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Can changes in litter quality drive soil fauna structure and functions?

Marie Sauvadet [a, 1], Matthieu Chauvat [b], Nicolas Brunet [c, 2], Isabelle Bertrand [a, d, *]

[a] INRA, UMR FARE, F-51100 Reims, France
[b] Normandie Univ, UNIROUEN, IRSTEA, ECODIV, F-76000 Rouen, France
[c] INRA, UR AgroImpact, F-02000 Barenton-Bugny, France
[d] INRA, UMR Eco&Sols, F-34060 Montpellier, France

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ABSTRACT

Crop residues restitution has significant impacts on soil biota, as it constitutes the main carbon (C) source in cultivated system, and differently alters belowground communities depending on its initial quality. However, functional consequences of such changes have mainly been studied considering few taxa, and less is known on the effects of biota differentiation in complex, un-manipulated communities. To evaluate the role of litters diverging qualities on soil fauna assemblages and functions during decomposition, we incorporated into the soil two litters of different qualities (high: pea or low: barley) in a long-term experimental research station studying the impacts of different cultural practices in Northern France. We measured initially and after 7 and 11 months the abundance and composition of main functional groups of soil fauna: bacterial-feeders, fungal-feeders, meso- and macro-detritivores. In parallel, we followed litter mass loss and quality, enzymatic activities (hydrolytic and oxidative), soil mineral N content, microbial and fungal biomass.

Pea and barley litter qualities gradually diverged across time due to the faster depletion of cellulose in pea (−38%) than in barley (−18%), leading to contrasting enzymatic activities despite similar mass loss for both litters. Microbial-feeders exhibited more changes between the sampling dates rather than between the different litters. Contrastingly, detritivores (meso- and macro-) mirrored divergence in quality of pea and barley litters across time with increasing composition dissimilarities after 0, 7 and 11 months. As a consequence, enzymatic activities were better explained by detritivores rather than by microbial-feeders composition. These relationships suggested a direct link between the identity of the taxa stimulated and the nature of the top-down regulation during litter decomposition.

1. Introduction

Litter decomposition is an essential process that drives biogeochemical cycles in soils (Sinsabaugh et al., 2002). Its effects on C and N cycling are primarily linked to litter chemical composition changing during decomposition. Litter C recalcitrance is increasing over time as the more labile compounds (the soluble and holocellulose fractions) degrade more rapidly compared to the recalcitrant ones (Berg and McClaugherty, 2008). Changes in litter quality during decomposition are mirrored by extracellular enzymes production, which reflects soil biota C and N acquisition strategies and enzymes efficiency (Sinsabaugh et al., 2002; Amin et al., 2014; Fanin et al., 2016). Several works found that during the decomposition process, litter chemical characteristics diverged, rather than converged (Berg and Mc Claugherty, 2008; Wickings et al., 2012). This qualities divergence has been attributed to soil biota, the main actor of litter decomposition; this assumption is supported by the strong differentiation of biota composition with litter type and stage of decomposition (Kaneko and Salamanca, 1999; Irmler, 2000; Osler et al., 2006; Szanser et al., 2011; Fujii and Takeda, 2012). Nevertheless, our knowledge of how changes in litter quality during decomposition impact soil biota structure and associated functions remains incomplete, in particular for soil fauna.

These effects are better known for microbial communities, with different affinities to litter components of bacteria and fungi being generally associated with labile and recalcitrant compounds degradation, respectively (e.g. de Boer et al., 2005). As a

* Corresponding author. INRA, UMR Eco&Sols, Place Pierre Viala, F-34060, Montpellier, France.
E-mail address: isabelle.bertrand@inra.fr (I. Bertrand).
[1] IRD, UMR Eco&Sols, F-34060 Montpellier, France.
[2] Agence de l'eau Rhône Méditerranée Corse, F-69007 Lyon, France.

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consequence, bacterial community is more differentiated with labile litter addition but converges rapidly to its initial state after few weeks, while fungal community differentiation along decomposition usually lasts longer (Tardy et al., 2015). These trends are usually mirrored at the higher trophic level with similar convergence – divergence patterns for nematodes bacterial- and fungal-feeders communities (Georgieva et al., 2005; Sauvadet et al., 2016a). Nematodes differentiation patterns are supposedly due to specific feeding preferences of nematodes taxa on microbial species (Blanc et al., 2006; Jousset et al., 2009). However, direct links between microbial-feeders composition and litter chemistry have been seldom studied. Most of the studies putting in relief the indirect influence of litter quality on microbial-feeders community structure did not follow the concomitant evolution of litter chemistry and fauna composition (Georgieva et al., 2005; Sauvadet et al., 2016a); we may thus wonder to which degree microbial-feeders will reflect litter diverging qualities, throughout the decomposition process, and whether they will exhibit the same specificity as direct litter-feeders such as detritivores. Indeed, relationships between detritivores communities and litter qualities are better known and present contrasting patterns between the taxa (Brown et al., 2000; Wolters, 2000; Fujii and Takeda, 2012; Chauvat et al., 2014; Ferlian et al., 2014). For instance, litter initial recalcitrance was associated to low abundance of macro-detritivores (e.g. Hendriksen, 1990) but to high abundance of meso-detritivores (e.g. Chauvat et al., 2014). However, little is known on the relationships between the theory of litter diverging quality and macro and meso-detritivores dynamic during the decomposition process. The question we intend to address is: does litter quality divergence during the decomposition process will drive macro-and meso-detritivores, as observed for bacterial–fungal-feeders successions?

Changes in fauna composition may have important effects on soil functioning (e.g. de Vries et al., 2013). While litter enzymatic degradation is mostly performed by microorganisms, top-down regulation exerted by soil fauna upon soil microorganisms tend to be a more important driver of soil functions than microbial community structure itself (Wickings et al., 2012; A'Bear et al., 2014; Sauvadet et al., 2016a; Trap et al., 2016). Fauna manipulation experiments put in relief the importance of taxa identity on intensity of top-down regulations (A'Bear et al., 2014; Trap et al., 2016). Indeed, top-down regulation by microbial-grazers may depend on (i) their feeding-preference, which can change microbial community structure according to the taxa grazed, and thus alter nutrient acquisition strategy (for example between bacterial and fungal pathway, e.g. de Vries et al., 2012), and on (ii) their consumption rates, which can also determine the rates of nutrient recycling (Blanc et al., 2006; Trap et al., 2016), and thus nutrient need of soil community for litter decomposition. However, little is known on the validity of these results for complex, un-manipulated communities, where several fauna species and functional groups affects simultaneously microbial community structure and functioning. In complex communities, top-down regulations depends on litter quality (Mamilov et al., 2001; Lenoir et al., 2007), however whether changes in chemical litter characteristics during the decomposition could be linked to soil fauna communities' divergence or convergence still needs to be answered.

The objective of this study was to determine the effects of litters of contrasting qualities on soil fauna structure and functions during decomposition. Here, we tested the effect of the addition of either a high (pea) or a low (barley) quality litter on the density and composition of four soil functional groups: the bacterial-feeding nematodes, the fungal-feeding nematodes, the meso-detritivores and the macro-detritivores and on enzymatic activities at three stages of decomposition: initial (time 0) and after 7 and 11 months. We hypothesized that (i) pea and barley litter qualities will diverge during decomposition, the proportion of lignin increasing differentially in the two litter types, (ii) this divergence will affect soil fauna structure at the early stage of decomposition for bacterial-feeding nematodes and macro-detritivores and at the late stage of decomposition for fungal-feeding nematodes and meso-detritivores thus (iii) leading to contrasting soil fauna structure–enzymes activities relationships between the two litters; we expect a direct link between enzymatic activities and the intensity of fauna functional groups differentiation.

2. Material and methods

2.1. Site description

The study was conducted on a French long term experimental station located in Estrées Mons, Northern France (49°873′N, 3°032′E). The experimental site is established since 2010 in order to study the impact of different cultural practices such as tillage, residues exportation and N fertilization on soil physicochemical properties, biological activities and environmental impacts (see Coudrain et al. (2016) for further details). We established plots in a field conducted in shallow tillage (8 cm depth) with crop residues restitution after the harvest. The soil was classified as a Luvisol Orthique (FAO classification) or a Typic Hapludalf (USDA classification). The soil texture is characterized by 16.8% clay, 76.3% silt and 3.8% sand with a mean pH (soil H_2O) of 7.8 in the top soil, and average soil C content is 8.7 g C kg^{-1}. Pea and barley had been grown in neighboring fields.

Two weeks prior the start of the experiment, the soil was prepared through shallow tillage (8 cm depth) and weeded with glyphosate in order to remove any living plants from the site; then, after the start of the experiment, hand-weeding was performed regularly. Pea and barley were incorporated at a dose of 10 t ha^{-1} in the 0–15 cm layer of 8 m^2 plots repeated randomly within four blocks distributed in our experimental zone. The plots within the blocks were separated by at least 2 m of distance. To prevent a "border effect", only the central 4 m^2 of each plot were sampled. The experiment started in October 2013 by mixing vigorously the litter with the top soil layer (0–15 cm). Each plot was delimited by wood pieces forming a square of 2 m side and 25 cm high. In order to evaluate litter mass loss and quality during decomposition, we buried litterbags at 8 cm depth (20 × 20 cm, 5 mm mesh size) in each plot at the beginning of the experiment. Each litterbag contained 5.0 g C of litter (dry weight), corresponding to 11.1 and 11.0 g DM of barley and pea, respectively.

Soil biota and abiotic parameters were followed in autumn 2013, spring 2014 and autumn 2014, corresponding respectively to 0, 7 and 11 months after litter addition. Time 0 was sampled on each of the 12 plots right after litter incorporation. The time scale between the sampling dates was determined in order to follow simultaneously the response of functional groups of heterogeneous life spans (microorganisms to earthworms) and to perform biota sampling at its optimal seasonal development stages (spring and autumn under our temperate climate). For the three campaigns, we collected soil samples (0–10 cm) to determine the mineral nitrogen content, microbial biomass, ergosterol, enzymatic activities, nematodes, micro-arthropods and macrofauna communities.

2.2. Litter mass loss and quality

A single litterbag per plot was sampled after 7 months of decomposition. After 11 months 3 litterbags per plot were collected in order to obtain enough materials for litter quality analyses. In the laboratory, litter from the litterbags were briefly washed under water in order to remove soil particles, and then dried at 37 °C