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Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland

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The consequences of predicted climate change on ecosystem processes is difficult to evaluate, because biodiversity is also susceptible to change resulting in complex interactions on ecosystem functioning. With an experimental approach, we aimed to understand how plant community diversity (through different plant litter mixtures) and climate change (through decreased precipitation) may impact microbial abundance and diversity and affect C and N cycling in a Mediterranean shrubland. Along a natural plant diversity gradient, we manipulated the amount of precipitation and followed leaf litter decomposition during one year. We found that multi-species litter mixtures had higher microbial abundance, lower bacterial diversity and higher fungal diversity than predicted from single-species litter. In addition, C and N release increased with increasing litter species richness. Microbial abundance and diversity were positively, but weakly, correlated to the litter mixture effects on C and N release. Drier conditions increased microbial diversity but had no effect on microbial abundance. The net release of N from decomposing litter was lower with reduced precipitation irrespective of litter species richness and composition, while that of C was higher or lower depending on litter species composition. The relationships between microbial communities and litter mixture effects on C and N release were altered under drier conditions. Our data provide clear evidence that microbial decomposers and the processes they drive, respond to changing plant community diversity and composition in a Mediterranean shrubland. We highlighted the importance of *Quercus coccifera* that appears to be a key species in shaping microbial communities and driving synergistic effects on C and N release more than the three other shrub species. Our study also suggests that shifts in the plant community composition may have stronger impacts on litter decomposition and nutrient cycling than relatively subtle changes in precipitation as simulated in our study.

1. Introduction

Decomposition of plant material is a key ecosystem function determining the carbon and nitrogen cycles to a great extent (Cadish and Giller, 1997; Bardgett, 2005). In most of natural ecosystems, litter material from different plant species decomposes together. Numerous studies have shown that mixtures of litter from different plant species decompose at different rates compared to what is expected from the component species (reviewed in Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Gessner et al., 2010). Among the mechanisms underlying these litter diversity effects, complementary resource use by the decomposer community may be particularly important for explaining synergistic litter mixing effects (Hättenschwiler et al., 2005). However, it is difficult to quantify this mechanism (Hättenschwiler et al., 2011), especially regarding the role of microbial decomposers. This limits the

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understanding of how resource diversity interacts with decomposer community effects on carbon and nitrogen cycling during decomposition. Indeed, soil microorganisms are the major drivers of litter decomposition and nutrient mineralization (Bardgett, 2005; de Graaff et al., 2010), but it is presently not well understood if and how litter mixture effects on decomposition are related to shifts in the structure and composition of the microbial decomposer community. Previous studies have provided some evidence that microbial biomass and diversity respond positively to litter mixing (Blair et al., 1990; Bardgett and Shine, 1999; Kominoski et al., 2007; Chapman et al., 2013), which could result from an increased diversity of substrates and associated niches for microorganisms (Tilman et al., 1997; Hooper and Vitousek, 1998; Hättenschwiler et al., 2011). Additionally, it has been shown that decomposition rates increased with increasing microbial diversity, due to complementarity and facilitation mechanisms that enhance microbial exploitation of organic matter (Robinson et al., 1993; Setälä and McLean, 2004; Tiunov and Scheu, 2005), in accordance with theoretical predictions (Loreau, 2001).

Abundance, community structure, and activity of soil microorganisms are strongly controlled by water availability (Angel et al., 2010; Schimel et al., 2007; Williams and Rice, 2007; Cregger et al., 2012; Kaisermann et al., 2013). Thus, climate change-related modifications in the precipitation regime are likely to affect the microbial decomposer community, with potential consequences on decomposition dynamics, carbon cycling and nutrient availability for plants (Hobbie, 1996; Aerts, 1997; Knapp et al., 2008). In Mediterranean ecosystems, water availability is the most important environmental constraint for decomposition, with biological processes being strongly regulated by the seasonally contrasting climate condition such as summer drought and episodic drying/rewetting cycles (Sardans and Peñuelas, 2013). Regional climate models predict an increase in both temperature and drought conditions in the Mediterranean region in the future (Giorgi and Lionello, 2008; Polade et al., 2014). These changes are expected to result in increased frequency, intensity and duration of drought, especially during the summer (Dubrovsky et al., 2014). Increased drought should lead to more limiting conditions for soil microorganisms and may provoke shifts in the microbial community composition (Pesaro et al., 2004; Schimel et al., 2007). Such changes of microbial communities are also likely affecting the decomposition process. However, the relationship between climate change, microbial community composition and decomposition is not well understood.

In this study, we examined litter decomposition in a field experiment in which we manipulated the amount of precipitation along a natural plant diversity gradient in a Mediterranean shrubland. We specifically investigated the decomposition of leaf litter mixtures along with their associated microbial communities compared to their respective single litter species treatments with or without reduced rainfall during one year. We hypothesized a positive effect of litter species diversity on microbial communities (i.e. increase of abundance and diversity) and on litter decomposition (i.e. increase of carbon and nitrogen release). We hypothesized a negative effect of drier conditions on microbial communities (i.e. decrease of abundance and diversity) and on litter decomposition (i.e. decrease in carbon and nitrogen release), as soil moisture has been reported as the most limiting environmental factor in Mediterranean ecosystems. Furthermore, we explored the potential relationships between microbial communities and carbon and nitrogen release. We hypothesized that the frequently observed non-additive litter mixture effects on litter decomposition are correlated to the abundance and diversity of fungal and bacterial decomposers. In a last hypothesis, we predicted that drier conditions would attenuate the non-additive litter mixture effects on litter decomposition as well as the potential relationships between microbial communities and non-additive litter mixture effects.

2. Materials and methods

2.1. Study site

The study site was located in the Massif de l'Etoile near Marseille, France (43° 22′ N, 5°25′ E) at 275 m above sea level (see Montès et al. (2008) for a detailed description of the study site). The mean annual precipitation is 552 mm and the mean annual temperature is 14.6 °C (mean values over the period 2002-2012 averaged across the two meteorological stations in Marignane (43°26′N, 5°12′E) and Marseille (43°15′N, 5°22′E) closest to our study site). The soil is classified as shallow rendzina developed over limestone bedrock with 66% of stones in the top 50 cm, a mean pH of 7.9, a mean C:N ratio of 18 and a mean CEC of 36.8 cmol kg^{-1} (means from 92 different soil samples taken in the study plots; see Shihan et al. (2017) for further details).

The vegetation is a woody shrub-dominated "garrigue", with shrub heights ranging between 0.2 and 1.4 m (Montès et al., 2008) and a heterogeneous cover ranging between 25% and 95%. Four woody shrub species dominate the community: *Quercus coccifera* L. (*Quercus*, with an average cover across all plots of 36%), *Cistus albidus* L. (*Cistus*, 18%), *Ulex parviflorus* Pourr. (Ulex, 10%), and *Rosmarinus officinalis* L. (*Rosmarinus*, 9%).

2.2. Experimental setup

The study site is characterized by a natural small-scale mosaic of assemblages of distinct compositions of the four dominating woody shrub species (i.e. *Quercus, Cistus, Rosmarinus* and *Ulex*) that allowed establishing a series of plots varying in species richness of these four species. Ninety-two 4 × 4 m plots were selected based on plant community composition in order to include all 15 possible combinations of the four dominant shrub species (i.e. 4 single-species litter, 6 two-species mixtures, 4 three-species mixtures, and one four-species mixture). The distance between plots varied from 1 to 30 m (Fig. S1). Each of the 15 different plant combinations was replicated six times, except for the four-species mixture that was replicated eight times. All plots were equipped with a 4 m × 4 m solid aluminum frame, held 2 m above the ground by aluminum posts at the outer border of the 16 m^2 plot area and fixed to the ground with reinforcing bars. Stainless steel gutters were mounted on top of the aluminum frame. Contrary to the rain exclusion plots, the gutters in the control plots were mounted upside down in order to let the precipitation fall on the vegetation. A supplementary PVC gutter and a pipe mounted at the border of the frame allowed to evacuate the rainwater away from the plots. Over the 6 replicates for each plant combinations (8 for the four-species mixture), 3 replicates were randomly assigned to control plots and the other 3 to rain exclusion plots (4 of each for the four-species mixture). The experimental rain exclusion was set up in October 2011. The exact amount of precipitation excluded was estimated using (i) rain gauges installed at ground level underneath the gutters in both control and rain-excluded plots and (ii) TDR100 probes (Campbell Scientific Inc., Logan, Utah) installed in seven control and eight rain-excluded plots at 10 cm soil depth and by (iii) determining the gravimetric humidity in the soil sampled in control and excluded plots. Compared to control plots, the rain exclusion plots received on average 12± 2% less rainfall. This exclusion resulted in an average lower soil humidity of −6.5% (that could reach between −13 and −24% during rain events) at 10 cm soil depth between control and rain exclusion plots (determined by