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The influence of litter composition across the litter–soil interface on mass loss, nitrogen dynamics and the decomposer community

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ABSTRACT

Many studies have investigated the influence of plant litter species composition on decomposition, but results have been context-dependent. Litter and soil are considered to constitute a decomposition continuum, but whether litter and soil ecosystems respond to litter identity and mixing in the same manner is unsure. In a field experiment utilizing 5 litter species and their mixture, we investigated whether the effects of litter identity and mixing on mass loss, nutrient dynamics, and decomposer communities are consistent across the litter–soil interface. In monoculture, mass loss and nitrogen (N) dynamics in the litter layer corresponded to the underlying soil N availability, demonstrating the continuum of resources from litter to soil. Litter microbial biomass and mesofauna abundance tended to be greater on litter with a faster decay rate and greater N release. However, soil decomposer abundance and diversity were not greater with higher soil N, causing litter and soil communities to respond differently to litter identity. Non-additive mass loss and N dynamics were observed after 6 months, and were correlated with non-additive litter microbial community composition and litter mesofauna communities, but all other aspects of the litter community and all measures of the soil community were additive. Decomposer communities and N dynamics did not respond similarly to the litter mixture across the litter–soil interface. This study is one of the few to comprehensively examine how a litter mixture influences decomposition dynamics and communities across the soil–litter interface, including multiple taxa and trophic levels. Our results demonstrate that processes associated with decomposition are decoupled for litter and soil, particularly in that litter showed non-additivity in mass loss, N release and decomposer community, but soil responses were largely additive.

1. Introduction

There is a well-established relationship between plant litter species identity and its decomposition (e.g., McClaugherty and Berg, 1987; Aber et al., 1990; Aerts, 1997). This relationship is probably due to the influence of litter chemical quality on decomposer community composition and activity (Wardle, 2002; Carrillo et al., 2012). Many studies have identified an influence of plant litter species composition on its decomposer community and plant litter mass loss (e.g., McClaugherty et al., 1985; Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Wardle et al., 2006; Ball et al., 2008; Gessner et al., 2010), including studies in heavily-managed and disturbed ecosystems such as agroecosystems (e.g., Beare et al., 1992; Moço et al., 2010).

Beyond the litter layer, litter composition also influences the underlying soil along what is frequently considered to be a decomposition continuum across the litter–soil interface (Melillo et al., 1989; Wardle et al., 2004). Under this concept, plant litter influences soil foodwebs based on litter chemical characteristics to therefore influence soil processes (Wardle et al., 2004). Soil communities have been shown to vary as a function of the surface litter resources (e.g., Vivanco and Austin, 2008; Ayres et al., 2009; Carrillo et al., 2011; Milcu et al., 2013), and thus may change with alterations to litter species composition. How the soil communities respond to changes in species composition of surface litter resources can have implications on the dynamics of nutrients and indigenous soil organic matter (Waldrop and Firestone, 2004), because soil communities are responsible for releasing up to 30% of nutrients available to plants (Verhoef and Brussaard, 1990; Setälä and Huhta, 1991; Bonkowski et al., 2000; Moore et al., 2003). Therefore, altered decomposition and decomposer communities in the litter layer in response to litter composition can result in altered

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carbon (C) and nitrogen (N) cycling dynamics in the underlying soil (Meier and Bowman, 2008; Carrillo et al., 2011; Szanser et al., 2011). An area of uncertainty within this framework is whether litter and soil systems respond with similar trends to different litter compositions. For example, most studies looking at the effect of litter composition on decomposer communities have focused on the communities inhabiting either the litter (e.g., Bjørnlund and Christensen, 2005; Wardle et al., 2006; Ball et al., 2009b) or the soil (e.g., Bending et al., 2002; Salamanca et al., 2006; Carrillo et al., 2011), but few have looked at the effects in both environments simultaneously (but see Szanser et al., 2011). However, it is crucial to distinguish the response of the litter communities from that of the soil communities because (a) they may utilize different organic matter pools as energy and nutrient resources and thus can play different roles in driving biogeochemical processes, and (b) interactions between the populations that compose each environment's community may influence C and nutrient cycling and organic matter pools (Fontaine et al., 2004). Studies have begun to identify a disconnect between litter and soil processes, suggesting that the factors regulating decomposition and community structure are not necessarily the same for each environment (Parton et al., 2007; Adair et al., 2008), even though they are part of the same "continuum". Therefore, it is important to identify how and why soil and litter communities might respond differently to changes in litter composition.

An interesting aspect of litter composition that can be tested using this framework is litter-mixing. Plant litter species mixing is one heavily-studied aspect of litter composition whose effects on decomposition dynamics has been investigated in many different types of ecosystems incorporating a wide variety of plant types. Some studies show that, when litter species are in mixture, the properties relating to decomposition appear to be additive, such that a mixture behaves as expected based on the average influence of the individual species involved (e.g., Wardle et al., 1997; Ball et al., 2008). Alternatively, other studies have found that emergent dynamics arise, leading to non-additive dynamics that differ from those expected based on the monocultures, either positively or negatively (e.g., Gartner and Cardon, 2004; Ball et al., 2009a; Chapman and Newman, 2010). For example, while monocultures of labile litter high in nutrients and low in structural compounds tend to provide a better resource for decomposers and support a larger decomposer community biomass, plant litter in mixture may support a more diverse decomposer community than a monoculture (Wardle, 2006; Chapman and Newman, 2010). This influence on decomposer diversity is likely due to the fact that organisms are divergent in their resource use, and thus community composition may change in response to a more diverse chemical and structural resource (Wardle, 2006; Makkonen et al., 2013). Complementarity among decomposer taxa could allow for more efficient resource use and therefore non-additively faster decomposition, despite results indicating that the saturation level may be very low (reviewed by Gessner et al., 2010). Non-additive effects might also be negative, if for example competition and microbial release of inhibitory substances lead to antagonistic interactions that prevent or reverse any positive mixing effects (see Hättenschwiler et al., 2005). Given the incredible diversity of plant chemical composition and decomposer communities around the world, studies have reported a wide variety of outcomes when mixing different litter types for mass loss, decomposer communities, and nutrient dynamics. Results are environmentally context dependent, for example due to soil environmental conditions (e.g., Li et al., 2011; McLaren and Turkington, 2011). Overall, this suggests that the consequences of changing litter species composition are not predictable based on knowledge of existing litter species studied independently, and demonstrating the complicated nature of the diversity-decomposition relationship (reviewed by Gessner et al., 2010).

Though the entire soil foodweb is hypothesized to be influenced by litter composition under the litter–soil continuum concept, the role of the litter decomposer community across various trophic levels in mixed-litter dynamics has not been well defined. The relationship between litter diversity and decomposer community has been studied mostly within individual trophic levels, rather than across the levels of the foodweb that are involved in decomposition or across the litter–soil interface. Without knowing the response of multiple taxa across levels of the foodweb, it is harder to identify cascading effects of litter resource diversity on community composition such as top-up or bottom-down effects that might influence decomposition dynamics (Gessner et al., 2010).

The traditional concept of the litter–soil continuum focuses on the unidirectional influence of litter on soil communities and processes. In addition to the fact that litter composition influences underlying soil communities, there may be feedbacks in which alterations to the soil community may influence decomposition of the plant litter mixture (e.g., Hättenschwiler and Gasser, 2005; Schädler and Brandl, 2005; Vos et al., 2011; Carrillo et al., 2012; Eisenhauer et al., 2012). For example, as mentioned above, we may observe complementarity among the litter and soil faunal community when taxa are functionally diverse or antagonism as the result of competition. However, evidence for this is scarce in terrestrial ecosystems (Gessner et al., 2010). Studies investigating the role of terrestrial decomposer biota present in litter mixing experiments have focused on large-body macrofaunal detritivores (Heemsbergen et al., 2004; Hättenschwiler and Gasser, 2005; Jacob et al., 2009; Vos et al., 2011, but see Schädler and Brandl, 2005; Eisenhauer et al., 2012). Gessner et al. (2010) recently pointed out that the lack of comprehensive studies indicates the need for experiments manipulating the complete size range of litter fauna and litter quality to properly assess the influence of the decomposer community on decomposition of litter mixtures.

We investigated two key aspects pertinent to the litter–soil continuum concept: litter-mixing and the soil fauna community. We sought to determine how different litter species of varying chemical quality and their mixture influence decomposition dynamics and community structure across the litter–soil interface, and how alterations to soil communities may alter these patterns. In a previous report, we found that the structure of the soil community can alter the effect of the surface litter chemical composition on N dynamics in the mineral soil. Specifically, the study reported that the presence of the larger fauna can magnify the stimulating effect that high-N litter has on N mineralization (Carrillo et al., 2011). By influencing the effect of litter quality on N dynamics, the larger fauna can alter the amount and temporal dynamics of N availability which, in turn, can have important implications for ecosystem productivity and long term nutrient cycling dynamics. In the current study, we hypothesized that 1) The effects of litter identity and litter-mixing on mass loss, N dynamics and biotic community structure will be consistent across the litter–soil interface, such that the magnitude and direction of litter identity and mixing effects would be similar for N dynamics and decomposer community in both the litter and soil, given the continuum of resources; and 2) The manipulation of larger-bodied meso- and macrofauna composition in the soil would affect decomposition processes across the interface, such that their presence would increase decomposition and N dynamics to enhance the effects of litter identity and litter-mixing. To gain a comprehensive understanding of multiple functions associated with decomposition, we measured the response of mass loss, mineral N released from litter and accumulated in the soil, and microbial, nematode, and microarthropod communities in the litter and soil.