



Earthworms differentially modify the microbiome of arable soils varying in residue management

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ABSTRACT

Earthworms are among the most important soil ecosystem engineers. Their effects on soil structure have been well documented, however, there is limited knowledge on how earthworms in the long term affect the soil microbiome, especially in arable soils. We investigated the soil microbiome of rice (cultivated under aerobic condition) and wheat fields in two consecutive seasons after manipulating earthworms and organic amendments for 14 years. Composition of soil prokaryotes and eukaryotes were analyzed by Illumina sequencing. Molecular network analysis suggest that in mulched rice fields earthworms foster species interlinked with many others and shift the dominance of prokaryotes from Planctomycetes to Proteobacteria. In contrast, in fields where residues were incorporated into the soil earthworms shifted the dominance of prokaryotes from Proteobacteria to Planctomycetes. Further, earthworms significantly increased the Proteobacteria-to-Acidobacteria ratio, a putative indicator of high nutrient turnover. Further, the ratio of prokaryote-to-eukaryote abundance was increased by earthworms when straw was incorporated into the soil. In conclusion, the results suggest that in the long term earthworms mainly modify the structure and functioning of prokaryote rather than eukaryote communities in arable fields. The effects of earthworms on the structure of microbial communities and microbial interactions are closely linked to resource management practices. The more pronounced effects of earthworms in treatments with residues mulched as compared to incorporated into the soil suggest that earthworm effects in part were due to bioturbation, i.e. mixing straw with mineral soil.

1. Introduction

For sustainable agriculture internal nutrient cycling based on biotic interactions needs to be strengthened (Matson et al., 1997). Therefore, in order to exploit the full potential of soil biota in sustainable agriculture, knowledge on the functioning of individual species but also interactions between species is mandatory. Such knowledge may be used for engineering soil communities fostering the sustainable management of agricultural systems (Bender et al., 2016; Mueller and Sachs, 2015).

The soil microbiome, representing the interconnected web of soil microorganisms, plays a key role in ecosystem functioning, including litter decomposition, nutrient cycling and feedbacks to plants (Bardgett and van der Putten, 2014; van der Heijden et al., 2008; Wagg et al., 2014). An increasing number of studies have demonstrated that soil physicochemical characteristics, vegetation, climate as well as soil type

play vital roles in structuring soil microbiomes (Fierer and Jackson, 2006; Lauber et al., 2009; Shade et al., 2013). Importantly, in addition to the structure of the soil microbiome, these factors also drive interactions in microbial communities essential for ecosystem functioning (Fuhrman, 2009). However, understanding of interactions among co-existing microbial taxa and their response to changes in abiotic and biotic factors in agricultural systems is still in its infancy (Barberan et al., 2012; Ling et al., 2016).

The soil microbiome consists of prokaryotes (mainly bacteria) and eukaryotes (mainly fungi and protists) as essential components of any terrestrial ecosystem. Due to their smaller body size, prokaryotes have faster turnover rate and higher carbon assimilation efficiency than eukaryotes with each characterized by distinct life histories, occupying different niches and performing different functions in soils (Rousk and Baath, 2011). For example, ammonia oxidation predominantly is performed by prokaryotes (Leininger et al., 2006), whereas aggregate

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formation and stabilization predominantly is due to the activity of saprotrophic and mycorrhizal fungi (Wilson et al., 2009). This has led to the classical view that soil food webs comprise two energy channels, the bacterial and fungal energy channel (Moore et al., 1988; Scheu et al., 2005). This concept, however, recently has been challenged by the fact that e.g., some rhizosphere bacteria may actually feed on saprotrophic fungi (Ballhausen and de Boer, 2016). Prokaryotes and eukaryotes are both indispensable components of any soil food web considering their variety of roles in nutrient cycling, and therefore knowledge on their response to variations in abiotic and biotic factors is mandatory.

Litter, as complex carbon resource entering agricultural soils via plant residues, affects not only soil physicochemical properties but also soil biota. Generally, residue amendment increases microbial biomass in parallel to soil organic carbon concentration (Lange et al., 2015; Marschner et al., 2003) as well as soil fauna abundance via providing food resources (Leroy et al., 2007). It has been stressed that both quality and quantity of residues are important factors in affecting soil biota, but effects of residue management regimes on soil biota and their functioning still are little understood (Scheunemann et al., 2015). Compared to leaving residues on the soil surface (mulching), incorporating residues into the soil results in a more homogeneous environment and increases resource availability to soil biota (Wu et al., 2015). However, litter decomposition may also be retarded if residues are incorporated into the soil as compared to leaving them on the soil surface (Li et al., 2013), and this likely is related to the structure and functioning of the soil microbiome. The slower decomposition of residues incorporated into the soil may also have been due to limited oxygen availability and related changes in the structure and functioning of the soil microbiome (Lüdemann et al., 2000).

Due to their large body size and high biomass in many ecosystems as well as their intensive burrowing activity, earthworms have been recognized as major ecosystem engineers affecting the structure and activity of other soil organisms including bacteria and fungi (Edwards et al., 1995; Jouquet et al., 2006). Through feeding, burrowing and casting they reinforce soil structure, thereby affecting soil moisture, gas diffusivity and nutrient dynamics (Bertrand et al., 2015; Edwards, 2004; Frouz et al., 2014). Via these modifications earthworms also alter the structure and functioning of the soil microbiome. However, these effects still are not well understood, e.g. earthworms have been found to stimulate soil microbial biomass due to increased litter input into the soil (bioturbation) (Frouz et al., 2014; Groffman et al., 2015), but also to reduce it, potentially via earthworms competing with microorganisms for food resources (Lachniet and Hendrix, 2001; Lubbers et al., 2017; Pang et al., 2012). Further, earthworms may not affect microbial biomass at all (Aghababaei et al., 2014). How can these inconsistent findings be reconciled? Most studies investigating earthworm - microbial interactions were conducted in the laboratory using microcosms and lasted only few months (Araujo et al., 2004; Frouz et al., 2014). There are only few long-term field experiments, investigating the impact of earthworms on soil microorganisms and soil processes (Bertrand et al., 2015; Lubbers et al., 2017).

High throughput sequencing allows investigating the structure of the soil microbiome at high taxonomic resolution (Bates et al., 2013). Further, advances in network analysis allow to explore interrelationships of microbial taxa and to disentangle keystone factors driving interactions among microbial taxa (Barberan et al., 2012; Berry and Widder, 2014; Layeghifard et al., 2017). In the present study, we explored long-term effects of earthworms on the soil microbiome by using high throughput sequencing of soil samples from an agricultural experiment established in 2001 varying organic matter amendment in a wheat and upland rice rotation agro-ecosystem. Our hypotheses were as follows: (1) straw incorporation into the soil favors earthworm activity and thereby shifts the microbiome towards the dominance of taxa with fast turnover rate, i.e. prokaryotes, and (2) through ecosystem engineering, earthworms increase soil heterogeneity and thereby the complexity of prokaryote communities and the whole microbial network.

2. Materials and methods

2.1. Study site

The experiment was established at the experimental field station of the Nanjing Agricultural University (118°85'E and 32°02'N) in 2001. The mean atmospheric temperature at the study site is 16.0 °C and the average annual precipitation is 1106 mm. The field was located close to the Nanjing Agricultural University campus and comprised a wheat and upland rice rotation agro-ecosystem, with rice being cultivated at 80% of the maximum soil water holding capacity throughout the growing season favoring the activity and density of earthworms, whereas wheat was cultivated without irrigation. Two factors, i.e. straw management and earthworms, were manipulated in a full factorial design resulting in four treatments: (1) maize straw incorporated into soil without earthworms, (2) maize straw incorporated with earthworms, (3) maize straw mulched on the soil surface without earthworms, and (4) maize straw mulched with earthworms. Individual plots were 2.8 × 1.0 m in size. They were separated by 15-cm-wide concrete frames ranging 60 cm into the soil and 20 cm above the ground. Each treatment was replicated three times with individual treatments being randomly ascribed to the plots. Maize straw was chopped to < 2 cm and added to experimental plots equivalent to 7500 kg ha⁻¹ at the beginning of each crop growth period. By adding C4 plant residue to a C3 plantation system allowed tracking residue C as affected by earthworms. However, these data will be reported elsewhere. The amount resembles the amount of residues typical for the cropping systems studied. Straw residues were homogeneously mixed into the top 5 cm of the soil or left on the soil surface (mulched) in the respective treatments. After residue addition, 30 ± 2 adult earthworm individuals of the endogeic species *Metaphire guillelmi* were added to the earthworm plots at a density of 70 g m⁻². The earthworms were added only if necessary, i.e., when their biomass has declined to less than 60 g m⁻². The number and species of earthworms were monitored after every harvesting stage annually. Typically, the soil structure was disturbed during that period by tillage for preparing subsequent crop seeding; hand sorting of 1 m² for collecting earthworms therefore added little to this disturbance. For establishment of control plots without earthworms electro-shocking was applied to substantially reduce earthworms (Bohlen, 1995). Only few earthworm individuals were observed by the end of each crop cultivation season in plots without addition of earthworms, and these earthworms were discarded. In contrast, earthworm biomass remained at a rather constant level of about 65 g m⁻² in earthworm treatments (Tao et al., 2009).

2.2. Soil physicochemical properties and sampling

The soil, classified as Orthic Acrisol, had a pH (H₂O) of 8.25 and contained 5.86 g kg⁻¹ soil organic C, 0.71 g kg⁻¹ total N, 11.4% clay, 84.1% silt and 4.5% sand at start of the experiment. Soil samples were taken before crops were harvested in October 2014 (rice) and June 2015 (wheat). In each plot eight soil cores of an area of 2.5 cm² to a depth of 20 cm were taken randomly using a steel corer and pooled as composite sample. Soil cores were transferred to the laboratory and sieved through 8 mm mesh. Aliquots were stored at -70 °C for molecular analysis and aired dried for physicochemical analysis. To determine total soil P (TP) and K (TK) soil samples were digested with HF-HClO₄. Available K (AK) and available P (AP) were extracted with ammonium acetate and sodium bicarbonate, respectively, and determined by flame photometry and molybdenum blue method, respectively (Lu, 1999). Soil pH was measured using a pH meter after shaking a soil - water suspension (1:5w/v) for 30 min. Total carbon (TC) and total nitrogen (TN) concentrations were measured using an elemental analyzer Vario Max CN (Elementar Analysensysteme, Hanau, Germany). Wet sieving was used to determine water-stable aggregate distribution (Six et al., 2000).

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