



## Responses of soil microbial communities to nutrient limitation in the desert-grassland ecological transition zone

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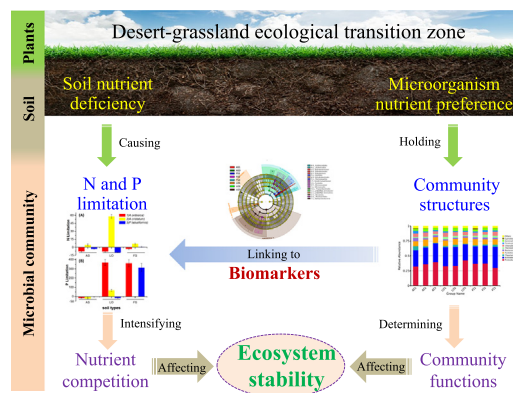
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### HIGHLIGHTS

- Soil microbial metabolisms were strongly limited by N and P in arid regions.
- Key biomarkers shaped microbial metabolic properties and community structures.
- Bacteria and fungus preference for nutrients alleviated the nutrient limitations.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Soil microorganisms are crucial to indicate ecosystem functions of terrestrial ecosystems. However, the responses of microbial communities to soil nutrient limitation in desert-grassland are still poorly understood. Hence, we investigated soil microbial community structures and metabolic characteristics in a desert-grassland ecological transition zone from the northern Loess Plateau, China, and explored the association of microbial communities with nutrient limitation via high-throughput sequencing. Threshold elemental ratios (TER) indicated that the microbial communities were strongly limited by nitrogen (N) under *A. ordosica* and *P. tabuliformis* communities. The phosphorus (P) limitation of microbial communities was observed in the aeolian sandy soil. The results imply that soil microbial communities had strong nutrient competition for N and P with aboveground vegetation in arid and oligotrophic ecosystems. The LEfSe and linear regression analysis revealed that the microbial taxa of *Micrococcales*, *Micrococcaceae* and *Herpotrichiellaceae* were significantly correlated with microbial N limitation. The *Thermoleophilia* taxa were significantly correlated with microbial P limitation. These biomarkers related to microbial nutrient limitation could be considered as the key microbial taxa to shape microbial communities and functions. Furthermore, N form had different effects on microbial communities, which  $\text{NH}_4^+$ -N strongly affected bacterial communities, whereas  $\text{NO}_3^-$ -N had a significant influence on fungal communities. The different responses indicate that soil microorganisms had corresponding nutrient preferences for bacterial and fungal

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communities, which might alleviate the nutrient limitations and environmental stress. This study provided important insights on microbial community structures linking to community functions and on the mechanisms governing microbial N and P limitation in arid land ecosystems.

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## 1. Introduction

Arid land ecosystems are widely considered to be vulnerable and unrecoverable under global climate change. Unlike agroecosystem with a large amount of fertilizers input (Carbonetto et al., 2014), arid natural ecosystems are characterized as continuous accumulation of organic matter and incessant consumption of soil nutrients especially for nitrogen and phosphorus (Craine et al., 2010; Cui et al., 2018). Low nutrient condition in arid ecosystem could result in strong competition of nutrient between microbes and plants (Inselsbacher et al., 2010; Ouyang et al., 2016), which potentially alter underground ecological functions and accelerate vegetation degradation in arid and oligotrophic ecosystems (Craine et al., 2010; Huang et al., 2016). Therefore, to understand microbial metabolism in arid land ecosystems is crucial to illuminate nutrient limitation of microbial communities as well as competition with vegetation.

Soil microbial community structures are powerfully affected by soil properties and environmental factors (Zhou et al., 2002). Such as, land use types (Tian et al., 2013; Zhao et al., 2015), soil fertility (Carbonetto et al., 2014; Zabaloy et al., 2016), and vegetation succession (Nacke et al., 2014; Zhang et al., 2016). Also, in its turn, microbial community structures have great effects on functions and metabolic characteristics (Boyle et al., 2008). Previous studies found that soil microbial communities in ultra-oligotrophic desert ecosystem were co-limited by C and either by N or P (Tapia-Torres et al., 2015). Waring et al. (2014) reported that soil microbial communities were limited by P in tropical soils due to microbial nutrient acquisition was regulated by climatic factors (such as mean annual temperature and precipitation). Our recent research also indicated that the microbial nutrient metabolisms in rhizosphere were co-limited by N and P in the arid area of the northern Loess Plateau (Cui et al., 2018). However, the linkage between microbial community structures and nutrient metabolism is still not well understood.

Normally, soil nutrient availability limits microbial metabolism as well as primary productivity in arid ecosystems (Bünemann et al., 2012; Xu et al., 2015). The nutrients utilized by soil microorganisms are decomposed from soil organic compounds and soil parent material elements (Sinsabaugh et al., 2009, 2015). In arid regions, soil available nutrients are easily fixed by soil particles and ions (Waring et al., 2014; Cui et al., 2018). For example, soil phosphorus can be easily bound with calcium and magnesium as insoluble substance (Cross and Schlesinger, 2001). Thus the decomposition of organic compounds via the extracellular enzyme of heterotrophic microorganisms is the key process of nutrient supply (Waring et al., 2014). Previous studies suggested that soil microbial communities had significantly effect on soil fertility and vegetation (Roszak and Colwell, 1987). Moreover, the processes of microbial nutrient metabolism can simultaneously supply energy and nutrients to aboveground plants (Kowalchuk et al., 2002; Lagerlöf et al., 2014). Thus, to understand the relationships between microbial community structures and nutrient metabolism could provide fundamental insight into these feedback patterns of microbial community and ecosystem function.

Soil microorganisms acclimate to environmental stress by reassigning key resources to nutrient acquisition mechanisms rather than their growth (Schimel et al., 2007; Duan et al., 2018). It has been reported that the ratio of C:N:P in microbial biomass is relatively constrained cross ecosystems compared to it in soil, thus the variations of nutrient ratio could indicate the shifts of nutrient allocation under altering demand (Cleveland and Liptzin, 2007). Ecoenzymatic activities involved in an intersection of ecological stoichiometry theory (EST)

with the metabolic theory of ecology (MTE) can help us to understand the energy and nutrient controls on microbial metabolism (Sinsabaugh et al., 2009, 2012). Meanwhile, Threshold Elemental Ratio (TER) can be used to define the shifts of microbial growth between nutrient limitation (represented by N or P, at high C:N or C:P ratios) and energy limitation (represented by C, lower C:N or C:P ratios) (Sterner and Elser, 2002). Hence, the application of those models and methods can assist to reveal microbial metabolic limitation in the ecological fragile regions.

The Loess Plateau is one of the most eroded regions in China and one of the most vulnerable ecosystems in the world (Li et al., 2011). The northern area of Loess Plateau is desert-grassland transition zone (Wen et al., 2007), which is a typical fragile ecosystem (Noymeir, 2003; Pointing and Belnap, 2012). Microbial nutrient limitation affects community metabolism function and soil nutrient cycling, and thus influences the sustainable development of aboveground and underground in ecosystems. Therefore, it is very important to understand the feedbacks of microbial functions to community structures with the mechanisms governing microbial nutrient limitation in the desert-grassland transition zone.

In this study, we hypothesized that: (1) soil microbial nutrient metabolism in desert-grassland transition zone is strongly suffered from nutrient limitation due to soil nutrients (N and P) deficiency and vegetation competition, (2) the key microbial taxa control the microbial nutrient limitation in desert-grassland transition zone. In addition, the effect of environmental factors on microbial community structures in ecological critical zone was also investigated.

## 2. Materials and methods

### 2.1. Study site and sampling

This research was carried out in natural grassland and artificial shrubland ecosystems. The sites were located in Jungar Banner of the northern Loess Plateau (latitude 40°10' to 39°35' N and longitude 110°35' to 111°23' E), China (Fig. S1). The mean annual temperature is 6.7 °C, with a mean minimum temperature in January of −7.6 °C and a mean maximum temperature in August of 36.5 °C. It is arid and semi-arid climate zones and the mean annual precipitation is 390 mm, with over 60% precipitation from July to September. The soil types in this area are Aeolian sandy soil in the northern side, Loess in the eastern side, and Feldspathic sandstone weathered soil in the western side (Calcic Cambisol, FAO classification). The dominant plant species in this area are natural *Artemisia ordosica*, natural *Agropyron cristatum*, and artificial *Pinu tabuliformis*.

Nine field experiment sites were established in the three soil types with three vegetation communities in August 2016 (Fig. S1). Under each soil type, there were three vegetation communities including the *Artemisia ordosica*, *Agropyron cristatum*, and *Pinu tabuliformis* plant communities. The descriptions of sampling sites were shown in Table 1. Each field experiment site was divided into 3 blocks. Ten quadrats (1 m × 1 m) with the same vegetation community were randomly selected as “W” pattern in each block. Soil cores from the topsoil (0–20 cm) were collected in each quadrat, and then mixed to one composite sample. Each composite sample was divided into three parts for future analysis. The first two parts were placed on ice box and transported to the laboratory within 2 days. The first part was immediately stored at −80 °C for soil genomic DNA extraction. The second part was passed through a 2.0 mm sieve and stored at 4 °C for measurement

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