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Long-term chronological shifts in bacterial communities and hydrolytic extracellular enzyme activities in the forty years following a land-use change from upland fields to paddy fields

Nan Jiang, Kai Wei, Lijun Chen*

State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China

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ABSTRACT

Here, we used a forty-year chronosequence of land-use change from upland fields to paddy fields to study short- and long-term temporal patterns in bacterial communities and extracellular enzyme activities (EEAs). Soil samples were collected at two depths (0–20 cm and 20–40 cm) from one upland field and six paddy fields that were established on former upland fields at different time points (1, 5, 10, 20, 30, and 40 years before the study). 454 barcoded-pyrosequencing was used to identify the bacteria residing in each soil sample. Following the land-use change, bacterial diversity was reduced and bacterial community composition changed in the short-term; however, communities demonstrated a certain level of resilience, returning in structure and composition to states that resembled their original states, prior to land-use change, during the first two decades. In addition, different bacterial responses were observed for the two soil depths. Soil chemical properties were associated with some of these changes; total phosphorus (TP), soil pH and Olsen phosphorus (OP) were significantly correlated with bacterial communities, while both soil pH and nutrient contents significantly affected the EEAs. In addition, we found evidence suggesting associations between EEAs and the abundance of specific bacterial genera, particularly to *Chloroflexi* and *Proteobacteria* . Overall, this study provides a temporal view of the bacterial community assembly and functional shifts following land-use change.

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1. Introduction

Bacteria, the most abundant and diverse group of soil organisms, produce extracellular enzymes (EEs) that catalyze important transformations in the carbon (C), nitrogen (N) and phosphorus (P) cycles (Acosta-Martinez et al., 2008; Stone et al., 2014). Land-use change is a common occurrence and may possibly disturb soil bacterial communities (Lauber et al., 2008; Osborne et al., 2011; Vink et al., 2014), and their extracellular enzyme activities (EEAs) (Salam et al., 1998; Wallenius et al., 2011). As the most important agronomic activity and productive practice (Liesack et al., 2000), paddy cultivation has increased steadily during recent decades to meet the demands of an increasing population (Liu et al., 2011; Wang and Gu, 2013). Shifts in the diversity and composition of bacterial communities and EEAs after conversion of natural ecosystems, such as forest and grassland, to cultivated land have been increasingly reported (Jesus et al., 2009; Suleiman et al., 2013). However, little is known about how a land-use change from upland to paddy fields influences the structural and functional responses of bacteria.

Any land-use change can possibly cause a disturbance. According to Allison and Martiny, there are three potential impacts on microbial communities caused by a disturbance. After a disturbance, the microbial composition might be resistant and not change, might be altered and rapidly return to the original composition (resilient), or might remain altered (Allison and Martiny, 2008; Suleiman et al., 2013). Long-term investigations are indispensable to determine the situation or stage. In addition, land-use change can have significant and long-lasting effects on soil chemical properties (Lauber et al., 2008), including soil pH, C/N ratio and total nitrogen (TN). These properties have usually been reported as important factors influencing microbial community composition, microbial diversity and soil enzyme activities (Caldwell, 2005; Hu et al., 2013; Lauber et al., 2009; Moritsuka et al., 2013). Moreover, during the growing season, a rice paddy soil is an artificial wetland whose water-saturated sediment has limited exposure to oxygen (Nicolaisen et al., 2004). After conversion of upland fields to paddy fields, ammonia-oxidizing bacteria have been shown to experience a slight decline in number and a significant shift in composition (Alam et al., 2013).

* Corresponding author.
E-mail addresses: ljchenchina@hotmail.com, ljchen@iae.ac.cn (L. Chen).

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Nevertheless, there is little further detail concerning the relationship between bacterial communities and soil attributes or EEAs in either ecological environment. Furthermore, different microbial communities occur at different soil depths (Fierer et al., 2003; Huang et al., 2013). However, whether the responses of bacterial communities to land-use change are dependent on soil depth remains unclear.

In the present work, to elucidate bacterial variability across a chronosequence after conversion of upland fields to paddy fields, we investigate bacterial communities that have been exposed to land-use changes over the course of four decades using 454 barcoded pyrosequencing. Our main objectives are to provide an investigation into bacterial responses to land-use change across a forty-year chronosequence and their relationships with temporal patterns in soil properties by (1) assessing the time-dependent changes in bacterial communities at two soil depths following a land-use change from upland to paddy fields in the Songnen Plain (55,900 km^2 farmland area) in Northeast China, (2) identifying the most important soil factors influencing the bacterial communities, and (3) examining the shifts in EEAs and their correlation with bacterial communities after the land-use change. The results of this study will expand our understanding of bacteria and its vital factors, including chemical properties and EEs, which influence the agricultural ecosystem.

2. Material and methods

2.1. Soil sampling, chemical analyses

The study sites include paddy fields that were established on former croplands in the Songnen Plain of northeast China (46.83–46.89°N, 127.09–127.11°E). Briefly, a total of seven time points (0, 1, 5, 10, 20, 30, and 40 years) after the land-use change were examined. Soil samples were collected after the rice-growing seasons. Area of each field was at least 1 ha and the fields were located less than 2 km apart. All plots were similar in soil type, the level topography, climate, and in irrigation and fertilizer use practices (except the upland). For each field, five random cores (as "S") were collected from the surface soils in the top 20 cm and the subsurface soils at 20-40 cm. Before the fields were used as paddy field they had been planted with maize with a conventional tillage management for more than 100 years. The soil samples were stored at −80 °C prior to molecular analyses and at 4 °C before chemical and enzyme analyses. The chemical and enzyme analyses were completed within two weeks. For chemical analyses, each sample was air-dried, sifted through a 2.0-mm mesh sieve and stored at an ambient laboratory temperature. The soil pH was determined using a 1:15 (w/w) soil/$BaCl_2$ (0.1 M) suspension using a glass electrode (Hendershot et al., 2007). The samples were sifted through a 100-mesh (0.15 mm) sieve for the total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP) analyses. TOC and TN were determined using a Vario MACRO cube analyzer (Elementar Analysensysteme Vario MACRO cube, Germany). TP was determined using the molybdate method following perchloric acid ($HClO_4$) digestion (Sparks et al., 1996). Olsen phosphorus (OP) was extracted using sodium bicarbonate prior to analyses (Sims, 2000).

2.2. Extracellular enzyme assays

Enzymes involved in soil C, N, and P cycling were selected. The activities of β-glucosidase (EC3.2.1.21, BGL) and *N*-acetyl-β-D-glucosaminidase (EC3.2.1.52, NAG) were determined in an assay using a fluorogenic substrate. This assay is based on a method described by Marx et al. (2001). The substrates for these enzymes were 4-methylumbelliferyl β-D-glucopyranoside and 4-methylumbelliferyl *N*-acetyl-β-D-glucosaminide, respectively, and were dissolved in 0.4% methyl cellosolve (0.1% final concentration in the assay). For each sample, soil suspensions were prepared as a 1:100 ratio of soil to deionized water (containing 1 mM NaN_3 to prevent microbial activity) by stirring on a magnetic stir-plate for 15 min (Turner and Romero, 2010). Soil suspensions (50 μL) were then pipetted into wells on a micro-well plate. Each well contained 100 μL of 200 μM substrate and 50 μL of 200 μM sodium acetate-acetic acid buffer adjusted to the soil pH. Plates were incubated for 30 min at 30 °C for a standard assay temperature. The reaction was terminated by adding 50 μL of 0.5 M NaOH. Fluorescence was measured immediately on a Tecan Infinite 200 PRO multifunctional microplate reader (TECAN Group Ltd., Mannedorf, Switzerland) with an excitation wavelength of 360 nm and an emission wavelength of 460 nm. Control wells were prepared for each substrate and contained substrate, buffer, and 1 mM NaN_3. Blank wells contained soil suspension and buffer only. Standard wells contained buffer, 1 nmol methylumbelliferone (MU), and either soil suspension or 1 mM NaN_3 to account for reduction of fluorescence in the presence of soil (quenching). All enzyme activities are expressed as nmol MU g^{-1} soil (dry-weight) min^{-1}. Each sample was repeated eight times.

The activities of alkaline phosphatase (EC3.1.3.1, AlP), acid phosphatase (EC3.1.3.2, AcP), phosphodiesterase (EC3.1.4.1, PD) and inorganic pyrophosphatase (EC3.6.6.1, IPP) were determined as described by Tabatabai (Tabatabai, 1994). In brief, AlP and AcP were assayed using *p* -nitrophenyl phosphate as the substrate with the buffer adjusted to pH 11.0 and 6.5, respectively. PD was assayed using bis-*p*-nitrophenyl phosphate as the substrate with the buffer adjusted to pH 8.0. IPP was assayed using sodium pyrophosphate decahydrate as the substrate. The activities of AlP, AcP, and PD were expressed as mg *p*-nitrophenol kg $^{-1}$ soil h $^{-1}$, and IPP activity was expressed as mg PO_4^{3-} –P kg $^{-1}$ soil h^{-1}.

2.3. Genomic DNA extraction and 454 pyrosequencing

To minimize error from site-specific differences, within each soil depth, equal masses of the five random soil samples from an individual field were thoroughly mixed to form one sample for the following experiments. The total genomic DNA was extracted from 1.0 g of each mixed soil sample using the E.Z.N.A.™ Soil DNA Kit (Omega, CT, USA) according to the manufacturer's instructions. The concentration and quality of the DNA was determined using a NanoDrop ND 2000 spectrophotometer (USA). The hypervariable V1–V3 regions of the 16S rDNA were amplified using the universal primers named 8F/533R (5′-AGAGTTTGATCCTGGCTCAG/5′-TTACCGCGGCTGCTGGCAC) (Baker et al., 2003). Both primers incorporated the FLX Titanium adaptors and a sample barcode sequence. The PCR experiments were performed in triplicate 20-μL reactions as follows: 5 min of initial denaturation at 95 °C; 25 reaction cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and elongation at 72 °C for 30 s; and a final extension at 72 °C for 5 min. Pooled triplicate reactions were purified using the AxyPrepDNA Gel Extraction Kit (Axygen, USA) according to the manufacturer's recommendations. The DNA concentration was determined using the QuantiFluor-ST PicoGreen double-stranded DNA assay (Promega, USA), and the quality was controlled for using an Agilent 2100 bioanalyzer (Agilent, USA). The pyrosequencing was performed using a Roche GS FLX + system(Roche, Switzerland) at Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China. Sequence data were submitted to the GenBank databases under the biosample accession numbers SAMN02925421–SAMN02925434 (SRR2043284).

2.4. Processing of pyrosequencing data

QIIME software (Caporaso et al., 2010) was used to trim all pyrosequencing reads according to a sliding window of 50 bp and a minimum average quality score of 20. After trimming, the reads

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