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## Bacterial succession along a long-term chronosequence of paddy soil in the Yangtze River Delta, China



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#### ABSTRACT

Conversion of tidal wetlands into paddy soils is an ancient and prevalent agricultural practice to meet increasing demand of food in the Yangtze River Delta of China, a coastal region where paddy soils originated. However, the impacts of tidal wetland reclamation and continuous rice cultivation at long time scales on soil bacterial communities remains poorly understood. In this study, we investigated temporal dynamics of bacterial communities using 16S rRNA gene pyrosequencing to delineate the patterns and drivers of soil bacterial succession along a long-term (2000 years) chronosequence of paddy field since reclamation from tidal wetlands. The results exhibited orderly changes in soil physicochemical characteristics and bacterial community composition with increasing rice cultivation time, indicating the occurrence of paddy soil development and bacterial succession since reclamation from tidal wetlands. Soil bacterial diversity significantly increased after reclamation of tidal wetlands. Succession of bacterial community composition was primarily linked with significant decrease in the relative abundances of Gammaproteobacteria and Planctomycetes and increase in those of Alphaproteobacteria and Firmicutes. Further analysis showed that long-term rice cultivation led to the enrichment of certain populations such as Rhodospirillaceae (within the class Alphaproteobacteria) and Clostridiaceae (within the phylum Firmicutes), which are potentially beneficial to higher rice yields. Canonical correspondence analysis indicated that at the time scale of millennia, the shift of bacterial community structure was mainly driven by the changes of soil physicochemical properties, especially cation exchange capacity and pH during paddy soil development. Overall, we demonstrate an orderly shift of soil bacterial communities towards higher productivity along with a 2000-year development of paddy soils after the tidal wetland reclamation, which was primarily associated with soil physicochemical alterations with time, and suggest that such chronosequence of paddy soils can serve as a test bed to delineate the relationship between microbial community and soil functions, particularly crop productivity.

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## 1. Introduction

The effects of changes in land use types on soil microbial communities has received growing attention in recent decade because of the critical importance of microorganisms in soil health and nutrient biogeochemical cycling. Significant changes in microbial community composition and functionality have been observed after ecosystem conversion, including wetlands or grassland to forest

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ecosystems (D'Angelo, Karathanasis, Sparks, Ritchey, Wehr-McChesney, 2005; Berthrong, Schadt, Pineiro, Jackson, 2009), restoration of agricultural soils to wetlands (Hartman, Richardson, Vilgalys, Bruland, 2008), and temporary upland conversion in paddy ecosystems (Chu, Morimoto, Fujii, Yagi, Nishimura, 2009). Nevertheless, these studies have mainly focused on the influences shortly after the transformation of ecosystems, it is unclear whether such changes in microbial communities were driven by different types of land use or merely reflected a transient response to disturbance of a steady-state ecosystem. To answer this question, it is imperative to explore the long-term dynamics of soil microbial communities after ecosystem conversion.

Soil chronosequence is considered to be a powerful tool for



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studying rates and directions of soil development (Huggett, 1998). It ascribes the detected differences among soils to the function of time only, since other environmental factors such as soil-forming factors are relatively constant (Huang et al., 2015). Due to this unique characteristic, soil chronosequence has been widely used to study patterns and drivers of shift in soil microbial communities at long time scales (i.e., succession) under natural conditions (Allison, Miller, Jastrow, Matamala, Zak, 2005; Tarlera et al., 2008; Moore et al., 2010). Tarlera et al. (2008) investigated the microbial community succession and bacterial diversity in soils that developed with 77,000 years of intermittent aeolian deposition, and revealed an orderly pattern of bacterial community development that was strongly linked with soil ecosystem development. However, information on the temporal dynamics of microbial communities in agricultural soils is rather limited, particularly at time scales spanning from centuries to millennia. This could be in part due to uncertainties of such studies, for example, artificially controlled management practices might have altered within hundreds or thousands of years (Cui et al., 2012). Nevertheless, Cui et al. (2012) have investigated soil bacterial community evolution during 500year development of agro-ecosystems, and suggested that even at long time scales, overall patterns of soil microbial succession could not be masked by short-term changes in management practices under a certain cropping system. Therefore, soil chronosequence could also provide a valuable opportunity for elucidating the patterns of microbial succession under long-term agricultural practices.

It has been well documented that reclamation of emergent wetlands in areas along coastline is a feasible and efficient approach to obtain agricultural land resources (Cheng, Yang, Cao, Ci, Yin, 2009).Paddy soils are of vital importance in food supply in China (Ding, An, Li, Zhang, Zhu, 2014), and reclamation and development of tidal wetlands towards paddy ecosystem is ancient and common in many coastal regions of China, especially in the Yangtze River Delta where rice cultivation history after reclamation from tidal wetlands can be traced back to thousands of years ago (Cao et al., 2006; Zong et al., 2007; Zhu et al., 2016). Previous studies on a 2000-year paddy soil chronosequence originated from tidal wetlands in the Yangtze River Delta showed that such ecosystem conversion and long-term development had altered the diversity/abundance of some specific microbial communities, including methane oxidizing bacteria (Ho, Lüke, Cao, Frenzel, 2011), and microbes involved in inorganic nitrogen (N) cycle such as N fixation, nitrification and denitrification (Bannert et al., 2011; Jiang et al., 2013). Although these studies have improved our understanding of the microbial succession under long-term paddy management, in which specific group of soil microbes were targeted, knowledge of the temporal dynamics of overall soil microbiota in tidal wetland derived paddy soils with different duration of rice cultivation time is still limited. This knowledge would provide useful suggestions for development of sustainable agriculture, given that microbial diversity is a major determinant of sustainable productivity of agricultural soils (van der Heijden, Bardgett, Van Straalen, 2008). Changes of bacterial communities have been reported after the reclamation of coastal wetlands to paddy soils (Cui et al., 2012). Soil physicochemical properties have been proposed to be crucial factors for shaping microbial communities (Fierer and Jackson, 2006; Freedman and Zak, 2015), and soil physicochemical alterations with time have been commonly found during soil development (Cheng et al., 2009; Zou, Fu, Cao, 2011). Additionally, soil productivity has been reported to be greatly enhanced with increasing rice cultivation time in a soil chronosequence derived from tidal wetlands (Hu et al., 2008). We thus hypothesize that bacterial succession may co-occur with long-term development of paddy soils since reclamation from the tidal wetlands, with selection of particular bacterial taxa which are potentially beneficial to higher rice yields.

To address this hypothesis, by using high-throughput 16S rRNA gene pyrosequencing (454) technique, we investigated the dynamics of bacterial diversity and community structure using a soil chronosequence up to 2000-year rice cultivation after reclamation from tidal wetlands in the Yangtze River Delta. The objectives of this study were (i) to examine if shifts in the bacterial communities have occurred along with the long-term soil chronosequence, and (ii) if a shift did occur, to investigate the relationship of environmental factors with this shift in bacterial communities.

### 2. Materials and methods

#### 2.1. Site description and soil sampling

Soil samples were collected from a land reclamation region on the south bank of Hangzhou Bay, Cixi city, Zhejiang Province, eastern part of China. This region has a north subtropical monsoon climate with a mean annual precipitation of 1325 mm and mean annual temperature of about 16.3 °C, and soils in this area are mainly originated from coastal sediments from the Yangtze River Delta (Cheng et al., 2009). More details of the study area such as geography, geochemistry and groundwater level were given by Cheng et al. (2009).

Paddy soil samples were collected from a soil chronosequence with 50-, 300-, 1000-, and 2000-year duration of rice cultivation (P50, P300, P1000 and P2000), and sediment samples were collected from the tidal wetland (PO) which typically stands for the parent materials of agricultural land reclamation through sea dike building. All these sites are located within an area of 40 km<sup>2</sup>, and the coordinates of sampling sites are as follows: P0, 30°19'N, 121°09'E; P50, 30°11'N, 121°21'E; P300, 30°06'N, 121°30'E; P1000, 30°10'N, 121°07'E; P2000, 30°05'N, 121°27'E. The duration of rice cultivation at each site was assessed based on the record in the County Annals of the Zhejiang Province, as well as in Cixi, Yuyao and Shangyu Counties (abstracted information in Chinese is available at http://www.cixi.gov.cn). In brief, within the chronosequence, all the paddy soils are developed from comparable parent materials (i.e., tidal wetlands) and under the identical ecological conditions, and their textures are mainly composed of silt-sized particles, which are similar to those of tidal wetlands (Roth et al., 2011). More detailed information of this chronosequence has been described in previous studies (Cheng et al., 2009; Zou et al., 2011).

Given that all the sampling sites are located in the same region and agricultural management has uniformly followed the central instructions of Technical Service Bureau since 1949 (time for the foundation of People's Republic of China), comparable management practices have been conducted for all paddy soils within the chronosequence. For all the paddy soils, rice cropping system was single-crop rice (*Oryza* sp.), and the types, rates, and approaches of fertilization, pesticide application and irrigation were similar among the fields (Zou et al., 2011). Additionally, all the paddy soils are farther than 10 km from the sea, and thus can't be directly flooded with seawater. The surface soils are not affected by groundwater because of the morphology of the soils (Bannert et al., 2011).

Field sampling was performed in late August 2009 during the grain filling stage of rice plants (visual observation). For each soil within the chronosequence, field samples were collected in triplicate plots (about 120 m<sup>2</sup> for each plot) from the top 15 cm of soil layer with a soil auger, each replicate containing at least five individual soil cores, which were completely homogenized to minimize heterogeneity. All samples were collected into sterile

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