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Natural revegetation of a semiarid habitat alters taxonomic and functional diversity of soil microbial communities

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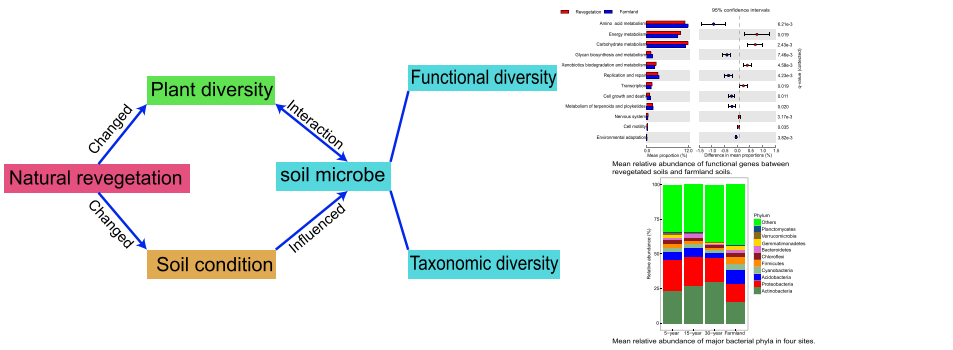
HIGHLIGHTS

- We analyzed the microbial taxonomic and functional diversity of revegetated soils.
- We used both 16S rRNA gene amplicon and shotgun metagenomic sequencing.
- The microbial taxonomic diversity increased with plant diversity.
- Soil organic matter was the best predictor of microbial community structure.
- Revegetation increased the potential of microbe-mediated nutrient cycling.

GRAPHICAL ABSTRACT



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ABSTRACT

Revegetation of degraded lands has a profound impact on the maintenance and stability of ecosystem processes. However, the impacts of this land use change on functional diversity of soil microbial communities are poorly understood. Here, using 16S rRNA gene amplicon and shotgun metagenomic sequencing, we compared the taxonomic and functional communities of soil microbiome, and analyzed the effects of plant diversity and soil chemical properties, in a chronosequence of restored ex-farmland that had been naturally revegetated to grassland over periods of 5, 15 and 30 years with adjacent farmland, on the Loess Plateau, China. We found that microbial taxonomic diversity was positively correlated with plant diversity and was higher in the revegetated sites. Functional diversity increased significantly in the oldest grassland. Actinobacteria, commonly considered a copiotrophic phylum, was more abundant in the revegetated sites, while Acidobacteria, an oligotrophic phylum, was more abundant in farmland. Furthermore, the structure of taxonomic and functional communities was significantly different between revegetated sites and farmland, and organic matter was the best environmental predictor in determining these microbial communities. Compared with the farmland, revegetation increased the proportion of genes associated with energy metabolism, carbohydrate metabolism and xenobiotics biodegradation and metabolism. Notably, the higher proportion of carbohydrate degradation gene subfamilies in the revegetated sites indicated higher levels of soil nutrient cycling. These results elucidate the significant shifts in belowground microbial taxonomic and functional diversity following vegetation restoration and have implications for ecological restoration programs in arid and semi-arid ecosystems.

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1. Introduction

Land degradation exerts a great impact on ecosystem services and threatens the survival of humans (Smith et al., 2016), especially in arid and semi-arid regions (Sun et al., 2015). Natural revegetation of degraded land is one of the most widely used restoration strategies, because the development of plant communities can effectively reduce soil erosion, improve biodiversity, and associated ecosystem services (Bullock et al., 2011; Liu et al., 2008). Yet, the restoration of ecosystem function is a long-term process that can vary with local climate and soil conditions (Munroe et al., 2013). Complex interactions between aboveground and belowground communities drive productivity and diversity in ecosystems and determine the successional establishment and development of biological communities (Kardol and Wardle, 2010; van der Putten et al., 2013). However, the majority of studies exploring ecosystem restoration focus on plants and little attention has been paid to soil microbial dynamics.

Plant-soil feedback processes play important roles in determining the structure and successional dynamics of both plant and microbial communities (Herrera Paredes et al., 2016). Plants can alter the abiotic soil environment, including pH, organic matter, carbon to nitrogen ratio and soil texture, through litter fall and root exudation, where such changes impact soil microbial diversity and community structure (Frouz et al., 2016; Schlatter et al., 2015). In turn, soil microbiome affect plant community composition and productivity through microbe-mediated organic matter decomposition and nutrient cycling and direct interactions with plants (van der Putten et al., 2016). In secondary succession of habitats, plant communities shift from fast to slow-growing species, with varying effects on plant diversity, community composition and biomass; there may also be changes in litter quality and quantity (Mahaming et al., 2009). Due to the strong interactions between plants, soil and microbes, successful habitat restoration should be concomitant with shifts in soil microbial communities.

Despite the importance of revegetation in ecological restoration, the impacts of revegetation processes on microbial taxonomic and functional diversity remain largely unknown. Previous studies have demonstrated that the composition of soil bacterial communities is affected by natural revegetation and its diversity increases with post-restoration time (Kuramae et al., 2010; Zhang et al., 2016), but they have mainly focused on taxonomic diversity of microbial communities that cannot accurately predict microbial functional characteristics owing to high functional redundancy (Allison and Martiny, 2008). It has been shown that better predictions of microbial responses to habitat change may be gained from functional genes rather than taxonomic traits (Burke et al., 2011). Therefore, assessment of changes in microbial gene functional diversity may better elucidate the impacts of revegetation on ecosystem restoration.

The Loess Plateau of China, characterized by extensive wind-blown sedimentary deposits, is one of the most eroded areas in the world due to its naturally erodible soil, complex terrain and frequent human disturbance (Fu et al., 2011). Various ecological construction strategies have been implemented since 1950s to reduce soil erosion and restore the environment, including the “Grain for Green” program in 1999, which aimed to convert farmland to forest, shrub and grassland (Deng et al., 2014). Recently, the plant communities (Kou et al., 2016; Sun et al., 2017) and corresponding belowground parameters, including soil chemical properties and microbial communities (Zhang et al., 2016) of naturally revegetated sites have been reported. However, these studies of the soil microbial communities were mainly based on amplicon sequencing that provided limited information about functional gene composition and diversity. Understanding the impacts of vegetation restoration on microbial taxonomic and functional communities is important for ecological monitoring and restoration assessment.

Here, we studied the soil microbial community at three naturally revegetated sites, which had been retired from agricultural use since the last 5, 15 and 30 years, and adjacent farmland on the Loess Plateau, China. By using Illumina HiSeq sequencing of 16S rRNA gene and metagenome, we aimed to (a) assess the influence of revegetation on the taxonomic and functional diversity of soil microbial communities and (b) determine the relationship between microbial and plant diversity and identify the major soil chemical properties that shape the structure of taxonomic and functional communities.

2. Materials and methods

2.1. Study site and soil sampling

Our study system is an active “Grain for Green” restoration site, located on the Loess Plateau, China (36°10′–36°17′ N, 106°21′–106°27′ E; altitude 1860–2000 m). The site is a semiarid habitat with temperate continental climate. The annual average precipitation is 424 mm, 60% of which occurs from July to September. The annual average temperature is 5 °C, ranging from a January minimum of −14 °C to a July maximum of 25 °C. Loessial soil (Calcaric Cambisols, FAO) and gray cinnamon soil (Haplic Greyxems, FAO) dominate. Since the 1980s, adjacent agricultural fields, which were similar in landscape position and cropping systems and had been cultivated for >30 years, were removed from production and fenced, to exclude livestock and anthropogenic disturbance, to allow natural revegetation. This has resulted in a series of secondary successional grasslands that differ in age.

In August 2014, we selected naturally revegetated grasslands that were 5-, 15- and 30-year old and adjacent, long-established cultivated farmland planted with corn. In each of the four study sites, three 1 × 1 m plots were arranged randomly within an area of 10 × 10 m. Within each plot, all plant species were identified and quantified (Sup. Table 1). We collected five topsoil cores (5 cm diameter × 10 cm depth) from each plots using an auger, which were pooled and transported to laboratory on ice. All soil samples were thoroughly homogenized and manually removed stones and roots. The single soil samples from each plot were then divided into two parts, where one was frozen at −80 °C for DNA extraction, and the remaining part was sieved (2 mm gauge) and air dried for soil chemical analyses. Soil organic matter (OM) content, total N (TN) content, available N (AN), available K (AK) and available P (AP) content and pH were determined as procedures previous described (Bao, 2000).

2.2. Soil DNA isolation, 16S rRNA gene sequencing and bioinformatic analysis

Total DNA was extracted from all soil samples using FastDNA® SPIN Kit (MP Biochemicals, Solon, OH, USA) with 500 mg of soil per sample following the manufacturer's recommendations. To obtain sufficient DNA quantity for sequencing and to ensure adequate representation of soil, five replicates were conducted and pooled for each sample. The V4–V5 region of bacterial 16S rRNA genes was PCR amplified using primer pair 515F (5′-GTG CCA GCM GCC GCG GTA A-3′) and 907R (5′-CCG TCA ATT CCT TTG AGT TT-3′) (Edwards et al., 2015), and all PCR amplifications were conducted in triplicate for each sample. Amplicon samples were sequenced on the paired 250-bp Illumina HiSeq 2500 platform (Illumina, Inc., CA, USA). Paired-end sequences were merged by FLASH (V1.2.7, http://ccb.jhu.edu/software/FLASH/), then quality filtered with QIIME (Caporaso et al., 2010). After removed chimeric sequences (Edgar et al., 2011), the remaining sequences were assigned to OTUs at similarities of 97% using UPARSE (Edgar, 2013). Taxonomic information was annotated for a representative sequence of each OTU by RDP classifier at a confidence of 80% (Wang et al., 2007).

2.3. Shotgun metagenomic sequencing and bioinformatic analysis

1 μg of the above-mentioned DNA extracted from each soil sample was prepared for shotgun metagenomic sequencing. The DNA samples