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1 **Can the comparison of above- and below-ground litter decomposition improve**  
2 **our understanding of bacterial and fungal successions?**

3

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16 **Abstract**

17 The relationship between litter quality and life strategy of soil microorganisms  
18 (copiotrophy vs oligotrophy) is important for understanding soil processes such as  
19 decomposition. Yet, whether and how this relationship may vary with the addition of  
20 substrates of contrasting quality (i.e., labile vs recalcitrant) has rarely been evaluated  
21 for both bacteria and fungi simultaneously. Using a 3-month incubation experiment  
22 with either maize leaves (enriched in soluble carbon (C)) or roots (enriched in  
23 structural C), we measured changes in litter quality in association with the  
24 composition of bacterial and fungal communities assessed *via* pyrosequencing after  
25 0, 15, 35 and 91 days. Overall, leaf addition led to a higher differentiation from the  
26 unamended soil for bacterial and early-decomposers fungal communities compared  
27 with root addition. This finding clearly indicates that the differentiation of microbial  
28 communities strongly depends on substrate quality for both bacterial and fungal  
29 communities. Further, the differentiation of bacterial communities after litter addition  
30 remained relatively similar throughout the incubation period. This suggests that many  
31 bacterial taxa are more adapted to complex C compounds than previously thought.  
32 Finally, our study underscores the limits of the copiotroph–oligotroph model at the  
33 phylum level and the necessity to work at a finer taxonomic resolution.

34

35 **Keywords**

36 Soil, pyrosequencing, decomposition, succession dynamics, microbial community  
37 structure.

38 In recent decades, the traditional view regarding the shift from bacteria to fungi as  
39 decomposition progresses has been challenged by several studies (Rousk and Frey,  
40 2015; Purahong et al., 2016). At the same time, the ecological attributes of both  
41 bacterial and fungal decomposers have been increasingly used in studies to better  
42 assess changes in carbon- (C) and nutrient-use efficiencies during litter  
43 decomposition: early decomposers (often assimilated to copiotrophs) have high  
44 nutritional requirements and preferentially consume rich and soluble substrates,  
45 whereas late-decomposers (often assimilated to oligotrophs) exhibit low growth rates  
46 and consume poor and complex C compounds (Fanin & Bertrand, 2016; Ho et al.,  
47 2017). Most substrates used to assess the validity of the copiotroph–oligotroph model  
48 are synthetic (*e.g.*, glucose and simple carbohydrates) or relatively labile (*e.g.*, leaf  
49 litter) (Goldfarb et al., 2011; Purahong et al., 2016; Tláskal et al., 2016). However,  
50 whether the addition of complex substrates naturally found across various  
51 ecosystems (as roots enriched in structural C compounds) has similar effects on the  
52 microorganisms' assemblages (copiotrophs vs. oligotrophs) during microbial  
53 succession is still an open question. To assess the importance of substrate quality on  
54 the differentiation of both bacterial and fungal communities in terms of  
55 copiotrophs/oligotrophs successions, we performed a controlled microcosm  
56 incubation experiment with two litters varying strongly in their physicochemical  
57 characteristics (maize leaves and roots), an unamended control (without litter) and  
58 followed microbial community structure by pyrosequencing at four sampling dates (0,  
59 15, 35 and 91 days). We hypothesized that (i) microbial communities will undergo the  
60 copiotrophs/oligotrophs successions for both litters, and (ii) within these successions,  
61 copiotrophic and oligotrophic taxa will be more favored by the amendment with maize  
62 leaves and roots, respectively.

63           The soil used for the experiment was a silty loam agricultural soil collected at  
64 an experimental research station (Estrees-Mons, northern France). The soil  
65 contained 8.70 mg C g<sup>-1</sup> soil and a mineral N content high enough to prevent N  
66 limitation for the decomposition of both litters (Sauvadet et al., 2016). Microcosms  
67 were built with soil sampled at a depth of 0-20 cm, with either no litter or 1 cm pieces  
68 of maize leaves or roots that were mixed into the soil at a depth of 0-5 cm and a rate  
69 of 4.8 g C kg<sup>-1</sup> soil mimicking a common crop residue quantity (about 7 t ha<sup>-1</sup>) after  
70 the growing season (e.g. Hiel et al., 2018). The microcosms were incubated at 15°C  
71 for 3 months, after which they were destructively sampled at four successive dates:  
72 0, 15, 35 and 91 days later (three replicates by treatment and sampling date). Carbon  
73 mineralization was measured in all the incubated microcosms using a CO<sub>2</sub> trap (1 M  
74 NaOH) titrated by continuous flow colorimetry using an autoanalyzer (TRAACS 2000,  
75 Bran and Luebbe). The litter was hand-sorted then washed in water and dried for one  
76 week at 37°C before soluble, cellulose, hemicellulose and the Klason lignin contents  
77 were measured (Sauvadet et al., 2016). The soil bacterial and fungal community  
78 structures were determined on soil alone (after leaves and roots were separated) at  
79 each sampling date by 454 pyrosequencing using 16S rRNA and 18S rRNA genes,  
80 respectively, as described by Terrat et al. (2012). Diversity analyses were performed  
81 on 5000 and 7500 reads for the 16S and 18S rRNA gene sequences of the bacterial  
82 and fungal communities, respectively, using the GnS-PIPE pipeline developed for the  
83 GenoSol platform (Institut National de la Recherche Agronomique [INRA], Dijon,  
84 France).

85           The microbial communities were then analyzed using the Bioconductor suite  
86 package and R software (<https://www.bioconductor.org>). Dissimilarities between the  
87 bacterial and fungal communities of each treatment at each sampling date were first

88 calculated using the Poisson distance at the genus level (after exclusion of genera  
89 who were unique across all samples), and then depicted graphically with nonmetric  
90 dimensional scaling (NMDS). Significant differences in Poisson distances between  
91 amended and unamended treatments were tested by analysis of variance (ANOVA)  
92 followed by post hoc tests using Fisher's least significant difference (LSD). In a  
93 second phase, we focused on the genera that were the most affected by litter  
94 amendments. To do so, the data were log-transformed (rlog function of the DESeq2  
95 R package) to obtain normality and minimize the differences between taxa with low  
96 abundances. We then performed a differential expression analysis (DESeq function  
97 of the DESeq2 R package) between soil communities that did not receive litter  
98 (unamended soil) and soil communities that did receive either leaves or roots at the  
99 corresponding sampling date. In this analysis, we considered only the genera that  
100 differed significantly in relative abundance from the community in unamended soils  
101 ( $P$ -value  $< 0.05$  adjusted with Benjamini-Hochberg corrections), which could be  
102 distinguished as either enriched (greater abundance than that in the unamended  
103 community) or depleted (lower abundance than that in the unamended community).  
104 More details of the DESeq analyses were reported by Edwards et al. (2015).

105         The leaf and root additions influenced the structure of both the bacterial and  
106 fungal communities at all sampling dates relatively to the unamended soils (Fig. 1a  
107 and 1b). Poisson distances between unamended and amended treatments were  
108 higher with leaves than roots addition for fungal communities at the earliest stage of  
109 decomposition (i.e., before  $400 \text{ mg C kg}^{-1}$  soil mineralized, Fig. 1d) and for bacterial  
110 communities at all sampling dates (Fig. 1c). These results highlight that the structure  
111 of bacterial and early-decomposers fungal communities depends directly on  
112 substrate quality (Table S1), and confirm previous reports demonstrating that many

113 bacterial and fungal taxa are strongly dependent upon C availability (van der Wal et  
114 al., 2013; Purahong et al., 2016; Ho et al., 2017). This further suggests that taxa  
115 feeding on recalcitrant C substrates are closer to communities living in unamended  
116 soils than opportunistic taxa feeding on freshly added labile C substrates. On the  
117 other hand, fungal community differentiation peak after 15 days of leaf  
118 decomposition, suggesting that these early-decomposers (presenting copiotrophic  
119 characteristics) could only develop when litter soluble content was high enough  
120 (Table S1). Interestingly, only fungal community presented such a peak; we could  
121 assume that bacterial differentiation occurred earlier (between 3 and 7 days in Tardy  
122 et al., 2015), yet our results support that fungi, and not only bacteria, takes an active  
123 part in early decomposition process. Further, the constant differentiation level of  
124 amended bacterial communities from their unamended counterpart supports the  
125 emerging idea that bacterial taxa can be better able to increase with the proportion of  
126 complex C compounds than previously thought (Rousk and Bååth, 2007; Rousk and  
127 Frey, 2015). However, as expected, high level of soluble C favor the differentiation of  
128 bacterial taxa which may also feed on products originating from fungal degradation  
129 (Purahong et al., 2016; Tláškal et al., 2016).

130         When studying microbial community composition, we found that only 6 out of  
131 59 genera (e.g., *Arthrobacter* or *Variovorax* for bacterial community, Table S2) and  
132 11 out of 57 genera (e.g., *Ascobolus* or *Heterobasidion* for fungal community, Table  
133 S3) were impacted by both litter types (Fig. 2). The idea that many microbial genera  
134 depend upon substrate quality is reinforced by the low redundancy between microbial  
135 genera at different sampling dates (Fig. 2); only a few bacterial genera remained  
136 enriched at all sampling dates (e.g., *Pseudomonas* during both leaves and roots  
137 decomposition, Table S2) and no fungal genus was consistently enriched or depleted

138 over time (Table S3). These results highlight the strong specificity of microbial genera  
139 to both litter quality and decomposition stage, which is partly overlooked when  
140 focusing only at the phylum level. Indeed, the bacterial genera impacted during litter  
141 decomposition belonged mainly to the three same phyla (i.e., Proteobacteria,  
142 Bacteroidetes and Actinobacteria), which are often regarded as copiotrophic in the  
143 literature (Ho et al., 2017). However, most phyla as Proteobacteria, had both  
144 enriched (e.g., *Variovorax*) and depleted genera (e.g., *Geobacter*) after litter  
145 additions, and this regardless of litter quality or sampling date (Table S2). This clearly  
146 indicates that different taxa within a phylum may present contrasting metabolic  
147 status. This further underscores the limits of the copiotroph–oligotroph model at the  
148 phylum level and the necessity to work at a finer taxonomic resolution (Philippot et  
149 al., 2010; Purahong et al., 2016; Ho et al., 2017).

150 We conclude that high quality substrate induces greater differentiation of early  
151 decomposers fungal communities and bacterial communities than low quality  
152 substrate. Further, both early- and late-decomposers showed a strong specificity to  
153 litter quality and decomposition stage at the genus level. Our results challenge the  
154 traditional concept of bacterial/fungal shift during decomposition and underline the  
155 necessity to identify more accurately life strategies of soil microbes at different  
156 taxonomic levels in order to improve our understanding of structure-function  
157 relationships and the role of microbial communities in ecosystem functions such as C  
158 mineralization and decomposition rates.

159

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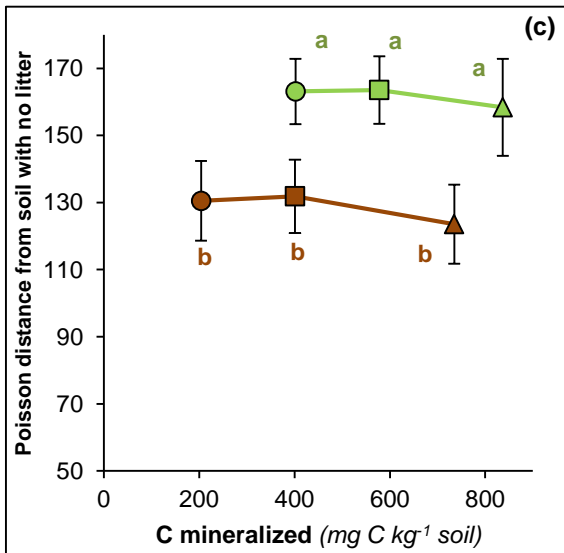
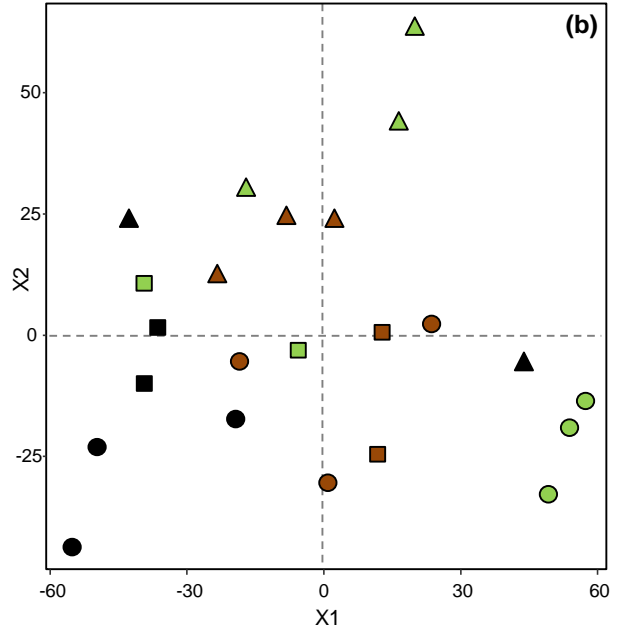
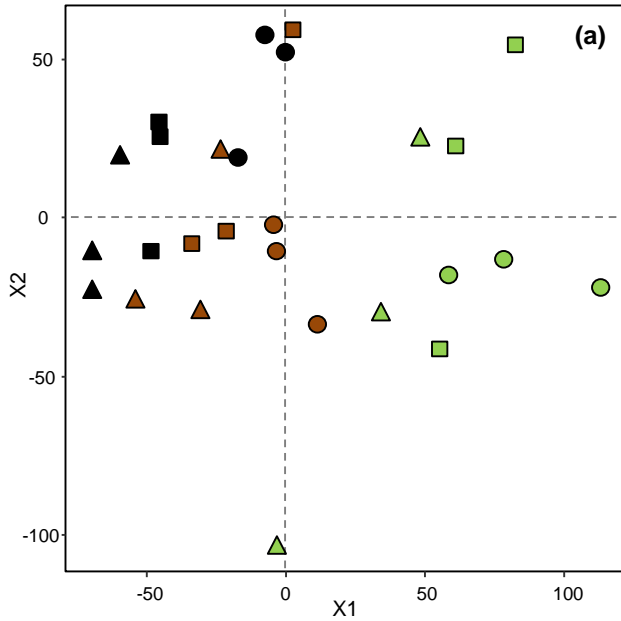
221 **Figure captions**

222 **Fig. 1.** Microbial community structure during the experiment represented by NMDS  
223 plots (a, b) and Poisson distances from the unamended community (c, d) using  
224 bacterial (a, c) or fungal (b, d) data. All figures are based on the Poisson distance  
225 calculated at the genus level. Abscissa axis of Fig. 1c and 1d are expressed as the  
226 cumulated amount of C mineralized, presented in Table S1. Significant differences  
227 between all sampling dates and litters were tested by ANOVA followed by post hoc  
228 Fisher tests and are represented by different letters for each graph.

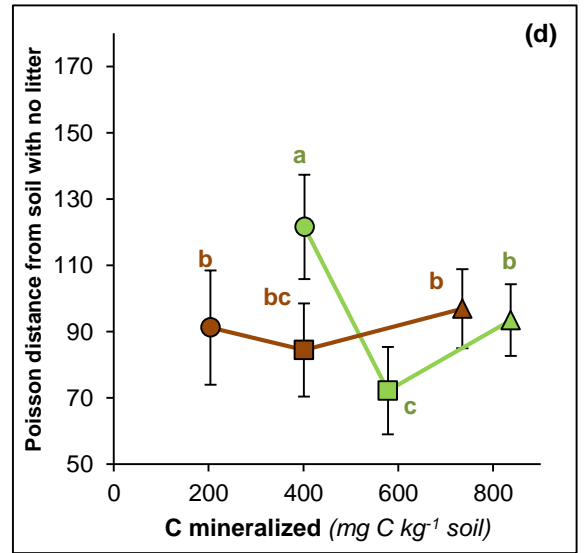
229 **Fig. 2.** Phylum identification of the enriched and depleted genera with maize leaf or  
230 root addition relative to the unamended soils for bacteria (a) and fungi (b).  
231 Abundance changes are expressed as  $\log_2$ fold (i.e.,  $\log_2[\text{sample}] - \log_2[\text{unamended}$   
232  $\text{community}]$ ). Only the genera which exhibit significant differences with the  
233 unamended community are considered (P-values < 0.05).

234

- Control after 0 days
- Control after 35 days
- ▲ Control after 91 days
- Leaves after 15 days
- Leaves after 35 days
- △ Leaves after 91 days
- Roots after 15 days
- Roots after 35 days
- ▲ Roots after 91 days

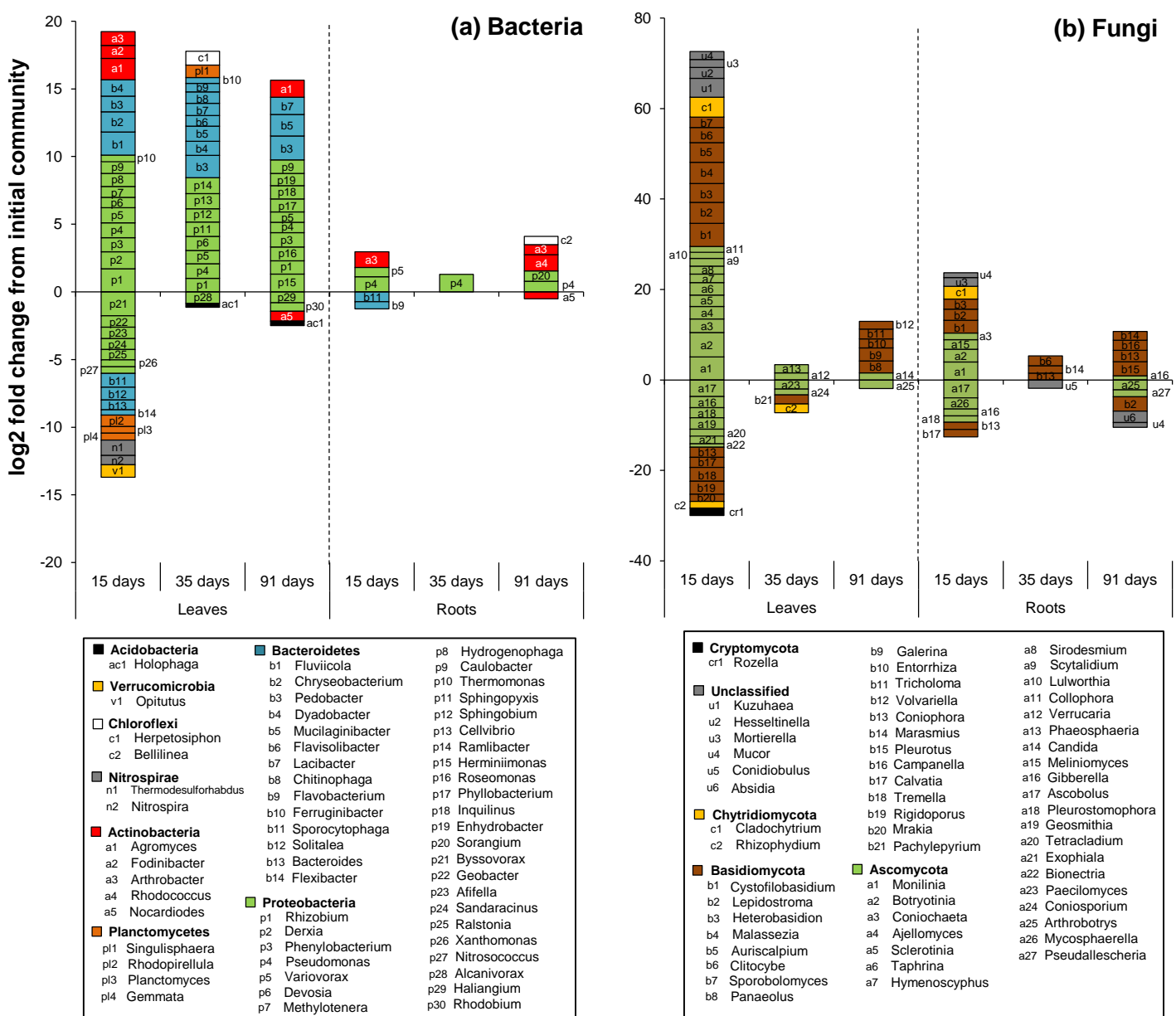


**Bacteria**



**Fungi**

**Fig. 1**



**Fig. 2**