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Relationships between fungal community composition in decomposing leaf litter and home-field advantage effects

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Abstract

1. Increasing evidence suggests that specific interactions between microbial decomposers and plant litter, named home field advantage (HFA), influence litter breakdown. However, we still have limited understanding of whether HFA relates to specific microbiota, and whether specialized microbes originate from the soil or from the leaf microbiome. Here, we disentangle the roles of soil origin, litter types, and the microbial community already present on the leaf litter in determining fungal community composition on decomposing leaf litter and HFA.
2. We collected litters and associated soil samples from a secondary succession gradient ranging from herbaceous vegetation on recently abandoned ex-arable fields to forest representing the end stage of succession. In a greenhouse, sterilized and unsterilized leaf litters were decomposed for 12 months in soils from early to late successional stages according to a full factorial design. At the end, we examined fungal community composition on the decomposing litter.
3. Fungal communities on decomposed late-successional litter in late-successional soil differed from those in early- and mid-successional stage litter and soil combinations. Soil source had the strongest impact on litter fungal composition when using sterilized litter, while the

impact of litter type was strongest when using unsterilized litter. Overall, we observed HFA, as litter decomposition was accelerated in home soils. Increasing HFA did not relate to the dissimilarity in overall fungal composition, but there was increasing dissimilarity in the relative abundance of the most dominant fungal taxon between decomposing litter in home and away soils.

4. We conclude that early, mid and late succession litter types did not exert strong selection effects on colonization by microorganisms from the soil species pool. Instead, fungal community composition on decomposing litter differed substantially between litter types for unsterilized litter, suggesting that the leaf microbiome, either directly or indirectly, is an important determinant of fungal community composition on decomposing leaves. HFA related most strongly to the abundance of the most dominant fungal taxa on the decomposing litter, suggesting that HFA may be attributed to some specific dominant fungi rather than to responses of the whole fungal community.

Keywords

Decomposition, microbial community, fungi, sequencing, ITS, succession

Introduction

The home-field advantage (HFA) hypothesis predicts that plant litter decomposition is accelerated in soil from the plant community where litter originates from compared to soil from other plant communities (Hunt *et al.* 1988; Gholz *et al.* 2000; Ayres *et al.* 2009; Veen *et al.* 2015). It has been proposed that HFA is the result of specific decomposer communities (Ayres *et al.* 2009; Austin *et al.* 2014; Palozzi & Lindo 2018). However, despite many studies on HFA (e.g. Vivanco & Austin 2008; Milcu & Manning 2011; Freschet, Aerts & Cornelissen 2012; Veen, Sundqvist & Wardle 2015; Li *et al.*

2017), few studies have attempted to demonstrate the involvement of specific decomposer communities (but see Chomel et al. 2015; Lin et al. 2018). As a result, we still have limited understanding as to what extent litter types accumulate specific decomposer communities during decomposition, and how HFA may relate to the microbiome of decomposing leaf litter. Here, we examine how variation in HFA relates to differences in fungal microbiome composition. Thus, we aim at a better understanding of the possible role of specialist decomposers in driving decomposition processes. We tested how soil source, litter type and priority effects of microbial communities on the leaf litter shape the microbiome of decomposed litter and how this relates to HFA effects.

Previous work has shown that the composition of the species pool, environmental filtering and selection effects, as well as priority effects all can be important drivers of community assembly and species composition in ecological communities (e.g. Grime 2006; Berg & Smalla 2009; Raaijmakers *et al.* 2009; Fukami *et al.* 2010; van der Wal, Ottosson & de Boer 2015; Zobel 2016). However, little is known about their importance in shaping the litter microbiome (Austin *et al.* 2014; Palozzi & Lindo 2018). The local species pool of the soil (Fierer & Jackson 2006) determines which species are available for colonizing plant litter during composition. Meanwhile, the quality of the litter may act as environmental filter and prevent the establishment of certain microorganisms (Kraft *et al.* 2015) resulting in litter-type specific microbial communities. In addition, microorganisms on plant litter may compete for nutrients and energy, creating a selection pressure (Ayres *et al.* 2009; Austin *et al.* 2014) that further shapes the litter community. Finally, the composition of the litter microbiome may be determined by the order in which species immigrate and colonize the litter during community assembly, leading to priority effects (Fukami 2015). These effects cause historical contingencies that control which species are able to colonize the litter at any moment in time (van der Wal, Ottosson & de Boer 2015).

The extent to which the litter microbiome depends on soil source, litter type and historical contingencies in the microbial community may help to understand the extent to which the various factors contribute to drive HFA effects. When litters have very distinct microbial communities in their home soils, they may experience stronger HFA effects than when communities in home and away soils have overlapping species composition. In addition, if litters take along their home phyllosphere microbiome (which can play a key role in shaping litter decomposer communities; (Voříšková & Baldrian 2013; Lin *et al.* 2015) to the away soils, then HFA may be reduced because some specialist decomposers could then be introduced into the new habitat on the litter. To date, little is known about the composition of the litter microbiome in home versus away soils in the context of HFA effects, particularly with regard to the role of the phyllosphere community. Nevertheless, previous work has indicated that plants can have specific saprophytic soil communities (Bezemer *et al.* 2010) and that their litters can support specific microbial communities (Keiser *et al.* 2011; Lin *et al.* 2018). As a result, when plant litters end up in a novel soil environment away from the plant species that has produced the litter, for example as a result of wind dispersal of dead leaves or of plant dispersal to novel environments, specific interactions between local soil decomposer communities and litter types may become disrupted resulting in reduced litter breakdown (Keiser *et al.* 2011; van der Putten 2012). Alternatively, if the phyllosphere community plays a key role in driving HFA effects, introducing the litter together with its original microbiome may maintain the connection with specific decomposers and hence rates of litter breakdown.

The aim of our study was to understand how soil source, litter type, and historical contingencies influence the fungal community composition of leaf litter during decomposition. In this study, we regard historical contingencies as the presence of an initial litter microbiome, which we modify by litter sterilization. In addition, we aimed to understand how variation in the composition of the fungal community on the decomposed litter might explain the observed patterns in HFA effects. In our study, we focus on fungal communities, as these are primary decomposers and many of them can degrade recalcitrant organic compounds that are abundant in plant residues (de

Boer *et al.* 2005; van der Wal *et al.* 2013; Voříšková & Baldrian 2013). We tested two hypotheses. The first hypothesis is that each of three factors, i.e., soil origin, litter type and historical contingency, drives the microbiome of decomposed litters. This is based on our expectation that each litter type would select a unique microbiome from the soil, because the HFA hypothesis predicts that HFA results from litters having specific decomposer communities. We also expected that litter microbiomes would be shaped in part by colonization from the soil in which they are incubated. As a result, when litters are placed away from their home soil they may not have access to all the decomposer specialists present in their home conditions. Finally, we expected that fungal communities initially present on litter would prevent colonization from the soil microbiome and exert a priority effect on fungal composition, compared to litters without fungi (as modified by sterilization). The second hypothesis is that the magnitude of the HFA is greater when the fungal composition on the decomposed home and away litter types is more dissimilar. Understanding which factors shape the microbiome on leaf litter and how differences between decomposed litters in their microbiomes explain the magnitude of home-field effects will help us to better understand how specific fungi may have contributed to HFA.

To test our hypotheses we set up a reciprocal transplant experiment using soils and litters from a well-repeated successional gradient of ex-arable fields in the Netherlands (Veen *et al.* 2018), in which early and mid-secondary successional stages were represented by ex-arable grasslands and late-successional stages were consisting of mixed pine and birch forest. Litters from each successional stage were left unsterilized or sterilized, in order to represent different historical contingencies of leaf microbiome, and incubated in soils from all stages in the greenhouse for 12 months, after which we determined litter mass loss and fungal community composition of the decomposed litter. Fungal community composition was measured at the end of the experiment, which integrates community development over the full course of the experimental period.

Methods

We set up a reciprocal litter transplant experiment in a greenhouse using soils and litters from early-, mid- and late-successional stages from a secondary successional gradient on ex-arable fields. The successional gradient was situated on nutrient-poor sandy soils in central Netherlands, in the nature area "De Veluwe", between Ede (52°04'20" N, 5°44'12") and Wolfheze (52°00'77" N, 5°48'58"). It was part of a well-established successional gradient of old fields (e.g. Kardol, Bezemer & van der Putten 2006; van de Voorde, van der Putten & Bezemer 2011; Morriën *et al.* 2017). Mean annual temperature was 10.7°C and mean annual precipitation approx. 840 mm in the ten years prior to our study, i.e. 2003-2012 (Royal Netherlands Meteorological Institute (KNMI)). Early-successional stages consisted of early-successional grasslands, dominated by fast-growing plant species such as the grasses *Elytrigia repens* and *Lolium perenne* and the forbs *Jacobaea vulgaris* and *Myosotis arvensis*. Mid-successional stages consisted of grasslands dominated by slower growing grasses such as *Anthoxanthum odoratum* and *Agrostis capillaris* and forbs, such as *Leucanthemum vulgare* and *Plantago lanceolata*. Late-successional stages consisted of mixed forest dominated by the trees *Betula pendula, Pinus sylvestris* and *Quercus robur* (Veen *et al.* 2018).

Experimental design

Soil and litter material was collected at the same time as material used by Veen *et al.* (2018) and we followed the same sampling design. Along the successional gradient we laid out six replicate transects that included early-, mid- and late-successional stages, resulting in 18 sampling locations (3 successional stages × 6 transects) from which litter and soil were collected. Successional stages within any given transect were at a distance of 300 m to 2200 m from each other, and transects were between 100 m and 7.5 km apart. For each sampling location, we used 4-8 randomly placed quadrats of 10 cm x 10 cm from an area of 2 m × 2 m. Between 25 October and 9 November 2012, in

each sampling location we collected ~10 g of freshly senesced leaf litter from the soil surface, resulting in a mixed litter sample that is representative of the local plant community. Then, in each quadrat we collected the soils underneath the litter from a depth of 0-10 cm below the soil surface. Samples from quadrats within a sampling location were homogenized, both for soil and litters, so that we had one homogenized litter and soil sample for each of the 18 sampling locations, which were kept as independent replicates throughout the whole experiment.

For each of the 18 soil samples we manually removed stones and large roots. A subsample of the soil from each location was used for analyzing moisture, organic matter, carbon, nitrogen and phosphorous content, as well as nitrate and ammonium availability (see Veen *et al.* 2018 for details). The rest of the soil was used to fill six 1L pots, with each of those pots receiving either sterilized or non-sterilized litter from early-, mid- or late-successional stages. The litter collected from each location was air-dried for at least 48 h until constant weight and cut into 5 mm fragments. A subsample of litter from each location was used to determine C, N, and P content (see Veen *et al.* 2018 for details). Half of the remaining litter from each location was sterilized using gamma-irradiation (25 KGray) to remove micro-organisms, whereas the other half was left intact. For litter from each location we filled three nylon mesh bags of 5 cm × 10 cm and mesh size 0.9 × 1 mm with 1 g of sterilized litter, and three with 1 g of non-sterilized litter. Mesh bags were buried in the pots according to a reciprocal transplant approach: within each transect, sterilized and non-sterilized litters originating from each successional stage (early, mid or late) were incubated in soils from all three successional stages (early, mid and late). This resulted in a total of 2 sterilization treatments (sterilized vs. non-sterilized) × 3 soil sources (early/mid/late successional stage) × 3 litter sources (early/mid/late successional stage) × 6 replicate transects = 108 pots, with 1 mesh bag per pot.

Pots were placed in a greenhouse under constant temperature and moisture conditions (see Veen *et al.* 2018 for details). After 12 months, mesh bags were harvested from all pots. From each bag a subsample was collected to measure fungal community composition. We measure fungal

community composition at 12 months because this integrates community development during the course of decomposition. The rest of the litter in the bag was gently rinsed on a 0.5-mm sieve to remove soil particles, dried at 60°C until constant weight and weighed to determine mass loss (which was corrected by adding the dry weight equivalent of the subsample that was used for analyzing fungal community composition).

DNA extraction, amplification and sequencing

Litter subsamples were frozen in liquid nitrogen and ground. Per subsample, we used 0.25 g fresh weight to isolate DNA using the PowerSoil DNA Isolation kit according to the manufacturer's instructions (MO BIO Laboratories, Carlsbad, California, USA). For each subsample we amplified the nuclear rDNA internal transcribed spacer (ITS) region using the fungal-specific primer pair with forward primer ITS 9 and reverse primer ITS 4 (Ihrmark *et al.* 2012), and added adapter sequences and 6-base-pair (bp) tags to each subsample. Polymerase chain reactions (PCRs) were performed in 25-µL reaction mixtures and contained of each 2.5 µL dNTP (400 µM) , 0.2 µL of FastStart Expand High Fidelity polymerase (Roche Applied Sciences, Indianapolis, Indiana, USA), 2.5 µL 10 × PCR buffer with MgCl2, 10 µmol/L of each of the two primers, and 1 µL DNA (~5–20 ng). Before performing PCR reactions, all samples were diluted ten times. For samples that did not produce (or produce enough) PCR products, we added 2.5 µl BSA (4 mg ml^{-1}) to the reaction mixture (Farell & Alexandre 2012). The temperature cycling PCR conditions involved denaturation at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s and 55C for 30 s, and then 72°C for 1 min. The final extension step was 72°C for 10 min. We confirmed the presence of expected sizes of PCR products by agarose-gel electrophoresis. Products of PCR reactions were pooled per sample (between three-nine PCR reactions per sample) and purified using a QIAquick PCR Purification Kit (Qiagen, Hilden, Germany, product number 28106). Quantification of DNA in the samples was done using a Fragment Analyzer (Advanced Analytical Technologies Inc.) with an NGS Standard Sensitivity kit (DNF-473-0500), and we

standardized the amount of DNA when pooling samples for sequencing by using 50 ng of DNA per sample. Samples were sequenced (Macrogen Company, Seoul, South Korea) on a Roche 454 automated sequencer and GS FLX system using titanium chemistry (454 Life Sciences, Branford, Connecticut, USA).

Bioinformatics

We analyzed DNA sequences for each subsample using a Snakemake workflow (Köster & Rahmann 2012) that follows the standard operating procedure for 454 data in MOTHUR version 1.33.2 (Schloss *et al.* 2009). We denoised and quality filtered flowgrams using the 'shhh.flows' command (Quince *et al.* 2011), which includes de-multiplexing and trimming of the flowgrams. We then analyzed ITS sequences with ITSx (version 1.0.10). Chimeric sequences were removed using the 'chimera.uchime' command (Edgar *et al.* 2011). Clustering of reads into OTUs was performed at a 97% identity threshold using EspritTree version 11152011 (2011). Sequences were aligned and classified with RDP using the command classify.seqs (Wang *et al.* 2007) against the UNITE database version (v6_sh_97, release 01.08.2015). For each OTU, a consensus taxonomy was determined based on the lowest taxonomic ancestor, using the 'classify.otu' command. Taxonomic classification and OTU clustering data were combined into the BIOM format (McDonald *et al.* 2012) for further downstream statistical analysis. Our data has been submitted to the European Nucleotide Archive (accession number: PRJEB24897; study name: ena-STUDY-NIOO-KNAW-09-02-2018-13:45:33:313-478). Prior to further analyses, we removed 15 samples that each had less than 230 reads, and all singletons from our dataset. We calculated the relative abundance for each OTU within a sample. Alpha-diversity (i.e., OTU richness and Shannon diversity index) was determined on rarefied data using the VEGAN package in R (Oksanen *et al.* 2018). We used FUNguild to determine the functional groups to which the OTUs in our dataset belong (Nguyen *et al.* 2016).

Data analysis

To test how soil source, litter type (both: early-, mid-, late-successional stage) and sterilization (sterilized vs. not sterilized) affected fungal community composition, we used the Bray-Curtis dissimilarity index from the vegan package (Oksanen *et al.* 2018) in a PERMANOVA analysis, with soil source, litter type, sterilization and their interactions and transect as a fixed factor. The relative abundances of the fungal OTU's were included as a multivariate response variable. To test for differences among treatments for each factor in the PERMANOVA test, we performed pairwise PERMANOVA comparisons between each combination of treatments as a post-hoc analysis. P-values were adjusted by the "BH" method in the p.adjust function in R (Benjamini & Hochberg 1995). Fungal community data were displayed using Nonmetric Multidimensional Scaling (NMDS) based on a Bray-Curtis distance matrix. In addition, we determined the number of reads per sample, OTU richness (total number of OTUs per sample) and OTU diversity (Shannon diversity) and we tested how soil source (early-, mid-, late-successional stage), litter type (early-, mid-, late-successional stage), and sterilization (sterilized vs. not sterilized) affected these indices using a general linear model. Here, soil source, litter type, sterilization and their interactions were tested as fixed factors, and transect as a random factor. To test how our treatments affected the relative abundance of each of the nine most dominant classes, we used general linear models with their relative abundance as a response variable, soil source, litter type, sterilization and their interactions as fixed factors, and transect as a random factor. To test how our treatments affected the relative abundance of functional groups we used the same model, but with the relative abundance of functional groups as a response variable. To assess how taxa of fungi changed across our soil and litter treatments we performed a network analyses at the level of fungal genera. These analyses were based on Spearman rank correlations between all pairs of genera for each combination of soil source and litter type for unsterilized litter and sterilized litter separately. Correlations between genera with $r>0.5$ or $r<-0.5$ ($P < 0.05$) were included in the network. We then determined clusters of

fungal genera by k-means clustering on the correlation matrix. Networks were visualized using igraph in R (Csardi & Nepusz 2006).

To determine HFA effects on litter mass loss after 12 months, we calculated the amount of Additional Decomposition at Home (ADH) (Ayres *et al.* 2009; Veen, Sundqvist & Wardle 2015). ADH was calculated for each litter sample and represents the percentage of additional mass loss in the home environment of that litter relative to all away environments within the same transect. We used t-tests to determine whether ADH values were significantly greater than zero for all treatments combined and for each of the treatment separately. To determine how soil source, litter type, litter sterilization and their interactions affected litter mass loss or ADH, we used a general linear model in which soil source, litter type and sterilization and their interactions were included as fixed factors and transect included as a random factor.

To test how shifts in fungal community composition relate to the observed litter mass loss, we used linear regression analyses with litter mass loss as a response variable and the NMDS scores for the fungal community as predictor variables. For this analysis, data from each pot was included as an individual observation, totaling 108 data points (i.e., 6 replicates × 3 sampling locations × 3 litter types × 2 sterilization treatments).To test how the relative abundance of dominant fungal taxa affected litter mass loss, we used a multiple regression analysis (again with each pot as an individual observation), with litter mass loss as a response variable and the relative abundance of the nine most dominant taxa (i.e., together composing >90% of the total community) as predictor variables. We selected only the nine most dominant fungi, because less abundant taxa occurred only in few plots.

To test how fungal dissimilarity between pots, both for the whole community (using Bray-Curtis dissimilarity measures) as well as for each of the dominant fungal taxa, related to dissimilarity in litter mass loss, we compared pairs of pots receiving home litter. For example, pots with early succession soil and early succession litter were compared to pots with mid succession soil and mid

succession litter and to pots with late succession soil and late succession litter within the same replicate transect. Fungal community dissimilarity was calculated using the Bray-Curtis dissimilarity index, and for dominant taxa we calculated dissimilarity in abundance as:

$$dissimilarity\ abundance = |log2\left(\frac{X_{iI}}{X_{jJ}}\right)| \quad (1)$$

where X_{iI} is the relative abundance of a dominant fungal taxon X in soil *I* incubated with litter *i*, and X_{jJ} is the relative abundance of fungal taxon X incubated in soil *J* incubated with litter *j*. To test how fungal community dissimilarity affected ADH we used a linear regression with ADH as a response variable, and Bray-Curtis distance, sterilization and their interaction as predictor variables. To test how dissimilarity in the relative abundance of dominant fungal taxa related to ADH we first used a multiple regression analyses with ADH as the response variable, and dissimilarity in abundance of the nine most dominant taxa as predictor variables. When dissimilarity in abundance of one of the abundant dominant taxa significantly explained variation in ADH, we performed a linear regression analysis with ADH as the response variable and dissimilarity in abundance, sterilization treatment and their interaction as predictor variables. For both the analyses on fungal community dissimilarity and on the dissimilarity in the abundance of the dominant fungal taxa, we only included data from litter incubated in "home" soils, i.e., in soils from the successional stage where they were soured from. As a result, we only used pots with early-successional litters and soils, pots with mid-successional litters and soils, and pots with late-successional litters and soils. This is because ADH is calculated per successional stage, and not for each individual transplant. In total this resulted in 3 pots per replicate gradient × 6 gradients × 2 sterilization treatments = 36 data points. Within each replicate gradient, we then compared fungal composition in a given litter sample to the composition in the litter samples from the other two pots to calculate the average dissimilarity in community composition or relative abundance, respectively.

To test how litter and soil chemical properties differed between successional stages, we used general linear models for each litter or soil property, using successional stage (early, mid, late) as a fixed factor, and transect as a random factor.

All analyses were performed in R version 3.4 (2013). We used the vegan package for multivariate statistics (Oksanen *et al.* 2018) and the lmerTest package for general linear models (Kuznetsova, Brockhoff & Christensen 2013). Data were tested for normality using a Q-Q plot and for homogeneity of variances with a Levene's test.

Results

Litter and soil chemical properties

Litter and soil chemical properties differed between successional stages (Table S1, S2). Soil organic matter content, ammonium concentration, total N and N:P ratio, and litter total C, C:P ratio and N:P were higher in late- than in early- and mid-successional stages, while pH, total soil P and total litter P were lower (Table S1, S2 in supporting information). Soil moisture and nitrate were highest in late- and lowest in mid-successional stages (Table S1, S2). Total soil C and C:N ratio, and litter total N and C:N ratio did not differ between successional stages (Table S1, S2).

Fungal community composition

Soil source, litter type, litter sterilization and their interactions explained >35% of the variation in litter fungal community composition at the end of the litter incubation period (Fig 1, Table 1). The factor that explained the highest proportion of variation in fungal composition was soil source (Table 1). On the first NMDS axis, fungal composition on litter incubated in late-successional soils was different from that on litter incubated in early- and mid-successional soils (Fig 1). A significant two-

way interaction between litter sterilization and soil source indicated that the impact of soil source was stronger for sterilized than for unsterilized litter on the first NMDS axis (Table 1, Fig 1). Litter type explained the second-highest proportion of total variation in fungal composition (Table 1). On the second NMDS axis, fungal communities on late-successional litter differed from those on early- and mid-successional litters (Fig 1). This effect was more pronounced in unsterilized than in sterilized litter, as revealed by a two-way interaction between litter type and litter sterilization. Litter sterilization explained a smaller proportion of total variation in litter fungal community composition on leaf litter, but its effect was still highly statistically significant (Table 1; Fig 1). Results were the same when we performed our analyses on rarefied data, used different dissimilarity indices or used data at the genus level.

The average number of reads per sample was 1235 ± 55 (mean ± SE, with a maximum 3013 of and a minimum of 232) and did not differ between treatments (Table S3 in supporting information). The average number of OTUs was 148 ± 5.5 (with a maximum of 291 and a minimum of 46) and was lower on sterilized (131 ± 6.6) than on unsterilized (167 ± 7.9) litter (Table S3). The average Shannon diversity index was lower for sterilized (3.59 ± 0.07) than for unsterilized (3.94 ± 0.08) litter (Table S3). The fungal classes with the highest relative abundance across all samples belonged to the classes Sordariomycetes (Ascomycota) and Agaricomycetes (Basidiomycota), which together made up 35-70% of the total fungal community depending on treatment combination (Fig 2, Table S4 in supporting information). The relative abundance of several fungal classes was affected by soil source, litter type and sterilization treatment, however these differences were not always reflected in posthoc analyses (Table S4). Sordariomycetes were higher in early- than late-succesional soils and lowest on late successional litters, and were higher on sterilized than unsterilized litter (Fig 2, Table S4). Dothideomycetes (Ascomycota) were higher in mid- than in late-successional soils, were generally higher on late- than on early- and mid-successional litters, and were lower on sterilized than on unsterilized litter. Leotiomycetes (Ascomycota) were highest in late-successional soils and on late successional litters, particularly when unsterilized. The relative abundance of an unclassified

taxon of Ascomycota was higher on late-successional litters than on early- and mid-successional litters, but only in early and mid-successional soils, as was indicated by the significant interaction between soil source and litter type. Also, on late-successional litters the unclassified Ascomycota were more abundant on unsterilized than on sterilized litter, but this was not the case for the other litter types, as was indicated by the interaction between litter type and sterilization. The abundance of Zygomycota was higher on sterilized than unsterilized litter and was lower on late-than on early- and mid-successional litters, but both effects occurred in late-successional soils only (Table S4).

Similar to the response of fungal classes, the relative abundance of fungal genera was determined by litter type, soil source, sterilization and their interactions (Table S5 in supporting information). For unsterilized litters, network analyses indicated that specific clusters of fungi occurred on early- and mid-successional litter types, while others occurred on late-successional litters (Fig. S1 and S2 in supporting information; for details on clusters and genera see Table S5). For sterilized litters, there were fewer connections than for unsterilized litters, and specific clusters of fungi occurred in early- and mid-successional soils, while others occurred mostly in late-successional soils (Fig S3 and S4 in supporting information, for details on clusters and genera see Table S5). On average 68% of our OTUs could be assigned to a fungal guild. This percentage was higher for sterilized (74%) than for unsterilized (62%) litter ($F_{1,63}$ = 25.11, P < 0.001), but did not differ between soil sources ($F_{2,63}$ = 0.57, P = 0.570) or litter types ($F_{2,62}$ = 2.33, P = 0.106). On average 52% of the identified fungi were potential saprotrophs. When correcting for the percentage of fungi that could be identified, we found that the relative abundance of potential saprotrophs was affected by soil source, litter type, sterilization and their interactions (Fig. S5 in supporting information). The relative abundance of saprotrophs was higher in sterilized than unsterilized litter ($F_{1,64}$ = 19.00, P <0.001). In addition, the relative abundance of saprotrophs was affected by a three-way interaction between soil source, litter type and sterilization ($F_{4,62}$ = 2.56, P =0.047) and a two-way interaction between soil source and litter type ($F_{4,63}$ = 6.18, P <0.001). These interactions emerged because the relative abundance of saprotrophs on mid-successional litter in late-successional soils was higher than on

early successional litter, while there was generally no difference between litter types for the other soil sources. Further, the relative abundance of saprotrophs was higher on sterilized late-successional litter in mid-successional soil than on sterilized mid-successional soils, while there was no difference between litter types in mid-successional soils for unsterilized litters (Fig. S5).

Litter mass loss and home-field advantage

Litter mass loss was affected by the main effects of litter type and soil source. Litter from late successional stages decomposed slower than litter from mid- and early successional stages, and litter decomposed slower in soils from late-successional stages than in soils from early- and mid-successional stages (Table S6, Fig 3a,c). Sterilization did not affect litter mass loss, and there were no interactive effects between sterilization, litter source and soil source (Table S6, Fig 3a,c). There were significant relationships between litter mass loss and sample scores on the first ($F_{1,81}$ = 19.40, P < 0.001, R^2 = 0.19) and second NMDS axis ($F_{1,81}$ = 5.45, P = 0.022, R^2 = 0.05), indicating that litter mass loss rates were related to fungal community composition after 12 months of decomposition. Multiple regression analyses with the nine most dominant fungal taxa showed that there was a negative relationship of litter mass loss with the relative abundance of an unclassified Ascomycota (t_{71} = -3.91, P < 0.001, R^2 = 0.29), but not with any of the other dominant taxa or groups of taxa.

Overall, home-field effects were positive (t_{33} = 2.44, P = 0.020). This indicates a general advantage for the different litter types of being decomposed in their home soil compared to in away soils (Fig 3b, d). There was a marginally non-significant effect of litter sterilization, but home-field effects tended to be lower for sterilized than for unsterilized litters ($F_{1,23}$ = 3.87; P = 0.061; Fig 3b,d). However, home-field effects did not differ between successional stages ($F_{2,23}$ = 2.67, P = 0.768; Fig 3b,d) and there was no interaction between successional stage and sterilization treatment ($F_{2,23}$ = 0.28, P = 0.761). There was no significant relationship between the magnitude of home-field effects

and the Bray-Curtis dissimilarity in fungal composition ($F_{1,24}$ < 0.01, P = 0.960; Fig 4a), irrespective of litter sterilization treatment ($F_{1,24}$ = 0.34, P = 0.566; Fig 4a). Multiple regression analyses showed that dissimilarity in the relative abundance of only one taxon could explain the magnitude of home-field effects, i.e., Sordariomycetes (Ascomycota), which was the most abundant taxon in the whole community.

Discussion

The aim of our study was to understand how soil source, litter type, and historical contingencies of the litter microflora affected fungal community composition on decomposed leaf litter and whether differences in fungal composition between litters could explain the magnitude of home-field advantage (HFA) for litter decomposition. By analyzing fungal community composition on decomposed litter, we attempted to obtain an integrated value corresponding with our integrated analysis of HFA during that same period. We found that the impact of soil source was stronger on sterilized than on unsterilized litter, while the impact of litter type on fungal composition was stronger for unsterilized than for sterilized litter. We found that not the dissimilarity in fungal composition, but the abundance of the most dominant fungal taxon corresponded with greater HFA.

The impact of soil source, litter type and sterilization on litter fungal composition

In line with our first hypothesis, we found that soil source, litter type, sterilization and their interactions all explained some of the total variation in fungal community composition on the decomposed litter. Soil source, and therefore the species pool in the soil, emerged as the most important driver of fungal composition on leaf litter. Large changes in soil fungal composition are known to occur as succession proceeds in this chronosequence (Hannula *et al.* 2017). However, litter type also had important effects on fungal composition, in that early-, mid- and late-successional

decomposed litter generally had different fungal communities. This may be the result of differences in chemical quality of the litter, as can be expected for old-field succession (Wardle 2002; Cortez *et al.* 2007; Milcu & Manning 2011), which may act as a filter for fungal colonization (Kraft *et al.* 2015). Therefore, in line with knowledge on the rhizosphere composition (Berg & Smalla 2009; Raaijmakers *et al.* 2009; Mommer *et al.* 2018) litter types can accumulate a unique microbiome (Conn & Dighton 2000; Aneja *et al.* 2006; Fanin, Hättenschwiler & Fromin 2014).

The effect of soil source was stronger for sterilized than for unsterilized litter, even after the 12 months of litter incubation in our experiment. This indicates that the phyllosphere microbiome on unsterilized decomposed litter may have provided resistance against invasion by fungi from the species pool in the soil (Mallon, Elsas & Salles 2015). Thus, under natural conditions, where plant litters are unsterilized, the leaf microbiome exerts a priority effect by influencing colonization of the decomposing litter by fungi from the soil (Fukami *et al.* 2010; Fukami 2015; van der Wal, Ottosson & de Boer 2015) and can drive fungal community composition (Voříšková & Baldrian 2013; Lin *et al.* 2015). Many previous controlled experiments studying HFA have used sterilized litter because, elimination of litter communities allows for testing the local adaptation of the soil community (Palozzi & Lindo 2018). Our comparison of sterilized and unsterilized litter suggests that specific decomposers may be imported together with the litter itself, at least to some extent.

Our findings are consistent with recent work showing that endophytes in phyllosphere can cause priority effects and play a key role in shaping decomposer communities on leaf litter (Voříšková & Baldrian 2013; Lin *et al.* 2015). As such, it has been shown that the phyllosphere microbiome (including both endo- and epiphytes) can differ between plant species (Persoh 2013) and genotypes (Wagner *et al.* 2016) and can depend on plant functional traits (Kembel *et al.* 2014) and environmental conditions (Kraft *et al.* 2015). Hence, shifts in plant composition and trait spectra along the successional gradient in our study (Morriën *et al.* 2017) may shape differences in phyllosphere microbiome and thus the decomposer community on leaf litter. Future work could

further advance this topic by focusing on the variation in phyllosphere communities at litter fall and the role of these communities in litter breakdown and HFA (Austin *et al.* 2014).

Relationship between fungal dissimilarity and home-field advantage

We found that litter mass loss differed between the litter types from the three successional stages and between the soils in which the litters were incubated, but this was not reflected in shifts in HFA between the successional stages. Overall, the litters in our experiment experienced HFA and the decomposed litters had unique fungal communities (Fig. 1). This is in line with a recent study (Lin *et al.* 2018), however, in contrast to our second hypothesis, we found that the magnitude of HFA effects did not relate to the dissimilarities between litters of the overall fungal community. Instead, variation in litter mass loss related to variation in fungal composition of the decomposed litter. It could be that in our work HFAs were weak because we sourced litter from mixed plant communities (Veen *et al.* 2015; Veen, Sundqvist & Wardle 2015), and hence that relationships between fungal composition and HFA are weak as well, so that they cannot be detected easily. Alternatively, biotic and abiotic environmental factors other than those that we have measured might play a role determining HFA (Palozzi & Lindo 2018). For example, larger soil fauna (Milcu & Manning 2011) or soil bacteria could also be important drivers of HFA, but these were not included in our greenhouse study or molecular analyses, respectively. Alternatively, variation in soil abiotic conditions, differences in litter quality or the presence of other soil organisms can interact with fungal decomposer communities to drive decomposition processes. This could modify the effect of specific interactions (due to specific decomposer communities or specific soil abiotic conditions) between litter and soil sources and therefore may have contributed to explain HFA effects (Austin *et al.* 2014; Veen *et al.* 2018). Therefore, there is a need to further elucidate the role of variation in soil physio-chemical conditions and biotic interactions in the soil for driving HFA effects (Palozzi & Lindo 2018).

Although, there were no clear relationships between variation in fungal composition and HFA, we found an almost significant reduction in HFA on sterilized litter (Fig. 3). This finding suggests that the removal of the phyllosphere community present at the time of litter collection eliminated specialists that otherwise cause HFA (Austin *et al.* 2014). Also, our results showed that increasing dissimilarity in the most abundant fungal taxon, i.e., Sordariomycetes, between home and away soils corresponded with stronger HFA. This class of fungi contains species that perform a wide variety of functions in the soil, ranging from plant parasitism to decomposition of recalcitrant organic material (Nguyen *et al.* 2016). It was the most abundant fungal class in our samples, suggesting that fungi may play a role in HFA if they are common enough. To further unravel the impact of individual fungal taxa on HFA will require disentangling the fungal community in more detail and performing transplant experiments with targeted fungal taxa or entire fungal groups.

In our experiment, we measured litter mass loss and fungal composition after 12 months of litter incubation. This informed on the changes that occurred in the fungal community integrated over the experimental period, both when we removed and did not remove the microbes from the phyllosphere at the start of the experiment. However, fungal composition and the strength of litter selection effects may vary during the process of litter breakdown, because fungal composition will be subject to succession during decomposition (Aneja *et al.* 2006; Voříšková & Baldrian 2013; van der Wal, Ottosson & de Boer 2015). Therefore, we recognize that measuring the fungal community throughout the full course of the 12 months might help us to increase understanding of the role of microbes in driving litter mass loss and HFA effects at the stages where most of the litter breakdown occurs. Future work should perform multiple destructive harvests and measure the temporal dynamics of HFA (Fanin, Fromin & Bertrand 2016) and litter microbiomes (Aneja *et al.* 2006; Voříšková & Baldrian 2013). Also, sampling fungal communities in the phyllosphere before or at the start of litter breakdown would allow to identify to what extent phyllosphere communities drive the

priority effects that we observed (Fukami *et al.* 2010; van der Wal, Ottosson & de Boer 2015) and contribute to explain HFA effects. Finally, integrating measurements on fungal biomass, fungal activity and species composition (see e.g. Morriën *et al.* 2017; Lin *et al.* 2018) may be essential to obtain a comprehensive understanding of the role of litter microbiomes for driving HFA (Props *et al.* 2017; Zhang *et al.* 2017).

Conclusions

We show that leaf litters at the end of a 12-month incubation period have unique decomposer communities, but particularly on unsterilized litter. This implies a priority effect, as fungi from the soil appeared more successful in colonizing sterilized than unsterilized litter. Our findings suggest that leaf litters select for fungal communities early on in the decomposition process or in their phyllosphere and those communities prevent invasion from the soil. Dissimilarity in the entire litter microbiome of the decomposed litter could not explain observed HFA effects. Instead, we found that the most abundant fungal taxon correlated with the magnitude of HFA. Therefore, we suggest that not the entire microbiome, but specific fungal species or taxa may be important for generating HFA effects. Our results show that decomposed plant litters can build up unique decomposer communities, which may have functional consequences for litter breakdown and may play a role in driving HFA. This finding helps to unravel the mechanisms that can drive HFA (Austin *et al.* 2014; Palozzi & Lindo 2018). In addition, our study suggests that the presence of specific decomposer taxa could feed back to plant growth and performance (Wardle *et al.* 2004) via accelerated litter breakdown and thus soil nutrient cycling. It will therefore be important to integrate the role of specific decomposers for litter breakdown into research on plant-soil feedback to further disentangle functional consequences of HFA (Kardol *et al.* 2015; Zhang, Van der Putten & Veen 2016).

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Author contributions

GFV, DAW and WHvdP designed the experiment. GFV carried out the experiment. GFV and TB performed the molecular work. GFV and LBS analyzed the data. GFV led the writing of the manuscript. All authors contributed to writing and revising of the manuscript and gave final approval for publication.

Data accessibility

Litter mass loss and environmental data are deposited in the Dryad Digital Repository doi:10.5061/dryad.527d3f9 (Veen *et al.* 2019). Sequencing data have been submitted to the European Nucleotide Archive (accession number: PRJEB24897; study name: ena-STUDY-NIOO-KNAW-09-02-2018-13:45:33:313-478). Our R code is available upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table 1

The influence of soil source (early, mid, late successional stage), litter type (early, mid, late successional stage), sterilization (no, yes) and their interactions on fungal community composition in the litter as tested using a PERMANOVA. Values in bold represent significant effects with $P < 0.05$.

Factor	**df**	**F**	**P**	**% explained variation**
replicate transect	**5, 61**	**2.6520**	**<0.001**	**11.5**
litter type	**2, 61**	**4.1988**	**<0.001**	**7.3**
soil source	**2, 61**	**5.8501**	**<0.001**	**10.1**
sterilization	**1, 61**	**6.2662**	**<0.001**	**5.4**
litter type × soil source	**4, 61**	**1.2619**	**0.048**	**4.4**
litter type × sterilization	**2, 61**	**1.7286**	**0.003**	**3.0**
soil source × sterilization	**2, 61**	**1.7023**	**0.002**	**2.9**
3-way interaction	4, 61	0.7509	0.990	2.6

Figure legends

Figure 1. NMDS plot of fungal community composition in unsterilized litter (left panel) and sterilized litter (right panel) at the end of the experiment. Litter source is indicated by different colors and soil source is indicated by different shapes. Different letters at the symbols indicate that treatments are significantly different from each other at $P < 0.05$ as tested in pairwise PERMANOVA analyses.

Figure 2. Relative abundance for the most abundant fungal classes in all different litters at the end of the experiment. Different panels represent different litter types, indicated by the names on the panels: Unsterilized = unsterilized litter, Sterilized = sterilized litter, Early = early-successional litter, Mid = mid-successional litter and Late = Late-successional litter. Within each panel, individual bars represent different soil sources: Early = early-successional soil, Mid = mid-successional soil and Late = Late-successional soil.

Figure 3. Mean litter mass loss (%) ± SE and Additional Decomposition at Home (ADH; %) ± SE for unsterilized litter (a,b) and sterilized litter (c,d). In panel (a) and (c) bars with different types of grey represent different litter types: Early = early-successional litter, Mid = mid-successional litter and Late = Late-successional litter. Bars topped by different letters are significantly different at $P<0.05$ as according to a Tukey posthoc test. Litter mass loss data were tested using a general linear model with soil source, litter type and sterilization as fixed factors (Table S3). ADH was tested using a general linear model with successional stage and sterilization as a fixed factor.

Fig 4. (a) Fungal community dissimilarity (Bray Curtis) and (b) the dissimilarity in abundance of Sordariomycetes (calculated as the logarithm of ratio of the relative abundance home and away) plotted against the percentage of Additional Decomposition at Home (ADH). Points represent individual litter samples. We only included data from litter samples incubated in soils collected from the same successional stage ("home combinations"), because ADH is calculated per successional stage, and not for each individual litter transplant. Relationships are tested using linear regression analyses.

Figure 1

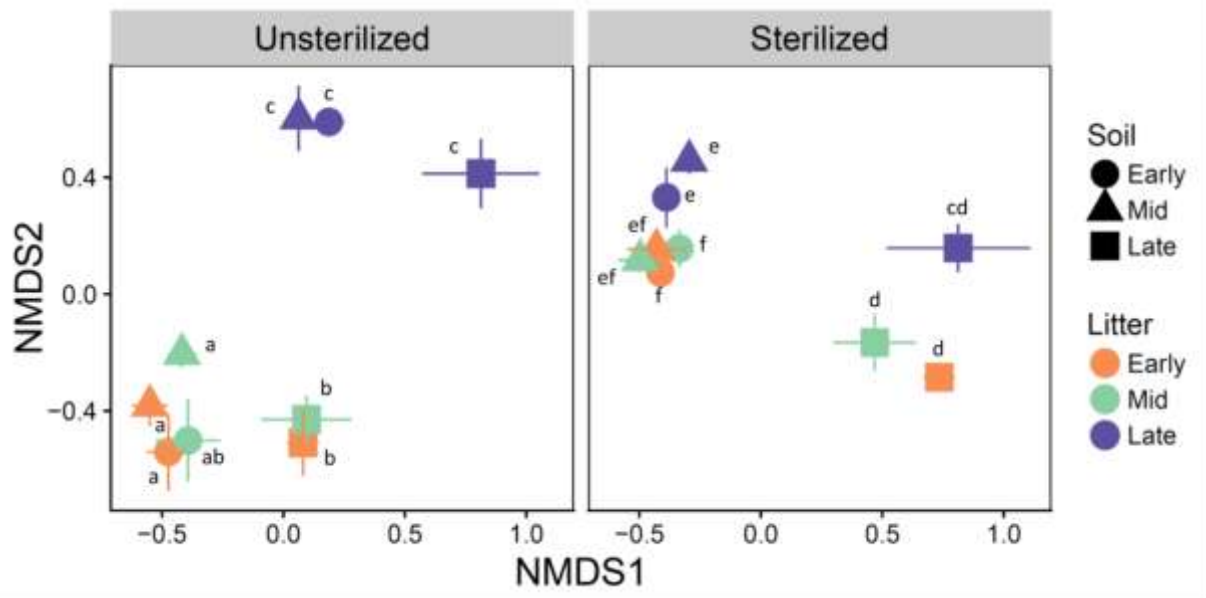

Figure 2.

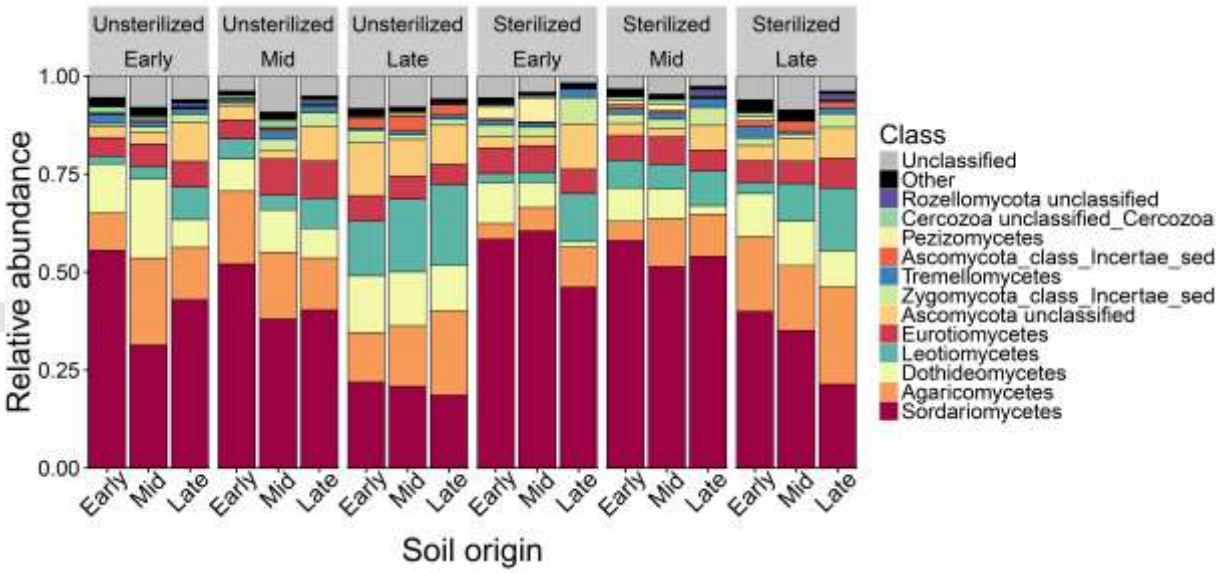

Figure 3

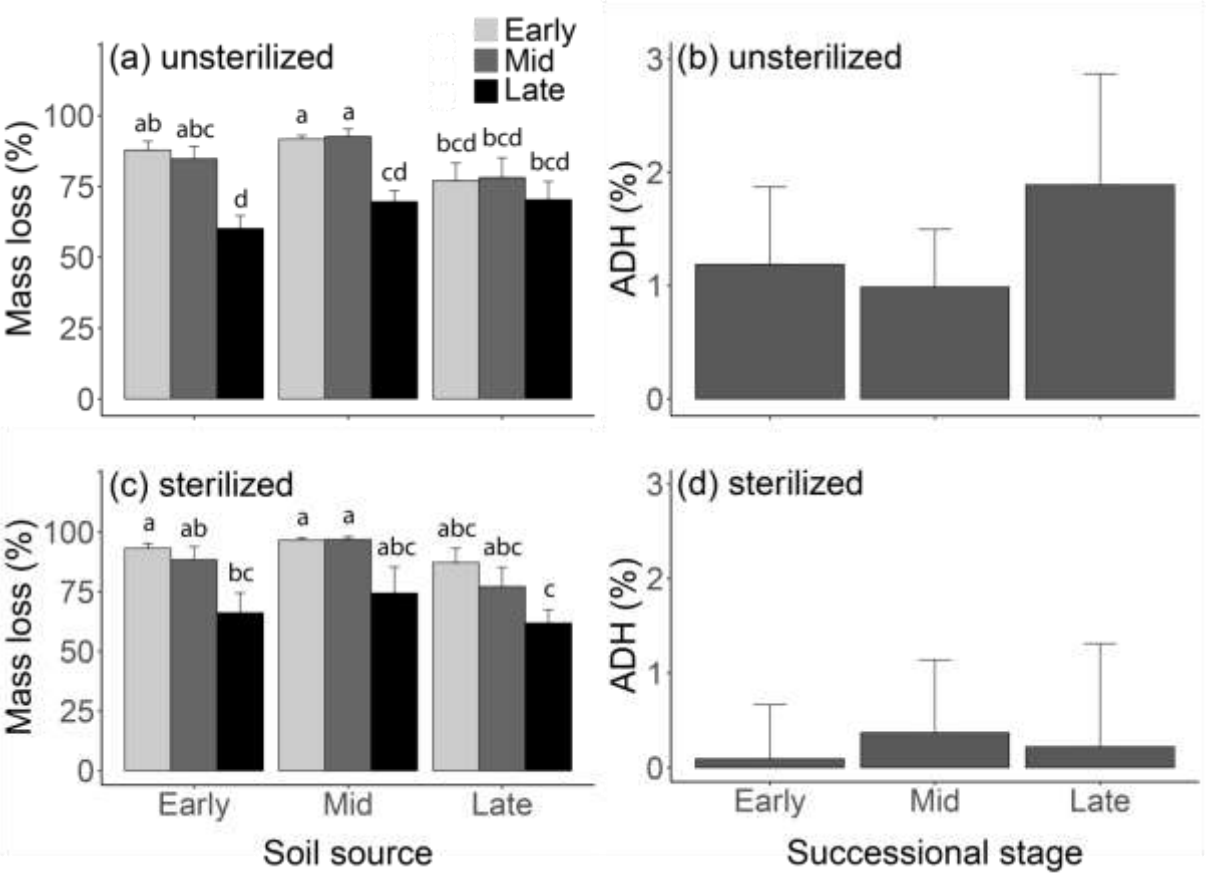

Figure 4