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The contributions of soil biota to litter mass loss and home-field advantage in temperate forests

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Abstract

Background Soil biotic communities play an important ecological role in driving the litter decomposition, and moreover the home-field advantage (HFA). However, whether and how these communities with different body sizes regulate litter mass loss and HFA is still unclear.

Methods We constructed a reciprocal transplantation microcosm decomposition experiment with the litter species and corresponding soil collected from three tree species distributed along an altitude gradient in Changbai Mountain in China (*Corylus mandshurica* Maxim. ex Rupr. at 700 m, *Fraxinus mandshurica* Rupr. at 1260 m, and *Betula ermanii* Cham. at 1800 m), respectively. We obtained a series of soil biotic communities with different body sizes through filtering soil solution with sieves ranging from 11 µm to 2 mm mesh. Microcosms were then inoculated with these community size fractions.

Results Biotic community size fractions positively influenced the litter mass loss, while the contributions of soil biotic groups to litter mass loss were negatively related to their body size. Compared with mesofauna and microfauna, soil microorganisms contributed more to litter mass loss. The contributions of soil biotic groups to HFA were influenced by the interaction between biotic body size and litter species. Moreover, we found close relationships between litter mass loss, HFA and litter quality in the initial stage of decomposition, while community size fractions contributed directly to litter mass loss in the relatively later stage.

Conclusion Our findings improve our understanding to the ecological role of different soil biotic communities in litter decomposition. It's crucial for accurately predicting the nutrient cycling in forest ecosystem under climate changes in the future.

Keywords Home-field advantage, Decomposer community, Body size, Reciprocal translocation, Decomposition stage

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Introduction

Litter decomposition serves as a fundamental biogeochemical process governing carbon cycling, nutrient mineralization, and soil organic matter formation in terrestrial ecosystems (Veen et al. 2015; Fanin et al. 2016). At a global scale, approximately 70% of the variations in litter decomposition rate can be explained by abiotic factors (e.g., temperature and moisture) and substrate quality metrics (Ayres et al. 2009; Fenoy et al. 2016). Notably, an increasing body of evidence shows that a significant proportion of the unexplained variations is linked to home-field advantage (HFA), which is attributed to the interactions between decomposers and local litter that decomposer communities can efficiently promote the decomposition of litter they often encounter (Ayres et al. 2009; Austin et al. 2014). This effect indicates that litter derived from its original habitat (home environment) is often decomposed more quickly than that in other habitats (away environment), with an average decomposition rate that is 7.5% faster across multiple ecosystem types (Veen et al. 2015). HFA provides a crucial mechanism from the perspective of the local adaptation of biotic communities, enabling us to understand the additional variations in litter decomposition. However, although the importance of microbial communities has been widely confirmed (Bardgett et al. 2014; Li et al. 2023a, b), uncertainties still remain regarding the contribution of decomposer communities with different body sizes to litter mass loss and HFA during the decomposition process (Milcu and Manning 2011; Lin et al. 2019).

Different soil biotic communities affect litter decomposition through various pathways (Li et al. 2020). For instance, the complex organic macromolecules in litter can be degraded into soluble small molecules through extracellular enzymes secreted by microorganisms (Ma et al. 2022; Zhang et al. 2022; Zhang et al. 2025a, b). In particular, fungi are typically regarded as the primary drivers in decomposing recalcitrant litter (i.e., higher lignin content or carbon:nitrogen ratio) (Lin et al. 2019; Osburn et al. 2022). Moreover, microfauna (body width less than 0.1 mm) such as nematodes can directly or indirectly affect the decomposition processes by their predation on microorganisms (Qiu et al. 2019). In addition, mesofauna (body width ranges from 0.1 mm to 2 mm, e.g., collembola and mites) can directly crush litter, which increases the contact area between litter surface and soil microflora, further promoting litter decomposition (Frouz 2018). Based on this, differences in the functionality of soil biota with different body sizes to litter decomposition may shape the intensity of HFA (Li et al. 2020). For instance, Garcia-Palacios et al. (2016) indicated that lignin-degrading enzyme systems of fungal communities may have evolved to be more catalytically efficient against local plants, and the fragmentation behaviour of mesofauna may amplify this biochemical adaptation. Therefore, exploring the synergistic effects of multiple-trophic groups and their dynamic contributions to litter mass loss and HFA at different stages of litter decomposition is necessary for understanding the potential mechanisms underlying elemental cycling drove by biodiversity.

The litter decomposition stage may influence the contributions of soil biota with different body sizes to HFA and litter decomposition rate (Hu et al. 2021; Chen et al. 2025). For instance, meso- and microfauna prefer to gnaw the litter characterised by more labile compounds (e.g., small molecule carbohydrates) in the initial phases (Li et al. 2021), which destroys the waxy layer or tough outer skin of the litter, providing a vast space for the attachment of microorganisms, and making them easily access nutrient-rich interior tissues. In the later period of litter decomposition, specialized microbial groups (e.g., saprophytic fungi, Actinobacteria) play an important role when facing residual litter typically with higher lignin and lower nitrogen availability (Qi et al. 2023), notably because they embrace complex and efficient enzyme systems to decompose the recalcitrant structural polymers (Fierer 2017; Argiroff et al. 2019). However, it is still unclear whether and how the effects of different soil biotic groups on litter decomposition changed under complex trophic interactions, even across different decomposition stages.

In addition to the decomposition stage, environmental factors (e.g., litter substrate and surrounding soil) can also modulate the contributions of different soil biotic groups to HFA by acting as selective filters, leading to body size-mediated niche partitioning (Kraft et al. 2015; Delgado-Baquerizo et al. 2020). For example, for litter with high carbon:nitrogen ratio, microbial decomposers often work collaboratively (e.g., cross-feeding) with mesofauna to break through decomposition bottlenecks (Luai et al. 2019; Bai et al. 2024; Shah et al. 2024). Regarding higher quality litter, they are typically associated with less HFA as they can be degraded by generalist decomposers (Veen et al. 2018; Wang et al. 2020, 2023). Moreover, local soil conditions can also influence the soil biotic communities and therefore determine the species pool that colonizes plant litter, resulting in specific litter-organism relationships (Fierer and Jackson 2006; Veen et al. 2019). Although litter quality and soil resources are considered as critical factors driving HFA during litter decomposition (Austin et al. 2014; Veen et al. 2018), there is a lack of knowledge concerning whether and how they interact and influence the effects of different soil biotic groups on HFA and litter decomposition rate.

The vertical vegetation gradient in temperate forest along the altitude in Changbai Mountain induces differential litter input and varied soil biotic community structure (Kang et al. 2023; Liu et al. 2023a; Sun et al. 2023). This provides a unique natural field to investigate the ecological mechanisms underlying HFA and litter decomposition. Therefore, in this study, we applied a litter-soil transplantation experiment, and separated soil biotic communities corresponding to different body size classes through sieving. We aim to reveal the contributions of different soil biotic groups to litter decomposition rate and HFA during decomposition process (Wagg et al. 2014; Peng et al. 2023). Given the direct ecological role of microorganisms in litter decomposition (Nielsen 2019; Li et al. 2020), we firstly hypothesized that the contribution of microorganisms to litter decomposition rate was greater than that of micro- and mesofauna (H_1). Based on this, we further hypothesized that the contribution of microorganisms to HFA was greater than that of micro- and mesofauna (H_2). This is because the faster turnover rate and wider adaptability of microorganisms may allow them to have more specialized species and hence produce a stronger HFA effect (Wang et al. 2013; Fujii et al. 2018; Nielsen 2019). Moreover, considering that the more complex enzyme systems is necessary to degrade recalcitrant compounds while nutrients in litter substrate gradually decrease during the decomposition process (Fierer 2017), we further hypothesized that the effects of soil biotic groups on litter mass loss and HFA varied in different litter decomposition stages (H_3).

Materials and methods

Experimental design and sample collection

The study was conducted in September 2021 at Changbai Mountain located in Jilin Province in Northeast China (E128°28′, N42°24′). We selected three representative tree species and collected the corresponding fallen leaves and soil samples, including *Corylus mandshurica* Maxim. ex Rupr. (litter C) at 700 m elevation (soil C), *Fraxinus mandshurica* Rupr. (litter F) at 1260 m elevation (soil F) and *Betula ermanii* Cham. (litter B) at 1800 m elevation (soil B) (Fig. 1).

At each elevation, three replicate plots were set with intervals of 200 m, and litter and soil samples were collected from 5 individuals per tree species at each plot, respectively. For each plot, we collected litter samples from 15 randomly placed 20 cm × 20 cm quadrats, and then soil samples were collected from a depth of 0–10 cm. We subsequently mixed these litter and soil samples as a composite sample. There was a total of 9 litter samples (3 litter species × 3 replicate plots) and 9 soil samples (3 soil identities × 3 replicate plots) were collected. The litter samples were oven-dried at 60 °C for 48 h, and then cut into 1 cm pieces to form standardized materials for further study. The soil samples were sieved through a 1 cm mesh to remove stones and plant debris, and then divided into two parts. One subsample was sterilized using gamma irradiation (35 kGray, isotron, Harbin, China) for further microcosm decomposition experiment (Li et al. 2023a, b), and the other subsample was used for extracting soil biotic communities.

Microcosm decomposition experiment

To assess the impacts of distinct soil biota with different body sizes on litter decomposition and HFA, three community size fractions were extracted (Wagg et al. 2014).

1. 2 mm: 300 mL phosphate buffer (1 g/L KH_2PO_4, pH = 6.5) was added into 300 g soil (water:soil = 1:1, w/w) in a 1 L beaker. Soil solution was stirred for 30 s followed by rested for 30 s, which was then sieved through a 2 mm sieve, and the filtrate was stored in a beaker. We sealed the beaker with a polyethylene film, and subsequently rinsed the sieve with water before the next operation.

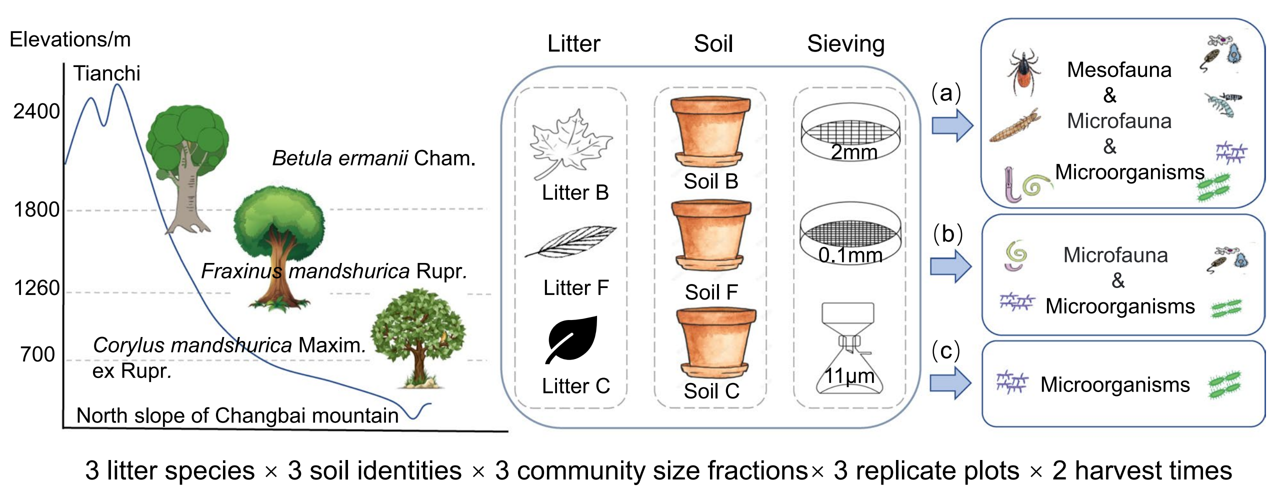

Fig. 1 Graphical illustration of the experimental design. A reciprocal litter transplantation microcosm experiment was performed with different litter species, soil identities and community size fractions derived from forests at altitude of 700 m, 1260 m, and 1800 m in Changbai Mountain. Litter—and soil—B, F and C represented that the litter and soil collected from *Betula ermanii*, *Fraxinus mandshurica* and *Corylus mandshurica*, respectively

2. 0.1 mm: The procedure as step 1 was followed. The soil filtrate that through the 2 mm sieve was sieved through a 0.1 mm sieve.
3. 11 μm: The procedure as step 2 was followed. The soil filtrate that through the 0.1 mm sieve was sieved through 11 μm filter paper (Whatman grade 1; 110 mm diameter) using a Brinell funnel.

After these operations, we assumed that the soil solution sieved through the 2 mm sieve contained mesofauna, microfauna, and microorganisms, and that sieved through the 0.1 mm sieve contained microfauna and microorganisms, while the soil solution sieved through the 11 μm sieve was regarded to mainly contain microorganisms (Li et al. 2020). We further verified that the diversity of soil biotic communities gradually decreased with reduced sieve size (Fig. S1).

We conducted a reciprocal transplantation design, in which litter C, litter F and litter B were decomposed in soil C, soil F, soil B across all size fractions of the soil biotic communities. Briefly, 600 g sterilized soil was placed in plastic containers (15 cm diameter, 9.5 cm height), which was then received 120 ml soil filtrate (Fig. S2). The microcosms were randomly placed, and the room temperature was maintained at 25 °C. One week later, a litter bag (12 cm × 8 cm, 2 mm mesh) filled with 2 g litter was buried in soil. The soil moisture content was maintained at 35% by adding sterilized water three times a week. Litter and soil samples were harvested after 3 and 5 months of decomposition. In total, we obtained 162 microcosms (3 litter species × 3 soil identities × 3 community size fractions × 3 replicate plots × 2 harvest times).

At each harvest time, each litter sample was gently brushed and then oven-dried at 60 °C for 48 h before weighing. Homogenized litter samples were ground with a ball mill for chemical analysis. Each soil sample was divided into three parts, one subsample was air-dried for physicochemical analysis, one subsample was stored at 4 °C for the analysis of soil enzyme activities, and another subsample was stored at −80 °C for extracting DNA of soil biotic communities.

Chemical analyses and DNA extraction and sequencing

Total carbon (TC) and total nitrogen (TN) of litter and soil were assessed using an automated elemental analyser (Elementar Analyser System Vario MACRO cube, Germany). The activity of two soil hydrolase enzymes related to C- and N-acquisition, i.e., β-1,4-glucosidase (BG) and β-1,4-N-acetylglucosaminidase (NAG), was measured following the methods of Tabatabai (1994) and Parham and Deng (2000). More details can be found in Appendix S1 in Supporting Information.

DNA of soil microorganisms and protozoans was extracted from 0.50 g fresh soil according to the standard protocols with the ALFA-SEQ Advanced Soil Kit (mCHIP, China), and nematode with the DNeasy Blood & Tissue Kit (QIAGEN, USA). The primer pairs 515F (5′-GTGCCAGCMGCCGCGG-3′)—907R (5′-CCGTCAATTCMTTTRAGTTT-3′) and ITS86F (5′-GTGAATCATCGAATCTTTGAA-3′)—ITS4R (5′-TCCTCCGCTTATTGATATGC-3′) were applied to amplify the V4 region of bacterial 16S rRNA and fungal ITS2 region, respectively. The primer pairs 3NDf (5′-GGCAAGTCTGGTGCCAG-3′)—C_1132rmod (5′-TCCGTCAATTYCTTTAAGT-3′) and Euk1391f (5′-GTACACACCGCCCGTC-3′)—EukBr (5′-TGATCCTTCTGCAGGTTCACCTA-3′) were used to amplify the 18S rRNA of eukaryote (Delgado-Baquerizo et al. 2020). PCR products were sequenced with the Illumina MiSeq PE300 platform. Bioinformatics processing was performed using VSEARCH (2.15.0), USEARCH (10.0.240) and UNOISE (7.0.1090). We further rarefied the sequences of each sample to a minimum number of sequences to reduce the interference of sequencing depth. The classification annotation of bacterial and fungal sequences was conducted with the RDP 18 and Unite 8.2 databases, respectively. We further classified fungi into different functional groups with the FUNGuild algorithm based on the 'Highly Probable' and 'Probable' confidence ranks (Nguyen et al. 2016). The classification annotation of nematode and protozoa was applied with the NT and PR2 databases, respectively. Specifically, protozoa were defined as all eukaryotic taxa in this study, except fungi, invertebrates (Metazoa), vascular plants (Streptophyta), algae and some slime moulds.

Data analysis

Litter mass loss (%) was determined with the Eq. (1):

$$Littermassloss(\%) = \frac{(littermass_0 - littermass_t)}{littermass_0} \times 100 \quad (1)$$

where *litter mass*$_0$ and *litter mass*$_t$ represented the litter weight at initial stage and harvest time *t*, respectively.

The additional decomposition at home (ADH) was calculated to determine the HFA in litter decomposition with the Eqs. (2)–(5) (Perez et al. 2013).

$$HDD_x = \left(D_{xX} - D_{yX}\right) + \left(D_{xX} - D_{zX}\right) \quad (2)$$

$$ADD_x = \left(D_{xY} - D_{yY}\right) + \left(D_{xZ} - D_{zZ}\right) \quad (3)$$

$$H = \left(HDD_x + HDD_y + HDD_z\right)/(n-1) \quad (4)$$

$$ADH_x = HDD_x - ADD_x - H \quad (5)$$

where D is the litter mass loss; HDD and ADD represented the differences in litter mass loss at home and away, respectively; H represented the total HFA for all litter species combined; n represents the number of litter species; and ADH_x was the additional decomposition at home for species x; x, y and z was the litter derived from the plant species x, y and z, respectively; X, Y and Z were the sites dominated by the species x, y and z, respectively.

The contributions of soil biota with different sizes to litter mass loss and HFA was calculated with Eqs. (6)–(8):

$$C_{\text{mesofauna}} = D_{2mm-0.1mm}/\text{Abs}(D_t) \times 100\% \quad (6)$$

$$C_{\text{microfauna}} = D_{0.1mm-11\mu m}/\text{Abs}(D_t) \times 100\% \quad (7)$$

$$C_{\text{microorganism}} = D_{11\mu m}/\text{Abs}(D_t) \times 100\% \quad (8)$$

where $C_{\text{mesofauna}}$, $C_{\text{microfauna}}$ and $C_{\text{microorganism}}$ represent the contributions of mesofauna, microfauna and microorganisms, respectively. $D_{\text{2mm-0.1 mm}}$ and $D_{\text{0.1 mm-11 μm}}$ represent the litter mass loss or HFA caused by mesofauna and microfauna, responding to the differences between 2 mm and 0.1 mm sieve treatments, and between 0.1 mm and 11 μm sieve treatments, respectively. $D_{\text{11μm}}$ represents the effects of microorganisms, and which was calculated as litter mass loss or HFA in the 11 μm sieve treatment. D_t represents the litter mass loss or HFA in the 2 mm sieve treatment.

Statistical analysis

Analysis of variance (ANOVA) was used to examine the effects of litter species, soil identity, community size fraction, harvest time and all possible interactions on the litter mass loss (%), and the effects of litter species, soil identity, biotic size class, harvest time and all possible interactions on the contributions of different soil biotic groups to litter mass loss. For HFA, the effects of community size fraction, litter species, harvest time, and their interactions were considered. For the contributions of different soil biotic groups to HFA, the effects of biotic size class, litter species, harvest time, and their interactions were considered. The normality of the model residuals was tested with the Shapiro–Wilk test, and the homogeneity of the variances was tested with the Bartlett test. Tukey's HSD test was used if the main effect was statistically significant ($P < 0.05$).

Dissimilarity of microbial and microfauna community was calculated using Bray–Curtis distance with the 'vegan' package in R. Linear regression analysis was used to determine the relationships between the community dissimilarity and HFA. Bootstrapped distributions of the slopes (K) describing the relationships between different soil biotic groups and HFA were visualized with the 'ggridges' package.

Structural equation models (SEM) were conducted using the 'lavaan' package to distinguish the drivers of HFA and litter decomposition rate at different decomposition stages (Rosseel 2012). A prior model was created with the soil source and community size fraction as exogenous variables, and the properties of litter, soil and enzyme activity were treated as endogenous variables, which were regarded as the influence mechanisms of decomposer communities to HFA and litter decomposition rate. Litter mass loss was considered as a response variable (Fig. S3). Specifically, in order to simplify our analyses and facilitating interpretations, the first axes were extracted to represent the variability in properties of litter, soil and enzyme activity based on the principal component analysis (PCA), respectively (Fig. S4). Model quality was assessed using the chi-squared value (χ^2), P value, comparative fit index (CFI), root mean square error of approximation (RMSEA) and goodness-of-fit (GFI) (Grace et al. 2010). Moreover, we also estimated the relationships between the litter mass loss, HFA and the properties of litter, soil and enzyme activity by Spearman correlation. All statistical analyses were performed in R version 4.1.2 (R Core Team 2018).

Results

The contributions of different soil biotic groups to litter mass loss

Litter mass loss (%) was affected by the two- and three-way interactions among litter species, soil identity and community size fractions (Table 1, Fig. 2), indicating that the effects of soil and litter sources on litter mass loss (%) differed among the three community size fractions. The mass loss (%) of litter C was greater than that of litter F and litter B in soil C for each soil community size fraction (Fig. 2a). The mass loss (%) of litter F was lower in the 2 mm and 11 μm community size fractions in soil F. In general, the litter mass loss (%) was positively related to the community size fraction (Fig. 2b). The contribution of soil biotic groups with different size classes to litter mass loss (%) was affected by the interaction among biotic size class, soil identity and litter species ($P < 0.001$) (Table 2; Fig. 3a). When litter decomposed in soil F, the contributions of different soil biotic groups significantly differed. Overall, the contributions of the community size fractions to litter mass loss (%) was negatively related to the organism sizes (Fig. 3b). Moreover, bacterial richness had positive effects on the mass loss (%) of litter B after both 3 and 5 months of decomposition, and the nematode and protozoa communities performed after 5 months of decomposition. There were positive correlations between

Table 1 Four-way ANOVA on the effects of community size fraction, soil identity, litter species and harvest time on litter mass loss

Variation	*Df*	*F* value	*Pr* (>*F*)
Community size fraction (C)	2	28.75	< 0.001
Soil identity (S)	2	41.52	< 0.001
Litter species (L)	2	4.78	0.01
Harvest time (H)	1	54.74	< 0.001
C×S	4	1.75	0.14
C×L	4	2.32	0.06
C×H	2	1.04	0.36
S×L	4	17.09	< 0.001
S×H	2	0.20	0.82
L×H	2	0.10	0.91
C×S×L	8	3.13	0.003
C×S×H	4	0.11	0.99
C×L×H	4	0.46	0.77
S×L×H	4	0.51	0.73
C×S×L×H	8	0.46	0.882

bacterial richness, fungal richness and the mass loss (%) of litter C (Fig. S5).

The contributions of different soil biotic groups to HFA

The HFA effect was affected mainly by litter species and its interaction with community size fraction ($P < 0.01$) (Table 3), indicating that the effects of different biotic groups on HFA differed across the forest environments. The HFA effects were lower for litter F at both two decomposition stages, in which the HFA effects of the 2 mm and 11 μm community size fraction treatments were negative (Fig. 4a). For litter C, the HFA effects were positive (Fig. 4a). The contributions of different soil biotic groups to HFA were affected mainly by biotic size class and its interaction with litter species ($P < 0.05$) (Table 4). The contribution of microfauna to HFA was lower than that of mesofauna and microorganisms in for litter F after 3 months of decomposition. The contribution of different soil biotic groups to HFA decreased with increasing body size for litter C, especially after 5 months of decomposition, while there was an opposite trend for litter B after 3 months (Fig. 4b). The correlation between the community dissimilarity of different soil biotic groups and the HFA varied across litter species, except for bacteria. After 3 and 5 months of decomposition, the community dissimilarity of nematode was positively related to the HFA for litter C ($P < 0.05$) (Fig. 5e, f).

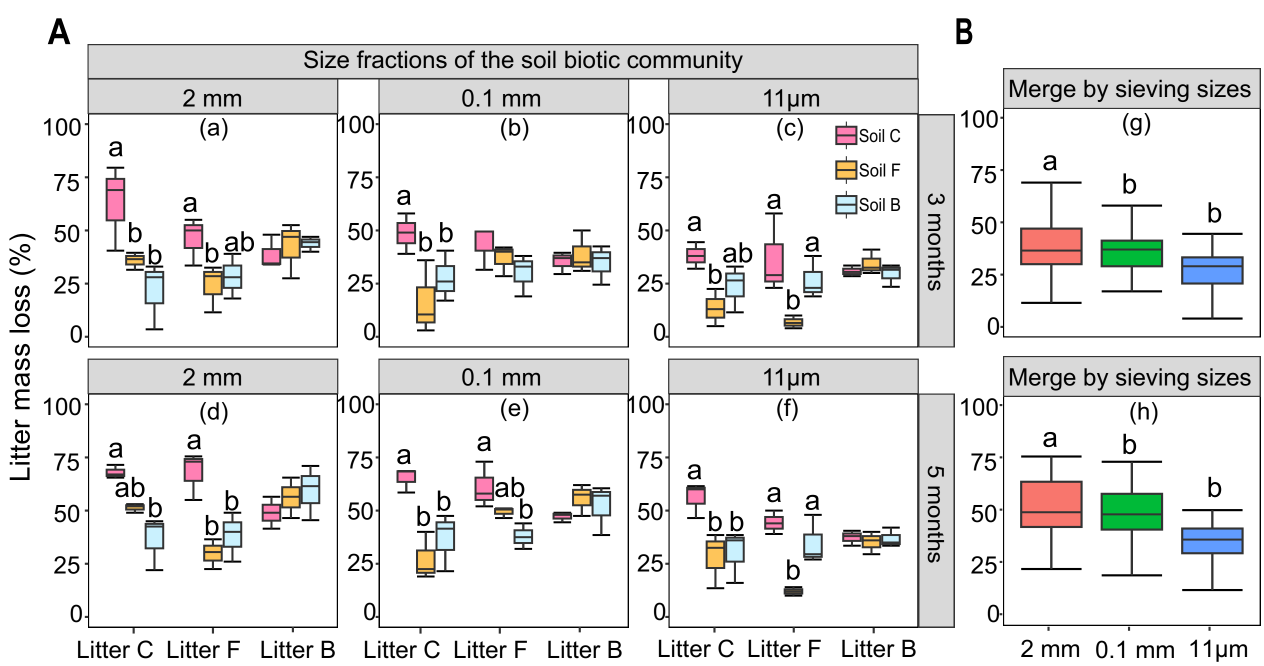

Fig. 2 Litter mass loss (%) of different combinations of litter species and soil identity across three community size fractions after 3 (a, b and c) and 5 (d, e and f) months of decomposition (**A**). Overall litter mass loss (%) across three community size fractions after 3 and 5 months of decomposition (**B**). Litter—and soil—B, F and C represented that the litter and soil collected from *Betula ermanii*, *Fraxinus mandshurica* and *Corylus mandshurica*, respectively. Different lowercase letters indicated significant differences at $P < 0.05$

Table 2 Four-way ANOVA on the effects of biotic size class, soil identity, litter species and harvest time on the contributions of different biotic groups to litter mass loss

Variation	*Df*	*F* value	*Pr* (> *F*)
Biotic size class (B)	2	41.50	< 0.001
Soil identity (S)	2	0.00	1.00
Litter species (L)	2	0.00	1.00
Harvest time (H)	1	0.00	1.00
B×S	4	4.31	< 0.01
B×L	4	3.05	< 0.05
B×H	2	0.97	0.38
S×L	4	0.00	1.00
S×H	2	0.00	1.00
L×H	2	0.00	1.00
B×S×L	8	6.73	< 0.001
B×S×H	4	1.25	0.30
B×L×H	4	0.86	0.49
S×L×H	4	0.00	1.00
B×S×L×H	8	1.49	0.17

Effects of community size fractions on litter decomposition at different decomposition stages

After 3 months of decomposition, community size fractions had indirect effects on the HFA and litter mass loss through influencing litter quality and soil enzyme activity (Fig. S6, Fig. 6a). In addition, we found that enzyme activity negatively influenced HFA, which was then promoted litter mass loss (Fig. 6a). In particular, positive correlations were found between litter mass loss, HFA and litter TC, litter TN and NAG activity, and moreover, litter mass loss was positively related to litter TC:TN (Fig. 6c). The BG: NAG was negatively related to litter mass loss and HFA, and BG activity was negatively correlated with HFA (Fig. 6c). After 5 months of decomposition, in addition to the indirect impact on litter mass loss through litter quality and enzyme activity (Fig. S7), community size fractions also had a direct effect (Fig. 6b). Moreover, we also found a direct effect of community size fractions on enzyme activity. We further showed significantly positive correlations between litter mass loss and NAG activity and BG: NAG (Fig. 6d).

Discussion

Contribution of soil biota with different body sizes to litter decomposition

We found that the litter decomposition rate increased with increased sieve size. This result was supported by the previous studies, and highlighted the importance of biodiversity in promoting litter decomposition (Wagg et al. 2014; Li et al. 2020). In line with our first hypothesis (H_1), we found that soil microbial community contributed the most to litter mass loss compared with other biotic groups. This may be attributed to their complex and efficient enzyme systems, which can breakdown

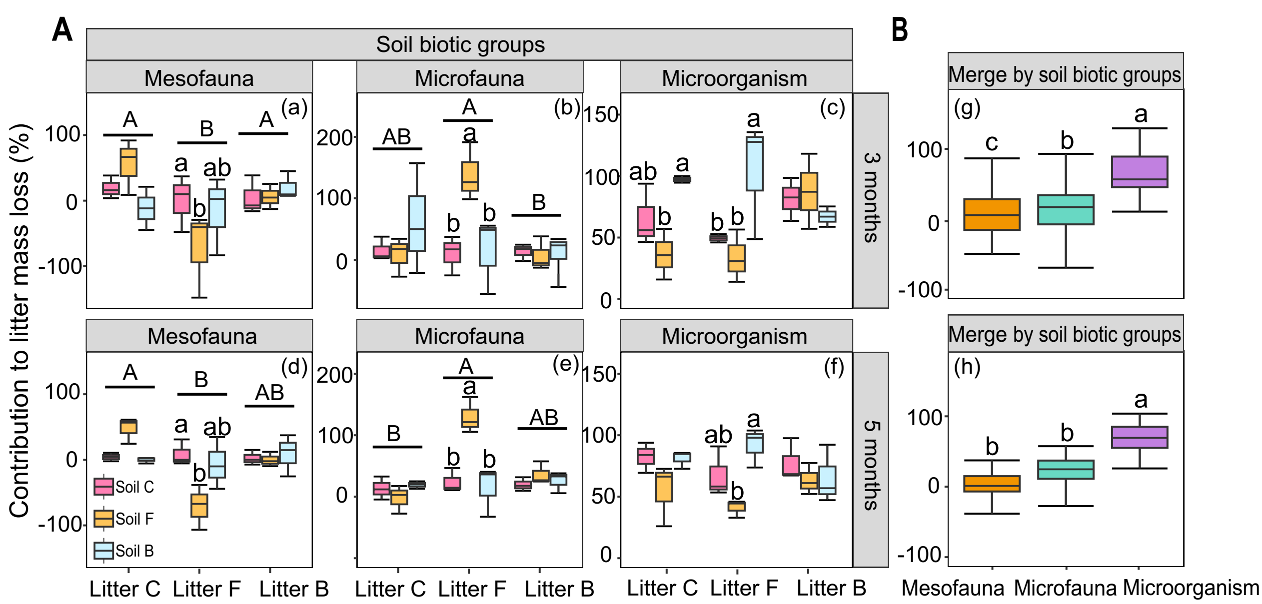

Fig. 3 The contributions of soil biotic groups with different sizes to litter mass loss (%) of different combinations of litter species and soil identity after 3 (a, b and c) and 5 (d, e and f) months of decomposition (**A**). Overall contributions of soil biotic groups with different sizes to litter mass loss (%) after 3 and 5 months of decomposition (**B**). Litter—and soil—B, F and C represented that the litter and soil collected from *Betula ermanii*, *Fraxinus mandshurica* and *Corylus mandshurica*, respectively. Different uppercase and lowercase letters indicated significant differences at *P* < 0.05

Table 3 Three-way ANOVA on the effects of community size fraction, litter species and harvest time on the home-field advantage (HFA)

Variation	*Df*	*F* value	*Pr* (> *F*)
Community size fraction (C)	2	2.76	0.076
Litter species (L)	2	32.18	< 0.001
Harvest time (H)	1	0.00	0.98
C × L	4	5.16	< 0.01
C × H	2	0.54	0.58
L × H	2	1.33	0.28
C × L × H	4	0.25	0.91

the recalcitrant carbon compounds (e.g., lignin) in litter, especially in the later decomposition stages (Zeng et al. 2018; Lin et al. 2019). Moreover, we also found that NAG activity was greater after 5 months of litter decomposition compared with 3 months, indicating that the greater decomposition ability was accompanied by higher nutrient requirements. Taken together, our results suggested that litter decomposition is a process mainly regulated by microbial communities (Elias et al. 2020).

The contribution of microfauna to litter mass loss was significantly lower than that of microorganisms, probably because microfauna predominantly influenced the decomposition rate indirectly by affecting microbial communities (Milcu and Manning 2011). Moreover, soil fauna preferred to high-quality litter, and the availability of labile components in litter substrate decreased during decomposition processes (Berg 2014; Peng et al. 2023; Zhang et al. 2023). Additionally, we found that the contribution of mesofauna to litter mass loss was the lowest. We speculated that the reason can be explained by their low abundance in soil, as a result, their contributions were more random and indirect (Wang et al. 2015; Song et al. 2021).

Contribution of soil biota with different body sizes to HFA

Contrary to our second hypothesis (H_2), we found that though microorganisms contributed the most to litter mass loss, it did not necessarily lead to a stronger HFA.

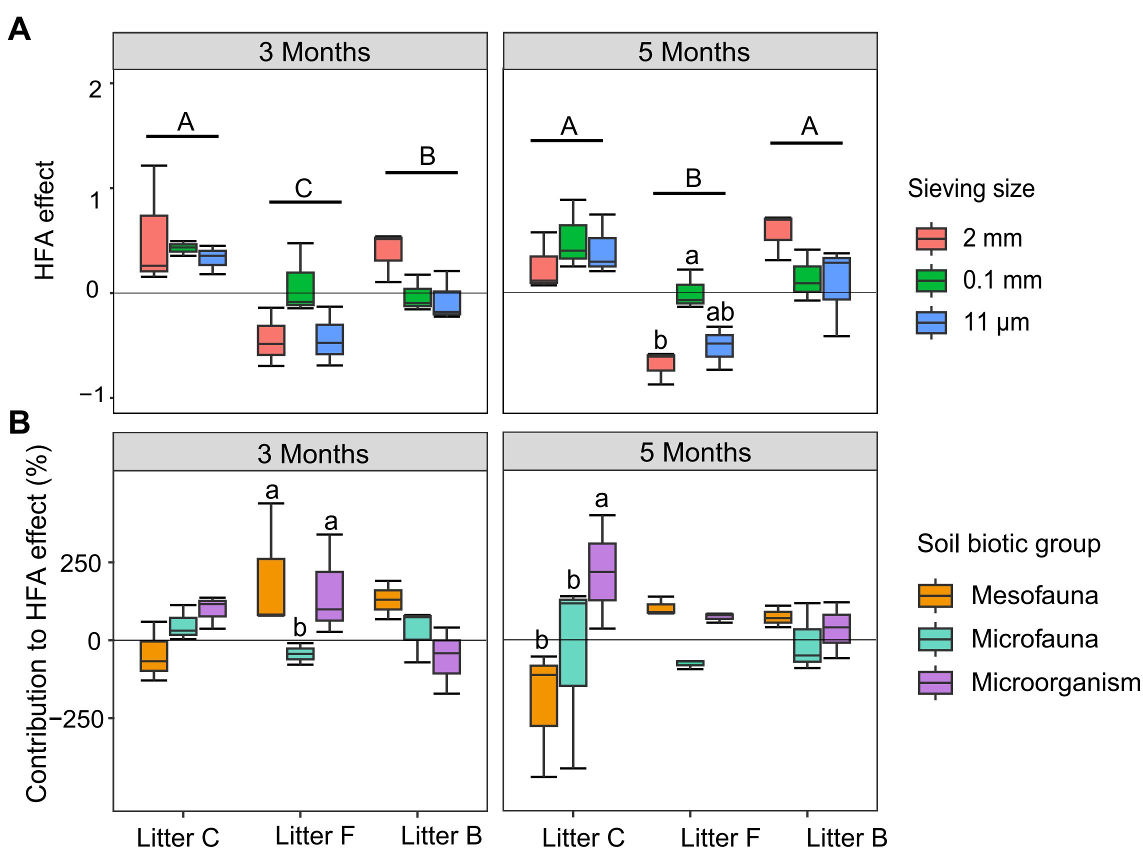

Fig. 4 The effects of different community size fractions on home-field advantage (HFA) across three litter species after 3 and 5 months of decomposition (**A**). The contributions of different soil biotic groups with different sizes to HFA across three litter species after 3 and 5 months of decomposition (**B**). Litter—B, F and C represented that the litter collected from *Betula ermanii*, *Fraxinus mandshurica* and *Corylus mandshurica*, respectively. Different uppercase and lowercase letters indicated significant differences at $P < 0.05$

Table 4 Three-way ANOVA on the effects of biotic size class, litter species and harvest time on the contribution of soil biota groups to home-field advantage (HFA)

Variation	*Df*	*F* value	*Pr* (> *F*)
Biotic size class (B)	4.32	2.76	< 0.05
Litter species (L)	2	0.00	1.00
Harvest time (H)	1	0.00	1.00
B × L	4	4.95	< 0.01
B × H	2	1.52	0.23
L × H	2	0.00	1.00
B × L × H	4	1.44	0.24

This finding reinforces the view that the contributions of different soil biotic groups HFA varied, and micro- and mesofauna can also regulate the litter decomposition processes by promoting the HFA under specific environmental conditions, even though their direct contributions to litter mass loss were slight (Li et al. 2021). Wang et al (2013) indicated that some saprophagous mites and collembola can affect decomposition directly by feeding or transforming litter, and their selective preference for different litter species can promote the HFA. In the vertical vegetation gradient in Changbai Mountain, a large number of oribatid mites have been proven to exist in the dark coniferous forests compared with the other forest types, which may contribute to the HFA (Liu et al. 2023a, 2023b).

Moreover, we found that the contribution of microorganisms to the HFA of litter C was greater than that of litter B. This may be attributed to the higher microbial diversity in litter C compared with litter B (Fig. S5). Previous studies have suggested positive effects of microbial richness on multifunctionality, and the potential mechanisms included an increase in the interactions within community (i.e., complementarity effects) and an increase in the existence likelihood key functional species (i.e., sampling effect) (Loreau and Hector 2001; Hooper et al. 2005). Species interactions are especially important for organic matter decomposition, which involves diversified metabolic routes and require the cooperation of diverse functional microorganisms to break down complex and recalcitrant polymers (Delgado-Baquerizo et al. 2017).

In addition to the diversity, community dissimilarity was also regarded as an important factor regulating HFA (Veen et al. 2019). We found that there was a stronger HFA for litter C in soil from low elevations, in which nematode community showed a higher dissimilarity between home and away field. Differences in soil biota community could arise from environmental filtering, leading to specific decomposers adapting to the local litter, further contributing to the HFA (Veen et al. 2015). However, we did not find similar patterns for fungal and bacterial communities, probably because the microbial communities were more diverse and contained many generalist taxa (Lucie et al. 2022).

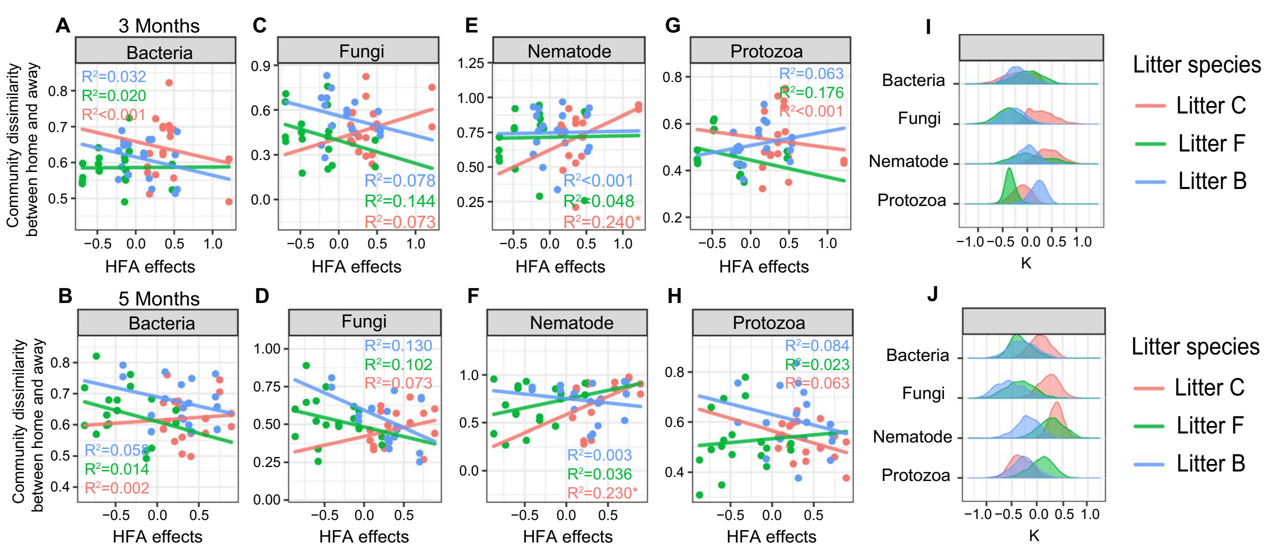

Fig. 5 The relationships between the community dissimilarity of bacteria (**A**, **B**), fungi (**C**, **D**), nematodes (**E**, **F**), protozoa (**G**, **H**) and the home-field advantage (HFA) across different litter species after 3 and 5 months of decomposition. Bootstrapped distributions of the slopes (*K*) describing the relationships between different soil biotic groups and HFA after 3 and 5 months of decomposition (**I**, **J**). Litter—B, F and C represented that the litter collected from *Betula ermanii*, *Fraxinus mandshurica* and *Corylus mandshurica*, respectively. *$P < 0.05$

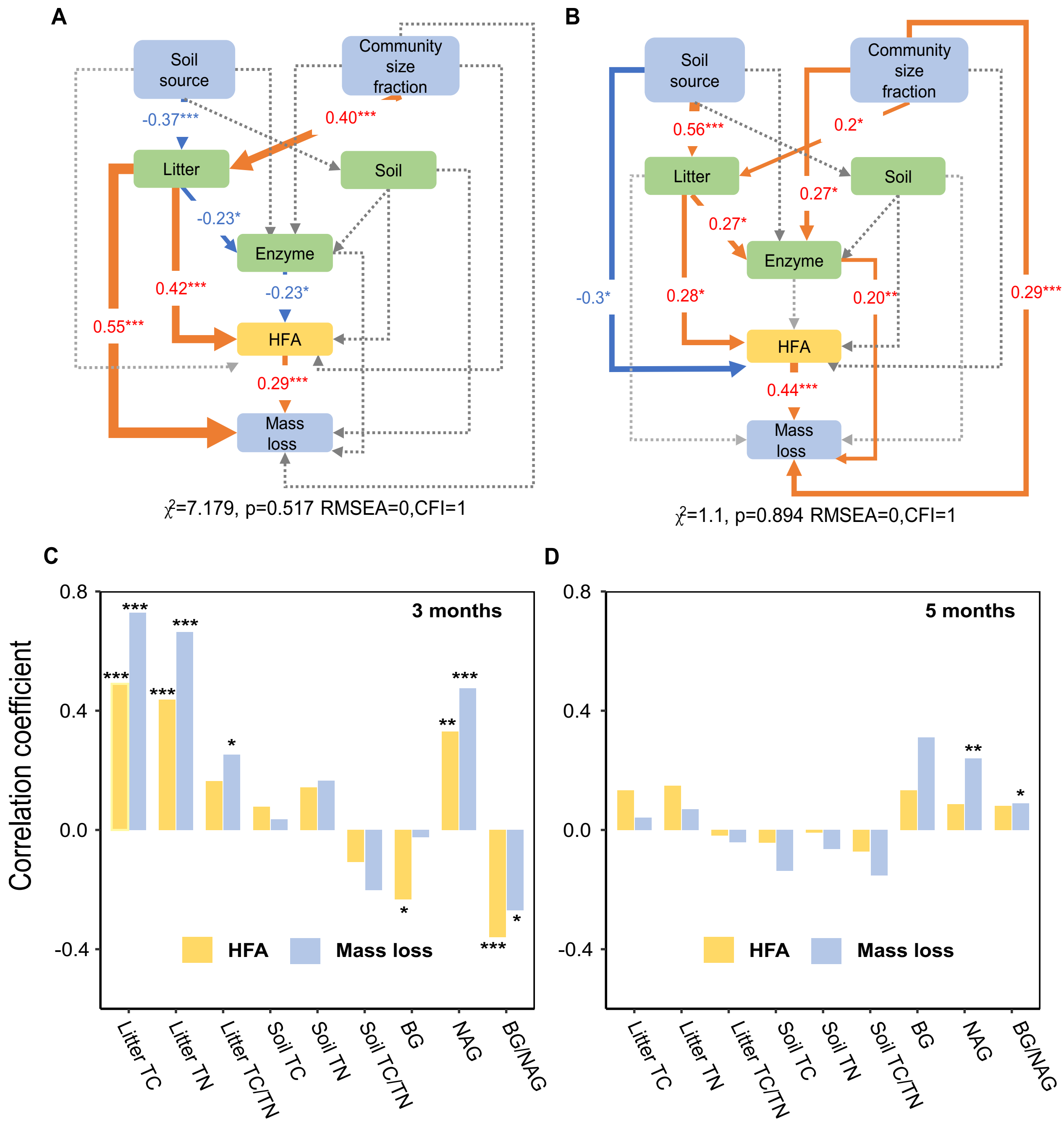

Fig. 6 Structural equation models (SEM) linking litter and soil features and biotic factors to litter mass loss and home-field advantage (HFA) at different decomposition stages (**A**, **B**). Standardized path coefficients were presented and visualized by the arrows, and blue and orange arrows represented the significant negative and positive effects, respectively ($P < 0.05$), while dashed black arrows indicated insignificant impacts ($P > 0.05$). Litter, soil and enzyme represented the first axis (PCA1) of principal component analysis (PCA) of litter properties (litter TC, litter TN and litter C:N), soil properties (soil TC, soil TN and soil C:N) and enzyme properties (BG, NAG and BG: NAG), respectively. Spearman's correlation coefficients between litter mass loss, HFA and the features of litter, soil and enzyme activity after 3 and 5 months of decomposition (**C**, **D**). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Trajectories of litter decomposition and HFA at different decomposition stages

Consistent with the third hypothesis (H_3), we found that soil organisms have different effects on litter mass loss and HFA at different stages. After 3 months of decomposition, community size fractions had indirect effects, mainly through litter quality such as TC and TN, on litter mass loss and HFA. Labile compounds such as small molecule carbohydrates and organic acids are accessible and are easily to be decomposed in most habitats at the earlier stage of decomposition (Djukic et al. 2018), resulting in similar decomposition rates and inapparent HFA. In line with this, Li et al. (2023a, b) indicated that stoichiometry imbalances between microbial communities and litter resources directly modulate litter decomposition rates at the earlier stage, independent of community composition changes of bacteria and fungi. These findings suggest that the interaction between soil decomposers, not just microbial decomposers, and suitable resources may be a potential mechanism underlying the HFA.

After 5 months of decomposition, we found that community size fractions affected the litter mass loss not only through litter quality but also through soil enzyme activity. During the decomposition processes, the available carbon and nutrients are gradually depleted, while the recalcitrant components such as lignin are accumulated in litter (Soong et al. 2020). Complex enzyme systems (e.g., peroxidases and manganese superoxide dismutase enzyme) are therefore required to participate in decomposition (Vivanco and Martiny 2025). Moreover, higher enzyme investment usually accompanied by the high N demand, notably because that N is essential for amino acid synthesis, protein production and hyphal growth (Fanin et al. 2016). In line with this, we found that the NAG activity was closely related to the litter mass loss.

This study highlights the different mechanisms by which soil organisms regulate litter decomposition at different stages, and this knowledge is important for optimizing litter decomposition models and predicting nutrient cycling in terrestrial ecosystems. However, our research period was relatively short, and this timeframe may not fully capture the complete decomposition process, particularly the late-stage breakdown of recalcitrant compounds such as lignin. In addition, compared with the field experiment, our results were obtained based on the microcosm approach characterized by more suitable conditions and simplified biological communities, which may lead to an overestimation on the ecological role of different soil biotic groups in litter decomposition (Zhang et al. 2025a, b). Therefore, comprehensively considering climate factors and extending the decomposition period to encompass the full decomposition trajectory will further increase our understanding of litter breakdown.

Conclusions

The results of our microcosm decomposition experiment provide new insights into the relative contributions of community size fractions to litter decomposition processes. We highlighted that the contributions of soil biotic communities to litter mass loss and HFA are affected by the interactions between body size and substrates features including litter and soil sources, and microbial communities are the main drivers to litter decomposition. We further showed that the mechanisms leading to litter mass loss and HFA are different at different decomposition stages; litter quality plays a crucial role in the earlier stage, while enzyme activity performs more at the later stage. Our findings supplement the researches on the ecological role of different soil biotic communities in regulating litter decomposition and help to improve decomposition models. This is of great significance for accurately predicting the variations in nutrient cycling caused by different litter input due to climate change.

Supplementary Information

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Additional file 1.

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Author contributions
YBL and QL designed the study. YXS and BL analysed the data. YXS, BL, YHL, XFD, YB, ZXX and YBL collected the samples and conducted the measurements. YXS, YBL, BL, and QL wrote the first draft, and all authors contributed to the editing of the paper. The authors declare that they have no competing interests.

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Data availability
The data will be made available upon request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors agreed and approved the manuscript for publication in Ecological Processes.

Competing interests
The authors declare that they have no competing financial interests.

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