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REGULAR ARTICLE

Fungi participate in driving home-field advantage of litter decomposition in a subtropical forest

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Abstract
Background and aims Home-field advantage (HFA) hypothesis predicts that plant litter decomposes faster beneath the plant species from which it was derived than beneath other plant species. However, it remains unclear, which groups of soil organisms drive HFA effects across a wide range of litter quality and forest types.
Methods We set up a reciprocal transplant decomposition experiment to quantify the HFA effects of broadleaf, coniferous and bamboo litters. Litterbags of different mesh sizes and high-throughput pyrosequencing of microbial rRNA gene were used to test the contribution of different decomposer groups to HFA effect.
Results The recalcitrant broadleaf litter and the labile bamboo litter exhibited HFA. Presence of meso-and macrofauna did not substantially change the HFA effects. Bacterial and fungal community composition on litters were significantly influenced by litter type. Bacterial community composition remained unchanged when the same litter was decomposed in different forest types, whereas fungal community composition on broadleaf and bamboo litters were significantly influenced by incubation site.
Conclusions Our data demonstrate specific association between fungal community composition and faster litter decomposition in the home site, suggesting that fungi probably participate in driving the HFA effect of broadleaf and bamboo litters.

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Introduction

Primary production and decomposition of detritus are two fundamental ecological processes on earth (Berg and McClaugherty 2014; Swift et al. 1979). Most primary production in terrestrial ecosystems enters the soil as litter or dead organic matter (Cebrian 1999). Decay of this material provides substantial nutrients and energy that supports detrital food webs, influencing soil fertility and the global carbon cycle (Berg and McClaugherty 2014; Gessner et al. 2010; Swift et al. 1979). It is commonly accepted that climate and litter quality are the main factors controlling litter decomposition at broad spatial scales (Meentemeyer 1978; Moore et al. 1999; Zhang et al. 2008). However, at the local scale a variety of biotic factors such as composition of decomposer communities or interactions among litter species can also influence decomposition rates (Austin et al. 2014; Ayres et al. 2009a; Gessner et al. 2010).

Among the potential mechanisms explaining the variability in decomposition rates at the local scale, several recent studies have reported that litter tends to decompose faster in the site from which it was derived (i.e. home site) than when placed in away sites, a phenomenon called 'home-field advantage' (HFA) (Ayres et al. 2009a; Gholz et al. 2000). Although the HFA effect for litter decomposition has gained much attention over the last decade (e.g. Ayres et al. 2009b; Milcu and Manning 2011; Chomel et al. 2015), many studies did not find any evidence of such an effect (e.g. Giesselmann et al. 2011; St John et al. 2011; Veen et al. 2015), thereby challenging the generalizability of this phenomenon in terrestrial ecosystems. Furthermore, most previous studies did not disentangle the true HFA effect, i.e. adaptation of soil biota to decomposition of litter at home, from the functional breadth hypothesis, i.e. the ability of soil biota to decompose more efficiently many different litter types at the same time (Fanin et al. 2016; Keiser et al. 2011, 2014). It is clear that magnitude of HFA effect is difficult to predict unless we uncover the underlying mechanisms of HFA effect of litter decomposition.

HFA could result from long-term ecological interactions between decomposer communities and litter that they encounter most often. In particular, microbial decomposers may differ in their ability and preference to utilize different carbon sources (Durall et al. 1994; Hanson et al. 2008; McGuire et al. 2010). Therefore, faster decomposition rates at home may arise because of niche differences among microbial communities at different sites. For instance, the high proportion of complex and/or toxic compounds contained in recalcitrant litter requires specialist decomposers to break them down (Ayres et al. 2009a; Milcu and Manning 2011). By contrast, the high proportion of rich and labile carbon compounds contained in some litters may stimulate competition among copiotrophic microbial decomposers. Therefore, faster decomposition rates may arise because of higher decomposer growth rate at home site. Based on this theoretical framework, it's likely that both low quality and high quality litter can decompose faster in their home sites, but for different reasons.

Despite the increasing recognition that HFA depends on the functional attributes of soil communities, little is known about the main groups of soil organisms (fauna, bacteria and fungi) contributing to HFA effects. It has been shown recently that the direction and strength of interaction between soil fauna and litter traits may vary among sites and biomes (Garcia-Palacios et al. 2013; Milcu and Manning 2011; Perez et al. 2013), suggesting an important context-dependency of HFA effects (Chomel et al. 2015; Milcu and Manning 2011). Such variability in the effects of soil fauna on decomposition rates may depend on their impact on microbial activity (Bardgett 2005; Berg and McClaugherty 2014). In addition, empirical evidence on the relative contribution of soil microorganisms to HFA are scarce in the literature (e.g. Fanin et al. 2016). In particular, the role of fungi and bacteria may differ across contrasting ecosystems and/or litter quality because of their differences in functional attributes and carbon requirements. Fungi are generally thought to possess stronger capacities than bacteria for decomposing recaciltrant plant material, whereas bacteria are thought to be more efficient at exploiting labile carbon compounds (de Graaff et al. 2010; Hunt et al. 1987; Paterson et al. 2008). However, whether, how and why the main contributors of HFA effect vary between labile and recalcitrant litters has received only a weak attention in the literature.

In this study, we aim to investigate HFA during leaf litter decomposition across contrasting ecosystems by performing a reciprocal litter transplantation experiment using three tree species (*Castanopsis eyrei*, *Cunninghamia lanceolata* and *Phyllostachys heterocycla*

cv. *Pubescens*) originating from three different forest types (broadleaf, coniferous and bamboo forests) in subtropical China. We used litterbags of two different mesh sizes and pyrosequencing technique to address the role of soil biota, i.e. soil fauna, bacteria and fungi, in explaining the HFA effects. More specifically, because of the supposedly specialized role of bacteria and fungi during litter decomposition (de Graaff et al. 2010; Hunt et al. 1987; Paterson et al. 2008), we hypothesized that different groups of decomposer microorganisms should dominate depend on the litter quality: fungi should be the main group of organism participating HFA effect in recalcitrant litter because of their greater functional capacities in using low quality carbon resource (H_1), and bacteria should be the main group of organism participating to HFA effects in labile litter because of their faster rate in resource acquisition and exploitation (H_2). Finally, given that some studies reported soil fauna play an important role in driving the HFA effects (e.g. Milcu and Manning 2011), we hypothesized that meso- and macrofauna presence should substantially enhance the strength of HFA effects (H_3).

Material and methods

Study site

We conducted this study in a subtropical forest within Gutianshan National Nature Reserve (GNNR, approximately 81 km^2 in area), located in the western part of Zhejiang Province, East China (29°8′18″ - 29°17′29″ N, 118°2′14″ - 118°11′12″ E). The region has a subtropical monsoon climate, with a mean annual temperature of 15.3 °C, and mean annual precipitation of 1964 mm (most of which occurs between March and September). The parent rock of the mountain range is granite, and the predominant soil types are red, red-yellow, yellow-red, and marsh soil. The GNNR comprises a large area of natural evergreen broadleaf forest (57% of the reserve area) dominated by *C. eyrei, Schima superba*, *Cyclobalanopsis glauca*, as well as coniferous plantations (*C. lanceolata* or *Pinus massoniana*), tea-seed oil plantations (*Camellia oleifera*) and bamboo plantations (*P. heterocycla* cv. *Pubescens*) (Lin et al. 2016).

Experimental design

We selected three forest types which differ significantly in species compositon for the study: broadleaf forest, coniferous forest, and bamboo forest. *C. eyrei*, *C. lanceolata* and *P. heterocycla* cv. *Pubescens* are the dominant tree species of the broadleaf, coniferous and bamboo forest, respectively (Table 1). The shortest and longest distance between any two forest sites is 1.6 and 4.6 km, respectively. We selected one plot at each forest site for the establishment of our litter decomposition experiment. All selected plots had similar altitude, slope and hence present similar microclimatic conditions. In January 2016, three soil cores (5 cm depth) were randomly collected within each plot for soil physicochemical analyses. Soil samples were air-dried, sieved with a 2-mm mesh and grounded. Four edaphic variables were measured: pH, soil organic carbon, total nitrogen and phosphorus (Table 1). Soil was shaken in 1 mol L^{-1} KCl solution, and pH was measured using a pH meter. Soil organic carbon was measured by dry combustion in a solid module (Shimadzu SSM-5000, Japan) coupled with a TOC/TN analyzer (Shimadzu TOC-L CPH, TNM-1, Japan). After digestion of soil powder with concentrated H_2SO_4 and 30% H_2O_2 (Jones 2001), total nitrogen was measured by using the TOC/TN analyser, and total phosphorus content was determined spectrophotometrically by using molybdenum blue method.

We installed a full reciprocal transplant decomposition experiment using the litterbag method in the three forest types. Leaf litter of the three dominant species, i.e. *C. eyrei, C. lanceolata* and *P. heterocycla* cv. *Pubescens* were used and we referred to these litter types hereafter as broadleaf litter, coniferous litter, and bamboo litter, respectively. Litter was collected after natural abscission using litter traps (1 m × 1 m) placed underneath tree canopies. Litter samples for each species were bulked, homogenised and oven dried at 40 °C for 48 h in the laboratory. Five subsamples of the dried material from each litter type were then oven dried at 60 °C to determine the weight conversion factor between 40 °C and 60 °C. To determine the contribution of soil fauna to decomposition we constructed two different types of litterbags: coarse mesh size (4-mm upper side and 0.5-mm lower side facing the soil surface to avoid loss of litter fragments during field exposure) and fine mesh size (25-μm on both side). The 25 μm mesh size allowed for the access of only microorganisms and microfauna, while the 4 mm mesh size also allowed meso-and macrofauna to enter the litterbag. Both types of litterbags were 10 cm × 15 cm in size, filled with approximately 3.0 g of 40 °C-dried litter, and labeled

Table 1 Tree community characteristics, soil chemical properties (0-5 cm depth) and initial litter quality of the three tree species

	Castanopsis eyrei	*Cunninghamia lanceolata*	*Phyllostachys heterocycla* cv. *Pubescens*
Site description			
Forest type	Broadleaf	Coniferous	Bamboo
Relative basal area (%)	55.1%	81.9%	84.5%
DBH range (cm)	1.0–65	1.5–27.8	7.0–13.5
Soil pH	3.72 ± 0.01	4.14 ± 0.04	3.88 ± 0.08
Soil organic C (mg g^{-1})	41.7 ± 7.5	19.1 ± 5.0	46.7 ± 12.7
Soil N (mg g^{-1})	2.90 ± 0.47	2.59 ± 0.52	5.63 ± 1.97
Soil P (mg g^{-1})	0.158 ± 0.006	0.092 e± 0.005	0.201 ± 0.05
Soil C/N	15.3 ± 3.8	7.9 ± 2.6	8.7 ± 0.7
Initial litter traits			
C (mg g^{-1})	467.2 ± 1.153^{a}	492.4 ± 2.395^{b}	391.8 ± 1.593^{c}
N (mg g^{-1})	9.80 ± 0.001^{a}	4.60 ± 0.001^{b}	7.60 ± 0.088^{c}
P (mg g^{-1})	0.207 ± 0.003^{a}	0.266 ± 0.024^{a}	0.228 ± 0.021^{a}
K (mg g^{-1})	1.861 ± 0.025^{a}	1.662 ± 0.159^{a}	2.481 ± 0.088^{b}
Mn (mg g^{-1})	0.795 ± 0.009^{a}	0.704 ± 0.076^{a}	0.949 ± 0.063^{b}
C/N	47.67 ± 0.118^{a}	107.04 ± 0.520^{b}	51.34 ± 0.422^{c}
Proximate lignin (mg g^{-1})	161.99 ± 7.95^{a}	266.66 ± 4.45^{b}	88.98 ± 6.30^{c}
Total phenols (mg g^{-1})	24.9 ± 0.08^{a}	18.1 ± 1.68^{b}	6.9 ± 0.06^{c}
Tannin (mg g^{-1})	15.0 ± 0.02^{a}	11.1 ± 1.52^{b}	0.2 ± 0.08^{c}

Relative basal area and range of tree diameter at breast height (DBH) were calculated based on a 20 m × 20 m census plot for each forest type. Data are mean ± SE ($n = 3$). Different letters indicate significant differences ($P < 0.05$) on the basis of one-way ANOVA followed by pairwise multiple comparisons (Tukey's HSD test)

with plastic tags. In total, 108 litter bags (3 incubation sites × 2 mesh size × 3 litter types × 6 replicates = 108) were used to determined decomposition rates. Three additional fine-mesh bags for each litter types and each incubation site (27 in total) were used to monitor the microbial communities of the decomposing litter. Six blocks beneath tree crowns of *C. eyrei*, *C. lanceolata* and *P. heterocycla* cv. *Pubescens* in broadleaf, coniferous and bamboo forest plots, respectively, were selected for litterbag incubation. The distance between any two blocks is at least 10 m. All litterbags were fixed on the surface of the forest floor using plastic nails after recently fallen litter was removed. After 222 days of exposure in the field (25th of January to 3rd of September, 2016) all litter bags were harvested and put in sealed polyethylene bags. In the laboratory, the remaining litter was removed from litterbags and gently brushed to remove adhering soil particles and other foreign materials. Samples were then dried at 60 °C and weighed to determine the remaining litter mass. Litter mass loss (M_l, %) was calculated as $M_l = (M_i - M_f)/M_i \times 100\%$, where M_i and M_f are the initial and final litter mass (dry at 60 °C), respectively. Litter mass loss data are available in the Electronic supplementary material.

Litter quality measurements

We used three replicates per species to assess litter quality. Total carbon (C) and nitrogen (N) concentrations were measured by dry combustion using an elemental analyzer (MACRO Cube Elemental Analyzer, Elmenta, Italy). C/N ratio was calculated based on the C and N concentrations. Phosphorus (P), potassium (K) and manganese (Mn) concentrations were measured using inductively coupled plasma emission spectroscopy (ICP-OES; Therma Jarrel-Ash, IRIS Advantage, MA, USA) after digestion of ground leaf litter material with concentrated HNO_3 and 30% H_2O_2 (Jones 2001). Proximate lignin was determined by the acid-detergent fiber method as described in Graça et al. (2005). Total phenols were extracted with a 75% acetone solution, and concentrations of total phenols, tannins were measured colorimetrically with the Folin-Ciocalteau reagent

following the method of Makkar (2003), using tannic acid as a standard.

Microbial community on decomposing litter

Litterbags for assessing microbial community structure (three replicate samples per treatment) were also harvested on September 3rd, 2016. They were placed in a heat insulation box cooled by ice immediately after collection and shipped to the laboratory in Chongqing University (< 24 h). Samples were stored in a − 80 °C freezer until further processing. We extracted DNA from 0.3 g of frozen leaf litter using FastDNA™ Spin Kit for Soil (116560–200, MPBIO, California, USA), according to the manufacturer's protocol and quantified the extracted DNA using NanoDrop 2000 (Thermo Fisher Scientific Inc., Wilmington, DE, USA).

The fungal and bacterial abundances were estimated by using quantitative real-time PCR (qPCR). A fragment of the fungal 18S rRNA gene was amplified using the forward primer 5′-GGCAAGTCTGGTGCCAG-3′ combined with reverse primer 5′- ACGGTATC T(AG)ATC(AG)TCTTCG-3′, while a fragment of the bacterial 16S rRNA gene was amplified using the forward primer 5′-ACTCCTACGGGAGGCAGCAG-3′ combined with reverse primer 5′-TACNVGGGTATCT AATCC-3′. Standard curves were generated using 10-fold serial dilutions of a plasmid (pGEM-T) containing the targeted gene inserts for the 18S and 16S rRNA gene, respectively. The qPCR reactions were performed in duplicate 10 μl mixtures, each containing 5 μl GoTaq® qPCR Master Mix Technical Manual (A6001, Promega, USA), 1 μl of each forward and reverse primers, and 2 μl sterile DNA-free water, and 1 μl standard or soil DNA samples. The reaction was carried out on an ABI ViiA ™ 7 Real Time PCR System (ABI, USA), using reaction conditions of 95°Cfor 3 min followed by 40 cycles of 95°Cfor 15 s, 60 °Cfor 30s and 72°Cfor 30s. Fungal and bacterial gene copy numbers were calculated according to the standard curves that relate the cycle threshold value to the known number of copies in the standards (Rousk et al. 2010).

Fungal and bacterial communities that colonized on litter were assessed using high-throughput sequencing methods. Fungal and bacterial amplicon libraries were obtained for pyrosequencing using custom fusion primers. The primer pair 338-F (5′- ACTCCTAC GGGAGGCAGCAG-3′) and 806-R (5′-GGACTACHVGGGTWTCTAAT-3′) were used to amplify the V3-V4 region of the bacterial 16S rRNA gene (Zhou et al. 2016), and the primer pair ITS1-F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2-2043R (5′-GCTGCGTTCTTCATCGATGC-3′) were used to amplify the fungal internal transcribed spacer (ITS) rRNA region (McGuire et al. 2013). Amplification was conducted on ABI GeneAmp® 9700 with the following settings: initial denaturation at 95 °C for 3 min, followed by 27 or 35 cycles separately for bacterial and fungal genes, consisting of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 45 s, and finally extension at 72 °C for 10 min. Each sample was amplified in triplicate and the three PCR products of each sample were pooled and purified. Samples were then evaluated for quantity and quality via electrophoresis with 2% agarose gel. The resulting gene amplicon samples were sequenced on the Illumina MiSeq platform (San Diego, CA, USA) at Majorbio BioPharm Technology Co., Ltd. (Shanghai, China), using paired-end 300-bp read lengths.

For both 16S and ITS genes, sequences were pre-processed and quality filtered before downstream analyses using Trimmomatic program (Bolger et al. 2014) and FLASH program (Magoc and Salzberg 2011). Reads containing ambiguous base "N" were removed. Reads were truncated at any site receiving an average quality score < 20 over a 50 bp sliding window, and any truncated reads shorter than 50 bp were discarded. Reads without exact barcode matching or > 2 nucleotide mismatches in primer matching were removed. Forward and reverse reads of same sequence with at least 10 bp overlap and < 20% mismatches were assembled into contigs. Reads that could not be assembled were also discarded. Singleton contigs were discarded and the remaining contigs were handled as OTUs (Operational Taxonomic Units). OTUs were clustered at 97% sequence similarity level for both fungal and bacterial sequences and an OTU table was created by identifying the number of sequences of each OTU in each sample using UPARSE program (Edgar 2013).

Data analysis

Data was tested for normal distribution using the Shapiro–Wilk test ($P > 0.05$) and homogeneity of variances using Breusch-Pagan test ($P > 0.05$). We used one-way ANOVA to test for interspecific differences in litter chemistry and post hoc comparisons between litter species were evaluated using Tukey's HSD. We performed

random forest analysis to assess which litter trait was the best factor explaining litter mass loss, with litter traits as explanatory variables and litter mass loss of all litterbags as response variable. We performed a three-way ANOVA to examine the effects of incubation site (broadleaf, coniferous, and bamboo forest), mesh size of litterbags (coarse and fine), litter type (broadleaf, coniferous and bamboo litter), as well as all possible interactions among these factors on litter mass loss. We then analysed the litter mass loss for each litter type individually using a two-way ANOVA in which the incubation site and mesh size of litterbag were treated as fixed effects and were allowed to interact.

We then performed the regression model developed by Keiser et al. (2014), which separates the overall ability of soil biota to decompose different litter types and the real HFA. The model states that litter mass loss is equal to litter ability (β_l, i.e. litter quality index) plus soil ability (γ_s, i.e. inherent functional capacity of soils) plus a home interaction (η_h, i.e. HFA), as follow (Keiser et al. 2014):

$$Y_i = \alpha + \sum_{l=1}^{N} \beta_l \, \text{Litter}_{l_i} + \sum_{s=1}^{M} \gamma_s \text{Soil}_{s_i} + \sum_{h=1}^{K} \eta_h \, \text{Home}_{h_i} + \varepsilon_i$$

where Y_i is the litter mass loss for observation i. α is the intercept term, represents the average litter mass loss for all observations in the dataset after controlling for litter, soil, and HFA effects. β_l is the ability of litter species l (from species 1 to N), γ_s is the ability of the soil community s (from community 1 to M), and η_h is the HFA of h (from home combinations 1 to K). The estimated parameters are β_l, γ_s and η_h. Both of $\sum_{l=1}^{N}\beta_l$ and $\sum_{s=1}^{M}\gamma_s$ were restricted to zero to prevent perfect collinearity (Keiser et al. 2014). Litter_l, Soil_s and Home_h are dummy variables that is set as 1 or 0 depending on the presence or absence of the litter species, soil community or home combination, respectively (Keiser et al. 2014). ε is the error term. Using this model, we calculated the litter quality index (β_l), the functional ability index of soil decomposer communities (γ_s), and the HFA index (η_h) on the litter mass loss. We analysed the data from fine- and coarse-mesh litterbags separately. We ran the models in SAS version 9.3 (SAS Institute 2010) using the SAS code provided in Keiser et al. (2014).

We used one-way ANOVA to test the effects of incubation site on the abundances of fungi and bacteria on decomposing litters and post hoc comparisons between incubation sites were evaluated using Tukey's HSD. We used nonmetric multidimensional scaling (NMDS) analysis to visualize the differences in the structure of bacterial and fungal community on decomposing litters. We then used permutational multivariate ANOVA (PERMANOVA) to test the effect of incubation site, litter type, and their interactions on bacterial and fungal communities with 9999 random permutations. We also ran PERMANOVA for each litter type separately. Bray-Curtis dissimilarity matrices were used in all the analyses.

We performed statistical analyses in the software R 3.3.1 (R Development Core Team 2016), using the R package 'randomForest' (Liaw and Wiener 2002) for random forest analysis, 'vegan' (Oksanen et al. 2016) for NMDS and PERMANOVA analysis. $P < 0.05$ was considered as statistical significance.

Results

Litter quality

Litter chemical traits differed significantly among the three litter types, except for the P content ($P < 0.05$; Table 1). The interspecific variability of litter chemistry was particularly apparent for N content, C/N ratio, proximate lignin, total phenols, and tannins contents which varied by 2.1-, 2.2-, 3.0-, 3.6-and 75-fold, respectively (Table 1). Litter quality strongly differed among the three litter types according to the two first axes of the PCA plot (Online Resource 1). Bamboo litter was segregated from broadleaf and coniferous along the first axis whereas broadleaf was opposite to coniferous along the second axis. Bamboo litter presented significantly lower content of tannins that was about 54-and 74-fold lower than coniferous and broadleaf litters, respectively (Table 1). Coniferous litter was characterized by significantly higher lignin content than other two litter types, and broadleaf litter was significantly higher in total phenols and tannins contents (Table 1). Overall, litter quality of bamboo litter was relatively higher than that of broadleaf and coniferous litter.

Litter mass loss and home-field advantage

After 222 days of exposure in the field litter mass loss differed significantly among the different litter types (ANOVA, $F_{2,105} = 15.3$, $P < 0.001$; Fig. 1), with the highest mass loss observed for bamboo litter ($24.6 \pm 1.2\%$), followed by coniferous litter ($24.3 \pm 0.6\%$) and broadleaf litter ($17.8 \pm 1.0\%$). Random forest analysis

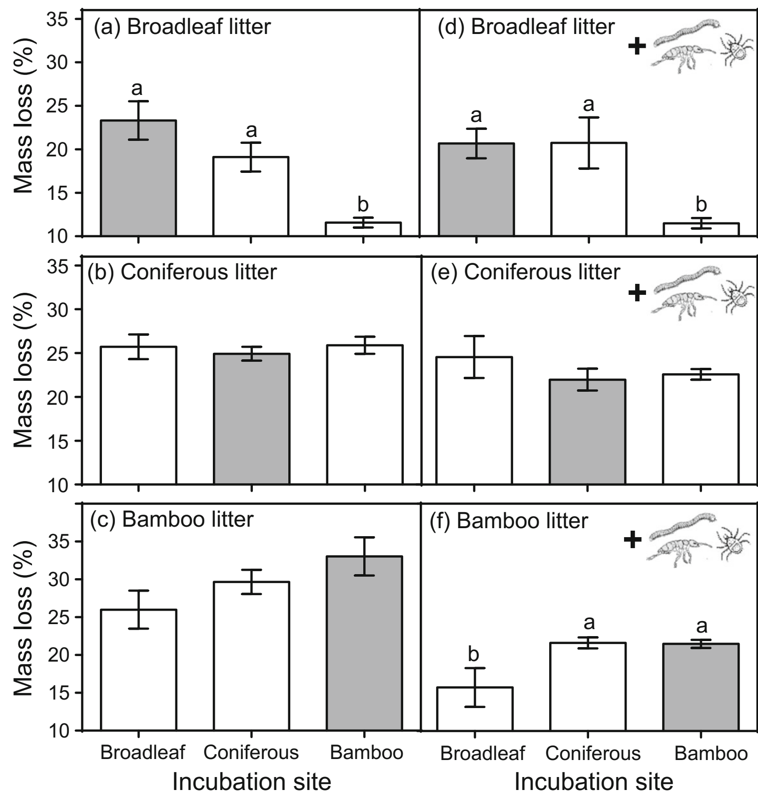

Fig. 1 Litter mass loss (%) of the three tree species that were enclosed in (**a**-**b**-**c**) fine-mesh (25 μm, left column) and (**d**-**e**-**f**) coarse-mesh (4 mm, right column) litterbags after 222 days of filed exporsure. Grey bar denotes the litter was decomposed in its home site. Error bars respresent ± SE ($n = 6$). Different letters above the bars indicate significant differences ($P < 0.05$; Tukey's hsd test)

showed that tannins content was the most important litter quality trait that influences litter mass loss (Online Resource 2). The Keiser's model showed that the litter quality index (β_l) estimates were higher for coniferous and bamboo litter compared to broadleaf litter (Fig. 2a).

Litter type explained the largest proportion (22.5%; $P < 0.001$) of the variation in litter mass loss (Table 2). Although there was no significant effect of incubation site ($P = 0.107$), the interaction between incubation site and litter type was the second most important driver explaining 20% of the variation in litter mass loss (Table 2). There were greater mass losses for broadleaf and bamboo litter when they were incubated in their home site than in away sites, but not for coniferous litter (Fig. 1). Consistently, the HFA index estimated from Keiser's model displayed a significant positive HFA index (η_h) for broadleaf and bamboo litter (Fig. 2b), confirming that they decomposed faster in the area dominated by the plant species from which they were derived. The functional ability index (γ_s) estimates showed that the coniferous forest had the highest functional ability to decompose all litter (Fig. 2c).

Mesh size of litterbag had a significant negative impact on mass loss for coniferous and bamboo litter ($P = 0.034$ and $P < 0.001$, respectively), but not for broadleaf litter ($P = 0.807$). This led to a significant interaction between mesh size and litter type on litter mass loss ($P < 0.001$; Table 2). In addition, HFA index (η_h) estimated from Keiser's model between fine-and coarse-mesh litterbags for each litter type had apparent overlapped standard errors (Fig. 2b).

Microbial community on decomposing litter

There was no significant effect of incubation site on the abundance of fungi (determined using qPCR) for broadleaf and coniferous litters (Fig. 3a, b). However, we found that the abundance of fungi was significantly higher when bamboo litter was incubated in its home site ($P < 0.05$; Fig. 3c). Incubation site had no significant effect on the bacterial abundance for all litter types (Fig. 3d–f).

Litter type was the most important variable explaining 20.8% of the the variation in the fungal community structure ($P < 0.001$; Table 3). Ordination plot from NMDS clearly distinguished the fungal communities of the three litter types (Fig. 4a). Although there was no significant effect of incubation site ($P =$

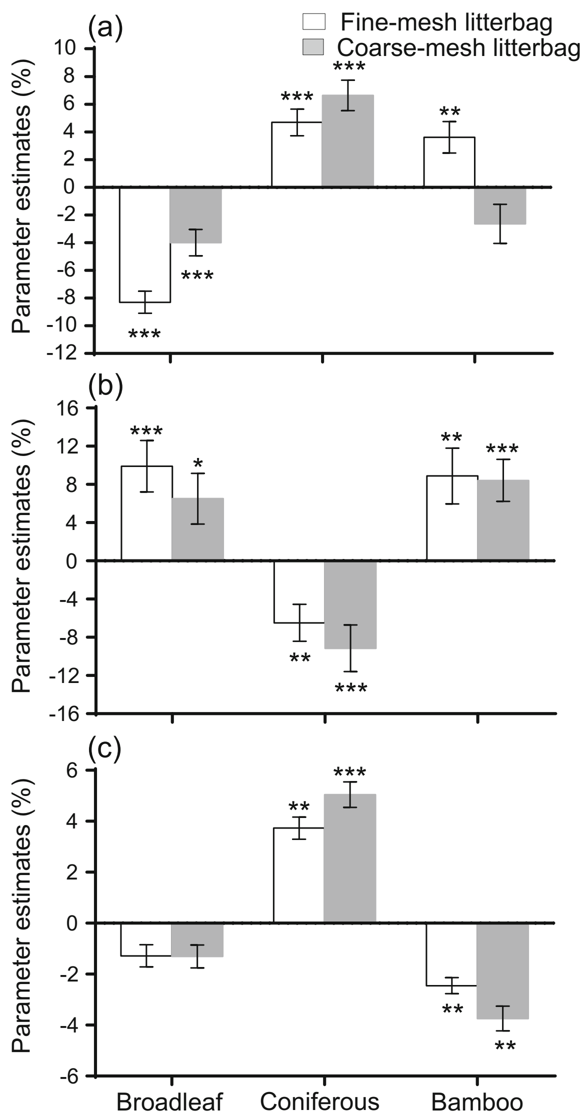

Fig. 2 Parameter estimates (mean ± SE, $n = 6$) of the litter mass loss calculated using the approach developed by Keiser et al. (2014) for (**a**) litter quality index, (**b**) home-field advantage (HFA) index and (**c**) functional ability index. Litter quality index relates to the relative ability of each different litter (broadleaf, coniferous and bamboo) to be decomposed by all the decomposer communities used in our study, HFA estimates the interaction between the litter decomposition and the decomposer communities in each forest (broadleaf, coniferous and bamboo), and functional ability quantifes the overall ability of decomposer community. Data from fine-and coarse-mesh litterbags were analysis separately. Positive values mean positive effect, while negative values means negative effect. Estimates that differ significantly from zero are indicated by asterisk (* $P < 0.05$, ** $P < 0.01$ and ***$P < 0.001$)

0.059; Table 3), the interaction between incubation site and litter type was the second most important driver, significantly explaining 16.3% of the variation in the fungal community structure ($P = 0.015$; Table 3). This was mainly driven by the significant effect of incubation site on fungi colonizing broadleaf and bamboo litter ($P = 0.003$ and $P = 0.035$, respectively), but not for coniferous litter ($P = 0.775$; Table 3).

Similar to what was observed for the fungal community, we found that the identity of litter species was the most important driver, significantly explaining 33.8% of the variation in the community structure of bacteria that colonised in the litter ($P < 0.001$; Table 3). Ordination plot from NMDS distinguished the bacterial communities of broadleaf litter from coniferous and bamboo litters (Fig. 4b). However, incubation site and interaction between incubation site and litter type had no significant effects on bacterial communities ($P = 0.584$ and $P = 0.329$, respectively; Table 3), in contrast to our findings regarding fungi.

Discussion

Due to the hyper-diverse nature of soil biota, soil organisms are thought to be functionally redundant in terrestrial ecosystems and soil community composition has long been ignored in global prediction models (Allison and Martiny 2008). Recently, ecologists have started to consider the functional differences among soil decomposer communities in driving ecosystem processes, and their results challenged the assumptions of functional redundancy (Delgado-Baquerizo et al. 2016; Fanin et al. 2016; Strickland et al. 2009). Consistent with previous reports across contrasting forest types (Ayres et al. 2009b; Chomel et al. 2015; Milcu and Manning 2011), we found HFA effects for two of three litter types, i.e. bamboo and broadleaf litter decomposed faster at home site (Table 2; Figs. 1, 2b). Furthermore, our study suggests that soil fungi participate actively in driving HFA effects for both labile and recalcitrant litters (Table 3; Fig. 4a), highlighting that a better understanding of plant-soil interactions is necessary for predicting how litter decomposition varies across contrasting ecosystems.

Litter quality as a major control of litter mass loss

It is generally accepted that initial litter quality strongly influences litter decomposition rates, with high-quality litter (e.g. high N content, low lignin, phenols and tannins contents) decomposing more rapidly than poor-quality

Table 2 ANOVA results for the effects of incubation site, mesh size, litter type and all possible interactions on leaf litter decompositon rate

Source of variation	df	SS	%SS	*F*	*P*
All litter					
Incubation site	2	81.9	1.7	2.3	0.107
Mesh size	1	489.8	10.5	27.4	**< 0.001**
Litter type	2	1055.4	22.5	29.5	**< 0.001**
Incubation site×mesh size	2	18.1	0.4	0.5	0.604
Incubation site×litter type	4	937.1	20.0	13.1	**< 0.001**
Mesh size×litter type	2	454.8	9.7	12.7	**< 0.001**
Incubation site×mesh size×litter type	4	36.6	0.8	0.5	0.727
Error	90	1608.8	34.4		
Broadleaf litter					
Incubation site	2	736.7	54.2	18.6	**< 0.001**
Mesh size	1	1.2	0.1	0.1	0.807
Incubation site×mesh size	2	27.8	2.0	0.7	0.504
Error	30	593.8	43.7		
Coniferous litter					
Incubation site	2	17.1	4.1	0.8	0.477
Mesh size	1	55.3	13.2	4.9	**0.034**
Incubation site×mesh size	2	8.0	1.9	0.4	0.703
Error	30	337.0	80.8		
Bamboo litter					
Incubation site	2	265.2	14.3	5.9	**0.007**
Mesh size	1	888.2	48.0	39.3	**< 0.001**
Incubation site×mesh size	2	18.9	1.0	0.4	0.662
Error	30	678.0	36.6		

Significiant effects ($P < 0.05$) are shown in bold. SS% represents the percentage sum of squares explained

litter (e.g. Coq et al. 2010; Melillo et al. 1982; Vivanco and Austin 2008). In agreement with this theory, we found that litter type explained the largest proportion of the variation in litter mass loss (Table 2). Random forest analysis showed that tannins content is the most important litter quality trait that influences litter mass loss (Online Resource 2). Higher tannins content can inhibit litter decomposition via inhibiting microbial growth and soil enzyme activity, forming insoluble complexes with biological polymers such as proteins (Chomel et al. 2016; Hättenschwiler and Vitousek 2000), and reducing litter palatability for soil fauna (Coq et al. 2010).

Interaction between decomposers and their substrates

Besides the effect of litter quality, we found that the interaction between decomposers and their substrates explained a significant, but low proportion of the variability in decomposition rates (Table 2). Contrary to the idea that HFA should be more pronounced for recalcitrant than labile litter (Ayres et al. 2009a; Chomel et al. 2015; Milcu and Manning 2011), we found that both the recalcitrant litter (broadleaf) and the relative labile litter (bamboo) exhibited HFA (Fig. 2b). Although high concentrations of complex and/or toxic compounds require specific decomposers with the enzymatic capacities to break them down, thereby generating HFA in recalcitrant substrates (Durall et al. 1994; Hanson et al. 2008; McGuire et al. 2010), our results suggested that HFA may also occur when litter resources are abundant and easily decomposable. This may arise because of selecting copiotrophic decomposer communities that are well adapted to exploit energy-rich resources at home site. This hypothesis was supported by the higher fungal biomass when the bamboo litter was decomposed in its home site (Fig. 3c).

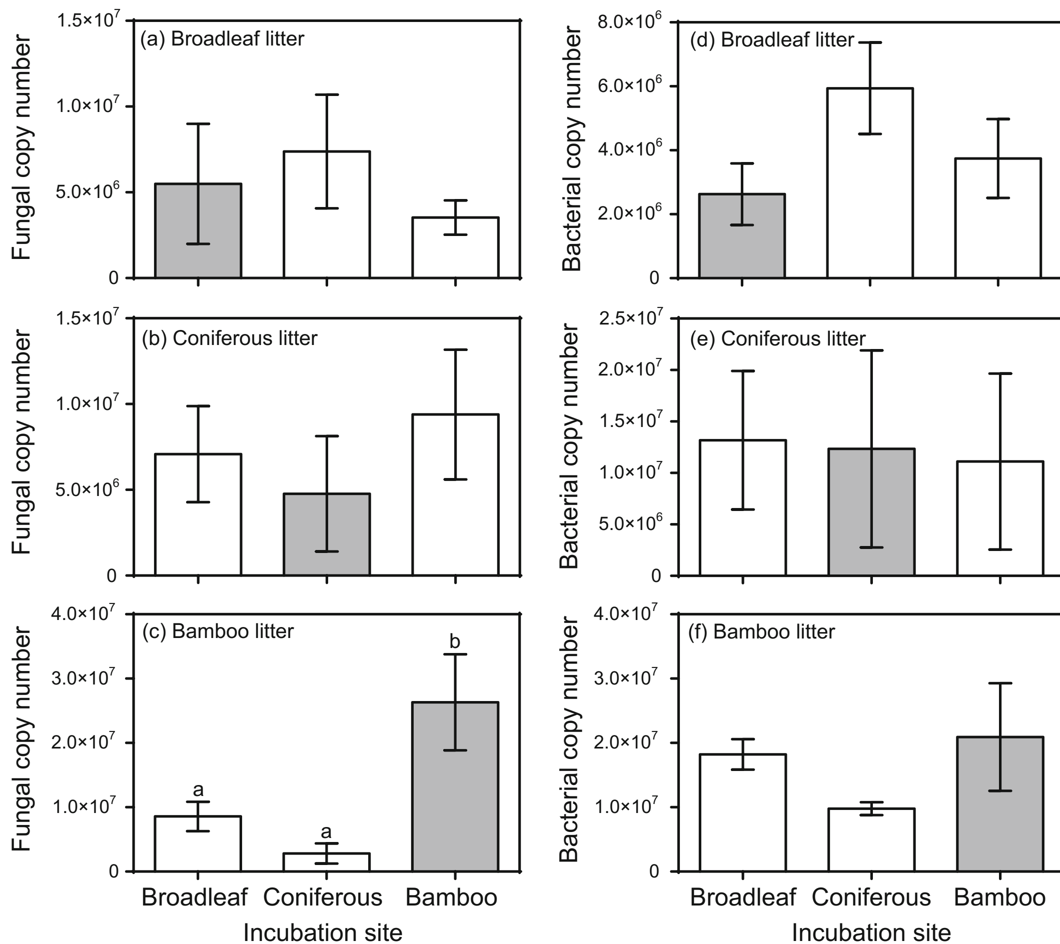

Fig. 3 The abundance of fungi (**a**-**c**) and bacteria (**d**-**f**) on decomposing litters, as indicated by the number of 18S and 16S ribosomal DNA (rDNA) copies measured using quantitative PCR (qPCR). Grey bar denotes the litter was decomposed in its home site. Error bars respresent ± SE ($n = 3$). Different letters above the bars indicate significant differences ($P < 0.05$; Tukey's HSD test)

Another way to address functional dissimilarity between contrasting microbial communities is the functional breadth hypothesis, i.e. the ability of soil biota to decompose more efficiently all litter types at the same time (Fanin et al. 2016; Keiser et al. 2011, 2014). Here, we found that all litter decomposed faster in the coniferous forest (Fig. 1), suggesting that the decomposer community has a broader functional ability to decompose various litter types. This was confirmed by the higher functional ability index (γs) for the coniferous forest (Fig. 2c). This may arise because the long-term coniferous litter inputs, rich in lignin and presenting high C/N ratios, shape a relatively poor and recalcitrant environment for the decomposer communities (Table 1), thereby stimulating their capacities to decay a wide range of substrates (Keiser et al. 2011).

Fungi participate in driving HFA effect

Because of the supposedly contrasting role of bacteria and fungi during litter decomposition, we tested the hypotheses that fungi and bacteria should be the main drivers of HFA in recalcitrant and labile litters, respectively. Our results provide support for our first hypothesis (H_1) that fungi are probable the main group of organisms participating to HFA effects in recalcitrant litter (i.e. broadleaf litter). More specifically, we found that incubation site explained 32.3% of the variation in the fungal community on broadleaf litter (Table 3), and NMDS plot showed that fungal communities on broadleaf litter were most dissimilar between litter incubated at home sites (i.e. broadleaf forest) and in the bamboo forest (Fig. 4a). Similarly, Chomel et al. (2015) reported greater fungal biomass in a

Table 3 PERMANOVA evaluating the effects of incubation site, litter type and their interactions on the fungal and bacterial community structure

		Fungal community				Bacterial community			
Source of variation	df	SS	%SS	*F*	*P*	SS	%SS	*F*	*P*
All litter									
Incubation site	2	0.96	7.9	1.3	0.059	0.34	4.8	0.9	0.584
Litter type	2	2.51	20.8	3.4	**< 0.001**	2.42	33.8	6.2	**< 0.001**
Incubation site×litter type	4	1.97	16.3	1.3	**0.015**	0.86	12.0	1.1	0.329
Error	18	6.63				3.53			
Broadleaf litter									
Incubation site	2	1.14	32.3	1.4	**0.003**	0.50	32.4	1.4	0.125
Error	6	2.40				1.04			
Coniferous litter									
Incubation site	2	0.63	20.3	0.8	0.775	0.45	22.4	0.9	0.650
Error	6	2.46				1.55			
Bamboo litter									
Incubation site	2	1.15	39.5	2.0	**0.035**	0.26	21.3	0.8	0.632
Error	6	1.76				0.94			

Significiant effects ($P < 0.05$) are shown in bold. SS% represents the percentage sum of squares explained

recalcitrant spruce plantation, supporting the idea that fungi are probably the most important contributors to HFA effects in recalcitrant environments.

By contrast, our results do not support our hypothesis (H_2) predicting that bacteria should be the main group of organisms participating to HFA effects in labile litter (i.e. bamboo litter). In particular, we did not find significant effect of the incubation site on bacterical community structure ($P = 0.65$, Table 3). On the contrary, incubation site explained 39.5% of the variation in fungal communities on the bamboo litter (Table 3), and NMDS plot showed that the dissimilarity among fungal communities on bamboo litter was highest between litter incubated at home (i.e. bamboo forest) and in the broadleaf forest (Fig. 4a). Contrary to what we expected, this result suggests that HFA effect in labile litter is probably not mediated by bacteria, but by fungi. This does not support the widely held views that bacterial-dominated decomposition pathways control the decomposition of more labile organic substrates (de Graaff et al. 2010;

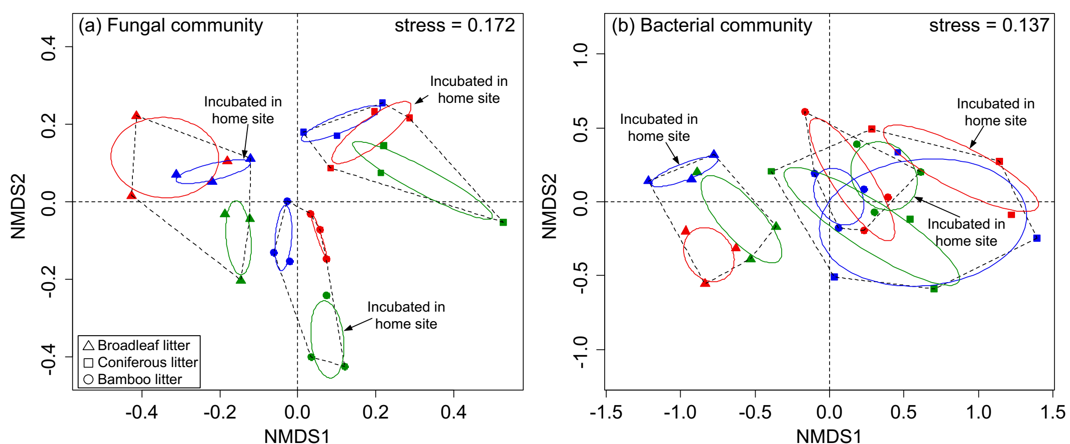

Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities depicting fungal (**a**) and bacterial (**b**) community composition for broadleaf, coniferous and bamboo litter which were incubated in broadleaf (blue colour), coniferous (red colour) and bamboo (green colour) forests. Samples that are closer together have similar microbial communities

Hunt et al. 1987; Paterson et al. 2008). In agreement with this result, Rousk and Frey (2015) have recently found an association between fungi and high-quality soil carbon after two decades of litter manipulation, challenging the traditional view of contrasting life strategies between bacteria and fungi during the decomposition process. It is also noteworthy that as response to litter quality changes during decomposition, fungal communities on litters may change (Voriskova and Baldrian 2013).

Meso-and macrofauna did not alter HFA effects

Our results do not support our third hypothesis (H_3) predicting that soil meso-and macrofauna would substantially enhance the strength of HFA effects. Instead, we found that HFA effects were relatively consistent between fine-and coarse-mesh litterbags (Fig. 2b). Depending on litter type and climate, there is considerable variation in the magnitude of soil fauna effect on litter decomposition (Bradford et al. 2002; Garcia-Palacios et al. 2013; Wall et al. 2008). For instance, Gonzalez and Seastedt (2001) showed that faunal contribution to litter decomposition varied from 1.6% to 66% and Coq et al. (2010) reported that the fauna effect varied about 20-folds among 16 litter types originating from the same tropical forest. Furthermore, Fujii et al. (2016) even found significantly negative fauna effect in a temperate forest in Japan. In line with this result, we found lower mass loss in coarse-mesh litterbags (Fig. 1), suggesting that the inclusion of meso-and macrofauna reduced litter decomposition probably because of grazing and/or disruption of microbial decomposer communities by soil fauna (Bradford et al. 2002; Crowther et al. 2012; Newell 1984). However, significantly lower mass loss in coarse-mesh litterbags were only found for coniferous and bamboo litters but not for the relatively recalcitrant broadleaf litter (Fig. 1; Table 2). This might be due to selective feeding on microbial decomposers by soil fauna (e.g. Bardgett et al. 1993).

Conclusion

We found that two out of three litter types, i.e. broadleaf (recalcitrant) and bamboo (labile) litter, exhibited HFA effects. This indicates that HFA is not restricted to either labile or recalcitrant litter types and suggests local adaptation of decomposer communities to the substrates that they encounter the most often. Further, we found that HFA effects of broadleaf and bamboo litter were probably driven by fungi, highlighting that specific plant-fungi interactions are important for litter decomposition.

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