



Long-term farming systems modulate multi-trophic responses

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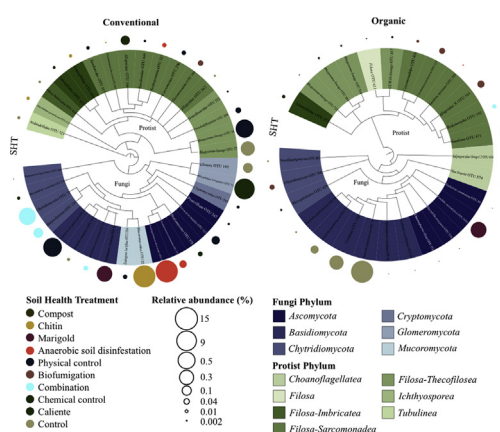
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HIGHLIGHTS

- The diversity of protist was stable at organic and conventional farming systems.
- The diversity of fungal community increased in organic farming.
- Organic farming increased the population of free-living nematodes and suppressed Meloidogynidae and Pratylenchidae plant parasitic nematodes.

GRAPHICAL ABSTRACT



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ABSTRACT

Soil microbiome and multi-trophic relationships are essential for the stability and functioning of agroecosystems. However, little is known about how farming systems and alternative methods for controlling plant pathogens modulate microbial communities, soil mesofauna and plant productivity. In this study, we assessed the composition of eukaryotic microbial groups using a high-throughput sequencing approach (18S rRNA gene marker), the populations of parasitic and free-living nematodes, plant productivity and their inter-relationships in long-term conventional and organic farming systems. The diversity of the fungal community increased in the organic farming system compared to the conventional farming system, whereas the diversity of the protist community was similar between the two farming systems. Compared to conventional farming, organic farming increased the population of free-living nematodes and suppressed plant parasitic nematodes belonging to Meloidogynidae and Pratylenchidae. Fungal diversity and community structure appeared to be related to nematode suppression in the system receiving organic fertilizer, which was characterized by component microbial groups known to be involved in the suppression of soil pathogens. Unraveling the microbiome and multi-trophic interactions in different farming systems may permit the management of the soil environment toward more sustainable control of plant pathogens.

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1. Introduction

The interaction and feedback of the microbiome with the soil biota regulate ecosystem functioning and primary productivity in soil agroecosystems (Carrascosa et al., 2015; Tedersoo et al., 2016). Fungi play an important role in soil ecosystems as obligate root symbionts, decomposers or soil-borne pathogens (Penton et al., 2014; Schneider et al., 2010; Xu et al., 2012). Soil mesofauna and protists fulfill diverse functions in soil ecosystems as well as in grazing by living organisms, decomposing organic matter and determining nutrient cycling (Paungfoo-Lonhienne et al., 2015). Top-down relationships may also regulate soil ecosystem processes and functioning. Greater community diversity and the presence of certain component species may promote soil services and enhance ecosystem stability by suppressing plant pathogens and reducing interspecific competition and promoting higher plant productivity (Saleem et al., 2013; Vivant et al., 2013).

Soils are managed with organic and inorganic fertilizers to increase crop yields (Tilman et al., 2002). Although the positive effects of conventional farming systems on nutrient availability and plant productivity are well described (Alaru et al., 2014), there is increasing concern that intensive agricultural management leads to ecosystem degradation, soil pollution and diversity loss (Reganold and Wachter, 2016). Compared with conventional systems, organic farming reduces the use of synthetic fertilizers and pesticides and mitigates the negative impacts of intensive management to promote sustainable production (Bonilla et al., 2012). Positive effects of organic farming include increased microbial diversity and heterogeneity (Kamaa et al., 2011; Lupatini et al., 2017), promotion of beneficial microorganisms (Postma et al., 2008), enhanced nutrient cycling (Mader et al., 2002), and reduced plant pathogens (Krauss et al., 2011). However, the understanding of the long-term benefits and limitations of organic farming systems remains incomplete (Schneider et al., 2014).

In addition to organic farming, non-chemical alternatives for inhibiting plant pathogens are gaining importance (Krauss et al., 2011; Mader et al., 2002). Methods based on biofumigation, Marigold treatment, chitin and compost efficiently suppress disease caused by plant-parasitic nematodes (Hooks et al., 2010; Oka, 2010; Piedrabuena et al., 2006; Sarathchandra et al., 1996). However, this disease suppression has been linked to factors other than direct effects on the target organisms (Topp et al., 1998). These methods can modulate the soil microbiome and promote the presence of microbial groups that are able to interact with each other and control pathogens in the soil (Cretoiu et al., 2013). Soil management might also affect free-living soil nematodes, which play an important role in soil functioning through food webs by regulating decomposition and mineralization processes (Quist et al., 2016). Promoting the broad application of alternative methods for pathogen control requires a better understanding of their impacts on the soil microbiome and soil mesofauna and the mechanisms involved in specific interactions (Bengtsson et al., 2005; Reilly et al., 2013; van Diepeningen et al., 2006).

Cultivation-based studies have shown that fungi and protists are abundant and ecologically important for soil processes (Saleem et al., 2013). Many taxonomic groups comprise species of potential and varying ecological importance that remain undetected by traditional morphology-based methods for determining community composition (Lentendu et al., 2014). To elucidate the relationships and functioning of these groups in agroecosystems, the responses of multi-trophic levels to agricultural management should be assessed simultaneously (Luo et al., 2015). Next-generation sequencing approaches allow the soil microbiome to be harvested at different taxonomic resolutions, thereby permitting the identification of microbial taxa associated with specific management practices in agricultural soils (Hartmann et al., 2015).

In this context, we simultaneously identified multiple organism groups in a long-term Soil Health Experiment (SHE) model system featuring a conventional farming system and an organic farming system. The organic and conventional farming systems were further divided

into component parts, namely soil health treatments (SHTs; non-chemical methods for plant pathogen control). We disentangled the effects of farming system and SHT on multiple taxonomic groups and their relationships via high-throughput sequencing of the 18S rRNA gene marker to determine the fungal and protist microbiomes and assessments of soil mesofauna and plant yield. We postulated the following hypotheses: (i) organic farming systems have a positive effect on the diversity of the fungal and protist microbiomes; (ii) organically managed systems increase the population of free-living nematodes and suppress the population of plant-parasitic nematodes by affecting their relationships with the fungal and protist groups; and (iii) multi-trophic components shift in concordance primarily due to similar responses to agricultural management. In the long-term, identifying microbial taxa and monitoring the collection of components in agroecosystems will facilitate the sustainable management of agricultural soils to improve ecosystem health.

2. Material and methods

2.1. The agricultural Soil Health Experiment (SHE) model system

The long-term Soil Health Experiment (SHE) located at Wageningen University Research (WUR) station in Vredepeel, in the southeast of the Netherlands (51° 32' 27.10" N and 5° 51' 14.86" E) was used to test our hypotheses. The site has been in agricultural cultivation since 1955. The SHE field (~6 ha) was established in 2006, and contains 160 plots (6 m × 6 m) arranged in a randomized block design and continuously managed according to conventional and organic farming systems. Conventional and organic systems only differ in fertilizer application and plant protection strategies. Both conventional and organic systems received similar amount of N, P, K nutrients per hectare/year according to fertilizer recommendations for the crops. Initially, all plots were fertilized with cattle slurry (38 m³ ha⁻¹). After that, the conventional system received mineral fertilizer (250 kg ha⁻¹ of mineral fertilizer) and common chemical plant protection (300 L ha⁻¹ Metam sodium - Monam 510 g a.i. L⁻¹) was carried out. The organic system exclusively received organic fertilizers (25,000 kg ha⁻¹ of farm yard manure) and when necessary was mechanical weeded. Each year between 2006 and 2013, a crop was grown on the entire experimental field: 2006: Wheat (Conv) or barley (Org); 2007: potato (Conv, Org); 2008: lily (Conv, Org); 2009: wheat (Conv) or barley (Org); 2010: potato (Conv, Org), 2011: carrot (Conv, Org), 2012: maize (Conv, Org), 2013: maize (Conv, Org).

2.2. The soil health treatments (SHT)

The soil health treatments (SHTs) used in this study was selected based on literature information regarding the efficiency in plant pathogen control. Nine SHTs were applied twice since 2006 until 2013 (from the end of July 2006 till May 2007 and from July 2009 till December 2009) within conventional and organic farming systems with four replicates per treatment: Compost (CO) - 50 t ha⁻¹ of mature compost (65% wood, 10% leaves and 25% grass and inoculated with *Trichoderma harzianum* - Orgapower) was incorporated in the 20 cm soil surface; Chitin (CH) - 20 t ha⁻¹ of chitin based on shrimp waste material (Gembr, Ecoline) was incorporated in the 20 cm soil surface; Marigold (MA) - *Tagetes patula* (cv. Ground Control) grown from July 2006 till January 2007 and incorporated in the 20 cm soil surface; Grass-clover (GC) - a combination of four grass species (4 kg ha⁻¹ cv. Tetraflorum, 7 kg ha⁻¹ cv. Miracle, 2 kg ha⁻¹ cv. Pomposo and 1 kg ha⁻¹ cv. Tomaso) and two clover species (1 kg ha⁻¹ cv. Riesling and 7 kg ha⁻¹ cv. Maro) was grown from 27 July 2006 till 12 March 2007 and incorporated in the 20 cm soil surface; Soil Anaerobic Disinfestation (AD) - 50 t ha⁻¹ of fresh organic matter (a mixture of different rye-grass species) was incorporated in the 20 cm soil surface on August 2006, irrigated with 20 mm and covered with a virtually impermeable film

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