



## Divergent assemblage patterns and driving forces for bacterial and fungal communities along a glacier forefield chronosequence

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### ABSTRACT

Despite the ubiquitous distributions and critical ecological functions of microorganisms in pedogenesis and ecosystem development in recently deglaciated areas, there are contrasting successional trajectories among bacteria and fungi, but the driving forces of community assembly still remain poorly resolved. In this study, we analyzed both bacterial and fungal lineages associated with seven different stages in the *Hailuoguo Glacier Chronosequence*, to quantify their taxonomic composition and successional dynamics, and to decipher the relative contribution from the bottom-up control of soil nutrients and altered vegetation as well as top-down pressures from nematode grazers. Co-occurrence networks showed that the community complexity for both bacteria and fungi typically peaked at the middle chronosequence stages. The overlapping nodes mainly belonged to Proteobacteria and Acidobacteria in bacteria, and Ascomycota and Basidiomycota in fungi, which was further supported by the indicator species analysis. Variation in partitioning and structural equation modeling suggested that edaphic properties were the primary agents shaping microbial community structures, especially at the early stages. The importance of biotic factors, including plant richness and nematode feeding, increased during the last two stages along with the establishment of a coniferous forest, eventually governing the turnover of fungal communities. Moreover, bacterial communities exhibited a more compact network topology during assembly, thus supporting determinism, whereas the looser clustering of fungal communities illustrated that they were determined more by stochastic processes. These pieces of evidence collectively reveal divergent successional trajectories and driving forces for soil bacterial and fungal communities along a glacier forefield chronosequence.

### 1. Introduction

Microbes are usually the first colonizers and keystone players to elicit a cascade of processes crucial for the development of higher-trophic level food webs, especially in many pristine environments, including glacier retreat areas (Bradley et al., 2016). Despite their ubiquity in terrestrial ecosystems and importance in ecological functioning, the diversity and distribution patterns of soil microbes at regional and global scales are far less understood than the respective distribution patterns of above-ground macro-organisms, such as plants and animals (Kazemi et al., 2016). The continuum of stages on glacier

forefronts represents an ideal framework to study trajectories of microbial succession, as many glaciers have well-documented recession rates, and thus, the distance from the glacier provides a proxy of the time of the retreat, allowing for the examination of microbial succession along a spatial chronosequence (Walker et al., 2010).

Broad ecological differences between bacterial and fungal organisms, such as growth rates, stress tolerance and substrate utilization, suggest that they could follow distinct trajectories and show contrasting dynamics during ecosystem succession (Hannula et al., 2017). In fact, a number of studies have investigated the effects of environmental factors on soil microbial abundance and community structure at different

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scales. Intriguing results from the pioneering studies of Brown and Jumpponen (2014) and Cutler et al. (2014) showed that bacteria and fungi exhibit contrasting successional trajectories. Brown and Jumpponen (2014) claimed that bacterial succession was influenced more by plant establishment than by the succession of fungal communities during pedogenesis. Furthermore, the presence of plants but not the plant identity itself played a crucial role in structuring bacterial communities along the chronosequence. In contrast, Cutler et al. (2014) found that fungi were closely linked to plant establishment but bacteria were less so. Moreover, bacterial communities seemed to converge along the chronosequence, whereas no evidence of convergence was found in the fungal community. The reasons for this discrepancy are uncertain, and our understanding of the patterns and drivers of soil microbial communities remains limited, hampering generalizations on the basis of available studies.

Besides the bottom-up control of nutrient quality and quantity from altered vegetation, microbial communities are also influenced by top-down pressure from nematodes and other grazers (Wardle, 2006). Soil nematodes use an exceptionally wide range of resources and form functional groups at each trophic level, thereby holding a central position in the food web (Grandy et al., 2016). Therefore, the development of holistic models that include the full soil-plant-microbe-nematode complex will provide important clues for understanding the whole ecosystem development. Recent empirical and theoretical studies have highlighted that both stochastic and deterministic processes govern the spatial distribution of microbial communities at different spatial and temporal scales (Caruso et al., 2011). Neutrality-based theories emphasize that communities are stochastically assembled by probabilistic dispersal, ecological drift or historical inertia (Hubbell, 2001). In contrast, according to deterministic models, successional changes are directional, with dissimilarities among patches and successional rates decreasing over time, as communities converge towards similar stable states resistant to further colonization and invasion (Clark, 2009). The knowledge gap is particularly pronounced in understanding the relative importance of these two processes as drivers for bacterial and fungal assemblages. The clustering of bacteria along the Lyman Glacier Chronosequence suggested that bacterial communities are compiled in a more deterministic fashion than fungal communities (Brown and Jumpponen, 2014). In contrast, in a steppe ecosystem in North China, Zhang et al. (2011, 2016) argued that environmental changes affect the assembly of bacterial communities primarily through stochastic processes. However, most previous studies have focused on only a single group of organisms or a single trophic level (but see e.g., Soinenen et al., 2007; Norfolk et al., 2015). Recently, Jonsson et al. (2016) investigated seven different groups of organisms and discovered a more deterministic pattern for beetle community changes, but a more stochastic pattern for litter fungal community changes along with the age of the ecosystem. It is reasonable to speculate that deterministic and stochastic processes can play different roles in contrasting organisms during different (early vs. late) successional stages (Powell et al., 2015; Jonsson et al., 2016). However, current evidence is mostly based on descriptive approaches, which may limit the evaluation of the relative importance between these two types of processes during ecosystem succession (Zhang et al., 2016).

The *Hailuogou Glacier Chronosequence* provides an excellent place to study the relationship between vegetation succession and soil development, as its relatively mild and humid climate allows for rapid moraine colonization by plants and promotes fast ecosystem development. Along the approximately 2 km-long belt, a series of sites representing different stages of vegetation succession can be readily recognized, from a barren stage supporting only some mosses to a lush forest stage. At this site, several studies have investigated specific processes or organisms, such as pedogenesis (He and Tang, 2008; Zhou et al., 2013), plant succession (Zhong et al., 1997; Yang et al., 2014), soil nematodes (Lei et al., 2015) and microbial changes (Sun et al., 2016a). However, the understanding of the mechanistic underpinnings

of community assembly is still highly fragmentary, especially for the holistic soil-plant-microbe-nematode complex.

In this study, we used high-throughput Illumina paired-end sequencing of the bacterial small-subunit ribosomal RNA (16S rRNA) gene and the fungal ribosomal internal transcribed spacer (ITS) to determine both bacterial and fungal lineages associated with decadal scale stages of soil development in the *Hailuogou Glacier Chronosequence*. Our main objectives were to disentangle fungal and bacterial successional dynamics and community assembly as well as to decouple the effects of plant establishment, soil development and nematode grazing on microbial successional trajectories. We hypothesized that: (1) bacterial and fungal communities show hump-shaped responses to soil ageing, and the chronosequence enters into its retrogressive phase after 120 years of succession mainly due to the decreased nutrient availabilities; (2) edaphic properties serve as the primary agents in shaping bacterial communities, while the increasing abundance of lignin-rich coniferous tree species at later stages of succession exerts a greater impact on fungal communities; (3) stochastic processes dominate in microbial and microfauna community assemblages at the early stages, while deterministic factors are more prevalent in plants and at the later stages. To the best of our knowledge, this is among the first attempts to integrate knowledge of the soil-plant-microbe-nematode complex in a glacier forefield, and it may provide a breakthrough for a more holistic view of ecosystem development in the warmer and increasingly ice-free future world (Grandy et al., 2016).

## 2. Materials and methods

### 2.1. Study sites

The *Hailuogou Glacier Chronosequence* area has been described in detail in Zhou et al. (2013) and Lei et al. (2015). Briefly, the mean annual precipitation is about 2000 mm, with most (over 68%) occurring between June and October. The mean annual air temperature is 3.8 °C, monthly averages ranging from −4.3 °C in January (lowest) to 12.7 °C in July (highest). The observed recession of the Hailuogou Glacier began in 1823, and it has accelerated markedly since the early 20th century. This study was conducted on seven sites undergoing long-term primary succession starting from bare soil, to pioneer communities and eventually to the climax vegetation communities at different ages after deglaciation and at different distances from the glacier terminus (Fig. S1; Lei et al., 2015). The approximate age for each stage studied was calibrated with chronologies according to tree-rings and soil erosion rates assessed by <sup>137</sup>Cs budget, and a seven-scale chronosequence (from stage 1, ca. 3 years since the glacier retreat, to stage 7, ca. 120 years; Fig. S1) was used.

### 2.2. Sampling design

At each chronosequence stage, three 5 × 5 m square experimental plots with a 10-m distance between the plots were established (except stages 1 and 2 where 2 × 2 m square plots with a 3-m distance between the plots were used due to the smaller area at the early stages). The taxa of plant communities were determined to the species level to assess plant richness, including tree, shrub and herb layers (Yang et al., 2014). If higher than 3 m, the tree biomass was calculated with the allometric equations reported by Zhong et al. (1997). The biomass of the shrub and herb layers was obtained through destructive sampling within the central 2 × 2 m of each subplot (Yang et al., 2014). All sampled plant material was sorted by species, and then oven-dried and weighted.

For soil sampling in mid-August 2016, a 50 × 50 cm quadrat was established in each of the three square plots at each stage, and five soil cores were collected from the center and each corner of the quadrat using a 5-cm diameter soil corer after removal of litter from soil surface by hand. The five soil cores were combined as one composite soil sample, and homogenized to pass through a 2-mm sieve after removing

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