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# Soil microbial responses to simulated climate change across polar ecosystems

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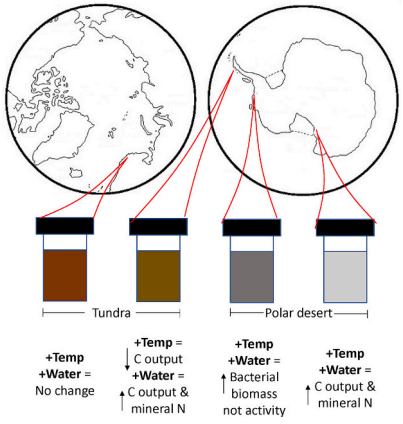
## HIGHLIGHTS

- Distant polar soils differed in their response to simulated climate change.
- Polar desert soil microbes were co-limited by temperature and water availability.
- Antarctic tundra soil microbes were climate-sensitive, but not the Arctic tundra.
- Higher temperature and water availability stimulated soil C mineralization.
- The varying sensitivity of polar ecosystems to climate could impact soil C storage.

## GRAPHICAL ABSTRACT

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## ABSTRACT

The polar regions are among the most biologically constrained in the world, characterized by cold temperatures and reduced liquid water. These limitations make them among the most climate-sensitive regions on Earth. Despite the overwhelming constraints from low temperatures and resource availability, many polar ecosystems, including polar deserts and tundras across the Arctic and Antarctic host uniquely diverse microbial communities. Polar regions have warmed more rapidly than the global average, with continued warming predicted for the future, which will reduce constraints on soil microbial activity. This could alter polar carbon (C) cycles, increasing $CO_2$ emissions into the atmosphere. The objective of this study was to determine how increased temperature and moisture availability impacts microbial respiration in polar regions, by focusing on a diversity of ecosystem types (polar desert vs. tundra) that are geographically distant across Antarctica and the Arctic. We found that polar desert soil microbes were co-limited by temperature and moisture, though C and nitrogen (N) mineralization were only stimulated at the coldest and driest of the two polar deserts. Only bacterial biomass was impacted at the less harsh of the polar deserts, suggesting microbial activity is limited by factors other than temperature and moisture. Of the tundra sites, only the Antarctic tundra was climate-sensitive, where increased temperature decreased C and N mineralization while water availability stimulated it. The greater availability of

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soil resources and vegetative biomass at the Arctic tundra site might lead to its lack of climate-sensitivity. Notably, while C and N dynamics were climate-sensitive at some of our polar sites, P availability was not impacted at any of them. Our results demonstrate that soil microbial processes in some polar ecosystems are more sensitive to changes in temperature and moisture than others, with implications for soil C and N storage that are not uniformly predictable across polar regions.

## 1. Introduction

The polar regions have warmed faster than any other part of the world (sensu McClintock et al., 2008; Post et al., 2019). In these climate-sensitive environments the effects of climate change are more intense, and therefore its effects can be readily observed. An increasing concern regarding climate warming is that these regions may be sources rather than sinks of atmospheric carbon (C), due to warming temperatures and ice melt in addition to a better understanding of $CO_2$ release beyond the summer season (Braybrook et al., 2021; Gray et al., 2018; Ouyang et al., 2020; Woosley and Millero, 2020). Soil microorganisms play a key role in regulating the release or storage of soil C (Bhattacharyya et al., 2022; Jansson and Hofmockel, 2020; Schuur et al., 2015). Climate-change related temperature variations may have significant implications for these cold-adapted microorganisms of the Arctic and Antarctic, where low temperatures generally reduce microbial activity in comparison to warmer temperatures (Cruz-Paredes et al., 2021; Goordial et al., 2016; Wang et al., 2021). Thus, understanding how climate-sensitive polar soil microbes respond to climate variations will improve our predictions of how polar C cycling will respond to climate change.

Increasing temperatures in both Arctic and Antarctic ecosystems have caused a flux of moisture release from permafrost and glacial melt (Overland et al., 2019; Tuckett et al., 2019), as well as increased snowfall in some polar regions but reduced snowpack in others, with altered timing of melt (AMAP, 2017; Medley and Thomas, 2019), leading to altered soil insulation and heat retention as well as moisture availability (Ayres et al., 2010; Loranty et al., 2018; Wang et al., 2020). Soil biological processes can be influenced by these water pulses and any associated nutrient changes (Ball et al., 2018; Gebauer and Ehleringer, 2000). As such, microbial communities in polar ecosystems have been found to respond to simulated climate change (e.g., Cruz-Paredes et al., 2021; Kim et al., 2018; Misiak et al., 2021; Newsham et al., 2016; Wang et al., 2021), due to the dominant limitation of biological activity by temperature and water availability. For example, tundra microbial communities, in response to reduced glacial cover, decompose soil organic matter at an accelerated rate with the addition of increased soil moisture (Fell et al., 2021; Sitch et al., 2007). Increased temperature and moisture availability influence soil respiration and soil C decomposition in both Antarctic and Arctic ecosystems (Ball and Virginia, 2015; Pradel et al., 2023; Rijkers et al., 2022), though not all studies note an effect of increased temperature (Newsham et al., 2019; Weedon et al., 2014).

Polar regions vary in their climate and geology, and therefore soil composition. As such, locations differ in temperature, moisture, nutrient availability, and biological communities. In a polar desert, soils are subject to low annual rainfall and temperature averages with the majority of the fresh water sequestered in glaciers and permafrost (Fountain et al., 1999; Kennedy, 1993). Such ecosystems can consist of largely unvegetated landscapes with poorly-developed soils that are nutrient and/or C-limited with minimal soil organic matter (Barrett et al., 2007; Barrett et al., 2005; Convey, 1996). In contrast, a tundra ecosystem can support much more plant and animal life, primarily during the summer season where organisms have access to free flowing water by way of glacial and permafrost melt and increased rates of precipitation (Edlund and Alt, 1989; Glanville et al., 2012; Rixen et al., 2022). Even so, decomposition of soil organic matter can be slow as cold temperatures, anaerobic conditions, and the edaphic environment limit microbial activity (Hobbie and Gough, 2004; Wallenstein et al., 2009; Walz et al., 2017). While ample research has been conducted in a variety of polar ecosystems, a comprehensive understanding of the effects of climate change on soil microbial C processing in polar regions requires coordinated study across geographic regions and ecosystem types, such as a tundra and polar desert that occur in both the Arctic and Antarctic (ACIA, 2005; Bliss et al., 1981). However, research understandably tends to focus on individual sites, rather than in orchestrated experiments across distant polar ecosystems. The few existing examples demonstrate consistent increases in microbial growth and abundance across Antarctic tundra ecosystems (Rinnan et al., 2009a; Yergeau et al., 2012), and differing responses of microbial community composition between a polar desert and tundra ecosystem on the Antarctic Peninsula (Dennis et al., 2013). Studies that compare results across sides of the Antarctic continent or across the Arctic and Antarctic, though, are rare, particularly in regard to how changes in the microbial community composition influences process rates for C and nutrient mineralization.

The objective of this study is to determine whether soil microbial communities from different tundra and polar desert ecosystems respond similarly to increased temperatures and associated water availability, particularly regarding their biomass, respiration rate, and associated nutrient mineralization. Understanding microbial communities' response to water and temperature variation can indicate whether the microbes present at these sites are limited by water scarcity and/or low temperatures, as opposed to other factors that may be indirectly influenced by climate change. We utilized soils from four sites across a broad geographic span located in either polar desert or tundra ecosystems that could help us gain a comprehensive understanding of the effects of climate change induced temperature and moisture variations in environmentally diverse locations throughout the polar regions. These sites included two fellfield desert sites in Antarctica, comprising a similar ecosystem type that are geographically distant from each other: one from Victoria Land in east Antarctica and the other from the southern Antarctic Peninsula in west Antarctica. We also included a tundra ecosystem on the Antarctic Peninsula that falls within the same "maritime" geographic categorization as one of the fellfield sites, thus constituting two different ecosystem types within a similar region. Finally, we included a tundra ecosystem in the Arctic, comprising a similar biome that is geographically distant from the Antarctic tundra.

We hypothesized that soil microbial communities located in the two Antarctic polar desert sites would be limited by both moisture availability and cold temperatures, such that climate manipulations of increased temperature and meltwater would increase microbial biomass and activity, regardless of the different geologic resources and biological communities. We also hypothesized that in the tundra ecosystems on both the Antarctic Peninsula and the Arctic, soil microbes would not be particularly limited by moisture availability due to their comparatively higher annual precipitation rate, and instead microbial respiration would increase most significantly in response to the incubation with only the higher temperature.

## 2. Methods

### 2.1. Study sites

Archived soil samples were utilized from four different sites: three located in Antarctica and one site from within the Arctic Circle (Fig. 1, Table 1). The Antarctic samples were sourced from a lake basin in the McMurdo Dry Valleys, as well as two sites along the Antarctic Peninsula: Mars Oasis on Alexander Island and Admiralty Bay on King George

Island. The Arctic samples were collected from Kilpisjärvi Biological Station, which is located north of the Arctic Circle in northern Finland. Soil samples from these four sites were available from prior field expeditions, and chosen to allow the comparison of ecosystem types and climate regions. Specifically, they represent (1) two polar deserts (McMurdo Dry Valleys and Mars Oasis) that are geographically separate within the Antarctic continent, (2) two different ecosystem types located within a geographically similar climate system on the Antarctic Peninsula (polar desert at Mars Oasis and tundra at Admiralty Bay), and (3) Antarctic vs. Arctic tundra ecosystems (Admiralty Bay vs. Kilpisjärvi). Admiralty Bay was the most highly vegetated Antarctic tundra site available from the sample archive, making it most comparable to the Arctic tundra site.

The McMurdo Dry Valleys are a polar desert located in mainland East Antarctica, representing one of the driest and coldest regions on Earth, with low mean annual temperature (MAT) and precipitation (MAP; Table 1). Soil was collected from the Lake Fryxell basin, where soils are categorized as Typic Haploturbels on Ross Sea drift (Bockheim et al., 2008; Bockheim and McLeod, 2008), with typically a shallow, 30–40 cm active layer depth during summer (Ball and Virginia, 2012). They are poorly developed and coarse (normally 95–99 % sand) underlain by 200–600 m of perennial permafrost, dry, and alkaline (Bockheim and McLeod, 2008; Burkins et al., 2000; Campbell and Claridge, 1987; Campbell et al., 1997). The soils are carbon-limited due to the low presence of soil organic matter (Ball et al., 2018; Burkins et al., 2000). Biology is constrained in this environment by moisture and temperature limitations; thus the Dry Valleys are limited to low biomass and diversity animal and plant communities, but sparse moss coverage and several taxa of invertebrates are present. Despite these constraints, the microbial communities in the Dry Valleys have been studied as being highly diverse albeit especially responsive to change within their environment (Cary et al., 2010; Convey, 2011).

Mars Oasis is also a polar desert but located instead in West Antarctica on Alexander Island off the Antarctic Peninsula. Due to the maritime climate of the Antarctic Peninsula, Mars Oasis is warmer with a higher MAP than the Dry Valleys (Table 1), and therefore water constraints are comparatively lower especially during the autumnal and summer months where meltwater can form streams and ponds (Ball et al., 2022; Bridge and Newsham, 2009). Underlying parent material consists of sandstone and mudstone (Bell, 1973). Soils collected from Mars Oasis are also poorly developed, coarse, and are characterized as sandy in texture (Convey and Smith, 1997). Similar to the Dry Valleys, some bryophyte species are observed near sources of water, but are absent moving further away from these sources where only some species of lichen are present (Convey and Smith, 1997; Maslen and Convey, 2006). There is a fairly diverse microbial and invertebrate community (Convey and Smith, 1997; Convey and Wynn-Williams, 2002; Maslen and Convey, 2006), but higher animals are also absent from this site.

The terrestrial ecosystem surrounding Admiralty Bay, located on King George Island, is an Antarctic tundra ecosystem (Kozeretska et al., 2010). It experiences a much greater MAP and a MAT than the polar deserts (Table 1). Precipitation rate is enhanced by the melting of accumulated winter snow caused by consistent positive air temperatures during the warmer months, which contributes to the 40–60 cm depth to permafrost during the summer months (Simas et al., 2008). The underlying parent material is tholeiite basalt (Birkenmajer, 1980). The soil is acidic, well-drained, and primarily of sandy-skeletal texture with a higher fraction of fine particles than the polar desert sites, categorized as Haploturbels (Simas et al., 2008). The climate allows Admiralty Bay to sustain an abundant plant community and relatively high microbial diversity, as well as higher life forms such as penguins and sea birds (Petry et al., 2016; Teixeira et al., 2010; Teixeira et al., 2013; Wentzel et al., 2019). Presence of higher animals near these soils strongly influences the nutrient levels of the soil and thus the microbial communities present in certain areas of Admiralty Bay (Tatur, 1989). The abundant and diverse plant community, including the two species of Antarctic vascular plants, is the reason that much of this area is an Antarctic Specially Protected Area.

Kilpisjärvi is a village in Finland located entirely within the Arctic Circle and classified as a low Arctic tundra ecosystem. While its MAT is comparable to the Antarctic tundra site, Kilpisjärvi's location is adjacent to the nearby Norwegian mountains which causes a rain shadow effect, limiting its MAP (Kauhanen, 2013). Soils present near water sources in Kilpisjärvi have a high amount of organic matter due to the scattered arcto-alpine vegetation which has a growing season of ~100 days in any given year (Kauhanen, 2013; Kumar et al., 2016). Soils form on dolomite parent material and are moderately developed (Kumar et al., 2016). Soil microbial variation is high, in part due to the presence of diverse animal species and complex vegetation (sensu Andersson and Jonasson, 1986; Kauhanen, 2013). This Arctic site was included to understand the effects of different climatic factors on the polar regions in relation to each other.

### 2.2. Field sampling

The archived soils were collected in January 2010 for the Dry Valleys, December 2014 for Mars Oasis, February 2016 for Admiralty Bay,

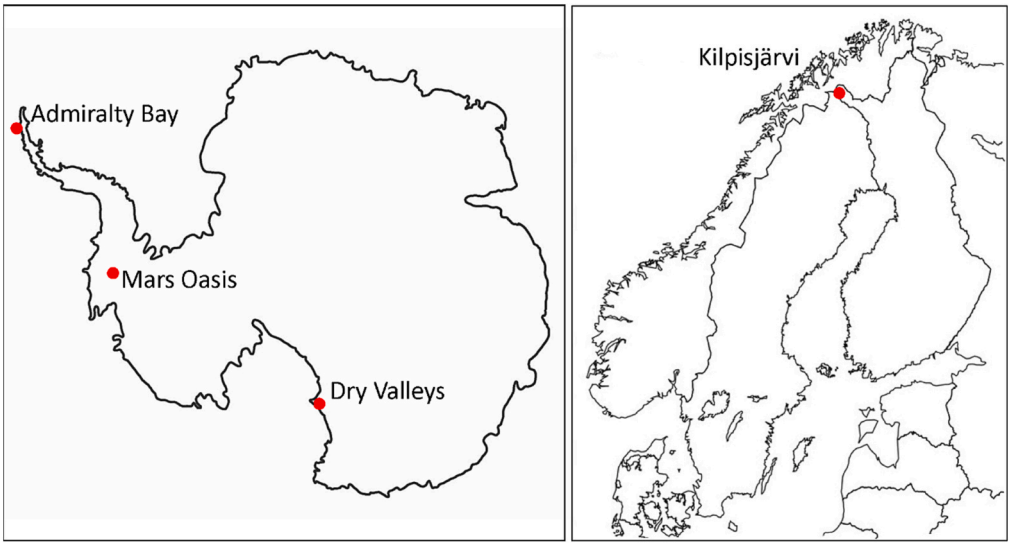


**Fig. 1.** Map showing the location of the three Antarctic (left panel) and one Arctic (right panel) sites.

and June 2019 for Kilpisjärvi. Surface soil samples (depth of 0–10 cm) were collected from beneath representative vegetative cover for the area using a clean plastic scoop and were stored in sterile plastic bags until bulked for this study. A composite bulk soil was made for both Mars Oasis and Admiralty Bay soils from 20 to 30 smaller samples collected randomly from a ~ 10,000 $m^2$ area beneath the dominant vegetation (moss and algae at Mars Oasis, moss and grass at Admiralty Bay) and bare soils. Five bulk soil samples were collected at Kilpisjärvi from a random selection of representative vegetation (moss and grass) over a 7500 $m^2$ area, which were combined equally to create a composite bulk sample. The Dry Valleys soil was a composite of two bulk soils collected near the Lake Fryxell basin from bare soils lacking vegetation, as is representative of the landscape. They were then stored at −20 °C and transported to Arizona State University until this experiment in 2019. Because the samples were stored in a biologically inactive state at −20 °C, and because the soil communities at all four sites would be adapted to seasonal thaw from deep-freezing events, it is assumed that the freeze-thaw process is equivalent among the samples despite frozen storage.

### 2.3. Soil respiration

Laboratory incubations were conducted to measure the biotic activity of the microbes as they respired and generated $CO_2$. Soils from the four sites were allowed to thaw for 24 h in a 3 °C fridge. Following methodology utilized in Ball and Virginia (2014), Dry Valley and Mars Oasis soils were sieved to <2 mm, whereas wetter soils from Admiralty Bay and Kilpisjärvi were hand sorted due to their high moisture content that made sieving difficult. Subsamples from each site were placed into 32 replicate incubation vessels per site, totaling 128 vessels. The incubation vessels were 4-oz acid-washed, glass canning jars. For the Dry Valleys and Mars Oasis, incubation vessels contained 40 ± 0.5 g soil, while 20 ± 0.5 g was used for Admiralty Bay and 15 ± 0.5 g for Kilpisjärvi. These variable soil masses were chosen to provide similar volume of soil vs. headspace across the four sites, given differences in bulk density. The jars were capped loosely with lids that had been modified to include a silicone septa.

Four incubation treatments were applied to the jars from each site, factorially manipulating both moisture and temperature. The Control group (C) were incubated in standard conditions of +3 °C, representing a standard summer temperature that would occur across all of the sites, with no addition of water. The Water treatment (W) jars were incubated at a standard temperature of +3 °C, and sterilized di-$H_2O$ was added to mimic conditions of higher soil moisture availability. Water was added at the rate of 75 μL/g soil following previous application rates on some of these soils (Ball et al., 2018; Ball et al., 2015). Therefore 3 mL were added to the polar desert sites, 1.5 mL to the Admiralty Bay soils, and 1.125 mL to Kilpisjärvi soils. The Temperature treatment (T) jars were incubated at an elevated temperature of +5 °C without any additional water to mimic conditions of an increase of 2 °C in global temperatures with climate change; and the Temperature + Water (TW) treatment jars received both the water addition and incubation at +5 °C to mimic conditions of both increased moisture availability and temperature. Soil water content and nutrient content of initial soil samples were measured prior to incubation (see Section 2.4).

The loosely capped jars allowed the gas within the jars to exchange with the air inside the incubators, preventing anaerobic conditions. At periodic intervals over the course of ~40 days, $CO_2$ flux was measured from each jar. The jars were tightly capped, flushed with air that was free of $CO_2$, then placed back in their incubators. The jars were left in their respective temperature conditions to allow $CO_2$ to accumulate over a period of 24 h for the low-C, low-biomass Dry Valleys and Mars Oasis jars or 6 h at Admiralty Bay and Kilpisjärvi, due to the comparatively high biomass present in the tundra soils (Kumar et al., 2016; Tatur, 1989). After this accumulation period, either 5-mL (low-flux Dry Valleys and Mars Oasis jars) or 2-mL (high-flux Admiralty Bay and Kilpisjärvi) air samples from within the headspace inside the jars were extracted using a syringe and injected into a LICOR infrared gas analyzer (LI-7000, LI-COR, Lincoln, NE). The accumulated $CO_2$ concentration was used to calculate net C mineralization rate using the equation:

$$(AW_C * [CO_2] * V)/(R * T)/(S * d)$$

where $AW_C$ is the atomic weight of C (12 g $mol^{-1}$), V is the headspace volume, R is the gas constant (0.082 L ppm $K^{-1}$ $mol^{-1}$), T is the incubation temperature (276.15 or 278.15 K), S is soil mass, and d is the days of $CO_2$ accumulation (Ball et al., 2018).

### 2.4. Soil chemistry

Soil chemistry was measured at the start and end of the ~40-day incubation, as well as one mid-point. To measure any comparative nutrient differences between periods of high and low microbial respiration, 50 % of the samples were randomly chosen to be destructively sampled when respiration was observed to fall after an initial peak during incubation period (referred to as "mid-point sampling"). The remaining samples were destructively sampled at the end of the incubation period ("final sampling"). The interval at which the midpoint sampling was conducted was dependent on the unique respiration dynamic of each site, and fell at day 8 for the polar desert soils and day 17 for the tundra sites.

Soil water content (SWC) was measured on 10 ± 0.5 g of soil from the Dry Valleys and Mars Oasis, 5 ± 0.5 g of soil from Admiralty Bay, and 2.5 ± 0.5 g of soil from Kilpisjärvi, given the different masses of starting soil and water holding capacities. Following Ball et al. (2015), the subsamples were dried at 105 °C for 24 h after which their moisture-free mass was measured. Sample extractable phosphate ($PO_4$-P) content was measured by extracting 10 ± 0.5 g of soil from the Dry Valleys and Mars Oasis sample jars and 5 ± 0.5 g soil from the more nutrient-rich Admiralty Bay and Kilpisjärvi soils in 50 mL of 0.5 M $NaHCO_3$ with a pH of 8.5, shaken at 180 rpm for 60 min. The extracts were then centrifuged for 10 min at 15,000 ×g and filtered through 0.45-μm nylon filter to remove any soil particles still present in the samples. The centrifuged samples were frozen until analyzed, at which point they were thawed, acidified with 3 mL of 6 N HCl to degas prior to analysis with a flow injection analyzer (Lachat QC8000). Inorganic N ($NO_3$ + $NO_2$-N and $NH_4$-N) was measured by extracting the same weights in 50 mL of 2 M KCl, then following the same method of being centrifuged, filtered, and then frozen until being run on a Lachat Autoanalyzer (Barrett et al., 2007). Additionally, an estimate of organic matter content was measured on initial soils by loss on ignition (LOI) where soil

**Table 1**
Climate and soil conditions across the four sites from which soils were collected for this study, including mean annual precipitation (MAP) and temperature (MAT), loss on ignition (LOI; a correlate for organic matter content), soil water content (SWC), pH, and electrical conductivity (EC; a correlate for salinity). LOI and SWC were measured in this study, while all other values are provided from the cited sources for these specific sites.

| | (mm) | MAT (°C) | LOI (%) | SWC (%g/g) | pH | EC (μS/cm) | Citations |
|---|---|---|---|---|---|---|---|
| Dry Valleys | <100 | <−15 | 0.95 ± 0.19 | 1.49 ± 0.05 | 9.74 ± 0.42 | 219.9 ± 119.0 | Ball et al. (2018); Fountain et al. (1999) |
| Mars Oasis | 209 | −8 | 3.30 ± 0.11 | 8.07 ± 0.62 | 7.38 ± 0.02 | 131.2 ± 4.9 | Ball et al. (2022) |
| Admiralty Bay | 771 | −2.7 | 7.23 ± 0.07 | 19.23 ± 0.61 | 5.43 ± 0.01 | 53.9 ± 0.9 | Ball et al. (2022) |
| Kilpisjärvi | 472 | −2 | 15.47 ± 0.09 | 67.64 ± 2.33 | 5.30 ± 0.09 | 680.1 ± 188.5 | Klein and Ball (n.d.); Kauhanen (2013) |

sample mass loss was measured after 3 h in a 550 °C in a muffle furnace (Ball et al., 2022).

### 2.5. Bacterial cell counts

Analyses include a combination of initial sampling and the bacterial biomass determined by the use of an epifluorescence microscope (Bottomley, 1994). From each sample jar, either 10 (Dry Valleys and Mars Oasis) or 5 g (Admiralty Bay and Kilpisjärvi) of soil was extracted in an acid-washed flask with 50 mL of autoclaved 1× phosphate buffered saline. The flasks were placed into a shaker at a gentle cycle of 100 rpm for 60 min. The resulting liquid samples were preserved using 0.2-μl-filtered formaldehyde to 4 % concentration. The samples were diluted to a ratio of 1:400 to adjust the density of cells and sedimentation to be more readily counted through a microscope. 2 mL of the dilutions were placed into an acid-washed and ethanol rinsed filtration manifold on a black 0.2 μm pore size polycarbonate filter (Ball and Virginia, 2014). 0.5 mL of 25× SYBR green nucleic acid gel stain was subsequently added and left to incubate for 15 min, then vacuum filtered. The filters were placed on slides with a drop of immersion oil for viewing through an epifluorescence microscope. Ten randomized fields were counted, categorized by shape and size using the following categories: small cocci, large cocci, small bacilli, and large bacilli. These categories were used to calculate biovolume per g of dry soil extracted.

### 2.6. Data analyses

All data were analyzed in R version 4.0.2 (The R Foundation). First, a 3-way Analysis of Covariance (ANCOVA) was conducted to test the effect of Site (4 levels), Treatment (4 levels), and Time (continuous covariate), as well as their interactions, on each of the response variables. Data were transformed to meet the assumptions of normality and heteroscedasticity using the "boxcox" function in package *MASS*. Two outliers were removed from the $NO_2 + NO_3$-N data and $PO_4$-P data each. Where site and treatment were significant, a post hoc Tukey HSD test was conducted using package *agricolae* to determine which sites and treatments significantly differed from each other. Because site was a significant factor for all metrics, often significantly interacting with treatment and/or time, we further analyzed each individual site using a similar 2-way ANCOVA to test for significant differences among treatments (4 levels) over time (continuous covariate) within each site.

## 3. Results

### 3.1. Carbon mineralization

For all sites, respiration varied over time (significant influence of time, Table 2), where the initial respiration pulse after thawing was short-lived and followed by a sharp decrease in carbon mineralization (Fig. 2). Sites also differed in how carbon mineralization proceeded over time (significant Site*Time, Table 2). Across all treatments, carbon mineralization from Dry Valley and Mars Oasis soils began to increase during the latter portion of the incubation period following a significant drop mid-incubation. Admiralty Bay and Kilpisjärvi soils exhibited on average a decrease of carbon mineralization over the incubational time period for all treatments.

The influence of climate treatment on respiration differed by sites (significant Site*Treatment, Table 2). This reflects the fact that only Dry Valleys and Admiralty Bay soils were significantly influenced by the treatments, and the differences among treatments was not uniform at these sites (Fig. 2). Soil from the Dry Valleys exhibited approximately double the carbon mineralization in response to TW over the other treatments (Fig. 2a). Dry Valley soils receiving W also responded with a slightly increased (1.2–1.5×) carbon mineralization rate in the later part

**Table 2**
Results of a three-way Analysis of Covariance testing the effect of site, treatment, and time (as a continuous covariate) on soil respiration and chemical properties throughout the 40-day incubation, both across all sites as well as individually at each site.

| | Respiration | | $NO_2 + NO_3$-N | | $NH_4$-N | | $PO_4$-P | | Bacterial biovolume | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $F_{df}$ | *P* | $F_{df}$ | *P* | $F_{df}$ | *P* | $F_{df}$ | *P* | $F_{df}$ | *P* |
| All sites | | | | | | | | | | |
| Site | $1081.5_{3,774}$ | **<0.001** | $95.0_{3,143}$ | **<0.001** | $1271.9_{3,145}$ | **<0.001** | $1735.8_{3,144}$ | **<0.001** | $19.3_{3,90}$ | **<0.001** |
| Treatment | $10.8_{3,774}$ | **<0.001** | $1.6_{3,143}$ | 0.187 | $2.2_{3,145}$ | 0.090 | $0.7_{3,144}$ | 0.531 | $2.1_{3,90}$ | 0.110 |
| Time | $969.5_{1,774}$ | **<0.001** | $215.8_{1,143}$ | **<0.001** | $5.7_{1,145}$ | **0.019** | $19.6_{1,144}$ | **<0.001** | $18.8_{1,90}$ | **<0.001** |
| Site*Treatment | $6.9_{9,774}$ | **<0.001** | $1.0_{9,143}$ | 0.443 | $2.1_{9,145}$ | **0.033** | $0.9_{9,144}$ | 0.530 | $3.6_{9,90}$ | **0.001** |
| Site*Time | $42.8_{3,774}$ | **<0.001** | $20.4_{3,143}$ | **<0.001** | $7.8_{3,145}$ | **<0.001** | $26.7_{3,144}$ | **<0.001** | $3.6_{3,90}$ | **0.016** |
| Treatment*Time | $7.2_{3,774}$ | **<0.001** | $0.4_{3,143}$ | 0.735 | $0.6_{3,145}$ | 0.592 | $0.3_{3,144}$ | 0.810 | $1.1_{3,90}$ | 0.335 |
| Site*Treat*Time | $1.2_{9,774}$ | 0.232 | $0.9_{9,143}$ | 0.541 | $1.2_{9,145}$ | 0.284 | $0.8_{9,144}$ | 0.622 | $0.9_{9,90}$ | 0.487 |
| Dry valleys | | | | | | | | | | |
| Treatment | $5.2_{3,174}$ | **0.002** | $0.6_{3,40}$ | 0.603 | $19.9_{3,40}$ | **<0.001** | $1.5_{3,40}$ | 0.232 | $2.4_{3,24}$ | 0.090 |
| Time | $180.3_{1,174}$ | **<0.001** | $82.1_{1,40}$ | **<0.001** | $26.9_{1,40}$ | **<0.001** | $26.1_{1,40}$ | **<0.001** | $20.3_{1,24}$ | **<0.001** |
| Treatment*Time | $2.3_{3,174}$ | 0.080 | $0.6_{3,40}$ | 0.634 | $8.9_{3,40}$ | **<0.001** | $0.6_{3,40}$ | 0.648 | $0.7_{3,24}$ | 0.568 |
| Mars Oasis | | | | | | | | | | |
| Treatment | $0.9_{3,174}$ | 0.440 | $0.7_{3,39}$ | 0.534 | $0.6_{3,40}$ | 0.641 | $0.2_{3,40}$ | 0.870 | $4.0_{3,24}$ | **0.019** |
| Time | $158.6_{1,174}$ | **<0.001** | $148.7_{1,39}$ | **<0.001** | $0.1_{1,40}$ | 0.730 | $72.8_{1,40}$ | **<0.001** | $1.8_{1,24}$ | 0.189 |
| Treatment*Time | $0.6_{3,174}$ | 0.641 | $0.5_{3,39}$ | 0.711 | $0.2_{3,40}$ | 0.864 | $0.3_{3,40}$ | 0.837 | $2.2_{3,24}$ | 0.110 |
| Admiralty Bay | | | | | | | | | | |
| Treatment | $20.3_{3,213}$ | **<0.001** | $5.7_{3,33}$ | **0.003** | $0.6_{3,33}$ | 0.616 | $0.6_{3,33}$ | 0.647 | $9.0_{3,21}$ | **<0.001** |
| Time | $508.5_{1,213}$ | **<0.001** | $11.6_{1,33}$ | **0.002** | $12.7_{1,33}$ | **0.001** | $20.9_{1,33}$ | **<0.001** | $0.4_{1,21}$ | 0.553 |
| Treatment*Time | $2.8_{3,213}$ | **0.042** | $3.9_{3,33}$ | **0.018** | $0.7_{3,33}$ | 0.538 | $1.3_{3,33}$ | 0.298 | $1.5_{3,21}$ | 0.257 |
| Kilpisjärvi | | | | | | | | | | |
| Treatment | $1.7_{3,213}$ | 0.162 | $1.1_{3,31}$ | 0.361 | $0.3_{3,32}$ | 0.809 | $1.0_{3,31}$ | 0.398 | $0.5_{3,21}$ | 0.657 |
| Time | $217.1_{1,213}$ | **<0.001** | $72.4_{1,31}$ | **<0.001** | $15.4_{1,32}$ | **<0.001** | $0.6_{1,31}$ | 0.433 | $2.6_{1,21}$ | 0.121 |
| Treatment*Time | $2.2_{3,213}$ | 0.090 | $0.3_{3,31}$ | 0.842 | $0.4_{3,32}$ | 0.768 | $0.8_{3,31}$ | 0.524 | $0.3_{3,21}$ | 0.856 |

P-values in bold are significant at $P < 0.05$ for emphasis.

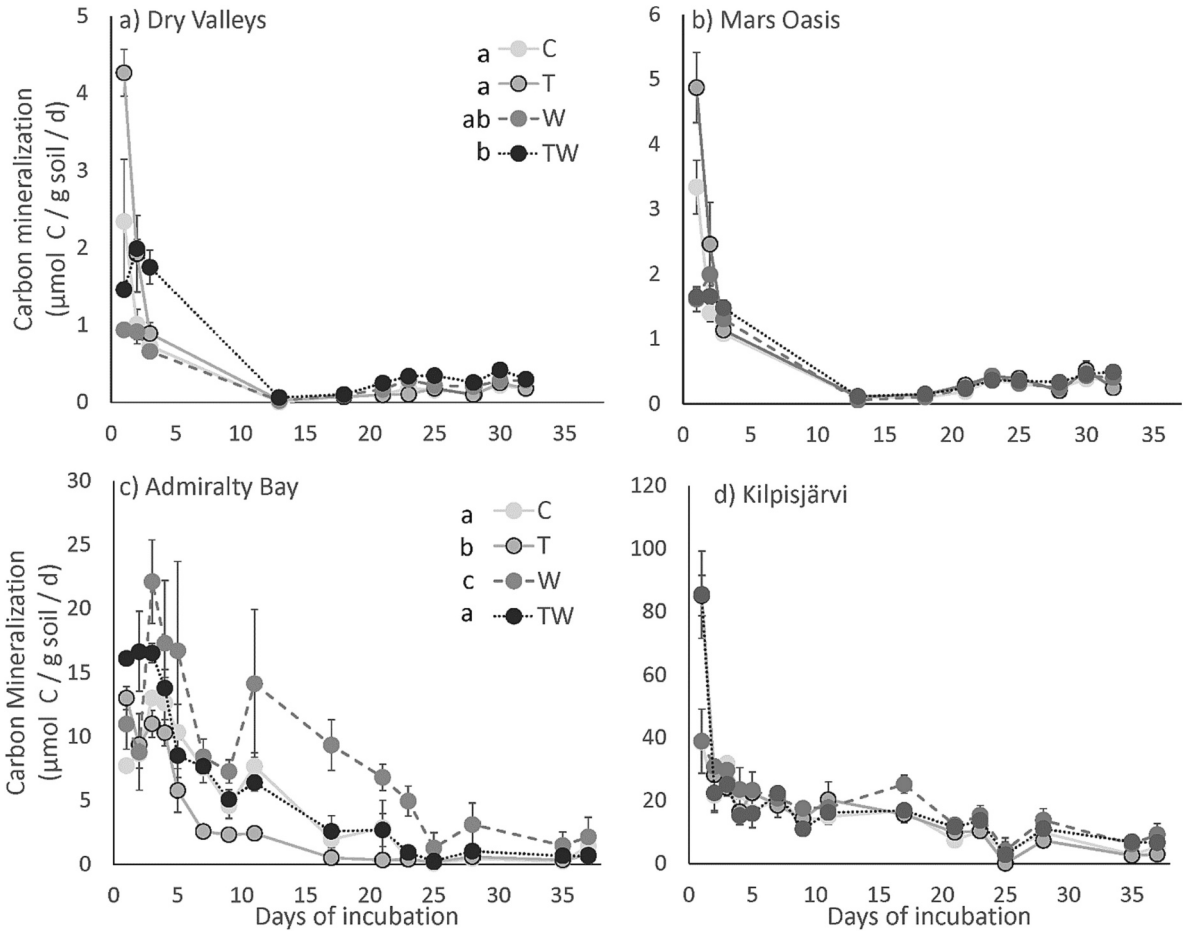


**Fig. 2.** Carbon mineralization over the course of the ~40-day incubation from soils at each of the four sites receiving four treatments: untreated or control (C), increased temperature (T), water additions (W), and both increased temperature and water additions (TW). Values represent mean ± standard error. Note the different scale of the y-axis for each site. Where treatments significantly differed from each other, the results of the post hoc Tukey HSD test are included in the legend, where treatments with the same letter do not differ significantly from each other.

of the incubation, though not significantly greater than the soils not receiving water. Temperature alone did not have an influence. In Admiralty Bay soils, carbon mineralization rate was stimulated by W compared to the control, reaching almost 20× higher rates, and reduced to one-quarter of the mineralization by T mid-incubation, with the differences among treatments diminishing over time (Fig. 2c). Respiration under TW was also initially 2× higher than C, but not significantly different when considered across the entire incubation (Table 2). Initial respiration was stimulated ~1.5× by T at Mars Oasis and halved by W and TW (Fig. 2b), and doubled by TW and T at Kilpisjärvi (Fig. 2d), but these were not sustained throughout the incubation and were therefore not statistically significant (Table 2).

### 3.2. Bacterial biovolume

Bacterial biovolume was significantly influenced by the climate treatments in the soils from the two Antarctic Peninsula sites: Mars Oasis and Admiralty Bay (Table 2). In the Mars Oasis soils, the TW soils had a 1.5–2× larger bacterial biovolume than the C and T soils (Fig. 3b). In the Admiralty Bay soils, it was the W treatment with a 1.5–3× larger biovolume than all other treatments (Fig. 3c). Despite the treatment effect on respiration in the Dry Valley soils, bacterial biovolume was not statistically influenced by treatment, though it did more than double from mid- to late-incubation, despite the low respiration rates in this second half of the incubation (Fig. 3a).

### 3.3. Soil nutrient content

Nutrient content varied across the four sites, and shifted over time, but there was not a clear effect of treatment when considered across the sites (Table 2). Within individual sites, individual nutrients only differed among the treatments at some sites, specifically $NH_4$-N in Dry Valley soils and $NO_2 + NO_3$-N in Admiralty Bay soils. Notably, $PO_4$-P was not significantly influenced by the climate treatments at any of the sites.

Dry Valley soils with added water (W and TW) had significantly, 4–8× greater $NH_4$-N content than those without (Fig. 4a). The T soils did not differ significantly from the control, both of which had consistently low $NH_4$-N throughout the incubation. Further, TW soils showed a consistent increase in $NH_4$-N throughout the incubation period, while the other treatments peaked at the midpoint and either decreased or remained constant. $NO_2 + NO_3$-N did not significantly differ among the treatments (Table 2), though they tended to be inverse of the $NH_4$-N concentrations, with the W and TW soils exhibiting the lowest overall concentration and the C the highest concentration (Fig. 5a). $PO_4$-P content peaked at a level 3× higher than initial by the midpoint sampling (Fig. 6a). Though differences by treatment were statistically negligible, the TW soils had the highest peak of concentration, followed by W.

Unlike the other polar desert site, mineral nutrients were not significantly influenced by treatment at Mars Oasis (Table 2). $NH_4$-N peaked mid-incubation after the peak of respiration, and then reduced to low levels, half the initial level of $NH_4$-N, by the end of the incubation (Fig. 4b). $NO_2 + NO_3$-N generally increased throughout the incubation

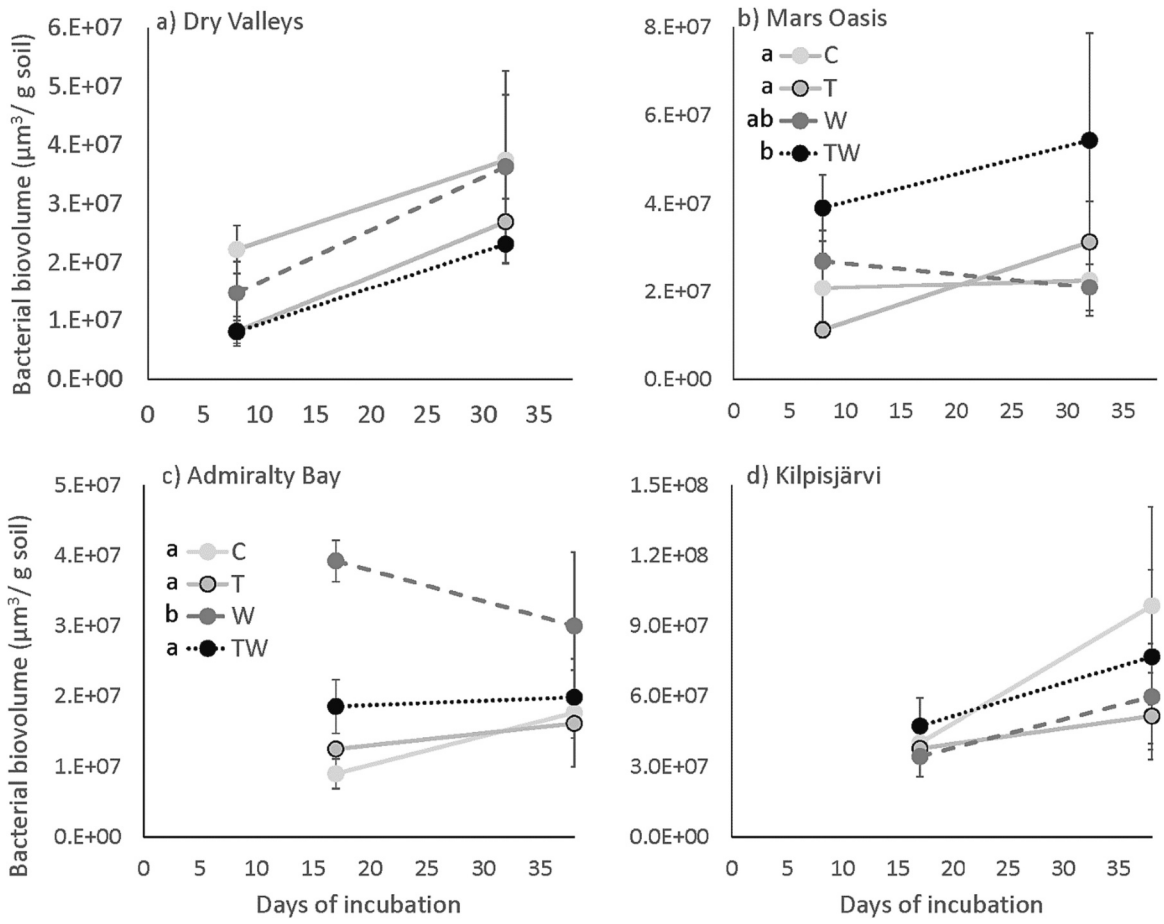


**Fig. 3.** Bacterial biovolume at the mid-incubation sampling and at final sampling of the soils over the course of the ~40-day incubation of soils from each of the four sites receiving four treatments: untreated or control (C), increased temperature (T), water additions (W), and both increased temperature and water additions (TW). Note the different scale of the y-axis for each site. Where treatments significantly differed from each other, the results of the post hoc Tukey HSD test are included in the legend, where treatments with the same letter do not differ significantly from each other.

to a level 8× higher than initial, while $PO_4$-P increased to 3× initial levels by mid-incubation and remained fairly constant throughout the end.

Soils from the tundra site on the Antarctic Peninsula, Admiralty Bay, responded to treatments in $NO_2 + NO_3$-N content (Table 2). The soils receiving water (W and TW) had significantly more $NO_2 + NO_3$-N than the T-only treatment, though only TW was significantly greater than the control, ending with 50-fold greater levels (Fig. 5c). Unlike the Antarctic polar desert sites, $NH_4$-N decreased by almost half from the start of the incubation, rather than increased (Fig. 4c), and $PO_4$-P levels decreased by about a quarter in the second half of the incubation (Fig. 6c).

Nutrient concentrations in Kilpisjärvi soils were not significantly influenced by the climate treatments (Table 2). $NH_4$-N behaved similarly to the polar desert soils, not the other tundra site, peaking mid-incubation. $NO_2 + NO_3$-N content increased over time by several orders of magnitude, peaking mid-incubation for the treatments not receiving water (C and T), and continuing to increase in those with water (TW and W), though these differences in the final sampling point were not statistically significant when considered across the entire incubation.

## 4. Discussion

### 4.1. Antarctic polar deserts

We hypothesized that soil microbes in the two polar deserts, regardless of their geographic distance in Antarctica, would be influenced by both temperature and water associated with climate change. We found this to be true for the Dry Valleys, which is the coldest and driest of the sites studied. While respiration marginally benefited from the addition of water alone, the largest increase was from the combination of temperature and water. Existing field studies at this site show that diel changes in temperature between 3 and 5 °C can yield a 1.3–2× increase in soil $CO_2$ efflux (Ball and Virginia, 2015), but experimental 2 °C warming alone did not influence $CO_2$ flux without the addition of water, which yielded small (1.2–1.4×) increases (Ball et al., 2009). However much like field studies from this and other fellfield sites (e.g., Ball et al., 2018; Van Horn et al., 2014; Yoshitake et al., 2007), this appears to be through increased activity rather than biomass, given that bacterial biovolume did not respond to climate treatments. However, the opposite was true at the other polar desert site, Mars Oasis, where bacterial biovolume was stimulated by TW, but not respiration. Thus, microbes at both polar deserts appeared to be co-limited by temperature and water, but responded differently in terms of whether biomass or activity was stimulated. While colimitation is supported by one study in the Dry Valleys (Ball et al., 2009), few studies exist in other polar deserts for comparison. Field studies at Mars Oasis found that 10 months of 1.3 °C warming decreased gram positive bacterial concentration by about a quarter, but not water (Dennis et al., 2013). In studies that independently investigate temperature and moisture, 4 years of ~2 °C warming and a natural 4 % difference in SWC yielded no effect on bacterial community composition or diversity (Newsham et al., 2010; Newsham et al., 2019). Further studies would be needed to determine if colimitation by temperature and water are a consistent control on soil

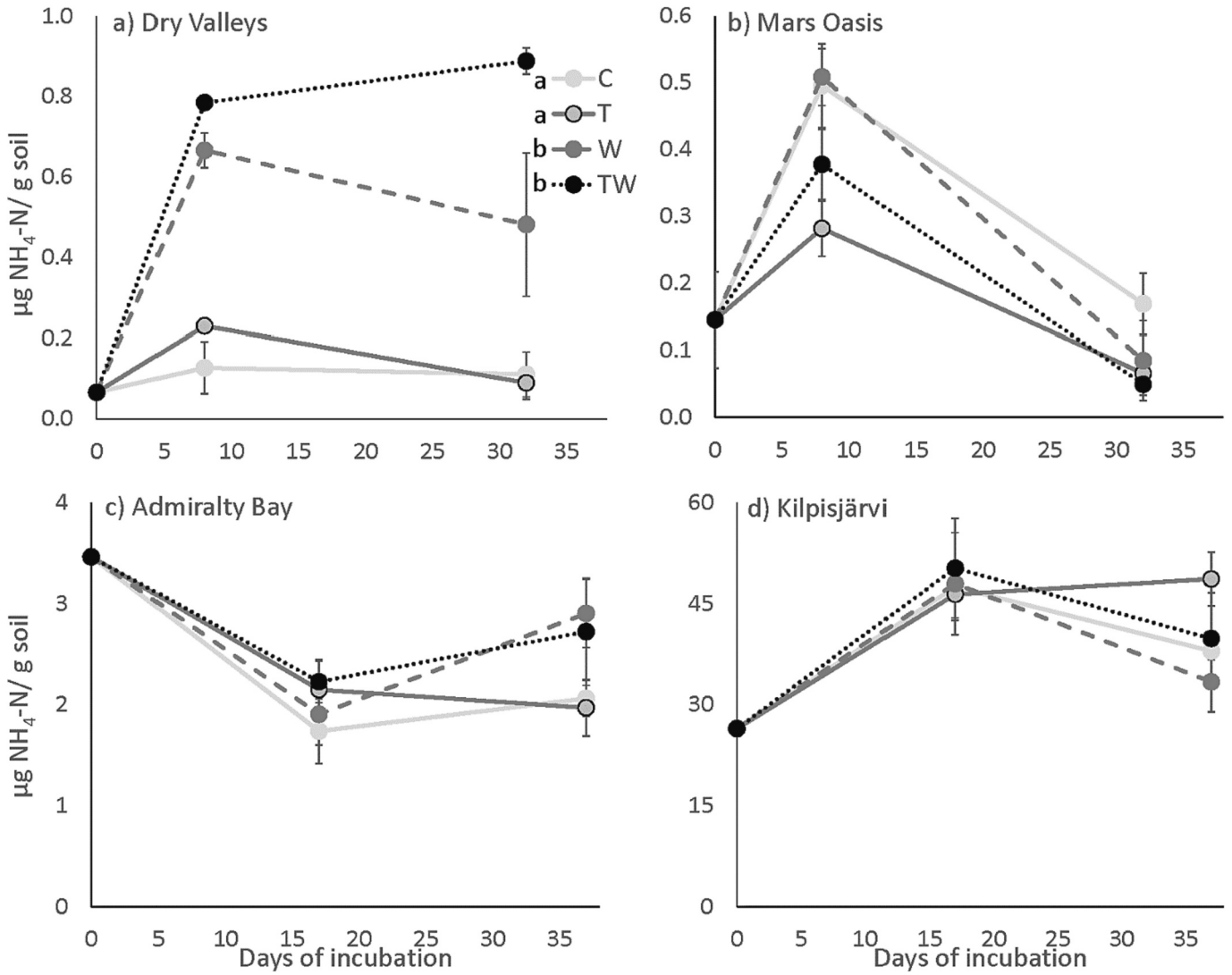


**Fig. 4.** Concentration of mineral ammonium in soil samples at three points over the course of the ~40-day incubation of soils from each of the four sites receiving four treatments: untreated or control (C), increased temperature (T), water additions (W), and both increased temperature and water additions (TW). Note the different scale of the y-axis for each site. Where treatments significantly differed from each other, the results of the post hoc Tukey HSD test are included in the legend, where treatments with the same letter do not differ significantly from each other.

respiration and nutrient activity in polar deserts.

While microbial biomass or respiration were co-limited by water and temperature, mineral nutrient content, specifically $NH_4$-N, was influenced only by the addition of water (whether alone or in combination with temperature) and only at the colder, drier polar desert site in the Dry Valleys. Therefore, though the combination of water and temperature was needed to stimulate respiration, ammonification was primarily limited by water. This suggests that carbon and nitrogen mineralization processes are decoupled in this polar desert. $NH_4^+$ is typically converted into $NO_2^-$ and $NO_3^-$ by nitrifying bacteria, but despite increased $NH_4^+$ with water addition, there was an insignificant effect of treatment on $NO_2^-$+ $NO_3^-$ content. It is possible that water addition stimulated decomposition of in situ organic material to enhance ammonification, without an immediate ability to utilize that extra N in nitrification. Previous research at this site has shown that soil microbes have a delayed response to additional N availability (Ball et al., 2018), and a longer-duration incubation might have shown a subsequent increase in $NO_2^-$+ $NO_3^-$ availability to mirror that of $NH_4^+$. However, both $NH_4$-N and $NO_2$ + $NO_3$-N increased from the start of the experiment, so there does appear to be an ability to nitrify the labile N that is inevitably released upon thawing the soils to begin the incubation. A more likely explanation is that $NH_4^+$ was only a minor fraction of the mineral N in these soils, causing the nitrification of the additional $NH_4^+$ to yield an undetectable difference in $NO_2$ + $NO_3$-N, which was more than an order of magnitude more abundant.

While activity in the colder, drier Dry Valleys appears to be more strongly limited by temperature and water availability, the relatively warmer and wetter Mars Oasis is less sensitive to the direct impacts of these small temperature fluctuations, given the lack of treatment effect on respiration or mineral nutrients. It is possible that an increase of 2 °C and 3 mL of water were both entirely within the natural climatic variation that microbes from Mars Oasis experience, where summer temperatures can fluctuate by almost 10 °C in magnitude (Convey et al., 2018), and therefore they may already be acclimated to these ranges. Newsham et al. (2019) also noted a lack of warming effect at this site. A study in the Arctic has demonstrated that seasonal variation in enzymatic activity outweighed the effects of experimental warming (Weedon et al., 2014). However, temperature had a negative impact at the other maritime Antarctic Peninsula site where temperature ranges are also greater. Another possibility is that the microbes are limited not simply by the climate but also the chemistry of the soil. As measured in Newsham et al. (2019), bacterial communities from Mars Oasis that

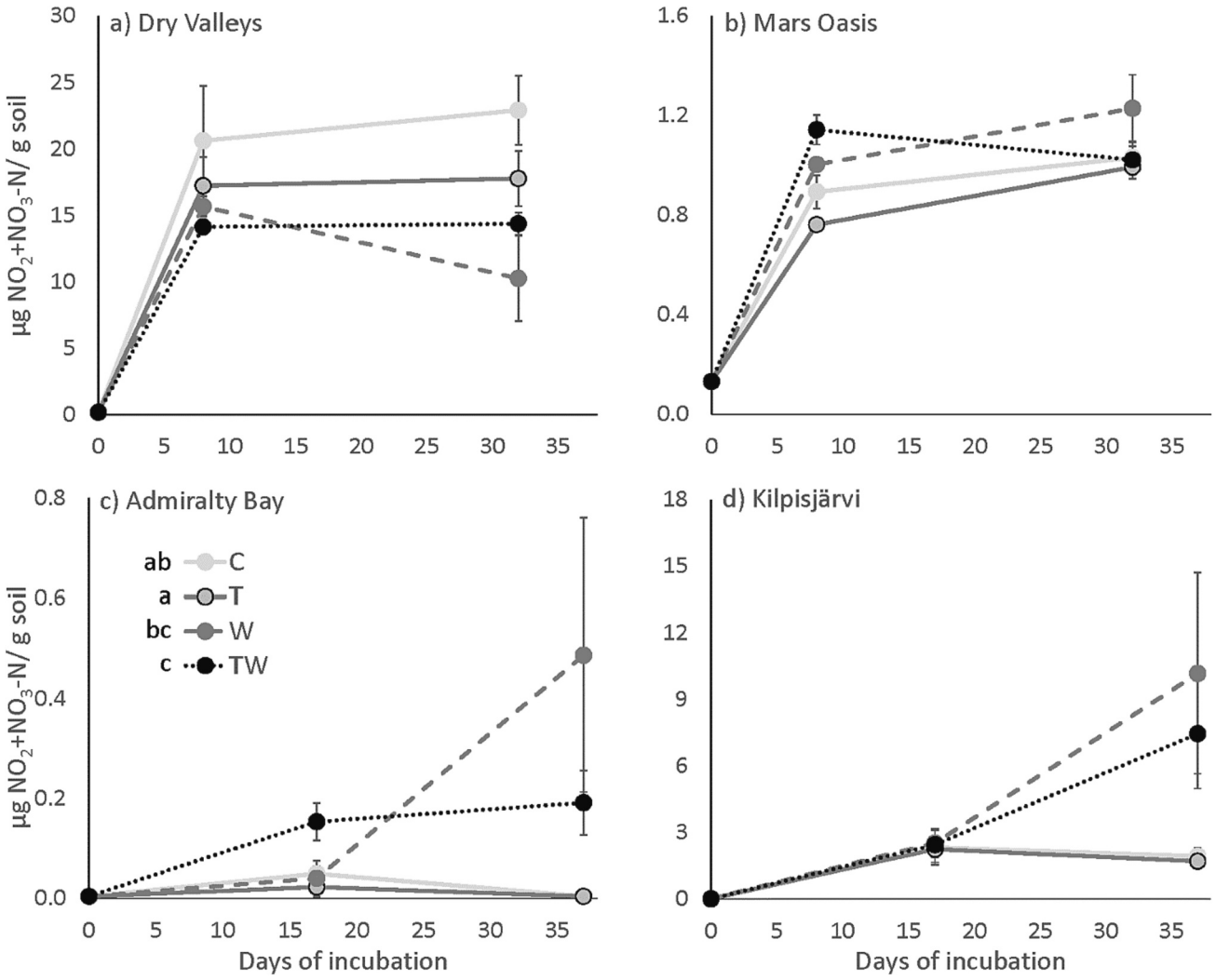


**Fig. 5.** Concentration of mineral nitrite and nitrate in soil samples at three points over the course of the ~40-day incubation of soils from each of the four sites receiving four treatments: untreated or control (C), increased temperature (T), water additions (W), and both increased temperature and water additions (TW). Note the different scale of the y-axis for each site. Where treatments significantly differed from each other, the results of the post hoc Tukey HSD test are included in the legend, where treatments with the same letter do not differ significantly from each other.

were subjected to higher than normal temperatures (without an increase in soil water content) did not show a significant change in microbial activity, but was stimulated by input of nitrogen. Therefore, it is not surprising that nutrient concentrations did not vary across treatments, as nutrient availability may be more of limiting factor than climate conditions. Mars Oasis soils in our incubation contained the least mineral N of the four sites, even lower than P content, and are therefore potentially more N limited. Interestingly, the stimulation of bacterial biovolume by TW could indicate that climate conditions were successful in stimulating microbial growth, but their activity became limited by other factors not addressed in this study. Other studies have shown negative impacts of increased temperature on the microbial community composition at Mars Oasis (Dennis et al., 2013; Misiak et al., 2021), and it is possible that the altered community while more abundant, was less active.

### 4.2. Antarctic Peninsula polar desert vs. tundra

Of the two sites located within the maritime climate region of the Antarctic Peninsula, it was the relatively warmer and wetter Admiralty Bay that was climate sensitive, and less so the colder, drier Mars Oasis where the only response to treatments was a stimulation of bacterial biovolume, but not activity, by TW. At Admiralty Bay, however, water additions increased soil respiration, bacterial biovolume, and $NO_2$ + $NO_3$-N. Microbial communities exposed to added moisture began to reproduce, respire, and mineralize $NH_4^+$ that was quickly converted into $NO_2^-$ and $NO_3^-$, resulting in no treatment differences in $NH_4^+$. However, increased temperature reduced both respiration and $NO_2^-$ + $NO_3^-$. Thus Admiralty Bay soils were moisture limited, at least in this laboratory setting where moisture content was held constant, and an increase in temperature without the presence of increased moisture availability was detrimental to the cold-adapted microbial communities native to these soils. While Mars Oasis may be primarily nutrient rather than climate limited, the much higher in situ organic (Table 1) and nutrient content (Figs. 4–6; Ball et al., 2022) at Admiralty Bay may cause climate conditions to be more limiting to growth and activity there.

Field studies on King George Island, home to Admiralty Bay, have found both no temperature response in C mineralization within this range of temperatures after 4 years of warming (Pradel et al., 2023) and a 20 % increase in bacterial biomass after 7 years of 1 °C warming (Kim et al., 2018). Thus, there appears to be variability within this island to the impacts of warming, possibly due to degree of warming, duration of study, or differences in vegetation cover and in situ habitat conditions. On nearby Signy Island, however, Yergeau et al. (2012) found that 3 years of a 0.7 °C warming in the field led to shift towards generalist

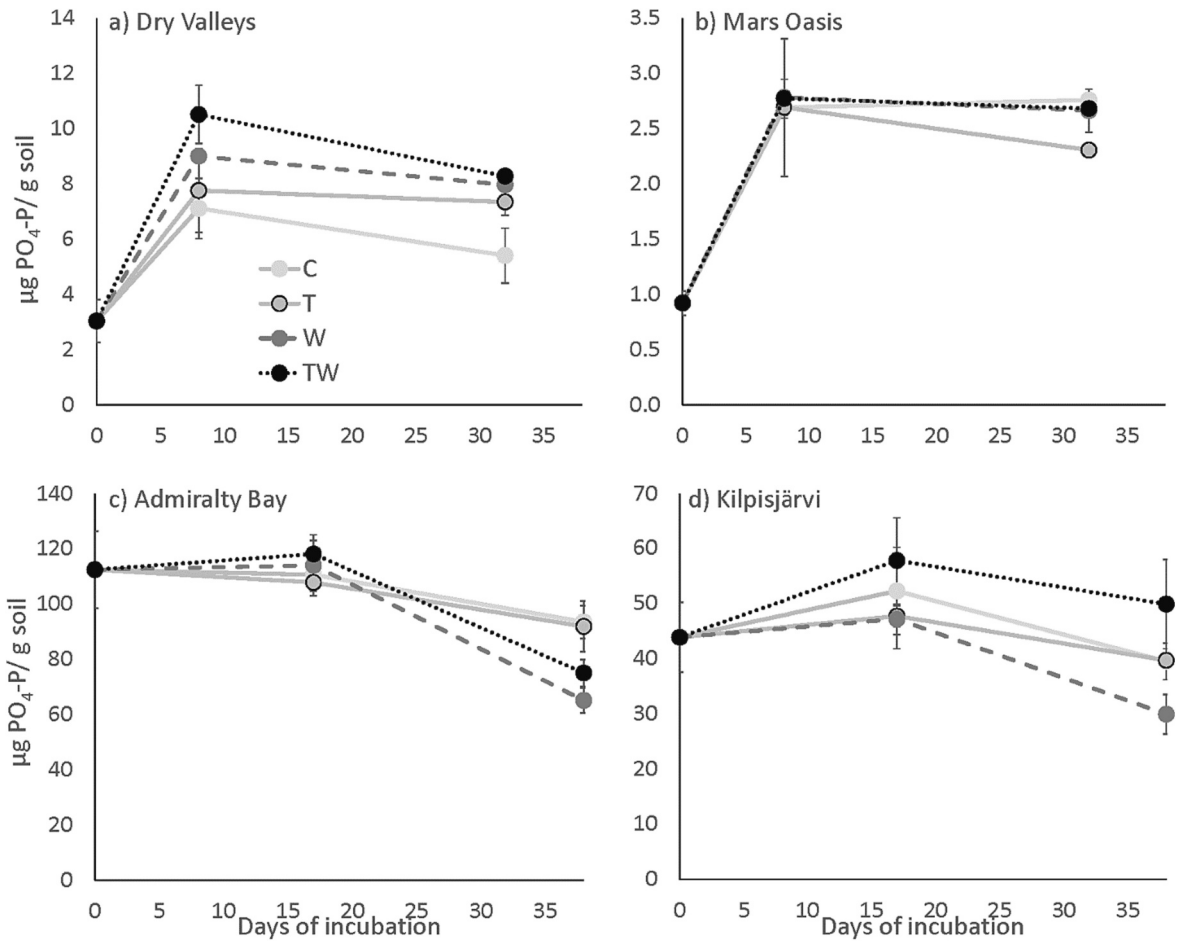


**Fig. 6.** Concentration of mineral phosphate in soil samples at three points over the course of the ~40-day incubation of soils from each of the four sites receiving four treatments: untreated or control (C), increased temperature (T), water additions (W), and both increased temperature and water additions (TW). Note the different scale of the y-axis for each site.

bacterial communities with a reduction in N-cycling gene families, and while that led to no change in soil nitrogen content in their study, this could be in line with our observed decrease in soil nitrogen under the warming treatment.

Interestingly, the climate-sensitive Admiralty Bay was stimulated by water addition, but inhibited by increased temperature. One recent study shows limited temperature sensitivity of soil respiration at this site below 20 °C (Pradel et al., 2023), while previous studies from other tundra ecosystems on the northern Antarctic Peninsula found respiration, microbial biomass, and nutrient mineralization to be stimulated by increased temperature and water (Benhua et al., 2014; Bokhorst et al., 2007; Kim et al., 2018) but bacterial and archaeal community composition to be relatively insensitive to small changes in temperature (Dennis et al., 2013; Kim et al., 2018). Our results confirm the water-limitation of these processes, but not temperature. These studies are all longer duration than the incubation reported here, and it is possible that the inhibitory effect of increased temperature was short-lived, and we would have seen acclimation (e.g., Rijkers et al., 2022) and stimulation had we run the incubation longer. In addition to broad-scale climatic differences, it is also possible that the geological and biological differences across the islands of the Antarctic Peninsula account for the different responses found in previous studies and ours. For example, often both soil physicochemical and vegetation differences across a geographic area explain landscape variation in soil carbon dynamics in polar ecosystems (Bradley-Cook and Virginia, 2018; Van Horn et al., 2014). There are few studies of the direct impacts of warming on soils for King George Island (where Admiralty Bay is located), to date focusing more on the plant and moss community (Cavieres et al., 2018; Prather et al., 2019; Shortlidge et al., 2016) and microbial community composition (Kim et al., 2018) rather than soil microbial processes (aside from Pradel et al., 2023), so further study would be needed to determine whether these short-term incubation results reflect field responses over the longer term.

### 4.3. *Antarctic vs. Arctic tundra*

The two tundra ecosystems, Admiralty Bay in Antarctica and Kilpisjärvi in the Arctic, are both comparatively wetter than the polar deserts with greater biodiversity, including plant life and higher animals. Due to the greater availability of soil water by higher precipitation and snowmelt, we predicted that the soil microbes are not limited by water, but by cold temperatures and therefore would exhibit highest activity in response to temperature. However, this was not supported by our data. At Admiralty Bay, in fact the opposite was true. As described above, the addition of water stimulated respiration, N mineralization, and bacterial biovolume, but temperature had a negative impact on respiration.

Of all four sites, Kilpisjärvi had the highest SWC and soil organic matter content, and supports the most diverse community of plants and higher life forms. Neither temperature nor water limitation were a factor for any of the metrics measured, despite temperature limitations generally understood for Arctic soil microbial processes (Blume-Werry et al., 2023). It is possible that, like Mars Oasis, Kilpisjärvi soils are primarily limited by some other factor such as nutrient content, but these soils contained relatively high levels of C, N, and P. More likely,

the parameters set for this experiment were too conservative and likely the microbes are already adapted to these variations. A 2 °C and 1.125 mL water addition may not have been enough to generate a response from the microbial community adapted to natural temperature and moisture fluctuations greater than this. Indeed, projections of Arctic temperatures indicate a much higher increase in temperature than the one modeled in this experiment (Overland et al., 2019), and a field study at this site measured responses at up a to 4 °C increases in daily maximum temperatures (Rinnan et al., 2009b). Other Arctic sites show doubling of soil respiration and microbial growth rates at temperature increases of 5 °C increments through ranges above those used in our study (Wang et al., 2021). A study from slightly more southerly Abisko, Sweden showed bacterial biomass and respiration increased over a doubling and tripling of soil moisture and temperature (Cruz-Paredes et al., 2021), representing greater ranges than we simulated here. Notably the one field study at Kilpisjärvi measured a reduction in soil N and microbial biomass after 10 years of warming, and it is possible that there may be a lag in response that was not captured during this short term incubation (Rinnan et al., 2009b). Further, our incubations focused on the direct response only of soil microbes, and therefore were conducted in the absence of plants that could influence soil microbial responses to climate change in field studies (Rinnan et al., 2009b).

Thus, the two tundra ecosystems studied differ in many characteristics that likely influence their climate sensitivity. Despite having a similar MAT, Kilpisjärvi soils are comparatively much higher in organic matter and nitrogen content (Table 1; Figs. 4–5) with a more diverse aboveground and belowground community, and supports a more abundant and active microbial community (Figs. 2–3) that appear to be insensitive to the small variability in climate altered by this study. Despite receiving more MAP, Admiralty Bay soils are water limited, even at the small range we tested. Vegetation differs significantly between the two tundras, which can alter the influence of temperature regimes in the Arctic (Bradley-Cook and Virginia, 2018; Grogan and Jonasson, 2005). Further, a meta-analysis showed a statistically insignificant response of soil respiration to temperature in low tundra Arctic ecosystems (Rustad et al., 2001), to which Kilpisjärvi is more similar.

### 4.4. Synthesis

Our results demonstrate that some polar ecosystems are more sensitive to changes in temperature and moisture than others. Overall, one of the two polar deserts (Dry Valleys) and one tundra ecosystem (Admiralty) were climate-sensitive, while the other site from each ecosystem type was less so. The two polar desert sites in Antarctica were co-limited by both temperature and water, though to different magnitudes. The Antarctic tundra was water-limited and negatively sensitive to temperature, whereas the wetter and warmer Arctic tundra site did not respond to the magnitude of climate change simulated in this study. Therefore, the consequences of climate change for polar C and nutrient dynamics will likely be ecosystem-dependent and not predictable uniformly across polar regions. Further, C and N dynamics do not appear to be completely linked. When C mineralization was stimulated by climate treatments, so was N availability (in at least one mineral form), but the C and N responses to each treatment did not entirely mirror each other.

Also, it is interesting that mineral N availability was impacted by climate at two sites, but mineral P availability was not impacted at all. This could be due to the fact that $NH_4^+$ and $NO_2^- + NO_3^-$ availability are more strongly tied to microbial activity than $PO_4^{3-}$. In all four sites, $PO_4^{3-}$ availability is higher than the predicted soil microbial stoichiometric N:P ratio of 7:1 (Cleveland and Liptzin, 2007), suggesting N is more limiting than P at these sites (Ball et al., 2018; Newsham et al., 2019). Any stimulation of their activity would therefore likely first influence N before P, and as with C, the response of N to climate change will be ecosystem-dependent. Future studies could explore the interaction of in situ stoichiometry with simulated climate change to determine whether this is a common or unique characteristic of polar ecosystems.

## CRediT authorship contribution statement

**Ana Khan:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft. **Becky A. Ball:** Conceptualization, Methodology, Supervision, Formal analysis, Resources, Data curation, Writing – review & editing.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Becky A Ball reports financial support was provided by National Science Foundation.

## Data availability

Data will be made available on request.

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