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published in
Fungal Ecology
2018

DOI (link to publisher)
10.1016/j.funeco.2017.11.003

document version
Publisher's PDF, also known as Version of record

citation for published version (APA)
Asplund, J., Kauserud, H., Bokhorst, S., Lie, M. H., Ohlson, M., & Nybakken, L. (2018). Fungal communities influence decomposition rates of plant litter from two dominant tree species. *Fungal Ecology*, *32*, 1-8. https://doi.org/10.1016/j.funeco.2017.11.003

Fungal Ecology 32 (2018) 1–8

Contents lists available at ScienceDirect

Fungal Ecology

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

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

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ARTICLE INFO

Article history:
Received 16 June 2017
Received in revised form
23 October 2017
Accepted 8 November 2017
Available online 28 November 2017

Corresponding Editor: Björn D. Lindahl.

Keywords:
Boreal and temperate forests
Fungi
Illumina DNA sequencing
Litter decomposition
Mesofauna
Plant–soil (below-ground) interactions

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,

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https://doi.org/10.1016/j.funeco.2017.11.003
1754-5048/

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

five remaining replicates were transferred to 50 ml Falcon tubes and directly placed in dry ice for transport to the lab. The material was then freeze-dried and ground to powder and stored at −80 °C until ergosterol and DNA extraction.

2.3. Ergosterol analysis

Total ergosterol (a proxy for fungal biomass) was extracted with saponification using a modified protocol after Gessner and Schmitt (1996). 8 ml 3 M KOH in ethanol was added to 100 mg powdered litter and incubated at 80 °C on a shaker in a water bath for 1 h. The mixture was then centrifuged at 2500 *g* for 15 min and the supernatant was diluted with 2 ml deionized water. Ergosterol was extracted from the supernatant by two successive applications of 5 ml hexane. The organic fractions were combined and evaporated using an Eppendorf Concentrator Plus 5301 (Eppendorf, Hamburg, Germany) and then re-suspended in 500 μl methanol. The extracts were analysed following Dahlman et al. (2002) on a 1200 Series HPLC (Agilent Technologies, Waldbronn, Germany). Ergosterol was separated on a reversed phase ODS ultrasphere column, 250 cm × 4.6 mm, particle size 5 mm (Beckman, Fullerton, USA), using MeOH as the mobile phase. The flow rate was 1.5 ml min^{-1} and the total analysis time 12 min. The detection wavelength was 280 nm, and the identification of ergosterol was based on retention time, online UV-spectra and co-chromatography of commercial standard of ergosterol (Sigma, St. Louis, USA).

2.4. DNA sequencing analyses

DNA was extracted from the 60 lyophilized litter samples using a modified CTAB-based extraction protocol (Murray and Thompson, 1980; Gardes and Bruns, 1993). DNA concentration was calculated from A260 on a NanoDrop for all samples. 300 ng of DNA was then subjected to PCR. ITS2 was amplified using the primers fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990). To enable multiplexing of the samples, a two base pair (bp) tag was attached at the 5′ end of both forward and reverse primers. Illumina sequencing introduces sequence-specific error due to phasing caused by specific sequence patterns (Nakamura et al., 2011). Therefore, sample-specific multiplex identification DNA tags (MIDs) of varying size (4–8) were designed to correct this bias. These MIDs were attached at both ends of the Illumina-specific adapter. One end (5′) of the adapter was phosphorylated and at the other end (3′) a "T" base was overhanged, to anneal with "A" overhanged on the PCR-amplified product. Solid-phase reversible immobilization (SPRI) beads were used for the purification of amplified PCR products. A paired-end (PE) adapter oligo mix were ligated to the fragments using T4 DNA ligase (New England Biolabs Ipswich, Massachusetts, USA). To cut "ideoxyU," located at the center of the Illumina adapter, 1 μL USER enzyme (New England BioLabs) was used. QPCR was used for library quantification to find the optimal end point (low CT value) of the PCR cycle, followed by 5′-end adaptor extension and library-enrichment PCR with 11 cycles, using Q5® high-fidelity DNA polymerase enzyme. The indexed NGS libraries were sequenced on an Illumina MiSeq, using paired-end 2 × 300 bp reads and the v3 sequencing reagents. For three of the samples (DNA extracts), 15 technical replicates were run to investigate the level of biases introduced during PCR, library preparation and sequencing combined.

2.5. Bioinformatics analyses

After sequencing, reads were paired using FLASH v.1.2.11 (Magoč and Salzberg, 2011) with a maximum overlap of 300 bp and a mismatch density of 0.3. Reads were de-multiplexed according to their respective indices. While the index design allows for error correction, the conservative decision was made to discard all reads with any index mismatch, to minimize the danger of misattributing reads to the incorrect sample. Barcode and primer sequences were removed, and paired amplicons were subjected to additional quality filtering using QIIME v1.8.0 (Caporaso et al., 2010) with the following criteria: (1) length between 250 and 550 bp, (2) average quality score >35 (indicates a per-base error probability of 0.0003), (3) <2 ambiguous bases, (4) maximum homopolymer length <10, (5) 0 barcode errors, (6) <2 errors in the forward primer, and (7) <2 errors in the reverse primer. Chimeric sequences were detected and removed from the dataset using UCHIME (Edgar et al., 2011) as implemented in QIIME v.1.8.0 under the default settings. Sequences from all runs were pooled and clustered into operational taxonomic units (OTUs) using an open-reference based implementation of the UCLUST algorithm (Edgar et al., 2011), as implemented in QIIME v1.8.0, with a 97% similarity cutoff. The UNITE + INSDC 97% clustered database (as per 01.08.2015) were used as reference centroids (Kõljalg et al., 2013). The most abundant sequence in each cluster was designated the representative sequence and given a taxonomic assignment using the RDP naïve Bayesian classifier (Wang et al., 2007) against the 01.08.2015 UNITE + INSDC 97% clustered database release (Kõljalg et al., 2013) for ITS2. Identified OTUs were categorized into the fungal guilds: saprotrophs, plant pathogens and ectomycorrhizal fungi based on the FUNGuild database (http://funguild.org). Sequence data (raw sequences, accepted sequences after filtering and representative sequences for all OTUs) as well as the final OTU/sample data matrix, have been deposited in the Dryad repository under http://dx.doi.org/10.5061/dryad.5k54f.

2.6. Statistical analyses

Mass loss and release of N during decomposition as well as ergosterol concentration were analysed using split-plot ANOVAs with forest type as the main plot factor and litter type and mesh size (coarse *vs* fine) as sub-plot factors. Abundance of springtails and mites in the litter-bags was only analysed for coarse litter-bags because the arthropods had no access to the fine-meshed bags. This was done with a generalized linear mixed model with block as random factor and assuming a Poisson distribution of errors. *P* values were derived from a Wald's χ^2-test.

We calculated the home-field advantage index (HFAI) following Ayres et al. (2009).

$$\mathrm{HFAI} = \left[\left(\frac{F_f}{F_f + P_f} + \frac{P_p}{P_P + F_p}\right) \Big/ \left(\frac{P_f}{F_f + P_f} + \frac{F_p}{P_P + F_p}\right)\right] \times 100 - 100$$

Where, F_f represents the mass loss of litter from species *F* in the forest *f*. The HFAI is the net value for both species and represents the percent faster mass loss of litter when it decomposes at home versus away. We used a single sample *t*-test to test whether the HFAI differed from 0.

Statistical analyse of differences in fungal community composition were carried out after sub-sampling of 1544 sequences per sample. Three samples with a markedly lower amount of sequences were excluded from the remaining analyses. The community compositions were visualized using non-metric multidimensional scaling (NMDS) on the basis of a Bray-Curtis distance matrix using the metaMDS function in the R package vegan (Oksanen et al., 2016). Ergosterol concentration and mass loss were fitted as vectors and the forest type × litter type combination and the mesh size treatment were fitted as factors onto the NMDS ordination using the function envfit (Oksanen et al., 2016) and 999 permutations. We

used the ordiellipse function (Oksanen et al., 2016) to plot the 95% confidence intervals (CI) of group scores of the four forest type × litter type combinations onto the NMDS ordination. To determine the relative importance of forest type *vs* litter type in explaining the fungal community compositions, we performed canonical correspondence analysis (CCA) with variation partitioning following Peres-Neto et al. (2006). All analyses were performed in R 3.2.5 (R Core Team, 2016). As illustrated in Fig S1 (in Supplementary data), there were some compositional variations between the technical replicates, but markedly smaller than between biological replicates, suggesting that we would be able to detect clear treatment effects, if they existed.

3. Results

There was no significant difference in the initial N or C concentrations of beech (N: 0.79 ± 0.03%; C: 46.3 ± 2.2%) and spruce litter (N: 0.84 ± 0.03%; C: 44.3 ± 1.6) ($P > 0.05$). The C: N ratio at the start was higher in beech litter (58.0 ± 1.1) than in spruce litter (52.7 ± 0.7) ($P < 0.01$).

We found a significant net home-field advantage of on average 24 ± 4% ($t = 6.47$, $P < 0.001$). The HFAI did not vary between litter-bags allowing or excluding microarthropods ($t = 0.62$, $P = 0.55$). Overall, litter mass loss was 1.5 times higher in the beech forest compared to the spruce forest (Table 1, Fig. 1). Furthermore, spruce litter lost 1.5 times more mass than beech leaves during the study period (Table 1, Fig. 1). However, the difference between beech and spruce litter mass loss was larger in the spruce forest than in the beech forest. Litter type described 3.8 times as much of the variance compared with forest type. The release of N during decomposition varied significantly between the two litter types (Table 1), as beech litter immobilised N during the study period while minor changes in N release were observed for spruce litter (Fig. 1). There were no differences in N release or immobilization between forest types for either of the litter types (Table 1).

Spruce litter had a higher fungal biomass than beech litter (Table 1, Fig. 1). We found no overall significant difference in fungal biomass between litter-bags placed in the different forest types. However, there was a significant forest type × litter type interaction term, as the fungal biomass in spruce litter was higher in the spruce forest while fungal biomass in beech litter was indifferent to forest type.

The fungal community composition was significantly different among the four litter type × forest type combinations – i.e. the 95% CIs of the group centroid of the four treatment combinations did not overlap (Fig. 2). Various Agaricomycetes dominated (~50%) in the beech litter while spruce litter was dominated by Ascomycota, especially Leotiomycetes (Fig. S2). *Mycena* spp. dominated the fungal community in the litter-bags placed in the beech forest, where they represented 44% of all sequences. Meanwhile, *Mycena* was much less common in the spruce forest, and in the spruce litter in the spruce forest, *Mycena* only represented 3% of the sequences. Instead, the ascomycete *Chalara* was the most common genus in spruce litter in the spruce forest, where it represented 15% of all sequences. The relative importance of forest type *vs* litter type in explaining the variation in the fungal community composition was approximately the same between the two groups (52.0% and 48.7% of total explained variation, respectively). The shared fraction was slightly negative (−0.7% of the explained variation), (see Fig. 3).

Springtail and mite abundance was higher (1.8 times) in spruce litter compared to beech litter irrespective of forest type (Table 2). Excluding microarthropods had no significant effect on either mass loss, N release or ergosterol concentration (Table 1). In addition, there was no significant interaction term involving the mesh size treatment. The exclusion of microarthropods had no effect on the fungal community compositions ($R^2 = 0.001$, $P = 0.95$).

4. Discussion

We found a significant home-field advantage, supporting our first hypothesis that litter decomposes more quickly in its home environment. The mass loss rate of beech litter almost halved when placed in a spruce forest. Spruce litter also decomposed slightly slower in the spruce forest. However, relative to the beech litter, spruce litter decomposed more rapidly in the spruce forest, implying a home-field advantage. Interestingly, the observed patterns of mass loss rates were concurrent with shifts in the fungal species composition in the litter, giving support for our second hypothesis. When placed in the spruce forest, beech litter was colonized by other types of fungi that supposedly are less efficient at decomposing beech. For instance, various species of *Mycena*, which are efficient saprotrophs, were much less abundant on beech litter in the spruce forest than in the beech forest. We did not find support for our final hypothesis that excluding microarthropods from litter-bags would increase the fungal biomass and change the species composition of fungi. We explore these findings and their implications below.

Accounting for general differences between litter and forest types, litter on average lost 24% more mass when incubated in its home environment. Previous reviews analysing HFA effects from a number of studies have found mean effects of 4%, 7.5% and 8% (Ayres et al., 2009; Wang et al., 2013; Veen et al., 2015). Ayres et al. (2009) found that only three out of 35 reciprocal tree-tree litter transplants had higher HFAI than the estimate of the present study. The strength of HFA seems to be context-dependent and tends to be most pronounced when litter types are more dissimilar in terms of litter quality (i.e. N:P ratio) or when the plant communities are very different (Veen et al., 2015). Home-field effects likely occur because microbial decomposers are specialized to break down litter from plants they associate with, and the influence of macro-faunal decomposers on HFA is probably relatively small (Keiser et al., 2011; Veen et al., 2015). The fact that we found no difference in HFA

Table 1
General linear model, with block as random factor, testing for the effect of forest type (beech *vs* spruce), litter type (beech *vs* spruce) and litter-bag mesh size (excluding *or* including mesofauna) mass loss and N release during decomposition and ergosterol concentration. Bold letters indicate significant effects at $P < 0.05$.

	Mass loss		N release		Ergosterol	
	DF	F (*P*)	DF	F (*P*)	DF	F (*P*)
Forest Type (F)	1,18	**24.89 (<0.001)**	1,18	2.63 (0.122)	1,8	2.07 (0.188)
Litter Type (L)	1,54	**93.81 (<0.001)**	1,54	**57.14 (<0.001)**	1,24	**81.54 (<0.001)**
Mesh Size Treatment (M)	1,54	2.15 (0.149)	1,54	0.10 (0.749)	1,24	0.91 (0.349)
F × L	1,54	**8.95 (0.004)**	1,54	1.65 (0.205)	1,24	**9.21 (0.006)**
L × M	1,54	1.25 (0.270)	1,54	0.19 (0.666)	1,24	0.05 (0.818)
F × M	1,54	0.73 (0.396)	1,54	0.33 (0.568)	1,24	0.00 (0.975)
F × L × M	1,54	0.10 (0.753)	1,54	0.03 (0.862)	1,24	0.01 (0.916)

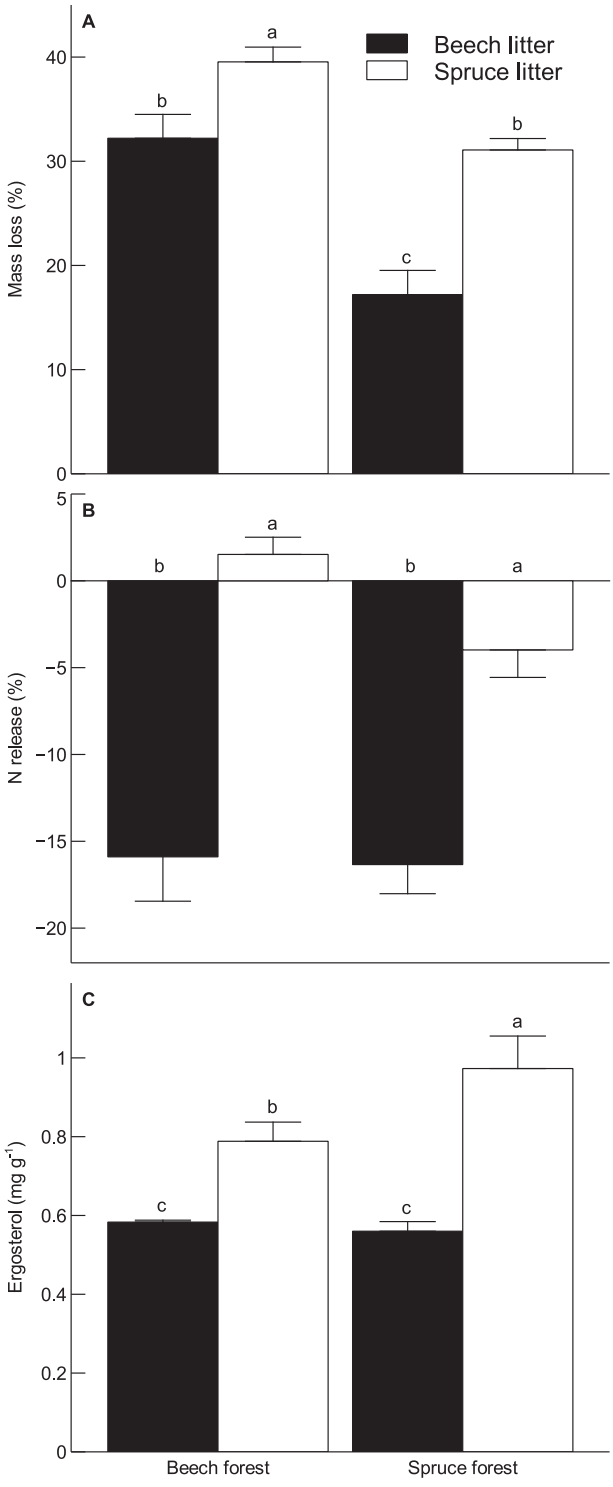

Fig. 1. Mean (±S.E.) of (A) mass loss and (B) nitrogen release during decomposition as well as (C) ergosterol concentration in litter-bags filled with either beech or spruce litter and placed in both beech and spruce forests. Negative nitrogen release represents net uptake of N during the incubation. Bars (within panels) topped with the same letter are not significantly different ($P < 0.05$, Tukey).

between litter-bags of different mesh size supports this conclusion. Even though many studies have found HFA effects, litter quality is the predominant factor controlling litter decomposition, which in some cases may overshadow the effects of plant-decomposer interactions (Fanin et al., 2016).

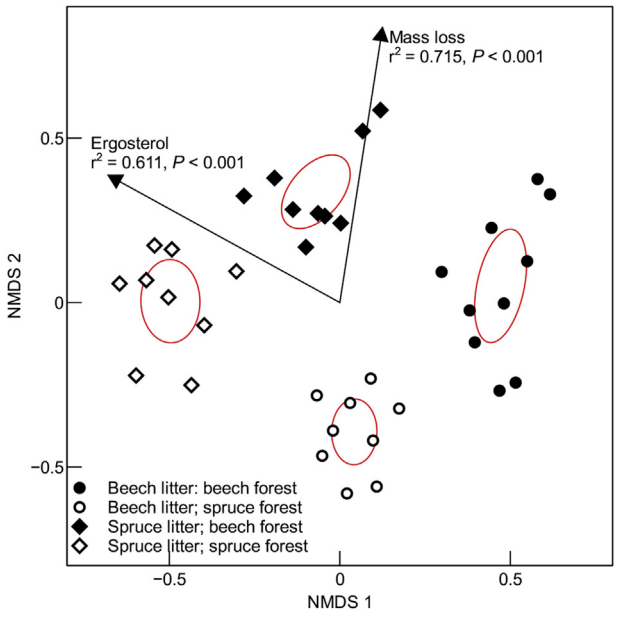

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination plots of the fungal community composition in litter-bags filled with beech or spruce litter placed in both beech and spruce forests. The diameter of the symbols reflects the mass loss of the litter. Ordination two-dimensional stress value was 0.16. The red rings are 95% confidence intervals of the respective litter × forest type centroid (based on SE - values). The arrows show the direction of increasing mass loss and ergosterol concentration in the samples and their length is proportional to the correlation between the variable and the ordination.

In our study, litter type was clearly more important than forest type in determining litter mass loss, in line with previous studies highlighting the importance of litter quality (Makkonen et al., 2012; Cleveland et al., 2014; Fanin et al., 2016). Beech litter decomposed slower than spruce litter regardless of whether it was placed in the spruce or the beech forest, possibly because of higher C: N values in the beech litter. Beech litter showed a net N immobilization during decomposition, while N release from spruce litter was marginal. Surprisingly, the net N immobilization from beech litter was identical between the two forest types, despite the fact that beech litter lost twice as much mass in the beech forest compared with in the spruce forest. This suggests that the N release pattern is the result of litter characteristics while the differences in mass loss rates are also driven by extrinsic factors. In contrast to our findings, previous studies showed no differences or quicker mass loss in beech litter compared with spruce litter (Vesterdal, 1999; Albers et al., 2004; Berger and Berger, 2012). This suggests that the relative litter quality of the two species varies between forests and that the outcome is context dependent. Furthermore, we found beech litter to be more responsive than spruce litter to incubation site in line with Vesterdal (1999), but contrasting to a German study where beech litter was unresponsive to incubation site (Albers et al., 2004). Vesterdal (1999) argued that the lower litter quality of spruce litter (in their study and in contrast to our study) should make it less affected by soil properties at the incubation site. We also observed least differences when spruce litter mass loss rates were compared between the spruce and beech forest, but spruce litter still decomposed faster than beech litter. The fungal community, as discussed below, therefore likely drives the observed differences in mass loss rates between spruce and beech litter.

Fungal community composition in the litter was dependent on the forest type in which the litter was incubated. This variation in fungal community composition may have caused the observed

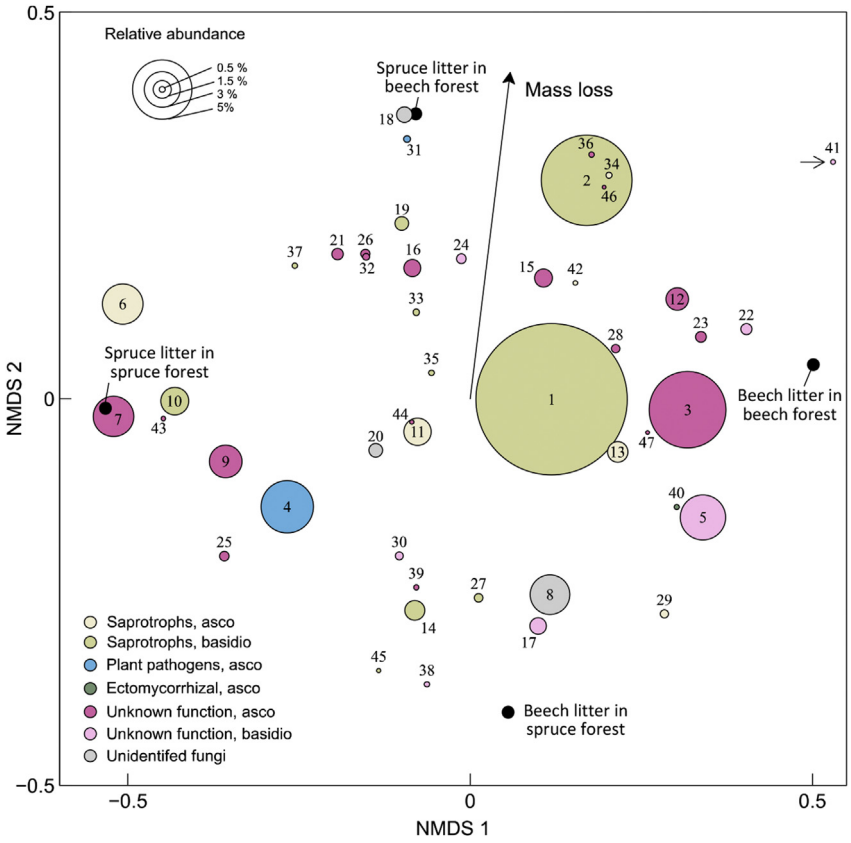

Fig. 3. Species plot derived from a non-metric multidimensional scaling (NMDS) of fungal communities in litter-bags filled with beech or spruce litter placed in both beech and spruce forests. The NMDS is based on all fungal operational taxonomic units (OTUs) present (1699), but only the 47 OTUs that on average represented at least 0.3% of the total amplicon, together adding up to 81% of the reads, are shown. The diameter of the dots indicate the relative abundance of each OTU. The arrow indicates direction of correlation between litter mass loss and the ordination. Numerical prefixes identify all OTUs: *Mycena* (1, 2, 10, 14, 27, 33, 35, 45), Helotiales (3, 7, 23, 44), *Coccomyces* (4), Agaricomycetes (5, 30), *Chalara* (6), Unknown fungi (8, 18, 20, 22, 41), Ascomycota (9, 12, 15, 25, 28, 36, 47), *Herpotrichia* (11), *Scleropezicula* (13), Hypocreales (16, 26), Cantharellales (17, 24), Mycenaceae (19), Leotiomycetes (21, 39), Hyaloscyphaceae (29), *Lophodermium piceae* (31), Hypocreaceae (32), *Chalara pseudoaffinis* (34), *Luellia* (37), Thelephoraceae (38), *Entoloma* (40), *Chlorencoelia* (42), Capnodiales (43), Dothideomycetes (46).

Table 2
Abundance (mean ± S.E.) of springtails and mites in litter-bags filled with beech or spruce litter and placed in both beech and spruce forests. χ^2 and *P* values are derived from general linear models with block as random factor. Values in **bold** denote significant effects at $P < 0.05$.

	Beech Forest		Spruce Forest		χ^2 (*P*)		
	Beech Litter	Spruce Litter	Beech Litter	Spruce Litter	Litter	Forest	L × F
Springtail	1.2 ± 0.4	2.8 ± 0.7	1.4 ± 0.7	1.8 ± 0.7	**5.08 (0.024)**	0.52 (0.470)	1.44 (0.230)
Mites	1.1 ± 0.3	1.6 ± 0.5	2.1 ± 0.7	4.1 ± 0.6	**6.76 (0.009)**	**11.75 (<0.001)**	0.38 (0.535)

differences in mass loss rates between the treatments, and thus contributed to the observed HFA effects. For instance, the slow mass loss of beech litter in the spruce forest could be due to the fungal species pool in this forest type being different and not coping equally with the presented litter types, despite similar fungal biomass (concentrations of ergosterol) in beech litter between forest types. The ascomycete genus *Chalara,* a common saprotroph in coniferous forests (Koukol, 2011), was the dominating genus on spruce litter in the spruce forest but these seldom colonized the beech litter. This indicates that the dominant saprotrophic fungi in the spruce forest were less able to decompose beech litter. On the other hand, the dominant saprotrophic fungi in the beech forest (genus *Mycena*) did colonize the spruce litter and even decomposed it faster than the native beech litter. *Mycena* spp. have a relatively high ability to decompose lignin, which could explain the higher mass loss rates in litter dominated by this genus (Boberg et al., 2011). In this light, the lower mass loss rates of beech in spruce forests are most likely the result of lacking key fungal decomposers, while spruce litter decomposed more easily, independently of the fungi present. It is worth mentioning that some recent studies have shown that fungal decomposers are often functionally redundant because key enzymes driving decomposition processes can be similar across geographic regions despite very little overlap in species composition (Talbot et al., 2014). However, this would imply low HFA effects in contrast to our observations of relatively large effects of incubating the litter in its home environment. Apart from influencing the decomposer community, tree species may impact on decomposition rates by changing physical and chemical characteristics of the forest floor (Joly et al., 2017).

We did not find any effect of microarthropods on mass loss, N release during decomposition, fungal biomass or fungal species composition. In line with our findings, Wise and Schaefer (1994) found no effect of mesofauna on the mass loss rate of beech litter. In contrast, some previous studies have found that springtails and

woodlice can alter the competition between fungal species and thus species composition (A'Bear et al., 2013; Crowther et al., 2013). We are not aware of any studies evaluating soil animals' effect on spruce litter mass loss, but we have previously shown that soil fauna do increase lichen mass loss rates in spruce forests (Asplund et al., 2013). Meanwhile, mesofauna can accelerate Scots pine litter mass loss (Berg et al., 1980). On a global scale, the effect of soil animals on decomposition is generally low in regions where biological activity is constrained by temperature and/or moisture (Wall et al., 2008). One explanation for the lack of micro-arthropod effect could be that high concentrations of polyphenols in spruce and beech litter reduce the palatability of the litter to soil animals (Neuhauser and Hartenstein, 1978). Similarly, secondary compounds in lichens can reduce the effect of microarthropods on lichen mass loss rates (Asplund et al., 2013).

Acknowledgement

We thank Tone Birkemoe for help setting-up the Tullgren apparatus. We acknowledge Courtney Nadeau and Marie Davey for DNA and bioinformatics analyses. Permit to conduct research in Brånakollane Nature Reserve was given by the County Governor of Vestfold (2013/3878). We thank Kjell Lie, on behalf of the forest owner, for kind help with access to the forest area. Two anonymous reviewers and Björn Lindahl provided insightful comments that helped to improve this manuscript. This study was funded by the Research Council of Norway (grant number 225018). The authors declare no conflict of interest.

Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.funeco.2017.11.003.

References

A'Bear, A.D., Murray, W., Webb, R., Boddy, L., Jones, T.H., 2013. Contrasting effects of elevated temperature and invertebrate grazing regulate multispecies interactions between decomposer fungi. PLoS One 8, e77610. https://doi.org/10.1371/journal.pone.0077610.

Albers, D., Migge, S., Schaefer, M., Scheu, S., 2004. Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce. Soil Biol. Biochem. 36, 155–164. https://doi.org/10.1016/j.soilbio.2003.09.002.

Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C., Schloter, M., 2006. Microbial colonization of beech and spruce litter—influence of decomposition site and plant litter species on the diversity of microbial community. Microb. Ecol. 52, 127–135. https://doi.org/10.1007/s00248-006-9006-3.

Asplund, J., Bokhorst, S., Wardle, D.A., 2013. Secondary compounds can reduce the soil micro-arthropod effect on lichen decomposition. Soil Biol. Biochem. 66, 10–16. https://doi.org/10.1016/j.soilbio.2013.06.013.

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol. Biochem. 41, 606–610. https://doi.org/10.1016/j.soilbio.2008.12.022.

Baldrian, P., 2016. Forest microbiome: diversity, complexity and dynamics. FEMS Microbiol. Rev. 41, 109–130. https://doi.org/10.1093/femsre/fuw040.

Bardgett, R.D., Wardle, D.A., 2010. Aboveground-belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change. Oxford University Press, Oxford.

Berg, B., Lohm, U., Lundkvist, H., Wirén, A., 1980. Influence of soil animals on decomposition of scots pine needle litter. Ecol. Bull. 401–409.

Berger, T.W., Berger, P., 2012. Greater accumulation of litter in spruce (*Picea abies*) compared to beech (*Fagus sylvatica*) stands is not a consequence of the inherent recalcitrance of needles. Plant Soil 358, 349–369. https://doi.org/10.1007/s11104-012-1165-z.

Bever, J.D., Westover, K.M., Antonovics, J., 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. J. Ecol. 85, 561–573. https://doi.org/10.2307/2960528.

Bezemer, T.M., Fountain, M.T., Barea, J.M., Christensen, S., Dekker, S.C., Duyts, H., van Hal, R., Harvey, J.A., Hedlund, K., Maraun, M., Mikola, J., Mladenov, A.G., Robin, C., de Ruiter, P.C., Scheu, S., Setälä, H., Šmilauer, P., van der Putten, W.H., 2010. Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. Ecology 91, 3027–3036. https://doi.org/10.1890/09-2198.1.

Boberg, J.B., Ihrmark, K., Lindahl, B.D., 2011. Decomposing capacity of fungi commonly detected in *Pinus sylvestris* needle litter. Fungal Ecol. 4, 110–114. https://doi.org/10.1016/j.funeco.2010.09.002.

Bokhorst, S., Wardle, D.A., 2013. Microclimate within litter bags of different mesh size: implications for the 'arthropod effect' on litter decomposition. Soil Biol. Biochem. 58, 147–152. https://doi.org/10.1016/j.soilbio.2012.12.001.

Bradford, M.A., Tordoff, G.M., Eggers, T., Jones, T.H., Newington, J.E., 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos 99, 317–323. https://doi.org/10.1034/j.1600-0706.2002.990212.x.

Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Peña, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. Nat. Methods 7, 335–336. https://doi.org/10.1038/nmeth.f.303.

Cleveland, C.C., Reed, S.C., Keller, A.B., Nemergut, D.R., O'Neill, S.P., Ostertag, R., Vitousek, P.M., 2014. Litter quality versus soil microbial community controls over decomposition: a quantitative analysis. Oecologia 174, 283–294. https://doi.org/10.1007/s00442-013-2758-9.

Cole, L., Bradford, M.A., Shaw, P.J.A., Bardgett, R.D., 2006. The abundance, richness and functional role of soil meso- and macrofauna in temperate grassland—a case study. Appl. Soil Ecol., Soil Biodivers. Upl. Grassl. 33, 186–198. https://doi.org/10.1016/j.apsoil.2005.11.003.

Crowther, T.W., A'Bear, A.D., 2012. Impacts of grazing soil fauna on decomposer fungi are species-specific and density-dependent. Fungal Ecol. 5, 277–281. https://doi.org/10.1016/j.funeco.2011.07.006.

Crowther, T.W., Boddy, L., Jones, T.H., 2011. Outcomes of fungal interactions are determined by soil invertebrate grazers. Ecol. Lett. 14, 1134–1142. https://doi.org/10.1111/j.1461-0248.2011.01682.x.

Crowther, T.W., Stanton, D.W.G., Thomas, S.M., A'Bear, A.D., Hiscox, J., Jones, T.H., Voříšková, J., Baldrian, P., Boddy, L., 2013. Top-down control of soil fungal community composition by a globally distributed keystone consumer. Ecology 94, 2518–2528. https://doi.org/10.1890/13-0197.1.

Dahlman, L., Zetherström, M., Sundberg, B., Näsholm, T., Palmqvist, K., 2002. Measuring ergosterol and chitin in lichens. In: Kranner, D.I.C., Beckett, P.D.R.P., Varma, P.D.A.K. (Eds.), Protocols in Lichenology. Springer Lab Manuals. Springer, Berlin Heidelberg, pp. 348–362.

Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27, 2194–2200. https://doi.org/10.1093/bioinformatics/btr381.

Ellingsen, V.M., Asplund, J., Ohlson, M., 2017. Spatial and temporal patterns in seed predation as revealed by reciprocal experiments and video surveillance in neighbouring beech and spruce forests. Scand. J. For. Res. 32, 105–114. https://doi.org/10.1080/02827581.2016.1215523.

Fanin, N., Fromin, N., Bertrand, I., 2016. Functional breadth and home-field advantage generate functional differences among soil microbial decomposers. Ecology 97, 1023–1037. https://doi.org/10.1890/15-1263.1.

Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. J. Ecol. 100, 619–630. https://doi.org/10.1111/j.1365-2745.2011.01943.x.

Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol. Ecol. 2, 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x.

Gessner, M.O., Schmitt, A.L., 1996. Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. Appl. Environ. Microbiol. 62, 415–419.

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob. Change Biol. 6, 751–765. https://doi.org/10.1046/j.1365-2486.2000.00349.x.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kühn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Glob. Ecol. Biogeogr. 21, 50–63. https://doi.org/10.1111/j.1466-8238.2010.00613.x.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., van der Putten, P.L.W.H., de Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience 50, 1049–1061.

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T., Reid, C.P.P., 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69, 1009–1016. https://doi.org/10.2307/1941256.

Hustoft, E., 2016. The Impact of Litter on Soil Quality and Regeneration of Norway Spruce (Picea Abies [L.] H.Karst) and European Beech (Fagus Sylvatica [L.])- an Experimental Approach (Master thesis). Norwegian University of Life Sciences.

Ihrmark, K., Bödeker, I.T.M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K.E., Lindahl, B.D., 2012. New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiol. Ecol. 82, 666–677. https://doi.org/10.1111/j.1574-6941.2012.01437.x.

Joly, F.-X., Milcu, A., Scherer-Lorenzen, M., Jean, L.-K., Bussotti, F., Dawud, S.M., Müller, S., Pollastrini, M., Raulund-Rasmussen, K., Vesterdal, L., Hättenschwiler, S., 2017. Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. New Phytol. 214, 1281–1293. https://doi.org/10.1111/nph.14452.

Keiser, A.D., Strickland, M.S., Fierer, N., Bradford, M.A., 2011. The effect of resource history on the functioning of soil microbial communities is maintained across time. Biogeosciences 8, 1477–1486. https://doi.org/10.5194/bg-8-1477-2011.

Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., Bates, S.T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G.W., Hartmann, M., Kirk, P.M., Kohout, P., Larsson, E., Lindahl, B.D., Lücking, R., Martín, M.P., Matheny, P.B., Nguyen, N.H., Niskanen, T., Oja, J., Peay, K.G., Peintner, U., Peterson, M., Põldmaa, K., Saag, L., Saar, I., Schüßler, A., Scott, J.A., Senés, C., Smith, M.E., Suija, A., Taylor, D.L., Telleria, M.T., Weiss, M., Larsson, K.-H., 2013. Towards a unified paradigm for sequence-based identification of fungi. Mol. Ecol. 22, 5271–5277. https://doi.org/10.1111/mec.12481.

Koukol, O., 2011. New species of *Chalara* occupying coniferous needles. Fungal divers. 49, 75–91. https://doi.org/10.1007/s13225-011-0092-2.

Kubartová, A., Ranger, J., Berthelin, J., Beguiristain, T., 2009. Diversity and decomposing ability of saprophytic fungi from temperate forest litter. Microb. Ecol. 58, 98–107. https://doi.org/10.1007/s00248-008-9458-8.

Magoč, T., Salzberg, S.L., 2011. FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinforma. Oxf. Engl. 27, 2957–2963. https://doi.org/10.1093/bioinformatics/btr507.

Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M., Aerts, R., 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecol. Lett. 15, 1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x.

McNaughton, S.J., Oesterheld, M., Frank, D.A., Williams, K.J., 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341, 142–144. https://doi.org/10.1038/341142a0.

Migge, S., Maraun, M., Scheu, S., Schaefer, M., 1998. The oribatid mite community (Acarina) of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. Appl. Soil Ecol. 9, 115–121. https://doi.org/10.1016/S0929-1393(98)00065-1.

Mikola, J., Bardgett, R.D., Hedlund, K., 2002. Biodiversity, ecosystem functioning and soil decomposer food webs. In: Loreau, M., Naeem, S., Inchausti, P. (Eds.), Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, pp. 169–180.

Murray, M.G., Thompson, W.F., 1980. Rapid isolation of high molecular weight plant DNA. Nucleic Acids Res. 8, 4321–4326. https://doi.org/10.1093/nar/8.19.4321.

Nacke, H., Goldmann, K., Schöning, I., Pfeiffer, B., Kaiser, K., Castillo-Villamizar, G.A., Schrumpf, M., Buscot, F., Daniel, R., Wubet, T., 2016. Fine spatial scale variation of soil microbial communities under European beech and Norway spruce. Front. Microbiol. 7 https://doi.org/10.3389/fmicb.2016.02067. Article 2067.

Nakamura, K., Oshima, T., Morimoto, T., Ikeda, S., Yoshikawa, H., Shiwa, Y., Ishikawa, S., Linak, M.C., Hirai, A., Takahashi, H., Altaf-Ul-Amin, M., Ogasawara, N., Kanaya, S., 2011. Sequence-specific error profile of Illumina sequencers. Nucleic Acids Res. 39, e90. https://doi.org/10.1093/nar/gkr344.

Neuhauser, E.F., Hartenstein, R., 1978. Phenolic content and palatability of leaves and wood to soil isopods and diplopods. Pedobiologia 18, 99–109.

Ohlson, M., Ellingsen, V.M., del Olmo, M.V., Lie, M.H., Nybakken, L., Asplund, J., 2017. Late-Holocene fire history as revealed by size, age and composition of the soil charcoal pool in neighbouring beech and spruce forest landscapes in SE Norway. Holocene 27, 397–403. https://doi.org/10.1177/0959683616660174.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. Vegan: community ecology package. R package, version 2.3-5. http://CRAN.R-project.org/package=vegan.

Paul, E.A., 2016. The nature and dynamics of soil organic matter: plant inputs, microbial transformations, and organic matter stabilization. Soil Biol. Biochem. 98, 109–126. https://doi.org/10.1016/j.soilbio.2016.04.001.

Pennanen, T., Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J., Fritze, H., 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. Microb. Ecol. 38, 168–179. https://doi.org/10.1007/s002489900161.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2.

Peršoh, D., 2015. Plant-associated fungal communities in the light of meta'omics. Fungal divers. 75, 1–25. https://doi.org/10.1007/s13225-015-0334-9.

Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39, 288–388. https://doi.org/10.2307/3544689.

Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter and soil: current knowledge and research needs. For. Ecol. Manag 309, 19–27. https://doi.org/10.1016/j.foreco.2013.02.034.

R Core Team, 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL: http://www.R-project.org/.

Sætre, P., 1998. Decomposition, microbial community structure, and earthworm effects along a birch–spruce soil gradient. Ecology 79, 834–846. https://doi.org/10.1890/0012-9658(1998)079[0834:DMCSAE]2.0.CO;2.

Salamon, J.-A., Scheu, S., Schaefer, M., 2008. The Collembola community of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. Pedobiologia 51, 385–396. https://doi.org/10.1016/j.pedobi.2007.10.002.

Scheu, S., Albers, D., Alphei, J., Buryn, R., Klages, U., Migge, S., Platner, C., Salamon, J.-A., 2003. The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. Oikos 101, 225–238. https://doi.org/10.1034/j.1600-0706.2003.12131.x.

Soong, J.L., Nielsen, U.N., 2016. The role of microarthropods in emerging models of soil organic matter. Soil Biol. Biochem., Special issue: Food web interactions in the root zone: influences on community and ecosystem dynamics 102, 37–39. doi:10.1016/j.soilbio.2016.06.020.

Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., Erlandson, S., Vilgalys, R., Liao, H.-L., Smith, M.E., Peay, K.G., 2014. Endemism and functional convergence across the North American soil mycobiome. Proc. Natl. Acad. Sci. 111, 6341–6346. https://doi.org/10.1073/pnas.1402584111.

Treseder, K.K., Lennon, J.T., 2015. Fungal traits that drive ecosystem dynamics on land. Microbiol. Mol. Biol. Rev. 79, 243–262. https://doi.org/10.1128/MMBR.00001-15.

Urbanová, M., Šnajdr, J., Baldrian, P., 2015. Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. Soil Biol. Biochem. 84, 53–64. https://doi.org/10.1016/j.soilbio.2015.02.011.

Uroz, S., Oger, P., Tisserand, E., Cébron, A., Turpault, M.-P., Buée, M., De Boer, W., Leveau, J.H.J., Frey-Klett, P., 2016. Specific impacts of beech and Norway spruce on the structure and diversity of the rhizosphere and soil microbial communities. Sci. Rep. 6, 27756. https://doi.org/10.1038/srep27756.

van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J., Wardle, D.A., 2013. Plant–soil feedbacks: the past, the present and future challenges. J. Ecol. 101, 265–276. https://doi.org/10.1111/1365-2745.12054.

Van Straalen, N.M., Rijninks, P.C., 1982. The efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod populations. Pedobiologia 24, 197–209.

Veen, G.F. (Ciska), Freschet, G.T., Ordonez, A., Wardle, D.A., 2015. Litter quality and environmental controls of home-field advantage effects on litter decomposition. Oikos 124, 187–195. doi:10.1111/oik.01374.

Vesterdal, L., 1999. Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce. Can. J. For. Res. 29, 95–105. https://doi.org/10.1139/x98-182.

Wall, D.H., Bradford, M.A., John, S.G.M., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., Dangerfield, J.M., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z., Ayuke, F.O., Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S., Henschel, J.R., Johnson, D.L., Jones, T.H., Kovarova, M., Kranabetter, J.M., Kutny, L., Lin, K., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabará, M.G., Salamon, J., Swift, M.J., Varela, A., Vasconcelos, H.L., White, D., Zou, X., 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob. Change Biol. 14, 2661–2677. https://doi.org/10.1111/j.1365-2486.2008.01672.x.

Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naïve bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Appl. Environ. Microbiol. 73, 5261–5267. https://doi.org/10.1128/AEM.00062-07.

Wang, Q., Zhong, M., He, T., 2013. Home-field advantage of litter decomposition and nitrogen release in forest ecosystems. Biol. Fertil. Soils 49, 427–434. https://doi.org/10.1007/s00374-012-0741-y.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633. https://doi.org/10.1126/science.1094875.

White, T.J., Bruns, T., Lee, S.B., Taylor, J.W., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfland, D.H., Sninsky, J.J., White, T.J. (Eds.), A Guide to Methods and Applications. Academic Press, San Diego, CA, USA, pp. 315–322. PCR Protocols.

Wise, D.H., Schaefer, M., 1994. Decomposition of leaf litter in a mull beech forest: comparison between canopy and herbaceous species. Pedobiologia 34, 269–288.