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Identity of biocrust species and microbial communities drive the response of soil multifunctionality to simulated global change

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ABSTRACT

Increasing N inputs and changing rainfall regimes will lead to drastic changes in multiple ecosystem functions such as nutrient cycling, organic matter decomposition and gas exchange in dryland ecosystems. As fundamental components of drylands, biological soil crusts (biocrusts) play important roles in the regulation of responses of multiple ecosystem functions to global environmental changes. Biocrusts are home to highly functional microbial communities; however little is known on the role of microbial communities associated with different biocrust species in regulating the response of multiple ecosystem functions to global change. Here, we conducted a microcosm experiment to evaluate the roles of biocrust-forming lichens (*Diploschistes thunbergianus*, *Psora crystallifera* and *Xanthoparmelia reptans*) in mediating the effects of simulated changes in rainfall frequency and nitrogen (N) addition on soil multifunctionality involving nutrient availability, greenhouse gas flux and enzyme activities. The three biocrust species supported different levels of soil bacterial diversity, and specific community composition as revealed by MiSeq sequencing. Biocrust species always promoted multiple functions related to carbon, nitrogen and phosphorus cycling compared to bare ground, with *X. reptans* having the highest effect on multifunctionality. Most importantly, the relative abundance of specific microbial communities associated with different lichen species modulates the response of multifunctionality to impacts of water frequency (negative) and N addition (positive). Our results suggest that biocrust species could regulate global change impacts on soil multifunctionality in drylands, although the strength and direction vary among the biocrust species. These findings highlight the importance of preserving biocrusts as hotspots of microbial genetic resources and ecosystem functioning in drylands.

1. Introduction

Drylands ecosystems are one of the most important biomes for global sustainability (Reynolds et al., 2007; Canfora et al., 2014, 2016). Predicted changes in rainfall regime could negatively influence soil biodiversity, essential ecosystem functions and services such as nutrient cycling and plant production in drylands (Wardle et al., 2004; Solomon, 2007; Maestre et al., 2015a; Delgado-Baquerizo et al., 2016a). In addition to climate change, elevated nitrogen (N) inputs from anthropogenic sources into drylands are simultaneously influencing ecosystems (Delgado-Baquerizo et al., 2016a), and reducing soil microbial diversity or altering community composition (Allison et al., 2008; Ramirez et al., 2010, 2012). Understanding the interactive effects of the global change drivers (e.g. altered rainfall patterns or N inputs) on soil microbial communities and ecosystem processes is essential to develop predictive

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frameworks for protecting ecosystem functioning under changing environments in drylands (Roose et al., 2016).

Biological soil crusts (biocrusts hereafter) are communities of mosses, lichens, cyanobacteria, and heterotrophs that colonize the surfaces of dryland soils (Belnap, 2003; Canfora et al., 2016), that can constitute up to 70% of the biotic cover of drylands (Belnap, 2003; Maestre et al., 2013; Ferrenberg et al., 2015). A growing body of literature had demonstrated that biocrusts (i.e. species and cover) are essential for the stability and productivity of dryland ecosystems, as they drive multiple ecosystem functions such as nutrient cycling and organic matter decomposition (Eldridge and Greene, 1994; Belnap, 2003; Yoshitake et al., 2010; Maestre et al., 2012a). In addition, previous studies had indicated the effect of biocrust species in controlling the total abundance and composition of soil microbial communities (Bates et al., 2012; Maier et al., 2014; Maestre et al., 2015b). Most important to our topic, biocrusts have been shown to play an essential role in controlling the response of ecosystem functioning to climate change (Reed et al., 2012; Maestre et al., 2013). For instance, a recent study highlighted the important role of biocrust-forming mosses in mitigating the negative impacts of global change (increasing aridity) on ecosystem multifunctionality (Delgado-Baquerizo et al., 2016c). In addition, species identity of biocrust-forming lichens modulated the response of soil processes (i.e. N cycling) to global change drivers (Liu et al., 2016). However, much less is known on the role of identity of biocrust species in regulating the response of ecosystem multifunctionality to global change. The response of soil microbial diversity and ecosystem multifunctionality associated with different biocrust species to global change (e. g. N inputs and changing rainfall frequency) remains largely unknown.

Biodiversity is a key factor regulating ecosystem functioning (Tilman et al., 1996, 2001; Jing et al., 2015), and loss of biodiversity is considered a major threat to ecosystem services (Hector et al., 1999; Wagg et al., 2014). However, our understanding of the relationship between microbial diversity and ecosystem functioning is much more limited. An increasing number of studies have provided evidence that microbial communities directly influence ecosystem functions and services in terrestrial ecosystems (Berg and Smalla, 2009; Singh et al., 2010; Bodelier, 2011; Trivedi et al., 2013; Bardgett and van der Putten, 2014; Wagg et al., 2014; Delgado-Baquerizo et al., 2016b). These functions include, but are limited to, decomposition of organic matter, nutrient acquisition and the regulation of greenhouse gas emissions. The different microbial communities living under different species of biocrusts may then greatly influence the response of soil functioning to global environmental change. Thus, given the importance of biocrusts for the sustainability of global drylands (Elbert et al., 2012), understanding the role of the microbial communities inhabiting the biocrusts is of paramount importance to predict the response of multiple ecosystem functions to on-going global changes.

Herein, we hypothesized that: i) identity of biocrust species will regulate the response of soil bacterial community to changes in N addition and rainfall frequency; and ii) microbial diversity and composition associated with different biocrust species will differentially modulate the response of multiple ecosystems functions to global change impacts. To test these hypotheses, we conducted a microcosm experiment to examine the potential direct and indirect (via microbial communities) role of biocrusts species, including *Diploschistes thunbergianus*, *Psora crystallifera* and *Xanthoparmelia reptans*, in mediating responses of soil multifunctionality (i.e. 15 functions involved in nutrient cycling and the regulation of greenhouse gas emission) to simultaneous changes in N amendment and precipitation frequency.

2. Materials and methods

2.1. Experimental design

For the microcosm experiment, we collected 120 soil cores (0–5 cm depth) from a semiarid area of Nyngan (31°34′, 147°12′E), New South Wales, Australia, where open areas between plant patches contained well-developed biocrust communities. The sampled soil cores covered with three lichens studied: *D. thunbergianus*, *P. crystallifera* and *X. reptans*. Each pot exclusively contains either bare ground, *D. thunbergianus*, *P. crystallifera* or *X. reptans*. Basic chemical characteristics of the soils before our incubation experiment are listed in Table S1. The experimental design had been described in detail previously in Liu et al. (2016). In brief, we established a microcosm study with a full factorial experimental design including three factors: identity of biocrusts species (*D. thunbergianus*, *P. crystallifera* and *X. reptans*), N amendment aligned with reported rates for N deposition (0 and 20 kg N ha^{-1} $year^{-1}$) and altered water frequency (i.e. high frequency, 3.61 mm each 3 days; moderate frequency, 7.22 mm each 6 days; and low frequency, 14.44 mm each 12 days). Bare soil was also treated as a procedure control vs. lichen species under the simulated global change conditions. The total amount of watering to these soil cores by the end of the experiment is exactly the same regardless of the altered frequency, which was adjusted to mimic the rainfall level during the spring season of previous year under field conditions. Moreover, N was added at the beginning of the experiment by dissolving NH_4NO_3 in water. The N addition and watering treatments were established to test whether biocrust-forming lichens can potentially drive the response of below-ground bacterial community and ecosystem multifunctionality to the global change drivers. Five replicated cores per combination of treatments were incubated for 72 days in a climate-controlled glass-house. Full details of incubation conditions are provided in the methods description within the Supplementary information. After the incubation, soil samples (0–4 cm depth) from different treatments were collected, carefully removing the above biocrusts. All the soil samples were mixed homogenously and passed through a 2.0 mm sieve, which were subsequently divided into two sub-samples. One sub-sample was stored at −20 °C for microbial DNA extraction, and another sub-sample was stored at 4 °C for the assessment of soil functions.

2.2. Single soil function analysis

In total, we tested for 15 soil variables as key ecosystem functions including (1) available nitrogen (AN), (2) potential nitrification rate (PNR), (3) microbial biomass N (MBN), (4) dissolved organic carbon (DOC), (5) microbial biomass carbon (MBC), (6) CO_2 flux, (7) CH_4 flux, (8) N_2O flux, (9) β-D-glucopyranoside (BG), (10) β-D-cellulosidase (CB), (11) β-xylosidase (XYL), (12) α-glucosidase (AG), (13) L-Leucine-7-amido-4-methylcoumarin hydrochloride (LAP), (14) phosphate (PHOS), and (15) *N*-acetyl-β-glucosaminidase (NAG). These selected variables are related to cycling of nitrogen (N), carbon (C) and phosphate (P), and the regulation of greenhouse gas emissions. Dissolved organic carbon and AN in the soils were extracted with 0.5 M K_2SO_4 in a ratio 1:5 by shaking at 200 rpm for 1 h and filtered using 0.45-μm Millipore filter paper (Liu et al., 2016). In parallel, the carbon in microbial biomass (MBC) and the N in microbial biomass (MBN) were evaluated using the fumigation-extraction method (Brookes et al., 1985; Vance et al., 1987). The selected enzyme activities including BG, CB, XYL, AG, LAP, PHOS and NAG were measured using 4-methyl umbelliferyl (MUB) substrate yielding the highly fluorescent cleavage products MUB upon hydrolysis (Wallenstein and Weintraub, 2008).