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Antarctic microbial communities are functionally redundant, adapted and resistant to short term temperature perturbations

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ABSTRACT

Climate change has the potential to induce dramatic shifts in the biodiversity and functionality of soil microorganisms in polar hyperarid ecosystems. In these depauperate soil ecosystems, microbial communities are vital as they represent the dominant input sources of essential nutrients. However, the effects of changing climate on extreme edaphic environments, such as the McMurdo Dry Valleys of Antarctica, remain poorly understood. To better understand these effects, we constructed soil microcosms and simulated temperature shifts over a 40-day period. Soil physicochemical analysis revealed low levels of key nutrients, with mean organic carbon and nitrogen contents of <0.1% and 11.55 ppm, respectively. We also applied 16S rRNA gene amplicon sequencing to determine taxonomic composition and enzyme assays to measure *in situ* activity. Our data showed a prevalence of ubiquitous soil taxa (Actinobacteria, Chloroflexi and *Deinococcus-Thermus*), with a smaller proportion of autotrophic phyla (i.e. Cyanobacteria). None of the major phyla showed relative abundance changes in response to temperature. We found very low extracellular enzyme activity levels across all samples and observed no significant differences among temperature treatments. Functional predictions (using PICRUSt) revealed the putative presence of key genes implicated in the cycling of carbon (*ppc, rbcl*) and nitrogen (*nifH*, *nirK*), in stress response and in DNA repair throughout all treatments. Overall, our results suggest that short-term temperature fluctuations do not alter microbial biodiversity and functionality in Antarctic soils. This study provides the first evidence that microbial communities within this edaphic extreme environment may be functionally redundant, adapted and resistant to short term climatic perturbations.

1. Introduction

Global temperatures are expected to rise by up to 6.4 °C within the next 100 years, largely due to the effects of anthropogenic climate change (IPCC, 2007; Singh et al., 2010; Clements et al., 2014). Rising temperatures lead to the melting of surface and shallow sub-surface ice, resulting in the mobilisation of water and nutrients in polar terrestrial habitats, which are large carbon reservoirs (Singh et al., 2010; Isbell et al., 2015). Microbial communities are the dominant biota within these terrestrial habitats and are also known mediators of key biogeochemical cycles, particularly carbon and nitrogen turnover (Singh et al., 2010; Cowan et al., 2014). It is therefore hypothesised that changes in soil microbial community diversity and function may lead to alterations in essential ecosystem cycles (Singh et al., 2010; Gutknecht et al., 2012). However, it remains unclear how soil microbial communities may respond to temperature increases (Cowan et al., 2014), especially within climatically sensitive regions such as the McMurdo Dry Valleys (MDVs) of Antarctica (Cowan and Ah Tow, 2004; Barrett et al., 2006; Pointing et al., 2009).

The MDV mineral soils represent an ideal ecosystem in which to assess the effects of climatic changes due to their trophic simplicity and microbially driven nature (Cowan and Ah Tow, 2004; Pointing et al., 2009). However, field studies are limited within the MDVs due to the challenging environmental conditions and strict regulations designed to protect the Antarctic region (Cowan and Ah Tow, 2004). Microcosms, which are laboratory based studies,

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allow the creation of artificial environments within which the effects of perturbations may be assessed under controlled conditions (Grenni et al., 2012; Martínez et al., 2014). Although microcosms cannot account for the complete complexity of the natural environment (Grenni et al., 2012), such studies have shown reliable results (Grenni et al., 2012; Blake et al., 2015) which are comparable to studies performed in the field (Treonis et al., 2002; Martínez et al., 2014).

The microbial diversity of MDV soils is surprisingly high (Aislabie et al., 2006; Niederberger et al., 2008; Dreesens et al., 2014; Richter et al., 2014). The microbial communities in these edaphic regions have also been shown to harbour the capacity for complex metabolic functions (Yergeau et al., 2007a; Hopkins et al., 2008; Chan et al., 2013), with multiple genes for key pathways in carbon and nitrogen cycling (Yergeau et al., 2007a; Chan et al., 2013). Soil respiration (Hopkins et al., 2006), extracellular enzyme activities (Hopkins et al., 2008) and acetylene reduction (a valid proxy for nitrogen fixation) (Niederberger et al., 2008) have all been detected in MDV soils. These studies indicate that microbial communities within the MDV region have the capacity to contribute to functional ecosystem processes (Barrett et al., 2006; Cowan et al., 2014).

Microbial communities within Antarctic soils may respond relatively rapidly to environmental changes (Stomeo et al., 2012; Tiao et al., 2012). For instance, the repositioning of a mummified seal carcass led to rapid (within three years) changes in the underlying soil microbial community structure (Tiao et al., 2012). In addition, a number of studies assessing microbial diversity and abiotic factors along Antarctic latitudinal gradients have shown that community structure and functionality may be potentially altered in response to temperature (Rinnan et al., 2009; Newsham et al., 2015), moisture (Stomeo et al., 2012) and soil physiochemical status (Lee et al., 2012; Stomeo et al., 2012). However, how MDV soil microbial communities may respond directly to climatic perturbations, as well as how rapidly, is still unclear (García-Palacios et al., 2015).

Two hypotheses concerning the predicted response of microbial communities to climatic change have been proposed. The community diversity hypothesis (Isbell et al., 2015) suggests functional redundancy among organisms and that losses in diversity will not lead to decreases in function. Alternatively, the keystone species hypothesis (Pold and DeAngelis, 2013) proposes that loss of a few key taxa will lead to lower functionality and thus there is little functional redundancy. In support of this hypothesis, studies have found that microbial abundance and diversity may increase in response to temperature changes, while maintaining functional capacity (Yergeau and Kowalchuk, 2008; Newsham et al., 2015). Similarly, a decline in microbial biomass in response to temperature can be associated with an increase in soil respiration (Laudicina et al., 2015). However, other studies have shown that higher temperatures lead to a decrease in microbial species richness (Jung et al., 2011; Dennis et al., 2013; Philippot et al., 2013). This may, in turn, lead to a reduction in functional gene abundance (Jung et al., 2011) and microbial activity (Hopkins et al., 2006; Philippot et al., 2013). Such conflicting results indicate that the exact effects of climatic changes on microbial diversity and functionality, and subsequent ecosystem processes, remain unresolved (García-Palacios et al., 2015).

Here, we examine the influence of short term temperature fluctuations on Antarctic soil microbial community diversity and potential functionality. Microcosms were constructed using soil samples collected from the MDVs. Three temperature treatments were then applied to the microcosms for a period of forty days, where a baseline sample was taken prior to the start of the experiment and samples were recovered periodically. We used 16S rRNA gene amplicon sequencing to assess microbial diversity changes. The activity of extracellular enzymes potentially involved in microbial nutrient acquisition were combined with PICRUSt and KEGG functional gene and pathway predictions to assess potential microbial functionality.

2. Materials and methods

2.1. Soil sample collection and physicochemical analysis

Approximately 4 kg of mineral soil was collected in the vicinity of Spalding Pond in the Taylor Valley region of the McMurdo Dry Valleys, Antarctica (77.65808°S, 163.09204°E) in January 2015 (Fig. 1). Soil was collected aseptically by retrieving the top 5 cm of soil within a 20 × 20 cm sampling area. Soil was placed in sterile plastic bags and stored at −30 °C. All necessary permits were obtained through Antarctica New Zealand and the New Zealand Ministry of Foreign Affairs and Trade (MFAT) to allow the removal of the soil. The soil was then shipped on dry ice to the Centre for Microbial Ecology and Genomics (CMEG) at the University of Pretoria, where it was stored at −80 °C. Soil physiochemical analyses were performed at the Department of Plant Production and Soil Science of the University of Pretoria on three replicate soil samples prior to the microcosm experiment. Soil particle size was determined using the hydrometer method, as previously described (Bouyoucos, 1962). Percentage organic carbon analysis was performed according to the Walkley and Black method (Walkley and Black, 1934). Soil pH was determined using a glass electrode with a water-to-soil ratio of 2.5:1, according to specifications previously provided (Coleman, 1967). Ion concentrations were determined using potassium chloride (Bremner and Keeney, 1966), ammonium acetate (Chapman, 1965) and P- Bray I (Bray and Kurtz, 1945) extractions. The cation exchange capacity of the soil was determined according to a previously described method (Gillman et al., 1983).

2.2. Microcosm set-up

To determine the effect of increasing and fluctuating temperatures on Antarctic soil microbial communities, a microcosm experiment was designed. Soil samples were randomly assigned to three temperature treatment groups. Temperature simulations were applied over a period of forty days, wherein samples were taken 10 days prior to the start of the experiment and in 5 day intervals thereafter (Figs. S1 and S2). The treatment groups consisted of a control temperature group, at 0 °C for the entire experiment and two temperature treatment groups. One treatment group, called “stable” was at a constant elevated temperature of 15 °C. The other treatment group, called “fluctuating” varied from 0 to 15 °C with 1.5 °C increments per day, remained at 15 °C for 10 days and was then decreased from 15 to 0 °C with 1.5 °C increments per day (Fig. S1). The start of the experiment is indicated as day 0, where the control and fluctuating treatment groups were at 0 °C, whereas the stable treatment group was at 15 °C. Ten days prior to the start of the microcosm experiment, the stable treatment group was increased from 0 to 15 °C with 1.5 °C increments per day (Fig. S1, day −10). Further details of the experimental procedure are present in Supplementary Methods and Materials and are available on the online version of this manuscript.

2.3. Microcosm experiment analysis

2.3.1. Microbial community analysis using illumina-based amplicon sequencing

DNA extractions were performed using a MoBio PowerSoil® DNA Isolation Kit (MoBio, Carlsbad, USA) according to the