

1 **Litter quality and environmental controls of home-field advantage effects on litter decomposition**

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13

14 **Abstract**

15 The 'home-field advantage (HFA) hypothesis' predicts that plant litter is decomposed faster than  
16 expected in the vicinity of the plant where it originates from (i.e., its 'home') relative to some other  
17 location (i.e., 'away') because of the presence of specialized decomposers. Despite growing evidence for  
18 the widespread occurrence HFA effects, what drives HFA is not understood as its strength appears highly  
19 variable and context-dependent. Our work advances current knowledge about HFA effects by testing  
20 under what conditions HFA is most important. Using published data on mass loss from 125 reciprocal  
21 litter transplants from 35 studies, we evaluated if HFA effects were modulated by macroclimate, litter  
22 quality traits, and the dissimilarity between 'home' and 'away' of both the quality of reciprocally  
23 exchanged litters and plant community type. Our results confirmed the occurrence of an overall,  
24 worldwide, HFA effect on decomposition with on average 7.5% faster decomposition at home. However,  
25 there was considerable variation in the strength and direction (sometimes opposite to expectations) of  
26 these effects. While macroclimate and average litter quality had weak or no impact on HFA effects,  
27 home-field effects became stronger (regardless of the direction) when the quality of 'home' and 'away'  
28 litters became more dissimilar (e.g. had a greater dissimilarity in N:P ratio;  $F_{1,42} = 6.39$ ,  $P = 0.015$ ).  
29 Further, home-field effects were determined by the degree of difference between the types of  
30 dominant plant species in the 'home' versus 'away' communities ( $F_{2,105} = 4.03$ ,  $P = 0.021$ ). We conclude  
31 that home-field advantage is not restricted to particular litter types or climate zones, and that the  
32 dissimilarity in plant communities and litter quality between the 'home' and 'away' locations, are the  
33 most significant drivers of home-field effects.

34 **Keywords**

35 Home-field advantage (HFA) hypothesis, plant-soil interactions, litter decomposition, litter transplant,  
36 plant functional traits, decomposer communities

37

38 **Introduction**

39 The decomposition of plant litter is a key determinant of nutrient and carbon cycling worldwide (Swift et  
40 al. 1979). Until recently soil organisms that break down plant litter were thought to be mostly generalist  
41 consumers. However, evidence is growing that plant species have species-specific decomposer  
42 communities (Scheu et al. 2003; McGuire et al. 2010), suggesting that plant-decomposer interactions  
43 show a higher level of specificity than has been previously thought (Strickland et al. 2009b; Bezemer et  
44 al. 2010). There is considerable variation in the quality of residues that plants return to the soil (Cornwell  
45 et al. 2008) and many decomposer organisms may be adapted to break down particular litter types  
46 (Ayres et al. 2009). As a result, the decomposition rate of plant litter has been hypothesized to be faster  
47 than expected in the vicinity of the plant from which it is derived (i.e., at home) than away from that  
48 plant, and this “at home” benefit has been referred to as ‘home-field advantage (HFA)’ (Hunt et al. 1988;  
49 Gholz et al. 2000; Ayres et al. 2009). As such, experiments using successive litter incubations suggest  
50 that over time decomposer communities can specialize on litter types they encounter, thereby  
51 accelerating litter breakdown (Hansen 1999; Keiser et al. 2011).

52 Studies testing the HFA hypothesis using reciprocal litter transplant experiments have found  
53 highly variable results. While some studies have shown that decomposition was accelerated at their  
54 home relative to away from it (e.g. Vivanco and Austin 2008; Strickland et al. 2009a; Jacob et al. 2010;  
55 Madritch and Lindroth 2011), others have showed similar or even reduced decomposition at home

56 compared to away (e.g. Ayres et al. 2006; McGuire et al. 2010; Giesselmann et al. 2011; St John et al.  
57 2011). Furthermore, although two recent analyses focusing on forest ecosystems found that litter  
58 decomposition was on average increased at home (Ayres et al. 2009; Wang et al. 2012), neither fully  
59 explored the reasons underlying the wide variation in magnitude and direction of HFA effects between  
60 litter transplants. In addition, the meta-analysis by Wang et al. (2012) contains limitations which may  
61 have confounded the outcome because it included non-reciprocal experiments, used multiple time  
62 points within studies as independent replicates, gave equal weight to all studies irrespective of size, and  
63 did not include several studies reporting relevant data. Consequently, to better understand when and  
64 how specialized decomposer communities interact with litter to influence potential HFA effects, it is  
65 necessary to further explore the role played by key drivers of this interaction such as litter quality, the  
66 type of plant community present and litter incubation conditions.

67         In addition, HFA effects are only one of several types of interactions that take place between  
68 litter quality and litter incubation conditions (Freschet et al. 2012). A further improvement of our  
69 understanding of litter-site interactions will require us to take into account that incubation conditions  
70 are determined not only by decomposer community composition and activity (sensu Milcu and Manning  
71 2011; Freschet et al. 2012; Makkonen et al. 2012), but also by litter mixture effects (Wardle et al. 1997),  
72 and abiotic factors such as nutrient leaching, photodegradation and freeze-thaw cycles (Hobbie and  
73 Chapin 1996; Gartner and Cardon 2004; Austin and Vivanco 2006); these factors all interact with the  
74 quality of an individual litter to influence its decomposition rates. Thus, since many litter-site  
75 interactions can have positive or negative effects on litter decomposition rates and therefore contribute  
76 strongly to the context-dependency of observed “HFA effects”, any analysis of HFA effects should  
77 explicitly account for other co-occurring litter-site interactions.

78 By performing a synthesis of 125 reciprocal litter transplants from 35 studies we move beyond  
79 previous studies by Ayres et al. (2009; 11 reciprocal transplant studies) and Wang et al. (2012; 25  
80 reciprocal transplant studies) by including grassland-grassland and grassland-forest transplantations,  
81 and by testing four specific hypotheses aimed at explaining the context-dependency of HFA effects. Our  
82 first hypothesis is that the magnitude of HFA effects decreases when macroclimatic conditions for litter  
83 breakdown become more favorable. Warmer and moister conditions favor higher activity of soil  
84 organisms and faster litter breakdown irrespective of litter quality (Hobbie 1996; Aerts 1997; Trofymow  
85 et al. 2002). In such conditions, specialized decomposers are less likely to have a substantial impact on  
86 plant litter breakdown rate, as compared to conditions that favor slow litter breakdown. Our second  
87 hypothesis is that the occurrence and magnitude of HFA effects is negatively affected by litter quality.  
88 When plants display functional traits associated with resource conservation (e.g., thick leaves, low leaf  
89 nitrogen concentration and high concentrations of defense compounds), their litter is usually of low  
90 nutritional value and recalcitrant to decomposers (Cornelissen 1996; Wardle et al. 1998). In contrast to  
91 easily degradable litter, decomposition of recalcitrant litter is likely to require specialized decomposers  
92 such as wood decomposing fungi (e.g., Milcu and Manning 2011).

93 Our third hypothesis follows the “substrate quality-matrix quality interaction (SMI) hypothesis”  
94 (Freschet et al. 2012), we tested whether HFA effects became larger when the quality of the dominant  
95 litter exchanged between home and away sites becomes more dissimilar and when litters are  
96 transplanted across sites with increasingly dissimilar plant communities (Ayres et al. 2009; Freschet et al.  
97 2012). This is because the soil biota associated with any plant community should be best adapted to  
98 decomposing litters that are of similar quality to those from the dominant species in that community  
99 (Strickland et al. 2009b; Freschet et al. 2012). Our fourth hypothesis is that the absolute magnitude of  
100 home-field effects (whether accelerating decomposition at home or away) increases with both the  
101 dissimilarity in quality of the dominant litter and the dissimilarity in plant communities between the

102 home and away sites. This hypothesis recognizes that home-field effects can be negative as well as  
103 positive, and aims to determine the context-dependence of decomposition rates without any *a priori*  
104 expectation of the directionality of these differences. As such, while increased positive home-field  
105 effects (i.e., HFA) with increasing litter and plant community dissimilarity can indicate a higher degree of  
106 specialization of decomposers (Ayres et al. 2009; Freschet et al. 2012) and/or other litter-site  
107 interactions driving accelerated decomposition at home, increased negative home-field effects reflect  
108 situations where litter-site interactions drive accelerated decomposition away. For instance,  
109 decomposers may be limited by nutrients and respond strongly to the input of high quality litter from  
110 elsewhere, resulting in accelerated decomposition away from home (i.e. litter mixture effects Gartner  
111 and Cardon 2004; Hättenschwiler et al. 2005). Absolute measures for the home-field effect represent  
112 the strength of litter-site interactions irrespective of the opposing effects of these positive and negative  
113 influences.

114

## 115 **Methods**

### 116 *Literature search and selection criteria*

117 We compiled a data set of reciprocal litter transplant experiments by searching both ISI Web of  
118 Knowledge and Google Scholar using the search keys: “home field” AND “decomposition”, and  
119 “reciprocal transplant” AND “litter”, with the most recent search performed on 10 April 2013. This  
120 search identified a total of c. 800 studies, and from these we selected studies that: (1) used reciprocal  
121 transplants of leaf litter between home and away sites, hence only including reciprocal transplant, in  
122 contrast to also including one-way transplants (such as done in the analysis by Wang et al. 2012),  
123 allowing us to correct for variation in home-field effects due to different local incubation conditions and  
124 inherent differences in rates of decomposition between home and away sites (see also Ayres et al.

125 2009); (2) measured the percentage of mass loss (or mass remaining) of the litter; (3) were carried out  
126 across terrestrial ecosystems only; and (4) transplanted the dominant plant species (or a mixture of  
127 several of the dominant species), as subordinate litter types will have weaker impacts than dominant  
128 litter types on the composition of the soil decomposer community, resulting in a weaker link between  
129 litter traits of subordinate plant species and HFA effects (Freschet et al. 2012). As most of the studies did  
130 not provide quantitative measurements on the abundance of litter types within home or away sites, we  
131 classified litter types as dominant or subordinate based on qualitative information on community  
132 composition presented in each of the studies.

133

#### 134 *Data extraction*

135 From each of the studies that met our selection criteria we recorded the litter mass that was  
136 decomposed at home ( $\bar{X}_H$ ) and away ( $\bar{X}_A$ ). When multiple litter species were transplanted within one  
137 study, we used each species as a separate observation. In line with the meta-analysis by Freschet et al.  
138 (2013), we used data for percentage mass loss from the final time of harvest within each of the studies  
139 in order to standardize the input information used to calculate k-values across all studies, irrespective of  
140 the type of experimental set-up (e.g., field, common garden, laboratory and greenhouse microcosms)  
141 and sampling intervals and temporal fluctuations in litter decomposition dynamics resulting from  
142 temporal shifts in environmental conditions.

143 In addition to data on litter mass loss, when available, we recorded initial litter quality (C, N, P  
144 and lignin concentrations, and C:N, N:P and lignin:N ratios), climate conditions (total annual rainfall and  
145 mean annual temperature), and the dissimilarity between the home and away communities; we  
146 propose that all factors have the potential to modulate the HFA effects. The dissimilarity between home

147 and away communities was classified in three categories based on whether they shared dominant  
148 species or dominant functional groups (i.e., trees, shrubs, grasses or forbs): (a) communities had the  
149 same dominant species and the same dominant functional group, (b) communities had different  
150 dominant species, but the same dominant functional group, or (c) communities had both different  
151 dominant species and functional groups. Finally, we also recorded study duration (months), mesh size of  
152 litterbags (mm), ecosystem type in three categories (forest, grassland or other).

153           When data were only available as figures, we used Datathief III (B. Tummers 2006,  
154 [www.datathief.org](http://www.datathief.org)) to extract data from figures. In those cases where the study did not present the  
155 information of interest, we contacted the authors. When authors did not respond after sending two  
156 reminders the study was excluded from the analyses. Climate data that was not presented in the papers  
157 was retrieved from the relevant national weather institutes or from [www.worldclimate.com](http://www.worldclimate.com) when  
158 possible.

159           In total, we collected 125 observations on reciprocal litter transplants from 35 independent  
160 studies (Fig. 1). We were not able to collect climate and litter quality data for all these studies. The  
161 number of studies/reciprocal transplants that were collected for each of the climate and litter quality  
162 variables are: mean annual precipitation (MAP) 34/119; mean annual temperature (MAT) 32/124; C  
163 14/57; N 22/86; P 8/44; lignin 17/58; C:N 18/72; N:P 8/44; and lignin:N 16/56.

164

#### 165 *Data analysis*

166 We calculated the home-field advantage index (HFAI) for each pair of reciprocal litter transplants  
167 (following Ayres et al. 2009). We use the HFAI to correct for inherent differences in rates of  
168 decomposition between habitat and litter types by directly comparing reciprocal transplants.



169           Given that the HFAI reflects all possible interactions between the transplanted litter and the  
170 environmental conditions at the incubation site and not only HFA effects, we refer to the difference in  
171 decomposition rate between home and away sites as litter-site interactions. Litter-site interactions can  
172 be either positive or negative, depending on whether decomposition is accelerated or decelerated at  
173 home respectively. In this context, we refer to HFA effects only when litter-site interactions are  
174 significantly positive.

175           For each observation on percentage litter mass loss (%ML) we determined the decomposition  
176 constant  $k$  using a negative exponential function  $\%ML = 100 - 100 e^{-kt}$  where  $t$  is the duration of litter  
177 incubation in years. The use of  $k$  allows us to compare decomposition rates between studies of different  
178 duration, because  $k$  is independent of time. We calculated the HFAI (Ayres et al. 2009), which represents  
179 the percentage by which the decomposition process is sped up or slowed down at home, as:

$$180 \quad \text{HFAI (\%)} = \left[ \left( \frac{A_{Rk_a} + B_{Rk_b}}{2} \right) / \left( \frac{A_{Rk_b} + B_{Rk_a}}{2} \right) \right] \times 100 - 100$$

181           where  $i_{Rk_j}$  represents the relative decomposition constant  $k$  of species  $i$  in environment  $j$ .

182           We tested whether, across all studies, HFAI was significantly higher than zero using a one-  
183 sample  $t$ -test, which would indicate an overall HFA effect. We then used general linear models (GLMs) to  
184 test whether field studies differed from laboratory and common garden studies and how mesh size and  
185 study duration influenced litter-site interactions. We defined laboratory and common garden  
186 experiments as studies that were carried out in pots or in plots where plants were grown for less than  
187 one year before litter was reciprocally transplanted. All other studies, including studies on forest  
188 plantations that were established for over one year, were considered field studies.

189           We used GLMs to test how mean macroclimatic conditions (MAP and MAT), mean litter quality  
190 (%N, %P, %lignin, C:N, N:P and lignin:N), the relative difference between the qualities of reciprocally

191 transplanted litters ( $\frac{|Quality_A - Quality_B|}{Quality_A + Quality_B}$ ), and community dissimilarity between home- and away sites  
192 affected the strength and direction of home-field effects. We could not test how the relative difference  
193 in climate conditions affected HFAI, because “home” and “away” climate conditions were the same in 32  
194 out of 35 studies. We used HFAI as a response variable, and each of the climate measures, litter quality  
195 and community dissimilarity variables were used as predictor variables. We used a compound symmetry  
196 covariance structure (with the intra-class correlation coefficient specified) to account for the hierarchical  
197 and non-independence grouping of the observations (Zuur et al. 2009), because in some cases multiple  
198 observations originate from the same study and some observations within studies shared “home” or  
199 “away” decomposition rates. By determining this correlation structure, we explicitly define the influence  
200 of the dependency of nested “home” and “away” contrasts in the variation of home-field effects.  
201 Because few studies presented all macroclimatic and litter quality data, we used separate models to test  
202 the influence of each of the macroclimate and litter quality variables on HFAI.

203 In addition, we also used GLMs with the absolute value for HFAI as a response variable to assess  
204 whether macroclimate, litter quality, dissimilarity in litter quality and community dissimilarity affected  
205 the *magnitude* of litter-site interactions, regardless of their direction.

206 All analyses were performed in R version 2.14 (R Development Core Team) using the ‘nlme’  
207 package for linear mixed effects models. We tested model residuals for normality using a Shapiro-Wilk  
208 test and found that most data were slightly left-skewed. However, evaluation of the regression residuals  
209 shows homoscedastic distributions across all values of the predicted values, and therefore the use of  
210 parametric analyses, i.e., GLMs, was justified.

211

## 212 **Results**

213 Across all studies decomposition was faster at home than away (Fig. 2). The HFAI showed 5.6% faster  
214 decomposition at home than away ( $t = 3.89, P < 0.001, df = 124$ ). Even though this result indicates  
215 positive litter-site interactions and thus a net HFA, the effect was relatively small. Moreover,  
216 decomposition ranged from 34.1% slower to 57.5% faster than expected at home, which indicates  
217 considerable variation in the magnitude and direction between observations.

218

### 219 *Experimental conditions*

220 The direction of litter-site interactions was different between studies conducted in the field and these  
221 carried out in laboratory or common garden conditions ( $F_{1,123} = 10.96, P = 0.001, R^2 = 0.08$ ; Fig 2). In the  
222 laboratory or common garden, decomposition was on average 6.0% ( $t = -2.24, P = 0.040, df = 16$ ) slower  
223 at home than away. In contrast, decomposition in the field was 7.5% faster at home than away ( $t = 4.79,$   
224  $P < 0.001, df = 107$ ). The magnitude and direction of litter-site interactions was affected neither by mesh  
225 size ( $F_{1,106} = 0.72, P = 0.397, R^2 = 0.01$ ) nor by study duration ( $F_{1,106} = 1.79, P = 0.183, R^2 = 0.02$ ).

226

### 227 *Macroclimatic conditions*

228 Litter-site interactions were not explained by mean annual temperature (MAT;  $F_{1,101} = 0.06, P = 0.810, R^2$   
229  $< 0.01$ ) or mean annual precipitation (MAP;  $F_{1,106} = 1.85, P = 0.177, R^2 = 0.02$ ). In addition, MAT ( $F_{1,101} =$   
230  $0.39, P = 0.533, R^2 < 0.01$ ) and MAP ( $F_{1,106} = 1.69, P = 0.196, R^2 = 0.01$ ) did not affect the magnitude of  
231 the interactions between litter and incubation site.

232

### 233 *Litter quality*

234 Average litter quality (i.e., the average quality of pairs of reciprocally transplanted litters) expressed in  
235 terms of C:N or N:P ratio affected litter-site interactions (Table 1), where the HFAI decreased with an  
236 increasing C:N ratio and tended to increase with an increasing N:P ratio. The other variables indicating  
237 litter quality did not affect litter-site interactions or the magnitude of litter-site interactions, regardless  
238 of the direction (Table 1).

239

#### 240 *Litter quality dissimilarity*

241 Overall, we found some indications that the strength of litter-site interactions increased when litter  
242 became more dissimilar. More specifically, litter-site interactions became significantly more positive  
243 when N:P ratio and lignin:N ratio differed more between home and away sites (Table 2). This was  
244 marginally significant when P and lignin contents became more dissimilar (Table 2). The magnitude of  
245 litter-site interactions increased with increasing dissimilarity in the quality of reciprocally exchanged  
246 litters, for litter lignin content, N:P ratio and lignin:N ratio (Table 2).

247

#### 248 *Community dissimilarity*

249 Litter-site interactions were affected by the dissimilarity in plant community composition between  
250 home and away sites ( $F_{2,105} = 4.03$ ,  $P = 0.021$ ,  $R^2 = 0.08$ ; Fig. 3a). Litter-site interactions were neutral for  
251 transplants between communities with the same dominant plant species (Fig 3a). They were  
252 significantly positive for litter transplants across communities with different dominant species from the  
253 same functional group, and they tended to be highest and positive for transplants across communities  
254 with different dominant plant species from different functional groups (Fig 3a). Similarly, litter-site  
255 interactions were affected by home and away ecosystem type ( $F_{2,103} = 3.39$ ,  $P = 0.038$ ,  $R^2 = 0.06$ ; Fig 4a).

256 For litter transplants between two grasslands litter-site interactions were neutral, while for transplants  
257 between two forests litter-site interactions were significantly positive. Litter-site interactions also  
258 tended to be positive between forests and grasslands (Fig 4a).

259 The magnitude (regardless of direction) of interactions between litter type and incubation site  
260 also affected by community dissimilarity ( $F_{2,105} = 10.23$ ,  $P < 0.001$ ,  $R^2 = 0.17$ ) and became increasingly  
261 stronger when plant communities became increasingly dissimilar (Fig 3b). Similarly, the magnitude  
262 (regardless of direction) of litter-site interactions depended on ecosystem type ( $F_{2,103} = 9.04$   $P < 0.001$ ,  $R^2$   
263  $= 0.15$ ) and was larger for grassland-forest transplants than for grassland-grassland and forest-forest  
264 transplants (Fig 4b).

265

## 266 **Discussion**

267 We found an overall positive effect of litter-site interactions on decomposition rate at home of 7.5%,  
268 indicative of HFA influencing decomposition processes. This effect is comparable to that measured in  
269 two previous analyses (Ayres et al. 2009; Wang et al. 2012), which respectively determined overall HFA  
270 effects of 8% and 4%. However, despite being statistically significant, the importance of HFA for  
271 decomposition processes appears relatively small in comparison to climatic and litter quality variables,  
272 which explain together around 70% of the variation in global decomposition rates (Trofymow et al.  
273 2002; Parton et al. 2007; Cornwell et al. 2008). Nevertheless, the tremendous variation in litter-site  
274 interactions (sometimes in opposite direction as expected by the HFA hypothesis) suggests that HFA  
275 effects may be context-dependent. For example, our results indicate that litter-site interactions become  
276 more strongly positive when the quality of litter and the composition of plant communities become  
277 more dissimilar (Figs. 3, 4), and hence of considerable importance in some settings. As such, the

278 importance of HFA for decomposition processes may potentially vary depending on both experimental  
279 and environmental conditions, as we now discuss.

280

### 281 *Experimental conditions*

282 Litter-site interactions were on average much weaker for laboratory and common garden studies than  
283 for field studies. This could emerge because laboratory and common garden experiments involve  
284 disturbances to the incubation medium (e.g., handling of soil, sowing of plant communities, exclusion of  
285 larger soil fauna) that in turn may disrupt plant-decomposer interactions and therefore HFA effects. As  
286 such, after a disturbance the development of a specialized decomposer community responsible for HFA  
287 effects may take longer than the duration of most laboratory experiments (Ayres et al. 2006). In contrast  
288 to the analysis by Wang et al. (2012), we did not find an effect of study duration on home-field effects,  
289 showing that HFA was equally able to occur in studies with short and long incubation time. The  
290 discrepancy between the results of these two analyses could have emerged from fundamental  
291 differences between the two analyses, such as Wang et al. (2012) using non-reciprocal experiments,  
292 treating multiple harvests for each litter over time as independent data points and including  
293 considerably fewer studies. Finally, we found that litter bag mesh size had no influence on litter-site  
294 interactions. This suggests a relatively small influence of macro-faunal decomposers on HFA and  
295 therefore supports the idea that HFA is primarily driven by microbes (Keiser et al. 2011).

296

### 297 *Macroclimate*

298 In contrast with our first hypothesis that specialized interactions between litter and decomposers were  
299 more important under colder and drier conditions, we found that litter-site interactions occur

300 worldwide and are not specifically bound to certain biomes or climatic conditions (Fig. 1). This is  
301 consistent with a recent litter transplant experiment across biomes by Makkonen et al. (2012), which did  
302 not find evidence for differences in adaptation of decomposer communities across highly contrasting  
303 climates. Our analyses show therefore that the degree of specialization in the soil decomposer  
304 community with regard to litter types is not strongly constrained by climatic conditions. This finding is in  
305 line with recent experimental study, which showed that climatic conditions (in terms of drought) had no  
306 impact on microbial specialization on different litter types after one year of litter incubation (Allison et  
307 al. 2013).

308

#### 309 *Litter quality*

310 While our second hypothesis predicted that HFA would increase when litter quality decreases because  
311 the breakdown of recalcitrant litters may require the action of highly specialized decomposers (Ayres et  
312 al. 2009; Milcu and Manning 2011), our results showed that positive interactions between litter type  
313 and incubation site occur for both low-quality and high-quality litters. This is in agreement with the  
314 findings of Freschet et al. (2012) that litters decomposed best in environments where the litter layer is  
315 of similar quality, and these of Fierer et al. (2007) and Strickland et al. (2009b) that microbial phyla  
316 sourced from low and high quality habitats performed better on low and high quality litter respectively.  
317 Further, Allison et al. (2013) showed that microbial communities can be adapted to decompose litter  
318 from nitrogen-amended plots, but not from control plots, indicating further that HFA may not  
319 necessarily increase when litter quality decreases.

320

#### 321 *Litter and community dissimilarity*

322 In support for our third hypothesis, i.e., the SMI hypothesis, we observed stronger HFA effects with an  
323 increase in dissimilarity between the quality of transplanted litters or between the types of plant  
324 community compared (Ayres et al. 2009; Freschet et al. 2012), showing that HFA effects are context-  
325 dependent. This may have consequences for litter decomposition rates at the community level, as well  
326 as at the level of individual plants. For instance, as a result of current global change plant species may  
327 rapidly expand their ranges (Morrien et al. 2010) and enter new communities where local plants may  
328 have contrasting functional traits. Under such conditions specialized decomposers will be absent and  
329 decomposition of litter from the range-expanding species will be slowed down. At the level of individual  
330 plants, neighboring plant species with a different chemical composition may each develop their own  
331 specialized decomposer community (Bezemer et al. 2010), resulting in locally adapted decomposer  
332 communities, thereby promoting HFA (Freschet et al. 2012).

333           The greater magnitude (independent of direction) of litter-site interactions with increasing litter  
334 and plant community dissimilarity indicates that the average strength of interactions between litter  
335 quality and the decomposer community become apparent when communities that are more dissimilar  
336 are considered (Table 2, Figs 3b and 4b), which is consistent with our fourth hypothesis. Higher positive  
337 litter-site interactions (i.e., HFA effects) with increasing litter and plant community dissimilarity are  
338 consistent with a higher degree of specialization of decomposers (Ayres et al. 2009; Freschet et al.  
339 2012). However, our finding that higher negative litter-site interactions also occur is less intuitive.  
340 Nonetheless, the latter may be possible when the quality of the transplanted litter differs from the  
341 average litter quality in its home community. In fact, the SMI hypothesis (an extension of the HFA  
342 hypothesis; Freschet et al. 2012), suggests that high quality litter could decompose slower than  
343 expected in a habitat where the overall litter quality is low, because under such conditions decomposers  
344 at home may not be specialized to breakdown that litter (Strickland et al. 2009b; Freschet et al. 2012).  
345 Moreover, in sites with low litter quality, decomposers may be limited by nutrients and respond strongly



346 to the input of high quality litter, resulting in litter decomposition faster than expected away from rather  
347 than at home (Gartner and Cardon 2004; Hättenschwiler et al. 2005), i.e. negative litter-site interactions.  
348 In addition, decomposer communities can also be specialized to many types of compounds that were  
349 not considered in this study (e.g., phenolics and alkaloids), but that can be important drivers of the  
350 interactions between litter quality and decomposers (Hättenschwiler and Vitousek 2000; Baldrian 2006).  
351 Further, litters from other plant organs such as stems and roots also have an impact on the decomposer  
352 activity that do not necessarily match that of leaves from the same species (Freschet et al. 2013).

353

#### 354 *Conclusions*

355 We conclude that, despite large variation in the strength and direction of litter-site interactions,  
356 detectable HFA effects can occur worldwide and across all litter types. Dissimilarity in both litter quality  
357 and dominant species among plant communities both contributed significantly in explaining the context-  
358 dependency of HFA effects. Additionally, the large remaining unexplained variation in the strength and  
359 direction of litter-site interactions suggests that other types of interactions between litter, decomposers  
360 and incubation conditions play substantial roles in controlling litter decomposition processes.

361 These results emphasize that further investigations of how variation in environmental factors  
362 (e.g. community litter quality), abiotic incubation conditions (e.g. macroclimate and soil fertility) and  
363 litter mixture effects (sensu Freschet et al. 2012; Makkonen et al. 2012) control litter-site interactions  
364 are needed. Moreover, such knowledge is necessary to fine-tune current large-scale decomposition  
365 models (Moorhead and Sinsabaugh 2006; McGuire and Treseder 2010; van der Wal et al. 2013).

366 Further, HFA offers considerable potential for better understanding plant-soil feedback, a two-  
367 step process whereby plants provide resources for both decomposers and for root-associated biota,

368 which in turn impact on the plants (Bever et al. 1997; Wardle et al. 2004). Until now, plant-soil  
369 feedbacks involving decomposers and root-associated organisms have been mainly studied in  
370 separation, with few studies explicitly considering whether plants undergo positive or negative  
371 feedbacks with the decomposer subsystem. Our understanding of feedbacks of plants with decomposers  
372 would benefit from explicit recognition of the role of HFA in influencing the release of nutrients from  
373 decomposing plant litter and the consequences for plant nutrition, growth and community structure  
374 (van der Putten et al. 2013).

375

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383

#### 384 **References (46)**

385 Aerts R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A  
386 triangular relationship. - *Oikos*, 79: 439-449.

387 Allison S.D. et al. (2013). Microbial abundance and composition influence litter decomposition response  
388 to environmental change. - *Ecology*, 94: 714-725.

389 Austin A.T. and Vivanco L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by  
390 photodegradation. - *Nature*, 442: 555-558.

391 Ayres E. et al. (2006). Do plant species encourage soil biota that specialise in the rapid decomposition of  
392 their litter? - *Soil Biol Biochem*, 38: 183-186.

393 Ayres E. et al. (2009). Home-field advantage accelerates leaf litter decomposition in forests. - *Soil Biol*  
394 *Biochem*, 41: 606-610.

395 Baldrian P. (2006). Fungal laccases - occurrence and properties. - *Fems Microbiol. Rev.*, 30: 215-242.

396 Bever J.D. et al. (1997). Incorporating the soil community into plant population dynamics: the utility of  
397 the feedback approach. - *J Ecol*, 85: 561-573.

398 Bezemer T.M. et al. (2010). Divergent composition but similar function of soil food webs beneath  
399 individual plants: plant species and community effects. - *Ecology*: 3027-3036.

400 Cornelissen J.H.C. (1996). An experimental comparison of leaf decomposition rates in a wide range of  
401 temperate plant species and types. - *J Ecol*, 84: 573-582.

402 Cornwell W.K. et al. (2008). Plant species traits are the predominant control on litter decomposition  
403 rates within biomes worldwide. - *Ecol Lett*, 11: 1065-1071.

404 Fierer N. et al. (2007). Toward an ecological classification of soil bacteria. - *Ecology*, 88: 1354-1364.

405 Freschet G.T. et al. (2012). Multiple mechanisms for trait effects on litter decomposition: moving beyond  
406 home-field advantage with a new hypothesis. - *J Ecol*, 100: 619-630.

407 Freschet G.T. et al. (2013). Linking litter decomposition of above and belowground organs to plant-soil  
408 feedbacks worldwide. - *J Ecol*, 101: 943-952.

409 Gartner T.B. and Cardon Z.G. (2004). Decomposition dynamics in mixed-species leaf litter. - *Oikos*, 104:  
410 230-246.

411 Gholz H.L. et al. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments:  
412 toward a global model of decomposition. - *Glob. Change Biol.*, 6: 751-765.

413 Giesselmann U.C. et al. (2011). Lack of home-field advantage in the decomposition of leaf litter in the  
414 Atlantic Rainforest of Brazil. - *Appl. Soil Ecol.*, 49: 5-10.

415 Hansen R.A. (1999). Red oak litter promotes a microarthropod functional group that accelerates its  
416 decomposition. - *Plant Soil*, 209: 37-45.

417 Hättenschwiler S. et al. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. In: *Annual*  
418 *Review of Ecology Evolution and Systematics*. Annual Reviews, pp. 191-218.

419 Hättenschwiler S. and Vitousek P.M. (2000). The role of polyphenols in terrestrial ecosystem nutrient  
420 cycling. - *Trends Ecol Evol*, 15: 238-243.

421 Hobbie S. and Chapin F.S., III (1996). Winter regulation of tundra litter carbon and nitrogen dynamics. -  
422 *Biogeochemistry*, 35: 327-338.

423 Hobbie S.E. (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. -  
424 *Ecol Monogr*, 66: 503-522.

425 Hunt H.W. et al. (1988). Nitrogen limitation of production and decomposition in prairie, mountain  
426 meadow and pine forest. - *Ecology*, 69: 1009-1016.

427 Jacob M. et al. (2010). Leaf litter decomposition in temperate deciduous forest stands with a decreasing  
428 fraction of beech (*Fagus sylvatica*). - *Oecologia*, 164: 1083-1094.

429 Keiser A.D. et al. (2011). The effect of resource history on the functioning of soil microbial communities  
430 is maintained across time. - *Biogeosciences*, 8: 1477-1486.

431 Madritch M.D. and Lindroth R.L. (2011). Soil microbial communities adapt to genetic variation in leaf  
432 litter inputs. - *Oikos*, 120: 1696-1704.

433 Makkonen M. et al. (2012). Highly consistent effects of plant litter identity and functional traits on  
434 decomposition across a latitudinal gradient. - *Ecol Lett*, 15: 1033-1041.

435 McGuire K.L. and Treseder K.K. (2010). Microbial communities and their relevance for ecosystem  
436 models: Decomposition as a case study. - *Soil Biol Biochem*, 42: 529-535.

437 McGuire K.L. et al. (2010). Slowed decomposition is biotically mediated in an ectomycorrhizal, tropical  
438 rain forest. - *Oecologia*, 164: 785-795.

439 Milcu A. and Manning P. (2011). All size classes of soil fauna and litter quality control the acceleration of  
440 litter decay in its home environment. - *Oikos*, 120: 1366-1370.

441 Moorhead D.L. and Sinsabaugh R.L. (2006). A theoretical model of litter decay and microbial interaction.  
442 - *Ecol Monogr*, 76: 151-174.

443 Morrien E. et al. (2010). Climate change and invasion by intracontinental range-expanding exotic plants:  
444 the role of biotic interactions. - *Ann. Bot.*, 105: 843-848.

445 Parton W. et al. (2007). Global-scale similarities in nitrogen release patterns during long-term  
446 decomposition. - *Science*, 315: 361-364.

447 Scheu S. et al. (2003). The soil fauna community in pure and mixed stands of beech and spruce of  
448 different age: trophic structure and structuring forces. - *Oikos*, 101: 225-238.

449 St John M.G. et al. (2011). No 'home' versus 'away' effects of decomposition found in a grassland-forest  
450 reciprocal litter transplant study. - *Soil Biol Biochem*, 43: 1482-1489.

451 Strickland M.S. et al. (2009a). Testing the functional significance of microbial community composition. -  
452 *Ecology*, 90: 441-451.

453 Strickland M.S. et al. (2009b). Litter quality is in the eye of the beholder: initial decomposition rates as a  
454 function of inoculum characteristics. - *Funct Ecol*, 23: 627-636.

455 Swift M.J. et al. (1979). *Decomposition in terrestrial ecosystems*. Blackwell Scientific, Oxford, UK.

456 Trofymow J.A. et al. (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of  
457 litter quality and climate. - *Can. J. For. Res.*, 32: 789-804.

458 van der Putten W.H. et al. (2013). Plant-soil feedbacks: the past, the present and future challenges. - *J*  
459 *Ecol*, 101: 265-276.

460 van der Wal A. et al. (2013). A thready affair: linking fungal diversity and community dynamics to  
461 terrestrial decomposition processes. - *Fems Microbiol. Rev.*, 37: 477-494.

462 Vivanco L. and Austin A.T. (2008). Tree species identity alters forest litter decomposition through long-  
463 term plant and soil interactions in Patagonia, Argentina. - *J Ecol*, 96: 727-736.

464 Wang Q. et al. (2012). Home-field advantage of litter decomposition and nitrogen release in forest  
465 ecosystems. - *Biol. Fertil. Soils*, 49: 427-434.

466 Wardle D.A. et al. (2004). Ecological linkages between aboveground and belowground biota. - *Science*,  
467 304: 1629-1633.

468 Wardle D.A. et al. (1998). Can comparative approaches based on plant ecophysiological traits predict the  
469 nature of biotic interactions and individual plant species effects in ecosystems? - *J Ecol*, 86: 405-  
470 420.

471 Wardle D.A. et al. (1997). Biodiversity and plant litter: Experimental evidence which does not support  
472 the view that enhanced species richness improves ecosystem function. - *Oikos*, 79: 247-258.

473 Zuur A.F. et al. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, USA.

474

475

476 **Table 1.** Influence of average litter quality (i.e. the average quality of pairs of reciprocally transplanted  
 477 litters) on litter-site interactions (top), and on the magnitude of litter-site interactions regardless of  
 478 direction (bottom) as revealed by general linear models (GLM) on the home-field advantage index (HFAI;  
 479 sensu Ayres et al. 2009).

	F	df	P	R <sup>2</sup>	n	
<i>Effect of litter quality on litter-site interactions</i>						
N	1.66	1, 83	0.201	0.02	85	
P	0.59	1, 42	0.447	0.01	44	
Lignin	0.10	1, 56	0.755	<0.01	58	
C:N	<b>4.68</b>	<b>1, 57</b>	<b>0.035</b>	<b>0.09</b>	<b>59</b>	<b>(-)</b>
N:P	<i>3.68</i>	<i>1, 42</i>	<i>0.062</i>	<i>0.08</i>	<i>44</i>	<i>(+)</i>
Lignin:N	0.50	1, 54	0.483	0.01	56	
<i>Effect of litter quality on the overall magnitude of litter-site interactions</i>						
N	1.22	1, 83	0.271	0.02	85	
P	0.94	1, 42	0.336	0.02	44	
Lignin	0.04	1, 56	0.833	<0.01	58	
C:N	2.20	1, 57	0.143	0.04	59	
N:P	2.16	1, 42	0.149	0.05	44	
Lignin:N	0.37	1, 54	0.544	0.01	56	

480 Values in boldface represent significant effects with  $P < 0.05$ , values in italic represent effects with  $P <$   
 481  $0.1$ . The direction of significant effects is indicated between brackets (+/-). F = F-value from the GLMs, df  
 482 = degrees of freedom, P = P-value, R<sup>2</sup> represents the % variance explained by the GLMs on HFAI, n =  
 483 number of observations, i.e. pairs of reciprocally transplanted litters.

484

485 **Table 2.** Influence of dissimilarity in litter quality (pairs of reciprocally transplanted litters) on litter-site  
 486 interactions (top) and the magnitude of litter-site interactions regardless of direction (bottom) as  
 487 revealed by general linear models (GLM) on the home-field advantage index (HFAI; sensu Ayres et al.  
 488 2009).

	F	df	P	R <sup>2</sup>	n	
<i>Effect of litter dissimilarity on litter-site interactions</i>						
N	1.66	1, 83	0.201	0.02	85	
P	3.61	1, 42	0.064	0.08	44	(+)
Lignin	3.70	1, 56	0.059	0.06	58	(+)
C:N	0.01	1, 57	0.925	<0.01	59	
N:P	<b>6.39</b>	<b>1, 42</b>	<b>0.015</b>	<b>0.13</b>	<b>44</b>	<b>(+)</b>
Lignin:N	<b>4.36</b>	<b>1, 54</b>	<b>0.040</b>	<b>0.09</b>	<b>56</b>	<b>(+)</b>
<i>Effect of litter dissimilarity on the overall magnitude of litter-site interactions</i>						
N	0.61	1, 83	0.439	0.01	85	
P	2.04	1, 42	0.160	0.05	44	
Lignin	<b>13.85</b>	<b>1, 56</b>	<b>&lt;0.001</b>	<b>0.20</b>	<b>58</b>	<b>(+)</b>
C:N	0.02	1, 57	0.888	<0.01	59	
N:P	<b>4.47</b>	<b>1, 42</b>	<b>0.040</b>	<b>0.10</b>	<b>44</b>	<b>(+)</b>
Lignin:N	<b>11.87</b>	<b>1, 54</b>	<b>0.001</b>	<b>0.18</b>	<b>56</b>	<b>(+)</b>

489 Values in boldface represent significant effects with  $P < 0.05$ , values in italic represent effects with  $P <$   
 490 0.1. The direction of significant effects is indicated between brackets (+/-). F = F-value from the GLMs, df  
 491 = degrees of freedom,  $P$  =  $P$ -value,  $R^2$  represents the % variance explained by the GLMs on HFAI, n = the  
 492 number of observations, i.e. pairs of reciprocally transplanted litters.



493 **Figure legends**

494 Figure 1. World map of litter-site interactions, expressed as the average home-field advantage index  
495 (HFAI) for each of the 31 field studies. Each circle represents one study (for details and references of  
496 each of the studies see Appendix 1). Circle size corresponds to the average magnitude of litter-site  
497 interactions (HFAI) per study. Circle shading represents the direction of litter-site interactions: white =  
498 accelerated decomposition at home; black = decelerated decomposition at home.

499

500 Figure 2. Magnitude and direction of litter-site interactions, expressed as the home-field advantage  
501 index (HFAI), for: all studies, laboratory and common garden studies only, and field studies only. Large  
502 dots show the mean HFAI and bars represent 95% confidence intervals. Numbers between brackets are  
503 the number of samples in each group. Asterisks indicate whether litter-site interactions differ from zero  
504 at  $P < 0.05$  \*,  $P < 0.01$  \*\* and  $P < 0.001$  \*\*\*. Significantly positive litter-site interactions indicate HFA  
505 effects.

506

507 Figure 3. Magnitude and direction (a) and absolute magnitude (independent of direction) (b) of litter-  
508 site interactions, expressed as the home-field advantage index (HFAI), for litter transplants across  
509 contrasting communities. Plant communities are characterized in three categories: communities with  
510 the same dominant species from the same functional group (top); these with different dominant  
511 species, but from the same functional group (middle); and these with different dominant species from  
512 different functional groups (bottom). Large dots show the mean (absolute) HFAI and bars represent 95%  
513 confidence intervals. Numbers between brackets are the number of samples in each group. In panel (a)  
514 asterisks indicate whether litter-site interactions differ from zero at  $P < 0.05$  \*,  $P < 0.01$  \*\* and  $P < 0.001$

515 \*\*\*. Significantly positive litter-site interactions in (a) indicate HFA effects. Different letters indicate  
516 significant differences between groups at  $P < 0.05$  (LSD test with Benjamini-Hochberg correction).

517

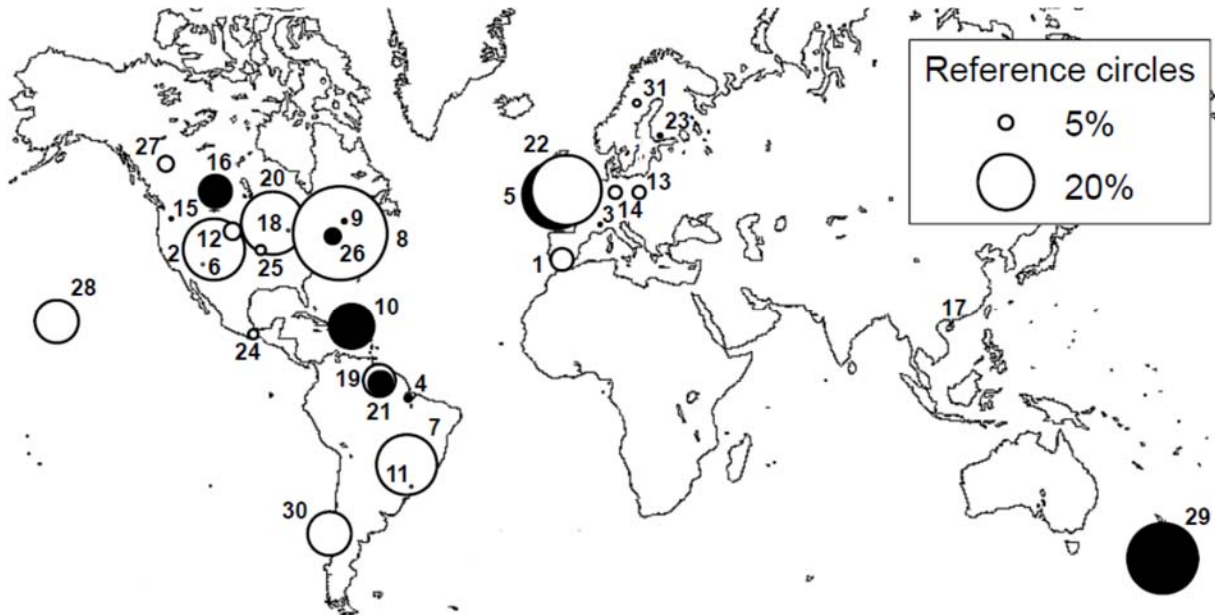
518 Figure 4. Magnitude and direction (a) and absolute magnitude (independent of direction) (b) of litter-  
519 site interactions, expressed as the home-field advantage index (HFAI), for litter transplants across  
520 grasslands, forests and between grasslands and forests. Large dots show the mean (absolute) HFAI and  
521 bars represent 95% confidence intervals. Numbers between brackets are the number of samples in each  
522 of the groups. In the left panels, asterisks indicate whether litter-site interactions differ from zero at  
523  $P < 0.05$  \*,  $P < 0.01$  \*\* and  $P < 0.001$  \*\*\*. Significantly positive litter-site interactions in (a) indicate HFA  
524 effects. Different letters indicate significant differences between groups at  $P < 0.05$  (LSD test with  
525 Benjamini-Hochberg correction).

526

527 **Figures**

528 **Figure 1**

529

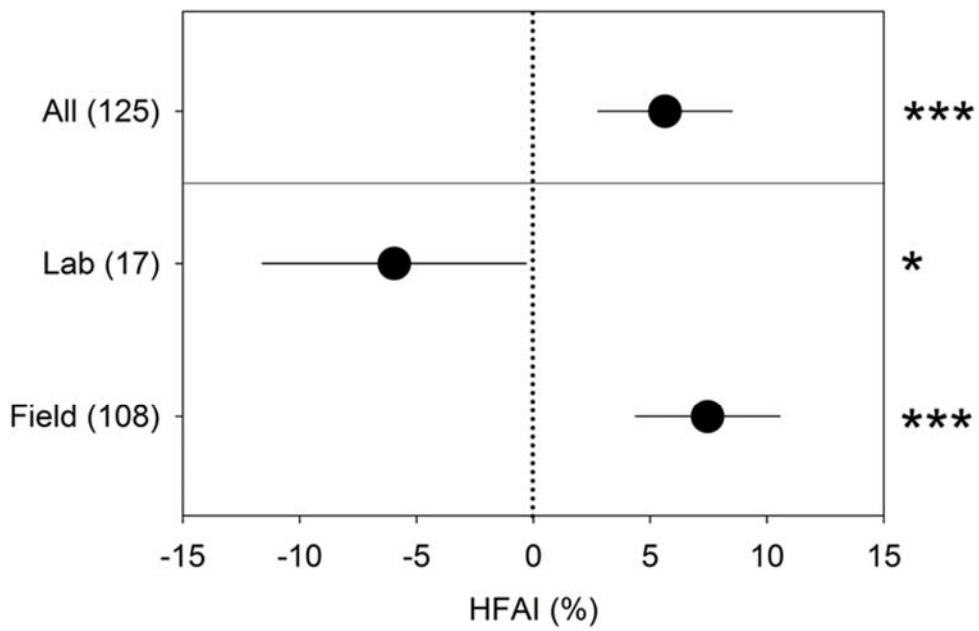


530

531

532

533 **Figure 2**



534  
535

