



Aggregate-related changes in network patterns of nematodes and ammonia oxidizers in an acidic soil



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ABSTRACT

Nitrification plays a central role in global nitrogen cycle, which is affected by biological interaction between soil microfauna and microorganisms. However, the complexity of soil biotic communities made it difficult to reveal organizational principles of the community and the interactions among species. Here, we used the network analysis to decipher the interactions between nematodes and ammonia oxidizers within aggregate fractions under 10-year manure application, and examine their associations with soil variables and potential nitrification activity (PNA). Three aggregate fractions included large macroaggregates (>2000 μm, LA), small macroaggregates (250–2000 μm, SA), and inter-aggregate soil and space (<250 μm, IA). Aggregate fractions showed a remarkable effect on association networks of nematodes and ammonia oxidizers. The average connectivity (*avgK*) and the number of edges in overall networks increased with increasing aggregate sizes, while the average geodesic distance (GD) followed the opposite trend. The LA network could be viewed as a better organized or a better operational soil food web with more functional interrelated members than the SA and IA networks. The modules related to PNA were significantly correlated and clustered together as meta-modules in networks of aggregate fractions. The role-shifts prevailed among the network members such as significant module memberships (MMs) and generalist/specialist operational taxonomic units (OTUs). A half of shared nodes were further identified as shared MMs, dominated by ammonia-oxidizing bacteria (AOB) especially for *Nitrosospira* cluster 3a and 10. Soil pH could explain partly the shift of module hubs in different networks, while grazing by bacterivores might account for three exclusively connectors related to *Nitrososphaera* clusters 1.1. The strongly coupled modules correlated positively to pH and total carbon (TC), regardless of aggregate fractions. The network analysis approach provided new insights into potential importance of network interactions between nematodes and ammonia oxidizers in soil nitrogen cycling.

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1. Introduction

Ammonia oxidation is the first and rate-limiting step in nitrification that plays a critical role in the global nitrogen cycle (Gruber and Galloway, 2008). Both ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB) are ubiquitously distributed in agricultural soils (Leininger et al., 2006) and derive energy from ammonia oxidation in support of their growth (Martens-Habbena et al., 2009). The inter-species interactions in microbial community play vital roles in determining the structure of microbial

community and in turn the ecosystem functioning (Fuhrman, 2009). Nevertheless, a comprehensive understanding of the interactions among these coexisting ammonia oxidizers and the resulting ecological functions in agricultural soils remains difficult.

Both abiotic and biotic soil components simultaneously affect the microbial community composition and their functions. The ecological importance of AOB and AOA may vary according to soil chemical properties, including ammonia concentration, pH and organic matter (He et al., 2012). Furthermore, soil is usually composed of a wide range of aggregate-sizes which depend on the association between mineral soil particles and organic matter and change with management practices (Tisdall and Oades, 1982). Soil microaggregates generally contain a great proportion of stable SOM

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and particulate organic matter (POM) (Oades, 1984), while macroaggregates contain relatively labile binding agents (i.e. roots, fungal hyphae, and microbial polysaccharides) and are less stable than microaggregates to the changes in land use and cultivation practice (Puget et al., 2000). Soil aggregates of different sizes provide spatially heterogeneous microhabitats for microorganisms, which are characterized by differences in organic carbon stabilization (Six et al., 1999) or by the fluxes of oxygen and water (Young et al., 2008). Specific microclimatic conditions within different aggregate size fractions affect microbial community composition and nitrification activity (Muruganandam et al., 2010). To our knowledge, there has been far less attention focused on evaluating how aggregate fractions affect the network structure of ammonia oxidizers under long-term manure application.

The biological interaction between soil microfauna and microorganisms in soil food web creates a complex microbial community (Neher, 2010) and affects soil nitrogen cycling (Rønn et al., 2012). Generally, grazing by bacterivorous nematodes can stimulate nitrification by enhancing AOB abundance and modifying AOB community composition in microcosms (Xiao et al., 2010) and field soils (Jiang et al., 2014). Furthermore, the microbial changes induced by root-parasitic nematodes are observed to promote soil microbial respiration and net N mineralization (Tu et al., 2003). To fully examine the biotic factors that control microbial ecological processes, we have in this study expanded our co-occurrence network analysis to include a broad variety of bacterivorous and plant-parasitic nematodes.

An ecological network is a representation of various biological interactions in an ecosystem in which species (nodes) are connected by positive and negative interactions (links) (Montoya et al., 2006). Positive correlations may suggest co-occurrence due to similar preferred conditions, commensalism or a mutualistic relationship between organisms cooperating within the same niche, whereas negative correlations may suggest the presence of predation and competition (Chow et al., 2014). Recent advance of metagenomic technologies, such as high throughput sequencing, provides revolutionary tools for analyzing diversity and structure of ammonia-oxidizing community, and the factors shaping these microorganisms (Mao et al., 2013), but these fundamental approaches scarcely describe the interactions among microbes within a community or with their environments. Although our ability to interpret these networks is still under development, current progresses in association network have greatly improved our understanding on the broad range of interactions among microbial populations that jointly buildup the typically complex communities characteristic for terrestrial ecosystems (Chaffron et al., 2010; Freilich et al., 2010). Furthermore, network analysis of taxonomic co-occurrence patterns offers new insights into keystone populations and significant module memberships in biotic community, and their responses to habitat conditions (Zhou et al., 2011; Deng et al., 2012), such as soil organic carbon (Sul et al., 2013). Documenting inter-taxa associations across complex and diverse ammonia-oxidizing community may help to ascertain the functional roles or environmental niches occupied by community members (even members of intra-taxa, such as AOA and AOB). It is particularly valuable information in agricultural soils annually receiving a large amount of nitrogen fertilizers, where the basic ecology and life history strategies of many microbial taxa remain unknown (Janssen, 2006). Exploring co-occurrence patterns between soil microorganisms can identify potential biotic interactions, habitat affinities, or shared physiologies that could guide more focused studies or experimental settings.

Here, we examined the changes of microfaunal–microbial interdependencies and their ecological functions at the aggregate level under a 10-year manure experiment in an acid soil. We

calculated co-occurrence patterns of nematodes and ammonia-oxidizing microorganisms and their correlations to soil properties and potential nitrification activity (PNA). We hypothesized that the aggregate fractions can affect network structure of nematodes and ammonia oxidizers by changing abiotic characteristics which defined microhabitats heterogeneity. Furthermore, we expected to discover the numerous interesting features of soil biotic community, including significant module memberships and possible keystone species. Finally, we identified soil environmental conditions that correlated positively or negatively with these relationships.

2. Materials and methods

2.1. Site description

The long-term fertilization experiment was initiated in 2002 at the Red Soil Ecological Experimental Station of the Chinese Academy of Sciences, located in Yingtan, Jiangxi Province, China (28° 15'N, 116° 55'E). This region has a subtropical humid monsoon climate with an annual average temperature and precipitation of 17.6 °C and 1795 mm, respectively. The soil is an acid loamy clay derived from Quaternary red clay (Udic Ferralsols in Chinese Soil Taxonomy and Ferric Acrisols in the FAO classification system). Four fertilization treatments (three replications each) were implemented in a completely randomized plot design (2 m wide × 2 m long × 1.5 m deep) with a rotation of monoculture maize (*Zea mays* L.): no manure (CK), low manure with 150 kg N ha⁻¹ y⁻¹ (LM), high manure with 600 kg N ha⁻¹ y⁻¹ (HM), and high manure with 600 kg N ha⁻¹ y⁻¹ and lime (HML, Ca(OH)₂ applied once every 3 years at 3000 kg ha⁻¹). Soil collection protocol and methods for edaphic properties, aggregate fractionation, nematodes, ammonia oxidizers and potential nitrification activity (PNA) have been described previously (Jiang et al., 2014).

2.2. Aggregate fractionation and sampling grouping

Three aggregate-size classes were manually fractionated through dry sieving of 100 g fresh soil on a series of 2 sieves (2000 μm and 250 μm) as follows: large macroaggregates (>2000 μm; LA), small macroaggregates (250–2000 μm; SA) and fine material (<250 μm). Small aggregates passing through a 250 μm sieve are considered too small for nematodes to enter and this fraction will thus be referred to as inter-aggregate soil and space (IA) (Briar et al., 2011). Fresh soil was dry-sieved because air drying compromised the *in situ* link between the aggregates obtained and their indigenous biota. Moreover, the dry-sieving procedure was adopted in order to avoid the loss of hydrotropic nematodes (Stock and Goodrich-Blair, 2012) and microbial biomass living on the surface of aggregate fractions (Oades, 1984) during wet-sieving. Soil was placed on a 2000 μm sieve, and then manually moved up and down 60 times during a period of 2 min. The material passing through the 2000 μm sieve was transferred to the next smaller-sized sieve (250 μm) for further fractionation, ultimately generating three aggregate fractions (LA, SA and IA). The subsamples of each aggregate fraction were used for nematode assemblages, ammonia oxidizers community and soil chemical analyses respectively. All these subsamples were put into three groups based on three aggregate fractions. Each group had 12 subsamples that contained four fertilization treatments (CK, LM, HM and HML) with three replicates. This grouping allowed us to construct and compare networks of soil biotic community at the aggregate level.

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