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Testing association between soil bacterial diversity and soil carbon storage on the Loess Plateau

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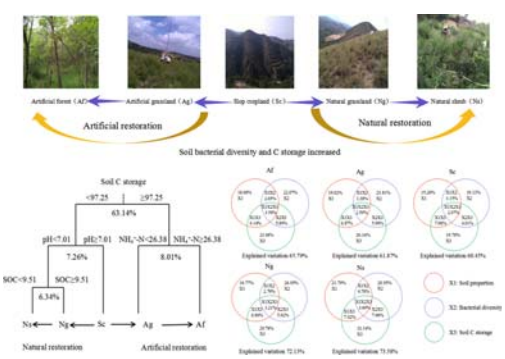
HIGHLIGHTS

- High-throughput 16S rRNA sequencing was used for soil bacterial community composition.
- Soil C storage and soil bacterial diversity increased due to vegetation restoration.
- A strong relationship between the dominant bacterial groups and soil C storage
- Soil bacterial diversity is closely related to soil C storage on the Loess Plateau.

GRAPHICAL ABSTRACT



Soil bacterial diversity was closely related to soil C storage on the Loess Plateau.

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ABSTRACT

Bacteria are widely distributed and play an important role in soil carbon (C) cycling. The impact of soil bacterial diversity on soil C storage has been well established, yet little is known about the underlying mechanisms and the interactions among them. Here, we examined the association between soil bacterial diversity and soil C storage in relation to vegetation restoration on the Loess Plateau. The dominant phyla among land use types (artificial forest, Af; natural shrubland, Ns; artificial grassland, Ag; natural grassland, Ng; slope cropland, Sc) were *Acidobacteria*, *Actinobacteria*, *Alphaproteobacteria*, and *Betaproteobacteria*, which transited from *Acidobacteria*-dominant to *Actinobacteria*-dominant community due to vegetation restoration. Soil C storage and the Shannon diversity index of soil bacterial community ($H_{Bacteria}$) showed the order Ns > Ng > Af > Ag > Sc, whereas no significant difference was found in Good's coverage ($p > .05$). Further, a strong relationship was observed between the relative abundance of dominant bacterial groups and soil C storage ($p < .05$). Additionally, soil bacterial diversity was closely related to soil C storage based on the structural equation model (SEM) and generalized additive models (GAMs). Specifically, soil C storage had the largest deterministic effects, explaining >70% of the variation and suggesting a strong association between soil C storage and soil bacterial diversity. Overall, we propose that further studies are necessary with a focus on the soil bacterial groups with specific functions in relation to soil C storage on the Loess Plateau.

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1. Introduction

Soil bacteria, one of the most abundant and diverse groups of microorganisms, play a vital role in regulation of ecological processes, such as soil carbon (C) cycling from the Earth Microbiome Project (EMP, http://www.earthmicrobiome.org) (Lloydprice et al., 2017; Thompson et al., 2017). Soil C-fixing bacteria are widespread in soil, indirectly altering the rate of soil C sequestration and C storage. For example, *Bradyrhizobium japonicum*, *Mycobacterium* sp., and *Burkholderia* sp., also harbor the *cbbL* gene which can thus fix C via the Calvin cycle, resulting in the increase of soil C storage (Könneke et al., 2014; Lynn et al., 2016). In turn, soil C storage in terrestrial ecosystems considers as an overarching factor for soil bacteria and constitutes an important component of the global C balance (Kennedy and Smith, 1995; Torn et al., 1997; Treseder and Allen, 2000; Xia et al., 2016). Most soil bacteria rely on soil C storage to obtain energy, so there was a closely relationship between soil bacteria and soil C storage. Consequently, a large number of studies have shown the close links between soil bacteria and soil C storage (Horner-Devine et al., 2004; Wardle et al., 2004; Torsvik and Øvreås, 2002). For example, soil bacteria are directly responsible for the turnover and decomposition of soil organic matter and therefore contribute to the enhancement of soil C storage (Lange et al., 2015; Ling et al., 2017). Meanwhile, soil bacteria indirectly affect soil C storage by increasing soil aggregation due to the degradation of microbial byproducts (Exbrayat et al., 2014; van Groenigen et al., 2014). In recent years, traditional explanatory theories have focused on the stabilization, decomposition, and transformation of soil C storage owing to the growing interest in soil C cycling (Pan et al., 2009; Liu et al., 2010; Berlemont et al., 2014). It is generally accepted that the magnitude of soil C storage is dependent on microbial involvement (Burke, 2015; Doetterl et al., 2015; Lange et al., 2015), as soil C storage is ultimately affected by soil bacterial diversity and community composition (Treseder and Allen, 2000; Nave et al., 2010; Lange et al., 2015). Although soil bacterial diversity and community composition have been largely examined (Lupwayi et al., 1998; Zhao and Gillet, 2011; Bissett et al., 2013; Sun et al., 2015; Yao et al., 2017a; Yao et al., 2017b), there are still unclear gaps in understanding of the relationship between soil C storage and soil bacterial diversity.

China's Loess Plateau is one of the deepest loess deposits and also one of the most eroded areas in the world (Fu et al., 2017). Last century, increasing population pressure and environmental damage resulted in the serious degradation in this region. Government launched a series of ecosystem deterioration engineering projects in the 1980s (Deng et al., 2014; Feng et al., 2016; Fu et al., 2017). Since 1999, the Grain-for-Green program has made remarkable contribution to China's vegetation restoration, which aims to restore degraded ecosystem services, by improving carbon sequestration, soil conservation and reducing floods. Now, the Loess Plateau has become the most successful ecological restoration zone (Fu et al., 2017). Following the Grain-for-Green and Natural Forest Protection projects for vegetation restoration, large loessial areas of sloping farmland have been converted to artificial forest and grassland (artificial vegetation restoration) or natural grassland and shrubs (natural vegetation restoration) (Chen et al., 2015; Feng et al., 2016; Fu et al., 2017). In this case, soil C storage is a critical index for evaluating the efficiency of vegetation restoration, and soil bacteria are vulnerable to vegetation restoration (Jin et al., 2014; Feng et al., 2017). Hundreds of studies have reported that soil C storage has greatly increased due to vegetation restoration in this region (Chen et al., 2007; Wang et al., 2010; Feng et al., 2013; Deng et al., 2014). While there is considerable disagreement on soil bacterial diversity in relation to vegetation restoration (Houghton et al., 1999; Post and Kwon, 2000; Guo and Gifford, 2002). In fact, a wide range of biotic and abiotic factors influence soil bacterial diversity, including soil type, climate, nutrient management, and the decomposition of soil microorganisms (Nair and Ngouajio, 2012; Heijden and Wagg, 2013). For example, Zeng et al. (2016) reported that soil bacterial diversity was closely related to the edaphic properties on the Loess Plateau. Similarly, a strong relationship between soil nutrients and soil bacterial diversity was found in natural grassland, and soil nutrients contributed a great deal to soil bacterial diversity (Zhang et al., 2015). By contrast, some surveys have found that environmental conditions were determinants in regulating soil bacterial diversity, and this discrepancy could be attributed to soil C storage at large scales (Liang et al., 2017; Xu et al., 2017). At regional scale, different mechanisms have been proposed to explain how soil bacterial diversity affects soil C storage, although some studies also revealed that soil bacteria had some resilience to disturbance (Hartzog et al., 2017; Samaritani et al., 2017). Thus, a central issue in microbial ecology is to investigate the interactions between soil bacterial diversity and soil C storage on the Loess Plateau.

To examine the association between soil bacterial diversity and soil C storage, five land use types (artificial forest, Af; natural shrubland, Ns; artificial grassland, Ag; natural grassland, Ng; slope cropland, Sc) on the Loess Plateau were selected. Three objectives of this study were to (i) determine and compare the soil bacterial diversity and soil C storage in relation to vegetation restoration, (ii) explore the dominant factors shaping soil bacterial diversity and soil C storage, and (iii) test the association between soil bacterial diversity and soil C storage. Therefore, we tested three hypotheses: (i) soil bacterial diversity and soil C storage are related to vegetation restoration, (ii) the dominant driving factors (soil properties) can contribute to soil bacterial diversity and soil C storage, and (iii) soil C storage is positively associated with soil bacterial diversity.

2. Materials and methods

2.1. Sampling areas

We carried out this study in Zhifanggou (Yanhe river) catchment in Ansai county (36°46′28″–36°46′42″N, 109°13′03″–109°16′46″E), located in the middle of the Yellow river on the Loess Plateau. The study area occupies a total area of approximately 8.72 km^2 and has a semi-arid climate and a deeply incised hilly-gully Loess landscape with heavy seasonal rainfall and periodic flooding. Hills cover 90% of the region, and with the steep slopes (40%) near cliffs, only 7% of this area can be used in agriculture. The average annual rainfall from 1970 to 2000 was approximately 497 mm, and there are distinct rainy and dry seasons. The rainy season occurs from July to October, with the August rainfalls amounting to >20% of the annual total. The average annual temperature was 9.1 °C along the elevation gradient. Most of the area lies at an altitude between 900 m and 1500 m and the zonal soil in this region is Calcaric Cambisol according to FAO-UNESCO Soil Map of the World (FAO and ISRIC, 1988) or Orthic Entisol according to Chinese Soil Taxonomy (Cooperative Research Group on Chinese Soil Taxonomy, 2001), which developed directly from the parent wind-deposited yellow material.

We selected 45 sites within five land use types: artificial forest, Af; artificial grassland, Ag; natural shrubland, Ns; natural grassland, Ng; slope cropland, Sc. These land use types initially developed from similar parental material and under the same climate but were eventually changed by differences in long-term land-use regimes. In addition, there were no signs of fire or natural disasters in this area over the past several decades based on historical sources. The loess is perfectly arable due to its fine grains, loose texture and high content of mineral nutrients. The types of vegetation in this area include artificial restoration (Af, Ag) on account of the Grain-for-Green Project since 1974 and natural restoration (Ns, Ng) on account of the prevention of grazing by fencing since 1938.

2.2. Experimental design

A field survey was conducted at the peak of the growing season in 2016 between July and September. The sampling sites were located at