



Decreased occurrence of carbon cycle functions in microbial communities along with long-term secondary succession

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ABSTRACT

The succession of microbial community structure and function is a central ecological topic; however, the mechanisms that underlie community assembly and promote temporal succession remain unclear. We studied microbial community-associated functional dynamics in a well-established secondary successional chronosequence that spans approximately 160 years of ecosystem development on the Loess Plateau of China, by sequencing both 16S and ITS rRNA genes and soil metagenomes, resulting in a total of 132.5 Gb of data. Notably, both bacterial and fungal communities shifted with succession, but the microbial community changed little from the pioneer forest stage (approximately 110 years) to the latter successional forest stage. Fungi showed higher variability with succession than bacteria, and the shift of both the bacterial and fungal communities was related more to the soil characteristics than to the litter characteristics. Shifts in soil microbial functions were associated with microbial phylogenetic changes, but microbial gene function also showed changes in the absence of phylogenetic changes at the late successional stages. The reduction in microbial C cycle genes was related to a decrease in litter decomposition ability, thus resulting in a steady state of nutrient cycle in the ecosystem. In addition, high microbial respiration in nutrient-rich soil does not necessarily indicate high microbial decomposition functions; the latter also depend on the abundance of related genes, on enzyme activity and on the physicochemical properties of the litter. Our study provides a metagenome profile of a successional chronosequence and provides insight into the mechanisms underlying the soil microbe-driven functional changes in nutrient cycles during succession.

1. Introduction

Secondary succession occurs in disturbed areas and is characterized by changes in plant coverage, composition, biomass, soil nutrient level, and soil erodibility (Finegan, 1984), which have attracted increased attention due to the increased amount of abandoned cropland (Grime, 2006; Van der Maarel and Franklin, 2012; Zhang et al., 2013). Microorganisms play an important role in the Earth's global biogeochemical cycles (Palomo et al., 2016) and are essential to soil functions, especially organic matter decomposition and nutrient cycling; they are therefore important in the regulation of plant productivity and community dynamics and in soil formation (Harris, 2009). Integrating microbial community structure and function into the study of ecological succession could provide considerable knowledge regarding the mechanisms that drive successional dynamics and that underlie microbe-driven nutrient cycles (Fierer et al., 2010), especially considering that little is known of the belowground microbial community that occurs

with long-term succession in an ecosystem.

Associations between plants and soil microorganisms are essential and unavoidable (Chabrierie et al., 2003). Some studies have addressed the changes in microbial communities that occur during succession; however, these works reported inconsistent results regarding community-level diversity. Kuramae et al. (2010) observed a decrease in microbial richness with field age, whereas Jangid et al. (2011) reported that bacterial diversity remained unchanged after > 50 years of succession, and Zhang et al. (2016) described an increase in diversity after 10 years of secondary succession. Furthermore, a few studies reported that fungal communities are more easily changed than bacterial communities by plants along a successional gradient (Cutler et al., 2014). In addition, due to the variation in soil substrates and the heterogeneity of ecosystems, the existence of common patterns of change in microbial communities undergoing succession remains unclear, as do the roles of the bacterial and fungal communities in this process. Moreover, whether microbial communities stabilize in the latter successional stage is

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unclear (Fierer et al., 2010). Thus, the complex patterns of microbial succession remain to be revealed.

Numerous studies have addressed how soil physicochemical properties change with succession and have reported that succession can enhance the nutrient availability of degraded soil and maintain soil fertility, which is strongly related to microbe functions (Cline and Zak, 2015; Cong et al., 2015; Kuramae et al., 2010). However, it remains unclear how microbial metabolic functions and soil properties develop concurrently during succession. Previous studies have mainly focused on microbial community structure (Banning et al., 2011; Jangid et al., 2011; Zhang et al., 2016), whereas functional shifts at the genetic level have attracted little attention. In terrestrial ecosystems, microorganisms act as major players in the C and nitrogen (N) cycles (Harris, 2009) and mediate the transfer of photosynthetic products from plants into soil (Heimann and Reichstein, 2008; Högberg et al., 2001). Voříšková and Baldrian (2013) reported that fungi are the key players in litter decomposition because of their ability to produce a wide range of extracellular enzymes, whereas bacteria are mainly involved in soil nutrient cycles, which easily shift with changes in soil physicochemical properties during succession (Dini-Andreote et al., 2016). However, it remains unclear whether changes in the abundance of specific microbial taxa in succession are related to changes in community functioning due to the close association of plant and soil microbial communities through bidirectional exchanges (Bever, 1994). Zhang et al. (2013) reported a decreasing decomposition rate during secondary succession from grassland to forest; however, the relationship between decomposition rate change and microbial functions remains unclear. In addition, the role of microbial function shifts in the C and N cycles along the successional gradient remains unknown.

Succession provides an opportunity to study changes in plant communities and in belowground microbial processes. However, studies of long-term succession usually involve primary succession (Schmidt et al., 2008; Williams et al., 2013), whereas studies of changes in the composition and function of belowground microbial communities during secondary succession have only been conducted on relatively small scales (Banning et al., 2011; Zhang et al., 2016). To the best of our knowledge, intact, long-term secondary succession over a 100-year period from abandoned land to grassland to shrub and forest and finally to predominantly stable plant communities has rarely been studied; as a result, the establishment of microbial communities and shifts in microbial function during such long-term succession are poorly understood. Here, we use a chronosequence in the Ziwlung forest region on the Loess Plateau of China with approximately 160 years of secondary succession to investigate the patterns of bacterial and fungal community succession that are associated with functional change. These patterns are investigated using microbial rRNA genes, shotgun metagenomic sequencing of total soil DNA and a suite of complementary approaches to reveal the responses of the structure and function of soil microbial communities to long-term secondary succession. In addition, we assessed the litter decomposition rate, the microbial respiration rate, the ratio of carbon (C)-use efficiency to N-use efficiency (CUE:NUE), and the related potential enzyme activity, all of which are related to litter decomposition, in the long-term secondary succession.

The major aims of this study are to assess how the microbial community and its potential functions change during secondary succession and how they subsequently influence litter decomposition and the process of succession and to identify the mechanisms driving nutrient cycling over the course of succession. We ask (1) What are the patterns of microbial community composition and functional shifts that occur along the long-term successional gradient? (here, we chose a site that was naturally regenerated on abandoned land and that has been transformed from grassland to shrubland and latter successional forest over approximately the past 160 years) (2) Which component (the bacterial community or the fungal community) is more sensitive to succession, and which factor (soil or litter properties) is more associated with soil microbial shifts? (3) How does microbial potential function

change with succession, and do shifts in microbial genes affect nutrient cycling and drive succession as feedback?

2. Materials and methods

2.1. Study area and soil sampling

This study was conducted at the Lianjiabian Forest Farm in the Ziwlung forest region in Gansu Province, China (35°03′–36°37′N, 108°10′–109°18′E, 1211–1453 m a.s.l.). This region covers a total area of 23,000 km² (Supplementary Figure S1). In this area, the annual temperature is 10 °C, the annual rainfall is 587 mm, and the soil pH ranges from 7.92 to 8.31. The region is covered in species-rich uniform forests with a forest canopy density ranging from 80% to 95%. The soil in the region is calcareous cinnamon soil (Ustalfs) that evolved from primary or secondary loess 50–100 m in depth (Jia et al., 2005; Zou et al., 2002).

Based on previous research in the study area, the secondary succession has naturally regenerated on abandoned cropland (maize and foxtail millet were the main rotational crops grown in these stands for > 15 years before afforestation). The arable land was abandoned at different times after the local inhabitants emigrated from this area due to famine, war and other disasters that have occurred since 1842; thus, various successional stages from grassland to shrubland and latter successional forest (*Q. liaotungensis*) have been observed in this region over approximately the past 160 years (Wang et al., 2010). Chen (1954) investigated the vegetation recovery in this area in the 1950s and found that *P. davidiana* made up 70% of the vegetation cover after approximately 100 years. Zou et al. (2002) investigated the vegetation succession in this area three times (in 1962, 1982 and 2000) and found that the *P. davidiana* forests were replaced by *Q. liaotungensis* forests after approximately 50 years; thus, the recovery period for *Q. liaotungensis* forests was approximately 160 years. The ages of shrub and herbaceous communities that have undergone less than 60 years of recovery were estimated by consultation with local elders and by taking into account land contracts between farmers and the government; the age of forest communities older than 60 years was also determined by evaluating tree rings and consulting relevant written sources (Zhong et al., 2017). Our group investigated the vegetation succession in 2005 (Wang et al., 2010) and 2015. We chose four vegetation recovery stages as the subject of the study: (1) the grassland stage (approximately 30 years, S1), in which *Bothriochloa ischaemum* (Linn.) Keng is the main herbaceous species; (2) the shrubland stage (approximately 60 years, S2), in which *Hippophae rhamnoides* (Linn.) is the main shrub species; (3) the pioneer forest stage (approximately 110 years, S3), which is dominated by *Populus davidiana* Dode; and (4) the latter successional stage (approximately 160 years, S4), which is dominated by *Quercus liaotungensis* Koidz.

The degree of temporal variability also plays an important role in soil microbial communities; however, because soil sampling is inherently destructive, the exact same location cannot be sampled repeatedly (Fierer, 2017). Furthermore, in the few cases in which temporal variation has been explicitly quantified, temporal variation is typically lower than spatial variation (Docherty et al., 2015; Lauber et al., 2013). Thus, in this study, we performed one-time sampling in late September 2015. When the leaves began to senesce, four independent replicate plots not less than 300 m apart and not more than 5 km apart were established for each stage; the difference in elevation between any two samples was less than 120 m. The sizes of the sample plots in the forest, shrub and herbaceous communities were 20 m × 20 m, 5 m × 5 m and 2 m × 2 m, respectively. All surveyed soils had developed from the same parent materials and had been vegetative for varying lengths of time.

Nine soil samples were randomly sampled and combined from the 0–20 cm soil layer (the humus layer was removed at the forest sites) in each replicate plot at each stage using a soil-drilling sampler (5 cm

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