Microbial Mat Abundance and Activity in the McMurdo Dry Valleys, Antarctica

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ABSTRACT

Primary productivity is a fundamental ecological process and an important measure of ecosystem response to environmental change. Currently, there is a considerable lapse in our understanding of primary productivity in hot and cold deserts, due to the difficulty of measuring production in cryptogam vegetation. However, remote sensing can provide long-term, spatially-extensive estimates of primary production and are particularly well suited to remote environments, such as in the McMurdo Dry Valleys (MDV) of Antarctica, where cyanobacterial communities are the main drivers of primary production. These microbial communities form multi-layered sheets (*i.e.*, microbial mats) on top of desert pavement. The cryptic nature of these communities, their often patchy spatial distribution, and their ability to survive desiccation make assessments of productivity challenging. I used field-based surveys of microbial mat biomass and pigment chemistry in conjunction with analyses of multispectral satellite data to examine the distribution and activity of microbial mats. This is the first satellite-derived estimate of microbial mat biomass for Antarctic microbial mat communities. I show strong correlations between multispectral satellite data (*i.e.*, NDVI) and ground based measurements of microbial mats, including ground cover, biomass, and pigment chemistry. Elemental (C, N) and isotopic composition (^{15}N, ^{13}C) of microbial mats show that they have significant effects on biogeochemical cycling in the soil and sediment of this region where they occur. Using these relationships, I developed a statistical model that estimates biomass (kg of C) in selected wetlands in the Lake Fryxell Basin, Antarctica. Overall, this research demonstrates the importance of terrestrial microbial mats on C and N cycling in the McMurdo Dry Valleys, Antarctica.

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GENERAL AUDIENCE ABSTRACT

Primary productivity is an essential ecological process and a useful measure of how ecosystems respond to climate change. Primary production is more difficult to measure in polar desert ecosystems where there is little to no vascular vegetation. Polar regions are also ecosystems where we expect to see significant responses to a changing climate. Remote sensing and image analysis can provide estimates of primary production and are particularly useful in remote environments. For example, in the McMurdo Dry Valleys (MDV) of Antarctica, cyanobacterial communities are the main primary producers. These microbial communities form multi-layered sheets (*i.e.*, microbial mats) on top of rocks and soil. These communities are cryptic, do not cover large areas of ground continuously, and are able to survive desiccation and freezing. All of these characteristics make assessments of productivity especially challenging. For my master's research, I collected microbial mat samples in conjunction with the acquisition of a satellite image of my study area in the MDV, and I determined biological parameters (*e.g.*, percent ground cover, organic matter, and chlorophyll-a content) through laboratory analyses using these samples. I used this satellite image to extract spectral data and perform a vegetation analysis using the normalized difference vegetation index (*i.e.*, NDVI), which determines areas in the image that contain vegetation (*i.e.*, microbial mats). By linking the spectral data to the biological parameters, I developed a statistical model that estimates biomass (*i.e.*, carbon content) of my study areas. These are the first microbial mat biomass estimates using satellite imagery for this region of Antarctica. Additionally, I researched the importance of microbial mats on nitrogen cycling in Taylor Valley. Using elemental and isotopic analyses, I determined microbial mats have significant effects on the underlying soil and nutrient cycling. Overall, this research demonstrates the importance of terrestrial microbial mats on C and N fixation in Antarctic soil environments.

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ATTRIBUTION

Chapter 2 is a manuscript in preparation for submission to *Polar Biology* in May 2019 and is co-authored with my advisor, J. E. Barrett, and collaborator Mark R. Salvatore. JEB helped to design and conduct the field work and assisted with data analysis. MRS assisted with image analysis. All co-authors contributed to manuscript revisions.

CHAPTER 1: INTRODUCTION

Primary productivity (*i.e.*, carbon fixation) and nitrogen fixation are fundamental biogeochemical processes and necessary measures of ecosystem response to global change (Running et al. 2000). In polar ecosystems and hot deserts specifically, there's a lapse in our understanding of primary productivity due to the difficulty in measuring sparse, patchy vegetation (Elbert et al. 2012). Additionally, while biogeochemical cycling has been well studied in aquatic systems, less is known about the biogeochemistry of vegetation in the transition zone between aquatic habitats and dry soils and its effects on the underlying soil and sediments. Most ecosystems have confounding factors that influence biogeochemical cycling; however, the McMurdo Dry Valleys, Antarctica is a simple system that is an ideal location to study biogeochemical cycling in these ecologically important transition zones.

The McMurdo Dry Valleys (MDV) are the largest ice-free area on the Antarctic continent of approximately 4,500 km^2 in Southern Victoria Land (Levy 2013) and consist of a polar desert landscape. The MDV are one of Earth's coldest, driest deserts with mean annual temperatures between -15 and -30°C and less than 50 mm of precipitation annually (Doran et al. 2002, Fountain et al. 2009). During the austral summers, glacial melt forms streams that flow for up to 10 weeks a year (McKnight et al. 1999). Although there are no vascular plants in the MDV, the streams and the sediment environments bordering them host diverse microbial communities. These microbial mat communities form multi-layered sheets in mats in both aquatic and terrestrial environments, consisting primarily of cyanobacteria (*Nostoc*, *Oscillatoria*, and *Phormidium*), green alga (*Prasiola*), and various diatom species, with filamentous cyanobacteria being the most abundant (Alger et al. 1997). MDV microbial mats can tolerate extreme fluctuations of freeze-thaw and dry-wet cycles (Dodds et al. 1995; Mcknight et al. 2007), and they spend winter in a desiccated, freeze-dried state and begin photosynthesizing within minutes of thawing and rehydration during the onset of stream flow (Vincent and Howard-Williams 1986; Mcknight et al. 2007). The microbial mats are different colors due to their photosynthetic and accessory pigments (McKnight et al. 1999). There are four microbial mat types in the MDV, and for simplicity they are classified by their colors: black, orange, red, and green. For my thesis, I focused on the black mats, dominated by the cyanobacteria *Nostoc* spp., and the orange mats, which are primarily the cyanobacteria *Oscillatoria* spp. Abundant moss communities, *Hennediella heimii* and *Bryum* spp., are also common near wetted stream margins and beside snow packs (Schwarz et al. 1992). While the orange mats exist mostly in the stream thalweg where flow is more consistent, the black mats are found along the wetted zone in areas not typically inundated by water (Alger et al. 1997).

The composition and physiology of MDV microbial mats have been widely studied; however, current investigation of microbial mat abundance and activity in the MDV is limited to annual surveys of aquatic mats in stream channels and benthic areas of lakes (Hawes et al. 2013, Kohler et al. 2015). The periphery of lake margins and stream riparian areas are ecologically significant transition zones, and negligible grazing (Treonis et al. 1999), lack of vascular vegetation, and minimal lateral inputs of water or organic material (Gooseff et al. 2011) make this stream-soil interface an ideal location to study microbial mat dynamics. Currently there are no systematic estimates of terrestrial productivity in the MDV, but remote sensing may provide a valuable tool for investigating the distribution and productivity of microbial mats in this region.

Remote sensing is the process of obtaining information about areas on the Earth from a distance, typically using aircraft or satellite. Spectral imaging combines spectroscopy and photography by collecting photographic image data from specific wavelength ranges that can then be spectrally analyzed. Materials on the surface of the Earth reflect or absorb specific wavelengths of the electromagnetic spectrum, depending on the composition of the materials. For example, vegetation, water bodies, and bare soil reflect and absorb different regions of the spectrum. Because of these variations in spectral signatures, image processing software can be used to process and analyze geospatial imagery for detecting and monitoring physical characteristics of the Earth. One remote sensing application in particular includes quantifying the distribution, biomass, and productivity of vegetation. Chlorophyll-a in vegetation has a unique spectral signature where it absorbs most of the light in the visible wavelength spectrum and has an abrupt change in reflectance in the near-infrared region, between 680 and 800 nm. This phenomenon was first described by Collins (1978) and is now commonly known as the “red edge”. The red edge is used in spectral analysis as the basis for vegetation indices which provide indicators for vegetation composition, photosynthetic activity, health, identification, and other biophysical and biochemical variables. Although less common, the spectral characteristics of cyanobacterial soil crusts in arid regions have been studied and correlated to chlorophyll concentration (Karnieli et al. 1999, Rodríguez-Caballero et al. 2017).

These remote sensing methods have yet to be applied with Antarctic microbial mats; however, a recent study by (Salvatore 2015) has demonstrated the biological utility of remote sensing in the Antarctic by detecting the spectral signature of chlorophyll-a within streams and wetted margins in the MDV using multispectral data from the WorldView-2 satellite (DigitalGlobe). The terrestrial microbial mats in particular show strong spectral signatures of chlorophyll-a compared to the microbial mats within stream thalwegs, where there is more of a water absorption signature in the spectral data (Salvatore 2015).

For Chapter 2 of my thesis, I confirmed the utility of multispectral WorldView-2 satellite data in detecting photosynthetic microbial mats in the MDV, and I examined the statistical relationships between NDVI and field-based observations. To estimate the spatial distribution of terrestrial microbial mats for selected sites in the Lake Fryxell Basin, I: 1) Obtained field survey data (*i.e.*, ground cover, AFDM, pigment content) of microbial mats in a variety of wetlands with high and low visually conspicuous mat cover, 2) Processed WorldView-2 multispectral satellite imagery of the Lake Fryxell Basin and derived vegetation indices, and 3) Examined correlations of the multispectral data with field survey data to develop a statistical model that estimates the biomass (kg of carbon) of microbial mats in selected wetland areas.

In addition to primary production, *i.e.*, carbon (C) fixation, nitrogen (N) fixation is also a key biogeochemical process facilitated by some cyanobacterial mats in extreme environments. The black terrestrial microbial mats, primarily *Nostoc* spp., contribute to C and N cycling in the lotic and lentic environments of the MDV (McKnight et al. 2004). While these biogeochemical processes have been studied in Antarctic aquatic ecosystems, *i.e.*, lakes and streams, less is known about these processes in the terrestrial microbial mats that occupy the transition zones between aquatic habitats and dry soils, which are highly sensitive to climate change in the McMurdo Dry Valleys (Doran et al. 2008). The MDV streams and soils are considered simple ecosystems, suggesting that physical factors may be most important in controlling biological processes in the region. For example, the soils of Taylor Valley occur on glacial tills of varying surface-exposure age and have been modified by lacustrine sedimentation thousands of years ago (Denton et al. 1989), and the waxing and waning of these lacustrine environments has significantly affected the distribution of organic matter and biota in the terrestrial environments of Taylor Valley (Burkins et al. 2000). It is crucial to understand the landscape history of the

MDV in order to understand the contemporary variation in ecological communities and ecosystem processes (Barrett et al. 2006).

The landscape-driven patterns in geomorphology of the MDV drive biogeochemical trends in the Taylor Valley soils (Burkins et al. 2000, Barrett et al. 2007). For example, Michalski et al. (2005) found that the origin of N in areas of the MDV is exclusively atmospheric, and as a result of this atmospheric deposition that has accumulated over time on glacial tills of varying surface exposure age, N has a natural west – east gradient in Taylor Valley, with it being most abundant to the west where landforms are older compared to the relatively young Ross Sea till in the east (Barrett et al. 2006, 2007). This natural N source gradient has distinct isotopic composition and could help determine the relative importance of N fixation vs. acquisition of atmospherically deposited N in microbial mat nutrition and soil N budgets.

Stable isotope signatures of ^{15}N and ^{13}C in microbial mats can provide insight into the biogeochemical cycling and physiological status of Taylor Valley microbial mats and underlying soils and sediments (*e.g.*, Kohler et al. 2018). Isotopic analysis of ^{13}C potentially provides insights about autotrophic dynamics of microbial mats, including whether they are water limited (Ehleringer and Dawson 1992), C limited (Lawson et al. 2004, Lyons et al. 2013), or have energy sources other than C fixed through photosynthesis, for example methane-based food webs (Paul et al. 2017). In terms of N, abiotic and biotic sources of N are common in the MDV due to the long surface exposure ages and N deposition and also the abundance of the N-fixing cyanobacteria *Nostoc*, and these sources can be inferred due to their distinct isotopic signatures.

For Chapter 3 of my thesis, my objectives were to: 1) Determine sources of N for terrestrial microbial mat communities in the Taylor Valley across an atmospheric depositional gradient, and 2) Assess whether microbial mats are influencing the C and N biogeochemistry of the underlying soils and sediments. I hypothesized that microbial mats further up Taylor Valley would be obtaining N from physical sources and microbial mats closer to the coast would be obtaining N through N-fixation. Microbial mats that are fixing N should have $\delta^{15}N$ values closer to 0‰, while those that are not fixing N in areas where N concentrations are naturally higher should have more depleted $\delta^{15}N$ signatures, since biological processes discriminate against heavier N (Montoya and McCarthy 1995).

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CHAPTER 2: ESTIMATING MICROBIAL MAT ABUNDANCE and ACTIVITY in the MCMURDO DRY VALLEYS, ANTARCTICA USING SATELLITE IMAGERY and GROUND SURVEYS

Co-authors: Mark R. Salvatore and J. E. Barrett; To be submitted to *Polar Biology* May 2019.

Abstract

Cyanobacterial mat communities are the main drivers of primary productivity in the McMurdo Dry Valleys, Antarctica. These microbial communities form laminar mats on desert pavement surfaces adjacent to and within glacial meltwater streams, ponds, and lakes. The cryptic nature of these communities, their patchy distribution, and their ability to survive desiccation make assessments of productivity challenging. We used satellite imagery coupled with *in situ* surveying, imaging, and sampling to systematically estimate microbial mat biomass in selected wetland regions in Taylor Valley, Antarctica. On January 19th, 2018, the WorldView-2 multispectral satellite acquired an image of our study areas, occurring within 10 days of when we surveyed and sampled seven 100 m^2 plots of abundant microbial mats for percent ground cover, ash-free dry mass (AFDM), and pigment content (chlorophyll-a, carotenoids, and scytonemin). The microbial mats were dominated by the cyanobacteria *Nostoc*, ranging from 30-70% coverage in plots. The plots contained organic matter ranging from 6.53 to 399 mg g^{-1} AFDM or 10 to 1132 g C m^{-2} microbial mat biomass. Chlorophyll-a content within the plots ranged from 0.61 to 48.5 μg g^{-1}. Scytonemin, a UV screening cyanobacterial sheath pigment, had concentrations ranging from 4.07 to 1163 μg g^{-1}. The satellite imagery was geo-referenced, atmospherically corrected, and processed using the normalized difference vegetation index (NDVI). Multispectral analyses revealed the strong absorption of visible light (~ 0.4–0.7 μm) and strong reflectance of near-infrared light (> 0.7 μm), consistent with photosynthetic materials, with average NDVI values of 0.09 to 0.28. Strong linear and logarithmic correlations of microbial mat ground cover (R^2 = 0.84), biomass (R^2 = 0.74), chlorophyll-a content (R^2 = 0.65), and scytonemin content (R^2 = 0.98) with logit transformed NDVI values demonstrate that satellite imagery can detect both the presence and key biological properties of microbial mats. Using the NDVI – biomass logarithmic relationship we developed, we estimate 21,715 kg of C (14.7 g C m^{-2}) exists in the Canada Glacier Antarctic Specially Protected Area. This is the first satellite-derived estimate of microbial mat biomass for this region of Antarctica.

Introduction

Autotrophic microbial communities are essential drivers of primary production in extreme ecosystems, such as hot and cold deserts (Elbert et al. 2012), where species of cyanobacteria, chlorophytes, lichens and moss form laminar mats or “crusts” with thicknesses ranging from millimeters to several centimeters (Prieto-Barajas et al. 2018). These biological soil crusts perform key ecological functions, including nutrient cycling and soil stabilization (Belnap 2003), which are particularly important in environments that lack vascular plants. The cryptic nature of these communities, their patchy distribution, and their ability to survive desiccation make assessments of biomass and productivity challenging, especially in polar deserts. For example, in the McMurdo Dry Valleys, Antarctica (76°30’-78°30’ S, 160-164° E), cyanobacterial mats are typically dormant for more than 10 months of the year and are sparsely distributed in terrestrial environments, with the greatest densities occurring on the margins of lakes, ponds, and streams. There are currently no systemic measurements of terrestrial production in the McMurdo Dry Valleys that are scalable beyond point level measurements of PAM fluorometry or gas exchange (Novis et al. 2007, Ball et al. 2009, Geyer et al. 2017) or that provide a record suitable for assessing interannual variation in productivity.

The McMurdo Dry Valleys (MDV) are the largest ice-free area on the Antarctic continent of approximately 4,500 km^2 in Southern Victoria Land (Levy 2013) (Figure 2.1). The MDV are one of Earth’s coldest, driest deserts with mean annual temperatures between -15 and -30°C and less than 50 mm of precipitation annually (Doran et al. 2002, Fountain et al. 2009). During the austral summers, glacial meltwater feeds streams that flow for up to 10 weeks a year (McKnight et al. 1999). These streams and the sediments and soils around them support diverse microbial communities that persist despite the extreme environment. Microbial mat communities form multi-layered sheets in mats in both aquatic and terrestrial environments in the MDV. These microbial mats consist primarily of cyanophyta (*Nostoc*, *Oscillatoria*, and *Phormidium*), chlorophyta (*Prasiola*) and bacillariophyta (various diatom species), with filamentous cyanobacteria being the most abundant (Alger et al. 1997). MDV microbial mats can tolerate extreme fluctuations of freeze-thaw and dry-wet cycles (Dodds et al. 1995; Mcknight et al. 2007). They spend winter in a desiccated, freeze-dried state and begin photosynthesizing within minutes of thawing and rehydration during the onset of stream flow (Vincent and Howard-Williams 1986; Mcknight et al. 2007).

While the composition and physiology of microbial mats have been studied, current investigation of microbial mat abundance and activity in the MDV is limited to annual surveys of aquatic mats in stream channels and benthic areas of lakes (Hawes et al. 2013, Kohler et al. 2015). Terrestrial mats occurring on the periphery of lake margins and stream riparian zones occupy ecological significant transition zones between aquatic habitats and dry mineral soils. These transition zones are ecologically important, as significant nutrient and biotic exchange occurs here (Ayres et al. 2007, Barrett et al. 2009). Negligible grazing (Treonis et al. 1999), lack of vascular vegetation, and minimal lateral inputs of water or organic material (Gooseff et al. 2011) in the MDV make this stream-soil interface an ideal location to research microbial mat dynamics.

Remote sensing and image analysis can provide long-term, spatially-extensive estimates of biomass and primary production and are particularly well suited to the study of remote environments. These techniques work best when features associated with primary production are surficial and readily visible from above, such as in the MDV where cyanobacterial communities are the main drivers of primary production. Remote sensing can be utilized for the determination of vegetation abundance and activity with one such means being the normalized difference vegetation index (NDVI), which evaluates the relationship of reflectance between 680 and 800 nm where photosynthetic materials exhibit a strong increase in reflectance. This is caused by chlorophyll-a in vegetation, which has a unique spectral signature where it absorbs most of the light in the visible wavelength spectrum, while scattering and reflectance by vegetation cell walls result in strong reflection signatures at near-infrared regions. This strong increase in reflectance, also known as the “red edge” (Collins 1978), is used in spectral analysis as the basis for vegetation indices, such as the NDVI. These indices have been used to derive fundamental vegetation properties, including vegetation composition, photosynthetic activity, health, identification, and other biophysical and biochemical variables, most notable in forestry and agricultural applications.

In the Arctic, satellite-derived NDVI has been combined with field survey data to quantify the abundance and biomass of tundra vegetation and mosses in the Arctic (Edwards and Treitz 2017, Hogrefe et al. 2017, Berner et al. 2018). Although less common, the biomass of cryptic cyanobacterial soil crusts in arid regions have also been quantified using this approach (Karnieli et al. 1999; Rodríguez-Caballero et al. 2017). These remote sensing methods have yet to be applied to Antarctic microbial mat communities. However, Salvatore (2015) demonstrated the biological utility of remote sensing in the Antarctic by detecting the spectral signature of chlorophyll-a from terrestrial microbial mats in the MDV using multispectral data from the WorldView-2 satellite (DigitalGlobe). Microbial mats inundated by water within the main channels of streams or in lake "moats" do not exhibit as prominent of a spectral signature of chlorophyll due to the absorption of water; however, the terrestrial cyanobacterial mats exhibit strong spectral signatures (Salvatore 2015). Since the MDV is a simple system lacking vascular vegetation, remote sensing is particularly useful here for isolating microbial mats.

In this study we confirm the utility of multispectral WorldView-2 satellite data in detecting photosynthetic microbial mats in the MDV, and we examine the statistical relationships between NDVI and field-based observations. To estimate the spatial distribution of terrestrial microbial mats for selected sites in the Lake Fryxell Basin, we: 1) Obtained field survey data (*i.e.*, ground cover, AFDM, and pigment content) of microbial mats in a variety of wetlands with high and low visually conspicuous mat cover, 2) Processed WorldView-2 multispectral satellite imagery of the Lake Fryxell Basin and derived vegetation indices, and 3) Examined correlations of the multispectral data with field survey data. By quantitatively linking field survey data and multispectral satellite data, we have developed a statistical model that estimates the biomass in kg of C of microbial mats in the Canada Glacier Antarctic Specially Protected Area (ASPA), the Green Creek and Bowles Creek wetland area, and a portion of the lower reach of McKnight Creek (Figure 2.8-2.10). These estimates represent the first attempt to use remote sensing data to derive such detailed microbial properties in the McMurdo Dry Valleys.

Methods

Study Site

All of the study sites are located within Taylor Valley, Antarctica where several glaciers feed streams in the austral summer that flow to perennially ice-covered Lake Fryxell (Figure 2.1). The MDV microbial mats are generally described by four mat types (black, orange, green, and red) based on their appearance, dominant taxa, and habitat preference within the stream (Alger et al. 1997). Located within distinct zones based on flow regime and soil/sediment water content, some mats exist mostly in the stream thalweg where flow is most consistent, while the cyanobacterial "black mats" are found along wetted margins not commonly inundated by stream flow where moisture is supplied by the hyporheic zone (Alger et al. 1997). These terrestrial microbial mats are dominated by the cyanobacteria *Nostoc* spp. While microbial mat abundance is inherently linked to the availability of water in MDV streams, it is also controlled by the characteristics of the streambeds (McKnight et al. 1999). This includes not only the stream gradient, but also the size and arrangement of the streambed particles. McKnight et al. (1999) found that microbial mats are most common in medium-gradient streams where the streambed consists of desert pavement with stable cobble composition. This information aided us in determining which streams would be most appropriate for this study.

We selected streams that had characteristics suitable for microbial mat growth and were already known to represent a range in the density of microbial mats that are representative of Taylor Valley (Alger et al. 1997, McKnight et al. 1999). Six 100 m^2 plots were established on the western side of Lake Fryxell, five of which are beside Canada Stream which is fed by the Canada Glacier. This area is within the Canada Glacier Antarctic Specially Protected Area (ASPA) (Figure 2.8), which was designated by the Antarctic Treaty System in 2002 as a significant biologically active area of great scientific value as one of the most productive and biologically diverse areas in the MDV. Glacial melt flows over a gently sloping area of approximately 100–200 m^2 before entering the Canada Stream channel; melt from the northern end forms small channels before flowing into the main channel, while melt from the southern end drains into a pond before entering the main channel (Conovitz et al. 1998). One plot is located in the wetted area north of the pond referred to as “the upper flush” and four others are located in the wetted area south of the pond, “the lower flush”, which are both biologically rich with abundant cyanobacteria, algae, and moss (Schwarz et al. 1992, Alger et al. 1997). On the southern side of Lake Fryxell, one plot was also established at Green Creek, which is also fed by the Canada Glacier and located beside Bowles Creek in an area we’ve classified as the Green Creek and Bowles Creek wetlands (Figure 2.9). The plot was positioned downstream of a melt pond beside the glacier in a shallow gradient area with visible microbial mat cover. An additional plot was established on the eastern side of Lake Fryxell beside McKnight Creek (Figure 2.10), which is fed by the Commonwealth Glacier. Compared to the six other plot locations at Canada Stream and Green Creek, the McKnight Creek plot is much further downstream from its source glacier and has a less stable, sandier substrate, poorly developed desert pavement, and patchier and less abundant microbial mats. Plot locations among each of the streams were selected in areas that were not inundated by water to ensure that the spectral signature was not dominated by water signatures.

Field Surveys

Locations of visually conspicuous microbial mats outside of stream channels were selected for plots beside Canada Stream, Green Creek, and McKnight Creek (Table 2.1). On January 9th and 10th 2018, four 100 m^2 plots (Canada Stream-1, Canada Stream-2, Canada Stream-3, and Canada Stream-4) were established adjacent to one another in the most productive area of the Canada Stream ASPA, the lower flush (Schwarz et al. 1992), using a tape measure (-77° 36′ 58.14″ S, 163° 2′ 28.97″ E). In the upper flush of the Canada Stream ASPA (-77° 36' 47.76" S, 163° 1' 52.54" E), a fifth 100 m^2 plot (Canada Stream-5) was established on January 11th, 2018. Two additional 100 m^2 plots were established beside McKnight Creek (-77° 35' 50.99" S, 163° 16' 10.15" E) and Green Creek (-77° 37' 30.29" S, 163° 3' 0.62" E) on January 12th and 25th, 2018, respectively.

Hemispherical photos of ground cover along with position data were taken every 5 m at each of the seven plots. The plot locations were marked using a high precision global navigation satellite system (GNSS) receiver (Septentrio ALTUS APS3G) which communicated with a GNSS reference receiver (Trimble NetR8) located at the Lake Fryxell Camp. The receiver unit used real time kinematic (RTK) positioning to gather locations with centimeter level accuracy. The hemispherical photos taken in the field were analyzed for microbial mat cover using ImageJ, an image analysis software. By converting the photos to binary black and white images, the software distinguished pixels representing microbial mats (black) from those representing bare soil or rocks (white). Each pixel was then classified as either white or black, and an estimate for percent cover was quantified using a histogram.

Using a random stratified sampling design, we surveyed and sampled 2 – 1 m^2 subplots within each of the first four Canada Stream plots, with location of sub-plots depending on the distribution of standing water in the plot. Point intercept surveys of ground cover and hydrological status were completed at 5 random numbers between 0 and 100 cm (*i.e.*, north to south at 40 and 80 cm, and west to east at 20, 60, and 100 cm) in each survey sub-plot to determine the 5 sampling locations for each sub-plot. Samples from each sub-plot were composited for a total of 10 samples from each 100 m^2 plot. The Canada Stream-5, McKnight

Creek, and Green Creek plots were surveyed and sampled at 9 locations every 5 m apart. At each of the sampling points within the 7 plots, we visually assessed the hydrologic status (*i.e*., inundated, saturated, wet or dry) and the ground cover type (*e.g*., soil, black mat, green moss, *etc*.). Microbial mats were each collected in 60 mL amber Nalgene bottles at the 9-10 sample points in each plot. The top layer of soil was collected for the areas that did not have visible mat, following the methods described in Barrett et al. (2004). All samples were kept cool in ice chests and transported back to McMurdo Station for analysis.

Laboratory Analysis

The microbial mat samples were stored in a freezer at -20°C at Crary Laboratory in McMurdo Station and then shipped to Virginia Tech in February 2018. Chlorophyll-a concentration was measured on the microbial mat samples with a spectrophotometer (Shimadzu UV-1601) at Virginia Tech on May 29th & 31st, 2018 using a protocol that corrects for scytonemin concentration, an accessory sheath pigment previously reported for this area (Vincent et al. 1993). Throughout the process, care was taken to avoid exposing the samples to light as chlorophyll-a is degraded by exposure to light. First, the samples were dried at 105°C for 24 hrs and one-half g of the sieved samples were added to 10 mL of 90% unbuffered acetone to extract the chlorophyll-a. The samples were then left overnight in a dark room for complete chlorophyll extraction. After centrifuging for 10 minutes at 4000 RPM, they were analyzed on the spectrophotometer using 10 mL cuvettes at 750, 663, 490, and 384 nm. The absorbances contributed by chlorophyll-a, carotenoids, and scytonemin were quantified at 663, 490, and 384 nm, respectively, using the trichromatic equations outlined in Garcia-Pichel and Castenholz (1991). The pigment concentrations were then determined using the Beer-Lambert Law with the extinction coefficients also outlined in Garcia-Pichel and Castenholz (1991).

The microbial mat samples were measured for ash-free dry mass (AFDM) by weighing approximately 0.25 g of oven-dried sample, combusting at 550°C for 60 min using a muffle furnace, and reweighing after cooling in a desiccator. Given the extremely low clay content of soils in this region (Barrett et al. 2006a), the rehydration of clays is assumed negligible so the methods did not include rewetting samples to account for the hydration of clays. Microbial mat biomass (mg organic matter (OM) cm^{-2}) was estimated from AFDM (mg g^{-1}) using bulk density measurements made at each site with a 2.27 cm^2 coring device. Similarly, pigments were also expressed on an areal basis (μg cm^{-2}) using bulk density measurements. To correlate spatially with NDVI, biomass and pigments were also scaled by percent cover. The areal-scaled biomass was then converted to biomass in g C m^{-2} by assuming organic matter is 53% C by weight.

Satellite Imagery Collection & Analysis

WorldView-2 (DigitalGlobe) multispectral satellite images of the Lake Fryxell Basin were collected during January 2018 to coincide with the timing of field surveys and sample collection as closely as possible. While multiple images were acquired during this time, only one image was cloud-free and was taken January 19, 2018. This image was georeferenced using ground control points and obtained from University of Minnesota's Polar Geospatial Center (PGC) through a cooperative agreement between the NSF and National Geospatial-Intelligence Agency (NGA). The image was subsequently processed to atmospherically corrected surface reflectance using the dark object subtraction-regression (DOS-R) and other methods in Salvatore et al. (2014) and Salvatore (2015) using the Environment for Visualizing Images (ENVI, Harris Geospatial) software. We then calculated the common normalized difference vegetation index (NDVI) parameter in ENVI, which is a common vegetation index used for determining whether an image contains photosynthesizing vegetation (Tucker 1979). NDVI was calculated as:

$$\mathrm{NDVI} = \frac{\rho_{\mathrm{NIR}} - \rho_{\mathrm{Red}}}{\rho_{\mathrm{NIR}} + \rho_{\mathrm{Red}}}$$

where ρ_{NIR} and ρ_{Red} represent the spectral reflectance measurements acquired in the near-infrared (770–895 nm, band 7) and red (630–690 nm, band 5) regions, respectively.

The plot GPS coordinates from the field were measured using GCS WGS 1984. To match the coordinate system of the satellite image, we re-projected the plot coordinates from GCS WGS 1984 to Polar Stereographic using ArcMap (ESRI) to open the NDVI product image and shapefile of the plot coordinates together. Using ArcMap, we converted the image raster file to points and then selected the pixels whose centroids fell within the 100 m^2 plot boundaries. Each plot corresponds to approximately 14-17 pixels with unique NDVI values. NDVI values of each selected pixel were exported and averaged to be compared to the survey data.

Statistical Analysis

Using R Statistical Software version 1.0.153, box plots were created for the field survey, chemistry, and NDVI data for each of the seven plots to visualize the variation within and among plots (R Core Team 2018). One-way analysis of variance (ANOVA) tests were performed on each data set to determine whether the means were statistically different among plots, and Tukey's Honest Significant Difference (TukeyHSD) tests were performed to determine which plots were statistically different from one another. To meet the assumptions for linear regression, NDVI values were logit transformed from proportional NDVI data to a continuous variable (Warton and Hui 2011). We performed a correlation analysis using the average logit(NDVI) plot values and the field survey and chemistry data (*i.e.*, AFDM and pigments) averaged and scaled using the percent cover of mats in each of the plots. Normality of residuals were confirmed visually using QQplots in R, and those variables with non-linear distribution of residuals were fit with a non-linear model, *e.g.*, logarithmic. Linear and logarithmic regressions of means between scaled plot data and logit(NDVI) values were fit in R.

To extrapolate total microbial mat biomass (g C m^{-2}) from the Canada Stream, Green Creek and Bowles Creek wetland area, and a portion of the lower reach of McKnight Creek, boundaries were defined in ENVI. The Canada Glacier ASPA boundaries were used to define the area for our Canada Stream extrapolations (Figure 2.8), while the Green Creek and Bowles Creek wetland area was defined based upon using the Canada Glacier and Lake Fryxell margin as boundaries (Figure 2.9). The delta of McKnight Creek had noticeably higher NDVI values, due to the proximity of Lake Fryxell and moat/lake microbial mats. Since this area is not comparable to the unstable, lower coverage substrate typical of McKnight Creek, the boundary was defined as the lower reach of McKnight Creek excluding the edge of the lake (Figure 2.10). NDVI values were then extracted from these areas in ENVI and logit transformed. Five NDVI values were excluded from the Canada Glacier ASPA dataset that were anomalously high (*i.e.*, between 0.45 and 0.64) due to manmade objects in the scene. The exponential relationship between logit(NDVI) and percent cover scaled biomass (g C m^{-2}) was applied to NDVI values > 0.09 (a vegetation threshold selected based on the average NDVI of our lowest coverage site, Green Creek). Biomass was quantified per pixel (5.95 m^2) and then summed together for a total biomass inventory in kg C at each of the sites.

Results

Field Survey Data

There was high density of microbial mat cover and organic matter content among all plots relative to typical dry soil surfaces that lack visual mat cover (*e.g.*, Burkins et al. 2000, Barrett et al. 2006). Black mat, which we report as *Nostoc,* was the majority of this cover, representing > 85% of microbial mat present in our ground surveys, and the remaining represented by mixed moss, likely *Bryum* (Schwarz et al. 1992), and epiphytic *Nostoc* communities. Plots were selected outside the main channels or thalwegs and less than 25% of plot sampling areas were inundated, *i.e.*, standing water, though a majority were near saturation. In the Canada Stream plots, 63% were wet to saturated with the remaining portion inundated with standing water. Percent microbial mat cover ranged from 33 to 85%, with the highest coverage in the Canada Stream "flush" areas and the lowest at the Green Creek and McKnight plots (ANOVA, df = 6, F = 14.31, $p < 0.0001$) (Table 2.2, Figure 2.2A). Organic matter content ranged from 6.53 to 399 mg AFDM g^{-1} (Figure 2.2B), with bulk densities of *Nostoc* and mixed moss and *Nostoc* mats of 0.64 to 0.81 g cm^{-2}. The Canada Stream plots had the overall highest biomass of microbial mats averaging 231–711 g C m^{-2}, while Green Creek and McKnight Creek had the lowest microbial mat biomass with averages of 69 +/- 52 g C m^{-2} and 144 +/- 113 g C m^{-2}, respectively (Table 2.3).

Chlorophyll-a, scytonemin, and carotenoid concentrations varied significantly among the seven study plots (ANOVA, df = 6, F = 4.35, $p < 0.01$; F = 5.04, $p < 0.001$; F = 5.01, $p < 0.001$, respectively) (Table 2.2): chlorophyll-a concentration ranged from 0.61 to 48.52 µg g^{-1}, scytonemin concentration ranged from 9.39 to 1163 µg g^{-1}, and carotenoid concentration ranged from 0.25 to 119.9 µg g^{-1} (Figure 2.3). McKnight Creek had the greatest average chlorophyll-a concentration of 24.44 µg g^{-1}, surpassing even the high-density Canada Stream plots (Figure 2.3A). Scytonemin concentrations were over an order of magnitude greater than the other pigment concentrations and highly variable, especially in the Canada Stream lower flush plots where scytonemin concentrations were highest (averaging 494.7–700.3 µg g^{-1}) (Figure 2.3B). One sample from Canada Stream-2 had extremely high pigment concentrations overall, with for example chlorophyll-a greater than 6 σ of the mean chlorophyll-a concentrations for all observations. Although this data point is not believed to be instrumental error, it was removed from the pigment box plots and the correlation analyses, because it was so far outside the centroid of the distribution and skewed all analyses.

NDVI Relationships

NDVI values extracted from the image at pixels determined to correspond with our plots ranged from 0.0719 to 0.365 with the highest values and the most variability seen in Canada Stream plots 1-4 (Figure 2.4). Although McKnight Creek had the highest average chlorophyll-a concentration, it had the second to lowest average NDVI value, 0.0964. Overall, the most productive sites (*i.e.*, Canada Stream) were the most variable in terms of AFDM, pigment concentration, and NDVI indices, but also had the highest % cover of microbial mats (Figure 2.2B, 2.3, 2.4).

Each of the biological parameters were significantly correlated to the multispectral data. Percent cover was significantly correlated to logit(NDVI) ($R^2 = 0.84$, $p = 0.004$, logit(NDVI) = 0.0169 * cover - 1.66), and percent cover scaled microbial mat biomass in g of C m^{-2} had a significant logarithmic relationship with logit(NDVI) ($R^2 = 0.74$, $p = 0.013$, logit(NDVI) = 0.283 * ln(biomass) - 2.24) (Figure 2.5). Percent cover scaled chlorophyll-a was significantly correlated to logit(NDVI) ($R^2 = 0.65$, $p = 0.028$, logit(NDVI) = 5.26 * chlorophyll - 1.07), and percent cover scaled scytonemin had the most significant relationship with logit(NDVI) ($R^2 = 0.98$, $p < 0.0001$, logit(NDVI) = 0.197 * scytonemin - 1.12) (Figure 2.6).

Upscaling

Using the observed relationship between biomass and NDVI, we predicted and extrapolated microbial mat biomass from NDVI to our respective study areas using the following equation: biomass = $1450 * e^{2.61 * \mathrm{logit(NDVI)}}$ ($R^2 = 0.74$, $p = 0.013$) (Figure 2.7). We estimated 21,715 kg of C in the Canada Glacier ASPA, an area of approximately 1,470,000 m^2 (Figure 2.8). This results in an average of 139 g C m^{-2} for vegetated areas of the Canada Glacier ASPA (*i.e.*, pixels > 0.09 NDVI). There was an estimated 2,115 kg of C in the Green Creek and Bowles Creek wetland area beside the Canada Glacier, an area of approximately 199,100 m^2 (Figure 2.9), yielding an average of 131 g C m^{-2} for vegetated areas. The lower reach of McKnight Creek, an area of 58,290 m^2, had a biomass estimate of 435 kg of C and an average of 114 g C m^{-2} for vegetated areas (Figure 2.10).

Discussion

Dense microbial mat communities are visible in the red and near-infrared wavelengths in satellite imagery of Taylor Valley, Antarctica. Above ~ 50% ground cover microbial mat communities in the vicinity of Canada Glacier (*i.e.*, Canada Stream and Green Creek sites in this study) returned NDVI values above 0.1, a value often used as a heuristic cut-off between barren areas and active vegetation. At the plot level, we have demonstrated that NDVI values are significantly correlated to *in situ* biological parameters of microbial mats in glacial wetland areas. We also present the first inventory estimates of C content in selected wetlands and stream regions: the Canada Glacier ASPA, Green Creek and Bowles Creek wetland area, and the lower reach of McKnight Creek.

Microbial Mat Abundance

Our results show high coverage of microbial mats in the Canada Stream flush areas (averaging 57-75% cover), agreeing with previous studies by Schwarz et al. (1992) and Alger et al. (1997) (Figure 2.2A). The plot location at McKnight Creek had a low to moderate cover of microbial mat, 43%, while our plot at Green Creek had the lowest cover, 37% (Figure 2.2A). McKnight et al. (1999) found that streams with stable, well-developed desert pavement, *e.g.*, Canada Stream and Green Creek, hosted the densest mats in Taylor Valley. In our study, McKnight Creek represents the low end of this spectrum, with unconsolidated sandy sediments constituting the majority of the plot surface. Previous studies have reported high density of microbial mats within the thalweg and riparian zone at Green Creek (Alger et al. 1997); however, the area we selected to establish the plot was on the stream margins where mats are not as abundant. This was to avoid surveying inundated areas, since currently there is little information regarding how water depth affects microbial mat spectral signatures in the MDV.

There are few scalable estimates of organic matter from the MDV literature for microbial mat biomass, but a previous vegetation study of the Canada Glacier flush areas where mixed moss and microbial mats occur reported unscaled biomass values of 95–125 mg OM cm^{-2} (Schwarz et al. 1992). Our average scaled biomass estimates for the Canada Glacier flush plots, 231–711 g C m^{-2}, correspond to unscaled biomass estimates of 69–180 mg OM cm^{-2}, which are comparable to those reported by Schwarz et al. (1992). The range of microbial biomass that we found of 69 g C m^{-2} at Green Creek to 711 g C m^{-2} at Canada Stream bracket values reported by

Moorhead et al. (2003) of 257 g C m^{-2} from organic matter cover on sediments and soils adjacent to Parera Pond, on the south side of Taylor Valley. In general, our results are intermediate between estimates of lake benthic mats at the high end, and lower mat biomass on the margins of small melt-water ponds and ephemeral streams in Taylor Valley.

Pigments

While sites in the Canada Glacier ASPA had the most consistently high chlorophyll-a content and the greatest NDVI values, the McKnight Creek plot had the overall highest concentration of chlorophyll-a on average, 24.44 μg g^{-1} (Figure 2.3A). However, McKnight Creek also had the most variation in chlorophyll-a concentrations (Figure 2.3A), among the lowest percent cover of microbial mats and thus, on an areal basis, significantly lower chlorophyll-a mass than the Canada Stream sites (Table 2.2, 2.3). It is notable that microbial mats at McKnight Creek occur at lower cover and biomass but appear to be highly active, with autotrophic indices (*i.e.*, Chl-a:AFDM) greater than those at Canada Stream (*i.e.*, 0.32 compared to 0.15 average for the flush). Based on these results and that McKnight Creek has less stable substrate consisting of sand rather than cobble observed at the other sites, there is likely a higher turnover of microbial biomass due to shearing stress at McKnight Creek. It is possible that these are younger mats in comparison to the microbial mats at Canada Stream and Green Creek, where the plots were in a more stable environment close to the source glacier with consistent but low flow and with low potential for shearing of microbial mats.

Our pigment analysis also indicates high concentration of scytonemin among the plots (Figure 2.3B). Scytonemin is a cyanobacterial sheath pigment and is commonly found in terrestrial cyanobacteria in extreme environments. Scytonemin is a “microbial sunscreen” as it has an absorption spectrum with a maximum absorbance in the near ultraviolet, allowing it to screen the cyanobacterial cells from damaging UV radiation (Garcia-Pichel and Castenholz 1991). In acetone, scytonemin has an absorption maximum at 384 nm, which was used in the trichromatic equations for determining pigment concentrations. Scytonemin has been found in cyanobacterial mats, desert biocrusts, and lithic environments (Abed et al. 2010, Vítek et al. 2014), and Vincent et al. (1993) reported extremely high concentrations in the MDV (~ 10 times that of chlorophyll-a) at Canada Stream. Vincent et al. (1993) found that the microbial mats were stratified with scytonemin and other sheath pigments enriched in upper layers of the mats, while the highest concentrations of chlorophyll-a were found in lower layers. Vincent et al. (1993) refers to this area as the "deep Chla maximum" where the chlorophyll-a is most protected by UV radiation by the surface layer of scytonemin and potentially other light-screening pigments.

While all the microbial mat samples from our study have detectable concentrations of scytonemin, the Canada Glacier lower flush area (*i.e*., Canada Stream 1-4) have the highest concentrations (ANOVA, df = 6, F = 5.04, $p < 0.001$) (Figure 2.3B). Average scytonemin concentrations for the Canada Glacier lower flush sites ranged from 495–700 μg g^{-1}, or 400–566 μg cm^{-2}, and are in the same range as values reported by Vincent et al. (1993), 425 μg cm^{-2}, for black microbial mats sampled at the delta of Canada Stream. Because these plots are located adjacent to the Canada Glacier in a wetland area where they are less likely to scour, the microbial mats existing here appear to be active and stable with multiple years of accumulation. The other plots are in areas of more consistent stream flow, where the microbial mats may be more ephemeral and younger with less time to have accumulated biomass and accessory pigments. Further work on the perennial nature of these microbial mat ecosystems in stable wetland environments could shed light on the importance of scytonemin and other "sunscreen" pigments to the spectral dynamics of these environments and their importance to energy balance, UV protection, and C budgets.

Scaling Ground-Based Observations to Orbital Spectral Data

The remotely determined NDVI values for the Canada Stream lower flush area (*i.e*., Canada Stream 1-4) were all above 0.2 and were the highest NDVI values detected in our study (Figure 2.4). NDVI values for Green Creek and McKnight Creek were below 0.1 (Figure 2.4). In typical remote sensing applications, an NDVI value of 0.1 or lower is usually interpreted as unproductive ground, barren rock or sand for example, and NDVI values between 0.2 and 0.5 are considered low biomass vegetation (*e.g.*, shrub and steppe vegetation). Although the NDVI averages for Green Creek and McKnight Creek are below 0.1, we are confident that the spectral signatures are in fact detecting microbial mat presence at these sites because bare soil in the regions surrounding the study areas had NDVI of even lower values of 0.06–0.07. The detection of cryptic, patchy microbial mats is not anticipated to be comparable to typical uses of NDVI vegetation detection of forests, crops, *etc*. Since this is the first study to confirm microbial mat detection in Taylor Valley via remote sensing and vegetation indices, we don't have limits of vegetation detection to compare our values to. Based on our results however, 0.09 was used as the threshold for vegetation detection in this analysis, which corresponds to the lowest NDVI average detected in the Green Creek plot where low, but significant, biomass of microbial mats was found, and where previous studies have reported active and diverse microbial mat communities (Alger et al. 1997, Esposito et al. 2006, Stanish et al. 2011, Kohler 2015).

Percent cover and microbial mat biomass were both significantly correlated with logit(NDVI) (Figure 2.5), notably higher than the correlation between chlorophyll-a and logit(NDVI) (Figure 2.6A), which suggests that the NDVI signature is driven more by biomass and ground cover than chlorophyll activity. This is supported by the strong linear correlation of scytonemin with logit(NDVI) ($R^2 = 0.98$, $p < 0.0001$) (Figure 2.6B). The darkening at visible wavelengths by scytonemin is equally, if not more, detectable in the NDVI parameter as the absorption of chlorophyll-a. These results (*i.e*., scytonemin has a stronger correlation with logit(NDVI) than chlorophyll-a does) appear to demonstrate how scytonemin is shielding underlying chlorophyll-a. While scytonemin is an accessory pigment and not involved in C fixation, its darkening at visible wavelengths and its strong reflection at NIR wavelengths was the most detectable signal in the spectral data and could be a useful indicator of perennial microbial mat biomass in satellite imagery.

These results demonstrate the utility and limitations of this method for examining cyanobacterial mat abundance and activity in the MDV. For example, the strong correlations of NDVI with percent cover, biomass, and scytonemin demonstrate that WV-2 imagery is highly effective at detecting and estimating the biomass of dense perennial microbial mat communities. However, the weaker correlation between chlorophyll-a and NDVI, driven by the anomalously high chlorophyll-a concentrations but low NDVI signals at McKnight Creek, point to the difficulty of using remote sensing to characterize productivity for microbial mat communities with patchy cover and/or low biomass. The microbial mat communities at McKnight Creek are clearly different from the other sites we examined in this study (*i.e*., low organic matter in combination with high chlorophyll-a), likely due to differences in stream channel morphology, substrate, and possibly the longevity of microbial mats. Additionally, the stronger correlation with scytonemin than with any other variable suggests that additional investigation of the spectral properties of these communities may inform new approaches of characterizing the distribution and activity of vegetation than traditional NDVI approaches. Although NDVI does not necessarily require chlorophyll-a correlations to detect biomass, shown here by the strong correlation between scytonemin, there are other "red-edge" approaches that might be more effective at detecting microbial mat *activity* through stronger chlorophyll-a correlations (Zhu et al. 2017).

Using NDVI to Estimate Carbon Inventories

Soils represent the vast majority of the McMurdo Dry Valley landscape. For example in Taylor Valley, soils occupy 105 km^2, followed by lakes (4.7 km^2), and streams (0.2 km^2) (Burkins et al. 2001). The majority of Taylor Valley soils are arid and do not typically have visible organic matter accumulations. For example, microbial mats and moss beds are found within and near streams and lakes; however, soils host fully functioning food webs and ecosystem processes even in some of the most arid environments (Adams et al. 2006, Barrett et al. 2006b, Lee et al. 2019). The majority of the organic C in Taylor Valley soils was thought to have originated from sediments deposited by previous high stands of pro-glacial lakes (Burkins et al. 2000). Burkins et al. (2001) estimated Taylor Valley lakes have 1250 g C m^{-2}, streams have a maximum of 600 g C m^{-2}, and soils have 150 g C m^{-2}, representing approximately 27%, 0.5%, and up to 72% of the total organic C in Taylor Valley when scaled to total ground cover, respectively. Our plot level averages for C content are comparable to Burkins et al. (2001) with Green Creek representing the lower end at 69 g C m^{-2} and the Canada Glacier lower flush plots representing the higher end at 242–711 g C m^{-2} of these stream biomass estimates.

Extrapolating from our biomass model (Figure 2.7), we estimated 21,715 kg of C in the Canada Glacier ASPA (Figure 2.8) and an average of 139 g C m^{-2} for vegetated areas (*i.e.*, pixels > 0.09 NDVI), which is surprisingly low compared to the values presented in Burkins et al. (2001) (*i.e.*, 600 g C m^{-2} for streams and 150 g C m^{-2} for soils), since the ASPA is considered one of the most biologically active sites in Taylor Valley. However, arid soils make up the majority of the ASPA area, and these areas were not included in previous studies of stream mats, organic matter, or C inventories (Schwarz et al. 1992, Alger et al. 1997). In the Green Creek and Bowles Creek wetland area (Figure 2.9), we estimated 2,115 kg of C, which yields an average of 131 g C m^{-2} for vegetated areas and is greater than that measured at the low coverage plot itself beside Green Creek, 69 g C m^{-2}. The lowest C estimate, 435 kg of C, was of the lower reach of McKnight Creek (Figure 2.10) and had an average of 114 g C m^{-2} for vegetated areas. The results from this extrapolation analysis are the first in this region of Antarctica using satellite imagery to estimate microbial mat biomass, and while these satellite derived estimates are unverified with ground-based spectral measurements, these values will be revisited with ongoing work. Particularly, there's limitation in extending these calculations to soils when the low-end NDVI relationships haven't been validated yet.

These results suggest that while stream riparian and glacial wetland microbial mat communities are hot-spots of organic matter and biodiversity, as reported by others (Schwarz et al. 1992, Geyer et al. 2013, 2014, 2017), satellite imagery is detecting significant stocks of organic matter even outside of stream channels. While our estimates don't significantly change previous C inventory exercises, they do point to ways in which improving the low end of NDVI detection could open up estimates of C in low-flow, or no-flow environments not previously considered in earlier accounts. Indeed, our NDVI-derived biomass estimates suggest that low productivity environments may have more C overall than the highly productive areas in the Canada Stream ASPA and other riparian environments. These results should be interpreted cautiously as NDVI values on the low end of these regression models are likely near the limits of biotic detection. However, this remote sensing application for detecting and estimating microbial mat abundance and activity, once validated, could be scaled to provide inventories of terrestrial C pools for the whole Lake Fryxell Basin, Taylor Valley, and potentially the entirety of the McMurdo Dry Valleys. Our continuing research is working towards the creation and validation of a remote sensing tool that will allow us to systematically estimate the distribution and activity of terrestrial microbial mats in the MDV. Future work will aim to relate climatic events (*e.g.*, high flow events) from the past (using archived satellite imagery) to determine how microbial mats respond to inter-annual climate variation and also potentially forecast how these primary producers may be affected in the future by a changing climate.

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Table 2.1. Locations where plots were established, including a qualitative comparison of their visual algal abundance and stream area stability.

Plot Location	Latitude	Longitude	Visual Algal Abundance	Stream Stability
Canada Stream-1	-77° 36' 58.12"	163° 2' 27.92"	high	moderate-gradient, stone pavement
Canada Stream-2	-77° 36' 57.92"	163° 2' 29.10"	high	moderate-gradient, stone pavement
Canada Stream-3	-77° 36' 58.37"	163° 2' 28.85"	high	moderate-gradient, stone pavement
Canada Stream-4	-77° 36' 58.17"	163° 2' 30.03"	high	moderate-gradient, stone pavement
Canada Stream-5	-77° 36' 47.76"	163° 1' 52.54"	high	moderate-gradient, stone pavement
Green Creek	-77° 37' 30.29"	163° 3' 0.62"	moderate	shallow-gradient, stone pavement
McKnight Creek	-77° 35' 50.99"	163° 16' 10.15"	low	shallow-gradient, sandy

Table 2.2. Degrees of freedom, F-values, and p-values from one-way ANOVA tests and plot comparisons of Tukey's Honest Significant Difference tests of percent cover, AFDM, chlorophyll-a, scytonemin, carotenoid, and NDVI data, where "CAN" refers to Canada Stream, "GRN" Green Creek, and "MCK" McKnight Creek.

	ANOVA			TukeyHSD (p < 0.05)
	df	F-value	p-value	Plot Comparison
Percent Cover	6	14.31	< 0.0001	CAN 1-5 > GRN, MCK
AFDM	6	4.14	0.00166	CAN 2 > GRN, MCK
Chlorophyll-a	6	4.35	0.00109	MCK > CAN 5, GRN
Scytonemin	6	5.04	0.00032	CAN 2-4 > GRN
Carotenoid	6	5.01	0.00034	CAN 2-4 > GRN
NDVI	6	70.01	< 0.0001	CAN 1-4 > GRN, MCK & CAN 5 > GRN

Table 2.3. Biomass in mg organic matter cm^{-2} and chlorophyll-a and scytonemin in μg cm^{-2} shown for the Canada Stream, Green Creek, and McKnight Creek plots expressed on an areal basis using the bulk density estimates. Data shown were also scaled by % cover to correlate spatially with NDVI.

						Scaled by % Cover		
	Bulk Density (g cm^{-2})	% Cover	Biomass (mg OM cm^{-2})	Chlorophyll-a (μg cm^{-2})	Scytonemin (μg cm^{-2})	Biomass (g C m^{-2})	Chlorophyll-a (g m^{-2})	Scytonemin (g m^{-2})
Canada Stream-1	0.81	66	69	10.8	400	242	0.071	2.65
Canada Stream-2	0.81	75	180	17.4	447	711	0.129	3.33
Canada Stream-3	0.81	63	102	16.6	566	342	0.105	3.58
Canada Stream-4	0.81	66	119	13.9	500	414	0.092	3.30
Canada Stream-5	0.81	57	76	6.1	252	231	0.035	1.45
Green Creek	0.75	37	35	5.6	144	69	0.021	0.53
McKnight Creek	0.64	43	63	15.7	232	144	0.068	1.00

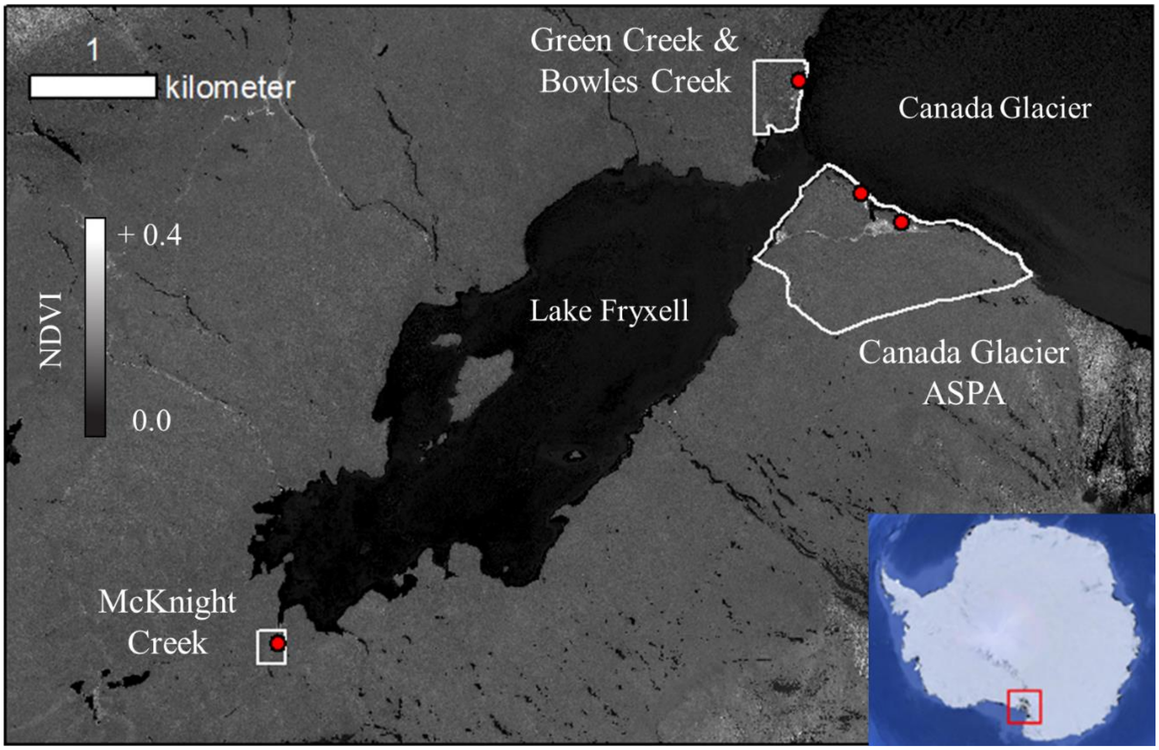

Figure 2.1. NDVI image of the Fryxell Basin with red pins denoting the 7 plot locations (Canada Stream, Green Creek, and McKnight Creek) with inset of Antarctica and Ross Island. Image acquired on January 19, 2018 by the WorldView-2 satellite (DigitalGlobe).

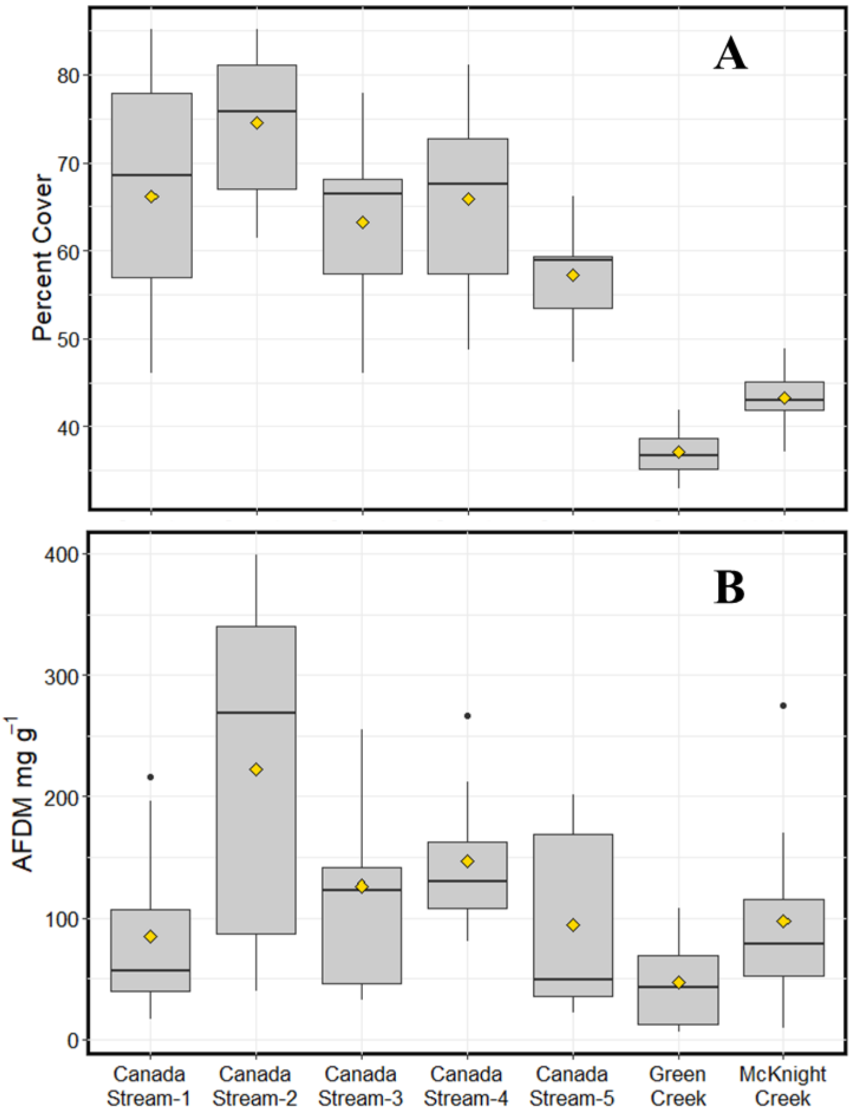

Figure 2.2. A. Percent cover and **B.** Ash-free dry mass (AFDM) from the Canada Stream, Green Creek, and McKnight Creek plots. Gold diamonds indicate the averages per plot. Black points indicate outliers defined as 1.5*interquartile range (IQR).

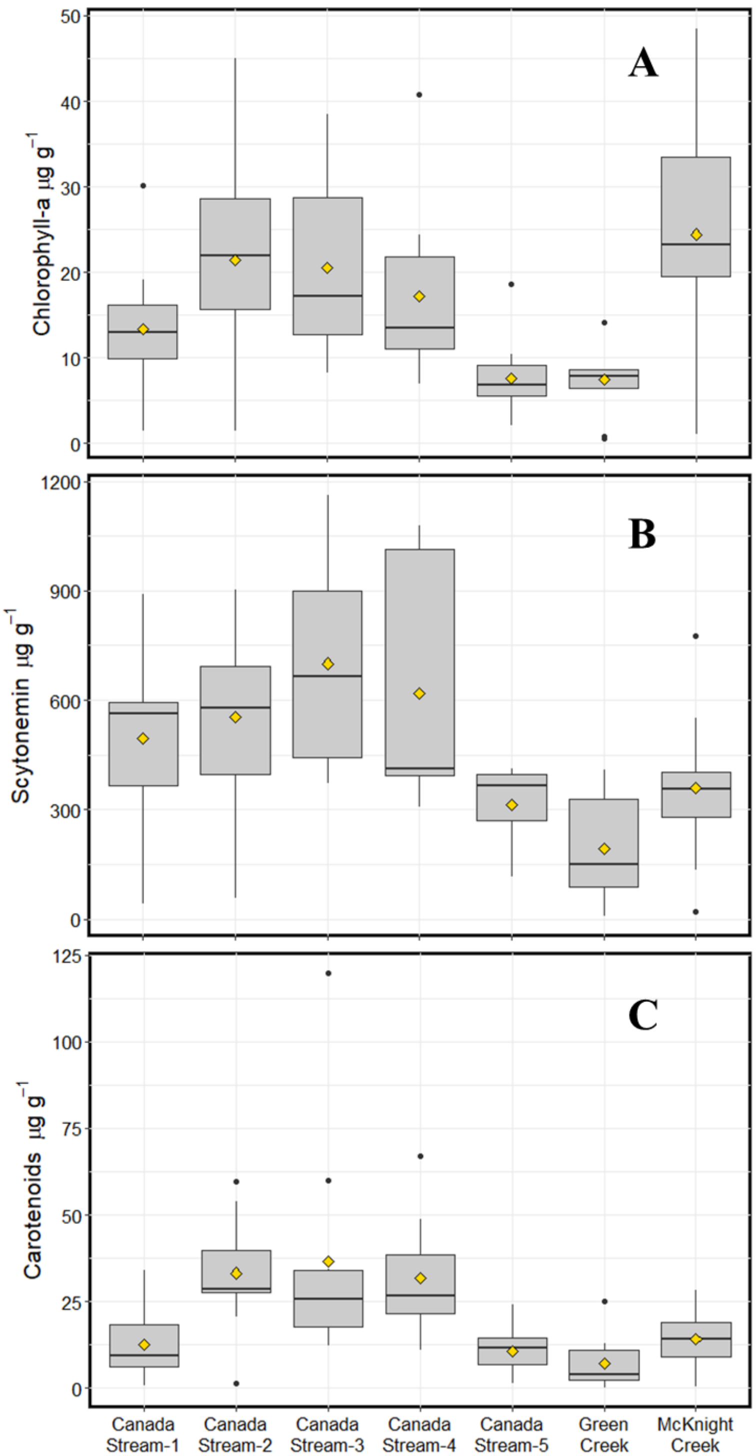

Figure 2.3. A. Chlorophyll-a, **B.** Scytonemin, and **C.** Carotenoid content from the Canada Stream, Green Creek, and McKnight Creek plots. Gold diamonds indicate the averages per plot. Black points indicate outliers defined as 1.5*IQR. One outlier 6, 3, and 4 standard deviations away from the mean was removed from the Canada Stream-2 chlorophyll-a, scytonemin, and carotenoid data, respectively.

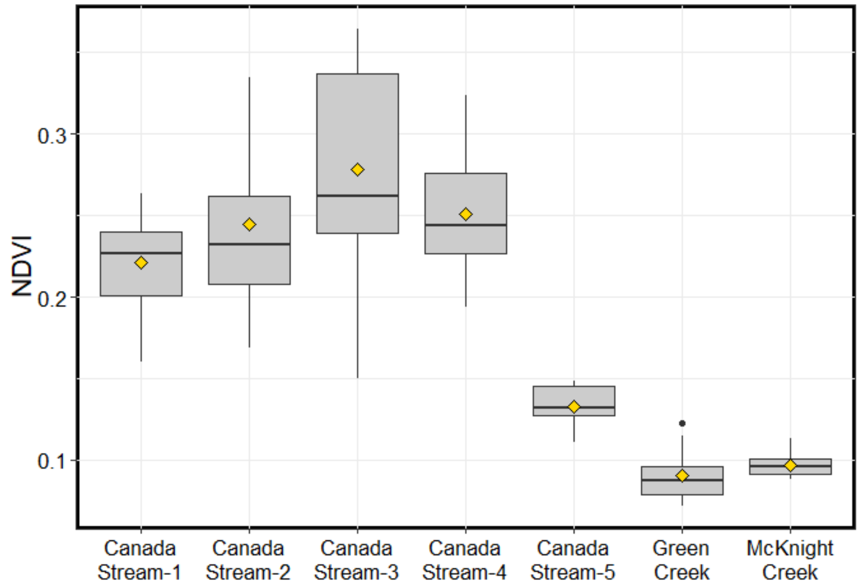

Figure 2.4. Box plots illustrating NDVI values from the Canada Stream, Green Creek, and McKnight Creek plots. Gold diamonds indicate the NDVI averages per plot. Black points indicate outliers defined as 1.5*IQR.

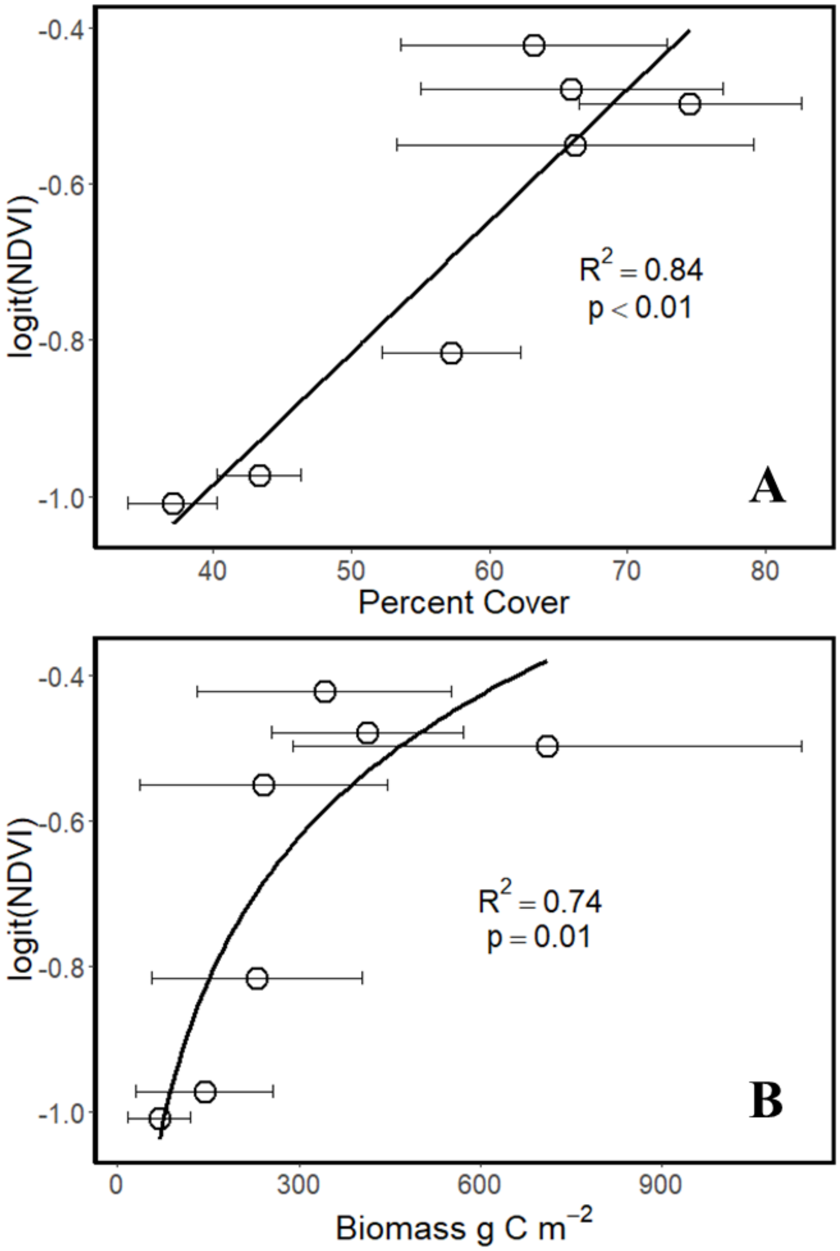

Figure 2.5. A. Significant linear relationship between percent cover and logit(NDVI) (R^2 = 0.84, p < 0.01, logit(NDVI) = 0.0169 * cover - 1.66). Error bars indicate population standard deviation. **B.** Significant logarithmic relationship between percent cover scaled biomass in g C m^{-2} and logit(NDVI) (R^2 = 0.74, p = 0.013, logit(NDVI) = 0.283 * ln(biomass) - 2.24). Error bars indicate population standard deviation.

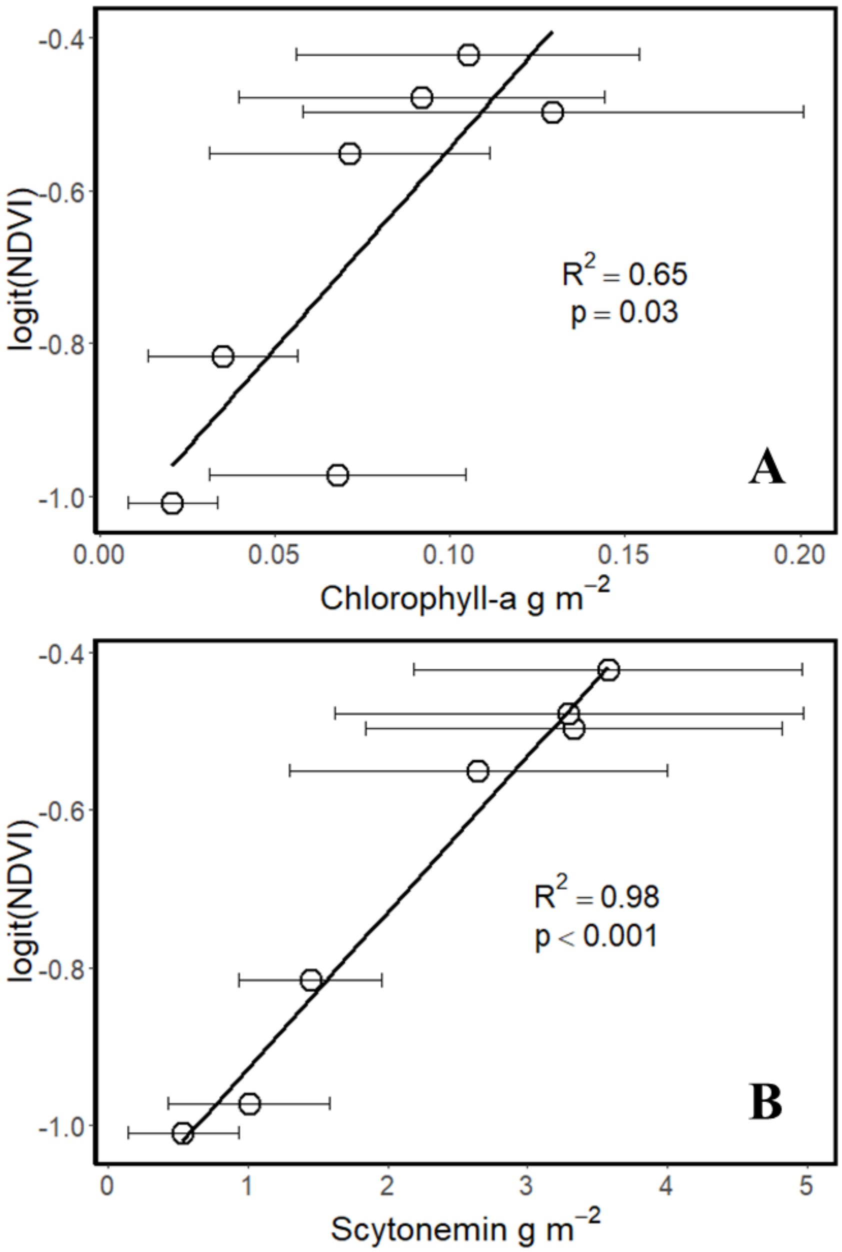

Figure 2.6. A. Significant linear relationship between percent cover scaled chlorophyll-a and logit(NDVI) ($R^2 = 0.65$, p = 0.028, logit(NDVI) = 5.26 * chlorophyll - 1.07). Error bars indicate population standard deviation. **B.** Highly significant linear relationship between percent cover scaled scytonemin and logit(NDVI) ($R^2 = 0.98$, $p < 0.001$, logit(NDVI) = 0.197 * scytonemin - 1.12). Error bars indicate population standard deviation.

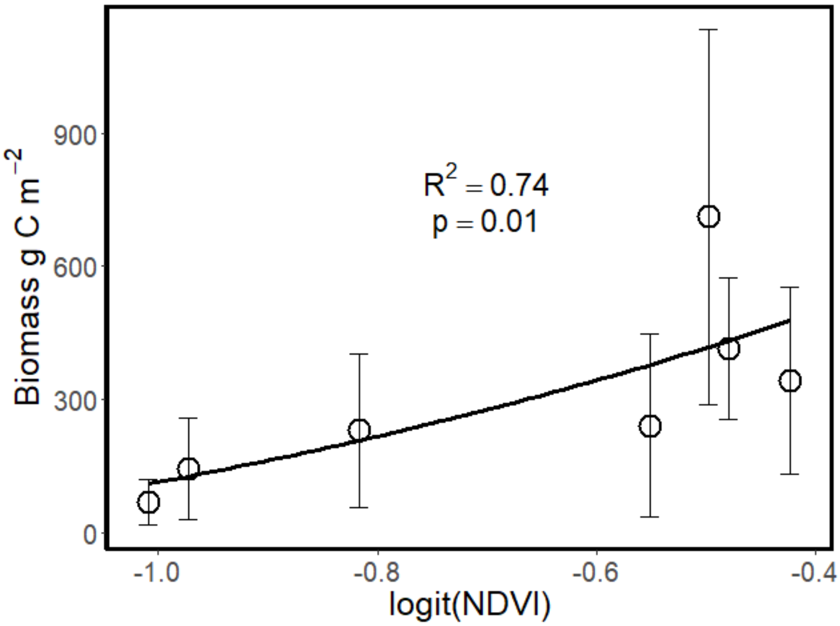

Figure 2.7. Significant exponential relationship between logit(NDVI) and percent cover scaled biomass in g C m^{-2} used for extrapolating biomass (R^2 = 0.74, p = 0.013, biomass = 1450 * $e^{2.61 * logit(NDVI)}$). Error bars indicate population standard deviation.

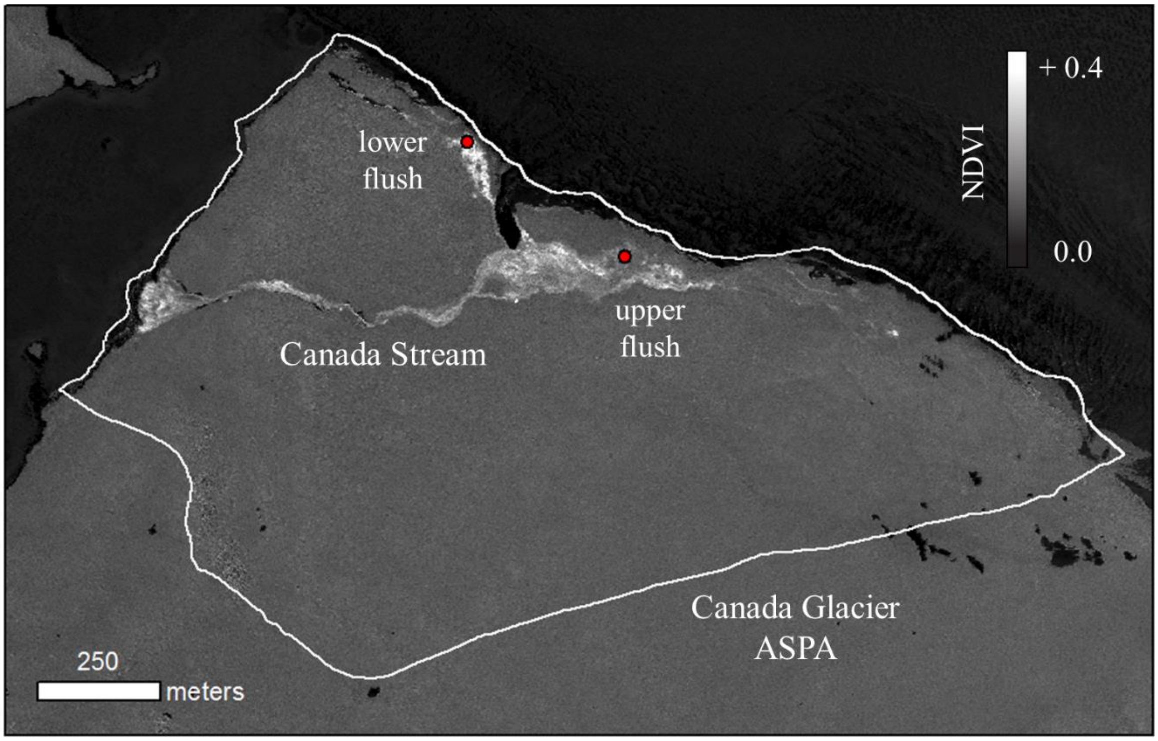

Figure 2.8. NDVI image of the Canada Glacier Antarctic Specially Protected Area (ASPA) (white boundary). The plots are shown in red for the upper flush and lower flush sites. Four plots were established adjacent to one another within the lower flush, and here they are denoted by a single pin. 21,715 kg of C were estimated in the Canada Glacier ASPA. Image acquired on January 19, 2018 by the WorldView-2 satellite (DigitalGlobe).

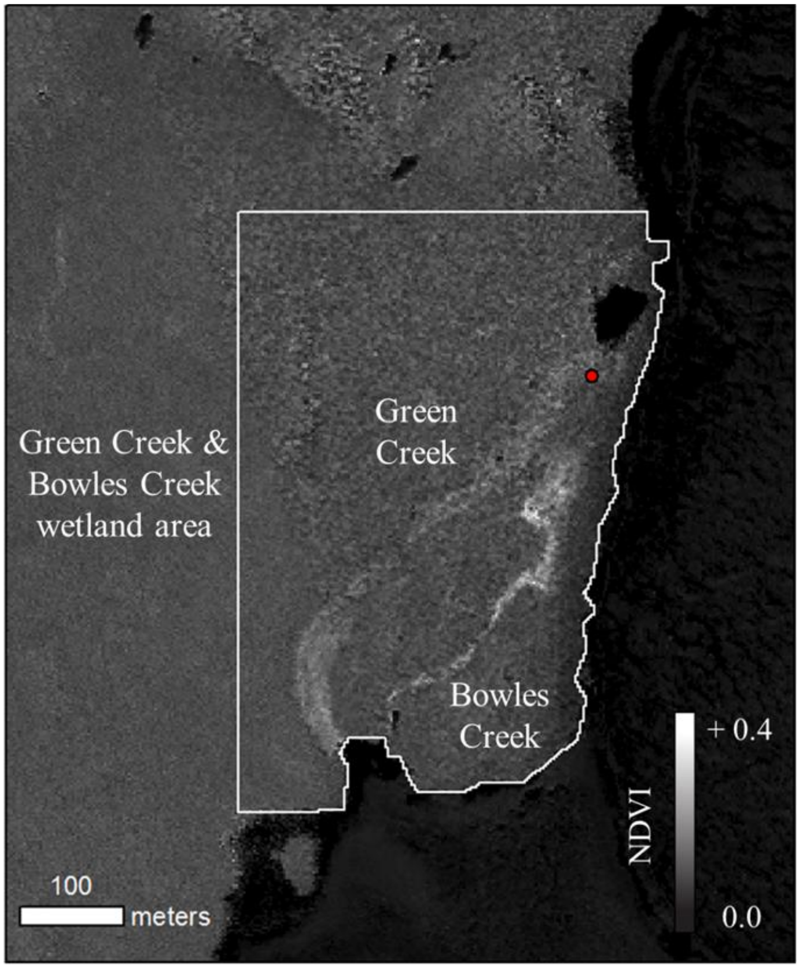

Figure 2.9. NDVI image of the Green Creek and Bowles Creek wetland area (white boundary). The plot is shown in red beside Green Creek. 2,115 kg of C were estimated for the Green Creek & Bowles Creek wetland area. Image acquired on January 19, 2018 by the WorldView-2 satellite (DigitalGlobe).

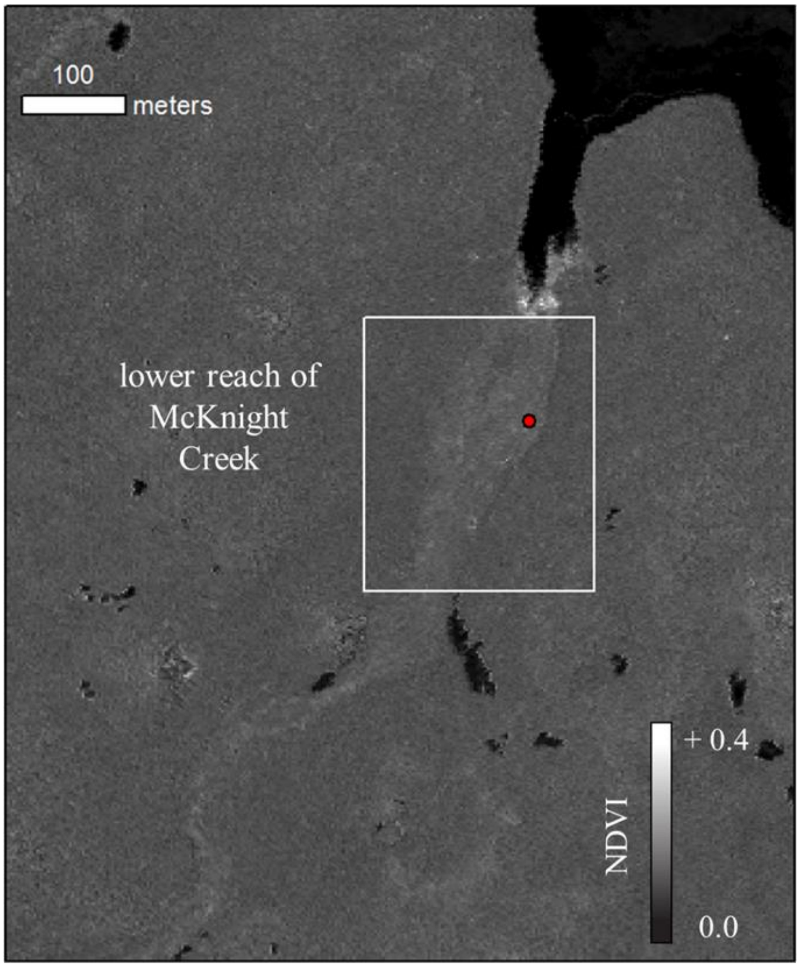

Figure 2.10. NDVI image of the lower reach of McKnight Creek (white boundary). The plot is shown in red beside McKnight Creek. 435 kg of C were estimated in the lower reach of McKnight Creek. Image acquired on January 19, 2018 by the WorldView-2 satellite (DigitalGlobe).

CHAPTER 3: GEOGRAPHIC VARIATION IN ^{15}N and ^{13}C NATURAL ABUNDANCE of TERRESTRIAL MICROBIAL MATS and SOILS IN TAYLOR VALLEY, ANTARCTICA

Abstract

Autotrophic microbial communities are the dominant primary producers in the McMurdo Dry Valleys (MDV), Antarctica, forming mats over soil and sediment surfaces. These microbial mat communities consist primarily of cyanobacteria and thrive in wetted areas and in the hyporheic zone of MDV streams that flow for up to 10 weeks a year. The mats are not only directly influenced by stream flow, but their distribution and activity are also influenced by geomorphology and potentially geochemistry. I examined microbial mat and underlying soil elemental and isotopic chemistry across an environmental gradient in Taylor Valley to characterize variation in the potential source pools of nitrogen used by these communities and their potential effect on local biogeochemical cycling. I sampled microbial mats and underlying soils from 6 locations occurring on different geological substrates and at a range of distances from the Ross Sea to measure their elemental (C, N) and isotopic ($\delta^{15}N$, $\delta^{13}C$) composition. Two of the sites were used as end-members, one beside the Ross Sea on the coast and one near the western end of Taylor Valley where there are different sources of N to the microbial mats, due to differing soil surface age and thus N depositional history. In terms of elemental chemistry, the microbial mats appear to be influencing the underlying soil by enriching the soil in C, which is important because the MDV are limited in C. The microbial mats at most of the sites had $\delta^{15}N$ of approximately 0‰, indicative of biological N fixation. Further up-valley, the microbial mats appeared to be acquiring N from abiotic sources associated with atmospheric deposition that is highly depleted in $\delta^{15}N$. These results demonstrate that microbial mats have a significant influence on the underlying soil C and N budgets, and that sources of N supporting microbial mats depend upon the functional capacity of the cyanobacteria community and the landscape history of the environment where they occur.

Introduction

Microbial mats are essential drivers of ecosystem processes in extreme ecosystems, such as hot and cold deserts (Elbert et al. 2012), where photosynthetic communities typically dominated by cyanobacteria form laminar mats or “crusts” over soil and sediment surfaces (Prieto-Barajas et al. 2018). In addition to primary production, *i.e.*, carbon (C) fixation, nitrogen (N) fixation is also a key biogeochemical process facilitated by cyanobacterial mats in extreme environments. In the McMurdo Dry Valleys (MDV), cyanobacteria, especially *Nostoc,* are important contributors to C and N cycling in lotic and lentic environments (McKnight et al. 2004), where in addition to low rates of photosynthesis (and hence low organic matter content), N is often a limiting nutrient to resident biota (McKnight et al. 1999). While these biogeochemical processes have been studied in Antarctic aquatic ecosystems (*i.e.*, lakes and streams), there is less known about these processes in the terrestrial microbial mats that occupy the transition zones between aquatic habitats and dry soils, which are highly sensitive to climate change in the McMurdo Dry Valleys (Doran et al. 2008).

The streams and soils of the McMurdo Dry Valleys are simple ecosystems in that there are no vascular plants, low species diversity, and no significant grazing of microbial mats (Treonis et al. 1999), suggesting that physical factors may be most important in controlling biological processes in this region. For example, the distribution and abundance of microbial mats in streams of the McMurdo Dry Valleys is strongly influenced by geomorphology (McKnight et al. 1999) and to a lesser extent by nutrient availability, especially inorganic N and phosphorus (Barrett et al. 2007, Kohler et al. 2016). The geomorphology of streams and soil surfaces in the McMurdo Dry Valleys is a legacy of geological events occurring over millennial time scales since their formation in the mid-Miocene as fjiord-like environments. Since then the movement of ice sheets, alpine glaciers, and the inundation and dry-down of proglacial lake environments have structured the current geochemical patterns observed in this region of Antarctica (Porter and Beget 1981, Lyons et al. 2000). For example, the soils of Taylor Valley, the focal system of the McMurdo Dry Valleys Long Term Ecological Research Program (*e.g.*, Gooseff et al. 2017), occur on glacial tills of varying surface exposure age and clast composition, and the entirety of Taylor Valley soils and sediments below ~ 300 m elevation have been modified by lacustrine sedimentation from Glacial Lake Washburn ~ 11,000–24,000 years ago (Denton et al. 1989). Specifically the rise and fall of the lacustrine environments has significantly affected the distribution of organic matter and biota in terrestrial environments of Taylor Valley and the physical limnology and biogeochemistry of the lakes that occur on the valley floor (Priscu 1995, Burkins et al. 2000). Understanding the landscape history of the MDV is crucial to understanding contemporary variation in ecological communities and ecosystem processes (Barrett et al. 2006).

Thus, regional and landscape-scale driven patterns in the geomorphology drive biogeochemical trends in the Taylor Valley soils (Burkins et al. 2000, Barrett et al. 2007): elevation influences microclimate; lithology of glacial tills and soils influences mineralogy and nutrient availability – particularly phosphorus; and distance from the ocean and surface exposure age of the landscape influences the depositional history with respect to the concentrations and composition of soluble ions in soil (Michalski et al. 2005, Welch et al. 2010, Lee et al. 2019). Barrett et al. (2006) describes the importance of different sources of N within the McMurdo Dry Valleys and partly attributes this to the differing ages and types of tills within a particular valley. For example, Michalski et al. (2005) found that the origin of N in some environments of the MDV is exclusively atmospheric after analyzing $\Delta^{17}O$ signatures of soil NO_3^- deposits in high elevation hyperarid environments. As a result of this atmospheric deposition that has accumulated over time on glacial tills of varying surface exposure age, N has a natural west – east gradient in Taylor Valley, with it being most abundant to the west, *i.e.*, landforms occurring in the west of the valley are older than the relatively young Ross Sea till in the east (Barrett et al. 2006, 2007). This natural gradient of N sources with distinct isotopic composition could help determine the relative importance of N fixation vs. acquisition of atmospherically deposited N in microbial mat mineral nutrition and soil N budgets.

Natural Abundance of C and N Stable Isotopes in the MDV

Stable isotope signatures of ^{15}N and ^{13}C in microbial mats can provide insight into the biogeochemical cycling and physiological status of Taylor Valley microbial mats and underlying soils and sediments (*e.g.*, Kohler et al. 2018). Isotopic analysis of ^{13}C potentially provides insights about autotrophic dynamics of microbial mats, *i.e.* are they water limited (Ehleringer and Dawson 1992), are they C limited (Lawson et al. 2004, Lyons et al. 2013), or are there energy sources other than C fixed through photosynthesis, for example methane-based food webs (Paul et al. 2017). Natural abundance of ^{13}C in plant material can vary both as a function of enzymatic efficiency of carboxylation and as a function of low pCO_2 in physically isolated environments where photosynthesis is occurring (O'Leary 1981), *e.g.*, under ice. Some processes result in ^{13}C enrichment (*e.g.*, CO_2 limitation (Lawson et al. 2004)) and some result in ^{13}C depletion (*e.g.*, C fixed through methane biogeochemistry (Paul et al. 2017)).

Abiotic and biotic sources of N are common in the MDV due to the long surface exposure ages and N deposition and also the abundance of N-fixing *Nostoc*. Black microbial mats dominate terrestrial surfaces where mats are present and on the periphery of lakes and many streams in the McMurdo Dry Valleys (Moorhead et al. 2003, Kohler et al. 2015, Power Chap. 2). Black microbial mats are dominated by the N-fixing cyanobacteria *Nostoc* (Alger et al. 1997), and their isotopic signature is near that of the atmospheric standard ($\delta^{15}N = \sim 0‰$), suggesting that they're obtaining N from biological N fixation (Shearer and Kohl 1986). Direct measurements of N fixation by recently re-hydrated microbial mats (Hawes et al. 1992) and in saturated hyporheic sediments (Niederberger et al. 2012) are evidence of the importance of N fixation in these communities.

Kohler et al. (2018) reported that stream microbial mats within the Fryxell Basin and even within the same stream can be acquiring N from biotic sources (N-fixing *Nostoc* upstream) *or* from abiotic sources, presumably of glacial meltwater origin. The $\delta^{15}N$ signatures of *Nostoc* mats were near the atmospheric standard, while orange and green mats were overall more variable and depleted in ^{15}N signatures, indicating an abiotic source of N (Kohler et al. 2018). Kohler et al. (2018) attributes this depletion to orange and green mats consisting mostly of taxa that have not been shown to fix N in the MDV, including *Oscillatoria* and *Prasiola*, respectively (Alger et al. 1997).

The objectives of this study were to: 1) Determine sources of N for terrestrial microbial mats communities in Taylor Valley across an atmospheric depositional gradient and 2) Assess whether microbial mats are influencing the C and N biogeochemistry of the underlying soils and sediments. I hypothesized that microbial mats further up Taylor Valley would be obtaining N from physical sources and microbial mats closer to the coast would be obtaining N through N-fixation. Microbial mats that are fixing N should have $\delta^{15}N$ values closer to 0‰, while those that are not fixing N in areas where N concentrations are naturally higher should have more depleted $\delta^{15}N$ signatures, since biological processes discriminate against heavier N (Montoya and McCarthy 1995).

Methods

Study Sites

Each of the study sites are located within Taylor Valley, Antarctica where alpine glaciers feed streams in the austral summer that flow to perennially ice-covered lakes on the valley floor (Figure 3.1). The MDV microbial mats are commonly described as four functional mat types (black, orange, green, and red) based on their appearance (color), dominant taxa, and habitat preference within the stream (Alger et al. 1997). The microbial mats are located within distinct zones based on flow regime and soil/sediment water content. Some of the mats exist mainly in the stream thalweg where flow is most consistent (*e.g*., orange mats, *Oscillatoria* spp.), while black mats are found along wetted margins not commonly inundated by stream flow but where water is supplied by the hyporheic zone (Alger et al. 1997). Terrestrial microbial mats are dominated by the cyanobacteria *Nostoc* spp. in most of the environments without active yearly flow.

I selected sites that were common to have vegetation and that spanned the atmospheric N deposition gradient along the Taylor Valley, from the coast to up-valley (Figure 3.1). Samples were collected from 6 locations: Hjorth Hill, McKnight Creek, Green Creek, Canada Stream, Canada Flush, and Wormherder Creek. All sites were selected from outside of the main channel of streams, *e.g*., three of the sites, Hjorth Hill, Canada Flush, and Wormherder Creek occur outside of stream channels and are fed by a combination of glacial and snow melt through subsurface flow.

To the easternmost side of Taylor Valley is Hjorth Hill (-77° 32.520' S, 163° 33.988' E) (Figure 3.2), the coastal end-member site, where there are several small snow-fed meltwater tracks and an abundance of moss and microbial mats. Black mat (*Nostoc* spp.), red moss and green moss were found at the Hjorth Hill sites (Figure 3.9A, B). Based on the identifications by Schwarz (1992) and Pannewitz et al. (2003), I identified the red moss sampled as *Hennediella heimii* and the green moss to genus as *Bryum* spp.

The middle gradient sites include McKnight Creek, Green Creek, Canada Stream, and the Canada Flush, all located within the Fryxell Basin (Figure 3.3). McKnight Creek is on the eastern side of Lake Fryxell and is fed by the Commonwealth Glacier (Figure 3.4, Figure 3.8A). The sampling area here was along the lower reach of the stream (-77° 35' 51.00" S, 163° 16' 10.03" E) in an area of patchy, less abundant microbial mats. The microbial mats found on the margins were exclusively black mats. On the southwestern side of Lake Fryxell, Green Creek is fed by the Canada Glacier, and the sampling area here was downstream of a melt-pond beside the glacier (-77° 37' 30.32" S, 163° 3' 0.58" E) in a shallow gradient area with visible black mat cover (Figure 3.5, 3.8B).

The Canada Stream and Canada Flush are located on the northwestern side of Lake Fryxell beside the Canada Glacier (Figure 3.6). This area is within the Canada Glacier Antarctic Specially Protected Area (ASPA), which was designated by the Antarctic Treaty System in 2002 as a significant biologically active area of great scientific value as one of the most productive areas in the MDV. Glacial melt flows over a gently sloping area of approximately 100–200 m^2 before entering the Canada Stream channel. Melt from the northern area of the Canada Glacier forms small channels before flowing into the main channel of Canada Stream, while melt from the southern area drains into a pond before entering the main channel (Conovitz et al. 1998). One sampling area, here referred to as the Canada Stream (Figure 3.8C), was located within the wetted area north of the pond before the stream channelizes (-77° 36' 47.77" S, 163° 1' 52.41" E) and consisted exclusively of black mat. The other sampling area, the Canada "Flush" (Figure 3.8D), was located in the wetted area south of the pond (-77° 36′ 58.14″ S, 163° 2′ 28.97″ E), "the lower flush", which is biologically rich with abundant cyanobacteria, algae, and moss (Schwarz et al. 1992, Alger et al. 1997). The samples I collected from the Canada Flush included black mat and also green moss with epiphytic black mat (Figure 3.9C). Moss from the Canada Flush has been identified as *Bryum argenteum, Bryum pseudotriquetrum, and Hennediella heimii,* previously known as *Pottia heimii* (Schwarz et al. 1992, Pannewitz et al. 2003). *Hennediella heimii,* darker in color, is known to occur along the edges of flowing water and on higher ground, while *Bryum argenteum,* green in color, occurs within areas of flowing water and commonly has epiphytic *Nostoc* colonies (Schwarz et al. 1992, Pannewitz et al. 2003). Moss samples collected from the Flush were classified to genus as *Bryum* spp.

To the west is Lake Bonney Basin, where my end-member western-most site was located. Bonney Riegel is a high terrace underlain by gneiss on the southern side of Lake Bonney (Figure 3.7). Wormherder Creek (-77° 43.556' S, 162° 18.926' E) at Bonney Riegel is an ephemeral groundwater seep that was first noted in January of 2002, during the warmest austral summer recorded in Taylor Valley (Lyons et al. 2005). Wormherder Creek is dry most years, except for high flow seasons, but it happened to be flowing in January of 2018. Orange mats (*Oscillatoria* spp.) were found in the stream thalweg and in the wetted margins of Wormherder Creek (Figure 3.9D).

Sample Collection

Vegetation samples were collected from areas with visible abundance of microbial mat and moss using 60 mL amber Nalgene bottles. The top 5 cm of soils or sediments were also collected from beneath the sampled mat. On January 9th and 10th 2018, 40 vegetation and soil samples were collected from within a 400 m^2 area of the Canada Flush of the Canada Glacier ASPA. Samples were collected using a random stratified sampling design; I sampled 8 – 1 m^2 subplots using a directional point intercept survey at 5 numbers between 0 and 100 cm (*i.e*., north to south at 40 and 80 cm, and west to east at 20, 60, and 100 cm). On January 11th, 12th, and 25th 2018, 9 samples were collected every 5 m from within a 100 m^2 area of Canada Stream, Green Creek, and McKnight Creek, respectively. The top layer of soil was collected for the areas that did not have visible mat to measure chlorophyll-a within desert pavement, following the methods described in Barrett et al. (2004). Three grab samples of orange microbial mat and the soil below were taken beside Wormherder Creek at Boney Riegel on January 24th. Additionally, grab samples of black microbial mat along with red and green moss (*Hennediella heimii* and *Bryum* spp., respectively) and the soil below were taken at five different locations at Hjorth Hill on February 1st. These sampling areas at Hjorth Hill included wetted areas beside small channels, snow melt areas, and potential groundwater seeps. For all sampling locations, the ground cover type was recorded for each sample (*i.e*., black mat, orange mat, green moss, or red moss). Location coordinates were taken using a handheld GPS unit. Samples were kept cool in ice chests and transported back to McMurdo Station where they were stored in a freezer at -20°C at Crary Laboratory before being shipped to Virginia Tech for analysis.

Laboratory Analysis

Frozen microbial mat and soil samples were left to thaw at 4°C overnight in a fridge. They were oven dried at 105°C for 24 hrs and were then sieved through a 4 mm sieve. The samples were kept dry in a desiccator between processing steps. In November 2018, the microbial mat and soil samples were prepared for analysis by first homogenizing them using a ball mill grinder for approximately 1.5–2 min, or until completely homogenized. Using a microbalance, 50 mg of soil were weighed into 11 x 8 mm tin capsules, and 10 mg of mat were weighed into 8 x 5 mm tin capsules. The tins were encapsulated tightly to prevent any sample from escaping. Care was taken in cleaning the work area, utensils, and tweezers with EtOH between each sample to reduce the possibility of cross contamination. The samples were analyzed using the Department of Forest Resources and Environmental Conservation's isotope mass ratio spectrometer (IRMS), IsoPrime 100 isotope analyzer (Elementar), at the FREC Analytical Lab, Virginia Tech. This instrument quantified total C and N for the microbial mats and soil using a vario MICRO cube elemental analyzer (Elementar) on the front end and then quantified $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios for each sample. The $\delta^{13}C$ standards used included, USGS24 Graphite, USGS40 L-Glutamic acid, Elementar Flour (B2155), and Elementar Protein (B2155), and the $\delta^{15}N$ standards used included, USGS40 L-Glutamic acid, USGS41 L-Glutamic acid, Elementar Flour (B2155), and Elementar Protein (B2155).

Statistical Analysis

Using R Statistical Software version 1.0.153, box plots were created for the $\delta^{15}N$, $\delta^{13}C$, % N, and % C data for each of the six sampling locations to visualize variation within and among locations (R Core Team 2018). One Canada Flush mat $\delta^{15}N$ outlier was > 4 standard deviations away from the mean and was removed from the dataset. One-way analysis of variance (ANOVA) tests were performed on each data set to determine whether the means were statistically different between sampling locations, and Tukey's Honest Significant Difference (TukeyHSD) tests were performed to determine which locations were statistically different from one another. Scatterplots were also created in R to visualize trends in the data between isotope type ($\delta^{15}N$ or $\delta^{13}C$) and sample type (microbial mat or soil).

Results

The microbial mats samples collected from Hjorth Hill were visually identified as green moss (*Bryum*), red moss (*Hennediella heimii*), and a combination of moss with epiphytic black mat (*Nostoc*). The samples collected from McKnight Creek, Green Creek, and Canada Stream were all identified as black mat (*Nostoc*), while the samples from the Canada Flush were *Nostoc* and a combination of *Bryum* with epiphytic *Nostoc*. Wormherder Creek microbial mats samples were identified as orange mat (*Oscillatoria*).

Microbial mat and soils varied significantly among the sample sites, both in their elemental C and N concentrations as well as their stable isotope signatures (Table 3.1). Overall, C and N content of the microbial mats was greater and much more variable than the soils, particularly at the McKnight Creek, Canada Stream, and Canada Flush sites (Figure 3.10, 3.11). Mat % N averages ranged between 0.1 and 0.5% N by weight and mat % C averages ranged between 1 and 5% by weight (Figure 3.10). Mat % N and % C differed significantly among the sites (ANOVA, df = 5, F = 3.41, $p < 0.01$; df = 5, F = 3.25, $p < 0.05$) with Canada Flush having the highest % N and % C composition (0.47 and 5.38%, respectively) (Figure 3.10).

All soils had low total N content, with some samples flagged at the detection limit of the instrument. Even the highest soil N concentrations were an order of magnitude below the N concentrations of mat, with averages ranging between 0.008 and 0.05% (Figure 3.11A). Soil C content averages ranged between 0.15 and 0.45% C by weight (Figure 3.11B), which is on the high end of values reported for Antarctic soils in this region (Burkins et al. 2000, Barrett et al. 2006), but within the range reported for soils collected from below mats (Ball and Virginia 2014). Soil N and C varied significantly among study sites (ANOVA, df = 5, F = 7.19, $p < 0.0001$; df = 5, F = 4.38, $p < 0.01$) with Canada Flush again having the highest concentrations (0.048 and 0.41%, respectively), and Wormherder Creek sediments having the lowest N and C content (0.007 and 0.18%, respectively) (Figure 3.11).

C and N Isotopic Composition

Microbial mat $\delta^{15}N$ differed significantly among locations (ANOVA, df = 5, F = 20.65, $p < 0.0001$), with average $\delta^{15}N$ signatures of between 5 and -5‰ in all sites with the exception of Wormherder Creek, where mats were highly depleted, averaging -16‰ $\delta^{15}N$, well outside the distribution of observations from all the other sites (Figure 3.12A). Canada Stream and Canada Flush microbial mats exhibited the most variation in ^{15}N signatures, with $\delta^{15}N$ between -2.2 and 4.7‰ and -4.6 and 2.9‰, respectively (Figure 3.12A). Mat $\delta^{13}C$ also differed among study sites (ANOVA, df = 5, F = 3.65, $p < 0.01$). Wormherder Creek had the most enriched $\delta^{13}C$ signatures, ~ -10‰ (Figure 3.12B), while several samples had extremely low $\delta^{13}C$ with averages < -40‰, particularly from Canada Flush, Canada Stream, and McKnight Creek (Figure 3.12B).

Soil $\delta^{15}N$ differed significantly among study sites (ANOVA, df = 4, F = 4.11, $p < 0.01$). Notably, N content of the Wormherder Creek samples was too low to reliably quantify N isotope ratios. Excepting Wormherder Creek, Canada Stream exhibited the most depleted values, ~ -1‰, on average (Figure 3.13A). Green Creek $\delta^{15}N$ had the most variability with values of -2.6 to 3.1‰, and several of the soil samples were too low in N content to measure a reliable N isotope ratio (Figure 3.13A). Soil $\delta^{13}C$ also differed by location (ANOVA, df = 5, F = 33.96, $p < 0.0001$) and was slightly more enriched on average compared to mat $\delta^{13}C$, consistent with the presence of carbonates and/or expectations of isotopic fractionation following biological processing of microbial mat C (Figure 3.13B). Wormherder Creek soils had the most enriched $\delta^{13}C$, ~ -5‰, similar to the $\delta^{13}C$ microbial mats from that site (Figure 3.13B).

Discussion

Microbial mats enrich the organic matter in the soils and sediments below them. Carbon and N content of microbial mats and soils was greatest in the Canada Flush and least in the Wormherder Creek site, illustrating a broad range of mat influence of underlying soil organic matter storage (Figure 3.14). The Canada Flush is among the most productive environments in the McMurdo Dry Valleys (Schwarz et al. 1992, Pannewitz et al. 2003, Power Chap. 2), while Wormherder Creek is an ephemeral stream with notable flow events observed once or twice per decade (Lyons et al. 2005). In general, the most productive microbial mat communities in the vicinity of Canada Stream contributed to the highest observed soil C and N content (Figure 3.14).

The ^{15}N signatures of microbial mats suggest that cyanobacterial mats are obtaining much of their N from biological N fixation in most of the locations sampled (Figure 3.16A). Biological N fixation has a $\delta^{15}N$ signature of 0‰ in theory but slightly depleted values of $\delta^{15}N$ are commonly reported, -2 – 0‰ (Shearer and Kohl 1986, Vitousek et al. 2013). Most of my observations of mat $\delta^{15}N$ signatures were within 1‰ of previously reported values indicating biological N fixation (Figure 3.16A). In contrast, the $\delta^{15}N$ signatures of microbial mats at Wormherder Creek were highly depleted in $\delta^{15}N$, suggestive of abiotic sources, *i.e.*, atmospheric deposition, previously reported for this region (Wada et al. 1981, Michalski et al. 2005). Additionally, the microbial mats at Wormherder Creek were exclusively orange mats, previously reported as *Oscillatoria* spp., which have not been shown to fix N in the MDV. This region of Taylor Valley has older surface exposure ages with a greater accumulation of N deposition and high soil NO_3^- content (Barrett et al. 2006, 2007), so it is likely that Wormherder Creek mats would be ^{15}N depleted because they are acquiring their N from abiotic sources (*e.g.*, pools of NO_3^- in soil). All other locations supported microbial mat communities consisting mainly of *Nostoc* or a mixture of moss and *Nostoc*, and microbial mats at these locations generally had ^{15}N signatures very close to atmospheric (*i.e.*, within 1-2‰ of $\delta^{15}N$).

My ^{15}N results are comparable to previous descriptions of regional trends in biogeochemistry of the McMurdo Dry Valleys; in warmer and wetter environments (Doran et al. 2002) with higher soil/sediment phosphorus availability (Bate et al. 2008) and higher AFDM of microbial mats (Kohler 2015), but where N is more limiting (Barrett et al. 2007), the role of N-fixation is more important and stream microbial mat $\delta^{15}N$ signatures are enriched, compared to areas of greater accumulated N deposition (*i.e.*, up-valley), where the mat $\delta^{15}N$ signatures are more depleted. In general, soils and sediments collected from under microbial mats were enriched in $\delta^{15}N$ compared to the mats (Figure 3.15A), suggesting that if the mats are the primary source of N in the underlying sediment, as expected, then losses of N are contributing to fractionation of N isotopes in soil pools to result in isotopic pools enriched relative to their sources, as observed in this study. Denitrification is one such loss process that could explain this enrichment of ~ 1-3‰ $\delta^{15}N$ in the underlying soils and sediments.

Microbial mats exhibited a very broad range in $\delta^{13}C$ signatures compared to $\delta^{15}N$ (Figure 3.16A) in contrast to previous work examining stable isotope signatures of soil organic matter in Taylor Valley, which showed that fairly tight clustering of $^{13}C/^{12}C$ ratios, indicative of either lake or marine derived C (Burkins et al. 2000). Photosynthesis produces $\delta^{13}C$ signatures typically between -10 and -32‰ (O'Leary 1988). The enriched values at Wormherder Creek are likely due to high carbonate concentrations in soils and mats (Lyons et al. 2013). The depleted $\delta^{13}C$ signatures, primarily at the Canada Flush, could be caused by methanogenesis (*i.e.*, production of CH_4) and/or methanotrophy (*i.e.*, oxidation of CH_4). Methanogenesis is known to occur in Lake Fryxell in the MDV (Smith et al. 1993). Karr et al. (2006) detected methanogens in Lake Fryxell sediments and possibly methanotrophs in the anoxic water column. It was found that methane production was occurring in the sediments and was being consumed in the anoxic water column, implying that methanotrophy was occurring in Lake Fryxell as well as methanogenesis (Karr et al. 2006). Since methanogenes and methanotrophs thrive in anaerobic environments and have been found in the MDV, it is possible that the depleted $\delta^{13}C$ at the Canada Flush could be produced from similar processes, evidence of methane biogeochemistry (Paul et al. 2017). The Flush is a wetland environment where fairly consistent, low flow is common, and the ground is typically saturated for several weeks during the austral summer due to its proximity to the Canada Glacier. It wouldn't be surprising that the soils in the Flush are seasonally anaerobic. More analyses would need to be performed to verify if methanogenesis and methanotrophy were indeed occurring in this area.

Organic matter in Taylor Valley lake moats has been shown to be significantly enriched in $\delta^{13}C$ compared to under-ice organic matter deeper in the lakes (Lawson et al. 2004). Compared to phytoplankton in the water column, the benthic moat mats have mucilage, a protective polysaccharide sheath coating, and form colonial assemblages, both which have been shown to limit CO_2 diffusion to assimilation sites (Des Marais and Canfield 1994), and this CO_2 diffusion limitation is attributed to be the main factor influencing the $\delta^{13}C$ isotopic composition of the benthic moat mats (Lawson et al. 2004). Moat benthic mats were also $\delta^{13}C$ enriched compared to under-ice deep benthic mats, because there is a supersaturation of CO^2 with depth, so the benthic mats were not shown to experience a diffusion limitation (Lawson et al. 2004). Doran et al. (1998) reported deep benthic mats in Lake Hoare were preferentially taking up ^{12}C due to the supersaturation of CO_2 with depth, showing that the mats were approaching full expression of the RUBISCO enzyme. Lawson et al. (2004) determined that deep benthic mats typically had $\delta^{13}C$ values between -20.1 and -35.0‰, while moat benthic mats had $\delta^{13}C$ between -2.7 to -20.2‰. In comparison, $\delta^{13}C$ of Wormherder Creek mats in this study were extremely enriched, approximately -10‰ (Figure 3.16A). This value is comparable to the range of $\delta^{13}C$ Kohler (2015) reports for Wormherder Creek, ~ -10 and -15‰. Additionally, $\delta^{13}C$ of dissolved inorganic carbon (DIC) at Wormherder Creek is reported as having extremely high $\delta^{13}C$ DIC values (~ 5‰) in the MDV (Lyons et al. 2013), and because microbial mats are known to isotopically discriminate CO_2 over DIC (Des Marais and Canfield 1994), Kohler (2015) attributed the enriched $\delta^{13}C$ of Wormherder Creek on the discrimination of CO_2. One other possible explanation for the enrichment of $\delta^{13}C$ at Wormherder Creek is the samples in this study were not acidified to account for natural carbonates in the samples.

$\delta^{13}C$ signatures cannot always be easily used to infer physiological status of autotrophs or to distinguish sources. For example, Burkins et al. (2000) used $\delta^{15}N$ and $\delta^{13}C$ signatures to identify sources of soil organic matter in Taylor Valley, and they found that $\delta^{13}C$ signatures for most sources overlapped, whereas the $\delta^{15}N$ signatures were distinct among marine, lacustrine, and terrestrial end-members. Kohler (2015) found that patterns in $\delta^{13}C$ signatures were less obvious, with only orange mats exhibiting distinct $\delta^{13}C$ signatures relative to other microbial mat functional types, *i.e.*, enrichment with increasing distance from the coast. Additionally, Lawson et al. (2004) also illustrated this difficulty in interpreting $\delta^{13}C$ signatures as they found significant variation in microbial mat $\delta^{13}C$ signatures within moat regions of four Taylor Valley lakes. Ultimately, ^{13}C signatures are useful for speculation about the physiology of the microbial mats but patterns in general are more difficult to infer compared to ^{15}N.

Because ^{13}C is differentially fractioning, it's difficult to use these findings to interpret microbial mat physiology solely from isotopic and elemental data without additional information. There are known processes that result in ^{13}C depletion (*e.g.*, methane biogeochemistry) and enrichment (*e.g.*, CO_2 limitation, carbonates) and this data set doesn't provide sufficient information to distinguish between them. I'm speculating that the extremely depleted $\delta^{13}C$ mat samples from Canada Flush are associated with methanotrophy and methanogenesis and that the enriched $\delta^{13}C$ mats at Wormherder Creek are associated with natural carbonates and CO_2 discrimination over DIC, but further analysis would need to be performed to determine more about microbial mat physiology and potential patterns.

Conclusions

Microbial mats are associated with sediments enriched in organic matter and total N, but this inferred influence of aboveground productivity on belowground organic matter does not result in a strong relationship between microbial mat stable isotope signatures and soil isotope signatures of ^{13}C and ^{15}N. Most of the microbial mats examined in this study have $\delta^{15}N$ signatures indicative of a biological N fixation source for their N content (*i.e.*, ~ 0‰ $\delta^{15}N$) with variation among the sites, including depleted signatures indicating some amount of abiotic sourcing and some enriched signatures suggesting isotopic fractionation occurring during loss mechanisms (*e.g.*, denitrification). The one exception to these ^{15}N signatures indicative of biological N fixation is the Wormherder Creek site which supported orange mats presumed to be non-biological N fixing taxa, *e.g. Phormidium*, and is on a glacial till sequence previously reported to be rich in abiotically derived NO_3^- sources highly depleted in $\delta^{15}N$. These results demonstrate that microbial mats do have a significant impact on the underlying soil C and N budgets, and that sources of N supporting microbial mats depend upon the functional capacity of the cyanobacteria community and the landscape history of the environment where they occur.

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Table 3.1. Degrees of freedom, F-values and p-values from one-way ANOVA tests and plot comparisons of Tukey's Honest Significant Difference tests of $\delta^{15}N$, $\delta^{13}C$, % N, and % C for microbial mat and soil samples, where "WRM" refers to Wormherder Creek, "CAN Stream" Canada Stream, "CAN Flush" Canada Flush, "GRN" Green Creek, and "MCK" McKnight Creek.

		ANOVA			TukeyHSD ($p < 0.05$)
		df	F-value	p-value	Plot Comparison
Mat	$\delta^{15}N$	5	20.65	< 0.0001	WRM < all sites
	$\delta^{13}C$	5	3.65	0.00640	WRM > CAN Stream
	% N	5	3.41	0.00819	CAN Flush > GRN
	% C	5	3.25	0.0109	CAN Flush > GRN
Soil	$\delta^{15}N$	4	4.11	0.00544	CAN Stream < CAN Flush, MCK
	$\delta^{13}C$	5	33.96	< 0.0001	WRM > all sites; CAN Flush < GRN, MCK, WRM
	% N	5	7.19	< 0.0001	CAN Flush > WRM, GRN, CAN Stream, MCK
	% C	5	4.38	0.00162	CAN Flush > GRN

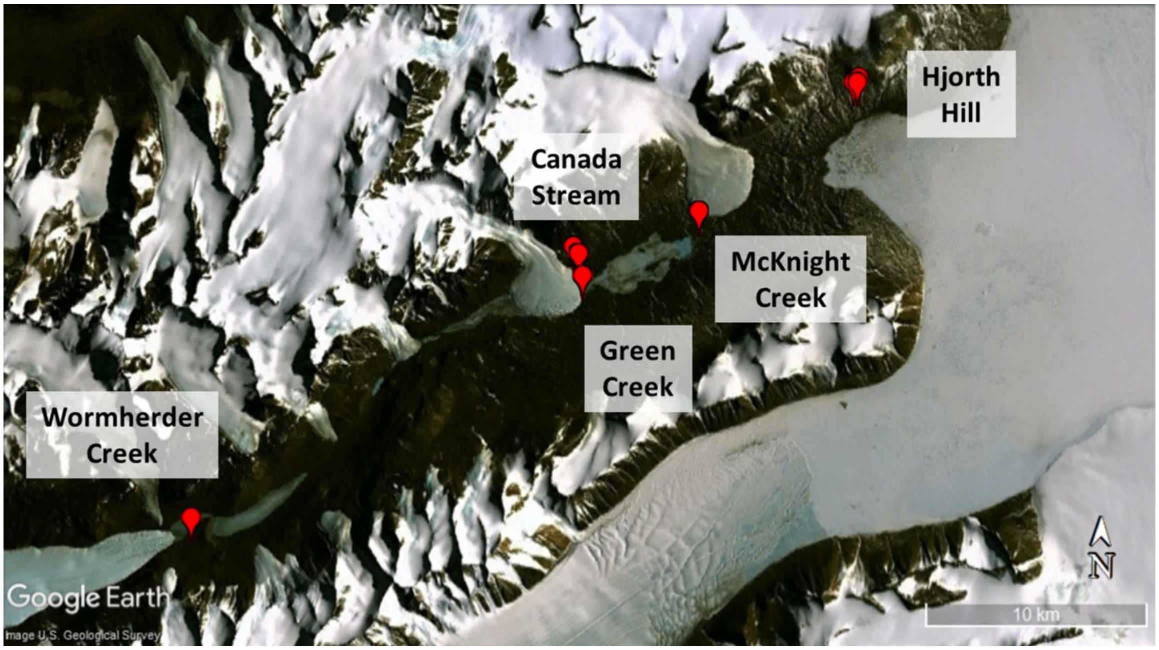

Figure 3.1. Satellite image of Taylor Valley and the six study sites. Image taken on 12/31/1998. © Google Earth

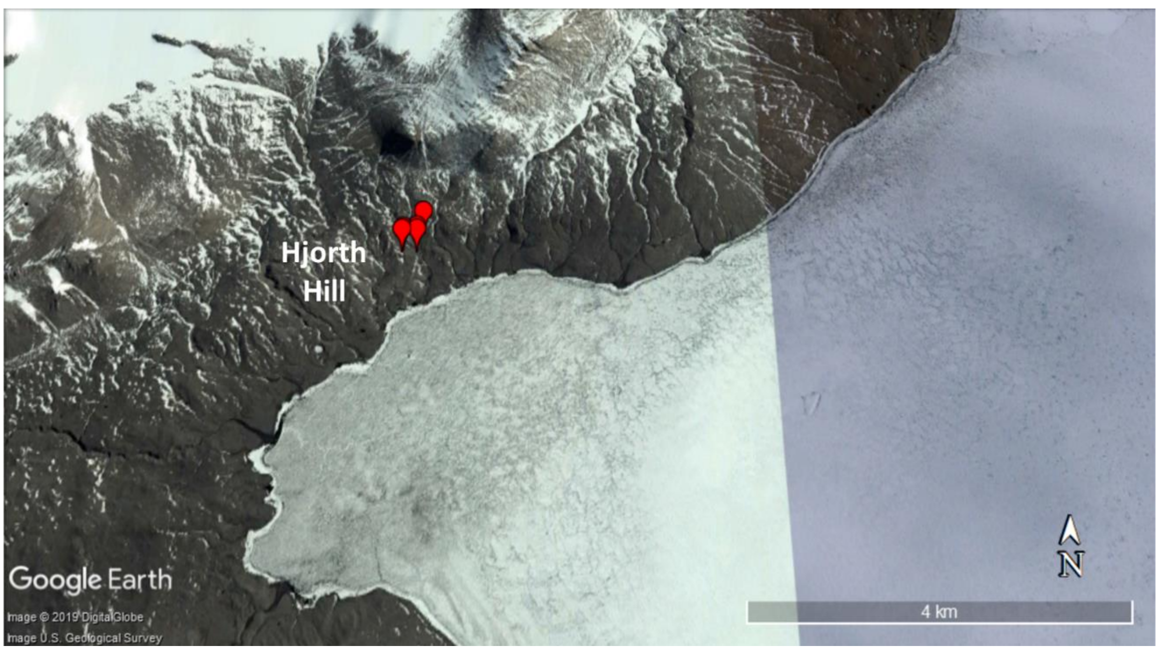

Figure 3.2. Satellite image of Hjorth Hill on the coast and the sampling locations. Images taken on 01/17/2010 and 01/20/2010. © Google Earth

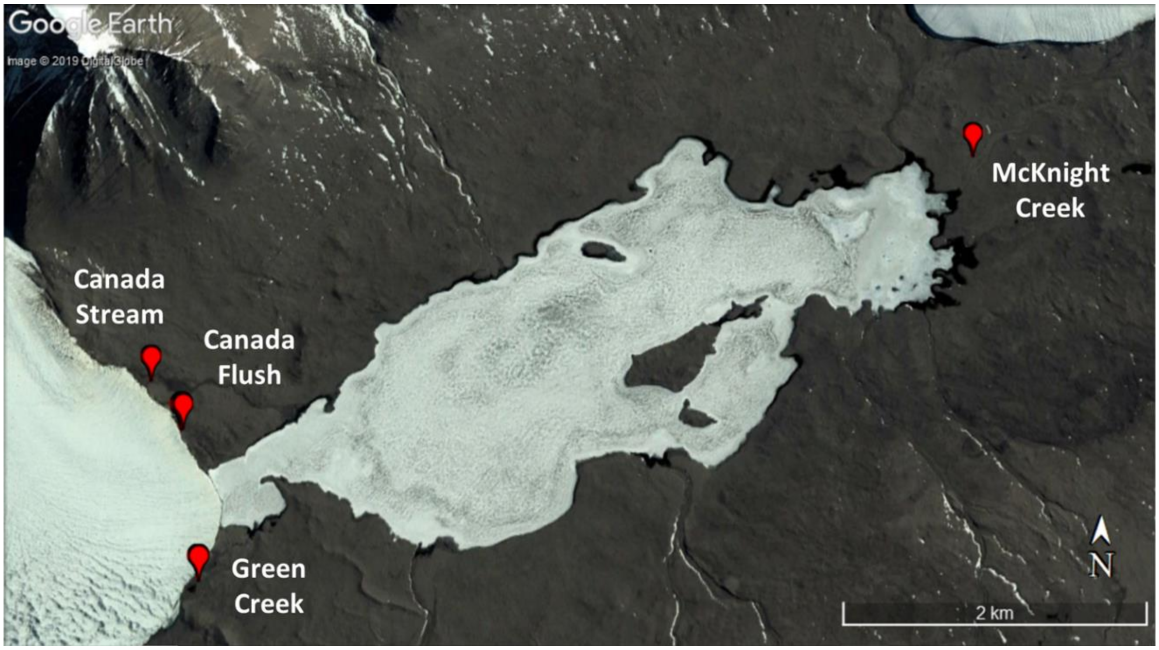

Figure 3.3. Satellite image of Lake Fryxell Basin and McKnight Creek, Green Creek, Canada Stream and Canada Flush. Image taken on 01/17/2010. © Google Earth

Figure 3.4. Satellite image of McKnight Creek and the sampling locations. Image taken on 01/17/2010. © Google Earth

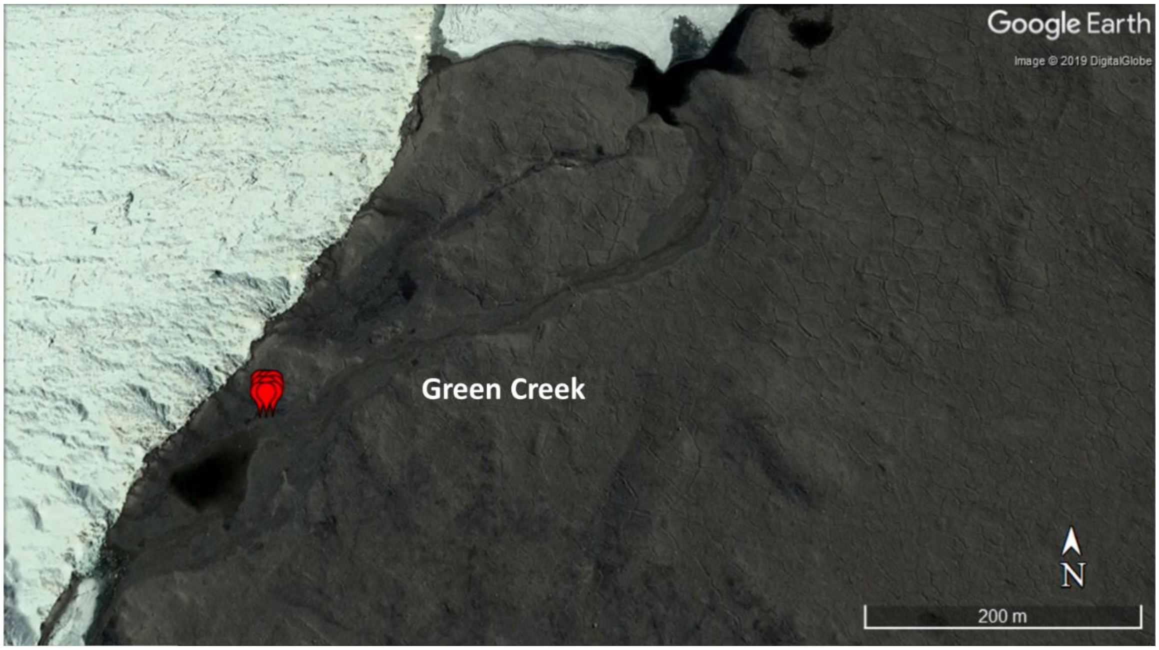

Figure 3.5. Satellite image of Green Creek and the sampling locations. Image taken on 01/17/2010. © Google Earth

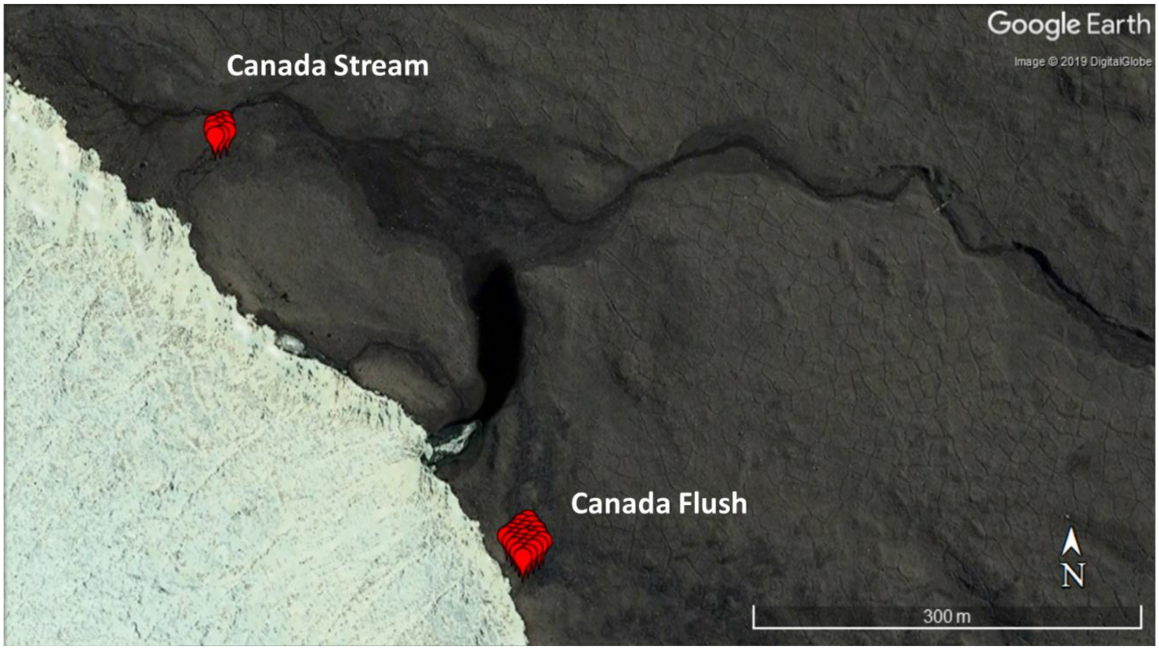

Figure 3.6. Satellite image of the Canada Glacier ASPA and the two sites: Canada Stream and Canada Flush. Image taken on 01/17/2010. © Google Earth

Figure 3.7. Satellite image of Bonney Riegel between the west and east lobe of Lake Bonney, including Wormherder Creek sample location. Image taken on 12/21/2013. © Google Earth

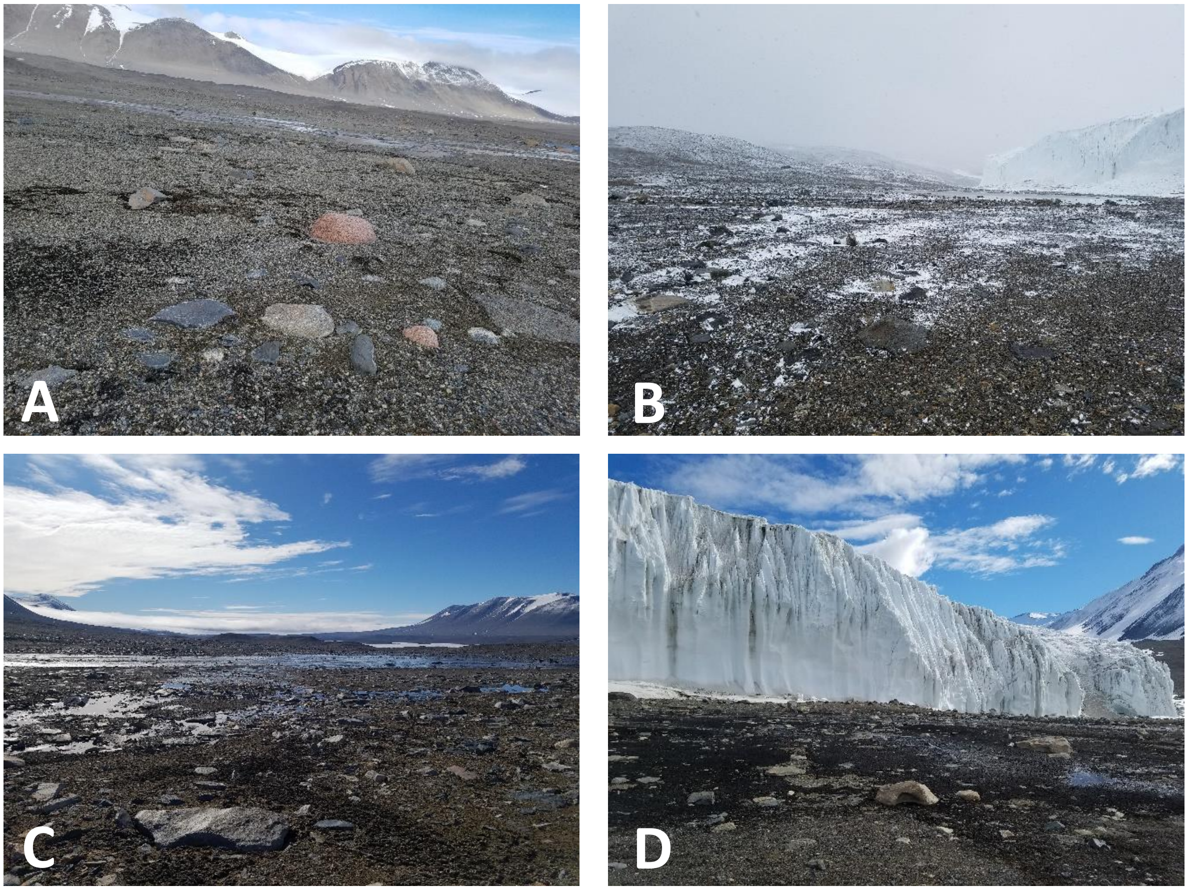

Figure 3.8. Study locations within Lake Fryxell Basin: **A.** McKnight Creek, **B.** Green Creek, **C.** Canada Stream, and **D.** Canada Flush. Photos taken by Sarah Power.

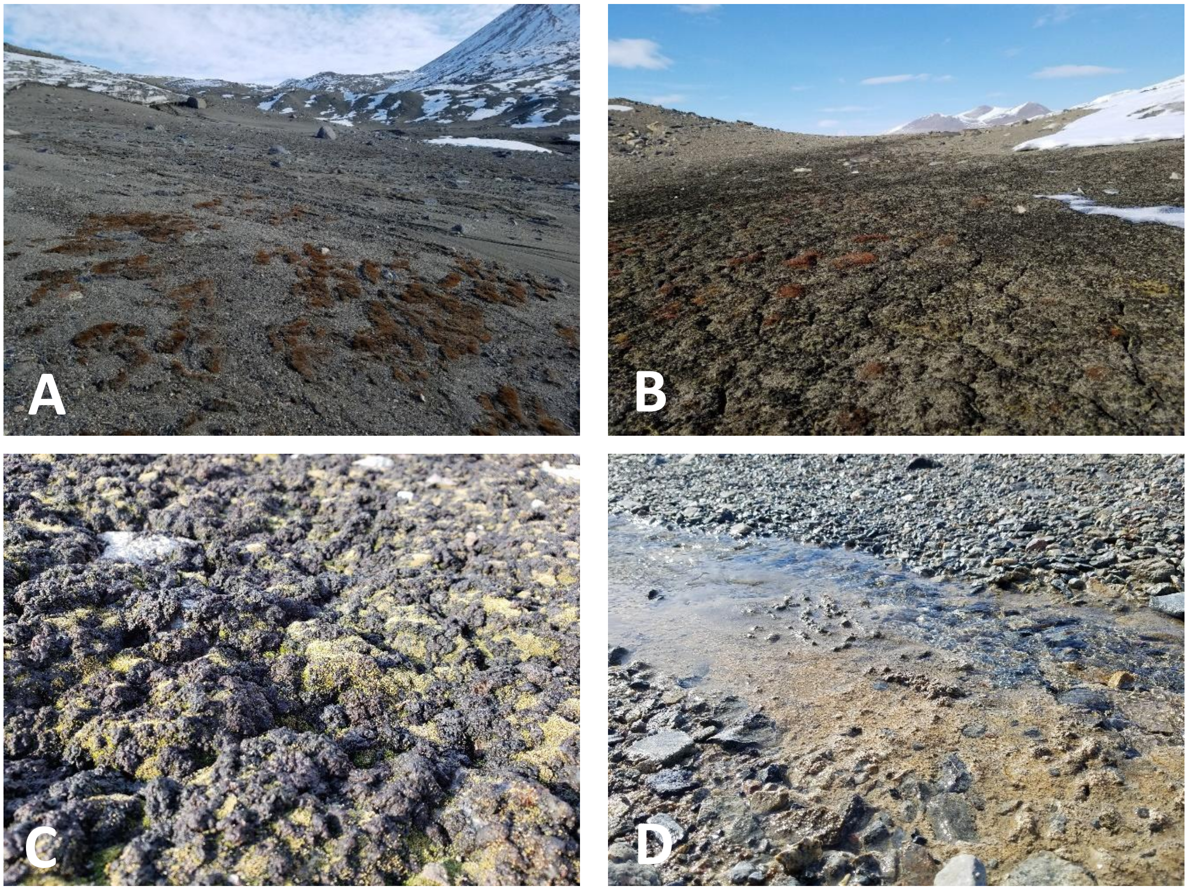

Figure 3.9. Vegetation types sampled at study sites: **A.** Red moss (*Hennediella heimii*) at Hjorth Hill, **B.** Black mat (*Nostoc*), red moss (*Hennediella heimii*) and green moss (*Bryum*) at Hjorth Hill, **C.** Green moss (*Bryum*) with epiphytic black mat (*Nostoc*) on top at Canada Flush, and **D.** Orange mat (*Oscillatoria*) at Wormherder Creek. Photos taken by Sarah Power.

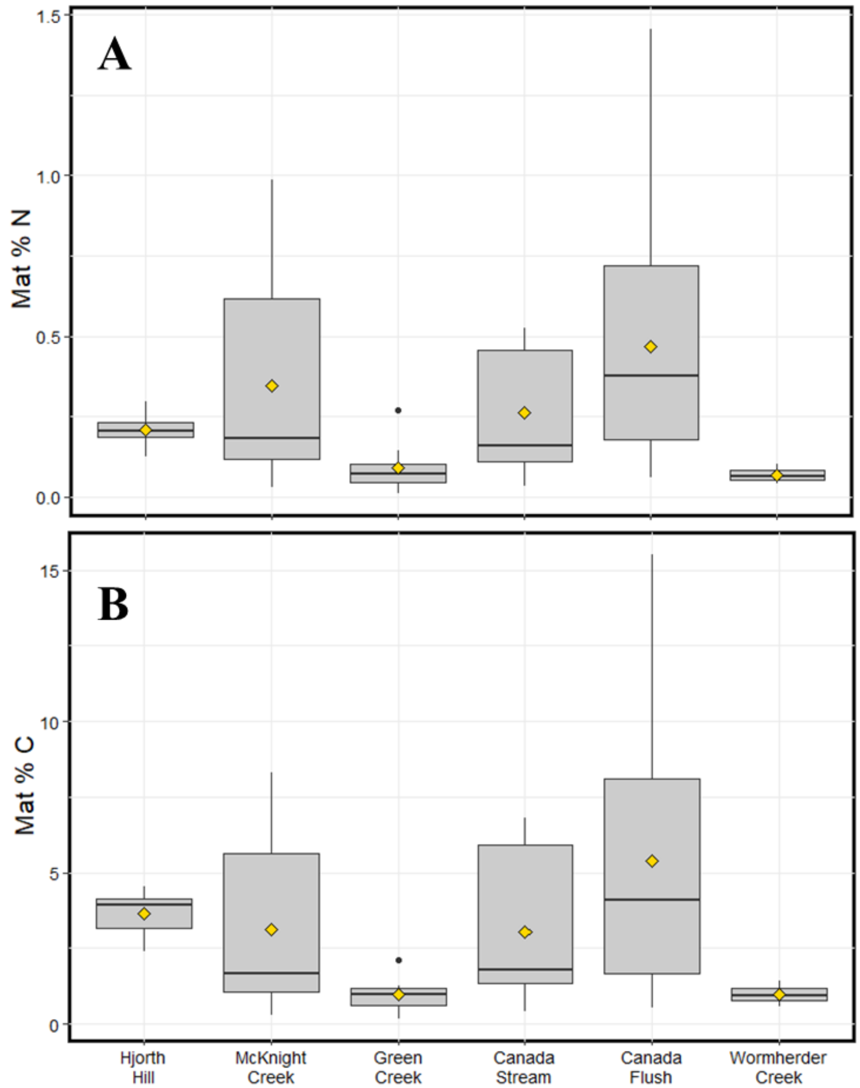

Figure 3.10. Microbial mat elemental composition: **A.** Percent N by weight and **B.** Percent C by weight for each study site oriented east to west. Gold diamonds indicate the averages per site. Black points indicate outliers defined as 1.5*interquartile range (IQR).

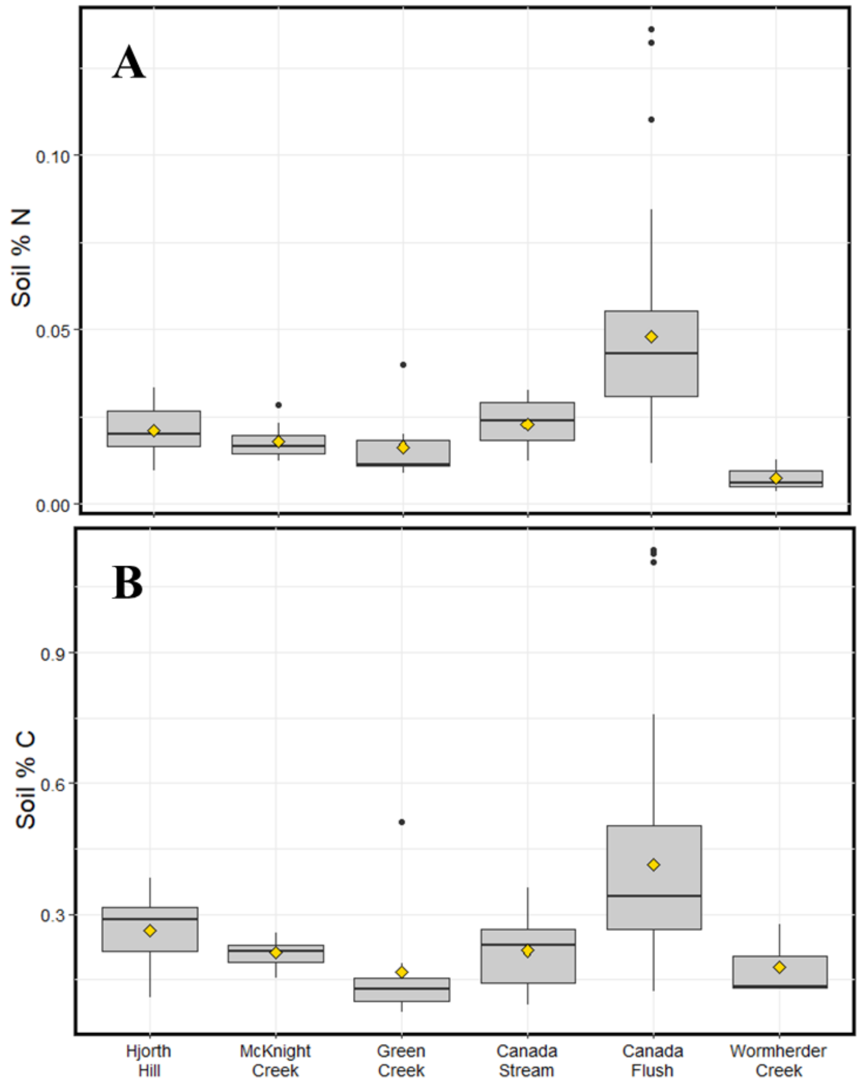

Figure 3.11. Soil elemental composition: **A.** Percent N by weight and **B.** Percent C by weight for each study site oriented east to west. Gold diamonds indicate the averages per site. Black points indicate outliers defined as 1.5*IQR.

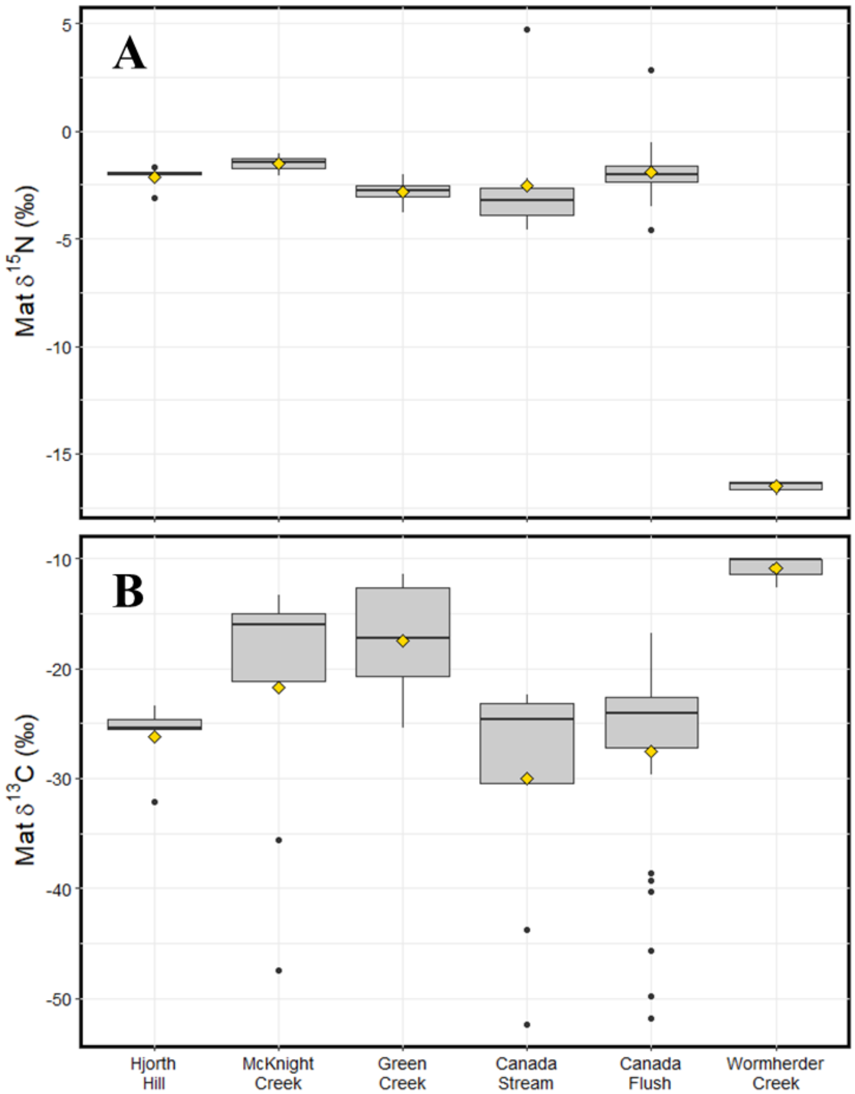

Figure 3.12. Microbial mat isotopic composition: **A.** $\delta^{15}N$ in ‰ and **B.** $\delta^{13}C$ in ‰ for each study site oriented east to west. Gold diamonds indicate the averages per site. Black points indicate outliers defined as 1.5*IQR. This figure excludes one mat $\delta^{15}N$ value from the Canada Flush was > 4 standard deviations away from the mean.

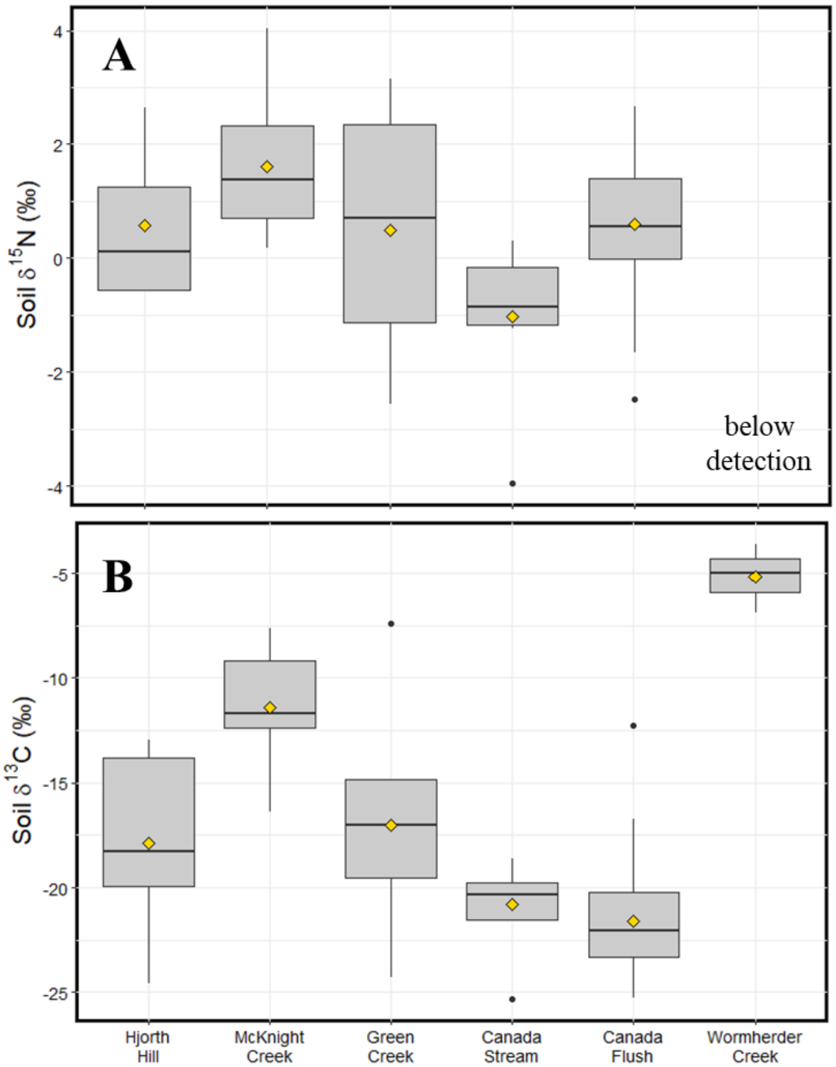

Figure 3.13. Soil isotopic composition: **A.** $\delta^{15}N$ in ‰ and **B.** $\delta^{13}C$ in ‰ for each study site oriented east to west. Gold diamonds indicate the averages per site. Black points indicate outliers defined as 1.5*IQR. Wormherder Creek soil samples were too low in % N to reliably quantify soil $\delta^{15}N$ values, so these values are not included in panel A.

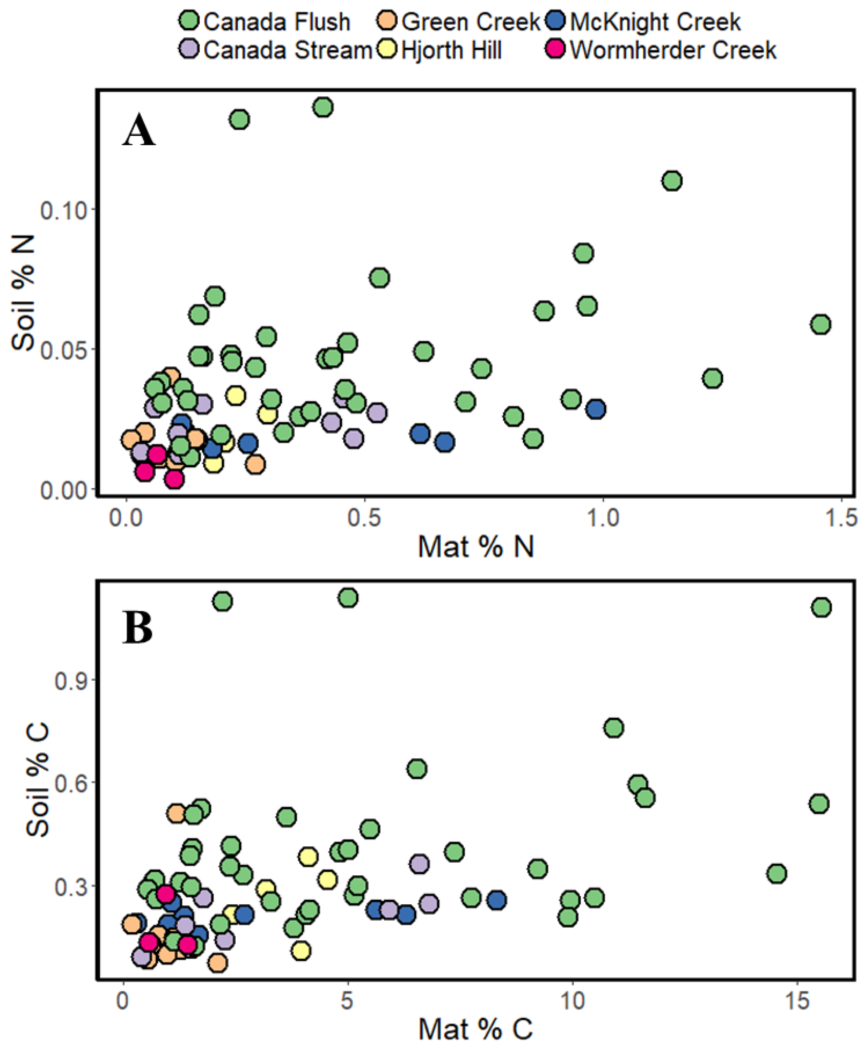

Figure 3.14. Comparison of elemental composition: **A.** Soil % N and microbial mat % N by weight and **B.** Soil % C and microbial mat % C by weight.

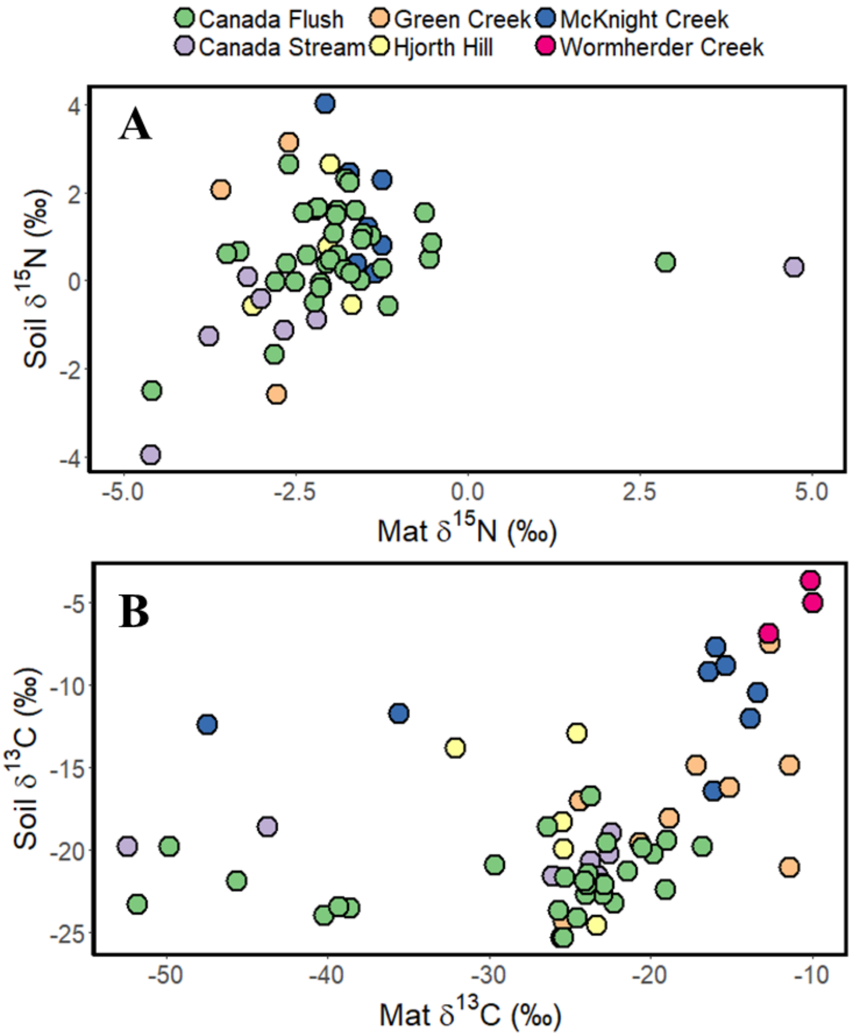

Figure 3.15. Comparison of isotopic composition: **A.** Soil $\delta^{15}N$ and microbial mat $\delta^{15}N$ in ‰ and **B.** Soil $\delta^{13}C$ and microbial mat $\delta^{13}C$ in ‰. Wormherder Creek soil samples were too low in % N to reliably quantify soil $\delta^{15}N$ values, so these values are not included in panel A.

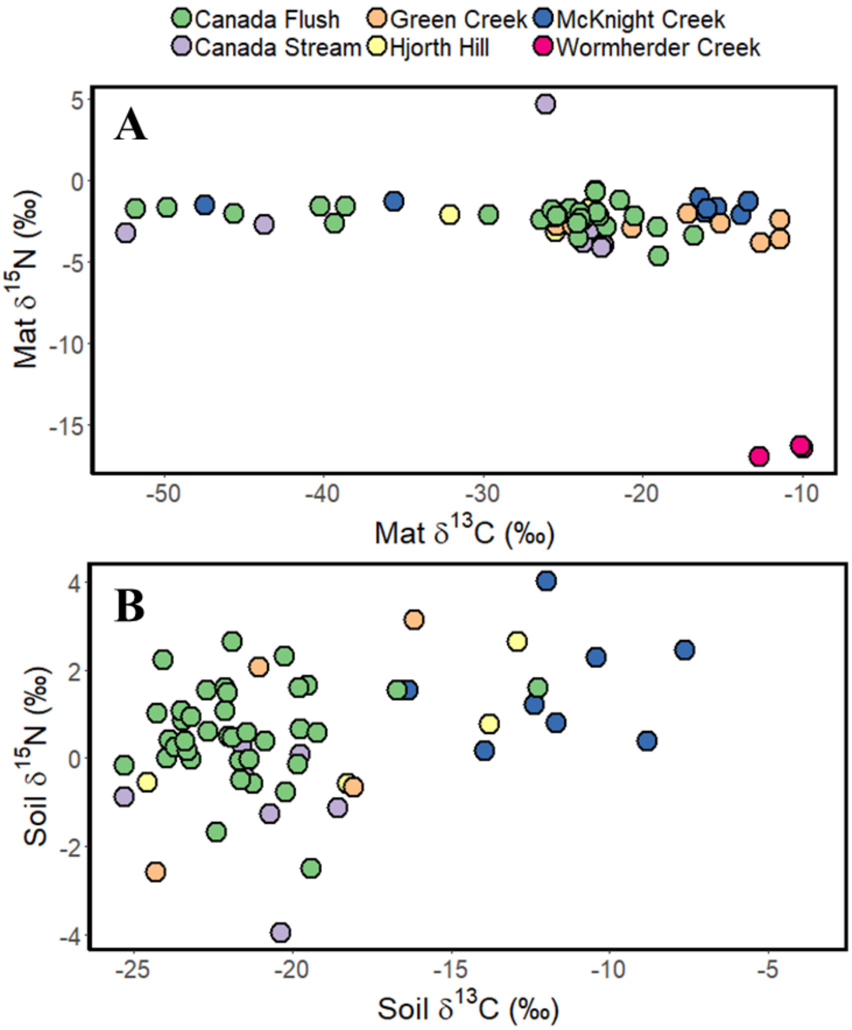

Figure 3.16. Comparison of isotopic composition: **A.** Microbial mat $\delta^{15}N$ and $\delta^{13}C$ in ‰ and **B.** Soil $\delta^{15}N$ and $\delta^{13}C$ in ‰. Wormherder Creek soil samples were too low in % N to reliably quantify soil $\delta^{15}N$ values, so these values are not included in panel B.

CHAPTER 4: CONCLUSION

This work has demonstrated the importance of terrestrial microbial mat communities on carbon (C) and nitrogen (N) fixation in Taylor Valley, Antarctica. Dense microbial mat communities are visible in the red and near-infrared wavelengths in satellite imagery. The strong correlations between NDVI and percent cover, biomass, and pigment content demonstrate that satellite imagery is highly effective at detecting and estimating the biomass of microbial mat communities in the McMurdo Dry Valleys (MDV). The C values presented here are the first biomass estimates for this region of Antarctica using satellite imagery. These biomass inventory estimates suggest that while stream channels and glacial wetlands are hot-spots of organic matter, there are significant amounts of organic matter outside of stream channels. This remote sensing application for detecting and estimating microbial mat abundance and activity, once validated, could be scaled to provide inventories of terrestrial C pools for the whole Lake Fryxell Basin, Taylor Valley, and potentially the entirety of the McMurdo Dry Valleys. My continuing research is working towards the creation and validation of a remote sensing tool that will allow systematic estimation of the distribution *and* activity of terrestrial microbial mats in the MDV. Future work will aim to relate climatic events (*e.g.*, high flow events) from the past (using archived satellite imagery) to determine how microbial mats respond to inter-annual climate variation and also potentially forecast how these primary producers may be affected in the future by a changing climate.

Microbial mats were also shown to have significant effects on soil and sediment biogeochemical cycling. The majority of the microbial mats I examined had $\delta^{15}N$ signatures indicative of a biological N fixation source for their N content; however, there were depleted signatures also, indicating some amount of abiotic N sourcing. Microbial mats do have a significant impact on the underlying soil C and N budgets, which is important because this system is so limited in C and N. Sources of N supporting microbial mats depend on the functional capacity of the microbial community and the landscape history of the environment where they occur.

There is a considerable lapse in our understanding of biogeochemical cycling in polar ecosystems and hot deserts, due to the difficulty in measuring sparse, patchy vegetation. A lack of systematic temporal and spatial records of terrestrial productivity hinders our ability to assess long-term microbial mat dynamics from responses to short- and long-term environmental changes in many desert and polar regions. However, this research demonstrates the importance of microbial mats on biogeochemical cycling, the need for long-term spatially extensive primary productivity estimates, and the utility and promise of remote sensing as a method to monitor microbial mat communities in polar regions.