INTRODUCTION

Litter decomposition is a crucial aspect of carbon and nutrient cycling (Swift et al., 1979). It is recognised that variation in the functional capacity of microbial communities is a key driver of decomposition processes (Bradford et al., 2017; Glassman et al., 2018; Keiser et al., 2011). Particularly, the idea that soil or litter microbial communities specialise towards local litter inputs and thereby accelerate litter breakdown, referred to as home-field advantage (HFA), has gained increasing attention over the last decade (Ayres et al., 2009; Lin et al., 2020; Palozzi & Lindo, 2018). Previous work showed that HFA effects can occur across many ecosystems (Fanin et al., 2016; Madritch & Lindroth, 2011; Milcu & Manning, 2011; Vivanco & Austin, 2008) and that such home-field effects may be driven by differences in the composition of fungal decomposer communities, shown both for the degradation of leaf litter and for other litter types.

Steering the soil microbiome by repeated litter addition

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Abstract

1. Microbial communities drive plant litter breakdown. Litters originating from different plant species are often associated with specialised microbiomes that accelerate the breakdown of that litter, known as home-field advantage. Yet, how and how fast microbial communities specialise towards litter inputs is not known.

2. Here we study effects of repeated litter additions on soil microbial community structure and functioning. We set up a 9-month, full-factorial, reciprocal litter transplant experiment with soils and litters from six plant species (three grasses and three trees). We measured fungal and bacterial community composition, litter mass loss and home-field effects.

3. We found that repeated litter additions resulted in convergence in fungal community composition driven by litter functional group (trees vs. grasses). Grasses enriched Sordariomycetes, while Tremellomycetes, Eurotiomycetes and Leotiomycetes were favoured by tree litter. Bacterial community composition, litter mass loss and home-field effects were not affected by litter incubation, but there was a relationship between fungal community composition and mass loss.

4. We conclude that repeated litter incubations can result in directional shifts in fungal community composition, while 9 months of litter addition did not change bacterial community composition and the functioning and specialisation of microbial communities.

5. Testing further how repeated litter inputs affect microbial functioning is essential for steering decomposer communities for optimal soil carbon and nutrient cycling.

KEYWORDS

bacteria, carbon cycling, decomposer community, decomposition, fungi, litter type, microbial community, saprotrophic fungi
Litter types are often associated with a species-specific microbiome in the detritusphere and in the soil (Prescott & Grayston, 2013). Species-specific microbiomes on litters (Aneja et al., 2006; Conn & Dighton, 2000; Lin et al., 2019) may develop because litter quality acts as an environmental filter for microbial colonisation (Kraft et al., 2015), as a result of competition between microorganisms for resources (Austin et al., 2014; Ayres et al., 2009) or due to historical contingencies induced by the phyllosphere microbiome (Lin et al., 2015; Veen, Snoek, et al., 2019; Voříšková & Baldrian, 2013). At the same time, decomposing litter itself may affect the composition and functioning of the microbial community in the soil under the litter (Fanin et al., 2014), which is probably driven by chemical inputs from the litter into the soil. For example, recent work has shown that adding woody substances to an agricultural soil steers the soil microbial community towards saprotrophic organisms and at the same time increases disease suppression (Clocchiatti et al., 2020). It remains, however, poorly understood whether repeated litter inputs can drive directional compositional and functional shifts in soil microbial communities, as has been found for litter microbiomes (Keiser et al., 2011).

The occurrence and magnitude of HFA effects is highly variable across studies (Ayres et al., 2009; Veen et al., 2015). Although it is not fully understood what drives variation in home-field effects, it appears that HFA becomes stronger when home and away litter types have a more distinct chemical composition (Barbe et al., 2017; Freschet et al., 2012; Veen et al., 2015). As a result, microbial communities favouring the breakdown of a certain litter type might also favour the breakdown of litter types with similar chemical traits, for example of litter types originating from the same plant functional groups (Freschet et al., 2012; Veen et al., 2015). This suggests that, in line with what we know from steering rhizosphere microbiomes (Fitzpatrick et al., 2018; Hannula et al., 2019), directional shifts in soil microbial taxonomic composition may not only depend on the plant species from which the litter is originating, but also on its functional group. However, to what extent litter types from different plant species or plant functional groups drive soil microbial community composition is almost fully unknown.

Litter-induced shifts in soil microbial composition can remain in the soil as biotic legacies with potential consequences for subsequent ecosystem processes (Ehrenfeld et al., 2005; Elgersma et al., 2012). For example, litter-induced shifts in microbial composition are shown to accelerate the breakdown of those litter inputs (Keiser et al., 2011). This will affect the availability of nutrients to plants and therefore influence plant nutrient uptake and growth (Kardol et al., 2015; Ke et al., 2015). Directional shifts in microbiome composition induced by repeated litter additions may also result in specialisation of microbial communities towards the new substrates and hence to HFA effects. To what extent HFA effects develop via repeated litter additions, and whether this differs between plant species or plant functional groups, is not known. Understanding how repeated addition of organic substrates results in the development of home-field effects is crucial for optimising soil carbon and nutrient cycling, for example in agro-ecosystems (Mariotte et al., 2018; Veen, Wubs, et al., 2019).

Here we test how repeated litter addition results in shifts in the composition and functioning of the soil microbiome. We use a repeated litter incubation experiment, where we confront the soil microbiome with their original litter input (i.e. matching the plant species where the soil originated from) or with a new litter input (i.e. litter derived from another plant species). We use litter and soils from three grass and three tree species to be able to distinguish whether effects play out at the level of plant species or at the level of plant functional groups. We use the incubated soils in a subsequent decomposition experiment to test how legacy effects of litter incubation affect subsequent litter breakdown and home-field effects. We specifically test three hypotheses. (a) Our first hypothesis is that repeated litter inputs result in directional shifts in the composition of the soil microbiome, in line with what we know from the litter microbiome (Keiser et al., 2011) and the plant rhizosphere (Hannula et al., 2019). We expect that the composition of soil microbiomes will be altered by litter inputs, such that it converges towards the soil microbiome originally associated with that litter input, with effects being more apparent at the level of plant functional groups than at the level of plant species (Freschet et al., 2012; Hannula et al., 2019). (b) Our second hypothesis is that directional shifts in microbial composition towards the new litter type have functional consequences. We expect that HFA effects for the original litter input become weaker with repeated addition of a new litter type. (c) Our third hypothesis is that repeated litter incubation leads to an increased affinity of the microbiome for the new litter type (Austin et al., 2014; Palozzi & Lindo, 2018), which will result in the occurrence of HFA effects for the new litter type. Our results will increase understanding to what extent decomposer microbiomes can be steered in order to exploit home-field effects for litter breakdown and carbon and nutrient cycling.

## MATERIALS AND METHODS

### 2.1 | Field sites

To test our hypotheses, we set up two controlled experiments. Soil and litter samples used in all experiments were collected from a long-term field site on the Veluwe, the Netherlands (Hannula et al., 2017; Kardol et al., 2006; Veen et al., 2018) situated between Ede (52°04′20″N, 5°44′12″) and Wolfheze (52°00′77″N, 5°48′58″). We sampled soils from six independent locations within the Veluwe field site. All locations were situated on sandy soils. Mean annual temperature was around 10.7°C and mean annual precipitation approximately 840 mm [Veen et al., 2018; Royal Netherlands Meteorological Institute (KNMI)]. Each location consisted of a semi-natural grassland and a surrounding broad-leaved forest (Veen et al., 2018).
2.2 | Experimental design

In the fall of 2016, we collected soils (8 December) and litter (3–27 October depending on timing of litter fall) from three grass species *Agrotis capillaris*, *Festuca rubra* and *Holcus lanatus* and three tree species *Betula pendula*, *Fagus sylvatica* and *Quercus robur* at each site. For the grass species we sampled soils within monoculture patches, for the tree species we sampled soils immediately underneath adult trees. For each plant species at each location we collected ~4 kg of soil from the top 10 cm by pooling ~6–10 individual soil cores. Soils were sieved over a 4-mm sieve. Soils were kept at 4°C until setup of the experiment. Litter, that is, recently senesced biomass, was collected as a bulk sample from locations where the plant species were highly abundant. Litter was cut into 1-cm fragments and sterilised by gamma irradiation (25 KGray). Using the soil and litter samples, we set up (a) a reciprocal transplant experiment where soils were incubated with all litter types during three subsequent periods of 3 months and (b) we used the incubated soils in a subsequent litter decomposition experiment where soils were confronted with original litter (i.e. litter type as in the field) or with the new litter (i.e. litter type used during the incubation in experiment (i)).

(i) Reciprocal litter incubation experiment

On 20 December 2016, we set up a full-factorial reciprocal litter transplant experiment with soils from the six replicated field locations. We filled microcosms with 240 g equivalent of dry weight soil. For each plant species at each location we set up seven microcosms which were incubated with 2 g of air-dried-sterilised plant litter from each plant species included in the experiment, according to a full-factorial design; and one mesocosm did not receive any litter (no-litter control). This resulted in a total of 6 replicates × 6 plant species × 7 litter treatments (i.e. six litter types, one no-litter control) = 252 microcosms (Figure 1). Litter addition to the same pots was repeated after 3 months and after 6 months (Figure 1).

At each litter addition, litter and soil were gently homogenised; the amount of litter added was similar to average rates of litter fall in temperate ecosystems (Penuelas et al., 2007). At each 3-month litter incubation period we also added 1 g of litter in a nylon mesh bag (mesh size 0.9 × 1.0 mm), which was inserted in the soil, in order to calculate litter mass loss. Microcosms were incubated in the dark at 60% water holding capacity (WHC), 20°C and 80% air humidity. Microcosms were organised to a randomised block design, with each replicated site considered as a block. After each 3-month litter incubation period, litter bags were harvested, cleaned and dried at 60°C to measure litter mass loss. Microcosms were weighed and watered to maintain WHC every 2 weeks. In addition, a soil subsample was collected at the start of the experiment and after each 3-month incubation period to measure soil abiotic and biotic conditions (details under ‘Soil and litter measurements’). At the start of the experiment subsamples of the litter were oven-dried, to be able to correct mass loss calculations for the amount of moisture still present in air-dried litter.

(ii) Litter decomposition feedback experiment

At the end of the reciprocal litter transplant experiment, that is, after 9 months of incubation, we collected a soil subsample from each microcosm from experiment (i) to set up a litter decomposition experiment. Each soil sample was split into two subsamples, used to set up two new microcosms using 50 ml falcon tubes: one microcosm was incubated with the litter type from the plant species where the litter (no-litter control). This resulted in a total of 6 replicates × 6 plant species × 7 litter treatments (i.e. six litter types, one no-litter control) = 252 microcosms (Figure 1). Litter addition to the same pots was repeated after 3 months and after 6 months (Figure 1). At each litter addition, litter and soil were gently homogenised; the amount of litter added was similar to average rates of litter fall in temperate ecosystems (Penuelas et al., 2007). At each 3-month litter incubation period we also added 1 g of litter in a nylon mesh bag (mesh size 0.9 × 1.0 mm), which was inserted in the soil, in order to calculate litter mass loss. Microcosms were incubated in the dark at 60% water holding capacity (WHC), 20°C and 80% air humidity. Microcosms were weighed and watered to maintain WHC every 2 weeks. In addition, a soil subsample was collected at the start of the experiment and after each 3-month incubation period to measure soil abiotic and biotic conditions (details under ‘Soil and litter measurements’). At the start of the experiment subsamples of the litter were oven-dried, to be able to correct mass loss calculations for the amount of moisture still present in air-dried litter.

*FIGURE 1* Overview experimental set up: (i) reciprocal feedback experiment with three sequential litter incubation periods (3 months each) to steer the composition and functioning of the soil microbiome, and (ii) litter decomposition feedback experiment to test how sequential litter incubations affect the breakdown and home-field effects of the original litter type (i.e. the original field litter type) and how legacy effects of field history affect the breakdown and home-field effects of the incubation litter type (i.e. the litter type used during sequential incubation). The set up for period 2 is not depicted in detail; it is exactly the same as the set up during periods 1 and 3. Shadings in the soil in period 3 indicate that the soil conditions may have changed in response to the incubation litter type.
soil originated from in the field, the other microcosm was incubated with the litter type that the soil had been incubated with during the reciprocal transplant experiment (Figure 1). Each microcosm received the equivalent of 0.50 g of dry soil and 0.50 g of dry litter (Keiser et al., 2011). This resulted in 252 soil subsamples × 2 litter types (i.e. the historical field litter type and the current incubation litter type; for the no-litter control samples we only incubated with the historical field litter) = 468 microcosms. We used small amounts of soil in this experiment in order to inoculate the soil microbiome, while minimising effects of soil physical and chemical conditions on litter breakdown (Keiser et al., 2011). Microcosms were incubated in the dark at 20°C, 60% WHC and 80% air humidity for 3 months and then freeze-dried to determine litter mass loss.

2.3 | Soil and litter measurements

At the start of the experiment we measured initial soil and litter chemical properties from all soil and litter types. A soil subsample was dried at 105°C for 24 hr to determine soil moisture content. Soil organic matter content was determined by loss-on-ignition in a muffle furnace (550°C, 4 hr). We determined pH in fresh soil samples with a Mettler Toledo pH metre after shaking the equivalent of 10 g dry weight soil in 25 ml of demi-water for 2 hr at 250 RPM. Inorganic nitrogen content (N-N\text{NO}_3 and N-N\text{NH}_4) was determined with an AutoAnalyzer (Quaatro, Seal Analytical) after shaking the dry weight equivalent of 10 g soil in 50 ml 1 M KCl (2 hr, 250 RPM). Soil inorganic nitrogen content was determined again after 9 months of litter incubation, that is, at the end of experiment (i). A soil subsample was dried at 40°C and ground and used to determine total soil C and N content with an element analyser (Flash 2000, Thermo Fisher Scientific). Soil P availability was measured as P-Olsen and measured with an AutoAnalyzer (Quaatro, Seal Analytical; Olsen, 1954). Litter C and N content were determined with an element analyser (Flash 2000, Thermo Fisher Scientific). Litter P content was determined by digestion with a 2.5% potassium persulphate solution. The obtained extract was measured colorimetrically with an AutoAnalyzer (Quaatro, Seal Analytical; Murphy & Riley, 1962). We determined lignin content using methanol–chloroform extractions and hydrolysis (Rowland & Roberts, 1994).

2.4 | Microbial community composition

We measured soil fungal and bacterial community composition in initial soils and after 3 and 9 months of litter incubation in experiment (i) by amplicon sequencing using the Illumina Miseq PE250 platform at BGI (Hong Kong). DNA was extracted from 0.25 g of soil using the Powersoil DNA isolation kit (Qiagen) according to the manufacturers’ protocol. We amplified DNA using polymerase chain reaction (PCR). Adapters and barcodes were added to samples by PCR for multiplexing and re-identification individual samples following sequencing. For fungi we used the primers IT54 and IT59 targeting the ITS2 region (Ihrmark et al., 2012) and the primers 515F and 806R (Caporaso et al., 2012) targeting the V4 region of the 16S rRNA gene in bacteria. ITS PCR was performed in 25-μl reaction mixtures and contained of each 2.5 μl dNTP 5 μM, 0.15 μl of FastStart Expand High Fidelity polymerase (Roche Applied Sciences), 2.5 μl 10× PCR buffer with MgCl₂, 1 μl MgCl₂ (25 mM), 1.25 μl BSA (4 mg/ml) 0.5 L of each of the two primers (10 mM) and 1 μl DNA (~5–20 ng). The temperature cycling PCR conditions involved denaturation at 95°C for 5 min, followed by 35 cycles of 95°C for 45 s and 55°C for 40 s, and then 72°C for 90 s. The final extension step was 72°C for 10 min. 16S PCR were performed in 25-μl reaction mixtures and contained 10 μl of 5 Prime Hot MasterMix 2.5x (QuantaBio), 1.25 μl BSA (4 mg/ml) 0.5 L of each of the two primers (10 mM) and 1 μl DNA (~5–20 ng). Before performing PCR, all samples were diluted 10 times to prevent inhibition. The temperature cycling PCR conditions involved denaturation at 95°C for 5 min, followed by 35 cycles of 95°C for 45 s and 55°C for 40 s, and then 72°C for 90 s. The final extension step was 72°C for 10 min. We confirmed the presence of PCR products of expected sizes by agarose gel electrophoresis. The PCR products were purified using Agencourt AMPure XP magnetic bead system (Beckman Coulter Life Sciences) with a volume ratio of PCR product to beads of 1:0.7. Purified PCR products were analysed in a Fragment Analyzer using a Standard Sensitivity NGS Fragment Analysis kit (1–6,000 bp) and following manufacturer’s instructions (Advanced Analytical Technologies GmbH).

2.5 | Bioinformatic analysis

The PIPITS pipeline was used for fungal sequences (Gweon et al., 2015; version 2.4, standard settings) with VSEARCH implemented to pair sequences. Shortly, we extracted the ITS2 region using ITSx (Bengtsson-Palme et al., 2013). Short reads (<100 bp) were removed, chimeric sequences were removed by comparing with UNITE uchime database (version 8.2) and clustering of reads into OTUs was performed at a 97% identity threshold. Sequences were aligned and classified using with RDP against the UNITE fungal database (Kõljalg et al., 2013; Nilsson et al., 2019). For bacteria, we used the DADA2 pipeline (version 1.14, forward reads were trimmed at 270 bp and reverse reads were trimmed at 200 bp; Callahan et al., 2016, p. 2). Consensus method was used to remove chimeric sequences. For bacteria we used the Silva database (version 132). Prior to statistical analysis, all sequences that did not belong to fungi or bacteria were removed. For bacteria, also sequences derived from mitochondria and chloroplasts were removed. All OTUs (fungi) and ASVs (bacteria) that occurred in less than three samples and with abundance of <0.01% were removed from the dataset. Samples with <1,000 or more than 80,000 reads were removed to ensure that read number did not affect community composition. One sample for fungal data (Holcus, experimental period 3) and one sample for bacteria (Quercus soil, blank, experimental period 1) were removed as outliers. Before analyses, data were normalised using cumulative sum scaling (CSS) which was suitable based on large number of samples (Pereira et al., 2018).
2.6 | Data analysis

To test the effects of sampling time, soil type and litter type on the community composition of bacteria and fungi, Permutational multivariate ANOVA (PERMANOVA) was used in 'vegan' (Oksanen et al., 2018) with 999 permutations and Bray–Curtis distance. The homogeneity of dispersion was inspected using betadispersion ('betadisper'). As the initial samples only included soils from different locations without litter addition (n = 30), they were analysed separately due to difference in sample numbers and dispersion. For the soils with litter addition, the interactive effects of the duration of litter addition, soil origin and litter type added were further investigated using PERMANOVA. NMDS (with Bray–Curtis) was used to visualise the effects of litter and soil type. We used general linear mixed models to determine how soil source, litter type and experimental period affected the relative abundances of fungal phyla and dominant/most abundant genera. Site (1|site), experimental period and mesocosm (period|mesocosm) were used as random factors to control for the experimental set up (sites as replicated blocks in field and greenhouse) for repeated measures respectively. In case the residuals were not normally distributed, arcsin square root transformation on relative abundances was used to ensure normality.

Before the analysis of the reciprocal litter incubation experiment (i) we standardised litter mass loss values to 90-day periods, in order to correct for differences in litter incubation length (range between 90 and 94 days). We then used a general linear mixed model to determine how soil source, litter type and experimental period affected litter mass loss. Site (1|site), experimental period and mesocosm (period|mesocosm) were used as random factors to control for the experimental set up (sites as replicated blocks in field and greenhouse) for repeated measures respectively. We tested the effect of soil source, litter type and experimental period on HFA effects (expressed as the percentage of additional decomposition at home; ADH) using a general linear mixed model with site and experimental period as random factors (period|site). For the first experimental period, we tested how field-effects differed between plant functional groups using a general linear model with transplant type (i.e. transplants between two grass species, two tree species or a grass and a tree species) as a fixed factor and site (1|site) as a random factor. Data from the litter feedback experiment (ii) were analysed from two different perspectives. First, we tested how litter incubation history (from experiment i) affected the mass loss and HFA of the original litter type, allowing us to analyse whether microbial lost affinity and thus HFA for the original litter type. We used general linear mixed models with mass loss and HFA as respective response variables, litter incubation history and litter type as fixed factors and site (1|site) as a random factor. We were not able to perform one full model for this experiment, because as a result of logistic constraints we did not include all full-factorial reciprocal transplants in this experiment (see Figure 1 for set up). For all analysis we used post-hoc Tukey’s HSD tests to test which treatments differed from each other. We explored for a normal distribution of residuals using Q-Q plots and a Shapiro–Wilks test and homogeneity of variances using a Levene’s test. All data were analysed in R version 3.6 (R Development Core Team, 2013) using the lme4 (Bates & Maechler, 2009) and lmerTest package (Kuznetsova et al., 2017) package.

3 | RESULTS

3.1 | Soil and litter properties

Soil and litter chemical properties differed between plant species (Table 1). Soils originating from grasses had higher pH ($F_{5,30} = 40.13$, $p < 0.001$) and phosphate availability ($F_{5,30} = 8.24$, $p < 0.001$), while soil organic matter content ($F_{5,30} = 10.35$, $p < 0.001$), moisture ($F_{5,30} = 8.21$, $p < 0.001$), total carbon (C; $F_{5,30} = 7.32$, $p < 0.001$), total nitrogen (N; $F_{5,30} = 3.04$, $p = 0.025$) and the C:N ratio ($F_{5,30} = 5.88$, $p < 0.001$) were lower. Mineral nitrogen availability was not significantly different between soil types ($F_{5,30} = 2.53$, $p = 0.050$).

Litter C ($F_{5,24} = 2.624.1$, $p < 0.001$) and lignin content ($F_{5,23} = 7.32$, $p < 0.001$) were generally higher in tree than grass litters, while litter N ($F_{5,24} = 238.0$, $p < 0.001$) and P content ($F_{5,24} = 1.115.0$, $p < 0.001$) were higher in grass than tree litters. Litter C:N ($F_{5,24} = 290.8$, $p < 0.001$), C:P ($F_{5,24} = 578.1$, $p < 0.001$) and lignin:N ratios ($F_{5,23} = 703.1$, $p < 0.001$) were higher in tree than grass litters, and the litter N:P ratio was higher in Betula and Fagus litter than in the other litter types ($F_{5,24} = 253.3$, $p < 0.001$).

(i) Reciprocal transplant experiment

3.2 | Microbial community composition

Initial fungal ($R^2 = 0.25$, $p < 0.001$) and bacterial ($R^2 = 0.20$, $p < 0.001$) composition differed between soil sources (Figure 1a,b). Most pronounced differences were found between soils sourced from grasses versus soils sourced from trees (Figure 1a,b). For fungal communities, repeated litter incubation resulted in shifts in composition over experimental periods (Figure 2) and shifts were both affected by the litter species (Figures S1 and S2) and the litter functional group (Figure S1 and S2). Fungal community composition generally converged by plant functional group, with shifts being most pronounced along the second NMDS axis (Figure 2; Figure S2). Here, communities in tree soils incubated with grass litters converged towards communities in soils sourced from grass soils incubated with grass litter and vice versa (Figure 2). The shifts in fungal composition over experimental periods were stronger for tree soils incubated with grass
TABLE 1 Initial soil and litter chemical properties. Data represent mean values ±SE for each of the plant species. Data were tested using a general linear model with plant species as a fixed factor. For each soil or litter variable, different letters indicate significant differences between litter types as tested in a Tukey’s HSD post-hoc analyses (p < 0.05).

| Soil properties | Betula | Fagus | Quercus | Agrostis | Festuca | Holcus |
|----------------|-------|-------|---------|----------|---------|--------|
| pH             | 2.98 ± 0.08 b | 2.96 ± 0.12 b | 3.43 ± 0.26 b | 4.74 ± 0.11 a | 4.88 ± 0.10 a | 4.75 ± 0.13 a |
| Soil moisture (%) | 25.1 ± 2.8 a | 28.6 ± 4.3 a | 23.6 ± 2.3 ab | 13.7 ± 0.9 b | 14.1 ± 0.41 b | 13.6 ± 0.8 b |
| SOM (%)        | 14.1 ± 2.6 a | 16.4 ± 2.20 ab | 11.9 ± 1.5 ab | 5.2 ± 0.5 c | 6.1 ± 0.1 bc | 5.1 ± 0.4 c |
| Available N (mg/kg) | 10.8 ± 2.8 b | 13.8 ± 2.2 ab | 15.9 ± 5.3 b | 4.2 ± 0.6 b | 7.6 ± 1.0 ab | 8.2 ± 1.2 ab |
| Available P (mg/kg) | 6.3 ± 0.7 b | 8.4 ± 1.3 b | 35.2 ± 16.1 b | 53.0 ± 7.5 a | 60.6 ± 5.8 a | 53.2 ± 7.8 a |
| Total C (%)    | 13.1 ± 1.8 a | 15.3 ± 2.8 a | 11.2 ± 1.7 ab | 5.4 ± 1.0 b | 6.0 ± 0.5 b | 5.4 ± 0.6 b |
| Total N (%)    | 0.57 ± 0.08 | 0.72 ± 0.17 | 0.56 ± 0.09 | 0.32 ± 0.08 | 0.33 ± 0.03 | 0.33 ± 0.05 |
| C:N ratio      | 23.4 ± 0.5 a | 22.5 ± 1.2 ab | 20.4 ± 1.6 abc | 17.5 ± 1.3 c | 18.2 ± 0.8 bc | 16.9 ± 1.0 c |

| Litter properties | Betula | Fagus | Quercus | Agrostis | Festuca | Holcus |
|-------------------|-------|-------|---------|----------|---------|--------|
| Litter C (%)      | 52.0 ± 0.08 a | 48.7 ± 0.04 b | 479 ± 0.11 c | 44.6 ± 0.02 d | 44.7 ± 0.04 d | 44.3 ± 0.02 e |
| Litter N (%)      | 1.76 ± 0.03 a | 1.00 ± 0.01 d | 1.08 ± 0.01 d | 1.21 ± 0.01 c | 1.42 ± 0.02 b | 1.20 ± 0.01 c |
| Litter P (%)      | 0.06 ± <0.01 e | 0.07 ± <0.01 e | 0.16 ± <0.01 d | 0.19 ± <0.01 c | 0.20 ± <0.01 b | 0.28 ± <0.01 c |
| Litter lignin (%) | 24.22 ± 0.24 a | 20.52 ± 0.24 b | 18.59 ± 0.21 c | 8.75 ± 0.10 e | 10.47 ± 0.24 d | 8.55 ± 0.25 e |
| C:N ratio         | 29.5 ± 0.5 a | 48.6 ± 0.3 a | 44.4 ± 0.6 b | 36.9 ± 0.2 c | 31.4 ± 0.4 d | 36.9 ± 0.4 c |
| C:P ratio         | 934.6 ± 30.1 a | 741.4 ± 11.6 b | 306.5 ± 2.7 a | 233.9 ± 2.7 d | 221.8 ± 5.0 d | 158.4 ± 1.6 e |
| N:P ratio         | 31.77 ± 1.57 a | 15.27 ± 0.20 b | 6.90 ± 0.07 c | 6.35 ± 0.10 c | 7.07 ± 0.23 c | 4.30 ± 0.07 c |
| Lignin:N ratio    | 13.75 ± 0.19 c | 20.44 ± 0.23 a | 17.26 ± 0.35 b | 7.23 ± 0.11 d | 7.35 ± 0.14 d | 7.11 ± 0.17 d |

litter than for grass soils incubated with tree litter, as was shown by an interaction between sampling time and soil source (R² = 0.02, p < 0.001; Figure 2). Both after 3 and 9 months of litter incubation fungal community composition was still different between the original soil sources (Figure S1c,d,e,f) even though the effect of original soil source got smaller in time (3 months R² = 0.29 and 9 months R² = 0.23, for both p < 0.001).

For bacterial communities, shifts in composition induced by repeated litter incubations were less pronounced (Figures S3 and S4). Bacterial communities remained different between soil sources during all experimental periods (Figures S3 and S4), but we did not find general effects of litter species or functional groups on bacterial community composition after 3 and 9 months of litter incubation (Figures S3 and S4). However, there were individual combinations of soil sources and litter types that led to unique bacterial communities. For example, in soils with a history of Betula, incubation with grass litter slightly shifted the bacterial community composition towards the composition found in soils sourced from grasses (Figure S4, R² = 0.05, p < 0.05).

We investigated in more detail which fungal classes explained the convergence in community composition driven by litter incubation (Figure 3; Figure S5). We found that the relative abundances of fungal classes changed depending on the litter incubation (Figure 3). Sordariomycetes were strongly enriched by litter addition in general; their relative abundance increased from 20% in initial soils to 75% in soils incubated with litter. The increase in relative abundance in Sordariomycetes was stronger for grass than for tree litter incubations (F₁,₃₉₁ = 183.10, p < 0.001), particularly in soils originating from trees, as was indicated by an interaction between soil source and litter type (F₁,₃₉₁ = 35.49, p < 0.001; Figure 3; Figure S6). Grass litter increased the relative abundance of Pezizomycetes, but only in grass soils (litter type: F₁,₃₉₁ = 38.32, p < 0.001; soil source x litter type: F₁,₃₉₁ = 40.94, p < 0.001; Figure 3). The addition of tree litter resulted in a higher relative abundance of Tremellomycetes (F₁,₃₉₁ = 6.545, p < 0.001), Eurotiumycetes (F₁,₃₉₁ = 155.50, p < 0.001), Leotiomyctes (F₁,₃₉₁ = 105.42, p < 0.001) and Dothidiomyctes (F₁,₃₉₁ = 74.45, p < 0.001; Figure 3; Figures S7–S9) than the addition of grass litter. For Eurotiumycetes and Leotiomyctes the effect of tree litter addition was stronger in tree than in grass soils (F₁,₃₉₁ = 20.42, and F₁,₃₉₁ = 18.52, for both p < 0.001). For Eurotiumycetes this was more apparent after 9 than 3 months of litter incubation, which was indicated by the interaction between litter source and experimental period (F₁,₃₉₁ = 17.56, p < 0.001) and a three-way interaction between soil source, litter type and experiment period (F₁,₃₉₁ = 7.46, p = 0.007; Figure S8). For Leotiomyctes the effect of litter addition was stronger in tree soils, as was indicated by an interaction between soil source and litter type (F₁,₃₉₁ = 18.52, p < 0.001; Figure S9). The relative abundance of Mortiriellomycota was higher in tree than in grass soils, but was not affected by litter type (Figure 3; F₁,₄₄₉ = 213.45, p < 0.001).

Within each of the fungal classes, we found that changes in the relative abundance of certain families were associated with litter...
incubation type. For Sordariomycetes the addition of grass litter favoured Chaetomium in both tree and grass soils (arcsin square root transformed relative abundance: litter type: $F_{1,391} = 110.81$, $p < 0.001$; interaction soil source × litter type: $F_{1,391} = 19.75$, $p < 0.001$). Furthermore, grass litter increased the relative abundance of Lasiosphaeriaceae, but only in grass soils (interaction soil source × litter type: $F_{1,391} = 55.81$, $p < 0.001$). Both these families are known to contain many saprotrophs (Figure S6). There were relatively more Trichoderma in tree soils especially after 3 months of decomposition (soil source: $F_{1,391} = 94.21$, $p < 0.001$; interaction soil source × experimental period: $F_{1,391} = 26.32$, $p < 0.001$) and grass litter promoted its abundance even further (interaction soil source × litter type: $F_{1,391} = 34.22$, $p < 0.001$). The most abundant Tremellomycetes in initial soils were Solicoccozyma, while adding litter increased the relative abundance of unknown Tremellomycetes (Figure S7). For Leotiomycetes communities, tree soils had higher relative abundance of Leotiomycetes than grass soils ($F_{1,391} = 128.71$, $p < 0.001$; Figure S8). In grass soils, Leotiomycetes communities were very simple and dominated by Helotiales. In tree soils, adding grass litter reduced diversity (Figure S8). The addition of tree litter in tree soils increased the relative abundances of Glutinomyces (litter type: $F_{1,391} = 45.18$, $p < 0.001$, litter type × soil source $F_{1,391} = 44.13$, $p < 0.001$), Hyaloscypha (specifically for Betula soils: soil source $F_{5,327} = 10.92$, $p < 0.001$), unknown Leotiomycetes (litter type: $F_{1,391} = 862.35$, $p < 0.001$, litter type × soil source $F_{1,391} = 42.53$, $p < 0.001$) and Pezoloma ericae (litter type: $F_{1,391} = 8.95$, $p < 0.005$, no interactions; Figure S8). The initial Dothideomycetes community contained ectomycorrhizal genera (Cenococcum), particularly in tree soils, but they disappeared during the experiment (i.e. they were still detected at 3 months, not at 9 months; effect of time $F_{1,391} = 58.13$, $p < 0.001$, soil source $F_{1,391} = 177.42$, $p < 0.001$, interaction soil source × time $F_{1,391} = 49.82$, $p < 0.001$, Figure S9). The Dothideomycetes community in grass soils was more diverse than in tree soils (Figure S10). Adding tree litter increased the relative abundance of total Dothideomycetes, with Leptosphaeria (litter type × soil source $F_{1,391} = 119.42$, $p < 0.001$) being promoted by tree litter in grass soils and Venturiales being promoted in tree soils (litter type × soil source $F_{1,391} = 13.22$, $p < 0.005$; Figure 2; Figure S9). The increase in the relative abundance of Eurotiomycetes over time in soils incubated with tree litter could be attributed to increase in relative abundance of Penicilli (litter type $F_{1,391} = 157.76$, $p < 0.001$) and Trichocomaceae species (litter type $F_{1,391} = 56.67$, $p < 0.001$; Figure S10), both classes known as good competitors and saprotrophs.

**FIGURE 2** Shifts in fungal community structure over time for (a) NMDS axis 1 and (b) NMDS axis 2. Lines from the same line type (i.e. solid, dashes etc.) represent fungal community composition in soils from the same source (indicated by the species names on the y-axis). Line colours represent different litter types, with the three brown shades being tree litter types and the three green shades being grass litter types. The mean shifts in fungal community composition (±SE) across litter types belonging to the same functional group (trees vs. grasses) are indicated by the thick lines. The thick brown lines represent mean NMDS score for tree litter incubations and the thick green lines mean NMDS score for grass litter incubations. In grass soils, Leotiomycetes communities were very simple and dominated by Helotiales. In tree soils, adding grass litter promoted its abundance even further (interaction soil source × litter type: $R^2 = 0.02$ ***). Furthermore, grass litter increased the relative abundance of unknown Tremellomycetes in initial soils were Solicoccozyma, while adding litter type × soil source: $F_{1,391} = 45.18$, $p < 0.001$, litter type × soil source: $F_{1,391} = 44.13$, $p < 0.001$).
FIGURE 3  Boxplots showing the relative abundance of major fungal classes (facets) for the different soil sources and litter incubation treatments. Relative abundances are shown at the level of plant functional groups: soil sources are divided in tree and grass soils (x-axis) and litter types are divided in tree and grass litters (different boxes)
3.3 | Litter mass loss and home-field advantage

Litter mass loss was affected by two-way interactions between soil source and litter type ($F_{25,568} = 1.77, p = 0.012$), between soil source and experimental period ($F_{5,568} = 6.00, p < 0.001$) and between litter type and experimental period ($F_{5,568} = 3.47, p = 0.004$). The interaction between soil source and litter type indicated that differences in mass loss between litter types depended on soil source. For example, mass loss did not differ between *Betula* and *Quercus* litter types for most soil sources, but in *Agrostis* and *Festuca* soils *Betula* litter decomposed faster than *Quercus* litter. Similarly, mass loss was similar between *Agrostis* and *Festuca* litters in most soil sources, but in *Agrostis* and *Holcus* soils *Agrostis* litter lost more mass than *Festuca* litter (Figure 4). The interactions involving experimental period showed that litter mass loss increased over the experimental periods for some litter types and soil sources (e.g. mass loss of *Betula* litter often increased with time), while it decreased or did not change for other litter types and soil sources (e.g. mass loss *Fagus* soils generally decreased with time; Figure 5). In addition, we found a main effect of soil source ($F_{5,568} = 3.33, p = 0.006$) and litter type ($F_{5,568} = 84.04, p < 0.001$) with *Fagus* soils and litters generally having the lowest mass loss and *Holcus* soils and litters generally having the highest mass loss. Also, there was a main effect of experimental period ($F_{1,37} = 6.88, p = 0.013$), with mass loss being lowest in the second experimental period and highest in the third experimental period (Figure 4). The three-way interaction between soil source, litter type and experimental period was not significant ($F_{25,568} = 0.92, p = 0.576$).

Overall, HFA was positive across all experimental periods (period 1: $t = 2.35, p = 0.025, df = 35$; period 2: $t = 3.32, p = 0.002, df = 35$; period 3: $t = 3.34, p = 0.002, df = 35$; Figure 5), but for most of the individual species HFA did not differ significantly from zero (t tests, $p > 0.05$; Figure 5). We only found significant HFA effects for *Fagus* in period 2 ($t = 3.62, p = 0.015, df = 5$) and 3 ($t = 3.67, p = 0.014, df = 5$), and for *Holcus* in period 2 ($t = 3.39, p = 0.019, df = 5$) and 3 ($t = 3.31, p = 0.021; df = 5$; Figure 5). HFA effects were not affected by plant species ($F_{2,77} = 0.98, p = 0.437$; experimental period ($F_{1,5} < 0.01, p = 0.995$) or their interaction ($F_{2,77} = 0.73, p = 0.723$), indicating that HFA effects did not significantly change over time. When we compared HFA for pairs of litter transplants (Ayres et al. 2009) for the first experimental period, we found that transplants occurring between grass and tree soils experienced higher HFA than those occurring between two grass soils ($F_{2,77} = 7.11, p = 0.001$; Figure S11), indicating that home-field effects occurred mostly at the level of plant functional groups.

We found a relationship between fungal community structure and litter mass loss after 3 months of litter incubation (ENVFIT: $R^2 = 0.32, p = 0.041$), but not anymore after 9 months (ENVFIT: $R^2 = 0.01, p = 0.358$), while both the NMDS1 and NMDS2 axes were correlated with mass loss in both periods (Pearson: NMDS1: $r = 0.358$; experimental period ($F_{1,5} < 0.01, p = 0.995$) or their interaction ($F_{2,77} = 0.73, p = 0.723$), indicating that HFA effects did not significantly change over time. When we compared HFA for pairs of litter transplants (Ayres et al. 2009) for the first experimental period, we found that transplants occurring between grass and tree soils experienced higher HFA than those occurring between two grass soils ($F_{2,77} = 7.11, p = 0.001$; Figure S11), indicating that home-field effects occurred mostly at the level of plant functional groups.

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between field history and current litter type (mass loss of
structure at 3 and 9 months respectively (Figure S12). Neither
the bacterial community structure (ENVI-FIT, 3 months: $R^2 = 0.19$,
$p = 0.58$, 9 months: $R^2 = 0.40$, $p = 0.06$) nor the NMDS axes for
the bacterial community were related to litter mass loss (data not
shown). However, there was a relationship between bacterial and
fungal community structure (both NMDS1; Pearson: $R^2 = 0.45$ at
3 months; $R^2 = 0.51$ at 9 months; both $p < 0.001$).

(ii) Litter decomposition feedback experiment

In the litter incubation experiment all soil microbiomes were in-
cubated with the original litter type (i.e. the litter type that matches
the soil history) or with the incubation litter type (i.e. the litter type
that was used during repeated incubations in experiment (i)). First,
current mass loss of the original litter type was not affected by
soil microbiomes originating from mesocosms with different litter
incubation histories ($F_{5,174} = 0.99$, $p = 0.424$). Mass loss differed,
however, between the litter types: for the original litter types grass
litters generally decomposed slower than tree litters (Figure S13;
$F_{5,174} = 9.30$, $p < 0.001$). There was no interaction between litter
incubation history and current litter type ($F_{5,174} = 0.45$, $p = 0.989$).
In contrast, current mass loss of the incubation litter type was still
affected by field history ($F_{5,175} = 14.85$, $p < 0.001$). Generally, these
litters decomposed faster with a soil microbiome originating from
grassland than from tree soils (Figure S14). In addition, for the incu-
bation litter types grass litters decomposed slower than tree litters
(Figure S14; $F_{5,175} = 61.16$, $p < 0.001$). There was no interaction be-
tween field history and current litter type ($F_{5,175} = 0.79$, $p = 0.747$).

Home-field advantage effects for the original litter type were
not different from zero ($t = -0.35$, $df = 35$, $p = 0.729$) and did not
differ between litter incubation history ($F_{5,30} = 0.28$, $p = 0.921$;
Figure S15a). Home-field advantage effects for the incubation litter
type did not differ from zero ($t = 0.34$, $df = 35$, $p = 0.734$) and did not
differ between field histories ($F_{5,30} = 0.18$, $p = 0.969$; Figure S15b).

4 | DISCUSSION

Litter types are often associated with specialised microbiomes
that accelerate the breakdown of that litter, known as HFA (Austin
et al., 2014; Palozzi & Lindo, 2018). In this study, we tested how and
how fast soil microbial community composition changed in response
to plant litter inputs, and whether community shifts led to the de-
velopment of HFA effects. We found that repeated litter additions
resulted in directional shifts in fungal composition. In addition, we
could relate the fungal decomposer community composition to litter
mass loss across the experiment. However, repeated litter additions
and shifts in microbial community composition did not result in the
development of HFA effects for the added litter type, suggesting
that observed changes in microbial communities might be still too
small to cause microbial specialisation.

4.1 | Directional shifts in soil microbial community
composition

In line with our first hypothesis that repeated litter inputs would
result in directional shifts in the composition of the soil microbio-
me, we found that fungal community composition converged by
the litter functional group type. The addition of grass litter to tree
soils resulted in fungal communities converging to those found in
graz soils incubated with grass litter and vice versa. This is po-
tentially driven by differences in chemical composition between
litter types (Fanin et al., 2014; Schneider et al., 2012), with plant
functional groups often being important explaining differences in
chemical traits and litter decomposability (Cornelissen, 1996; Díaz
et al., 2004). In contrast to our findings for fungal communities, we
did not find strong shifts in the community composition of bacte-
ria. That effects were particularly apparent for fungal communities
may not be surprising given that fungi play a key role in the
breakdown of more recalcitrant organic compounds (van der Wal
et al., 2013). However, earlier work also showed a turnover in bac-
terial functioning and community composition during decomposi-
tion (Heijboer et al., 2018; Herzog et al., 2019). In our study we
did not find shifts in bacterial community composition in response
to litter inputs for most litter types, except in Betula soils with
glass litter addition. It might be that fungi are more specialised to
certain litter types, while bacteria use simpler carbon compounds
from litter and degradation products of fungi and thus respond less
strongly to litter inputs as such. Yet, we expected that some bacte-
rna found in later stages of decomposition, such as Actinobacteria
and Acidobacteria, would have responded to litter inputs (Heijboer
et al., 2018; Herzog et al., 2019).

Our findings are in line with previous work showing that the
addition of organic amendments in agricultural soils can affect
fungal biomass and community compositions in soils (Clocchiatti
et al., 2020; Moll et al., 2015; Reardon & Wuest, 2016) and that leaf
litters (Asplund et al., 2018; Keiser et al., 2011; Lin et al., 2019; Veen,
Snoek, et al., 2019) and decomposing wood (Purahong et al., 2019)
are associated with unique microbiomes on their surface. We now
progress on this understanding and show that repeated additions of
a certain organic input can result in the development of litter-specific
soil fungal communities (Fanin et al., 2014; McTee et al., 2017). In
our approach we used sterilised litter in order to prevent the intro-
duction of ‘home’ decomposers from the phyllosphere with the litter
itself and focused on how interactions between soil and litter
addition affected litter mass loss and the microbes present in the soil.
However, litter-specific microbes originating from the phyllosphere
may also play a role in driving litter breakdown and home-field ef-
facts (Austin et al., 2014; Lin et al., 2015). It will be essential that
future work explicitly considers how litter-specific phyllosphere communities interact with soil communities to impact decomposition. This will aid our understanding of how litter inputs can steer the soil microbiome, which may provide opportunities for creating legacy effects in soils that may help to optimise carbon and nutrient cycling and thereby sustainable agriculture (Clocchiatti et al., 2020; Mariotte et al., 2018; Veen, Wubs, et al., 2019).

The shifts in fungal community composition in response to litter of different plant functional groups were driven by changes in the relative abundance of certain fungal taxa. The key fungi in grass soils were initially Sordariomycetes and especially Chatomycotaceae and Podospora, while in tree soils Trichoderma and Chaetomycotaceae were the main fungi present. We showed that adding grass litter shifted the fungal community towards Sordariomycetes and Pezizomycetes, while adding tree litter enriched the ascomycete classes Dothideomycetes, Eurotiomycetes, Leotiomycetes and the basidiomycete taxa Tremellomycetes. Most of the taxa that were enriched by the litter addition are known saprotrophs and can decompose both lignin and cellulose. However, our finding that different litter functional groups stimulated different fungal taxa suggests that the fungi do have preference for certain litter types, probably because the capacity to degrade specific organic compounds varies between taxa (Schneider et al., 2012; Song et al., 2010; van der Wal et al., 2013). Although, it still challenging to predict exact functions for all functional groups that were enriched in our study (Osono, 2020) it is known that for example the Basidiomycota Trichosporonaceae, which belongs to the Tremellomycetes and was enriched by tree litter, can decompose hemicellulose and assimilate phenolic compounds, but is not able to degrade lignin. In addition, Xylariales were enriched in grass soils incubated with tree litters and are known for lignolytic activity (Osono, 2020). The Chaetomiaceae, enriched by grass litter, are able to degrade lignin, but may also increase in abundance when enough available nitrogen is present, for example in high-quality litter (Clocchiatti et al., 2020). Our findings are in line with earlier studies showing that the Ascomycota, which are early colonisers of litter and the main decomposers in our study, are litter type specific (Štursová et al., 2020).

For many of the fungal classes and genera we found that effects of litter addition on their relative abundance were dependent on the soil source. This impact of soil source suggests strong historical contingencies (Keiser et al., 2011), where current microbial community composition is still affected by the environment where the community is sourced from (Asplund et al., 2018). Although experimental litter inputs were able to shift community composition, these soil histories appeared important for shaping microbial communities, and remained visible during the entire experiment. In addition, the effects of soil source had a strong impact on the fungal species being enriched, for example, species of Penicillium were enriched only in tree soils with tree litter. This finding suggests that priority effects played a key role in shaping the decomposer communities (Fukami, 2015; Fukami et al., 2005; van der Wal et al., 2015; Veen, Snoek, et al., 2019). The impact of historical contingencies and priority effects might become less pronounced over time (Clocchiatti et al., 2020; Hannula et al., 2019; Keiser et al., 2011). In contrast, litter type may become more important, which was confirmed by our finding that the effect of litter type driving fungal community composition became stronger over the experiment, leading to convergence towards a new litter-specific community. Finally, some fungal species were found under ‘home’ combinations of soil source and litter type (see supplement), indicating specific interactions between fungi and litter types depending on the soil source (Lin et al., 2019; Veen, Snoek, et al., 2019).

4.2 Litter mass and home-field advantage

In contrast with our second hypothesis that directional shifts in microbial community composition would affect litter decomposition, we did not find changes over time in litter breakdown and HFA effects. This is contrasting to earlier work on the litter microbiome, showing that repeated litter incubations affected microbial community composition on leaf litter and also resulted in accelerated mass loss over time (Keiser et al., 2011). It could be that directional functional shifts mediated by the soil microbiome may develop over longer periods of time or require stronger changes in microbial community composition. Alternatively, shifts in community composition may not directly lead to changes in microbial functioning, because there is a substantial functional redundancy in soil microorganisms, particularly for general functions like litter breakdown (Allison & Martiny, 2008; Louca et al., 2018). However, earlier work showed that different microbial communities can have a distinct ability to degrade certain plant litter types (Keiser et al., 2014; Strickland et al., 2009), which is also at the basis of the HFA hypothesis (Austin et al., 2014; Palozzi & Lindo, 2018). Moreover, recent studies found relationships between microbial community composition and the rate of litter decomposition (Glassman et al., 2018; Lin et al., 2019; Purahong et al., 2019; Veen, Snoek, et al., 2019). Also, even though litter breakdown was not affected by repeated litter inputs, other ecosystem functions such as disease suppression, may be enhanced (Clocchiatti et al., 2020).

Our finding that repeated litter addition and associated shifts in soil fungal community composition did not lead to changes in process rates, makes it challenging to use litter to steer functioning of microbial communities. It might be that more pronounced shifts in microbial communities, for example stronger enrichment of decomposers of recalcitrant components, for example, Basidiomycetes, would impact functioning. To assess whether and how such shifts can be achieved by repeated litter inputs and can be used for soil management, longer term and more detailed measurements on microbial functioning are required in future research. It will then be essential to use a functional gene approach or 13C-labelled substrates (Costa et al., 2020; Hannula et al., 2017; Hannula & Van Veen, 2016; Štursová et al., 2012) to trace how microbial communities process carbon originating from different litter types.

In contrast with our second and third hypotheses, we did not find that home-field effects decreased over time for the original
litter input, or developed for the new litter input, indicating that repeated litter additions did not change the affinity of the microbiome for the received input. Instead, our findings revealed that there are long-lasting legacy effects of the field history on litter breakdown, as the soil origin was still affecting litter mass loss after three 3-month periods of the litter incubation treatment. This finding is in line with earlier research and suggests strong historical contingencies for litter breakdown (Asplund et al., 2018; Keiser et al., 2011). This contrasts ideas on microbial similarity proposing that microbial functioning is strongly driven by current environmental conditions as a result of redundancy (Allison & Martiny, 2008; Louca et al., 2018). Although, home-field effects did not change over time, we found that home-field effects were generally positive for transplants occurring between trees and grasses, in line with earlier work (Freschet et al., 2012; Veen et al., 2015). Our result supports the idea that specialised microorganisms not only accelerate the breakdown of litter types from the plant species they are associated with, but also of other litter types that have similar chemical properties (Freschet et al., 2012). This idea is also supported by our finding that litter addition results in directional shifts in the soil microbiome at the level of plant functional groups.

5 | CONCLUSIONS

We conclude that repeated litter incubations can steer microbial community composition, particularly of fungi. However, this did not lead to shifts in decomposition processes at least within the time frame of our study. Future research should disentangle further how repeated addition of organic inputs can drive microbial specialisation in the longer term, because this can be used to optimise carbon and nutrient cycling and thereby aid sustainable soil management (Clochchiatti et al., 2020; Mariotte et al., 2018; Veen, Wubs, et al., 2019).

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AUTHORS’ CONTRIBUTIONS

G.F.V. conceived and designed the experiment; G.F.V., F.C.t.H. and C.W. carried out the experiment; G.F.V. and S.E.H. analysed the data; G.F.V. wrote the manuscript with the contribution of all authors. All authors approved the final version of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Mass loss and environmental data belonging to this article have been archived in Dryad Digital Repository https://doi.org/10.5061/dryad.jwstqj8d (Veen et al., 2021). Sequence data have been submitted to the European Nucleotide Archive (accession number: PRJEB38778; study name: ena-STUDY-NIOO-KNAW-09-06-2020-10:04:43:840-281).

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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