

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

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- 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

species than those originating from richer environments, i.e. the functional breadth (FB) hypothesis; and/or (ii) decomposer communities may be specialized towards the litter they most frequently encounter, i.e. the home-field advantage (HFA) hypothesis. Nevertheless, the functional dissimilarities among contrasting microbial communities, which are generated by the 27 FB and the HFA, have rarely been simultaneously quantified in the same experiment, and their relative contributions over time have never been assessed. To test these hypotheses, we 29 conducted a reciprocal transplant decomposition experiment under controlled conditions using 30 litter and soil originating from four ecosystems along a land-use gradient (forest, plantation, 31 grassland and cropland) and one additional treatment using <sup>13</sup>C labelled flax litter allowing us to 32 assess the priming effect (PE) in each ecosystem. We found substantial effects of LQ on carbon 33 mineralisation (more than two-thirds of the explained variance), whereas the contribution of the 34 soil type was fairly low (less than one-tenth), suggesting that the contrasting soil microbial 35 communities play only a minor role in regulating decomposition rates. Although the results on 36 PE showed that we overestimated litter-derived CO<sub>2</sub> fluxes, litter-microbe interactions contributed significantly to the unexplained variance observed in carbon mineralisation models. 38 The magnitudes of FB and HFA were relatively similar, but the directions of these mechanisms 39 were sometimes opposite depending on the litter and soil types. FB and HFA estimates 40 calculated on parietal sugar mass loss were positively correlated with those calculated on 41 enzymatic activity, confirming the idea that the interaction between litter quality and microbial 42 43 community structure may modify the trajectory of carbon mineralisation via enzymatic synthesis. We conclude that although litter quality was the predominant factor controlling litter 44 mineralisation, the local microbial communities and interactions with their substrates can explain 45 a small (< 5%) but noticeable portion of carbon fluxes.

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

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#### Introduction

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54 The decomposition of plant litter is one of the most important processes influencing the global carbon cycle, the mineralisation of nutrients, soil fertility, and the formation of soil 55 organic matter in terrestrial ecosystems. Almost 40 years ago, Meentemeyer (1978) proposed that climate and litter quality are the main factors explaining plant litter decomposition at the 57 global scale. In the decades since, many studies have confirmed this pattern at the continental 58 scale (e.g., Aerts 1997, Gholz et al. 2000, Trofymow et al. 2002, Powers et al. 2009), but the 59 factors contributing to the unexplained variation in local decomposition processes and their 60 relative contributions remain uncertain (Bradford et al. 2014). A variety of drivers modifying the 61 trajectory of decomposition rates have been proposed, including diversity effects (Heemsbergen 62 et al. 2004, Gessner et al. 2010), solar radiation (Austin and Vivanco 2006), the temporal 63 concordance between tree phenology and soil decomposers (Pearse et al. 2014), and the structure of the soil fauna and microbial communities (Wall et al. 2008, Strickland et al. 2009a). It has also been suggested that interactions between the litter quality and decomposer communities may 66 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. 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 71 Avres 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 73 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 75 hypotheses addressing the effects of plant-soil interactions on carbon mineralisation during the 76 decomposition of plant litter in a variety of contrasting ecosystems (Fig. 1). The selected land-77 use gradient, which ranges from cropland, plantation, and grassland to forest on a common soil 78 substratum and varies in vegetation cover and disturbance frequency, offers a great opportunity 79 to accurately assess the relative importance of substrate quality and microbial community on 80 81 litter decomposition. 82 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 83 various carbon forms, are the main predictors influencing the decomposition rate (Aber et al. 84 1990, Aerts 1997, Cornwell et al. 2008). In a reciprocal litter transplant study using 16 different 85 species across four different biomes, Makkonen et al. (2012) showed that a small subset of litter 86 traits explained most of the variation in litter mass loss, suggesting that the decomposition 87 process is largely independent of the local decomposer communities. Because of these 'litter trait 88 89 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 90 contents) and the persistence of recalcitrant litters that are more resistant to decay (e.g., rich in 91 lignin and secondary metabolites). For example, along a land-use gradient, grass litter, which 92

represents an energy-rich and labile substrate, should decompose faster in all types of ecosystems compared to the poorer and more recalcitrant forest litter (Fig. 1a). Support for this hypothesis is derived from a multitude of decomposition studies in which a range of litter types were allowed 95 to decompose across a variety of ecosystems (e.g., Gholz et al. 2000, Hobbie et al. 2006, 96 Makkonen et al. 2012). 97 Second, the 'functional breadth' (FB) hypothesis stipulates that decomposer communities 98 from recalcitrant litter environments have a wider functional ability than those originating from richer environments, meaning that they more efficiently decompose various litter types that vary 100 widely in their chemical and physical characteristics (van der Heijden et al. 2008, Keiser et al. 101 2011). Because of the past resource history that may influence whether microbial communities 102 are functionally 'broad' or 'narrow' (Keiser et al. 2014), differences in the carbon mineralisation 103 rates during litter decomposition should result from different catabolic capacities among contrasted decomposer communities. Thus, all litter species should decompose faster in the 105 forest soil than in any other ecosystem because of a higher capability of the forest soil microbial community to decompose a wide range of litter substrates (Fig. 1b). Consistent with this 107 108 hypothesis, Strickland et al. (2009b) demonstrated that poor and recalcitrant litter was decomposed more efficiently by decomposer communities originating from forested habitats, 109 whereas easily degradable litter was decomposed equivalently by all communities of 110 decomposers from different types of ecosystems. These results indicate that microbial 111 112 communities may be functionally dissimilar for the degradation of recalcitrant litter substrates and consequently that changes in ecosystem processes may also be strongly influenced by the 113 functional ability of distinct decomposer communities (Strickland et al. 2009a).

115 Finally, the 'home-field advantage' (HFA) hypothesis suggests that litter decomposes faster in an area dominated by the plant species from which it derives (i.e., at home) rather than 116 in an area dominated by another plant species (i.e., away) (Gholz et al. 2000). Because of this 'local adaptation' of the decomposer community, differences in carbon mineralisation rates 118 during litter decomposition should result from the match between a litter type and its own 119 environment. For example, forest litter should decompose faster in forest soil, whereas wheat 120 litter should decompose faster in cropland soil (Fig. 1c). In agreement with this hypothesis, 121 numerous studies have documented that plant litters decompose fastest in their local environment 122 (e.g., de Toledo Castanho and de Oliveira 2008, Vivanco and Austin 2008, Strickland et al. 123 2009a, Wallenstein et al. 2010). Although the HFA hypothesis has generated great attention, 124 several empirical studies did not find any evidence of such affinity between litter and microbes at 125 home (Ayres et al. 2006, Gießelmann et al. 2011, St John et al. 2011, Veen et al. 2015), sparking an important debate about the generalizability of this mechanism (see Austin et al. 2014 for a 127 review). This 'affinity effect' between decomposers and their substrates has been recently 128 129 amended with the 'substrate-matrix interaction' hypothesis (Freschet et al. 2012), which states that the composition of the decomposer community should reflect the average quality of the litter 130 matrix rather than species-specific home litter effects, in particular in biomes dominated by 131 multiple and chemically contrasted plant species. Despite these recent advances, few studies 132 have addressed carbon dynamics over time in relation to simultaneous changes in litter quality, 133 134 the local microbial community, and their functional abilities, although such an effort is essential 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 microbe interactions in a reciprocal transplant experiment of contrasting litters and their 138 associated soils originating from a land-use gradient (forest, plantation, grassland and cropland) 139 across a one-hectare plot. Because little is known about whether the previously described 140 mechanisms are transient or persistent over time, we specifically followed the kinetics of carbon 141 mineralisation over 202 days and 21 dates to better grasp the variability of responses generated 142 by the interactions between soil microbial communities and litter types. In order to ensure that 143 the mineralisation of 'older' organic matter via 'fresh' litter addition did not alter our conclusions 144 on litter-microbe interactions, we also measured the mineralisation of soil organic matter 145 following the addition of <sup>13</sup>C labelled flax litter (*Linum usitatissimum* L.) for assessing the 146 contribution of priming effect (PE) in each ecosystem. To investigate the triangular relationships 147 involving litter quality, the decomposer community and enzymatic activities for explaining the observed affinity effects, we analysed at three time points (at 27, 97, and 202 days) the mass loss 149 rates of the main sugars within the cell wall, the microbial community structure via twenty-four 150 selected PLFA markers, and the activities of four hydrolytic enzymes. We employed a new 151 model recently developed by Keiser et al. (2014) that allowed us to simultaneously test our three 152 main hypotheses by calculating the estimated parameters for LQ, FB and HFA and their effects 153 on carbon mineralisation. Finally, by assessing the effects of these parameters on the mass loss 154 of parietal sugars and on enzymatic activities, we addressed for the first time whether the effects 155 156 of FB and HFA on carbon mineralisation depend on the functional ability of the soil decomposer communities. 157

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#### 159 Methods

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161 Microcosm design

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

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

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#### 206 Carbon mineralisation

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

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224 Priming effect

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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 photoperiod) were monitored to mimic spring conditions. The plants were grown on rockwool

plugs under hydroponic conditions using nutrient solutions as described by Devienne et al. (1994). The plants were continuously labelled with  $^{13}$ C by using the same  $^{13}$ CO<sub>2</sub> bottles throughout the entire growth cycle. Flax stem was collected at maturity ( $\delta^{13}$ C = 2870‰, atom% excess = 3.056), homogenised, incubated at a rate equivalent to 10 g C kg<sup>-1</sup> dry soil (2.13 g of dry mass) and carbon mineralisation was measured as described above. Flax litter represented a mid-range quality, characterized by intermediate content of nitrogen, lignin, and soluble compounds and showed cumulative carbon mineralisation comprised between *Gramineae* and woody plant species with an average of 5232 mg C kg<sup>-1</sup> soil (see Appendix C for more details).

The <sup>13</sup>C–CO<sub>2</sub>/<sup>12</sup>C–CO<sub>2</sub> ratio was determined by adding 10 ml of 0.5 M BaCl<sub>2</sub> to NaOH solutions and the resulting precipitate of BaCO<sub>3</sub> was separated by vacuum filtration (glass fiber filter) and dried at 80°C for 8 hours. The BaCO<sub>3</sub> precipitate was weighed in a tin cap with the addition of a catalyst (PbO<sub>2</sub>), and the isotope ratio <sup>13</sup>C/<sup>12</sup>C of the precipitate was measured with an elemental analyzer (Eurovector, Milan, Italy) coupled to a mass spectrometer (Delta S Advantage, Thermo Fisher Scientific, Bremen, Germany). The priming effect (PE) was calculated with the following equation:

244 PE =  $[^{12+13}CO_2$ -amended -  $^{13}CO_2$ -amended] -  $^{12}CO_2^{ctrl}$ 

where  $^{12+13}$ CO<sub>2</sub>-amended and  $^{12}$ CO<sub>2</sub><sup>ctrl</sup> are the cumulative amounts (mg kg $^{-1}$ ) of mineralized

carbon in the soil with and without litters, respectively, and <sup>13</sup>CO<sub>2</sub>-amended represents the litter-

247 derived carbon.

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249 Litter chemical analyses

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251 To characterise the parietal sugars initially and at days 27, 97, and 202, the plant litter samples were subjected to a cell wall preparation process that consisted of extracting the neutral 252 detergent fibre (NDF) fraction as described by Goering and Van Soest (1970). The soluble 253 fraction was removed by boiling between 0.7 to 1 g of litter in deionised water at 100°C for 30 254 min and then performing an extraction with a neutral detergent solution at 100°C for 60 min to remove the cytoplasmic components and obtain the NDF fraction. All residues from the cell wall 256 preparations were dried for one week at 30°C and ground to 80 µm. The parietal sugars were 257 then analysed as previously described (Machinet et al. 2011). Briefly, 10 mg of the NDF residue 258 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 hydrolysis with 1 M H<sub>2</sub>SO<sub>4</sub> for 2 h at 100°C. The monosaccharides released by the acid 260 hydrolysis were separated by high-performance anion-exchange chromatography (HPAEC) on a 261 CarboPac PA-1 column (Dionex ICS 5000+, Thermo-Scientific, Sunnyvale, CA, USA). The 262 monosaccharide composition was analysed, and nine sugars were quantified using 2-deoxy-D-263 ribose as an internal standard and standard solutions of the following neutral carbohydrates: L-264 arabinose, D-glucose, D-xylose, D-galactose, L-rhamnose, D-mannose, L-fucose, D-galacturonic 265 acid and D-glucuronic acid. The parietal sugars were calculated as the sum of all of the 266 267 monosaccharides. 268 The lignin content of the litter subsamples was approximated as the acid-non-

The lignin content of the litter subsamples was approximated as the acid-nonhydrolysable residue remaining after sulphuric acid hydrolysis according to the Klason lignin determination method (Monties 1984). Briefly, 300 mg of litter was suspended in 3 ml of 12 M H<sub>2</sub>SO<sub>4</sub> for 2 h at room temperature. The suspensions were then diluted to 1 M with deionised 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.

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276 Enzymatic activities

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278 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 279 constituents of organic matter. The following enzymes were selected to represent the degradation 280 281 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 282 assays were conducted by homogenising 2.75 g of the soil-litter mixture in 91 ml of 50 mM 283 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 285 repeat pipettor. Additional quench control replicates of the soil slurry and 4-methylumbelliferone 286 (MUB) standard curves (0-100 µM concentrations) were included with each sample. The soil 287 slurries were incubated with fluorometric substrates for 3 h at 25°C. After the incubation period, 288 the plates were centrifuged for 20 min at 3000 rpm, after which 250 µl of supernatant was 289 transferred from each well into a black, flat-bottomed 96-well plate that was scanned using a 290 microplate reader (SpectraMax Gemini, Molecular Devices, CA, USA) with an excitation 291 wavelength of 365 nm and an emission wavelength of 450 nm. All enzymatic activities were first 292 calculated in nmol g<sup>-1</sup> soil h<sup>-1</sup> and were then corrected for the contribution of the corresponding 293 soil type by subtracting the enzyme activities of the 'no-litter' soil. These values were 294 subsequently integrated over time (mmol kg<sup>-1</sup> soil) following Sinsabaugh et al. (2002).

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297 Microbial community structure

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

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315 Data analysis

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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

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

The relative contribution of the litter quality, functional breadth, and home-field advantage in explaining the carbon mineralisation was estimated using the model developed by Keiser et al. (2014). This model states that carbon mineralisation ( $Y_i$ ) is equal to litter ability ( $\beta_l$ ) 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

where Yi is the carbon mineralisation for observation i,  $\beta_l$  is the ability of litter species l (from species 1 to N),  $\gamma_s$  is the ability of the soil community s (from community 1 to M),  $\eta_h$  is the HFA of h (from home combinations 1 to h), and Homeh = Litterh \* Soilh when h and h are home-field pairings. The parameters to be estimated are h0, h1, h2 intercept term is defined by h2 and represents the average carbon mineralisation rate for all observations in the dataset after controlling for litter, soil and home-field pairings. Negative parameter estimates indicate lower carbon mineralisation than the average rate observed across all samples in the device. The error term is defined by h2. 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 cumulative carbon mineralisation. Keiser's model was also used to determine the relative 342 contributions of FB ( $\gamma_s$ ) and HFA ( $\eta_h$ ) in explaining the sugar mass loss (computed for the sum 343 of all parietal sugars) and enzymatic activities (computed for the sum of the four net integrated 344 345 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 relationships between these two sets of variables. All of the statistical tests were performed using 347 R software (version 3.1.1, The R Foundation for Statistical Computing, Vienna, Austria) and 348 SAS software (version 9.0, SAS institute, NC, USA).

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#### 351 **Results**

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353 Litter quality and carbon mineralisation

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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. 365 ranging from 3463 to 6649 mg C kg<sup>-1</sup> 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 368 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. 369 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<sup>-1</sup> 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 <sup>13</sup>C litter-amended soils. Although PE increased in the forest soil to similar levels than in cropland and plantation soils after 97 days of decomposition, 375 grassland soil always showed lower PE, with a difference of 78 mg C kg<sup>-1</sup> 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. 378

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

386 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 387 mineralisation independently of the sampling date (Table 1). Among the different litter traits, the 388 lignin:N and C:N ratios were poor predictors of the mineralisation rates (p > 0.05, Appendix F). 389 By contrast, the lignocellulose index (LCI) showed strong negative correlations with the carbon 390 mineralisation rates for each litter type individually but also globally using the entire dataset ( $r^2$ 391 = 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 393 of the cropland, forest and plantation litter types were influenced by the soil type and by a soil type × time interaction that decreased from 0-27 to 98-202 days (Table 2). The soil net carbon 395 mineralisation rates for the grass litter showed only an effect of the soil type for the period 28-97 396 days and significant soil type × time interactions at 0-27 and 98-202 days (Table 2, see also Appendix G for the general model). 398

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00 Microbial community structure and enzymatic production

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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

409 microbial community structure, the ordination plot from NMDS clearly distinguished the communities from the four soil types (Fig. 3A). The microbial communities were plotted 410 according to a pattern in which the first axis depicted the land-use gradient from cropland to 411 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 414 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 419 (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 421 3B). In contrast, time and its interaction with the soil type explained 25% and 19% of the 422 variability in enzymatic patterns, respectively. 423 424

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

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When estimating the  $\beta_l$  (LQ),  $\gamma_s$  (FB), and  $\eta_h$  (HFA) metrics from the net carbon mineralisation data, we found that  $\beta_l$  was the metric that showed the largest variation (Fig. 4), with values ranging from -1725 to +1426 mg C mineralised kg<sup>-1</sup> 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

432 degraded fastest across all of the ecosystems (Fig. 2A). Overall, we observed an initial and rapid increase or decrease in  $\beta_l$  for the grass and forest litters, followed by a slow decline in carbon 433 mineralisation over the incubation period (Fig. 4A). Meanwhile, a transition period occurred for 434 the cropland and plantation litters between 0 and 27 days, followed by a regular increase or 435 decrease in  $\beta_l$ , suggesting that the notion of litter quality for the soil decomposers may vary from 436 the short to the long term (Fig. 4A). When estimating the functional ability  $\gamma_s$  that varied from -437 249 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 lesser extent, the microbial community from the grassland soil also displayed positive  $\gamma_s$  values, 440 with an increasing functional ability after a time lapse of approximately 100 days. In contrast, the plantation and cropland soil types presented negative  $\gamma_s$  values over the course of the incubation experiment, indicating that these communities were unable to degrade a wide range of 443 qualitatively contrasting litter types (Fig. 4B). Finally, when evaluating whether a litter type 444 decomposed faster in an area dominated by the plant species from which it derived, we observed 445 an increasing affinity effect  $\eta_h$  when the plantation soil microbial community matched its own 446 litter (Fig. 4C). Similarly, we found a positive  $\eta_h$  between the grass litter and its own 447 environment, but this effect was transient over time and decreased after 140 days. No significant 448 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 decomposed more rapidly elsewhere than in its own environment (Fig. 4C). 451 452 When calculating the parameter estimates corresponding to the effects of FB ( $\gamma_s$ ) and HFA  $(\eta_h)$  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

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

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#### 464 Discussion

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466 Little is known regarding how the triangular interactions involving litter quality, the decomposer community, and enzymatic activities can modify the trajectory of carbon dynamics 467 within a land-use gradient. To quantify the relative contributions of litter quality (LQ), functional breadth (FB), and home field advantage (HFA) (Fig. 1), we implemented a reciprocal litter-soil 469 transplant decomposition experiment over 202 days. Despite the relatively similar decomposition patterns across all soil-litter combinations, we found a twofold variation in the magnitude of carbon mineralisation among the most chemically contrasting litter types at the end of the 472 incubation period (Fig. 2A), and distinct mineralisation rates for a given litter type incubated 473 with different soil inoculums (Table 2). Our results confirm that litter decomposition is mainly 474 influenced by litter quality, but indicate that the local microbial communities and interactions 475 with their substrates also explained a subtle (< 5%) but significant part of the variation in carbon 476 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 resource history can play a significant role during litter decomposition. In light of the new 479 advances provided by our incubation experiment, we propose a new theoretical concept based on 480 enzymatic activities for addressing the issue of functional dissimilarity of contrasting microbial 481 communities originating from a variety of ecosystems. 482

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Litter quality as a major control of carbon mineralisation 484

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

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Testing the functional importance of microbial communities

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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 mineralisation during the course of the experiment (Table 1). However, when accounting for the 502 initial variability among the different ecosystems, the soil type explained only 2 to 4% of the 503 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 232 505 mg C kg<sup>-1</sup> between 27 to 202 days, meaning that we overestimated litter-derived CO<sub>2</sub> 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 508 509 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 511 variation in decomposition rates.

513 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 516 communities originating from forested habitats display a greater ability to degrade various substrates compared to those originating from more labile litter environments. Although we 518 cannot substantiate the notion that litter quality is 'in the eye of the beholder' (Strickland et al. 519 520 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, 521 investigating the temporal dynamics of carbon mineralisation allowed us to determine that the 522 523 capacities of soil microbes are not set in stone. For example, the FB of the grassland microbial

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524 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 526 that additional mechanisms may influence the ability of a community to be functionally 'broad' 527 or 'narrow'. Although we cannot judge with certainty, the gene and protein expression, the 528 physicochemical characteristics of the surrounding environment, the diversity of soil 529 530 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 531 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 533 did those originating from 'agro-systems', which likely influenced the contrasting functional 534 abilities observed among the four different soil types. 536 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 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 proportionally more rapidly in this ecosystem. Although the interpretation of HFA results should 541 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, 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 metaanalysis 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.

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

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To date, functional dissimilarities of soil microbial communities generated by FB and 556 HFA have not been separately quantified (but see Keiser et al. 2014), and our study is one of the 557 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, 559 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 561 enzymes (Fig. 5), suggesting that the extracellular enzymatic activities are the main driver of the 562 563 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 564 any direct relationship between the PLFA-based community structure and the hydrolytic enzyme 565 566 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 567 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

570 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 573 litters presenting positive plant-soil interactions, lignin generally exhibited greater FB and HFA 574 effects compared to more labile monosaccharides after an approximately 100-day delay (see 575 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 577 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 579 groups of macrofauna by sieving, we cannot ignore that the variability in micro- and mesofauna 580 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 582 communities, particularly in the poorest sites (e.g., Milcu and Manning 2011, Perez et al. 2013), 583 increasing the diversity of decomposers in the field will likely reveal a more complex situation than that observed in our microcosm experiment. 585

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587 Conclusions

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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

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

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#### 788 **Tables**

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

Carrer of Carriedian	10	Raw data				Net data			
Source of variation	df	%SS	F	P-value	%SS	F	P-value		
27 days									
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	$0.45^{\mathrm{NS}}$		
Error	32	0.9			1.0				
97 days									
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				
202 days									
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				

<sup>792</sup> 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 carbon mineralisation rates.

T :44 - 11 - 11 - 11	Incubation period	Soil type			Soil type x Time			
Litter type		df	F	P-value	df	F	P-value	
	0 - 27 days	3, 8	10.76	0.0035	18, 48	21.11	< 0.0001	
Cropland	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	$0.52^{NS}$	
	0 - 27 days	3, 8	13.10	0.0019	18, 48	11.38	< 0.0001	
Forest	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	$0.40^{ m NS}$	
	0 - 27 days	3, 8	2.96	$0.10^{NS}$	18, 48	8.12	< 0.0001	
Grassland	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 <sup>NS</sup>	18, 48	10.62	< 0.0001	
	0 - 27 days	3, 8	6.48	0.016	18, 48	14.27	< 0.0001	
Plantation	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	$0.06^{\mathrm{NS}}$	

<sup>795</sup> *Note*: Results were analysed based on litter types and incubation periods. Significant differences796 are displayed in boldface.

Total

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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	P-value	$r^2$
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	$0.94^{ m NS}$	0.01
Residuals	114	0.07	0.00			0.19
Total	143	0.39				
B Enzymes	df	SS	MS	F.model	P-value	$r^2$
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

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

0.40

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#### 803 **Figures**

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

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

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soil.

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,

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849 D-mannose, L-fucose, D-galacturonic acid and D-glucuronic acid. The net integrated enzymatic

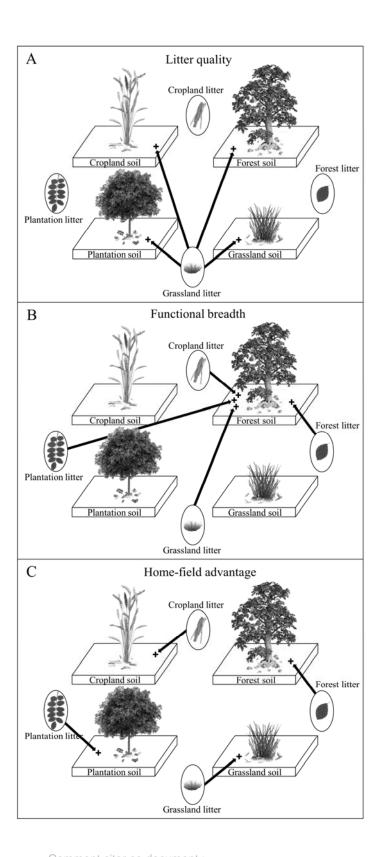
850 activity is the mean of all of the carbon-related enzymes ( $\beta$ -1,4-glucosidase,  $\beta$ -D-cellobiosidase,

851  $\alpha$ -glucosidase, and  $\beta$ -xylosidase) after correction by the 'no-litter treatment' soil.

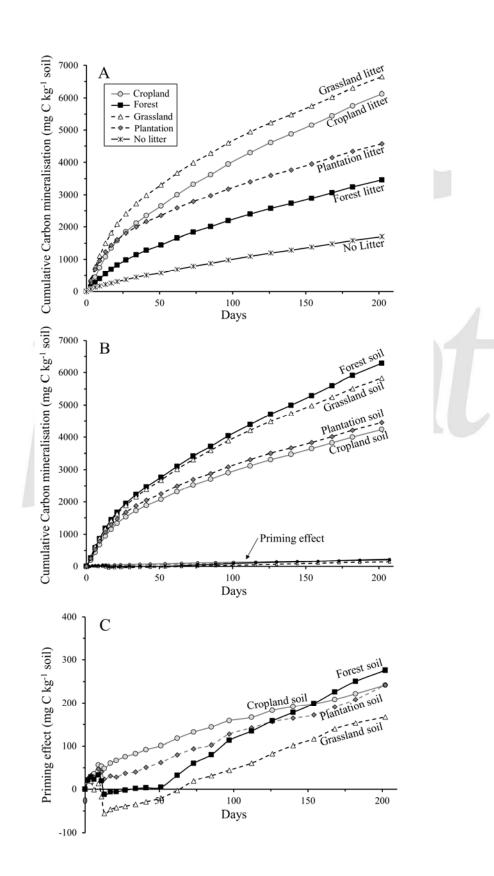


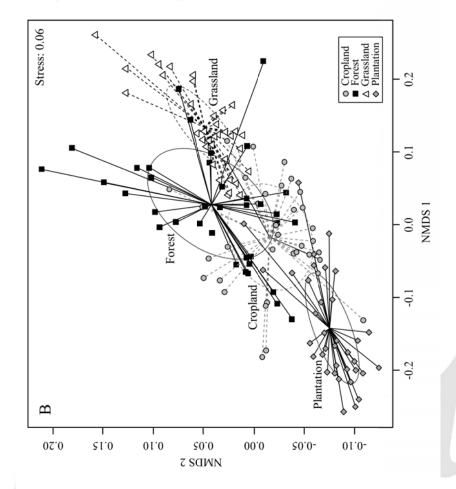
#### 852 Figure 1.

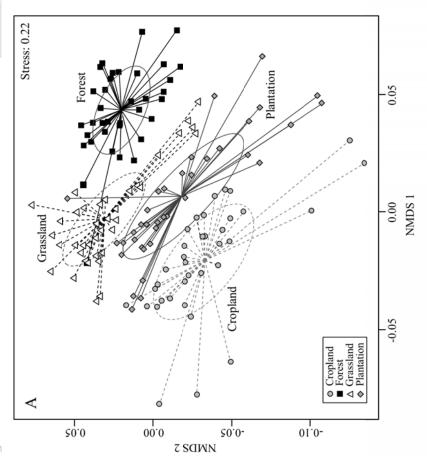
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#### 853 Figure 2.





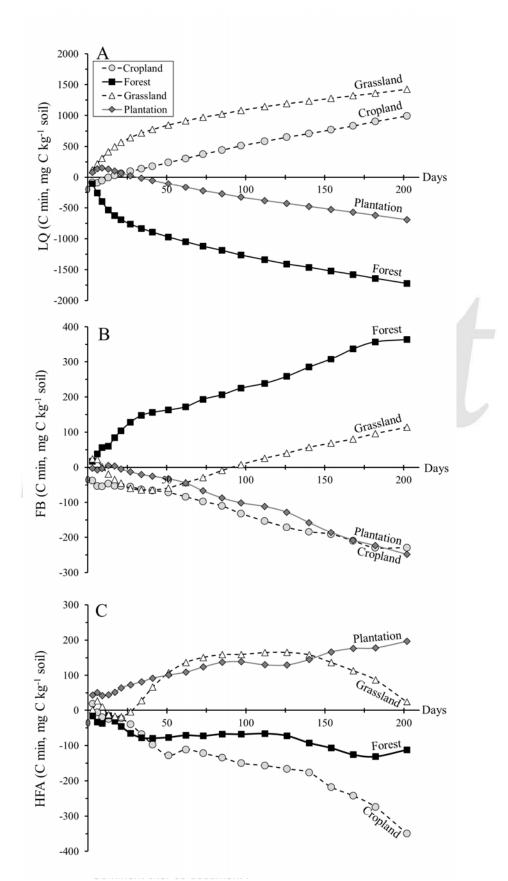


854 Figure 3.

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855 Figure 4.



856 Figure 5.

