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Fungal communities influence decomposition rates of plant litter from two dominant tree species

Johan Asplund [a, *], Håvard Kauserud [b], Stef Bokhorst [c], Marit H. Lie [a], Mikael Ohlson [a], Line Nybakken [a]

[a] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
[b] Section for Genetics and Evolutionary Biology (Evogene), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway
[c] Department of Ecological Science, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

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ABSTRACT

The home-field advantage hypothesis (HFA) predicts that plant litter decomposes faster than expected underneath the plant from which it originates. We tested this hypothesis in a decomposition experiment where litters were incubated reciprocally in neighbouring European beech and Norway spruce forests. We analysed fungal communities in the litter through DNA metabarcoding and evaluated the effect of mesofauna (mites and springtails) on litter mass loss by using different litter-bag mesh sizes. Accounting for general differences in decomposition between litter and forest types, we found a significant home field advantage of 24%. Litter decomposed faster in the beech forest but spruce litter decomposed faster than beech litter. Fungal communities showed a clear dependency on both forest and litter type. Mesofauna did not affect litter mass loss rates or microbial species composition.

1. Introduction

Commonly, 50–99% of the aboveground net primary production is not consumed by animals (McNaughton et al., 1989). Instead, this material becomes plant litter that enters the belowground decomposer subsystem, and during the last two decades the interactions between above- and belowground biota have been increasingly recognized as key-drivers of ecosystem function (Bever et al., 1997; Wardle et al., 2004; Bardgett and Wardle, 2010; Treseder and Lennon, 2015; Paul, 2016). The link between the above- and belowground subsystems has proven to be tight as belowground decomposer communities are largely structured by the vegetation, with plant species, plant diversity and biomass being the most important factors (Sætre, 1998; Pennanen et al., 1999; Hooper et al., 2000; van der Putten et al., 2013; Peršoh, 2015). Any changes in the vegetation will thus directly, or indirectly, result in corresponding changes in the decomposer community that may involve significant changes in the activity and composition of the community (Bardgett and Wardle, 2010).

Plants rely on the decomposer community to recycle nutrients from dead organic plant material. Fungi are among the main microbial decomposers of plant litter, being able to decompose the recalcitrant constituents (Baldrian, 2016). Many plant species even have a distinct soil decomposer community adapted to breakdown the plant's own litter (Bezemer et al., 2010). The plant species-specific nature of many decomposer communities suggests that plant litter is decomposed faster underneath the plant from which it originates than under other plant species, and this hypothesis has been coined “home-field advantage” (HFA) (Hunt et al., 1988; Gholz et al., 2000; Ayres et al., 2009). The main mechanism for the HFA is that the decomposer community is adapted to a certain litter quality (Freschet et al., 2012), and that litter from outside, with a different structural and chemical composition, is harder to decompose. The HFA effect on litter has been estimated to increase litter decomposition on average by 4–8% but values up to 58% have been reported. (Ayres et al., 2009; Wang et al., 2013; Veen et al., 2015). The emergence of new plant species with novel traits in many ecosystems, due to human introductions and expansions driven by climate change,

* Corresponding author.
E-mail address: johan.asplund@nmbu.no (J. Asplund).

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may have large impacts on local carbon and nutrient cycling rates. The distribution limit of European beech is expected to expand substantially towards the north at the expense of spruce due to climate warming (Hickler et al., 2012) but little is known about the consequences for litter decomposition rates.

Fungal species composition in forest litter and soil is largely governed by dominant trees (Prescott and Grayston, 2013; Urbanová et al., 2015). A recent study comparing the microbial community under seven forest trees found that 36% of the dominant fungal OTUs were restricted to one or two tree species and that the tree species-specificity is larger in litter than in soil (Urbanová et al., 2015). Microbial communities in the mineral soil are significantly different between spruce and beech forests (Nacke et al., 2016; Uroz et al., 2016). Previous papers have examined microbial species composition in litter from beech and spruce in relation to decomposition (Aneja et al., 2006; Kubartová et al., 2009). However, in these studies litter was not transplanted reciprocally between the forest types, and the HFA was not addressed.

During later decomposition stages, primary fungal colonisers may constitute a substrate for secondary fungi and bacteria (Baldrian, 2016), leading to a complex interdependency between litter types and associated microbes. In addition, the microbial community growing on litter forms part of the diet of detritivores such as microarthropods. Soil microarthropods affect litter decomposition by consuming and fragmenting litter, or by influencing microbial communities through grazing on fungal networks and fecal production (Petersen and Luxton, 1982). Fungal-feeding microarthropods can be highly selective, and their grazing can therefore lead to significant changes in composition, biomass and activity of microbial communities, resulting in both negative and positive effects on decomposition (Mikola et al., 2002; Cole et al., 2006; Crowther et al., 2011; Crowther and A'Bear, 2012). Even though it is well established that soil microarthropods play a role as decomposers in the below ground biota, relatively little is known about their relative importance as compared to that of the microbial decomposer community (Soong and Nielsen, 2016). However, because the soil microarthropod community composition differs between forest types (Migge et al., 1998; Scheu et al., 2003; Salamon et al., 2008) it is likely that its relative contribution in the decomposition process will depend on the dominating tree species in a given forest ecosystem.

We have performed a litter-bag experiment in neighbouring European beech (*Fagus sylvatica*; hereafter beech) and Norway spruce (*Picea abies*; hereafter spruce) forests where we placed beech and spruce litter in both forests. We used two types of litter-bag mesh sizes to include or exclude the soil invertebrate mesofauna, such as mites and springtails (Bokhorst and Wardle, 2013). We extracted and analysed DNA from the fungal community through DNA metabarcoding analyses to elucidate its species composition. We used this experimental set-up to test the following hypotheses: (i) Litter will decompose quicker when placed under the species from which it originated; (ii) Fungal community composition in leaf litter differs between contrasting forest and litter types; (iii) Excluding microarthropods from litter-bags will increase the fungal biomass and change the species composition of fungi. By testing these three hypotheses, we aimed to elucidate the relative roles of the fungal and soil microarthropod communities on litter mass loss rates in two dominant European forest types.

2. Materials & methods

2.1. Study site and litter material

The study site was a natural beech forest covering about 20 ha (Brånakollane, Vestfold, Norway S; 59°20′ N; 10°06′ E; 200 m a.s.l.) and a neighbouring Norway spruce forest. The forest floor vegetation is generally sparse, in particular in the beech forest, and consists mainly of *Oxalis acetosella* and *Anemone nemorosa*. In addition, there is *Vaccinium myrtillus* and some bryophytes, mainly the feather mosses *Hylocomium splendens* and *Pleurozium schreberi,* in the spruce forest. There is a sharp and distinct border between the two forest types, as part of the original beech forest was clear-cut in 1956 and planted with spruce. As such, apart from forest types, the two forest sites represent analogous environmental conditions in terms of underlying bedrock, subsoil, microtopography, and soil hydrology. According to a previous study at this site, there is no significant difference in soil pH between the beech (4.19 ± 0.1) and the spruce (4.09 ± 0.1) forests (Hustoft, 2016). See Ellingsen et al. (2017) and Ohlson et al. (2017) for more information about the sites and their forest history.

In October 2013, we collected recently senesced beech leaves from the trees and brown spruce needles from living spruce twigs. The litter was then left to air-dry (for 4 d). Initial mass prior to decomposition was determined air-dry and the values were converted to oven-dry mass values using the ratio between air-dry and oven-dry mass obtained from measurements on an additional 5 × 1 g of litter for each species. The weight control litter samples were first air-dried and then dried at 70 °C for 48 h after which they had constant weights. For both litter-types, concentration of N at start was determined on five sub-samples of the start material using a vario MICRO cube elemental analyser (Elementar, Hanau, Germany).

2.2. Experimental design

Litter mass loss rates were measured in litter-bags of approximately 12 × 6 cm with either fine (50 μm × 50 μm) or coarse (1 mm × 1.2 mm) meshed nylon net. The fine mesh allows decomposer microbes entry but excludes all Acari and Collembola from the litter, while the coarse mesh allows access by these animals as well as by some larger detritivores (Bradford et al., 2002). The microclimatic differences are minimal between these two mesh sizes, and any differences in mass loss rates are assumed to be related to invertebrate activity (Bokhorst and Wardle, 2013). On November 6, 2013, the litter-bags were placed in the field on top of the humus layer and covered with the naturally occurring litter (beech: 1.4 ± 0.1 kg m^{-2}, spruce: 2.2 ± 0.3 kg m^{-2}). 120 bags filled with 1 g of litter were set-up in a split-plot design, with forest type as the main plot factor and litter type and mesh size (coarse *vs* fine mesh) as sub-plot factors. In each forest type, 10 blocks were set up and we placed one bag of each litter type × mesh size treatment combination in each block. In five of the 10 blocks, we placed one additional bag of each litter type × mesh size treatment combination. This bag was used for analysis of the fungal community. The bags were collected on October 6, 2014. In the field, 10 of the replicates were carefully transferred to 50 ml plastic jars and stored cool until the next day. Arthropods were then extracted from the litter with a Tullgren apparatus (Van Straalen and Rijninks, 1982) for 4 d and the animals were collected and preserved in 70% ethanol. Mass remaining after decomposition was determined by drying at 70 °C for 48 h (after first drying the samples in the Tullgren apparatus) and mass loss was expressed as the proportion of initial oven dry mass that was lost during placement in the field. The material was then ground into powder with a ball mill and concentration of N was determined as described above. Release of N during decomposition was calculated as the total mass × nutrient concentration before incubation minus that after incubation, and was expressed as a proportion of the total mass × nutrient concentration before incubation (Wardle, 2002). The contents of the