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1 SOILS, SEC # • RESEARCH ARTICLE

2

3 **Litter decomposition in peatlands is promoted by mixed plants**

4

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24

25 **Abstract**

26 *Purpose.* The carbon sink function of peatlands is primarily driven by a higher production than decomposition of  
27 the litter *Sphagnum* mosses. The observed increase of vascular plants in peatlands could alter the decomposition  
28 rate and the carbon (C) cycle through a litter mixing effect, which is still poorly studied. Here, we examine the  
29 litter mixing effect of a peat moss (*Sphagnum fallax*) and two vascular plants (*Pinus uncinata* and *Eriophorum*  
30 *vaginatum*) in the field and laboratory-based experiment.

31 *Materials and methods.* During the laboratory incubation, mass loss, CO<sub>2</sub> production and dissolved organic carbon  
32 concentration were periodically monitored during 51 days. The collected data were then processed in a C dynamics  
33 model. The calculated enzymatic activity was correlated to the measured  $\beta$ -glucosidase activity in the litter. In the  
34 field experiment, mass loss and CO<sub>2</sub> production from litter bags were annually measured for three years.

35 *Results and discussion.* Both laboratory and field experiments clearly show that the litter mixture, i.e. *Sphagnum-*  
36 *Pinus-Eriophorum*, had a synergistic effect on decomposition by enhancing the mass loss. Such enhanced mass  
37 loss increased the water extractable C and CO<sub>2</sub> production in the litter mixture during the laboratory experiment.  
38 The synergistic effect was mainly controlled by the *Sphagnum-Eriophorum* mixture that significantly enhanced  
39 both mass loss and CO<sub>2</sub> production. Although the  $\beta$ -glucosidase activity is often considered as a major driver of  
40 decomposition, mixing the litters did not cause any increase of the activity of this exo-enzyme in the laboratory  
41 experiment suggesting that other enzymes can play an important role in the observed effect.

42 *Conclusions.* Mixing litters of graminoid and *Sphagnum* species led to a synergistic effect on litter decomposition.  
43 In a context of vegetation dynamics in response to environmental change, such a mixing effect could alter the C  
44 dynamics at a larger scale. Identifying the key mechanisms responsible for the synergistic effect on litter  
45 decomposition, with a specific focus on the enzymatic activities, is crucial to better predict the capacity of  
46 peatlands to act as C sinks.

47

48 **Keywords**  $\beta$ -glucosidase • Carbon dynamics models • Catalysis • CO<sub>2</sub> production • Dissolved organic carbon •  
49 Litter mixture effect

50

51 **1. Introduction**

52 *Sphagnum*-dominated peatlands accumulate organic matter (OM) as peat at a rate of ca. 20 to 30 g C m<sup>-2</sup> year<sup>-1</sup>  
53 (Francez 2000; Rydin et al. 2013). At global scale, peatlands are estimated to store about 270 to 547 Pg C as peat  
54 (1 Pg = 10<sup>15</sup> g), representing ca. 15-30% of the world's soil carbon (C) stock in an area accounting for only 3-5%  
55 of the land surface (Turunen et al. 2002; Yu et al. 2010). This high rate of C accumulation is due to peculiar  
56 environmental and soil conditions, i.e. waterlogging, anoxia, acidity, low temperature, and specific plant species  
57 composition that ultimately hamper the microbial litter decomposition so resulting in a net accumulation of OM  
58 as peat (e.g. Gorham, 1991; Holden, 2005). In particular, *Sphagnum* mosses have a key role for peat accumulation  
59 as they are able to create unfavorable conditions for decomposer activities by producing a recalcitrant litter and by  
60 promoting waterlogged and acidic conditions (Van Breemen 1995). As a result, *Sphagnum* mosses gain in  
61 competitive ability against vascular plants, whose litter is much more easily decomposable (Bragazza et al. 2007,  
62 2009), thereby acting as effective ecosystem engineers (Van Breemen 1995).

63 Human-induced environmental changes are expected to modify plant species abundance in peatlands, in  
64 particular by favoring vascular plants at the expense of *Sphagnum* mosses under a warmer climate (Buttler et al.,  
65 2015; Dieleman et al., 2015). Although previous studies have shown that warming can modify the rate of litter  
66 decomposition in peatlands (Thormann et al., 2004; Bragazza et al. 2016) and that decomposition rates of  
67 *Sphagnum* are lower than those of vascular plants (Hoorens et al., 2010), few studies have addressed the issue of  
68 a litter mixture effect in peatlands (Hoorens et al. 2010; Krab et al. 2013; Gogo et al. 2016). Most of the studies  
69 on litter decomposition in peatlands have focused on single plant species, although in natural conditions litters  
70 mainly consist of a mixture of multiple plant species (Salamanca et al. 1998). Litters in mixture can decompose  
71 faster (synergistic effect) or slower (antagonistic effect) than the same litter type alone (non-additive effect  
72 (Gartner and Cardon, 2004). Almost 70% of mixed-species litter exhibited non-additive mass loss with a  
73 prevalence of synergistic effects (Gartner and Cardon, 2004). Such modifications of the decomposition rate due to  
74 litter mixture could affect the imbalance between primary production and decomposition in peatlands in response  
75 to a vegetation dynamics and, ultimately, the capacity of peatlands to act as C sinks. Despite the crucial role of  
76 litter decomposition in controlling C dynamics and peat accumulation in peatlands, we have still little  
77 understanding of how the mixture litter affects decomposition.

78 As change in leaf litter quality can affect enzyme production by soil microbes (Hu et al. 2006), litter mixture  
79 could also change enzyme activities, which may result in a non-additive effect. For example,  $\beta$ -glucosidase is  
80 commonly described as an important exo-enzyme involved in C-cycling, and therefore primarily in the

81 decomposition of cellulose (Kourtev et al. 2002; Sinsabaugh et al. 2002), so that it could be a key-player in the  
82 non-additive effect of litter mixture. Nevertheless, the role of enzymes in relation to litter decomposition still needs  
83 to be elucidated.

84 In order to understand the effect of a litter mixture of *Sphagnum* mosses and vascular plants on OM  
85 decomposition and C dynamics in peatlands, we performed a decomposition experiment under laboratory and field  
86 conditions. Experimental laboratory data were then used to calibrate a C dynamics model proposed by Gogo et al.  
87 (2014), using three C compartments: the solid (mass loss), the dissolved (Water Extractable Organic Carbon,  
88 WEOC) and the gaseous components (CO<sub>2</sub>-C). In this model, the litter is catalyzed by exo-enzymes at a rate “c”  
89 to produce soluble organic C, i.e. WEOC, which is used for respiration at a rate “r” by microorganisms. The model  
90 gives a catalysis rate for each litter that contributes to overall catalytic activity. The field experiment was performed  
91 to assess whether there was agreement between laboratory and field decomposition tests by focusing on mass loss  
92 and CO<sub>2</sub> production. Overall, the aims of this work were: (i) to determine the occurrence of a litter mixture effect  
93 for three different plant species during decomposition; (ii) to elucidate the role of β-glucosidase activity during  
94 litter decomposition; (iii) to relate the catalysis rate from the C dynamics modeling to the activity of hydrolytic  
95 enzymes.

96

## 97 **2. Materials and methods**

### 98 **2.1 Study site and litter sampling**

99 Plant litter material for laboratory and field experiments was collected at the Forbonnet peatland in Frasné (France,  
100 N46°49'35" E 6°10'20", 840m). The site is a *Sphagnum*-dominated peatland with a mean annual temperature of  
101 7.5°C and annual rainfall amount of 1400 mm (Laggoun-Défarge et al. 2008; Delarue et al. 2011). The vascular  
102 plant cover mainly consists of *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Andromeda polifolia*, *Vaccinium*  
103 *oxycoccos* and *Carex limosa* (Buttler et al. 2015) with a recent increased abundance of trees of the genus *Pinus* in  
104 response to a decline in peat water content, as observed in many bogs in the study region (Frelechoux et al. 2000).  
105 Overall, the moss layer is primarily dominated by *Sphagnum fallax* and *S. magellanicum*. Litter samples of  
106 *Eriophorum vaginatum* (E) and *Pinus uncinata* (P) were composed, respectively, of senescent leaves and needles.  
107 Litter samples of *Sphagnum fallax* (S) corresponded to the decaying part just below the green photosynthesizing  
108 apical part (Bragazza et al. 2007). After having been air-dried, sub-samples of each litter type were oven dried at  
109 50°C for 48 hours in order to calculate the dry weight.

110

111 2.2 Laboratory experiment

112 **Sample preparation and incubation** - For the laboratory experiment, samples of one gram for seven litter types  
113 were prepared. Litter types were formed by single litter of *Sphagnum fallax* (S), *Eriophorum vaginatum* (E) or  
114 *Pinus uncinata* (P), and by the following mixtures: *Sphagnum fallax* + *Eriophorum vaginatum* (SE), *Sphagnum*  
115 *fallax* + *Pinus uncinata* (SP), *Pinus uncinata* + *Eriophorum vaginatum* (PE) and *Sphagnum fallax* + *Pinus uncinata*  
116 + *Eriophorum vaginatum* (SPE). Litter samples received 20 mL of peatland water overnight in order to inoculate  
117 microorganisms (Hoorens et al. 2002). The excess water was removed with a tissue and the litter samples were  
118 placed in aluminum cups with small holes at the bottom to allow air circulation. The cups were placed on a 0.4 L  
119 pot containing 20 mL of saturated solution of K<sub>2</sub>SO<sub>4</sub> to maintain moist conditions. Each pot with its cup was  
120 covered with perforated aluminum foil to allow air circulation. All pots were placed in an incubator (Aralab 1200)  
121 at 20°C and 95% of relative humidity. A total of 105 litter samples (pots) were prepared in order to have 3 replicates  
122 for each of the 7 litter types and 5 periodical harvests. At intervals of 0, 1, 14, 28 and 51 days after incubation, we  
123 measured CO<sub>2</sub> production, water extractable organic carbon (WEOC) release, litter mass loss, β-glucosidase  
124 activities and C content in 3 replicats of each litter type.

125 **Laboratory measurements** - The CO<sub>2</sub> production was measured with a GMP343 Vaisala probe after placing the  
126 litter sample (pots) in a 2.34 L chamber. The measurement took 15 minutes. The slope of CO<sub>2</sub> increased over time  
127 within the chamber (in μmol CO<sub>2</sub>. mol air<sup>-1</sup>.sec<sup>-1</sup>) and was used to calculate a cumulative C release (g C g<sup>-1</sup> initial  
128 C litter). The WEOC from each sample was obtained after rinsing the incubated litter three times with 50 mL of  
129 distilled water and followed the method described in Delarue et al. (2011). The extract was filtered through a 0.45  
130 μm membrane filter. Dissolved organic carbon (DOC) in water extract was determined with a Shimadzu TOC  
131 5000A (Total Organic Carbon Analyzer). The particles on the 0.45 μm filter and the remaining litter were dried at  
132 50°C during two days and then weighed to obtain the remaining mass (mass loss = initial mass – remaining mass)  
133 in g OM g<sup>-1</sup> initial litter mass. The C in each litter sample was then measured with an elementary analyzer  
134 (Thermo-FLASH 2000 CHNS/O Analyzer). This normalized the three C pools in g C g<sup>-1</sup> initial C litter, thus  
135 making possible to input data in the C dynamics models. The activity of β-glucosidase was measured by adding to  
136 0.5 mL of water extracted litter, 3.5 mL of 4-Methylumbelliferyl β-D-glucopyranoside, a substrate for β-  
137 glucosidase activities which is transformed into 4-Methylumbelliferone (MUF). After one hour of incubation, the  
138 concentration of MUF was determined by fluorescence using an excitation wavelength of 330 nm and an emission  
139 wavelength of 450 nm and was compared to standard solution. Measured values obtained in the litter mixtures

140 were compared to calculate additive values (expected) after Hoorens et al. (2010), which are means of the values  
141 as measured in the decomposition of the single species litter type.

142 **C dynamic modeling** - The experimental design was similar to that published by Gogo et al. (2014, 2016). These  
143 authors conceptualized the model assuming that solid OM is catalyzed by exo-enzymes, leading to soluble OM,  
144 which is then absorbed by microorganisms and used as an energy source for different microbial functions (enzyme  
145 production, maintenance, growth). Then, the soluble organic C is respired and released into the environment in the  
146 form of CO<sub>2</sub>. The applied model followed Schimel and Weintraub (2003) but was simplified to make it  
147 experimentally testable (Supplementary Fig. S6). It is composed of three compartments: (i) the “L” compartment  
148 corresponding to the C fraction contained in the litter (solid fraction), (ii) the “W” compartment corresponding to  
149 the C fraction in the WEOC (dissolved fraction) and (iii) the “G” compartment corresponding to the C fraction in  
150 the cumulative CO<sub>2</sub> released by microbial respiration (gaseous fraction). C flow from the L to the W compartment  
151 at a rate corresponding to the exo-enzyme catalysis rate. C flows from the W to the G compartment at a rate  
152 corresponding to the respiration rate. Equations describe the simultaneous change in time of the state variable (L,  
153 W, and G) and the reaction rates (Gogo et al. 2014; Supplementary Fig. S6). At any time, the sum of all these three  
154 fractions is equal to 1. The three fractions corresponding to C stocks (solid, soluble, gaseous) were experimentally  
155 measured. The catalysis rate “c” and the respiration rate “r” were tuned at the same time to fit the stock values of  
156 the model to those experimentally assessed. When the reaction rates are allowed to change in the course of the  
157 experiment, the goodness of fit is improved. The reaction rates were allowed to follow a negative exponential  
158 decrease with time. The following parameters describe the shape of the curve: “a+b” = the initial reaction rate, “a”  
159 = the final rate, “m” = decay rate with time of the reaction rate (Rovira and Rovira, 2010). Observed rates obtained  
160 in litter mixture were compared to calculate additive rates, which are means of the catalysis and respiration rates  
161 measured in decomposition of the single species litter type. The root mean square error (RMSE) was calculated  
162 for each litter type in order to represent model performance. The RMSE is calculated by squaring individual errors,  
163 summing them, dividing the sum by their total number (N), and then taking the square root of this quantity:

$$RMSE = \sqrt{\sum \frac{(y_{pred} - y_{meas})^2}{N}}$$

164  
165 The RMSE was normalized to the mean of observed data and multiplied by 100 to obtain the Normalized Root

166 Mean Square Error (NRMSE) in percentage (%): 
$$NRMSE = 100 \times \frac{RMSE}{\bar{y}}$$

167

168           2.3 Field experiment

169   The litterbag experiment was performed at the Forbonnet peatland in order to annually measure mass loss and CO<sub>2</sub>  
170   production during three years of field incubation. Litterbags (0.5 mm mesh) were prepared with one gram of litter  
171   of S, P, E and in a mixture of the three species (SPE). For the SPE litter mix, each species contributed equally to  
172   the final weight of the litter bag. Litter bags were placed vertically in the moss carpet and buried at 5 cm depth on  
173   November 2009 in lawns, which represent the major feature in this bog, avoiding hummocks where there was tree  
174   encroachment. Twelve samples were prepared for each of the four litter treatments that were periodically collected  
175   after one, two and three years of incubation. Litter mass loss was calculated as percentage of remaining mass of  
176   initial litter mass. The CO<sub>2</sub> flux was measured immediately after collection in a 835 cm<sup>3</sup> chamber with a Li-Cor  
177   LI-8100 analyser and expressed as fluxes (in µg CO<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> dry weight).

178

179           2.4 Statistics

180   The role of litter mixture in affecting the measured variables was compared to the corresponding additive  
181   calculated values (expected) from the litter decomposition of each single species. Two-way ANOVA was applied  
182   to investigate differences in the measured variables for both the field and laboratory experiments where the selected  
183   factors were “litter types” (observed vs additive) and “time (years or days) of measurements. Post-hoc Tukey’s  
184   Honestly Significant Differences (HSD) tests were performed to determine significant differences within groups.  
185   Differences were considered as a trend for  $p < 0.1$  (noted with: -) and significant at  $p < 0.05$  and referred to by \* =  
186    $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . Modeled curves for temporal changes of variables in the laboratory  
187   incubation experiment were calculated from the C dynamics model. All statistical analyses were done using R  
188   3.1.1 software.

189

190   **3. Results**

191           3.1 Laboratory experiment

192   During the laboratory incubation of the single litter type, *Sphagnum fallax* (S) litter was characterized by a mass  
193   loss, DOC release and CO<sub>2</sub> production significantly different compared to *Pinus uncinata* (P) and *Eriophorum*  
194   *vaginatum* (E) litter (Fig. 1). The S, E and P litters contained, respectively, 42.4, 50.9 and 47.7 % of C (Table 1).  
195   These contents were constant in time and between additive (calculated values) and measured values in mixture  
196   litter (Table 1). When compared to the decomposition calculated from the single plant litter (additive mean values),  
197   the observed *Sphagnum + Pinus + Eriophorum* (SPE) mixture showed a significantly higher mass loss (i.e. lower

198 remaining C) ( $p < 0.001$ ), a higher WEOC ( $p < 0.05$ ) as well as a higher production of  $\text{CO}_2$  ( $p: 0.063$ ) (Fig. 2). The  
199 litter mixture of *Sphagnum* + *Eriophorum* (SE) significantly ( $p < 0.001$ ) increased mass loss and  $\text{CO}_2$  production  
200 by 13% after 51 days of incubation, as compared to the additive effect (Fig. 2, Table 2). The C dynamics in the SP  
201 and PE mixtures did not significantly differ from the additive effect of the single species (Fig. 2, Table 2) although  
202 the litter mixture of *Pinus* and *Eriophorum* (PE) showed a tendency to decrease litter mass loss and  $\text{CO}_2$  production  
203 ( $p: 0.069$  and  $0.097$ , respectively).

204

### 205 3.2 Field experiment

206 After three years of field incubation, the decomposition of single litter of *S. fallax* was slower than that of vascular  
207 plants ( $p < 0.001$ ) (Fig. 3, Table 3). *S. fallax* litter showed significant differences for  $\text{CO}_2$  production compared to  
208 *Pinus uncinata* ( $p < 0.001$ ) and *Eriophorum* litter ( $p < 0.05$ ). There was a significant effect of litter mixture during  
209 field decomposition, with a mass loss higher (ca. 19%) than that expected from the single species additive effect  
210 ( $p < 0.01$ ) (Fig. 4), while the  $\text{CO}_2$  production in the mixture litter did not differ from the additive effect (Fig. 4,  
211 Table 3).

212

### 213 3.3 Catalysis of C dynamics models and $\beta$ -glucosidase activities

214 The model fitted well the measured values with a lower NRMSE (sum between 2.82 and 9.41 %; Supplementary  
215 Table S5) compared to Gogo et al. (2014). The catalysis rate decreased with incubation time in each litter type  
216 (Table 4). In *Sphagnum* litter, this rate was initially very fast and decreased rapidly to become slower than vascular  
217 plant litters. The catalysis rates measured in *Sphagnum-Eriophorum* (SE) and *Sphagnum-Pinus-Eriophorum* (SPE)  
218 mixtures were always greater than expected from the mean of single litter species at each time of measurement  
219 (Table 4). This corresponded to higher C mass loss, WEOC and  $\text{CO}_2$  production.

220 At the beginning of incubation,  $\beta$ -glucosidase activity was similar in all litter types but afterward it significantly  
221 increased in *Eriophorum* and *Pinus* litters, while remaining constant in *Sphagnum* litter (Supplementary Fig. S7).  
222 Mixing litters did not affect  $\beta$ -glucosidase activities so that there were no significant differences between observed  
223 and calculated additive values (Fig. 5). Overall,  $\beta$ -glucosidase activities increased with incubation time, whereas  
224 the catalysis rate decreased (Fig. 5; Table 4) so that the catalysis rate was inversely correlated to the  $\beta$ -glucosidase  
225 activity ( $r^2: 0.52$ ;  $p < 0.001$ ; Supplementary Fig. S8).

226

## 227 4. Discussion

#### 228 4.1 Occurrence of a synergistic effect

229 The laboratory incubation experiment clearly showed that the litter mixture of *Sphagnum-Eriophorum* as well  
230 as *Sphagnum-Pinus-Eriophorum* had a synergistic effect on mass loss and CO<sub>2</sub> production compared to the  
231 corresponding additive effect. Similar results were obtained with a mixture of *Sphagnum* litter and graminoid  
232 species (Hoorens et al. 2002; Gogo et al. 2016). Such synergistic interaction on decomposition has been explained  
233 by differences in litter chemistry such as N concentration (Hoorens et al. 2002). However, similar N concentration  
234 was found in our litter types. Mixing different litters can produce both chemical diversity and microhabitat  
235 complexity so supplying an increased diversity of substrates to the decomposers (Gartner and Cardon, 2004). Also,  
236 special attention in future studies should be devoted to the improvement of microclimatic condition such as the  
237 water content of individual litter in mixture through water flow from the wettest to the driest litter. The hypothesis  
238 is that through such water flow the conditions are improved in the driest litter, without decreasing to large extent  
239 the conditions of the wettest litter (Gogo et al., 2017).

240 The field experiment also showed an increase of decomposition by mixing *Sphagnum + Eriophorum + Pinus*  
241 litter. *Sphagnum fallax* decomposed at a slower rate than *Pinus uncinata* and *Eriophorum vaginatum* litter as  
242 observed elsewhere by Hobbie (1996). Curiously, we expected to have higher CO<sub>2</sub> production in combination with  
243 higher litter mass loss, but, instead, the highest CO<sub>2</sub> production was measured in *Sphagnum* litter with the slowest  
244 mass loss. The high capacity of *Sphagnum* litter to maintain capillary water could have contributed to retaining  
245 water that had previously percolated through the upper photosynthetically active centimeters of the *Sphagnum*  
246 carpet. This percolating water may have been enriched in labile C that could stimulate CO<sub>2</sub> production.  
247 Furthermore, the capillary structure of *Sphagnum* is known to host rich microbial communities, including  
248 microbial predators, i.e. amoebae (Jassey et al., 2013) in the living apical part and we cannot exclude the possibility  
249 that this might have affected the decaying part in the long field run. This could explain the decoupling observed  
250 between mass loss and respiration rate.

251 Laboratory incubation was a short experiment in which environmental factors and C input and output were  
252 well controlled. Conversely, field experiments spanned over three years and thus represent litter mass loss as it  
253 occurs in natural field conditions. In both laboratory and field experiments, mixing *Sphagnum* with *Eriophorum*  
254 and *Pinus* litter had a synergistic effect on litter decomposition. Such non-additive effects have already been  
255 reported for other ecosystems (Wu et al. 2013; Zhang et al. 2014), although the reasons are still unclear. Many  
256 studies have tried to explain such an effect by nutrient exchanges between litters (Vos et al. 2013), litter chemical  
257 quality (Meier and Bowman 2010) or changes in habitat characteristics (Lecerf et al. 2011). Nevertheless, only

258 very few studies have addressed this effect at microbial scale and established links between microbial communities  
259 and litter decomposition (Chapman et al. 2013).

260

261 4.2 Role of  $\beta$ -glucosidase in early C dynamics the early decomposition stages???

262

263 Contrary to our hypothesis, no significant increases were noticed in  $\beta$ -glucosidase activity between the  
264 observed and the additive values during the laboratory experiment, suggesting that, at least in the early stages of  
265 decomposition (i.e. the first 28<sup>h</sup> days), the synergistic mixture effect does not originate from the stimulation of this  
266 hydrolytic enzyme.

267 By comparing the measured enzymatic activities to the modeled catalysis rates, the *Sphagnum* litter showed  
268 values similar to those obtained by Gogo et al. (2014) and Gogo et al. (2016), with a fast rate in the early stage of  
269 decomposition, and slower but constant values thereafter ( $< 0.002 \text{ gC.g}^{-1}\text{C.d}^{-1}$ ). Contrary to our hypothesis, a  
270 negative link was established between modeled catalysis rates and  $\beta$ -glucosidase activities. Such a link between  
271 litter enzyme activities and decomposition rates was already assessed with hydrolases and the results showed that  
272 this relationship was weak (Allison and Vitousek, 2004). These authors suggested that mass loss occurred  
273 independently of enzyme activities with compounds that may leached out of the litter. As this last one, the really  
274 different litter types could not allowed to connect the enzymes activities with the decomposition rates.  
275 Furthermore, fast catalysis rate in the initial decomposition stage was not related to the  $\beta$ -glucosidase activity but  
276 maybe more to the phenol oxidase activity particularly in the case of *Sphagnum* litter (Sinsabaugh et al. 2002).  
277 Indeed, it has been shown that phenol oxidase enzymes by degrading inhibitory phenolic compounds, allow other  
278 enzymes to act on soil organic C and as a consequence regulate the stability of a vast C store in the soil following  
279 the hypothesis of 'enzyme latch' mechanism (Freeman et al., 2001).

280 Linking microbial extracellular enzyme production and litter decomposition modeled catalysis rates could  
281 provide information on the mechanisms of decomposition and non-additive effect (Sinsabaugh et al. 2002).  
282 However, using different litter types (which can change litter quality, nutrient availability and pH) such a  
283 correlation could not be demonstrated. Enzymatic degradation is still necessary to degrade complex and insoluble  
284 litter compound and relating modeled catalysis rates and enzymatic activities are likely to provide powerful models  
285 that remains poorly understood.

286

### 287 4.3 Sensitivity of the WEOC compartment

288 Mixing *Sphagnum* with *Pinus* litters did not increase OM decomposition but affected the WEOC  
289 compartment, i.e. the dissolved C pool in the laboratory-based experiment. This dissolved fraction described as  
290 the pool that is mostly sensitive to any modification in litter decomposition (e.g. Gogo et al. 2014) is considered  
291 as a transitory compartment between solid and gaseous pools, which contains a low C-content compared to the  
292 other pools. Thus, an increase in litter decomposition would have a strong effect on this compartment as observed  
293 for the *Sphagnum-Eriophorum-Pinus* litter mixture. The *Sphagnum-Eriophorum* mixture did not increase the  
294 WEOC content as this pool is a ‘dynamic’ compartment that is rapidly transformed into a gaseous C pool. The  
295 WEOC increase in *Sphagnum-Pinus* litter could indicate a modification in litter decomposition, which was still  
296 not perceived in the solid or gaseous compartments however.

297

### 298 4.4 Implication in a scenario of vegetation dynamics

299 Like Hoorens et al. (2002) and Gogo et al. (2016), our study showed that mixing graminoid and *Sphagnum*  
300 litters together induces a synergistic effect on decomposition. This has important implication for estimating litter  
301 decomposition rates in peatlands. These species-specific interactions appeared to be modulated by the changing  
302 climate through modifications of litter chemistry (Hoorens et al., 2002). In the context of global change and its  
303 role in causing a shift in the relative abundance of *Sphagnum* and vascular plants in peatlands (Dieleman et al.,  
304 2015), synergistic effects of mixed litters on decomposition is likely to play a critical role for the C dynamics at  
305 ecosystem level.

306

## 307 **5 Conclusions**

308 On the global scale, the C-sink capacity of *Sphagnum* peatlands could be affected by the litter mixture effect.  
309 This calls for further studies on non-additive effects of litter mixture, with a focus on elucidating the specific  
310 enzymatic mechanisms behind such interactions, with the ultimate goal of incorporating them in global  
311 biogeochemical models.

312

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316 Région Centre – Val de Loire (ARD 2020 program and CPER 2015 -2020). The authors are also indebted to the  
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319

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408

409 **Table captions**

410 TAB. 1: C content (%), N content (%) and C:N ratio for the *Sphagnum* (S), *Pinus* (P), *Eriophorum* (E), *Sphagnum-*  
411 *Pinus* (SP), *Sphagnum-Eriophorum* (SE), *Pinus-Eriophorum* (PE) and *Sphagnum-Pinus-Eriophorum* (SPE) litters.

412

413 TAB 2. Levels of significance from the post-hoc tests for comparison of *Sphagnum-Pinus* (SP), *Sphagnum-*  
414 *Eriophorum* (SE), *Pinus-Eriophorum* (PE) and *Sphagnum-Pinus-Eriophorum* (SPE) litter mixture effect (additive  
415 vs observed) by incubation time on the remaining solid C, water extractable organic carbon (WEOC) and cumulated  
416 of CO<sub>2</sub> - C production during the laboratory experiments. Asterisks represent significant differences (NS = not  
417 significant, - p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

418

419 TAB 3. Levels of significance from the post-hoc tests for comparison of *Sphagnum-Pinus-Eriophorum* (SPE) litter  
420 mixture effect (additive vs observed) by incubation time on the remaining solid C and CO<sub>2</sub> production during the  
421 field experiments. Asterisks represent significant differences (NS = not significant, - p < 0.1, \*p < 0.05, \*\*p <  
422 0.01, \*\*\*p < 0.001).

423

424 TAB. 4: Catalysis rate (mg C .g<sup>-1</sup>C.d<sup>-1</sup>) obtained from the C-fluxes model over time for *Sphagnum* (S), *Pinus* (P),  
425 *Eriophorum* (E), *Sphagnum-Pinus* (SP), *Sphagnum-Eriophorum* (SE), *Pinus-Eriophorum* (PE) and *Sphagnum-*  
426 *Pinus -Eriophorum* (SPE). The model was calibrated with data from the laboratory incubation experiment.  
427 Calculate additive rates values are means from the catalysis rates measured in the decomposition of the single  
428 species litter.

429 **Figure captions**

430 FIG. 1: Mean (±SE, n=3) remaining solid C (a), water extractable organic carbon (WEOC) (b) and CO<sub>2</sub> - C  
431 production (c) in single species litter decomposition of *Sphagnum fallax* (◐, S), *Pinus uncinata* (Δ, P) and  
432 *Eriophorum vaginatum* (◊, E) during the laboratory incubation. Lines represent the corresponding fitted curves  
433 from the model for each type of litter. Asterisks represent significant differences (NS = not significant, - p < 0.1,  
434 \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

435 FIG. 2: Additive (■) and observed (□) mean ( $\pm$ SE, n=3) of remaining solid C (i), WEOC (ii) and cumulative  
436 CO<sub>2</sub> - C (iii) of *Sphagnum+Pinus+Eriophorum* (a), *Sphagnum+Eriophorum* (b), *Pinus+Eriophorum* (c) and  
437 *Sphagnum+Pinus* (d) litter mixture decomposition during the laboratory incubation. Additive values are the  
438 weighed means from the values measured in the decomposition of the single species litter. Lines represent the  
439 corresponding fitted curves from the model. Asterisks represent significant differences (NS = not significant, - p<  
440 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

441 FIG. 3: Mean ( $\pm$ SE, n=12) remaining mass (a) and CO<sub>2</sub> production (b) of *Sphagnum fallax* (○, S), *Pinus*  
442 *uncinata* (Δ, P) and *Eriophorum vaginatum* (◇, E) litter from field litter bags experiment. Asterisks represent  
443 significant differences (NS = not significant, - p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

444 FIG. 4: Additive (■) and observed (□) mean ( $\pm$ SE, n=12) of remaining litter mass (a) and CO<sub>2</sub> production (b)  
445 from litter mixtures of *Sphagnum*, *Pinus* and *Eriophorum* (SPE) during field litter bags experiment. Additive  
446 values were calculated as the weighed mean of the values from litter decomposition of single plant species litter.  
447 Asterisks represent significant differences (NS = not significant, - p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001).

448 FIG. 5: Additive (■) and observed (□)  $\beta$ -glucosidase activities of *Sphagnum+Pinus+Eriophorum*,  
449 *Sphagnum+Eriophorum*, *Pinus+Eriophorum* and *Sphagnum+Pinus* litter mixtures ( $\pm$ SD, n=3). Asterisks represent  
450 significant differences (NS = not significant, - p < 0.1, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001). Only values from 0  
451 to 28 days of incubation are given because a contamination occurred for the  $\beta$ -glucosidase activities samples at 51  
452 days.

453

454 **Tables**

455 Table 1.

Composition	Litters						
	S	P	E	SP	SE	PE	SPE
C (%)	42.4	50.9	47.7	46.8	45.2	49.7	46.9
N (%)	1.8	1.7	1.9	1.6	1.9	1.9	1.7
C:N	23.7	29.2	25.8	30.1	23.3	26.9	26.8

456

457 Table 2.

		Main effect		Post hoc test				
		Litter type (expected vs observed)	Time (days)	0	1	14	28	51
SP	Solid C		***					
	WEOC	-						
	Cumul CO <sub>2</sub> -C		***					
SE	Solid C	***	***					***
	WEOC							
	Cumul CO <sub>2</sub> -C	***	***					***
PE	Solid C	-	***					
	WEOC		***					
	Cumul CO <sub>2</sub> -C	-	***					
SPE	Solid C	*	***					
	WEOC	*	***					
	Cumul CO <sub>2</sub> -C	-	***					

458

459 Table 3

		Main effect		Post hoc test		
		Litter type (expected vs observed)	Time (years)	1	2	3
SPE	Solid C	**	***			*
	CO <sub>2</sub> production		***			

460

461

462 Table 4

Litters	Time (days)
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		0	1	14	28	51
S		7.87	6.61	1.91	1.66	1.65
P		2.57	2.54	2.18	1.84	1.40
E		4.02	3.51	2.22	2.20	2.20
SP	observed	3.44	3.33	2.34	1.84	1.54
	additive	3.05	5.18	1.83	1.62	1.61
SE	observed	3.57	3.51	2.86	2.34	1.77
	additive	3.41	3.34	2.57	2.00	1.44
PE	observed	3.79	3.5	1.87	1.62	1.59
	additive	3.47	3.26	2.08	1.88	1.85
SPE	observed	3.29	3.23	2.63	2.11	1.46
	additive	3.10	3.05	2.45	1.93	1.31

463

464 **Figures**

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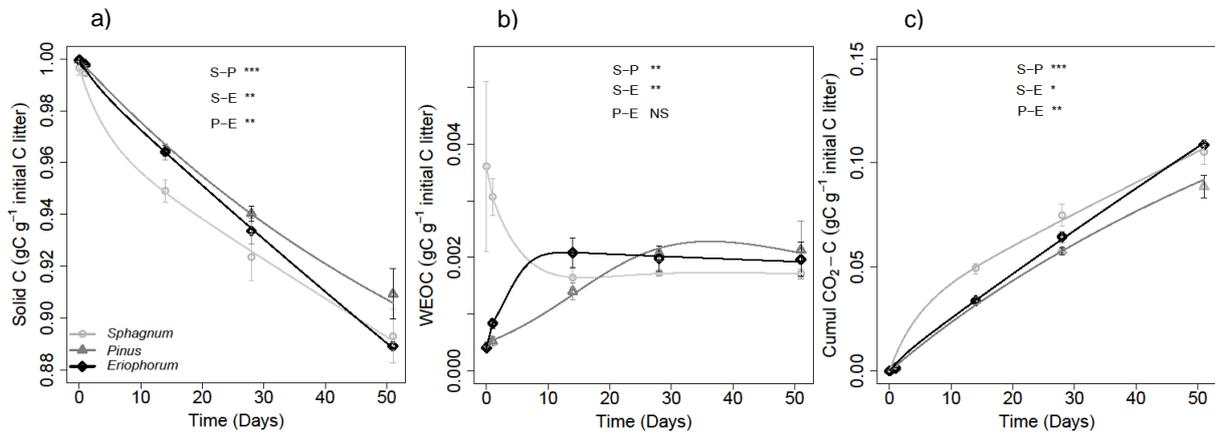
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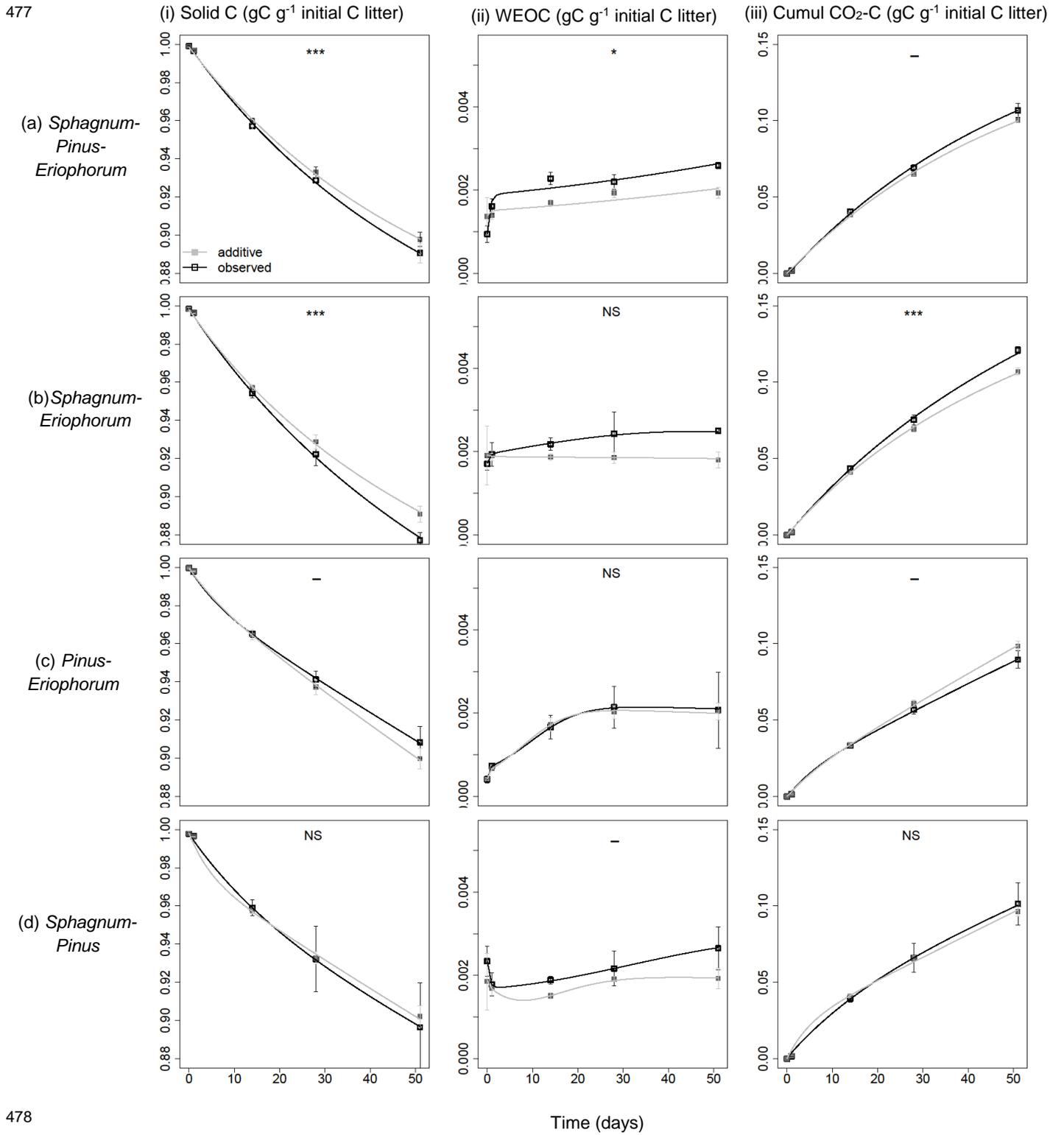


473 Fig. 1

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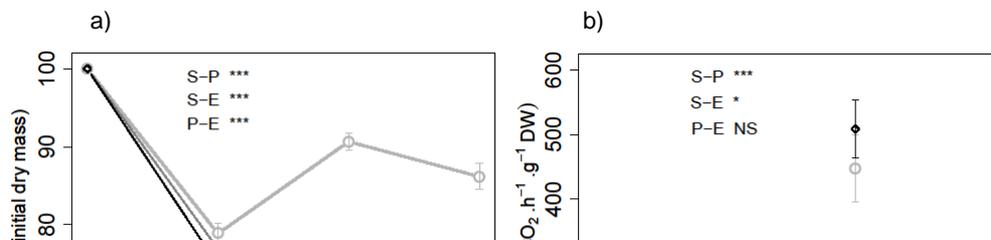
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480 Fig. 2

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Fig. 3

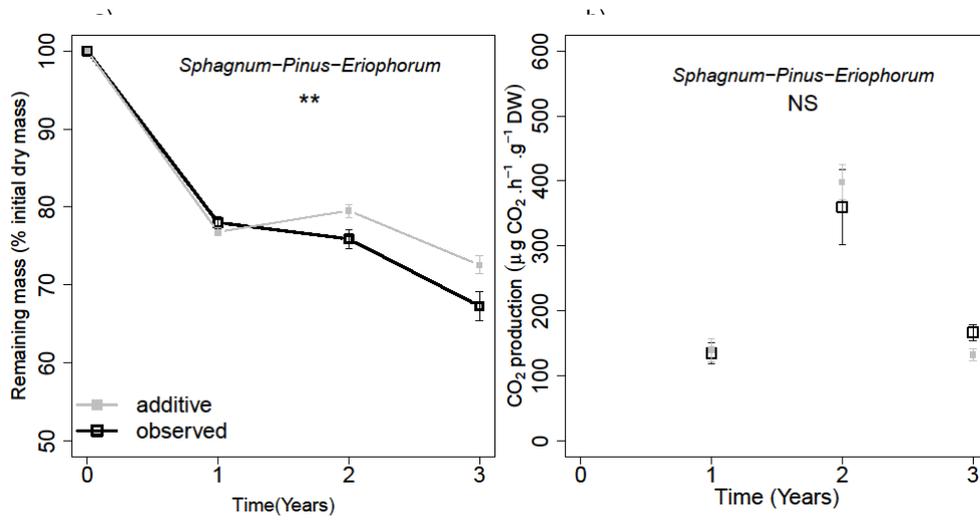
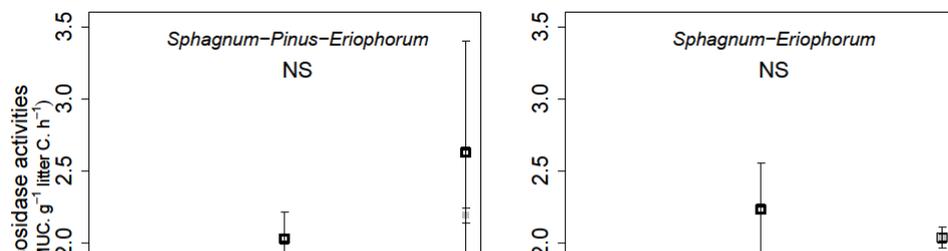


Fig. 4



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529 Fig. 5

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531 **Supplementary data**

532 **Table**

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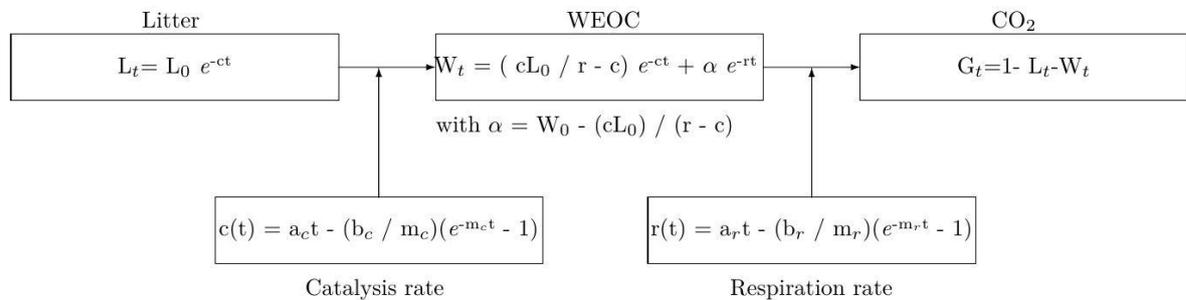
534 Supplementary Table S5: Percentage normalized root mean square error (% NRMSE) for the solid (L), dissolved  
 535 (W), gaseous (G) pools and the sum of them for the *Sphagnum* (S), *Pinus* (P), *Eriophorum* (E), *Sphagnum-Pinus*  
 536 (SP), *Sphagnum-Eriophorum* (SE), *Pinus-Eriophorum* (PE) and *Sphagnum-Pinus -Eriophorum* (SPE) models of  
 537 C dynamics.

Pools	Litters						
	S	P	E	SP	SE	PE	SPE
L	0.28	0.19	0.11	0.11	0.13	0.09	0.1
W	0.28	4.08	1.89	0.19	0.48	0.84	5.54
G	5.75	5.14	2.49	2.52	2.52	2.51	1.98
Sum	6.31	9.41	4.49	2.82	3.13	3.45	7.61

538

539 **Figures**

540

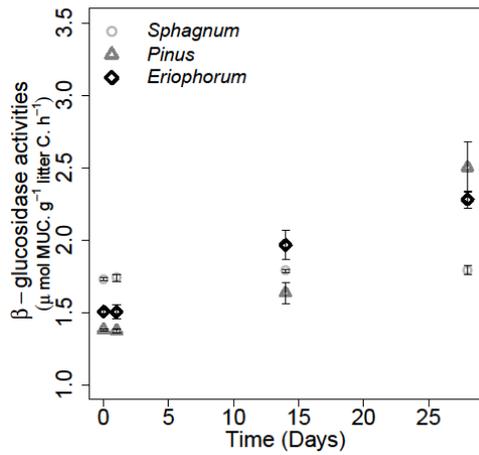


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542 Supplementary FIG. S6: Model of the C flow in the litter decomposition process. Three compartments  
 543 corresponding to the solid (litter), aqueous (WEOC), and gaseous (cumulative C-CO<sub>2</sub> respired) forms of C are  
 544 indicated. Solid lines indicate the rates of catalysis and respiration. The L pool flows into the WEOC at the catalysis  
 545 rate “c” and the WEOC is respired at the rate “r” (adapted from Gogo et al. 2014).

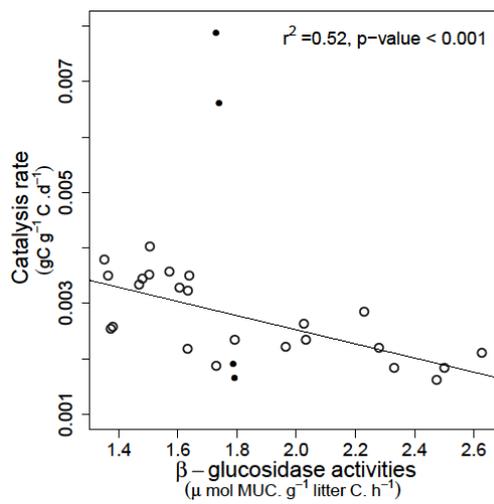
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549 Supplementary FIG. S7:  $\beta$ -glucosidase activities in *Sphagnum* ( $\circ$ ), *Pinus* ( $\Delta$ ) and *Eriophorum* ( $\diamond$ ) litter during  
 550 the laboratory incubation ( $\pm$ SD,  $n=3$ ). Only values from 0 to 28 days of incubation are given because a  
 551 contamination occurred for the  $\beta$ -glucosidase activities samples at 51 days.



552

553 Supplementary FIG. S8: Linear regression between catalysis rates and  $\beta$ -glucosidase activities. Each point  
 554 represents the  $\beta$ -glucosidase activities measured associated to the catalysis rate obtained for each litter type at a  
 555 time  $t$ . The  $r^2$  was calculated with all litters at the exception of *Sphagnum* ones ( $\bullet$ ).