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# Functional breadth and home-field advantage generate functional differences among soil microbial decomposers

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1 **Title:** Functional breadth and home-field advantage generate functional differences among soil  
2 microbial decomposers

3

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17

18 **Running title:** Functional ability of soil microbes

19

20 **Abstract. (350 words)** In addition to the effect of litter quality (LQ) on decomposition, increasing  
21 evidence is demonstrating that carbon mineralisation can be influenced by the past resource  
22 history, mainly through following two processes: (i) decomposer communities from recalcitrant  
23 litter environments may have a wider functional ability to decompose a wide range of litter

24 species than those originating from richer environments, i.e. the functional breadth (FB)  
 25 hypothesis; and/or (ii) decomposer communities may be specialized towards the litter they most  
 26 frequently encounter, i.e. the home-field advantage (HFA) hypothesis. Nevertheless, the  
 27 functional dissimilarities among contrasting microbial communities, which are generated by the  
 28 FB and the HFA, have rarely been simultaneously quantified in the same experiment, and their  
 29 relative contributions over time have never been assessed. To test these hypotheses, we  
 30 conducted a reciprocal transplant decomposition experiment under controlled conditions using  
 31 litter and soil originating from four ecosystems along a land-use gradient (forest, plantation,  
 32 grassland and cropland) and one additional treatment using  $^{13}\text{C}$  labelled flax litter allowing us to  
 33 assess the priming effect (PE) in each ecosystem. We found substantial effects of LQ on carbon  
 34 mineralisation (more than two-thirds of the explained variance), whereas the contribution of the  
 35 soil type was fairly low (less than one-tenth), suggesting that the contrasting soil microbial  
 36 communities play only a minor role in regulating decomposition rates. Although the results on  
 37 PE showed that we overestimated litter-derived  $\text{CO}_2$  fluxes, litter-microbe interactions  
 38 contributed significantly to the unexplained variance observed in carbon mineralisation models.  
 39 The magnitudes of FB and HFA were relatively similar, but the directions of these mechanisms  
 40 were sometimes opposite depending on the litter and soil types. FB and HFA estimates  
 41 calculated on parietal sugar mass loss were positively correlated with those calculated on  
 42 enzymatic activity, confirming the idea that the interaction between litter quality and microbial  
 43 community structure may modify the trajectory of carbon mineralisation *via* enzymatic synthesis.  
 44 We conclude that although litter quality was the predominant factor controlling litter  
 45 mineralisation, the local microbial communities and interactions with their substrates can explain  
 46 a small (< 5%) but noticeable portion of carbon fluxes.

47

48 **Keywords:** aboveground-belowground, functional equivalence, functional redundancy,  
 49 functional similarity, litter decomposition, local adaptation, microbial community structure,  
 50 plant-soil interactions.

51

52 **Introduction**

53

54       The decomposition of plant litter is one of the most important processes influencing the  
 55 global carbon cycle, the mineralisation of nutrients, soil fertility, and the formation of soil  
 56 organic matter in terrestrial ecosystems. Almost 40 years ago, Meentemeyer (1978) proposed  
 57 that climate and litter quality are the main factors explaining plant litter decomposition at the  
 58 global scale. In the decades since, many studies have confirmed this pattern at the continental  
 59 scale (e.g., Aerts 1997, Gholz et al. 2000, Trofymow et al. 2002, Powers et al. 2009), but the  
 60 factors contributing to the unexplained variation in local decomposition processes and their  
 61 relative contributions remain uncertain (Bradford et al. 2014). A variety of drivers modifying the  
 62 trajectory of decomposition rates have been proposed, including diversity effects (Heemsbergen  
 63 et al. 2004, Gessner et al. 2010), solar radiation (Austin and Vivanco 2006), the temporal  
 64 concordance between tree phenology and soil decomposers (Pearse et al. 2014), and the structure  
 65 of the soil fauna and microbial communities (Wall et al. 2008, Strickland et al. 2009a). It has  
 66 also been suggested that interactions between the litter quality and decomposer communities may  
 67 locally influence decomposition rates due to decomposers' different perceptions and/or  
 68 specialisations toward specific substrates (Hunt et al. 1988, Gholz et al. 2000, Strickland et al.  
 69 2009b). Nonetheless, important uncertainties remain regarding the magnitude and direction of

70 these interactions (Ayres et al. 2006, Chapman and Koch 2007, Freschet et al. 2012). In  
 71 particular, little is known about the kinetics of litter-decomposer interactions over time (but see  
 72 Ayres et al. 2009a), and positive or negative effects may depend on the interactions between the  
 73 initial litter quality, the stage of decomposition, and the local decomposer community (Strickland  
 74 et al. 2009a, Wickings et al. 2012, Wallenstein et al. 2013). In this context of multiple biotic and  
 75 abiotic factors regulating the decomposition rate at a local scale, we focused on a set of  
 76 hypotheses addressing the effects of plant-soil interactions on carbon mineralisation during the  
 77 decomposition of plant litter in a variety of contrasting ecosystems (Fig. 1). The selected land-  
 78 use gradient, which ranges from cropland, plantation, and grassland to forest on a common soil  
 79 substratum and varies in vegetation cover and disturbance frequency, offers a great opportunity  
 80 to accurately assess the relative importance of substrate quality and microbial community on  
 81 litter decomposition.

82 First, the ‘litter quality’ (LQ) hypothesis suggests that the intrinsic physical and chemical  
 83 characteristics of leaf litter, commonly measured as the C:N and lignin:N ratios or the quality of  
 84 various carbon forms, are the main predictors influencing the decomposition rate (Aber et al.  
 85 1990, Aerts 1997, Cornwell et al. 2008). In a reciprocal litter transplant study using 16 different  
 86 species across four different biomes, Makkonen et al. (2012) showed that a small subset of litter  
 87 traits explained most of the variation in litter mass loss, suggesting that the decomposition  
 88 process is largely independent of the local decomposer communities. Because of these ‘litter trait  
 89 controls’, differences in carbon mineralisation rates during litter decomposition should result  
 90 from the higher consumption of easily degradable litters (e.g., rich in soluble and holocellulose  
 91 contents) and the persistence of recalcitrant litters that are more resistant to decay (e.g., rich in  
 92 lignin and secondary metabolites). For example, along a land-use gradient, grass litter, which

93 represents an energy-rich and labile substrate, should decompose faster in all types of ecosystems  
 94 compared to the poorer and more recalcitrant forest litter (Fig. 1a). Support for this hypothesis is  
 95 derived from a multitude of decomposition studies in which a range of litter types were allowed  
 96 to decompose across a variety of ecosystems (e.g., Gholz et al. 2000, Hobbie et al. 2006,  
 97 Makkonen et al. 2012).

98         Second, the ‘functional breadth’ (FB) hypothesis stipulates that decomposer communities  
 99 from recalcitrant litter environments have a wider functional ability than those originating from  
 100 richer environments, meaning that they more efficiently decompose various litter types that vary  
 101 widely in their chemical and physical characteristics (van der Heijden et al. 2008, Keiser et al.  
 102 2011). Because of the past resource history that may influence whether microbial communities  
 103 are functionally ‘broad’ or ‘narrow’ (Keiser et al. 2014), differences in the carbon mineralisation  
 104 rates during litter decomposition should result from different catabolic capacities among  
 105 contrasted decomposer communities. Thus, all litter species should decompose faster in the  
 106 forest soil than in any other ecosystem because of a higher capability of the forest soil microbial  
 107 community to decompose a wide range of litter substrates (Fig. 1b). Consistent with this  
 108 hypothesis, Strickland et al. (2009b) demonstrated that poor and recalcitrant litter was  
 109 decomposed more efficiently by decomposer communities originating from forested habitats,  
 110 whereas easily degradable litter was decomposed equivalently by all communities of  
 111 decomposers from different types of ecosystems. These results indicate that microbial  
 112 communities may be functionally dissimilar for the degradation of recalcitrant litter substrates  
 113 and consequently that changes in ecosystem processes may also be strongly influenced by the  
 114 functional ability of distinct decomposer communities (Strickland et al. 2009a).

115 Finally, the ‘home-field advantage’ (HFA) hypothesis suggests that litter decomposes  
 116 faster in an area dominated by the plant species from which it derives (i.e., at home) rather than  
 117 in an area dominated by another plant species (i.e., away) (Gholz et al. 2000). Because of this  
 118 ‘local adaptation’ of the decomposer community, differences in carbon mineralisation rates  
 119 during litter decomposition should result from the match between a litter type and its own  
 120 environment. For example, forest litter should decompose faster in forest soil, whereas wheat  
 121 litter should decompose faster in cropland soil (Fig. 1c). In agreement with this hypothesis,  
 122 numerous studies have documented that plant litters decompose fastest in their local environment  
 123 (e.g., de Toledo Castanho and de Oliveira 2008, Vivanco and Austin 2008, Strickland et al.  
 124 2009a, Wallenstein et al. 2010). Although the HFA hypothesis has generated great attention,  
 125 several empirical studies did not find any evidence of such affinity between litter and microbes at  
 126 home (Ayres et al. 2006, Gieβelmann et al. 2011, St John et al. 2011, Veen et al. 2015), sparking  
 127 an important debate about the generalizability of this mechanism (see Austin et al. 2014 for a  
 128 review). This ‘affinity effect’ between decomposers and their substrates has been recently  
 129 amended with the ‘substrate-matrix interaction’ hypothesis (Freschet et al. 2012), which states  
 130 that the composition of the decomposer community should reflect the average quality of the litter  
 131 matrix rather than species-specific home litter effects, in particular in biomes dominated by  
 132 multiple and chemically contrasted plant species. Despite these recent advances, few studies  
 133 have addressed carbon dynamics over time in relation to simultaneous changes in litter quality,  
 134 the local microbial community, and their functional abilities, although such an effort is essential  
 135 for assessing the unexplained variation in decomposition rates caused by litter-microbe  
 136 interactions at the local scale.



137 Here, we tested these three non-exclusive hypotheses by examining the plant litter–  
 138 microbe interactions in a reciprocal transplant experiment of contrasting litters and their  
 139 associated soils originating from a land-use gradient (forest, plantation, grassland and cropland)  
 140 across a one-hectare plot. Because little is known about whether the previously described  
 141 mechanisms are transient or persistent over time, we specifically followed the kinetics of carbon  
 142 mineralisation over 202 days and 21 dates to better grasp the variability of responses generated  
 143 by the interactions between soil microbial communities and litter types. In order to ensure that  
 144 the mineralisation of ‘older’ organic matter *via* ‘fresh’ litter addition did not alter our conclusions  
 145 on litter-microbe interactions, we also measured the mineralisation of soil organic matter  
 146 following the addition of <sup>13</sup>C labelled flax litter (*Linum usitatissimum* L.) for assessing the  
 147 contribution of priming effect (PE) in each ecosystem. To investigate the triangular relationships  
 148 involving litter quality, the decomposer community and enzymatic activities for explaining the  
 149 observed affinity effects, we analysed at three time points (at 27, 97, and 202 days) the mass loss  
 150 rates of the main sugars within the cell wall, the microbial community structure *via* twenty-four  
 151 selected PLFA markers, and the activities of four hydrolytic enzymes. We employed a new  
 152 model recently developed by Keiser et al. (2014) that allowed us to simultaneously test our three  
 153 main hypotheses by calculating the estimated parameters for LQ, FB and HFA and their effects  
 154 on carbon mineralisation. Finally, by assessing the effects of these parameters on the mass loss  
 155 of parietal sugars and on enzymatic activities, we addressed for the first time whether the effects  
 156 of FB and HFA on carbon mineralisation depend on the functional ability of the soil decomposer  
 157 communities.

158

159 **Methods**

160

161 *Microcosm design*

162

163 Litter and soil were collected from a one-hectare plot within the ‘AgroParisTech’ site,  
 164 Paris-Grignon (48°50’N, 1°56’E). We identified four areas in close proximity to one another  
 165 representing the four different systems that were present in our study site, i.e., cropland  
 166 (48°51’11.7.8’’N, 1°56’15.5’’E), deciduous forest (48°51’15.3’’N, 1°56’01.7’’E), grassland  
 167 (48°51’17.0’’N, 1°55’44.0’’E), and tree plantation (48°51’16.4’’N, 1°55’30.4’’E). The shortest  
 168 and longest distances between two sites were 250 and 900 m, respectively. Wheat (*Triticum*  
 169 *aestivum* L.), beech (*Fagus sylvatica* L.), fescue (*Festuca arundinacea* Schreb.), and black locust  
 170 (*Robinia pseudoacacia* L.) were the dominant plant species in each respective ecosystem. In the  
 171 forest and grassland ecosystems, which present greater plant diversity than the monospecific  
 172 wheat culture and black locust plantations, we selected sampling areas within nearly pure stands  
 173 to prevent litter mixing and difficulties in interpreting the results due to potential diversity  
 174 effects. Forest and plantation litters were collected as recently fallen leaf litter, grass litter was  
 175 collected as standing-dead material, and cropland litter was collected just after the wheat harvest  
 176 in October 2013. In the laboratory, all of the litter samples were sorted to remove the fruits,  
 177 seeds, and roots, cut into approximately 1 cm pieces using scissors, homogenised, and dried at  
 178 40°C. Litter was sterilised by autoclaving (121°C, 20 min) twice in succession to maximise the  
 179 chance that the decomposer communities were introduced only *via* the soil and not by the litter  
 180 material, but we acknowledge that autoclaving may have altered the initial litter chemistry. The  
 181 litter chemical quality was determined using standard methods after sterilisation (see Appendix  
 182 A for a detailed description of the litter chemical parameters and determination methods).

183 Mineral soil was collected from three different areas in each ecosystem by digging  $25 \times 25 \text{ cm}^2$   
 184 holes to a depth of 10 cm, representing three independent samples series per land-use type. The  
 185 soil was passed through a 2-mm sieve, homogenised, and then stored at  $4^\circ\text{C}$  until use (see  
 186 Appendix B for a detailed description of the soil characteristics).

187 The soil samples (100 g dry mass) were mixed with the litter samples at a rate equivalent  
 188 to  $10 \text{ g C kg}^{-1}$  dry soil (between 2.05 and 2.22 g of dry mass) in 850 ml glass jars and incubated  
 189 for 202 days at  $20^\circ\text{C}$ . Based on preliminary tests and previous incubation experiments (e.g.,  
 190 Bertrand et al. 2007, Amin et al. 2014), 2 g of litter was considered as the best compromise  
 191 between the need to retrieve enough material for our chemical analyses after 202 days of  
 192 decomposition and the quantity necessary for optimizing the stimulation of soil microbial  
 193 communities. The mixture was adjusted to and maintained at a potential of  $-80 \text{ kPa}$ , which  
 194 corresponds to  $221\text{-}230 \text{ g kg}^{-1}$  of air-dried-soil water content (approximately 50% water-holding  
 195 capacity) and favours microbial activity (Bertrand et al. 2007). The soil moisture was maintained  
 196 throughout the incubation period by weighing the microcosms twice per month and readjusting  
 197 with deionised water when necessary. We used a reciprocal transplant design (i.e., all of the litter  
 198 types crossed with all of the soil types) plus additional ‘no-litter’ soil samples. In total, 9  
 199 replicates per treatment were constructed, permitting the destructive harvest of replicates on  
 200 incubation days 27, 97, and 202 for chemical, enzymatic and microbial community analyses. On  
 201 each sampling date and for each microcosm, a subsample of the remaining litter material was  
 202 carefully retrieved, cleaned of soil particles, and dried at  $37^\circ\text{C}$  for parietal sugar and lignin  
 203 analyses. Two additional subsamples of soil and litter mixtures were immediately frozen at -  
 204  $20^\circ\text{C}$  for further PLFA analyses and enzymatic assays.

205

206 *Carbon mineralisation*

207

208 Carbon mineralisation was measured in triplicate for each soil × litter type combination in  
 209 the presence of a CO<sub>2</sub> trap (15 ml of 1 M NaOH) at [3, 6, 9, 13, 17, 21, and 27], [34, 41, 51, 62,  
 210 73, 85, and 97], and [112, 126, 140, 154, 168, 182, and 202] days after the start of incubation.  
 211 Specifically, the microcosms harvested on days 27, 97, or 202 were the same microcosms from  
 212 which we measured the carbon mineralisation rates during the three periods, i.e., 3–27, 28–97, or  
 213 98–202 days of incubation. This measurement trend resulted in 21 sampling dates divided into  
 214 three incubation periods composed equally of 7 sampling dates. The carbon dioxide production  
 215 rates (mg C kg<sup>-1</sup> soil day<sup>-1</sup>) and cumulative carbon mineralisation (mg C kg<sup>-1</sup> soil) were corrected  
 216 for the contribution of the corresponding soil type by subtracting the carbon mineralisation of the  
 217 ‘no-litter’ soil (except when ‘raw data’ are mentioned in the text). It should be noted that the  
 218 carbon mineralisation was analysed for all of the microcosms (i.e., 3 sets of 3 replicates) on day  
 219 27, whereas only 2 sets and 1 set of microcosms were collected on days 97 and 202, respectively,  
 220 since the first and second sets of microcosms had already been destructively harvested. The  
 221 concentrations of CO<sub>2</sub> trapped in the NaOH solution were measured by continuous flow  
 222 colourimetry using an auto-analyser (TRAACS 2000, Bran & Luebbe, Norderstedt, Germany).

223

224 *Priming effect*

225

226 Labelled <sup>13</sup>C flax stem were obtained from growing flax seeds (*Linum usitatissimum* L.)  
 227 in an airtight growth chamber in which conditions (air moisture, air temperature and  
 228 photoperiod) were monitored to mimic spring conditions. The plants were grown on rockwool

229 plugs under hydroponic conditions using nutrient solutions as described by Devienne et al.  
 230 (1994). The plants were continuously labelled with  $^{13}\text{C}$  by using the same  $^{13}\text{CO}_2$  bottles  
 231 throughout the entire growth cycle. Flax stem was collected at maturity ( $\delta^{13}\text{C} = 2870\text{‰}$ , atom%  
 232 excess = 3.056), homogenised, incubated at a rate equivalent to  $10 \text{ g C kg}^{-1}$  dry soil (2.13 g of  
 233 dry mass) and carbon mineralisation was measured as described above. Flax litter represented a  
 234 mid-range quality, characterized by intermediate content of nitrogen, lignin, and soluble  
 235 compounds and showed cumulative carbon mineralisation comprised between *Gramineae* and  
 236 woody plant species with an average of  $5232 \text{ mg C kg}^{-1}$  soil (see Appendix C for more details).

237 The  $^{13}\text{C}\text{-CO}_2/^{12}\text{C}\text{-CO}_2$  ratio was determined by adding 10 ml of 0.5 M  $\text{BaCl}_2$  to NaOH  
 238 solutions and the resulting precipitate of  $\text{BaCO}_3$  was separated by vacuum filtration (glass fiber  
 239 filter) and dried at  $80^\circ\text{C}$  for 8 hours. The  $\text{BaCO}_3$  precipitate was weighed in a tin cap with the  
 240 addition of a catalyst ( $\text{PbO}_2$ ), and the isotope ratio  $^{13}\text{C}/^{12}\text{C}$  of the precipitate was measured with  
 241 an elemental analyzer (Eurovector, Milan, Italy) coupled to a mass spectrometer (Delta S  
 242 Advantage, Thermo Fisher Scientific, Bremen, Germany). The priming effect (PE) was  
 243 calculated with the following equation:

$$244 \text{ PE} = [^{12+13}\text{CO}_2\text{-amended} - ^{13}\text{CO}_2\text{-amended}] - ^{12}\text{CO}_2^{\text{ctrl}}$$

245 where  $^{12+13}\text{CO}_2\text{-amended}$  and  $^{12}\text{CO}_2^{\text{ctrl}}$  are the cumulative amounts ( $\text{mg kg}^{-1}$ ) of mineralized  
 246 carbon in the soil with and without litters, respectively, and  $^{13}\text{CO}_2\text{-amended}$  represents the litter-  
 247 derived carbon.

248

249 *Litter chemical analyses*

250

251 To characterise the parietal sugars initially and at days 27, 97, and 202, the plant litter  
 252 samples were subjected to a cell wall preparation process that consisted of extracting the neutral  
 253 detergent fibre (NDF) fraction as described by Goering and Van Soest (1970). The soluble  
 254 fraction was removed by boiling between 0.7 to 1 g of litter in deionised water at 100°C for 30  
 255 min and then performing an extraction with a neutral detergent solution at 100°C for 60 min to  
 256 remove the cytoplasmic components and obtain the NDF fraction. All residues from the cell wall  
 257 preparations were dried for one week at 30°C and ground to 80 µm. The parietal sugars were  
 258 then analysed as previously described (Machinet et al. 2011). Briefly, 10 mg of the NDF residue  
 259 was allowed to swell in 125 µl of 12 M H<sub>2</sub>SO<sub>4</sub> for 2 h at 20°C and was then subjected to acid  
 260 hydrolysis with 1 M H<sub>2</sub>SO<sub>4</sub> for 2 h at 100°C. The monosaccharides released by the acid  
 261 hydrolysis were separated by high-performance anion-exchange chromatography (HPAEC) on a  
 262 CarboPac PA-1 column (Dionex ICS 5000+, Thermo-Scientific, Sunnyvale, CA, USA). The  
 263 monosaccharide composition was analysed, and nine sugars were quantified using 2-deoxy-D-  
 264 ribose as an internal standard and standard solutions of the following neutral carbohydrates: L-  
 265 arabinose, D-glucose, D-xylose, D-galactose, L-rhamnose, D-mannose, L-fucose, D-galacturonic  
 266 acid and D-glucuronic acid. The parietal sugars were calculated as the sum of all of the  
 267 monosaccharides.

268 The lignin content of the litter subsamples was approximated as the acid-non-  
 269 hydrolysable residue remaining after sulphuric acid hydrolysis according to the Klason lignin  
 270 determination method (Monties 1984). Briefly, 300 mg of litter was suspended in 3 ml of 12 M  
 271 H<sub>2</sub>SO<sub>4</sub> for 2 h at room temperature. The suspensions were then diluted to 1 M with deionised  
 272 water, heated at 100°C for 3 h and filtered. The remaining litter was dried at 105°C and the ash

273 content was determined after 4 h of combustion at 500°C. The lignin content was calculated as  
 274 the mass difference before and after combustion.

275

276 *Enzymatic activities*

277

278 At days 27, 97, and 202, we used a method by Bell et al. (2013) to measure the potential  
 279 activity of four hydrolytic soil enzymes, which degrade a range of substrates that are common  
 280 constituents of organic matter. The following enzymes were selected to represent the degradation  
 281 of C-rich substrates:  $\beta$ -1,4-glucosidase,  $\beta$ -D-cellobiosidase,  $\alpha$ -glucosidase, and  $\beta$ -xylosidase (see  
 282 Appendix D for details regarding the initial enzymatic activity of each system). In brief, the  
 283 assays were conducted by homogenising 2.75 g of the soil-litter mixture in 91 ml of 50 mM  
 284 TRIS buffer (pH 7.8 for forest or grassland, pH 8.1 for cropland and plantation) in a blender for  
 285 1 min. The soil slurries were then added to a 96-deep-well microplate using an eight-channel  
 286 repeat pipettor. Additional quench control replicates of the soil slurry and 4-methylumbelliferone  
 287 (MUB) standard curves (0-100  $\mu$ M concentrations) were included with each sample. The soil  
 288 slurries were incubated with fluorometric substrates for 3 h at 25°C. After the incubation period,  
 289 the plates were centrifuged for 20 min at 3000 rpm, after which 250  $\mu$ l of supernatant was  
 290 transferred from each well into a black, flat-bottomed 96-well plate that was scanned using a  
 291 microplate reader (SpectraMax Gemini, Molecular Devices, CA, USA) with an excitation  
 292 wavelength of 365 nm and an emission wavelength of 450 nm. All enzymatic activities were first  
 293 calculated in  $\text{nmol g}^{-1} \text{ soil h}^{-1}$  and were then corrected for the contribution of the corresponding  
 294 soil type by subtracting the enzyme activities of the ‘no-litter’ soil. These values were  
 295 subsequently integrated over time ( $\text{mmol kg}^{-1} \text{ soil}$ ) following Sinsabaugh et al. (2002).

296

297 *Microbial community structure*

298

299 The microbial community structure was determined at days 27, 97, and 202 by an  
 300 analysis of the group-specific phospholipid fatty acids (PLFAs) according to the protocol  
 301 described by Fanin et al. (2014) (Appendix D for details regarding the initial community  
 302 composition of each system). From each microcosm, a 10 g frozen soil subsample was used for  
 303 total lipid extraction in a single-phase mixture of chloroform:methanol:phosphate buffer at pH  
 304 7.4 (1:2:0.8 by vol.), eluted selectively, and subjected to a mild methanolysis. The resulting  
 305 PLFAs were analysed on a gas chromatograph equipped with a flame ionisation detector  
 306 (Agilent 6890, Agilent Technologies, Palo Alto, USA) with a 60 m × 0.25 mm × 0.15 µm DB-23  
 307 column (Agilent Technologies, Palo Alto, USA) and by gas chromatography–mass spectrometry  
 308 (Shimadzu QP2010 plus, Shimadzu Corporation, Suzhou, China). We retained the following 24  
 309 PLFAs as indicators of the microbial community structure: branched and saturated PLFAs i15:0,  
 310 a15:0, i16:0, i17:0, and a17:0 (Gram-positive bacteria); mono-unsaturated and cyclopropyl  
 311 PLFAs 16:1ω7c, cy17:0, 18:1ω7c, and cy19:0 (Gram-negative bacteria) 18:1ω9, 18:2ω6,9  
 312 (fungi), 10me-16:0 and 10me-18:0 (Actinobacteria); and i14:0, 14:0, 15:0, 16:0, 17:0, i18:0,  
 313 18:0, 18:1ω5c, C18:3ω3, 20:0 and 20:4ω6 (general indicators).

314

315 *Data analysis*

316

317 To examine the effects of the soil and litter types on the cumulative carbon  
 318 mineralisation, we performed a two-way ANOVA using the raw (total cumulative carbon



319 mineralisation) or net data (cumulative carbon mineralisation corrected using ‘no-litter’ soils).  
 320 We then individually analysed the net mineralisation rates for each litter type using linear mixed  
 321 models in which the soil type and time were treated as fixed effects and were allowed to interact.  
 322 The microcosm identity was included as a random effect to account for the repeated sampling of  
 323 the microcosms across time. Using Bray-Curtis dissimilarity matrices, we ran non-metric  
 324 multidimensional scaling (NMDS) to visualise the differences in structure and catabolic ability  
 325 of the microbial community (as relative proportions of PLFAs and of the four enzymatic  
 326 activities) and then performed permutational multivariate ANOVAs to test the significance of the  
 327 litter type, soil type, and time for explaining the observed variations.

328 The relative contribution of the litter quality, functional breadth, and home-field  
 329 advantage in explaining the carbon mineralisation was estimated using the model developed by  
 330 Keiser et al. (2014). This model states that carbon mineralisation ( $Y_i$ ) is equal to litter ability ( $\beta_l$ )  
 331 plus soil ability ( $\gamma_s$ ) plus a home interaction term ( $\eta_h$ ):

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

332  
 333 where  $Y_i$  is the carbon mineralisation for observation  $i$ ,  $\beta_l$  is the ability of litter species  $l$  (from  
 334 species 1 to  $N$ ),  $\gamma_s$  is the ability of the soil community  $s$  (from community 1 to  $M$ ),  $\eta_h$  is the HFA  
 335 of  $h$  (from home combinations 1 to  $K$ ), and  $\text{Home}_h = \text{Litter}_l * \text{Soil}_s$  when  $l$  and  $s$  are home-field  
 336 pairings. The parameters to be estimated are  $\beta_l$ ,  $\gamma_s$  and  $\eta_h$ . The intercept term is defined by  $\alpha$  and  
 337 represents the average carbon mineralisation rate for all observations in the dataset after  
 338 controlling for litter, soil and home-field pairings. Negative parameter estimates indicate lower  
 339 carbon mineralisation than the average rate observed across all samples in the device. The error  
 340 term is defined by  $\varepsilon$ . Using this model, we calculated a quality index (LQ), the ability of soil

341 microbial communities (FB), and the interactions between litter and soil (HFA) on the net  
 342 cumulative carbon mineralisation. Keiser's model was also used to determine the relative  
 343 contributions of FB ( $\gamma_s$ ) and HFA ( $\eta_h$ ) in explaining the sugar mass loss (computed for the sum  
 344 of all parietal sugars) and enzymatic activities (computed for the sum of the four net integrated  
 345 enzymatic activities). We then explored the correlations between the parameter estimates for FB  
 346 and HFA on the parietal sugar mass loss and on the net integrated enzymes to visualise potential  
 347 relationships between these two sets of variables. All of the statistical tests were performed using  
 348 R software (version 3.1.1, The R Foundation for Statistical Computing, Vienna, Austria) and  
 349 SAS software (version 9.0, SAS institute, NC, USA).

350

## 351 **Results**

352

### 353 *Litter quality and carbon mineralisation*

354

355 Multiple litter traits varied significantly among the four litter types. For instance, the C:N  
 356 ratio varied by almost eightfold, ranging from 18.4 to 140.9 between the plantation (*R.*  
 357 *pseudoacacia*) and cropland (*T. aestivum*) litters, respectively, whereas the bulk litter lignin  
 358 concentration varied by a factor of 2.5 between the forest (*F. sylvatica*) and grass (*F.*  
 359 *arundinacea*) litters (39.3% and 15.5%, respectively; see Appendix A for more details). The  
 360 variability of the litter chemistry was particularly apparent when considering parietal sugars,  
 361 especially between forest and cropland litter types, with more than threefold variation in the  
 362 glucose and xylose concentrations. The polyphenol contents were the highest in the forest and

363 plantation litters, as was the lignocellulose index, ranging from 0.22 and 0.24 for cropland and  
 364 grass litters to 0.65 and 0.67 for forest and plantation, respectively.

365 The cumulative carbon mineralisation over 202 days varied according to the litter types,  
 366 ranging from 3463 to 6649 mg C kg<sup>-1</sup> of soil for the forest and grassland litters, respectively (Fig.  
 367 2A). The variation in the average cumulative carbon mineralisation between the soil types was,  
 368 however, less important than was that observed between the litter species, with a minimum of  
 369 4237 mg C kg<sup>-1</sup> for the cropland soil and a maximum of 6287 mg C kg<sup>-1</sup> for the forest soil (Fig.  
 370 2B, see also Appendix E for details on the control soils). Priming effect (PE) varied over time  
 371 with a maximum of 232 mg C kg<sup>-1</sup> on average after 202 days (Fig. 2C, Appendix C). After a  
 372 mineralisation flush during the first 7 days, PE increased steadily for cropland and plantation  
 373 soils while it was negative for grassland and forest soils, meaning that the SOM mineralisation  
 374 was higher in the control than in the <sup>13</sup>C litter-amended soils. Although PE increased in the forest  
 375 soil to similar levels than in cropland and plantation soils after 97 days of decomposition,  
 376 grassland soil always showed lower PE, with a difference of 78 mg C kg<sup>-1</sup> on average compared  
 377 with the three other ecosystems (Fig. 2C). Overall, PE corresponded to 3.6 to 6.6% of net carbon  
 378 mineralisation between 27 and 202 days.

379 Using raw data for the total cumulative carbon mineralisation measured in the four  
 380 ecosystems, we observed that the average percentage of variance explained by the soil type  
 381 increased during the course of the incubation, ranging from of 9.6% at the beginning to 32.1% at  
 382 the end of the experiment. By contrast, the average contribution of the litter type decreased from  
 383 89.3 to 66.9% during the same time (Table 1). However, when considering the net data  
 384 (cumulative carbon mineralisation corrected by ‘no-litter’ soils), the soil type explained only 1.9  
 385 to 4.0% of the variation in the net carbon mineralisation over 202 days, suggesting that this effect

386 is more subtle when the initial soil variation among ecosystem types is considered (Table 1). In  
 387 this latter model, the litter species explained 94% of the average variance of carbon  
 388 mineralisation independently of the sampling date (Table 1). Among the different litter traits, the  
 389 lignin:N and C:N ratios were poor predictors of the mineralisation rates ( $p > 0.05$ , Appendix F).  
 390 By contrast, the lignocellulose index (LCI) showed strong negative correlations with the carbon  
 391 mineralisation rates for each litter type individually but also globally using the entire dataset ( $r^2$   
 392 = 0.47,  $p < 0.05$ , Appendix F). Finally, when the effect of each litter type was investigated  
 393 separately over the course of the incubation, the dynamics of the net carbon mineralisation rates  
 394 of the cropland, forest and plantation litter types were influenced by the soil type and by a soil  
 395 type  $\times$  time interaction that decreased from 0-27 to 98-202 days (Table 2). The soil net carbon  
 396 mineralisation rates for the grass litter showed only an effect of the soil type for the period 28-97  
 397 days and significant soil type  $\times$  time interactions at 0-27 and 98-202 days (Table 2, see also  
 398 Appendix G for the general model).

400 *Microbial community structure and enzymatic production*

401  
 402 Most of the PLFA markers showed significant differences among the soil and litter type  
 403 combinations, indicating that the soil microbial community structure was affected by multiple  
 404 parameters (Fig. 3A, Table 3). Over the course of the incubation, the soil type and the identity of  
 405 the decomposing leaf litter were the most significant factors, explaining an average of 36% and  
 406 18%, respectively, of the variability in the community structure (Table 3). To a lesser extent,  
 407 time (12%) and its interaction with the soil type (9%) or litter type (4%) also explained a  
 408 significant part of the observed variation. Consistent with the reported differences in the

409 microbial community structure, the ordination plot from NMDS clearly distinguished the  
 410 communities from the four soil types (Fig. 3A). The microbial communities were plotted  
 411 according to a pattern in which the first axis depicted the land-use gradient from cropland to  
 412 forest and the second axis separated the agro-systems (cropland and plantation) from the less  
 413 intensively managed ecosystems (forest and grassland).

414         Similar to what was observed for the microbial community structure, we found that the  
 415 soil type was the most important driver, explaining 28% of the variation in the enzymatic activity  
 416 (Fig. 3B, Table 3). The soil type was visually confirmed as a main driver of enzymatic activity  
 417 when the NMDS plot was observed, although this result was clearer from the PLFA data. In the  
 418 NMDS plot, a clear segregation occurred along the first two axes between the plantation and  
 419 cropland soils on the one hand (down left), and the forest and grassland soils on the other hand  
 420 (top right) (Fig. 3B). The litter types and their interaction with time or soil only slightly  
 421 influenced the patterns of enzyme activities in the different soil-litter type combinations (Table  
 422 3B). In contrast, time and its interaction with the soil type explained 25% and 19% of the  
 423 variability in enzymatic patterns, respectively.

424

425 *Major controls of litter carbon mineralisation and their relations to enzymatic activity*

426

427         When estimating the  $\beta_l$  (LQ),  $\gamma_s$  (FB), and  $\eta_h$  (HFA) metrics from the net carbon  
 428 mineralisation data, we found that  $\beta_l$  was the metric that showed the largest variation (Fig. 4),  
 429 with values ranging from -1725 to +1426 mg C mineralised kg<sup>-1</sup> soil on average across the soil  
 430 and litter type combinations. The grass and cropland litters showed the highest LQ index  
 431 compared to the plantation and forest litters (Fig. 4A), confirming that more labile litter types

432 degraded fastest across all of the ecosystems (Fig. 2A). Overall, we observed an initial and rapid  
 433 increase or decrease in  $\beta_l$  for the grass and forest litters, followed by a slow decline in carbon  
 434 mineralisation over the incubation period (Fig. 4A). Meanwhile, a transition period occurred for  
 435 the cropland and plantation litters between 0 and 27 days, followed by a regular increase or  
 436 decrease in  $\beta_l$ , suggesting that the notion of litter quality for the soil decomposers may vary from  
 437 the short to the long term (Fig. 4A). When estimating the functional ability  $\gamma_s$  that varied from -  
 438 249 to + 364 mg C mineralised kg<sup>-1</sup> soil, we observed that the ‘ability’ of decomposer  
 439 communities was highest and increased during the experiment for the forest soil (Fig. 4B). To a  
 440 lesser extent, the microbial community from the grassland soil also displayed positive  $\gamma_s$  values,  
 441 with an increasing functional ability after a time lapse of approximately 100 days. In contrast, the  
 442 plantation and cropland soil types presented negative  $\gamma_s$  values over the course of the incubation  
 443 experiment, indicating that these communities were unable to degrade a wide range of  
 444 qualitatively contrasting litter types (Fig. 4B). Finally, when evaluating whether a litter type  
 445 decomposed faster in an area dominated by the plant species from which it derived, we observed  
 446 an increasing affinity effect  $\eta_h$  when the plantation soil microbial community matched its own  
 447 litter (Fig. 4C). Similarly, we found a positive  $\eta_h$  between the grass litter and its own  
 448 environment, but this effect was transient over time and decreased after 140 days. No significant  
 449 HFA was found for the forest ( $p > 0.05$  for the whole incubation period), and a disadvantage to  
 450 decomposing at home was found for the cropland litter, indicating that this litter type  
 451 decomposed more rapidly elsewhere than in its own environment (Fig. 4C).

452         When calculating the parameter estimates corresponding to the effects of FB ( $\gamma_s$ ) and  
 453 HFA ( $\eta_h$ ) on the parietal sugar mass loss and net integrated enzymes, we observed positive  
 454 correlations between these two parameters across the various systems, indicating that a higher

455 ‘functional ability’ or ‘affinity effect’ on the decomposition process was related to a higher  
 456 enzymatic activity (Fig. 5, see also Appendix H for more details). In agreement with the carbon  
 457 mineralisation results, we observed positive  $\gamma_s$  estimates for both the enzymatic activity and  
 458 sugar mass loss in the forest ecosystem, whereas the  $\eta_n$  estimates were highest in the plantation  
 459 and grassland (Fig. 5). Specifically, the positive effects that FB and HFA had on parietal sugars  
 460 were mainly related to xylose and glucose dynamics during the early phase of decomposition,  
 461 whereas after 100 days of decomposition, lignin appeared to increase in importance as a factor  
 462 explaining the FB and HFA effects (Appendix I).

463

464 **Discussion**

465

466 Little is known regarding how the triangular interactions involving litter quality, the  
 467 decomposer community, and enzymatic activities can modify the trajectory of carbon dynamics  
 468 within a land-use gradient. To quantify the relative contributions of litter quality (LQ), functional  
 469 breadth (FB), and home field advantage (HFA) (Fig. 1), we implemented a reciprocal litter-soil  
 470 transplant decomposition experiment over 202 days. Despite the relatively similar decomposition  
 471 patterns across all soil-litter combinations, we found a twofold variation in the magnitude of  
 472 carbon mineralisation among the most chemically contrasting litter types at the end of the  
 473 incubation period (Fig. 2A), and distinct mineralisation rates for a given litter type incubated  
 474 with different soil inoculums (Table 2). Our results confirm that litter decomposition is mainly  
 475 influenced by litter quality, but indicate that the local microbial communities and interactions  
 476 with their substrates also explained a subtle (< 5%) but significant part of the variation in carbon  
 477 mineralisation (Table 1). Neither the amplitude nor the ranking of the priming effect (PE)

478 changed the main conclusions on FB and HFA results, strengthening the idea that the past  
 479 resource history can play a significant role during litter decomposition. In light of the new  
 480 advances provided by our incubation experiment, we propose a new theoretical concept based on  
 481 enzymatic activities for addressing the issue of functional dissimilarity of contrasting microbial  
 482 communities originating from a variety of ecosystems.

483

484 *Litter quality as a major control of carbon mineralisation*

485

486 In agreement with our first hypothesis, the litter quality consistently explained more than  
 487 two-thirds of the carbon mineralisation, confirming that litter traits are the best predictors of  
 488 carbon dynamics (Makkonen et al. 2012, Cleveland et al. 2014). In contrast to the often assumed  
 489 relevance of the bulk nitrogen concentration or the lignin:N ratio of leaf litter, we found that the  
 490 variability in the carbon mineralisation rates among the different litter species was primarily  
 491 explained by the degree of recalcitrance of plant cell walls (Appendix F). These results suggest  
 492 that the complexity of the cell wall network can retard or enable the access of microorganisms to  
 493 easily degradable litter compounds and that simple estimators of the cell wall structure such as  
 494 the lignocellulose index (LCI) are useful indicators for assessing mineralisation rates using  
 495 predictive models at a local scale (Moorhead and Sinsabaugh 2006, Moorhead et al. 2014).

496

497 *Testing the functional importance of microbial communities*

498

499 Whether contrasting microbial communities are functionally equivalent regarding  
 500 ecosystem processes remains an essential issue for our prediction of the carbon balance along a



501 land-use gradient. Overall, the soil type explained 9 to 32% of the variation in carbon  
 502 mineralisation during the course of the experiment (Table 1). However, when accounting for the  
 503 initial variability among the different ecosystems, the soil type explained only 2 to 4% of the  
 504 variation, suggesting that the response induced by the litter-microbe interactions was smaller in  
 505 our study than in other reports (Ayres et al. 2009b). The PE increased on average from 57 to 232  
 506 mg C kg<sup>-1</sup> between 27 to 202 days, meaning that we overestimated litter-derived CO<sub>2</sub> fluxes by  
 507 3.6 to 6.6% in our models. In addition, PE was lower in grassland soils over the course of the  
 508 incubation experiment (Fig. 3C), indicating that caution must be taken when considering the  
 509 variation of litter-microbe interactions between grassland and the other soil types. However, the  
 510 relative consistency among soil types (CV = 27%) explaining 0.03 to 1.18% in the variation in  
 511 net carbon mineralisation suggest that other factors besides PE also significantly influenced the  
 512 variation in decomposition rates.

513         Among the potential mechanisms to explain the responses induced by plant-soil  
 514 interactions, microorganisms may differ in their abilities to degrade contrasting litter species, i.e.,  
 515 in their FB (Keiser et al. 2014). In agreement with this second hypothesis, all of the tested litter  
 516 types decomposed more rapidly in the forest soil (Fig. 4B), confirming that microbial  
 517 communities originating from forested habitats display a greater ability to degrade various  
 518 substrates compared to those originating from more labile litter environments. Although we  
 519 cannot substantiate the notion that litter quality is ‘in the eye of the beholder’ (Strickland et al.  
 520 2009b), our results confirm that contrasting microbial communities may differ in their functional  
 521 abilities for decomposing various litter species (Strickland et al. 2009a). More importantly,  
 522 investigating the temporal dynamics of carbon mineralisation allowed us to determine that the  
 523 capacities of soil microbes are not set in stone. For example, the FB of the grassland microbial

524 community, which had not faced complex substrates in their recent history, became positive and  
 525 increased steadily after 100 days (Fig. 4B). This result is particularly surprising given that the  
 526 fingerprint of the past resource is often invoked to explain plant-microbe interactions, suggesting  
 527 that additional mechanisms may influence the ability of a community to be functionally ‘broad’  
 528 or ‘narrow’. Although we cannot judge with certainty, the gene and protein expression, the  
 529 physicochemical characteristics of the surrounding environment, the diversity of soil  
 530 decomposers, and/or the presence of specific groups of decomposers may all explain the  
 531 functional ability dynamics. An alternative explanation would be that although we consciously  
 532 selected one species in almost pure stands for the ecosystems of grassland and forest, microbial  
 533 communities from these two ecosystems encountered a wider variety of chemical substrates than  
 534 did those originating from ‘agro-systems’, which likely influenced the contrasting functional  
 535 abilities observed among the four different soil types.

536 Another way to address functional dissimilarity between contrasting microbial  
 537 communities is the HFA hypothesis, which investigates whether microbes decompose litter that  
 538 is derived from a ‘home’ site more efficiently than litter that is derived from a ‘away’ site (Gholz  
 539 et al. 2000). Here, although the forest litter decomposed fastest in its own environment, we did  
 540 not find any evidence for an HFA effect in the forest soil because all of the litters decomposed  
 541 proportionally more rapidly in this ecosystem. Although the interpretation of HFA results should  
 542 be treated with caution since their variability is greater than that of LQ and FB, we found a small  
 543 positive HFA when the plantation and grassland litters matched their own environment,  
 544 indicating that soil microbial communities originating from these two environments were ‘pre-  
 545 adapted’ to decomposing substrates they were accustomed to encountering (Fig. 4C).  
 546 Counterintuitively, we demonstrated here that HFA is not systematically greater with increasing

547 litter recalcitrance and that ‘affinity effects’ between microorganisms and their resources can  
 548 also be observed on more labile substrates. This idea has been recently supported by a meta-  
 549 analysis of 125 reciprocal litter transplants, in which Veen et al. (2014) concluded that HFA  
 550 effects were not related to particular litter types but were stronger when the litter quality between  
 551 ‘home’ and ‘away’ sites was more dissimilar.

552

553 *Microbial community structure and enzymatic activities: how can we explain the functional*  
 554 *dissimilarity?*

555

556 To date, functional dissimilarities of soil microbial communities generated by FB and  
 557 HFA have not been separately quantified (but see Keiser et al. 2014), and our study is one of the  
 558 first to determine their relative contribution over time. Here, we found that the magnitude of  
 559 these two mechanisms was similar but that the directions of these effects were, in some cases,  
 560 opposite depending on both the litter and soil types (Fig. 4). The functional dissimilarity  
 561 generated by the effects of FB and HFA on parietal sugar mass loss were closely linked to soil  
 562 enzymes (Fig. 5), suggesting that the extracellular enzymatic activities are the main driver of the  
 563 interactions between litter quality and the decomposer communities. Surprisingly, despite the  
 564 large variations in microbial groups among the different ecosystems (Fig. 3A), we did not find  
 565 any direct relationship between the PLFA-based community structure and the hydrolytic enzyme  
 566 production. This result begs the question as to whether the relationship between the composition  
 567 of soil communities and the enzymatic synthesis is causal at the local scale. Similarly, Purahong  
 568 et al. (2014) recently demonstrated a decoupling between the microbial community structure and  
 569 hydrolytic, but not oxidative, enzymatic activities. At minimum, these data indicate that the

570 enzymes necessary for degrading complex molecules are under the direct control of specific  
 571 groups of decomposers (i.e. fungi), and thus that any effect of community structure on  
 572 decomposition should be accentuated when one is interested in more recalcitrant leaf litter  
 573 compounds (Wallenstein et al. 2013). In agreement with this theory, we found that in most of the  
 574 litters presenting positive plant-soil interactions, lignin generally exhibited greater FB and HFA  
 575 effects compared to more labile monosaccharides after an approximately 100-day delay (see  
 576 Appendix I). Consequently, because contrasting microbial communities can change the course of  
 577 the decomposition process (Wickings et al. 2012), we believe that models predicting carbon  
 578 mineralisation should include parameters that explicitly represent the variability in the functional  
 579 abilities of decomposers (Treseder et al. 2012). However, although we excluded all the major  
 580 groups of macrofauna by sieving, we cannot ignore that the variability in micro- and mesofauna  
 581 diversity may have also contributed to the plant-soil interactions. Because higher trophic levels  
 582 have been shown to largely contribute to the interaction between litter and decomposer  
 583 communities, particularly in the poorest sites (e.g., Milcu and Manning 2011, Perez et al. 2013),  
 584 increasing the diversity of decomposers in the field will likely reveal a more complex situation  
 585 than that observed in our microcosm experiment.

586

587 *Conclusions*

588

589 Our fully factorial microcosm experiment provides new insight into the relative effects of  
 590 litter quality and microbial community on decomposition rates. The effect of soil type on carbon  
 591 mineralisation suggests that microbial communities have a subtle but significant role in  
 592 regulating decomposition rates. In particular, the mass loss of various parietal compounds in a

593 given litter type can vary strongly between microbial communities from contrasting soil types.  
 594 Whether microbial diversity or soil physico-chemical properties are directly responsible for the  
 595 local variability observed in enzymatic activities nevertheless remains a complex question. In  
 596 other words, if microbial diversity is critical to enzymatic synthesis, then the absence of specific  
 597 groups due to ecosystem disturbance might have substantial impacts on the local carbon fate. If  
 598 not, enzymatic activity across various lineages of soil organisms should converge to optimise  
 599 resource acquisition and thus the functional traits of soil microbes would be more relevant than  
 600 their identity for predicting the ecosystem processes (Talbot et al. 2014). However, the relatively  
 601 small amount of variation that was explained by the litter-microbe interactions compared to that  
 602 which was explained by litter quality suggests that the composition of the microbial community  
 603 plays only a minor role in regulating the decomposition rates along our land use gradient. This  
 604 result questions the relevance of increasing efforts to understand the role of resource-consumer  
 605 interactions during litter decomposition in various ecosystems. Although this issue is  
 606 challenging, more attention should be paid to determining whether fundamental knowledge about  
 607 microbial diversity will considerably improve our predictions of carbon mineralisation and  
 608 enzymatic activities.

609

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611

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626

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628

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784

785 **Ecological Archives**

786 Appendices A-I are available online:

787

788 **Tables**

789 Table 1. ANOVA results with the percentage sums of squares explained (%SS) for the effects of  
 790 soil, litter type and their interactions on the cumulative carbon mineralisation. Raw data or net  
 791 data (corrected by control soils) were used.

Source of variation	df	Raw data			Net data		
		%SS	F	<i>P</i> -value	%SS	F	<i>P</i> -value
<i>27 days</i>							
Soil type	3	9.6	114.3	< <b>0.0001</b>	1.9	21.2	< <b>0.0001</b>
Litter type	3	89.3	1066.6	< <b>0.0001</b>	96.8	1066.6	< <b>0.0001</b>
Soil type × Litter type	9	0.3	1.0	0.45 <sup>NS</sup>	0.3	1.0	0.45 <sup>NS</sup>
Error	32	0.9			1.0		
<i>97 days</i>							
Soil type	3	22.9	430.3	< <b>0.0001</b>	2.4	35.0	< <b>0.0001</b>
Litter type	3	76.1	1431.7	< <b>0.0001</b>	96.4	1431.7	< <b>0.0001</b>
Soil type × Litter type	9	0.4	2.6	<b>0.024</b>	0.5	2.6	<b>0.024</b>
Error	32	0.6			0.7		
<i>202 days</i>							
Soil type	3	32.1	791.0	< <b>0.0001</b>	4.0	69.0	< <b>0.0001</b>
Litter type	3	66.9	1647.8	< <b>0.0001</b>	94.7	1647.8	< <b>0.0001</b>
Soil type × Litter type	9	0.5	4.2	<b>0.0011</b>	0.7	4.2	<b>0.0011</b>
Error	32	0.4			0.6		

792 *Note:* Significant differences are displayed in boldface.

793 Table 2. Results of linear mixed models to test for the effects of soil type and time on the net  
794 carbon mineralisation rates.

Litter type	Incubation period	Soil type			Soil type x Time		
		df	F	<i>P</i> -value	df	F	<i>P</i> -value
<i>Cropland</i>	0 - 27 days	3, 8	10.76	<b>0.0035</b>	18, 48	21.11	< <b>0.0001</b>
	28 - 97 days	3, 8	8.83	<b>0.0064</b>	18, 48	5.30	< <b>0.0001</b>
	98 - 202 days	3, 8	37.60	< <b>0.0001</b>	18, 48	0.96	0.52 <sup>NS</sup>
<i>Forest</i>	0 - 27 days	3, 8	13.10	<b>0.0019</b>	18, 48	11.38	< <b>0.0001</b>
	28 - 97 days	3, 8	20.42	< <b>0.0001</b>	18, 48	6.14	< <b>0.0001</b>
	98 - 202 days	3, 8	10.75	<b>0.0035</b>	18, 48	NS	0.40 <sup>NS</sup>
<i>Grassland</i>	0 - 27 days	3, 8	2.96	0.10 <sup>NS</sup>	18, 48	8.12	< <b>0.0001</b>
	28 - 97 days	3, 8	34.69	< <b>0.0001</b>	18, 48	1.50	0.13 <sup>NS</sup>
	98 - 202 days	3, 8	2.69	0.12 <sup>NS</sup>	18, 48	10.62	< <b>0.0001</b>
<i>Plantation</i>	0 - 27 days	3, 8	6.48	<b>0.016</b>	18, 48	14.27	< <b>0.0001</b>
	28 - 97 days	3, 8	13.57	<b>0.0017</b>	18, 48	10.74	< <b>0.0001</b>
	98 - 202 days	3, 8	147.99	< <b>0.0001</b>	18, 48	1.77	0.06 <sup>NS</sup>

795 *Note:* Results were analysed based on litter types and incubation periods. Significant differences

796 are displayed in boldface.

797 Table 3. PERMANOVA evaluating the effects of soil type, litter type and time on (A) the  
798 microbial community structure and (B) enzymatic activities.

A Microbial community structure	df	SS	MS	F.model	<i>P</i> -value	<i>r</i> <sup>2</sup>
Soil type	3	0.14	0.05	71.6	< <b>0.0001</b>	0.36
Litter type	3	0.07	0.02	36.8	< <b>0.0001</b>	0.18
Time	2	0.05	0.24	36.9	< <b>0.0001</b>	0.12
Litter type × Time	6	0.04	0.01	9.2	< <b>0.0001</b>	0.09
Soil type × Time	6	0.02	0.00	4.1	< <b>0.0001</b>	0.04
Soil type × Litter type	9	0.00	0.00	0.7	0.94 <sup>NS</sup>	0.01
Residuals	114	0.07	0.00			0.19
Total	143	0.39				

B Enzymes	df	SS	MS	F.model	<i>P</i> -value	<i>r</i> <sup>2</sup>
Soil type	3	0.11	0.037	66.3	< <b>0.0001</b>	0.28
Litter type	3	0.02	0.005	9.4	< <b>0.0001</b>	0.04
Time	2	0.10	0.050	88.5	< <b>0.0001</b>	0.25
Litter type × Time	6	0.01	0.001	2.7	<b>0.012</b>	0.02
Soil type × Time	6	0.08	0.013	22.6	< <b>0.0001</b>	0.19
Soil type × Litter type	9	0.02	0.002	4.2	< <b>0.0001</b>	0.05
Residuals	114	0.06	0.001			0.16
Total	143	0.40				

799 *Note:* Permutational multivariate ANOVA were performed to examine the relative influences of  
800 soil type, litter type, time, and the interactions between these three explanatory variables on the  
801 variation in the microbial community PLFA-based structure and enzymatic activities over the  
802 course of the incubation experiment.



803 **Figures**

804 Fig. 1. Schematic diagrams of the interactions between litter quality and soil microbial  
 805 communities during decomposition as expected when considering (A) the initial litter quality  
 806 (LQ) hypothesis: carbon mineralisation throughout decomposition is a function of initial litter  
 807 quality, with the most labile litters showing the highest carbon mineralisation rates in all  
 808 environments; (B) the functional breadth hypothesis (FB): decomposer communities from  
 809 recalcitrant ecosystems have a wider functional ability to decompose a wide range of chemical  
 810 compounds, with all litter types showing the highest carbon mineralisation rates in  
 811 poor/recalcitrant litter environments; and (C) the home-field advantage (HFA) hypothesis:  
 812 decomposer communities are locally adapted to their own litter, with each litter type  
 813 decomposing fastest in an area dominated by the plant species from which it was derived than in  
 814 an area dominated by another plant species. Based on the degree of recalcitrance of plant cell  
 815 walls that varied strongly between *Gramineae* and woody plant species, and on the nitrogen  
 816 content that was almost threefold higher in the grassland litter compared with the cropland litter,  
 817 we defined the relative ranking of litter quality as following: *F. arundinacea*, *T. aestivum*, *R.*  
 818 *pseudoacacia* and *F. sylvatica*. The + sign indicates that the carbon mineralisation rate is higher  
 819 for the plant-soil interactions, which are illustrated by arrows in the different panels. All + signs  
 820 represent patterns of variation rather than absolute values.

821

822 Fig. 2. Raw cumulative carbon mineralisation obtained for each (A) litter type and (B) soil type.  
 823 Each point represents a mean across all types of soils or among the different litters under  
 824 decomposition at a given time. Priming effect obtained after the addition of <sup>13</sup>C labelled flax

825 litter was represented for each ecosystem type (C). A negative priming effect indicates that SOM  
 826 mineralisation is higher in the control than in the residue-amended treatment.

827

828 Fig. 3. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis distances  
 829 of (A) microbial community composition (stress = 0.22) and (B) enzymes (stress = 0.06).  
 830 Different symbols represent the different types of soil: cropland (grey circles), forest (black  
 831 squares), grassland (white triangles), and plantation (dark grey diamonds). The lines correspond  
 832 to the distance between the calculated centroid and the projection of the different samples per  
 833 soil. The ellipses represent the average projection area of the samples from the centroid of each  
 834 soil.

835

836 Fig. 4. Parameter estimates of the net cumulative carbon mineralisation calculated using the new  
 837 approach developed by Keiser et al. (2014) for (A) LQ, (B) FB, and (C) HFA. LQ relates to the  
 838 relative ability of each different litter to be mineralized by all the decomposer communities used  
 839 in our experiment. FB quantifies the overall functional ability of each decomposer community.  
 840 HFA estimates the interaction between the litter decomposition and the decomposer communities  
 841 in each ecosystem.

842

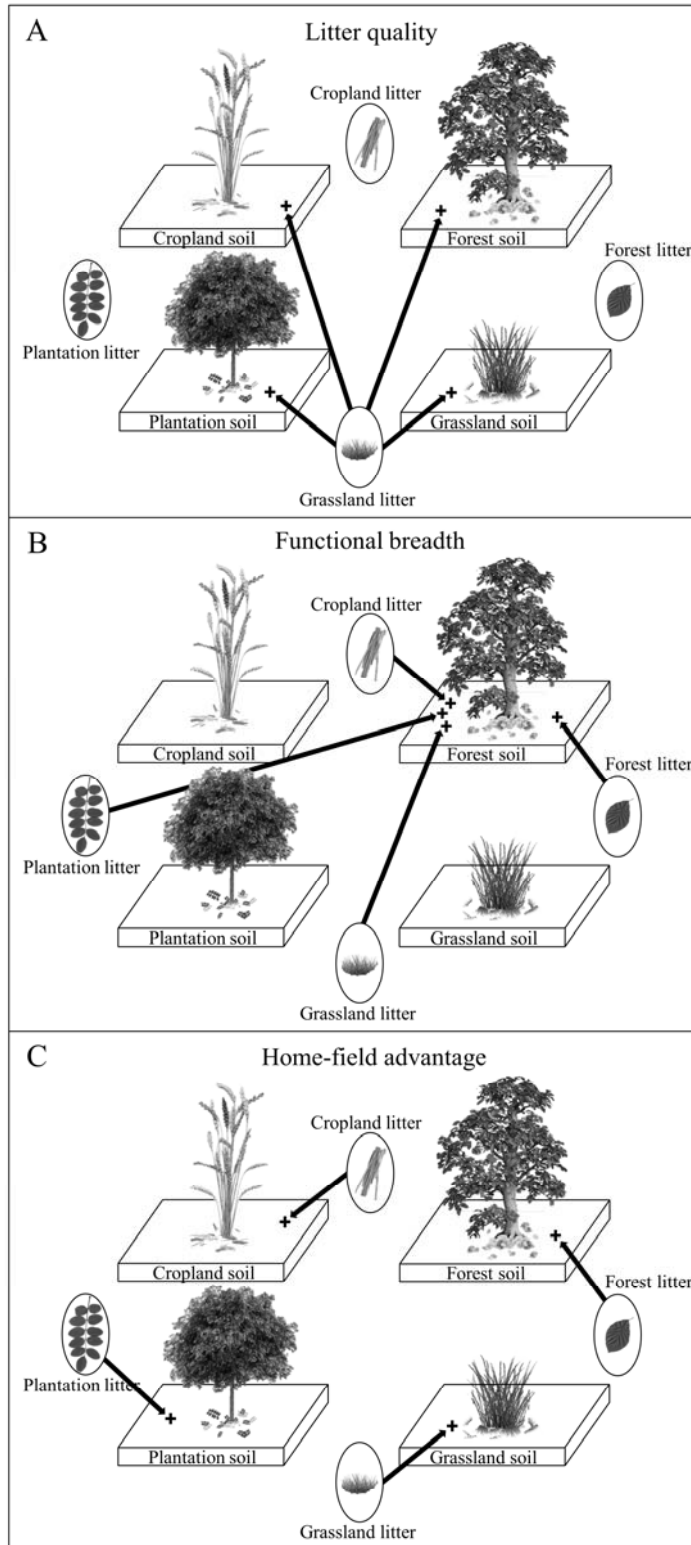
843 Fig. 5. Correlations between the parameter estimates of sugar mass loss as a function of the net  
 844 integrated enzymatic activity, which was calculated using the model presented in Fig. 4. The  
 845 parameter estimates represent the expected parietal sugar mass loss or enzymatic synthesis for  
 846 either FB (white symbols) or HFA (grey symbols): cropland (circles), forest (squares), grassland  
 847 (triangles), and plantation (diamonds). The parietal sugar mass loss is the mean of all of the  
 848 monosaccharides in the cell wall: L-arabinose, D-glucose, D-xylose, D-galactose, L-rhamnose,

849 D-mannose, L-fucose, D-galacturonic acid and D-glucuronic acid. The net integrated enzymatic  
850 activity is the mean of all of the carbon-related enzymes ( $\beta$ -1,4-glucosidase,  $\beta$ -D-cellobiosidase,  
851  $\alpha$ -glucosidase, and  $\beta$ -xylosidase) after correction by the 'no-litter treatment' soil.

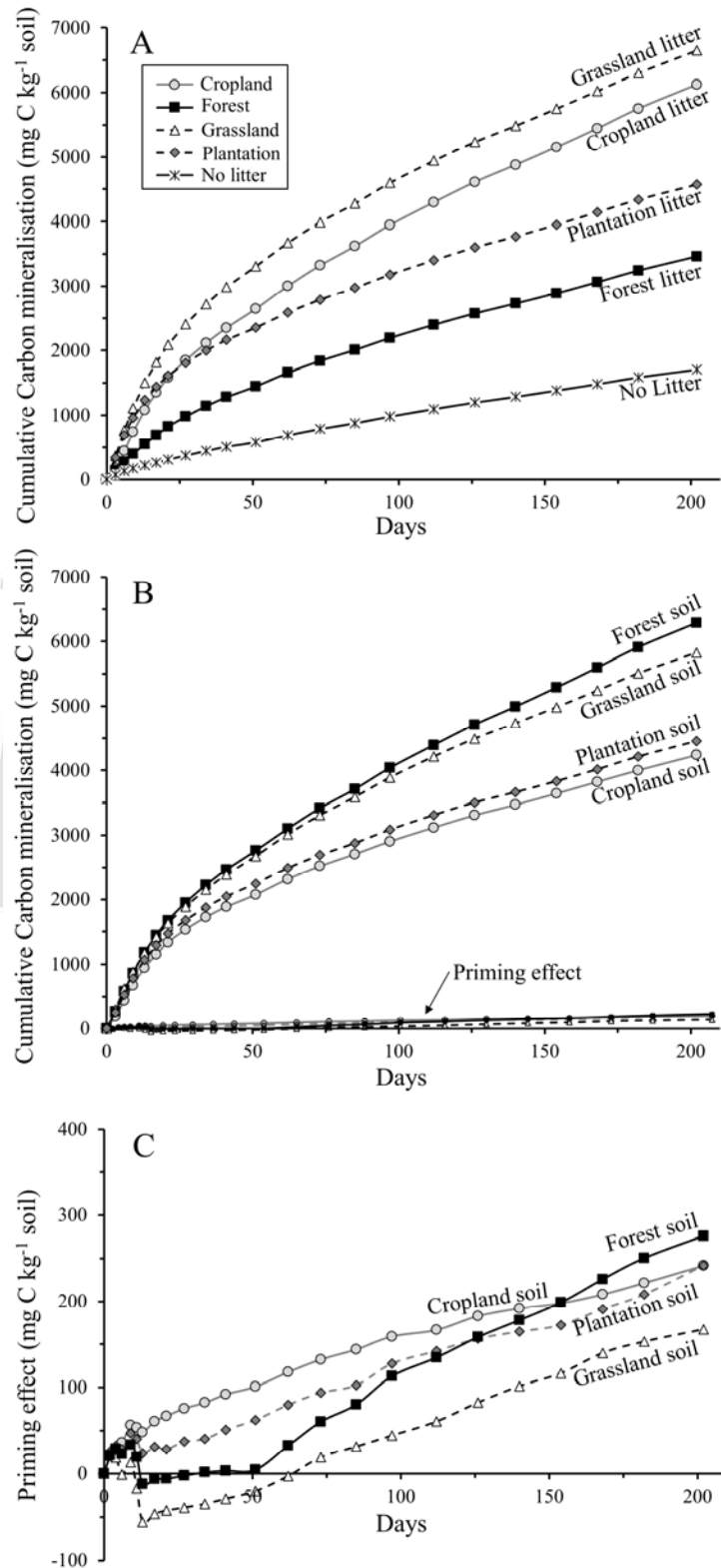
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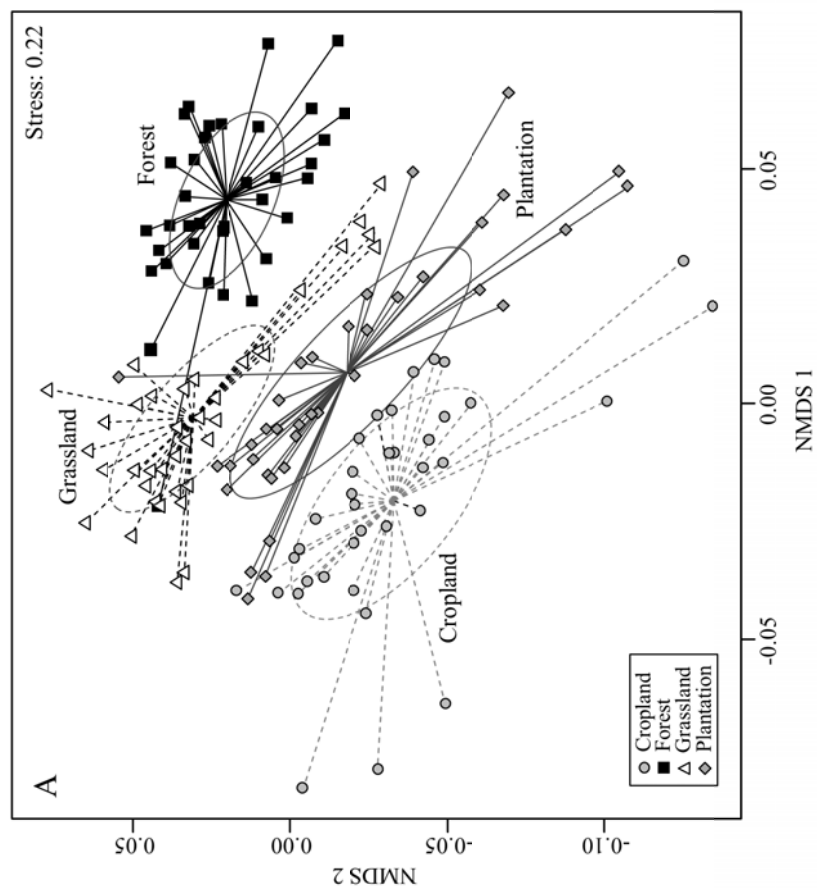
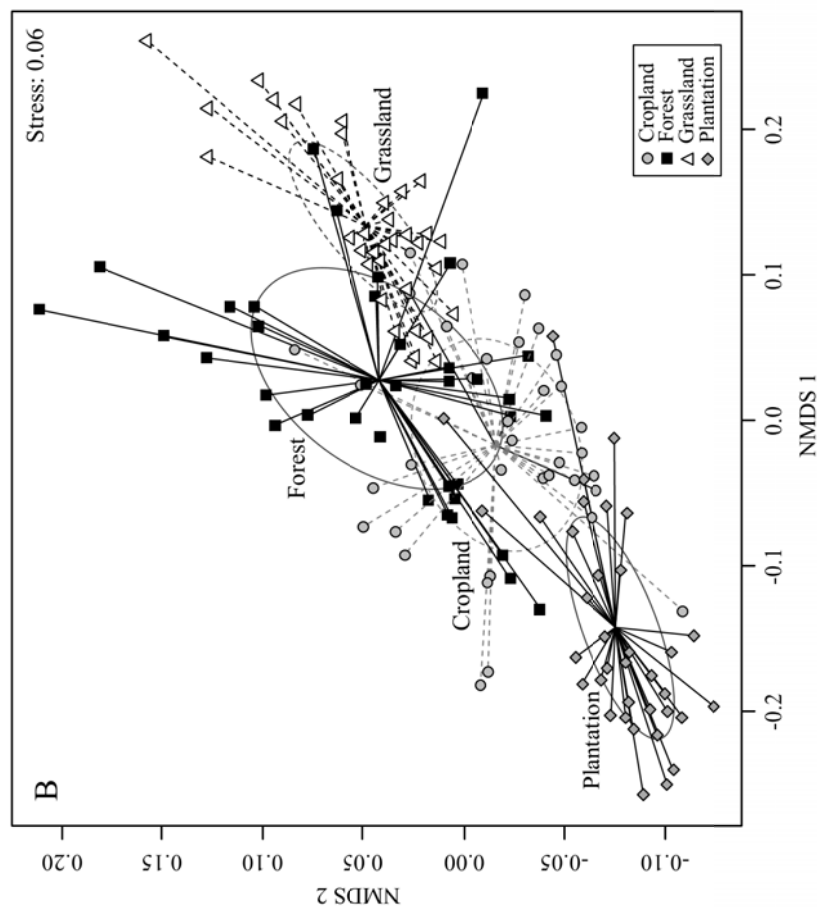
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852 Figure 1.



853 Figure 2.



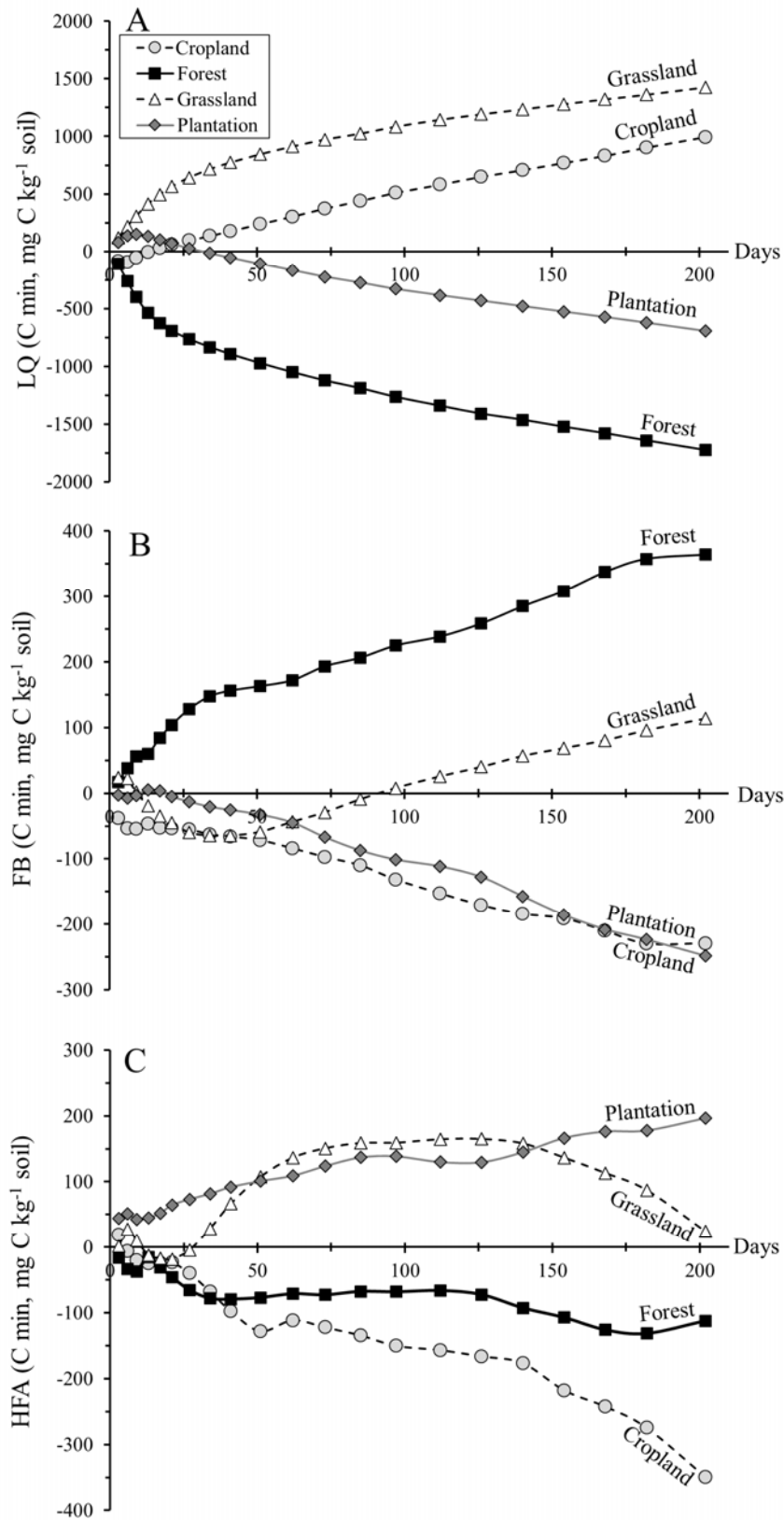


854 Figure 3.

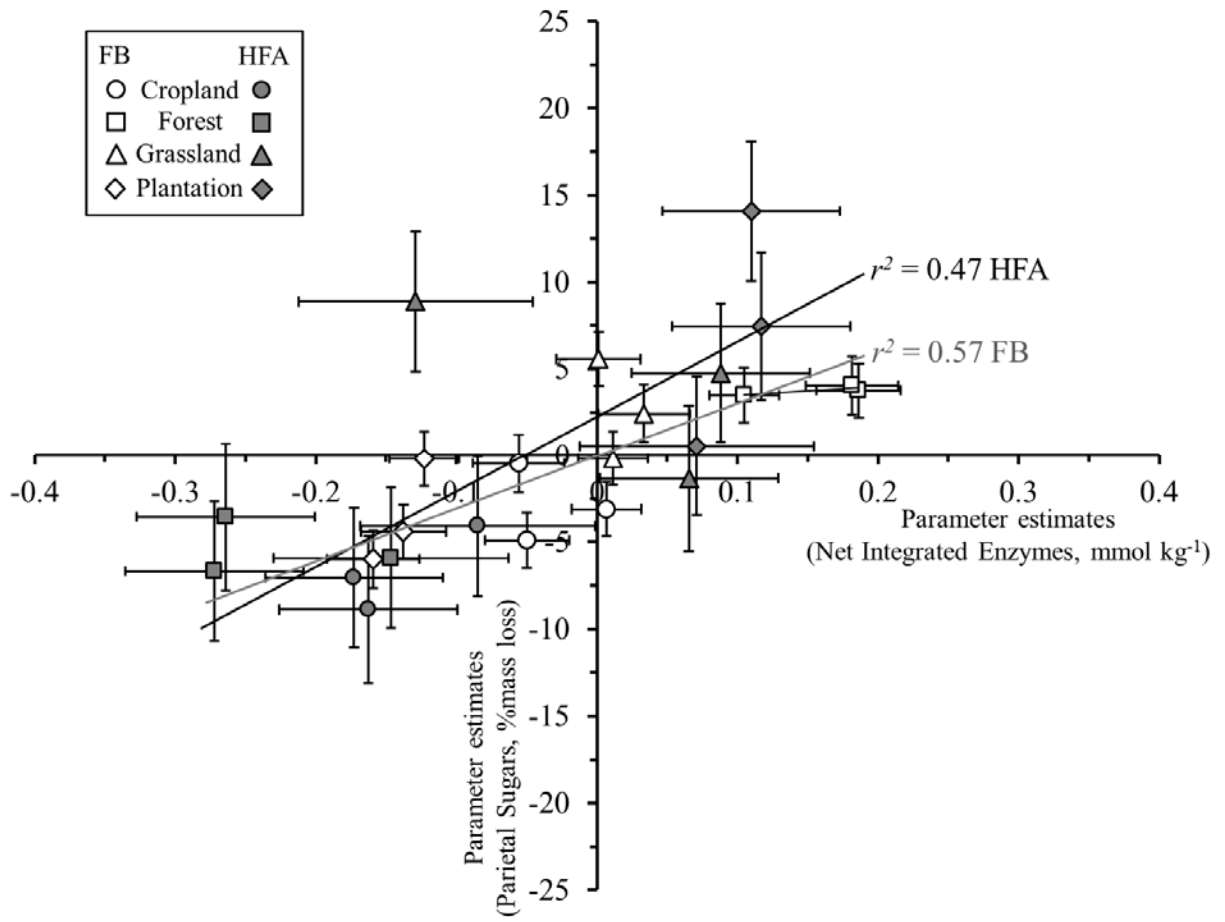
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855 Figure 4.



856 Figure 5.



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