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Biological Sciences

Microbial mat activity and soil biogeochemistry across variable phosphorus availability in Taylor Valley, Antarctica

Sarah N. Power[1], Ernest D. Osburn[2] and John E. Barrett[1]

[1]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA and [2]Department of Plant and Soil Sciences, University of Kentucky, Lexington, KY, USA

Abstract

Primary production is fundamental to ecosystems, and in many extreme environments production is facilitated by microbial mats. Microbial mats are complex assemblages of photo- and heterotrophic microorganisms colonizing sediment and soil surfaces. These communities are the dominant producers of the McMurdo Dry Valleys, Antarctica, where they occupy lentic and lotic environments as well as intermittently wet soils. While the influence of microbial mats on stream nutrient dynamics and lake organic matter cycling is well documented, the influence of microbial mats on underlying soil is less well understood, particularly the effects of microbial mat nitrogen and carbon fixation. Taylor Valley soils occur across variable levels of inorganic phosphorus availability, with the Ross Sea drift containing four times that of the Taylor drifts, providing opportunities to examine how soil geochemistry influences microbial mats and the ecological functions they regulate. We found that inorganic phosphorus availability is positively correlated with microbial mat biomass, pigment concentration and nitrogen fixation potential. Additionally, our results demonstrate that dense microbial mats influence the ecological functioning of underlying soils by enriching organic carbon and total nitrogen stocks (two times higher). This work contributes to ongoing questions regarding the sources of energy fuelling soil food webs and the regional carbon balance in the McMurdo Dry Valleys.

Keywords: Carbon; cyanobacteria; nitrogen fixation; phosphorus; pigments; soil ecology

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Introduction

Primary production is a fundamental ecosystem process that supports food webs and ecosystem energy flow. In environments where environmental stressors are common (e.g. saline conditions, intense ultraviolet (UV) radiation), microbial mats, consisting mainly of cyanobacteria but also including green algae and moss, are often foundational components of the autotrophic community. Microbial mats typically occur as laminated millimetre- to centimetre-thick colonial communities on the surface of soils and sediments in extreme environments such as deserts, hypersaline ponds and hydrothermal hot springs (Stal & Caumette 2011, Prieto-Barajas *et al.* 2018). Microbial mats are self-sustaining communities that govern nutrient cycles and create a habitat supporting a diverse community of organisms (Davey & O'Toole 2000, Guerrero *et al.* 2002, Bolhuis *et al.* 2014, Prieto-Barajas *et al.* 2018). In the polar desert of the Antarctic McMurdo Dry Valleys, microbial mats are present within and along the margins of glacial-melt streams, lakes, wetlands, snow-influenced soils and even surface lake and glacial ice (Paerl & Priscu 1998, McKnight *et al.* 1999, Power *et al.* 2020, Stone *et al.* 2024). The microbial mats of this region are dominated by cyanobacteria but also contain other autotrophic and heterotrophic prokaryotic taxa (Van Horn *et al.* 2016), as well as green algae, diatoms, mosses and invertebrates (e.g. nematodes, rotifers and tardigrades; Alger *et al.* 1997, Simmons *et al.* 2009). The highly variable and physiologically stressful conditions of Antarctica (e.g. low nutrient availability, freeze/thaw cycles and intense UV radiation; Hawes *et al.* 1992, Vincent *et al.* 1993) require key adaptations of resident biota to these harsh environments.

The terrestrial surfaces of the McMurdo Dry Valleys have been influenced by the waxing and waning of glacial ice, which left behind glacial drifts consisting of soil and rock material (Bockheim *et al.* 2008). This landscape history has created significant variation in inorganic phosphorus (P) availability across the Taylor Valley in particular, where differences in till lithology and weathering rates have resulted in areas containing high and low P (Bate *et al.* 2008, Heindel *et al.* 2017, 2018). Previous studies have demonstrated a link between P availability and nitrogen (N) fixation in aquatic and terrestrial systems, where high-P environments favour N-fixing organisms (Howarth *et al.* 1988, Andersson *et al.* 2015, Tierney & Wurzburger 2024). Moreover, we suggest the variation in P availability across Taylor Valley may influence the distribution and activity of terrestrial microbial mats, as these communities are known to contain active N-fixers (Coyne *et al.* 2020). Previous studies have also demonstrated that the abundance and composition of microbial mat communities are influenced by the local geomorphology and hydrology (McKnight *et al.* 1999, Stanish *et al.* 2011, Kohler *et al.* 2015, Levy *et al.* 2020), but no work has systematically examined the influence of geochemical variation

Corresponding author: Sarah Power; Email: snpower@vt.edu

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in nutrient availability (e.g. Barrett *et al.* 2007, Bate *et al.* 2008, Welch *et al.* 2010) on microbial mat distribution, composition and activity.

In many ecosystems, microbial mats make important material (e.g. carbon (C) and N fixation) and functional (soil cohesion and UV protection) contributions to the environments they occupy (Prieto-Barajas *et al.* 2018). In the McMurdo Dry Valleys, cyanobacteria-dominated microbial mats are the dominant primary producers and strongly influence organic matter budgets (Parker *et al.* 1982, Burkins *et al.* 2000, Lawson *et al.* 2004) and N economies (Hawes *et al.* 1992, Kohler *et al.* 2018, 2023) of the lake, stream and sediment environments they occupy. For example, while stream water chemistry is modulated by upstream glacial-melt conditions and hyporheic interactions that alter the biogeochemistry (Gooseff *et al.* 2002, 2003, Maurice *et al.* 2002), microbial mat communities also influence water chemistry through biological uptake, recycling and downstream export of N and P (Gooseff *et al.* 2004, McKnight et al. 2004, Kohler *et al.* 2018).

Most studies of microbial mats in the McMurdo Dry Valleys have been conducted in or adjacent to perennial aquatic landscape features (i.e. streams, ponds and lakes; Moorhead *et al.* 2003, Gooseff *et al.* 2004, McKnight *et al.* 2007, Stone *et al.* 2024). Intermittently wet soils and ephemeral, un-channelized streams have received comparatively less attention, even though these landscapes occupy large proportions of the area, and the functioning of microbial mats and biocrusts is relevant to ongoing questions regarding the sources of energy fuelling the simple soil food webs and the regional C balance (e.g. Burkins *et al.* 2000, Barrett *et al.* 2006a, Power *et al.* 2024b,c). Moreover, strong geochemical variation in inorganic P (e.g. Barrett *et al.* 2007, Welch *et al.* 2010) may influence the distribution and activity of microbial mats by controlling their N-fixation potential.

The objective of our study was to investigate the relationships between underlying soil chemistry and microbial mat distribution, composition and function in Taylor Valley, Antarctica. We expected to observe a feedback relationship whereby soil geochemistry (i.e. variation in inorganic P) influences microbial mat occurrence, and in turn the density of microbial mats influences the underlying soil geochemistry. Specifically, we characterized the taxonomic composition, underlying soil geochemistry and pigment composition of microbial mats distributed across two glacial drifts in the Taylor Valley, and we further examined the influence of variable soil inorganic P content on microbial mats and their N-fixation potential, as well as the influence of microbial mats on the C and N budgets of the underlying soils.

Materials and methods

Site description

The McMurdo Dry Valleys (Fig. 1) are the largest contiguous ice-free area on the Antarctic continent, with ~4500 km^2 of exposed soil, stream and lake ecosystems (Levy 2013). They are one of Earth's coldest and driest deserts, with mean annual temperatures between -15°C and -30°C and less than 50 mm water equivalent of snowfall annually (Fountain *et al.* 2010, Obryk *et al.* 2020). Glacial meltwater during the summer (i.e. 24 h of daylight) feeds streams that flow for an average of 4–9 weeks per year (Wlostowski *et al.* 2016). These streams drain into perennially ice-covered lakes along the floor of most of the valleys, supporting microbial mats within and along the margins of the streams and lakes (McKnight *et al.* 1999). Additionally, other sources of moisture (e.g. snow patches, wetlands and groundwater seeps; Levy *et al.* 2024) are also activated during the summer, and many of these wetted environments also support microbial mats (Gooseff *et al.* 2013).

The parent material of soils in the region are composed of glacial drift deposits (i.e. unsorted rock/soil material deposited from glacial ice or meltwater). In Taylor Valley, where this study was conducted, the soils form from three types of glaciations: 1) advances from the grounded Ross Sea Ice Sheet from the east, 2) advances of glaciers from the East Antarctic Ice Sheet to the west and 3) advances of alpine glaciers along the Taylor Valley walls (Bockheim *et al.* 2008). These glaciations are thought to have occurred over the past 10,000 to 10 million years (Bockheim *et al.* 2008), resulting in very different exposure ages and, given the regional variation in bedrock composition and mineralogy, distinct clast compositions (Denton *et al.* 1989, Bate *et al.* 2008, Bockheim *et al.* 2008). The Ross Sea drift is on the eastern side of Taylor Valley (Fig. 1) and was deposited more recently than the Taylor drifts on the western side of Taylor Valley. Soil P content is most abundant on the Ross Sea drift due to the weathering of apatite, which is more abundant on these drifts relative to the Taylor Valley sequence (Barrett *et al.* 2007, Bate *et al.* 2008, Heindel *et al.* 2017, 2018). The geochemistry of the drifts in Taylor Valley has been previously described (e.g. Barrett *et al.* 2007, Bate *et al.* 2008); however, the impacts of the variation in soil geochemistry on microbial mat composition and activity have not been studied. Additionally, while

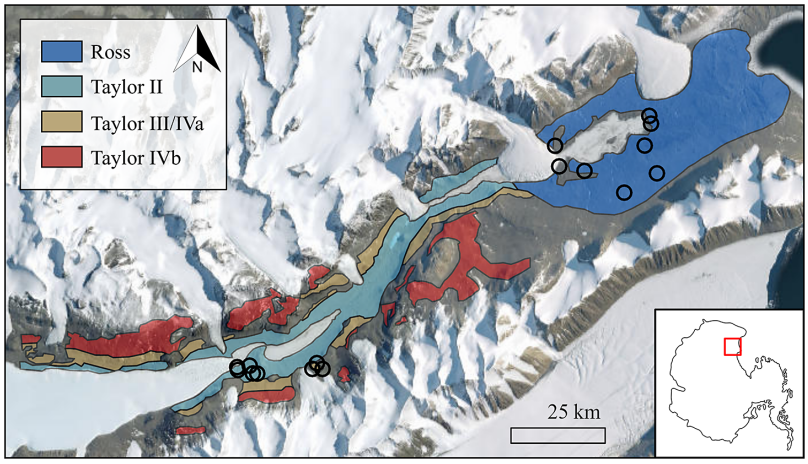


Figure 1. Map of eastern Taylor Valley with 16 field sites indicated by open black circles. Inset on bottom right identifies the McMurdo Dry Valleys, Antarctica, with a red square. Ross Sea, Taylor II, Taylor III/IVa and Taylor IVb drifts are delineated by colour, modified from Bockheim *et al.* (2008). Esri basemap imagery © Earthstar Geographics.

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the influence of microbial mats on stream chemistry has been well documented (e.g. McKnight et al. 2004, Kohler *et al.* 2018), the influence of microbial mats, due to their N- and C-fixation potential in particular, on underlying soils alongside stream margins is less well understood.

Studies of microbial mats in the McMurdo Dry Valleys have described them primarily by their visible colour, along with the hydrological conditions of their habitat (Alger *et al.* 1997, McKnight *et al.* 1999, Stanish *et al.* 2011, Kohler *et al.* 2015). A useful typology has emerged from these studies that is based on dominant pigments and visible colour: black, orange, green and red mats (Alger *et al.* 1997). The black mats primarily occupy intermittently saturated areas at the margins of lentic and lotic landscapes and beside melting snow patches, whereas orange, green and red mats primarily occupy seasonally inundated areas generally within the thalweg of stream channels (Howard-Williams *et al.* 1986, Alger *et al.* 1997, Kohler *et al.* 2015). While this colour typology should be understood as a description of community type rather than specific taxa, the generalization that black mats are dominated by *Nostoc*, green mats by chlorophytes and orange and red mats by *Oscillatoria* is supported by early microscopy (e.g. Parker *et al.* 1982, Vincent & Howard-Williams 1986, Alger *et al.* 1997) and later molecular sequencing approaches (e.g. Van Horn *et al.* 2016).

Field sampling

In December 2019 and January 2020, we sampled microbial mats and underlying soils at 16 sites located on the Ross Sea (n = 8) and Taylor drifts (n = 8) of Taylor Valley, Antarctica (Fig. 1 & Table S1). These sites included landscapes that were intermittently wet environments, such as alongside stream channels, pond margins and snowmelt patches. Sampling locations were often within 1 m of water sources but not within standing water. We did not select sites within the thalweg of incised stream channels or in the inundated areas of lakes and ponds as our focus was on the contribution of microbial mats to terrestrial soils. Stream-to-soil ecotones are not always clear in this region (e.g. Harris *et al.* 2007, Gooseff *et al.* 2013, Wlostowski *et al.* 2019), but we sought landscape surfaces that were not subject to channelized stream flow, where lotic processes dominate the biogeochemistry and community composition of microbial mats (Gooseff *et al.* 2004, Kohler *et al.* 2015, Zoumplis *et al.* 2023). Dominant colour typology composition (orange mats, typically described as dominated by *Oscillatoria*, or black mats, typically considered *Nostoc*-dominated) was noted for each location (e.g. Alger *et al.* 1997).

We identified a 0.5 × 0.5 m area of microbial mat at each site (e.g. Fig. 2) and sampled five plugs of mat material (from the centre and the four corners) using a sterilized #13 brass cork borer (2.27 cm^2) for organic matter content, pigment analysis and molecular analysis separately, for a total of 15 plugs. Directly beneath each sampled microbial mat we also collected the underlying soil (0–5 cm depth) using a sterilized cork borer for later geochemical and molecular analysis. Geochemical comparisons to existing, published soil data from the same drift sequences in the vicinity of our sampling sites were conducted (see 'Discussion' section), as no bare soils (i.e. soils without overlaying microbial mats) were collected during this field sampling campaign. The five microbial mat and underlying soil samples were composited into one soil and one microbial mat sample per site per analysis. All samples were kept frozen at -20°C in complete darkness until subsequent analyses were performed.

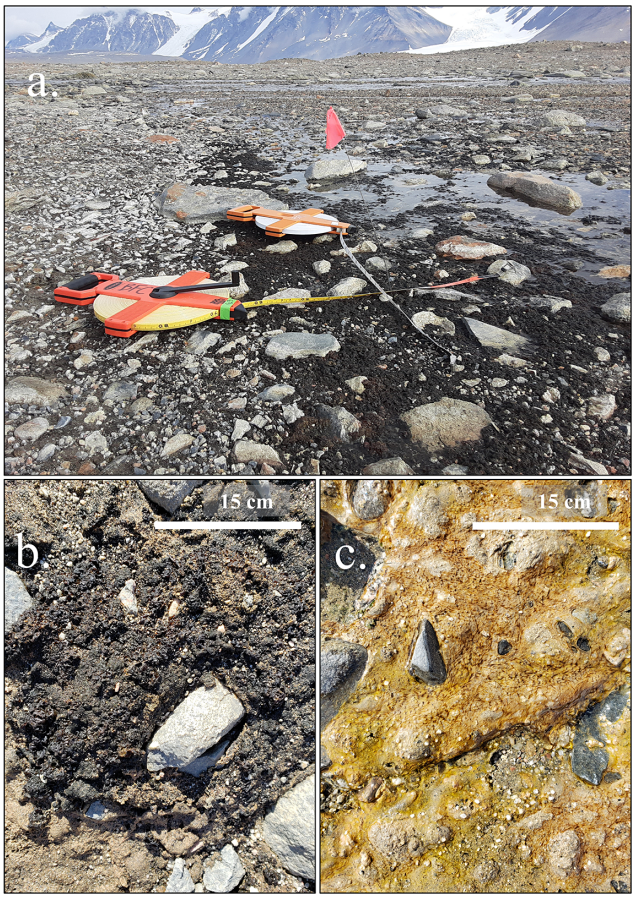


Figure 2. Photographs of **a.** 0.5 × 0.5 m plot of a dense black microbial mat alongside Crescent Stream (R07, Ross Sea drift), **b.** a dense black microbial mat alongside an unnamed ephemeral stream near Taylor Glacier (T15, Taylor drifts) and **c.** a dense orange microbial mat alongside an unnamed stream near Taylor Glacier (T14, Taylor drifts). Photographs taken by E.D. Osburn and S.N. Power.

Soil geochemical analyses

Gravimetric water content (GWC) was measured for each of the soil samples, determined as the mass of water lost after oven drying the soils at 105°C for 24 h. Soil pH and electrical conductivity (EC) were measured using 1:2 and 1:5 soil:deionized H_2O slurries, respectively, using a YSI pH meter (YSI, Yellow Springs, OH, USA) and Orion Star conductivity meter (Thermo Fisher Scientific, Waltham, MA, USA). We also extracted inorganic N (NH_4^+ and NO_3^-) in 2 M potassium chloride and inorganic P (PO_4^{3-}) in 0.5 M sodium bicarbonate. We interpret this extractable (soluble) nitrate, ammonium and phosphate as the biologically available N and P in the soil. Major anions were extracted using 1:5 dilutions of soil:deionized H_2O. Inorganic N and P were measured on extracts using a Lachat QuikChem flow injection analyser (Hach Company, Loveland, CO, USA; Prokopy 1995, Knepel 2003). Major anion concentrations were analysed on a Dionex Ion Chromatograph (Thermo Fisher Scientific, Waltham, MA, USA; Pfaff 1993); only sulphate (SO_4^{2-}) and chloride (Cl^-) had consistent concentrations above minimum detection levels. Additionally, we measured soil organic carbon (SOC) and total nitrogen (TN) using an Elementar Vario MAX Cube analyser (Elementar Americas, Inc., Mount Laurel, NJ, USA) after fumigating samples with concentrated hydrochloric acid to remove the influence of carbonates on SOC values (Walthert *et al.* 2010).

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Microbial mat organic matter and pigment analyses

Each microbial mat sample was measured for organic matter content as ash-free dry mass (AFDM) by oven drying at 100°C for 24 h, weighing the dry mass, combusting at 550°C for 15 h using a muffle furnace, weighing the ashed mass after cooling in a desiccator and estimating AFDM as the mass lost during ashing per mass of dry material (Dean 1974, Heiri *et al.* 2001, Santisteban *et al.* 2004). Additionally, pigment composition and concentration (Table S2) were estimated at the Paerl Lab, University of North Carolina, using high-performance liquid chromatography (HPLC; Mantoura & Llewellyn 1983, Van Heukelem 1992, 1994, Jeffrey *et al.* 1997). Pigments were extracted from the microbial mat samples in 100% acetone for 24 h before analysis on the Shimadzu HPLC system (Shimadzu Scientific Instruments, Columbia, MD, USA). The HPLC separated the pigments and measured the absorbance of the extracts by scanning 340–700 nm every 1.28 s. These data were analysed using Shimadzu's *LabSolutions Lite* software and a combination of peak retention time, absorbance spectrum shape/signature, maximum wavelength and the similarity match of the unknown pigment to a standard to identify the various pigments (Jeffrey *et al.* 1997). Pigments were then quantified from their peak areas, calculated at 388 nm for scytonemin and reduced scytonemin and 440 nm for all other pigments. A multipoint calibration curve was generated by injecting volumes of known quantities of pure pigment standards (DHI, Denmark) and then calculating the peak areas of those pigments. The standards' peak areas were then used to calculate the slopes (response factor) for all pigments, which were multiplied by the samples' peak areas of the chromatogram at 388 or 440 nm to quantify the pigments extracted in $\mu g\ g^{-1}$ dry mat.

DNA extraction and quantitative polymerase chain reaction

We determined the relative abundance of all nitrogenase (*nif*) genes, which are indicators of N-fixation potential, using shotgun metagenome sequencing and the absolute abundance of *nifH* specifically using quantitative polymerase chain reaction (qPCR) for both the microbial mats and underlying soils. DNA was extracted from ~1.5 g soil and ~ 0.5–1.0 g microbial mat material using the DNeasy PowerSoil kit (QIAGEN), and the extracts were quantified using a Qubit 2.0 fluorometer (Thermo Fisher Scientific). For qPCR, we used the IGK3/DVV primer set (Ando *et al.* 2005) because it exhibits less bias than other *nifH* primer sets (Gaby & Buckley 2017). Samples were amplified in triplicate and PCR reactions contained 10 µl Quantitect SYBR Green qPCR Mastermix (QIAGEN), 3 µl of 10 µM working stocks of each of the forward and reverse primers (for final primer concentrations of 1.5 µM) and 4 µl of DNA template for a total reaction volume of 20 µl. The high primer concentration we used was intended to maximize the efficiency of the qPCR reactions (Gaby & Buckley 2017). Thermal cycling conditions were as follows: 15 min at 95°C followed by 40 cycles of 15 s at 95°C, 30 s at 56°C and 30 s at 72°C. Standard curves were generated by amplifying serial dilutions of the target regions, with amplification efficiencies of 84.5% for the microbial mat samples and 74.2% for the soil samples, and both R^2 values > 0.99. For the qPCR gene standard, we used the *nifH* gene sequence from *Nostoc punctiforme* strain PCC 73102, which has a high similarity (99%) to Antarctic *Nostoc* sequences (Jungblut & Neilan 2010). Amplification specificity was assessed using melt curve analysis. The *nifH* gene copy numbers were corrected for dry soil mass and wet mat mass.

Metagenomic sequencing and taxonomic assignment

DNA libraries were prepared for shotgun metagenome sequencing using a KAPA HyperPrep Kit (Roche Molecular Systems, Inc.). Libraries were sequenced on an Illumina NextSeq500 in a 150 bp paired-end sequencing run at the Duke University School of Medicine Sequencing and Genomic Technologies Shared Resource. Raw sequence reads were uploaded to MG-RAST (accession# mgp95386) for merging of paired ends, quality control and annotation using the recommended MG-RAST default parameters (Meyer *et al.* 2008). Functional annotations were performed by aligning the metagenomic sequences to the SEED Subsystems database (Overbeek *et al.* 2014), while taxonomic annotations were performed using the RefSeq and SILVA databases. For all functional and taxonomic annotations, we used an e-value cutoff of 1e-5, a sequence similarity threshold of 80% and a minimum alignment length of 20 bp. After processing with MG-RAST, we retained an average of ~7.2 million sequences per sample, ranging from ~4.3 million to ~8.9 million sequences per sample. Of these sequences, an average of 3.91% failed quality control, 1.10% were rRNA genes, 41.25% were annotated proteins and 57.65% were unknown proteins. To quantify N-fixation gene relative abundances, we summed all sequences annotated as *nif* genes for each sample and expressed *nif* gene relative abundance as the percentage of all annotated reads.

Taxonomy was assigned to the processed reads using the NCBI RefSeq and SILVA (version 138.1) databases. We determined community composition by analysing the relative abundance of prokaryotic taxa that classified to at least a phylum (bacterial or archaeal). All eukaryotic taxa and any taxa unclassified to a phylum were removed from the analysis. To account for differences in sequence depth among samples, we used rarefied sequence counts. The rarefaction curves for the RefSeq data saturated, whereas the ones for the SILVA data did not; thus, we based our interpretations and conclusions primarily on the RefSeq results.

Statistical analyses

All statistical analyses were performed in *R Statistical Software* (R Core Team 2021). Figures were created in *R* using the *ggplot2* package (Wickham 2016). One-way analysis of variance (ANOVA; *aov* function, *stats* package; R Core Team 2021) was used to determine differences in soil geochemistry across drift types. Relative abundance of prokaryotic genera was determined using the following packages: *vegan* for the rarefaction curve analysis (Oksanen *et al.* 2022), *funrar* for relative abundance calculation (Grenié *et al.* 2017) and *reshape*, *tidyr*, *plyr* and *stringr* for data manipulation before visualizing the relative abundance (Wickham 2007, 2011, 2023, Wickham *et al.* 2023). Diversity was assessed using alpha (Shannon) and beta (Bray-Curtis dissimilarity) diversity metrics with the *diversity* function in the *vegan* package. A one-way ANOVA was used to determine differences in Shannon diversity by mat type. Bray-Curtis dissimilarity was calculated using the *vegdist* function in the *vegan* package after converting the data to relative abundances. A non-metric multidimensional scaling (NMDS) ordination was created with permutational analysis of variance (PERMANOVA) to visualize and analyse differences in prokaryotic community composition between mat type (*metaMDS* and *adonis2* functions, *vegan* package).

One-way ANOVAs were also performed to assess differences in AFDM and pigment concentrations by mat type. We used principal component analysis (PCA) to visualize the relative abundance of pigments across sites (*princomp* function, *stats* package;

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envfit function, *vegan* package), and we used PERMANOVA to assess mat type differences with Euclidean distance matrices. Additionally, the dispersion of the pigment relative abundance was calculated by mat type (*betadisper* function, *vegan* package), and a one-way ANOVA was used to assess the significance of the difference in dispersion by mat type. The relationships between metagenomic-derived *nifH* relative abundance and the qPCR-derived number of *nifH* genes for soils and microbial mats were assessed using Pearson correlation coefficients (r). Differences in *nif* and *nifH* gene abundance for the soils and microbial mats were assessed by mat type using one-way ANOVAs.

We applied polynomial regressions between AFDM and SOC, TN and the relative abundance of *nif* in soils. Assumptions of linear and polynomial regression were assessed, including normality (Q-Q plot assessment, Shapiro-Wilk normality test; *shapiro.test* function, *stats* package), homoscedasticity (Breusch-Pagan test; *bptest* function, *lmtest* package; Zeileis & Hothorn 2002) and no autocorrelation (Durbin-Watson test; *dwtest* function, *lmtest* package), and the data met all assumptions for polynomial regression. Spearman correlation coefficients (ρ) were calculated to assess relationships between the inorganic P of the underlying soils and microbial mat parameters including AFDM, relative abundance of *nif* and pigment concentrations of chlorophyll-*a*, scytonemin, β-carotene and canthaxanthin, as the distribution of these data did not meet the assumptions required for parametric analyses. We also used PCA to visualize variation in N and P availability, AFDM, *nif* gene relative abundance and scytonemin concentration among sites, and we assessed differences by mat type using PERMANOVA with Euclidean distance matrices. Additionally, the dispersion of these results was calculated by mat type (*betadisper* function, *vegan* package), and a one-way ANOVA was used to assess the significance of the difference in dispersion by mat type. For all statistical analyses, $P < 0.05$ was considered statistically significant.

Results

Distribution of 'black' and 'orange' microbial mats

Dense black microbial mats were the most conspicuous mat type in the intermittently wet environments we sampled on the Ross Sea drift, where we encountered dense black mats at the margins of streams and downhill of seasonal snowpacks (Fig. 2 & Table S1). Orange mats are abundant in the thalweg of the streams in this part of Taylor Valley, as has been previously described (Howard-Williams *et al.* 1986, Alger *et al.* 1997, Kohler *et al.* 2015), but they were not apparent in the drier 'terrestrial' environments we examined in this study. The Taylor drifts had a lower abundance of microbial mats overall in comparison to the Ross Sea drift. Unlike the Ross Sea drift, we were able to identify and sample orange mat communities on the Taylor drifts outside of the thalweg of streams, typically on hillslopes downhill from large snowpacks that feed ephemeral wetland landscapes (e.g. landscapes that do not support flowing surface water in most years, such as the Wormherder Creek wetland; Harris *et al.* 2007, Wlostowski *et al.* 2019). Black mats were less common on the Taylor drifts but were found along ephemeral stream margins. We sought to collect an equal distribution of black and orange mats across the drift types; however, the observed occurrences of mat types resulted in an asymmetrical distribution of mat types across the drift sequences.

Soil geochemical characterization below microbial mats

Soil geochemical characteristics below microbial mats varied among the plots, mainly associated with differences between the Ross Sea and Taylor drifts. Soil pH, inorganic P, SOC and TN were significantly higher in samples collected from the Ross Sea compared to the Taylor drifts (ANOVA, $P < 0.05$; Table I). For example, Ross Sea drift soil contained four times more biologically available inorganic P compared to the Taylor drifts, with an average of 2.36 μg P g^{-1} dry soil compared to 0.60 μg P g^{-1} dry soil, and four times lower N:P ratios than the Taylor drift samples. The average extractable, inorganic N:P ratios (by mass) of the Ross Sea and Taylor drift samples were 0.87 and 3.78, respectively. SOC was two times higher in the Ross Sea drift samples compared to the Taylor drifts, with an average of 1.79 mg C g^{-1} dry soil compared to 0.85 mg C g^{-1} dry soil. TN was also two times higher in the Ross Sea drift samples compared to the Taylor drifts, with an average of 0.19 mg N g^{-1} dry soil compared to 0.11 mg N g^{-1} dry soil. Soil GWC, EC, NH_4^+, NO_3^-, SO_4^{2-} and Cl^- were not significantly different between the Ross Sea and Taylor drift samples (Table I).

Community composition of microbial mats

Community composition varied among the microbial mat samples, mainly associated with differences between black and orange mats. Taxonomy assigned using the RefSeq and SILVA databases generated similar results, with only small differences in relative abundance at the phylum level (primarily for Cyanobacteria, Proteobacteria and Bacteroidetes; Figs 3a & S1a), and no meaningful differences at the genus level, which were dominated by cyanobacteria taxa (Figs 3b & S1b). At the phylum level, all microbial mat types sampled consisted primarily of a mix of Cyanobacteria, Proteobacteria and Bacteroidetes (Fig. 3a). In black mats of both the Ross Sea and Taylor drifts, Proteobacteria was the most abundant phylum, followed by Cyanobacteria and Bacteroidetes. In contrast, orange mats were dominated by Cyanobacteria at the phylum level. At the genus level, every microbial mat sample contained a large proportion of rare genera

Table I. Mean physicochemical variables for soils underlying microbial mats averaged by glacial drift composition: Ross Sea drift ($n = 8$) and Taylor drifts ($n = 8$) with ± 1 standard deviation. One-way analysis of variance tests were run between Ross Sea and Taylor drift soils for each parameter, and superscript letters represent differences (measurements with dissimilar letters were significantly different from each other, $P < 0.05$).

	GWC	pH	EC	NH_4^+	NO_3^-	PO_4^{3-}	SO_4^{2-}	Cl^-	SOC	TN
	g/g		μS cm^{-1}	μg N g^{-1} dry soil	μg N g^{-1} dry soil	μg P g^{-1} dry soil	μg S g^{-1} dry soil	μg Cl g^{-1} dry soil	mg C g^{-1} dry soil	mg N g^{-1} dry soil
Ross Sea drift	0.18^a ± 0.03	7.55^a ± 0.18	22.00^a ± 6.52	1.88^a ± 3.19	0.48^a ± 0.16	2.36^a ± 1.14	3.93^a ± 2.10	6.58^a ± 2.13	1.79^a ± 0.44	0.19^a ± 0.04
Taylor drifts	0.18^a ± 0.02	7.34^b ± 0.19	13.89^a ± 7.75	0.56^a ± 0.05	0.42^a ± 0.04	0.60^b ± 0.38	3.60^a ± 1.94	4.34^a ± 2.04	0.85^b ± 0.58	0.11^b ± 0.06

EC = electrical conductivity; GWC = gravimetric water content; SOC = soil organic carbon; TN = total nitrogen.

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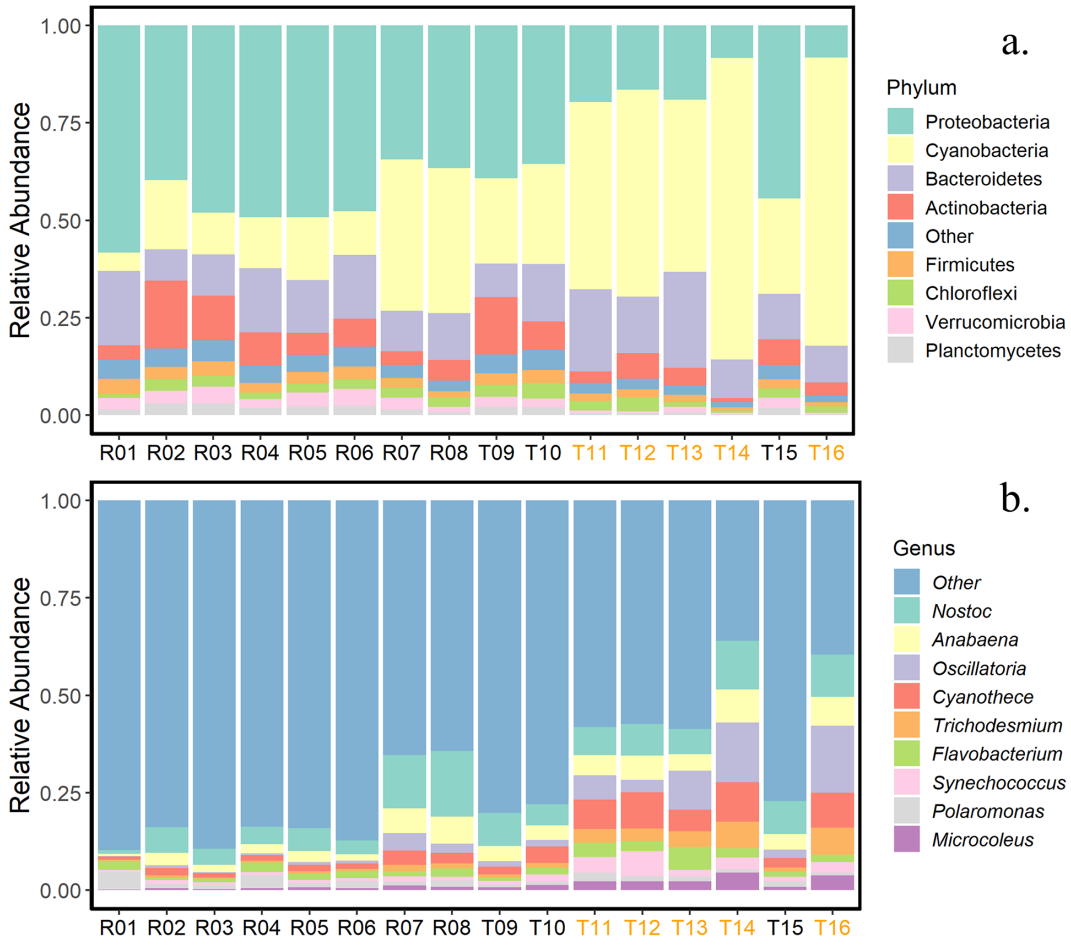


Figure 3. Relative abundances of **a.** prokaryotic phyla and **b.** prokaryotic genera identified within each of the 16 samples using the NCBI RefSeq sequence library. The remaining prokaryotic taxa of less than 1.4% are represented in 'Other'. Samples collected from the Ross Sea drift begin with 'R' (i.e. R01–R08), and samples collected from the Taylor drifts begin with 'T' (i.e. T09–T16). The *x*-axis label colours represent whether the samples were collected from black or orange microbial mats based upon visual field surveys.

(i.e. genera constituting less than 1.4% of sequences), contributing to more than 50% of the relative abundance in most of the samples (Fig. 3b). Black mats had a greater proportion of rare genera compared to orange mats. The cyanobacteria in black mats were predominantly *Nostoc*, whereas in orange mats *Oscillatoria* was typically the most abundant taxa, followed by *Nostoc* and *Cyanothece*. Shannon diversity was significantly greater in black mats, with an average of 5.19 compared to an average Shannon diversity of 4.17 in orange mat communities (ANOVA, $P < 0.05$). Black and orange mat community compositions were significantly different (PERMANOVA, $P = 0.001$), and NMDS visualization using Bray-Curtis dissimilarities exhibited significant differences in taxonomic composition between the mat types (Fig. 4).

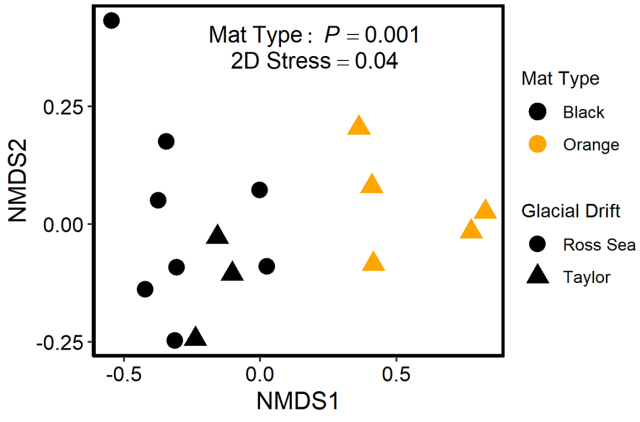


Figure 4. Non-metric multidimensional scaling (NMDS) ordination of the community composition (by genera) of each mat type using Bray-Curtis dissimilarities. The shown *P*-value is the mat type effect from permutational analysis of variance.

Organic matter content and pigment characterization of microbial mats

Organic matter content as AFDM and pigment concentration varied among the samples, mainly associated with differences in black and orange microbial mats. AFDM ranged over an order of magnitude from 12.7 to 185.8 mg g^{-1} dry mat and was significantly greater in black mats than in orange mats (ANOVA, $P < 0.05$; Table II). Black microbial mats contained three times the mass of organic matter than orange mats, with an average of 78.5 mg AFDM g^{-1} dry mat.

The microbial mats sampled contained photosynthetic and accessory pigments common to many cyanobacteria: chlorophylls, multiple carotenoids and extracellular sheath pigments. Out of 23 pigments analysed using HPLC (Table S2), nine pigments had detectable concentrations present within the sampled microbial

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Table II. Average ash-free dry mass (AFDM) and pigment concentrations averaged by microbial mat type: black mats ($n = 11$) and orange mats ($n = 5$) with ± 1 standard deviation. One-way analysis of variance tests were run between black and orange mats for each parameter, and superscript letters represent differences (measurements with dissimilar letters were significantly different from each other, $P < 0.05$).

	AFDM	Total pigment concentration	Scyto	Scyto- Red	Myxo	Zea	Chl-*a*	Chl-*b*	B-Car	Cantha	Echine
	mg g^{-1} dry mat	μg g^{-1} dry mat	μg g^{-1} dry mat								
Black mat	78.5^a ± 43.6	267.5^a ± 129.5	225.3^a ± 112.9	38.5^a ± 17.0	0^a ± 0	0.005^a ± 0.006	2.67^a ± 1.85	0.02^a ± 0.04	0.011^a ± 0.004	0.75^a ± 0.79	0.26^a ± 0.28
Orange mat	24.9^b ± 12.0	3.9^b ± 3.0	1.4^b ± 1.4	1.1^b ± 1.5	0.03^b ± 0.05	0.004^a ± 0.003	1.26^a ± 0.87	0.01^a ± 0.01	0.002^b ± 0.001	0.01^a ± 0.01	0.07^a ± 0.04

B-Car = *β*-carotene; Cantha = canthaxanthin; Chl-*a* = chlorophyll-*a*; Chl-*b* = chlorophyll-*b*; Echine = echinenone; Myxo = myxoxanthophyll; Scyto = scytonemin; Scyto-Red = reduced scytonemin; Zea = zeaxanthin.

mats (Table II). Black microbial mats had 68 times the total pigment concentration (267.5 μg g^{-1} dry mat on average) of orange mats (3.9 μg g^{-1} dry mat on average; ANOVA, $P < 0.001$; Table II). Scytonemin, reduced scytonemin, myxoxanthophyll and *β*-carotene concentrations were significantly different between black and orange mats (ANOVA, $P < 0.05$; Table II). Black mat pigment composition was dominated by scytonemin, which totalled > 83% of the total pigment relative abundance on average. Black mats contained 165 times the concentration of scytonemin compared to orange mats, with an average of 225.3 μg g^{-1} dry mat. Similarly, black mats also contained greater concentrations of reduced scytonemin: 35 times the amount measured in orange mats. Black mats contained six times the concentration of *β*-carotene than orange mats; however, *β*-carotene accounted for a greater relative abundance of the total pigment abundance of orange mats. Similarly, black mats contained, on average, a greater concentration of chlorophyll-*a*, whereas the relative abundance of chlorophyll-*a* was greater in orange mats. Multivariate visualization (PCA) of pigment relative abundance illustrates statistically significant differences among black and orange microbial mat communities based on microbial mat type (PERMANOVA, $P = 0.001$), with orange mats containing a greater variation in pigment type (ANOVA on dispersion, $P < 0.01$; Fig. 5). For example, three of the orange mat samples contained myxoxanthophyll (T12, T13, T14), whereas none of the black mat samples did.

Many of these pigments are photoprotective pigments that are important for microbial communities in the UV-intense McMurdo Dry Valleys, especially for 'terrestrial' communities that lack ice or water cover to aid in light absorption (Vincent *et al.* 1993). Scytonemin is a photoprotective, extracellular sheath pigment (Garcia-Pichel *et al.* 1992) that dominates black and orange mats. Differences in pigment composition were associated with differences in taxonomic composition even within black and orange mats. For example, samples R08 and T13 are notable outliers in the ordination of pigment content (Fig. 5). T13 contained the lowest relative abundance of scytonemin (10.7%) and the highest relative abundance of myxoxanthophyll (8.5%). Field observations indicated that R08 was a dense colony of *Nostoc* with a reddish colour in contrast to the other black mat samples and had the highest concentration of canthaxanthin (2.9 μg g^{-1} dry mat; 1% relative abundance), an orange-red ketocarotenoid. The taxonomic composition of R08 was also different from most of the other sampled black mats, with less rare taxa present and the highest relative abundance of *Nostoc*.

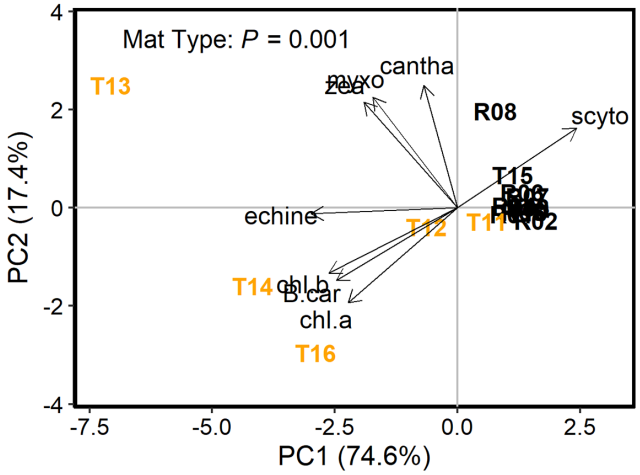


Figure 5. Principal component (PC) analysis ordination on correlation of the relative abundances of the pigments identified in the 16 microbial mat samples, where 'scyto' is scytonemin, 'myxo' is myxoxanthophyll, 'zea' is zeaxanthin, 'chl.a' is chlorophyll-*a*, 'chl.b' is chlorophyll-*b*, 'B.car' is *β*-carotene, 'cantha' is canthaxanthin and 'echine' is echinenone. Samples collected from the Ross Sea drift begin with 'R' (i.e. R01–R08), and samples collected from the Taylor drifts begin with 'T' (i.e. T09–T16). The label colours represent whether the samples were collected from black or orange microbial mats. Vectors represent correlations of the relative abundance of each pigment with PC analysis ordination axes (all displayed correlations are statistically significant, $P < 0.01$). The shown *P*-value is the mat type effect from permutational analysis of variance.

Nif gene characterization of microbial mats and soils

There was a significant linear correlation between the metagenomic-derived *nifH* relative abundance and the qPCR-derived number of *nifH* genes for soils ($r = 0.73$, $P < 0.01$) and microbial mats ($r = 0.72$, $P < 0.01$). The gene copy number and relative abundance of *nif* and *nifH* for mats and underlying soils (from both qPCR and metagenomics methods) were significantly different between black and orange mats (ANOVA, $P < 0.05$; Table III). Overall, black microbial mats had greater gene copy numbers and relative abundances of *nif* and *nifH* genes compared to orange mats.

Relationships among microbial mats and underlying soil geochemistry

Significant correlations between the microbial mats and the soils underlying them were apparent, particularly in the mat characteristics (i.e. AFDM and pigment content) and the soil geochemistry.

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Table III. Average nitrogen fixation gene abundance for black mats (n = 11) and orange mats (n = 5) with ± 1 standard deviation. Data are separated by those derived from metagenomic methods and quantitative polymerase chain reaction (qPCR) methods. The measures of nitrogen fixation potential are represented by the relative abundance of all *nif* genes and gene abundance of *nifH* specifically. One-way analysis of tests were run between black and orange mats for each parameter, and superscript letters represent differences (measurements with dissimilar letters were significantly different from each other, $P < 0.05$).

	Metagenomic method				qPCR method	
	nif mat	*nif* soil	*nifH* mat	*nifH* soil	*nifH* mat	*nifH* soil
	nif gene relative abundance		*nifH* gene relative abundance		No. *nifH* genes g^{-1} wet mat	No. *nifH* genes g^{-1} dry soil
Black mat	0.103^{a} ± 0.051	0.056^{a} ± 0.018	0.0078^{a} ± 0.0067	0.0026^{a} ± 0.0023	3.8×10^{7a} ± 2.8×10^{7}	1.2×10^{7a} ± 8.1×10^{6}
Orange mat	0.007^{b} ± 0.002	0.026^{b} ± 0.008	0.0001^{b} ± 0.0002	0.0001^{b} ± 0.0001	3.1×10^{6b} ± 1.1×10^{6}	3.0×10^{6b} ± 2.9×10^{6}

Table IV. Spearman correlation coefficients (ρ) between the inorganic phosphorus concentration of underlying soils and microbial mat parameters. Values in bold indicate statistically significant relationships based on $P < 0.05$.

	AFDM	Mat *nif*	Chl-*a*	Scyto	B-Car	Cantha
PO_4^{3-}	**0.53** $P = 0.037$	**0.58** $P = 0.020$	**0.57** $P = 0.024$	0.50 $P = 0.051$	**0.63** $P = 0.010$	0.47 $P = 0.066$

AFDM = ash-free dry mass; B-Car = β-carotene; Cantha = canthaxanthin; Chl-*a* = chlorophyll-*a*; Scyto = scytonemin.

Soil inorganic P was significantly correlated with mat AFDM, *nif*, chlorophyll-*a* and β-carotene concentrations (ρ = 0.53, 0.58, 0.57 and 0.63, respectively, $P < 0.05$; Table IV). Additionally, the AFDM of the microbial mats was positively correlated with underlying SOC, TN and the relative abundance of *nif* in the soils (R^2 = 0.66, $P < 0.001$; R^2 = 0.57, $P < 0.01$; R^2 = 0.44, $P < 0.05$, respectively; Fig. 6). A PCA ordination of N and P availability, AFDM, *nif* relative abundance and scytonemin concentration exhibits statistically significant separation of microbial mat types (PERMANOVA, P = 0.001), with black mats containing a greater variation in biogeochemical parameters (ANOVA on dispersion, $P < 0.05$; Fig. 7). This ordination illustrates a strong association between the black mat samples and inorganic P and TN, whereas orange mat samples were less related to variation in inorganic P and TN.

Discussion

Glacial drift composition influences soil chemistry and microbial mats

The landscape history and glacial drift composition of Taylor Valley influences its soil chemistry, which in turn influences its microbial mat distribution, composition and activity. The terrestrial surfaces of the Ross Sea drift in the east and more coastal region have greater P availability than Taylor drifts due to higher apatite in the drift clast composition and greater weathering (Bate *et al.* 2008, Heindel *et al.* 2017, 2018). Our data show that the soils underlying the microbial mats on the Ross Sea drift contained significantly more inorganic P and SOC in comparison to the soils underlying the microbial mats on the Taylor drifts (Table I). Inorganic N content was not significantly different between the Ross Sea and Taylor drifts, probably due to the flushing of N (particularly nitrate) in these intermittently wet environments where microbial mats are most encountered. We suggest that the greater content of SOC in soils collected from the Ross Sea drift is associated with greater availability of soil inorganic P, which potentially enhances the capacity of microbial mats to fix N and C. Interpreting these observations through the lens of landscape history provides better understanding of the contemporary variation in microbial mat composition and functioning.

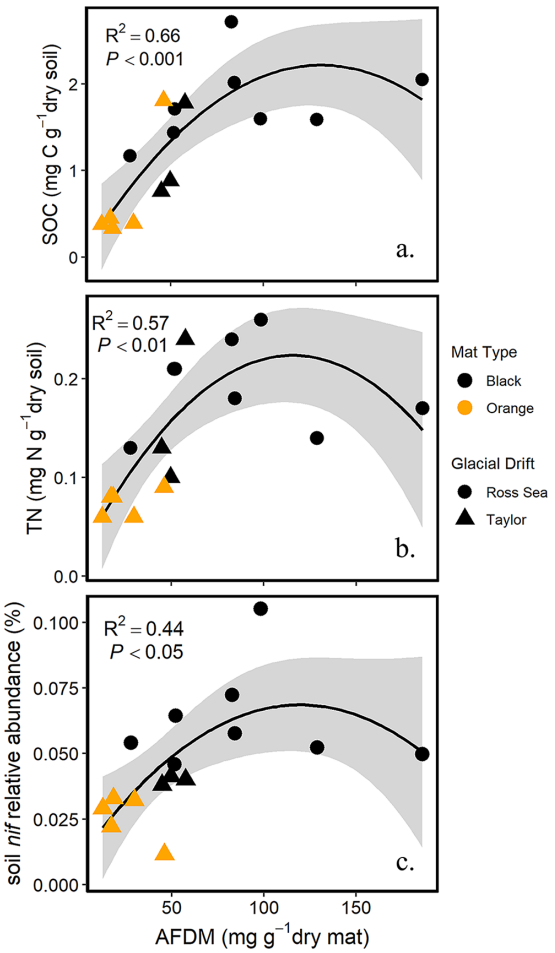


Figure 6. Polynomial regressions of **a.** soil organic carbon (SOC), **b.** total nitrogen (TN) and **c.** relative abundance of soil *nif vs* microbial mat organic matter content as ash-free dry mass (AFDM). Symbol colours distinguish black and orange microbial mats, and symbol shapes distinguish on which glacial drift the mats were sampled. The 95% confidence intervals of the regression lines are shown in grey.

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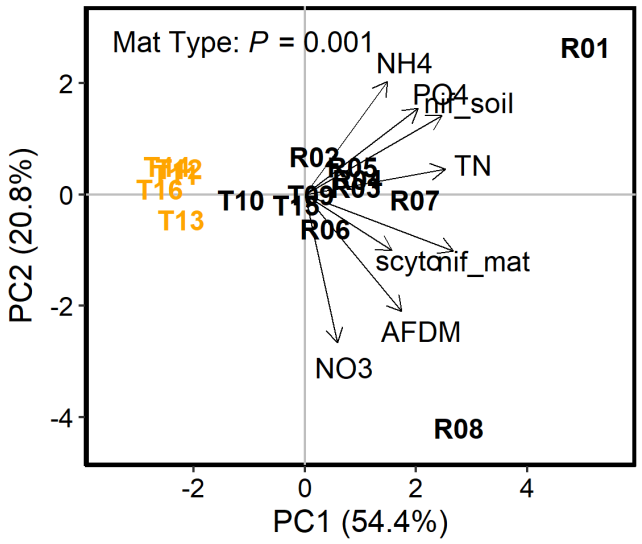


Figure 7. Principal component (PC) analysis ordination on correlation of the N and P availability of underlying soils, organic matter content as ash-free dry mass (AFDM), *nif* gene relative abundance and scytonemin concentration of the 16 microbial mat samples. Samples collected from the Ross Sea drift begin with 'R' (i.e. R01–R08), and samples collected from the Taylor drifts begin with 'T' (i.e. T09–T16). The colours represent whether the samples were collected from black or orange microbial mats. Vectors represent correlations of each parameter with PC analysis ordination axes (all displayed correlations are statistically significant, $P < 0.05$, while NH4 is marginally significant, $P < 0.1$). The shown *P*-value is the mat type effect from permutational analysis of variance.

In the intermittently wet environments outside of the stream channels that we sampled, black microbial mats were more common on the Ross Sea drift, whereas orange mats were more common on the Taylor drifts. The utility of this colour typology is validated by our data showing that the prokaryotic community composition was distinct between the two mat types (Figs 3 & 4). Specifically, *Nostoc*-dominated 'black' mats, regardless of underlying glacial drift composition, hosted a complex and diverse community of autotrophic and heterotrophic microbes across many bacterial phyla with a high proportion of rare taxa, whereas the orange mats consisted primarily of cyanobacteria (*Oscillatoria*) and had lower Shannon diversity values. This clear distinction in microbial diversity and the associated variation in pigment content and composition (Fig. 5) support a simple comparison of the different characteristics of these two mat types and their potential influences on underlying soil properties and processes. For example, black microbial mats contained significantly more organic matter in the form of AFDM, higher absolute and proportional scytonemin contents, as well as higher N-fixation potential, and they appeared to be preferentially located on P-rich soils (Tables II & III). Moreover, inorganic P concentration was significantly correlated with microbial mat organic matter content (AFDM), N-fixation potential and pigment concentration (Table IV).

Although the asymmetrical distribution of black and orange mats across the two drifts prevents conclusive inferences from being drawn regarding the influence of geochemistry on microbial mat distribution and activity, we hypothesize that the greater abundance of P on the Ross Sea drift may select for a greater abundance of active N-fixers, such as *Nostoc*. Specifically, our data suggest that the distribution of *Nostoc* black mats is strongly associated with higher inorganic P, possibly because there is a greater advantage of active N fixation when ample P is present. For example, high P availability has been shown to favour N-fixers in freshwater environments outside of Antarctica (Howarth *et al.* 1988, Andersson *et al.* 2015, Tierney & Wurzburger 2024). The greater apparent occurrence of orange mats on the lower-P Taylor drifts may be because they are more competitive in an environment where the strongly N-fixing black mats are at less of an advantage. Although there are orange mats on the Ross Sea drift, they are primarily located within the stream thalweg, where inorganic P is typically limiting and has been weathered out (Bate *et al.* 2008, Heindel *et al.* 2017, 2018) and where their isotopic composition suggests that turnover of N from *Nostoc* further upstream supports their nutrient requirements (Kohler *et al.* 2018). We sampled exclusively at the stream margins, where we could not locate any orange mats on the Ross Sea drift. We encourage further studies on these terrestrial communities to determine the underlying mechanisms of their distribution along varying inorganic P concentrations. Although a variety of climate, hydrological and geomorphological factors contribute to the abundance, distribution and functioning of microbial mats (McKnight *et al.* 1999, Stanish *et al.* 2011, Kohler *et al.* 2015, Levy *et al.* 2020, Power *et al.* 2024b), our work here demonstrates how soil geochemistry and landscape history also influence the prevalence of terrestrial microbial mats.

Microbial mats enrich underlying soil organic matter

While our data show that the geochemical variation in inorganic P along Taylor Valley is a factor influencing microbial mat distribution, microbial mats also make significant contributions to the chemical compositions of the underlying soils, especially to their greater SOC and TN (Fig. 6). Although in this study we did not sample soils from uncolonized areas, previous studies conducted in the same general area and on the same drifts have reported four times less SOC on areas uncolonized by mats (0.43 mg C g^{-1} dry soil on the Ross Sea drift and 0.19 mg C g^{-1} dry soil on the Taylor drifts; Barrett et al. 2006b) compared to the SOC values we estimated beneath microbial mats (1.79 mg C g^{-1} dry soil on the Ross Sea drift and 0.85 mg C g^{-1} dry soil on the Taylor drifts; Table I). Similarly, soils without microbial mats were shown to contain three to nine times less TN (0.02 mg N g^{-1} dry soil on the Ross Sea drift and 0.03 mg N g^{-1} dry soil on the Taylor drifts; Barrett et al. 2006b) compared to the TN values we estimated here for soils underlying microbial mats (0.19 mg N g^{-1} dry soil on the Ross Sea drift and 0.11 mg N g^{-1} dry soil on the Taylor drifts; Table I).

All samples contained a high abundance of *nif* and *nifH* genes, suggesting a strong N-fixation potential in both black and orange microbial mats, as has been previously shown primarily for black microbial mats in the McMurdo Dry Valleys (e.g. Kohler *et al.* 2018, 2023, Coyne *et al.* 2020). In addition, although all nine of the most abundant genera of the black and orange mats are known to be common N-fixers, both metagenomic approaches and qPCR indicated that the *Nostoc*-dominated black mats had significantly greater N-fixation potential than the *Oscillatoria*-dominated orange mats, as has been previously reported (Howard-Williams *et al.* 1989, Kohler *et al.* 2018, Coyne *et al.* 2020). The high N-fixation potential of these mat types probably accounts for the higher TN content in the underlying soils due to N fixation of the overlaying microbial mats.

Aquatic microbial mats influence stream chemistry in Taylor Valley (e.g. McKnight et al. 2004, Kohler *et al.* 2018) through biological uptake, recycling and export downstream. For example, using stable isotope approaches, Kohler *et al.* (2018) showed that black mats were the dominant N-fixers in Von Guerard Stream and that N was repeatedly recycled and assimilated downstream as

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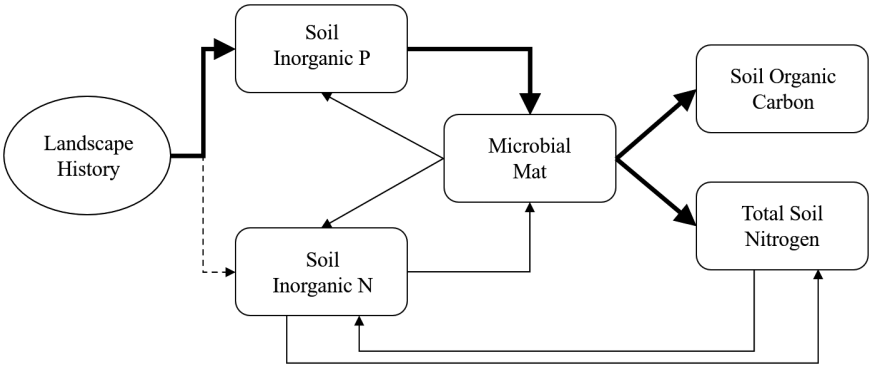


Figure 8. Conceptual model illustrating the hypothesized causal relationships between glacial drift composition, soil nutrients and organic matter and microbial mats based upon our observations in this study. Arrows indicate significant material fluxes between stocks. Bold arrows indicate the strongly positive relationships described in this study, whereas the dashed arrow indicates a weaker positive relationship.

other sources of N were exhausted. Our data show that terrestrial microbial mats at the margins of streams also influence underlying soil geochemistry. Although the differences in soil inorganic P are of geochemical origin from the weathering of greater apatite content on the Ross Sea drift (Bate *et al.* 2008, Heindel *et al.* 2017, 2018), the greater TN found in the soils underlying microbial mats is probably of biotic origin from N fixation by the cyanobacterial mats.

Differences in N-fixation potential may also explain the microbial responses to physical stressors in the Antarctic environment, such as UV radiation. For example, Fleming & Castenholz (2008) reported a connection between scytonemin synthesis and N sources and availability. In a laboratory experiment they showed that *Nostoc* synthesized significantly more scytonemin while fixing N than when utilizing available nitrate or ammonium (Fleming & Castenholz 2008). Fleming & Castenholz (2008) hypothesized that a restriction in N availability could cause an increase in UV radiation sensitivity in *Nostoc*, which therefore signals the increase in scytonemin synthesis. In our field-based studies, we found a significant, positive correlation between scytonemin concentration and *nif* relative abundance as N-fixation potential ($r = 0.56$, $P < 0.05$; Fig. 7). Although a mechanism for this remains unexamined, we hypothesize that this relationship may also be associated with greater UV stress under conditions of N limitation. The McMurdo Dry Valleys experience exceptionally high UV radiation, and it is possible that the increase in scytonemin with mats that have a higher N-fixation potential is due to greater photosensitivity. Alternatively, scytonemin may be produced in larger quantities to protect the nitrogenase enzyme complex, which has been shown to be sensitive to UV radiation (Kumar *et al.* 2003, Singh *et al.* 2023).

Our work here and previous studies support the notion that microbial mats impart an 'island of fertility' effect (*sensu* Schlesinger *et al.* 1990) on local soils and sediments through their influence on organic matter availability and N availability (Hawes *et al.* 1992) and through promoting diverse soil fauna communities (e.g. nematodes, tardigrades, rotifers and ciliates; Simmons *et al.* 2009). Specifically, our results demonstrate that terrestrial microbial mats are composed of diverse organisms that fix both C and N and contribute leached organic matter and nutrients into underlying soils. Previous studies have shown that the same holds true for aquatic microbial mats contributing organic matter and nutrients into stream waters as well, thereby supporting diverse soil and sediment communities (Moorhead *et al.* 2003, Simmons *et al.* 2009, Stanish *et al.* 2011, Kohler *et al.* 2018). Moreover, previous work has also shown that microbial mats have a homogenizing effect on the underlying soil bacterial communities in this region (i.e. bacterial communities below microbial mats support similar taxonomic compositions regardless of glacial drift composition or overlaying microbial mat type; Risteca 2023). In addition to influencing soil nutrient cycles and community composition, microbial mats can also influence soil hydrology due to their low permeability, which promotes higher moisture content in the soils below them (Perillo *et al.* 2019) and provides shelter from wind and UV radiation. These are essential functions, especially in the harsh and nutrient-poor terrestrial environment of the McMurdo Dry Valleys. Current (Nielsen *et al.* 2023, 2024, Barrett *et al.* 2024) and anticipated (Vignon *et al.* 2021) changes in climate and hydrology will have unknown influences on the distribution and activity of microbial mats in the McMurdo Dry Valleys. For example, greater snowfall or even rain in a potentially warmer climate regime would probably expand microbial mat habitats to currently arid and inactive soils, whereas increased föhn winds and associated drier conditions could decrease low-density microbial mats in currently marginal habitats. Any future changes in microbial mat distribution and activity will probably have marked effects on underlying soil biota and chemistry.

Conclusion

Here, we show how geochemical variation in inorganic P influences the occurrence, composition and ecological functioning of microbial mats, the dominant primary producers of many extreme ecosystems. The 'terrestrial' microbial mats we examined in this study enhance underlying soil C and N cycling and provide important sources of the energy and N fuelling soil food webs. Thus, understanding the distribution and activity of terrestrial microbial mats is essential to the regional C balance. This work highlights the recursive nature of the relationships between microbial mats and the soils underlying them and presents a conceptual model (Fig. 8) that could be useful for anticipating how changes in climate and regional weather events could alter microbial mat distribution and activity, and thereby the soil food webs and overall organic matter budgets in this region.

Supplementary material. To view supplementary material for this article, please visit http://doi.org/10.1017/S0954102025000094.

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Data availability. All data presented in this study are archived in the Environmental Data Initiative (EDI) repository (Power *et al.* 2024a). Metagenomic sequences are available on the MG-RAST database under project ID mgp95386: https://www.mg-rast.org/linkin.cgi?project=mgp95386.

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Competing interests. The authors declare that they have no competing interests.

Ethical standards. Permission to enter the Canada Glacier Antarctic Specially Protected Area (ASPA 131) and sample soils and microbial mats was given by the National Science Foundation Division of Polar Programs through Antarctic Conservation Act Permit.

Author contributions. All authors contributed to the design of the study and the field sampling. SNP and EDO conducted sample preparation and laboratory analyses. SNP led the statistical analyses and interpretation with support from EDO and JEB. All authors contributed to the writing and editing of the manuscript.

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