



The dynamics of soil micro-food web structure and functions vary according to litter quality



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ABSTRACT

Anthropogenic pressures on agricultural soils are known to alter the properties of soil food webs, which may affect ecosystem functions and the capacity to deliver services. Cropping systems fuel belowground biota by supplying litter, but litter quality varies from year to year. In this study, we hypothesized that (i) the structure and function of the soil biota may respond strongly to the quality of crop residue, and (ii) this response may vary with the complexity of the food web. To test this hypothesis, a 3-month incubation experiment was performed using soil columns filled with a silty loam agricultural soil (Estrées-Mons, Northern France), and plant litter was incorporated into the 0–5-cm layer. The quality of the litter was modulated by using either high quality (maize leaves) or low quality materials (maize roots), and two levels of biotic complexity were tested by introducing or not introducing an ecosystem engineer (*Lumbricus terrestris*, anecic earthworm) into the columns. We then investigated litter decomposition and enzymatic activities, as well as the biomass and diversity of the bacterial, fungal and nematode communities. The C mineralization and enzymatic profiles varied according to litter quality, and the most obvious differences were observed in the hydrolytic enzymes and phenol oxidase. Micro-food web interactions and structure were mainly impacted by litter type and the time since litter incorporation, and as expected, we observed a temporal succession of cellulolytic organisms followed by lignolytic organisms. This progression was mirrored by the nematode community; the ratio of fungal feeders/bacterial feeders increased between 35 and 91 days. Initial litter quality primarily impacted bacterial and fungal community structure, and the development of the bacterial channel was greater with the addition of leaf litter. This was related to an increase in specific, favored phyla, *Bacteroidetes* and *Proteobacteria*, whereas *Actinobacteria* increased more with the addition of root litter. However, we could not statistically link the changes in the structure of the microbial communities over time with those in enzyme activity, which led us to assume that other factors, such as top-down regulation, are more important than microbial community structure in the determination of the enzyme secretions in the soil. Finally, the addition of earthworms did not significantly impact litter decomposition and had a low impact on micro-food web structure and interactions. However, the presence of *L. terrestris* did modify the enzymatic secretions, probably through its endemic microbial population, as well as the stimulation of microbial activity through predation.

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1. Introduction

Soils are complex systems that are intimately linked to crucial ecosystem services, such as organic matter decomposition and the regulation of C and N fluxes (Haygarth and Ritz, 2009). However, agricultural soils must be managed to address the challenges of

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food production as well as environmental conservation, and reconciling productivity and sustainability has become a driving force behind the development of alternative agricultural practices. Soil biota are known to play a major role in essential ecological functions (Wagg et al., 2014) and the sustainability of the ecosystem services delivered to humans. Belowground biotic communities are strongly impacted by crop residues, which constitute their main source of trophic energy (Kim and Dale, 2004), and crop residues can be of high quality (i.e., easily degradable by soil organisms) or of rather low quality (i.e., made of complex C forms). The aerial parts of crop plants are rich in soluble components and are of high quality compared to roots, which are rich in cell wall components (Amin et al., 2014). Indeed, aerial and underground plant parts together constitute a model to study residue recalcitrance (Amin et al., 2011, 2014) and its impact on soil ecosystem services, such as carbon storage. However, the relative consequences of the different types of litter on soil communities remain unknown. Litter quality changes during decomposition, and its recalcitrance increases over time as the more labile compounds (the soluble and holocellulose fractions) degrade more rapidly compared to the recalcitrant compounds (Berg and McClaugherty, 2008). These dynamics are reflected in temporal modifications to the structure of microbial communities, such as the bacterial-fungal successions that occur during decomposition (e.g., Henriksen and Breland, 2002), and these changes in the bacteria and fungi have direct consequences for the dynamics of their predators. In particular, a successional shift in nematodes from bacterial feeders toward fungal feeders during litter decomposition has been reported (Georgieva et al., 2005). Furthermore, the addition of litters with contrasting initial quality impacts the structures of soil communities differently; the addition of labile litter leads to a greater increase in soil biomass and promotes bacterial energy channels, while recalcitrant litter induces fewer changes in biota biomass and favors fungal energy channels (e.g., Coleman et al., 2004). However, sufficient data on the functional consequences of structural changes in the soil food web after litter addition are currently not available.

The functions of soil biota are often assessed by measuring soil extracellular enzymes (EE) because they reflect the metabolic requirements of the organisms and regulate the degradation of organic matter and the supply of C and N (Sinsabaugh, 2010). The production of EE is dependent on the type of microorganism and its nutrient requirements (Baldrian et al., 2010; Sinsabaugh, 2010), and it usually mirrors the dynamics of litter degradation. However, litters with different chemical qualities may require varying amounts of different enzymes for C mineralization (Amin et al., 2014), and these differences may be directly linked to the contrasting structures of the microbial communities that develop during decomposition. However, other studies have suggested the potential importance of competing biotic interactions during EE production (Romaní et al., 2006), particularly the top-down regulatory functions of bacterial and fungal feeders (A'Bear et al., 2014; Trap et al., 2015) that increase microbial turnover and, subsequently, enzymatic secretions. Although the results of most studies support the importance of top-down regulation, the intensity of the process appears to be highly dependent on the identity of both the predators and the prey (A'Bear et al., 2014). Most of the published work related to this aspect is focused on the impact of litter N content on top-down regulation (Mamilov et al., 2001; Lenoir et al., 2007), but to our knowledge, the impact of litter C quality has not been studied. Nevertheless, the intensity of top-down regulation tends to increase with the amount of prey organisms in the soil (Thakur and Eisenhauer, 2015), so we may expect to increase top-down regulation with the addition of labile litter. On the other hand, most studies are focused on the effect of the meso- and

macrofauna, and less is known about the evolution of microfaunal top-down regulation during litter decomposition. The top-down regulation of microfauna should be similarly affected by contrasting litter quality. Furthermore, the presence of larger soil fauna (meso- and macrofauna) can also affect the relationships between the microfauna and microorganisms (Kaneda and Kaneko, 2008; Bastow, 2011). In particular, “ecosystem engineers”, such as earthworms, are known to affect soil micro-food webs both directly (through predation) and indirectly (through the modification of soil abiotic factors by bioturbation) (Lavelle et al., 1997; Bertrand et al., 2015). Thus, the presence of earthworms usually leads to changes in the structure and function of several components of the micro-food web (Bernard et al., 2012; Boyer et al., 2013) and modifies the bottom-up impacts on soil communities (Maraun et al., 2001).

Understanding the role of food webs in C and N cycles has been the focus of numerous studies due to the growing interest in agricultural soils (e.g., de Vries et al., 2013), but information about the consequences of crop residue degradation on food web structure and function remains limited. Most of the available data on the influence of litter decomposition on food web assemblages and functions has been acquired from studies of grasslands or forests (e.g., Wardle et al., 2006), but the effects could be different in agroecosystems due to the contrasting C dynamics, soil characteristics, biota biomass and management practices, such as residue quality, mechanical tillage, and mineral fertilization. However, to our knowledge, few studies have investigated the parallel differentiation of microorganisms and microbial feeders following the addition of litters of contrasting quality in an undisturbed micro-food web without biota manipulation, such as defaunation or species inoculation.

Our main objective was to understand the relationships between the structure and dynamics of soil micro-food webs and the production of enzymes during the decomposition of crop litters of contrasting quality (maize leaves or maize roots) in soil under controlled conditions. We also sought to evaluate how the presence of an “ecosystem engineer”, the anecic earthworm *Lumbricus terrestris*, might modify the biotic assemblages and their functions. We hypothesized that (i) litter addition will have a strong impact on the soil micro-food web. Maize leaf addition will mainly target bacterial pathways, and fungal pathways will be targeted by maize root addition. (ii) Top-down regulation will be greater with leaf addition and will be influenced by the structure and dynamics of micro-food webs through enzymatic secretions. Finally, (iii) *L. terrestris* will change abiotic and biotic conditions and thereby change micro-food web structure and functions.

2. Materials and methods

2.1. Soil and litter preparation

The study soil was classified as an Orthic Luvisol (FAO classification) or a Typic Hapludalf (USDA classification) and was obtained from a cultivated field in northeast France (49°80'N, 3°60'E). Organic C, clay, silt and sand contents were 8.70 mg C g⁻¹ soil, 16.8%, 76.3% and 3.8%, respectively, on a soil dry weight basis (Bertrand et al., 2006), and pH (soil H₂O) was 7.5. Soil samples were collected in spring 2013 at three depths: 0–5 cm, 5–10 cm and 10–20 cm. The soil was then sieved at 6 mm, and crop residue and soil macrofauna were manually removed. Soil moisture was fixed at a potential of –80 kPa (corresponding to 200 g H₂O kg⁻¹ dry soil), and the initial N mineral content was 38.0 ± 0.34 mg N kg⁻¹ dry soil (see paragraph 2.5). The soil was placed in PVC columns with a diameter of 15.3 cm and a depth of 20 cm (5.1 kg dry soil in total) after reconstituting the 0–5, 5–10 and 10–20-cm layers. Each soil layer was introduced into the column at its original bulk density:

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