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Species identity of biocrust-forming lichens drives the response of soil nitrogen cycle to altered precipitation frequency and nitrogen amendment

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ABSTRACT

Biological soil crusts (biocrusts) are fundamental components of drylands worldwide, and are of great importance for the regulation of ecosystem functioning. However, little is known on the role of species identify of biocrust-forming lichens in mediating the response of nitrogen (N) cycling to concurring global environmental change. Here, we conducted a microcosm study to evaluate how the species identity of biocrust-forming lichens (*Diploschistes thunbergianus*, *Psora crystallifera* and *Xanthoparmelia reptans*) regulate key processes of N cycling in response to simulated changes in rainfall frequency and N addition. We explicitly considered both direct and indirect effects (i.e. driven via microbial diversity and abundance) of global changes on N availability and losses using structural equation models. Our results showed that species of biocrust-forming lichens differentially mediated effects of N amendment and altered rainfall frequencies on belowground nitrate availability and N_2O flux rate. For instance, soils under *P. crystallifera* species showed the highest increase in nitrate content in response to N amendment under low rainfall frequency. Moreover, soils under *D. thunbergianus* showed the highest N_2O flux under high rainfall frequency without N addition. Interestingly, soils under *X. reptans* showed lowest and highest resistance in nitrate availability and N_2O flux, respectively, in response to N addition regardless of different rainfall frequencies. Strikingly, we only found an indirect impact of either rainfall frequency or N amendment on the nitrate availability (but not N_2O flux) driven via the ammonia-oxidizing community under *X. reptans*. Our results provide evidence that the species identity of biocrust-forming lichens modulates the response of N cycling to global change drivers. These findings have implications for predicting the potential consequence of altered rainfall patterns and environmental N inputs in dryland ecosystems.

1. Introduction

Dryland ecosystems cover 41% of earth's land surface and support over 38% of the total global population (Reynolds et al., 2007; Maestre et al., 2012). These ecosystems are highly vulnerable to ongoing global environmental changes (Schlesinger et al., 1996; Reynolds et al., 2007; Maestre et al., 2012; Dai, 2013; Delgado-Baquerizo et al., 2013a). Climate change models predict major changes in rainfall amounts and patterns in drylands worldwide during the second half of this century (Solomon, 2007). In parallel to climate change, environmental nitrogen (N) inputs resulting from anthropogenic activities is changing the N cycle in terrestrial ecosystems (Vitousek et al., 1997; Cui et al., 2013), affecting ecosystem processes (Phoenix et al., 2012; Concilio and Loik, 2013). Despite global change drivers are known to interact in their impacts

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on ecosystem services, we have limited knowledge on how the interaction between important factors such as decreasing rainfall frequency and increasing N inputs will affect ecosystem functioning in drylands (e. g. N cycle) and influence microbial communities; which carry out vital ecosystem functions (Fay et al., 2008; Delgado-Baquerizo et al., 2014). In drylands, water and N are the most important factors limiting resources for plant and microbial activity (Hooper and Johnson, 1999; Austin, 2011). Thus, understanding the underlying mechanisms that control effects of water (i.e. precipitation frequency) and N (N amendment) on nutrient availability is particularly important for managing soil fertility and ecosystem productivity in dryland ecosystems (Robertson and Groffman, 2007; LeBauer and Treseder, 2008).

Biological soil crusts (biocrusts hereafter) are photosynthetic, diazotrophic communities of bacteria, fungi, algae, lichens and moss that colonize the surfaces of dryland soils and are prominent surface features in all natural drylands (Belnap, 2003). Biocrusts are important to the stability and productivity of dryland ecosystems where plants are typically sparse (Eldridge and Greene, 1994; Belnap et al., 2008; Lindo and Gonzalez, 2010; Zelikova et al., 2012). Previous studies have demonstrated that biocrusts play crucial roles in mediating key processes of N turnover, such as N fixation, nitrification and denitrification (Belnap, 2003; Johnson et al., 2007; Strauss et al., 2012; Abed et al., 2013; Delgado-Baquerizo et al., 2013c; Kidron et al., 2015). Much less, however, is known about the importance of biocrusts on the diversity and abundance of particular microbial communities such as those related to N processes. Aboveground components of biocrusts have been reported to influence the structure of associated soil bacterial communities (Maestre et al., 2013; Maier et al., 2014), as well as functional groups related to N transformation such as ammonia-oxidizing prokaryotes (Marusenko et al., 2013; Delgado-Baquerizo et al., 2014, 2015). The availability of N for plants and microbes is predominantly mediated by particular microbial communities that carry out important processes such as nitrification and denitrification (Robertson and Groffman, 2007). These processes ultimately control N inputs and losses in terrestrial ecosystems. Thus, complex interactions between biocrusts and microbial communities may synchronously mediate effects of climate change (i.e. altered rainfall patterns) and N inputs on the N cycling in drylands (Delgado-Baquerizo et al., 2014).

Despite the well-known influence of biocrusts on the regulation of soil nutrient cycles and microbial communities, little is known about how identities of biocrust-forming species (e.g. lichen species), and their associating microbial communities, modulate the impact of global change drivers on nutrient cycling. A recent study suggested that, similar to vascular plants, biocrust-forming lichens have species-specific effects on soil nutrient cycling and microbial abundance (Delgado-Baquerizo et al., 2015). However, the role of different biocrust-forming species in controlling the response of nutrient cycling (here N transformation processes) to global environmental change remains unresolved. Improving our understanding on the role of different species of biocrust-forming lichens in controlling multiple global change impacts on the N cycle is crucial for accurately forecasting their impacts on dryland ecosystems, the largest biome on Earth. Yet no previous study has evaluated how individual species of biocrust-forming lichens modulate the responses of key N cycling processes to interactive global environmental disturbances such as N inputs and altered rainfall frequencies, which are threatening the proper functioning of drylands worldwide (Reynolds et al., 2007; Solomon, 2007; Phoenix et al., 2012; Concilio et al., 2013).

Herein, we conducted a microcosm study to evaluate the potential role of biocrust-forming lichen species (*Diploschistes thunbergianus*, *Psora crystallifera* and *Xanthoparmelia reptans*) in controlling responses of soil N cycling (i.e. nitrate availability and N_2O flux) to simultaneous changes in rainfall frequency and N additions. We explicitly considered both direct and indirect effects mediated via the diversity and abundance of microbial communities related to N availability and losses using structural equation modeling. We hypothesized that: i) the species identity of biocrust-forming lichens will drive the response of N cycle processes (i.e. nitrification and denitrification) to disturbances from added N and altered rainfall frequencies; ii) different species of biocrust-forming lichens will differentially modulate the resistance of the N cycle to N addition alongside different watering frequencies; and iii) changes in microbial diversity linked to different lichen species will influence the response of N availability to the interactive impacts from the disturbance factors.

2. Materials and methods

2.1. Experimental design

Samples for the microcosm study were collected from Nyngan (31°34′, 147°12′E), New South Wales, Australia. The climate in this region is semiarid, with a mean annual rainfall and temperature of 431 mm and 18.7 °C, respectively (1920–2014). Open areas between plant-patches contained well-developed biocrust communities dominated by the lichens studied: *D. thunbergianus*, *P. crystallifera* and *X. reptans*. Sampling was carried out in May 2014 within a 50 m × 50 m area under each of the most abundant biocrust-forming lichens. All lichens randomly distributed within the same flat ground (Fig. S1). We randomly collected 30 intact soil cores (5 cm diameter and 5 cm height PVC tubes), as well as their respective lichen thalli, for each of the species studied (exclusively covered by *D. thunbergianus*, *P. crystallifera* and *X. reptans* in each case) and another 30 cores of bare ground areas. A total of 120 soil cores were collected (30 for each of the three biocrusts studied and bare ground areas; Fig. S1). All these soil cores were collected from open areas between plants avoiding areas under plant canopies. After sampling, soil cores were transported to the laboratory and air-dried at room temperature for three weeks before starting the microcosm experiment. Previous studies have found that air drying dose not appreciably alter variables such as C and N we studied (Zornoza et al., 2006; Delgado-Baquerizo et al., 2014). The soil is classified as alfisol with a content of 54% sand, 13% silt and 32% clay. Some basic chemical characteristics of the soils (0–4 cm depth, removing the above biocrusts) were obtained before our incubation experiment and are listed in Table 1.

We established a full factorial microcosm experimental design with three factors: biocrust-forming species (three lichen species and bare ground areas), N amendment (0 and 20 kg N ha^{-1} $year^{-1}$) and changes in watering 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; Fig. S2). Five replicated cores per combination of treatments, (120 pots in total) were incubated for 72 days. It is important to note that the amount of water added to the different pots at the end of the experiment is exactly the same; with the only change being watering frequency. The amount of water added was adjusted to mimic the exact amount of water (via rainfall) these soils received during the spring season of the previous year under field conditions. N amendment was conducted at the beginning of the experiment by adding NH_4NO_3 with the first watering (0.78 mg per soil core, an amount that is comparable to many previous studies, Ramirez et al., 2010; Ochoa-Hueso et al., 2013). These N additions and watering treatments were selected to evaluate the potential role of species identity of biocrust-forming lichens in driving the response of the N cycle to future global change impacts. Thus, our treatments are within the limits