



## Precipitation modifies the effects of warming and nitrogen addition on soil microbial communities in northern Chinese grasslands



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### ABSTRACT

Terrestrial ecosystems experience simultaneous shifts in multiple drivers of global change, which can interactively affect various resources. The concept that different resources co-limit plant productivity has been well studied. However, co-limitation of soil microbial communities by multiple resources has not been as thoroughly investigated. Specifically, it is not clearly understood how microbial communities respond to shifts in multiple interacting resources such as water, temperature, and nitrogen (N), in the context of global change. To test the effects of these various resources on soil microorganisms, we established a field experiment with temperature and N manipulation in three grasslands of northern China, where there is a decrease in precipitation from east to west across the region. We found that microbial responses to temperature depended upon seasonal water regimes in these temperate steppes. When there was sufficient water present, warming had positive effects on soil microorganisms, suggesting an interaction between water and increases in temperature enhanced local microbial communities. When drought or alternating wet–dry stress occurred, warming had detrimental effects on soil microbial communities. Our results also provide clear evidence for serial co-limitation of microorganisms by water and N at the functional group and community levels, where water is a primary limiting factor and N addition positively affects soil microorganisms only when water is sufficient. We predict that future microbial responses to changes in temperature and N availability could be seasonal or exist only in non-drought years, and will strongly rely on future precipitation regimes.

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### 1. Introduction

Soil microorganisms require multiple essential resources (e.g., water, carbon (C), nitrogen (N), and phosphorus (P)) to produce energy and synthesize cellular macromolecules, and they depend on environmental factors such as temperature, soil moisture content, pH, and salinity (Atlas and Bartha, 1998). It is crucial to better understand how these resources and environmental constraints

influence soil microbial communities in the context of global change. This is attributable to the fact that global change drivers simultaneously and interactively alter multiple resources (IPCC, 2007; Castro et al., 2010; Rousk et al., 2011) and potentially modify the microbial mediation of ecosystem C and nutrient cycling. Thus, the influence of resources and environmental constraints on microbial communities may have far-reaching effects on ecosystem feedback in relation to global change (de Vries et al., 2006, 2007; Allison et al., 2010; Feng et al., 2010; Dijkstra et al., 2011; Zhang et al., 2011).

Optimal foraging theory predicts that organisms should allocate energy in such a way that they are equally limited by different resources, in order to maximize net resource uptake per unit time

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(Bloom et al., 1985; Chapin et al., 1987). There have been various theories about how the simultaneous limitation of multiple resources or co-limitation occurs, including independent co-limitation at the level of individual organisms (Saito et al., 2008), populations, or communities (Harpole et al., 2011). These theories serve as a framework in which to investigate co-limitation by multiple resources, which is defined as an instance when organisms are successfully able to utilize one resource depending upon sufficient supply of another resource (Gleeson and Tilman, 1992; Saito et al., 2008; Harpole et al., 2011). The definition of co-limitation has developed from single resource limitation, as stated in Liebig's law of the minimum (Liebig, 1855). At the community level, Harpole et al. (2011) classified categories as independent, simultaneous, or serial co-limitation. The community-level co-limitation of microorganisms may simply reflect biochemical-level co-limitation only when all of the species in a community are co-limited by the same resources. However, community-level co-limitation by multiple resources is usually quite complicated to detect or interpret, because of species-specific physiological needs or adaptations (Schimel et al., 2007), and it can be especially difficult considering shifts in multiple nutrients and environmental constraints due to global change.

Water occupies 70–90% of the cell mass of microorganisms (Atlas and Bartha, 1998) and often co-limits soil microbial communities along with other factors. A body of evidence has demonstrated that warming may interact with water fluctuation to affect soil microbial communities in arid and semi-arid ecosystems (Allison and Treseder, 2008; Liu et al., 2009; Nielsen and Ball, 2015). Warming can reduce soil microbial biomass and activities in the cell by inducing water-stress on microorganisms (Zhang et al., 2005; Rinnan et al., 2007, 2009; Liu et al., 2009). Alternatively, warming may suppress microbial growth indirectly by reducing plant growth and consequently providing less nutrient and energy input into soils (Allison and Treseder, 2008; Hoepfner and Dukes, 2012). In contrast, improved water availability may negate the negative effect of warming; for instance, there is a counter-intuitive increase in soil moisture under warming conditions, which is driven indirectly by plant senescence (Zavaleta et al., 2003). As such, the dependence of warming effects upon water fluctuation can be predicted, especially in arid or semi-arid ecosystems.

Similarly, N effects on soil microbial communities may strongly depend upon water regimes (Herman et al., 1993; Grizzle et al., 2010; Bi et al., 2011). A previous study showed that the addition of water and N had a synergistic effect on the population of N<sub>2</sub>-fixing bacteria (Herman et al., 1993). High amounts of water availability can enhance the responses of soil microbial communities to N deposition as well (Grizzle et al., 2010). These findings are not surprising because water physically influences microbially mediated N processes (Schimel et al., 1996). Moreover, N addition can exert a pronounced influence on soil microbial activities, but only under high water availability (Bi et al., 2011), suggesting a serial co-limitation of water and N. Additionally, microbial communities from different climate regimes, and therefore diverse evolutionary histories of adaptation, may respond differently to changes in either water or temperature fluctuations (Schimel et al., 2007; Balser and Wixon, 2009). We predicted that the serial community-level co-limitation of water and N generally exists in temperate grasslands, given that water is a predominantly limiting factor in temperate ecosystems (LeBauer and Treseder, 2008; Liu et al., 2009) and is usually linked to N availability or cycling rates (Schimel et al., 1996).

To test whether and how soil microbial communities are co-limited by multiple resources, which dramatically and simultaneously shift in the context of global change, we established an experiment in which we were able to manipulate warming and N

addition continually since April 2006 in three temperate grasslands of northern China. The three temperate grasslands are along a decreasing natural precipitation gradient and include a meadow (440 mm annual rainfall), a semi-arid steppe (380 mm annual rainfall), and a desert steppe (313 mm annual rainfall). To further compare global change in natural weather regimes, we also carried out measurements during two years that had contrasting levels of precipitation. This allowed us to examine how both local climate regimes and natural fluctuations in weather from year to year alter microbial responses to temperature and N addition. We hypothesized that these global change drivers would alter multiple resources, among which (1) water and temperature could interactively influence soil microorganisms, (2) water and N could serially co-limit soil microorganisms at the community level, and (3) differences could exist in both microbial responses and in interactions between treatments among the three temperate steppes. We theorized that this would be due to water deficiency in the semi-arid and the desert steppes and the local adaptation of microbial communities to the two ecosystems regularly affected by droughts.

## 2. Materials and methods

### 2.1. Field sites

We conducted field experiments in three temperate grasslands of northern China. Concurrent changes in temperature, precipitation, and N deposition were recorded in these temperate zones of northern China (IPCC, 2007; Liu et al., 2007, 2010; He et al., 2007; Zhang et al., 2008b). Three grasslands, including a meadow steppe, a semi-arid steppe, and a desert steppe, were included in this experiment. The meadow steppe is located in Changling County in the southwestern region of the Songnen Plain of Northeast China, and stands at the eastern edge of the Eurasian steppe (Fig. 1 and Table 1). The semi-arid and desert steppes are situated in Duolun County and the Siziwang Banner of Inner Mongolia, respectively (Fig. 1 and Table 1). All three steppes are in a continental temperate climate. There is a gradual decrease in the mean annual precipitation from the meadow to the semi-arid steppe, then finally to the desert steppe (Fig. 1 and Table 1). The soils in the meadow steppe, semi-arid steppe and desert steppe are characterized as Chernozem with high sodic and saline content, Haplic Calcisols and Kastanozem, respectively, according to the Food and Agriculture Organization (FAO) classification (Table 1). In comparison with the meadow and the desert steppe, the soil of the semi-arid steppe has higher concentrations of organic C and N, but a lower pH (Table 1). The dominant plant species in the meadow steppe are *Leymus chinensis*, *Puccinellia tenuiflora*, *Calamagrostis epigejos*, *Chloris virgata*, and *Suaeda glauca*. The vegetation of the semi-arid steppe is dominated by *Stipa krylovii*, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, and *Agropyron cristatum*, while that of the desert steppe is dominated by *Stipa breviflora*, *A. frigida* and *Cleistogenes mutica*.

### 2.2. Experimental design

The experiment was established in April 2006 and lasted for 4 years. Three sites (a meadow, a semi-arid and a desert steppe), were used to set up plots in which the temperature or N concentrations could be manipulated. In the semi-arid steppe, we used a randomized block design with 6 treatments including: control (C), continuous warming per day (W, 24 h), N addition (N), warming plus N addition (WN), daytime warming (6:00 a.m.–6:00 p.m., 12 h) and nighttime warming (6:00 p.m.–6:00 a.m., 12 h) (Xia et al., 2009). All treatments were replicated 6 times. Thirty-six 3 × 4 m

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