



Long-term warming rather than grazing significantly changed total and active soil procaryotic community structures

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ABSTRACT

There is a paucity of knowledge in understanding the effects of warming and grazing on soil microbes and their active counterparts, especially on the Tibetan Plateau which is extremely sensitive to global warming and human activities. A six-year field experiment was conducted to investigate the effects of asymmetric warming and moderate grazing on total and active soil microbes in a Tibetan *Kobresia* alpine meadow. Soil bacterial abundance and 16S rDNA transcriptional activity were determined using real-time PCR. Total and active soil procaryotic community structures were analyzed through MiSeq sequencing based on 16S rDNA and rRNA, respectively. The results showed that the soil procaryotic community was more sensitive to the warming than the grazing. The warming significantly decreased soil microbial respiration rates, 16S rDNA transcription activity, and dispersion of total procaryotic community structures, but significantly increased the α diversity of active procaryotes. Warming also significantly increased the relative abundance of oligotrophic microbes, whereas decreasing the copiotrophic lineage proportions. The functional profiles predicted from the total procaryotic community structures remained unaffected by warming. However, the rRNA-based predictions suggested that DNA replication, gene expression, signal transduction, and protein degradation were significantly suppressed under the warming. The grazing only significantly decreased the 16S rDNA transcription and total procaryotic richness. Overall, these findings suggest that warming can shift soil procaryotic community to a more oligotrophic and less active status, highlighting the importance of investigating active microbes to improve our understanding of ecosystem feedbacks to climate change and human activities.

1. Introduction

The unequivocal global warming profoundly alters terrestrial biodiversity and ecosystem functioning, which, in turn, can influence the ongoing global climate changes (IPCC, 2013). Accordingly, soil microbes have been intensively examined in temperature manipulation investigations by virtue of their vital roles in determining ecosystem feedbacks (Melillo et al., 2017; Oliverio et al., 2017; Romero-Olivares et al., 2017). Furthermore, the interactive effects between warming and human activities (e.g., grazing) on soil microbes have also been observed in a number of studies (Li et al., 2016; Zhang et al., 2016b). However, most of these studies only focused on the responses of total

soil microbial communities (Knox et al., 2017; Zhang et al., 2017; Zhang et al., 2016b). The active microbes have rarely been investigated due to the difficulties in soil labeling and RNA extractions (Che et al., 2016a). Nevertheless, soil microbes have a wide range of vitality, with a small active population being active, while the majority is dormant (Fierer, 2017; Lennon and Jones, 2011). Compared to total soil microbes, active soil microbes usually show higher sensitivity to environmental changes (Barnard et al., 2015; Che et al., 2015; Xue et al., 2016b), and are more connected with soil functionality (Che et al., 2016b). Therefore, examining the effects of warming and human activities on active soil microbial communities can improve our understanding of ecosystem feedbacks to the future climate changes.

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In the recent decade, rRNA-based methods (e.g., rRNA sequencing) have been widely employed to identify active soil microbial communities (Barnard et al., 2015; Che et al., 2015; Che et al., 2016b; Mueller et al., 2016) for the following reasons. First, rRNA genes (rDNAs) are the most widely-used molecular markers to determine microbial abundances and community compositions (Che et al., 2016b). Second, rRNAs are indispensable for protein synthesis, and in some pure cultures, their cellular concentration correlate well with microbial growth rates (Kerckhof and Kemp, 1999; Muttray and Mohn, 1999; Perez-Osorio et al., 2010). Third, the dormancy and decease of microbes usually accompany rRNA degradation (Lahtinen et al., 2008; Segev et al., 2012). Fourth, the rRNA-based methods can identify active microbes without labeling, which avoids disturbance and captures more reliable active microbial profiles. Moreover, the invention and popularization of the commercial soil RNA extraction kits have largely solved the difficulties in soil RNA extraction (e.g., Che et al., 2017). Consequently, a combination of the rDNA- and rRNA-based methods can systematically determine the responses of both total and active soil microbes (Che et al., 2016a; Che et al., 2016b).

Tibetan Plateau, known as the third pole of our planet, is extremely sensitive to global warming (Chen et al., 2013; Chen et al., 2015; Liu and Chen, 2000) and human activities, particularly livestock grazing (Chen et al., 2013; Zhou et al., 2005). There are 23.2 Pg of organic carbon (2.5% of the global pool) stored in the Tibetan soils (Wang et al., 2002), and thus even a slight variation in this organic carbon pool can result in a considerable feedback to the global warming. Soil microbes, especially the active populations, play a key role in determining the dynamics of soil organic carbon pools (Che et al., 2016b). Moreover, they have been also recognized as a vital factor for influencing the sustainability of Tibetan alpine meadows (Che et al., 2017). Therefore, determining the individual and combined effects of warming and grazing on soil microbial community is not only important for predicting the Tibetan ecosystem feedbacks to global warming, but also crucial to providing a basis for optimizing the grazing strategies under the climate change.

In Tibetan alpine meadows, the previous studies suggested that warming significantly increased soil respiration, litter mass losses, phosphomonoesterase activity, soil nutrient contents, and belowground biomass, and significantly affected soil N₂O emission and plant community composition (Hu et al., 2010; Lin et al., 2011; Luo et al., 2010; Luo et al., 2009; Rui et al., 2011; Rui et al., 2012; Wang et al., 2012). Compared to warming, the effects of grazing were generally weak and sometimes converse (Jiang et al., 2016; Wang et al., 2012). The most significant effect of grazing was the decrease in litter input (Luo et al., 2009). In addition, significant warming-grazing interactive effects were observed in several studies (Li et al., 2016; Rui et al., 2011; Wang et al., 2012). Responses of soil microbes to warming and grazing were analyzed in a few investigations (Li et al., 2016; Yang et al., 2013; Zhang et al., 2016a; Zhang et al., 2016b). However, as mentioned above, these studies only assessed the total soil microbes, while the effects of warming and grazing on the active soil microbes have never been investigated in this region. In addition, although soil microbes should be sensitive or responsive to the aforementioned changes, significant effects of warming and grazing on total soil bacterial communities were seldom observed in the previous studies (Li et al., 2016; Zhang et al., 2016b).

Therefore, in this study, we aimed to investigate the main and interactive effects of warming and grazing on total and active soil prokaryotes in a *Kobresia* alpine meadow on the Tibetan Plateau. Bacterial abundance and 16S rRNA transcriptional activity were determined using 16S rDNA and rRNA copies, respectively. Total and active prokaryotic community structures were analyzed using Miseq sequencing based on 16S rDNA and rRNA, respectively. On the basis of the aforementioned findings, we hypothesized that: 1) warming and grazing exerted more profound effects on active prokaryotes than total prokaryotes in soils; 2) warming stimulated soil microbial activity and 16S

rDNA transcription; and 3) soil prokaryotes were less sensitive to grazing than warming, but grazing could partially offset the effects of warming.

2. Materials and methods

2.1. Study site

This research was conducted at the Haibei Alpine Meadow Ecosystem Research Station (37° 37' N, 101° 12' E), situated in the northeast of the Tibetan Plateau. With an average elevation of 3200 m, this region has a typical plateau continental climate. The mean annual temperature and precipitation were -1.7°C and 570 mm, respectively (Zhao et al., 2006). The soil was classified as Gelic Cambisols (WRB, 1998). The vegetation of our study site was dominated by species such as *Potentilla nivea*, *Kobresia humilis*, and *Elymus nutans* (Wang et al., 2012). The average coverages of graminoids, forbs, and legumes were about 86%, 86%, and 28%, respectively (Wang et al., 2012). A detailed description of the experimental site can be found in our previous studies (Jiang et al., 2016; Ma et al., 2015).

2.2. Experimental design

The field treatments first started in May 2006 and continued until 2012 to reveal the effects of warming and grazing on alpine meadow ecosystems. The experimental design has been provided in our previous studies (Jiang et al., 2016; Luo et al., 2009). It was a two-way factorial design with four replicates. In total, 16 orbicular plots (3 m diameter) were established in the field with a randomized complete block design. The interval between every two adjacent plots was 3 m.

The experimental warming was achieved by an infrared heating system named free-air temperature enhancement (FATE) that has been detailed by Luo et al. (2009). The canopy temperature increase in the warming plots was 1.2°C during the day and 1.7°C at night in the growth seasons (May to September), while it was 1.5°C in the daytime and 2.0°C at night in the non-growth seasons (October to April). These temperature increases were in accordance with the predictions of global warming (IPCC, 2013). In each plot, type-K thermocouples (Campbell Scientific, Logan, Utah, USA) were used to automatically measure soil temperature at 0–5 and 5–10 cm. All temperature data were recorded and stored in CR1000 dataloggers.

From August 2006 to October 2010, the grazing plots were grazed by Tibetan domestic sheep (*Ovis aries*; Table 1). One or two sheep were fenced in the plots for 1 to 2 h to remove plant to approximately half of the canopy height. The details of the sheep grazing treatments have been described in our previous study (Rui et al., 2012). In November 2011 and April 2012, instead of sheep grazing, clipping was employed to simulate winter grazing (Table 1). The clipping removed approximately 90% of the grass litter. Overall, these grazing treatments were

Table 1
Methods of grazing treatments.

Time	Methods	Intensity ^a
August 2006	Sheep grazing	50%
July 2007	Sheep grazing	50%
August 2007	Sheep grazing	50%
September 2007	Sheep grazing	50%
July 2008	Sheep grazing	50%
August 2008	Sheep grazing	50%
July 2009	Sheep grazing	50%
August 2009	Sheep grazing	50%
July 2010	Sheep grazing	50%
August 2010	Sheep grazing	50%
November 2011	Clipping	90%
April 2012	Clipping	90%

^a The grazing intensity was indicated by the variations of canopy height.

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