



# Soil bacterial community shifts driven by restoration time and steppe types in the degraded steppe of Inner Mongolia

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## ABSTRACT

Degraded grassland can be restored through management practices such as fencing to protect land from overgrazing. However, little is known about the dynamics of underground microbial communities and their associated ecological function during the restoration process. In this study, we investigated changes in the soil bacterial community composition with varying restoration time in the *Leymus chinensis* steppe. We also studied the differences in the soil bacterial community composition between a *Leymus chinensis* steppe and a *Stipa grandis* steppe at the same restoration time in the Inner Mongolia of China. Results showed that restoration of the degraded steppe through fencing significantly changed the bacterial community composition through the restoration time. The relative abundances of Chloroflexi and Cyanobacteria decreased significantly with restoration. However, the relative abundances of copiotrophic Proteobacteria and Bacteroidetes increased. Significant changes for many dominant taxa occurred between 7 and 13 years of restoration time in the *Leymus chinensis* steppe. Shifts in the composition of bacterial communities with fencing and grazing were driven by multiple factors, including soil moisture, pH, nutrients (organic carbon and nitrogen, etc.). Network analysis of soil bacterial community compositions showed that the three largest modules in co-occurrence networks were separated by fencing, grazing and steppe type. This study revealed the successions of underground microbial communities associated with steppe restoration management over time.

## 1. Introduction

Livestock grazing constitutes a major use of grassland with extensive economic and environmental consequences. Heavy grazing has caused the degradation of large areas of grassland in the Inner Mongolia steppe of China. The effects of livestock grazing on the ecosystem structure and function (plant community coverage and biomass, plant diversity and species, soil carbon (C) and nitrogen (N) contents, soil microbial biomass C and N, greenhouse gas emissions) have been studied intensively (Tang et al., 2016; Wolf et al., 2010; Wu et al., 2014).

Fencing is regarded as an effective management practice for restoring degraded grassland ecosystems. Fencing can increase above ground plant biomass, subsequently increasing the soil organic C and N

derived from litter decomposition and root exudation (Bai et al., 2012; Wu et al., 2014). Low concentrations of soil organic C and N,  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N in the free grazing treatment suggest that grazing has negative effects on soil N pools (Wang et al., 2006; Wright et al., 2004). Animal urine and feces plus high moisture evaporation (causing salt accumulation on the surface) on the heavily grazed steppe may increase in surface soil pH (Li et al., 2013). Vegetation, soil pH and soil organic C and N concentrations can be recovered after fencing the degraded steppe with varying restoration times (Chen and Tang, 2016; Zhou et al., 2012). Moderate grazing can promote the restoration of degraded grassland by modulating plant diversity and species (Quan et al., 2015). In the restoration process, changes in soil nutrients, pH, moisture and other conditions likely create or modify ecological niches for both

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above and below ground communities. These modifications are affected by multiple factors, such as restoration time, climate and steppe types.

Microbes are a crucial part of the ecosystem by driving biogeochemical cycles. Total C and N contents in the soil are identified as key factors that affect microbial biomass and activity (Holt, 1997). Patches of bare soil caused by grazing lead to loss of soil organic matter (Kölbl et al., 2010), which in turn affects microbial biomass and activity. It is well known that soil microbial communities are closely associated with plant communities. Most microorganisms are heterotrophs that require nutrients provided by plants. Soil microorganisms will also decompose organic matter and litter, providing available nutrients for plant growth (Wu et al., 2014). Low plant biomass may decrease the nutrients available to microorganisms, subsequently decreasing bacterial diversity (Qi et al., 2010; Zhou et al., 2010). However, another study showed that soil bacterial communities are not influenced by plant restoration. Instead, they are influenced by soil environmental properties and spatial effects for the restored grassland (Murphy and Foster, 2014).

A previous study showed that short-term fencing of a degraded steppe significantly increased bacterial diversity compared with free grazing and long-term fencing sites in a typical steppe of Inner Mongolia (Zhou et al., 2012). Bacterial diversity changes are not likely monotonically with an increased grazing intensity (Zhou et al., 2010). Intermediate grazing intensity can increase soil bacterial diversity, but there is no significant difference in bacterial diversity between non-grazed and heavily grazed sites. Other studies indicate that soil microbial responses are modulated by soil texture in restored grassland (Bach et al., 2010), and the microbial diversity does not increase, but the microbial community structure and functionality are influenced by soil restoration (Bastida et al., 2013). However, previous studies based on low-resolution microbial profiling methods, such as terminal restriction fragment length polymorphism (T-RFLP) and denatured gradient gel electrophoresis (DGGE) (Bach et al., 2010; Zhou et al., 2012), are not able to discern whether particular taxonomic groups are more or less sensitive to the restoration process.

The Inner Mongolian steppe lies in the eastern part of the Eurasia grassland, which is the largest contiguous grassland area in the world. However, the relationships of bacterial community responses to restoration time and types of degraded steppe have not been recorded in Inner Mongolia. Two important typical steppes, *Leymus chinensis* and *Stipa grandis*, are widely distributed in this region. Water availability is the most important factor limiting aboveground plant community composition, diversity and biomass (Bai et al., 2008). Precipitation in the *Leymus chinensis* steppe region is usually higher than in the *Stipa grandis* steppe. Thus, the responses of the soil bacterial community to restoration may differ in different types of steppe.

In this study, we investigated the responses of soil bacterial communities to fencing restoration of degraded steppe in Inner Mongolia using the pyrosequencing technique. The purpose of the study was to detect changes of bacterial community compositions along with the fencing restoration time and the effects of different steppe types on the changes of bacterial community compositions during the restoration. Another purpose was to identify key driving factors changing the composition of bacterial communities during fencing restoration.

## 2. Materials and methods

### 2.1. Study site descriptions

The study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116°42' E, 43°38' N, with an average elevation of 1100 m above sea level), Inner Mongolia of China. The mean annual temperature is 0.3 °C, with the mean monthly temperature ranging from −21.6 °C in January to 19.0 °C in July. The mean annual precipitation is 346.1 mm with 60% to 80% occurring during the growing season from May to August. The first 24-ha grazing field in

the *Leymus chinensis* steppe was fenced against large animal grazing for 33 years from 1979 to 2012 (L79F). In 1999, its neighboring 25-ha field was fenced for 13 years until 2012 (L99F). The field outside the 33-yr and 13-yr fenced sites (L79G/L99G) was free grazed. Near the 1979-fenced field, a site was fenced in 2005 for 7 years until 2012 (L05F). Outside the fence, it was free grazed (L05G). The highly degraded *Stipa grandis* steppe was fenced for 33 years from 1979 to 2012 (S79F). Similar free grazing activity continued outside the fenced area (S79G). Precipitation is higher in the *Leymus chinensis* steppe (annual mean 358 mm) than in the *Stipa grandis* steppe (annual mean 323 mm). Soil in the *Leymus chinensis* steppe is classified as dark chestnut, and that in the *Stipa grandis* steppe is classified as typical chestnut soil.

### 2.2. Soil sample collection and soil properties measurement

Soil samples were collected in mid-July, 2012. Five sampling lines inside the fence and five corresponding lines outside and vertical to the fence were established every 10 m. We collected five individual soil cores with a diameter of 5 cm at a 0–10 cm depth and 10 m apart for each core along each sampling line, and pooled them into one sample. Finally, five replicate samples from five sampling lines were collected for each treatment.

Soil samples were transported to the lab on ice, stored at −20 °C until the genomic DNA was extracted (within a month). Part of the sample was sieved with a 2 mm mesh and stored at 4 °C to measure soil properties such as soil pH, NH<sub>4</sub><sup>+</sup>-N, total organic C (TOC), total N (TN) and microbial biomass C (C<sub>mic</sub>) and N (N<sub>mic</sub>), soil basal respiration (R) and respiratory quotient (Q<sub>CO2</sub>), as described by Yao et al. (2014).

### 2.3. DNA extraction, PCR amplification and pyrosequencing

Soil genomic DNA was extracted using a method described by Lueders et al. (2003). To amplify the V4-V5 hypervariable regions of 16S rRNA genes, the universal primer 515F/909R was used in the PCR (Baker et al., 2003). PCR and other experimental procedures were described in detail by Li et al. (2014). The barcoded amplicons were pooled in an equimolar concentration for 454 pyrosequencing using a GS FLX system (454 Life Sciences, Branford, CT).

### 2.4. Pyrosequencing data analysis

A QIIME Pipeline (<http://qiime.org/tutorials/tutorial.html>) was used to sort and trim the raw sequencing data based on barcode and sequence quality (length > 300 bp, average base quality score > 30). A Uchime algorithm was used to remove chimera sequences (Edgar et al., 2011). Operational taxonomic units (OTUs) were classified at the threshold of 97% identity. Each sample was rarefied to the soil sample exhibiting the lowest number of reads (2979 sequences) for both alpha and beta diversity analyses, and the rarefaction curves were generated from the observed species. Taxonomy was assigned using the Ribosomal Database Project classifier (Wang et al., 2007). The original sequence data are available at the European Nucleotide Archive by accession PRJEB11649 (<http://www.ebi.ac.uk/ena/data/view/PRJEB11649>).

### 2.5. Statistical analysis

Principal coordinates analysis (PCoA) was used to evaluate general structural changes of bacterial communities in Fast UniFrac (<http://bmf.colorado.edu/fastunifrac/>). PerMANOVA analysis with the weighted PCoA scores as input data was conducted to assess the statistical significances among our datasets in the PAST (<http://folk.uio.no/ohammer/past/>). The correlations among bacterial community dissimilarities with environmental variables were evaluated using the (partial) Mantel test in PASSaGE (<http://www.passagesoftware.net/>). Variance partitioning analysis (VPA) was used to quantify the relative contributions of environmental variables by using the R package Vegan

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