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Bacterial communities in soil mimic patterns of vegetative succession and ecosystem climax but are resilient to change between seasons

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ABSTRACT

Organism succession during ecosystem development has been researched for aboveground plant communities, however, the associated patterns of change in below-ground microbial communities are less described. In 2008, a study was initiated along a developmental sand-dune soil chronosequence bordering northern Lake Michigan near Wilderness Park (WP). It was hypothesized that soil bacterial communities would follow a pattern of change that is associated with soil, plant, and ecosystem development. This study included 5 replicate sites along 9 soils ($n = 45$) ranging in age from ~105 to 4010 years since deposition. Soil bacterial community composition and diversity were studied using bacterial tag-encoded FLX amplicon pyrosequencing of the 16S rRNA gene. Bray–Curtis ordination indicated that bacterial community assembly changed along the developmental soil and plant gradient. The changes were not affected by seasonal differences, despite likely differences in plant root C (e.g. exudates), temperature, and water availability in soil. Soil base cations (Ca, Mg) and pH declined, showing log-linear correlations with soil age ($r \sim 0.83$, 0.84 and 0.81; $P < 0.01$). Bacterial diversity (Simpson's $1/D$) declined rapidly during the initial stages of soil development (~105–450 y) and thereafter (>450 y) did not change. Turnover of plant taxa was also more rapid early during ecosystem development and correlated with bacterial community structural change ($P < 0.000001$; $r = 0.56$). It is hypothesized that plants help to drive pedogenic change during early (<450 y) soil development (e.g. pH decline, cation leaching) which drive selection of soil bacterial communities. In mature soils (~450–4000 y), resilient and stable soil bacterial community structures developed, mimicking steady-state climax communities that were observed during latter stages of primary plant succession. These relationships point to possible feedbacks between plant and bacterial communities during ecosystem development.

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1. Introduction

Microorganisms are key drivers of global biogeochemical cycles and are considered the most abundant and diverse organisms on earth (Torsvik et al., 2002; Falkowski et al., 2008). Despite their vast diversity, the biogeography of microbes on small and large scales is poorly understood (Ranjard et al., 2010). Previous studies have shown that environmental factors, such as quantity and quality of available soil carbon (Blaalid et al., 2011), nitrogen (Eaton et al., 2011), texture (Monroy et al., 2012), land-use history (Jangid et al., 2008; Drenovsky et al., 2010) and season (Williams, 2007) influence soil microbial community structure. Studies of bacterial community change during early (~100 y) ecosystem development adjacent to retreating glaciers have generally shown that bacterial communities are highly dynamic during early ecosystem development (Nemergut et al., 2007; Schutte et al., 2009), but that patterns of change are not always easy to discern or to relate to soil and vegetative properties (Wu et al., 2012; Zumsteg et al., 2012). Over shorter-time scales, in contrast, bacterial communities have been shown to be relatively static between seasons and across a variety of land use types (Jangid et al., 2008, 2010). How bacterial communities become structured over seasons and during the natural process of soil accrual, weathering and nutrient transformations (pedogenesis) over much longer time scales could provide clues to the underlying mechanisms and feedbacks that regulate community assembly (Green and Bohannan, 2006; Green et al., 2008).

Numerous studies have researched above-ground and below-ground feedbacks, for example, implicating soil microbes as

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important determinants of plant diversity and productivity (Ehrenfeld et al., 2005; Kara et al., 2008; Van Der Heijden et al., 2008). Above-ground plant community composition, in turn has a major influence on the microbial community by driving changes in litter quality, soil acidity and soil moisture (Porazinska et al., 2003; Kardol et al., 2007; Mitchell et al., 2011; Zhang et al., 2011). It is not well-known, however, how these processes of long-term ecosystem development, vegetative succession, and pedogenesis are related to changes in soil microbial communities (Wardle et al., 2012). If above- and below-ground subsystems are linked and feedback, then patterns of bacterial and plant community change should also show relationships with pedogenesis over hundreds, and thousands of years of ecosystem development. Describing how bacterial communities change during ecosystem development could thus provide fundamental insight into above and below-ground linkages and ultimately whether these feedbacks underlie patterns of community and ecosystem function.

Differences in bacterial community composition and diversity across a series of developmental sand-dune soil chronosequences bordering northern Lake Michigan and ranging in age from ~105 to 4010 years since deposition were studied. A pyrosequencing-based approach was used to characterize phylogenetic changes in soil bacterial communities across the chronosequence. The primary hypothesis was that bacterial communities would follow patterns of change associated with the relatively long-term processes of pedogenesis and primary vegetative succession. The effect of season was also tested to observe whether shorter-term environmental change regulates bacterial community structure. Succession is defined as a non-random "pattern of change" in communities through time (Wardle et al., 2012).

2. Materials and methods

2.1. Site description

The study site consists of a series of beach-dune ridges bordering Lake Michigan (N 45.72729, W 84.94076), and located in Emmett County of northern lower Michigan. Periods of unusually moist conditions altering with dry spells associated with swelling and receding of Lake Michigan formed a series of ~108 eolian deposited dune ridges running parallel to the shoreline with depositional ages from present day to ~4500 years (Lichter, 1995). The dune ridges have a parent material originating from glacial deposits and Paleozoic bedrock underlying the lake basin. Fine sands deposited on the lake shore are dominated by quartz but contain numerous other minerals in minor quantities. The youngest soils (~100 y) are mapped as dunes which then develop into Deer Park sands (soil series) and described taxonomically as mixed, frigid, Spodic Udipsamments. The oldest soils (>1475 y) tend to be mapped to the Roscommon series, and are mixed, frigid Mollic Psammaquents. The chronology of the dunes was estimated using Accelerated Mass Spectroscopy (AMS) radiocarbon dating of macrofossil remains from each dune (Lichter, 1995). The ridges are approximately 2.5 km long, 10–30 m wide, and vary between 3 and 5 m high to 15 m high parabolic dunes inland (Lichter, 1998a). A previous study (Lichter, 1998b) has shown that patterns of primary succession with grasses and shrubs on younger dunes change into mixed coniferous forests that dominate older dunes.

2.2. Soil and vegetative sampling

Five replicate soil samples were taken at (10-m) intervals across transects (35–120 m) along each dune's crest. From each sampling location, 5–6 sub-sample cores were collected from the incipient A–E horizon (0–15 cm, 5-cm dia.), homogenized, stored in sterile Whirlpak® bags, and frozen immediately in coolers with dry ice. Five replicate samples were also collected along the beach to simulate the material that might be the source of the dune ridges (time zero). Soils were thawed briefly (25–30 min) to clean extraneous roots and other organic materials by passage through a 4-mm sieve. Samples were collected in August (Summer) and December (Winter) of 2008.

Along each replicate soil age, plant species composition, tree density, and percentage canopy cover was measured (5×20 m^2). The tree composition and density were measured by counting the number of species within the sampling area and measuring DBH (Diameter Breast Height), respectively. Understory species cover was measured at five random locations within the sampling area using a 1 sq. m quadrat. Two quadrats were randomly placed on each sampling spot along each replicated age. Understory species were identified and their percentage cover was estimated by visual observation as agreed by two observers. For the vegetation data, species that were rare (occurred in 3 or fewer plots) were removed. The tree species canopy cover was estimated by fitting the DBH measurement into a conifer crown radius model (Dequiedt et al., 2011).

2.3. Soil characteristics

Soil organic matter content was measured by loss on ignition (560 °C) in dry soils (104 °C) by subtracting the mass difference before and after ignition. Carbon content on dry soils was measured using a Elementar vario Max CN. Carbonate content was estimated as described by Amundson et al. (1988). The mineralizable C was estimated by measuring the cumulative CO_2-C released over 1 month. Incubations were carried out using 1 L canning jars filled with 100 g of soil (−0.03 MPa) and sealed with a lid fitted with a rubber septum. Soil pH was measured on 1:2 soil and 0.01 M $CaCl_2$ mixture. Soil extractable cations were extracted and analyzed according to the Mehlich-3 extraction protocol (Maron et al., 2011, Table 1).

2.4. DNA extraction and pyrosequencing

Total community DNA was extracted from 0.5 g of soil using ZR Soil Microbe DNA Kit (Zymo Research, Orange, California) with minor modifications in the manufacturer's protocol as described in Garcia et al. (2011), inventoried, and stored at −80 °C. PCR amplification of the bacterial 16S rRNA V3 region, purification and processing for pyrosequencing was carried out using primers and conditions as described by Garcia et al. (2011). Samples were initially denatured at 95 °C for 3 min, then amplified by using 22 cycles of 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 1 min. Samples were further purified to remove PCR inhibitors using *OneStep*™ PCR Inhibitor Removal Kit (Zymo Research). The final mixed amplicon pool was submitted to the Environmental Genomics Core Facility at the University of South Carolina for pyrosequencing with Roche® GS FLX sequencing (Branford, CT, USA), yielding 108,273 reads (260-bp average length).

2.5. Processing of 16S rRNA gene data

A two-step pipeline was established to analyze the 16S rRNA gene sequence data. QIIME (Caporaso et al., 2010) was used to quality trim the raw sequences for primers and chimeras and to sort them based on the barcodes. The denoised data were then analyzed using MOTHUR v1.22.0 (Schloss et al., 2009). The sequences were aligned using SILVA reference database and a distance matrix was generated in MOTHUR followed by filtering

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