Taxonomic and functional diversity of microbial mat communities in the McMurdo Dry Valleys, Antarctica is driven by variation in soil geochemistry

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ABSTRACT

Microbial communities play critical roles in biogeochemical cycles of aquatic and terrestrial ecosystems, but studies of soil microbial communities have been limited by the diversity and complexity found in most ecosystems. Here we report on work investigating the functional diversity of microbial mat and underlying soil communities in the McMurdo Dry Valleys of Antarctica across a gradient of phosphorus availability on glacial tills of distinct age and mineral composition in Taylor Valley, Antarctica. Microbial mat and soil DNA were extracted and sequenced on an Illumina NextSeq500 in a 150 bp paired end format. Raw sequences were uploaded to the MG-RAST server for processing and annotation. Community taxonomic and functional annotation were determined using the RefSeq and SEED Subsystem databases, respectively. The results revealed significant variation in microbial mat community taxonomic composition between the two tills, strongly associated with visual assessment of mat morphology, *e.g.*, “black” and “orange” mats, and soil N:P ratios. The underlying soil microbial communities did not exhibit significant differences in diversity between the two tills, but community composition varied significantly across gradients of soil chemistry, particularly extractable-phosphate content even within tills. The relative abundance of biogeochemistry-relevant pathways determined from the SEED database varied amongst soil microbial communities between the two tills. For example, microbial mat communities exhibited

significant variation in the relative abundance of key nitrogen and phosphorus metabolism associated genes strongly associated with the underlying soil N:P. These results suggest that spatial variation in geochemistry influences the distribution and activity of microbial mats, but that the microbial mats themselves also exert a significant homogenizing effect on the underlying soil communities and some of the key biogeochemical processes they facilitate.

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GENERAL AUDIENCE ABSTRACT

Microbial communities play critical roles in the processes of aquatic and terrestrial ecosystems. Still, studies of soil microbial communities have been limited by the complex nature of the ecosystems we study. This study examined the diversity of microbial communities in the McMurdo Dry Valleys of Antarctica, specifically looking at how different levels of phosphorus availability in the soil affected microbial function. We used DNA sequencing and databases to determine the taxonomic and functional makeup of these communities. We found that while the microbial mat communities varied significantly based on soil chemistry and appearance, the underlying soil microbial communities did not. We also found evidence suggesting that the microbial mats played a role in regulating some of the key ecosystem processes in the soil. Overall, this study sheds light on how microbial communities are impacted by their environment and how they, in turn, impact their surroundings.

DEDICATION

This thesis is dedicated to my nephews Maddux, Caleb, Declan, and Xander Fawcett, who constantly remind me of the wonder this world has to offer. Never stop chasing your dreams, and always be willing to learn and grow!

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Introduction

Microorganisms can be found in nearly every habitat on Earth (Bar-On et al., 2018; Dolan, 2018; Ghiorse & Wilson, 1988; Šantl-Temkiv et al., 2022). Viable microbes have been isolated from some of the most inhospitable environments, including deep-subseafloor sediments (Dolan, 2018; Kallmeyer et al., 2012) and the Antarctic continent (Priscu & Christner, 2003; White, 1996). The functional diversity of these communities is immense, with microorganisms playing key roles in all biogeochemical processes on Earth (Crowther et al., 2019; Falkowski et al., 2008), including the macronutrient cycles of carbon, nitrogen, and phosphorus (Gächter & Meyer, 1993; Hayatsu et al., 2008; Schimel & Schaeffer, 2012). Understanding environmental drivers of microbial communities has been a fundamental focus of microbial ecology for several decades. However, most of these studies have focused on taxonomic diversity and composition without explicitly considering functional capacity of the microbial community.

The complex interplay between environmental factors such as nutrient availability, temperature, pH, and habitat type plays a crucial role in shaping the functional diversity of microbial communities. Recently the field has expanded from several studies focused on the environmental drivers of microbial functional diversity and potential, providing insight to these multifaceted relationships between a community and its environment. For example, (Alsop et al., 2014) demonstrated that it is possible to determine the ordering of community functional potential along a geochemical gradient without geochemical data, emphasizing the significance of understanding geochemical drivers of microbial functional diversity. A range of studies in terrestrial and aquatic systems have demonstrated that diversity and availability of resources, changes in

nitrogen and water availability, and physical changes in the environment all influence microbial functional diversity (Guo et al., 2018; Pacheco et al., 2021; Zhang et al., 2019). With a deeper understanding of geochemical controls on microbial communities, it is possible to predict a community's composition of major taxonomic groups and to predict functional diversity from known geochemical and stoichiometric parameters of the environment.

The elemental stoichiometry of carbon (C), nitrogen (N), and phosphorus (P) in terrestrial ecosystems and organisms are key to understanding the reciprocal relationship between the chemistry of biota and their geochemical environment (Elser & Hamilton, 2007; Elser et al., 2000). Microbial communities display varying ratios of these essential elements (C:N:P), with tendencies toward a general stoichiometry dictated by biochemistry and environmental availability of macronutrients (e.g., Cleveland & Liptzin, 2007). For example, changes in the relative availability of C:N:P can influence microbial community composition and activity, with emergent effects on ecosystem processes such as carbon and nutrient cycling (Fanin et al., 2019; Moorhead et al., 2013; Sinsabaugh et al., 2013; X. Wei et al., 2020). Microbial biomass C:N:P has been implicated in regulating organic matter decomposition rate, which alters productivity and nutrient availability of the ecosystem (Zhu et al., 2018). Therefore, the significance of microbial stoichiometry emphasizes the need for a deeper understanding of the environmental factors that influence microbial diversity and function, and the effect these communities have on subsequent ecosystem processes.

In the McMurdo Dry Valleys of Antarctica spatial patterns in soil geochemistry and soil communities are structured by a range of processes operating over multiple

spatial scales (Barrett et al., 2004; Feeser et al., 2018) which elicit general patterns in geochemistry useful for testing hypotheses about ecological stoichiometry (Aanderud et al., 2018; Ball et al., 2018; Xue et al., 2023). For example, soils develop on underlying tills deposited during previous glacial events over thousands to millions of years (Barrett, Virginia, Parsons, et al., 2006). Soils are further subject to cryoturbation, chemical weathering, biological processing of organic matter, and hydrological processes creating a heterogeneous mosaic of soils across broad (valley to region), and fine (landscape) scales (Feeser et al., 2018; Van Horn et al., 2014). The resulting biogeochemical patterns are integral to understanding the distribution and activity of the resident soil biota (Adams et al., 2006; Barrett, Virginia, Parsons, et al., 2006; Geyer, 2014; Poage et al., 2008).

Earlier studies focused on characterizing the spatial patterns in availability of carbon (C), nitrogen (N), and phosphorus (P) across this heterogeneous landscape (examples). Total P and extractable phosphate are primarily influenced by till mineralogy and exposure age, while soil N typically displayed a positive relationship with surface exposure age reflecting abiotic accumulation of aerosols, *e.g.*, nitrate over millennial time scales (Barrett et al., 2005, 2007; Bate et al., 2008; Bockheim, 1997). The McMurdo Dry Valleys are further characterized by a landscape highly structured by environmental gradients influenced by proximity to liquid water and microclimate influenced by energy balance and temperature, which feedback on one another, amplifying the effects of these environmental conditions on soil and soil communities (Andriuzzi et al., 2018; Barrett et al., 2005; Barrett et al., 2006; Bate et al., 2008; Gooseff et al., 2007). Thus, landscape history and geomorphology structure the terrestrial and aquatic environments of the

McMurdo Dry Valleys, yet few studies have documented how biota influence ecosystem functioning in this extreme environment.

Cyanobacteria are the dominant primary producers in the region, specifically in lake benthic zones, stream channels, and intermittently wet soils occurring as cm thick mats of colonial cyanobacteria cells co-occurring with heterotrophic bacteria (McKnight et al., 2007; Van Horn et al., 2016; Wharton et al., 1983). Microbial mats are typically distinguished as black, orange, red, or green based upon visual appearance and habitat preference (Alger et al., 1997; McKnight et al., 1999, 2004). For example, orange mats are dull to bright orange in color and mostly associated with the thalweg of stream channels (McKnight et al., 1999) or with the surface of ephemeral melt/thaw channels, and characterized by high relative abundance of *Oscillatoria* spp. In contrast, black mats are typically reported in stream riparian zones outside the main channel and in nivation hollows under or down-gradient from ephemeral snow-patches (Power et al. in review).

The goal of this study was to test the hypotheses that the functional diversity of microbial mat communities is strongly influenced by variation in soil geochemistry, *e.g.*, phosphate concentrations and soil N:P ratios, and to examine the influence of microbial mats on the underlying soil communities and biogeochemistry. I predicted that bacterial assemblages from similar mat type, *i.e.*, black and orange would be similar regardless of soil type if these visual and morphological assessments of microbial mats are meaningful. Moreover, I anticipate community functional diversity will be influenced by intrinsic characteristics of the assemblage, *e.g.*, dominant taxa and the diversity metrics of the community, and extrinsic properties of the distinct soils located on the Ross till in eastern Taylor Valley and from Taylor tills in western Taylor Valley, McMurdo Dry Valleys,

Antarctica. Specifically, I predicted that soils with low availability of phosphate would have greater metabolic functions associated with P acquisition and conservation, while higher nutrient availability, e.g., total and dissolved N, would increase the relative abundance of functions associated with the breakdown and assimilation of nutrients.

Materials and Methods

Site Description and Sampling

This study took place in Taylor Valley, Antarctica, the principal site of the McMurdo Dry Valleys Long Term Ecological Research Program. Microbial mats and soils were collected from two distinct glacial till sequences in the Lake Fryxell and Lake Bonney basins of Taylor Valley, Antarctica (Figure 1). These tills, Ross and Taylor, exhibit significant differences in soil P availability associated with differences in till mineralogy, resulting in a range of soil N:P ratios. This variation in N:P ratios is a product of landscape history soils and sediments occurring on the Ross till, which is enriched in rocks with high apatite content exhibiting high P availability (Bate et al., 2008), while soils occurring on the Taylor till parent material typically have significantly lower P availability (Bate et al., 2008). Soil N availability, in contrast, is often a function of exposure age, with more recently exposed Fryxell soils (~10,000 years old) exhibiting generally lower N as a result of less opportunity for atmospheric NO_3^- deposition in comparison to older soils occurring on Taylor till series (~100,000-250,000 years old) which can accumulate higher concentration of NO_3^- (Burkins et al., 2000, Barrett et al., 2006). This predictable variation in soil N:P represents an ideal opportunity to investigate

geochemical and stoichiometric constraints on soil and microbial mat communities and their potential ecosystem functions.

From December 2019 – January 2020 microbial mat and underlying soils (0-10 cm depth) were collected from 16 locations where visible microbial mats were evident with 8 plots each sampled from the Ross and Taylor tills in Taylor Valley, McMurdo Dry Valleys, Antarctica. Microbial mats were opportunistically located outside of stream channels or lake margins, and visually identified as black mats (n = 11) or orange mats (n = 5).

Sampling took place in wetted areas of the landscape outside of channelized streams or lake margins, but where sufficient water from snowpack or permafrost thaw regularly occurs, e.g., in ephemeral melt seeps, and wet depressions downslope of snowpacks. In each location, a 0.5 m^2 section of wet, active mat were identified and 5 plugs of mat material (from the center and four corners of the 0.5 m^2 section) were collected using a sterilized 13 mm diameter cork borer. Additionally, a sterilized cork borer was used to collect the underlying soil from a 5 cm depth core directly beneath each sampled microbial mat plug. The 5 mat and 5 soil subsamples from each location were placed in separate whirlpak bags (one for mat material, one for soil), resulting in one composite mat sample and one composite soil sample per location. A subsample of each soil sample was removed and stored at 4 ^{o}C prior to chemical analyses (see below). Remaining soil and microbial mat material were stored at -20 °C and shipped frozen to Virginia Tech for DNA extraction and molecular analyses

Soil Chemical Analyses

Electrical conductivity of collected soils was determined in a 1:5 soil to DI H_2O slurry using a YSI conductivity meter. Soil pH was determined in a 1:2 soil to DI H_2O slurry using an Orion pH meter. Soil ammonium and nitrate concentrations were determined in 2 *M* KCl extracts while phosphate concentrations were determined in 0.5 *M* $NaHCO_3$ extracts. Extracts for ammonium, nitrate, and phosphate were analyzed on a Lachat QuickChem Flow injection analyzer (Hach Company, Loveland, CO, United States), and express as µg element per g soil dry weight equivalent. Total organic C and total nitrogen were measured on dried, milled soil using an Elementar vario MAX cube (Elementar Americas Inc., Mt. Laurel, NJ, United States), and expressed as milligrams element per gram soil dry weight equivalent. Gravimetric water content (GWC) of all soils was measured by mass loss after drying at 105 °C for 24 hours and all soil chemical properties are presented on an oven-dried basis.

DNA Extraction and Shotgun Metagenome Sequencing

DNA was extracted from ~1.5 g soil and ~ 0.5 – 1.0 g microbial mat material using the Qiagen DNeasy PowerSoil kit (Qiagen, Valencia, CA, United States) and extracts were quantified using a Qubit 2.0 Fluorometer (Thermo Fisher Inc., Waltham, MA, United States). DNA libraries were prepared for shotgun metagenome sequencing using a KAPA HyperPrep Kit (Kapa Biosystems, Inc., Basel, Switzerland). 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 for merging of paired ends, quality control, and annotation using the recommended MG-RAST default parameters

(Meyer et al., 2008). Taxonomy was assigned to the processed reads using the NCBI RefSeq database while functional annotations were performed using the SEED Subsystems database (Overbeek et al., 2014). Following processing by MG-RAST, we retained an average of ~7.2 million sequences per sample, ranging from ~4.3 million to ~ 8.9 million. Of these sequences, an average of 3.91% failed QC, 1.10% were rRNA genes, 41.25% were annotated proteins, and 57.65% were unknown proteins. All metagenomes are publicly available on the MG-RAST database under project ID mgp95386.

Analyses of Microbial Community Composition and Diversity

All microbial community composition data was analyzed at the phylum and genus levels. Alpha diversity of the microbial communities was determined by calculating Shannon-Weiner diversity (H') indices using the diversity() function from the 'vegan' (Oksanen et al., 2020) package. Using the aov() function from the 'stats' package, a one-way analysis of variance (ANOVA) test was used to compare H' values between the two tills. Before assessing beta diversity, all samples were standardized using the decostand() function from the 'vegan' package. The 'total' standardization method was used. Dissimilarity indices were calculated from the standardized community data using the vegdist() function and the "bray" argument from the 'vegan' package. A permutational multivariate ANOVA was ran for each distance matrix using the adonis2() function from the 'vegan' package. The Bray-Curtis distances were also analyzed with nonmetric multidimensional scaling (NMDS) using the metaMDS() function from the 'vegan' package. Vectors were produced from intrinsic (species) and extrinsic (soil chemistry) variables using the envfit() function from the 'vegan' package. The output provided the

coordinates of the heads of the vectors. The values were scaled by their correlation (square root of the r2 value) to demonstrate how strong the predictors are. This means that weaker predictors will have shorter arrows while stronger predictors have longer arrows. This is further adjusted to scale to the plot on which the vectors will go. Combined with the NMDS plot, these data were used to assess relationships visually and statistically among and across microbial assemblages and environmental factors.

Analysis of Microbial Community Functional Potential

Microbial community functional potential was assessed using feature count tables obtained from MG-RAST after metagenomic sequences from each library were annotated using the SEED subsystems database. Features associated with nitrogen and phosphorus metabolism were identified at subsystem level 1 (highest level) and all associated features were pulled at subsystem level 3 (detailed functional assignments of the features in question). These data were read into a DESeqDataSet object using the DESeqDataSetFromMatrix() function from the 'DESeq2' (Love et al., 2014) package. All count data stored in the object were normalized for differential abundance analysis of features using the DESeq() and results() functions from the 'DESeq2' package. Normalization is carried out using a median of ratios approach which divides counts specific to each sample by a determined size factor derived using median ratios of specific feature counts relative to the geometric mean for each feature. Normalized counts were then used to compare counts between samples and to analyze the differential abundance of each feature.

Statistical analyses

Summary statistics and assumption testing of soil chemistry data were calculated for each parameter. Summary statistics were calculated using the 'rstatix' (Kassambara, 2023a) package. Before hypothesis testing, the data were tested to confirm that they are normally distributed and that their variance is homogenous. The normality of soil chemistry data was determined through an outlier test, Shapiro-Wilke's tests, and homogeneity of variance were also derived using 'rstatix.' All normally distributed soil chemistry data (pH, GWC, C:N, phosphate, ammonium, nitrate) were analyzed to determine significant variation between the two tills through an independent samples t-test using the Weltch t-test from the 'rstatix' package. All data that were identified as having a non-normal distribution (electrical conductivity, soil organic C, total nitrogen, nitrate) were analyzed using a nonparametric Mann-Whitney U test from the 'stats' package (R Core Team, 2013).

All statistical analyses and visualizations were completed using R version 4.0.5 (R Core Team, 2021) using the ggplot2 (Wickham, 2016), reshape2 (Wickham, 2007), biomformat (McMurdie & Paulson, 2022), phyloseq (McMurdie & Holmes, 2013), vegan (Oksanen et al., 2020), lme4 (Bates et al., 2015), funrar (Grenié et al., 2017), emmeans (Lenth et al., 2023), cowplot (Wilke, 2020), ape (Paradis & Schliep, 2019), ggpubr (Kassambara, 2023b), BiocGenerics (Huber et al., 2015), tidyverse (Wickham & RStudio, 2023), pheatmap (Kolde, 2019), RColorBrewer (Neuwirth, 2022), dendsort (Sakai & Biederstedt, 2021), knitr (Xie et al., 2023), dplyr (v1.1.1,Wickham et al., 2023) packages.

Results

Soil Properties

Soil moisture did not vary significantly between the Ross and Taylor till samples (0.181 and 0.175 gravimetric water content, respectively, p=0.66), though soil moisture in the Ross till samples exhibited more variation (0.127 to 0.23 gravimetric water content) than in the Taylor till samples (0.141 to 0.193 gravimetric water content). Similarly, electrical conductivity was low and relatively uniform across sites sampled, with no significant differences between the two tills (22.0µS/cm and 13.9 µS/cm, respectively) (p=0.1) or underlying mat types. The mean soil pH in samples collected from the Ross till was significantly higher (p=0.049) than in the Taylor till samples (7.55 and 7.34, respectively). Though soil pH was higher in Ross, Taylor soil pH was more variable (7.13 to 7.70) compared to the Ross till (7.37 to 7.92). Soil pH in these study sites is up to 2 units lower than some more alkaline soils in Taylor Valley (Campbell et al., 1998), and electrical conductivity is also very low. This is likely the result of an increased availability of liquid water in these sites, which has been implicated in the leaching of alkaline cations and flow of material in and out of the system (Chytrý et al., 2007; Gooseff et al., 2011).

Soil organic carbon (SOC) was significantly higher in samples collected from the Ross tills than in samples from the Taylor tills (p = 0.021). Ross SOC was, on average, ~2.1 times higher than Taylor SOC, with a range of 1.17 to 2.72 mg C g soil^{-1} in Ross samples and 0.33 to 1.81 (units) in Taylor samples. Total soil N in samples collected from Ross Sea tills was~1.8 times higher on average than Taylor till total soil N, with a range of 0.13 to 0.25 mg N g soil^{-1} for samples collected from the Ross till, and 0.06 to 0.24 mg N g soil^{-1} for samples collected from the Taylor till (p = 0.0098). One extreme

outlier was identified in Taylor plot #1 with a total nitrogen of 0.24 mg N g soil^{-1}. Soil C:N was relatively uniform across the two sites, with no significant difference in mean soil C:N between Ross and Taylor tills (9.52 and 8.10, respectively, $p = 0.083$). However, C:N in Taylor till soil samples was highly variable (4.13 to 20.11) compared to Ross samples which ranged from 6.15 to 12.06.

Extractable-phosphate was significantly higher in soils collected from the Ross Sea tills than in those collected from the Taylor till ($p = 0.0039$), with Ross soil phosphate concentrations ~4 times higher than those in soils collected from Taylor till soils. Phosphate concentrations ranged from 2.054 to 8.807 µg P g soil^{-1} for soils collected from the Ross till and from 0.087 to 2.793 µg P g soil^{-1} on the Taylor till.

There was no significant difference observed in KCl-extractable ammonium or nitrate concentrations between the Ross and Taylor soils ($p = 0.083$ and 0.33, respectively). Ammonium concentrations in Ross plot #1 were more than 3X the interquartile range (0.193) of all measurements at 10.304 µg N g soil^{-1}, and nitrate concentrations in Ross plot #8 were more than 3X the interquartile range (0.113) of all measurements at 0.902 µg N g soil^{-1}. Mean DIN was significantly higher in soils collected from the Ross till than in Taylor soils ($p = 0.0054$), and more variable (0.977 to 10.723 µg N g soil^{-}1) compared to DIN in Taylor which had a range of 0.864 to 1.063 µg N g soil^{-1}.

Alpha Diversity of Microbial Mat and Soil Communities

Mat community Shannon diversity did not vary across the two sites at the phylum level ($p = 0.13$), but diversity did vary significantly between Ross and Taylor at the genus level ($p = 0.03$). Ross till microbial mat communities tended to be more diverse

than those occurring on Taylor tills, with mean H' of 5.19 and 4.57, respectively. At both the phylum and genus levels, black mats were significantly more diverse than orange mats (Phylum: $p = 0.001$; Genus: $p < 0.001$). Black mats had an average H' of 1.73 and 5.20 at the phylum and genus levels, respectively, while orange mat had an average H' of 1.29 and 4.18. At the phylum level, mat community diversity was not significantly correlated with any abiotic soil properties. At the genus level, mat community diversity was positively correlated with SOC (t = 2.13, $p = 0.05$, r-Pearson = 0.5), Total nitrogen (t = 2.91, $p = 0.01$, r-Pearson = 0.61), and phosphate (t = 2.29, $p = 0.04$, r-Pearson = 0.52).

Microbial mat community evenness (Pielou's J) did not vary significantly across the Ross and Taylor tills at the phylum level ($p = 0.13$), but evenness did vary significantly at the genus level ($p = 0.03$). On average, Ross till communities were more even (J = 0.801) than Taylor till communities (J = 0.705). However, at both the phylum ($p = 0.001$) and genus ($p < 0.001$) levels, black mat communities were significantly more even than orange mat communities. On average, black mats displayed greater evenness than orange mats at both the phylum (0.495 and 0.37, respectively) and genus (0.802 and 0.645, respectively). At the phylum level, mat community evenness was not significantly correlated with any abiotic soil properties, however at the genus level, mat community evenness was positively correlated with SOC (t = 2.13, $p = 0.05$, r-Pearson = 0.5), total nitrogen (t = 2.91, $p = 0.01$, r-Pearson = 0.61), and extractable phosphate (t = 2.3, $p = 0.04$, r-Pearson = 0.52).

Soil community diversity (H') was similar across both tills and mat type at the phylum (Site: $p = 0.46$; Mat: $p = 0.79$) and genus (Site: $p = 0.70$; Mat: $p = 0.22$) levels. Soil diversity at both the phylum and genus levels was negatively correlated with soil pH

(Phylum: t = -2.37, p = 0.03, r-Pearson = -0.53; Genus: t = -2.41, p = 0.03, r-Pearson = -0.54), conductivity (Phylum: t = -3.44, p = 0.004, r-Pearson = -0.68; Genus: t = -2.78, p = 0.01, r-Pearson = -0.6), and C:N (Phylum: t = -3.2, p = 0.006, r-Pearson = -0.65; Genus: t = -4.79, p < 0.001, r-Pearson = -0.79).

Soil microbial community evenness (J) was also relatively consistent across the two tills and overlying mat types at both the phylum (Site: p = 0.46; Mat: p = 0.79) and genus (Site: p = 0.70; Mat: p = 0.22) levels. Community evenness in soils at both the phylum and genus levels was negatively correlated with soil pH (Phylum: t = -2.37, p = 0.03, r-Pearson = -0.53; Genus: t = -2.41, p = 0.03, r-Pearson = -0.54), conductivity (Phylum: t = -3.44, p = 0.004, r-Pearson = -0.68; Genus: t = -2.78, p = 0.01, r-Pearson = -0.6), and C:N (Phylum: t = -3.2, p = 0.006, r-Pearson = -0.65; Genus: t = -4.79, p < 0.001, r-Pearson = -0.79).

Microbial Community Composition

The composition of overlying microbial mat communities was highly variable at both the phylum and genus levels when analyzed by site and mat type (Figures 2a & 2b). Apart from Taylor #1, 2, and 7, the Taylor till samples appear to have distinct communities from the Ross samples (Figures 2a & 2b). Notably, all the Ross till samples and Taylor plots #1, 2, and 7 were visually categorized as “black mats”, while Taylor plots #3, 4, 5, 6, and 8 were identified as “orange mats” based upon visual assessment. The key distinction between black and orange mats, apart from the physical color of the mat, is the dominant taxa revealed by my analyses. Black mats are generally dominated by the cyanobacterial genera *Nostoc*, while orange mats are dominated by *Nostoc* and *Oscillatoria* (Figure 2b).

At the phylum level, microbial mat and soil communities were dominated by the same five phyla (Figure 2a & 2c). There were 18 phyla in Ross or Taylor tills and 28 phyla in orange or black mats identified as being significantly more abundant (Table 3). Of the 18 phyla exhibiting differential abundance by site, 17 were more abundant in mats collected from the Ross till, and one was more abundant on the Taylor till. Of the 28 phyla exhibiting differential abundance by mat type, 27 were more abundant in black mats, and one was more abundant in orange mats. In the mat communities, the five most abundant phyla represented a majority of the reads from Ross and Taylor tills (88.1% and 92.1%) and black and orange mats (88.0% and 94.7%). Proteobacteria was the dominant phylum in samples from the Ross till and black mats (45.3% and 43.8%) while Cyanobacteria dominated in Taylor tills and orange mats (46.0% and 59.2%). Proteobacteria ($t = 3.79$, $p = 0.003$), Firmicutes ($t = 2.43$, $p = 0.03$), Verrucomicrobia ($t = 3.49$, $p = 0.004$), and Planctomycetes ($t = 2.50$, $p = 0.03$) were all significantly more abundant in samples from the Ross till than in Taylor tills (Table 3). Cyanobacteria ($t = -3.09$, $p = 0.01$) were significantly more abundant in samples from the Taylor till than in the Ross till. Proteobacteria ($t = 8{,}74$, $p < 0.001$), Actinobacteria ($t = 2.87$, $p = 0.01$), Firmicutes ($t = 4.92$, $p < 0.001$), Verrucomicrobia ($t = 6.59$, $p < 0.001$), Planctomycetes ($t = 7.59$, $p < 0.001$), and Acidobacteria ($t = 6.38$, $p < 0.001$) were significantly more abundant in black mats. Cyanobacteria ($t = -5.16$, $p < 0.001$) were significantly more abundant in orange mats (Table 3). There were no phyla significantly differentially abundant in soil communities with respect to site or mat type (Table 4).

At the genus level, microbial mat communities varied greatly by both till and mat type (Figure 2b; Table 5). A total of 48 genera occurring in Ross or Taylor tills and 530

genera in black or orange mats were identified as significantly more abundant. Of the 48 genera found to be differentially abundant by site, 45 were more abundant in mats collected from the Ross till, and three were more abundant in mats collected from the Taylor till. Of the 530 genera found to be differentially abundant by mat type, 509 were more abundant in black mats, and 21 were more abundant in orange mats. Of the dominant genera, *Burkholderia* (t = 3.74, p = 0.002) and *Acidovorax* (t = 2.51, p = 0.009) were significantly more abundant in mats collected from the Ross till, while *Cyanothece* (t = -3.80, p = 0.005), *Microcoleus* (t = -3.36, p = 0.01), *Trichodesmium* (t = -3.17, p = 0.01), *Lyngbya* (t = -3.10, p = 0.02), *Anabaena* (t = -2.15, p = 0.05), *Oscillatoria* (t = -2.56, p = 0.03), and *Synechococcus* (t = -2.85, p = 0.02) were significantly more abundant in samples collected from the Taylor till (Table 5). *Burkholderia* (t = 7.66, p < 0.001) and *Acidovorax* (t = 3.10, p = 0.009) were also significantly more abundant in black mats, while *Cyanothece* (t = -7.11, p < 0.001), *Microcoleus* (t = -4.81, p = 0.007), *Trichodesmium* (t = -4.94, p = 0.007), *Lyngbya* (t = -4.52, p = 0.01), *Anabaena* (t = -3.08, p = 0.01), *Oscillatoria* (t = -3.36, p = 0.03), and *Synechococcus* (t = -3.28, p = 0.03) were significantly more abundant in orange mats (Table 5).

The ten most abundant genera varied by till and mat type (Fig. 2b; Table 5). *Nostoc*, *Oscillatoria*, *Cyanothece*, *Flavobacterium*, and *Anabaena* were among the ten most abundant genera for till and mat type. *Polaromonas*, *Acidovorax*, *Methylibium*, and *Burkholderia* were among the ten most abundant for Ross tills and black mat (Table 5). Ross tills and black mats differed by two top genera; *Chitinophaga* were more abundant in Ross tills, but not in black mats, while *Sphingomonas* were more abundant in black mat but not in Ross tills. *Trichodesmium*, *Synechococcus*, *Microcoleus*, *Lyngbya*, and

Arthrospira were the other five most abundant taxa in both orange mats and in samples collected from Taylor tills.

With the exception of a few dominant genera at certain sites, soil microbial communities were relatively homogenous at both the phylum and genus levels across both the Ross and Taylor sites (Figures 2c & 2d; Table 4 & 6). At the phylum level, soils were overwhelmingly dominated by the bacterial phyla Proteobacteria, Actinobacteria, Cyanobacteria, Bacteroidetes, and Firmicutes (Figure 2c). On average, these five phyla represented a majority of the reads identified in Ross and Taylor soil samples (~82% and ~80%) and in soils collected from under black and orange mats (80.5% and 82.2%). *Nostoc*, was the most abundant genera in soils across both sites (Ross: 3.42%, Taylor: 2.09%) and soils under black mats (2.80%); *Nostoc* was the second most abundant genera in soils under orange mats (2.39%) with *Oscillatoria* being the most abundant genera (2.78%). However, at the genus level, soils did not appear to be dominated by any particular genera (Figure 2d).

There was little variation in the relative abundance of dominant genera and phyla in soil microbial communities with respect to overlying microbial mat type. There were no phyla identified as being significantly more abundant in either Ross or Taylor tills or under black and orange mats (Table 4). However, there were 29 bacterial genera present in Ross or Taylor tills and 53 genera under black or orange mats, which displayed significantly different abundances with respect to site or overlying mat type. For example, the genera *Chitinophaga* was significantly more abundant in Taylor till soils ($t = -2.964$, $p = 0.0122$; Table 6). On average, *Chitinophaga* was identified in 1.40% of reads from soils collected from the Taylor till and 1.09% of reads from soils collected

from the Ross till. Of the 29 genera exhibiting differential abundance by till, 19 were more abundant in Ross tills, while 10 were more abundant in Taylor tills (Table 6). Of the 53 differentially abundant genera by mat type, 50 were more abundant under black mats, while three were more abundant in soils collected from beneath orange mats (Table 6).

Community Composition and Beta Diversity

The trends observed in community alpha diversity and composition data were supported by Global non-metric Multidimensional Scaling Analysis (NMDS) ordination, which exhibited clear distinctions in microbial community composition between black and orange mats (Figure 3A). In contrast there was no distinction in soil microbial community composition observed either across tills or beneath the orange and black mats (Figure 3B; Table 7).

Results of Permutational Analysis of Variance (PERMANOVA) suggested that till and mat type share significant correlation with Bray Curtis distances of microbial mat bacterial communities (Table 7). Though till was identified as being a driver of mat community separation, the black mat samples collected from the Taylor till cluster more closely with the Ross till samples of the same mat type suggesting that mat type is the overriding influence in the patterns of community composition and beta diversity observed. Ordinations of microbial mat communities separated between the black and orange mat types and across geochemical gradients associated with phosphate, ammonium, and total nitrogen especially within the Ross till (Figure 3A).

The environmental variables most significantly correlated with community structure (envfit; all $p < 0.05$) were soil phosphate ($R^2 = 0.70$), total nitrogen ($R^2 = 0.57$), ammonium ($R^2 = 0.55$), and DIN ($R^2 = 0.56$). Mat type, as expected, was the categorical

variable most significantly correlated with microbial mat community structure (p = 0.001; R^2 = 0.70). In contrast to the overlying microbial mats, soil communities did not exhibit significant separation with respect to till or mat type. Instead, variation in soil communities was most strongly associated with soil properties such as phosphate, conductivity, and C:N (Figure 3B). These environmental variables were significantly correlated with soil microbial community structure (all $p < 0.05$; PO4_P: R^2 = 0.43, EC: R^2 = 0.45, C:N: R^2 = 0.58).

Analysis of Mat and Soil Metagenome Functional Capacity

I focused the functional component of my metagenomic analysis on identifying variation in bacterial function at the SEED subsystems level 3 along a gradient of soil P and soil N:P. Metagenomic functional profile separated by till, with 53.09% of assigned functions represented in Ross till samples compared with 46.91% of functional profiles associated with Taylor tills. Generally, 50.95% of assigned functions were associated with black mat samples, while 49.05% of assigned functions were associated with orange mats. These trends in soil microbial functional abundance were consistent when analyzing exclusively nitrogen or phosphorus metabolism subsystems separately.

The proportional abundance of nitrogen and phosphorus metabolism functional subsystems were slightly more dynamic in mat samples compared to soil samples. On average, 51.28% of assigned functions belonged to mat samples from the Ross till, while 48.72% were from microbial mats from the Taylor till. When separated by mat type, black mat samples represented 51.33% of assigned reads, while 48.67% were from orange mat samples. However, when proportional abundance was analyzed by functional pathway (*i.e*. nitrogen metabolism or phosphorus metabolism), it was clear that the

relative abundance of nitrogen metabolism functions (with the exception of nitrogen fixation) was higher in orange mat samples (51.56%; black – 48.44%), while P metabolism functions were higher in black mat samples (54.26%; orange – 45.74%). A similar pattern of functional subsystems was also evident for all Ross till samples and Taylor plots #1, 2, and 7, which were all black mats and dominated by *Nostoc* (see above). All functional subsystems reported had a $p < 0.05$ and absolute value of LFC > 1.

Microbial mat communities displayed clear variation in functional potential by both site and mat type (Figure 4). Hits to nitrogen metabolism functional categories cyanate hydrolysis (LFC = 1.05; $p = 0.002$) and nitrate and nitrite ammonification (LFC = 1.44, $p < 0.001$) were significantly more abundant in microbial mats from the Taylor till samples, while nitrogen fixation (LFC = 1.44; $p = 0.01$) and dissimilatory nitrite reductase (LFC = 2.97; $p = 0.002$) were significantly more abundant in black microbial mats from the Ross tills.

Similar to earlier analyses of microbial mat community composition and diversity, the functional potential of mat samples was highly variable when analyzed by the mat type. Black mats had a significantly greater relative abundance of hits to amidase clustered with urea and nitrile hydratase functions (LFC = 2.14; $p < 0.001$), dissimilatory nitrite reductase (LFC = 2.84; $p = 0.002$), and nitrogen fixation (LFC = 3.05; $p < 0.001$). The functional categories ammonia assimilation (LFC = 1.28; $p < 0.001$), cyanate hydrolysis (LFC = 1.36; $p < 0.001$), and nitrate and nitrite ammonification (LFC = 1.90; $p < 0.001$) were significantly more abundant in orange mat samples than in black mat samples.

Microbial mat community phosphorus metabolism functions did not appear to correlate with till type (Figure 5), but several phosphorus metabolism subsystems were differentially abundant between black and orange mats. On average, hits to the phosphorus metabolism-associated subsystem for high-affinity phosphate transporter (LFC = 1.11; $p < 0.001$) were higher in orange mat samples, while hits to phosphate binding DING proteins (LFC = 2.33; $p < 0.001$), phosphoenolpyruvate phosphomutase (LFC = 1.20; $p < 0.001$), and phosphonate metabolism (LFC = 1.89; $p < 0.001$) were all significantly more abundant in black mats (Figure 5).

Nitrogen and phosphorus metabolism functions did not vary significantly between soils collected from Ross or Taylor tills (Figure 4 & 5), however, soils under black mats tended to have a higher normalized relative abundance of hits to nitrogen fixation (LFC = 1.03; $p < 0.001$), with soils from under black mats containing ~2x the normalized number of hits to nitrogen fixation than orange mat soil samples (Figure 5).

The trends observed in community composition and diversity data were also observed in the community functional profile and supported by NMDS ordination. Microbial mat communities separated by mat type along NMDS1 (Figure 6A), while soil communities appear to separate by glacial till along both NMDS1 & 2 (Figure 6B). Results of PERMANOVA suggested that till and mat type display significant correlation with Bray Curtis distances of microbial mat functional hits (Till: ADONIS Pr(>F) = 0.006; Mat: ADONIS Pr(>F) = 0.001). Soil community functional potential also displayed a significant correlation with till type (ADONIS Pr(>F) = 0.007). The separation in mat communities by mat type along NMDS1 appears to correlate strongly

with functional roles, while within mat variation appears to be driven by soil edaphic and geochemical properties (Figure 6A).

The functional subsystems intrinsic to the ordination data most significantly correlated with community function of microbial mats (envfit; all $p \leq 0.002$) were ammonia assimilation ($R^2 = 0.88$), cyanate hydrolysis ($R^2 = 0.92$), denitrification ($R^2 = 0.76$), nitrate and nitrite ammonification ($R^2 = 0.88$), nitrogen fixation ($R^2 = 0.83$), nitrosative stress ($R^2 = 0.77$), high affinity phosphate transporter ($R^2 = 0.95$), P uptake in cyanobacteria ($R^2 = 0.94$), phosphate binding DING proteins ($R^2 = 0.78$), phosphate metabolism (0.91), phosphoenolpyruvate phosphomutase ($R^2 = 0.67$), and phosphonate metabolism ($R^2 = 0.84$). The soil properties most significantly correlated with mat community function were SOC ($R^2 = 0.44$; $p = 0.013$), total nitrogen ($R^2 = 0.68$; $p = 0.001$), phosphate ($R^2 = 0.67$; $p = 0.002$), ammonium ($R^2 = 0.48$; $p = 0.012$), and DIN ($R^2 = 0.48$; $p = 0.030$).

Several functional subsystems and soil properties were correlated with soil community functional potential (Figure 6B). The functional subsystems most significantly correlated with soil community function (all $p \leq 0.002$) were allantoin utilization ($R^2 = 0.84$), ammonia assimilation ($R^2 = 0.78$), cyanate hydrolysis ($R^2 = 0.86$), dissimilatory nitrite reductase ($R^2 = 0.80$), nitrate and nitrite ammonification ($R^2 = 0.88$), nitrogen fixation ($R^2 = 0.73$), high affinity phosphate transporter and control of PHO regulon ($R^2 = 0.88$), P uptake in cyanobacteria ($R^2 = 0.81$), phosphate metabolism ($R^2 = 0.76$), and phosphoenolpyruvate phosphomutase ($R^2 = 0.65$). The most significant soil properties correlated with soil community function (all $p < 0.02$) were EC ($R^2 = 0.56$), total nitrogen ($R^2 = 0.42$), C:N ($R^2 = 0.57$), and phosphate ($R^2 = 0.83$).

Discussion

Microbial mats are unique communities of microorganisms that are often found throughout arid ecosystems, which comprise over one third of the Earth's terrestrial surface (Golla, 2021; Prieto-Barajas et al., 2018). These complex consortiums of microorganisms play major roles in key ecosystem processes (i.e., primary production, nutrient cycling) and influence underlying soils and the organisms found therein (de los Ríos et al., 2015; Prieto-Barajas et al., 2018; Sohm et al., 2020). Due to their global presence through many of Earth's most fragile ecosystems, I set out to identify patterns of microbial community composition (*e.g.*, cyanobacteria mats and soil heterotrophic bacterial communities) and functional diversity along a well-characterized environmental gradient of phosphate availability and N:P ratios in Taylor Valley, Antarctica. Using metagenomic approaches, I tested my predictions that 1) microbial community composition and functional diversity would vary with soil nutrient content (i.e., phosphate, N:P) across the tills and mat types sampled, and 2) that soil community composition and function would vary with respect to the overlying microbial mat type (*i.e.*, black or orange mats *sensu* Alger et al. 1997). In general, visually distinct microbial mats (i.e., black and orange) demonstrated separate microbial communities with differing functional diversity, both appearing to be significantly influenced by soil phosphate and N:P ratios. Additionally, underlying soil communities were surprisingly similar regardless of the soil type and overlying mat community. This study provides a valuable understanding of how soil nutrient stoichiometry structures microbial mat communities in nutrient limited environments. Furthermore, the data herein will help inform future studies on the complex biotic controls over nutrient cycling in arid ecosystems, as well as

understanding the relationship between microbial mats and local soil microbial communities.

Microbial Mats Harbor Distinct Bacterial Communities with Differing Functional Diversity

Globally, microbial mats are known to be complex microbial communities that grow on surfaces in aquatic or terrestrial environments and are characterized by a stratified structure and high diversity of microorganisms (Prieto-Barajas et al., 2018). In my study system, designations of mat type are based on the physical appearance of the mat, i.e., black or orange, which has been associated with the dominant taxa present, i.e., *Nostoc* spp. or *Oscillatoria* spp (Alger et al., 1997; Coyne et al., 2020). It is important to note, the designations, black and orange, do not define discrete communities that do not vary, rather they define predictable communities with black and orange denoting two community types composed of many unique taxa (Figure 2B).

Variation in microbial mat community diversity and composition was most evident between the black and orange mats, which is no surprise as these samples were derived from visually distinct microbial assemblages. Though microbial mat communities also differed across the two till types, the clustering of microbial mat communities in the Taylor plots #1, 2, and 7 with the Ross till samples (Fig. 2b & 3a) appears to be driven by the overlying black mats and illustrates an overriding influence of microbial mat type over local soil geochemistry and edaphic characteristics. Contrary to the hypothesized association of till geochemistry with microbial community composition, these data suggest that the visually distinct mat type is a stronger indicator of the microbial

community present in the mats. In line with the established visual identification methods of microbial mats in the McMurdo Dry Valleys (Alger 1997) and subsequent studies within the system, my results further support that the visual differences in black and orange microbial mats are the direct result of the dominant taxa present in the community and a valid method for identification purposes (McKnight et al., 1999, 2004).The genera *Nostoc* and *Oscillatoria* were generally the most abundant members of black and orange mats, respectively. These filamentous cyanobacteria are known to dominate microbial mat communities in both the Antarctic and Arctic polar regions, representing the dominant primary producers and key nitrogen fixers in polar systems devoid of vascular plants and their symbionts (de los Ríos et al., 2004, 2015; Vincent et al., 2000).

Variation in functional diversity between black and orange mats was in line with previous studies in the McMurdo Dry Valleys. With respect to nitrogen metabolism, black mats appear to focus their resources on nitrogen fixation, while orange mats displayed a greater relative abundance of functions associated with the uptake of inorganic nitrogen and conversion to nitrogen compounds readily available for microbial metabolism. Black mats have been shown to surpass the nitrogen fixation rates of other microbial mat types in the system (Kohler et al., 2018), sometimes demonstrating rates of dinitrogen fixation similar to those documented in warmer, more temperate environments (Sohm et al., 2020). These data also provide insights into the nitrogen metabolism potential of orange mat communities, suggesting that orange mats may play a major role in local nitrogen cycling (Vincent et al., 1993; Vincent & Howard-Williams, 1986). In terms of phosphorus metabolism, orange mats, which occurred generally on soils with low phosphorus availability, may focus their energy on the acquisition of phosphate

readily available in the environment through the use of high affinity phosphate transporters, while black mats may invest energy in both the degradation of phosphorus containing molecules to phosphate and subsequent uptake and assimilation of the phosphate. These results suggest that black mat communities may not just increase the presence of biologically available ammonium in the system but also increase available phosphate, two key nutrients required for the healthy growth and reproduction of microorganisms within the mats. My study also contributes a clearer understanding of the potential influences microbial mats have on the availability and exchange of nutrients from mats to the sub-soils where these nutrients could be subject to leaching and hydrological transport. These results suggest that the diverse microbial communities found in microbial mats play critical roles in soil health, nutrient cycling, and primary production in their host systems (Bottos et al., 2008).

Soil Phosphate and N:P Ratios Influence Microbial Mat Communities and Functional Diversity

Abiotic factors are the dominant influential factors in the assembly and diversity of microbial communities over broad spatial gradients or geographies (Hanson et al., 2012). For example, soil pH, relative soil moisture, and availability of labile carbon (C) and nitrogen (N) have all been shown to influence microbial community assembly and diversity (Fierer & Jackson, 2006; Nemergut et al., 2010). In my study, multiple indices of microbial diversity (H’ and J) were significantly correlated with C, N, and P availability in soils. This result is consistent with my prediction that microbial community taxonomic composition would be influenced by geochemical constraints

(e.g., soil phosphate, total nitrogen, N:P). Elevated levels of soil organic C and available nitrogen in underlying soils relative to typical soils reported in other studies (Barrett et al., 2006; Fritsen et al., 2000) is likely the result of the high abundance of nitrogen fixing taxa and primary. production within mat communities including *Trichodesmium*, *Anabaena*, and *Cyanothece*. Thus, changes in resident bacterial taxa can have broad implications on environmental functionality. Previous studies have demonstrated that soils low in P tend to harbor nitrifying taxa and high P soils tend to have a greater abundance of denitrifies while increases in soil C and N tend to have implications for total community functionality (O'Neill et al., 2022). Further analysis of microbial mat community structure using Bray-Curtis distances and NMDS ordination revealed a significant relationship between microbial mat community structure and geochemistry with a significant correlation to phosphate, ammonium, and total nitrogen on microbial mats. The influence of mat type as the distinguishing factor in relation to community structure was consistent with my findings of mat community alpha diversity metrics. These data further support my hypothesis that microbial mat communities are structured along geochemical gradients of phosphate and N:P. Moreover, these results align with experimental data from (Kohler et al., 2016), which demonstrated that N and P have a distinct effect on the taxa present and community structure of microbial mats within stream channels of the McMurdo Dry Valleys.

Microbial mat community functional profiles tended to distinguish along geochemical gradients. Specifically, this separation was significantly correlated to SOC, phosphate, total nitrogen, ammonium, and dissolved inorganic nitrogen. These results, in tandem with similar findings from community level analyses, directly inform the main

objective of my study to identify the influences of soil geochemistry on the functional potential of microbial mat communities. Furthermore, several studies have demonstrated that variations in soil stoichiometry (i.e., soil P and N) alter the functional profile of these microbial communities through shifts in community composition and stoichiometry. For example, some systems have shown increases in soil P alter the functional profile of microbial communities towards increased P immobilization, while increases in soil N decrease the solubilization and mineralization of P by microorganisms (Dai et al., 2020). Additionally, the mineralization of P by microorganisms is driven by their demand for C (Heuck et al., 2015). Therefore, soil chemical stoichiometry is vital in the maintenance of microbial mediated ecosystem function (Luo et al., 2020).

Microbial Mats May Exert a Homogenizing Influence on Underlying Soils' Community and Function

Soil microbial communities across the globe tend to be heterogenous assemblages of various bacterial taxa, structured by several variations in environmental factors, including soil moisture, pH, temperature, SOC, nutrient availability, elevation, and seasonality (Delgado-Baquerizo et al., 2018; Nunan et al., 2020; Peng et al., 2022). Studies in the MDV system have also demonstrated great heterogeneity in soil microbial communities across the system. These communities have demonstrated distinct communities with respect to several abiotic factors, displaying increased dissimilarity with increasing distance between resident soils (Bottos et al., 2008)

In this study, soil microbial communities were remarkably homogenous regardless of glacial till of origin and overlying mat types. Given the distinct overlying

microbial mat habitat, I expected distinct underlying soil microbial communities with respect to mat type. However, these data contradict my initial hypothesis regarding the influence of mat type on underlying microbial communities. These results are in contrast to previous findings, which have shown soil microbial communities are highly heterogeneous across the McMurdo Dry Valleys landscape (Buelow et al., 2016; Lee et al., 2018; Schwartz et al., 2014; S. T. S. Wei et al., 2016). Soil microbial communities were also functionally homogenous. A trend that has now been observed in microbial mat-associated soil communities at both the taxonomic and functional levels. From these data, there are two predictions that could explain the patterns observed. First, microbial mats in the system colonize soils with a specific microbial community present. Though this is logically sound, it is ecologically unlikely, especially given the documented heterogeneity of the system. An alternate explanation is that the physical and biotic presence of the microbial mats provides a unique microhabitat for the underlying soils relative to uncovered soils from the region.

Microbial mat communities carry out a variety of ecosystem processes, including primary production and nitrogen fixation across a range of mat harboring ecosystems (i.e., sand flats, hypersaline systems, hot springs, and polar regions) (Des Marais, 2003; Giovannoni et al., 1987; Severin & Stal, 2008; Stal et al., 2010; Steunou et al., 2006). Future studies would benefit greatly from assessing the contribution of organic material and other nutrient species from microbial mats to their underlying soils and sediments. Moreover, microbial mats excrete complex exopolysaccharides and other compounds that can stabilize soil structure (Federico rossi), increase water retention (adessi), soil organic matter, and increase solubility of key limiting nutrients to microbial growth (Adessi et al.,

2018; Des Marais, 1995, 2003; Rossi & De Philippis, 2015). Combined, these insights suggest microbial mats provide an ideal microhabitat for underlying soils that are not only related to the community composition and functioning of the mats, but rather the physical presence of the mat over the soil and the homogenous habitat they provide and particularly the input of organic matter from the microbial mats themselves.

Conclusion

I conclude that spatial variation in geochemistry, especially soil P availability influences distribution and diversity of microbial mats, but microbial mat composition determines the functioning of microbial mat and soil microbial communities, especially with respect to nitrogen cycling. Previous studies have demonstrated distinct geochemistry between the Ross and Taylor tills, demonstrating soil nitrogen content is higher in Taylor tills than Ross tills (Barrett et al., 2007; Barrett et al., 2006). However, the soil chemistry data from microbial mat covered soils suggests higher nitrogen content in Ross till soils. The higher than expected soil nitrogen content in the Ross till plots could be due to the presence of black microbial mats, suggesting these mats are not only the dominant primary producer but also a key nitrogen fixer in a habitat with very sparse distribution of non-vascular vegetation (Power et al., 2020). Soils underlying the relatively favorable microhabitat of microbial mats exhibit little variation in most of the soil properties explored in this study, suggesting microbial mats have a homogenizing influence on soil community structure and soil processes. In the context of Antarctica, these data suggest that mat communities and the associated heterotrophic assemblage in the underlying soil may homogenize the biogeochemical and compositional properties of soils while increasing the habitability of

soils for organisms found within. The McMurdo LTER has documented how hydrologic connectivity links glacial, terrestrial, and aquatic ecosystems in this region, but important questions about the role of biota in modulating these linkages remain. In this work we have shown that microbial communities are gatekeepers in the cycling and mobility of nitrogen and phosphorus on two glacial tills and soils with distinct mineralogy and chemistry.

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TABLES

Table 1: Sample plots (n = 16) with corresponding mat type, latitude, longitude, SOC, total N, and phosphate

Sample Name	Mat Type	Latitude	Longitude	SOC (mg/g)	Total N (mg/g)	Phosphate (µg/g)
ROSS1	Black	-77.59846	163.26842	1.6	0.26	8.807
ROSS2	Black	-77.61371	163.25754	1.17	0.13	4.647
ROSS3	Black	-77.61382	163.04385	1.44	0.21	4.036
ROSS4	Black	-77.60246	163.27255	1.59	0.14	6.96
ROSS5	Black	-77.62435	163.05362	1.71	0.21	4.308
ROSS6	Black	-77.62669	163.11385	2.02	0.18	2.054
ROSS7	Black	-77.63781	163.20866	2.72	0.24	2.461
ROSS8	Black	-77.62792	163.28668	2.05	0.17	2.898
TAYLOR1	Black	-77.72675	162.46495	1.78	0.24	0.739
TAYLOR2	Black	-77.72767	162.48909	0.88	0.1	0.847
TAYLOR3	Orange	-77.72469	162.47571	0.39	0.06	0.949
TAYLOR4	Orange	-77.73006	162.33351	0.33	0.08	0.918
TAYLOR5	Orange	-77.72599	162.31544	1.81	0.09	1.457
TAYLOR6	Orange	-77.72674	162.2858	0.45	0.08	1.281
TAYLOR7	Black	-77.7282	162.28732	0.76	0.13	2.793
TAYLOR8	Orange	-77.72993	162.323	0.38	0.06	0.087

Table 2: Mean (± SE) and P values of soil edaphic and geochemical properties separated by Ross (n = 8) and Taylor (n = 8) tills. Wilcoxon test was used for non-normal soil property data and these are denoted with an asterisk.

Parameter	Parental Till		*P* value
	Ross	Taylor	
Gravimetric water content	0.181 ± 0.032[A]	0.175 ± 0.018 [A]	0.66
Electrical conductivity			
(µS/cm)	22.0 ± 6.97[A]	13.9 ± 8.28 [A]	0.1
pH	7.55 ± 0.194[A]	7.34 ± 0.201 [B]	0.049
Soil Organic Carbon (mg/g)	1.79 ± 0.474 [A]	0.848 ± 0.616 [B]	0.021
Total Nitrogen (mg/g)	0.192 ± 0.046 [A]	0.105 ± 0.059 [B]	0.0098
C:N	9.52 ± 2.29 [A]	8.10 ± 5.04 [B]	0.083
PO4_P (µg/g)	4.52 ± 2.32 [A]	1.13 ± 0.783 [B]	0.0039
NH4_N (µg/g)	1.89 ± 3.40 [A]	0.562 ± 0.048 [A]	0.083
NO3_N (µg/g)	0.493 ± 0.173 [A]	0.418 ± 0.039 [A]	0.33
DIN (µg/g)	2.38 ± 3.37 [A]	0.979 ± 0.067 [B]	0.0054

Table 3: Mean normalized counts and P values determined by t-tests of the phyla identified as being present in microbial mat communities, showing the differences between tills (Ross or Taylor) and microbial mat type (black or orange).

Phylum	Ross	Taylor	Std. Error	P value	Black	Orange	Std. Error	P value
Acidobacteria	30459	19735	5995	0.096	31650	10680	3278	1.79E-05
Actinobacteria	213702	160632	60173	0.393	226621	100368	44057	0.012
Aquificae	2865	1880	396	0.027	2848	1328	306	9.99E-04
Bacteroidetes	361433	389633	66665	0.680	349330	433180	87627	0.383
Candidatus.Poribacteria	500	262	98	0.031	482	158	65	2.31E-04
Chlamydiae	2532	1615	363	0.024	2475	1191	292	0.001
Chlorobi	15067	11352	1936	0.077	14607	10136	1896	0.042
Chloroflexi	61345	64583	12996	0.808	67679	52591	15839	0.380
Chrysiogenetes	654	436	79	0.019	626	368	62	0.001
Cyanobacteria	510073	1255516	241178	0.010	549170	1616768	206649	0.002
Deferribacteres	1458	927	207	0.023	1420	692	154	4.21E-04
Deinococcus.Thermus	13683	13552	1852	0.944	14324	12064	2305	0.369
Dictyoglomi	806	503	130	0.035	804	325	84	7.58E-05
Elusimicrobia	432	275	67	0.035	425	195	54	0.002
Fibrobacteres	580	362	96	0.045	542	316	92	0.032
Firmicutes	81201	55164	10640	0.028	80355	41402	7877	4.73E-04
Fusobacteria	1962	1367	278	0.053	1888	1173	257	0.019
Gemmatimonadetes	16208	9252	3876	0.098	17019	3294	2000	1.25E-05
Lentisphaerae	1972	1023	315	0.010	1852	718	258	7.56E-04
Nitrospirae	3634	1968	671	0.029	3503	1256	433	2.32E-04
Planctomycetes	54739	27099	11079	0.026	54598	10824	5788	5.96E-06
Proteobacteria	1236900	651521	154849	0.003	1194996	392482	91854	4.90E-06
Spirochaetes	6800	4807	948	0.059	6499	4274	869	0.026
Synergistetes	1754	1047	242	0.012	1724	689	164	8.66E-05
Tenericutes	600	529	80	0.391	588	512	105	0.499
Thermotogae	3202	1999	470	0.023	3163	1362	343	3.41E-04
Unclassified Bacteria	4001	2815	652	0.091	4069	1955	457	5.88E-04
Verrucomicrobia	85899	37439	13850	0.004	81183	18737	9486	1.59E-05
Crenarchaeota	1216	805	203	0.064	1232	523	144	5.53E-04
Euryarchaeota	12167	9805	1219	0.073	12156	8413	997	0.004
Korarchaeota	84	43	14	0.013	82	23	9	1.33E-05
Nanoarchaeota	5	7	3	0.661	5	8	5	0.596
Thaumarchaeota	184	163	37	0.571	203	109	25	0.002

Table 4: Mean normalized counts and P values determined by t-tests of the phyla identified as being present in soil communities underlying microbial mats, showing the differences between tills (Ross or Taylor) and microbial mat type (black or orange).

Phylum	Ross	Taylor	Std. Error	P value	Black	Orange	Std. Error	P value
Acidobacteria	69938	86330	13519	0.251	79696	74698	17793	0.789
Actinobacteria	394878	424877	57821	0.613	387192	459787	76129	0.384
Aquificae	5241	5969	700	0.320	5711	5371	920	0.726
Bacteroidetes	297075	332807	28357	0.229	299059	349881	35315	0.205
Candidatus.Poribacteria	1991	1783	303	0.505	2079	1465	322	0.103
Chlamydiae	4375	4006	528	0.497	4498	3513	467	0.061
Chlorobi	19855	20420	1705	0.746	20718	18860	2085	0.409
Chloroflexi	84033	92170	9047	0.391	89175	85739	12953	0.802
Chrysiogenetes	969	1068	109	0.388	1045	960	140	0.566
Cyanobacteria	351976	348674	152014	0.983	303117	454181	213671	0.513
Deferribacteres	2511	2745	325	0.486	2714	2439	420	0.539
Deinococcus.Thermus	20944	24416	2219	0.148	22587	22884	3179	0.929
Dictyoglomi	1496	1624	202	0.540	1601	1469	273	0.650
Elusimicrobia	824	904	110	0.483	892	801	140	0.542
Fibrobacteres	705	836	98	0.204	734	851	141	0.448
Firmicutes	134290	144154	15854	0.546	142269	132519	21492	0.669
Fusobacteria	2743	2878	293	0.653	2887	2643	357	0.520
Gemmatimonadetes	24076	25813	4138	0.682	25174	24439	5817	0.905
Lentisphaerae	2427	2659	233	0.343	2599	2420	306	0.582
Nitrospirae	15627	13410	2422	0.376	16204	10811	2458	0.067
Planctomycetes	106947	104492	15664	0.878	114200	87061	15665	0.125
Proteobacteria	1153418	1024028	73956	0.113	1156014	940683	92694	0.074
Spirochaetes	8752	8991	759	0.758	9118	8328	880	0.402
Synergistetes	2991	3209	389	0.587	3195	2892	522	0.587
Tenericutes	873	901	59	0.640	902	854	72	0.533
Thermotogae	5399	5884	704	0.506	5810	5271	933	0.587
Unclassified Bacteria	7358	8206	928	0.380	7831	7674	1304	0.909
Verrucomicrobia	99188	125004	13034	0.075	112325	111593	17319	0.968
Crenarchaeota	2427	2692	379	0.500	2597	2477	534	0.830
Euryarchaeota	19632	21492	2159	0.408	20822	19992	2995	0.793
Korarchaeota	178	202	33	0.493	199	171	38	0.494
Nanoarchaeota	12	13	3	0.507	14	10	3	0.145
Thaumarchaeota	628	1123	280	0.108	800	1042	372	0.540

Table 5: Mean normalized counts and P values determined by t-tests of the 100 most abundant genera identified as being present in microbial mat communities, showing differences between till (Ross or Taylor) and microbial mat type (black or orange).

Genus	Ross	Taylor	Std. Error	P value	Black	Orange	Std. Error	P value
Nostoc	191041	230280	56973	0.508	194339	246565	49167	0.307
Oscillatoria	34131	194940	62813	0.035	37681	283616	73255	0.027
Cyanothece	49525	170913	31938	0.005	57425	226365	23732	0.001
Anabaena	87221	146774	27785	0.051	92138	171689	25788	0.013
Trichodesmium	19343	94830	23901	0.014	22140	133967	22798	0.007
Flavobacterium	45343	68528	16595	0.194	42614	88443	20017	0.076
Synechococcus	24267	74767	17733	0.024	27241	98523	21842	0.029
Microcoleus	16151	61397	13421	0.010	18842	82624	13227	0.007
Polaromonas	51961	31049	13567	0.157	45286	33185	12129	0.336
Lyngbya	9911	52561	13761	0.016	11559	74525	13876	0.009
Pedobacter	30031	35506	5816	0.370	28977	41111	7658	0.180
Arthrospira	8300	43920	11143	0.014	9544	62556	10276	0.006
Chitinophaga	34140	28490	4422	0.225	33435	26651	5906	0.302
Cytophaga	24181	33143	5555	0.143	24208	38460	7477	0.123
Spirosoma	25490	29669	3717	0.293	27030	28789	5259	0.751
Synechocystis	11085	35265	7079	0.009	12321	47053	6235	0.003
Acidovorax	40757	16293	9732	0.035	35867	12373	7560	0.009
Nodularia	17714	31159	5596	0.031	18998	36400	5352	0.011
Burkholderia	37465	17975	5181	0.002	35544	10508	3264	0.000
Sphingomonas	33068	20500	8663	0.169	35217	8231	4841	0.000
Roseiflexus	22738	25448	5009	0.599	25679	20605	6051	0.434
Streptomyces	27689	22281	8153	0.518	30182	13553	5904	0.014
Methylibium	40225	12025	8375	0.007	35591	5298	6098	0.000
Caulobacter	32909	17031	9794	0.129	33712	5737	6246	0.001
Brevundimonas	33101	16424	11414	0.169	33619	5280	7987	0.003
Xanthomonas	29754	16618	8150	0.129	29038	10311	6941	0.020
Chthoniobacter	32311	13985	6120	0.010	31175	5488	3843	0.000
Bacteroides	24839	16848	6395	0.244	22643	16883	5590	0.321
Pseudomonas	26954	14892	2883	0.001	25661	10499	1945	0.000
Microcystis	8190	24595	4383	0.005	9232	32144	3157	0.000
Acaryochloris	7348	24037	4639	0.007	8714	31045	4756	0.006
Albidiferax	30034	8480	12368	0.124	24863	6924	9275	0.081
Leptothrix	30771	8425	7848	0.020	26769	3822	5800	0.002
Dyadobacter	16701	16877	2591	0.947	16588	17232	3673	0.868

Rhodobacter	23357	10987	3606	0.004	22049	6442	2381	0.000
Sorangium	21093	12395	3600	0.030	20949	7492	2535	0.000
Erythrobacter	22237	11546	4242	0.025	21824	6039	2606	0.000
Sphingobium	20912	12948	5326	0.157	22181	5380	2994	0.000
Thermosynechococcus	5885	20798	4409	0.010	6746	27852	4306	0.006
Unclassified Flavobacteriales	11005	17126	4392	0.195	10205	22558	5180	0.067
Rhodopseudomonas	20849	11001	3724	0.021	20923	4928	1723	0.000
Mycobacterium	18812	12223	4969	0.207	19234	7341	3470	0.004
Sphingopyxis	18583	12078	4107	0.136	19636	5858	2319	0.000
Gloeobacter	8820	17249	2216	0.004	9724	20316	2234	0.004
Methylobacterium	18495	11717	4309	0.142	19769	4846	2175	0.000
Bradyrhizobium	19212	10638	3565	0.034	19547	4757	1612	0.000
Geobacter	16979	10636	2300	0.016	16473	7942	1705	0.000
Candidatus.Solibacter	17276	10909	3441	0.087	17922	5668	1820	0.000
Frankia	14485	12081	4017	0.559	15562	8269	3209	0.041
Myxococcus	15241	10104	2616	0.071	15648	6127	1684	0.000
Chloroflexus	13301	11536	2800	0.541	14601	7615	2431	0.021
Gramella	11779	11415	2143	0.868	11271	12313	2807	0.725
Gemmatimonas	16186	9289	3871	0.100	17006	3347	2013	0.000
Cupriavidus	17157	7557	2630	0.003	16105	4112	1671	0.000
Anaeromyxobacter	15068	8993	2616	0.036	15158	5149	1658	0.000
Variovorax	15994	7279	2821	0.011	14406	5543	2350	0.002
Nocardioides	12505	9996	4740	0.605	13212	6936	3782	0.120
Bacillus	12717	9594	1505	0.059	12815	7504	1209	0.003
Opitutus	16408	6811	2980	0.007	15257	3585	2177	0.000
Novosphingobium	13950	8474	2793	0.071	14374	4256	1586	0.000
Mucilaginibacter	10093	10044	1331	0.971	9848	10552	1931	0.732
Herpetosiphon	6165	12442	3214	0.087	6731	14962	4832	0.161
Marivirga	9184	10279	1800	0.554	9045	11242	2321	0.386
Planctomyces	14359	6750	2667	0.013	14030	2907	1454	0.000
Gemmata	13196	7681	4066	0.196	14206	2149	2261	0.000
Crocosphaera	3618	12064	2270	0.005	4096	16080	1535	0.000
Mesorhizobium	12966	6901	2927	0.057	13184	2782	1625	0.000
Microscilla	7523	9609	1564	0.211	7716	10436	2093	0.251
Clostridium	11561	7026	2198	0.067	10978	5586	1670	0.006
Haliangium	11813	6800	2429	0.058	11729	3977	1716	0.001
Roseomonas	11826	6767	2828	0.096	12370	2535	1496	0.000
Rhodopirellula	12251	5864	1988	0.006	11833	2951	1134	0.000
Algoriphagus	8010	7958	1480	0.972	7752	8495	1889	0.709
Rhizobium	11192	6339	1909	0.027	11368	3040	877	0.000

Sinorhizobium	11073	6192	1874	0.025	11234	2909	836	0.000
Plesiocystis	8391	7071	2096	0.541	8199	6702	2942	0.633
Stenotrophomonas	10616	5748	3192	0.150	10332	3452	2685	0.024
Shewanella	9214	6364	1081	0.020	8878	5395	986	0.006
Verminephrobacter	10982	4861	2072	0.015	9949	3461	1588	0.001
Ralstonia	11021	4757	1624	0.002	10245	2705	1086	0.000
Rhodococcus	9030	6394	2490	0.308	9486	3808	1772	0.006
Stigmatella	9334	6135	1746	0.090	9693	3426	1064	0.000
Sphingobacterium	6504	7054	1121	0.633	6286	7864	1477	0.335
Dechloromonas	12902	2547	6797	0.171	10493	1633	5002	0.107
Rhodospirillum	9580	5448	1595	0.026	9740	2615	689	0.000
Chlorobium	7979	5942	1075	0.083	7684	5369	1008	0.043
Verrucomicrobium	10317	4445	1365	0.001	9528	2658	1092	0.000
Roseobacter	9252	5235	1371	0.015	9218	2899	682	0.000
Unclassified Verrucomicrobia	9700	4822	1608	0.009	9356	2651	1000	0.000
Bordetella	9741	4540	1329	0.002	9238	2526	803	0.000
Deinococcus	5403	7055	1090	0.165	5794	7185	1701	0.455
Oscillochloris	6799	6243	1631	0.739	7593	4162	1534	0.058
Leadbetterella	5792	6255	983	0.646	5721	6690	1351	0.506
Cylindrospermopsis	2984	7799	1346	0.005	3414	9742	1295	0.004
Salinispora	6416	6485	3213	0.983	8039	2955	2217	0.040
Ruegeria	8179	4736	1286	0.022	8221	2577	632	0.000
Polaribacter	5616	5867	1252	0.844	5299	6714	1581	0.409
Desulfovibrio	7352	4795	946	0.017	7236	3518	655	0.000
Delftia	8731	3677	1821	0.022	7806	2680	1409	0.003
Arthrobacter	6957	5089	1712	0.295	7086	3686	1432	0.035

Table 6: Mean normalized counts and P values determined by t-tests of the 100 most abundant genera identified as being present in soil underlying microbial mat separated by both till of origin (Ross or Taylor) and microbial mat type (black or orange).

Genus	Ross	Taylor	Std. Error	P value	Black	Orange	Std. Error	P value
Nostoc	97206	54675	25998	0.124	79618	67849	33456	0.736
Streptomyces	53442	59326	7524	0.449	53226	63330	10448	0.381
Oscillatoria	35903	52774	36909	0.658	28661	78829	54479	0.406
Cyanothece	41320	49561	17668	0.651	37528	62848	24733	0.358
Chthoniobacter	38431	52455	6615	0.057	44759	46950	8826	0.811
Candidatus.Solibacter	39098	48385	7732	0.256	44681	41674	10261	0.780
Anabaena	49417	35500	15888	0.397	41151	45336	21267	0.851
Burkholderia	40104	35946	3368	0.244	40494	32593	4330	0.133
Polaromonas	41157	32740	8243	0.325	38813	32845	8140	0.480
Chitinophaga	31068	39936	2976	0.012	33522	39857	4347	0.197
Flavobacterium	29848	37066	7983	0.390	28439	44496	11088	0.216
Mycobacterium	34505	34630	4803	0.980	33452	37023	6477	0.605
Frankia	29827	34830	4961	0.336	29742	38019	7074	0.301
Roseiflexus	28382	31101	2676	0.336	30042	29082	3822	0.812
Xanthomonas	28536	29378	3576	0.818	29931	26813	3504	0.396
Geobacter	28785	28128	3759	0.864	29965	25137	4132	0.283
Sorangium	28584	27308	3825	0.744	29603	24302	4397	0.273
Pedobacter	24889	28846	2225	0.099	25242	30442	2823	0.123
Planctomyces	26853	28285	3830	0.714	29087	24228	4062	0.269
Conexibacter	23006	28151	6567	0.455	22864	31550	10003	0.432
Synechococcus	22937	27084	4126	0.335	22296	30982	5085	0.149
Gemmata	28246	25190	4922	0.545	30404	18607	3949	0.014
Gemmatimonas	24102	25821	4141	0.685	25191	24456	5818	0.905
Pseudomonas	25735	23945	1454	0.252	26089	22091	1794	0.084
Anaeromyxobacter	23426	24909	2941	0.623	25100	22116	3509	0.428
Trichodesmium	17606	25237	14714	0.616	14808	35972	21534	0.378
Acidovorax	27814	19943	4545	0.115	25674	19929	4166	0.191
Nocardioides	22431	22710	4348	0.950	21218	25548	4109	0.316
Cytophaga	19640	23397	2794	0.205	19800	25298	3845	0.217
Sphingomonas	23353	21294	3173	0.527	23601	19512	3851	0.331
Spirosoma	20201	22999	1587	0.105	20575	23854	2228	0.204
Bradyrhizobium	22564	20285	2790	0.428	23221	17471	2747	0.073

Myxococcus	20190	21963	2366	0.467	21735	19627	2759	0.472
Rhodopirellula	20418	21126	2629	0.792	21850	18402	2907	0.277
Bacillus	19096	21176	1990	0.320	20368	19627	2750	0.798
Unclassified Verrucomicrobia	17202	22825	2529	0.048	19906	20250	3380	0.922
Bacteroides	21337	18446	4504	0.540	20659	18202	3385	0.482
Rhodopseudomonas	21259	17849	2405	0.178	21466	15347	2178	0.022
Methylibium	23439	14842	3987	0.056	21647	13627	3617	0.045
Methylobacterium	19072	17034	2016	0.330	19327	15249	2283	0.126
Candidatus.Koribacter	15692	19415	2996	0.240	17823	16959	3892	0.832
Cupriavidus	18354	16116	1627	0.196	18439	14587	2079	0.127
Rhodococcus	15987	17047	2307	0.654	15662	18398	3090	0.417
Clostridium	17027	16413	2387	0.801	17533	14933	2437	0.316
Pirellula	16968	16007	2549	0.712	17704	13810	2810	0.212
Microcoleus	13383	16173	8128	0.738	11500	21989	11608	0.412
Opitutus	15422	16550	1620	0.504	16757	14290	1775	0.209
Dyadobacter	14076	16214	1080	0.069	14479	16609	1489	0.211
Erythrobacter	14510	14926	2263	0.858	14592	14994	3307	0.908
Caulobacter	17567	12449	2426	0.057	16527	11666	2560	0.090
Haliangium	14079	15054	2046	0.641	15550	12402	1757	0.099
Albidiferax	18128	10856	4818	0.170	16172	10796	3867	0.188
Chloroflexus	14096	14090	1250	0.996	14683	12794	1667	0.312
Blastopirellula	14468	13896	2067	0.786	15146	12059	2319	0.230
Stigmatella	12900	14094	1590	0.466	13860	12699	1918	0.566
Sphingobium	14027	13089	2115	0.664	14196	12153	2702	0.481
Rhodobacter	15147	11660	2910	0.256	13749	12644	4216	0.804
Leptothrix	17085	10301	3459	0.080	15598	9503	2998	0.062
Lyngbya	9660	14178	8306	0.599	8173	20160	12177	0.377
Sphingopyxis	13062	12970	1970	0.964	13251	12498	2787	0.798
Salinispora	12208	13332	1773	0.538	12391	13603	2361	0.629
Verrucomicrobium	11354	14362	1339	0.046	12830	12919	1764	0.961
Nitrospira	14243	11905	2235	0.314	14707	9481	2213	0.051
Acidobacterium	11193	13777	2114	0.247	12734	11938	2743	0.782
Mesorhizobium	13234	10780	1314	0.084	13178	9431	1026	0.003
Sinorhizobium	12280	10919	1052	0.219	12373	9900	1218	0.094
Rubrobacter	10037	12169	2203	0.359	10525	12374	3431	0.616
Arthrospira	8263	12172	6901	0.585	7050	17186	10117	0.369
Desulfovibrio	10864	11485	1142	0.597	11506	10444	1482	0.504
Herpetosiphon	9259	12124	1136	0.035	10051	12099	1867	0.327
Rhizobium	11906	10348	990	0.139	11973	9265	1011	0.035
Variovorax	12486	9532	1779	0.123	11513	9900	1872	0.409
Gramella	9912	11058	800	0.175	10029	11488	1036	0.216
Arthrobacter	10214	10597	1354	0.782	9826	11681	1309	0.191
Bordetella	11337	10114	1023	0.258	11473	9081	1316	0.134
Gloeobacter	9590	11017	781	0.089	9840	11322	890	0.139
Novosphingobium	9868	10700	1759	0.647	9930	11063	2678	0.692

Ralstonia	11181	9711	953	0.151	11152	8893	1261	0.138
Synechocystis	9028	10443	3178	0.665	8224	13061	4304	0.316
Stenotrophomonas	9993	10398	1405	0.778	10522	9476	1437	0.486
Chlorobium	9942	10232	823	0.729	10370	9465	948	0.375
Saccharopolyspora	9462	10231	1278	0.559	9350	10938	1788	0.418
Shewanella	9979	10073	585	0.876	10303	9417	694	0.253
Kribbella	9232	9952	1464	0.631	8909	11093	1714	0.251
Sphaerobacter	9272	10210	1556	0.559	9877	9442	2207	0.852
Mucilaginibacter	8446	9653	623	0.075	8679	9864	869	0.231
Nodularia	10112	7667	3338	0.477	8527	9686	4477	0.806
Janibacter	9913	8053	2766	0.517	8982	8986	2180	0.999
Ktedonobacter	8360	9572	1352	0.388	9076	8724	1841	0.856
Deinococcus	7675	9707	754	0.024	8367	9404	1192	0.423
Nitrobacter	9320	8294	1205	0.409	9538	7199	1145	0.074
Micromonospora	7965	8830	1264	0.506	8181	8875	1617	0.684
Pelobacter	8733	8451	1120	0.804	9052	7581	1237	0.275
Brevundimonas	12143	5611	2612	0.034	10471	5371	2393	0.051
Kineococcus	7856	8390	1226	0.670	7514	9462	1183	0.136
Geodermatophilus	7576	8553	1236	0.443	7397	9533	1509	0.213
Rhodospirillum	8978	7546	653	0.050	8964	6719	691	0.022
Nitrosococcus	7811	8412	815	0.476	8318	7657	1064	0.560
Unclassified Flavobacteriales	6788	8522	2104	0.431	6358	10507	2899	0.220
Verminephrobacter	8902	6998	987	0.080	8506	6726	948	0.086

Table 7: Permutational Analysis of Variance (PERMANOVA) results for comparisons of bacterial assemblages based on Bray-Curtis distance matrices.

	Microbial Mat Communities			**Soil Communities**		
Variable	**R^2**	**F Statistic**	**Pr(>F)**	**R^2**	**F Statistic**	**Pr(>F)**
Till	0.33225	6.9659	0.007	0.05721	0.8496	0.471
Mat	0.57764	19.147	0.001	0.09816	1.5238	0.169

FIGURES

Figure 1: Map of the study region with glacial till series indicated by colored overlay and sample plots identified as red stars.

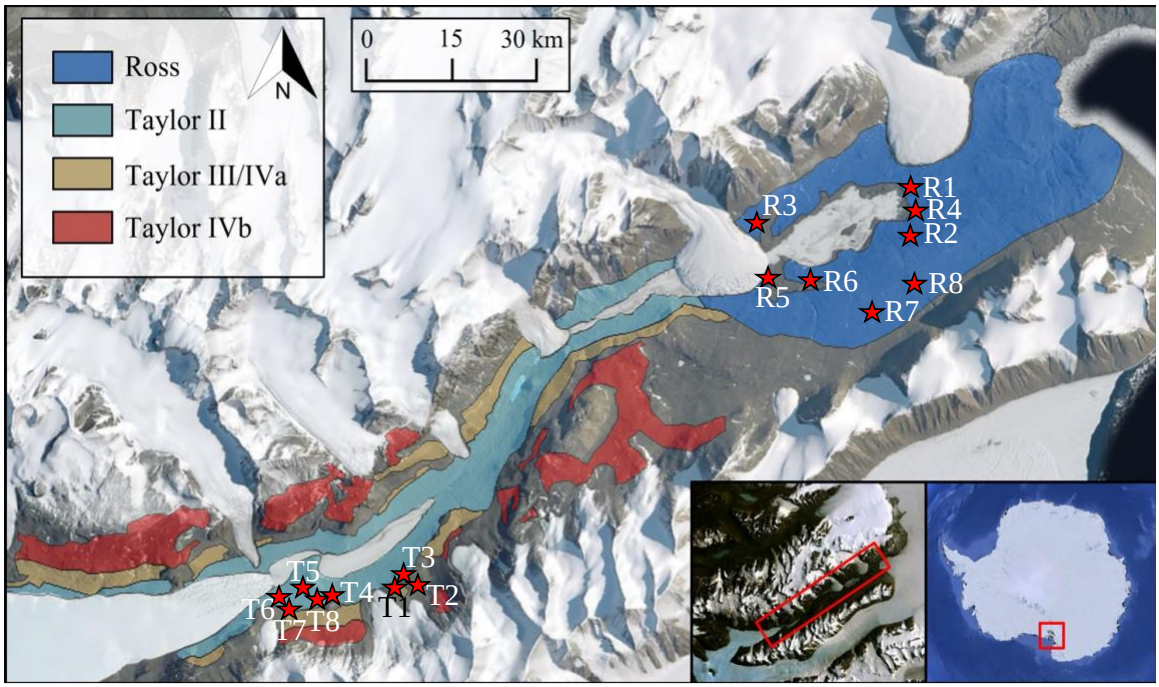


Figure 2: Relative abundance of top mat phyla (2A) and genera (2B) and top soil phyla (2C) and genera (2D). Top phyla and genera were determined to be any phylum or genus representing an arbitrary percentage (1%) of all sequences across samples. Associated mat type indicated as B_ for black mats and O_ for orange mats.

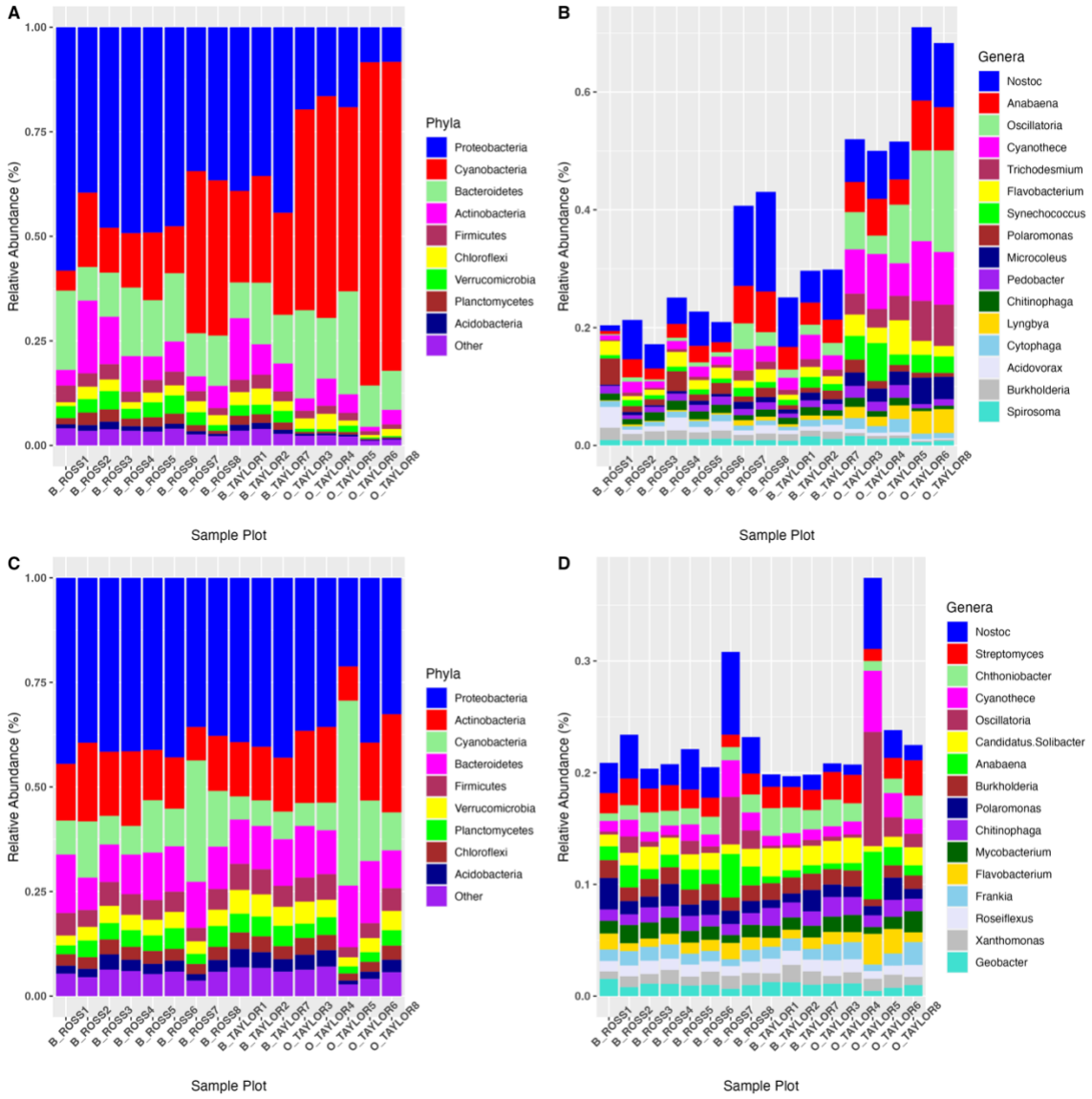
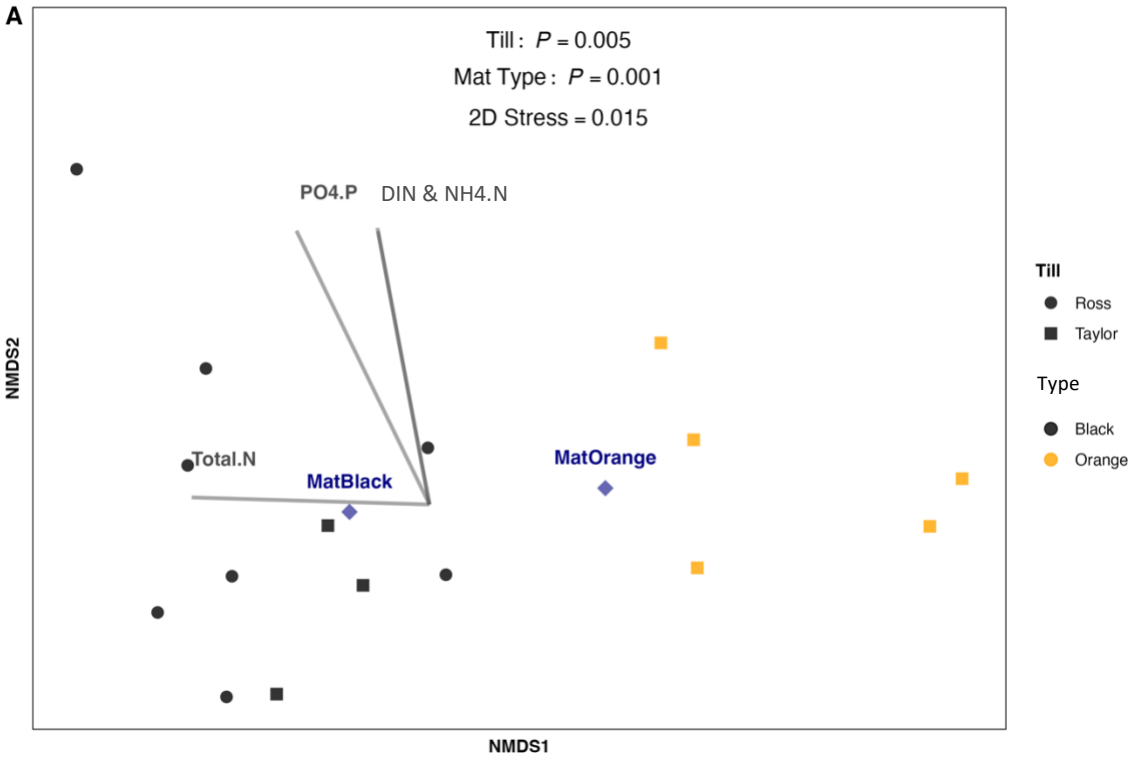


Figure 3: Non-metric multidimensional scaling ordination of mat (3A) and soil (3B) bacterial communities from sites along a gradient of biologically available soil N & P using Bray-Curtis dissimilarity distances. Parental till is indicated by the shape of the data points (Circle: Ross till; Square: Taylor till) and mat type is indicated by data point color (color corresponds to specific mat color). Vectors for soil edaphic and geochemical properties correlated with microbial community composition are included and radiate out from the origin. Stress value of ordination 3A 0.045. Stress value of ordination 3B 0.052.


A
Till : P = 0.005
Mat Type : P = 0.001
2D Stress = 0.015
PO4.P
DIN & NH4.N
Total.N
MatBlack
MatOrange
NMDS2
NMDS1
Till
Ross
Taylor
Type
Black
Orange

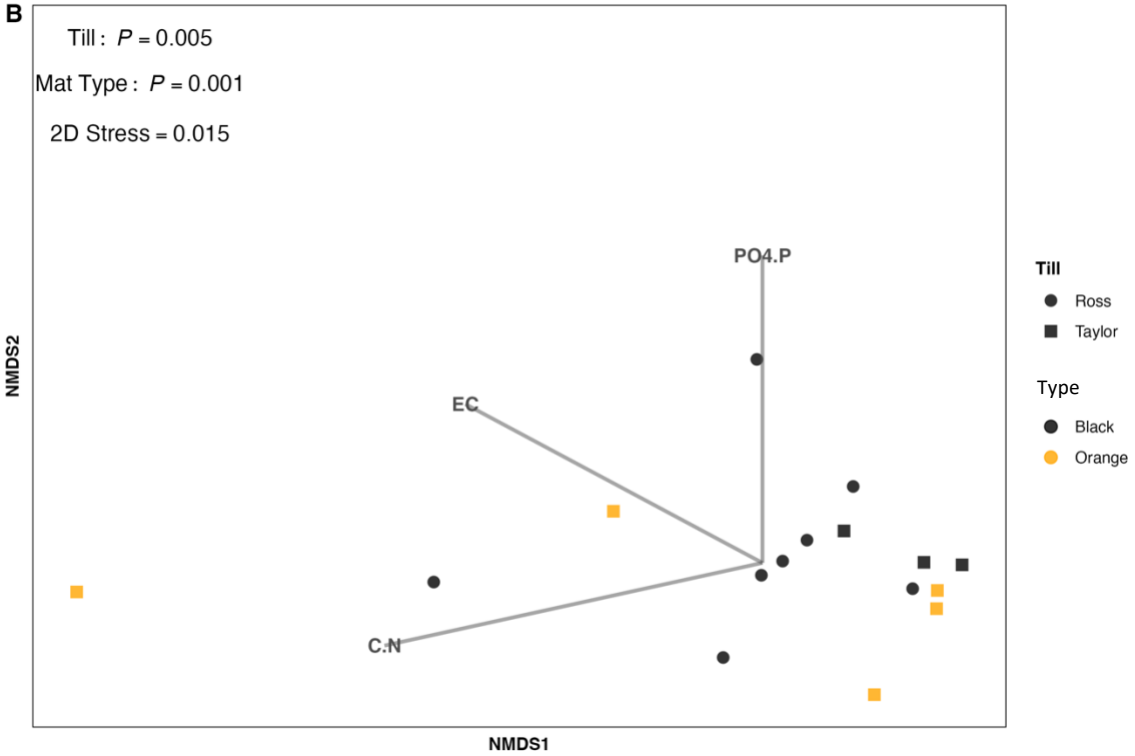

B
Till : P = 0.005
Mat Type : P = 0.001
2D Stress = 0.015
PO4.P
EC
C:N
NMDS2
NMDS1
Till
Ross
Taylor
Type
Black
Orange

Figure 4: Heatmap of log 2-fold change for differentially abundant features at SEED subsystem level 3 in microbial mats. The SEED subsystems database is a protein database with hierarchically organized gene families. The database has 5 levels, increasing in functional resolution at higher levels.

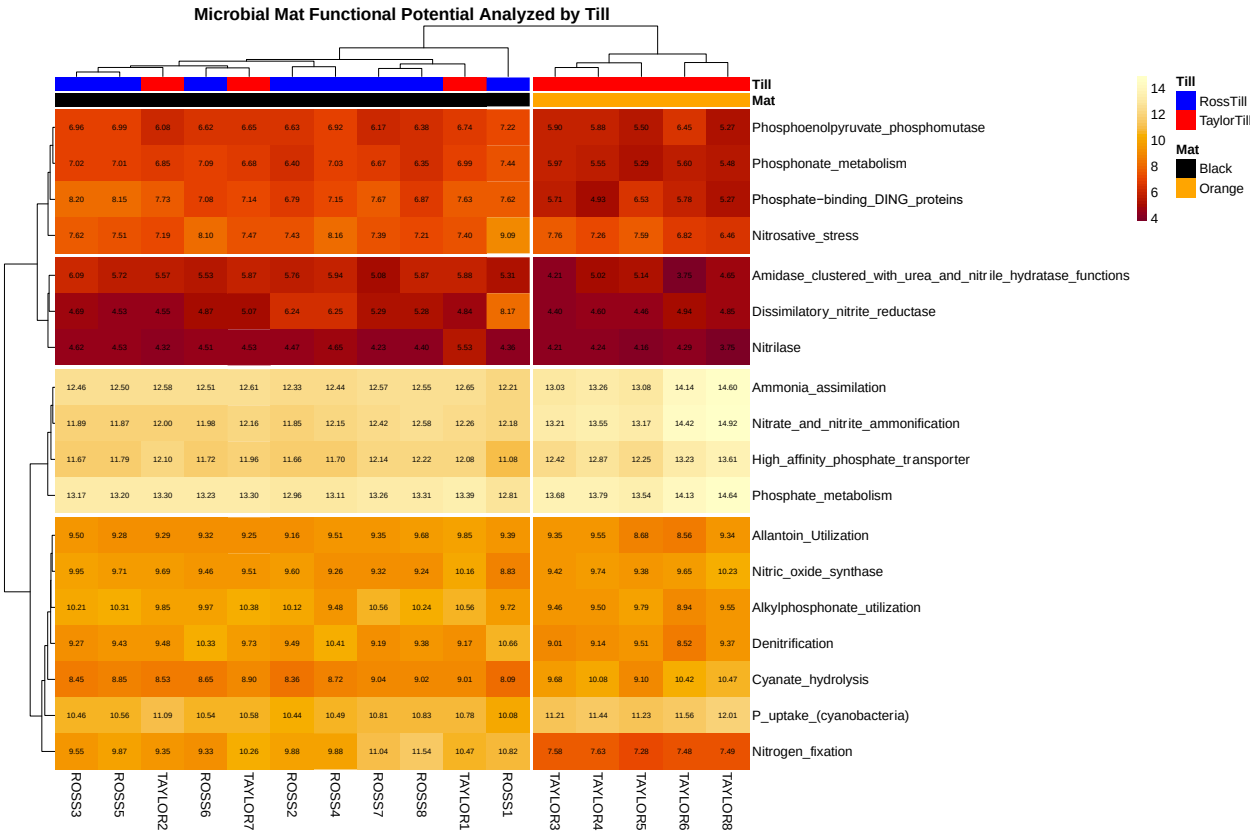


Figure 5: Heatmap of log 2-fold change for differentially abundant features at SEED subsystem level 3 in soils. The SEED subsystems database is a protein database with hierarchically organized gene families. The database has 5 levels, increasing in functional resolution at higher levels.

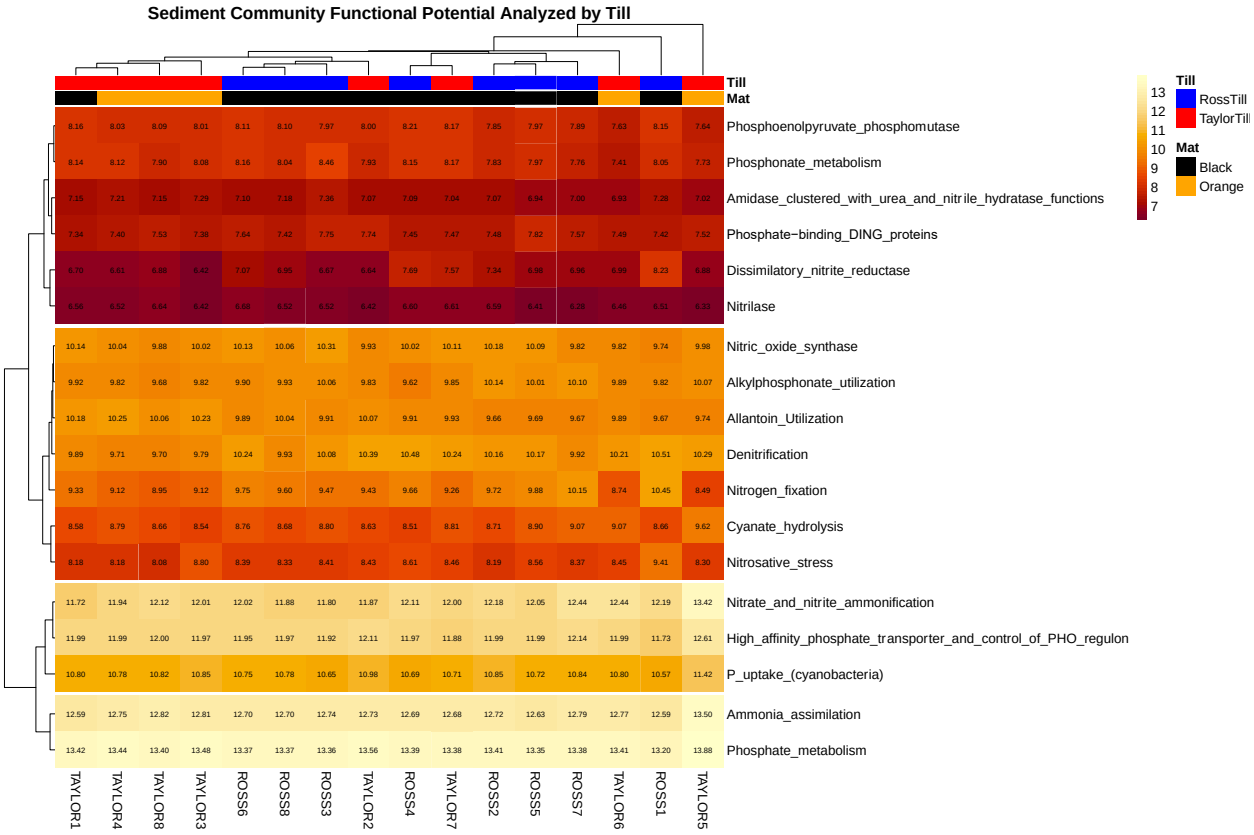
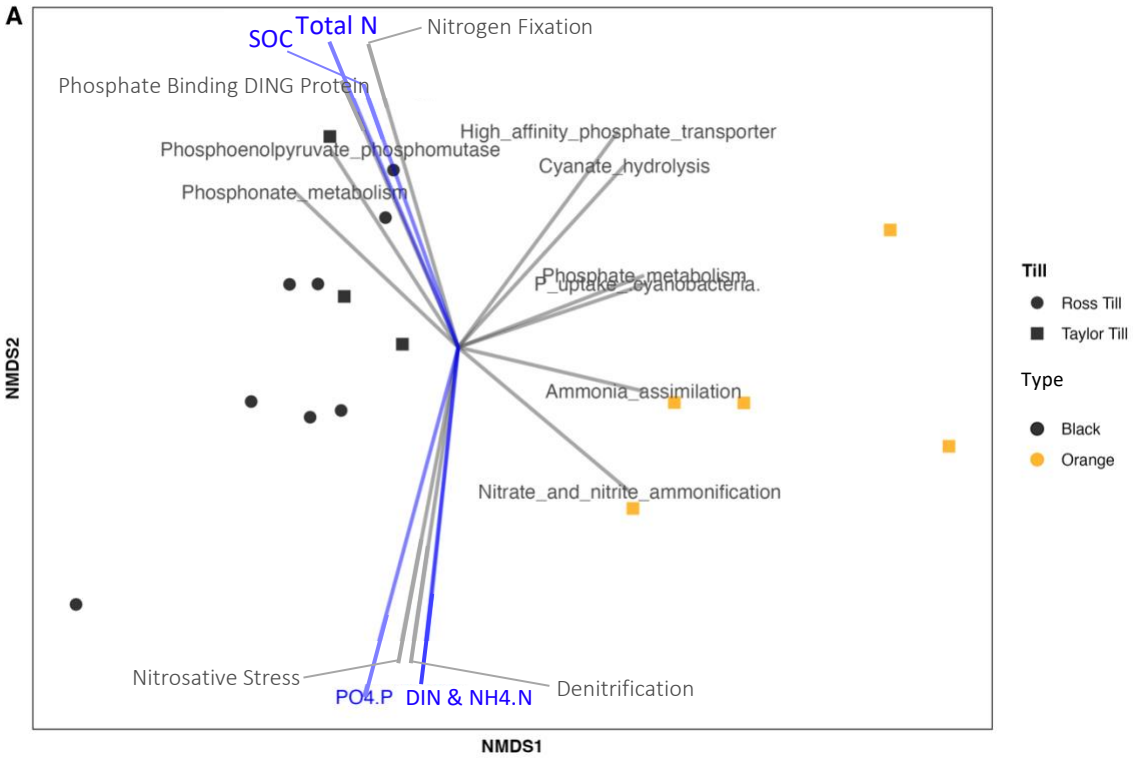
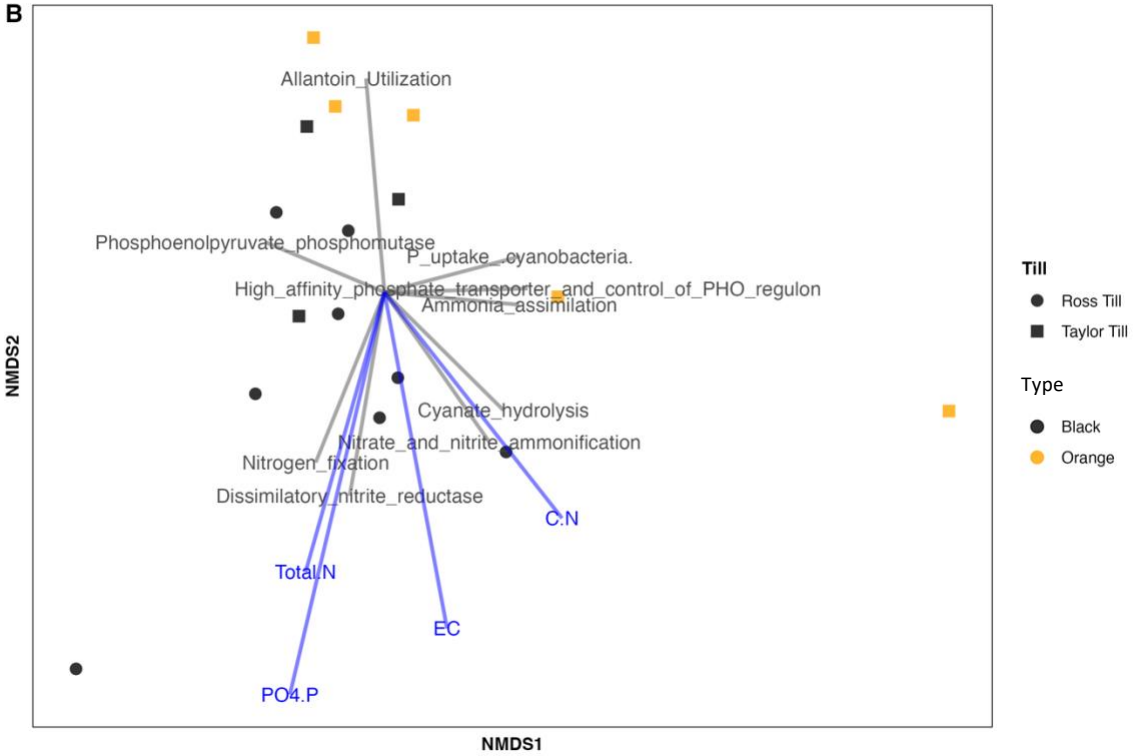


Figure 6: Non-metric multidimensional scaling ordination of mat (6A) and soil (6B) bacterial community functional potential from sites along a gradient of biologically available soil N & P using Bray-Curtis dissimilarity distances. Parental till is indicated by the shape of the data points (Circle: Ross till; Square: Taylor till) and mat type is indicated by data point color (color corresponds to specific mat color). Vectors for functional (intrinsic variables) and soil edaphic/geochemical properties correlated with microbial community functional potential are included and radiate out from the origin. Stress value of ordination 5A 0.041. Stress value of ordination 5B 0.078.


A
SOC
Total N
Nitrogen Fixation
Phosphate Binding DING Protein
High_affinity_phosphate_transporter
Phosphoenolpyruvate_phosphomutase
Cyanate_hydrolysis
Phosphonate_metabolism
Phosphate_metabolism
P_uptake_cyanobacteria.
Ammonia_assimilation
Nitrate_and_nitrite_ammonification
Nitrosative Stress
PO4.P
DIN & NH4.N
Denitrification
NMDS2
NMDS1
Till
Ross Till
Taylor Till
Type
Black
Orange


B
Allantoin_Utilization
Phosphoenolpyruvate_phosphomutase
P_uptake_cyanobacteria.
High_affinity_phosphate_transporter_and_control_of_PHO_regulon
Ammonia_assimilation
Cyanate_hydrolysis
Nitrate_and_nitrite_ammonification
Nitrogen_fixation
Dissimilatory_nitrite_reductase
C.N
Total.N
EC
PO4.P
NMDS2
NMDS1
Till
Ross Till
Taylor Till
Type
Black
Orange