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Resolving Functional Resilience of Microbial Communities to Climate-Induced Change

in the McMurdo Dry Valleys of Antarctica

A thesis

submitted in fulfilment

of the requirements for the degree

of

Doctor of Philosophy in Biological Sciences

at

The University of Waikato

by

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2022

Statement of Authorship

I hereby declare that this is a submission of my own work, and to the best of my knowledge does not contain material that has been previously published by another individual, nor has it been used for the awarding of another degree.

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Thesis Abstract

The McMurdo Dry Valleys of Antarctica are an abiotically driven ecosystem characterized by having a very simple trophic structure dominated by microbial communities, whose diversity is shaped by extreme abiotic gradients, particularly extreme aridity and oligotrophy. Regional isolation and dispersal limitations have concurrently led to the emergence of heterogeneous microbial communities with highly localized dominant taxa across the region. These taxa were selected based on specialized genetic and physiological adaptations accumulated during long-term isolation, which conferred an advantage to endure the physical and chemical stress. Models predict that over the coming decades, climate change will trigger hydrological changes in the system with potential consequences for its microbial communities and, subsequently, ecosystem-level processes. The capacity of the Antarctic microbiome to absorb change while maintaining its structural and/or functional attributes will determine the extent to which predicted environmental changes will threaten the system's stability.

This research starts by developing and validating a space-for-time sampling approach using variations in geochemical factors that follow alterations in water availability as time progresses and to which biological communities respond. This approach was replicated across the six major lakes in the Wright and Taylor valleys, and builds on previous examples of environmental gradients, which used arbitrary distance-based metrics as sampling design, incorporating significant yet uncharacterized *in situ* geochemical variability. The approach developed here enabled the acquisition of a comprehensive dataset that predicts, with confidence, that future hydrological changes will significantly alter the composition and diversity of microbial communities historically adapted to arid and oligotrophic conditions. The latter will result in significant changes in the metabolic activity of pathways associated with carbon, nitrogen, phosphorous and sulphur cycles, with an increase in functional diversity and activity as the system becomes wetter. This work further provides first time evidence that carbon fixation via atmospheric chemosynthesis is the primary active pathway for carbon acquisition under extreme aridity in polar deserts, being replaced by photosynthetic carbon fixation with prolonged exposure to wetness.

To complement predictions made *in situ* using a space-for-time approach, this research incorporated temporal observations using manipulative experiments, performed in a Polar Desert Environmental Chamber (PDEC), to test the sensitivity and resilience of microbial communities to short-term wetting disturbances. It demonstrated that co-existing microbial taxa respond asynchronously during wetting and drying periods, which indicates dry soil communities comprise co-existing taxa with preferences for different environmental conditions. It also experimentally showed, for the first time, the capacity of microbial communities from this region to recover from short-term wetting events associated with the ability of dry-adapted taxa, mostly affiliated with Actinobacteriota and Acidobacteria phyla, to persist during the wetting period.

Through the incorporation of large-scale spatial transects in conjunction with manipulative experiments, this research delivered a fundamental evidence-based anticipation of the compositional and functional aspects that are likely to change in the McMurdo Dry Valleys ecosystem in response to alterations in water dynamics as well as on the microbial attributes that enhance the ecosystem's functional resilience to climate change.

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CHAPTER I

Introduction and Literature Review

1 .1 Introduction

The impacts of disturbance on ecosystems are of considerable interest among ecologists. Yet, one of the most significant conundrums in ecology remains unanswered: the relationship between biodiversity, function, and ecosystem stability. Ecosystems are structured according to the interplay of different ecological factors, which include biotic interactions, environmental selection, and stochastic events, acting at different temporal and spatial scales. For the vast majority of the terrestrial ecosystems around the globe (e.g., tropical and temperate forests, grasslands, agricultural fields, among others), these ecological factors are constantly affecting complex relationships established between historical and contemporary environmental conditions and microbial communities, viruses, and a wide diversity of eukaryotic life. Nonetheless, such trophic complexity makes it challenging to de-couple and therefore understand the role of microbial communities in conferring biological stability to an ecosystem. Constituting about 15% of the global biomass (Bar-On et al. 2018) and being considered the life support system of the biosphere, bridging above and below-ground ecosystem interactions (Stevnbak et al. 2012; Cavicchioli et al. 2019), the resilience of microbial communities to environmental change is a crucial part of a complex process that determines the stability of an ecosystem to disturbances. It is therefore essential to assess the properties and mechanisms that drive the response of the ecosystem's microbiome to environmental disturbances and how it may impact its functioning and resilience to environmental change.

Ecosystems with low trophic complexity represent, arguably, the best scenarios to study microbial resilience to environmental change. The Antarctic continent, in particular, is a cold and remote place, where some regions haven't gone through significant environmental changes over the last centuries (Convey 2010). The geographic isolation combined with strong gradients of environmental variability and hostile conditions determined how life has evolved

and adapted to a wide range of niches, resulting in the diversity of organisms, functional traits, and strategies currently observed in the system (Cary et al. 2010; Thibault et al. 2012; Lebre et al. 2017, 2021; Ortiz et al. 2021). Terrestrial Antarctic ecosystems, particularly, are an attractive model system since the great majority if its area is depauperate of vertebrates and plants, being instead dominated by very simple (mostly microbial) and well-adapted organisms that can persist and establish under extreme polar environmental conditions.

The Antarctic continent is considered one of the most sensitive regions to climate change (Convey 2010) with its predictable consequences being a subject of intense scientific scrutiny for the last few decades (Shaw et al. 2014; Hughes et al. 2015b, c; Wauchope et al. 2019). The high number of endemic species observed even at regional scales and the specialized genetic and physiological adaptations accumulated during long term isolation put them at increased risk from potential invasive species as a result of increased connectivity between different Antarctic bioregions (Lee et al. 2017b). However, current knowledge on how Antarctic terrestrial systems function and whether changes in environmental factors that regulate biological diversity will affect the current functional stability of the system is still scarce. Until recently, the concept of resilience has been rarely assessed in Antarctic regions, and the structural and functional changes in microbial communities have rarely been accounted for as part of Environmental Impact Assessments required by the Protocol on Environmental Protection to the Antarctic Treaty (Hughes et al. 2015b). Yet, the simplicity and intact nature of Antarctic terrestrial ecosystems, make these ideal to develop hypotheses and a framework to study the ecological functioning in this region, which will help to better predict the effects of climate change and human activities in Antarctica.

This literature review is divided into six sections. It starts with an overview of the multiple concepts of resilience followed by an explanation of why the McMurdo Dry Valleys are a model system to study resilience. It then describes recent signs of change observed in the McMurdo Dry Valleys and the sensitivity of microbial communities to those contemporary environmental changes. It also summarises the current understanding of the functional attributes of the McMurdo Dry Valleys terrestrial microbiome, giving a perspective of the role of metagenomic and metatranscriptomic studies in advancing our insights regarding the functionality of the terrestrial microbiome. It then concludes by presenting the proposed approach with the primary goals and discusses the properties of microbial communities that confer stability and resilience to an ecosystem, as well as the ecological methods used to

measure resilience such as the use of space-for-time approaches in conjunction with manipulative experiments.

1.2 Defining resilience in ecological systems

The concept of resilience has multiple definitions with no current agreement (Gunderson 2000). Yet, in ecological studies, resilience is viewed as an insurance against the loss of valued functions in the system when a disturbance occurs (Thrush et al. 2009). As such, defining this concept is essential to understand and predict the system's response to undesirable changes (Downes et al. 2013). In natural sciences, the definition of resilience often reflects one of two concepts: "engineering resilience" or "ecological resilience" (Holling 1973; Pimm 1984), depending on whether the system is assumed to have one global stable state or multiple stable states (Figure 1).

Engineering resilience takes one unique stable state so that when the system is disturbed, resilience represents its ability to recover from the disturbance and return to its pre-disturbance condition (Pimm 1984). A study performed by Shade et al. (2012) is an example of using this concept where ARISA fingerprints showed that bacterial communities sampled from a lake epilimnion and hypolimnion changed after those layers were mixed, but were able to recover to a pre-disturbance state as abiotic conditions such s temperature and oxygen were restored (Shade et al. 2012). Another example was the recovery of one individual’s gut microbiome after prolonged travel and change in diets (David et al. 2014).

Ecological resilience, developed by Holling, assumes that ecosystems go through multiple stable states driven by environmental changes, biological colonization, or stochastic events (Holling 1973). According to Holling's concept, resilience is defined as the magnitude of disturbance that an ecosystem can absorb before it shifts into a new stable state (Holling 1973; Gunderson 2000). For example, during a rainfall manipulation experiment the composition of microbial communities supplemented by natural rain showed minimal and short-loved shifts compared to the ambient controls, despite profound treatment-related changes in the overlying grassland (Cruz-Martínez et al. 2009).

Despite the proposals of unifying engineering and ecological concepts of resilience (Song et al. 2015), there is no current one-size-fits-all definition of resilience. Therefore the concept should be defined and optimized considering the research question, ecosystem’s

dynamics, type of disturbance, and the time frame dedicated to the study (Botton et al. 2006; Shade et al. 2012; Song et al. 2015).

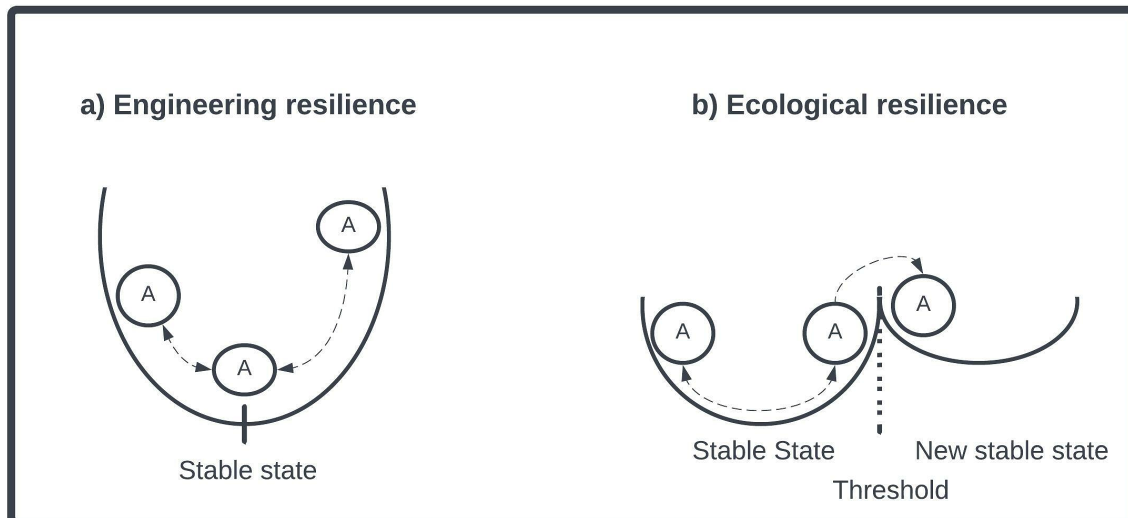

Figure 1 - Schematic representation of **(a)** engineering resilience and **(b)** ecological resilience (adapted from Sterk et al. 2017). Engineering resilience (a) assumes that systems have one stable state, therefore it is defined as the system's ability to recover to its pre-disturbance state. Ecological resilience (b) assumes that ecosystems go through different stable states and it is defined as the amount of disturbance that an ecosystem can withstand before shifting into a new stable state.

1.3 Antarctic ice-free regions: the McMurdo Dry Valleys a model system to study resilience

Antarctic ice-free regions are a portrait of nature at its most simple state. The pristine and distinct landscape comprises mountain ranges, ice-covered lakes, streams, ponds, glaciers, and heterogeneous soils (Figure 2) (Cary et al. 2010). These regions are highly regarded areas for ecological conservation and protection within the Antarctic continent (Shaw et al. 2014), since they harbor almost the entirety of the continent's biodiversity (Convey 2010; Lee et al. 2017b). Ice-free regions comprise about 0.3% of the Antarctic continent and cover coastal areas and small regions scattered within the continent. The largest site is the McMurdo Dry Valleys (MDVs) in Victoria Land (Terauds et al. 2012).

The McMurdo Dry Valleys are a polar desert with a mean annual temperature of -15 to -30 °C, with daily temperature fluctuations greater than 20°C (Cary et al. 2010). The soils are highly arid, oligotrophic, and salty partly due to low precipitation (3-50 mm mainly in the form of snow) and strong katabatic winds that trigger evaporation and sublimation of the falling snow (Cary et al. 2010). The majority of water in the system is generated from the melt of glacier surfaces, being subsequently fed into the system through ephemeral streams leading to ice-covered lakes (Fountain et al. 1999). Underneath the surface soil lies a vast layer of permafrost, mainly in the ice-cemented or dried frozen forms (Bockheim et al. 2007). The active layer depth is correlated with the climate, ranging from < 20 cm to 70 cm depending on the elevation and proximity to the coast (Campbell and Claridge 2006; Fountain et al. 2014). The sublimation of moisture from ice-cemented permafrost contributes to ice loss from the soils to the atmosphere (Fountain et al. 2014). The rate of this physical process depends on the air temperature, relative humidity, wind speed, sediment moisture, solar radiation, and particle surface area (Law and Van Dijk 1994), and it can lead to significant topographic and hydrological changes in the terrestrial systems (Fountain et al. 2014).

The landscape of the MDVs resembles an ecosystem at the first stages of colonization, displaying a very simple trophic structure where vascular plants or vertebrates are absent (Figure 2). The low liquid water availability (typically < 2% mass water content) and geographical isolation hamper the colonization, establishment, and persistence of complex organisms (Convey and Smith 2005), only allowing for endemic, mostly microbial and microinvertebrate species to persist as a result of years of adaptation to extreme weather conditions. In this abiotically driven system, the capacity for adaptation to local environmental conditions plays a more significant role than biotic interactions between species (Lee et al. 2019). As a result, we can expect that early warning signs of change will be primarily given by alterations in endemic species' composition and functioning as a response to changes in environmental conditions that they respond to.

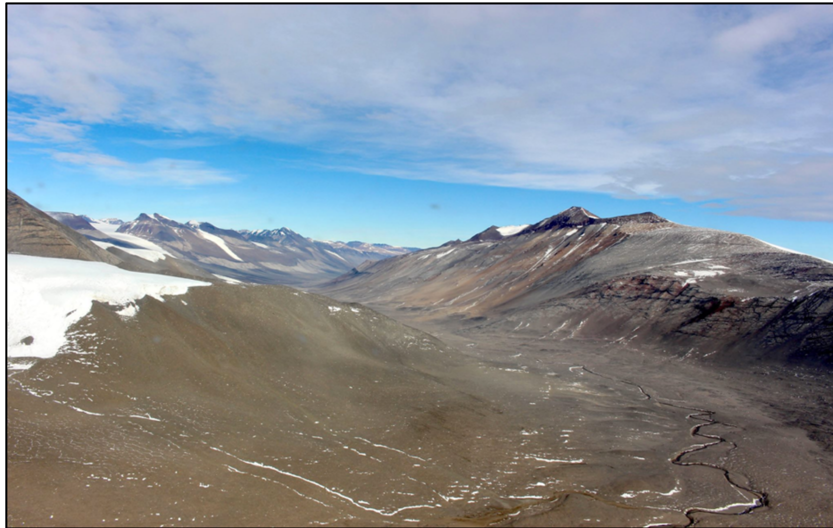

Figure 2-Wright Valley and Onyx River pictured in the McMurdo Dry Valleys, Victoria Land, Antarctica (Maria Monteiro, 2016).

1.4 Signs of change in Antarctic ice-free regions

The Antarctic continent has undergone colossal climatic and ecological changes, which aligns with Holling's concept of system stability over geological temporal scales. Biotic and organic geochemical climate proxies suggest that approximately 55 to 48 million years ago, parts of the Antarctic continent were a forest due to the lower temperature gradients between the poles and the equator and higher CO_2 levels in the atmosphere (Pross et al. 2012). Nonetheless, for at least last 15 million years, Antarctica has been a "white continent". Despite the apparent visual stability, the continent is changing prompted by climate change (Fountain et al. 2014, 2016; Levy et al. 2018).

According to the Intergovernmental Panel on Climate Change, ice loss from Antarctica's ice sheet has tripled over the past decade (IPCC, 2021). The continued ice melting and glacier retreat due to warming trends could lead to an expansion of Antarctic ice-free areas by up to 25% by the end of this century. Such events will increase the connectivity between different Antarctic regions, which poses a significant threat to native populations that have been isolated for extended periods and could be outcompeted by new colonizers (Hughes et al. 2015a; Lee et al. 2017a; Siegert et al. 2019).

In the Antarctic Peninsula, the increase in temperature and moisture led to a significant increase in biological activity and biomass prompted by the growth of moss, an increase in fungal diversity, and the establishment of non-native plant species (Chown et al. 2012; Newsham et al. 2016; Amesbury et al. 2017). This occurrence has been referenced as the "greening effect" (Amesbury et al. 2017), and it is expected to increase if warming trends continue at 0.56°C per decade as in the past 50 years (Turner et al. 2005).

In the McMurdo Dry Valleys, local climate changes impact the system's hydrology, which is tightly connected to its ecology (Fountain et al. 2014; Gooseff et al. 2017; Lyons et al. 2021). Extreme warm events have been triggering the melting of glacier surfaces and glacier runoff (Bergstrom et al. 2021), the increase in the stream water flux, the melt of buried ice (Lyons et al. 2021), and the expansion of closed-basin lakes across the region (Castendyk et al. 2016; Levy et al. 2018). The consequent expansion of wet zones and increased meltwater supply will significantly impact the landscape and stability of terrestrial biota, which has been highly adapted to historical aridity (Gooseff et al. 2017; Bergstrom et al. 2021). For instance, nutrients and minerals previously deposited in the dried soil and ice will be leached by increased water flows, altering conductivity and pH gradients (Barrett et al. 2009). The increase in water availability and the consequent geochemical changes in the soils will likely impact the structural and functional *status quo* of the system with the possible loss of endemic dry-adapted organisms (Van Horn et al. 2014; Niederberger et al. 2015; Hughes et al. 2015a; Buelow et al. 2016; Niederberger et al. 2019; Monteiro et al. 2022). The capacity of the Antarctic microbiome to absorb change while maintaining its structural and/or functional attributes will determine the extent to which predicted environmental changes will threaten the system's stability.

1.5 Microbial communities as sentinels of change in the McMurdo Dry Valleys

Antarctic soils were considered inhospitable for a long time (Flint and Stout 1960). However, with the implementation of culture-independent studies by Norman Pace (Pace et al. 1986), it was quickly understood that the Antarctic terrestrial ecosystems harbor a great microbial diversity, well established and adapted to face the extreme polar conditions (Niederberger et al. 2008; Casanueva et al. 2010).

The most abundant phyla present in the soils belong to Actinobacteria, Cyanobacteria,

Bacteroidetes, Acidobacteria, and Proteobacteria (Cary et al. 2010). Nevertheless, many organisms routinely sequenced still have an unknown taxonomical classification (Lambrechts et al. 2019). The distribution and composition of microbial communities diverge at both fine and large scales (Aislabie et al. 2006; Niederberger et al. 2008; Cowan et al. 2011a; Lee et al. 2012; Sokol et al. 2013; Chong et al. 2015) due to contemporary and historical abiotic gradients present in the soils. Water availability is regarded as the primary driver of community diversity in the MDVs polar deserts (Niederberger et al. 2015; Bottos et al. 2020; Monteiro et al. 2022), and it is also positively linked to increased photosynthetic primary productivity (McKnight et al. 2007; Wood et al. 2008). Moreover, changes in conductivity, pH, and UV radiation have also been found to affect the distribution and diversity of the terrestrial microbiome (Aislabie et al. 2008, 2012; Chong et al. 2012; Lee et al. 2012; Stomeo et al. 2012; Sokol et al. 2013; Van Horn et al. 2014; Bottos et al. 2020). Despite the MDVs being mostly abiotically driven (Bottos et al. 2020), Cyanobacteria diversity has been linked with increased fungal and multicellular diversity (Lee et al. 2019), which emphasizes the role of these primary producers in the structure of these ecosystems. Wind and water dynamics influence the diversity of Cyanobacteria across the landscape (Sokol et al. 2013) and the presence of water on their activity (McKnight et al. 2007). Wind dispersal also has a significant role in microbial dispersion, particularly in those adapted to long-range dispersal, such as spore-forming bacteria like Firmicutes (Bottos et al. 2014). Still, most of the Antarctic “airborne” community seems to be poorly correlated with the local community (Archer et al. 2019). Therefore, although the dispersal mechanism may have a significant role in the dispersion of specific microbial taxa, geochemistry still plays an essential role in establishing most microbial taxa.

A few studies have demonstrated how sensitive and fast responding the MDV terrestrial microbiome is to environmental disturbances (McKnight et al. 2007; Tiao et al. 2012; Buelow et al. 2016; Niederberger et al. 2019). McKnight et al. (2007) observed an increase in primary productivity one week after a former dried cyanobacterial mat was re-hydrated. The transplantation of a mummified seal carcass in the MDV revealed the capacity of the Antarctic soil microbiome to respond quickly (i.e., within a few years) to alterations in relative humidity with consequences to local diversity (Tiao et al. 2012). More recently, *in situ* wetting experiments showed fast compositional and structural changes in the dry-adapted soil microbiome when water was added to the soils, with the increase in taxa affiliated to Bacteroidota, Acidobacteria and Cyanobacteria (Buelow et al. 2016; Niederberger et al. 2019).

The above examples demonstrate the capability of Antarctic terrestrial microbial communities to respond quickly to alterations in the environment, which to some extent demonstrate a possibility for them to be used as biological sentinels for change in the system (Shade et al. 2012). Additionally, some studies also reported a decrease in diversity after the disturbance (Tiao et al. 2012; Buelow et al. 2016), which can have consequences to the functioning of the ecosystem unless a level of functional redundancy is present within the community. Otherwise, changes in community composition may modify important ecosystem processes, such as the compositional shifts observed within nitrifying communities, during a drought experiment, which lead to increases in nitrification N_2O emission rates at the end of the drought period (Séneca et al. 2020). It is then important to understand how changes in community composition may affect the system's functioning and stability.

1.6 Functional attributes of the McMurdo Dry Valleys terrestrial microbiome

Most MDV studies have primarily focused on the structural attributes of microbial communities. One main reason has been methodological difficulties in extracting DNA and RNA from low-biomass soils. Nonetheless, the development of DNA/RNA extraction and sequencing kits for low biomass samples, with the advances in metagenomic and metatranscriptomic techniques, have started to reveal the functional attributes of polar desert microbial communities (Zaikova et al. 2019; Zoumplis et al. 2023).

Amplicon sequencing targeting functional or phylogenetic genes in combination with measurements of biological processes (e.g. N-fixation rates), and experimental assays, provided a glimpse into the role, distribution and diversity of distinct microbial functional groups in the soils. For instance, the analysis of *nifH* gene abundance demonstrated that heterotrophic diazotrophs make a significant contribution to N_2 fixation in the MDV soils (Niederberger et al. 2012; Coyne et al. 2020). While autotrophic Cyanobacteria appear to be the first colonizers in wet environments, over time, with increased stability and biomass, heterotrophic diazotrophs will play a significant role in expanding the functional capacity of sourcing nitrogen into the system, possibly contributing to functional redundancy of the community (Coyne et al. 2020). Another functional screening across different Antarctic habitats found the presence of genes and taxa involved in denitrification and nitrification pathways (Chan et al. 2013), with the latter being primarily driven by either Bacteria or

Archaea depending on the environmental conditions (Magalhães et al. 2014; Monteiro et al. 2020).

With metagenome sequencing, a non-targeted sequencing approach of the community's DNA, we are now able to move forward from a targeted approach of specific functional groups to a more comprehensive functional profile of a given community. For instance, a comparative metagenomic study revealed that genes involved in stress response pathways, such as osmotic shock tolerance, radiation stress, and nutrient depletion, were found to be relatively abundant in MDV samples (Fierer et al. 2012; Ortiz et al. 2020). In contrast, genes involved with antibiotic resistance were poorly represented (Fierer et al. 2012). This result indicates that in an extreme abiotically driven system, microbial competition is less important than acquiring adaptations that allow long-term survival (Fierer et al. 2012; Chan et al. 2013). Metagenomic studies and activity assays have also demonstrated that diverse bacteria inhabiting polar desert soils can maintain their energy needs by scavenging trace gases (H_2, CO_2, and CO) from the atmosphere and fixing carbon through the Calvin-Benson-Bassham cycle (Ji et al. 2017a; Ortiz et al. 2021; Ray et al. 2022). It is understood that hydrogen-oxidizing and CO-oxidizing pathways support primary production in the oligotrophic dry soils, where photosynthetic producers are not abundant or present, and therefore helping to sustain the heterotrophic members of the community (Ortiz et al. 2021).

Despite the progress achieved by metagenomic studies, a few hurdles still need to be addressed. First, the vast majority of Antarctic microorganisms are thought to be inactive, dormant, or able to alternate between different metabolic pathways (Lambrechts et al. 2019). As such, just because a particular pathway is present in the dataset doesn't necessarily mean it is active. That leads to the possibility that the DNA from non-viable cells can still be extracted, sequenced, and annotated (Carini et al. 2016). The use of metatranscriptomics can partially alleviate this hurdle by explicitly targeting the viable and active part of the community. In other words, it provides a snapshot of the gene expression pattern of a community under the influence of a specific environmental condition in a given particular sample and given time point.

Nonetheless, the interpretation of metatranscriptomics needs to be contextualized since the signals expressed by the community might reflect an immediate response to a daily environmental variation or even to the sampling procedure and not necessarily the functional state of the sample under a particular disturbance. Therefore it would be necessary to de-couple what might be an immediate response of the community towards a transient change from the

actual functions of the community under a specific particular state of change. The combination of metagenomic and metatranscriptomic datasets would likely deliver the best results as it can reveal the functional potential of a community layered with functional activity linked to specific taxa (Aguiar-Pulido et al. 2016). For instance, a "multi-*omics*" study performed with Antarctic paleomats showed that these may contain viable and non-dormant bacteria with diverse metabolic functions, mainly related to stress response and DNA repair, which can be understood as a sign of resilience (Zaikova et al. 2019a).

Yet, several drawbacks to metagenomic and metatranscriptomic studies still need to be accounted for before extrapolating information or drawing conclusions. For instance, we cannot assume that nucleic acids are extracted equally from each cell, and complete coverage of all genes from a community is not yet achievable (Hart et al. 2015). Genes are still being misannotated, databases are incomplete, and we are still limited by the genes and functions we know based on cultivated microorganisms (Prosser et al. 2015).

1.7 Framework to study resilience in the MDVs

1.7.1 Measuring resilience in a slow-changing ecosystem

Long-term monitoring studies are critical to monitor different processes in the natural environment and generate broad spatial and temporal scale datasets that help further science and environmental policy (Kratz et al. 2003a; Rustad 2008a). Moreover, monitoring studies are essential for discovering unusual or extreme events and detecting an altered response pattern over time, helping formulate questions and providing a context for developing better experimental designs. Nonetheless, conducting these studies in Antarctica demands considerable logistic and funding efforts and significant institutional and collaborative commitments to be sustained (Convey and Peck 2019). Moreover, permit restrictions and the long-lasting impacts of human presence in the soils (O’Neill et al. 2015) impose significant limitations on the performance of experimental field manipulations in parts of the continent. For the those reasons, it is necessary to find complementary strategies to long-term studies to help anticipate the consequences of predicted environmental change in the functioning of polar desert ecosystems.

1.7.2 Space-for-Time approaches

Space-for-time approaches use existing environmental gradients representative of past or future environments as time progresses. It is based on the assumption that spatial and temporal variation is equivalent (Pickett 1989). This approach has been primarily used to study ecological succession patterns across several environments (e.g. plant succession) and soil development dynamics (Johnson and Miyanishi 1979; Walker et al. 2010a; Blois et al. 2013). More recently, it also has been adopted in microbial ecology studies (Yang et al. 2014; Yan et al. 2017; Colby et al. 2020). Nonetheless, ecosystems can be shaped by many processes independent of time or environmental change. Factors such as daily environmental variation or stochastic events which can affect microbial communities may reduce the reliability of space-for-time approaches (Blois et al. 2013). Moreover, the covariance of several independent environmental factors, which cannot be controlled for during spatial analyses or might not even be accounted for, may vary more across space than through time. Therefore, space-for-time approaches underperform when the trajectory of change is variable, when the rate of change is too quick or when the records of environmental change in the system have been poorly recorded (Johnson and Miyanishi 1979; Wogan and Wang 2018)

In polar regions, space-for-time approaches have been previously applied to study the effect of soil exposure during glacial retreat, and the relationship between the stage of development of the soil with the structure of microbial communities (Aislabie et al. 2012; Mateos-Rivera et al. 2018). These previous examples implied the use of transects, mostly using a distance-based metric as sampling design, which incorporates significant yet uncharacterised *in situ* geochemical variability. Without knowledge of the ecological niche characteristics or empirical measurements of key deterministic drivers of community distribution along the gradient, reflective of the temporal change of interest, this approach can mislead the interpretation of the results. Alternatively, this same approach could focus on smaller-scale variations of specific environmental factors that communities respond to, also representative of predicted changes in the system (Cummings et al. 2018). As mentioned before, changes in the local climate have triggered hydrologic responses across the MDVs, which have the potential to alter geochemical gradients in the soils with impacts on biological communities (Barrett et al. 2009). Wetness gradients, for instance, can be used to validate the space-for-time sampling approach to assess the impacts of climate-related hydrological changes on the terrestrial microbiome in the MDVs. Characterizing the structural and functional elements of

microbial communities along those gradients and identifying the level of functional redundancy within dry to wet-like communities can help predict the resilience of MDV ecosystems to future increases in water availability.

1.7.3 Manipulative experiments

Experimental manipulations are a standard approach to studying ecological and causal relationships. It requires a description of the experimental settings before the disturbance and a time set for when the disturbance occurs. Therefore, experimental manipulations are often described as "before-after-control-impact" (Shade et al. 2012a; De Palma et al. 2018) and can be designed to test the effect of a single or multiple factors and their interactions during “pulse” or “press” disturbances, assuming that each factor is independent (Shade et al. 2012a).

When coupled with process rate measurements, time-series experiments provide significant insight into the response of biological communities to a range of stressors, therefore becoming ideal to test the broad nature of resilience of Antarctic communities and offering unlimited opportunities for hypothesis testing. The majority of manipulative experiments conducted in Antarctic soils were performed *in situ* with the most significant studies involving warming and wetting simulations (Tiao et al. 2012; Ball and Virginia 2014; Buelow et al. 2016; Niederberger et al. 2019). Nonetheless, the performance of field manipulative experiments faces several challenges. Firstly, it is limited by permit restrictions ,and requires substantial logistic and personal efforts. For instance, the duration of the experiment can be restricted by tight time frames allocated to field access and it often requires the presence of researches on-site throughout the experiment (Niederberger et al. 2019). These can significantly limit any continuous monitoring of biological response to the disturbance that is being tested. Otherwise, if the experiments need to be run over long periods of time, they will most likely need to be left unattended in remote locations year-round without control for unpredictable events (McKnight et al. 2007; Tiao et al. 2012), which increases the risk of results being misinterpreted. Secondly, comparative to long-term monitoring programs, or space-for-time approaches, the spatial extent of the manipulation is often limited. Therefore, generalized assumptions should be made with caution since results may not be representative of patterns and processes occurring at larger spatial scales (De Palma et al. 2018). Lastly, methodological

limitations or the lack of proper simulation of the predicted disturbance has introduced inconsistent results, decreasing the reliability of past studies (Convey and Smith 2005).

Perhaps the best practice is to use multiple methods of observation (e.g. long-term observations, space-for-time approaches and manipulative experiments) (Figure 3), while taking advantage of their differences. In other words, inferences made by one method should be validated from data using other methods. The latter will contribute to comparable and more detailed observations, and increase confidence and reliability in the results interpretation, broadening the scope of the information that will become available.

1.7.4 Microbial attributes that confer resilience to environmental disturbances

As mentioned at the start of this review, despite the multiple definitions of resilience, several taxonomic and functional attributes of microbial communities can still be used as proxies for increased resilience to environmental disturbance (Allison and Martiny 2008; Shade et al. 2012a; Philippot et al. 2021).

Historically, biodiversity has been strongly associated with increased resilience and stability of an ecosystem (Oliver et al. 2015a, b). This consensus, first developed by macro-ecological studies, is known as the insurance hypothesis. It stems from the principle that the higher the number of species, the better the chances are that ecological processes are provisioned by different species, despite possible compositional changes (Yachi and Loreau 1999). Considering the abundance and diversity of microorganisms in an ecosystem and their role in their functioning (Cavicchioli et al. 2019), it is essential to consider how microbial biodiversity affects ecosystem processes. Studies have demonstrated that microbial diversity enhances functional diversity and stability in terrestrial ecosystems (Delgado-Baquerizo et al. 2016; Feng et al. 2017; Wu et al. 2022). However, the relationship between microbial diversity and resilience isn't always clear (Wertz et al. 2007; Roger et al. 2016). Different factors, such as the level of functional redundancy within specific functional microbial guilds, species interactions, life-history strategies, historical contingencies, or even how microbial diversity is experimentally manipulated, can drive different conclusions (Bardgett and Caruso 2020b). For instance, Wertz et al (2007) reported that a decrease in diversity did not affect the resilience of denitrifiers and nitrite-oxidizing communities (Wertz et al. 2007). However, the study used a series of dilutions to manipulate bacterial diversity and equalize it across different treatments.

Such an approach often requires a regrowth phase, which could favour the growth of opportunistic species. Additionally, it used a random elimination of microbial species, which may not be representative of a real scenario where environmental factors constitute critical selective filters on microbial communities.

Functional redundancy, here defined as the ability of a process being carried out at the same rate by different taxa, can be observed when compositional changes observed in response to a disturbance do not reflect functional changes in the ecosystem (Louca et al. 2018a). It is, however, difficult to characterize functional redundancy at the microbial community level since microbial processes are more likely to be redundant than others, depending on the genetic complexity of the trait (Martiny et al. 2013a). For instance, complex metabolic pathways such as photosynthesis are more phylogenetically conserved (Nelson and Ben-Shem 2004) than those related to nutrient assimilation, respiration, and decomposition traits, which involve a few gene clusters (Martiny et al. 2013a). As such, the association between community composition and functional redundancy could depend on the phylogenetic distribution of a particular functional trait and the selective effect of environmental changes on that trait. However, there is still limited knowledge about the distribution of functional traits across different taxa due to the lack of genomic and physiological information from most microorganisms (Fierer et al. 2014). For example, the metabolic capability of Archaea to oxidise ammonia has only been discovered in the past fifteen years (Könneke et al. 2005). Similarly, the ability to fixate carbon through hydrogen oxidation (atmospheric chemosynthesis) has only recently been discovered as a widespread process occurring across several ecosystems (Ray et al. 2022).

Recently, trait-based approaches have been given more consideration for the outcome of resilience research (Fierer et al. 2014; Malik et al. 2020). The functioning, stability, and resilience of microbial communities depend on the metabolic activity and life-history strategies employed by the community members, which can be shaped by ecological interactions, historical contingencies, and stochastic or deterministic environmental variability at both spatial and temporal scales (Bardgett and Caruso 2020b). Life-history strategies correspond to a set of metabolic and physiological traits associated with resource and energy acquisition for cellular activity (e.g., metabolic pathways related to C, N, and P cycles), stress resistance (e.g., sporulation, dormancy, DNA-repair) and growth (rRNA operon copy numbers) (Roller et al. 2016). Different traits can be favoured under different environmental conditions, which

highlight the trade-offs underpinning soil community coexistence (Polz and Cordero 2016). For instance, these can be observed in the form of asynchronous species responses to perturbations (Evans and Wallenstein 2014). Some studies have gone to the extent of classifying microbes as opportunistic, sensitive, and tolerant, while others have proposed the terms copiotrophs and oligotrophs (derived from R-K strategies developed in macro ecological studies) based on growth rates and resource use efficiency (Fierer et al. 2007; Evans and Wallenstein 2014). It is expected that under conditions of high stress, such as oligotrophy, aridity, or high UV radiation, those who allocate most of their energetic resources into stress-tolerance traits or the regulation of metabolic pathways toward more efficient use of specific resources at the cost of rapid will prevail. Identifying genomic features related to these life-history strategies, concurrently involved with the maintenance of ecological processes and mechanisms that help to reduce local extinctions, can help provide clues into an ecosystems' resilience to environmental change.

1.8 Research Chapters and Goals

The research presented in this thesis was carried out as part of an NZARI Type-B collaborative research programme focused on the resilience of Antarctic biota and ecosystems. This thesis is focused on understanding the stability and resilience of Antarctic terrestrial ecosystems from a microbial compositional and functional perspective. The goal is to provide novel insights into the attributes of microbial communities considered to be related to the ecosystem resilience and to give a functional perspective of the impacts of climate change on the McMurdo Dry Valleys ecosystems.

The chapters in this thesis have been prepared in a publication format, with chapter 2 published, chapter 3 currently under review, and chapter 4 in preparation for submission. An overview of the following chapters is outlined below:

Chapter II presents the development and validation of a space-for-time sampling approach to assess the impacts of climate-related hydrological changes on the terrestrial microbiome in a polar desert. The latter was performed by sampling 15 geochemically defined wetness gradients from the shore of four closed-basin and two open-basin lakes across the Wright and Taylor valleys. We demonstrated that predictions of a wetter system will directly affect the stability of microbial communities historically adapted to ultra-aridity and

oligotrophy by altering significantly the composition and diversity of these communities. We also demonstrated that contemporary and historical changes in water availability can be resolved by subtle structural and compositional re-arrangements of microbial communities along geochemically defined environmental gradients. These observations could only be depicted when sampling approaches are determined by the spatial variability of geochemical drivers along environmental gradients and replicated across comparable environments that differ in historical exposure to the driving factor.

This chapter has been published in *Frontiers in Microbiology* as:

Monteiro MR, Marshall AJ, Hawes I, et al (2022) Geochemically Defined Space-for-Time Transects Successfully Capture Microbial Dynamics Along Lacustrine Chronosequences in a Polar Desert. Front. Microbiol. 12

Chapter III validates the ability to perform off-continent manipulative experiments using a Polar Desert Environmental Chamber (PDEC) to study the impacts of environmental change on biological communities from the McMurdo Dry Valleys. Our goal was to test in laboratory conditions the response of microbial communities to a wetting and re-drying event and compare the observed response with field observations, including the observations and predictions made using a space-for-time approach. Work of this kind has the potential to expand the ability to perform temporal experiments and address predictions for biological response to single or multiple disturbances without the temporal, logistic, and permit constraints, or the anthropogenic impacts associated with field-based work. We demonstrated that coexisting taxa with different environmental preferences (e.g. affiliated to Actinobacteriota, Proteobacteria, Acidobacteria and Bacteroidota phyla) initially drive fast compositional shifts in dry soils. The latter offers insights into the diversity of metabolic functions and strategies inherent in the MDV terrestrial microbiome. We further demonstrated that compositional changes during four weeks of wetting were not permanent, with the conservation of drought-resistant taxa underpinning resilient communities that oscillates in response to a periodic wetting/re-drying event.

This chapter has been published in the journal *Polar Biology* as:

Monteiro, M.R., Marshall, A.J., Lee, C.K. et al. (2023) Bringing Antarctica to the lab: a polar desert environmental chamber to study the response of Antarctic microbial communities to climate change. *Polar Biol*.46

Chapter IV focused on the community's functional aspects that are likely to change in response to the increase in water availability. It further aims to identify functional attributes of microbial communities that regulate the resilience of abiotically driven terrestrial systems to climate change. This chapter combined metagenomic and metatranscriptomic sequencing to assess the functional potential and functional activity of metabolic and stress-response pathways along the defined wetness gradients from the stable Lake Brownworth. It demonstrated that the increase in water availability will increase microbial functional richness and activity of pathways associated with Carbon, Nitrogen and Phosphorous acquisition. It also identified levels of functional redundancy and metabolic plasticity within the community as well as a wide range of traits linked to stress tolerance to multiple abiotic stresses. Those attributes are associated with increased microbial resilience to environmental disturbances. It further showed that, under dry conditions, carbon fixation is mainly regulated by Actinobacteriota through atmospheric chemosynthesis. As the soils become wetter, this process carbon is mainly fixed by photosynthesis regulated by Cyanobacteria. This chapter currently under preparation to be submitted for publication.

Chapter V highlights general conclusions and presents future directions from this work.

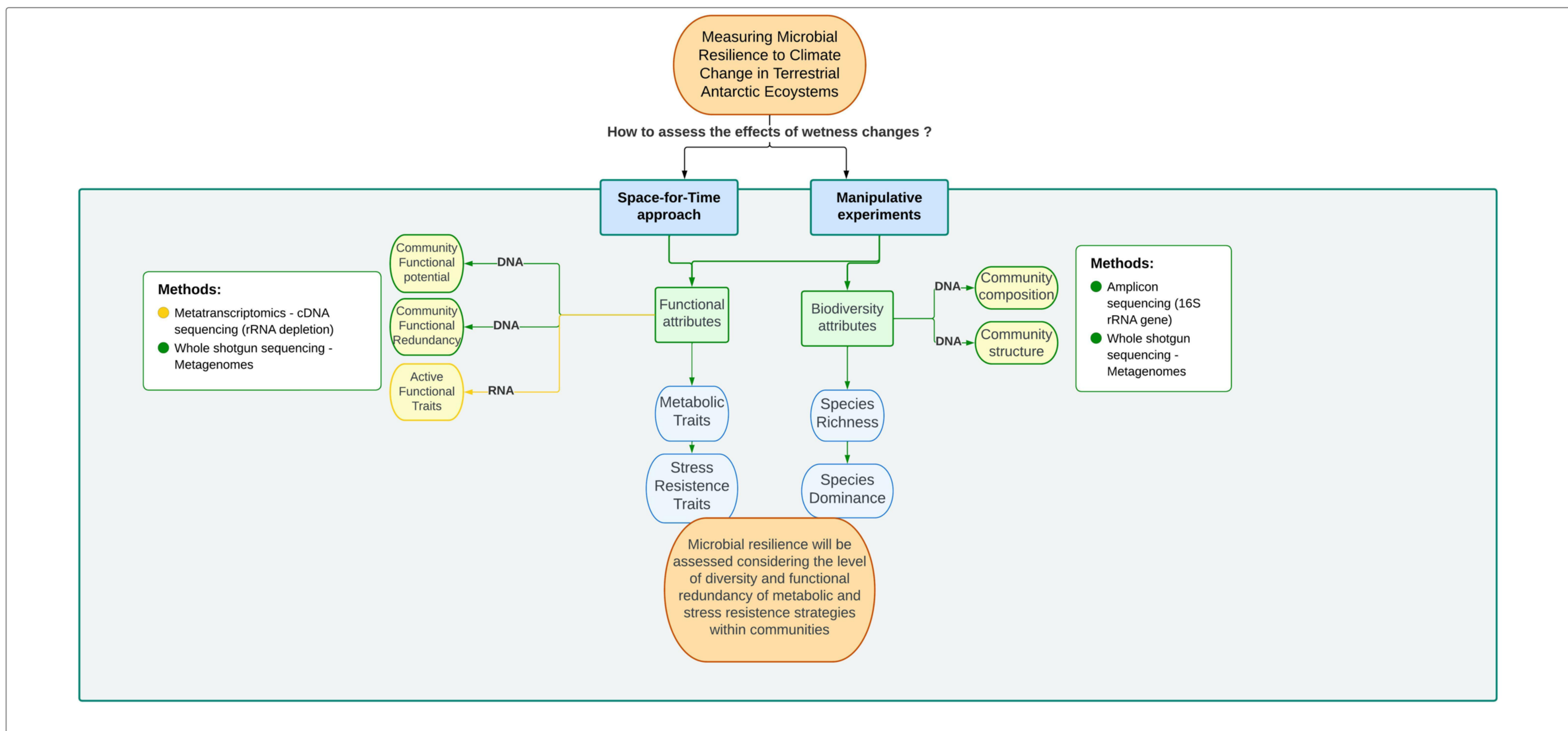

Figure 3 – Proposed framework to study resilience in the McMurdo Dry Valleys.

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CHAPTER II

Geochemically defined space-for-time transects successfully capture microbial dynamics along lacustrine chronosequences in a polar desert.

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2.1 - Abstract

The space-for-time substitution approach provides a valuable empirical assessment to infer temporal effects of disturbance from spatial gradients. Applied to predict the response of different ecosystems under current climate change scenarios, it remains poorly tested in microbial ecology studies, partly due to the trophic complexity of the ecosystems typically studied. The McMurdo Dry Valleys of Antarctica represent a trophically simple polar desert projected to experience drastic changes in water availability under current climate change scenarios. We used this ideal model system to develop and validate a microbial space-for-time sampling approach, using the variation of geochemical profiles that follow alterations in water availability and reflect past changes in the system. Our framework measured soil electrical conductivity, pH, and water activity in situ to geochemically define 17 space-for-time transects from the shores of four dynamic and two static Dry Valley lakes. We identified microbial taxa that are consistently responsive to changes in wetness in the soils and reliably associated with long-term dry or wet edaphic conditions. Comparisons between transects defined at static (open-basin) and dynamic (closed-basin) lakes highlighted the capacity for geochemically defined space-for-time gradients to identify lasting deterministic impacts of historical changes in water presence on the structure and diversity of extant microbial communities. We highlight the potential for geochemically defined space-for-time transects to resolve legacy impacts of environmental change when used in conjunction with static and dynamic scenarios, and to inform future environmental scenarios through changes in the microbial community structure, composition, and diversity.

2.2 – Introduction

Long-term ecological observations provide valuable information for studying the impacts of climate change. They form excellent resources to detect climate trends and patterns over time, study slow or highly variable ecological processes, validate modelled predictions of change, and support environmental policies (Kratz et al. 2003b; Rustad 2008b). However, the maintenance of these continuous observations is generally dependent on long-term financial and logistic security from local institutions and governments. When time and funding are a constraint, or when long-term studies are not feasible, space-for-time substitution models are an attractive alternative to forecast long-term climate impacts on ecosystems (Blois et al. 2013).

Space-for-time substitution approaches, such as ecological chronosequences, rely on the assumption that factors responsible for spatial turnover in species abundance are similar to those responsible for temporal turnover (Pickett 1989; Wogan and Wang 2018). First used to study plant succession and soil development (Pickett 1989; Johnson and Miyanishi 2008; Walker et al. 2010b), it has recently been adapted to predict impacts of climate change on microbial communities (Wilhelm et al. 2013; Yang et al. 2014; Yan et al. 2017; Colby et al. 2020). However, despite its common use, the reliability of this approach has been questioned, particularly when its primary assumption is not met or tested (Blois et al. 2013; Damgaard 2019). For instance, deterministic and stochastic processes can both affect how different microbial groups assemble over different space and time scales (Caruso et al. 2011). Therefore, space-for-time sampling designs should consider the scale and history of the sampling site and discuss the legacy impacts left by historical processes that have known lasting effects on microbial communities (Chase and Myers 2011; Dini-Andreote et al. 2015; Zhou and Ning 2017). Without *a priori* knowledge of the ecological niche characteristics or empirical measurements that constrain the deterministic drivers of species variation, space-for-time sampling approaches may lead to a naive interpretation of the community, missing spatial/temporal context, and impairing any comparisons between replicated gradients. Ideally, to validate the use of this approach to assess the temporal effects of climate change on an ecosystem's microbiome, a baseline study is required in an ecosystem that lacks trophic complexity and includes well-characterized deterministic gradients of species distribution.

The McMurdo Dry Valleys (MDV) are the largest ice-free area in Antarctica and represent one of Earth's coldest and driest regions (Cary et al. 2010). These polar deserts exhibit high spatial variability in geochemistry, climate, and landscape characteristics, resulting in a

patchy distribution of a simple and unique biota functionally dominated by microbial communities (Cary et al. 2010; Lee et al. 2012; Kwon et al. 2017; Feeser et al. 2018; Bottos et al. 2020). Since the environmental conditions select against the establishment of vascular plants and limit complex trophic interactions, the MDV represents an ideal natural laboratory to validate space-for-time as a tool to study climate-related disturbances on microbial communities. Recent changes in the local climate have triggered hydrologic responses across the MDV (Castendyk et al. 2016; Fountain et al. 2016; Levy et al. 2018). This is especially relevant in closed-basin lakes, which are described as lakes that do not have an outlet channel for water to flow out. Examples of these type of lakes include Lake Vanda, Lake Bonney, and Lake Fryxell in the Taylor and Wright Valleys, where the water level has risen (Castendyk et al. 2016; Levy et al. 2018). Water level rise triggers the expansion of the adjacent wetted margins, which imposes selective pressures on the established microbial communities adapted to long-term dry conditions (Van Horn et al. 2014; Niederberger et al. 2015, 2019; Buelow et al. 2016; Lee et al. 2018; Coyne et al. 2020; Ramoneda Massague et al. 2021). Our work and others have previously used simplistic sampling approaches based on physical distance to better understand how microbial community diversity responds to geochemical changes along an environmental gradient (Yang et al. 2014; Niederberger et al. 2015; Yan et al. 2017; Feeser et al. 2018; Lee et al. 2018). These studies assume that geochemical variables along a gradient change gradually and linearly with distance. However, interacting environmental factors may not continuously change along a distance-based gradient (Kappes et al. 2010), nor are microbial communities randomly distributed along natural gradients, being continuously under the influence of deterministic, stochastic, or a combination of both processes.

In this study, our goal was to develop and validate a space-for-time sampling approach to assess the impacts of climate-related hydrological changes on the terrestrial microbiome in a polar desert, using a wetness gradient. We achieved this by determining whether extant microbial community attributes (e.g., changes in structure and diversity) across replicated geochemically defined space-for-time transects could reconstruct past wetting events within the MDV. To ensure the robustness of the transects, we first methodically characterized the spatial variability of local geochemical parameters (water activity, electrical conductivity, and pH) at the chosen sites. Transects were established across static (open-basin with outflow) and dynamic (closed-basin with no outflow) lakes to identify if the structure, diversity, and composition of the microbial community could be used to assess historic versus more recent impacts of water availability. Open-basin lakes are expected to be less impacted by increased

glacial meltwater and groundwater flow due to the presence of an outflow channel which drains the overflow. Therefore, wetted areas surrounding these lakes are expected to expand at lower rates and be more stable, comparatively to those surrounding closed-basin lakes which reflect more recent and predicted hydrological disturbances in the system (Castendyk et al. 2016). We demonstrate the strength of extant microbial community attributes for reconstructing past impacts of hydrological changes and support the capacity for space-for-time to be developed as a robust tool to understand future impacts of change under current climate warming scenarios.

2.3 - Material and Methods

2.3.1 - Site description, space-for-time transects, and sampling.

We geochemically defined seventeen space-for-time soil transects, representing a wetness gradient from the shores of six lakes during the 2016 and 2017 Antarctic field seasons. The lakes span the length of the Wright (Lake Brownworth and Lake Vanda) and Taylor (Spaulding Pond, Lake Fryxell, Lake Hoare, and Lake Bonney) valleys (Figure 1, Table 1). Lake Brownworth and Spaulding Pond are open-basin lakes, meaning that they have an outlet channel through which water flows out. The presence of the outlet regulates the water level in these lakes (Levy et al. 2018). Transects defined from these lakes are referred to in this study as static (as having more static water levels). Lakes Vanda, Fryxell, Bonney, and Hoare are closed-basin lakes, which do not have an outlet channel for water to flow out of the lake. The water levels in these lakes are dynamic on multiple time scales but, over the last 100 years, are thought to have been intermittently rising (Castendyk et al. 2016; Levy et al. 2018; Ramoneda Massague et al. 2021). Transects defined from these lakes are referred to in this study as dynamic (as having more dynamic water levels). For each lake, except for Lake Hoare, three space-for-time transects were defined along the wetness gradient. At Lake Hoare, only two transects were sampled due to snowfall while sampling.

In these soils, pH, electrical conductivity (EC) and water activity (WA) have been described in several studies as being the key drivers of community assembly in the MDV (Barret et al., 2009; Bottos et al., 2020; Niederberger et al., 2015, 2019; Feeser et al., 2018; George et al., 2021; Van Horn et al., 2014). These metrics were measured in the field to identify *in situ* geochemical gradients across transects from all water bodies within which three geochemical zones were identified (Table 1 and Supplementary Figure S2). This process

involved performing measurements with an average spacing of 50 cm from the existing water level within a transition zone to observe the natural variation of these geochemical variables along the wetness gradient (Supplementary Figure S1 and S2). The first zone represented a water-saturated wet zone characterized by comparatively higher water activity (average of 1) and the lowest electrical conductivity (138 ± 81 µS) (sampling point 1). With increasing distance from the lake shore, water content remained high, but conductivity increased several times (938 ± 1591 µS) (sampling points 2 and 3). This was used to define the second zone, representative of a transition zone. The third zone represented a dry zone, characterized by the lowest measured water activity and lower electrical conductivity (341 ± 443 µS) (sampling points 4 and 5).

Briefly, electrical conductivity and pH were determined from a 1:5 slurry of soil to Milli-Q water (Thermo Scientific Orion meter, USA) (Lee et al. 2012). Water activity was measured using a PawKit meter (AquaLab, NZ), following the manufacturer's instructions. Infield measurements of electrical conductivity and pH were confirmed under laboratory conditions using Thermo Scientific Orion meter and the same slurry technique, but with the addition of 0.5 mL of 0.01M $CaCl_2$ per sample (Minasny et al., 2011; Lee et al., 2012). Soil moisture content was determined according to Lee et al. (2012). The elevation of each sampling point along the transects was surveyed in relation to the lakeshore (sampling point 1) using a laser levelling system (Topcon Laser Systems, USA).

For microbial community analysis, we aseptically collected surface soil samples (top 2 cm) with a sterile spatula from the five geochemically predefined sampling points. Spatulas were washed and then sterilized with ethanol wipes between sampling points and sampling sites. In total, across the six lakes, seventeen space-for-time transects were sampled, resulting in 85 soil samples. Individual samples were thoroughly mixed in a sterile Whirl-Pak® bag and then distributed into sterile 50 mL Falcon tubes. Samples were initially stored in the field on ice for 24 hours before being transferred to dry ice and transported to Scott Base (the New Zealand Antarctic Research Station), where they were maintained a - 60°C until DNA extraction. The remaining samples in each Whirl-Pak® bag were used to confirm moisture content, electrical conductivity, and pH analysis under laboratory conditions. These samples were kept cold at 4 °C until processed.

2.3.2 - Microbial Community Analysis

Total DNA was extracted from approximately 1 g of soil using a modified version of the CTAB (cetyl-trimethyl-ammonium-bromide) bead-beating method (Coyne et al., 2001). For each batch of DNA extractions, a negative control was included to ensure the identification of possible contamination. DNA concentration was determined using the Qubit dsDNA HS Assay Kit (ThermoFisher Scientific, USA). The bacterial and archaeal microbial community was targeted through the V4 region of the 16S rRNA gene was amplified in triplicate using the fusion-primer set 515F/806R (Parada et al., 2016) and sequenced using Ion PGM chemistry. Briefly, 20 μL PCR reactions each contained: 1 ng of total DNA, dNTPs (240 μM), $MgCl_2$ (6 mM), bovine serum albumin (0.24 μM), forward and reverse fusion primers (0.2 μM), 1 U of Platinum Taq polymerase (Invitrogen Inc., Carlsbad, California) and PCR buffer (1.2×). The following PCR conditions were used: 94 ºC for 3 min, followed by 30 cycles at 94 ºC for 45 sec, 50 ºC for 1 min, 72 ºC for 1.5 min, and a final extension step at 72 ºC for 10 min. For each PCR run, negative amplification was confirmed for each DNA extraction batch control. Triplicate PCR amplicons were pooled, and the expected amplicon size was confirmed via electrophoresis with a 1% agarose TAE gel. PCR products were cleaned and each sample concentration was normalised with SequalPrep™ (ThermoFisher Scientific, USA). Normalised samples were pooled at an equimolar concentration into a single library for sequencing. Amplicon sequencing was performed using the Ion PGM™ System for Next Generation Sequencing (ThermoFisher Scientific, USA) at the Waikato DNA Sequencing Facility (University of Waikato, New Zealand).

Raw sequences were filtered with Ion PGM™ software to remove low-quality and polyclonal reads. The remaining sequences were processed using a combination of Mothur (v.1.40.5) and USEARCH 10 (v10.0.24) software (Schloss et al., 2009; Edgar, 2010, 2013). Forward and reverse primers were identified within the sequences and trimmed using the python script fastq_strip_barcode_relabel.py supplied by UPARSE (v10.0.240). Sequences without forward and reverse primers were discarded. The remaining sequences were trimmed based on the length and the number of homopolymers sourced by Mothur script (Schloss et al., 2009). All reads with expected error rates higher than 2.5 were discarded using USEARCH (Edgar, 2010), and all reads were truncated to 350 bp. Through dereplication, unique sequences were identified and their abundances quantified. Sequences were sorted, singletons removed, and the remaining sequences were clustered into representative OTUs using the UPARSE-

OTU algorithm combined with the GOLD database to detect and remove chimeras (Bernal et al., 2001; Edgar, 2013). Reads were finally clustered into operational taxonomic units (OTUs) using UCLUST with a similarity threshold of 97%. Sequences that did not map to any OTU were discarded. Taxonomy was inferred using SINA (v1.2.11) and the SILVA SSU database (v 138) (Pruesse et al. 2012). A 0.005% cutoff was applied to the raw OTU counts across the dataset to remove poorly represented OTUs (Bokulich et al. 2013). Filtered OTUs were subsequently removed from the sequence Fasta file. Sequences were aligned using a Multiple Alignment using Fast Fourier Transform with default settings (MAFFT v7.429-gimkl-2020a) and a phylogenetic tree was generated using FastTree (v2.1.11).

2.3.3 - Statistical analysis

All statistical and visualization analyses were computed in R (v3.5.2, R Core Team, 2000) using the following packages: phyloseq (v1.26.1) (McMurdie and Holmes 2013), vegan (v2.5) (Oksanen et al. 2012), picante (v1.8) (Kembel et al. 2010), ggplot2 (v3.2.1) (Wickham et al., 2016), ggpubr (v0.4.0), compositions (van den Boogaart and Tolosana-Delgado 2008), and randomForest (v4.6) (Liaw and Wiener, 2002). Alpha diversity was calculated on a non-rarefied dataset using richness and phylogenetic diversity (PD) indexes. Differences in library sizes were tested on both rarefied and non-rarefied data with no significant impact on the data interpretation. Diversity differences between transect zones and lakes were tested using one-way ANOVA. Normality assumptions were tested using a Shapiro-Wilk test, and the assumption of homogeneity of variances was tested using a Levene's test. For the relationship between the microbial diversity and the log transformed moisture content and electrical conductivity, correlation analyses (Pearson) were applied. For beta diversity analysis we transformed the data using a total sum normalization. Beta diversity was calculated using weighted UniFrac phylogenetic pairwise distances (Lozupone and Knight 2015) and visualized in a principal coordinates analysis (PCoA). A PERMANOVA analysis, using Adonis function in vegan package (Oksanen et al. 2012), tested the dissimilarities among communities from different groups (lakes, and zones within the wetness gradients). The variation between samples from the three wetness zones described along the transects was tested using a permutational multivariate analyses of dispersion (betadisp) from vegan package (Anderson et al. 2006). A Random Forest model (Liaw and Wiener 2001) was used to detect the most reliable and relevant top 20 OTUs to predict the different zones along the wetness gradients. Raw

counts were transformed using a centered log-ratio (clr) before classification and regression models. OTUs were selected based on the MeanDecreaseAccuracy values, which measures the extent to which a variable (OTU) improves the accuracy of the forest in predicting the classification. Higher values indicate that the OTU improves the prediction. To evaluate the phylogenetic community assembly among species within each sample we calculated the mean nearest taxon distance (MNTD) and the nearest taxon index (NTI) using "taxa.labels" null model, with 999 iterations, using the function 'ses.mntd' from the R package picante. The NTI was quantified as the number of standard deviations that the observed MNTD was from the mean of the MNTD null distribution, multiplying by -1. For a single community, observed NTI values > +2 or <–2 indicate phylogenetic clustering of species or phylogenetic overdispersion, respectively. NTI values between –2 and 2 usually indicates the influence of a stochastic assembly (Stegen et al. 2012). To compare community assembly processes along the moisture gradients, we calculated the Beta Nearest Taxon Index (βNTI). Following Stegen et al. (2013), the βNTI is the number of standard deviations that the observed beta mean nearest taxon distance (βMNTD) is from the mean of the null distribution. It indicates how much the observed difference between a pair of communities differs from a null distribution. Similarly to NTI, values > +2 or <–2 indicate phylogenetic clustering of species or phylogenetic overdispersion, respectively, while values between –2 and 2 usually indicates the influence of a stochastic assembly (Stegen et al. 2013). β-NTI pairwise comparisons were plotted against increasing differences in moisture content. A Euclidean distance matrix was calculated using pH, electrical conductivity, water activity, moisture content, and elevation log-transformed and normalized data. ANOSIM was performed on the resemblance matrix to test the significance of the dissimilarities between the predefined zones of the wetness gradients. Sampling locations were plotted using Quantarctica (v3.1) (Matsuoka et al., 2021).

2.4 - Results

2.4.1 - Characterisation of space-for-time wetness transects

Seventeen geochemically defined space-for-time transects were parametrized using measurements of elevation, soil moisture content, electrical conductivity, pH, and water activity from both dynamic (n = 11 transects; Lake Vanda, Lake Bonney, Lake Hoare, and Lake Fryxell) and static (n = 6 transects; Lake Brownworth and Spaulding Pond) lakes across the Wright and Taylor Valleys (Figure 1, Table 1). Across all transects, elevation increased

from wet (sampling point 1) to dry (sampling points 4 and 5) soils (from 0 to 135 ± 19 cm), and soil moisture content decreased in the same direction (from 17.25 ± 3.07 to 0.54 ± 0.54 %) (Figure 2, Table 1). Electrical conductivity was lowest in wet and dry soil samples (138 ± 81 µS and 341 ± 443 µS respectively), achieving the highest values and variation within the transition zone (938 ± 1591 µS) (Figure 2, Table 1). Water activity decreased from wet to dry soils in Lake Vanda, Lake Bonney, Lake Brownworth, and Lake Hoare and remained stable across the wetness gradient in Spaulding Pond and Lake Fryxell (Figure 2, Table 1). The variability in soil pH across the wetness gradients was lake-specific (Figure 2, Table 1). The significance of the distinction between the three wetness zones (wet, transition, and dry) was confirmed with non-parametric testing (ANOSIM, $R = 0.69$, p-value < 0.01, 999 permutations) (Figure S3).

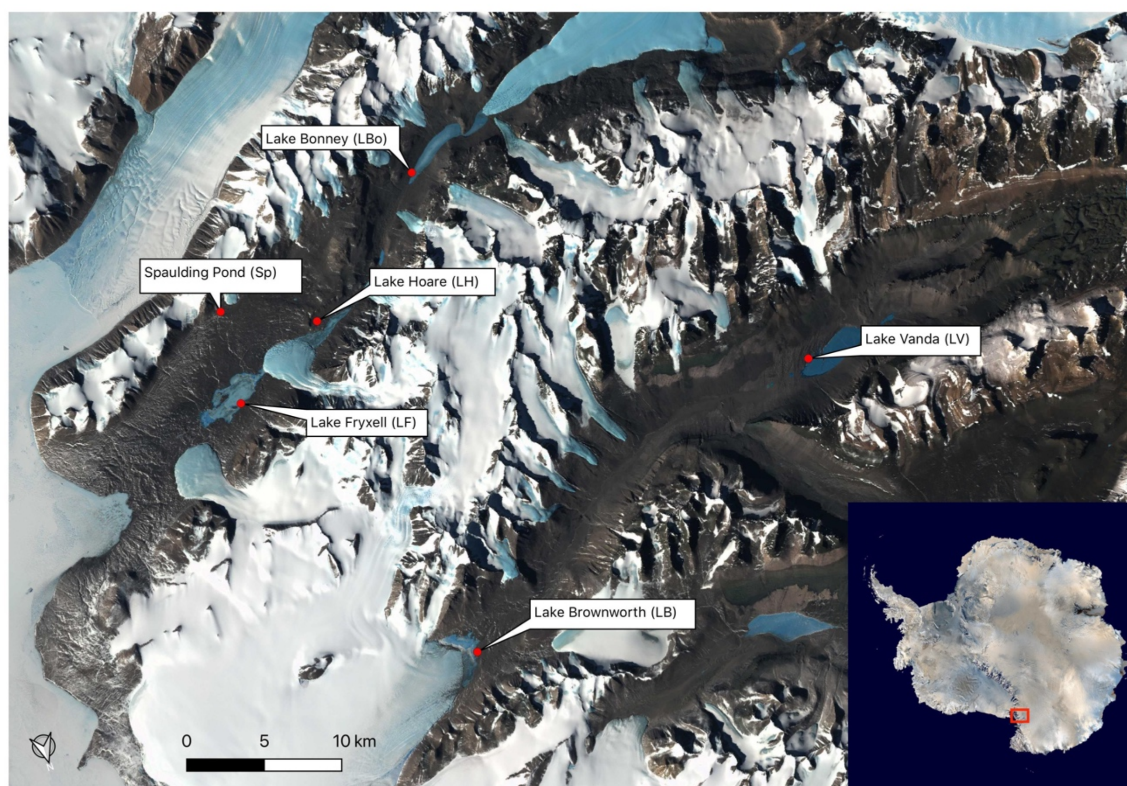

Figure 1 – Sampling locations in Wright Valley and Taylor Valley

Lake	Lat and Long	Valley	Transect Section	Gradient	Sampling Point	Elevation (cm)	Distance from shoreline (m)	EC (μS)	WA	pH	Moisture (%)
Lake Brownworth (LB)	S77.42414 E162.73761	Wright	Wet	Static	1	0	0	25.45 (10.9)	1	7.3 (0.42)	16.77 (3.28)
			Transition		2	14.33 (1.5)	5 (3.6)	71.7 (36.6)	1	7.8 (0.11)	11.30 (1.58)
			Transition		3	36.13 (3.53)	7.35 (3.44)	321 (194.7)	0.77 (0.25)	7.89 (0.10)	6.40 (2.90)
			Dry		4	45.73 (1.41)	8.25 (3.27)	205.7 (87.2)	0.43 (0.11)	7.87 (0.16)	0.74 (0.46)
			Dry		5	92.17 (6.17)	13.7 (3.05)	61.2 (54.5)	0.33 (0.05)	7.87 (0.32)	0.35 (0.6)
Lake Vanda (LV)	S77.53408 E161.62372	Wright	Wet	Dynamic	1	0	0	160 (42.23)	1	8.06 (0.11)	18.65 (1.58)
			Transition		2	15.8 (3.34)	2.3 (0.58)	796.8 (154)	0.93 (0.11)	7.9 (0.10)	8.74 (2.9)
			Transition		3	35 (3.37)	3.7 (0.64)	2340 (2303)	0.46 (0.38)	7.63 (0.11)	1.06 (0.55)
			Dry		4	45.63 (9.27)	4.83 (1.04)	156.2 (155)	0.26 (0.06))	7.57 (0.15)	0.14 (0.12)
			Dry		5	138.85 (6.15)	11 (1.41)	72.1 (40.44)	0.25 (0.07)	7.45 (0.07)	0.11 (0.14)
Lake Bonney (LBo)	S77.69933 E162.53149	Taylor	Wet	Dynamic	1	0	0	83.1 (19.1)	1	8 (0.24)	17.07 (0.28)
			Transition		2	9.83 (0.29)	1	705.7 (302.2)	1	8.44 (0.41)	11.30 (17.63)
			Transition		3	84.67 (2.57)	5.97 (0.05)	5300 (1503)	0.31 (0.02)	8.10 (0.15)	2.06 (0.6)
			Dry		4	105 (8.41)	7.5 (0.87)	1269.77 (344.24)	0.40 (0.26)	8.19 (0.07)	1.75 (0.94)
			Dry		5	116.25 (2.48)	8	1217.9 (712.90)	0.28 (0.05)	8.25 (0.13)	0.63 (0.40)

Lake Hoare (LH)	S77.63271 E162.93942	Taylor	Wet	Dynamic	1	0	0	160 (61.05)	1	8.47 (0.03)	11.93 (0.51)
			Transition		2	13.25 (1.06)	1	788.25 (761.90)	1	8.76 (0.27)	8.60 (2.58)
			Transition		3	43.75 (1.06)	2.5 (0.7)	475.85 (136.11)	0.46 (0.64)	9.05 (0.16)	2.94 (1.16)
			Dry		4	57.5 (0.70)	3 (0.70)	267.4 (154)	0.6	8.75 (0.30)	1.19 (0.12)
			Dry		5	136 (14.85)	7	133.6 (31.96)	0.8	8.75 (0.20)	0.42 (0.35)
Lake Fryxell (LF)	S77.60336 E163.13921	Taylor	Wet	Dynamic	1	0	0	159 (82.53)	1	8.22 (0.12)	16.90 (1.59)
			Transition		2	6 (4.58)	1	633.20 (275.07)	0.98 (0.04)	8.25 (0.30)	12.82 (3.58)
			Transition		3	52.17 (2.57)	7.67 (1.15)	1582.33 (302)	0.98 (0.01)	8.20 (0.02)	6.45 (2.38)
			Dry		4	64.33 (2.52)	8.83 (1.04)	106.26 (34.93)	1 (0.05)	8.47 (0.03)	1.86 (0.53)
			Dry		5	161 (0.12)	19.83 (0.76)	161.12 (99.83)	1 (0.02)	8.69 (0.20)	1.42 (0.37)
Spaulding Pond (Sp)	S77.65936 E163.12224	Taylor	Wet	Static	1	0	0	210.63 (107.97)	1	7.69 (0.24)	20.63 (4.44)
			Transition		2	14.83 (2.47)	1.83 (1.04)	765.63 (403.19)	1	8.71 (0.25)	11.87 (2.52)
			Transition		3	27.17 (8.46)	3.67 (1.15)	469.17 (304.77)	1	8.69 (0.19)	4.85 (3.07)
			Dry		4	68.83 (3.25)	7 (2.65)	198.60 (88.51)	0.78 (0.14)	8.53 (0.11)	0.40 (0.16)
			Dry		5	122.33 (20.14)	14.67 (1.15)	355.47 (231.73)	0.88 (0.16)	8.44 (0.27)	0.56 (0.10)

Table 1. Soil samples collected across all space-for-time transects and associated geochemical data. Values represent the average and standard deviations of the measurements across replicated transects (n=3), except for Lake Hoare (n = 2). Elevation from the shoreline (cm), distance from the shoreline (m), Electrical conductivity (EC) (μS), water activity (WA), pH, and soil moisture (%)

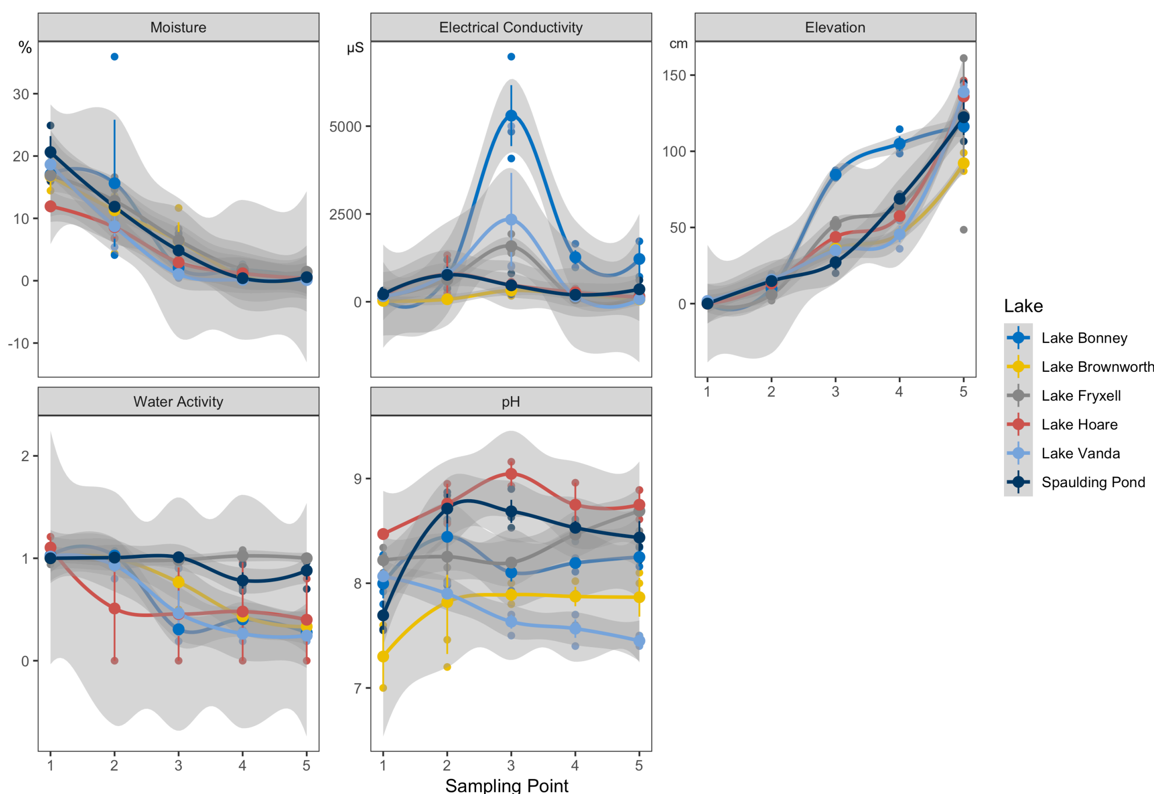

Figure 2 - Soil moisture content (%), electrical conductivity (μS), elevation (m), water activity (WA), and pH profiles along the space-for-time transects profiled from all major lakes (n=3, except for Lake Hoare n=2) in Taylor and Wright valleys.

2.4.2 - Sequencing Results and Quality Control

After filtering out low-quality and short sequence reads, we obtained a total of 2,084,605 sequence reads and 4,098 OTUs at 97% sequence similarity (Supplementary Table S1). We then filtered the low abundant OTUs using a 0.005% relative abundance cutoff across the entire OTU dataset and removed 72% of the initial OTUs. The remaining 28% (1,133 OTUs) comprised 97% of the initial reads. A significant correlation exists between the ordinations of the initial and filtered datasets (m12 squared: < 0.001; Procrustes Correlation: 0.99; p-value < 0.01, 999 permutations). We removed thirty-two OTUs classified as Chloroplast using the SILVA database, leaving a dataset containing 1,101 OTUs for downstream analysis. Sixteen percent of the remaining OTUs were unclassified at the phylum level. The Procrustes Correlation between the ordination matrices with and without the unclassified phyla was significant (m12 squared: < 0.001; Procrustes Correlation: 0.99; p-value < 0.01, 999 permutations). As a result, we retained the unclassified OTUs in the analysis.

2.4.3 - Microbial community diversity along space-for-time wetness transects

We observed significant differences in species phylogenetic diversity (PD) within the dry, transition, and wet transect zones from each lake (Supplementary Figure S4; p-value < 0.01). Spaulding Pond consistently presented the most diverse community along the wetness gradients and Lake Vanda the least diverse community (Supplementary Figure S4). Except for Lake Vanda and Lake Bonney, PD correlated positively with soil moisture content (p-value < 0.05; Figure 3A). Soil electrical conductivity correlated negatively with PD (p-value < 0.05; Figure 3B) only in Lake Bonney transects, likely driven by the comparatively high electrical conductivity (5300 µS) measurements.

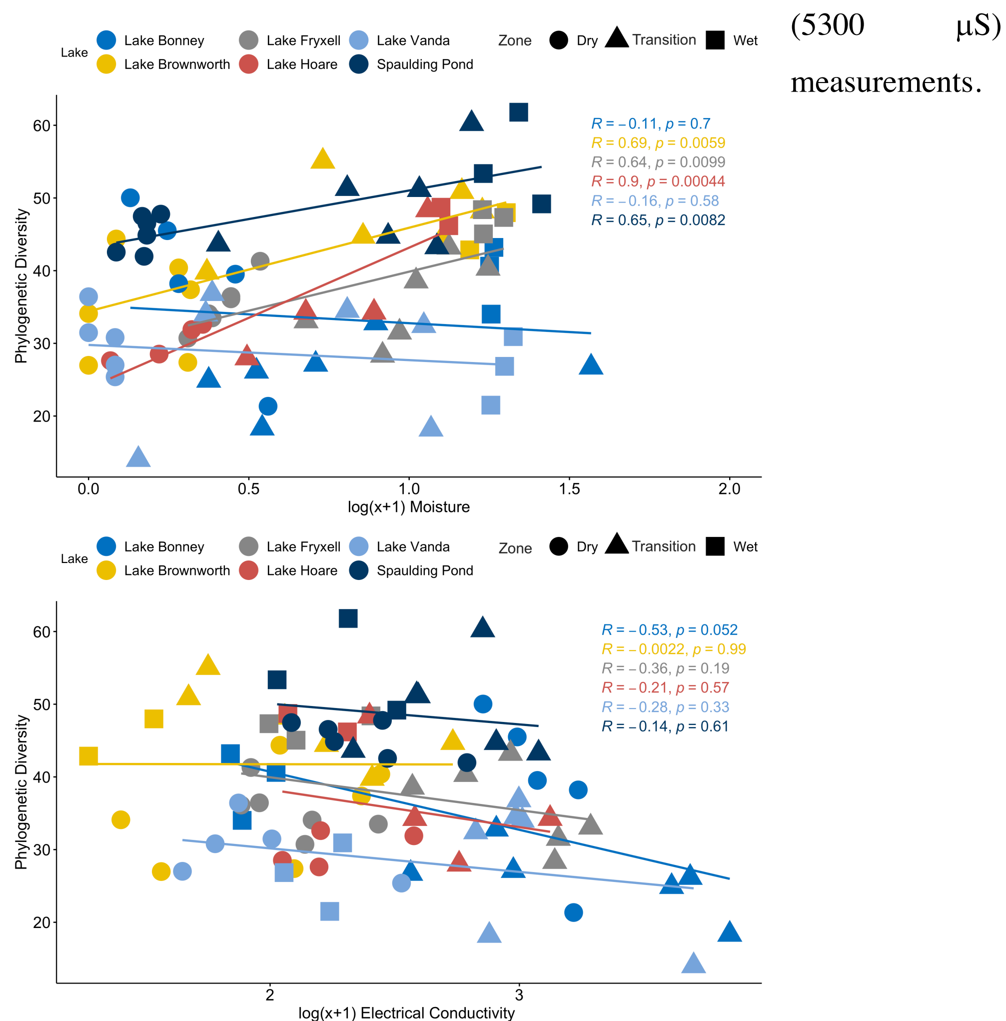

Figure 3 – (A) Relationship between Phylogenetic Diversity (PD) and moisture content (%) measured across the SFT. transects from Lake Brownworth (static transects), Lake Bonney (dynamic transects), Lake Fryxell (dynamic transects), Lake Hoare (dynamic transects), Spaulding Pond (static transects), and Lake Vanda (dynamic transects). **(B)** Relationship between Phylogenetic Diversity (PD) and electrical conductivity (μS) measured across the SFT. transects from Lake Brownworth; Lake Bonney, Lake Fryxell, Lake Hoare, Spaulding Pond, and Lake Vanda.

2.4.4 - Microbial community composition along space-for-time wetness transects

The soil microbial community was represented by 24 phyla, with 98% of reads classified within the top 10 phyla (Supplementary Figure S5). These dominant 10 phyla maintained their representation across all lakes sampled, with a variation in relative abundance reflective of the moisture zone. *Bacteroidota* (0.31 ± 0.08), *Proteobacteria* (0.24 ± 0.08), and *Cyanobacteria* (0.19 ± 0.11) were consistently abundant in wet soils. *Bacteroidota* (0.28 ± 0.09), *Proteobacteria* (0.18 ± 0.10), and *Actinobacteriota* (0.15 ± 0.13) were highly abundant in the transition zones. Dry zones were dominated by members of *Actinobacteriota* (0.30 ± 0.07), *Bacteroidota* (0.20 ± 0.05), *Proteobacteria* (0.11 ± 0.03) and *Acidobacteriota* (0.10 ± 0.06) phyla. In Lake Bonney, taxa affiliated with the phyla *Cyanobacteria* and *Firmicutes* presented a relatively high abundance in transition zone (0.16 ± 0.08 and 0.14 ± 0.16, respectively) and dry samples (0.36 ± 0.09 and 0.09 ± 0.09, respectively).

2.4.5 - Microbial community structure along space-for-time wetness transects

Community beta-diversity from communities from the dry zones of space-for-time transects varied significantly between lakes (PERMANOVA, $R^2 = 0.69$, $F = 11.55$, p-value < 0.01; Supplementary Figure S6A), sharing only 32% of the OTUs (Figure S7A). Microbial communities from the wet zones of space-for-time transects were significantly different between lakes (PERMANOVA, $R^2 = 0.73$ $F = 4.47$, p-value < 0.01; Supplementary Figure S6B), sharing only 16% of the OTUs (Figure S7B).

Along the space-for-time transects, communities collected in the dry zone were structurally distinct from those collected in the wet zone (PERMANOVA, $R^2 = 0.27$, $F = 14.11$, p-value < 0.01) (Figure 4).

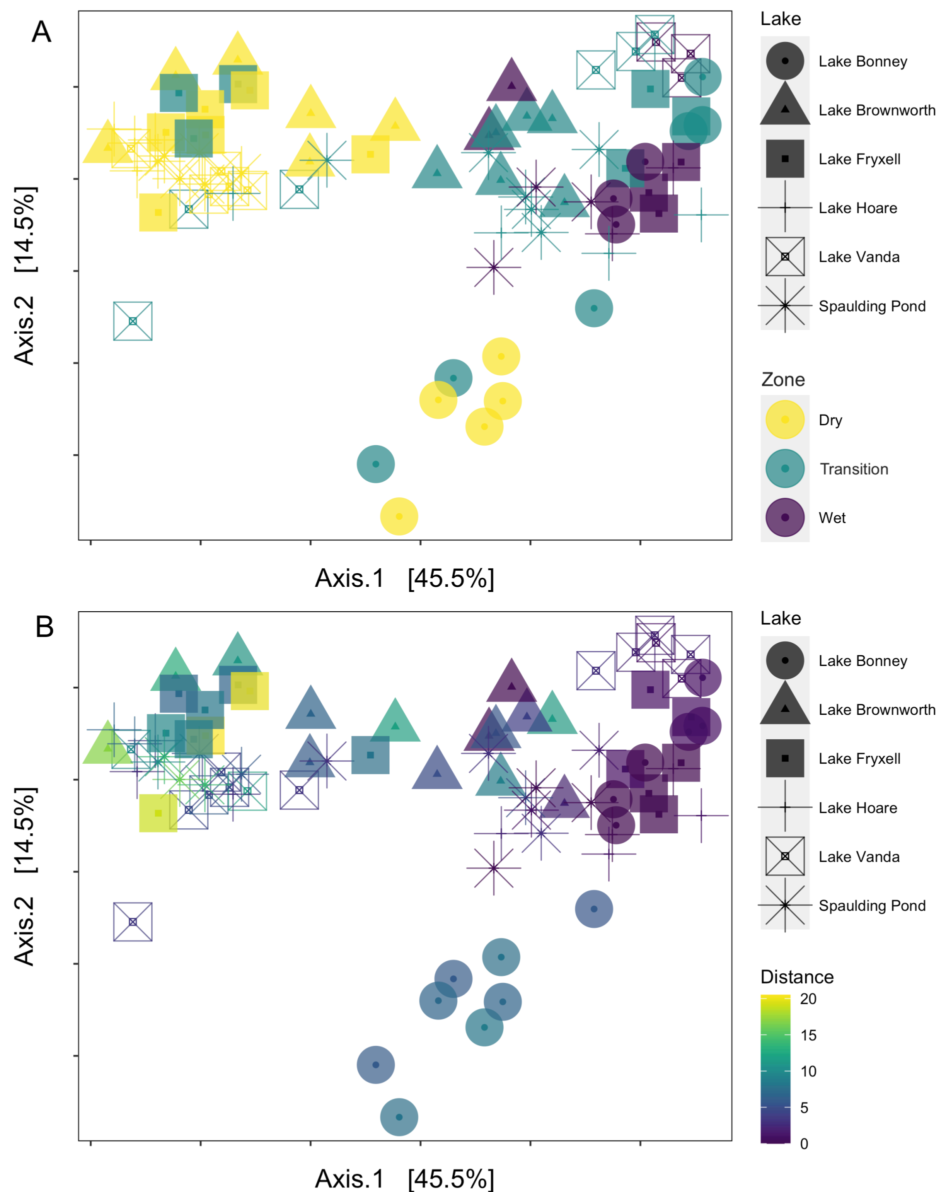

Figure 4 – Principal coordinate analysis (PCoA) of microbial community compositional data based on a weighted UniFrac distance matrix. Figure 4A the samples are coloured by transect zone. Figure 4B the samples are coloured according to their distance from the lake shore.

For each lake, significant clustering of the communities by zone was identified (Figure 5). However, only the Lake Brownworth Spaulding Pond and Lake Hoare transects met the premise for homogenous dispersion (Figure 5A; beta-dispersion > 0.05). For all dynamic lake transects (apart from Lake Hoare), the dispersion of communities within the transition zone was significantly different (beta-dispersion < 0.05) (Supplementary Table S2). Except for Lake Hoare, the transition zone community across all dynamic lake transects was segregated into two clusters, with one of the clusters intercepting with the dry soil community cluster on

sampling point 3 (ellipses at 95% confidence level) (Figure 5C-E). The latter was not observed in the stable lake transects collected from Lake Brownworth (Figure 5A) or Spaulding Pond (Figure 5B).

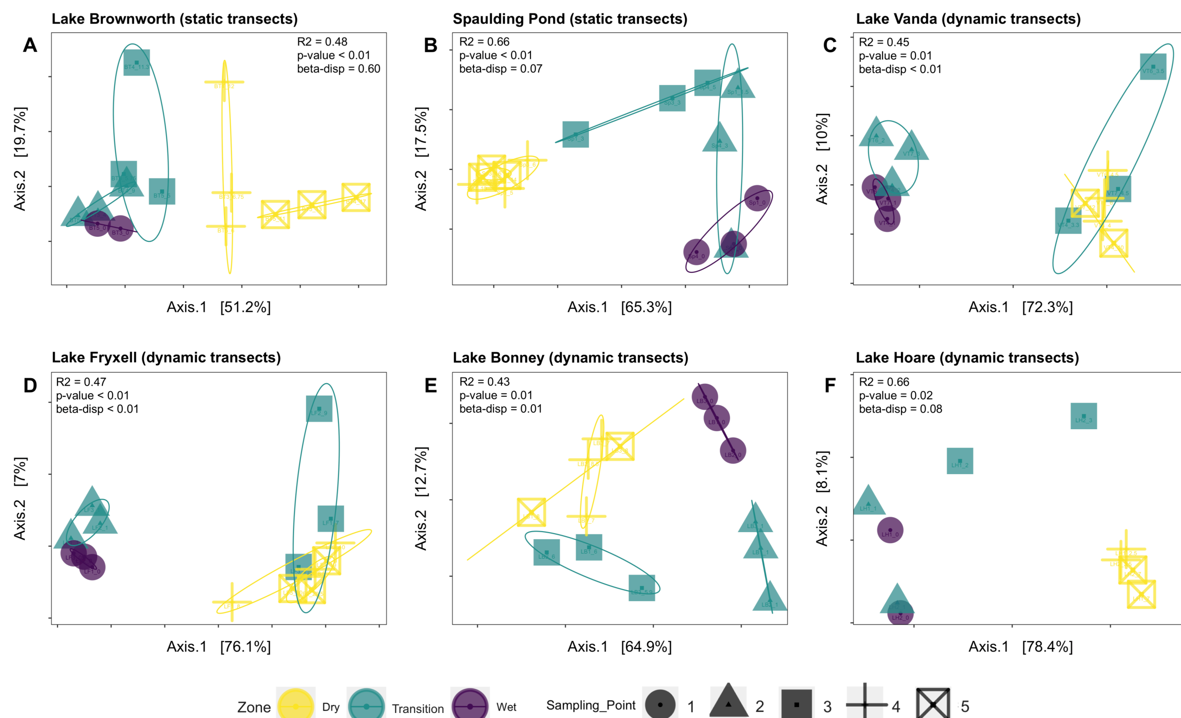

Figure 5 - Principal coordinate analysis (PCoA) of microbial community data based on a weighted UniFrac distance matrix for each lake along each transect: A – Lake Borwnworth (static transects); B – Spaulding Pond (static transects); C – Lake Vanda (dynamic transects); D – Lake Fryxell (dynamic transects); E - Lake Bonney (dynamic transects); F – Lake Hoare (dynamic transects). The significance between weighted UniFrac distances was calculated using PERMANOVA. The assumption for homogeneity of group dispersion was tested with betadisper function. Ellipses on the PCoA plot highlight the deviations from the mean for each clustered group of samples) representative of different sections of the transects (95% confidence level).

Phylogenetic community composition within each sample revealed a trend leaning towards a deterministic assembly of the community governed by environmental selection (NTI>2) (Figure S8A). That effect was higher, and consistent in the dry soils (sampling point 5) and tended to decrease towards the wet zone (sampling point 1) of the gradient, except for Lake Bonney and Lake Vanda, where no trend was identified (Figure 6). In contrast to NTI values, βNTI values distribution showed a median close to 0 but with skewed distribution stretching beyond the +2 significant threshold (Figure S8A). This reflects the influence of deterministic processes for a given pairwise comparison. However, pairwise comparisons regressed against differences in moisture content indicates a large influence of stochasticity with a weak relation to moisture content (Figure S8B).

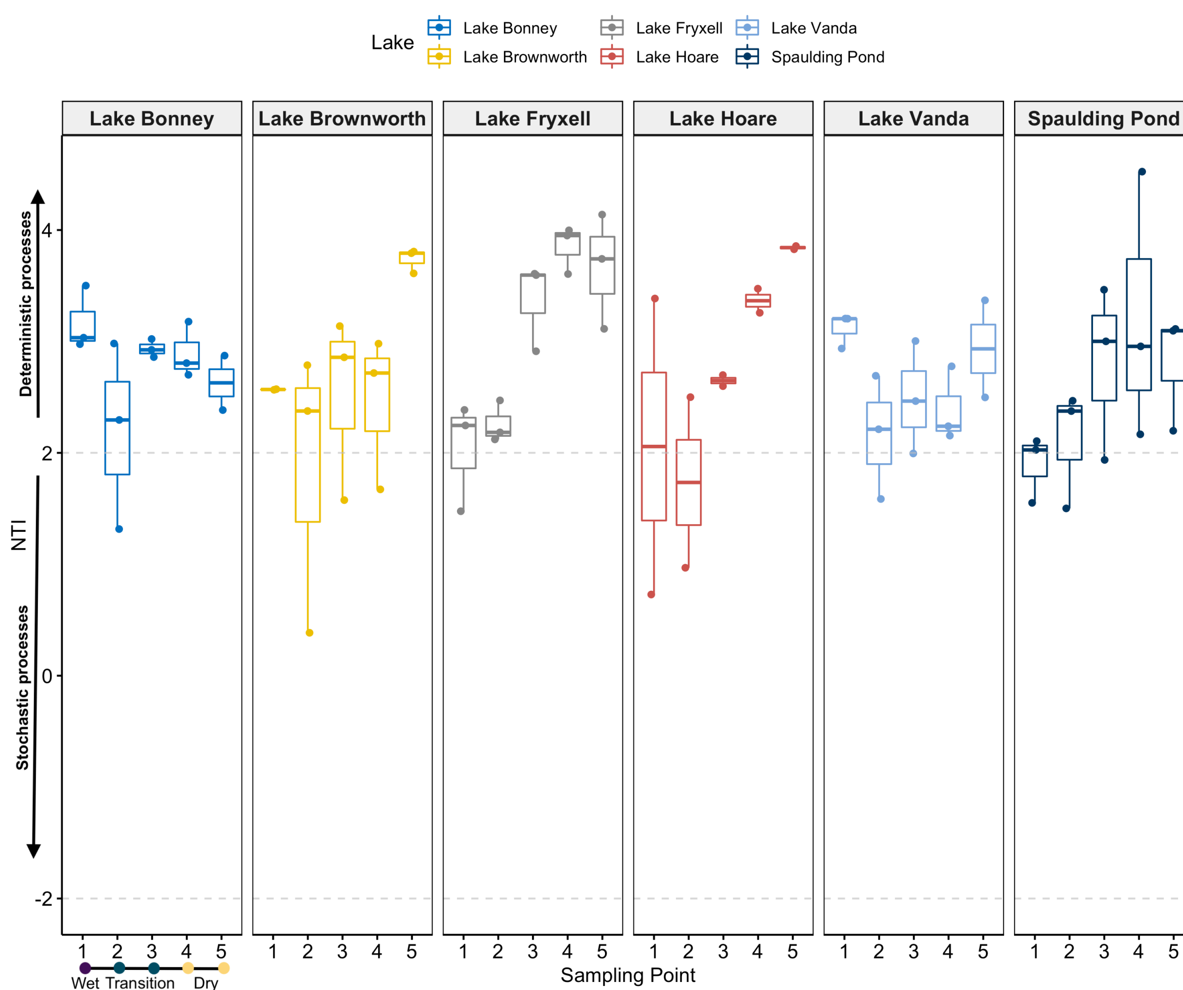

Figure 6 – NTI values for each single community sampled along space-for-time transects at each lake. Dashed grey lines at the −2 and +2 values delimitate the significance thresholds from the null expectation. NTI values < -2 or > +2 suggests that phylogenetic turnover is less or greater than the null expectation, and it is related to deterministic processes. NTI values ranging between -2 and 2 is usually considered signifying the influence of stochastic assembly.

2.4.6 - Microbial taxa as sentinels for change

Soil moisture content was the primary non-categorical variable driving microbial community structure patterns (PERMANOVA, $R^2 = 0.25$, $F = 26.48$, p-value < 0.01; Table 2). A random forest approach identified that 64.8% of the variance in the community could be explained by moisture content (RF, no of trees: 10001, mean of squared residuals 19.88). Taxa affiliated to *Actinobacteriota, Chloroflexi, Deinococcota, Verrucomicrobiota, Proteobacteria, Acidobacteriota, Abditibacteriota,* and *Bacteroidota* were the major taxa driving differences between wet and dry soils (out-of-bag estimate of error rate for the transect section classification: 24.4%) (Figure 7A). OTUs affiliated to *Actinobacteria,* order *Solirubrobacterales*; *Chloroflexi*, order *Kallotenuales*; *Deinococcota*, order *Deinococcales; Acidobacteria*, order Blastocaellales, and *Abditibacteriota,* order *Abditibacteriales,* were exclusively associated to dry and transition zone soils (Figure 7B, Supplementary Table S3). Our model also identified the OTU assigned to *Verrucomicrobiota*, order *Verrucomicrobiales* (genus *Luteolibacter)* as an important OTU to classify wet soils (Figure 7B, Supplementary Table S3). Members of *Bacteroidota* and *Proteobacteria* phyla were associated with both dry or wet soil conditions. *Bacteroidota* taxa related to wet soil conditions belonged to the *Flavobacterium* and *Ferruginobacter* genus (order *Flavobacteriales* and *Chitinophagales),* whereas the genus *Segitobacter* (order *Chitinophagales*) was more abundant in dry soils. Within *Proteobacteria*, 4 OTUs affiliated to the genus *Sphingorhabdus* (order *Sphingomonadales*), *Thermomonas and Pseudoxanthomonas* (order *Xanthomonadales*), and genus *Brevundimonas* (order *Caulobacterales*) were associated with wet soil conditions, whereas the genus *Sphingomonas* (order *Sphingomonadales*) were associated with the dry zone of the gradient (Figure 7B, Supplementary Table S3).

	F model	Statistic R2	Significance (p-value)
Moisture (%)	26.48	0.25	< 0.01
pH	1.36	0.02	0.22
Electrical Conductivity (µS)	5.28	0.06	< 0.01

Table 2. PERMANOVA test using soil moisture content (%), pH, and electrical conductivity on microbial communities along the moisture transects, based on PERMANOVA dissimilarity

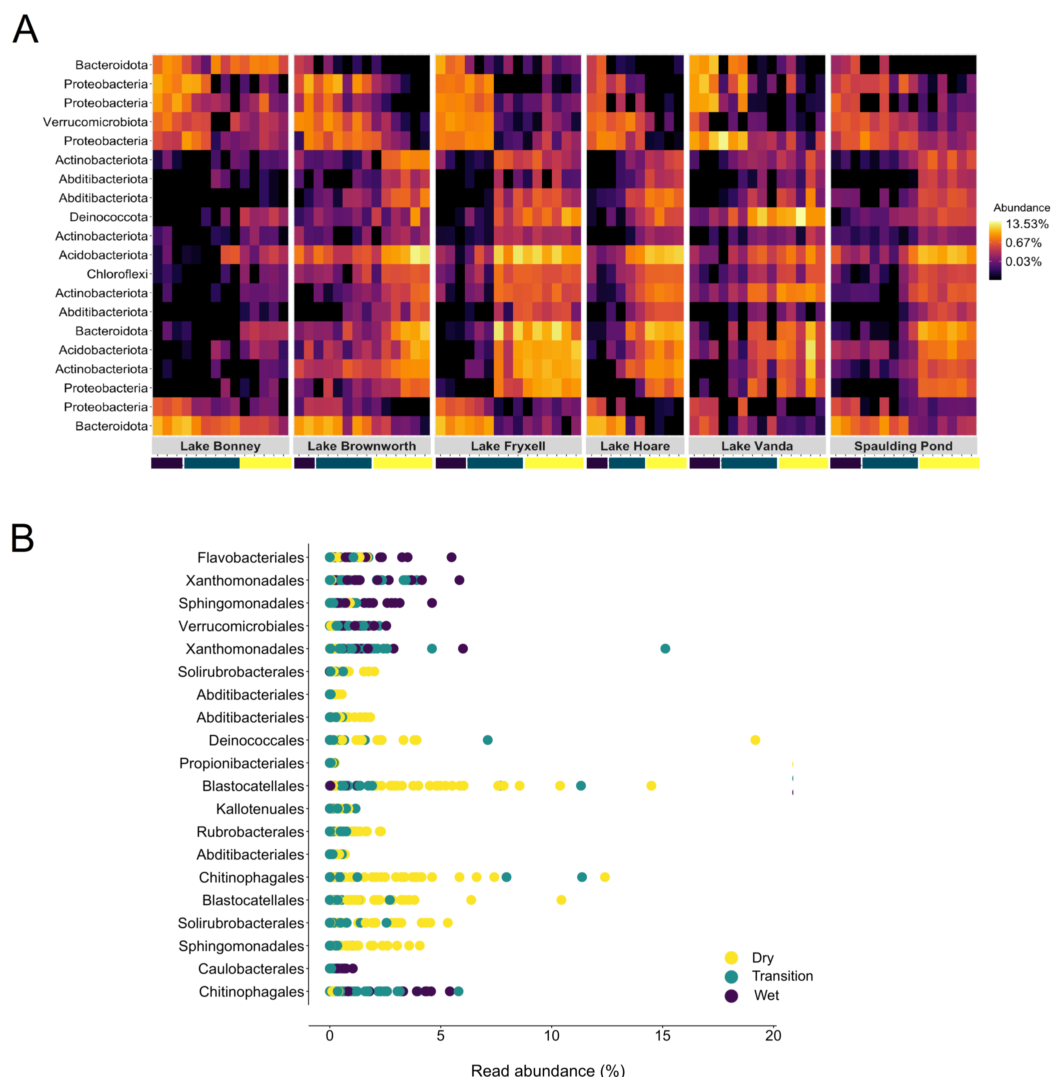

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Figure 7 – (A) Heatmap of the top twenty bacterial OTUs classified by Random Forest classification analysis as the most important to discriminate between the different sections of lake transects. Each row represents each OTU at the phylum level, and the colour of the box indicates the relative abundance of each OTU, with yellow depicting high relative abundance and black low relative abundance. **(B)** Rank abundance plot of the correspondent top 20 OTUs identified across the different sections of the SFT transects at the order level

2.5 - Discussion

Here we sought to validate the application of space-for-time as a reliable approach to forecast the impacts of climate-related hydrological changes on the terrestrial microbiome in a polar desert. We chose the soil ecosystem of the McMurdo Dry Valleys (MDV) as a natural, trophically simple, and well-characterized system where single environmental drivers (such as water availability) have a profound and quantifiable impact on the resident microbial community (Van Horn et al. 2014; Niederberger et al. 2015, 2019; Buelow et al. 2016; Lee et al. 2018; Coyne et al. 2020; Bottos et al. 2020; Ramoneda Massague et al. 2021). Our sampling approach starts by highlighting the importance of selection of sites along spatial gradients based on field determinations of critical environmental drivers of species distributions and their patterns across space. This will help to select sites at consistent points along different ecotones, which can be missed when arbitrary measures such as distance are chosen (Figure 2). Secondly, we point out the importance of repeating space-for-time transects across multiple units within the ecosystem to fully harness the characteristics of environmental variability. Lastly, we considered the detailed historical background on ecosystem response to climate change and defined transects in relatively stable and dynamic environmental scenarios. The MDV offers access to multiple lake systems with variable rates and timing of change. Closed-basin lakes, in particular, are quite sensitive to climate change, which is reflected by historic and current changes in water level and salinity (Castendyk et al. 2016; Levy et al. 2018). Across all sampled lakes Lake Vanda and Lake Bonney have experienced the biggest water level rise, followed by Lake Fryxell and Lake Hoare (Levy et al. 2018). Open-basin lakes, in contrast, may change at slower rates due to an established outlet that rapidly drains glacial meltwater and groundwater flow (Levy et al. 2018). Transects defined in open-basin lakes set the background state for longer periods of stability, whereas transects defined in closed-basin lakes mirror more recent and predicted hydrological disturbances in the system.

2.5.1 - Historical legacy of water availability reflected by the structure and composition of microbial communities

By comparing geochemically defined space-for-time transects from lake systems with relatively stable or dynamic water levels, we were able to resolve the legacy impacts of water presence on microbial community structure (Figure 4). Only within transects defined from

Lake Brownworth, and to a lesser extent Spaulding Pond (static transects), did the microbial community display specific structural patterns reflecting the three geochemical zones identified (Figure 5 A-B). The high degree of zone specificity (wet, transition, and dry) in community structuring from these lakes aligns with an extended period of more stability due to the presence of an outflow (Levy et al. 2018). In contrast, from the dynamic closed-basin lake transects, the clear spatial segregation of the transition zone communities into one of "dry" or "wet"-like community could reflect a response related to legacy of water level changes in these lakes, not detected by the defined geochemical metrics, which respond on a different time scale. Particularly in Lake Vanda, Lake Bonney, and Lake Fryxell (Figure 5 C-E), which have risen between 1.6 and 4.1 m from 2001 to 2017 (Levy et al. 2018), no distinct transitional zone community was recognisable (Figure 7A). Our findings support recent monitoring of Lake Vanda water levels, which indicate that this lake has been continually rising at a rate of 22 cm/year since 1947 (Castendyk et al. 2016). The lack of zone specificity in the microbial community structure at this lake likely reflects that at the time of sampling, microbial communities collected at the geochemically defined transition between transition and dry zones were likely to have been recently wet (potentially hours to days) and remain similar to a dry soil community. In contrast, communities exposed to wetness for more extended periods resemble a more long-term wet soil community. Similar temporal shifts were observed by Ramoneda Massague and colleagues (2021) in moat samples collected along a depth gradient in Lake Vanda. Microbial assemblages collected from the higher depths diverged from those collected at the lake shore, being likely influenced by pre-existing terrestrial microbes in recently inundated soils (Ramoneda Massague et al., 2021). The consistency of our results across closed-basin lake transects suggests that a geochemically defined space-for-time sampling approach can be applied across polar systems to monitor change through the lasting legacy impacts of water availability on assembly mechanisms that shape extant microbial community structure.

Upon observing different spatial structuring of microbial communities, we evaluated whether microbial community assembly patterns within and between communities along the moisture gradient were driven by deterministic or stochastic processes, or by a combination of both. Contrary to a previous observation (Lee et al. 2018), the NTI values observed for each sample across all 17 geochemically defined space-for-time transects indicate that the degree of phylogenetic relatedness among the individuals in a community is likely driven by environmental selection (NTI $>$ 2) (Figure 6). In the MDV, the dry soils are typically

oligotrophic, with minimal water content (< 2%) and high salt concentrations (Cary et al. 2010), which collectively exclude a significant range of taxa that cannot tolerate such selective pressures (Chase 2007; Stegen et al. 2012). Nonetheless, overall patterns of community assembly along increasing differences in moisture content (βNTI values) suggest a considerable but variable influence of stochastic and, to a lesser extent, deterministic processes, with a weak relation to differences in moisture content (Figure S8). While this was surprising considering the NTI values, it suggests that, at a regional scale, community assembly is driven by stochastic processes, but phylogenetic differences within communities are driven by deterministic processes that favour the occurrence of closely related taxa. Such a pattern could indicate that microbial traits that confer adaptability are phylogenetically not well-conserved across the region. Alternatively, it could also result from the distribution of spore-forming, or dormant bacteria in dry or highly conductive soils (Lee et al., 2018), or from differences in diversity between lakes or along the gradients. Overall, we suggest that deterministic and stochastic processes play a role in community assembly, however further extensive analyses are required to understand how deterministic and stochastic components change communities as moisture content changes in the soils.

The impact of moisture as a key driver of microbial diversity was evident at all lakes studied except in Lake Bonney and Lake Vanda (Figure 3A). The presence of water in an available state for life has quantifiable impacts on soil microbial diversity within polar deserts (Bottos et al., 2020; Buelow et al., 2016; Niederberger et al., 2015, 2019). Nonetheless, its positive impact can be suppressed by the effect of soil conductivity (Van Horn et al. 2014; Feeser et al. 2018; Bottos et al. 2020; George et al. 2021). This was the case of Lake Bonney, where the high levels of soil conductivity affected the microbial diversity along the wetness gradient (Figure 3B), creating a niche that only allows for taxa capable of tolerating high osmotic stress (e.g. *Firmicutes*) to thrive. Lake level rise caused by increased glacial runoff in Lake Bonney facilitates the leaching and movement of accumulated meteoric salts, altering soil geochemistry, particularly pH and conductivity (Barrett et al. 2009). High conductivity measurements in these soils support our evidence for the greater prevalence of deterministic processes driving *within* community assembly in Lake Bonney and, to a lesser extent, in Lake Vanda, where the moisture content and relatively higher salt concentration in the soils may have a constant selective effect on the community. Both lakes are located further inland, where soils are characteristically older, more developed, and with higher salt concentrations and with different chemistry, compared to coastal soils (Bockheim 2002). These could also be factors

for such disparities in community diversity and composition along transects sampled from these two inland lakes. Although pH has been suggested to be a critical factor driving spatial patterns of microbial communities (Tripathi et al. 2018), in this study, pH changes within and between space-for-time transects did not have a significant effect on community diversity.

Specific phyla and orders of microbial taxa associated with long-term dry and wet conditions can provide a metric to assess early signs of change (Figure 7). Despite the variability in the structure of microbial communities among wet soil samples, OTUs affiliated with *Verrucomicrobiota* were consistent indicators of long-term wet conditions, whereas OTUs affiliated with *Proteobacteria* and *Bacteroidetes* were associated with both wet and dry conditions. On the other hand, *Actinobacteria*, *Acidobacteria*, *Chloroflexi,* and *Deinococcota* taxa significantly and consistently enriched communities from dry soils, corroborating our previous observations conducted in the MDVs (Niederberger et al. 2015, 2019; Zhang et al. 2020). A recent study by Lee et al. (2018) found similar taxonomic trends, with *Acidobacteria* and *Actinobacteria* being less abundant with higher moisture content. We then provide strong evidence that the presence of discrete taxa within the phyla *Actinobacteria* (family *Solirubrobacteraceae*), *Acidobacteria* (subdivision 4 genera *Blastocatella),* and *Deinococcota* (genus *Truepera*) are ubiquitously associated with long-term dry edaphic conditions. This could be a result of metabolic specialization in the shape of very limiting long-term dry, oligotrophic, and ionizing (UV radiation) conditions to life. Taxa belonging to the family *Solirubrobacteraceae* are currently known for their capability to metabolize atmospheric trace gases contributing to primary production in the dry oligotrophic soils (Ji et al. 2017b), and members of the genus *Truepera* are known for being extremely resistant to ionizing radiation, which is considered a strong stress factor in arid desert soils (Cary et al. 2010). The alleviation of specific stress conditions will impose selective pressures on these highly adapted taxa. As such, any quantifiable taxonomic changes among these taxa can be developed as sentinels for increased temporal exposure to moisture within the MDVs soils, which from a structural standpoint shows a heightened sensitivity of the terrestrial Antarctic microbiome to hydrological changes.

2.5.2 - Validation of the space-for-time approach

The space-for-time approach employs ecological structures within contemporary environmental gradients to project ecological responses to changes in the environment over

time. Primarily applied to study slow ecological processes, this approach is informative when factors that drive community change are equivalent across space and time (Blois et al. 2013). From a microbial ecology perspective, the geochemical profile of a system is often highlighted as an important, if not the primary deterministic force driving community assembly, particularly in ecosystems with low trophic complexity or where diversity is environmentally constrained (Chase 2007). Yet, sampling designs along spatial gradients are often conducted following distance points (Yang et al. 2014; Niederberger et al. 2015; Yan et al. 2017; Feeser et al. 2018; Lee et al. 2018) rather than being based on the spatial variability of geochemical factors, to which biological communities respond to, along a constrained gradient. The patterns of geochemical drivers across space may not be continuous along a gradient, therefore without characterizing them, geochemical boundaries that may drive community assembly within the gradient are likely to be missed, contributing to extant microbial community heterogeneity.

In an environmentally constrained system, such as the Antarctic polar deserts, we demonstrate that contemporary and historical environmental changes (e.g., water availability) can be resolved by subtle structural and compositional re-arrangements of the microbial communities along geochemically defined environmental gradients. These observations could only be depicted when sampling approaches are determined by the spatial variability of geochemical drivers along environmental gradients and replicated across comparable environments that differ in historical exposure to the driving factor. The validation of our space-for-time transects relies on the observed interdependence between structural and compositional community shifts across space, with the temporal exposure to wet conditions.

Given the accelerated rate of climate change across the globe (IPCC, 2021), the ongoing increasing lake levels (Castendyk et al., 2016; Levy et al., 2018), and the expected increase in snow and ground ice melt (Linhardt et al., 2019) will lead to drastic changes in the MDVs landscape, hydrology and ecology (Fountain et al., 2014). For instance, a recent study conducted in a high Arctic lake demonstrated that the taxonomic and functional diversity of dominant microbes can be impacted by an increase in glacial runoff as a consequence of rapid climate change (Colby et al., 2020). Our study, demonstrates that predictions of a wetter system will directly affect the stability of microbial communities currently adapted to dry and ultra-oligotrophic conditions, resulting in significant compositional and diversity changes across the system. Such environmental and taxonomical changes have the potential to lead to alterations in primary productivity, carbon and nitrogen cycling, and energy fluxes across the

system (Coyne et al. 2020; Monteiro et al. 2020; Karen et al. 2021). Whilst microorganisms underpin the stability and functionality of polar deserts ecosystems, these are still rarely considered in policy development and lack any protective status within the Antarctic Treaty (Hughes et al., 2015). This study highlights that microbial communities are highly sensitive to change and closely reflect changes in the environment. Therefore, as in more temperate environments (Cavicchioli et al. 2019), microbial communities should be considered by policy-makers as primary sentinels for current and historical changes in the Antarctic systems.

Data Availability

Raw DNA sequences generated for the current study are available from the NCBI Sequence Read Archive (SRA) under the accession number PRJNA764757.

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CHAPTER III

Bringing Antarctica to the lab: A polar desert environmental chamber to study the response of Antarctic microbial communities to climate change

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3.1 - Abstract

Polar deserts contain unique and sensitive communities responsive to climate-associated habitat changes. However, unlike temperate desert ecosystems, characterizing and predicting the responses of polar ecosystems to environmental change remains a significant challenge due to logistical constraints. Here we aim to demonstrate the use of a custom-designed Polar Desert Environmental Chamber (PDEC) to perform off-continent experimental ecological research. We did so by characterizing the structure and composition of arid edaphic bacterial communities collected from the McMurdo Dry Valleys during a simulated wetting event. The results were discussed in light of previous field observations. Rapid structural and compositional changes were observed during wetting and re-drying treatments. Those were driven by changes in the relative abundance of co-existing taxa, which fluctuated asynchronously over time in response to the treatments. While selection was the main ecological factor influencing communities during dry conditions or the initial wetting, with prolonged exposure to wetness, neutral processes began to drive community assembly. Ultimately, these observations reflect different adaptative responses from microbial taxa to water stress, which can be argued as beneficial to increasing resilience in polar deserts. Our findings demonstrate that experiments conducted in PDEC provide valuable contextual data on community response to environmental change and can accelerate our ability to assess biological thresholds to change within polar desert ecosystems. We advocate that, with careful consideration of key emulated environmental attributes, laboratory-based Antarctic research can complement fieldwork to achieve a nuanced and evidence-based understanding of the ecology of Antarctica's ice-free regions.

3.2 - Introduction

Terrestrial Antarctica encompasses the largest polar desert and one of the most extreme environments on Earth. The continent is mostly ice-covered, resulting in the majority of its terrestrial biodiversity being constrained to the 1% ice-free soil, patchily distributed across the continent (Lee et al. 2017). The largest ice-free region on the continent is the McMurdo Dry Valleys (MDV), a hyperarid and ultraoligotrophic polar desert (Doran et al. 2002; Bockheim et al. 2007; Cary et al. 2010). Due to the lack of precipitation, liquid water is only ephemerally available during the Austral summer when the combination of air temperature, relative humidity, wind speed, and solar radiation favor the melting of glaciers and the ablation of permafrost (Law and Van Dijk 1994; Fountain et al. 2014). The intensity and frequency of these physical processes can increase water availability by expanding lakes and transiently wet areas such as streams, moats, and water tracks, thereby affecting this region's ecology.

Antarctic ice-free regions are considered natural laboratories, well-suited for studying the relationship between environmental variability, biodiversity, and ecosystem functioning due to the lack of trophic complexity (Convey et al. 2014). In these regions, microorganisms make up for most biomass and diversity, exhibiting a diverse repertoire of metabolic strategies that facilitate survival and acquisition of energy and carbon despite the severe moisture and nutrient limitations (Ortiz et al. 2021). Microbial distribution, diversity, and function are intimately linked to historical and contemporary abiotic conditions (Lee et al. 2019; Bottos et al. 2020). As a result, these are arguably the most responsive biological entities to environmental change, functioning as biological sentinels for climate change in the system (Monteiro et al. 2022). Field observations and *in situ* manipulative experiments have driven tremendous progress in predicting and demonstrating the sensitivity of microbial response to present-day changes in Antarctic environmental conditions, particularly to changes in water availability (McKnight et al. 2007; Tiao et al. 2012; Van Horn et al. 2014; Buelow et al. 2016; Niederberger et al. 2019; Monteiro et al. 2022). Initial observations by McKnight et al. (2007) detected an increase in primary productivity from a former dried cyanobacterial mat one week after the channel, which had not received substantial water flow for two decades, was re-hydrated. Later, an unprecedented four-year experimental manipulation involving the transplantation of a mummified seal carcass in the MDV revealed the capacity of the Antarctic soil microbiome to respond to contemporary alterations in relative humidity in timeframes considerably shorter than previously thought (Tiao et al. 2012). More recently, Niederberger et al. (2019), through the simulation of a natural wetting event by re-diverting a meltwater

stream into a historically dry soil area in the Miers Valley, showed significant structural and compositional shifts in the soil microbial communities over seven weeks. These compositional changes co-occurred with the onset of significant declines in the relative abundance of Actinobacteriota, a recognized dominant phylum in dry soils, and an increase of Cyanobacteria and other taxa commonly found in MDV wetted areas, such as Proteobacteria and Bacteroidetes (Monteiro et al. 2022). However, there is still limited information regarding the thresholds and subsequent ability of the Antarctic soil microbiome to recover from changes in its local environment.

Many aspects of change in Antarctic ice-free regions manifest slowly and incrementally over time, and tracking ecological changes over decades is logistically challenging to execute (Convey and Peck 2019). Firstly, the restricted time frame allocated to field access significantly limits any continuous monitoring of biological response to environmental change. Without the constant collection of time series data, the risk of ecological bias within predictions increases by the mismatch between the range of scales at which climate change and biological response occur during temporal studies (Bütikofer et al. 2020). Currently, field manipulations require an extraordinary logistic and personal effort to be achieved, such as the presence of researchers on-site for the duration of the experiment (Niederberger et al. 2019) or, in the case of long-term manipulations, the decision to leave the experiment in place unattended in remote locations year-round without control for unpredictable events (McKnight et al. 2007; Tiao et al. 2012). The latter poses a risk to the quality of the research since it increases the chances of incorporating extraneous variables, making interpreting results difficult or inaccurate. Secondly, strict international regulations plus the requirement for permits and substantial financial and logistic support impose significant limitations on the performance of experimental field manipulations in parts of the continent. For instance, in the MDV, only a few experiments have been successfully performed *in situ* (McKnight et al. 2007; Tiao et al. 2012; Van Horn et al. 2014; Buelow et al. 2016; Niederberger et al. 2019). Lastly, research activities can leave long-lasting impacts on the soils and their communities (Hughes et al. 2015; O'Neill et al. 2015), which contradicts one of the Antarctic Treaty's founding principles, the preservation of the continent.

Given the relatively low biological complexity present on the Antarctic continent compared to more temperate or tropical regions, experimental manipulations conducted off-continent, under settings representative of the natural environment, can create a powerful means of hypothesis testing without the permit, temporal and logistical limitations, or

anthropogenic impacts associated with field studies. When conducted in parallel with and validated by *in-situ* observations, laboratory experiments enable the collection of time series from long and short-term controlled disturbances while reducing the complexity of confounding variables and ecological processes in the field. The latter gives a deeper and more controlled perspective on the niche-based and stochastic processes that govern community assembly during environmental change. Moreover, considering the expected increase in the timing and frequency of wetting events around ice-free areas (Fountain et al. 2014; Lee et al. 2017), off-continent laboratory experiments can manipulate brief or prolonged cycles of wetting events, helping to identify the ecological thresholds and tipping points of biological communities. The question remains: can we emulate ice-free Antarctic systems and biological responses in the laboratory?

Here we demonstrate the ability to study the impacts of environmental change on biological communities from the MDV using a Polar Desert Environmental Chamber (PDEC) custom-designed to emulate permafrost ablation, air temperature, relative humidity, and light conditions observed in Antarctic ice-free systems. We validated the PDEC by comparing the response of the MDV soil microbiome to wetting events with previous field observations, particularly to a seven-week wetting experiment performed in Miers Valleys (Niederberger et al. 2019). We subjected previously collected MDV soils to a continuous wetting treatment (eight weeks) and re-drying treatment (four weeks wet/ four weeks dry). We demonstrate that with adequate and controlled infrastructure, manipulative laboratory experiments are a complementary approach to Antarctic field studies, providing a mechanism for addressing predictions for biological response to single or multiple disturbances. Work of this kind can be expanded to incorporate a variety of perturbations expected to occur in Antarctic ice-free regions, including warming, productivity changes, or species introduction, coupled to activity measurements, which can be performed without the temporal, logistic, and permit constraints nor the anthropogenic impacts associated with field-based work.

3.3 - Methods

3.3.1 - Soil sampling and processing

During the New Zealand Antarctic field season in 2018, surface soil samples (0 – 2 cm) geochemically characterized as dry were aseptically collected with a sterile spatula 10 meters from the shore of Lake Hoare (Eastern side) in Taylor Valley, in the McMurdo Dry Valleys,

Antarctica (Monteiro et al. 2022). Lake Hoare located 15 km from the coast, profiles mean annual air temperatures of -14.8 °C and an average mean relative humidity of 66% (Doran et al. 2002). It has the lowest mean yearly solar flux in the Dry Valleys due to its position adjacent to the Aasgard Range (Doran et al. 2002). Samples were stored at -20 °C for one day, transported to Scott Base, back to New Zealand on dry ice, and stored at -60 °C until processed.

3.3.2 - Polar Deserts Environmental Chamber

The experimental design was conducted in a modified Contherm Global5000 Environmental Chamber (CAT 5400/RHS) explicitly designed to emulate key environmental attributes and processes that affect soil microbial communities in ice-free polar deserts (PDEC – Polar Deserts Environmental Chamber) (Figure S1) (Contherm Scientific Limited, New Zealand). Permafrost is a major controlling factor in the dynamics of Antarctic terrestrial ecosystems, and it is ubiquitously present in ice-free regions (Bockheim et al. 2007). As such, it was fundamental to emulate permafrost conditions in our experimental design. The construction of the underlying permafrost layer started using soils sampled in depth increments in the Miers Valley in 2013. The bulk dry soil was autoclaved and reconstructed inside an insulated acrylic box (54 x 49 x 54 cm) by mixing it with sterile water until a mud-like consistency was achieved (Figure 1). The permafrost container has a low-temperature cooling coil set to -15 ºC to freeze the mixture (Figure 1, Figure S1). Four large open-ended master cylindric containers (12.5 x 35.5 cm) were placed 10 cm inside the soil mixture. Once the soil mixture froze, we filled the large master cylinders to the top using the same autoclaved Miers Valley soil. To emulate permafrost ablation processes, which are dynamic processes influenced by air relative humidity, temperature, and wind**,** the PDEC has the capacity to constantly remove moisture from the chamber through refrigeration. The reduction of relative humidity was assisted by placing a set of fans inside the chamber, which increases air circulation close to the surface of the soil and disturbs the boundary layer. The latter creates an imbalance between the surface of the ice in the permafrost and the percentage of vapor water inside the chamber, causing moisture to move upward and creating a gradient in humidity within the overlying soil (Figure S2) (Law and Van Dijk 1994). The gradient in humidity was recorded by placing six humidity sensors (HOBO Micro Station Logger) 5 cm apart from the bottom to the top 2 cm in one master cylinder. Humidity changes were recorded in 5 min intervals during the eight weeks of the experiment (Figure 1).

Above the permafrost container, we set a light sourcing system (FUTURELED, Berlin) specifically constructed using LEDs emitting light at all wavelengths across the visible spectra and into the near UV. The light system was set 30 cm above the soils and calibrated to provide similar quality spectra and 50% of the incoming light intensity experienced in the MDVs during the Austral summer (please refer to the methods in the supplementary material) (Figure S2). The temperature inside the chamber was set to be maintained at 5 ºC, as required to maintain the relative humidity inside the chamber of 50%, a value within the range observed in the field (Doran et al. 2002).

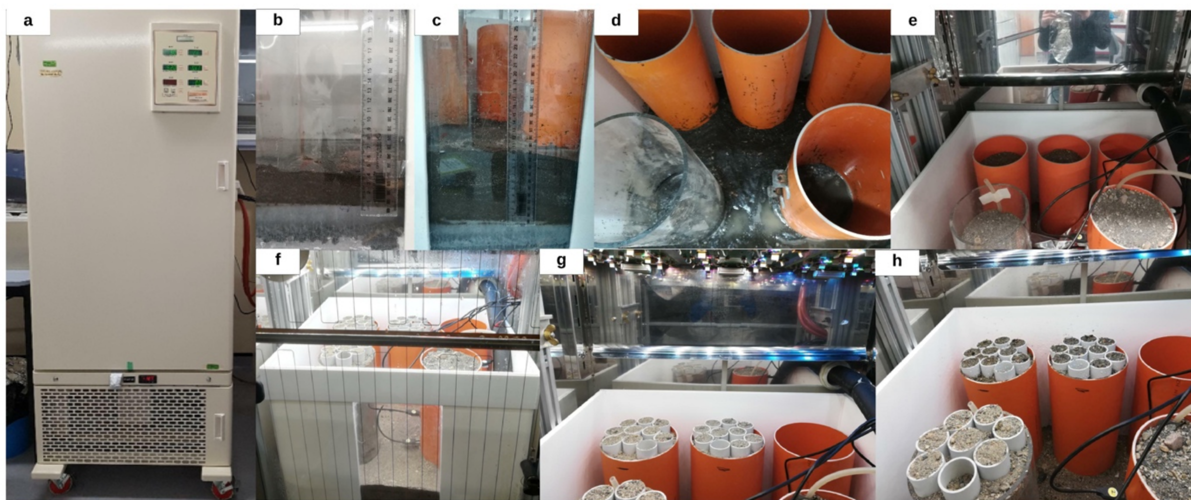

Figure 1 – (a) Polar Desert Environmental Chamber (PDEC) designed to emulate temperature, relative humidity, light, and permafrost observed in the McMurdo Dry Valleys. A digital thermostat shows the permafrost container's current temperature, and an LCD on the door shows the current temperature and relative humidity values inside the chamber; (b-d) the different phases involved in the reconstruction of the permafrost; (b) mixing of the second layer of autoclaved dry soil collected in Miers Valley with sterile water inside the permafrost container; (c/d) insertion of four master cylinders 10 cm down the soil mixture; (d) soil freezing; (e) filling the cylinders with additional sterile dry soil; (f) view of the permafrost container with the master cylinders in place and the small open-ended test cylinders on top filled with Lake Hoare dry soils. Humidity loggers were set on the front right cylinder; (g) view of the small cylinders containing Lake Hoare soil on top of the master cylinders and the light system above; (h) experimental set up after the soils were wet.

3.3.3 - Experimental setup

Before the start of the experiment, the entire chamber was cleaned with 80% (vol/vol) ethanol. All incubation cylinders and materials used during the experiment were cleaned with 80% (vol/vol) ethanol and sterilized with UV light for 30 min before setup. On top of the three large master cylinders, we placed ten small open-ended test cylinders containing 40 g of untreated, dry soil collected from Lake Hoare in 2018. Each set of ten test cylinders was subjected to one of the three different treatments for a total of eight weeks: in the dry control, the soils remained dry throughout the experiment (dry control); in the wetting treatment, the soils were sprayed with 8 ml of sterile Milli-Q water twice a day to stay wet; in the wetting/re-drying treatment, the soils were sprayed with 8 ml of sterile Milli-Q water twice a day for the first four weeks and then, they were left to dry gradually for the following four weeks of the experiment (Figure S1). Samples were incubated under 24 h daylight conditions. The chamber conditions were monitored daily, and samples were collected from each treatment before the start of wetting, when all the soils were dry (T0), and after 24 hours (T1), one week (T2), four weeks (T3), five weeks (T4), and eight weeks (T5) from the start of the experiment. After T3, the soils from the wetting/re-drying treatment stopped being wetted. The time points T4 and T5 mark five and eight weeks, respectively, since the start of the experiment and one and four weeks since the soils in the wetting/re-drying treatment stopped being wet. At T0, before the experiment started, one small cylinder placed on top of each master cylinder, representative of each treatment, was removed, and one soil sample from each small cylinder was extracted and stored at -60 °C until processed. Considering that at T0, all soils were still dry and that all soil samples used in this experiment came from the same field sample, these samples were called the T0 control (n=3). From T1 until T5, we aseptically removed one of the small cylinders from each treatment and collected three replicates of soil per treatment (n = 3). These samples were stored at -60 °C until processed. Two additional field samples were used as a field control to ensure that the starting chamber-based community structure reflected what was found in the field. Soil moisture content within each experimental treatment was determined at T5, according to Monteiro et al. (2022).

3.3.4 - DNA extraction, sequencing, and data processing

Forty-eight experimental samples (16 from each treatment) were collected from the manipulation experiment and processed alongside two additional samples from the field. Total

DNA extraction, the PCR amplification of the 16S rRNA gene, and NGS library preparation were conducted according to Monteiro et al. (2022). Amplicon sequencing was performed using the Ion PGM™ System for Next Generation Sequencing (ThermoFisher Scientific) at the Waikato DNA Sequencing Facility (University of Waikato, New Zealand).

Sequencing primers and indexing barcodes were removed with cutadapt (v2.3) (Martin 2011). A total of 1,387,788 reads across 50 samples were processed using DADA2 (v1.14.1) (Callahan et al. 2016) to generate amplicon variants (ASVs) in R (v3.6.2) (R Development Core Team, 2010). Taxonomical identity was assigned to each variant using the SILVA database (v138) (Quast et al. 2012). ASVs classified as mitochondria, chloroplast, eukaryotes, or without any taxonomical assignment at the Phylum level were removed from the dataset. ASVs not present at T0 or having less than 100 reads across the entire dataset (relative abundance threshold of 0.007%) were removed from our analysis as a control for potential contamination and to help to reduce the noise across the dataset (Bokulich et al. 2013).

3.3.5 - Statistical analysis

All statistical and visualization analyses were computed in R (v4) (R Development Core Team, 2010) using the following packages: phyloseq (v1.26.1) (McMurdie and Holmes 2013), vegan (v2.5) (Oksanen et al. 2012), Picante (v1.8) (Kembel et al. 2010), ggplot2 (v3.2.1) (Wickham 2016), and DeSeq2 (Love et al. 2014). Alpha diversity using richness and phylogenetic diversity indexes were calculated using a non-rarefied dataset. Diversity differences among groups were tested using one-way ANOVA. Normality assumptions were tested using Shapiro-Wilk test, and the assumption of homogeneity of variances was tested using the Levene's test. Beta diversity was calculated on a transformed dataset using a total sum normalization and log-ratio transformation (Coenen et al. 2020) and visualized in a principal coordinates analysis (PCoA) using a weighted UniFrac phylogenetic pairwise distance (Lozupone and Knight 2015). Calculated pairwise distances between samples of each treatment relative to the Dry Control treatment visualized using boxplots generated using ggpubR (Kassambara and Kassambara 2020) (v0.4.0). PERMANOVA was applied to identify differences in beta-diversity between different treatments at each time point. The test was perfomed using *adonis* from vegan R package (Oksanen et al. 2012). We used *betadisp* to test for the homogeneity of group dispersions, included in the same package. For differential analysis, raw read counts of ASVs were log2 transformed and modeled using a negative binomial generalized linear model

implemented in the DESeq2 package in R (Love et al. 2014). ASVs identified as significantly different resulted from comparisons between wetting treatment and wetting/re-drying treatment relative to the dry control at each time point. An adjusted p-value below 0.01 was considered significant. To evaluate what ecological factors underly the microbial composition with changes in water availability, we calculated phylogenetic community assembly among species within each sample using the mean nearest taxon distance (MNTD) and the nearest taxon index (NTI) using "taxa.labels" null model, with 999 iterations, using the function 'ses.mntd' from the R package Picante (v1.8.2). The NTI was quantified as the number of standard deviations that the observed MNTD was from the mean of the MNTD null distribution, multiplying by -1. For a single community, observed NTI values > +2 or <−2 indicate phylogenetic clustering of species or phylogenetic overdispersion, respectively. NTI values between −2 and 2 usually indicate the influence of a stochastic assembly (Stegen et al. 2012).

3.4 - Results

3.4.1 - Chamber monitoring

The chamber maintained a constant 5 °C, 50% relative humidity, and -15 °C in the lower permafrost. Before starting the experiment, Lake Hoare soils presented a moisture content of 0.4 ± 0.3%, pH of 8.75 ± 0.2, and electrical conductivity of 268 ± 267 μS. A power failure affected the chamber and interrupted the permafrost freezing process 29 days into the experiment leading to an increase in the chamber's temperature and consequent alteration of the relative humidity and defrosting of the permafrost layer for three consecutive days (Figure S2). This event was recorded after T3 sampling, and likely contributed to the variance observed at T4 and T5 in the dry control samples. We did not identify other impacts in samples submitted to wetting (Figure 2).

3.4.2 - Sequencing analysis

After quality control steps, we identified 2,779 ASVs. Chimera check identified 431 bimeric sequences, which were subsequently removed, generating 2,348 unique ASVs and 1,339,818 reads (average length 215 bp) across 50 samples. Filtering out low abundant ASVs (< 0.007% cutoff, representative of less than 100 reads across the entire dataset) removed 59%

of the initial ASVs. The additional removal of ASVs classified as mitochondria (0 ASVs), chloroplast (2 ASVs), eukaryotes (7 ASVs), not classified at the Phylum level (204 ASVs), not present or with only one sequence at T0 (48 ASVs), removed an additional 27% of the ASVs. The remaining dataset comprised 1,108,012 sequences representing 82% of the initial sequencing data and 706 ASVs.

3.4.3 - Temporal dynamics of community diversity during the wetting treatment

We observed a significant decrease in α-diversity, measured using Faith's Phylogenetic Diversity, after two months of wetting (T5) (one-way ANOVA, F-value: 114.91, *p*-value=2.58e-08, Figure S3a, Table S1). Differences in α-diversity remained significant in relation the control at the same time point (one-way ANOVA, F-value: 112.84, *p*-value=1.74e-05, Figure S3b, Table S1). Nonetheless, no significant differences were encountered among the dry controls throughout the experiment (Figure S3). Additional α-diversity measures supported this trend: the observed number of ASVs, Chao1 richness, and Shannon index (data not shown).

Microbial community β-diversity changed with time and treatment (Figure 2). Samples were clustered by sampling time point across the primary axis (55% of the variability within the dataset) and treatment across the secondary axis (22% of the variability within the dataset) (Figure 2). During the four weeks of constant wetting (T0-T3), β-diversity increased between wetted samples and the dry controls, for each respective time (Figure 3). Once the wetting ceased (T3), β-diversity decreased between the control and communities submitted to the re-drying process (T5) (Figure 3). For each time point, we observed significant differences in β - diversity between the respective control samples and the treated samples (T1-PERMANOVA: F model = 9.40, *p*-value = 0.03; T2-PERMANOVA: F model = 20.61, *p*-value = 0.02; T3-PERMANOVA: F model = 28.17, *p*-value = 0.03; T4-PERMANOVA: F model = 66.44, *p*-value = 0.01; T5-PERMANOVA: F model = 118.97, *p*-value = 0.01). The assumptions to conduct a PERMANOVA test were tested and met.

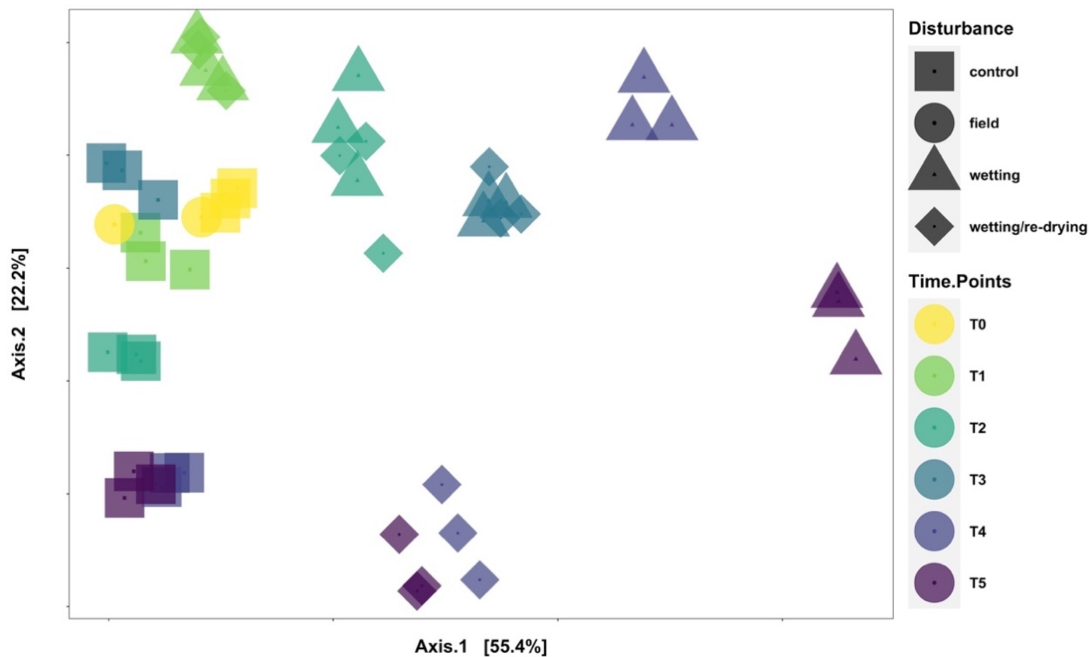

Figure 2 - Principal coordinate analysis (PCoA) plot of weighted UniFrac distance. PCoA was used to plot the beta diversity of microbial communities throughout the experiment using the weighted UniFrac distance matrix.

Communities from the dry control samples were compositionally and structurally similar to field samples at T0 (Figure2). However, we observed variability within the control samples during the experiment (Figure S4a). While sources for this variability could be related to initial acclimatization to the conditions in the chamber, the highest variation occurred after the chamber breakdown (between T3 and T4), which would have been in response to an increase in temperature and changes in relative humidity (Figure S2). While changes in temperature and relative humidity may have caused a response from dry communities or communities in the early days of the re-drying step (Figure S4a/c), the degree of such response was still less pronounced than the response observed to wetting (Figure S4d). Additionally, we do not expect that such an event had a significant effect on communities that remained wet since the dissimilarity distances between wet samples and the control continuously increased in the same direction (either in relation to the T0 control or in relation to the respective time point control) (Figure S4b; Figure 3). This observation suggests the effects of changes in moisture dominates microbial communities from ice-free regions over alterations in temperature. Nonetheless, it also highlights the sensitivity of these communities to subtle environmental changes, and the importance of accurately emulating conditions in manipulative

laboratory experiments to avoid generating incorrect interpretations of the results and inaccurate predictions.

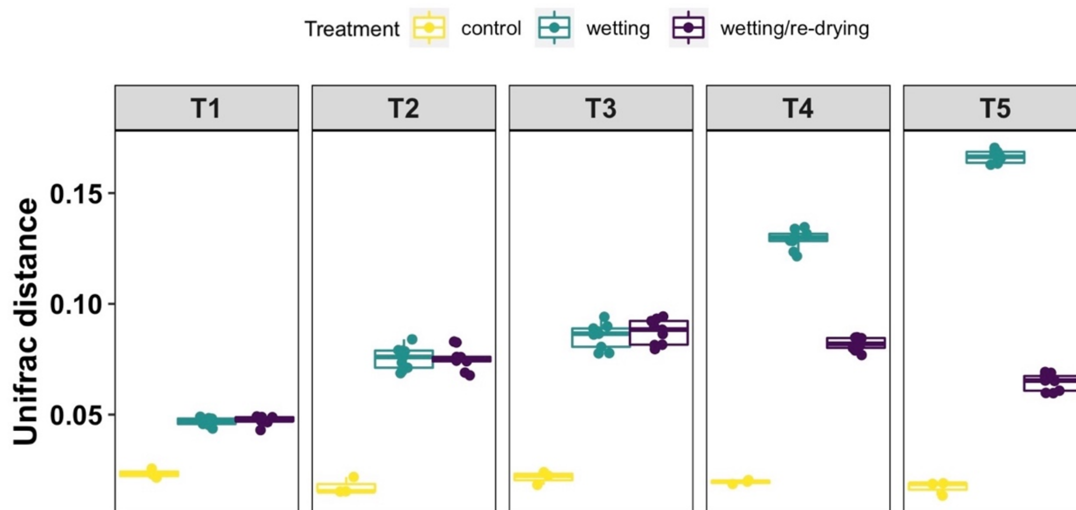

Figure 3 - Weighted UniFrac distance values representative of each pairwise comparison calculated between a wetting or wetting/re-drying sample versus the control, and pairwise comparisons between controls, at each respective time point identified by the panel. After T3, the soils from the wetting/re-drying treatment stopped being wetted.

3.4.4 - Microbial compositional changes during the wetting treatment

Temporal changes in the relative abundances of microbial taxa were analyzed by aggregating all taxa at the phylum (Figure 4) and family (Figure 5) levels. Four major bacterial phyla dominated dry soil communities alongside the field samples: Actinobacteriota (39%), mainly composed of the family Solirubrobactereaceae; Bacteroidota (20%), primarily consisting of the family Chitinophagaceae; Acidobacteriota (11%), mainly represented by the family Blastocatellaceae, and Proteobacteria (10%) primarily consisting of the Alphaproteobacteria family Sphingomonadaceae. This structure remained consistent in the dry control soils throughout the entirety of the experiment (Figure 4).

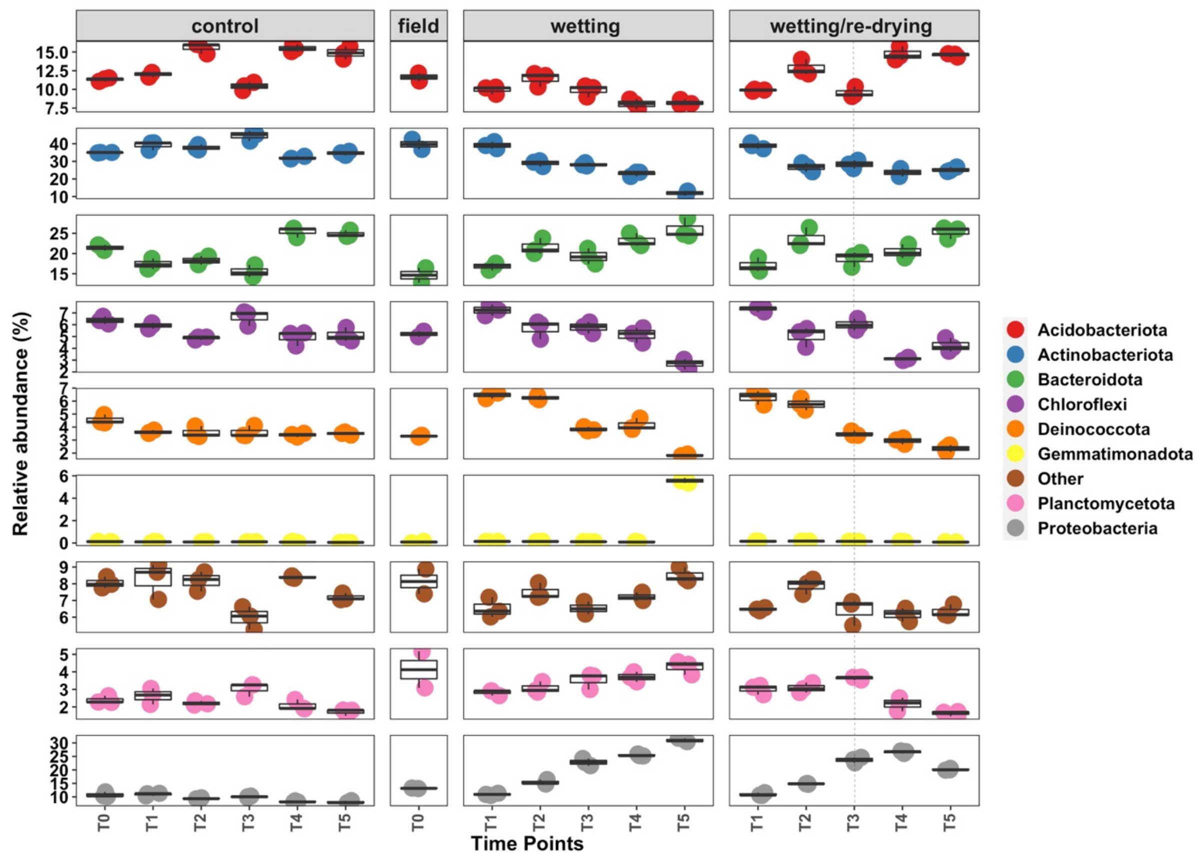

Figure 4 – Temporal dynamics of the eight most dominant phyla during the Control, Wetting, and Wetting/re-drying treatments. Panels show the relative sequence abundance (%) changes of the eight most abundant phyla during the eight weeks of the PDEC manipulative experiment. T0 was taken before the start of the experiment with T1 taken 24h after, T2 one week after, and T3 four weeks after. At T3, soils submitted to the wetting/re-drying treatment stopped being wet. At T4, soils submitted to the wetting treatment were wet for five weeks, and soils submitted to the wetting/re-drying treatment haven't received any water input for one week. The last time point, T5, represents eight weeks of daily wetting and four weeks of the drying period.

During the wetting treatment and the initial 4-week wet phase of the wetting/re-drying treatment, the phylum Proteobacteria (representing 10% of the initial community) doubled in relative sequence abundance to 23% from T0 to T3. By the end of the experiment (T5), the relative sequence abundance of this phyla was three times higher (from 10% to 31%) compared to the initial sample (T0) in the wetting treatment (Figure 4). The Proteobacteria family Sphingomonadaceae (Alphaproteobacteria) dominated the community apart from T3 when it was succeeded by taxa belonging to the Oxalobacteraceae family (Fig 5A). After one week of constant wetting (T2 onwards), we observed a continuous increase in the Comamonadaceae and Xanthomonadacea, both belonging to the subdivision Gammaproteobacteria, which

became significant after five weeks of wetting (Kruskal-Wallis: chi-squared = 13.5, df = 4, *p*-value = 0.001; chi-squared = 12.9, df = 4, *p*-value = 0.01, respectively) (Figure 5A). Alongside Proteobacteria, members of the low abundant phylum Planctomycetota increased steadily by 2.5% in their relative sequence abundance throughout the wetting treatment (Figure 4). Bacteroidota phylum had an overall increase of 5% with constant wetting treatment compared to the relative abundance at the beginning of the experiment (T0) (Figure 4). However, throughout the wetting treatment, different families showed an asynchronous response toward this perturbation (Figure 5D). In contrast, the relative sequence abundance of the Actinobacteriota phylum declined from 39% to 11% in response to wetting (Figure 4). A 23% reduction in relative sequence abundance across all detected Actinobacteriota families signs the negative impact of wetting in this phylum (Figure 5B). Taxa within the Acidobacteriota and Chloroflexi also decreased relative sequence abundance by 3% after eight weeks of continuous wetting (Figure 4). Such decline was more pronounced in the Blastocatellaceae family (Figure 5C). Low abundant phyla, such as Deinococcota, despite an initial increase by 0.02% in relative sequence abundance with wetting, decreased by 0.05% from T2 to T5 (Figure 4).

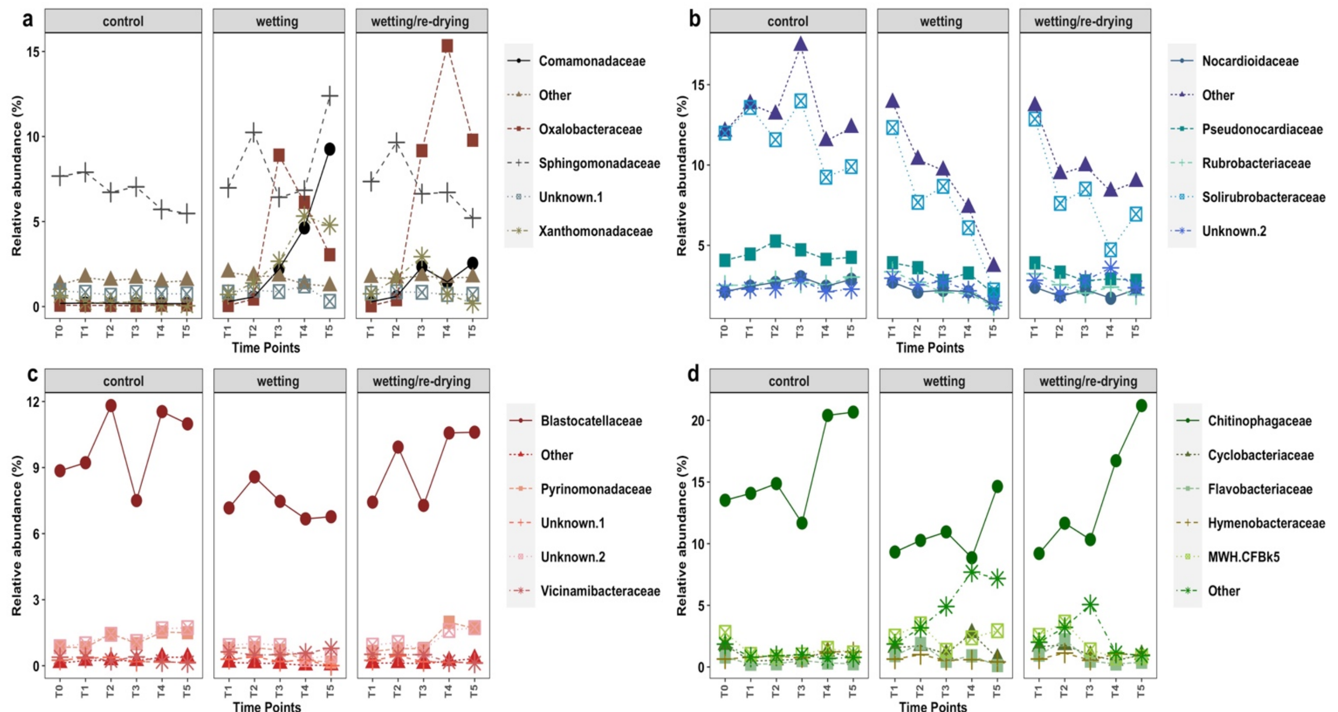

Figure 5 – Relative abundance of the top five most abundant bacterial families from the four most abundant phyla in the community at different time points during the control, wetting, and wetting/re-drying treatments. (a) Proteobacteria; (b) Actinobacteriota; (c) Acidobacteriota; (d) Bacteroidota.

3.4.5 - Microbial compositional changes during the wetting/re-drying treatment

Four weeks after the wetting ceased, the relative sequence abundance of Proteobacteria decreased by 3%. By the end of the experiment (T5), it was 10% less abundant than the samples that were kept wet (Figure 4). The response to the re-establishment of dry conditions was particularly evident for the dominant families Sphingomonadaceae and Comamonadaceae, which decreased their relative sequence abundance, and for Oxalobacteraceae family which increased their relative sequence abundance during the first week of re-drying (Figure 5A). In contrast, after four weeks of drying (T5), the relative sequence abundance of Actinobacteriota was 14% higher than those in the wetting treatment but still comparatively 9% lower than the dry control samples (Figure 4). The family Solirubrobactereacea in particular, showed a slow recovery after the drying process started (Figure 5B). Acidobacteriota were 5% more abundant than those in the wetting treatment and reached a similar relative sequence abundance to those observed in the dry control samples (15%) (Figure 4). Blastocatellaceae and Pyrinomonadaceae families showed signs of a quick recovery one week after the drying process started (T4) (Figure 5C). Despite the positive response to wetting, the Bacteroidota phylum increased in relative sequence abundance in one week after the drying process started (T4), being 3% more abundant than the dry control, by the end of the experiment (T5) (Figure 4). The latter was mainly driven by the 8% increase in relative sequence abundance of the family Chitinophagaceae compared to the beginning of the experiment (T0). All other Bacteroidota families declined in relative sequence abundance with the re-establishment of dry soil conditions (Figure 5D).

3.4.6 - Differentially abundant ASVs during wetting and wetting/re-drying periods

We used DESeq2 to identify the ASVs that were differentially abundant between the treated samples and the control after 24 hours (T1), one week (T2), four weeks (T3), five weeks (T4), and eight weeks (T5) (Figure 6). At T1, T2, and T3, we identified 96, 144, and 116 ASVs significantly different between the wetting treatment and the control. The number of ASVs continued to increase at T4 and T5, with 202 and 194 ASVs significantly different from the control. Of the identified ASVs, those that became less abundant than the control ($\log_2$ fold change, $LFC < 0$) continuously increased with the exposure to wet conditions, from 36% (T1) to 58% (T5), while those that became more abundant with wetting decreased from 64% (T1) to 42% (T5) (Figure S5, Table S2).

In the wetting/re-drying treatment, the number of ASVs significantly different from the control was similar to those identified in the wetting treatment, with 105, 139, and 119 ASVs found at T1, T2, and T3, respectively. However, one week after the wetting ceased (T4), we only identified 54 ASVs as significantly different from the control, decreasing to 48 ASVs one month after (T5) (Figure 6, Table S2). By the end of the experiment (T5), communities submitted to an initial wetting disturbance followed by a re-drying event resembled the dry control communities more than the wet counterparts (Figure 3 and Figure 6). Of the identified ASVs, those that became less abundant than the control during the wetting phase (T1 to T3) represented 41% of the identified ASVs. During the re-drying phase, the percentage of ASVs that became more abundant than the control increased from 59% (T3) to 65% (T5) (Figure S5, Table S2).

Most ASVs affiliated to the phyla Actinobacteriota, Bacteroidota (family Chitinophagacea), Chloroflexi, and Acidobacteriota decreased relative sequence abundance with wetting. In contrast, the relative sequence abundance of ASVs affiliated with Proteobacteria, Bacteroidota, and Planctomycetota increased during wetting (Figure 6).

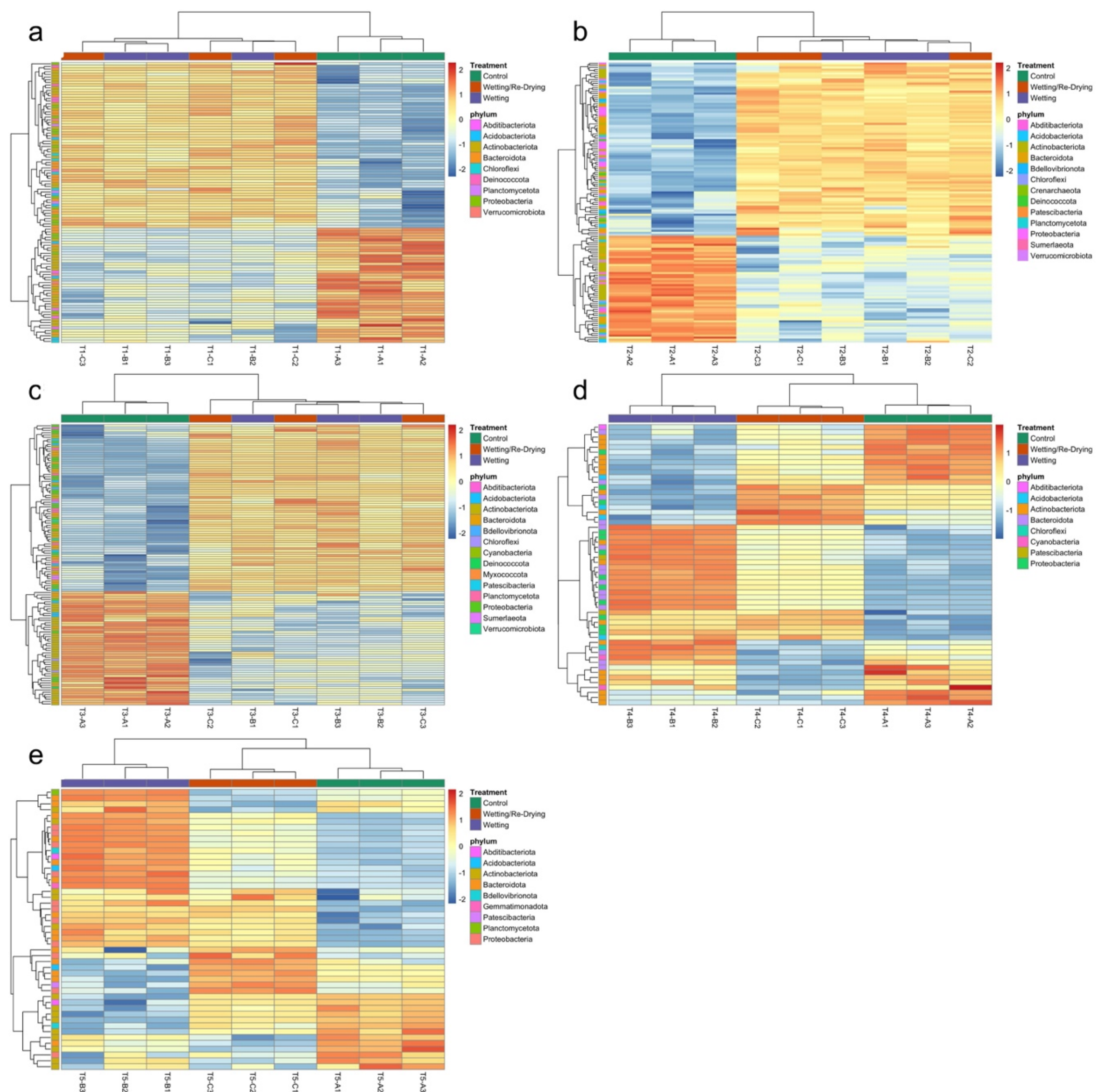

Figure 6 – (a-e) Heatmaps indicating the number of significant amplicon sequence variants (ASVs) identified by DeSeq2 analysis, for each time point. Comparisons were made between each treatment (wetting and wetting/re-drying) and the control at **(a)** T1, **(b)** T2, **(c)** T3, **(d)** T4 and **(e)** T5. Cells were colored using the normalized read counts (log+1) from DeSeq2 analysis, with a posterior scale by row transformation. Different colored cells in the leftmost columns indicate the phylum affiliation for each ASV identified. Colored cells in the highest part of the heatmap identify dataset characteristics such as the type of treatment.

3.4.7 - Phylogenetic structure of the communities during the wetting treatment

Microbial communities displayed significant phylogenetic clustering in dry soils (Dry control NTI mean values: 2.18 ± 0.18) during the experiment. This pattern was significantly affected by prolonged wetting (one-way ANOVA: F-value = 76.08, *p*-value = 1.9e-07), depicted by a shift towards a stochastic assembly of the community after four weeks of daily wetting (T3) (wetting treatment NTI mean values: 1.34 ± 0.68; wetting/re-drying treatment mean values: 1.70 ± 0.29) (Figure 7). We observed a second shift after T3 once wetting ceased and the re-drying phase started (Figure 7).

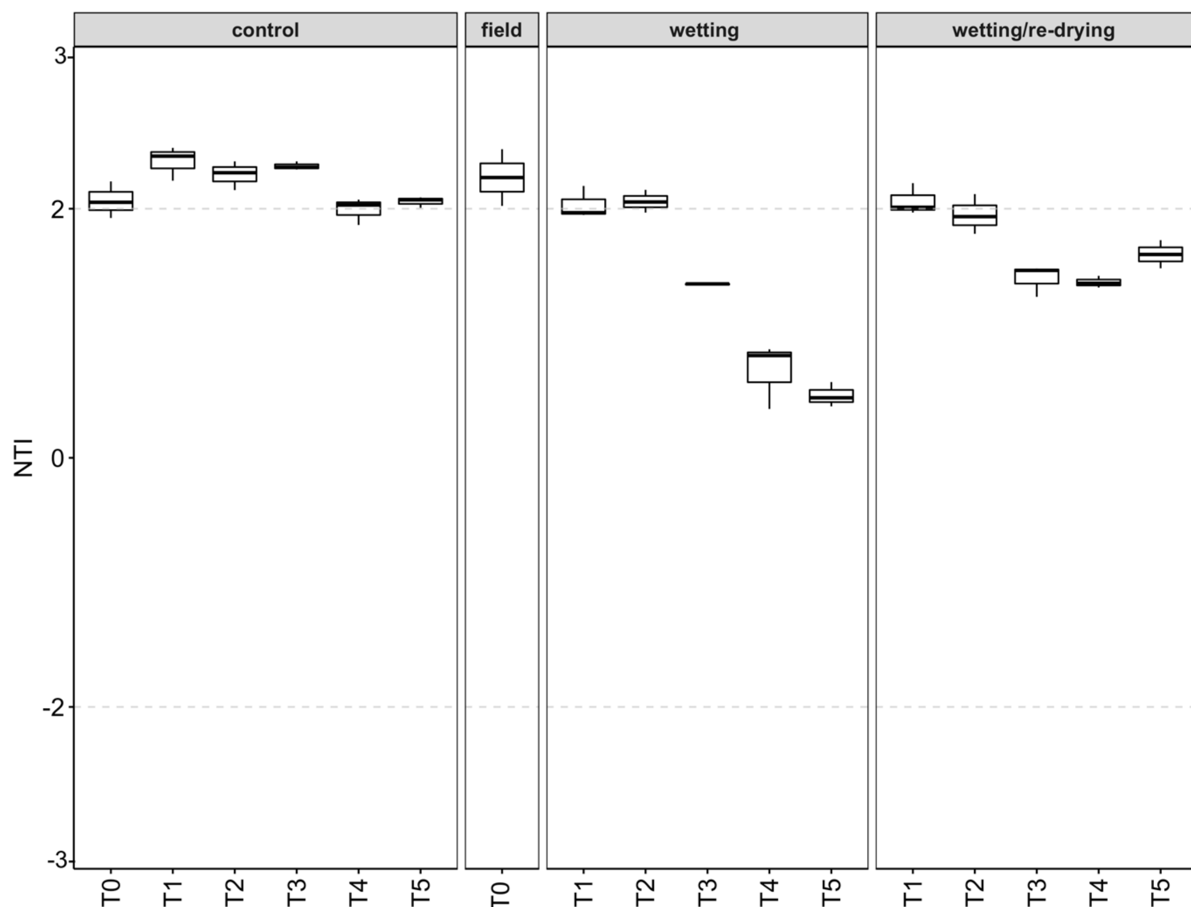

Figure 7 - NTI values for every community sampled from each treatment and control over the time course of the experiment. Dashed gray lines at the −2 and + 2 values delimitate the significance thresholds from the null expectation. NTI values < −2 or > + 2 suggest that phylogenetic turnover is less or greater than the null expectation and is related to deterministic processes. NTI values ranging between –2 and 2 are usually considered to signify the influence of stochastic assembly

3.5 - Discussion

The climate is changing in Antarctica, resulting in impacts that will likely affect the diversity and stability of terrestrial communities (Lee et al. 2017). Long-term observations are invaluable for documenting ecosystem changes, providing more comprehensive reports of ecosystem processes that occur over prolonged periods. However, the demands of budgets, the logistical constraints associated with long-term monitoring programs challenge the maintenance of these programs. Moreover, the time required to resolve patterns of change and draw inferences can take years to decades (McKnight et al. 2007; Tiao et al. 2012), which can delay the applicability of the results within rapidly evolving decision-making processes.

Several studies have looked at the impact of wetting on ecosystems and microbial life (Wallenstein and Evans, 2014; Barnard et al. 2013, 2015, 2020). However. Antarctic research is held under a strict code of conduct to help reduce or eliminate the human impact on the continent. As a result, research conducted in the field requires permits, which can limit the type and the number of experimental manipulations undertaken *in situ*. In this study, we aimed to demonstrate the ability to perform controlled experiments outside the continent as a complementary approach to field observations to study the response of the Antarctic biota to environmental change. The ability to accelerate changes predicted to occur in the ecosystem under realistic controlled conditions of temperature, relative humidity, and light in the laboratory, with replication, will help identify the tipping point and thresholds of current stable communities under climate change scenarios (Lee et al. 2017). Moreover, the ability to precisely emulate permafrost conditions and physical processes, such as the ablation of ice from the underlying permafrost that may influence below-ground communities, is an essential requirement to reliably simulate the physical and chemical environment that regulates the Antarctic terrestrial microbiome. For instance, the unfortunate event of the chamber breakdown within this study and the subsequent response of the microbial community observed in the control samples further emphasizes the need to accurately emulate key environmental attributes in a manipulative laboratory experiment, and the importance of the inclusion of controls to enhance the internal validity of the experiment. The effectiveness of our approach was further validated by comparing our results with previous field observations similarly focused on wetting events conducted in the McMurdo Dry Valleys. Our primary reference experiment was performed in the Miers Valley, where community changes were monitored for seven weeks after a stream was re-diverted into historically dry soil (Niederberger et al. 2019).

We observed significant structural and compositional changes in the microbial communities after one day of wetting, which persisted throughout the eight weeks of constant wetting (Figure 3). Those were consistent with the compositional shifts and turnover rates reported by Niederberger et al. (2019) and reflected, to some extent, the variation in community composition observed along wetness gradients in the Wright and Taylor valleys (Monteiro et al. 2022). Proteobacteria exhibited a positive response to wetting, with relative sequence abundance tripling after eight weeks of constant wetting compared to the dry control, becoming the most dominant phylum under wet conditions. The increase, during the first month of wetting, was mainly driven by the Alphaproteobacteria family Sphingomonadacea and Gammaproteobacteria families Oxalobactereaceae, Comamonadaceae, and Xanthomonadaceae (Figure 5A), which have been previously associated with wet soils in the dry valleys (Monteiro et al. 2022). Conversely, we observed an overall decline in the relative sequence abundance of Actinobacteriota, Acidobacteriota , and Deinococcota during the eight weeks of constant wetting compared to the dry control (Figure 4). Particularly for Actinobacteriota, the most dominant phylum in dry soils, the sensitivity to wetting persisted at the family level (Figure 5B). These clear taxa-specific abundance-changes hints at the possibility that a phylogenetic coherence might exist within Actinobacteriota to their sensitivity to wetting (Evans and Wallenstein 2014), which has been observed in previous wetting/dry-down experiments (Barnard et al. 2013, 2015). The latter, implies that these taxa should share traits that are key to adapting to extreme aridity. Part of these drought tolerance traits can be related to the capability to sporulate, the thickness of cell walls, and the ability to produce and accumulate organic osmolytes (e.g., proline, glycine, trehalose) to help adjust to the osmotic stress (Barnard et al. 2020).

Although the rapid responsiveness of microbial communities to wetting events has been well described or predicted in the MDV (Buelow et al. 2016; Van Horn et al. 2014; Lee et al. 2018; Monteiro et al. 2022; Niederberger et al. 2015, 2019; Tiao et al. 2012), evidence for subsequent recovery is still scarce. Our results indicate that microbial communities from historically dry soils can recover from short-term wetting events (Figure3, Figure 6). However, it is possible that long term exposure to wet conditions alters the structure and dominance patterns of the community to a point that the legacy effect of the disturbance could affect the ability to recover (Monteiro et al. 2022). These observations are relevant since climate predictions suggest that MDV soils will likely become more frequently wet during the summer due to warming (Fountain et al. 2014). The shift in community structure once wetting ceased

was mainly driven by the rapid increase in relative sequence abundance of Acidobacteriota and Bacteroidetes family Chitinofagaceaea to values identical to the dry control, the relative decline in Proteobacteria and Bacteroidota families (apart from Chitinofagaceaea) and the much slower relative increase of Actinobacteriota, a pattern associated with drought-resistors (Figure 4 and Figure 6) (Brangarí et al. 2021). The potential conservation of drought-resistant taxa during the wetting period and fast relative increase during the drying period are essential traits for community resilience and stability of the ecosystem (Manzanera 2021). These attributes have been associated with the historical legacy of the harsh conditions that preceded the disturbance (Jiang and Patel 2008; Evans and Wallenstein 2014; Hawkes et al. 2017; Brangarí et al. 2021).

The Niederberger et al. (2019) field experiment discussed whether dispersal mechanisms could have driven early compositional changes in the community. Our PDEC-controlled study demonstrates that community changes could be attributed to the fast responsiveness of resident members of dry soil communities to wetting (Figure 4). Since ecological processes such as dispersion cannot be accounted for during our laboratory experiment, the asynchronous changes in the relative abundance of dominant phyla and families to quick alterations in water availability indicate that dry soils communities are composed of coexisting taxa with different preference for environmental conditions. Ultimately, it could suggest that dry soil communities maintain different physiological aptitudes and metabolisms which are relevant attributes to increase the ecosystem's stability during short wetting disturbances. Concurrently, these highly responsive taxa could be used as biological indicators for recent changes in water availability in Antarctic terrestrial systems (Monteiro et al. 2022), adding further evidence on how sensitive communities inhabiting polar deserts are to those changes.

Following the observed asynchronous response at the phylum and family levels with changes in water availability, we examined which ecological factor best explained the structuring of the community during the experiment. In dry soil communities and during the initial exposure to wetness (one week), we observed the prevalence of phylogenetic clustering through selection (NTI values > 2) (Figure 7). This result is consistent with previous *in situ* observations using wetness gradients (Monteiro et al. 2022), and provides further evidence that communities emerge through strong environmental filtering leading to niche segregation in dry or recently wet soils. Under historical aridity conditions, taxa are likely selected based on traits related to stress mitigation or efficient resource utilization under ultra oligotrophy and extreme aridity. For instance, recent genomic analyses suggest that the highly abundant

Actinobacteriota can use atmospheric trace gases (e.g., H_2, CO) to support aerobic respiration and carbon fixation in desert soils (Bay et al. 2021; Ortiz et al. 2021). Likewise, Acidobacteriota are better adapted to compete when resources are limited (Fierer et al. 2007), with some members of this phylum capable of oxidizing hydrogen from the atmosphere to sustain energy requirements (Greening et al. 2015). However, we observed that quick changes in water availability could compromise the survival of well-adapted taxa to extreme aridity. For instance, species historically adapted to low water potential have less tolerance to immediate hydrological shocks during wetting, resulting in cell lysis (Schimel et al. 2007). In contrast, the consequent release of cellular material from sensitive taxa into the soils may benefit opportunistic heterotrophic taxa, which rely on rapid and efficient growth, rather than investing significant resources in stress mitigation strategies.

After one week of continuous exposure to wetness, the prevalence of phylogenetic clustering started to decrease, and neutral processes began to determine community composition (NTI between - 2 and 2) (Figure 7). We believe this could result from increased stochasticity coincident with the decline in selective pressures associated with desiccation/moisture stress and rapid increase in newly available carbon sources from the death and lysis of more sensitive taxa (Dini-Andreote et al. 2015). At this stage, we postulate that the relative increase in resource availability from cell lysis of sensitive taxa enabled a broad range of taxa to utilize newly available resources (e.g., different carbon substrates) (Martiny et al. 2013b), thereby decreasing the competition among coexisting taxa and leading to a more stochastic assembly of the community (Chase 2010). The increase in the relative abundance of Gammaproteobacteria, associated with higher productivity soils in the MDV (Niederberger et al. 2008), provides evidence for a potential increase in resource availability.

We identified two significant differences between the PDEC experiment and the analogous field wetting experiment (Niederberger et al. 2019). Firstly, we did not observe a significant increase in Cyanobacteria during our wetting treatment, which contrasts with the 18% increase reported after seven weeks of wetting in the field experiment (Niederberger et al., 2019). Cyanobacteria are major primary producers in Antarctic ice-free regions, exhibiting an excellent capacity to persist under arid conditions and considerable dispersal abilities (McKnight et al. 2007; Wood et al. 2008). As such, one explanation for the absence of Cyanobacteria increase in our experiment could be related to the difficulty of simulating dispersion processes in close systems such as the PDEC, which otherwise would naturally occur in the field, particularly during a natural wetting event (Niederberger et al. 2019).

Alternatively, it is also possible that the conditions in PDEC were not ideal for Cyanobacteria to thrive or the storing conditions pre-manipulation (-60 °C) impaired these taxa from growing. Secondly, we observed a significant decrease in alpha diversity relative to the dry control during the wetting treatment, particularly after two months of continuous wetting (Figure S3). This observation contrasts with the two-fold increase in species richness observed during the seven weeks field experiment (Niederberger et al. 2019) and the positive associations between water availability and diversity observed in the field (Lee et al. 2018; Monteiro et al. 2022; Niederberger et al. 2008). Yet, the positive associations between wetness and diversity aren't always consistent. For instance, three years after a mummified seal was moved to a new location in the MDV, the authors observed significant structural changes in the soil microbiome underneath the seal, correlated with changes in relative humidity and a significant reduction in diversity (Tiao et al. 2012). We then hypothesize that under wet conditions and in the absence of primary producers or biomass imports through wind or water dispersion, the potential decrease in resource availability over time could have increased resource competition affecting community diversity.

While in this study, we described community changes from a compositional and structural standpoint, further studies are necessary to address the association between composition and functional attributes of microbial communities during wetting events. Ultimately, a better understanding of the functional attributes underpinning the response of dry soil microbial taxa and how those are affected during wetting events will improve our ability to predict the ecological consequences of hydrological changes in the MDV ecosystem and other Antarctic ice-free regions.

3.6 - Conclusion and Significance

Overall the similarities in the results obtained through our laboratory experiment, emulating the microbial response to a wetting event, with those previously observed in the field validates the use of a PDEC as a complementary tool to study the temporal response and resilience of communities from Antarctic ice-free regions to climate change. We demonstrated that coexisting taxa with different environmental preferences initially drive fast structural shifts in dry soils. The latter offers insights into the diversity of metabolic functions and strategies inherent in the MDV terrestrial microbiome. We further demonstrated that compositional changes during four weeks of wetting were not permanent, with the conservation of drought-

resistant taxa underpinning resilient communities that oscillates in response to a periodic wetting/re-drying event.

Despite the limitations associated with laboratory-controlled experiments, such as the simulation of dispersal mechanisms (e.g. wind and water) which are relevant for the distribution of biomass in ice-free regions (Wood et al. 2008), the ability to adequately simulate a naturally low diversity system while maintaining the benefits of a controlled setting offers unlimited opportunities for hypothesis testing. When supported by field studies, such observations will help define the tipping points of community response to environmental disturbances in the Antarctic ice-free regions. Future experiments could be expanded to include single or synergetic physical, chemical, and biological disturbances, predicted to become more frequent in the system due to climate change (Hughes and Convey 2010), to understand how these will impact ecosystem functions and resilience. Lastly, the human presence associated with fieldwork activities in the continent can leave long-lasting disturbances in the ice-free soils affecting Antarctica's wilderness and aesthetic values as well as habitat suitability for its biota (Convey 2010; O'Neill et al. 2015). As such, efforts to develop infrastructure that enables remote and more sustainable research practices on ice-free regions should be encouraged and part of frameworks aimed to conserve and manage Antarctica's unique biodiversity and environment, one of the founding principles of the Antarctic Treaty.

Data Availability

The raw DNA sequences have been deposited in SRA under the BioProject accession number PRJNA912229.

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CHAPTER IV

Role of dominant taxa driving functionality under climate change in the terrestrial ecosystems of the McMurdo Dry Valley

4.1 - Abstract

Antarctic polar deserts are an abiotically-driven system projected to undergo changes in climate by the end of the century, which will significantly impact its ecology. As the main drivers of ecosystem functioning, the impacts of climate change on microbial communities will dictate the future states and functionality of polar desert ecosystems. Earlier investigations demonstrated that changes in water availability have profound implications on microbial structure and diversity, driven by shifts in the proportions of dominant taxa within communities. However, an evidence-based prediction of the impact of changes in dominance patterns on the functional status of the ecosystem is still lacking. Here we present a multi-omics resolved analysis of the effect of increased water availability on polar deserts' soil microbiome. We provide a functional perspective to previous structural and compositional changes observed in the soil microbiome and highlight the role of dominant taxa in maintaining critical traits associated with carbon, nitrogen, and phosphorous acquisition, energy conservation processes, as well as ecological resilience in an abiotically driven system. We demonstrated that dominant Actinobacteriota regulate metabolic traits for carbon fixation, P acquisition, and energy conservation under intense abiotic stress. We also found evidence that dominant Actinobacteriota persist actively in communities sampled across a wetness gradient, which is an important attribute associated with enhanced functional resilience to future wetness changes in the system. With the increase in water availability, we can expect an increase in functional activity and diversity regulated by a more diverse group of taxa, such as those affiliated to Cyanobacteria, Bacteroidota and Acidobacteriota, and potentially in conjunction with rare taxa.

4.2 - Introduction

In an ecological context, resilience is unarguably viewed as the ecosystem's insurance to cope with change (Thrush et al., 2009). Considering ecosystems are not homeostatic, ecological resilience is the ability of the community to persist or functionally adapt to temporal changes in environmental conditions. As a result, it may not depend solely on the continuity of ecological processes during disturbances, the rates of which can change over time, but also on the maintenance of mechanisms that reduce the probability of local extinctions, thereby increasing the ability to recover after the disturbance (Bardgett and Caruso 2020a; Philippot et al. 2021). Ecosystem resilience can be measured at different spatial and temporal scales and levels of ecological organization. As a result, a framework to study resilience should initially be developed and defined *a priori* to take into account the ecological level(s) at which ecological processes are analyzed, the functional traits that are most relevant for the system in question, and the type of disturbance.

Given the role of microbial communities in bridging above and below-ground ecosystem interactions and supporting ecosystem functioning (Stevnbak et al. 2012; Cavicchioli et al. 2019), an increasing number of studies have discussed the different attributes of microbial communities that regulate their capacity to respond and recover from environmental change (Allison and Martiny 2008; Avise et al. 2008; Shade et al. 2012a, b; Louca et al. 2018b; Bardgett and Caruso 2020a). Evidence shows that microbial diversity is essential to maintain functional diversity in terrestrial ecosystems, thereby increasing stability and resilience (Delgado-Baquerizo et al. 2016). The higher the number of species, the better the chances are that ecological processes can be provisioned by different microbial taxa regardless of the compositional changes occurring within the community. Nonetheless, microbial diversity is not homogeneously distributed, and in some environments, microbial taxa contribute disproportionately to community composition. For instance, a global survey demonstrated that a few bacterial taxa dominate soil communities, exhibiting strong preferences for a given set of environmental conditions (Delgado-Baquerizo et al. 2018). In some cases, such preference was found to be coherent at higher taxonomic levels (e.g., different members of Acidobacteriota exhibit affinities for acidic soils) (Philippot et al. 2010). These observations have recently started to raise questions about the ecological and functional role of dominant taxa as the backbone of community resistance and resilience (Fierer et al. 2014),

similar to what has been observed in macro-ecology studies (Grime 1998; Smith and Knapp 2003).

Microbial diversity results from the interplay of different ecological drivers, such as biotic interactions, environmental selection, and stochastic events, all acting at different temporal and spatial scales (Stegen et al. 2012; Dini-Andreote et al. 2015; Aguilar and Sommaruga 2020) and sometimes over distinct functional groups (Caruso et al. 2011). In some environments, such as in some hot and polar deserts, the influence of abiotic drivers greatly exceeds any other intrinsic factors (Andrew et al. 2012; Lee et al., 2019). Under those circumstances, coexistent populations are more likely to be selected based on physiological, morphological, or metabolic characteristics that collectively confer better ecological adaptation to a particular niche (e.g., moisture, pH, UV-radiation, salinity, oxygen) (Schimel et al. 2007). The latter may result in the emergence of dominant groups whose traits may fully characterize the current ecological state. Under such scenarios, the loss of dominant taxa will have larger impacts on ecosystem functioning than changes in diversity per se (via loss/gain in rare taxa).

The McMurdo Dry Valleys are considered an extreme polar desert ecosystem resulting in minimal biotic interactions due to their trophic simplicity and ultra-low biomass levels (Cary et al. 2012, Lee et al. 2019). Instead, extreme abiotic physicochemical gradients, particularly the lack of water availability, play a fundamental role in determining endemic biotic community distribution, structure, composition, and functionality (Bottos et al. 2020). Field and manipulative studies demonstrated substantial variation in the proportion of different microbial phyla with changes in water availability (Van Horn et al. 2014; Niederberger et al. 2015, 2019; Buelow et al. 2016; Monteiro et al. 2022), with the clear emergence of taxa dominance patterns, particularly in dry soils (Monteiro et al. 2023 - unpublished). However, a functional perspective on the value of traits associated with carbon (C), nitrogen (N), and phosphorous (P) acquisition and energy conservation processes expressed by dominant taxa for the stability and resilience of this abiotically-driven ecosystem to climate change is still lacking.

Here we tested the hypothesis that dominant active microbial taxa regulate core metabolic functions in polar ecosystems where environmental selection is the primary driver of community diversity. To test this hypothesis, we first identified the dominant metabolic functions associated with C, N, and P acquisition and stress-related pathways present and active within microbial communities across a wetness gradient previously defined according to the

spatial variability of environmental factors to which microbial communities respond to (Monteiro et al. 2022). We then attempted to identify the primary active members of the community, using a binning approach, and compared the dominant metabolic pathways present and expressed by the most active metagenome-assembled genomes (MAGs). We used a previously defined wetness gradient surrounding Lake Brownworth in the McMurdo Dry Valleys as our experimental system due to strong abiotic factors constraining the microbial community diversity and structure (Monteiro et al. 2022). To interrogate our hypothesis, we sought to address the following questions: (1) Do changes in water availability impact the functional activity of microbial communities? (2) Is there a loss in the metabolic capability or/and transcriptional activity for core metabolic traits for C, N, and P acquisition in the community with changes in wetness? (3) Which stress-response pathways are expressed by microbial communities with changes in water availability? (4) Will the loss of dominant taxa significantly impact essential microbial ecosystem services associated with C, N, and P acquisition? By answering these questions, we hope to understand the underlying mechanisms that shape microbial community resilience in an abiotically driven polar desert and have an evidence-based prediction of future functional states as a result of changes in water availability in the system under current climate change predictions for the region.

4.3 - Material and Methods

4.3.1 - Site description

Lake Brownworth (S77.42414 E162. 73761) is a small, shallow proglacial lake located 277 m above sea level at the seaward end of the Wright Valley next to the terminus of the Lower Wright Glacier in Victoria Land, Antarctica (Shaw and Healy 1980). The lake's formation coincided with the retreat of Wright Lower Glacier (9000 years B.P.) (Shaw and Healy 1980). The lake is mainly fed by meltwater discharges from the adjacent margins of the Lower Wright Glacier and by several alpine glaciers on the northern side, where the Upper Onyx River starts (Howard-Williams et al. 1986; Chinn and Mason 2016). The presence of an outflow feeding the Onyx River acts as a draining system for meltwater discharges into and out of the lake. As such, despite the annual or daily variation in meltwater discharges, these feeder streams may have a minimal impact on the dimensions of the lake (Levy et al. 2018).

4.3.2 - Sample and metadata collection, and nucleic acids extraction

A total of 15 soil samples were collected along three wetness gradients, as described in Monteiro et al. (2022). Briefly, five sampling points were defined from the shore of Lake Brownworth towards dry soil, considering the variability of soil conductivity, water activity, and pH along the wetness gradient. The sampling points represented one wet, two transition, and two dry soil samples (Monteiro et al. 2022). Soils used for later RNA extraction were immersed in 15ml falcon tubes with RNA later, and initially stored inside a dry Shipper to be kept frozen while in the field. They were later transported to Scott Base in dry ice and maintained at –60°C until RNA extraction.

Total DNA was extracted from 0.8 g of soil using a bead-beating method with a CTAB protocol as previously described samples (Coyne et al. 2001). Procedural controls were included during each batch of extractions. All DNA extracts were quantified using the Qubit dsDNA High Sensitivity Assay Kit (Thermo Fisher Scientific, USA).

Total RNA was extracted from a total of six samples across two gradients (three samples in each transect). These samples represented one wet, one transition, and one dry soil sample per gradient. Total RNA was extracted from 17 g of soil using the RNA PowerSoil kit from MO BIO (Carlsbad, CA, USA) in conjunction with the RNA Clean and Concentrator kit (Zymo Research, USA). Since we used approximately eight times more soil quantity than the one recommended in the RNA PowerSoil kit protocol, we adjusted the reaction volumes proportionally throughout the MO BIO protocol.

Before extractions, all surfaces were sterilized with 70% ethanol and RNase AWAY (Thermo Fisher Scientific, USA). The concentration of the total RNA was determined using the Qubit RNA HS Assay Kit (Thermo Fisher Scientific, USA). To prevent genomic DNA carryover, samples were treated with TURBO™ DNase (Ambion Life Technologies). The removal of genomic DNA from the total RNA samples was confirmed by PCR using the DNase-treated sample as a template and the 926R/515F primer set (Parada et al. 2016).

4.3.3. - Soil physicochemical analysis

Geochemical variables associated with each sample, namely the percentage of moisture, pH, and electrical conductivity, were measured as described previously by Monteiro et al. (2022). We performed additional measurements of total carbon, total nitrogen, ^{14}C, and ^{15}N isotopes, and trace elements. Briefly, samples for trace element analysis were prepared according to Lee et al. (2012) and analyzed in an ICP-MS (University of Waikato) following acid digestion and an in-house procedure based on the US EPA method 200.8 (Creed et al. 1994). For measurements of total carbon (TC), total organic carbon (TOC), total nitrogen (TN), and isotopic analysis, 2 grams of soils were dried, ground to a fine powder, and poured into a glass scint vial. These were then sent to the Center for Stable Isotope Biogeochemistry (UC Berkeley, California, US) to be further processed and analyzed using in-house procedures (Table S1/S2).

4.3.4 - Metagenome and metatranscriptome library construction and sequencing

Metagenome libraries from 15 samples were constructed and sequenced at the Genewiz sequencing facility (GENEWIZ China & Suzhou Lab), following the facility's protocols. Libraries were prepared using NEB Ultra II DNA Library Prep Kit for Illumina® (New England BioLabs) and sequenced in one lane on the Illumina HiSeq platform (2x150bp).

Total RNA was first treated with the Ribo-Zero rRNA depletion kit for Bacteria (Illumina, USA), following the manufacturer's protocol. Six RNA sequencing libraries were prepared using NEBNext® Ultra™ RNA Library Prep Kit for Illumina® (New England BioLabs). The quality of each barcoded library was confirmed with a BioAnalyser 2100 expert High Sensitivity DNA assay (Agilent Technologies). Libraries were sequenced in one lane on the Illumina Hiseq platform (2x150bp) at the Genewiz sequencing facility (GENEWIZ China & Suzhou Lab).

4.3.5 - Metagenomes and metatranscriptomes quality assessment and sequencing coverage

The quality of the raw metagenomic reads from each sample was checked with FastQC (v0.11.7) (Andrews 2010) and then processed with the BBTools package (Bushnell 2014). Briefly, the 3′-adaptors and 5′-adaptors were stripped, contaminants such as PhiX and other artifacts were removed, and the reads were filtered with a minimum quality score of 20. Two error-correction steps were incorporated into the pipeline to identify possible erroneous reads. First, we used Tadpole from the BBTools package with default parameters, followed by SPADES (v3.14.0) error correction step (Bankevich et al. 2012). The quality of the processed and error-corrected reads was re-assessed with FastQC (v0.11.7) before the co-assembly. The estimation of each metagenome coverage was first evaluated with Nonpareil using the quality-controlled reads and K-mer alignment method (Rodriguez-R et al. 2018).

The quality of the raw metatranscripts was checked with FastQC v0.11.7 (Andrews 2010). Erroneous transcripts were identified and removed with RCorrector (v1.0.4) default settings (Song and Florea 2015). Trim Galore! (v0.6.4) wrapper was used to remove sequencing adapters, filter bases with quality scores below 5 (Andrews et al. 2015), and remove transcripts with an error allowance greater than 0.1 and lengths below 36 bases. The presence of rRNA carry-over in the datasets was assessed with SortmeRNA (v2.1), and any residual rRNA identified was removed (Kopylova et al. 2012)

4.3.6 - Metagenomic community composition

The microbial community composition in each metagenomic dataset was determined by classifying reads using L16/L10E *rplP* universal single-copy ribosomal marker proteins with SingleM v0.13.2 (https://github.com/wwood/singlem). Briefly, “singlem pipe” was run on each metagenome and then summarised to produce a combined OTU table with all samples. Output tables for the *L16/L10E rplP* single-copy ribosomal marker proteins were then processed in R to generate phyla profiles (Team 2013).

4.3.7 - Metagenomes co-assembly and binning

SPADES quality filtered paired-end reads from each metagenome (n=15) were co-assembled using *de novo* MEGAHIT (v1.1.4), with a minimum contig length of 500 bp (Li et al. 2015). The quality of the assembly was inspected with MetaQUAST (v5.0.2) (Mikheenko et al. 2016). Coverage data based on mapping genomic and transcriptomic reads back to the co-assembly were calculated using coverM "contig mode" and "bwa-mem method" (https://github.com/wwood/CoverM), with default settings, and Salmon (salmon quant, "--validate-mappings", "meta"), respectively (Patro et al. 2017).

Metagenome-assembled genomes (MAG) were generated using contigs from the co-assembly step and from additional individual assemblies using SPADES (--meta) (Bankevich et al. 2012). The contigs longer than 1500 bp were binned using Metabat2 and Maxbin2 (Wu et al. 2016; Kang et al. 2019). Briefly, the reconstructed bins were aggregated, dereplicated with dRep (Olm et al. 2017), and the most high-quality genome bins were predicted using DASTool v1.1.1 (Sieber et al. 2018). A total of 170 bins were generated, which were then checked for completeness and contamination using CheckM --lineage_wf v1.0.13 (Parks et al. 2015). Using MIMAG standard as a reference (Bowers et al. 2017), low-quality bins or bins that failed the contamination threshold of $> 10\%$ were refined using MAGpurify v2.1.2 to remove possible contamination for genome quality improvement (Nayfach et al. 2019). In total, we recovered 143 MAGs, 56 of which were high quality and 87 medium quality according to the MIMAG standard (Bowers et al. 2017). The completeness and contamination of each MAG were assessed using CheckM (Parks et al. 2015). MAGs taxonomy was determined using GTDB-Tk v0.2.2 (Chaumeil et al. 2022) and illustrated using Pavian (Breitwieser and Salzberg 2020) to create the Sankey plot.

4.3.8 - Metagenome community representation in the co-assembly and MAGs

We used SingleM v0.13.2 (https://github.com/wwood/singlem) to calculate how much of the community was represented in our co-assembly and MAGs. We ran the subcommand "singlem pipe" on each metagenome, co-assembly, and high-medium quality MAGs to find discrete operational taxonomic units (OTUs) based on the presence of 14 single-copy marker genes. Each table comprising 14 single-copy marker genes was compared using the subcommand "singlem appraise" to determine how much of a community in each metagenome

was represented in the co-assembly or by the set of metagenome-assembled genomes (MAGs). To calculate the percentage of the community represented in our co-assembly and MAGs at the genus level, the OTUs were clustered at 89% average nucleotide identity (ANI). The argument "–imperfect" was used to accommodate some sequence differences.

4.3.9 - Read mapping, MAGs relative abundance and activity

MAGs coverage was calculated by mapping metagenomic and metatranscriptomic reads to high-medium quality MAGs using the CoverM subcommand "coverm genome" with default settings and Salmon (salmon quant, "--validate-mappings", "meta"), respectively. The relative abundance and functional activity of the MAGs in each sample were calculated using CoverM by mapping both metagenomic and metatranscriptomic reads to the MAGs with more stringent parameters to avoid spurious hits which could inflate the results: "coverm genome -m relative abundance --min-read-aligned-percent 0.75 --min-read-percent-identity 0.95 --min-covered-fraction 0". Since only a small portion of the reads mapped to the MAGs (Table S13/S14), we further normalized the relative abundance of each MAG in each sample by dividing the genomic/transcriptomic abundance of each MAG by the summarised genomic/transcriptomic abundance of all MAGs present in each sample. A rank abundance plot was computed with the normalized transcriptomic abundance calculated for each MAG across all samples with a cutoff of 4% to define the most active MAGs across our dataset.

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4.3.10 - Co-assembly functional annotation and gene/transcripts quantification

Open reading frames (ORFs) were predicted from the co-assembly using Prodigal v2.6.3 (-p meta) (Hyatt et al. 2010). The nucleotide sequences of the predicted ORFs were clustered at 99% identity using CD-HIT v4.8.1 to produce a nonredundant reference gene catalog (Fu et al. 2012). This catalog was annotated using DIAMOND BLASTX (default settings) with an 80% query coverage threshold (Buchfink et al. 2015). Nucleotide sequences were aligned against a metabolic marker database that included 51 metabolic marker genes (Leung and Greening 2021) and filtered following Jordaan et al. (2020) percent identity thresholds (Jordaan et al. 2020). For the phosphorous cycle gene annotation, we used the PCycDB database with a 70% identity cut-off (Zeng et al. 2022). To find genes associated with stress tolerance associated with polar deserts, the nonredundant reference gene catalog was

further annotated with eggNOG-mapper (v5.0) using diamond sequence aligner with an 80% query coverage threshold (Cantalapiedra et al. 2021). Gene abundance was quantified from the reference gene catalog by mapping quality filtered reads from each metagenome to the nonredundant catalog of genes present in the co-assembly using CoverM “contig --min-read-aligned-percent 0.75 --min-read-percent-identity 0.95 --min-covered-fraction 0”, with bwa alignment mode and subsequently normalizing the counts to RPKM (reads per kilobase of transcript per million reads mapped). Transcripts abundance was quantified using Salmon (salmon quant, “--validate-mappings”, “meta”) by mapping quality filtered transcripts to the nonredundant catalog of genes and normalizing read quantifications from each metatranscriptome to TPM (transcripts per million) (Patro et al. 2017).

4.3.11 - MAGs functional annotation and gene/transcripts quantification.

MAGs open reading frames (ORFs) were predicted using Prodigal v2.6.3 (-p single) (Hyatt et al. 2010). The nucleotide sequences from the predicted ORFs were annotated for metabolic marker genes using DIAMOND BLASTX (default settings) with an 80% query coverage threshold and the same settings described above for the co-assembly (Buchfink et al. 2015). Gene abundance was quantified by mapping quality filtered reads from each metagenome to the MAGs ORFs using CoverM “contig --min-read-aligned-percent 0.75 --min-read-percent-identity 0.95 --min-covered-fraction 0”, with bwa alignment mode and subsequently normalizing the counts to RPKM. Transcript abundance was quantified using Salmon (salmon quant, “--validate-mappings”, “meta”) by mapping quality filtered transcripts to the MAGs ORFs and normalizing read quantifications from each metatranscriptome to TPM (Patro et al. 2017).

4.4. - Results

4.4.1 - Sequencing

Illumina shotgun sequencing produced, on average, 7 Gb (s.d ±3) of metagenomic reads across the 15 soil samples (Table S3). Comparisons of diversity and coverage between the 15 metagenomes, using NonPareil, indicate that wet, transition, and dry soil metagenomes had an average diversity coverage of 60%, 63%, and 72%, respectively (Figure S1_NonPareil curves,

Table S3). The soil diversity index, calculated with NonPareil, ranged between 18.6 and 21.4 (Table S3). All metagenomes were co-assembled with Megahit generating a total of 4,798,308 contigs, with 4,797,652 contigs greater than 500 bp and 633,634 contigs greater than 1500 bp (Table S4). On average, Illumina shotgun sequencing of the 6 RNA libraries produced 18 Gb (s.d ± 12) of transcripts across the six sequenced samples (Table S3).

4.4.2 - Metagenome community composition and representativity in the co-assembly

Microbial community composition across the wetness gradients comprised 54 phyla (Figure S2; Table S5), with the top 10 most abundant phyla (mean relative abundance > 0.01 across the dataset) identified as Acidobacteriota, Actinobacteriota, Bacteroidetes, Chloroflexi, Cyanobacteria, Gemmatimonadetes, Patescibacteria, Planctomycetes, Proteobacteria and Verrucomicrobia (Figure S2; Table S5). Dry soil metagenomes were dominated by Actinobacteriota (69%), followed by Acidobacteriota (7%) and Chloroflexi (6%). Metagenomes from transition soils were dominated by Actinobacteriota (33%), Proteobacteria (18%), and Bacteroidetes (15%). Wet soils metagenomes were dominated by Bacteroidetes (23%), Proteobacteria (21%), and Actinobacteriota (20%) (Figure S2; Table S5).

Estimates based on conserved single-copy marker genes indicated that, on average, 88% of the taxa identified in the unassembled metagenomic reads were successfully represented in the co-assembly. An average of 94% of the populations present in dry soil metagenomes were successfully co-assembled. In contrast, only 79% of the populations present in wet soil metagenomes were successfully co-assembled (Table S6).

Coverage data, based on mapping rates from reads and transcripts to the co-assembly, aligned with the recovery estimates, with an average of 90% of the metagenomes mapping to the co-assembly and 65% of the transcripts mapping to the co-assembly (Table S6). Reads from dry soils metagenomes had the highest mapping rates to the co-assembly, followed by reads from the transition soils and reads from the wet soils.

4.4.3 -Functional capacity and functional activity of core metabolic traits

At the community level, the annotation of selected marker genes for energy acquisition identified a dominance and high transcription of genes associated with aerobic respiration, TCA cycle, and oxidative phosphorylation across the wetness gradient (Figure 1A/B, Table S7/S8).

Carbon fixation via the Calvin-Benson cycle was the most dominant and active pathway identified across the gradient, based on *rbcL* abundance and transcription. Rubisco genes were significantly more abundant in dry soil metagenomes, but at a transcriptional level, the most transcribed type was associated with chemosynthetic type IE (Figure 2A; Figure S4; p-value < 0.05). At the transcriptional level, *rbcL* transcripts were more abundant and diverse in wet soils, and particularly associated with the type IB, IC and ID (Cyanobacteria and phototrophic bacteria) (Figure 1A/B, Figure 2A, Figure S5, Figure S6, p-value < 0.05). We also identified the presence and transcription of marker genes associated with other carbon fixation pathways in wet soils, such as the reverse TCA cycle, the 3-hydroxypropionate/4-hydroxybutyrate, but not in dry soils (Figure 1, Figure S4/S5/S6/S7).

The presence and transcription of maker genes associated with phototrophy (RHO, PSI, PSII) indicates that this metabolic trait is present and active along the wetness gradient. Yet, despite the high variability, wet soil communities had the highest abundance of marker gene transcripts for photosystems I and II (Figure S6). In contrast, marker genes and transcripts for trace gas metabolism, mainly carbon monoxide and hydrogen oxidation pathways, were more abundant in dry soils than in transition and wet soils (Figure 1A/B, Figure 2B and Figure S6; p-value < 0.05).

The diversity and abundance of genes and transcripts associated with nitrogen cycling were consistently higher in transition and wet soils compared to dry soils (Figure 1A/B, Figure S4/S5/S6). Marker genes for nitrification (*amoA*) and nitrogen fixation genes (*nifH*) were detected in wet, and transition soils but could not be detected in the majority of dry soil samples (Figure 1 A/B). The most active nitrogen cycling pathways in wet and transition soils were related to reductive steps of the cycle, particularly complete denitrification, with fewer transcripts mediating dissimilatory nitrate reduction to ammonium (*nrfA*) (Figure S5).

Marker genes associated with the two-component system, phosphotransferase system, and transporters were present across the gradient, with higher abundance in wet soils (Figure

1/A/B, Figure S4, Table S7/S8). Transcript abundance associated with these phosphorous pathways was higher in the transition soils (Figure 1/A/B, Figure S4, Table S7/S8). Lastly, marker genes associated with sulfur cycle pathways, particularly sulfide oxidation (*FCC, Sqr*) and SOX systems (*SoxB*), were present across the wetness gradients (Figure 1A) with very low gene and transcript abundances (Figure S6).

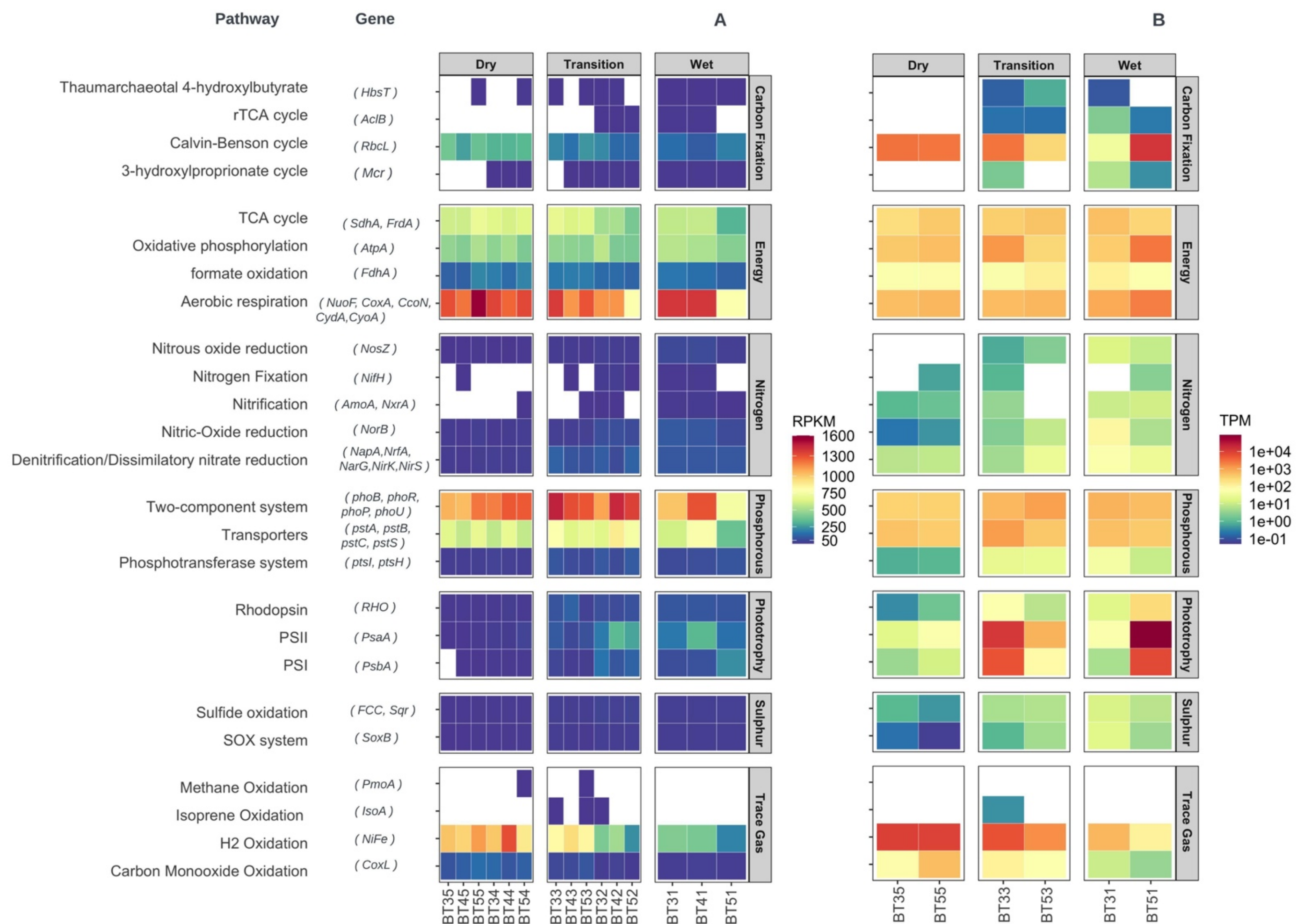

Figure 1 –Functional capacity and transcription of core metabolic pathways identified at the community level across a geochemically defined wetness gradient. A - Heatmap showing the presence and abundance of marker-genes associated to core metabolic pathways along the wetness gradients. The abundance of marker-genes for each pathway are displayed as reads per kilobase million (RPKM). **B –** Heatmap showing the transcript abundance for marker-genes associated to core metabolic pathways along the wetness gradients. The abundance of each transcript was calculated in transcripts per million (TPM). When more than one gene was used to represent a pathway, the RPKM and TPM abundances were summed. Blank white cells represent zero values.

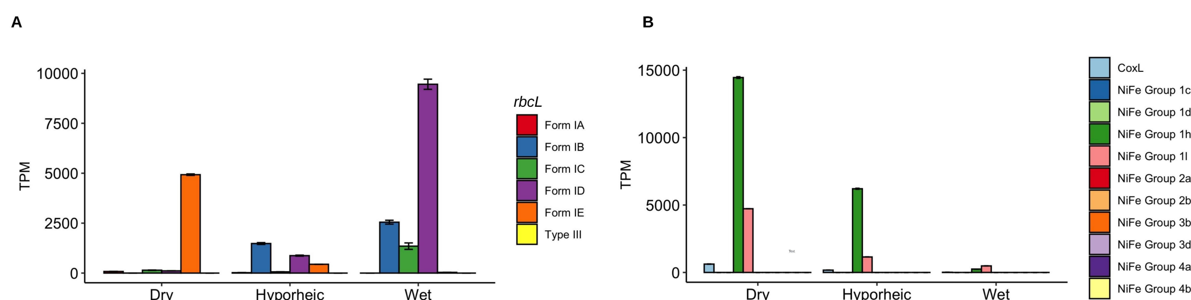

Figure 2 – A - Normalised transcript abundance of Rubisco genes found along the wetness gradients. **B -** Normalised transcript abundance of NiFe hydrogenases and CO dehydrogenase found along the wetness gradients.

4.4.4 - Stress-response pathways across the wetness gradients

Molecular chaperones such as *GroEL* and *DnaK*, which have a role in minimizing biomolecular damage, were highly expressed in communities across the wetness gradients (Figure 3A/B; Figure S7, Table S9/S10). Genes related to UV-resistance (*uvrABC, recA*) were the most abundant across the transect, particularly in dry soils (Figure 3A, Table S9/S10). However, due to the high variability in the abundance of transcripts associated with UV-resistance genes in both transition and wet soils, no significant differences were identified across the transect (Figure S7B). Genes and transcripts involved with desiccation, osmotic stress, sporulation, and those associated with the universal stress protein (USP) were significantly more abundant in dry soils than in wet soils (Figure 3, Figures S7, p-value < 0.05). Although genes associated with DNA repair were significantly more abundant in dry soils, from an activity point of view, transcripts were more abundant in wet soil (Figure 3, Figures S7, p-value > 0.05). The abundance of transcripts associated with DNA repair was highly variable within wet and transition soils (Figure 3, Figures S7, Table S9/S10). Genes related to cold and heat shock proteins were more abundant in dry soils (p-value < 0.05), but no differences in transcript abundances across the transect were identified (Figure 3, Figures S7, Table S9/S10).

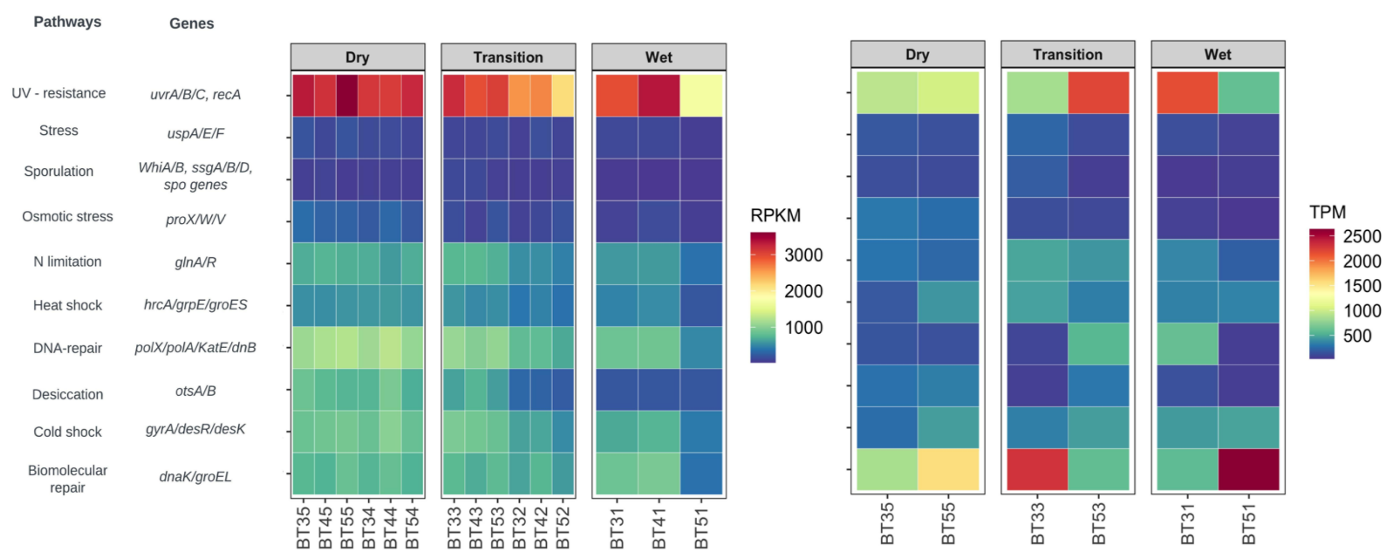

Figure 3 - Functional capacity and activity of stress-related pathways at the community level. A - Heatmap showing the presence and abundance of stress-related pathways along the wetness gradients. The abundance of marker-genes for each pathway are displayed as reads per kilobase million (RPKM). **B –** Heatmap showing the abundance of gene transcripts associated to stress-related pathways along the wetness gradients. The abundance of each transcript was calculated in transcripts per million (TPM) with Salmon. When more than one gene transcript was used to represent a pathway, the RPKM and TPM abundances were summed.

4.4.5 - MAGs composition, coverage, and representativity in the community

To address the hypothesis that the dominant taxa maintain community function, we recovered 143 MAGs, These were represented by 56 high-quality MAGs (completion > 90%, contamination < 5%) and 87 medium-quality (completion > 50%, contamination < 10%) (Table S11). The 143 MAGs reflected 142 Bacteria and one Archaea (*Nitrosocosmicus* sp). Taxonomic classifications using GTDB show that MAGs spanned 11 phyla, with the majority being affiliated with the Actinobacteriota (68 MAGs), Bacteroidota (22), Cyanobacteria (12), Proteobacteria (12) and Chloroflexota (11) (Figure S8).

On average, 42% of the populations present in the unassembled metagenomes were represented in our MAGs (Table S12). Clustering the single-marker genes at 89% ANI (an approximate representation of genus-level clusters) demonstrated that our recovered MAGs represented 56% of the genera present in dry soil unassembled metagenomes, but only 22% of the genera present in the wet soil unassembled metagenomes (Table S12). Genomic and transcriptomic read mapping to the 143 MAGs supported the recovery estimates, with dry unassembled metagenomes and metatranscriptomes consistently better represented and covered (Table S12).

4.4.6 - Potential for key metabolic functions governing carbon and nutrient cycles within MAGs

To gain insight into the metabolic capacity of the 143 MAGs, we analysed the presence of metabolic marker genes in our MAGs (Figure S9). The capability to derive energy through aerobic respiration via the TCA cycle and oxidative phosphorylation was widespread among our MAGs (85% of MAGs on average) (Figure S9). Carbon fixation pathways were restricted to the Calvin-Benson cycle and the archaeal Thaumarchaeotal 4-hydroxybutyrate pathway. The presence of *rbcL* gene was found in ten of the twelve Cyanobacteria MAGs, twenty-eight of the sixty-eight Actinobacteriota MAGs, and one Bacteroidota MAG. As expected, the marker gene for the Thaumarchaeotal 4-hydroxybutyrate pathway was only found in the Archaea MAG (Thermoproteota phylum). Marker genes for phototrophy, particularly for photosystems I and II, were only present in Cyanobacteria and one Proteobacteria from the Rhodobacter family. Rhodopsin genes were found in seven Bacteroidota, three Actinobacteriota, and one Deinococcota from the Trueperacea family. The capability to oxidase atmospheric trace gases, particularly hydrogen (NiFe group1h/l and NiFe group 2a), was widespread across different MAGs, including fifty-four Actinobacteriota, eight Chloroflexota, six Bacteroidota, four Gemmatimonadota, five Proteobacteria, five Acidobacteriota, two Verrucomicrobiota and two Cyanobacteria (Nostocaceae family). The capacity to oxidize carbon monoxide was restricted to fifteen Actinobacteriota and one Acidobacteria (Figure S9).

The capacity for nitrification was only found in the archaeal MAG. We identified a *NifH* genes in three Cyanobacteria MAG (genus *Hassallia, Nodularia* and *Nodosilineas).* In contrast, the capacity for the reductive pathways associated with nitrogen cycling was present in four Bacteroidetes MAGs, three Actinobacteriota MAGs, two Acidobacteriota MAGs, one Planctomycetota, and one Proteobacteria MAG. Marker genes for the two-component system associated with phosphorous starvation were present across ten phyla, with *PhoB* present across all Cyanobacteria, Proteobacteria, Deinococcota, and Planctomycetota MAGs, and in fifty-five Actinobacteriota, ten Bacteroidota, two Acidobacteriota, two Chloroflexota MAGs and one Gemmatimonadota MAG. Phosphate transporters (e.g., *pstB*) were present across seven phyla, including Gemmatimonadota, Planctomycetota, Verrucomicrobiota (all MAGs), four Cyanobacteria, five Acidobacteriota, forty-six Actinobacteriota, and nine Proteobacteria. Pathways related to the sulfur cycle were only found in three Proteobacteria and one Actinobacteriota MAG (Figure S9).

4.4.7 - Key metabolic functions governing MAG carbon and nutrient cycling

To address our main hypothesis, we focused on the community's most dominant and active members. Only the MAGs in which normalized transcript relative abundance in each sample was higher than 4% were selected for further analysis (Figure S10). The latter resulted in the selection of 18 functionally active MAGs across the wetness gradient, 15 of which were equally highly abundant (Figure 4).

Functional activity and dominance patterns across the wetness gradients varied. In dry soils, Actinobacteriota were the most active phylum. In wet and transition soils, the most active members of the community were more diverse, and comprised Acidobacteriota, Cyanobacteria, and Bacteroidota MAGs (Figure 4). The patterns observed in the dry soils and, to a lesser extent, transition soils reflect dominance patterns observed previously by 16S amplicon sequencing (Monteiro et al. 2022) and, in this study, by shotgun metagenomic sequencing (community composition was classified using L16/L10E *rplP* single-marker gene retrieved from metagenomic reads). However, the patterns observed in the wet samples did not reflect previous results (Figure S2).

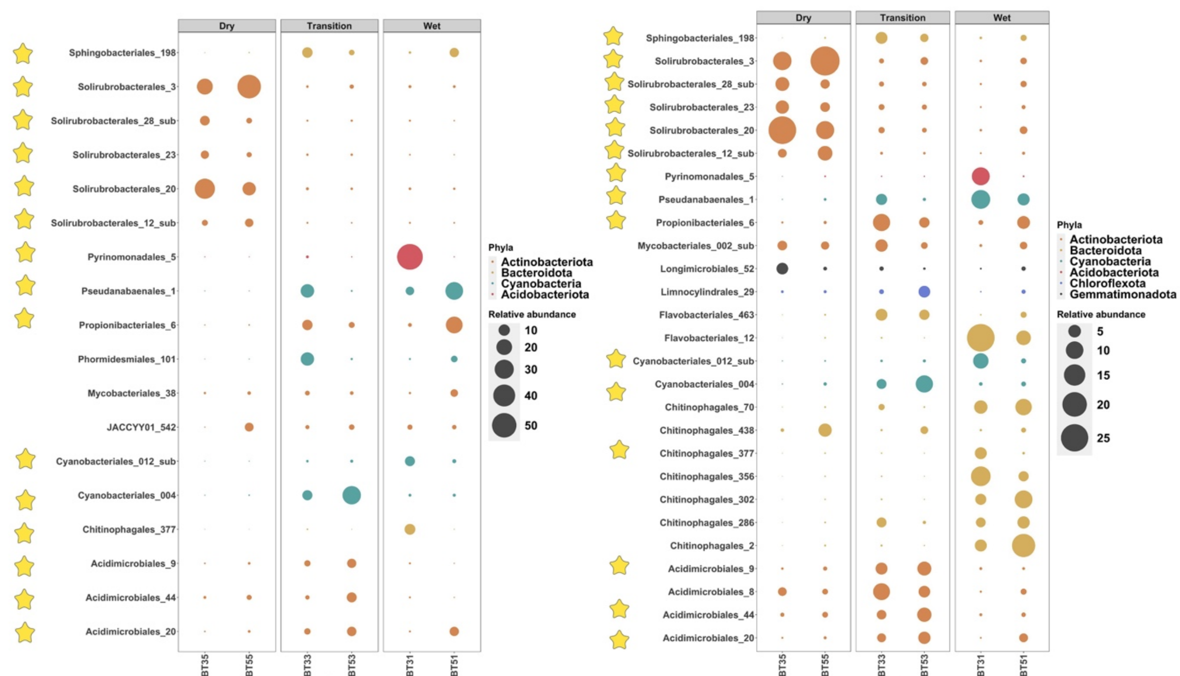

Figure 4 – A – Top 4% most active MAGs found in each sample based on the normalised abundance of transcripts mapping to the MAGs was higher than 4%, calculated using CoverM. **B –** Top 4% most abundant MAGs found in each corresponding metagenome, based on the normalised abundance of metagenomic reads mapping to the MAGs. The abundance of genomic reads mapping to the MAGs was calculated using CoverM. Stars identify the MAGs that were consistently in the top 4% of most active and abundant MAGs.

Considering energy conservation pathways, a high abundance of marker gene transcripts associated with aerobic respiration, oxidative phosphorylation, and TCA cycle was well supported by several dominant MAGs associated with four phyla (Figure 5). In dry soils, marker gene transcripts for the TCA cycle (*SdhA*) and aerobic respiration (*NuoF, CoxA*) were the most abundant transcripts related to energy conservation pathways and solely associated with Actinobacteriota MAGs, mostly associated with the Solirubrobacterales order. The latter were also actively transcribing hydrogen oxidases (Figure 6). In transition soils, Cyanobacteria and Actinobacteriota MAGs were actively transcribing genes associated with oxidative phosphorylation (*AtpA*), aerobic respiration (*NuoF, CoxA) and* the TCA cycle (*SdhA).* In wet soils, those genes were found to be transcribed also by active Acidobacteriota (Chitinophagales_377) and Bacteroidota (Pyrinomonadales_5) MAGs (Figure 5).

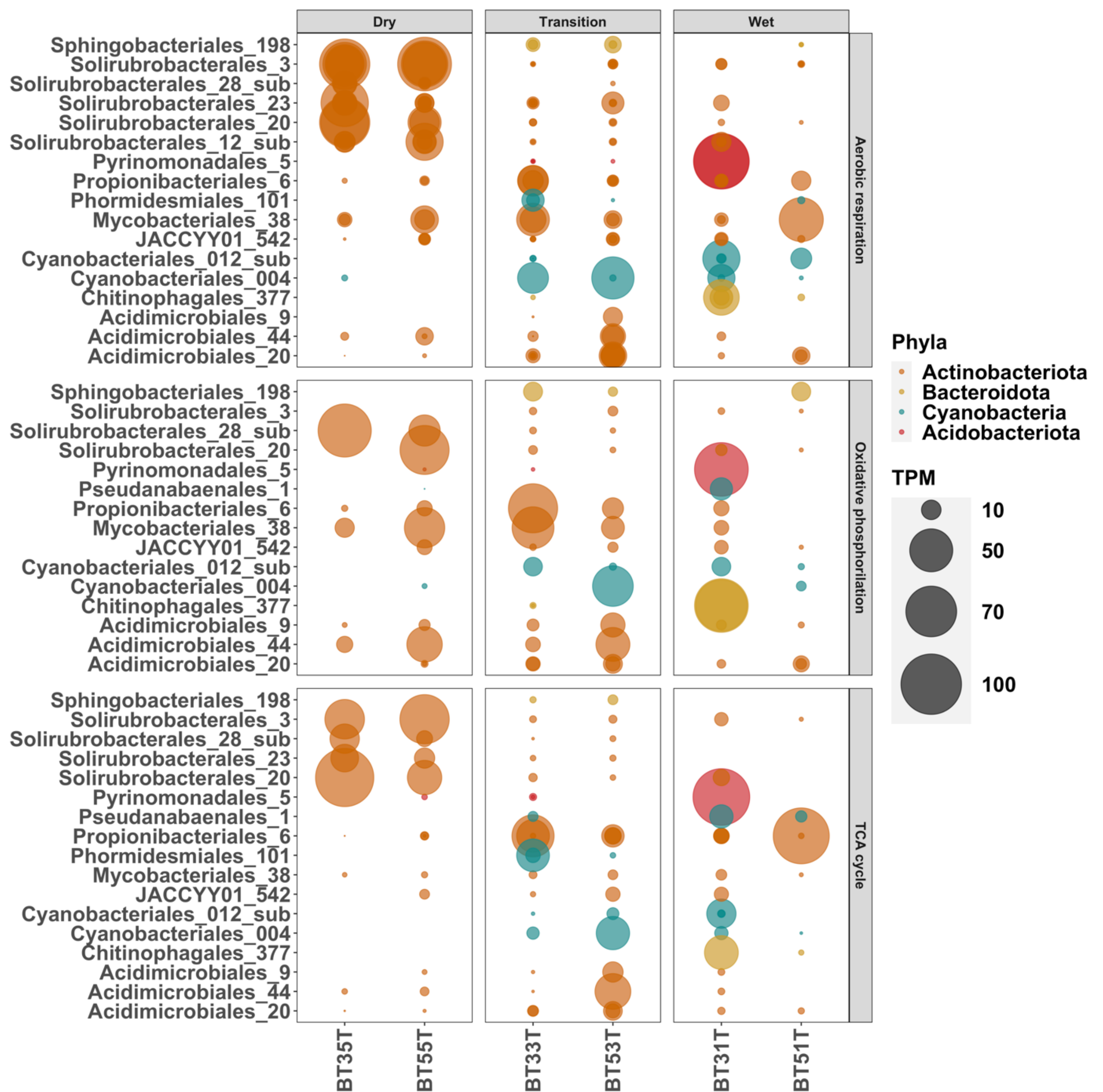

Figure 5 - Normalized abundance of transcripts of key genes associated with energy conservation pathways such as the TCA cycle (*SdhA*), aerobic respiration (*NuoF, CoxA)* and oxidative phosphorylation (*AtpA*), expressed by the top 4% most active MAGs. Values are shown in transcripts per million reads (TPM).

Marker genes for trace gas metabolism, particularly hydrogen oxidation, and phototrophic metabolism, particularly photosystems I and II (PSI and PSII), were the most transcribed metabolic genes by the most active MAGs (Figure 6A/B). Hydrogen oxidation transcripts (*NiFe*) were found in thirteen highly active Actinobacteriota MAGs, eleven of which were equally highly abundant in dry soil samples (Figure 6A; Figure 4). The latter indicates that functionally active and dominant Actinobacteriota MAGs are the main drivers of

trace gas metabolism at this location. Five MAGs all belonging to the order Solirubrobacterales (Solirubrobacterales_3, Solirubrobacterales_20, Solirubrobacterales_28_sub, Solirubrobacterales_23, and Solirubrobacterales_12_sub) had the highest *NiFe* transcript abundance (maximum of 3269 TPM, 2969 TPM, 483 TPM, 392TPM, and 301 TPM, respectively) in dry soils. *NiFe* transcripts associated with those five MAGs were also found in transition and wet soils, albeit at substantially lower abundance (average of 6 and 4 TPM in transition and wet soils, respectively). The maximum abundance of *NiFe* transcripts in wet samples was found in one Bacteroidota MAG (Chitinophagales_377 – 83 TPM). Marker genes for carbon monoxide oxidation (*CoxL*) were also actively transcribed by three Actinobacteriota in dry soils but at substantially lower abundance (average of 7 TPM).

In wet and transition soils, highly active Cyanobacteria were the main drivers of a phototrophic metabolism (Figure 5B). In particular, we found a high abundance of marker gene transcripts for PSI and PSII associated with Cyanobacteria MAGs representative of the orders Pseudanabaenales (Pseudanabaenales_1 – 6011 TPM, *PsbA*), Cyanobacteriales (Cyanobacteriales_004 - 2789 TPM, *PsbA*) and Phormidesmiales (Phormidesmiales _101 - 1606 TPM, *PsaA*). Marker genes for bacterial rhodopsins were only transcribed in two dominant Actinobacteriota, representative of the orders Propionibacteriales and Mycobacteriales, with a maximum value of 14 TPM in a wet sample.

Carbon fixation via the Calvin-Benson cycle was the only active pathway identified in our most functionally active MAGs (Figure 6C). In dry soils, the *rbcL* gene was transcribed by Actinobacteriota MAGs, particularly in MAGs representative of the orders Solirubrobacterales (Solirubrobacterales_3 – 3076 TPM; Solirubrobacterales_28_sub – 364 TPM; Solirubrobacterales_23 – 252 TPM; Solirubrobacterales_20 - 1815 TPM; Solirubrobacterales_12_sub – 242 TPM, maximum values) . In wet and transition soils, the *rbcL* gene was transcribed by phototrophic Cyanobacteria MAGs (Pseudanabaenales_1 - 2193 TPM) (Figure 6C). The most active Actinobacteriota MAGs transcribing NiFe genes were also found to be transcribing rbcL genes and were all associated with the order Solirubrobacterales (Figure 6).

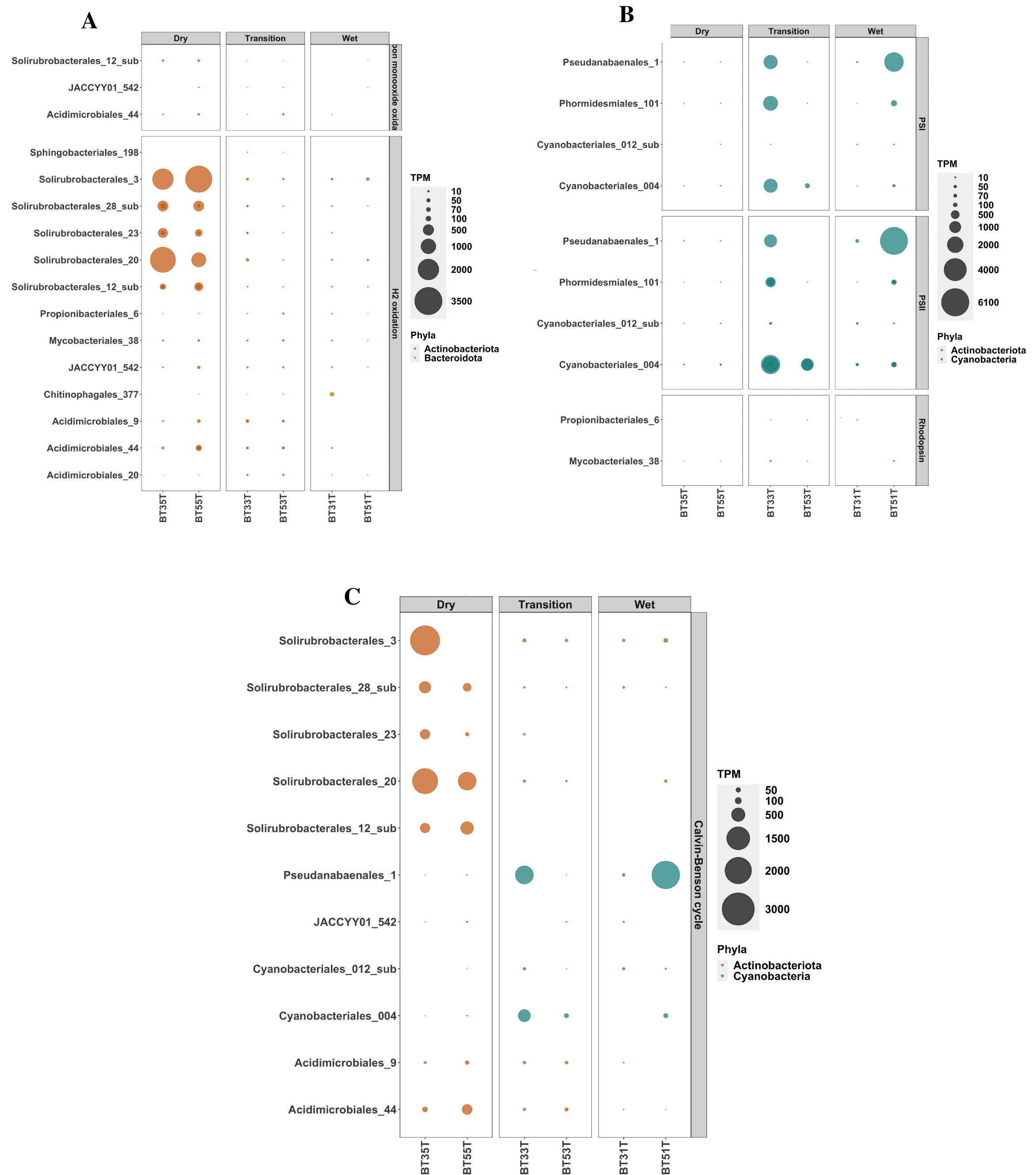

Figure 6 – Normalized abundance of transcripts of key genes for **(A)** Trace gas metabolism (NiFe) **(B)** Phototrophy (PsaA,PsbA, RHO) and **(C)** Carbon fixation (rbcL), expressed by the top 4% most active MAGs. Values are shown in transcripts per million reads (TPM).

We observed an absence in transcriptional activity of most marker genes associated with N cycling pathways by our dominant active MAGs. Only marker gene transcripts for the reductive pathways of the nitrogen cycle (denitrification – *NorB;* denitrification/dissimilatory nitrate reduction - *NarG*, and *NapA*) were mapped to our most functionally active MAGs. Additionally, those were solely transcribed in wet and transition soils by Acidobacteriota

(Pyrinomonadales_5 – 207 TPM maximum value) and Actinobacteriota (Propionibacteriales_6 - 31 TPM; Acidimicrobiales_9 - 8 TPM maximum values) MAGs, despite their active presence in dry soils (Figure 7).

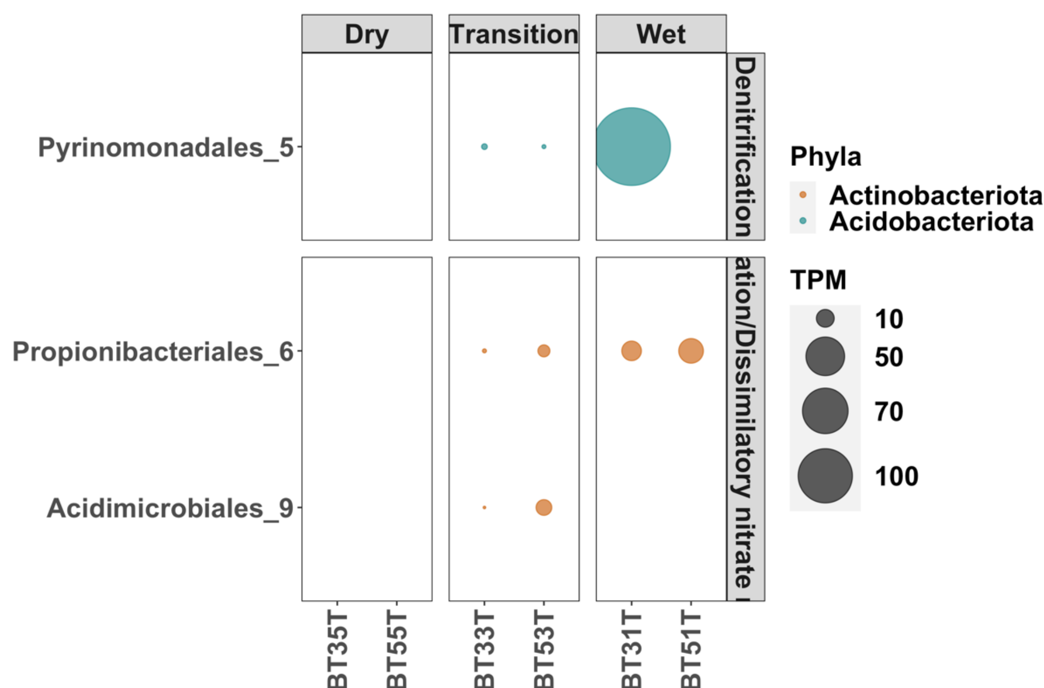

Figure 7– Normalized abundance of transcripts of marker genes for reductive pathways of the nitrogen cycle (*NorB*, *NarG*, and *NapA*), expressed by the top 4% most active MAGs. Values are shown in transcripts per million reads (TPM).

Pathways for phosphorus acquisition were well expressed in eighteen functionally active MAGs. In dry soils, marker genes associated with the two-component system and the transporter system (*pst* complex) were highly expressed by Actinobacteriota (Figure 8). One Actinobacteriota MAG, representative of the Solirubrobacterales order (Solirubrobacterales_20), was particularly associated with a high transcription of the *phoB* gene (214 TPM), which is related to P starvation. Contrastingly, in transition and wet soils, the transcription of genes associated with P acquisition pathways was higher in Cyanobacteria MAGs but also identified in Bacteroidota, Acidobacteriota, and Actinobacteriota MAGs. Marker genes for the transporter system (*pst* complex) were highly expressed in wet and transition soils and mainly by Cyanobacteria MAGs (Pseudanabaenales_1 – 731 TPM in

transition soils;) and Acidobacteriota MAGs (Pyrinomonadales_5 – 127 TPM in wet soils) (Figure 8).

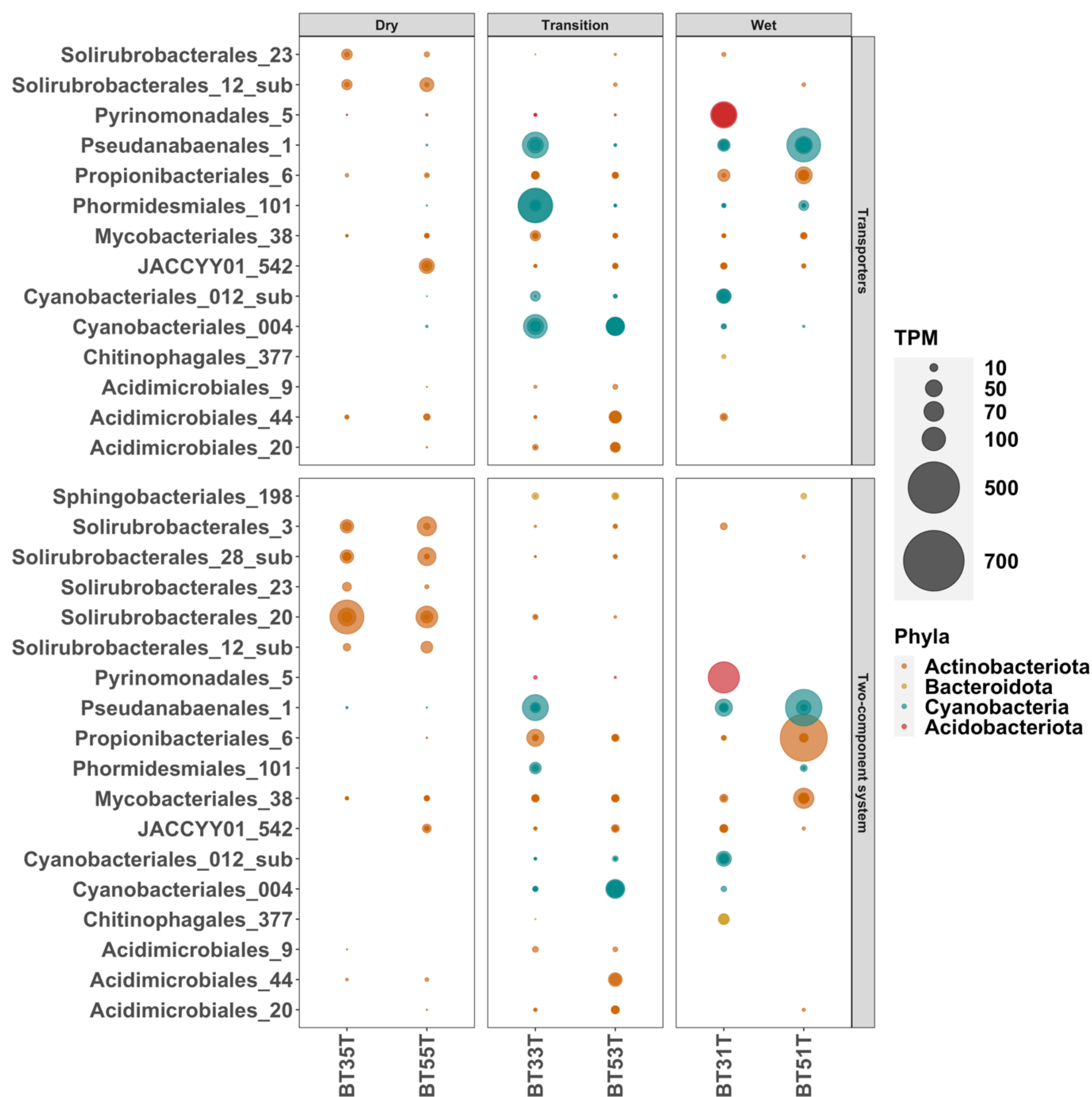

Figure 8 - Normalized abundance of transcripts of key genes for the phosphorous transport system (*pstS*, *pstB*, *pstC*, *pstA*) and the two-component system (*phoB*, *phoP*, *phoR*, *phoU*), expressed by the top 4% most active MAGs. Values are shown in transcripts per million reads (TPM).

4.5 - Discussion

In this study, we aimed to provide a functional perspective on the impacts of differences in water availability on polar desert ecosystems and further identify functional attributes of microbial communities that enhance the resilience of these abiotically driven systems to environmental change. Previous descriptive studies identified the dominance of specific bacterial taxa across extreme gradients in aridity and oligotrophy (Lee et al. 2012; Archer et al. 2017; Monteiro et al. 2022), but a functional perspective on the role of dominant taxa and their significance for the functional resilience of abiotically driven systems is still lacking. Here, we set out to test the hypothesis that these dominant microbial taxa are active and preserve essential metabolic functions (C, N, and P acquisition and energy conservation) to maintain microbial ecosystem services. Functional resilience, defined in this study as the ability of ecological processes to be continued during a wetness gradient, will be underpinned by the functional traits associated with dominant microbial taxa and their capacity to adapt to environmental change. To test our hypothesis, we identified and compared how changes in water availability affect the functional activity of prevalent traits associated with C, N, and P acquisition at the community level and by the most active microbial taxa identified along the wetness gradient representative of future hydrological changes in the system.

4.5.1 - Changes in water availability will affect the functional activity of pathways related to C, N, and P acquisition within microbial communities.

Our data shows that the functional capacity for carbon fixation via the Calvin-Benson cycle was the most dominant and consistent autotrophic process along the wetness gradient (Figure 1). With increased water availability, we observed significant alterations in the abundance and activity signatures for alternative autotrophic carbon-fixation pathways. In dry soil communities, the co-expression of genes involved in trace gas oxidation (*NiFe, CoxL* genes) and chemosynthetic carbon fixation (*rbcL* chemosynthetic type IE) by active Actinobacteriota MAGs (order Solirubrobacterales) was a dominant process in the community and provided evidence of an active community persisting in extreme oligotrophy through atmospheric chemosynthesis (Ji et al. 2017b; Ray et al. 2022). This result supports the importance of this trait as a carbon source in such nutrient-depleted edaphic conditions. Moreover, considering that metabolic water is an end-product of hydrogen oxidation, the

potential generation of water through this process could help sustaining hydration under such extreme aridity (Ortiz et al. 2021). We also observed that this process was still active along the wetness gradients, due to the persistence of taxa regulating it along the gradient, yet, at much lower levels. As water availability increases along the gradient, the high transcription levels of marker genes for photosynthetic activity (PSI and PSII) and *rbcL* genes (type IB) suggest a transition to phototrophy where Cyanobacteria become the main primary producers in wet soils. In addition, we also found a higher diversity of *rbcL* genes (type IA/C/D/E) being transcribed in wet conditions, along with increased activity signatures for alternative autotrophic carbon fixation pathways, namely the 3-hydroxypropionate, the Thaumarchaeotal 4-hydroxybutyrate, and the reductive tricarboxylic acid cycle. These results confirm that despite the dominant role of Cyanobacteria in driving primary production, other microbial groups potentially associated with phototrophic bacteria will also actively contribute to primary production during longstanding wet and potentially anaerobic conditions (Tabita 2007; Tahon et al. 2016). We expect that the observed higher functional diversity of active autotrophic pathways in wet conditions, compared to dry soils, is likely related to the amelioration of environmental stresses and the subsequent creation of niches for a higher diversity of primary producers to grow. Considering polar deserts lack significant vegetation, the persistence and co-occurrence of diverse autotrophic microbial taxa along the wetness gradient may be essential to maintain fixed carbon production service during transient changes in water availability.

We also observed significant differences in the activity of metabolic pathways related to N cycling across the wetness gradients (Figure 1B). We detected minimal expression of *nifH* at the community level along the gradient, with the highest abundance of *nifH* transcripts identified in wet samples. These results suggest that nitrogen fixation is not a dominant metabolic process and is mainly limited to wet soils, where a higher abundance of diazotrophs has been typically observed (Niederberger et al. 2012; Coyne et al. 2020). Instead, the most active nitrogen cycling pathway was denitrification and, to a lesser extent, dissimilatory nitrate reduction, which was thought to be a minor process in Antarctic soils (Cary et al. 2010). Similar to what has been observed in another hyperarid desert (Shen et al. 2019, 2022), this result provides strong evidence that the potential increase in nitrate bioavailability with increased wetness will make it the dominant nitrogen input source in polar desert soils.

Pathways for P acquisition were highly expressed across the gradient, particularly those associated with the two-component and Pst phosphate transporter systems (Figure 1B). Phosphorous, commonly found as inorganic phosphate, is a key element for metabolic and energy-producing pathways in bacteria (Hudek et al. 2016; Oliverio et al. 2020), but its abundance varies across the dry valleys system (Blecker et al. 2006). The high expression of genes associated with the two-component system and high-affinity phosphorus transporters (e.g., *phoR*/*phoB* and *pst* complex) indicate that P was limited in the soils across the wetness gradient. As a result, pathways that increase the efficiency of P uptake in P-limited soils are necessary to maintain critical microbial services in the system.

4.5.2 - Maintenance of functional capacity at the community level insures the continuity of ecological processes during environmental change.

Despite the differences in functional activity, we observed that most marker genes for C, N, and P acquisition were present across the wetness gradient, with a few exceptions. This pre-existing capacity for core metabolic function within the microbial communities is pivotal to increasing the ecosystem's functional resilience since it ensures the persistence of function under a range of environmental changes (Griffiths and Philippot 2013). For instance, an experiment conducted in the Arctic showed that despite short-term changes in temperature affecting microbial composition, the functional potential of the community was not altered (Yang et al. 2021). Moreover, this functional capacity could also potentially underpin previously observed capacity for microbial communities to respond quickly to changes in a polar desert environment (McKnight et al. 2007; Van Horn et al. 2014; Niederberger et al. 2019).

Considering the documented taxonomic shifts observed during changes in water availability (Monteiro et al. 2022; Monteiro et al. 2023, Niederberger et al. 2019), the maintenance of a core functional capacity within the community suggests the presence of functionally redundant species in microbial communities as previously observed in other ecosystems (Louca et al. 2016, 2018; Yang et al. 2021). Conversely, the maintenance of function could also be associated with the physiological ability of cryptobiotic taxa and persistence of stress-adapted taxa which were selected based on their capabilities to withstand

multiple abiotic stresses (e.g., dormancy, desiccation, resource-limitation, UV-radiation) (Schimel et al. 2007; Goberna et al. 2014; Malik et al. 2020; Brangarí et al. 2021).

4.5.3 - Stress-resistance traits underpin microbial persistence under extreme abiotic stress.

Across the wetness gradients, we observed a high abundance of genes and transcripts associated with several stress-response pathways, consistent with the different kinds of abiotic stress known to impact microbial communities in the system (Figure 2) (Cary et al. 2010). UV resistance genes (*uvrA*, *recA*) and genes involved with biomolecular repair mechanisms (chaperones *dnaK*, *groEL*) were the most abundant stress-resistance genes and transcripts identified across the wetness gradients, highlighting the importance of UV resistance as a fundamental physiological adaptation to persist in polar desert terrestrial ecosystems (Wynn-Williams and Edwards 2002). As expected, genes associated with desiccation-induced damage and osmotic stress (*otsA*/*B, proX*/*W*/*V*) were more abundant and active in dry soils than their wet counterparts. The significantly higher expression of genes associated with trehalose biosynthesis (*otsA*/*B*) in dry soils indicates that communities actively produce and accumulate solutes to counteract the osmotic stress. Surprisingly, we did not identify a high abundance or transcription of genes related to dormancy/sporulation as might be expected in desert soils (Fierer et al. 2012b; Man et al. 2020). Though we focused on a small set of sporulation genes, given the functional activity profiles described, we provide evidence for the persistence of an active community under longstanding aridity and oligotrophy and suggest that dormancy might not be a dominant process as previously thought (Goordial et al. 2016; Man et al. 2020).

4.5.4 - Dominant active taxa maintain core metabolic functions in abiotically-driven systems.

In our dry soil communities, the top four percent functionally active MAGs were affiliated with the Actinobacteriota, demonstrating that members of this dominant phylum, often observed globally in arid desert soils, are functionally active and versatile (Figure 4). Furthermore, we demonstrated that chemosynthetic carbon-fixation, phosphorous acquisition, and energy conservation pathways, identified in this study as dominant active metabolic

processes in dry soil communities and widespread across different phyla, were highly expressed by Actinobacteriota MAGs (Figures 5, 6, 7 and 8). This result supports our hypothesis that dominant drought-resistant Actinobacteriota regulate essential metabolic functions associated with P acquisition, energy conservation, and primary productivity under extreme aridity. We did not identify functional activity associated with nitrogen cycling pathways in functionally active MAGs from the dry soils. This result could potentially suggest that less dominant taxa regulate N inputs in dry soils. Otherwise, N inputs may be driven by hypolithic communities (cryptic microbial biofilms that develop under rocks as a stress avoidance strategy) rather than surface soil communities, as previously observed in cold and hot deserts (Cowan et al. 2011b; Ramond et al. 2018). Considering that N-fixation is a high-energy process (Ortiz et al. 2020a) it is possible that for surface soil communities, trade-offs associated with the investment of energy into stress-resistance traits could decrease microbial function (Schimel et al. 2007).

In contrast to what we observed in dry soils, the taxonomic composition of the most functionally active MAGs from transition and wet soils was more diverse, comprising Cyanobacteria, Bacteroidetes, Acidobacteriota, and Actinobacteriota (Figure 4). Our previous study demonstrated that with increased persistence of wet conditions, environmental selection becomes weaker and neutral processes gain a more critical role in driving community assembly (Monteiro et al. 2022). The latter could potentially reflect the lack of strong dominance patterns in wet and transition metagenomes. Despite the low representation of Cyanobacteria in wet soil metagenomes, transcript data revealed that Cyanobacteria MAGs were the most active taxa in wet and transition soils. The elevated transcriptional activity of genes associated with photosynthetic activity and carbon fixation via Calvin-Benson suggests that Cyanobacteria may represent keystone taxa that play a large role as primary producers with increased water availability.

We did not find evidence for the expression of genes associated with alternative autotrophic carbon fixation pathways, such as the reverse TCA cycle and the 3-hydroxypropionate, in dominant MAGs from the transition and wet soils. Those could be instead regulated by rare taxa. Moreover, although complete pathways for denitrification were active at the community level, none of the most active MAGs in transition and wet soils possessed a complete metabolic capacity for this step. These observations could be an artifact of the fact that our high and medium-quality MAGs were not complete genomes. Yet, it could

also be possible that with the alleviation of environmental stresses and increase in resource availability with the persistence of wet conditions, indicated by the presence of active Actinobacteriota photoheterophs, the diversity, and activity of core metabolic functions could be maintained by both the dominant and rare taxa. We propose future work to explore the potential for partnerships between dominant and rare taxa due to an increase in microbial connectivity under persistent wet environmental conditions and relatively higher primary productivity in the Dry Valleys. Work of this kind could give new insights into the contributions of biotic interactions in the Dry Valleys ecosystems, as recently suggested for multicellular organisms (Lee et al. 2020).

Lastly, we identified the persistence (yet at a lower abundance) of dominant autotrophic MAGs along the wetness gradient (Figure 6). For instance, one MAG belonging to the Acidimicrobiales order (MAG Acidimicrobiales_9) appeared active in both dry, transition and wet soils (Figure 4), engaging in atmospheric chemosynthesis in the dry soils and respiring nitrate in transition soils (Figures 6 and 7). The latter contrasts with the observation that abundant specialized taxa are specific to their habitat (Mariadassou et al. 2015) and further demonstrates the potential for some dominant taxa to accommodate environmental fluctuations by switching between different metabolic processes (metabolic plasticity) according to resource availability. The latter can have significant consequences for community-level processes and ecosystem resilience, with these metabolically plastic taxa securing the maintenance of functional diversity during environmental change (Nimmo et al. 2015; Bardgett and Caruso 2020a).

4.6 - Conclusions

In summary, we conclude that the increase in water availability in polar desert soils will promote significant structural and functional changes in the community, with a significant increase in the abundance and transcription of a broader range of metabolic genes associated with energy conservation, carbon, nitrogen, and phosphorous acquisition. We further showed that dominant taxa are responsible for maintaining metabolic traits for carbon fixation, P acquisition, and energy conservation under the intense abiotic stress imposed in these arid polar systems. We also identified the persistence of dominant, active drought-resistant taxa along the wetness gradient, which is a strong attribute for increased resilience in the system. With the

persistence of wet conditions, we demonstrated that the diversity and activity of core metabolic functions are maintained by a more diverse group of dominant taxa, potentially in conjunction with rare taxa as a result of increased resource availability, alleviation of abiotic stresses and subsequent creation of more diverse edaphic niches.

4.7 - Methodological considerations

As demonstrated in this study, metagenomic and metatranscriptomic studies provide a powerful tool for relating microbial communities' functional capacity and metabolic activity across an abiotic gradient. Nonetheless, higher sequencing depth might be required to capture the full diversity present in a sample depending on the question and the community's diversity. Although metagenomic sequencing provided good coverage of dry soil diversity (expected to be low), which was subsequently well represented at the co-assembly and MAG level, our sequencing depth was not enough to cover the diversity in wet soils. As a result, the representation of wet communities at the co-assembly and recovered MAGs was poorer than the dry soils (79% and 22%, respectively, in wet soils; 94% and 56%, respectively, in dry soils). By sequencing all samples from our field-replicated transects, we are confident that we are providing robust estimations that consider environmental heterogeneity and variability in the system. Moreover, we also observed differences in the relative abundances of Cyanobacteria between the metagenomes and previous amplicon data (Monteiro et al., 2022). Of the possible explanations, one could be attributed to potential primer pair bias towards specific taxa, therefore overestimating the relative abundance of those taxa. Otherwise, it could result from the underrepresentation of Cyanobacteria in genomic databases.

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CHAPTER V

Summary, Conclusions and Future Work

5.1. – Proposed framework and aims

Models predict that the warming climate will affect Antarctic terrestrial ecosystems with severe consequences to local biota and consequently to the ecosystem's functioning (Lee et al. 2017a). The ability of Antarctic terrestrial ecosystems to endure environmental change without their functioning being affected will depend on the resilience of local communities to changes in their environment. Due to the lack of vegetation and low trophic complexity, microbial diversity comprises the majority of the biomass and biodiversity in Antarctic terrestrial systems, having a primary role in regulating biogeochemical processes, including controlling the system's primary productivity (Cary et al. 2010). Therefore, finding compositional and functional attributes that enable microbial resilience to disturbance is crucial in predicting the fate of Antarctic terrestrial ecosystems in response to climate change (Bardgett and Caruso 2020b).

Assessing the resilience of ecosystems to climate change is a complicated process, partly because of the complexity and dynamic nature of the majority of ecosystems studied (Angeler and Allen 2016). Terrestrial Antarctic ecosystems, on the other hand, provide the best model to test underlying mechanisms that increase resilience since the complexity that characterizes other ecosystems (e.g., biotic interactions, vegetation, high biodiversity) is reduced in Antarctica. Nonetheless, the remote location of the continent, the restricted time frame allocated to field access, and strict regulations regarding site occupation, human impacts, and sample collection impose significant limitations on the performance of long-term observational studies to study environmental change. As such, this thesis aims to create a framework using a combination of spatial and temporal observations that enables quick and acurate predictions on how future changes in water availability resulting from warming trends (Levy et al. 2018) will impact the compositional, structural, and functional attributes of microbial communities historically adapted to extreme aridity and oligotrophy. The results from this thesis will ultimately give insights into the resilience of Antarctic terrestrial ecosystems to change.

5.2 – Thesis summary

This thesis is part of a broader, multi-disciplinary collaborative program (NZARI Type B proposal) to assess the resilience of Antarctic terrestrial, aquatic, and marine ecosystems to climate change. Focusing on the terrestrial component of the program, the overarching goal of this thesis was to identify compositional and functional attributes of microbial communities from the McMurdo Dry Valleys associated with increased resilience of these terrestrial ecosystems to climate change, particularly to changes in water availability. The comprehensive dataset used for this thesis involved a spatial and temporal analysis, which included a combination of field observations and manipulative laboratory experiments that enabled robust spatial and temporal evidence-based predictions of the impacts of hydrological changes on the functioning of this polar ecosystem. This thesis so far resulted in one peer-reviewed publication (https://doi.org/10.3389/fmicb.2021.783767), one manuscript submitted to Polar Biology, which is under review at the time of this thesis submission (https://doi.org/10.21203/rs.3.rs-2110177/v1), and a third manuscript soon to be submitted for publication.

Collectively, the work presented in this thesis provides an unprecedented understanding of the impacts of hydrological changes on the compositional and functional attributes of microbial communities from the McMurdo Dry Valleys. At both spatial and temporal scales, the results from this thesis show that alterations in water availability will affect the composition and structure of microbial communities and will significantly alter microbial dominance patterns across the systems. The presence and dominance of specific microbial taxa could be used during field surveys as biological indicators of increased soil moisture conditions. This work further demonstrates that despite microbial compositional changes, the functional capacity within the community will persist due to the identification of functional redundancy within the community, and taxa that can persist or metabolically adapt to temporal changes in water availability. Both are strong attributes for increased resilience in the system. However, the activity and the diversity of ecosystem processes will change significantly with the alterations in water availability. Under longstanding aridity and oligotrophy, dominant chemosynthetic taxa persist actively in the community and maintain metabolic traits for carbon fixation (atmospheric chemosynthesis), P acquisition, and energy conservation. The increase and persistence of wet conditions in the system, as a result of global warming, will enhance functional activity and the diversity of metabolic genes associated with energy conservation, carbon, nitrogen, and phosphorous acquisition. Whilst carbon-fixation through atmospheric

chemosynthesis will still be an active process in a wetter environment, pathways associated with energy conservation, carbon, nitrogen, and phosphorous acquisition will likely be maintained by a more diverse group, including dominant photosynthetic taxa, potentially in conjunction with rare taxa, due to increased resource availability, alleviation of abiotic stresses, and subsequent creation of more diverse edaphic niches.

5.2.1 – Chapter 2 - main findings and contributions

The goal of this chapter was to develop and validate a space-for-time sampling approach using variations in geochemical profiles that follow alterations in water availability as time progresses. For that purpose, soil electrical conductivity, pH, and water activity were measured from the shore of six lakes across the Wright and Taylor valleys to geochemically define seventeen wetness gradients. This approach contrasts previous sampling designs along environmental gradients that followed arbitrary distance points rather than according to the spatial variability of environmental factors to which microbial communities respond. By considering the variability of critical ecological drivers of species distribution along the wetness gradients, I could choose the samples with consistent conditions across the transects, which were representative of different ecotones. The effort to maintain consistency in both sampling strategy and definition of wetness gradients ensured robust comparisons between transects from other locations, which fully enabled harnessing the environmental variability across the region.

With such a comprehensive dataset, using 16S rRNA gene amplicon sequencing, I was able to identify with confidence significant compositional and structural changes in microbial communities that will likely occur as water becomes more available in the system. For example, on the association of specific phyla and orders of microbial phyla with long-term dry or wet conditions, I provided evidence for using microbial taxa as biological sentinels for early signs of change in the system. The results from this chapter also pointed out that water availability will decrease selective pressures (dominant in dry soils) and increase microbial diversity and the influence of stochastic processes regulating community assembly in many locations across the McMurdo Dry Valleys. However, high values of soil conductivity, particularly in older and more inland locations (e.g., Lake Bonney), can also create niches where only taxa resistant to osmotic stress can thrive.

Additionally, by replicating and comparing space-for-time transects defined from stable and dynamic lakes, the detailed historical background of the ecosystem's response to climate change was considered, which is fundamental when implementing a space-for-time approach (Blois et al. 2013). While transects from open-basin lakes reflected more extended periods of stability, those from close-basin lakes reflected more recent hydrological changes. By comparing both, I was able to resolve both the legacy and more contemporary impacts of changes in water availability on the structure of microbial communities.

Overall, this chapter developed and validated a space-for-time approach through which predictions that water availability changes will directly affect the composition, structure, and diversity of microbial communities across the system could be made. It further highlighted the sensitivity of the terrestrial microbiome to local climate changes across the system.

5.2.2 – Chapter 3 - main findings and contributions

To complement predictions made *in situ* using a space-for-time approach (chapter 2), I used a time-series approach to test the sensitivity and resilience of microbial communities to changes in water availability. The manipulative study was performed by emulating a wetting disturbance in a custom-made polar desert environmental chamber (PDEC). The study of a disturbance to measure a community's resilience often requires the application of "pulse" impacts of different intensities and frequencies over time (Bardgett and Caruso 2020b). It is essential during these approaches to include a baseline of temporal variability (i.e., a control). Nonetheless, manipulative experiments in Antarctic terrestrial ecosystems are limited by logistics and permit restrictions which can significantly restrict the type and duration of fieldwork. Moreover, fieldwork can leave significant impacts on the system (O'Neill et al. 2015), which contradicts one of the Antarctic Treaty's founding principles, the preservation of the continent.

In chapter 3, I reported rapid structural and compositional changes during wetting and re-drying treatments, reflective of changes in the relative abundance of co-existing taxa, which fluctuated asynchronously over time in response to the wetting and re-drying treatments. Consistent with *in situ* observations described in chapter 2, dry soil samples were dominated by taxa affiliated with Actinobacteriota. The ubiquitous dominance of Actinobacteriota in dry soils suggests that these taxa have an essential role in driving ecosystem functioning under

extreme aridity and oligotrophy by sharing traits that are key to adapting to a broader range of stressors. Nonetheless, Actinobacteriota was found to be very sensitive upon wetting, which follows previous evidence that species historically adapted to low water potential have less tolerance to immediate hydrological shocks during wetting, resulting in cell lysis (Schimel et al. 2007). Conversely, Proteobacteria exhibited a positive response to wetting, tripling their relative abundance after eight weeks of constant wetting and becoming the most dominant phylum under wet conditions. Considering that several members of Proteobacteria have been identified as copiotrophs (Fierer et al. 2007), the significant increase in this taxa could reflect a relative increase in resource availability from cell lysis after wetting. The potential relative increase in resource availability could also explain the observed shift from deterministic to a more stochastic community assembly with increased exposure to wet conditions, also previously depicted in chapter 2.

Moreover, by stopping the wetting disturbance and returning the soils to a dry state, I identified the ability of microbial communities from polar deserts to recover from short-term wetting events. Such recovery was potentially driven through the conservation of dry-adapted taxa during the wetting period, which has been recognized as an essential trait for community resilience and the stability of ecosystems (Manzanera 2021).

I identified two significant differences between the PDEC and field wetting experiments. First, an increase in Cyanobacteria abundance or bacterial diversity was not observed with wetting, contrasting the observations depicted during field observations. These differences highlight some limitations of conducting manipulative experiments in a closed system, where ecological factors such as dispersion cannot be replicated despite naturally occurring in the system, particularly with increasing hydrological connectivity.

5.2.3 – Chapter 4 - main findings and contributions

Chapters 2 and 3 assessed structural and compositional attributes of microbial communities that will be impacted and/or increase resilience to alterations in water availability in the system. Both chapters and previous studies demonstrated substantial variation in the proportion of different microbial phyla with changes in water availability, with the emergence of dominance patterns, particularly in dry soils (Niederberger et al. 2015, 2019; Monteiro et al. 2022). However, to this date, there has been a lack of studies focusing on the functional changes that polar desert ecosystems might undergo with climate change. Chapter 4 focused on the

community's functional aspects that are likely to change in response to the increase in water availability. It also aimed to identify functional attributes of microbial communities that regulate the resilience of the abiotically driven terrestrial systems to climate change. To address those aims, metagenomic and metatranscriptomic sequencing were combined to assess the functional potential and functional activity of core metabolic and stress-response pathways along the defined wetness gradients from the stable Lake Brownworth. Considering the observations made in chapters 2 and 3, this chapter set out to test the hypothesis that dominant active microbial taxa maintain core metabolic functions associated with C, N, and P acquisition and energy conservation in ecosystems where environmental selection is the primary driver of community diversity.

In summary, the analysis shows that an increase in water availability will increase microbial functional activity and diversity of pathways related to C, N, and P acquisition and energy conservation. The enhanced functional activity and diversity are likely associated with alleviating environmental stresses in conjunction with increased connectivity and resource availability, creating niches for a higher diversity of microbial taxa to establish. Looking at metabolic functional activity across the wetness gradients, the disparities between wet and dry soils were evident. In dry soils, transcriptomic evidence shows that carbon fixation likely occurs through atmospheric chemosynthesis, which dominant Actinobacteriota regulate. These taxa also regulate the phosphorous acquisition and energy conservation pathways providing important insights into the critical functional role of dominant drought-resistant Actinobacteriota under extreme aridity in the McMurdo Dry Valleys.

Moreover, the identification of several dry soil dominant taxa across the wetness gradient suggests the capability of specific taxa to accommodate environmental fluctuations by switching between different metabolic processes (metabolic plasticity) according to resource and energy availability. The capacity of taxa to withstand disturbance is critical for increased resilience, as it secures the maintenance of functional diversity during environmental change (Shade et al. 2012a; Brangarí et al. 2021). Interestingly, functional activity associated with nitrogen cycling pathways was not associated with functionally dominant taxa in dry soils, which indicates possible trade-offs related to the investment of energy into stress-resistance traits that may decrease the ability to use certain types of inorganic nutrients.

With increased wetness, photosynthesis will likely become the primary carbon fixation pathway performed by Cyanobacteria. Nonetheless, alternative autotrophic carbon fixation

pathways will also be present and active at the community level, increasing the functional redundancy level for pathways related to carbon inputs in the system. Nitrogen fixation was not a dominant process and was restricted to transition and wet soils. Considering nitrogen fixation is an energetically expensive process, under extreme aridity, the process is restricted to hypolithic communities that live under rocks to avoid oxidative and osmotic stresses (Cowan et al. 2011b; Ramond et al. 2018). The high transcriptional activity for gene markers associated with denitrification in transition and wet soils gives insights into the potential use of bioavailable nitrate as a source of nitrogen in polar desert soils, similar to what has been observed in other deserts (Shen et al. 2019, 2022). Yet, this requires further investigation. In contrast to dry soils, transition and wet soils were composed of a more diverse functionally dominant taxa, comprising Cyanobacteria, Bacteroidetes, Acidobacteriota, and Actinobacteriota. The analysis of the functional role of these dominant taxa further supports potential partnerships between dominant and rare taxa with increased persistence of wet conditions.

Finally, despite the differences in functional activity, most marker genes for C, N, and P acquisition and energy conservation pathways were present across the wetness gradient at the community level. The analysis further showed evidence for a certain level of functional redundancy in the community and a wide range of traits linked to stress tolerance to multiple abiotic stresses. This is pivotal to increasing the functional resilience of the ecosystem since it ensures function persistence under environmental change.

5.3 – Future work

This research provides a comprehensive framework, with spatial and temporal components, that should be used as a foundation for future resilience studies conducted in similar abiotically driven systems. The scope of this research could be further expanded and tested in ecosystems with increasing trophic complexity, where the relative effects of biotic interactions are stronger.

In chapter 2, comparisons between stable versus dynamic gradients identified subtle structural rearrangements of microbial communities reflective of the legacy impacts of water availability on microbial communities. The natural progression is to compare the functional attributes of stable and dynamic communities to provide insights into the resilience of

communities adapted to more dynamic conditions. For instance, several studies have reported that communities exposed to disturbances or a more dynamic environment are more resilient to disturbances (Evans and Wallenstein 2014; Rillig et al. 2015; de Vries et al. 2018). As such, in the Dry Valleys system, it would be worth testing whether microbial attributes that confer resilience to environmental change are enhanced in communities that are established and developed in more dynamic settings. Such an idea could be tested *in situ* by comparing the functional attributes of microbial communities described in this thesis in Lake Brownworth with those in Lake Vanda since both lakes are located in the same valley and are connected by the Onyx river.

The hypothesis that communities in dynamic settings will show higher resilience to climate change than those living in relative stability could be further tested in our PDEC, explored in chapter 3. Chapter 3 used DNA-based technologies to describe the temporal response of microbial communities to a short-term wetting disturbance. It will be useful to expand the study and provide a complementary functional perspective to the observed structural and compositional changes in the soil microbiome in response to wetting. The latter would give a temporal perspective on which metabolic and stress-response traits are activated or suppressed with increased exposure to wetness and could further clarify, in a controlled scenario, the role of dominant taxa in driving functional shifts. These could be combined with stable isotope-informed genome-resolved metagenomics to identify the organisms that become active during the disturbance (Starr et al. 2018). Down the line, PDEC manipulative studies could incorporate more complex designs to test different kinds of disturbance with different frequencies and duration. Ultimately those would be useful to test whether microbial communities have increased resilience to frequent disturbances, whether they move to alternative functional states, and whether they are still capable of returning to their pre-disturbance state.

Lastly, the research in chapter 4 represents the first attempt to characterize and predict functional changes and resilience in the McMurdo Dry Valleys due to changes in water dynamics. Given the environmental heterogeneity present in the system (Lee et al. 2012), it will be important to extend the functional analysis to other locations to gain a deeper understanding of how divergent functional activity and diversity is across the system. Furthermore, considering that current models depicted that biotic interactions make crucial contributions in the McMurdo Dry valleys (Lee et al. 2019), it will be worth extending the

analysis to give new insights into potential networks between microbes, eukaryotes or viruses and how those can influence the systems resilience to climate change.

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Appendix A

Supplementary Material for Chapter II

Supplementary Figures and Tables

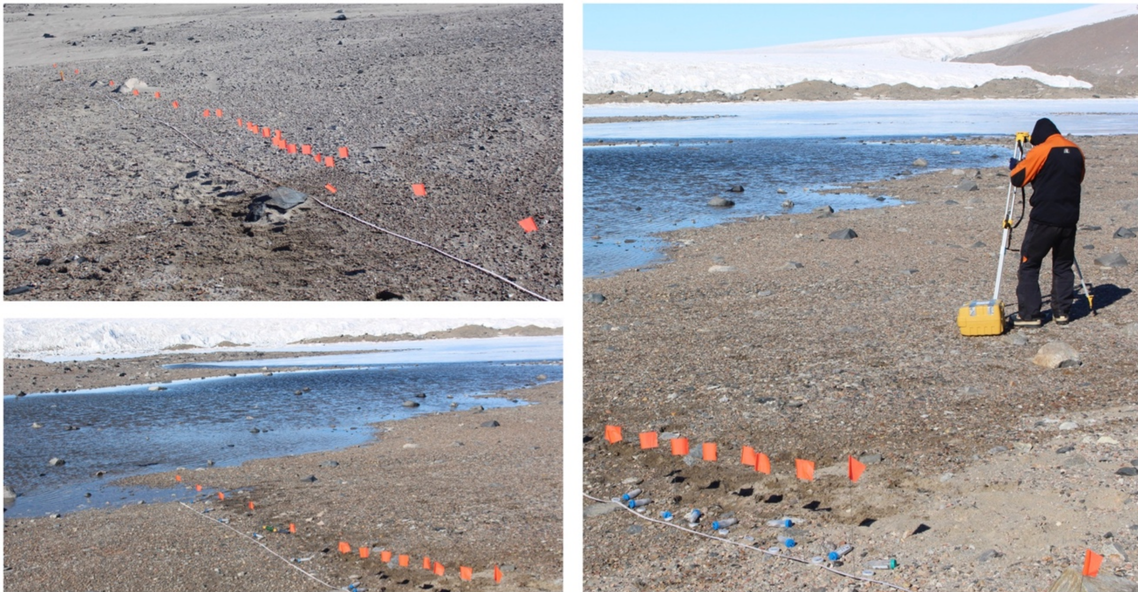

Figure S1 – Photos of space-for-time transects defined in Lake Brownworth during 2016/2017 field season. Before determining the sampling points, geochemical parameters of water activity, conductivity, and pH were measured along several points across the wetness gradients (averaging every 50 cm from the shore of the lake into the dry soil).

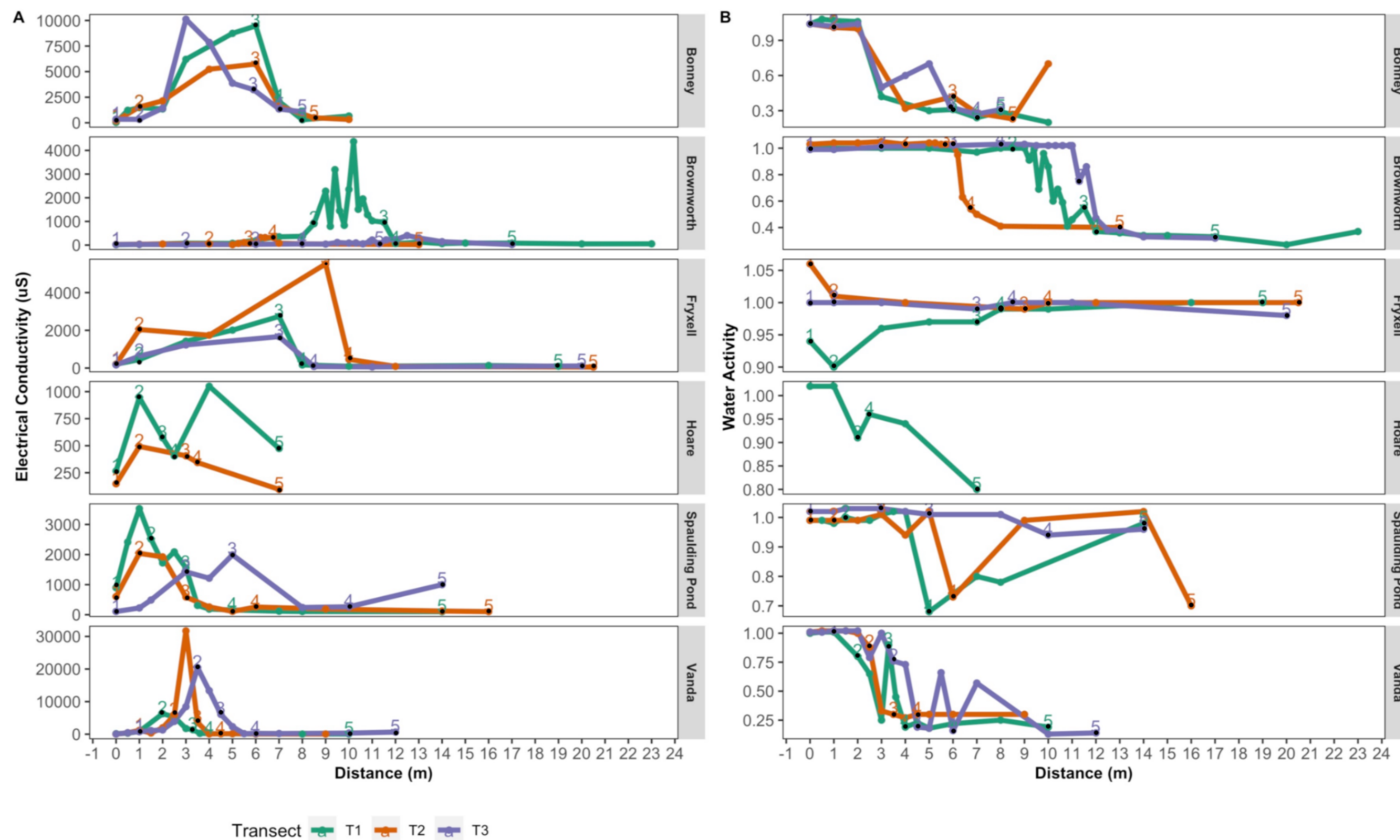

Figure S2 – Electrical conductivity (A) and water activity (B) profiles measured along the wetness gradient before defining the sampling points in Lake Bonney, Lake Brownworth, Lake Fryxell, Lake Hoare, Spaulding Pond and Lake Vanda. The location of each sampling point across distance can be depicted in the figures by the numbers

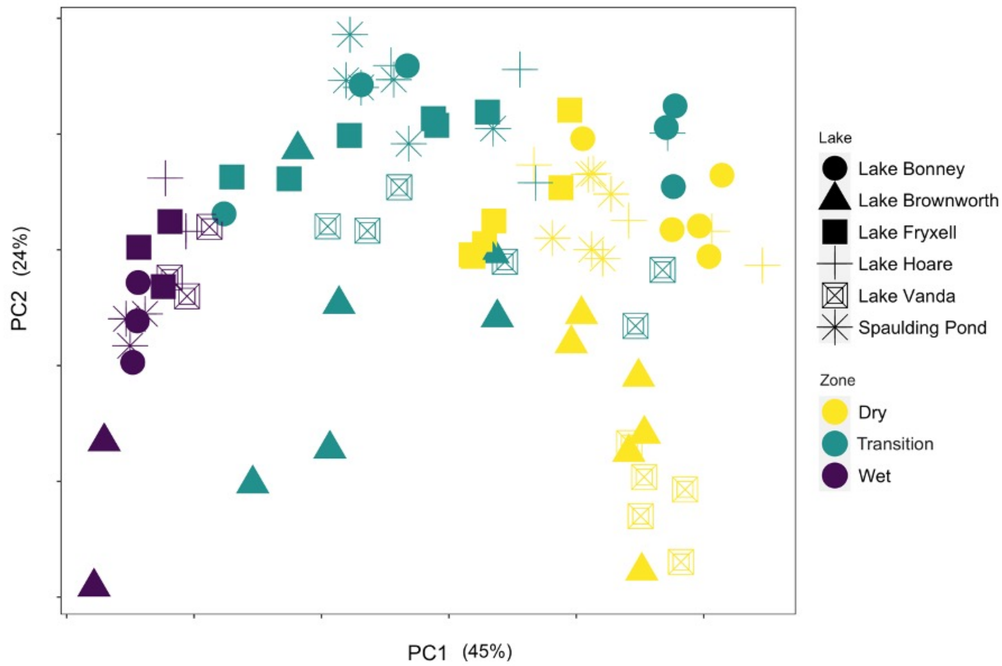

Figure S3 - PCoA ordinations based on the samples geochemical profiles. An Euclidean distance matrix was calculated using geochemical data collected in the field (elevation, pH, conductivity, water activity, and soil moisture content) after being log (x+1) transformed and normalized.

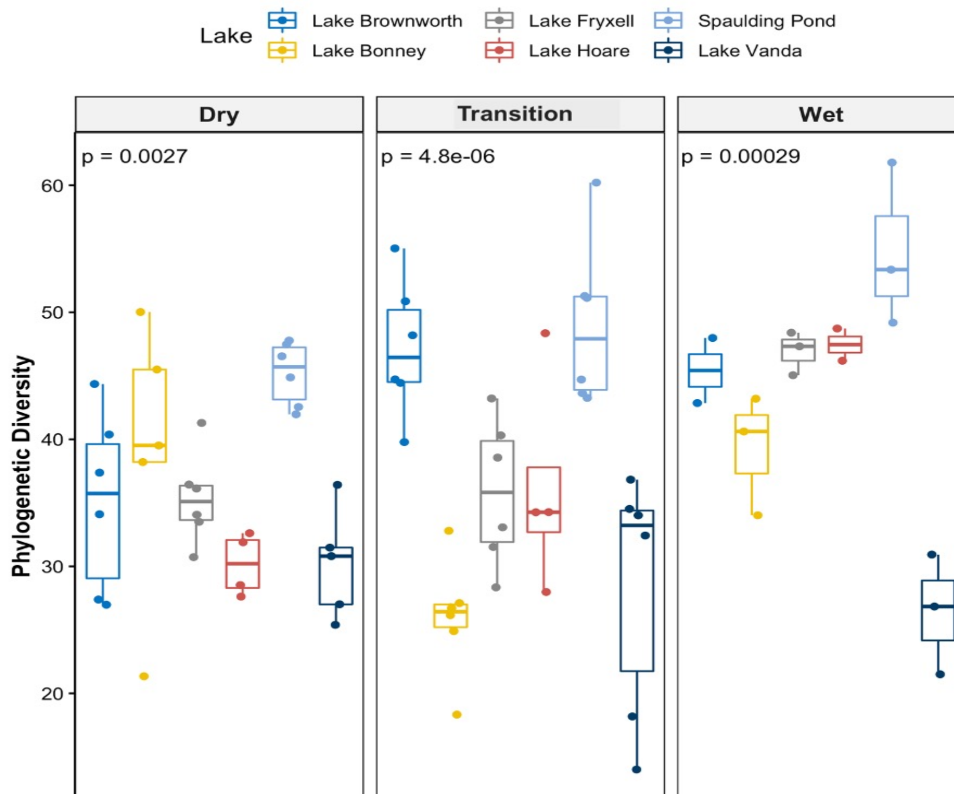

Figure S4 - Estimated OTU phylogenetic diversity (PD) of the microbial communities between different lakes on wet, transition, and dry sections of space-for-time transects. The error bars represent standard deviations of means.

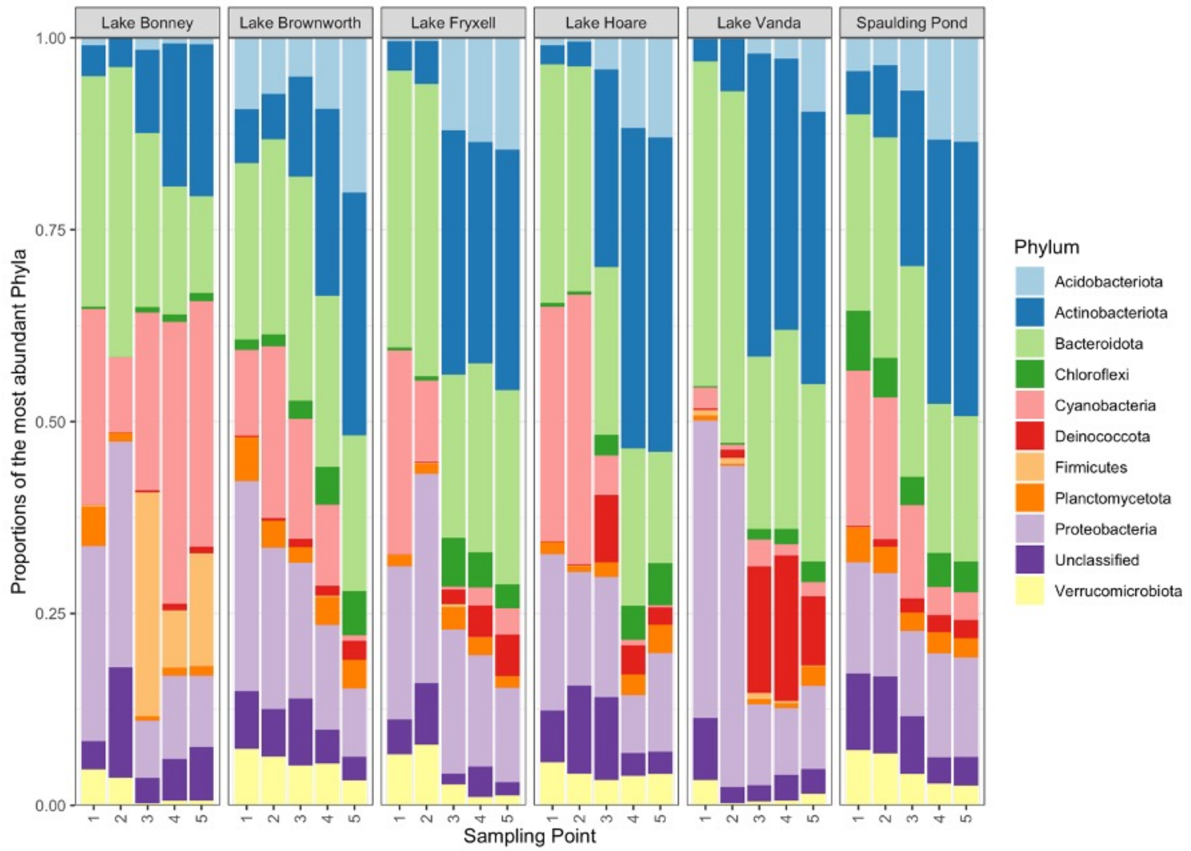

Figure S5 - Relative abundance of the most dominant bacterial phyla along space-for-time transects from each lake.

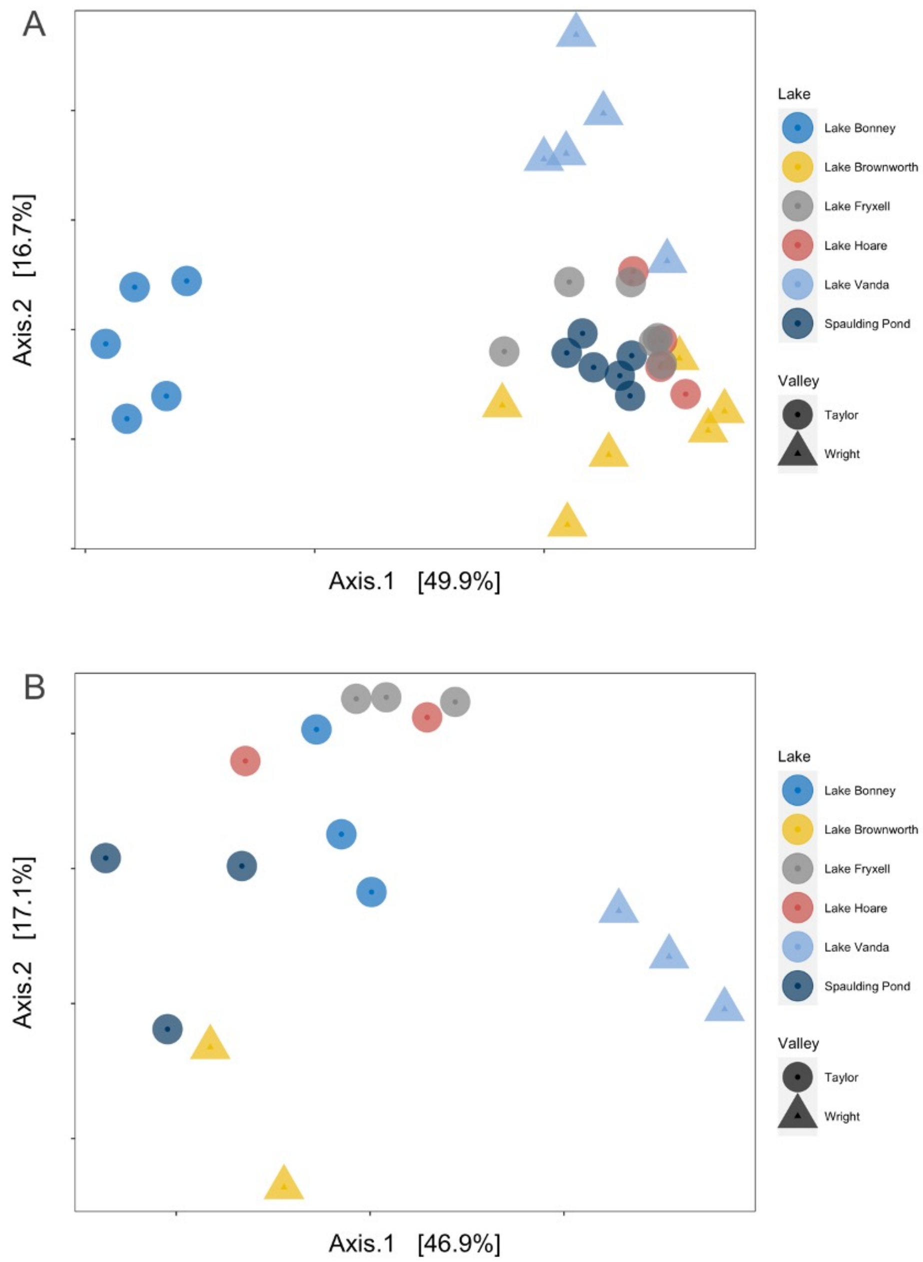

Figure S6 - Principal coordinate analysis (PCoA) of the microbial community compositional data from dry (A) and wet zones of all lake transects (B), using a weighted UniFrac distance matrix.

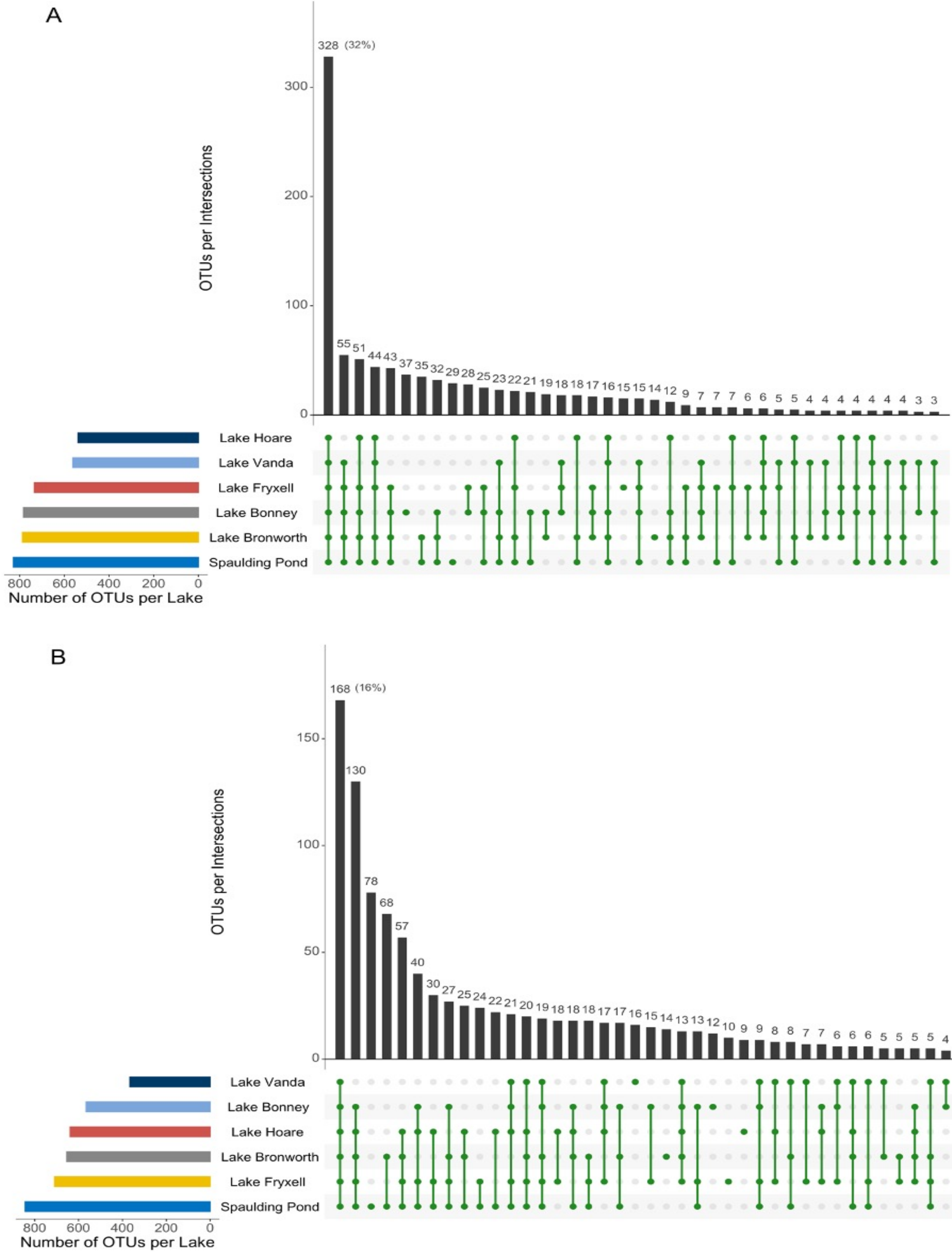

Figure S7 - UpSet plots showing the number of OTUs shared in the dry (A) and wet zones (B) of all lake transects.

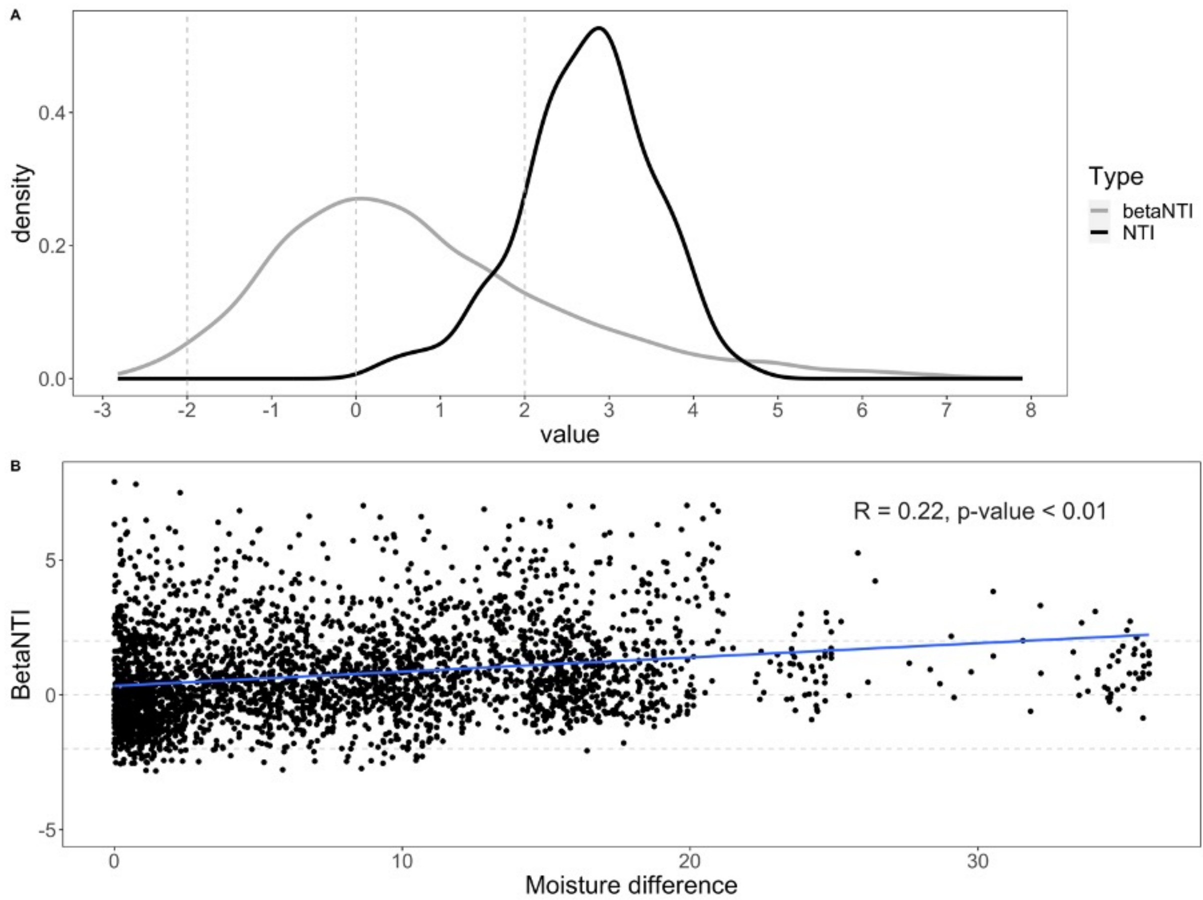

Figure S8 - A **-** density plot estimating the distributions of the nearest taxon index (NTI) and its between-community analogue (βNTI). Dashed grey lines at the −2 and +2 values delimitate the significance thresholds from the null expectation; B – βNTI values for all pairwise community comparisons regressed against the difference in moisture content between communities. The linear regression model is shown as the blue line. Dashed grey lines at the −2 and +2 values delimitate the significance thresholds from the null expectation.

ID	DNA yield (ng/g wet soil)	Raw reads	after QC	%	Length	after 0.005% culling	%	Transect	Sampling Point	Transect Section	Lake	Valley
BT3_0	421	71260	14670	21	350	11812	80.52	BT3	1	Wet	Lake Brownworth	Wright Valley
BT3_13	226	90447	23881	26	350	23704	99.26	BT3	5	Dry	Lake Brownworth	Wright Valley
BT3_4	250	97889	31299	32	350	28616	91.43	BT3	2	Transition	Lake Brownworth	Wright Valley
BT3_5.75	119	54774	13697	25	350	12706	92.76	BT3	3	Transition	Lake Brownworth	Wright Valley
BT3_6.75	890	67625	16549	24	350	15725	95.02	BT3	4	Dry	Lake Brownworth	Wright Valley
BT4_0	338	754	*all filtered out*	N/A	N/A	N/A	N/A	BT4	1	Wet	Lake Brownworth	Wright Valley
BT4_11.3	283	106305	36986	35	350	36375	98.35	BT4	3	Transition	Lake Brownworth	Wright Valley
BT4_12	55	64777	20699	32	350	20201	97.59	BT4	4	Dry	Lake Brownworth	Wright Valley
BT4_17	268	78018	23426	30	350	23265	99.31	BT4	5	Dry	Lake Brownworth	Wright Valley
BT4_9	381	74493	21563	29	350	19910	92.33	BT4	2	Transition	Lake Brownworth	Wright Valley
BT5_0	34	79955	20410	26	350	18982	93.00	BT5	1	Wet	Lake Brownworth	Wright Valley
BT5_11	188	68071	19455	29	350	18697	96.10	BT5	5	Dry	Lake Brownworth	Wright Valley
BT5_2	52	83741	24715	30	350	23621	95.57	BT5	2	Transition	Lake Brownworth	Wright Valley
BT5_5	186	100393	24025	24	350	22968	95.60	BT5	3	Transition	Lake Brownworth	Wright Valley
BT5_6	225	101765	25823	25	350	24260	93.95	BT5	4	Dry	Lake Brownworth	Wright Valley
LB1_0	1040	58481	20693	35	350	20070	96.99	LBo1	1	Wet	Lake Bonney	Taylor Valley
LB1_1	710	88682	35015	39	350	34462	98.42	LBo1	2	Transition	Lake Bonney	Taylor Valley
LB1_6	1	32458	18327	56	350	17934	97.86	LBo1	3	Transition	Lake Bonney	Taylor Valley
LB1_7	23	44974	19124	43	350	18743	98.01	LBo1	4	Dry	Lake Bonney	Taylor Valley
LB1_8	2	78858	43415	55	350	42284	97.39	LBo1	5	Dry	Lake Bonney	Taylor Valley
LB2_0	328	60379	21580	36	350	20521	95.09	LBo2	1	Wet	Lake Bonney	Taylor Valley
LB2_1	338	59666	23457	39	350	23272	99.21	LBo2	2	Transition	Lake Bonney	Taylor Valley
LB2_6	1	6141	3153	51	350	3060	97.05	LBo2	3	Transition	Lake Bonney	Taylor Valley
LB2_8.5	9	7805	4095	52	350	4037	98.58	LBo2	4	Dry	Lake Bonney	Taylor Valley
LB3_0	854	80353	23225	29	350	22466	96.73	LBo3	1	Wet	Lake Bonney	Taylor Valley
LB3_1	366	70635	29784	42	350	29581	99.32	LBo3	2	Transition	Lake Bonney	Taylor Valley
LB3_5.9	1	26788	14393	54	350	14021	97.42	LBo3	3	Transition	Lake Bonney	Taylor Valley
LB3_7	15	57730	24798	43	350	24159	97.42	LBo3	4	Dry	Lake Bonney	Taylor Valley
LB3_8	25	82881	35679	43	350	34207	95.87	LBo3	5	Dry	Lake Bonney	Taylor Valley
LF1_0	1000	78490	27712	35	350	26974	97.34	LF1	1	Wet	Lake Fryxell	Taylor Valley
LF1_1	1080	70882	29129	41	350	28647	98.35	LF1	2	Transition	Lake Fryxell	Taylor Valley
LF1_19	996	48830	23147	47	350	22714	98.13	LF1	5	Dry	Lake Fryxell	Taylor Valley
LF1_7	102	71815	29989	42	350	29688	99.00	LF1	3	Transition	Lake Fryxell	Taylor Valley
LF1_8	400	57759	23345	40	350	23005	98.54	LF1	4	Dry	Lake Fryxell	Taylor Valley
LF2_0	1140	67334	25658	38	350	24617	95.94	LF2	1	Wet	Lake Fryxell	Taylor Valley
LF2_1	1200	35663	16264	46	350	15627	96.08	LF2	2	Transition	Lake Fryxell	Taylor Valley
LF2_10	1120	85438	31455	37	350	31267	99.40	LF2	4	Dry	Lake Fryxell	Taylor Valley
LF2_20.5	722	54496	18718	34	350	18516	98.92	LF2	5	Dry	Lake Fryxell	Taylor Valley
LF2_9	23	77692	28618	37	350	28406	99.26	LF2	3	Transition	Lake Fryxell	Taylor Valley
LF3_0	1160	83743	31708	38	350	30424	95.95	LF3	1	Wet	Lake Fryxell	Taylor Valley
LF3_1	45	62712	23181	37	350	22492	97.03	LF3	2	Transition	Lake Fryxell	Taylor Valley
LF3_20	684	83802	31824	38	350	31228	98.13	LF3	5	Dry	Lake Fryxell	Taylor Valley
LF3_7	181	55089	21624	39	350	21366	98.81	LF3	3	Transition	Lake Fryxell	Taylor Valley
LF3_8.5	836	86817	34639	40	350	34105	98.46	LF3	4	Dry	Lake Fryxell	Taylor Valley
LH1_0	514	73457	27980	38	350	26925	96.23	LH1	1	Wet	Lake Hoare	Taylor Valley
LH1_1	618	76223	26387	35	350	25883	98.09	LH1	2	Transition	Lake Hoare	Taylor Valley
LH1_2	76.4	20742	9738	47	350	9617	98.76	LH1	3	Transition	Lake Hoare	Taylor Valley
LH1_2.5	133.4	57758	22544	39	350	22286	98.86	LH1	4	Dry	Lake Hoare	Taylor Valley
LH1_7	926	94313	34362	36	350	34033	99.04	LH1	5	Dry	Lake Hoare	Taylor Valley
LH2_0	876	71305	27076	38	350	25982	95.96	LH2	1	Wet	Lake Hoare	Taylor Valley
LH2_1	682	89187	33839	38	350	32736	96.74	LH2	2	Transition	Lake Hoare	Taylor Valley
LH2_3	86.4	68540	22653	33	350	22273	98.32	LH2	3	Transition	Lake Hoare	Taylor Valley
LH2_3.5	182.2	74620	26945	36	350	26645	98.89	LH2	4	Dry	Lake Hoare	Taylor Valley
LH2_7	524	57092	18664	33	350	18431	98.75	LH2	5	Dry	Lake Hoare	Taylor Valley
Sp1_0	1040	62267	18894	30	350	17158	90.81	Sp1	1	Wet	Spaulding Pond	Taylor Valley
Sp1_1.5	1080	89714	34991	39	350	32404	92.61	Sp1	2	Transition	Spaulding Pond	Taylor Valley
Sp1_14	111	68442	28012	41	350	27337	97.59	Sp1	5	Dry	Spaulding Pond	Taylor Valley
Sp1_3	824	94708	40310	43	350	39262	97.40	Sp1	3	Transition	Spaulding Pond	Taylor Valley
Sp1_5	1060	87065	37406	43	350	35910	96.00	Sp1	4	Dry	Spaulding Pond	Taylor Valley
Sp3_0	888	137905	52784	38	350	46087	87.31	Sp3	1	Wet	Spaulding Pond	Taylor Valley
Sp3_1	822	98758	36016	36	350	31029	86.15	Sp3	2	Transition	Spaulding Pond	Taylor Valley
Sp3_16	1000	72169	28614	40	350	27871	97.40	Sp3	5	Dry	Spaulding Pond	Taylor Valley
Sp3_3	952	92425	37294	40	350	35588	95.43	Sp3	3	Transition	Spaulding Pond	Taylor Valley
Sp3_6	640	48311	20398	42	350	19830	97.22	Sp3	4	Dry	Spaulding Pond	Taylor Valley
Sp4_0	1020	67494	24497	36	350	21489	87.72	Sp4	1	Wet	Spaulding Pond	Taylor Valley
Sp4_10	982	88463	30574	35	350	29514	96.53	Sp4	4	Dry	Spaulding Pond	Taylor Valley
Sp4_14	990	72375	25536	35	350	25093	98.27	Sp4	5	Dry	Spaulding Pond	Taylor Valley
Sp4_3	992	78510	29776	38	350	27872	93.61	Sp4	2	Transition	Spaulding Pond	Taylor Valley
Sp4_5	950	79454	28219	36	350	25979	92.06	Sp4	3	Transition	Spaulding Pond	Taylor Valley
VT4_1	19	65763	17173	26	350	16892	98.36	VT4	1	Wet	Lake Vanda	Wright Valley
VT4_10	141	59432	19335	33	350	19166	99.13	VT4	5	Dry	Lake Vanda	Wright Valley
VT4_2	17	83147	29868	36	350	29434	98.55	VT4	2	Transition	Lake Vanda	Wright Valley
VT4_3.3	19	80386	24525	31	350	24089	98.22	VT4	3	Transition	Lake Vanda	Wright Valley
VT4_4	31	81458	21858	27	350	21660	99.09	VT4	4	Dry	Lake Vanda	Wright Valley
VT6_1	30	65536	19713	30	350	19470	98.77	VT6	1	Wet	Lake Vanda	Wright Valley
VT6_2	17	121604	57601	47	350	57262	99.41	VT6	2	Transition	Lake Vanda	Wright Valley
VT6_3.5	19	39133	14230	36	350	13975	98.21	VT6	3	Transition	Lake Vanda	Wright Valley
VT6_4.5	31	71480	23208	32	350	23132	99.67	VT6	4	Dry	Lake Vanda	Wright Valley
VT6_9	58	293	*all filtered out*	N/A	N/A	N/A	N/A	VT6	5	Dry	Lake Vanda	Wright Valley
VT7_1	92	50732	15103	30	350	14858	98.38	VT7	1	Wet	Lake Vanda	Wright Valley
VT7_12	40	53999	17835	33	350	17669	99.07	VT7	5	Dry	Lake Vanda	Wright Valley
VT7_3	5	72277	25442	35	350	25009	98.30	VT7	2	Transition	Lake Vanda	Wright Valley
VT7_4.5	27	79156	25321	32	350	24945	98.52	VT7	3	Transition	Lake Vanda	Wright Valley
VT7_6	15	51649	18937	37	350	18644	98.45	VT7	4	Dry	Lake Vanda	Wright Valley

Table S1 - Raw reads, sequencing and quality filtering statistics of 16S rRNA gene reads

Lake Fryxell	p-value
Transition-Dry	<0.01
Wet-Dry	0.44
Wet- Transition	<0.001
Lake Bonney	**p-value**
Transition -Dry	0.02
Wet-Dry	0.7
Wet- Transition	0.01
Lake Hoare	**p-value**
Transition -Dry	0.11
Wet-Dry	0.89
Wet- Transition	0.36
Sapulding Pond	**p-value**
Transition -Dry	0.06
Wet-Dry	0.43
Wet- Transition	0.68
Lake Vanda	**p-value**
Transition -Dry	<0.01
Wet-Dry	0.74
Wet- Transition	<0.01
Lake Brownworth	**p-value**
Transition -Dry	0.94
Wet-Dry	0.57
Wet- Transition	0.71

Table S2 - Tukey multiple comparisons of means for beta-dispersion (betadisp) results between the three different zones for each lake transect.

OTU ID	Kingdom	Phylum	Class	Order	Family	Genus	Specie
OTU312	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Flavobacterium	Unclassified
OTU6	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Segetibacter	Unclassified
OTU40	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Ferruginibacter	Unclassified
OTU93	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales	Rubritaleaceae	Luteolibacter	Unclassified
OTU150	Bacteria	Chloroflexi	Chloroflexia	Kallotenuales	AKIW781	Unclassified	Unclassified
OTU27	Bacteria	Deinococcota	Deinococci	Deinococcales	Trueperaceae	Truepera	Unclassified
OTU164	Bacteria	Abditibacteriota	Abditibacteria	Abditibacteriales	Abditibacteriaceae	Abditibacterium	Unclassified
OTU280	Bacteria	Abditibacteriota	Abditibacteria	Abditibacteriales	Abditibacteriaceae	Abditibacterium	Unclassified
OTU72	Bacteria	Abditibacteriota	Abditibacteria	Abditibacteriales	Abditibacteriaceae	Abditibacterium	Unclassified
OTU25	Bacteria	Acidobacteriota	Blastocatellia	Blastocatellales	Blastocatellaceae	Blastocatella	Unclassified
OTU9	Bacteria	Acidobacteriota	Blastocatellia	Blastocatellales	Blastocatellaceae	Blastocatella	Unclassified
OTU31	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Pseudoxanthomonas	Unclassified
OTU44	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadaceae	Thermomonas	Unclassified
OTU126	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingorhabdus	Unclassified
OTU33	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas	Unclassified
OTU1839	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Brevundimonas	Unclassified
OTU73	Bacteria	Actinobacteriota	Rubrobacteria	Rubrobacterales	Rubrobacteriaceae	Rubrobacter	Unclassified
OTU39	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales	Solirubrobacteraceae	Unclassified	Unclassified
OTU134	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales	67-14	Unclassified	Unclassified
OTU2208	Bacteria	Actinobacteriota	Actinobacteria	Propionibacteriales	Nocardioidaceae	Marmoricola	Unclassified

Table S3 – Top twenty bacterial OTUs classified by Random Forest analysis as the most important to discriminate between the different zones of lake transects. The importance of OTUs is determined by the Mean Decrease in Accuracy from permuting the values in each feature. Mean Decrease in Accuracy contains a measure of the extent to which a variable improves the accuracy of the forest in predicting the classification.

Appendix B

Supplementary Material for Chapter III

Supplementary Methods

Polar Deserts Environmental Chamber - Contherm Global5000 Environmental Chamber

Our environmental chamber, Contherm Global5000 Environmental Chamber (CAT 5400/RHS), is a modification of the Contherm RHS models, which were explicitly designed to emulate the McMurdo Dry Valleys' environmental conditions (Figure S1) (Contherm Scientific Limited, New Zealand). This chamber has been designed to give the widest choice of operating conditions consistent with high reliability and low cost. The normal temperature range inside the chamber can be set to between -10 °C and 50 °C, with a temporal variation of ± 0.5 °C and a spatial variation of ± 1 °C. Relative humidity (RH) inside the chamber can be displayed between 0% and 100% RH, with a typical control range from 40 to 95% RH. However, the correct temperature must be set to achieve the desired RH (Supplementary material Fig. S1).

This chamber has a permafrost container to simulate permafrost conditions within the soils. Permafrost soil is ubiquitously distributed in the Dry Valleys, mainly in the ice cemented or dried frozen forms (Bockheim et al. 2007). The sublimation of moisture from ice-cemented permafrost contributes to ice loss from the soils to the atmosphere (Fountain et al. 2014). The rate of this physical process depends on the air temperature, relative humidity, wind speed, sediment moisture, solar radiation, and particle surface area (Law and Van Dijk 1994), and it can lead to significant topographic and hydrological changes in the terrestrial systems (Fountain et al. 2014). To simulate this physical process in the chamber's permafrost, we set up RH and temperature to 50% and 5 °C, respectively. These are also the RH and temperature conditions typically experienced in the field (Doran et al. 2002). Additionally, three fans were installed in the upper part of the chamber and activated to help reduce the relative humidity inside the chamber. The reduction of relative humidity creates an imbalance between the surface of the ice in the permafrost and the percentage of vapor water inside the chamber, triggering sublimation of the permafrost 37 mm below and creating a gradient in humidity within the overlying soil.

The permafrost container has a cold cooling coil, which can be set to -20 °C. To ensure maximum permafrost efficiency, 25 mm polystyrene insulation was installed around the side and under the container before filling the container with autoclaved soil. A permafrost temperature sensing probe is attached to a floating length of wire to position it at the site of

interest. A digital thermostat shows the permafrost bin's current temperature, and an LCD on the door shows the information on the current status of the chamber and current settings (Figure S1).

The chamber has been fitted with a LED light sourcing system (FUTURELED, Berlin) which spectrum quality is similar to the one experienced in the MDV but the intensity is about 50% of the experienced in the field as a result of potential cooling issues (Supplementary material Fig. S2, Table S1).

Experimental setup

Inside the permafrost container, autoclaved dry soil, previously collected from the MDVs, was mixed with sterile water until a mud-like consistency was achieved. Four large open cylindric containers (12.5 x 35.5 cm) were placed 10 cm inside the soil mixture. The cooling system was turned on and set to -15°C. Once the soil mixture was frozen, the large open cylindric containers were filled with the same autoclaved dry soil. On top of each cylinder, ten small cylinders (3 cm height) were set and filled with 40 g of dry soil collected 20 m south of Lake Hoare, homogenized (Supplementary material Fig. S1). Before the start of the experiment, the chamber was cleaned with 80% (vol/vol) ethanol. All cylinders and materials used during the experiment were cleaned with 80% (vol/vol) ethanol and sterilized with UV light for 30 min before setup.

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Supplementary Figures and Table

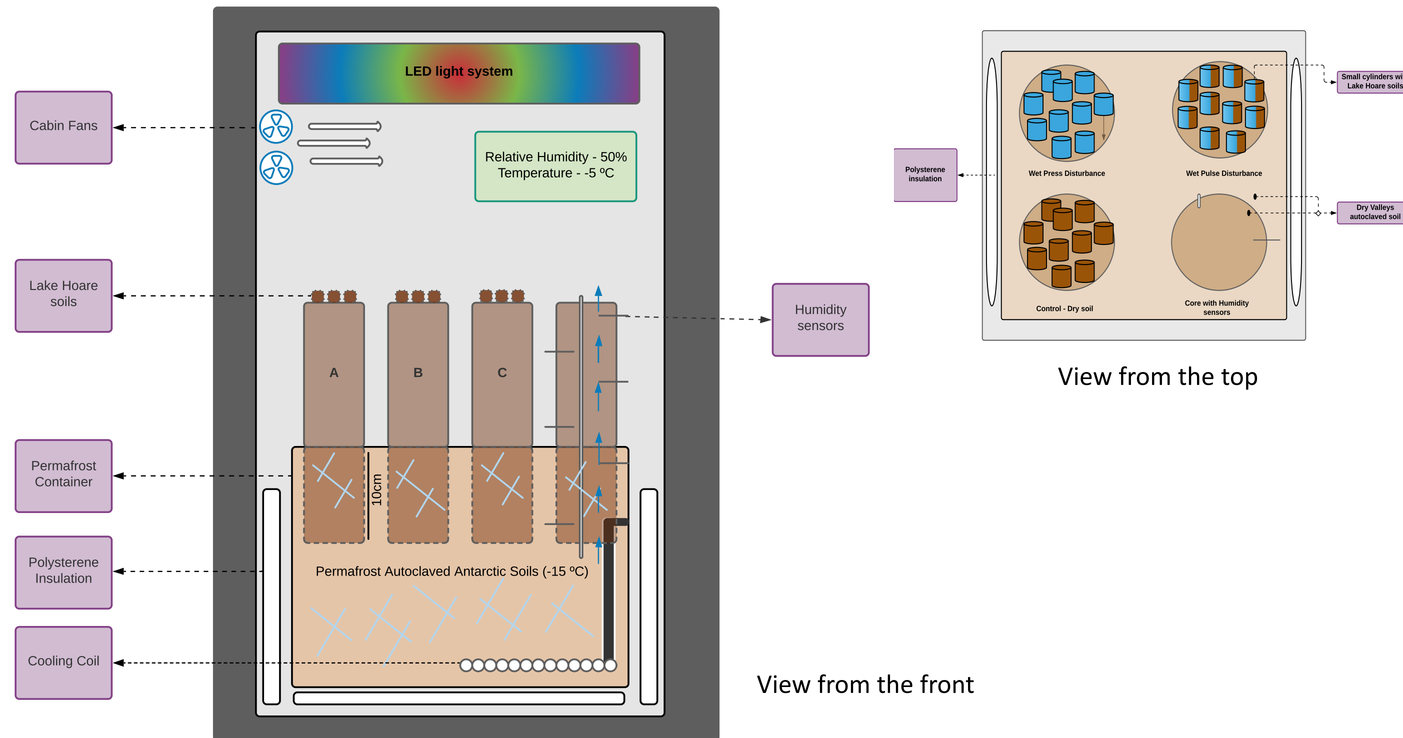
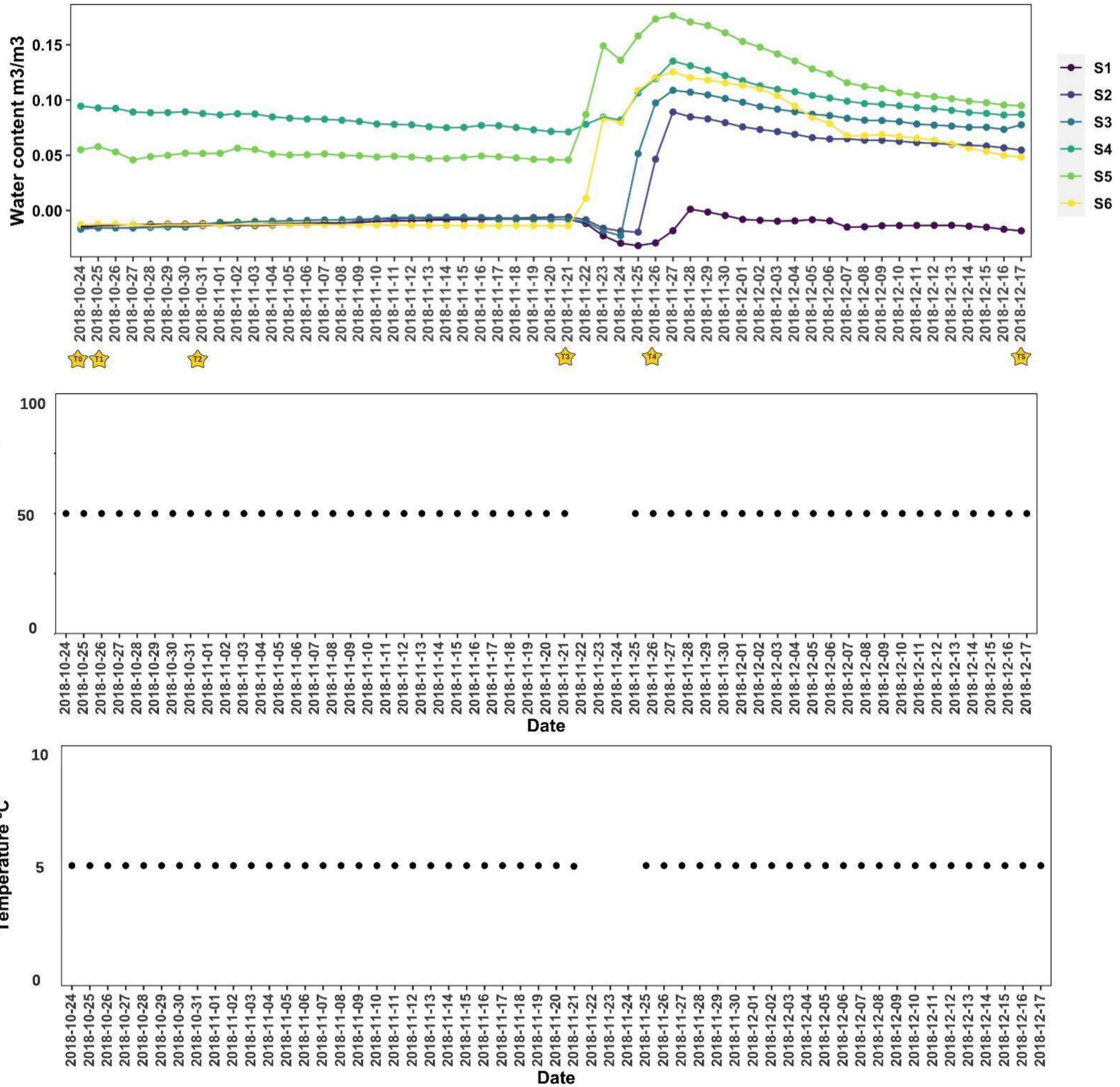


Figure S1 – Set up of PDEC and wetting experiment

a



b

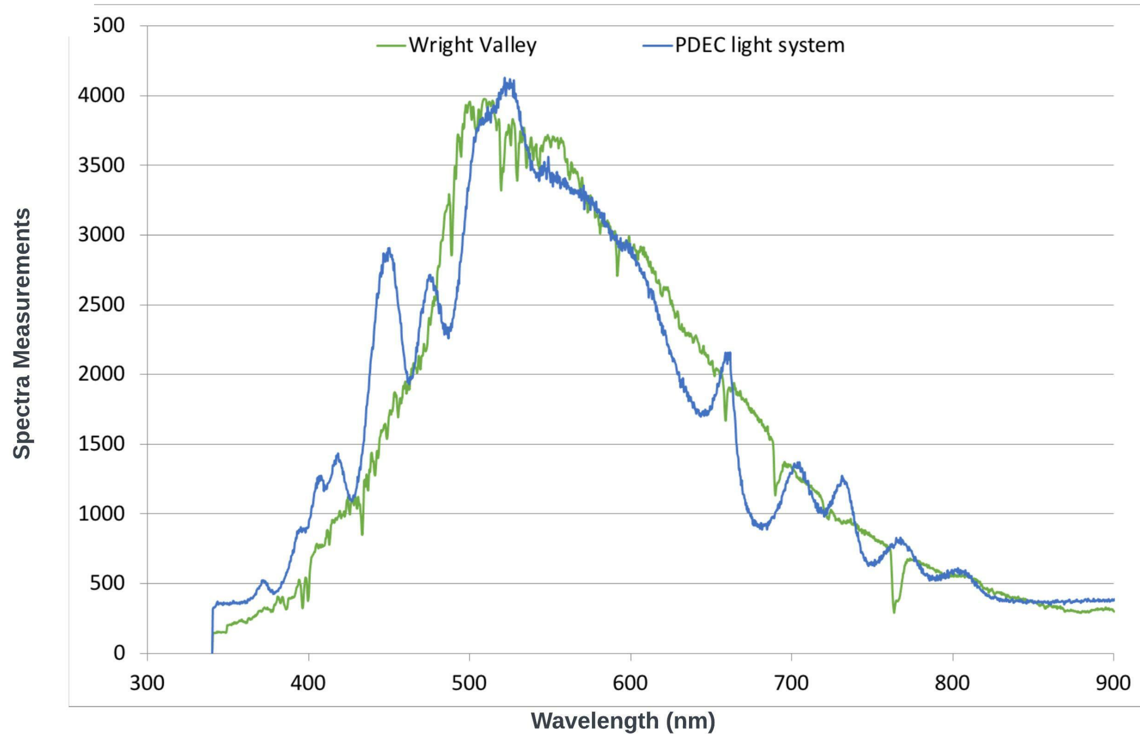
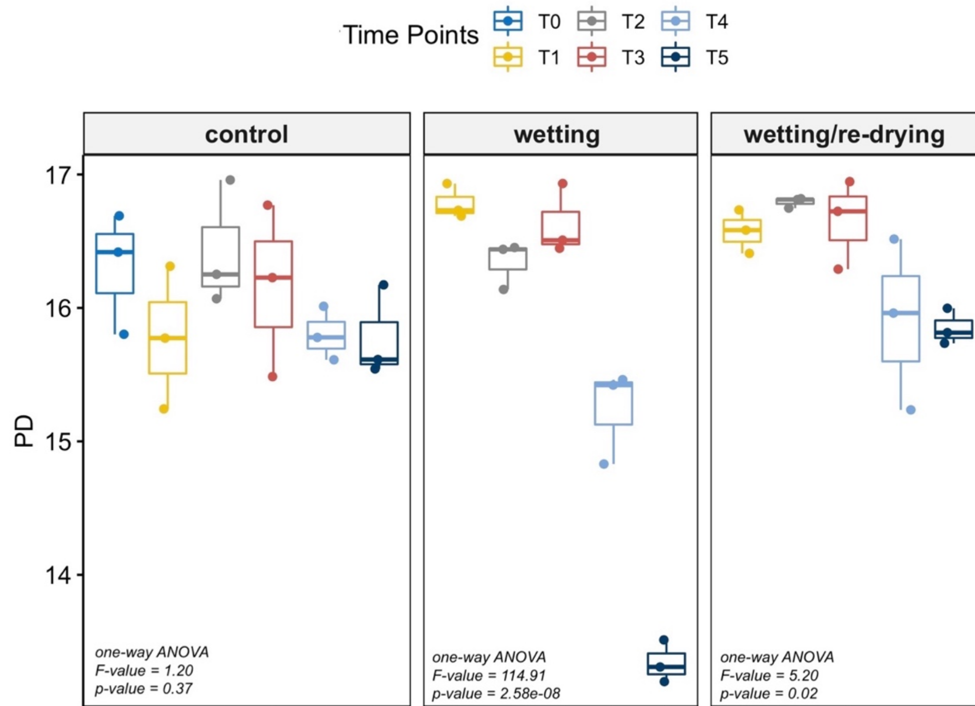


Figure S2 – a) Humidity sensor readings (m3/m3) during the experiment. Sensor 1 (S1) was positioned on the top of the fourth core (25 cm from the bottom end), followed by sensor 2 (S2 - 21 cm from the bottom end), sensor 3 (S3 - 15 cm from the bottom end), sensor 4 (S4 - 11 cm from the bottom end), sensor 5 (S5 - 5 cm from the bottom end) and finally sensor 6 positioned at the bottom of the fourth core (1 cm from the bottom end). On the 21st of November, the chamber had a power failure which affected the permafrost and the humidity content throughout the core. Despite taking weeks to be stabilized, the humidity records at the top of the core were less affected than those recorded at the bottom. Missing points in the temperature and relative humidity panels represent the days when the chamber was not working properly, therefore data couldn't be displayed. Stars symbolise the days when samples were taken. Samples at T3 were taken before the chamber breakdown **b)** Relative measurements of the quality/profile of the light spectra in the Wright Valley, compared to the light spectra from our light sourcing system inside the PDEC.

a



b

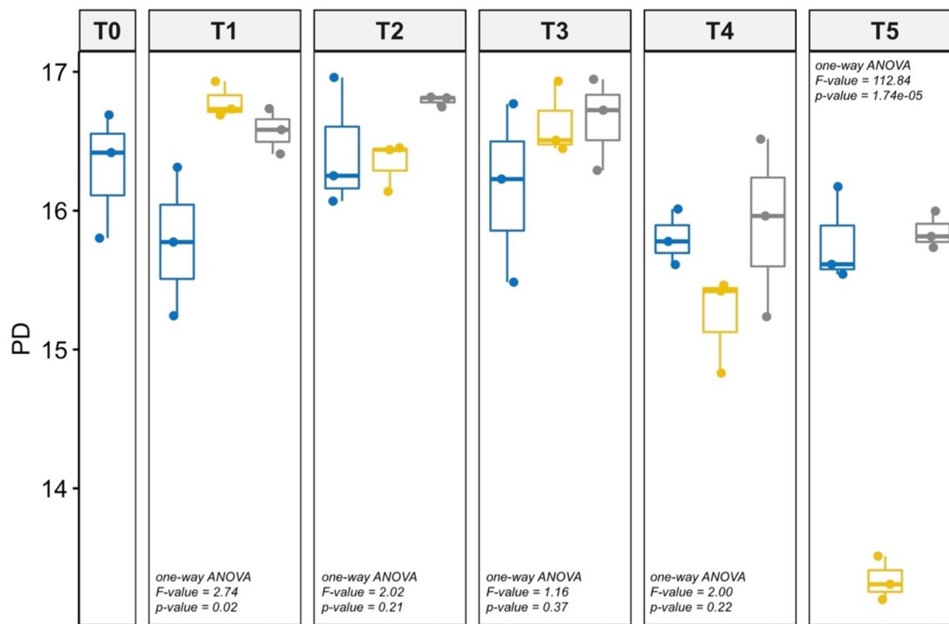


Figure S3 – Patterns of prokaryotic α-diversity measured using phylogenetic diversity (Faith's Phylogenetic Diversity) across time for each treatment (a) and between the treatments and the control for each time point (b). At T0 all samples were still dry (at that point the experiment hadn't started), and therefore were denominated as part of the control.

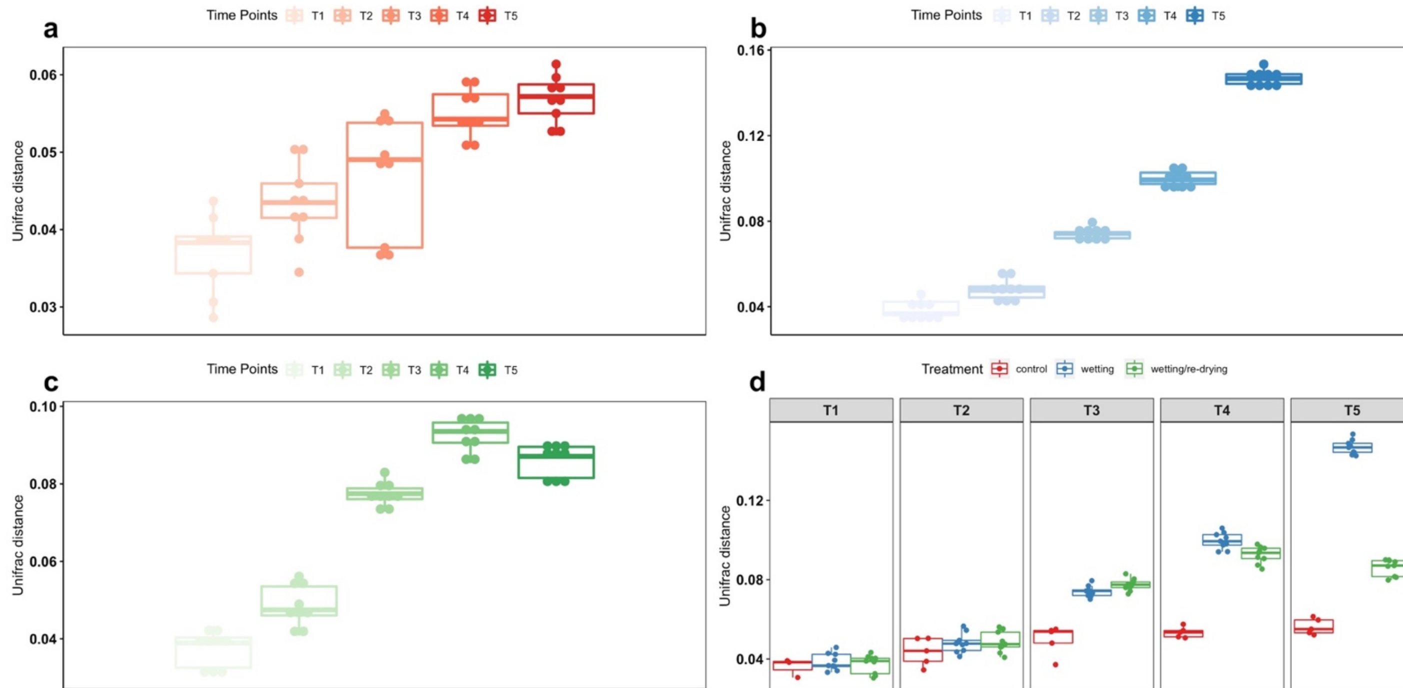


Figure S4 – Weighted UniFrac distance values representative of each pairwise comparison calculated between **a)** the control samples at each time point versus the control samples at T0; **b)** wetting treatment samples versus the control samples at T0; **c)** wetting/re-drying samples versus the control samples at T0. Plot **d)** represents the combination of the previous three plots in one plot, to better compare the differences observed in each treatment in relation to the T0 control, for each time point.

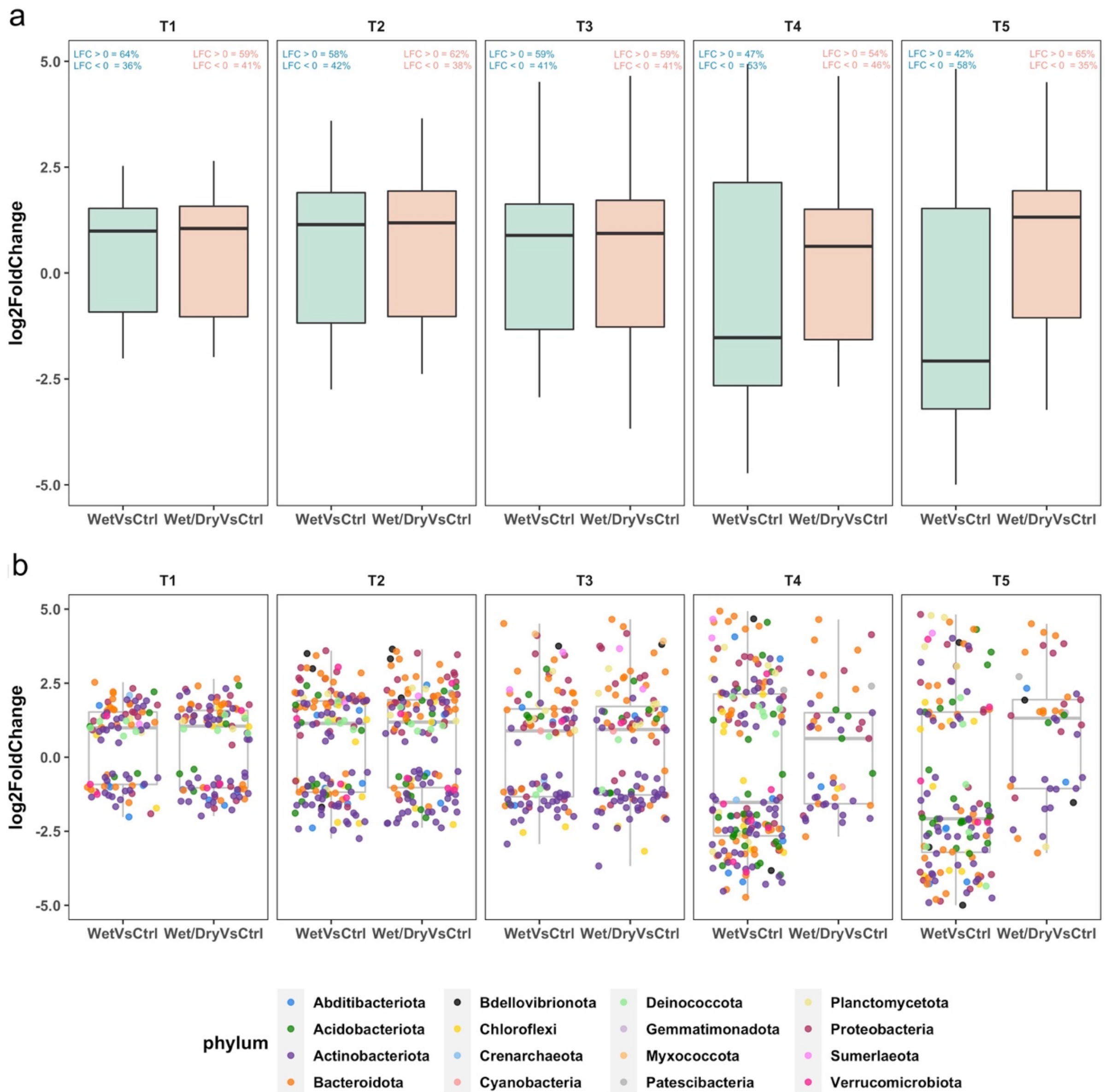


Figure S5 – **(a)** The $\log_2$ fold values for differential abundant ASVs detected using DESeq2 analysis between wetting treatment versus the control (light blue) and wetting/re-drying treatment versus the control (light pink) for each time point. Values on top of each panel show the percentage of ASVs with a positive log-fold change (LFC > 0) or negative log-fold change (LFC < 0). **(b)** Taxonomic affiliations of each ASV identified in our differential abundance analysis (DESeq2).

Table S1 – Significance of alpha diversity using one-way ANOVA and Tukey's post-hoc test for the wetting and wetting/re-drying treatments

Tuckey's test for the wetting treatment	
Comparisons	***p*-value adjusted**
T2-T1	0.2120
T3-T1	0.9181
T4-T1	**<0.001**
T5-T1	**<0.001**
T3-T2	0.5787
T4-T2	**0.0012**
T5-T2	**<0.001**
T4-T3	**<0.001**
T5-T3	**<0.001**
T5-T4	**<0.001**

Tuckey's test for the wetting-re-drying treatment	
Comparisons	***p*-value adjusted**
T2-T1	0.9278
T3-T1	0.9983
T4-T1	0.1825
T5-T1	0.1359
T3-T2	0.9848
T4-T2	0.0553
T5-T2	**0.0405**
T4-T3	0.1202
T5-T3	0.0886
T5-T4	0.9996

Comparison	Time Point	Significant ASVs	Total	Significant ASVs (%)	LFC > 0	% LFC > 0	LFC < 0	% LFC < 0
Wetting Vs Control	T1	96	285	34%	61	64%	35	36%
Wetting Vs Control	T2	144	289	50%	84	58%	60	42%
Wetting Vs Control	T3	116	286	41%	68	59%	48	41%
Wetting Vs Control	T4	202	273	74%	95	47%	107	53%
Wetting Vs Control	T5	194	271	72%	81	42%	113	58%
Wetting/Re-drying Vs Control	T1	105	285	37%	62	59%	43	41%
Wetting/Re-drying Vs Control	T2	139	289	48%	86	62%	53	38%
Wetting/Re-drying Vs Control	T3	119	286	42%	70	59%	49	41%
Wetting/Re-drying Vs Control	T4	54	273	20%	29	54%	25	46%
Wetting/Re-drying Vs Control	T5	48	271	18%	31	65%	17	35%

Table S2 – Number and percentage of differentially abundant ASVs identified with our DESeq2 analysis between each treatment and the control at each time point. LFC - Log Fold Change.

Appendix C

Supplementary Material for Chapter IV

Supplementary Figures and Tables

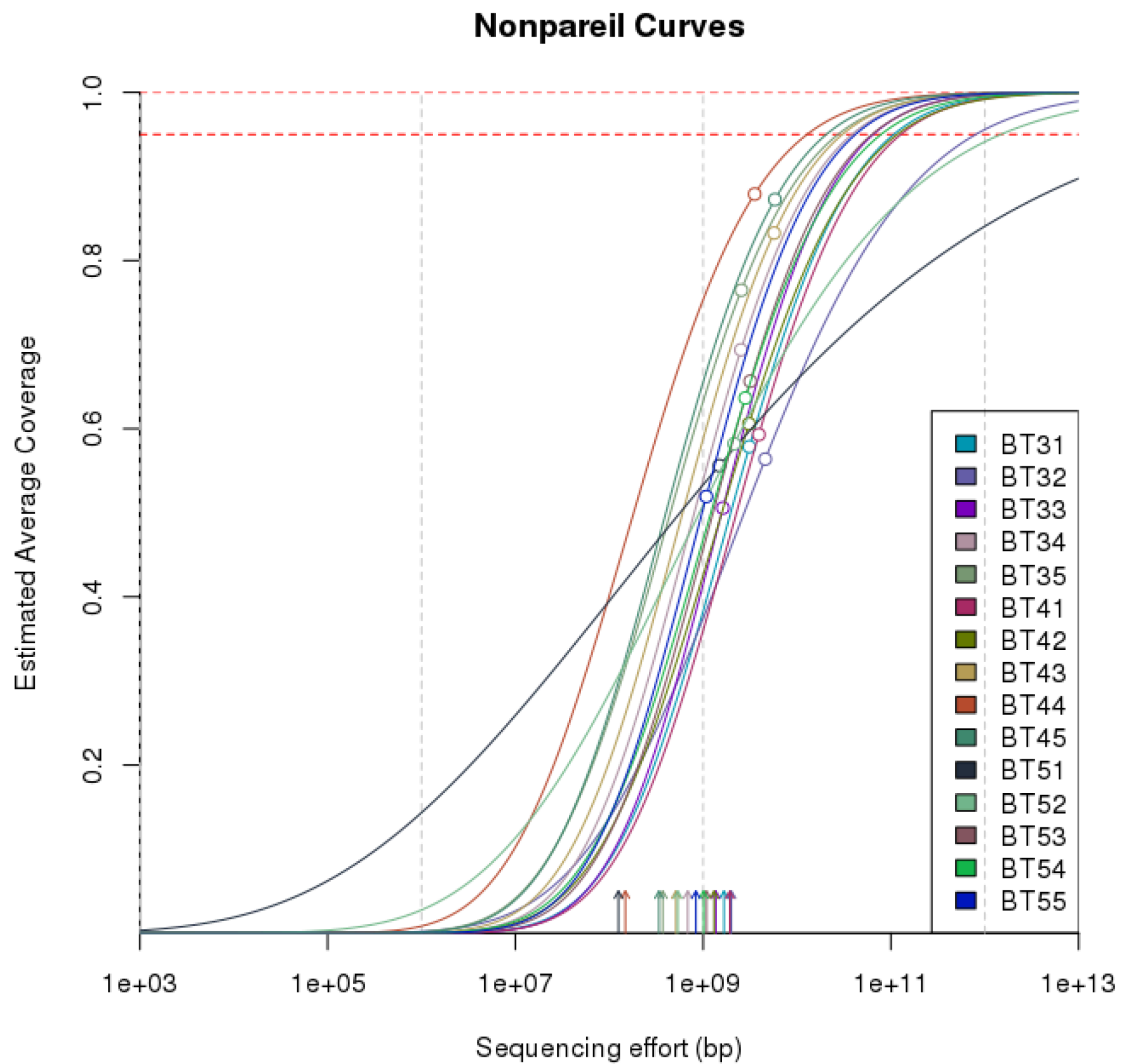


Figure S1 - Nonpareil curves for each sampled community analysed in this study using *k*-mer. The lines indicate coverage estimates from projection curves. Horizontal red dashed lines indicate 95 and 99% coverage.

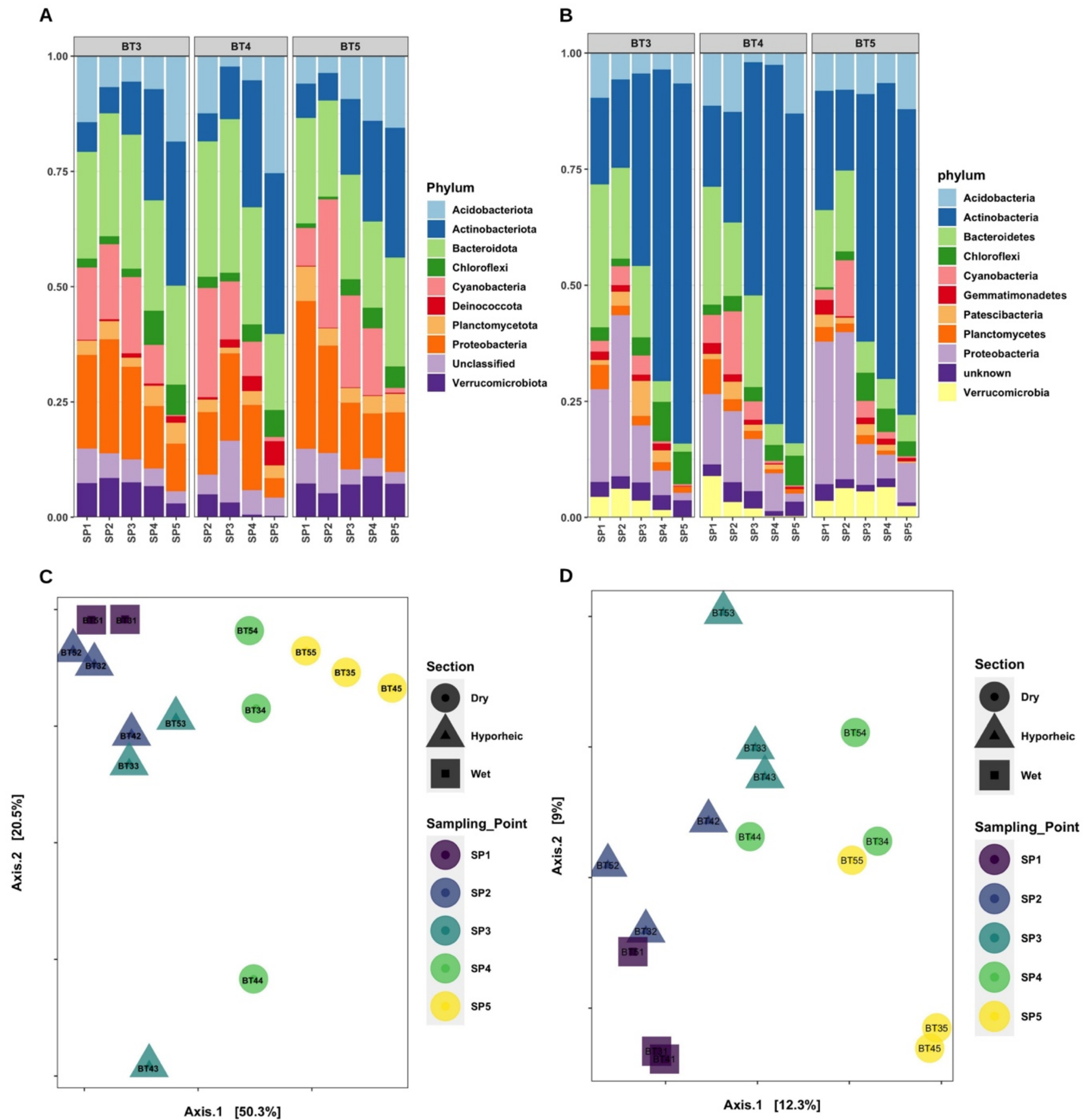


Figure S2 - **(A)** The relative abundance of the most abundant prokaryotic phyla (mean relative abundance > 0.01) using 16S amplicon sequencing (Monteiro et al., 2022) along the wetness gradients defined in Lake Brownworth. **(B)** The relative abundance of the most abundant prokaryotic phyla (mean relative abundance > 0.01) in the metagenomes, from the wetness gradients defined in Lake Brownworth, using *L16/L10E rplP* single-marker gene. In both bar plots phyla which mean relative abundance across all 15 samples was < 0.1% are not represented. **(C)** Beta-diversity of microbial communities along the wetness gradients calculated using the Unifrac distance and the 16S amplicon sequencing data (Monteiro et al., 2022). **(D)** Beta-diversity of microbial communities along the wetness gradients calculated using Bray-Curtis distance and the *L16/L10E rplP* single-marker gene.

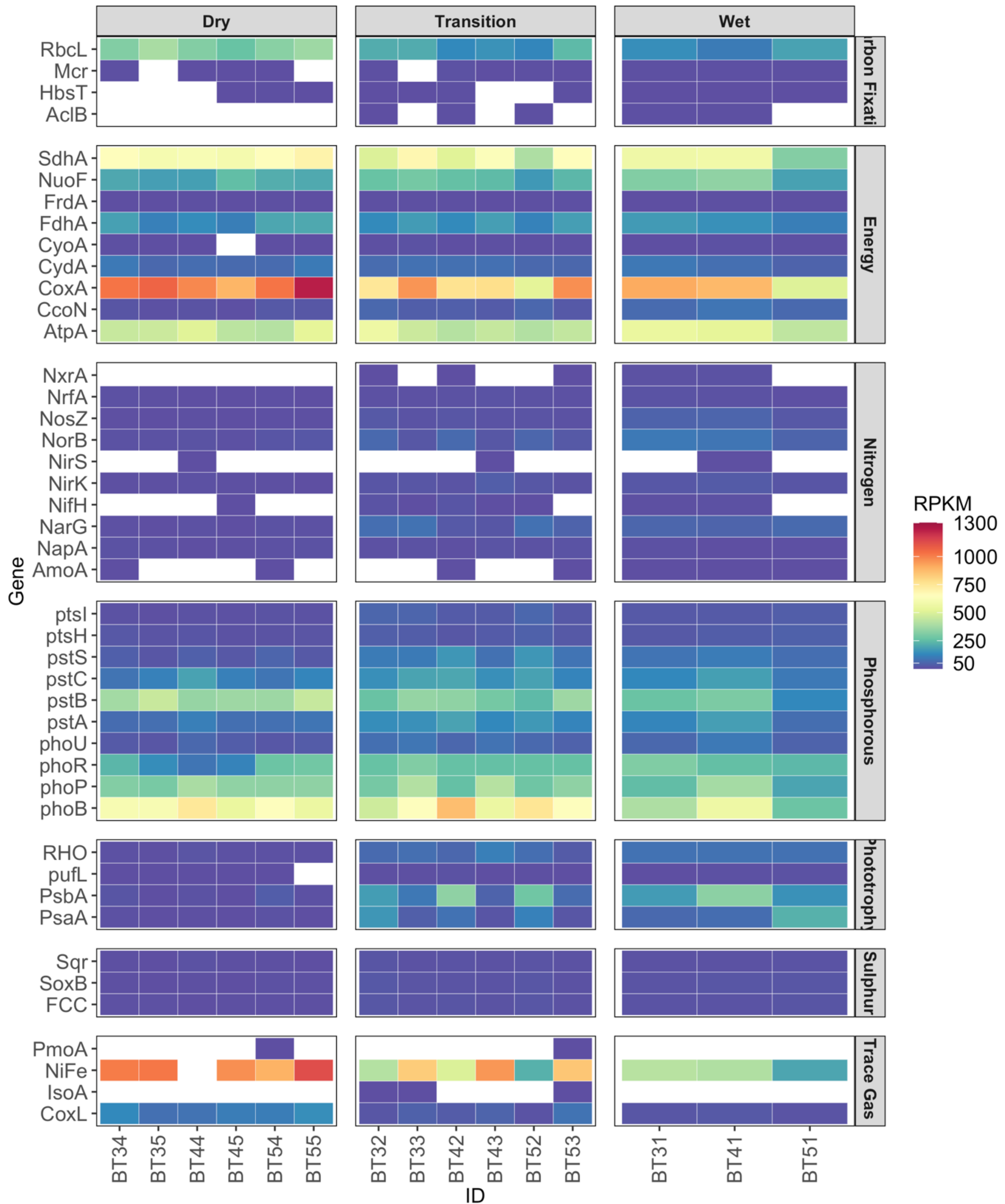


Figure S3 - Abundance (RPKM) of metabolic marker genes associated with carbon fixation, energy acquisition, trace gas metabolism, phototrophy, nitrogen, sulphur and phosphorous cycle. Gene abundance was calculated with CoverM "contig" mode using "bwa" alignment and the following parameters: min-read-align 0.75 and min-read-id 0.95. RPKM values calculated for ORFs with the same gene annotation were summed. Blank cells represent zero values

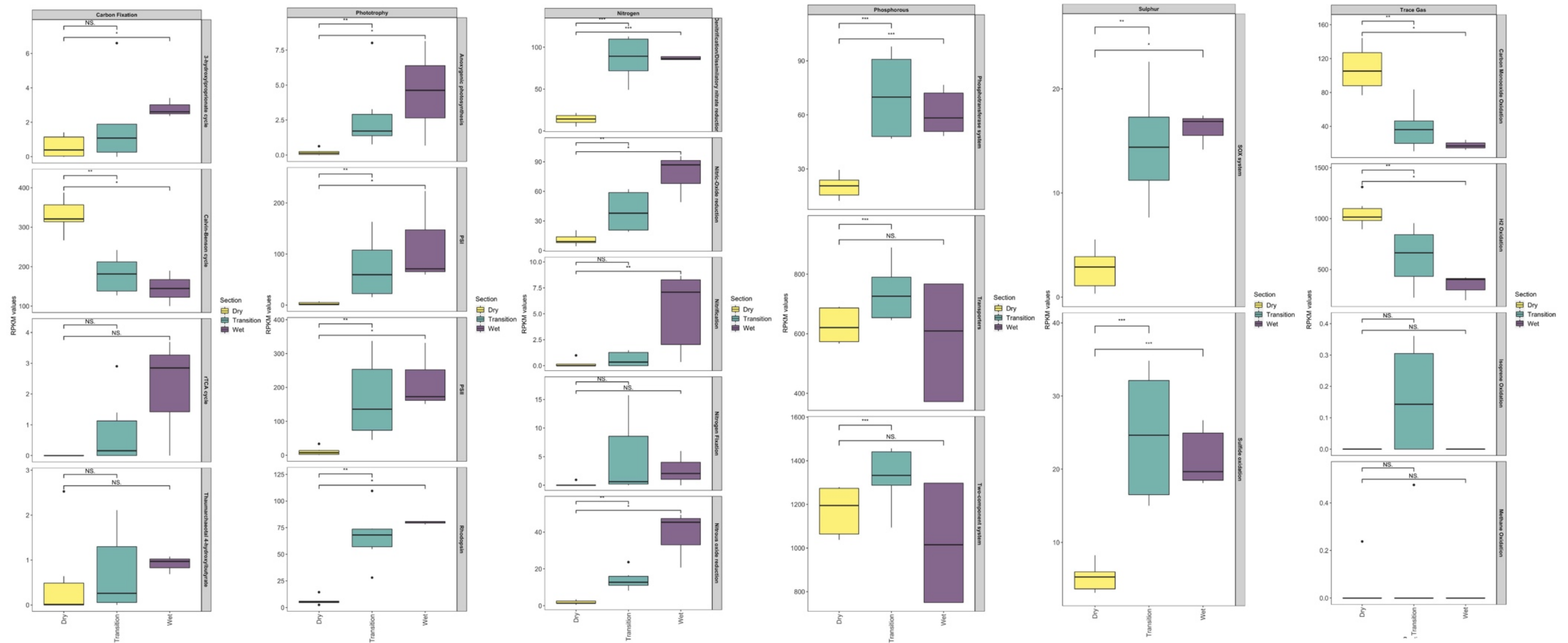


Figure S4 - Comparison of the abundance of metabolic pathways (RPKM) across the three sections of the gradient. Each section has a n=6 samples, except for wet soils where n=3 samples . Asterisks indicate statistically significant differences ($p < 0.05$) using Wilcox-test**.**

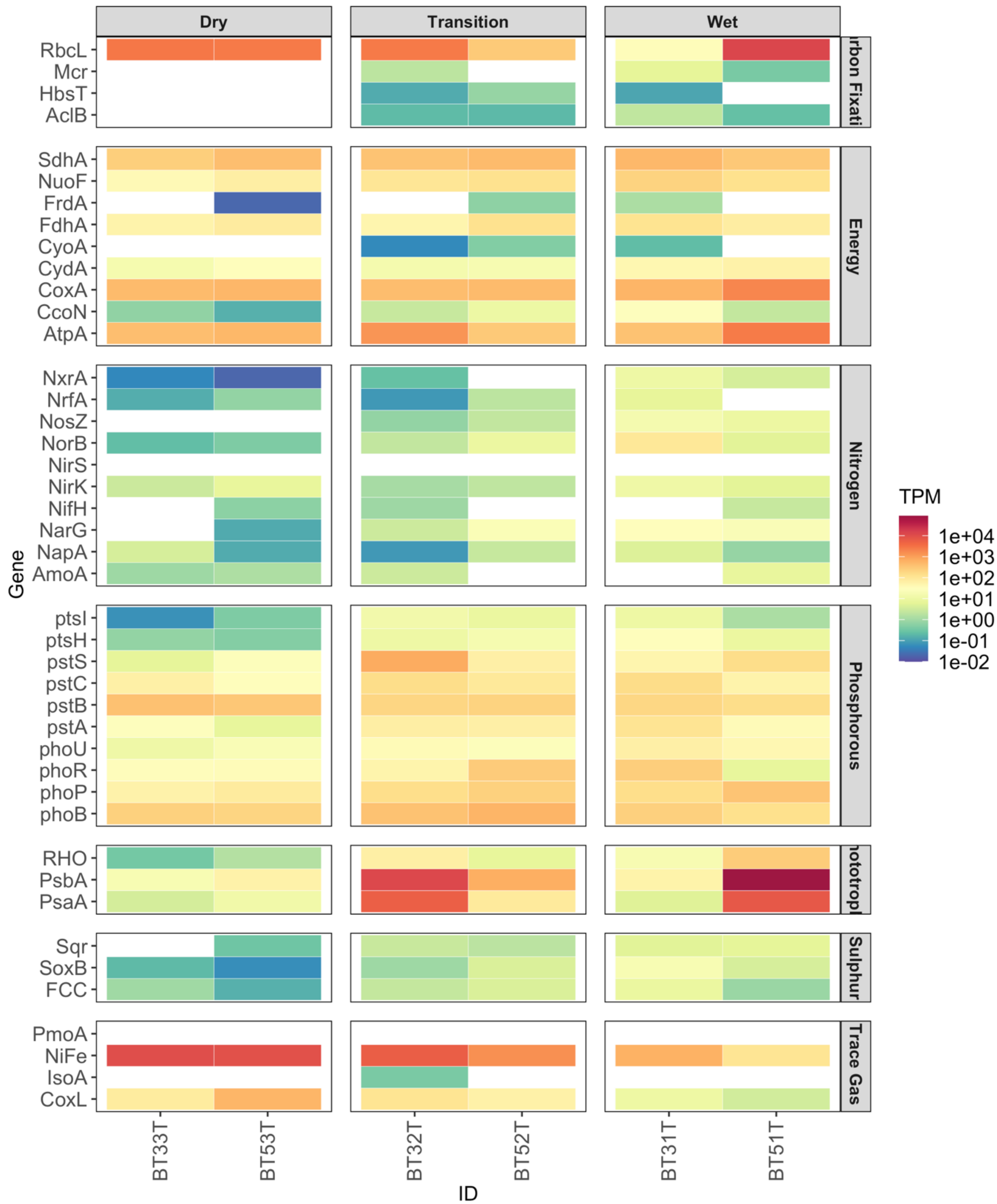


Figure S5 – Transcripts abundance (TPM) associated to metabolic marker genes related to carbon fixation, energy acquisition, trace gas metabolism, phototrophy, nitrogen, sulphur and phosphorous cycle. Transcript abundance was calculated with Salmon "--validate-mappings". TPM values calculated for ORFs with the same annotation were summed. Colours were log scaled. Blank cells represent zero values.

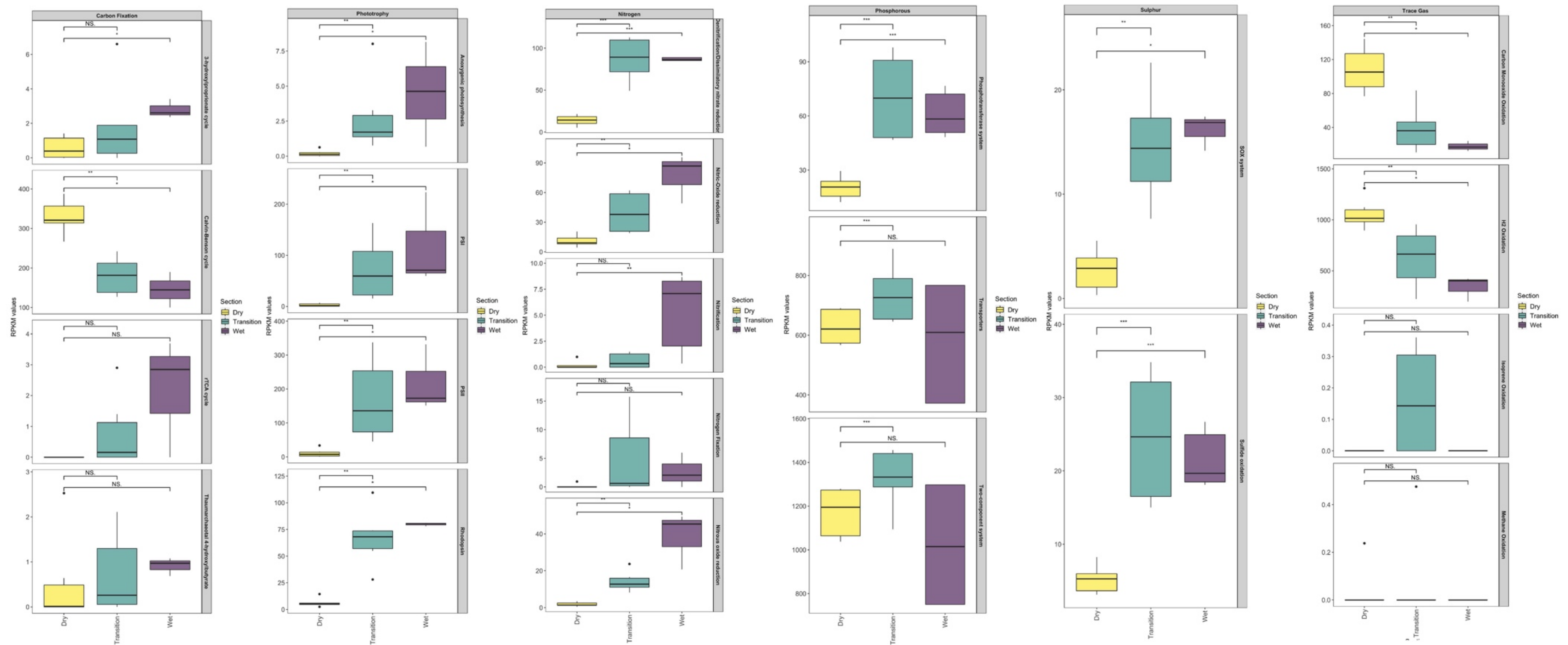
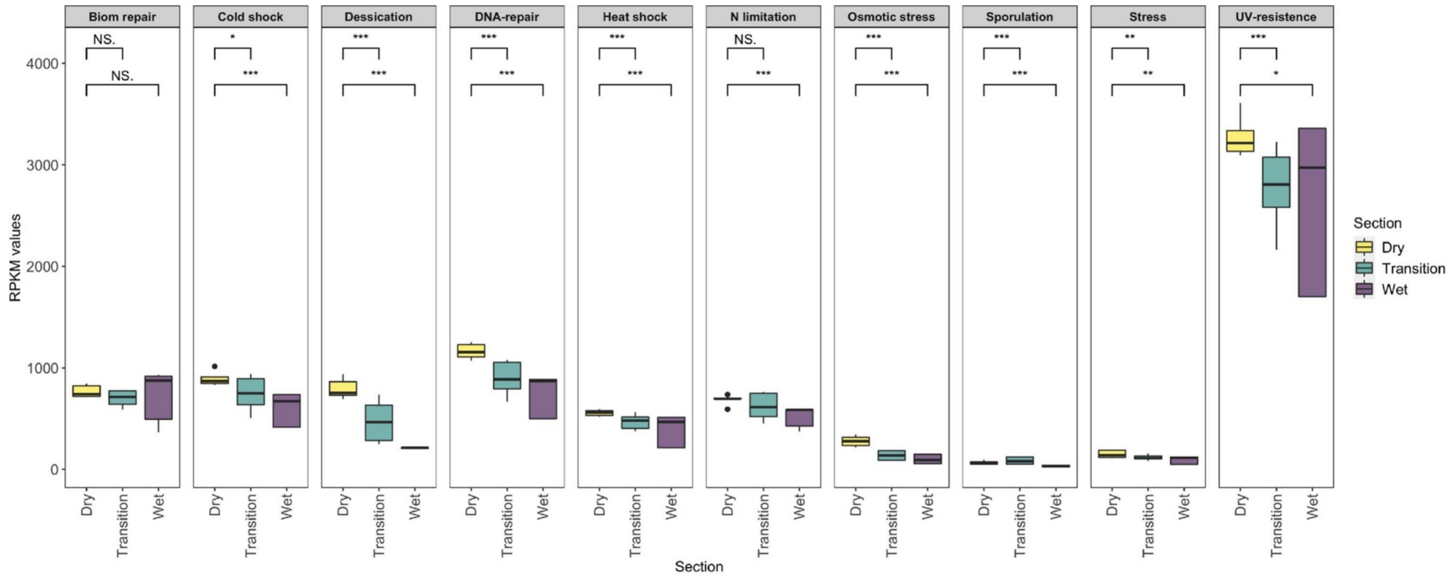


Figure S6 - Comparison of metabolic transcripts abundance (TPM) across the three sections of the gradient. Each section has a n =2 samples. Asterisks indicate statistically significant differences ($p < 0.05$) in the abundance of transcripts related to each respective metabolism between dry, transition and wet samples using Wilcox test.



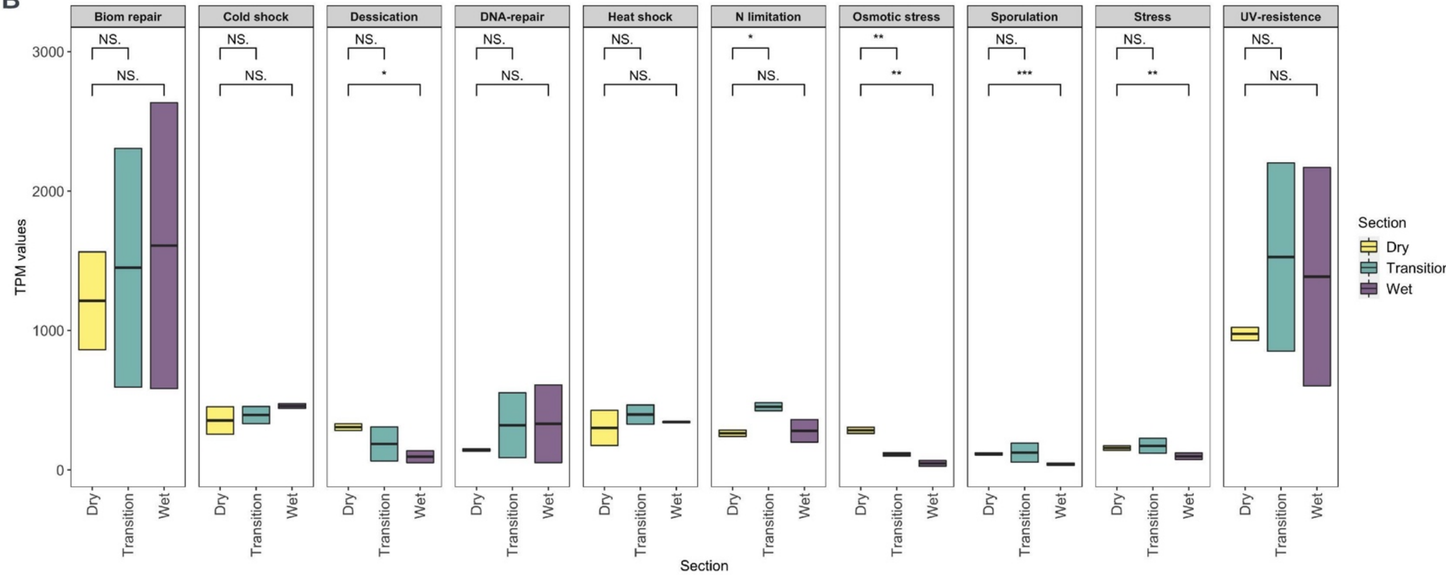


Figure S7 - A – Box plots comparing the presence and abundance of stress-related pathways along the three sections of the wetness gradients. The abundance of marker genes representative of each pathway were calculated in RPKM with CoverM. When more than one gene was used to represent a pathway, the RPKM abundances were summed. Biom repair stands for biomolecular repair mechanisms. Asterisks indicate statistically significant differences ($p < 0.05$) using Wilcox test. **B** – Box plots comparing the abundance of gene transcripts associated to stress-related pathways along the wetness gradients. The abundance of each transcript was calculated in TPM with Salmon. When more than one gene transcript was used to represent a pathway, the TPM abundances were summed. Biom repair stands for biomolecular repair mechanisms. Asterisks indicate statistically significant differences ($p < 0.05$) using Wilcox test.

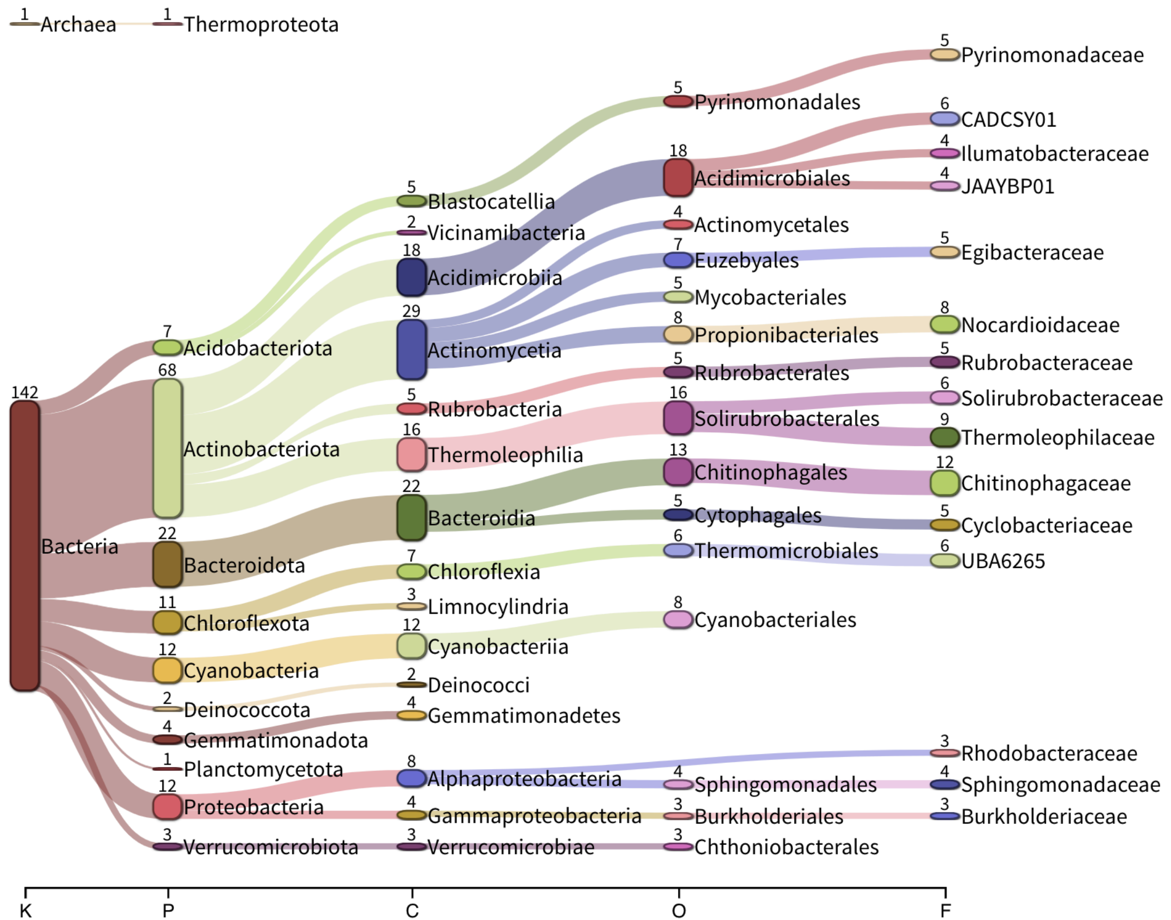


Figure S8 – Sankey plot based on assigned taxonomy at the phylum, class, order and family levels, with the top 16 taxa shown at each level. Numbers indicate the number of MAGs recovered for each taxonomic level.

Figure S9 – Bubble plot depicting the metabolic potential of the 143 Med-High quality MAGs. The size of the bubble represents the number of MAGs associated with each phyla that encode a marker gene for the metabolic pathway of interest. The colours represent the average genome completeness. The values inside the parenthesis represent the total number of MAGs with the respective phylum affiliation

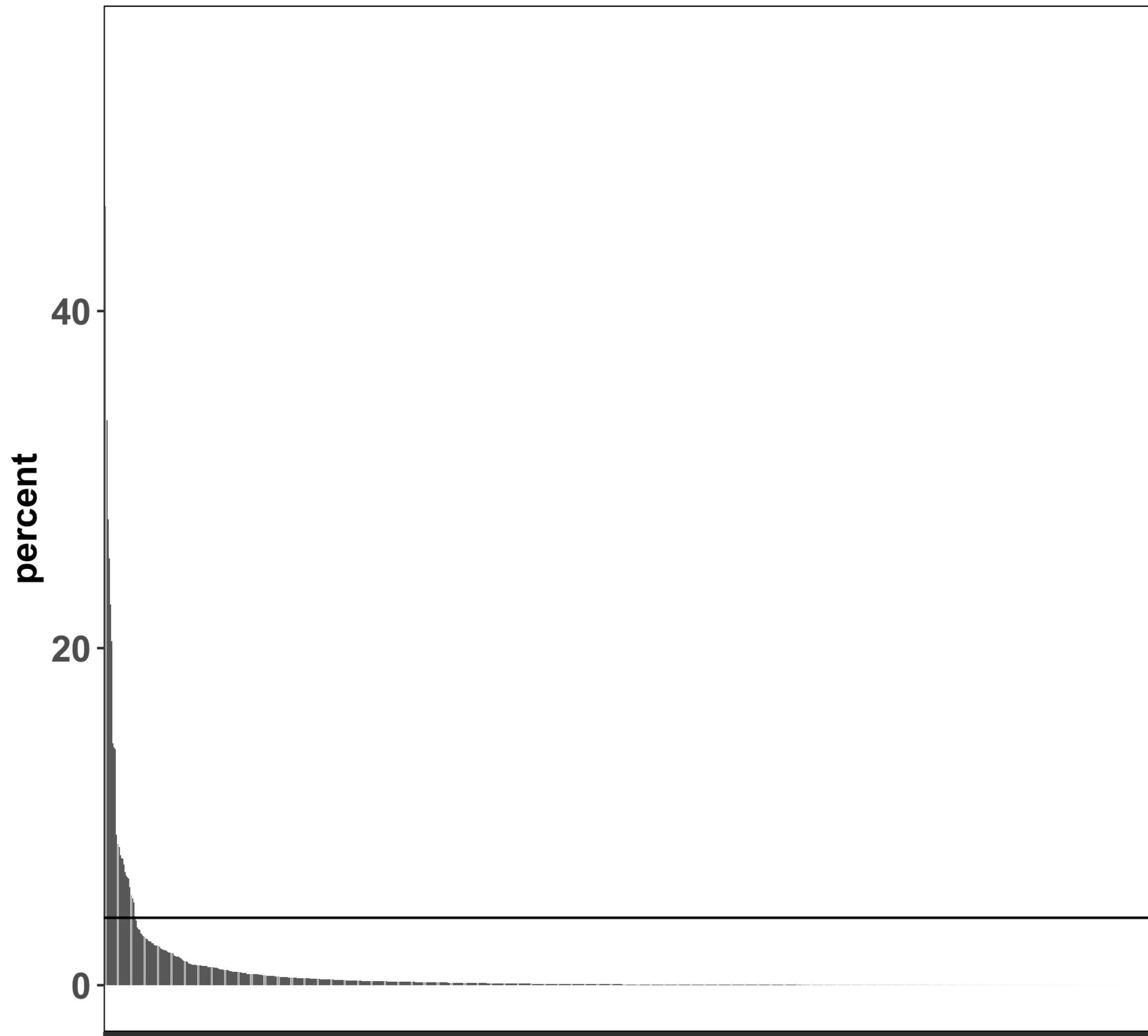


Figure S10 – Rank frequency plot of active MAGs across the wetness gradient. Line depicts the 4% relative abundance mark.

Table S1 - Metadata collected for each sample representative of the geochemically defined wetness gradient.

ID	Sample name	Sampling Point	Transect	Section	Distance (m)	Electrical Conductivity (uS)	Water Activity	pH	% Moisture	% TC	% TOC	%TN
BT31	BT3_0	1	BT3	Wet	0	17.70	1.00	7.00	14.45	0.05	0.04	< det lim
BT32	BT3_4	2	BT3	Transition	4	46.10	1.00	7.20	13.60	0.05	0.03	< det lim
BT33	BT3_5.75	3	BT3	Transition	6	167.30	1.00	7.80	11.67	0.05	0.03	< det lim
BT34	BT3_6.75	4	BT3	Dry	7	231.60	0.50	7.90	1.08	0.04	0.03	< det lim
BT35	BT3_13	5	BT3	Dry	13	35.60	0.40	8.10	0.00	0.05	0.03	< det lim
BT41	BT4_0	1	BT4	Wet	0	12.64	0.99	7.61	15.17	0.05	0.03	< det lim
BT42	BT4_9	2	BT4	Transition	9	55.40	1.00	7.46	4.38	0.04	0.03	< det lim
BT43	BT4_11.3	3	BT4	Transition	11	255.70	0.80	7.87	1.34	0.04	0.03	< det lim
BT44	BT4_12	4	BT4	Dry	12	277.10	0.50	8.02	0.91	0.04	0.03	< det lim
BT45	BT4_17	5	BT4	Dry	17	123.80	0.30	8.00	1.04	0.06	0.03	< det lim
BT51	BT5_0	1	BT5	Wet	0	33.20	1.00	7.60	19.09	0.04	0.02	< det lim
BT52	BT5_2	2	BT5	Transition	2	113.60	1.00	8.80	15.91	0.04	0.02	< det lim
BT53	BT5_5	3	BT5	Transition	5	539.90	0.50	8.00	6.18	0.04	0.02	< det lim
BT54	BT5_6	4	BT5	Dry	6	108.50	0.30	7.70	0.22	0.04	0.02	< det lim
BT55	BT5_11	5	BT5	Dry	11	24.20	0.30	7.50	0.00	0.05	0.02	< det lim

Table S2 – Trace elemental analysis conducted in each sample representative of the geochemically defined wetness gradient. Elemental concentrations are in ppm.

Samples	BT31	BT32	BT33	BT34	BT35	BT41	BT42	BT43	BT44	BT45	BT51	BT52	BT53	BT54	BT55
Silver*	<0.002	<0.002	<0.002	<0.002	<0.002	<0.002	<0.002	<0.002	0.00	<0.002	0.02	<0.002	<0.002	<0.002	<0.002
Arsenic	<0.0005	0.00	0.00	<0.0005	0.00	<0.0005	0.00	<0.0005	0.00	<0.0005	<0.0005	0.00	<0.0005	<0.0005	0.00
Aluminium	13.00	17.20	23.40	15.30	18.30	14.20	16.90	16.30	12.90	11.60	17.60	24.50	16.80	19.10	14.70
Barium	0.03	0.04	0.05	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.04	0.04	0.03
Beryllium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bismuth	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Boron	<0.005	<0.005	<0.005	<0.005	<0.005	0.01	<0.005	0.01	<0.005	<0.005	<0.005	0.01	0.01	0.01	<0.005
Calcium	7.89	10.50	14.00	9.40	11.00	8.18	9.41	9.51	7.76	8.44	10.80	14.90	11.60	12.90	9.57
Cadmium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cobalt	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Chromium	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Caesium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copper	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.04	0.05	0.04	0.04	0.03
Iron	10.30	12.30	14.30	11.90	12.30	12.10	14.50	12.90	12.10	11.60	11.90	16.30	12.70	13.90	11.30
Germanium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mercury	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Potassium	1.30	1.90	2.30	1.80	1.90	1.90	2.70	2.20	2.00	2.00	1.90	2.50	2.20	2.10	1.60
Lanthanum	0.02	0.03	0.03	0.02	0.03	0.02	0.04	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04
Lithium	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Magnesium	3.84	4.63	5.76	4.06	4.37	4.04	5.14	4.22	3.94	3.74	4.51	6.61	5.21	5.44	4.41

Manganese	0.16	0.18	0.21	0.19	0.19	0.19	0.22	0.20	0.19	0.20	0.17	0.23	0.18	0.21	0.16
Molybdenum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sodium	1.21	2.00	2.69	2.38	1.85	1.27	2.04	2.13	2.38	1.33	1.74	2.45	2.33	2.12	1.54
Nickel	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02
Phosphorus	0.59	0.59	0.63	0.58	0.57	0.59	0.68	0.59	0.60	0.59	0.53	0.75	0.60	0.71	0.62
Lead	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubidium	0.01	0.01	0.02	0.01	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01
Sulfur*	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10	<10
Antimony	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Selenium	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.00	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Tin	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005
Strontium	0.03	0.04	0.06	0.04	0.04	0.03	0.04	0.04	0.03	0.03	0.04	0.05	0.04	0.04	0.03
Thallium	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.00	<0.0001	<0.0001	<0.0001	<0.0001	0.00	<0.0001	<0.0001	<0.0001
Uranium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vanadium	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.02	0.02
Yttrium	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Zinc	0.07	<0.3	<0.3	0.05	<0.3	0.05	<0.3	0.05	0.05	0.06	<0.3	<0.3	0.05	<0.3	0.06

Table S3 –Metagenomes and metatranscriptomes sequencing results

				Metagenomes						Trancriptomes		
Sample	**Sampling Point**	**Transect**	**Section**	**Raw Base (G)**	**Raw reads**	**Read counts after QC**	**% QC reads**	**Nonpareil Coverage**	**Nonpareil Diversity**	**Raw Base (G)**	**Raw reads**	**Transcript counts after QC**
BT31	1	BT3	Wet	7.5	24913764	20892054	83.9	59.3	21.2	18.7	62324086	6767949
BT32	2	BT3	Transition	10.0	33420383	30769561	92.1	60.7	21.4			
BT33	3	BT3	Transition	4.0	13264156	10991266	82.9	49.9	21.1	28.8	96140418	33120604
BT34	4	BT3	Dry	5.8	19211196	16956543	88.3	68.8	20.4			
BT35	5	BT3	Dry	5.4	18139815	17113844	94.3	75.8	19.7	8.9	29534539	19196407
BT41	1	BT4	Wet	8.9	29696301	26401334	88.9	61.3	21.4			
BT42	2	BT4	Transition	7.8	26138866	20699149	79.2	61.0	21.0			
BT43	3	BT4	Transition	11.9	39675272	38115573	96.1	81.2	20.1			
BT44	4	BT4	Dry	7.6	25322441	23824684	94.1	86.3	18.8			
BT45	5	BT4	Dry	12.0	39967470	38877199	97.3	84.9	19.6			
BT51	1	BT5	Wet	4.3	14167465	10186123	71.9	60.7	18.6	12.8	42515590	10101098
BT52	2	BT5	Transition	4.9	16411942	14482860	88.2	63.1	20.0			
BT53	3	BT5	Transition	7.2	24112890	21366234	88.6	62.9	20.9	16.3	54314776	7049385
BT54	4	BT5	Dry	6.4	21496028	18909392	88.0	63.5	20.7			
BT55	5	BT5	Dry	3.8	12735537	7488408	58.8	51.9	20.5	38.7	128943998	86527328

Table S4 – Co-assembly statistics

	Co-assembly
# contigs	4798308
# contigs (>= 1000 bp)	1321158
# contigs (>= 1500 bp)	633,634
# contigs (>= 5000 bp)	70193
# contigs (>= 10000 bp)	18772
# contigs (>= 25000 bp)	2407
# contigs (>= 50000 bp)	310
Total length (>= 1000 bp)	2817996273
Total length (>= 5000 bp)	667515412
Total length (>= 10000 bp)	322136242
Total length (>= 25000 bp)	88404262
Total length (>= 50000 bp)	20535137
Largest contig	179226
Total length	5144032997
GC (%)	58.12
N50	1112
N90	565
L50	1087581
L90	1090927

Table S5 – Relative abundance of each phyla present along the wetness gradients sampled in lake Brownworth and identified using the the *L16/L10E rplP* single-marker gene.

Section	Phylum	Mean relative abundance	Mean relative abundance (%)	sd	Number of Samples
Dry	Acidobacteria	0.1	7.2	0.0	6
Dry	Actinobacteria	0.7	68.9	0.1	6
Dry	Aquificae	0.0	0.0	0.0	6
Dry	Armatimonadetes	0.0	0.0	0.0	6
Dry	Asgardarchaeota	0.0	0.0	0.0	6
Dry	Bacteroidetes	0.0	4.2	0.0	6
Dry	Bdellovibrionota	0.0	0.7	0.0	6
Dry	Chloroflexi	0.1	5.5	0.0	6
Dry	Crenarchaeota	0.0	0.0	0.0	6
Dry	Cyanobacteria	0.0	0.6	0.0	6
Dry	Deinococcota	0.0	0.3	0.0	6
Dry	Desulfobacterota	0.0	0.0	0.0	6
Dry	Desulfuromonadota	0.0	0.0	0.0	6
Dry	Elusimicrobia	0.0	0.0	0.0	6
Dry	Epsilonbacterota	0.0	0.0	0.0	6
Dry	Euryarchaeota	0.0	0.0	0.0	6
Dry	Fibrobacteres	0.0	0.1	0.0	6
Dry	Firmicutes	0.0	0.1	0.0	6
Dry	Firmicutes_A	0.0	0.2	0.0	6
Dry	Firmicutes_B	0.0	0.1	0.0	6
Dry	Firmicutes_C	0.0	0.0	0.0	6
Dry	Firmicutes_D	0.0	0.1	0.0	6
Dry	Firmicutes_E	0.0	0.1	0.0	6

Dry	Firmicutes_F	0.0	0.0	0.0	6
Dry	Firmicutes_G	0.0	0.0	0.0	6
Dry	Gemmatimonadetes	0.0	0.7	0.0	6
Dry	Marinimicrobia	0.0	0.0	0.0	6
Dry	MBNT15	0.0	0.0	0.0	6
Dry	Myxococcota	0.0	0.1	0.0	6
Dry	Nitrospinota	0.0	0.1	0.0	6
Dry	Nitrospirota	0.0	0.0	0.0	6
Dry	Omnitrophica	0.0	0.0	0.0	6
Dry	Patescibacteria	0.0	0.9	0.0	6
Dry	Planctomycetes	0.0	0.9	0.0	6
Dry	Proteobacteria	0.0	4.9	0.0	6
Dry	SAR324	0.0	0.0	0.0	6
Dry	Spirochaetes	0.0	0.1	0.0	6
Dry	Synergistetes	0.0	0.2	0.0	6
Dry	Thermotogae	0.0	0.0	0.0	6
Dry	unknown	0.0	1.1	0.0	6
Dry	Verrucomicrobia	0.0	1.9	0.0	6
Transition	Acidobacteria	0.1	6.6	0.0	6
Transition	Actinobacteria	0.3	33.1	0.2	6
Transition	Aquificae	0.0	0.1	0.0	6
Transition	Armatimonadetes	0.0	0.2	0.0	6
Transition	Asgardarchaeota	0.0	0.0	0.0	6
Transition	Bacteroidetes	0.2	15.2	0.0	6
Transition	Bdellovibrionota	0.0	0.8	0.0	6
Transition	Chloroflexi	0.0	3.2	0.0	6
Transition	Crenarchaeota	0.0	0.1	0.0	6
Transition	Cyanobacteria	0.1	6.6	0.0	6

Transition	Deinococcota	0.0	0.4	0.0	6
Transition	Desulfobacterota	0.0	0.2	0.0	6
Transition	Desulfuromonadota	0.0	0.0	0.0	6
Transition	Elusimicrobia	0.0	0.1	0.0	6
Transition	Epsilonbacterota	0.0	0.2	0.0	6
Transition	Euryarchaeota	0.0	0.0	0.0	6
Transition	Fibrobacteres	0.0	0.0	0.0	6
Transition	Firmicutes	0.0	0.2	0.0	6
Transition	Firmicutes_A	0.0	0.1	0.0	6
Transition	Firmicutes_B	0.0	0.1	0.0	6
Transition	Firmicutes_C	0.0	0.0	0.0	6
Transition	Firmicutes_D	0.0	0.0	0.0	6
Transition	Firmicutes_E	0.0	0.0	0.0	6
Transition	Firmicutes_F	0.0	0.0	0.0	6
Transition	Firmicutes_G	0.0	0.0	0.0	6
Transition	Gemmatimonadetes	0.0	1.1	0.0	6
Transition	Marinimicrobia	0.0	0.0	0.0	6
Transition	MBNT15	0.0	0.0	0.0	6
Transition	Myxococcota	0.0	0.4	0.0	6
Transition	Nitrospinota	0.0	0.0	0.0	6
Transition	Nitrospirota	0.0	0.1	0.0	6
Transition	Omnitrophica	0.0	0.1	0.0	6
Transition	Patescibacteria	0.0	3.1	0.0	6
Transition	Planctomycetes	0.0	2.0	0.0	6
Transition	Proteobacteria	0.2	18.2	0.1	6
Transition	SAR324	0.0	0.0	0.0	6
Transition	Spirochaetes	0.0	0.1	0.0	6
Transition	Synergistetes	0.0	0.2	0.0	6

Transition	Thermotogae	0.0	0.0	0.0	6
Transition	unknown	0.0	1.5	0.0	6
Transition	Verrucomicrobia	0.0	4.3	0.0	6
Wet	Acidobacteria	0.1	9.2	0.0	3
Wet	Actinobacteria	0.2	19.7	0.0	3
Wet	Aquificae	0.0	0.0	0.0	3
Wet	Armatimonadetes	0.0	0.2	0.0	3
Wet	Asgardarchaeota	0.0	0.0	0.0	3
Wet	Bacteroidetes	0.2	23.2	0.1	3
Wet	Bdellovibrionota	0.0	1.0	0.0	3
Wet	Chloroflexi	0.0	1.8	0.0	3
Wet	Crenarchaeota	0.0	0.0	0.0	3
Wet	Cyanobacteria	0.0	3.3	0.0	3
Wet	Deinococcota	0.0	0.3	0.0	3
Wet	Desulfobacterota	0.0	0.0	0.0	3
Wet	Desulfuromonadota	0.0	0.0	0.0	3
Wet	Elusimicrobia	0.0	0.0	0.0	3
Wet	Epsilonbacterota	0.0	0.0	0.0	3
Wet	Euryarchaeota	0.0	0.0	0.0	3
Wet	Fibrobacteres	0.0	0.0	0.0	3
Wet	Firmicutes	0.0	0.2	0.0	3
Wet	Firmicutes_A	0.0	0.3	0.0	3
Wet	Firmicutes_B	0.0	0.1	0.0	3
Wet	Firmicutes_C	0.0	0.0	0.0	3
Wet	Firmicutes_D	0.0	0.0	0.0	3
Wet	Firmicutes_E	0.0	0.0	0.0	3
Wet	Firmicutes_F	0.0	0.0	0.0	3
Wet	Firmicutes_G	0.0	0.0	0.0	3

Wet	Gemmatimonadetes	0.0	2.3	0.0	3
Wet	Marinimicrobia	0.0	0.0	0.0	3
Wet	MBNT15	0.0	0.0	0.0	3
Wet	Myxococcota	0.0	0.8	0.0	3
Wet	Nitrospinota	0.0	0.0	0.0	3
Wet	Nitrospirota	0.0	0.2	0.0	3
Wet	Omnitrophica	0.0	0.9	0.0	3
Wet	Patescibacteria	0.0	1.6	0.0	3
Wet	Planctomycetes	0.1	5.0	0.0	3
Wet	Proteobacteria	0.2	21.1	0.1	3
Wet	SAR324	0.0	0.0	0.0	3
Wet	Spirochaetes	0.0	0.0	0.0	3
Wet	Synergistetes	0.0	0.0	0.0	3
Wet	Thermotogae	0.0	0.0	0.0	3
Wet	unknown	0.0	1.5	0.0	3
Wet	Verrucomicrobia	0.1	5.4	0.0	3

Table S6 – Metagenome community representation at the co-assembly level calculated with SingleM. Coverage of the co-assembly based on the percentage of mapped metagenome reads and transcripts to the co-assembly. Read mapping was calculated with CoverM (contig mode) using default settings, Transcripts mapping was calculated with Salmon using the --*validate-mappings* option.

				SingleM	CoverM	Salmon
Metagenome	**Transect Section**	**num_assembled**	**num_not_found**	**Co-assembly community representation (%)**	**Co-assembly read mapping (%)**	**Co-assembly transcripts mapping (%)**
BT31	**Wet**	9166	2659	77.5	81.4	36.9
BT32	**Transition**	15399	2476	86.1	86.7	
BT33	**Transition**	5050	920	84.6	89.5	71.2
BT34	**Dry**	9218	797	92.0	93.3	
BT35	**Dry**	10782	285	97.4	96.3	86.5
BT41	**Wet**	9249	3016	75.4	80.9	
BT42	**Transition**	7873	2208	78.1	86.2	
BT43	**Transition**	19953	1166	94.5	94.8	
BT44	**Dry**	13446	462	96.7	97.1	
BT45	**Dry**	23271	566	97.6	96.5	
BT51	**Wet**	3795	673	84.9	90.0	54.8
BT52	**Transition**	4986	849	85.4	91.5	
BT53	**Transition**	10390	1228	89.4	92.4	70.6
BT54	**Dry**	9173	1035	89.9	92.1	
BT55	**Dry**	3697	441	89.3	92.4	74.1

Table S7 – RPKM values for metabolic pathways associated with carbon fixation, energy acquisition, trace gas metabolism, phototrophy, nitrogen, sulphur and phosphorous cycle. Metabolic marker gene coverage was calculated with CoverM "contig" mode using "bwa" alignment and the following parameters: min-read-align 0.75 and min-read-id 0.95. Metabolic marker gene abundances associated to the same pathway with grouped and the RPKM values summed .

Metabolism	Pathway	Genes	BT31	BT32	BT33	BT34	BT35	BT41	BT42	BT43	BT44	BT45	BT51	BT52	BT53	BT54	BT55
Carbon Fixation	**3-hydroxylproprionate cycle**	HbsT	3	2	0	1	0	3	7	0	1	0	2	2	0	1	0
Carbon Fixation	**Calvin-Benson cycle**	RbcL	145	213	209	313	388	100	132	154	315	267	190	127	242	326	367
Carbon Fixation	**rTCA cycle**	AclB	4	0	0	0	0	3	1	0	0	0	0	3	0	0	0
Carbon Fixation	**Thaumarchaeotal 4-hydroxylbutyrate**	HbsT	1	0	0	0	0	1	2	0	0	0	1	0	2	3	1
Energy	**Aerobic respiration**	NuoF, CoxA,CcoN,CydA,CyoA	1387	1139	1370	1340	1306	1388	1138	1131	1245	1207	799	802	1290	1328	1562
Energy	**formate oxidation**	FdhA	170	136	173	184	112	148	136	180	140	107	107	117	180	200	204
Energy	**Oxidative phosphorylation**	AtpA	546	561	461	452	461	527	414	449	510	427	435	407	442	413	525
Energy	**TCA cycle**	SdhA, FrdA	570	501	685	654	600	579	514	633	615	595	318	401	654	654	700
Nitrogen	**Denitrification/Dissimilatory nitrate reduction**	NapA, NrfA, NarG, NirK, NirS	89	101	110	18	10	85	49	77	13	5	86	113	72	21	15
Nitrogen	**Nitric-Oxide reduction**	NorB	96	61	20	8	9	87	62	19	10	4	49	52	24	15	21
Nitrogen	**Nitrification**	AmoA, NxrA	7	1	0	0	0	9	1	0	0	0	0	0	1	1	0
Nitrogen	**Nitrogen Fixation**	NifH	2	11	0	0	0	6	16	1	0	1	0	1	0	0	0
Nitrogen	**Nitrous oxide reduction**	NosZ	45	24	11	1	0	49	17	11	1	1	21	14	8	3	3
Phosphorous	**Phosphotransferase system**	ptsI,ptsH	48	91	83	30	16	58	48	57	24	12	77	98	47	19	22
Phosphorous	**Transporters**	pstA, pstB,pstC,pstS	609	654	790	567	664	767	890	646	691	573	372	757	695	577	687
Phosphorous	**Two-component system**	phoB, phoR, phoP,phoU	1015	1095	1457	1185	1064	1297	1441	1311	1279	1038	750	1355	1288	1273	1205
Phototrophy	**PSI**	PsaA	60	163	37	6	0	71	82	15	2	0	223	116	17	7	1
Phototrophy	**PSII**	PsbA	173	178	93	15	1	331	337	45	9	1	151	279	67	34	6
Phototrophy	**Rhodopsin**	RHO	81	64	74	6	3	80	55	109	14	6	78	72	28	5	5
Sulphur	**SOX system**	SoxB	14	23	15	3	0	17	14	10	3	1	17	18	8	6	4
Sulphur	**Sulfide oxidation**	FCC, Sqr	20	35	23	6	5	18	27	17	8	4	27	32	15	6	3
Trace Gas	**Carbon Monooxide Oxidation**	CoxL	17	17	42	134	77	24	30	48	82	106	12	11	84	105	144
Trace Gas	**H2 Oxidation**	NiFe	420	411	830	1009	1019	402	497	954	1310	972	198	224	846	896	1124
Trace Gas	**Isoprene Oxidation**	IsoA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trace Gas	**Methane Oxidation**	PmoA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S8 – TPM values for metabolic pathways associated with carbon fixation, energy acquisition, trace gas metabolism, phototrophy, nitrogen, sulphur and phosphorous cycle. Metabolic marker gene coverage was calculated with Salmon "—validate-mappings" option. The abundance of metabolic marker gene associated to the same pathway were grouped and the TPM values summed .

Metabolism	Pathway	Genes	BT31T	BT33T	BT35T	BT51T	BT53T	BT55T
Carbon Fixation	**3-hydroxylproprionate cycle**	HbsT	6.4	1.9	0.0	0.4	0.0	0.0
Carbon Fixation	**Calvin-Benson cycle**	rbcL	34.5	2585.3	2726.4	13352.4	291.4	2539.8
Carbon Fixation	**rTCA cycle**	AclB	2.2	0.2	0.0	0.2	0.2	0.0
Carbon Fixation	**Thaumarchaeotal 4-hydroxylbutyrate**	HbsT	0.1	0.1	0.0	0.0	0.7	0.0
Energy	**Aerobic respiration**	NuoF, CoxA,CcoN,CydA,CyoA	853.5	559.9	525.9	2110.0	619.8	626.5
Energy	**formate oxidation**	FdhA	118.5	49.3	53.5	72.0	128.7	78.5
Energy	**Oxidative phosphorylation**	AtpA	370.4	1328.8	419.8	2482.4	293.6	520.2
Energy	**TCA cycle**	SdhA, FrdA	509.4	362.2	246.9	307.3	470.0	420.2
Nitrogen	**Denitrification/Dissimilatory nitrate reduction**	NapA, NrfA, NarG, NirK, NirS	53.6	4.2	7.0	27.7	28.3	8.3
Nitrogen	**Nitric-Oxide reduction**	NorB	94.8	2.3	0.2	5.6	8.8	0.4
Nitrogen	**Nitrification**	AmoA, NxrA	10.2	3.2	0.9	11.4	0.0	1.4
Nitrogen	**Nitrogen Fixation**	NifH	0.0	0.9	0.0	2.5	0.0	0.6
Nitrogen	**Nitrous oxide reduction**	NosZ	15.2	0.7	0.0	9.2	2.3	0.0
Phosphorous	**Phosphotransferase system**	ptsI,ptsH	42.3	23.5	0.8	9.9	24.4	0.9
Phosphorous	**Transporters**	pstA, pstB,pstC,pstS	508.6	1162.8	480.1	390.4	428.5	375.5
Phosphorous	**Two-component system**	phoB, phoR, phoP,phoU	694.9	616.2	332.2	539.3	1104.5	337.4
Phototrophy	**PSI**	PsaA	5.1	5572.4	3.7	7279.2	84.6	12.2
Phototrophy	**PSII**	PsbA	54.6	12099.6	18.3	87275.1	696.8	57.3
Phototrophy	**Rhodopsin**	RHO	17.5	65.1	0.3	267.8	7.0	1.6
Sulphur	**SOX system**	SoxB	18.2	0.9	0.2	3.9	4.4	0.1

Sulphur	**Sulfide oxidation**	FCC, Sqr	13.9	5.1	0.9	7.0	6.2	0.5
Trace Gas	**Carbon Monooxide Oxidation**	CoxL	9.9	113.2	76.8	3.5	59.5	544.6
Trace Gas	**H2 Oxidation**	NiFe	630.1	5838.4	9930.9	108.8	1518.0	9249.8
Trace Gas	**Isoprene Oxidation**	IsoA	0.0	0.4	0.0	0.0	0.0	0.0
Trace Gas	**Methane Oxidation**	PmoA	0.0	0.0	0.0	0.0	0.0	0.0

Table S9 - – RPKM values for stress-related genes associated with stress-related pathways namely biomolecular repair damage, cold and heat shock, desiccation, DNA-repair, nitrogen limitation, osmotic stress, sporulation, UV-resistance and universal stress responses. Stress-related marker gene coverage was calculated with CoverM "contig" mode using "bwa" alignment and the following parameters: min-read-align 0.75 and min-read-id 0.95. Stress-related marker gene abundances associated to the same pathway with grouped and the RPKM values summed.

Pathway	Genes	BT31	BT41	BT51	BT32	BT42	BT52	BT33	BT43	BT53	BT34	BT44	BT54	BT35	BT45	BT55
Biom repair	dnaK, groEL	875.3	931.9	367.2	640.2	744.5	590.9	772.8	683.6	778.5	734.5	823.8	713.6	749.9	719.8	845.0
Cold shock	gyrA, desR, desK	671.2	737.2	415.2	636.0	649.9	505.5	939.6	892.2	847.7	845.6	1014.5	833.0	858.5	881.1	911.2
Desiccation	otsA/B	214.2	213.5	202.9	316.2	285.9	249.0	632.9	735.6	614.1	734.3	938.1	693.1	863.0	775.8	731.9
DNA-repair	polX, polA, KatE, dnB	871.3	886.4	498.6	798.7	794.0	667.6	1077.4	974.7	1053.9	1115.9	1253.1	1071.4	1107.7	1194.3	1229.7
Heat shock	hrcA, grpE, groES	467.7	513.1	214.1	403.1	457.5	375.2	564.8	503.0	516.7	577.7	594.5	557.0	531.6	519.8	563.5
N limitation	glnA/R	585.7	590.3	373.5	519.2	520.2	451.7	750.2	763.2	705.7	695.5	592.6	695.9	697.1	737.0	702.4
Osmotic stress	proX/W/V	92.0	148.7	56.1	84.7	116.5	185.4	157.7	89.0	190.3	234.7	317.4	216.6	343.4	282.3	272.6
Sporulation	WhiA/B, ssgA/B/D, spo genes	40.2	24.5	30.4	50.4	52.2	79.0	124.8	123.6	82.7	74.0	70.9	51.7	64.6	94.3	50.2
Stress	uspA/E/F	121.3	116.0	50.5	82.7	155.7	103.9	109.1	109.4	131.3	135.7	143.1	109.4	191.4	117.3	188.8
UV-resistance	uvrA/B/C, recA	2973.1	3359.5	1702.2	2582.2	2654.2	2163.3	3226.4	2958.0	3075.7	3133.2	3094.3	3253.7	3338.1	3176.2	3610.3

Table S10 – TPM values for stress-related genes associated with stress-related pathways namely biomolecular repair damage, cold and heat shock, desiccation, DNA-repair, nitrogen limitation, osmotic stress, sporulation, UV-resistance and universal stress responses. Stress-related marker gene coverage was calculated with Salmon "—validate-mappings" option. Stress-related marker gene abundances associated to the same pathway with grouped and the TPM values summed .

Pathway	Genes	BT31T	BT33T	BT35T	BT51T	BT53T	BT55T
Biom repair	dnaK, groEL	583.0	2307.6	861.9	2634.2	593.3	1564.0
Cold shock	gyrA, desR, desK	441.2	332.0	256.2	474.8	455.1	452.5
Desiccation	otsA/B	137.6	63.8	281.9	51.7	308.9	331.3
DNA-repair	polX, polA, KatE, dnB	609.7	87.2	151.1	52.0	552.5	135.1
Heat shock	hrcA, grpE, groES	339.8	466.0	174.9	346.7	328.8	428.0
N limitation	glnA/R	361.5	482.4	285.6	199.2	424.6	240.0
Osmotic stress	proX/W/V	66.7	124.5	306.2	26.9	98.1	262.0
Sporulation	WhiA/B, ssgA/B/D, spo genes	32.3	192.2	122.7	49.6	55.2	105.9
Stress	uspA/E/F	121.5	226.8	173.0	74.5	119.3	140.0
UV-resistance	uvrA/B/C, recA	2170.5	851.5	928.1	602.6	2202.8	1022.1

Table S11 - Summary table representing each metagenome-assembled-genome (MAG) produced in this study. The completeness and contamination were calculated using CheckM. The quality of each MAGS was assigned according to MIMAGs standards. Classification was assigned using GTDB-tk (R06-RS202).

MAGs ID	Completeness	Contamination	Quality	Classification
co-assembly_metabat.473.contigs_cleaned	74.02	9.17	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JAAYBF01;s__
co-assembly_metabat.67.contigs	75.04	3.02	Medium	d__Bacteria;p__Deinococcota;c__Deinococci;o__Deinococcales;f__Trueperaceae;g__;s__
co-assembly_metabat.455.contigs	75.39	9.4	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__;s__
co-assembly_metabat.178.contigs	75.46	3.95	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JACCZP01;s__
co-assembly_metabat.82.contigs	76.48	0	Medium	d__Bacteria;p__Planctomycetota;c__Planctomycetia;o__Pirellulales;f__Pirellulaceae;g__;s__
co-assembly_metabat.77.contigs	76.6	4.53	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__JACCUS01;s__
BT44_metabat.14.contigs	76.68	1.81	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Actinomycetales;f__Quadrisphaeraceae;g__;s__
co-assembly_metabat.362.contigs	77.55	4.63	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ginsengibacter;s__
co-assembly_metabat.370.contigs	77.95	2.07	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__JACDHG01;s__
co-assembly_metabat.200.contigs	78.95	9.37	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Egibacteraceae;g__WHTC01;s__
co-assembly_metabat.24.contigs	79.1	6.8	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Streptosporangiales;f__;g__;s__

BT54_metabat.9.contigs	79.32	8.49	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__CADCVQ01;s__
co-assembly_metabat.36.contigs	80.26	8.88	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__JACCYI01;s__
BT45_metabat.42_sub.contigs	80.51	3.13	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__JADDRA01;s__
BT45_metabat.52.contigs	80.58	1.98	Medium	d__Bacteria;p__Chloroflexota;c__Limnocylindria;o__Limnocylindrales;f__CSP1-4;g__Palsa-1032;s__
co-assembly_metabat.184.contigs	80.67	2.2	Medium	d__Bacteria;p__Gemmatimonadota;c__Gemmatimonadetes;o__Longimicrobiales;f__Longimicrobiaceae;g__;s__
co-assembly_metabat.333.contigs	81.02	4.45	Medium	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Sphingomonadales;f__Sphingomonadaceae;g__Sphingomicrobium;s__
co-assembly_metabat.524.contigs	81.16	5.04	Medium	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__SIO1D9;g__;s__
co-assembly_metabat.284.contigs	81.43	2.2	Medium	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__;s__
BT43_metabat.67.contigs	81.48	4.18	Medium	d__Bacteria;p__Chloroflexota;c__Limnocylindria;o__QHBO01;f__QHBO01;g__JACDBZ01;s__
co-assembly_metabat.324.contigs	81.74	5.87	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JAAYBP01;g__Aquihabitans;s__
BT32_metabat.14.contigs	81.75	1.3	Medium	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Sphingomonadales;f__Sphingomonadaceae;g__Allosphingosinicella;s__

co-assembly_metabat.545.contigs	81.81	2.22	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ferruginibacter;s__
BT35_metabat.23.contigs	82.24	1.29	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JAAYBF01;s__JAAYBF01 sp013812005
co-assembly_metabat.472.contigs	82.4	4.4	Medium	d__Bacteria;p__Proteobacteria;c__Gammaproteobacteria;o__Xanthomonadales;f__Xanthomonadaceae;g__Luteimonas;s__
co-assembly_metabat.267.contigs	82.52	2.2	Medium	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__JACCVC01;s__
co-assembly_metabat.204.contigs	82.6	6.55	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JACDCH01;g__VFJN01;s__
co-assembly_metabat.438.contigs	82.64	3.45	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__JACDAZ01;s__
co-assembly_metabat.141.contigs	82.67	9.74	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JAAYBF01;s__
BT35_metabat.12_sub.contigs	82.69	2.28	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JAAYBF01;s__
BT54_metabat.20.contigs	82.92	6.59	Medium	d__Bacteria;p__Verrucomicrobiota;c__Verrucomicrobiae;o__Chthoniobacterales;f__UBA10450;g__JACCTI01;s__JACCTI01 sp013812515
co-assembly_metabat.340.contigs	83.44	8.55	Medium	d__Bacteria;p__Acidobacteriota;c__Vicinamibacteria;o__Vicinamibacterales;f__2-12-FULL-66-21;g__JACCXG01;s__JACCXG01 sp013697225

co-assembly_metabat.232.contigs	83.5	8.17	Medium	d__Bacteria;p__Proteobacteria;c__Gammaproteobacteria;o__Burkholderiales;f__Burkholderiaceae;g__Ramlibacter;s__
co-assembly_metabat.121.contigs	84	8.21	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JACDCH01;g__;s__
co-assembly_metabat.126.contigs	84.05	2.05	Medium	d__Bacteria;p__Actinobacteriota;c__Rubrobacteria;o__Rubrobacterales;f__Rubrobacteraceae;g__JACDDK01;s__
BT41_metabat.2.contigs	84.2	3.04	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ferruginibacter;s__
co-assembly_metabat.507.contigs	84.43	9.16	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JAAYBP01;g__JAAYBP01;s__
co-assembly_metabat.16.contigs	84.56	3.53	Medium	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Rhodobacterales;f__Rhodobacteraceae;g__Amaricoccus;s__
co-assembly_metabat.243.contigs	84.64	9.55	Medium	d__Bacteria;p__Verrucomicrobiota;c__Verrucomicrobiae;o__Chthoniobacterales;f__Chthoniobacteraceae;g__;s__
co-assembly_metabat.130.contigs	84.66	2.56	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Euzebyaceae;g__Euzebya;s__
co-assembly_metabat.451.contigs	85.15	2.91	Medium	d__Archaea;p__Thermoproteota;c__Nitrososphaeria;o__Nitrososphaerales;f__Nitrososphaeraceae;g__Nitrosocosmicus;s__Nitrosocosmicus sp013694585
co-assembly_metabat.406.contigs	85.19	1.99	Medium	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__;s__
co-assembly_metabat.416.contigs	85.46	4.76	Medium	d__Bacteria;p__Gemmatimonadota;c__Gemmatimonadetes;o__Gemmatimonadales;f__GWC2-71-9;g__JACDDX01;s__

co-assembly_metabat.302.contigs	85.57	8.45	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ferruginibacter;s__
BT34_metabat.14.contigs	86.01	1.34	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__;s__
co-assembly_metabat.392.contigs	86.03	2	Medium	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Chamaesiphonaceae;g__Crinalium;s__
co-assembly_metabat.420.contigs	86.21	7.79	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JAAYBF01;s__
co-assembly_metabat.377.contigs	86.23	6.9	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Parafilimonas;s__
co-assembly_metabat.448.contigs	86.24	5.16	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__JACCUZ01;f__JACCUZ01;g__JACCUZ01;s__
BT45_metabat.56.contigs	86.73	1.17	Medium	d__Bacteria;p__Actinobacteriota;c__Rubrobacteria;o__Rubrobacterales;f__Rubrobacteraceae;g__SCSIO-52909;s__
co-assembly_metabat.224.contigs	87.06	3.37	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__;s__
co-assembly_metabat.148.contigs	87.12	6.87	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__JACCXZ01;s__
BT31_maxbin.012_sub.contigs	87.17	6.28	Medium	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Microcoleaceae;g__Microcoleus;s__
co-assembly_metabat.72.contigs	88.2	6.65	Medium	d__Bacteria;p__Actinobacteriota;c__Rubrobacteria;o__Rubrobacterales;f__Rubrobacteraceae;g__SCSIO-52915;s__

BT43_metabat.26.contigs	88.21	4.04	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__CADCSY01;s__
BT43_maxbin.002_sub.contigs	88.21	2.69	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Mycobacteriales;f__SCTD01;g__;s__
BT31_metabat.5.contigs	88.46	5.42	Medium	d__Bacteria;p__Acidobacteriota;c__Blastocatellia;o__Pyrinomonadales;f__Pyrinomonadaceae;g__;s__
BT35_metabat.28_sub.contigs	88.6	0.85	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__;s__
BT53_metabat.29.contigs	88.86	3.7	Medium	d__Bacteria;p__Chloroflexota;c__Limnocylindria;o__Limnocylindrales;f__CSP1-4;g__Palsa-1032;s__
BT44_metabat.37_sub.contigs	88.87	1.05	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Sporichthyales;f__Sporichthyaceae;g__;s__
BT35_metabat.9.contigs	89.03	6.83	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__JACDHG01;s__JACDHG01 sp013821195
co-assembly_metabat.478.contigs	89.08	4.7	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__;s__
co-assembly_metabat.253.contigs	89.17	1.8	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Egibacteraceae;g__JACCTL01;s__
BT43_metabat.62.contigs	89.32	2.56	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__Ilumatobacteraceae;g__Ilumatobacter;s__
co-assembly_metabat.380.contigs	89.42	3.41	Medium	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Rhodobacterales;f__Rhodobacteraceae;g__Amaricoccus;s__

co-assembly_metabat.493.contigs	89.47	3.1	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__;f__;g__;s__
co-assembly_metabat.384.contigs	89.68	2.71	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Segetibacter;s__Segetibacter sp002050375
BT45_metabat.59.contigs	89.74	1.28	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__JADDRA01;s__
co-assembly_metabat.97.contigs	89.9	6.38	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Mycobacteriales;f__Geodermatophilaceae;g__JACCTY01;s__JACCTY01 sp013695665
BT43_maxbin.037_sub.contigs_cleaned	89.94	8.01	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Sphingobacteriales;f__Sphingobacteriaceae;g__Daejeonella;s__
co-assembly_metabat.292.contigs	89.95	1.73	Medium	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__JACCYX01;s__
BT44_metabat.33_sub.contigs	90.09	2.99	High	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__Ilumatobacteraceae;g__Ilumatobacter;s__
co-assembly_metabat.171.contigs	90.63	9.35	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JACCVG01;s__
BT45_metabat.16.contigs	90.65	4.7	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Egibacteraceae;g__JACCTL01;s__
co-assembly_metabat.213.contigs	90.67	5.5	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Segetibacter;s__

co-assembly_metabat.412.contigs	90.92	2.83	High	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermobaculales;f__Thermobaculaceae;g__JACDAU01;s__JACDAU01 sp013695265
BT45_metabat.20_sub.contigs	90.95	0.63	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Actinomycetales;f__Dermatophilaceae;g__Ornithinicoccus_A;s__
co-assembly_metabat.466.contigs	91	4.17	High	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Sphingomonadales;f__Sphingomonadaceae;g__Sphingomicrobium;s__Sphingomicrobium sp013817375
BT45_metabat.3.contigs	91.55	0	High	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JACCUC01;s__JACCUC01 sp013812485
co-assembly_metabat.260.contigs_cleaned	91.79	9.07	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JAAYBP01;g__JAAYBP01;s__
co-assembly_metabat.177.contigs	92.19	8.36	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Segetibacter;s__
BT43_metabat.8.contigs	92.23	1.28	High	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__CADCSY01;g__JADDRA01;s__
co-assembly_metabat.101.contigs	92.26	2.85	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Phormidesmiales;f__Phormidesmiaceae;g__Nodosilinea;s__
BT45_metabat.34.contigs	92.31	0.85	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Egibacteraceae;g__JACCTL01;s__JACCTL01 sp013812395
BT42_metabat.12.contigs	92.45	0.22	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Microcoleaceae;g__Microcoleus;s__

co-assembly_metabat.286.contigs	92.57	3.61	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ferruginibacter;s__
co-assembly_metabat.535.contigs	92.63	1.76	High	d__Bacteria;p__Acidobacteriota;c__Blastocatellia;o__Pyrinomonadales;f__Pyrinomonadaceae;g__OLB17;s__OLB17 sp013695195
BT45_metabat.35.contigs	92.73	5.98	Medium	d__Bacteria;p__Acidobacteriota;c__Blastocatellia;o__Pyrinomonadales;f__Pyrinomonadaceae;g__GCA-002050365;s__
BT32_metabat.8.contigs	92.74	3.47	High	d__Bacteria;p__Acidobacteriota;c__Blastocatellia;o__Pyrinomonadales;f__Pyrinomonadaceae;g__QHXQ01;s__
BT35_metabat.20.contigs	92.82	0.86	High	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Thermoleophilaceae;g__JACCZP01;s__JACCZP01 sp013695885
co-assembly_metabat.256.contigs	92.9	4.36	High	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Rhizobiales;f__Rhizobiaceae;g__Mangrovicella;s__
co-assembly_metabat.542.contigs	92.94	5.95	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__JACCYY01;f__JACCYY01;g__JACCYY01;s__JACCYY01 sp013696235
co-assembly_metabat.169.contigs	92.95	1.3	High	d__Bacteria;p__Actinobacteriota;c__Rubrobacteria;o__Rubrobacterales;f__Rubrobacteraceae;g__JACDGB01;s__JACDGB01 sp013815485
co-assembly_metabat.38.contigs	93.1	8.54	Medium	d__Bacteria;p__Acidobacteriota;c__Vicinamibacteria;o__Vicinamibacterales;f__Vicinamibacteraceae;g__;s__
BT44_metabat.29.contigs	93.16	4.27	High	d__Bacteria;p__Acidobacteriota;c__Blastocatellia;o__Pyrinomonadales;f__Pyrinomonadaceae;g__GCA-002050365;s__

co-assembly_metabat.527.contigs	93.22	3.39	High	d__Bacteria;p__Deinococcota;c__Deinococci;o__Deinococcales;f__Trueperaceae;g__;s__
co-assembly_metabat.162.contigs	93.34	5.14	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__JAAYBP01;g__Aquihabitans;s__
co-assembly_metabat.179.contigs	93.39	7.32	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Mycobacteriales;f__Geodermatophilaceae;g__JACCTY01;s__JACCTY01 sp013695685
BT43_metabat.52.contigs	93.41	2.3	High	d__Bacteria;p__Gemmatimonadota;c__Gemmatimonadetes;o__Longimicrobiales;f__Longimicrobiaceae;g__;s__
BT31_metabat.12.contigs	93.57	2.01	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Flavobacteriales;f__Flavobacteriaceae;g__Flavobacterium;s__
BT32_metabat.24.contigs	93.99	0.59	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Nostocaceae;g__Nodularia;s__
BT35_metabat.17_sub.contigs	94.1	3.18	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Mycobacteriales;f__Geodermatophilaceae;g__JACCQS01;s__JACCQS01 sp013811975
co-assembly_metabat.206.contigs	94.4	6.69	Medium	d__Bacteria;p__Proteobacteria;c__Gammaproteobacteria;o__Burkholderiales;f__Burkholderiaceae;g__Rubrivivax;s__
co-assembly_metabat.70.contigs	94.53	4.07	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__Ferruginibacter;s__
BT53_metabat.9.contigs	94.63	7.26	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__GCA-2861595;g__;s__
BT43_metabat.59.contigs	94.79	0.3	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Cytophagales;f__Cyclobacteriaceae;g__Anditalea;s__

co-assembly_metabat.45.contigs	94.91	6.33	Medium	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__JACCVL01;s__JACCVL01 sp013696365
BT43_metabat.5.contigs	95.27	2.7	High	d__Bacteria;p__Verrucomicrobiota;c__Verrucomicrobiae;o__Chthoniobacterales;f__UBA10450;g__JACCTI01;s__JACCTI01 sp013695905
co-assembly_metabat.279.contigs	95.41	7.66	Medium	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Cytophagales;f__Cyclobacteriaceae;g__;s__
BT53_metabat.20.contigs	95.42	6.41	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__Ilumatobacteraceae;g__Ilumatobacter;s__
co-assembly_metabat.207.contigs	95.44	4.05	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__Egibacteraceae;g__JACCXR01;s__JACCXR01 sp013696915
BT43_maxbin.001.contigs	95.49	0.94	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Cytophagales;f__Cyclobacteriaceae;g__Rhodonellum;s__
co-assembly_metabat.383.contigs	95.54	0.31	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Cytophagales;f__Cyclobacteriaceae;g__ANT-B6;s__
BT41_metabat.1.contigs	95.75	0.83	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Pseudanabaenales;f__Pseudanabaenaceae;g__Pseudanabaena;s__
BT33_metabat.6.contigs	95.77	3.59	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Propionibacteriales;f__Nocardioidaceae;g__Nocardioides;s__
BT43_metabat.38.contigs	95.87	2.16	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Mycobacteriales;f__SCTD01;g__SCTD01;s__

BT43_metabat.6.contigs	95.96	1.32	High	d__Bacteria;p__Actinobacteriota;c__Rubrobacteria;o__Rubrobacterales;f__Rubrobacteraceae;g__Rubrobacter_A;s__
co-assembly_metabat.546.contigs	95.99	1.85	High	d__Bacteria;p__Proteobacteria;c__Gammaproteobacteria;o__Burkholderiales;f__Burkholderiaceae;g__Lautropia;s__
BT35_metabat.14.contigs	96.1	3.16	High	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__CADCVQ01;s__
BT53_maxbin.004.contigs	96.1	0.22	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Microcoleaceae;g__Microcoleus;s__
co-assembly_metabat.157.contigs	96.34	5.13	Medium	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__Ilumatobacteraceae;g__JACDHN01;s__JACDHN01 sp013821025
co-assembly_metabat.356.contigs	96.36	3.48	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__Chitinophagaceae;g__JAAFHG01;s__
BT43_metabat.29.contigs	96.38	1.09	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Phormidesmiales;f__Phormidesmiaceae;g__Phormidesmis;s__Phormidesmis sp002286735
co-assembly_metabat.463.contigs	96.56	0.79	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Flavobacteriales;f__Flavobacteriaceae;g__Aquaticitalea;s__
BT43_metabat.33.contigs	96.59	0	High	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Rhodobacterales;f__Rhodobacteraceae;g__Paracoccus;s__
BT43_metabat.19.contigs	96.74	0	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Phormidesmiales;f__Phormidesmiaceae;g__Phormidesmis;s__Phormidesmis foveolarum

co-assembly_metabat.271.contigs	96.85	4.95	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Actinomycetales;f__Dermatophilaceae;g__Ornithinicoccus_A;s__
BT44_metabat.19.contigs	97.01	0.85	High	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__CADCVQ01;s__
co-assembly_metabat.235.contigs	97.34	8.68	Medium	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__Solirubrobacteraceae;g__JACCYI01;s__
co-assembly_metabat.504.contigs	97.37	1.52	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Chitinophagales;f__BACL12;g__JADKAC01;s__
BT45_metabat.26.contigs	97.38	0	High	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__JACCVC01;s__JACCVC01 sp013698305
BT44_metabat.26.contigs	97.8	2.2	High	d__Bacteria;p__Gemmatimonadota;c__Gemmatimonadetes;o__Longimicrobiales;f__Longimicrobiaceae;g__JAFAYN01;s__
BT43_metabat.32.contigs	97.84	1.51	High	d__Bacteria;p__Actinobacteriota;c__Thermoleophilia;o__Solirubrobacterales;f__70-9;g__;s__
BT44_maxbin.011.contigs	98.01	1.11	High	d__Bacteria;p__Proteobacteria;c__Alphaproteobacteria;o__Sphingomonadales;f__Sphingomonadaceae;g__Sphingomicrobium;s__
co-assembly_metabat.309.contigs	98.04	2.14	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Cytophagales;f__Cyclobacteriaceae;g__;s__
BT45_metabat.21.contigs	98.11	0.1	High	d__Bacteria;p__Chloroflexota;c__Chloroflexia;o__Thermomicrobiales;f__UBA6265;g__;s__
co-assembly_metabat.198.contigs	98.27	1.13	High	d__Bacteria;p__Bacteroidota;c__Bacteroidia;o__Sphingobacteriales;f__Sphingobacteriaceae;g__Daejeonella;s__

BT43_metabat.9.contigs	98.47	0.62	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Actinomycetales;f__GCA-002748415;g__;s__
co-assembly_metabat.276.contigs	98.91	4.09	High	d__Bacteria;p__Chloroflexota;c__Anaerolineae;o__Caldilineales;f__Caldilineaceae;g__Litorilinea;s__
BT32_metabat.27.contigs	99.11	0.74	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Chamaesiphonaceae;g__;s__
BT43_metabat.44.contigs	99.15	2.14	High	d__Bacteria;p__Actinobacteriota;c__Acidimicrobiia;o__Acidimicrobiales;f__AC-14;g__CADCTB01;s__
co-assembly_metabat.435.contigs	99.15	0.85	High	d__Bacteria;p__Actinobacteriota;c__Actinomycetia;o__Euzebyales;f__;g__;s__
BT42_metabat.10.contigs	99.76	4.64	High	d__Bacteria;p__Cyanobacteria;c__Cyanobacteriia;o__Cyanobacteriales;f__Nostocaceae;g__Hassallia;s__

Table S12 – The proportion of metagenome community recovered in Med-HQ MAG using SingleM --imperfect --sequence_identity 0.89. Coverage data based on mapping genomic and transcriptomic reads back to MAGs using CoverM and Salmon, respectively.

	SingleM	**CoverM (default settings)**	**Salmon**
Metagenome	**Proportion of the community recovered in the MAG (%)**	**MAGs Coverage (%)**	**MAG Transcript Coverage (%)**
BT31	22.1	38.1	2.02
BT32	22.0	34.7	
BT33	39.4	46.9	21.05
BT34	51.7	50.6	
BT35	63.1	59.6	17.94
BT41	25.2	39.8	
BT42	30.4	44.0	
BT43	50.8	49.0	
BT44	67.9	60.8	
BT45	61.5	58.3	
BT51	20.0	43.6	7.89
BT52	28.8	47.4	
BT53	44.9	49.9	10.73
BT54	45.4	48.5	
BT55	47.1	55.2	10.85
Average	41.4	48.4	11.75
Dry	56.1	55.5	14.40
Wet	22.4	40.5	4.96
Transition	36.1	45.3	15.89

Table S13 - Summary table representing each metagenome-assembled-genome (MAG) relative abundance. The relative abundance (%) was calculated with CoverM using "genome" mode and "bwa" alignment with following parameters: min-read-align 0.75 and min-read-id 0.95. Values have not been normalised.

Bin ID	Min RA (%)	Max RA (%)	BT31	BT32	BT33	BT34	BT35	BT41	BT42	BT43	BT44	BT45	BT51	BT52	BT53	BT54	BT55
BT35_metabat.17_sub.contigs	**0.006**	**0.941**	0.006	0.026	0.084	0.386	0.941	0.006	0.038	0.038	0.063	0.674	0.015	0.016	0.096	0.183	0.235
co-assembly_metabat.466.contigs	**0.001**	**0.507**	0.001	0.003	0.104	0.088	0.001	0.001	0.004	0.213	0.507	0.001	0.004	0.005	0.021	0.003	0.004
co-assembly_metabat.178.contigs	**0.001**	**0.535**	0.001	0.003	0.009	0.028	0.158	0.001	0.003	0.004	0.007	0.535	0.006	0.005	0.008	0.019	0.046
co-assembly_metabat.406.contigs	**0**	**0.136**	0	0.002	0.007	0.096	0.136	0	0.004	0.002	0.001	0.074	0.002	0.001	0.061	0.061	0.056
co-assembly_metabat.284.contigs	**0**	**0.268**	0	0.001	0.002	0.002	0.001	0	0	0.002	0.268	0.024	0.001	0.001	0.001	0.001	0.001
BT42_metabat.10.contigs	**0**	**3.5**	0.004	0.006	0.011	0.002	0	0.028	3.5	0.005	0.014	0.001	0.029	0.052	0.008	0.005	0.006
co-assembly_metabat.157.contigs	**0.001**	**0.186**	0.001	0.003	0.009	0.031	0.186	0.001	0.084	0.002	0.003	0.159	0.004	0.005	0.123	0.128	0.139
co-assembly_metabat.507.contigs	**0.001**	**0.466**	0.001	0.004	0.012	0.017	0.052	0.001	0.003	0.015	0.005	0.466	0.007	0.007	0.008	0.008	0.012
co-assembly_metabat.72.contigs	**0.005**	**0.27**	0.016	0.015	0.023	0.201	0.27	0.008	0.039	0.017	0.005	0.232	0.007	0.005	0.045	0.081	0.124
BT44_metabat.33_sub.contigs	**0.001**	**0.601**	0.001	0.009	0.031	0.022	0.005	0.001	0.061	0.054	0.601	0.006	0.008	0.025	0.035	0.008	0.005
BT43_metabat.52.contigs	**0.004**	**1.85**	0.004	0.035	0.072	0.32	1.508	0.006	0.017	1.85	0.115	0.999	0.03	0.026	0.018	0.046	0.042
co-assembly_metabat.362.contigs	**0**	**0.212**	0.002	0.066	0.103	0.018	0	0.002	0.177	0.016	0.001	0	0.028	0.049	0.212	0.004	0.002
co-assembly_metabat.260.contigs_cleaned	**0.001**	**0.197**	0.001	0.001	0.005	0.005	0.065	0.001	0.002	0.004	0.01	0.197	0.002	0.002	0.004	0.006	0.006
co-assembly_metabat.383.contigs	**0**	**0.903**	0	0.001	0.002	0.008	0	0	0	0.046	0.903	0.009	0.002	0.003	0.001	0.001	0.002
BT43_maxbin.001.contigs	**0.002**	**4.594**	0.002	0.005	0.029	0.008	0.002	0.003	0.095	4.594	0.028	0.003	0.035	0.026	0.018	0.013	0.023
BT53_maxbin.004.contigs	**0.003**	**6.195**	0.024	0.035	0.472	0.279	0.003	0.024	0.222	0.069	0.026	0.004	0.038	6.195	1.688	0.812	0.033
BT44_metabat.37_sub.contigs	**0.002**	**1.823**	0.002	0.013	0.055	0.06	0.023	0.002	0.006	0.059	1.823	0.509	0.015	0.019	0.02	0.018	0.023
BT45_metabat.26.contigs	**0.001**	**1.468**	0.001	0.007	0.021	0.033	0.046	0.001	0.002	0.021	1.468	0.846	0.011	0.012	0.006	0.007	0.014
co-assembly_metabat.340.contigs	**0.001**	**0.22**	0.001	0.004	0.013	0.22	0.096	0.001	0.073	0.003	0.002	0.003	0.002	0.002	0.023	0.022	0.008
co-assembly_metabat.130.contigs	**0**	**0.314**	0	0	0.002	0.001	0	0	0	0.003	0.314	0.001	0.001	0.001	0.001	0.001	0.001
BT54_metabat.20.contigs	**0.001**	**0.588**	0.021	0.007	0.014	0.02	0.005	0.011	0.008	0.005	0.001	0.001	0.005	0.006	0.475	0.588	0.495
co-assembly_metabat.38.contigs	**0**	**0.173**	0	0.005	0.02	0.01	0.002	0.001	0.173	0.146	0.002	0.001	0.004	0.022	0.048	0.012	0.003
BT31_maxbin.012_sub.contigs	**0.002**	**0.654**	0.654	0.04	0.017	0.007	0.002	0.097	0.038	0.003	0.003	0.003	0.042	0.173	0.033	0.017	0.004
BT45_metabat.3.contigs	**0.009**	**3.983**	0.009	0.037	0.101	1.413	3.983	0.015	0.016	0.016	0.072	2.56	0.079	0.068	0.294	1.533	3.815
co-assembly_metabat.286.contigs	**0**	**1.522**	0.245	0.668	0.472	0.001	0	0.008	0.244	0.001	0.001	0	0.316	1.522	0.038	0.002	0.004
BT43_maxbin.002_sub.contigs	**0.014**	**4.495**	0.014	0.101	0.762	0.59	1.006	0.025	0.081	4.495	0.512	2.449	0.107	0.125	0.215	0.199	0.262
BT44_metabat.19.contigs	**0.006**	**3.744**	0.006	0.027	0.159	0.858	0.076	0.013	0.11	0.347	3.744	0.074	0.034	0.037	0.392	0.3	0.118

co-assembly_metabat.333.contigs	**0**	**0.338**	0	0.001	0.005	0.002	0.001	0.001	0.001	0.003	0.338	0.001	0.001	0.002	0.003	0.002	0.002
BT45_metabat.20_sub.contigs	**0.002**	**0.608**	0.002	0.012	0.035	0.076	0.19	0.003	0.007	0.034	0.06	0.608	0.008	0.008	0.017	0.017	0.026
co-assembly_metabat.324.contigs	**0.001**	**0.358**	0.001	0.004	0.009	0.022	0.358	0.001	0.002	0.002	0.004	0.192	0.003	0.003	0.005	0.012	0.021
BT35_metabat.14.contigs	**0.006**	**0.886**	0.006	0.015	0.084	0.841	0.886	0.008	0.166	0.076	0.123	0.052	0.01	0.01	0.16	0.13	0.08
BT45_metabat.35.contigs	**0.004**	**0.469**	0.004	0.011	0.008	0.006	0.059	0.005	0.015	0.004	0.005	0.469	0.005	0.004	0.008	0.01	0.02
co-assembly_metabat.451.contigs	**0**	**0.224**	0.107	0.016	0.015	0.012	0	0.095	0.224	0	0.001	0	0.06	0.005	0.107	0.1	0.025
co-assembly_metabat.271.contigs	**0.001**	**0.367**	0.001	0.005	0.037	0.044	0.006	0.001	0.01	0.367	0.021	0.019	0.005	0.009	0.021	0.01	0.007
BT35_metabat.23.contigs	**0.004**	**1.991**	0.004	0.013	0.147	0.949	1.991	0.005	0.046	0.146	0.139	1.142	0.025	0.024	0.116	0.247	0.377
co-assembly_metabat.276.contigs	**0**	**0.223**	0	0.002	0.019	0.037	0.001	0	0.016	0.15	0.223	0.025	0.002	0.009	0.024	0.003	0.002
co-assembly_metabat.171.contigs	**0.001**	**0.139**	0.001	0.003	0.01	0.061	0.137	0.001	0.002	0.003	0.014	0.139	0.002	0.002	0.006	0.012	0.02
co-assembly_metabat.370.contigs	**0.001**	**0.389**	0.002	0.003	0.135	0.389	0.033	0.001	0.037	0.056	0.005	0.043	0.003	0.003	0.012	0.019	0.027
BT43_metabat.6.contigs	**0**	**0.59**	0	0.002	0.009	0.022	0.006	0.001	0.027	0.331	0.59	0.074	0.004	0.004	0.003	0.003	0.006
co-assembly_metabat.384.contigs	**0.002**	**0.282**	0.002	0.016	0.006	0.079	0.282	0.003	0.004	0.003	0.004	0.214	0.003	0.002	0.003	0.014	0.203
BT43_metabat.8.contigs	**0.006**	**2.704**	0.006	0.032	1.476	1.371	0.791	0.012	0.155	2.704	1.396	0.922	0.066	0.059	0.736	0.586	0.117
co-assembly_metabat.292.contigs	**0.001**	**0.138**	0.001	0.005	0.015	0.021	0.098	0.001	0.02	0.138	0.028	0.109	0.003	0.004	0.021	0.011	0.009
co-assembly_metabat.524.contigs	**0**	**0.181**	0.002	0.016	0.067	0.002	0	0.022	0.052	0.181	0.011	0	0.021	0.011	0.015	0.004	0.003
co-assembly_metabat.162.contigs	**0.001**	**0.496**	0.001	0.003	0.011	0.012	0.031	0.001	0.002	0.006	0.014	0.496	0.004	0.004	0.008	0.009	0.009
BT43_metabat.32.contigs	**0**	**0.42**	0.001	0.001	0.019	0.117	0	0.001	0.023	0.42	0.024	0	0.005	0.004	0.004	0.003	0.005
BT32_metabat.27.contigs	**0**	**0.831**	0.025	0.831	0.008	0	0	0.004	0.076	0.001	0.001	0	0.014	0.118	0.001	0	0.001
co-assembly_metabat.206.contigs	**0**	**0.195**	0.002	0.023	0.067	0.002	0	0.002	0.084	0.129	0.003	0	0.015	0.195	0.042	0.017	0.003
co-assembly_metabat.169.contigs	**0.002**	**0.368**	0.003	0.009	0.013	0.368	0.192	0.002	0.029	0.003	0.006	0.206	0.005	0.006	0.044	0.139	0.228
co-assembly_metabat.97.contigs	**0.002**	**0.322**	0.005	0.069	0.087	0.006	0.002	0.006	0.253	0.011	0.008	0.003	0.035	0.088	0.322	0.046	0.014
co-assembly_metabat.267.contigs	**0**	**0.414**	0	0.003	0.004	0.005	0.414	0.001	0.002	0.003	0.018	0.086	0.002	0.002	0.003	0.003	0.004
BT43_metabat.26.contigs	**0.006**	**0.867**	0.006	0.03	0.28	0.069	0.031	0.007	0.087	0.867	0.526	0.028	0.029	0.139	0.256	0.113	0.035
co-assembly_metabat.438.contigs	**0.003**	**0.741**	0.007	0.028	0.011	0.29	0.094	0.007	0.175	0.003	0.003	0.012	0.041	0.009	0.299	0.536	0.741
co-assembly_metabat.77.contigs	**0.001**	**0.324**	0.001	0.004	0.011	0.034	0.202	0.002	0.004	0.007	0.009	0.324	0.004	0.004	0.011	0.019	0.059
co-assembly_metabat.204.contigs	**0.001**	**0.589**	0.014	0.059	0.271	0.03	0.002	0.009	0.076	0.007	0.002	0.001	0.019	0.02	0.589	0.111	0.013
BT41_metabat.1.contigs	**0.001**	**4.866**	0.989	0.704	0.612	0.003	0.002	4.866	0.081	0.005	0.011	0.001	0.303	1.953	0.036	0.013	0.018
co-assembly_metabat.302.contigs	**0**	**0.686**	0.321	0.126	0.005	0	0	0.122	0.008	0	0.001	0	0.686	0.064	0.001	0.001	0.002
co-assembly_metabat.45.contigs	**0.001**	**0.339**	0.001	0.007	0.053	0.339	0.193	0.002	0.045	0.036	0.005	0.13	0.004	0.005	0.016	0.017	0.021
BT43_metabat.33.contigs	**0**	**0.767**	0	0.001	0.005	0.005	0	0.001	0.004	0.767	0.006	0.001	0.006	0.004	0.002	0.002	0.005
BT43_metabat.5.contigs	**0.001**	**0.471**	0.003	0.008	0.021	0.021	0.005	0.004	0.022	0.471	0.002	0.001	0.005	0.007	0.016	0.018	0.011
BT34_metabat.14.contigs	**0.003**	**1.225**	0.004	0.012	0.068	0.823	0.244	0.003	0.012	0.025	0.015	1.225	0.016	0.019	0.044	0.041	0.095
BT53_metabat.29.contigs	**0.002**	**0.746**	0.002	0.018	0.091	0.04	0.052	0.003	0.103	0.01	0.006	0.013	0.027	0.053	0.746	0.045	0.025
co-assembly_metabat.148.contigs	**0.004**	**0.645**	0.005	0.04	0.105	0.013	0.01	0.004	0.406	0.011	0.008	0.007	0.014	0.03	0.645	0.194	0.04
co-assembly_metabat.82.contigs	**0**	**0.188**	0	0.001	0.007	0.009	0	0	0.003	0.188	0.002	0	0.001	0.004	0.001	0.003	0.001

BT35_metabat.28_sub.contigs	**0.006**	**4.549**	0.006	0.032	0.103	0.782	2.194	0.008	0.024	0.13	4.549	2.673	0.072	0.07	0.088	0.508	0.344
BT44_metabat.26.contigs	**0**	**1.977**	0	0.001	0.008	0.034	0.003	0	0.001	0.02	1.977	0.004	0.007	0.008	0.002	0.003	0.006
co-assembly_metabat.224.contigs	**0.001**	**0.23**	0.001	0.003	0.008	0.018	0.203	0.001	0.002	0.002	0.004	0.23	0.003	0.003	0.006	0.006	0.012
co-assembly_metabat.472.contigs	**0**	**0.231**	0	0.003	0.007	0.064	0	0	0.028	0.23	0.231	0	0.005	0.009	0.004	0.001	0.003
BT45_metabat.34.contigs	**0.003**	**1.806**	0.003	0.02	0.06	0.923	0.39	0.004	0.014	0.019	0.026	1.806	0.023	0.025	0.047	0.069	0.142
co-assembly_metabat.141.contigs	**0.001**	**0.397**	0.002	0.002	0.011	0.397	0.016	0.001	0.007	0.002	0.005	0.004	0.002	0.002	0.033	0.083	0.049
co-assembly_metabat.542.contigs	**0.004**	**0.474**	0.064	0.047	0.094	0.314	0.004	0.038	0.143	0.004	0.006	0.039	0.046	0.022	0.474	0.425	0.339
co-assembly_metabat.67.contigs	**0**	**0.271**	0	0.002	0.005	0.003	0.001	0	0.001	0.01	0.271	0.024	0.001	0.001	0.001	0.001	0.001
BT35_metabat.20.contigs	**0.01**	**9.201**	0.01	0.067	0.172	1.858	9.201	0.014	0.014	0.022	0.052	3.765	0.113	0.109	0.099	0.498	1.436
BT43_metabat.38.contigs	**0.009**	**1.314**	0.009	0.075	0.279	0.083	0.062	0.019	0.122	1.314	0.17	0.093	0.06	0.09	0.161	0.056	0.049
co-assembly_metabat.420.contigs	**0.001**	**0.34**	0.001	0.004	0.007	0.068	0.34	0.001	0.003	0.004	0.007	0.041	0.003	0.002	0.01	0.039	0.134
co-assembly_metabat.412.contigs	**0.001**	**0.103**	0.001	0.002	0.011	0.065	0.07	0.001	0.003	0.001	0.001	0.103	0.001	0.001	0.009	0.025	0.036
co-assembly_metabat.535.contigs	**0.001**	**0.633**	0.011	0.088	0.021	0.003	0.001	0.004	0.633	0.001	0.001	0.002	0.022	0.006	0.098	0.042	0.011
co-assembly_metabat.198.contigs	**0**	**0.703**	0.01	0.66	0.703	0.002	0	0.01	0.27	0.009	0.002	0	0.07	0.529	0.353	0.009	0.004
co-assembly_metabat.16.contigs	**0**	**0.468**	0	0.003	0.012	0.013	0.002	0	0.003	0.108	0.468	0.018	0.003	0.004	0.004	0.002	0.004
co-assembly_metabat.207.contigs	**0.001**	**0.769**	0.001	0.009	0.04	0.11	0.769	0.002	0.043	0.009	0.008	0.237	0.007	0.009	0.023	0.02	0.02
co-assembly_metabat.377.contigs	**0**	**0.378**	0.378	0.004	0.002	0.001	0	0.222	0.002	0.001	0	0	0.007	0.003	0.001	0.001	0.002
BT45_metabat.16.contigs	**0.002**	**1.006**	0.002	0.009	0.025	0.153	0.347	0.002	0.011	0.012	0.027	1.006	0.011	0.012	0.017	0.022	0.034
co-assembly_metabat.24.contigs	**0.001**	**0.959**	0.001	0.005	0.019	0.05	0.062	0.001	0.003	0.007	0.009	0.959	0.008	0.007	0.009	0.013	0.029
co-assembly_metabat.545.contigs	**0**	**0.636**	0.003	0.003	0.005	0.001	0	0.006	0.636	0.001	0.001	0	0.003	0.016	0.005	0.001	0.001
BT45_metabat.56.contigs	**0.006**	**0.423**	0.029	0.01	0.03	0.145	0.392	0.021	0.027	0.013	0.006	0.423	0.008	0.007	0.052	0.105	0.118
co-assembly_metabat.356.contigs	**0**	**1.088**	1.088	0.031	0.004	0	0	0.198	0.004	0	0.001	0	0.21	0.005	0.001	0.001	0.002
BT44_metabat.14.contigs	**0.002**	**1.073**	0.002	0.017	0.131	0.241	0.007	0.004	0.032	0.507	1.073	0.033	0.017	0.033	0.145	0.034	0.02
co-assembly_metabat.126.contigs	**0**	**0.385**	0	0.003	0.005	0.02	0.108	0.001	0.004	0.037	0.009	0.385	0.002	0.002	0.003	0.004	0.005
co-assembly_metabat.253.contigs	**0.001**	**0.727**	0.001	0.01	0.029	0.557	0.727	0.002	0.022	0.004	0.007	0.159	0.008	0.012	0.029	0.019	0.022
co-assembly_metabat.243.contigs	**0**	**0.212**	0.001	0.001	0.002	0.001	0	0.001	0.003	0.212	0.001	0	0.002	0.002	0.001	0.001	0.001
co-assembly_metabat.256.contigs	**0**	**0.294**	0.001	0.001	0.015	0.012	0.001	0	0.004	0.044	0.294	0.002	0.002	0.002	0.007	0.003	0.002
co-assembly_metabat.448.contigs	**0.006**	**0.575**	0.008	0.024	0.575	0.462	0.027	0.006	0.077	0.327	0.018	0.007	0.017	0.027	0.491	0.087	0.023
BT43_metabat.67.contigs	**0.001**	**0.292**	0.001	0.024	0.121	0.094	0.017	0.001	0.087	0.292	0.047	0.007	0.008	0.02	0.181	0.039	0.043
co-assembly_metabat.463.contigs	**0**	**1.071**	0.002	0.469	0.694	0.001	0	0.005	1.071	0.004	0.005	0	0.067	0.646	0.563	0.005	0.005
co-assembly_metabat.121.contigs	**0.001**	**0.523**	0.001	0.012	0.047	0.189	0.321	0.001	0.045	0.005	0.004	0.169	0.008	0.009	0.349	0.523	0.101
BT35_metabat.12_sub.contigs	**0.004**	**0.918**	0.004	0.013	0.024	0.395	0.813	0.005	0.006	0.017	0.184	0.272	0.012	0.01	0.019	0.156	0.918
co-assembly_metabat.235.contigs	**0.001**	**0.433**	0.001	0.001	0.004	0.006	0.433	0.001	0.002	0.002	0.006	0.095	0.003	0.003	0.004	0.007	0.016
co-assembly_metabat.101.contigs	**0.001**	**0.685**	0.005	0.026	0.538	0.001	0.001	0.021	0.685	0.084	0.031	0.001	0.023	0.079	0.063	0.005	0.003
BT35_metabat.9.contigs	**0.004**	**0.727**	0.008	0.014	0.075	0.496	0.727	0.004	0.024	0.031	0.034	0.329	0.01	0.01	0.076	0.163	0.362
BT42_metabat.12.contigs	**0**	**2.843**	0.011	0.005	0.036	0.012	0	0.088	2.843	0.007	0.006	0.001	0.008	0.312	0.058	0.029	0.006

BT45_metabat.52.contigs	**0.003**	**0.968**	0.003	0.014	0.058	0.368	0.968	0.003	0.025	0.006	0.029	0.337	0.01	0.012	0.094	0.094	0.209
co-assembly_metabat.177.contigs	**0.001**	**0.149**	0.001	0.006	0.004	0.009	0.088	0.002	0.003	0.003	0.002	0.149	0.002	0.002	0.002	0.004	0.026
BT32_metabat.14.contigs	**0.01**	**0.399**	0.018	0.399	0.067	0.148	0.041	0.01	0.232	0.187	0.062	0.02	0.021	0.057	0.112	0.219	0.075
co-assembly_metabat.493.contigs	**0.002**	**1.208**	0.002	0.011	0.036	0.402	1.208	0.002	0.015	0.006	0.011	0.195	0.009	0.011	0.019	0.023	0.024
co-assembly_metabat.546.contigs	**0.001**	**0.196**	0.004	0.052	0.162	0.051	0.003	0.002	0.095	0.196	0.027	0.001	0.017	0.064	0.17	0.041	0.01
co-assembly_metabat.504.contigs	**0**	**0.632**	0.002	0.008	0.026	0	0	0.001	0.632	0.002	0.001	0	0.007	0.538	0.05	0.001	0.002
co-assembly_metabat.473.contigs_cleaned	**0.002**	**0.23**	0.003	0.008	0.016	0.23	0.061	0.003	0.004	0.004	0.004	0.004	0.004	0.002	0.042	0.132	0.153
BT43_maxbin.037_sub.contigs_cleaned	**0.003**	**0.382**	0.013	0.215	0.145	0.044	0.004	0.017	0.246	0.382	0.034	0.003	0.042	0.186	0.055	0.021	0.016
BT31_metabat.5.contigs	**0**	**0.895**	0.895	0.003	0.002	0	0	0.063	0.005	0	0.001	0	0.003	0.002	0.003	0.002	0.004
BT44_metabat.29.contigs	**0.002**	**1.424**	0.002	0.015	0.081	0.008	0.006	0.004	0.177	0.209	1.424	0.01	0.01	0.04	0.02	0.011	0.01
BT41_metabat.2.contigs	**0**	**1.38**	0.384	0.122	0.009	0.001	0	1.38	0.011	0.001	0.003	0	1.194	0.012	0.002	0.002	0.006
co-assembly_metabat.527.contigs	**0.003**	**0.189**	0.003	0.006	0.014	0.006	0.116	0.003	0.004	0.009	0.006	0.189	0.017	0.017	0.006	0.006	0.015
BT53_metabat.9.contigs	**0.003**	**1.085**	0.013	0.036	0.714	0.096	0.037	0.003	0.05	0.071	0.032	0.032	0.01	0.012	1.085	0.255	0.054
co-assembly_metabat.380.contigs	**0.001**	**0.173**	0.001	0.014	0.058	0.173	0.037	0.002	0.12	0.067	0.005	0.006	0.005	0.009	0.129	0.06	0.023
BT43_metabat.19.contigs	**0**	**0.796**	0	0.002	0.011	0.001	0	0.002	0.011	0.796	0.006	0	0.005	0.006	0.001	0.006	0.003
BT43_metabat.59.contigs	**0**	**1.251**	0	0.001	0.004	0.003	0	0.002	0.005	1.251	0.005	0	0.007	0.005	0.001	0.002	0.004
co-assembly_metabat.392.contigs	**0**	**0.376**	0.003	0.086	0.376	0.001	0	0.003	0.011	0.059	0.004	0	0.029	0.315	0.316	0.017	0.002
co-assembly_metabat.179.contigs	**0.004**	**0.421**	0.004	0.022	0.108	0.421	0.053	0.005	0.246	0.226	0.015	0.049	0.013	0.034	0.231	0.117	0.035
BT43_metabat.62.contigs	**0.001**	**0.316**	0.001	0.012	0.096	0.023	0.009	0.001	0.12	0.316	0.088	0.004	0.01	0.044	0.053	0.01	0.006
co-assembly_metabat.36.contigs	**0.001**	**0.147**	0.001	0.002	0.004	0.007	0.056	0.002	0.001	0.003	0.007	0.147	0.002	0.002	0.004	0.008	0.017
co-assembly_metabat.435.contigs	**0**	**1.374**	0	0.002	0.006	0.002	0.001	0.001	0.017	0.039	1.374	0.024	0.005	0.008	0.003	0.002	0.005
co-assembly_metabat.200.contigs	**0.001**	**0.247**	0.001	0.004	0.009	0.027	0.247	0.001	0.006	0.002	0.002	0.04	0.003	0.002	0.014	0.031	0.055
BT31_metabat.12.contigs	**0**	**2.193**	2.193	0.013	0.005	0	0	0.038	0.002	0	0.001	0	0.453	0.047	0.001	0.001	0.003
co-assembly_metabat.416.contigs	**0**	**0.24**	0.005	0.017	0.24	0.165	0.004	0.002	0.104	0.001	0.001	0	0.003	0.004	0.088	0.014	0.003
co-assembly_metabat.70.contigs	**0**	**0.581**	0.481	0.58	0.166	0.001	0	0.544	0.174	0.002	0.003	0	0.581	0.024	0.006	0.005	0.005
BT54_metabat.9.contigs	**0.006**	**1.047**	0.006	0.026	0.108	0.399	0.113	0.014	0.146	0.06	0.04	0.053	0.013	0.012	0.385	1.047	0.237
BT53_metabat.20.contigs	**0.003**	**0.827**	0.003	0.275	0.375	0.035	0.018	0.005	0.231	0.031	0.025	0.01	0.154	0.564	0.827	0.126	0.024
BT45_metabat.42_sub.contigs	**0.002**	**2.324**	0.002	0.008	0.091	0.137	0.06	0.002	0.02	0.136	2.324	0.296	0.015	0.018	0.053	0.057	0.032
co-assembly_metabat.309.contigs	**0.001**	**1.013**	0.001	0.003	0.005	0.017	0.08	0.002	0.011	1.013	0.011	0.027	0.006	0.006	0.002	0.002	0.005
BT32_metabat.24.contigs	**0**	**0.748**	0.005	0.748	0.003	0	0	0.009	0.014	0	0.001	0	0.003	0.008	0	0	0.001
co-assembly_metabat.184.contigs	**0**	**0.247**	0	0.001	0.003	0.002	0.001	0	0.002	0.001	0.247	0.029	0.001	0.001	0.001	0.002	0.002
BT43_metabat.44.contigs	**0.004**	**1.894**	0.015	0.036	0.438	0.179	0.141	0.004	0.163	1.894	0.183	0.077	0.032	0.032	1.138	0.663	0.117
BT43_metabat.9.contigs	**0.004**	**2.213**	0.004	0.034	0.318	0.027	0.007	0.009	0.083	2.213	0.088	0.015	0.05	0.229	0.233	0.033	0.029
co-assembly_metabat.455.contigs	**0**	**0.289**	0.001	0.001	0.022	0.188	0.003	0	0.001	0.077	0.289	0.003	0.003	0.003	0.03	0.007	0.004
BT45_metabat.21.contigs	**0**	**0.251**	0	0.001	0.003	0.011	0.031	0	0.001	0.001	0.013	0.251	0.001	0.001	0.001	0.001	0.003

BT43_metabat.29.contigs	**0**	**0.653**	0	0.005	0.06	0.001	0	0.012	0.193	0.653	0.031	0.001	0.005	0.006	0.009	0.002	0.003
co-assembly_metabat.478.contigs	**0.001**	**0.244**	0.001	0.001	0.008	0.003	0.002	0.001	0.002	0.244	0.006	0.001	0.004	0.004	0.007	0.005	0.004
BT45_metabat.59.contigs	**0.002**	**2.696**	0.003	0.008	0.045	0.045	0.397	0.002	0.006	0.03	0.115	2.696	0.025	0.023	0.023	0.023	0.038
co-assembly_metabat.213.contigs	**0**	**0.538**	0.038	0.109	0.152	0.001	0	0.013	0.347	0.004	0.003	0	0.219	0.538	0.01	0.004	0.003
co-assembly_metabat.279.contigs	**0.001**	**0.319**	0.001	0.002	0.003	0.003	0.002	0.002	0.01	0.319	0.006	0.001	0.002	0.004	0.001	0.001	0.001
BT33_metabat.6.contigs	**0.026**	**1.535**	0.049	0.586	1.535	0.049	0.026	0.038	0.113	0.056	0.035	0.033	0.342	1.31	0.578	0.056	0.028
BT32_metabat.8.contigs	**0**	**0.882**	0.179	0.882	0.007	0.002	0.001	0.039	0.245	0.001	0.002	0	0.073	0.004	0.026	0.065	0.077
BT44_maxbin.011.contigs	**0.002**	**1.088**	0.002	0.007	0.016	0.023	0.01	0.004	0.009	0.024	1.088	0.012	0.007	0.009	0.017	0.014	0.014
co-assembly_metabat.232.contigs	**0**	**0.267**	0.044	0.099	0.11	0.001	0	0.055	0.165	0.004	0.003	0	0.123	0.267	0.041	0.009	0.002

Table S14 - Summary table representing expression activity of the MAGs by mapping transcriptomic reads from each sample to the MAGs with CoverM using "genome" mode and "bwa" alignment with following parameters: min-read-align 0.75 and min-read-id 0.95. Values have not been normalised.

Bin ID	Min RA (%)	Max RA (%)	BT31T	BT33T	BT35T	BT51T	BT53T	BT55T
BT35_metabat.17_sub.contigs	**0.006**	**0.494**	0.010	0.050	0.494	0.006	0.068	0.167
co-assembly_metabat.466.contigs	**0.000**	**0.025**	0.001	0.024	0.000	0.001	0.025	0.000
co-assembly_metabat.178.contigs	**0.001**	**0.322**	0.001	0.006	0.322	0.001	0.008	0.091
co-assembly_metabat.406.contigs	**0.000**	**0.073**	0.000	0.005	0.073	0.000	0.034	0.042
co-assembly_metabat.284.contigs	**0.000**	**0.002**	0.000	0.002	0.001	0.000	0.000	0.000
BT42_metabat.10.contigs	**0.000**	**0.149**	0.002	0.149	0.000	0.006	0.104	0.001
co-assembly_metabat.157.contigs	**0.001**	**0.142**	0.001	0.004	0.108	0.003	0.079	0.142
co-assembly_metabat.507.contigs	**0.001**	**0.022**	0.001	0.002	0.022	0.001	0.007	0.004
co-assembly_metabat.72.contigs	**0.002**	**0.177**	0.015	0.016	0.177	0.002	0.051	0.132
BT44_metabat.33_sub.contigs	**0.001**	**0.041**	0.001	0.040	0.006	0.005	0.041	0.003
BT43_metabat.52.contigs	**0.001**	**0.520**	0.004	0.016	0.520	0.001	0.011	0.009
co-assembly_metabat.362.contigs	**0.001**	**0.113**	0.001	0.051	0.001	0.009	0.113	0.001
co-assembly_metabat.260.contigs_cleaned	**0.000**	**0.018**	0.001	0.001	0.018	0.000	0.003	0.003
co-assembly_metabat.383.contigs	**0.000**	**0.000**	0.000	0.000	0.000	0.000	0.000	0.000
BT43_maxbin.001.contigs	**0.000**	**0.026**	0.000	0.026	0.004	0.002	0.017	0.002
BT53_maxbin.004.contigs	**0.005**	**6.310**	0.025	2.411	0.005	0.047	6.310	0.011
BT44_metabat.37_sub.contigs	**0.002**	**0.023**	0.002	0.019	0.019	0.007	0.023	0.010
BT45_metabat.26.contigs	**0.000**	**0.035**	0.000	0.006	0.035	0.000	0.003	0.002
co-assembly_metabat.340.contigs	**0.001**	**0.124**	0.002	0.011	0.124	0.001	0.034	0.005

co-assembly_metabat.130.contigs	**0.000**	**0.003**	0.000	0.003	0.000	0.000	0.000	0.000
BT54_metabat.20.contigs	**0.000**	**0.443**	0.055	0.009	0.002	0.000	0.443	0.034
co-assembly_metabat.38.contigs	**0.001**	**0.054**	0.001	0.040	0.003	0.010	0.054	0.002
BT31_maxbin.012_sub.contigs	**0.003**	**0.471**	0.471	0.091	0.004	0.093	0.108	0.003
BT45_metabat.3.contigs	**0.028**	**9.881**	0.028	0.092	8.713	0.036	0.249	9.881
co-assembly_metabat.286.contigs	**0.000**	**0.090**	0.065	0.090	0.000	0.060	0.036	0.000
BT43_maxbin.002_sub.contigs	**0.015**	**0.740**	0.015	0.656	0.740	0.149	0.178	0.255
BT44_metabat.19.contigs	**0.005**	**0.873**	0.005	0.593	0.203	0.006	0.873	0.323
co-assembly_metabat.333.contigs	**0.000**	**0.002**	0.001	0.001	0.000	0.000	0.002	0.001
BT45_metabat.20_sub.contigs	**0.002**	**0.102**	0.002	0.012	0.102	0.006	0.015	0.009
co-assembly_metabat.324.contigs	**0.001**	**0.088**	0.001	0.001	0.088	0.002	0.004	0.009
BT35_metabat.14.contigs	**0.002**	**1.231**	0.006	0.099	1.231	0.002	0.271	0.089
BT45_metabat.35.contigs	**0.001**	**0.027**	0.007	0.001	0.027	0.001	0.005	0.002
co-assembly_metabat.451.contigs	**0.000**	**0.039**	0.026	0.022	0.000	0.018	0.039	0.007
co-assembly_metabat.271.contigs	**0.001**	**0.021**	0.001	0.021	0.004	0.005	0.014	0.003
BT35_metabat.23.contigs	**0.003**	**2.099**	0.005	0.076	2.099	0.003	0.059	0.364
co-assembly_metabat.276.contigs	**0.000**	**0.039**	0.000	0.039	0.002	0.003	0.028	0.001
co-assembly_metabat.171.contigs	**0.002**	**0.123**	0.002	0.006	0.123	0.002	0.005	0.020
co-assembly_metabat.370.contigs	**0.001**	**0.077**	0.002	0.077	0.007	0.001	0.009	0.012
BT43_metabat.6.contigs	**0.000**	**0.002**	0.000	0.002	0.001	0.000	0.002	0.001
co-assembly_metabat.384.contigs	**0.003**	**0.104**	0.003	0.007	0.104	0.006	0.003	0.026
BT43_metabat.8.contigs	**0.003**	**0.958**	0.005	0.958	0.936	0.003	0.541	0.087

co-assembly_metabat.292.contigs	**0.002**	**0.117**	0.002	0.024	0.117	0.006	0.021	0.044
co-assembly_metabat.524.contigs	**0.002**	**0.607**	0.002	0.607	0.002	0.092	0.017	0.005
co-assembly_metabat.162.contigs	**0.001**	**0.014**	0.001	0.002	0.014	0.004	0.009	0.005
BT43_metabat.32.contigs	**0.000**	**0.008**	0.001	0.008	0.001	0.000	0.002	0.001
BT32_metabat.27.contigs	**0.000**	**0.197**	0.010	0.036	0.000	0.197	0.000	0.000
co-assembly_metabat.206.contigs	**0.000**	**0.050**	0.002	0.050	0.000	0.026	0.031	0.001
co-assembly_metabat.169.contigs	**0.002**	**0.223**	0.004	0.007	0.104	0.002	0.048	0.223
co-assembly_metabat.97.contigs	**0.003**	**0.292**	0.011	0.117	0.003	0.066	0.292	0.043
co-assembly_metabat.267.contigs	**0.001**	**0.240**	0.001	0.003	0.240	0.001	0.002	0.002
BT43_metabat.26.contigs	**0.008**	**0.168**	0.008	0.108	0.020	0.034	0.168	0.027
co-assembly_metabat.438.contigs	**0.005**	**0.121**	0.010	0.005	0.035	0.012	0.121	0.026
co-assembly_metabat.77.contigs	**0.001**	**0.159**	0.001	0.017	0.159	0.014	0.013	0.112
co-assembly_metabat.204.contigs	**0.004**	**0.284**	0.022	0.076	0.004	0.110	0.284	0.049
BT41_metabat.1.contigs	**0.002**	**4.482**	0.333	4.482	0.005	2.601	0.026	0.002
co-assembly_metabat.302.contigs	**0.000**	**0.214**	0.052	0.003	0.000	0.214	0.001	0.000
co-assembly_metabat.45.contigs	**0.002**	**0.239**	0.002	0.202	0.239	0.005	0.015	0.042
BT43_metabat.33.contigs	**0.000**	**0.001**	0.000	0.001	0.000	0.001	0.000	0.000
BT43_metabat.5.contigs	**0.005**	**0.053**	0.005	0.053	0.015	0.007	0.023	0.020
BT34_metabat.14.contigs	**0.005**	**0.166**	0.005	0.047	0.166	0.006	0.056	0.084
BT53_metabat.29.contigs	**0.003**	**0.622**	0.003	0.094	0.168	0.018	0.622	0.091
co-assembly_metabat.148.contigs	**0.008**	**0.756**	0.008	0.141	0.009	0.020	0.756	0.037
co-assembly_metabat.82.contigs	**0.000**	**0.003**	0.000	0.003	0.000	0.000	0.001	0.000

BT35_metabat.28_sub.contigs	**0.005**	**3.055**	0.010	0.046	3.055	0.005	0.048	0.458
BT44_metabat.26.contigs	**0.000**	**0.001**	0.000	0.000	0.001	0.000	0.000	0.000
co-assembly_metabat.224.contigs	**0.001**	**0.174**	0.001	0.003	0.174	0.002	0.005	0.010
co-assembly_metabat.472.contigs	**0.000**	**0.015**	0.001	0.008	0.000	0.015	0.004	0.000
BT45_metabat.34.contigs	**0.004**	**0.230**	0.007	0.027	0.230	0.004	0.053	0.133
co-assembly_metabat.141.contigs	**0.001**	**0.075**	0.002	0.007	0.020	0.001	0.041	0.075
co-assembly_metabat.542.contigs	**0.010**	**1.243**	0.107	0.310	0.010	0.123	0.446	1.243
co-assembly_metabat.67.contigs	**0.000**	**0.006**	0.000	0.006	0.001	0.000	0.002	0.001
BT35_metabat.20.contigs	**0.020**	**14.323**	0.020	0.141	14.323	0.024	0.065	2.998
BT43_metabat.38.contigs	**0.013**	**0.449**	0.013	0.449	0.103	0.421	0.168	0.144
co-assembly_metabat.420.contigs	**0.002**	**0.420**	0.003	0.009	0.420	0.002	0.015	0.232
co-assembly_metabat.412.contigs	**0.000**	**0.043**	0.001	0.006	0.029	0.000	0.008	0.043
co-assembly_metabat.535.contigs	**0.001**	**0.069**	0.032	0.015	0.001	0.010	0.069	0.006
co-assembly_metabat.198.contigs	**0.002**	**2.617**	0.017	2.617	0.002	0.659	0.464	0.006
co-assembly_metabat.16.contigs	**0.000**	**0.006**	0.001	0.002	0.001	0.000	0.006	0.001
co-assembly_metabat.207.contigs	**0.001**	**0.390**	0.002	0.022	0.390	0.001	0.015	0.009
co-assembly_metabat.377.contigs	**0.000**	**0.560**	0.560	0.021	0.002	0.001	0.001	0.000
BT45_metabat.16.contigs	**0.004**	**0.341**	0.004	0.029	0.341	0.005	0.019	0.081
co-assembly_metabat.24.contigs	**0.001**	**0.040**	0.001	0.005	0.040	0.001	0.007	0.024
co-assembly_metabat.545.contigs	**0.000**	**0.006**	0.002	0.005	0.000	0.002	0.006	0.000
BT45_metabat.56.contigs	**0.001**	**0.135**	0.012	0.009	0.135	0.001	0.036	0.068

co-assembly_metabat.356.contigs	**0.000**	**0.068**	0.029	0.001	0.000	0.068	0.000	0.000
BT44_metabat.14.contigs	**0.003**	**0.135**	0.003	0.135	0.003	0.018	0.129	0.006
co-assembly_metabat.126.contigs	**0.000**	**0.029**	0.001	0.002	0.029	0.000	0.003	0.008
co-assembly_metabat.253.contigs	**0.003**	**0.540**	0.003	0.024	0.540	0.004	0.035	0.021
co-assembly_metabat.243.contigs	**0.000**	**0.004**	0.001	0.004	0.000	0.004	0.001	0.001
co-assembly_metabat.256.contigs	**0.000**	**0.007**	0.001	0.006	0.000	0.000	0.007	0.000
co-assembly_metabat.448.contigs	**0.011**	**0.812**	0.011	0.812	0.027	0.028	0.591	0.014
BT43_metabat.67.contigs	**0.002**	**0.204**	0.002	0.204	0.042	0.010	0.113	0.056
co-assembly_metabat.463.contigs	**0.001**	**0.653**	0.003	0.653	0.001	0.255	0.269	0.001
co-assembly_metabat.121.contigs	**0.001**	**0.232**	0.001	0.023	0.232	0.001	0.162	0.078
BT35_metabat.12_sub.contigs	**0.008**	**1.105**	0.008	0.041	1.023	0.008	0.015	1.105
co-assembly_metabat.235.contigs	**0.001**	**0.487**	0.002	0.003	0.487	0.001	0.006	0.015
co-assembly_metabat.101.contigs	**0.002**	**4.407**	0.009	4.407	0.002	0.309	0.044	0.002
BT35_metabat.9.contigs	**0.005**	**0.227**	0.010	0.034	0.227	0.005	0.051	0.168
BT42_metabat.12.contigs	**0.000**	**0.373**	0.009	0.373	0.000	0.002	0.241	0.001
BT45_metabat.52.contigs	**0.003**	**0.453**	0.005	0.035	0.453	0.003	0.051	0.118
co-assembly_metabat.177.contigs	**0.001**	**0.019**	0.001	0.001	0.019	0.002	0.001	0.001
BT32_metabat.14.contigs	**0.035**	**0.144**	0.053	0.078	0.103	0.035	0.144	0.139
co-assembly_metabat.493.contigs	**0.003**	**1.010**	0.003	0.026	1.010	0.003	0.018	0.029
co-assembly_metabat.546.contigs	**0.011**	**0.201**	0.011	0.201	0.021	0.023	0.151	0.015
co-assembly_metabat.504.contigs	**0.000**	**0.041**	0.001	0.013	0.000	0.002	0.041	0.000

co-assembly_metabat.473.contigs_cleaned	**0.004**	**0.173**	0.004	0.016	0.053	0.004	0.048	0.173
BT43_maxbin.037_sub.contigs_cleaned	**0.005**	**0.335**	0.012	0.335	0.005	0.145	0.066	0.026
BT31_metabat.5.contigs	**0.001**	**3.471**	3.471	0.128	0.005	0.002	0.007	0.001
BT44_metabat.29.contigs	**0.004**	**0.042**	0.004	0.032	0.042	0.008	0.014	0.010
BT41_metabat.2.contigs	**0.000**	**0.123**	0.058	0.004	0.000	0.123	0.001	0.000
co-assembly_metabat.527.contigs	**0.000**	**0.106**	0.001	0.002	0.106	0.000	0.001	0.002
BT53_metabat.9.contigs	**0.002**	**1.442**	0.010	0.818	0.036	0.002	1.442	0.071
co-assembly_metabat.380.contigs	**0.003**	**0.200**	0.003	0.060	0.011	0.004	0.133	0.200
BT43_metabat.19.contigs	**0.000**	**0.035**	0.000	0.035	0.000	0.009	0.001	0.001
BT43_metabat.59.contigs	**0.000**	**0.000**	0.000	0.000	0.000	0.000	0.000	0.000
co-assembly_metabat.392.contigs	**0.000**	**1.026**	0.006	1.026	0.000	0.013	0.072	0.001
co-assembly_metabat.179.contigs	**0.008**	**0.154**	0.008	0.059	0.016	0.008	0.154	0.033
BT43_metabat.62.contigs	**0.001**	**0.156**	0.001	0.156	0.008	0.005	0.069	0.002
co-assembly_metabat.36.contigs	**0.001**	**0.047**	0.002	0.002	0.047	0.001	0.005	0.019
co-assembly_metabat.435.contigs	**0.000**	**0.003**	0.000	0.001	0.000	0.000	0.003	0.000
co-assembly_metabat.200.contigs	**0.001**	**0.319**	0.003	0.004	0.319	0.001	0.015	0.073
BT31_metabat.12.contigs	**0.000**	**0.061**	0.031	0.002	0.000	0.061	0.000	0.000
co-assembly_metabat.416.contigs	**0.005**	**0.775**	0.013	0.775	0.005	0.019	0.128	0.007
co-assembly_metabat.70.contigs	**0.000**	**0.176**	0.074	0.038	0.001	0.176	0.006	0.000
BT54_metabat.9.contigs	**0.003**	**0.521**	0.006	0.096	0.096	0.003	0.521	0.244
BT53_metabat.20.contigs	**0.009**	**1.529**	0.009	0.861	0.028	0.667	1.529	0.075
BT45_metabat.42_sub.contigs	**0.000**	**0.069**	0.002	0.069	0.054	0.000	0.050	0.023

co-assembly_metabat.309.contigs	**0.000**	**0.033**	0.000	0.001	0.033	0.000	0.001	0.000
BT32_metabat.24.contigs	**0.000**	**0.014**	0.002	0.010	0.000	0.014	0.000	0.000
co-assembly_metabat.184.contigs	**0.000**	**0.001**	0.000	0.001	0.000	0.000	0.001	0.000
BT43_metabat.44.contigs	**0.002**	**1.723**	0.009	0.352	0.181	0.002	1.723	0.344
BT43_metabat.9.contigs	**0.004**	**0.430**	0.004	0.430	0.010	0.183	0.164	0.018
co-assembly_metabat.455.contigs	**0.000**	**0.023**	0.000	0.009	0.003	0.000	0.023	0.007
BT45_metabat.21.contigs	**0.000**	**0.011**	0.000	0.001	0.011	0.000	0.001	0.001
BT43_metabat.29.contigs	**0.001**	**0.504**	0.001	0.504	0.001	0.029	0.020	0.003
co-assembly_metabat.478.contigs	**0.001**	**0.006**	0.001	0.003	0.001	0.002	0.006	0.002
BT45_metabat.59.contigs	**0.001**	**0.495**	0.001	0.027	0.495	0.001	0.016	0.031
co-assembly_metabat.213.contigs	**0.000**	**0.353**	0.023	0.121	0.000	0.353	0.015	0.000
co-assembly_metabat.279.contigs	**0.000**	**0.001**	0.000	0.001	0.000	0.000	0.001	0.000
BT33_metabat.6.contigs	**0.011**	**2.559**	0.051	2.559	0.011	2.318	0.538	0.014
BT32_metabat.8.contigs	**0.001**	**0.182**	0.182	0.011	0.001	0.027	0.063	0.099
BT44_maxbin.011.contigs	**0.001**	**0.023**	0.004	0.002	0.003	0.001	0.023	0.006
co-assembly_metabat.232.contigs	**0.001**	**0.091**	0.058	0.055	0.001	0.091	0.043	0.002

Appendix D

Co-authorship Forms

THE UNIVERSITY OF WAIKATO

Co-Authorship Form

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

Thesis Chapter 2: Monteiro, M. R., Marshall, A. J., Hawes, I., Lee, C. K., McDonald, I. R., & Cary, S. C. (2021). Geochemically defined space-for-time transects successfully capture microbial dynamics along lacustrine chronosequences in a polar desert. Frontiers in microbiology, 12.

Nature of contribution by PhD candidate	Data collection and analysis. Writing and editing of the manuscript
Extent of contribution by PhD candidate (%)	90%

CO-AUTHORS

Name	Nature of Contribution
Alexis J. Marshall	Provided input during data analysis, manuscript preparation and editing
Ian Hawes	Conceived and designed the project. Helped in data collection and provided input during manuscript editing
Charles K. Lee	Conceived and designed the project. Provided input during manuscript editing
Ian R. McDonald	Helped in data collection and provided input during manuscript editing
S. Craig Cary	Conceived and designed the project. Helped in overall study direction. Provided input during manuscript preparation and editing

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and

Name	Signature	Date
Alexis Marshall	[signature]	01 11 2022
IAN McDONALD	[signature]	1/11/22
Charles Lee	[signature]	2022-11-15
Craig Cary	[signature]	29/11/2022
Ian Hawes	IAN HAWES	16/01/2023

Co-Authorship Form

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Please indicate the chapter/section/pages of this thesis that are extracted from a co-authored work and give the title and publication details or details of submission of the co-authored work.

Thesis Chapter 3: Monteiro, M. R., Marshall, A. J., Lee, C. K., McDonald, I. R., & Cary, S. C. (under review in Polar Biology). Bringing Antarctica to the lab: A polar desert environmental chamber to study the response of Antarctic microbial communities to climate change

Nature of contribution by PhD candidate	Experimental set-up. Data collection and analysis. Writing and editing of the manuscript
Extent of contribution by PhD candidate (%)	90%

CO-AUTHORS

Name	Nature of Contribution
Alexis J. Marshall	Provided input during data analysis, manuscript preparation and editing
Charles K. Lee	Conceived and designed the polar desert environmental chamber. Provided input during experimental set-up and manuscript editing
Ian R. McDonald	Provided input during experimental set-up and manuscript editing
S. Craig Cary	Conceived and designed the polar desert environmental chamber. Provided input during experimental set-up, manuscript preparation and editing

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and

Name	Signature	Date
S. Craig Cary	[signature]	6/1/2023
Ian McDonald	[signature]	6/1/2023
Charles Lee	[signature]	2023-01-11
Alexis Marshall	[signature]	16/01/2023

July 2015