Soil Biology and Biochemistry 125 (2018) 27–36

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Contrasting responses of bacterial and fungal communities to plant litter diversity in a Mediterranean oak forest

Mathieu Santonja[a,b,c,d,*,1], Quentin Foucault[a,e,1], Anaïs Rancon[a], Thierry Gauquelin[a], Catherine Fernandez[a], Virginie Baldy[a], Pascal Mirleau[a,**]

[a] Aix Marseille Univ., Univ. Avignon, CNRS, IRD, IMBE, Marseille, France
[b] Univ Rennes, CNRS, ECOBIO UMR 6553, F-35000, Rennes, France
[c] Ecole Polytechnique Fédérale de Lausanne (EPFL), School of Architecture, Civil and Environmental Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Station 2, 1015, Lausanne, Switzerland
[d] Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Site Lausanne, Case postale 96, 1015, Lausanne, Switzerland
[e] Molecular Ecology Group, Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, 60325, Frankfurt am Main, Germany

ARTICLE INFO

Keywords:
Bacteria
Fungi
Litter decomposition
Litter traits
Mediterranean forest
Plant-soil interaction

ABSTRACT

Tree species diversity of forested ecosystems control the diversity of leaf litter inputs to the soil, with cascading effects on the microbial communities colonizing decomposing litter. However, the extent to which bacterial and fungal communities inhabiting the litter layer are affected by shifts in tree species diversity is not well understood. To investigate the role of litter species diversity, litter species identity and litter functional traits on bacterial and fungal communities of a typical Mediterranean oak forest, we set up a yearly field litterbag experiment that considered leaf litter mixtures of four abundant species: *Quercus pubescens*, *Acer monspessulanum*, *Cotinus coggygria* and *Pinus halepensis*. We found that both bacterial and fungal communities varied strongly during decomposition but showed distinct succession patterns. Both communities were also strongly influenced by litter species diversity, litter identity and litter functional traits. The intensity and the direction of these effects varied during decomposition. Litter diversity effects were mediated by litter species composition rather than litter species richness, highlighting the importance of litter species identity - and associated litter traits - as drivers of microbial communities. Both the "mass-ratio hypothesis", measured through the community weighted mean (CWM) litter traits, and the "niche complementarity hypothesis", measured through the functional dissimilarity (FD) of litter traits, contributed to litter diversity effects, with a greater relative importance of FD compared to CWM, and with an overall stronger impact on fungal- than on bacterial-communities. Interestingly, increasing FD was related to decreasing bacterial diversity, but increasing fungal diversity. Our findings provide clear evidence that any alteration of plant species diversity produces strong cascading effects on microbial communities inhabiting the litter layer in the studied Mediterranean oak forest.

1. Introduction

Alterations of plant communities due to ongoing global change, including climate, land-use and resource availability changes, have already been observed and are presumed to continue (Vitousek et al., 1997; Walther et al., 2002; van der Knaap et al., 2018). Studies of the relationship between plant species diversity and ecosystem functioning have received growing attention in the last decade (Diaz and Cabido, 2001; Loreau et al., 2001). The majority of such studies investigated how plant diversity affects litter decomposition efficiency (Gartner and Cardon, 2004; Hättenschwiler et al., 2005), but only a few have examined how it affects the organisms running the process (Bardgett and Shine, 1999; Leloup et al., 2018). Soil microorganisms are indeed major drivers of litter decomposition and mineralization (Bardgett, 2005; de Graff et al., 2010) and their responses to changes of leaf litter diversity should interact with the decomposition process efficiency.

Litter microbial communities are strongly influenced by the quantity and the quality of litter inputs from the plant community (Calderon et al., 2001; Lalor et al., 2007). Differences in litter quality among tree species have been reported to affect the abundance and composition of soil bacterial and fungal communities (Grayston et al., 1998; Aponte et al., 2013; Prescott and Grayston, 2013). Both nitrogen (N) and

* Corresponding author. Aix Marseille Univ., Univ. Avignon, CNRS, IRD, IMBE, Marseille, France.
** Corresponding author.
E-mail addresses: mathieu.santonja@gmail.com (M. Santonja), pascal.mirleau@imbe.fr (P. Mirleau).
[1] equal contribution to the work.

https://doi.org/10.1016/j.soilbio.2018.06.020
Received 13 April 2018; Received in revised form 12 June 2018; Accepted 19 June 2018

phosphorus (P) availabilities actually shape microbial decomposer communities as they are often limiting elements in the soil and play a central role in resource competition (Cleveland and Liptzin, 2007; Mooshammer et al., 2014). Other plant litter traits such as secondary metabolites are recognized to repress the biomass and activity of microbial communities (Fierer et al., 2001; Ushio et al., 2013; Chomel et al., 2014, 2016). For instance, Chomel et al. (2014) observed a negative correlation between phenolic concentrations and fungal biomass during litter decomposition in a Mediterranean pine forest, calling attention to the inhibitory effect of phenolic compounds from pine leaf litter toward fungi (Kainulainen et al., 2003; Kraus et al., 2003; Hättenschwiler et al., 2005). Likewise, Amaral and Knowles (1998) reported that monoterpenes inhibited the activity and growth of certain soil microbial groups while stimulating others.

However, in most natural ecosystems, litter material from various plant species decomposes together. As key actors of litter decomposition, microbial communities are likely responding to the variation in species composition of the litter input that determines litter functional diversity. According to the "mass-ratio hypothesis" (Grime, 1998), ecosystem properties are strongly related to the relative input of each species, implying that functional traits of the dominant plant species mainly determine ecosystem function (Garnier et al., 2004) and thus the litter trait control over microbial communities changes along community-weighted mean (CWM) trait values. Alternatively, the "niche complementarity hypothesis" argues that the functional diversity (FD) of trait-values promotes an ecosystem's functioning (Petchey and Gaston, 2006; Diaz et al., 2007), for instance, by improving the availability of complementary resources for microbial communities (Wardle et al., 1997; Barantal et al., 2014; Handa et al., 2014). These two mechanisms can operate simultaneously by affecting microbial communities as a result of plant (litter) composition change. However, our knowledge about the relative importance of these theories in controlling microbial decomposer communities is very limited.

The influence of tree species diversity on litter microbial communities has been studied in boreal, temperate and tropical ecosystems, while information from Mediterranean ecosystems is extremely scarce (e.g. Shihan et al., 2017; Santonja et al., 2017a, 2017b). Mediterranean forests have a different species composition than temperate forests due to the Mediterranean climate characteristics that have shaped species distribution (Quézel and Médail, 2003). Remarkable contrasts of temperature and humidity across seasons, and in particularly the summer drought period, correspond to particular leaf litter traits, including secondary metabolites (Chomel et al., 2014, 2016; Hashoum et al., 2017), that have the potential to influence microbial decomposer communities (Schimel et al., 2007; Williams and Rice, 2007; Brockett et al., 2012).

In this study we assessed the potential consequences of a forest composition shift on microbial communities associated with decomposing leaves, including both loss and gain of tree species. We conducted a full-factorial *in situ* decomposition experiment over a gradient of litter species diversity in a Mediterranean downy oak forest. Downy oak (*Quercus pubescens* Willd.) is broadly distributed from northern Spain to the Caucasus (Quézel and Médail, 2003), and is the dominant species structuring many forests of the northern parts of the Mediterranean basin. We used leaf litter from the three dominant woody plant species naturally present in the forest (*Q. pubescens*, *Acer monspessulanum* L. and *Cotinus coggygria* Scop.) and one pine species (*Pinus halepensis* Mill.), which may become more frequent in downy oak forest in the future in response to climate change (i.e. under warmer and drier environment; Gaucherel et al., 2008; Bede-Fazekas et al., 2014). We aimed to determine the effects of (i) litter species richness, (ii) litter species composition, (iii) litter species identity and (iv) litter functional trait values on the dynamics of microbial communities, during one-year leaf litter decomposition. Using fingerprinting methods, we explored in parallel fungal and bacterial community dynamics at six time points, expecting to reveal differences across microbial decomposers groups that have distinct trophic niches (Boer et al., 2005; Buée et al., 2009; Lopez-Mondejar et al., 2015). We hypothesized that H1: microbial diversity and community structure associated to decomposed leaves or needles change with decomposition time, as the litter quality changes over the course of decomposition (Snajdr et al., 2011; Baldrian et al., 2012); H2: microbial diversity increases with the increase of litter species richness, by increasing resource diversity and microhabitat heterogeneity; H3: microbial community parameters (diversity and community structure) are also determined by the plant identity in the litter mixture, as differences of litter quality among plant species would lead to distinct effects on microbial community parameters; H4: microbial diversity responds to "niche complementarity hypothesis" rather than to "mass-ratio hypothesis", as litter mixtures with contrasting litter quality improve the availability of different resources and microhabitat for microorganisms. We also hypothesized that H5: the relationships between microbial decomposers and litter diversity decrease with decomposition time, as resource diversity changes during leaf litter decomposition, leading to homogenization of litter quality across litter mixtures.

2. Materials and methods

2.1. Study site

This study was conducted in the Oak Observatory at the OHP (O_3HP) experimental site located in the research center "Observatoire de Haute Provence", 60 km north of Marseille, South of France (43°56′115″ N, 05°42′642″ E). The site is 680 m above sea level, and presents a mean annual temperature of 11.9 °C and a mean annual precipitation of 830 mm (1967–2000 period, WMO standard temperature and precipitation: 1960–2003 St Michel l'Observatoire/Meteo France 04192001; 2003–2010 Dauphine/Meteo France 04068001 - on and close to the OHP, respectively). Temperature and rainfall during the experiment showed a seasonal distribution characteristic of a Mediterranean climate, with maximum rainfall in June and October, maximum temperature in July and August, and a dry summer season lasting less than two months, typical of a supramediterranean bioclimatic stage (Supplementary Fig. S1). According to the French Référentiel Pédologique (Baize and Girard, 1998), the soil is a pierric calcosol (with S horizon between limestone rocks) or a calcarisol when limestone appears less than 25 cm deep. The pH is between 6.5 and 7.5 for the A horizon and 7.5 the for S horizon. According to the WRB classification (IUSS Working group WRB, 2006) the soil can be classified as a mollic leptosol.

The study site is a Mediterranean natural old-growth oak forest belonging to the site Natura 2000 "FR9302008 Vachères", in which 53 different plant species were identified. This forest already existed in the late 18th century (Hilaire et al., 2012) and was managed for centuries by coppicing. *Q. pubescens* (Downy oak: 75% coverage) and *A. monspessulanum* (Montpellier maple: 25% coverage) are the two dominant tree species, with understory vegetation dominated by *C. coggygria* (smoke tree: 30% coverage). *P. halepensis* (Aleppo pine) is present very close to the downy oak forest but only in open environments.

2.2. Experimental set-up

This experiment used litter of four species: *A. monspessulanum, C. coggygria*, *P. halepensis* and *Q. pubescens* that will be named *Acer*, *Cotinus*, *Pinus* and *Quercus* hereafter. Freshly abscised leaves of the four species were collected over the whole period of maximum litter fall from October to November using litter traps suspended under the relevant species. Leaves were dried at ambient temperature and stored until the beginning of the experiment.

Leaf litter decomposition was studied for 320 days using the litterbag method (Swift et al., 1979). Litterbags measuring 20 cm × 20 cm with a mesh size of 4 mm were filled with 10 g of dry leaf litter and