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

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Abstract

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

Introduction

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

Studies testing the HFA hypothesis using reciprocal litter transplant experiments have found highly variable results. While some studies have shown that decomposition was accelerated at their home relative to away from it (e.g. Vivanco and Austin 2008; Strickland et al. 2009a; Jacob et al. 2010; 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.

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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

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

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

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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

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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).

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383

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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^2	n	
Effect of litter quality on litter-site interactions						
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	**4.68**	**1, 57**	**0.035**	**0.09**	**59**	**(-)**
N:P	*3.68*	*1, 42*	*0.062*	*0.08*	*44*	*(+)*
Lignin:N	0.50	1, 54	0.483	0.01	56	
Effect of litter quality on the overall magnitude of litter-site interactions						
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^2 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^2	n	
Effect of litter dissimilarity on litter-site interactions						
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	**6.39**	**1, 42**	**0.015**	**0.13**	**44**	**(+)**
Lignin:N	**4.36**	**1, 54**	**0.040**	**0.09**	**56**	**(+)**
Effect of litter dissimilarity on the overall magnitude of litter-site interactions						
N	0.61	1, 83	0.439	0.01	85	
P	2.04	1, 42	0.160	0.05	44	
Lignin	**13.85**	**1, 56**	**<0.001**	**0.20**	**58**	**(+)**
C:N	0.02	1, 57	0.888	<0.01	59	
N:P	**4.47**	**1, 42**	**0.040**	**0.10**	**44**	**(+)**
Lignin:N	**11.87**	**1, 54**	**0.001**	**0.18**	**56**	**(+)**

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.

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).
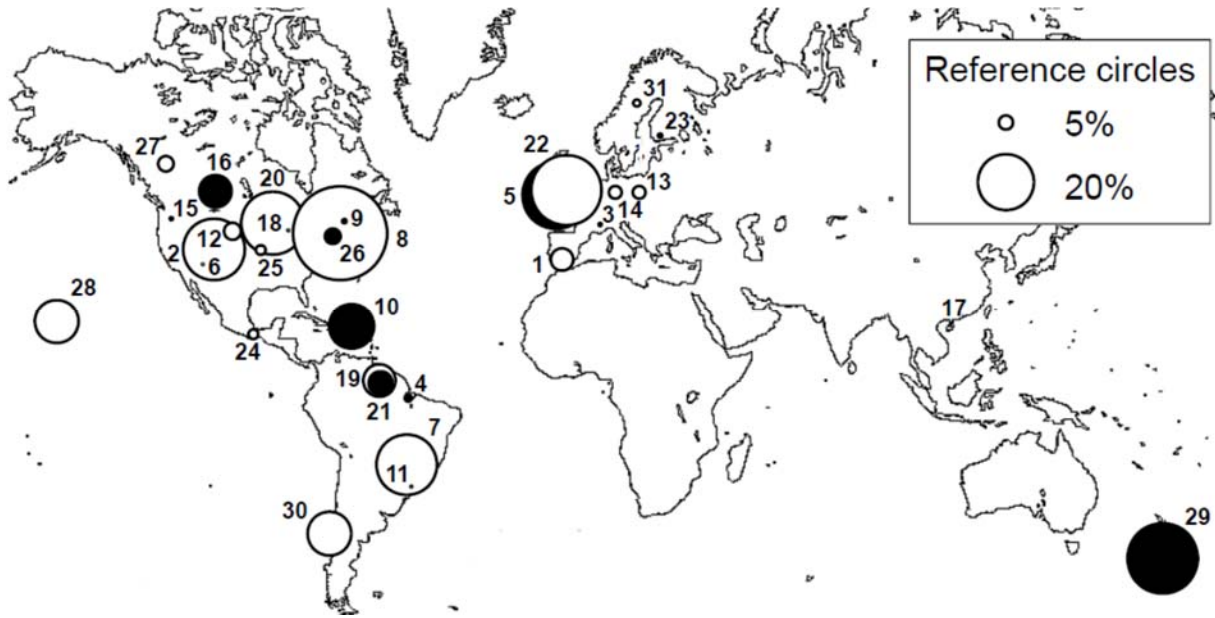
517

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
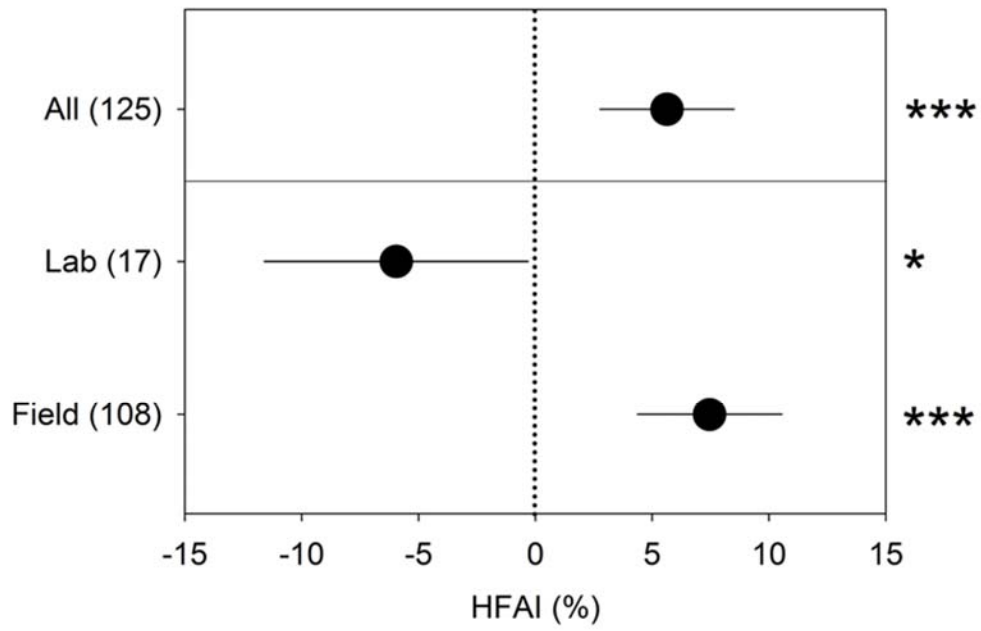
525   Benjamini-Hochberg correction).

526

Figures

528 **Figure 1**
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533   **Figure 2**

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536 **Figure 3**

539 **Figure 4**