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# Aboveground litter quality is a better predictor than belowground microbial communities when estimating carbon mineralization along a land-use gradient

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## A R T I C L E I N F O

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## ABSTRACT

Because of the vegetation cover and anthropogenic disturbances, land-use management strongly influences soil heterotrophic decomposers. Yet, little is known about whether contrasting microbial communities originating from different ecosystems are functionally similar, and only a few studies have disentangled the direct and indirect effects of resource quality on both microbial communities and carbon mineralization rates. To assess the relative importance of aboveground litter quality and belowground microbial communities on litter decomposition, we conducted a reciprocal transplant experiment under controlled conditions using four litters (Triticum aestivum, Fagus sylvatica, Festuca arundinacea and Robinia pseudoacacia) and four soils (culture, plantation, grassland and forest) originating from a land-use gradient. We followed the kinetics of carbon mineralization over 21 dates spanning a 202-day period to assess the variability of responses generated by the plant-soil interactions. Furthermore, at four time points (at 0, 27, 97 and 202 days), the mass loss rates for the main sugars within the cell wall, the microbial biomass (fumigation-extraction), the microbial community structure via phospholipid fatty acid (PLFA), and the activities of four carbon-related hydrolytic enzymes were investigated to assess the functional significance of microbial communities. Our results demonstrated that the importance of soil types and heterotrophic decomposers on carbon mineralization rates was minor (1.2% of the variance explained) compared with the predominant role of litter quality. The structure of the microbial communities responded strongly to both long-term land-use changes and short-term litter additions; specifically, (i) higher proportions of fungi were observed in natural ecosystems compared with agro-systems, and (ii) an opportunistic subset of the bacterial community was stimulated after litter additions. Even if the land-use management and litter quality can shape the microbial community structure in a foreseeable way, we found an important degree of plasticity in the responses of contrasting decomposer communities. In particular, the enzymatic efficiency (defined as the amount of enzyme produced by unit of carbon mineralized) differed among litters but not among soil types, suggesting that the threshold between carbon allocation to growth and acquisition depended more on the 'resource-use strategies' of the soil microorganisms than on the community structure. The recalcitrant litters stimulated 'efficient' communities characterized by low enzymatic activities, microbial biomass and respiration rates at the opposite of labile litters that stimulated 'wasteful' communities characterized by higher activities and metabolic quotient (defined as the amount of carbon respired by unit of biomass). In addition to the direct effects of litter quality, the path analysis reinforced our conclusion that the functional traits of microorganisms via their enzymatic activities are more relevant than their identity for predicting carbon mineralization. Thus, although multiple and coordinated responses of soil microbes can improve our understanding of carbon fluxes, shifts in the plant community composition caused by land-use conversion will have a stronger impact on predictions of carbon mineralization than short-term changes in the microbial community composition.

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#### 1. Introduction

Over the last 15 years, an increasing body of literature has shown that the aboveground and belowground components of ecosystems are strongly linked through a variety of direct and indirect interactions (e.g., Wardle et al., 2004; Bardgett and Wardle, 2010). In the short-term, vegetation is of the most importance in highly diverse heterotrophic soil food webs due to the production of qualitatively and quantitatively different resource inputs via litter fall and rhizodeposition (Paterson, 2003; Xu et al., 2013). Over longer periods, plants can influence multiple soil characteristics, such as pH, organic carbon and nutrient contents, microclimatic conditions, and soil texture (Augusto et al., 2002; Russell et al., 2007; Mueller et al., 2012), simultaneously modifying the physicochemical conditions in which heterotrophic microorganisms reproduce and grow. Because of the intimate relationship between vegetation and soil decomposers, any changes in the composition of aboveground plant communities may strongly affect the structure, activity and functions of belowground microbial communities and vice versa (Zak et al., 2003; Van Der Heijden et al., 2008). For example, microbial community composition has been shown to vary locally among plant species (Orwin et al., 2010; Knelman et al., 2012), environmental gradients (Allison et al., 2007; Holden et al., 2013), and, to a larger extent, biomes (Fierer et al., 2009, 2012).

Despite the high variability observed in community composition at different spatial and temporal scales, the causal relationship between community structure and microbial-driven processes is subject to important uncertainties, and the validity of its use for estimating carbon mineralization among a variety of ecosystems is currently being debated (McGuire and Treseder, 2010; Treseder et al., 2012). According to Allison and Martiny (2008), three explanations support the validity of the assumption that the microbial communities are equivalent. After a disturbance (e.g., changes in resource quality, habitat and/or climate), soil microbial communities may be (i) resistant and not change; (ii) resilient and rapidly return to the original composition; or (iii) functionally similar, meaning that the ecosystem process rates are not altered by shifts in the community composition. If none of these three conditions are exhibited, then modifications in the microbial community structure will impact essential ecological functions, such as litter decomposition. Thus, a more precise evaluation of the role of soil microbes in ecosystem functioning is required to accurately assess whether and how key functional groups can be altered by changes in the environment and whether the processes they drive are performed to the same extent by structurally distinct microbial communities.

Because of the differences in growth forms, stoichiometric requirements, and functional abilities between bacteria and fungi (Keiblinger et al., 2010; Strickland and Rousk, 2010; Fanin et al., 2013), it is unlikely that these two broad groups of microbial decomposers are similarly influenced by alterations in their resources and habitats. Although the soil fungi:bacteria (F:B) ratio has been shown to be sensitive to the soil pH and C:N ratios of organic matter (Fierer et al., 2009), leaf and/or root traits can also be considered good predictors of their relative proportions (de Vries et al., 2012; Legay et al., 2014). For example, recalcitrant litter is often associated with higher fungal biomass, which has a high functional capacity to decompose complex plant polymers, such as lignin (Romani et al., 2006; McGuire et al., 2010). Conversely, adding labile substrates stimulates an opportunistic subset of the bacterial biomass (Cleveland et al., 2007; Fierer et al., 2007), such as gram-negative bacteria (GN), which have been shown to behave more copiotrophically than gram-positive bacteria (GP) in the presence of plant-derived carbon compounds (Kramer and Gleixner, 2008; Fanin et al., 2014). Thus, modifying soil properties and litter traits among a variety of ecosystems should theoretically shape the microbial community structure in a foreseeable way, with potential consequences for the enzymatic activities and fates of different carbon forms (Wickings et al., 2012; Wallenstein et al., 2013). In particular, the enzymatic efficiency, defined as the relationship between mineralized carbon and enzyme activities over time (Sinsabaugh et al., 2002), should depend of the proportion of each functional group with higher efficiency when oligotrophic microbes are more abundant within the community (Amin et al., 2014). Nevertheless, this hypothesis has never been assessed across soils that differ in their past resource history, and whether the enzymatic efficiency varies among distinct microbial communities remains an open question.

To understand the relative importance of the soil microbial community structure relative to litter traits along a variety of ecosystems, we investigated the composition and functional importance of soil microbes by conducting a reciprocal transplant experiment with litter and soil originating from a land-use gradient on the same soil substratum (forest, plantation, grassland and culture). We focused on the long-term effects of the land use on the differentiation of soil microbial communities and on how the short-term effects of litter addition impact specific groups of decomposers over 202 days of incubation. To test whether habitat and resource changes can predictably shape the soil microbial composition, we hypothesized that (H1) the F:B ratios should vary along the land-use gradient from agrosystems to natural ecosystems, with higher ratios in soils characterized by low pH and high C:N ratios and that (H2) labile substrate additions should stimulate copiotrophic GN bacteria, with the relative proportion of oligotrophic GP bacteria increasing as decomposition proceeds. To test whether decomposer communities are functionally dissimilar, we hypothesized that (H3) carbon mineralization and the decomposition of various carbon forms should vary by soil type and that (H4) enzymatic efficiency should be higher in recalcitrant litter environments that are characterized by a greater abundance of oligotrophic organisms (i.e, forest soil). Finally, to test whether the overall structure of the soil microbial community is important for assessing carbon mineralization along the land-use gradient, we created a model based on the entire dataset to disentangle the effects of litter quality from the effects of community structure on mineralization rates. We hypothesized that (H5) in addition to the direct control of litter traits, the indirect effects via the responses of belowground decomposer communities explain a significant amount of the variation of carbon fluxes along the land-use gradient.

#### 2. Materials and methods

### 2.1. Experimental design

#### 2.1.1. Litter and soil collection

We conducted a microcosm experiment using litter and soil from four different ecosystems, namely, wheat culture, black locust plantation, grassland, and deciduous forest, along a land-use gradient on a common soil substratum within the 'AgroParisTech' site at Grignon (48°50'N, 1°56'E), which is 40 km southwest of Paris. Because the vegetation cover and management intensity varied over decades for the different ecosystems (except for the plantation at <10 years), we will refer to these as 'long-term effects' of land use throughout the article. The selected ecosystems were chosen to be in close proximity, specifically, on a plot of approximately one hectare, to avoid large variations in soil properties (see Appendix A for a detailed description of the soil characteristics). We chose to work on ecosystems originating from the same soil substratum to assess whether the shifts generated in the vegetation cover and the effects of the disturbance frequencies would influence microbial traits on a small spatial scale. The original physicochemical conditions (pH, organic matter) of each ecosystem were retained to limit the changes in the structure of the microbial Download English Version:

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