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Letters

Home-field advantage of litter decomposition differs between leaves and fine roots

Introduction

Litter decomposition is a fundamental process influencing carbon dynamics and nutrient cycling in terrestrial ecosystems. In the 20th century, it was commonly accepted that climate, litter quality and soil biota hierarchically influenced the decomposition process from the large to the local scale (Swift *et al.*, 1979; Coûteaux *et al.*, 1995). However, recent studies have suggested that decomposer communities are much more important in driving litter decomposition than previously thought, mainly because aggregate data at large spatial scales are falsely assumed to represent causative relationships at small spatial scales (Bradford *et al.*, 2014, 2017). In particular, microbial functioning may depend on complex interactions between microbial decomposers and their substrates such as plant litter (Jackrel *et al.*, 2019; Lin *et al.*, 2019). The home-field advantage (HFA) hypothesis predicts that decomposers are more efficient with the plant litters they most frequently encounter (Gholz *et al.*, 2000; Ayres *et al.*, 2009b; Austin *et al.*, 2014; Palozzi & Lindo, 2018). This hypothesis has been empirically tested in various ecosystems via reciprocal litter transplant experiments (Ayres *et al.*, 2009a; Milcu & Manning, 2011; Fanin *et al.*, 2016; Lu *et al.*, 2017; Palozzi & Lindo, 2017; Veen *et al.*, 2018; Jackrel *et al.*, 2019; Lin *et al.*, 2019), and HFA was shown to increase decomposition rates by 7.5% on average (Veen *et al.*, 2015a). However, the vast majority of studies demonstrating HFA effects used leaf litter, and whether the results are consistent with root litter has seldom been tested.

Fine roots account for a substantial amount of litter inputs in terrestrial ecosystems, and play a major role in carbon and nutrient cycling through their afterlife 'effects' (Jackson *et al.*, 1997, 2017; Freschet *et al.*, 2013). Because HFA may arise due to the specialization of microbial communities towards their substrates, especially when the substrate is recalcitrant (Milcu & Manning, 2011), root litter should generate important HFA effects because of the necessity to synthesize specific oxidative enzymes to breakdown complex organic compounds. Yet, the very limited empirical experiments evaluating HFA effects using roots have reported positive, neutral or negative effects (Freschet *et al.*, 2012a; Jacobs *et al.*, 2018; Minerovic *et al.*, 2018), perhaps as a consequence of an important variability in litter chemistry between 'home' and 'away' sites (Veen *et al.*, 2015a). Hence, it is difficult to generalize the specialization of microbial communities towards root litter decomposition. Furthermore, whether HFA effects are coherent between different plant organs originating from the same species (e.g. leaves and roots), has never been evaluated in the same experiment. Because leaves and roots of the same species commonly differ substantially in their chemical compositions (Freschet *et al.*, 2012b; Ma *et al.*, 2016; Sun *et al.*, 2018), different substrate qualities may stimulate contrasting microbial communities characterized by varying metabolic requirements and catabolic capacities (Sauvadet *et al.*, 2019). Therefore, we hypothesize that the concordance in HFA effects between aboveground and belowground plant parts depends on the (dis)similarity in litter chemistry between leaves and roots, that is, plant species having a greater similarity in their chemical traits between leaves and roots should present relatively similar HFA effects (hypothesis 1). Furthermore, because litter recalcitrance is thought to be one of the main drivers controlling HFA due to a higher degree of specialization of microbial communities (Milcu & Manning, 2011), we hypothesize that root litters should display greater HFA effects than leaf litters because they are often more recalcitrant (hypothesis 2).

Materials and Methods

We performed an 1132-d reciprocal litter transplant experiment among three forest sites using litters collected from the dominant tree species in each site: broadleaf (*Castanopsis eyrei*), coniferous (*Cunninghamia lanceolata*) and bamboo (*Phyllostachys heterocycla* cv *Pubescens*) (see Supporting Information Methods S1 for more details of the study sites). Freshly fallen leaf litters were collected using litter traps to prevent infection by soil biota of the 'home' site. Roots were extracted from the soil and washed on a sieve under running water. Fresh fine roots ($\Phi < 2$ mm) were picked out and sterilized using chloroform vapour. Litter quality was characterized by 14 chemical traits related to element concentration, stoichiometry and carbon quality (Table S1; details about trait measurements are in Methods S1). In each site, six randomized blocks, with a distance of at least 10 m between each block, were selected for litterbag incubation. Each litterbag (15 cm × 10 cm with a mesh size of 25-μm, which allows microbial decomposers to enter the litterbags), was filled with *c.* 3.0 g litters, and labelled with a plastic tag. Although soil fauna may also significantly affect the magnitude of the HFA effects in some ecosystems (Milcu & Manning, 2011), previous results in our study sites showed that soil fauna did not substantially contribute to driving the HFA (Lin *et al.*, 2019). In total, we placed six litterbags per litter type in each block for six successive harvests during the first year (94 and 222 d), second year (392 and 583 d) and third year (827 and 1132 d) after the start of the incubation, resulting in a total of 648 litterbags used in this study (three sites × six blocks × six litter types × six harvest times). Leaf litterbags were anchored on the forest floor and root litterbags were buried in the soil. Following harvest, the litter samples were

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cleaned under tap water, oven-dried at 60°C for 48 h and weighed. Litter mass loss (%) was calculated as $(M_i - M_f)/M_i \times 100$, where M_i and M_f are initial and final litter dry mass, respectively.

We ran nonmetric multidimensional scaling (NMDS) on the 14 chemical litter traits to visualize the variation in litter quality among the different litter types, and then performed a permutational multivariate analysis of variance (PERMANOVA) to test the significant effects of species, organ type and their interaction on litter chemical traits. We also calculated dissimilarity among the different litter types using the Euclidean distance. The effects of litter species, incubation site, harvest time and their interactions on mass loss of leaves or fine roots, respectively, were analysed using linear mixed effects models with a first-order auto-regressive variance structure to account for temporal pseudo-replication. To improve the reliability of our statistical inference, we selected the most parsimonious models based on the lowest AICc (Akaike's information criterion corrected for small sample sizes). In addition, the HFA index was estimated at each harvest time by running the regression model proposed by Keiser *et al.* (2014) (see Methods S1 for detailed description of the statistical analyses).

Results and Discussion

The NMDS ordination separated relatively well the six litter types along the two first NMDS axes (Fig. 1), which were associated to chemical traits known to directly affect litter decomposition rates such as nutrients (i.e. nitrogen (N), phosphorus (P), potassium (K), manganese (Mn)), carbon forms (i.e. total phenols, lignin, tannins) and stoichiometric ratios (N : P, C : P, lignin : N) (Swift *et al.*, 1979; Melillo *et al.*, 1982; Keiluweit *et al.*, 2015; Chomel *et al.*, 2016; Sun *et al.*, 2018). Litter chemistry differed significantly between different species ($P < 0.001$; Table S2). Litter chemical traits also differed significantly between plant organs ($P < 0.001$; Table S2), especially for the bamboo and coniferous species (Fig. 1). Specifically, bamboo litters were the most labile among the six litter types (Table S1), and both leaves and roots were generally located at the high quality end of the NMDS axes (Fig. 1). By contrast, broadleaf litters were more recalcitrant in comparison to bamboo litters and were generally located at the low quality end of the NMDS axes (Fig. 1), especially for the fine root litter (Table S1). In line with our expectations, bamboo and broadleaf litters generally exhibited higher and lower litter mass loss, respectively (Fig. 2). Coniferous was intermediate between bamboo and broadleaf litters. Overall, coniferous fine root litter was more recalcitrant than leaf litter, mainly because of higher concentrations in total phenols and tannins (Table S1), which may explain the lower mass loss of fine root litter compared with leaf litter over the course of the experiment (Fig. 2).

We found a significant tree species × incubation site interaction effect on leaf litter mass loss ($F_{4,40} = 13.23$, $P < 0.001$; Table 1), suggesting that leaf litter decomposition depends on the environment in which it decomposes (Ayres *et al.*, 2009a; Milcu & Manning, 2011; Lu *et al.*, 2017; Veen *et al.*, 2018; Lin *et al.*, 2019). This is mainly the result of lower leaf litter mass loss of broadleaf species in its 'away' site, especially in the bamboo forest (Fig. 2). By contrast, there is no significant tree species × incubation site interaction effect on fine root litter mass loss ($F_{4,40} = 0.78$, $P = 0.546$; Table 1). Accordingly, we found that HFA effects were generally inconsistent between leaves and fine roots over 1132 d of decomposition (Fig. 2). In addition, although the similarity in litter

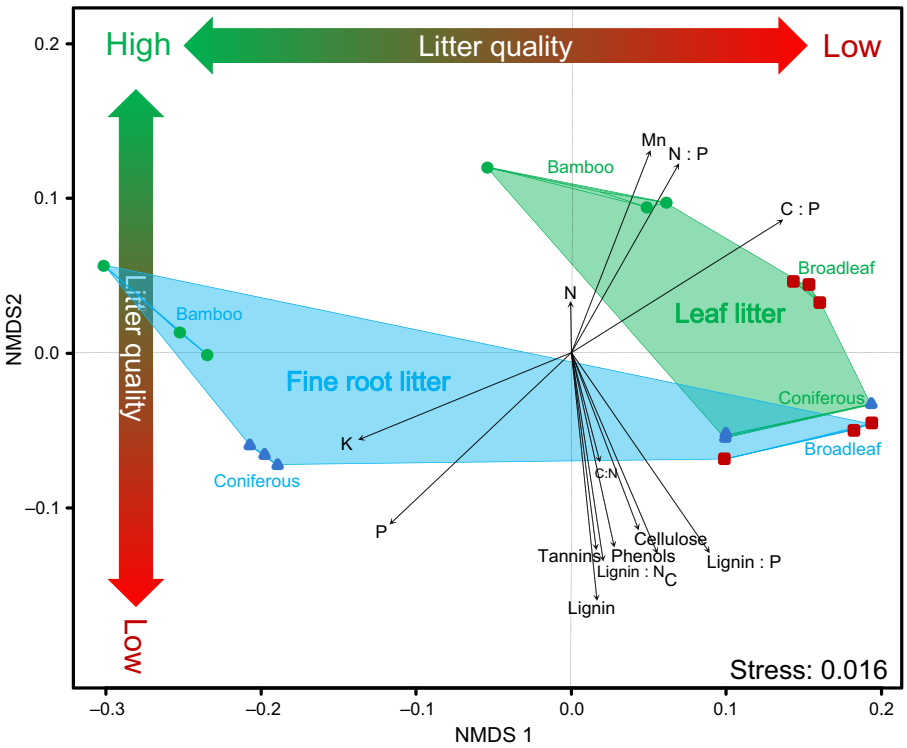

Fig. 1 Nonmetric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity matrices depicting litter chemical traits. Different organs were grouped by polygons (leaf in green; fine root in blue). Litter quality is reflected by the direction of the different nutrient components.

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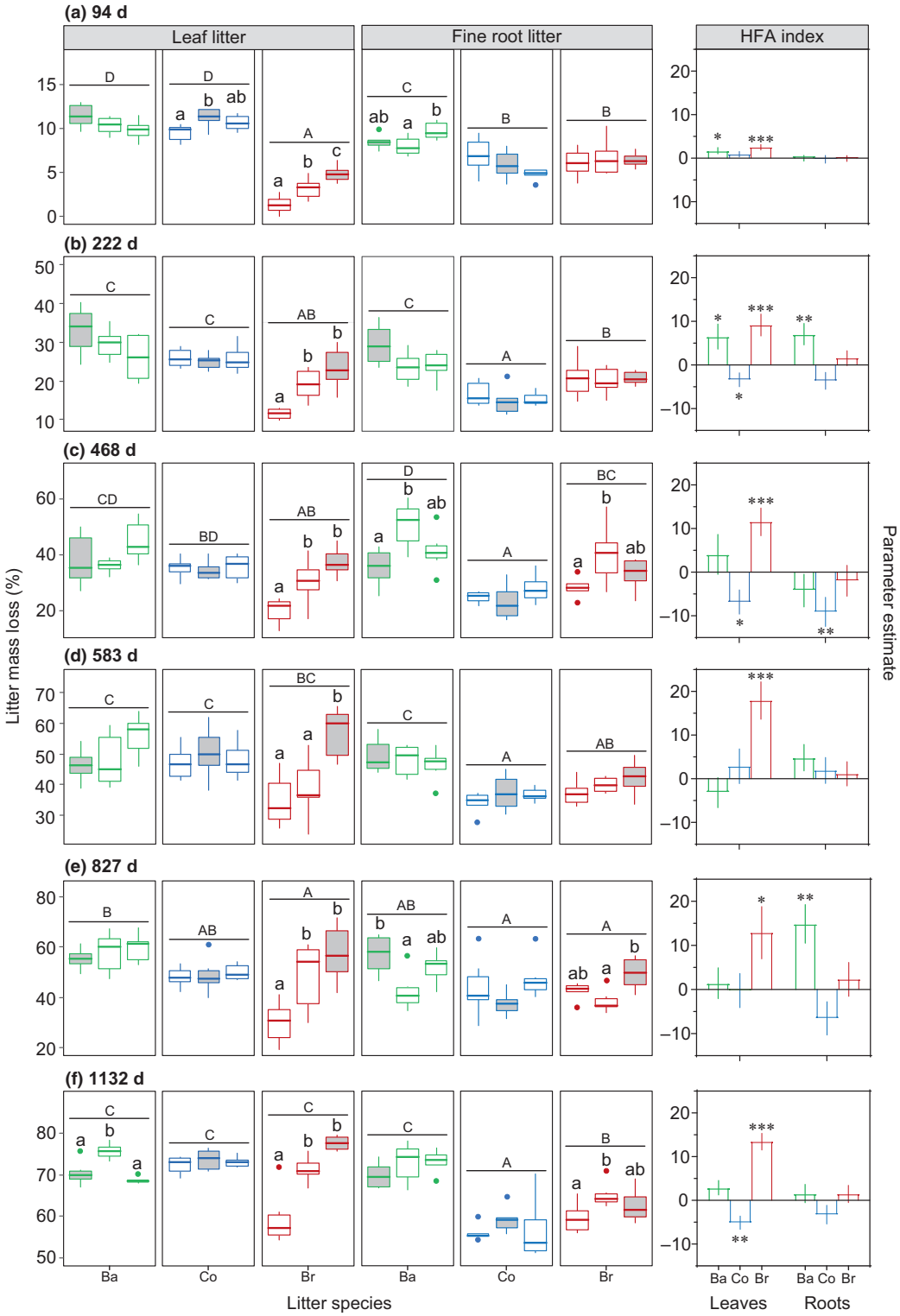

Fig. 2 Litter mass loss and home-field advantage (HFA) index of the six harvest times. At each harvest time (a–f), the left panels show the litter mass loss (%) of different organs (leaves and fine roots) for the three species that were reciprocally decomposed in the three forest sites and the right panel shows the HFA index estimated using the equation developed by Keiser *et al*. (2014). Ba, Bamboo species; Co, coniferous species; Br, broadleaf species. In the left panels, boxes represent the central 50% of the data and the whiskers on the boxes represent the 95% quantiles ($n = 6$). Within each panel, the different boxes from the left to the right represent the litter that was decomposed in the bamboo, coniferous and broadleaf sites, respectively. The grey closed boxes denote the litter that was decomposed in its 'home' site. Different lowercase letters indicate significant differences in litter mass loss among different incubation sites within each of the six litter types, while uppercase letters indicate significant differences among the six litter types (Tukey's HSD test, $P < 0.05$). In the right panels, a positive bar value means a 'home-field advantage', that is, litter decomposes faster beneath the plant species it derived from than beneath other species. Error bars represent ± SE ($n = 6$), asterisks indicate estimates significantly different from zero with: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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Table 1 Results from the most parsimonious linear mixed effects model to test for the effects of species, incubation site, harvest time and their interactions on mass loss of leaf and fine root litter, respectively (see Supporting Information Table S4 for model selection procedure).

	Leaf litter		Fine root litter	
	F-value	*P*-value	*F*-value	*P*-value
Variable				
Species	$F_{2,40}=36.24$	**<0.001**	$F_{2,40}=71.16$	**<0.001**
Site	$F_{2,40}=20.77$	**<0.001**	$F_{2,40}=1.05$	0.358
Time	$F_{1,269}=2327.41$	**<0.001**	$F_{1,269}=2275.74$	**<0.001**
Species × site	$F_{4,40}=13.23$	**<0.001**	$F_{4,40}=0.78$	0.546
Model performance				
logLik	−1097.78		−1071.02	
AICc	2224.90		2171.40	
ω_i	1.00		0.96	

Values in bold typeface represent significant effect with $P<0.05$; ω_i, model weight.

chemistry between leaves and roots varied in the order broadleaf > bamboo > coniferous (Table S3), the broadleaf species showed the highest degree of difference in HFA effects between leaves and roots, that is leaf litter exhibited significant HFA effects throughout the 1132-d of decomposition, but fine root litter did not (Fig. 2). The only case for which both leaf and root litters displayed significant HFA effects was for the bamboo litter after 222-d of decomposition (Fig. 2). Yet, this species showed a relatively low degree of similarity in litter chemistry between leaves and roots (Table S3). Therefore, these results contradict our first hypothesis predicting that plant species having a greater similarity in their chemical traits between leaves and roots should present a greater similarity in HFA effects, and suggest that the interactions between microbes and their substrates depend on the plant organ considered.

Interestingly, we found that root litter rarely showed significant HFA effects compared with leaf litter (Fig. 2). Contrary to our second hypothesis, these findings highlight that HFA effects are not higher for low litter quality compared with relatively high quality litter (Veen *et al.*, 2015b; Palozzi & Lindo, 2017; Lin *et al.*, 2019). In line with these results, previous microcosm incubation and field studies have also reported that root litter decomposition did not exhibit significant HFA effects (Jacobs *et al.*, 2018; Minerovic *et al.*, 2018). One potential explanation could be due to the differences in microhabitats along the soil profile. Leaf litter decomposes on the forest floor that is covered by freshly fallen litter, which is relatively rich in nutrients and labile carbon compounds, whereas root litter decomposes within the soil, in which the organic matter is heavily decomposed and more recalcitrant (Adl, 2003). These different resource conditions may generate significant differences in the composition and activity of microbial communities along the litter–soil continuum (Sterkenburg *et al.*, 2018). In particular, the microbial communities from recalcitrant environments may have a wider functional capacity than those originating from richer environments, meaning that they more efficiently decompose root litters that vary widely in their chemical characteristics (functional breadth hypothesis; Keiser *et al.*, 2011, 2014; Fanin *et al.*, 2016), thereby decreasing their specialization toward the litters they most frequently encounter. Alternatively, although we buried fine root litter in the soil close to the adult trees of targeted species, the soil environment is likely more heterogeneous than the forest floor because it includes fine root litters from many other coexisting tree species. Therefore, the adaptation of specialist decomposers to individual species might be less important in an environment in which the resources are highly diverse and mixed. Furthermore, we cannot exclude that the difference in microclimatic conditions along the soil profile, with notably higher water content in the soil, may also affect decomposer communities and reduce the differences in decomposition rates for root litter (Fanin *et al.*, 2019a). Additional studies simultaneously manipulating leaves and roots on the forest floor and in the soil will be necessary to disentangle the effects of microclimatic conditions from those of resource environment on HFA effects.

Conclusions

By using a long-term reciprocal litter transplant experiment, we sought to test whether HFA patterns were consistent between leaves and fine roots. We found that HFA effects were generally inconsistent between plant organs, either across or within species, thereby underlining that leaf and root litters need to be considered separately when evaluating the adaptation of decomposers to their substrates. These results have several implications. First, they emphasize that HFA is not more pronounced for recalcitrant (i.e. roots) than labile litter (i.e. leaves) (Veen *et al.*, 2015b; Palozzi & Lindo, 2017), and they demonstrate that HFA may also occur when litters are relatively rich in nutrients and labile carbon compounds (Lin *et al.*, 2019). Second, the results highlight that there is often some decoupling between the aboveground and belowground subsystems in terrestrial ecosystems (Cameron *et al.*, 2019; Delgado-Baquerizo *et al.*, 2019; Fanin *et al.*, 2019b), and this finding begs the question of whether the position at which soil communities perform decomposition is important to understand the local adaption of microbes to their sustrates. Finally, our results over a thousand days of incubation demonstrate an important temporal variability in HFA effects (Ayres *et al.*, 2009a; Fanin *et al.*, 2016; Veen *et al.*, 2018), indicating that the succession in microbial communities may be also an important factor to predict the variability in plant–soil interactions over time. We conclude that plant–microbe interactions contribute significantly to nutrient and carbon cycling, but these interactions may strongly depend on the plant organ considered and the environmental conditions at the local scale.

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Author contributions

DL designed the research. DL, PD, GY and HW performed the experiments with input from SQ, LZ, YY, XM and KM. DL carried out all of the statistical analyses with input from NF. DL and NF wrote the first draft of the manuscript. All authors contributed to manuscript completion and revision.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Descriptions of the study site, litter traits measurements and statistical analyses.

Table S1 Initial litter chemical traits of leaf and fine root litters for each of the three species used in this study.

Table S2 PERMANOVA statistics for the effects of species, organs and their interaction on litter chemical traits.

Table S3 Dissimilarity of chemical traits between leaf and root litters calculated with the Euclidean distance index among different litter types.

Table S4 Results of the model selection procedure of the linear mixed effects models used to test for the effects of species, incubation site, harvest time and their interactions on mass loss of leaf and fine root litter, respectively.

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