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New insights into the role of microbial community composition in driving soil respiration rates

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ABSTRACT

Microbial community plays critical roles in driving soil carbon (C) cycling in terrestrial ecosystems. However, we lack empirical evidence to demonstrate the role of microbial community in driving soil respiration - a key ecosystem process for global sustainability and climate regulation. Here, we used a long-term field experiment including multiple management practices, to identify, via statistical modeling, the role of microbial community composition in influencing soil respiration. We analyzed major soil properties and microbial (both bacterial and fungal) abundance, diversity and community composition. We found that different management regimes led to different soil respiration rates. Most importantly, microbial community composition explained a unique portion of the variation in soil respiration, which cannot be accounted for by key respiration drivers such as soil properties and other microbial attributes (richness and total abundance). Microbial biomass and fungal richness were also identified as key drivers of soil respiration. Our results indicate that inclusions of microbial compositional data in Earth system models can be potentially used to improve our capacity to predict changes in soil C balance under changing environments.

1. Introduction

Soils store four times as much carbon (C) as plant and atmospheric pools (Singh et al., 2010; Karhu et al., 2014), and soil respiration releases about 60 Pg C annually from the land surface (Shao et al., 2013). Both C sequestration and soil respiration are critical processes controlling key ecosystem functions such as climate regulation, nutrient cycling and plant productivity (Singh et al., 2010; Victoria et al., 2012). Global climate change and human disturbances including intensive agricultural practices are increasing the amount of C emitted to the atmosphere with important implications for the climate regulation of Earth (Nazaries et al., 2015; Spohn et al., 2016). Because of this, predictions of soil C balance in terrestrial ecosystems have become a global priority during the last decades with the development of Earth system models as primary tools (Luo et al., 2016).

Soil respiration is driven by both biotic and abiotic factors (Walker et al., 2004; Monson et al., 2006; Orwin et al., 2016). Previous studies have demonstrated the importance of geographic location (Campbell et al., 2004; Whitaker et al., 2014), climate (temperature and rainfall) (García-Palacios et al., 2012; Karhu et al., 2014), soil properties (Delgado-Baquerizo et al., 2016a) and plant features (Raich and Tufekciogul, 2000; Knowles et al., 2015) as key predictors of soil respiration. However, current models are not able to accurately predict the variation in soil C stocks and respirations, leading to a high level of uncertainty for these predictions. Identifying new major predictors of soil respiration that allow the improvement of predictive models is one of the major challenges that we are facing today. Most recently, the inclusion of microbial processes (reflected by microbial biomass and enzyme activities) has been reported to improve the prediction of soil C fluxes at the global scales (Allison et al., 2010; Wieder et al., 2013). Similarly, microbial diversity has been reported to drive multiple soil functions including soil respiration (Delgado-Baquerizo et al., 2016b; Liu et al., 2017). Further, in addition to microbial biomass and diversity, other microbial parameters such as community composition

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(relative abundance of phylotypes) may greatly improve our prediction for soil respiration (Whitaker et al., 2014), given the strong positive relationships between microbial composition and the functional genes that regulate soil respiration (Trivedi et al., 2016). However, the importance of soil microbial community composition in driving soil respiration remains poorly understood and largely unexplored; and no experimental approach has been used to address this important gap of knowledge.

A growing number of studies had emphasized the significance of microbial community composition in driving soil processes and functions including gaseous emission, decomposition, nutrient cycling and plant production (Fierer et al., 2007; Peter et al., 2011; Trivedi et al., 2013, 2016). We argue that current knowledge on microbial life strategies and functional attributes can be used to markedly improve our prediction of soil respiration rates. For example, previous studies suggested that ecological functional categories of copiotrophs and oligotrophs have specific roles in utilizing soil organic C (SOC) for respiration (Fierer et al., 2007; Ramirez et al., 2012; Trivedi et al., 2013). Thus, copiotrophs such as Bacteroidetes, Alphaproteobacteria and Gammaproteobacteria are expected to have higher respiration rates compared to oligotrophs including Actinobacteria, Acidobacteria and Deltaproteobacteria (Fierer et al., 2007; Bastian et al., 2009; Singh et al., 2010; Trivedi et al., 2013). In addition, bacteria are considered to have lower C use efficiency compared to fungi (Austin et al., 2004; Waring et al., 2013). All these suggest that differences in microbial community composition could potentially explain a unique portion of the variation in soil respiration.

Herein, we posit that community composition of fungi and bacteria can potentially help explain unique portions of the variation in soil respiration which cannot be accounted for by other key drivers of soil respiration including soil properties, land management practices (i.e. inorganic and organic fertilization) and other key microbial attributes such as microbial biomass or community richness. To test our hypothesis, we collected soils from a long-term field experiment including multiple combined applications of inorganic and organic fertilizers including nitrogen (N), phosphorus (P) and potassium (K) (NPK), livestock manure, wheat straw, and commercial organic fertilizers. These agricultural practices are well-known to simultaneously modify soil abiotic properties, microbial biomass, and community richness and composition (Sun et al., 2015, 2016), which in turn provides a unique opportunity to empirically identify the role of relative importance of soil microbial community in driving soil respiration responses to the combined fertilization after accounting for key soil properties.

2. Materials and methods

2.1. Experimental design and soil sampling

The long-term experiment was established in Linquan county, Anhui province, China (33°04′58N, 115°13′42E), in October 2010. Mean annual temperature in this region is 15.3 °C and mean annual precipitation is 892 mm. The experimental plots (10 × 5 m in size) were subject to wheat-corn rotation, and the locations were selected using a randomization approach. The soil in this site belongs to a lime concretion black soil (Eutric Acrisols) (Zhang et al., 2016), with 23% clay and 48% silt content. The initial pH of the soil was 5.72, which had 0.73% organic C, 80.16 mg kg^{-1} available N, 16.92 mg kg^{-1} available P and 116.7 mg kg^{-1} available K. This experiment included nine treatments with three replicate plots for each: (1) control, no fertilization; (2) chemical NPK fertilizers application (NPK); (3) 50% NPK fertilizers plus 6000 kg fresh cow manure ha^{-1} y^{-1} (NPK + CM); (4) 50% NPK fertilizers plus 6000 kg fresh pig manure ha^{-1} y^{-1} (NPK + PM); (5) NPK fertilizers plus all of preceding crop wheat straw (NPK + ST); (6) 50% NPK fertilizers plus 6000 kg pig manure and wheat straw from all of preceding crop (NPK + PM + ST); (7) 50% NPK fertilizers plus 6000 kg cow manure and wheat straw from all of preceding crop (NPK + CM + ST); (8) 30% NPK fertilizers plus 3600 kg commercial organic fertilizer ha^{-1} y^{-1}(NPK + OCM), which is made of cow manure; (9) 30% NPK fertilizers plus 3600 kg commercial organic fertilizer (NPK + OPM), which is made of pig manure. The NPK fertilizer comprised urea (300 kg N ha^{-1} y^{-1}), superphosphate (120 kg P_2O_5 ha^{-1} y^{-1}) and potassium chloride (100 kg K_2O ha^{-1} y^{-1}). These different proportions of NPK fertilizers with corresponding organic matter were applied to manipulate the relative balance of nutrients in the soil for crop growing. All chemical fertilizers and organic matter were applied once before sowing of the winter wheat in October, and the quantities of nutrient yearly added to the plots is showed in Table S1. The wheat straws were cut into small pieces of ~10 cm in length before use. Surface soil (0–15 cm) from each plot was collected in June 2016 after the harvest of wheat (*Triticum* spp.). Soil samples were sealed in plastic bags, and shipped back to the laboratory in an iced cooler. All the soil samples were mixed homogenously, passed through a 2.0 mm sieve, followed by dividing into two sub-samples. One subsample was stored at −20 °C for microbial analysis, and another subsample was stored at 4 °C for the analysis of soil properties.

2.2. Soil properties and respiration rate analysis

Soil water content was determined by oven-drying the samples at 105 °C, and soil texture was analyzed using the pipette method (Gee and Bauder, 1986). Soil pH was measured using a fresh soil to water ratio of 1: 2.5 with a Delta pH-meter, and soil organic carbon (SOC) was determined using the K_2CrO_7 oxidation titration method (Walkley & Black, 1934). Total carbon (TC) and total nitrogen (TN) were measured on a LECO macro-CN analyzer (LECO, St. Joseph, MI, USA). Inorganic N and labile carbon in the soils were extracted with 0.5 M K_2SO_4 in a ratio of 1:5 by shaking at 200 rpm for 1 h and filtered through 0.45-μm Millipore filter paper. Total C and N concentrations in the extracts were analyzed by TOC analyzer with total nitrogen unit (TOC-L Analyzer, Shimadzu, Japan). In parallel, the carbon in microbial biomass (MBC) was determined using the fumigation-extraction method (Vance et al., 1987). For each measurement of respiration rate, approximately 10 g of fresh soil (within 48 h after sampling) was incubated in a 120 ml container at 25 °C for 24 h. At the end of this period, CO_2 concentrations in headspace were measured using an Agilent-7890a gas chromatograph equipped with a flame ionization detector (FID) and an electron capture detector (ECD) (Agilent Technologies, Wilmington, DE, USA). Soil respiration rates were calculated from the net accumulation of CO_2 over time.

2.3. Soil microbial community characterization

The total genomic DNA was extracted from 0.30 g of soil using the MoBio PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) following the manufacturer instructions. The concentration and quality of isolated DNA was checked using a NanoDrop® ND-2000c UV–Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The abundance of bacteria and fungi were evaluated by quantifying *16S rRNA* and *ITS* gene copy number on an iCycler iQ5 thermocycler (Biorad, USA) using the primer pairs Eub338F/Eub518R (Cregger et al., 2012) and ITS1-5.8S (Fierer et al., 2005), respectively.

To evaluate the microbial community composition, the V4 region of the bacterial *16S rRNA* gene and *ITS* of fungi were amplified using the primer pairs of 338F/806R (Liu et al., 2016) and ITS1F/2043R (Zhao et al., 2016b), respectively. The 50 μl PCR reaction mixtures consisted of 25 μl PremixTaq™ (Takara Biotechnology, Dalian, China), 1 μl of each primer (10 μM), 3 μl of template DNA, and 20 μl of sterilized ddH_2O. The resultant PCR products were purified using the Wizard® SV Gel and PCR Clean-Up System (Promega, San Luis Obispo, USA). The purified amplicons were equimolarly mixed, and 2 × 250 bp paired-end sequencing was carried out on an Illumina Miseq sequencer (Illumina Inc., San Diego, USA). Raw reads generated from the MiSeq