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

Nicolas Fanin, Nathalie Fromin, Isabelle Bertrand

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

3

4 **List of authors:** Nicolas Fanin^{1,2}, Nathalie Fromin^{3,4}, Isabelle Bertrand^{1,5,6}.

5

6 **Postal addresses:** ¹INRA, UMR 614 Fractionnement des AgroRessources et Environnement, 2

7 esplanade Roland Garros, F-51100 Reims, France; ²Department of Forest Ecology and

8 Management, Swedish University of Agricultural Sciences, Umeå, Sweden, ³Centre d'Ecologie

9 Fonctionnelle et Evolutive (CEFE), CNRS – Université de Montpellier – Université Paul Valéry

10 Montpellier – EPHE, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France, ⁴PROMES –

11 CNRS, 7 rue du Four Solaire, F66120 Odeillo, France, ⁵INRA, UMR Eco&Sols, 2 Place Viala,

12 34060 Montpellier Cedex 1, France, ⁶Corresponding author: Isabelle Bertrand,

13 isabelle.bertrand@supagro.inra.fr

14

15 **E-mail addresses:** nicolas.fanin@slu.se, nathalie.fromin@cefe.cnrs.fr,

16 isabelle.bertrand@supagro.inra.fr

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}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 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

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

First, the ‘litter quality’ (LQ) hypothesis suggests that the intrinsic physical and chemical characteristics of leaf litter, commonly measured as the C:N and lignin:N ratios or the quality of various carbon forms, are the main predictors influencing the decomposition rate (Aber et al. 1990, Aerts 1997, Cornwell et al. 2008). In a reciprocal litter transplant study using 16 different species across four different biomes, Makkonen et al. (2012) showed that a small subset of litter traits explained most of the variation in litter mass loss, suggesting that the decomposition process is largely independent of the local decomposer communities. Because of these ‘litter trait controls’, differences in carbon mineralisation rates during litter decomposition should result from the higher consumption of easily degradable litters (e.g., rich in soluble and holocellulose contents) and the persistence of recalcitrant litters that are more resistant to decay (e.g., rich in 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, Gießelmann 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 ^{13}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°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 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°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 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°C for parietal sugar and lignin
 203 analyses. Two additional subsamples of soil and litter mixtures were immediately frozen at -
 204 20°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 CO₂ 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⁻¹ soil day⁻¹) and cumulative carbon mineralisation (mg C kg⁻¹ 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 CO₂ 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 ¹³C 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}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 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 BaCl_2 to NaOH
 238 solutions and the resulting precipitate of BaCO_3 was separated by vacuum filtration (glass fiber
 239 filter) and dried at 80°C for 8 hours. The BaCO_3 precipitate was weighed in a tin cap with the
 240 addition of a catalyst (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 (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 H₂SO₄ for 2 h at 20°C and was then subjected to acid
 260 hydrolysis with 1 M H₂SO₄ 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 H₂SO₄ 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

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

275

276 *Enzymatic activities*

277

At days 27, 97, and 202, we used a method by Bell et al. (2013) to measure the potential activity of four hydrolytic soil enzymes, which degrade a range of substrates that are common constituents of organic matter. The following enzymes were selected to represent the degradation of C-rich substrates: β -1,4-glucosidase, β -D-cellobiosidase, α -glucosidase, and β -xylosidase (see Appendix D for details regarding the initial enzymatic activity of each system). In brief, the assays were conducted by homogenising 2.75 g of the soil-litter mixture in 91 ml of 50 mM TRIS buffer (pH 7.8 for forest or grassland, pH 8.1 for cropland and plantation) in a blender for 1 min. The soil slurries were then added to a 96-deep-well microplate using an eight-channel repeat pipettor. Additional quench control replicates of the soil slurry and 4-methylumbelliferone (MUB) standard curves (0-100 μ M concentrations) were included with each sample. The soil slurries were incubated with fluorometric substrates for 3 h at 25°C. After the incubation period, the plates were centrifuged for 20 min at 3000 rpm, after which 250 μ l of supernatant was transferred from each well into a black, flat-bottomed 96-well plate that was scanned using a microplate reader (SpectraMax Gemini, Molecular Devices, CA, USA) with an excitation wavelength of 365 nm and an emission wavelength of 450 nm. All enzymatic activities were first calculated in nmol g⁻¹ soil h⁻¹ and were then corrected for the contribution of the corresponding soil type by subtracting the enzyme activities of the 'no-litter' soil. These values were subsequently integrated over time (mmol kg⁻¹ 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 (β_l)
 331 plus soil ability (γ_s) plus a home interaction term (η_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 , β_l is the ability of litter species l (from
 334 species 1 to N), γ_s is the ability of the soil community s (from community 1 to M), η_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 β_l , γ_s and η_h . The intercept term is defined by α 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 ε . Using this model, we calculated a quality index (LQ), the ability of soil

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

350

351 **Results**

352

353 *Litter quality and carbon mineralisation*

354

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

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

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

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

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

Microbial community structure and enzymatic production

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

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

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

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

When estimating the β_l (LQ), γ_s (FB), and η_h (HFA) metrics from the net carbon mineralisation data, we found that β_l was the metric that showed the largest variation (Fig. 4), with values ranging from -1725 to +1426 mg C mineralised kg⁻¹ soil on average across the soil and litter type combinations. The grass and cropland litters showed the highest LQ index compared to the plantation and forest litters (Fig. 4A), confirming that more labile litter types

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

When calculating the parameter estimates corresponding to the effects of FB (γ_s) and HFA (η_h) on the parietal sugar mass loss and net integrated enzymes, we observed positive 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 γ_s estimates for both the enzymatic activity and
 458 sugar mass loss in the forest ecosystem, whereas the η_h 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

land-use gradient. Overall, the soil type explained 9 to 32% of the variation in carbon mineralisation during the course of the experiment (Table 1). However, when accounting for the initial variability among the different ecosystems, the soil type explained only 2 to 4% of the variation, suggesting that the response induced by the litter-microbe interactions was smaller in our study than in other reports (Ayres et al. 2009b). The PE increased on average from 57 to 232 mg C kg⁻¹ between 27 to 202 days, meaning that we overestimated litter-derived CO₂ fluxes by 3.6 to 6.6% in our models. In addition, PE was lower in grassland soils over the course of the incubation experiment (Fig. 3C), indicating that caution must be taken when considering the variation of litter-microbe interactions between grassland and the other soil types. However, the relative consistency among soil types (CV = 27%) explaining 0.03 to 1.18% in the variation in net carbon mineralisation suggest that other factors besides PE also significantly influenced the variation in decomposition rates.

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

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

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

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

552

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

555

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

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

586

587 *Conclusions*

588

Our fully factorial microcosm experiment provides new insight into the relative effects of litter quality and microbial community on decomposition rates. The effect of soil type on carbon mineralisation suggests that microbial communities have a subtle but significant role in 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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- 785 **Ecological Archives**
- 786 Appendices A-I are available online:
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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-value</i>	%SS	F	<i>P-value</i>
<i>27 days</i>							
Soil type	3	9.6	114.3	< 0.0001	1.9	21.2	< 0.0001
Litter type	3	89.3	1066.6	< 0.0001	96.8	1066.6	< 0.0001
Soil type × Litter type	9	0.3	1.0	0.45 ^{NS}	0.3	1.0	0.45 ^{NS}
Error	32	0.9			1.0		
<i>97 days</i>							
Soil type	3	22.9	430.3	< 0.0001	2.4	35.0	< 0.0001
Litter type	3	76.1	1431.7	< 0.0001	96.4	1431.7	< 0.0001
Soil type × Litter type	9	0.4	2.6	0.024	0.5	2.6	0.024
Error	32	0.6			0.7		
<i>202 days</i>							
Soil type	3	32.1	791.0	< 0.0001	4.0	69.0	< 0.0001
Litter type	3	66.9	1647.8	< 0.0001	94.7	1647.8	< 0.0001
Soil type × Litter type	9	0.5	4.2	0.0011	0.7	4.2	0.0011
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	P-value	df	F	P-value
<i>Cropland</i>	0 - 27 days	3, 8	10.76	0.0035	18, 48	21.11	< 0.0001
	28 - 97 days	3, 8	8.83	0.0064	18, 48	5.30	< 0.0001
	98 - 202 days	3, 8	37.60	< 0.0001	18, 48	0.96	0.52 ^{NS}
<i>Forest</i>	0 - 27 days	3, 8	13.10	0.0019	18, 48	11.38	< 0.0001
	28 - 97 days	3, 8	20.42	< 0.0001	18, 48	6.14	< 0.0001
	98 - 202 days	3, 8	10.75	0.0035	18, 48	NS	0.40 ^{NS}
<i>Grassland</i>	0 - 27 days	3, 8	2.96	0.10 ^{NS}	18, 48	8.12	< 0.0001
	28 - 97 days	3, 8	34.69	< 0.0001	18, 48	1.50	0.13 ^{NS}
	98 - 202 days	3, 8	2.69	0.12 ^{NS}	18, 48	10.62	< 0.0001
<i>Plantation</i>	0 - 27 days	3, 8	6.48	0.016	18, 48	14.27	< 0.0001
	28 - 97 days	3, 8	13.57	0.0017	18, 48	10.74	< 0.0001
	98 - 202 days	3, 8	147.99	< 0.0001	18, 48	1.77	0.06 ^{NS}

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-value</i>	<i>r</i> ²
Soil type	3	0.14	0.05	71.6	< 0.0001	0.36
Litter type	3	0.07	0.02	36.8	< 0.0001	0.18
Time	2	0.05	0.24	36.9	< 0.0001	0.12
Litter type × Time	6	0.04	0.01	9.2	< 0.0001	0.09
Soil type × Time	6	0.02	0.00	4.1	< 0.0001	0.04
Soil type × Litter type	9	0.00	0.00	0.7	0.94 ^{NS}	0.01
Residuals	114	0.07	0.00			0.19
Total	143	0.39				

B Enzymes	df	SS	MS	F.model	<i>P-value</i>	<i>r</i> ²
Soil type	3	0.11	0.037	66.3	< 0.0001	0.28
Litter type	3	0.02	0.005	9.4	< 0.0001	0.04
Time	2	0.10	0.050	88.5	< 0.0001	0.25
Litter type × Time	6	0.01	0.001	2.7	0.012	0.02
Soil type × Time	6	0.08	0.013	22.6	< 0.0001	0.19
Soil type × Litter type	9	0.02	0.002	4.2	< 0.0001	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 ^{13}C labelled flax

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

827

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

835

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

842

Fig. 5. Correlations between the parameter estimates of sugar mass loss as a function of the net integrated enzymatic activity, which was calculated using the model presented in Fig. 4. The parameter estimates represent the expected parietal sugar mass loss or enzymatic synthesis for either FB (white symbols) or HFA (grey symbols): cropland (circles), forest (squares), grassland (triangles), and plantation (diamonds). The parietal sugar mass loss is the mean of all of the 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 (β -1,4-glucosidase, β -D-cellobiosidase,
 851 α -glucosidase, and β -xylosidase) after correction by the 'no-litter treatment' soil.

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852 Figure 1.

853 Figure 2.

854 Figure 3.

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855 Figure 4.

856 Figure 5.