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1 **Grassland-cropland rotation cycles in crop-livestock farming systems regulate priming effect**  
2 **potential in soils through modulation of microbial communities, composition of soil organic**  
3 **matter and abiotic soil properties.**

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22 Partitioning

23

## 24 **Abstract**

25 Soils can act as a carbon sink, and the chemical and biological transformation of vegetal litter into soil  
26 organic matter (SOM) is widely influenced by land-use and other biogeochemical parameters.  
27 However, the increase of new carbon inputs to soil has the potential to trigger the mineralization of  
28 stabilized SOM, a process called priming effect.

29 The objective of this manuscript is to investigate, at a landscape scale (5km<sup>2</sup>), the factors influencing  
30 the susceptibility of SOM to priming effect. To achieve this objective, physical, chemical, and  
31 metagenomics analyses were conducted on 88 soil samples and successively combined with  
32 agronomical data and soil incubation for the quantification of carbon fluxes.

33 Variance partitioning models highlighted that priming effect is controlled by complex interactions of  
34 biotic and abiotic factors, which include soil chemistry, quality of SOM, shape and abundance of  
35 microbial communities. Fluorescence properties of the dissolved organic matter has been found as a  
36 strong descriptor for priming effect. Depending on the time of crop rotation devoted to grassland, two  
37 different components leading to priming effect were identified. The introduction of grassland for 40-  
38 60% of the time of rotation achieved the lowest susceptibility to priming effect, and higher indexes of  
39 microbial diversity, whereas higher or lower proportions of time of the rotation devoted to grassland  
40 resulted in an increase of priming effect and a decrease of bacterial evenness.

41

## 42 **1. Introduction**

43 A sustainable land management aims to guarantee adequate productivity in agriculture and, at the  
44 same time, to provide several ecosystem services (Haines-Young and Potschin, 2010). Among  
45 marketed ecosystem services, the production of food, fiber and biofuel are the most acknowledged  
46 ones, but there are other non-marketed ecosystem services dealing with water and climate regulation,  
47 as well as cultural and aesthetic services (Swinton et al., 2007). Powlson et al. (2011) described soil  
48 fertility and the accumulation of soil organic matter (SOM) among the most important services  
49 provided by sustainable agricultural practices. There is a scientific consensus about the benefits  
50 provided by higher SOM contents, and a major concern regarding the decline of SOM stocks  
51 (Kirschbaum, 1995; Minasny et al., 2017; Six et al., 1998; Tiessen et al., 1994).

52 The contents of organic matter (OM) in a soil result from the differences between carbon (C) inputs,  
53 mainly as aboveground and belowground plant biomass or amendments, and outputs via SOM  
54 decomposition by microorganisms, runoff and leaching of particulate and dissolved organic C. The  
55 actual stock of OM in a soil is thus regulated by transformation processes resulting to its stabilization,  
56 or its mineralization. The microbial degradation of SOM is a function of its physical accessibility and  
57 chemical composition (Kuzyakov and Blagodatskaya, 2015). The addition of exogenous organic  
58 matter has been reported to alter SOM decomposition, either by boosting (Chen et al., 2014; Fontaine  
59 et al., 2003) or impeding it (Guenet et al., 2010) due to the so-called priming effect (PE) (Bingeman et  
60 al., 1953; Kuzyakov et al., 2000).

61 A considerable effort is necessary to elucidate SOM dynamics and fluxes, especially PE, since they are  
62 influenced by a plethora of biotic (interactions with plants, bacteria, fungi, micro fauna) (Tardy et al.,  
63 2015) and abiotic factors (content and type of minerals, water balance, atmospheric conditions)  
64 (Dignac et al., 2017), acting from micro- to macro-scales (Kuzyakov and Blagodatskaya, 2015). The  
65 fluxes of C in soil may differ strongly from one land-use to another, mediated by shifts in the  
66 distribution of microbial communities and functionality, different types and amounts of C returned to  
67 soil, and various plant/soil interactions (Baumann et al., 2013; Dignac et al., 2017; Frank et al., 2002;  
68 Tardy et al., 2015). Land-use can change SOM contents drastically, especially in the case of soils  
69 devoted to intense anthropic activities (reclamation for urban or agricultural purposes) (Lal and  
70 Stewart, 1990). The inclusion of grassland in crop rotation has been highlighted as a way to maintain  
71 or improve soil quality in agroecosystems (Glover et al., 2010; Lemaire et al., 2015) and to increase  
72 soil C stocks (Smith, 2014; Solomon et al., 2007) because of the modification of both SOM accrual  
73 and degradation dynamics (Panettieri et al., 2017). A considerable fraction of C fluxes resulting from  
74 the priming effect is assumed to be driven by processes taking place in the rhizosphere (de Graaff et  
75 al., 2014; Fontaine et al., 2003), and more extended and dense root networks are generally observed in  
76 grassland soils (Jackson et al., 1996; Panettieri et al., 2017). Therefore, the effects of grassland derived  
77 C inputs on PE needs attention in order to estimate the potential effect of the introduction of  
78 grasslands into crop rotations on agroecosystems C balance.

79 Kuzyakov et al. (2000) described the mechanisms behind the increased C mineralization responsible  
80 of the “real priming effect”, triggered by the addition of labile C sources and/or C-rich  
81 rhizodeposition, among other factors. Recent studies have been focused on the PE produced by mining  
82 of nitrogen and preferential substrate use (Chen et al., 2014), energy starvation, microbial competition  
83 and co-metabolisms (Louis et al., 2016; Tardy et al., 2015), or regulation by redox transformation of  
84 soil minerals (Finley et al., 2018; Keiluweit et al., 2015). However, the quantification of the PE  
85 mechanism is still limited by methodological uncertainties and by both spatial and temporal variability  
86 in its occurrence (Bastida et al., 2019). Moreover, there are concerns about the accuracy of prediction  
87 models for global C stocks in which the trigger of SOM mineralization provided by PE is not taken  
88 into account (Guenet et al., 2018).

89 Considering these scientific challenges, the present study has been designed to evaluate the effects of  
90 land-use on PE at a landscape scale. Recent studies have been focused on the global assessment of PE  
91 predictors (Bastida et al., 2019), but few studies have been targeted at the landscape scale (Craig et al.,  
92 2015; Helgason et al., 2014; Walz et al., 2017) and none of them included cropped soils. Unveiling the  
93 magnitude and the dynamics of PE in agricultural landscapes is mandatory to calibrate land-use  
94 policies. The objective of the project was to identify the factors controlling PE, having a  
95 comprehensive approach by integrating soil physical and chemical properties, indexes of soil  
96 microbial communities, and agronomic practices in a 5-km<sup>2</sup> agricultural area in the region of Brittany  
97 (France). The site is characterized by high density of pig farming and by the co-existence of mixed  
98 annual crops and grasslands (pastures or hayfields, being permanent or included in the rotations). We  
99 hypothesized that (i) PE at the landscape scale is related to the community composition of soil  
100 microorganisms interacting with the amount and type of OM, and that (ii) land-use management has a  
101 significant impact on C fluxes associated with PE.

102 To test these hypotheses, soil samples were analyzed using a multidisciplinary approach in which soil  
103 physical, chemical, and biological variables were tested as descriptors of PE fluxes measured in  
104 incubation condition with addition of <sup>13</sup>C-labeled wheat litter.

105

## 106 2. Materials and methods

### 107 2.1. Study area and soil sampling

108 Soil samples were collected from a 5 km<sup>2</sup> agricultural area, in the Brittany region (Kervidy-Naizin  
109 catchment, N 47.99; W 2.84, France) in June 2013. About 85% of the surface of the sampling area is  
110 devoted to agriculture. The crops covering the larger surfaces are maize and grassland (covering 30%  
111 of the agricultural surface each), followed by other cereals (25%) and vegetables (10%). The  
112 catchment is an Observatory for Research on the Environment related to agricultural watersheds  
113 (SOERE-RBV Critical Zones, [www6.inra.fr/ore\\_agrhys](http://www6.inra.fr/ore_agrhys)). The climate is oceanic, with a yearly  
114 average temperature of 11°C (1994-2013) and mean yearly rainfall of 830 mm. The elevation ranges  
115 between 98 and 140 m with mild slopes oriented towards the Naizin river network. Coordinates of the  
116 sampling points were distributed using a systematic triangular grid to integrate the maximum of the  
117 spatial heterogeneity of the area.

118 Most soils are well-drained Cambisol (upslope), and some poorly drained Haplic Albeluvisols are  
119 located in the foot-slope farms (IUSS Working Group WRB, 2015). Parent material consists of schist  
120 and alluvial deposits. The soil texture, measured by standardized 5-fraction granulometry (NF X 31–  
121 107, AFNOR, 2003), is silty-loam and relatively uniform among the whole area.

122 Surface composite soil samples were collected at a 0-15 cm depth with a 5 cm wide auger. The  
123 composite soil samples were made by mixing individual soil cores into one homogeneous sample,  
124 sieved in the field ( $\varnothing < 5\text{mm}$ ), stored at 4°C during the transportation to the lab, and split into two  
125 subsamples. The first subsample was air-dried and stored at 4°C for incubation and chemical analyses.  
126 The other subsample was freeze-dried and stored at -20°C until molecular biology analyses were  
127 performed. Soil drainage classes and Beven's topographic wetness indexes (Beven and Kirby, 1979)  
128 were derived respectively from a detailed soil map (Walter and Curmi, 1998) and from a 20-m digital  
129 elevation model. In the framework of the project, farmers were surveyed regarding farming practices,  
130 crop rotations, number of cropped species, the quantity of mean annual C input by crop and grassland  
131 residues, C input by animal manure as well as the quantity of mineral fertilizers applied each year, on  
132 an 11-year period (Viaud et al., 2018).

133 In this study, 100 independent samples were collected from different farms and divided in five  
134 different land-use classes considering the frequency of grassland, expressed as percentage of the  
135 rotation time devoted to grassland, as the classification parameter. Main cropped species other than  
136 grassland were Maize (silage or grain) in monoculture, or in rotation with cereals (winter wheat,  
137 winter barley and triticale), rapeseed, and vegetables. Regarding the descriptors of crop rotation, the  
138 number of cropped species, considering grassland a unique specie, was the other variable added to the  
139 variance partitioning model, further variables were adding too much complexity to the study and thus  
140 discarded. The lower and upper limits of the land-use classification were permanently cropped soils  
141 (PC n=42), and permanent grassland soils (PG n=7), respectively. Three land-uses were selected using  
142 the different frequency of grassland adopted by farmers on the 11-year period before soil sampling:  
143 low-frequency (LO, from 10 to 30% of time dedicated to grassland, n=13), mid-frequency (MI, 40-  
144 60% of time under grassland, n=13), and high-frequency (HI, 70-90% of time under grassland, n=13).  
145 All the grassland farms were mown regularly to feed animals.

146 After this classification, 88 independent samples respected the criteria of classification, 12 samples  
147 collected in wetland, wasteland land and orchards were not considered because of their low  
148 representativeness of the area.

149

## 150 2.2. Soil physical and chemical analyses

151 Each measure of soil physical and chemical parameters is a calculated mean of three replicates. The  
152 mean weight diameter (MWD) of the air-dried soil aggregates was calculated using the aggregate  
153 fractionation method ISO/FDIS 10930 (AFNOR, 2012) derived from the “slow re-wetting” and soil  
154 wet sieving procedure described by Le Bissonnais (1996). Bulk density was calculated on a 0-15 cm  
155 surface soil layer, using an 8-cm diameter manual soil core sampler. Samples were weighed and dried  
156 at 105°C for 48h to determine gravimetric water content and bulk density.

157 The total organic C and N contents (TOC and TN) and C isotopic signatures ( $\delta^{13}\text{C}$ ) of the soil samples  
158 were measured by dry combustion (NF ISO 10694 AFNOR, 1998, and NF ISO 13878, AFNOR  
159 1995)) on an elemental analyzer linked to an isotopic-ratio mass spectrometer (EA-IRMS, VarioMicro

160 Cube linked to an Isoprime, Elementar). The stable carbon isotope ratios,  $^{13}\text{C}/^{12}\text{C}$  expressed as  $\delta^{13}\text{C}$ ,  
161 are calculated against Vienna Pee Dee Belemnite (VPDB) standard.

162 Moreover, soils were analyzed for the concentrations of oxalate-extractable Si, Fe, Al (NF ISO 22036,  
163 (AFNOR 2009), Cu (NF X 31- 120 on EDTA extracted samples (AFNOR 2003b), extractable Olsen's  
164 P (NF ISO 11263, (AFNOR 1995b) and pH in a 1:5 water suspension (NF ISO 10390, (AFNOR  
165 2005)).

166 Pressurized hot-water-extractable organic carbon (WEOC) was obtained using a solvent extractor  
167 (ASE200, Dionex Corporation, Sunnyvale, USA) on 5 g of soil, according to the method of Guigue et  
168 al. (2014). The C concentration in the extracts was measured in a first aliquot by thermal oxidation and  
169 NDIR detection (TOC 5000A, Shimadzu), after the addition of 2M HCl (10  $\mu\text{l}$  per ml of sample) to  
170 remove inorganic C. The results of WEOC content were expressed as WEOC contribution to TOC  
171 content of soils. The UV-light absorbance of the extracts at 254 nm ( $\text{UV}_{254}$ ) was measured with a  
172 Jenway 6715 spectrophotometer and the specific ultraviolet absorbance ( $\text{SUVA}$  in  $\text{l mg C}^{-1} \text{cm}^{-1}$ ) was  
173 calculated as an indicator of their content in aromatic moieties (Chin et al., 1994; Weishaar et al.,  
174 2003). Another aliquot of the sample was used to measure the pH, then freeze-dried and used for the  
175 determination of  $\delta^{13}\text{C}$  of WEOC by EA-IRMS.

176

### 177 2.3. Excitation-emission matrices of fluorescence and PARAFAC modeling

178 For fluorescence measurements, triplicates of water-extracted samples ( $n=3\times 88$ ) were analyzed using  
179 the same settings as in Guigue et al. (2014), with excitation wavelengths ranging from 220 to 500 nm,  
180 and emission wavelengths from 250 to 600 nm. The whole dataset corresponding to 264 data matrices  
181 (excitation wavelength  $\times$  emission wavelength  $\times$  fluorescence intensity) was processed for PARAFAC  
182 modeling using drEEM toolbox 0.2.0 (Murphy et al., 2014) with Matlab R2016a under Linux. The  
183 inner-filter effect was corrected using absorbance spectra during the preprocessing steps. Rayleigh and  
184 Raman scatter peaks were excised and substituted with interpolated data using the *smootheem* function  
185 of the drEEM toolbox. The fluorescence signal measured at excitation wavelengths shorter than 250  
186 nm was noisy, exerting disproportionate leverage on the model, and were thus cut for all EEMs. Each  
187 EEM was normalized to its total signal, so that the effect of sample intensity was removed before the



188 modeling phase (Murphy et al., 2013). The normalization was reversed after the modeling so that the  
189 output values presented correspond to the concentration in the original sample. Outliers identified by  
190 their high leverages (n=11) were removed before fitting the final model. A 3-component model  
191 explaining 99.7% of the dataset, having a CORCONDIA of 43.4% and which was successfully split-  
192 validated was retained as the final model. The component contribution to each sample fluorescence  
193 signal were exported as Fmax in Raman Unit (RU), and then normalized to the DOC concentration in  
194 the measured aliquot so that the reported Fmax value is expressed in RU per C unit and serves as an  
195 indicator of the composition of OM in the samples. The three components of fluorescence identified  
196 by the PARAFAC model, named CP1<sub>(fluor)</sub>, CP2<sub>(fluor)</sub> and CP3<sub>(fluor)</sub>, comprised two excitation spectral  
197 peaks and a single emission peak (Fig. 1). The OpenFluor online database  
198 (<https://openfluor.lablicate.com>) was consulted to match the spectral properties of obtained  
199 components with previously identified fluorophores (Murphy et al., 2014).

200

#### 201 2.4. Soil microbial communities

202 A characterization of communities of soil microorganisms was carried out after the pre-incubation and  
203 just before incubation, following the method proposed by Tardy et al. (2015). For each soil sample, the  
204 biomass was derived from the total quantity of crude DNA extracted from 1 g of lyophilized soil using  
205 the ISO 10063 method (Dequiedt et al., 2011; Plassart et al., 2012). Prior to PCR amplification, DNA  
206 was purified using a MinElute gel extraction kit (Qiagen Courtaboeuf, France) at INRA Genosol  
207 Platform (Dijon, France). Bacterial and fungal diversity were resolved by 454 pyrosequencing,  
208 targeting respectively the 16S rRNA V3-V4 gene fragment (about 400 bases) and an 18S rRNA gene  
209 fragment of about 350 bases. The primer sets were respectively: F479 (5'-  
210 CAGCMGCYGCNGTAANAC-3')/R888 (5'-CCGYCAATTCMTTTRAGT-3') (Terrat et al., 2012);  
211 and FR1 (5'-AICCATTCAATCGGTAIT-3')/FF390 (5'-CGATAACGAACGAGACCT-3') (Plassart  
212 et al., 2012). A second PCR was run on purified products from first PCR, adding 10 based-pair  
213 multiplex identifiers (MID) at 5' position to the primers for subsequent sample identification. Final  
214 purification and pyrosequencing were carried out on a GS Roche 454 sequencing system.

215 Bioinformatics analyses were carried out using the GnS-Pipe of the Genosol Platform (Terrat et al.,  
216 2012). Raw reads of 16S and 18S were sorted according to MID sequences, then filtered on their  
217 length, number of ambiguities, and primer sequences. A homogenization procedure by random  
218 selection close to the lowest dataset (2,886 and 3,286 high-quality sequences for 16S and 18S rRNA  
219 genes, respectively) was carried out to avoid biased comparison of the communities. The dereplicated  
220 reads were aligned using infernal alignment and clustered at a 95% similarity threshold into  
221 operational taxonomic units (OTU) by grouping rare reads to abundant ones and not counting  
222 differences in homopolymer lengths (Terrat et al., 2012). Single Singletons constituted by unclustered  
223 reads detected only once were filtered based on the quality of their taxonomic assignment. Bacterial  
224 (16S) and fungal (18S) OTUs were organized into contingency tables reporting the number of reads  
225 for each OTU in each sample. In this study, bacterial and fungal richness were expressed as number of  
226 OTUs, whereas Pielou's diversity index  $J'$  assessed the evenness of the species (Pielou, 1966).

227

## 228 2.5. Carbon mineralization and priming effect measurements

229 The mineralization of SOM was measured during an 80-day incubation experiment. For each sample,  
230 six hermetically sealed 150-ml plasma flasks were filled with 30 g of dry soil and then brought to 60%  
231 of water holding capacity (WHC). To avoid the overestimation of C mineralized in the first days due  
232 to the disturbance by soil manipulation and rewetting and to allow soils to reach a more stable state,  
233 microcosms were pre-incubated for three weeks at 20°C before starting the monitored phase of the  
234 incubation.

235  $^{13}\text{C}$ -labeled wheat residues (7 atom%  $^{13}\text{C}$ ) originated from mature wheat plants (harvested 110 days  
236 after sowing) cultivated under controlled conditions (Groupe de Recherches Appliquées en  
237 Phytotechnologie, CEA Cadarache, France). More precisely, seeds of wheat (*Triticum aestivum* cv  
238 Caphorn) were germinated at 4°C in darkness. Plantlets were grown in a mix of sand (1/4) and perlite  
239 (3/4) in an air-tight chamber which allowed accurate regulation of atmospheric gas composition and  
240 environmental parameters. The plants were watered with half-diluted Hoagland's nutrient solution and  
241  $\text{CO}_2$  concentration was maintained at  $380\mu\text{l l}^{-1}$ . The partial pressures of both  $^{13}\text{CO}_2$  and  $^{12}\text{CO}_2$  in the

242 chamber were continuously monitored by Near Infrared Spectroscopy to determine  $^{13}\text{C}$  enrichment of  
243 the  $\text{CO}_2$ . Regulation was achieved by automatic injection of pure (>99% atom%  $^{13}\text{C}$ )  $^{13}\text{CO}_2$   
244 (CortecNet, Paris, France).

245 The microcosms were either amended with  $^{13}\text{C}$ -residues of wheat (5 mg  $\text{g}^{-1}$  of dry weight soil), which  
246 had been finely ground in a bead beater to obtain a powder (wheat residues  $\text{C}_{\text{org}} = 42.1\%$ , C:N ratio =  
247 77.7, and  $^{13}\text{C}$  labelling = 7.01%), or were not amended (control). Wheat residues were used as  
248 “model” C-input to assess the response of microbial activity to addition of a given quality of plant  
249 material in all soils. Although they were not amended with wheat, control microcosms were  
250 mechanically disturbed as amended microcosms. The 528 microcosms (88 samples  $\times$  2 treatments  
251 ( $^{13}\text{C}$ -amended and control)  $\times$  3 replicates) were incubated in the dark for 105 days under controlled  
252 temperature (20°C) and moisture (60% WHC) conditions.

253 The volume of  $\text{CO}_2$  produced, used as an index of soil respiration, was sampled after 3, 7, 14, 21, 28,  
254 42, 63, and 80 days. Microcosms were aerated by flushing with air at each sampling date to avoid the  
255 perturbation of microbial activity mediated by increased  $\text{CO}_2$  concentration. Therefore, the measured  
256 soil respiration corresponded to the  $\text{CO}_2$  accumulated in the microcosm headspace between two  
257 sampling dates.

258 At each sampling date, the gaseous phase was sampled in 10 ml airtight flasks, to measure the  $\text{CO}_2$   
259 concentrations using an Agilent 7890B GC equipped with a thermal conductivity detector coupled to  
260 an automatic sampler (Agilent HS7697A Headspace), and in 12 ml airtight flasks, to measure the  $^{13}\text{C}$ -  
261  $\text{CO}_2$  enrichment on a Trace Gas analyzer (Micromass) linked to an isotopic-ratio mass spectrometer  
262 (Isoprime, Elementar). In this study, only the cumulative values of respired  $\text{CO}_2$  at the end of the  
263 incubation are reported.

264 The multi-point calibration for  $\text{CO}_2$  concentrations and  $^{13}\text{CO}_2$  were both carried out using a GasMix  
265 diluter, AlyTech. For the isotopic  $^{13}\text{CO}_2$  measurements, a variable  $^{13}\text{C}$  enrichment, ranging from  
266 natural abundance (1.08%) to 90% of  $^{13}\text{C}$  was used. The accuracy of the calibration, expressed as the  
267 difference in  $^{13}\text{C}$  percentage between the theoretical and the measured values was less than 0.3%  
268 ( $R^2=0.99$ ).

269 The use of <sup>13</sup>C-labeled wheat litter allowed to discriminate the contribution to total respiration ( $R_T$ )  
270 expressed in  $\mu\text{g C-CO}_2 \text{ g}^{-1} \text{ soil}$  of the SOM- and litter-derived respiration ( $R_S$  and  $R_L$ , respectively)  
271 using mass-balance equations:

272 Eq. (1) 
$$[R_T] = [R_S] + [R_L] \quad \text{and} \quad [R_T] \times \delta_T = [R_S] \times \delta_S + [R_L] \times \delta_L$$

273 Eq. (2) 
$$[R_S] = \frac{[R_T] \times (\delta_T - \delta_L)}{\delta_S - \delta_L}$$

274 Where  $\delta_i$ ,  $i \in \{T, S, L\}$  is the <sup>13</sup>C signature of the total, SOM- and litter-derived respired CO<sub>2</sub>,  
275 respectively. For the calculation, we made the assumption that the isotopic fractionation between the  
276 solid fraction (soil or litter) and the CO<sub>2</sub> produced by its mineralization was negligible. Based on these  
277 equations, the priming effect was calculated as following:

278 Eq. (3) 
$$[R_{\text{priming effect}}] = [R_{T \text{ amended}}] - [R_{T \text{ control}}] - [R_L]$$

279 and expressed as mg of C-CO<sub>2</sub> primed per g of dry weight soil (PE-DW) and per TOC unit (PE/TOC).  
280 For this study, values of PE are expressed as cumulative values of CO<sub>2</sub> emitted during the incubation.

281

## 282 2.6. Data analyses

283 The analyses were performed with R (R Core Team, <http://www.r-project.org/>) using “vegan”, “car”,  
284 and “leaps” packages (Fox and Weisberg, 2011; Lumley, 2017; Oksanen et al., 2018). Correlation  
285 heatmap was generated using “corrplot” package (Wei and Simko, 2017). A variance partitioning  
286 approach was used to identify the most significant explanatory variables for the PE, following the  
287 method proposed by Chemidlin Prévost-Bouré et al. (2014). Using the Spearman’s correlation matrix,  
288 variables with a coefficient  $\rho \geq 0.8$  were selected and only one of each pair has been included into the  
289 models, to avoid collinearity. As a second step, a model selection was conducted by simultaneously  
290 minimizing the Bayesian Information Criterion (BIC) and maximizing the adjusted  $R^2$  using the  
291 function *regsubset* (“leaps” package). On this subset of explanatory variables, a forward selection  
292 procedure was applied to identify the model with the highest  $R^2$ . The amounts of variance for PE  
293 explained by each descriptor, intended as marginal and shared variance, were determined by canonical  
294 variation partitioning, whereas the adjusted  $R^2$  was determined by redundancy analysis. The variance

295 inflation factors (VIF) for each descriptor were calculated using the *vif* function (“car” package). The  
296 descriptors with a  $VIF \leq 3$  were selected for the regression model, limiting the effect of collinearity on  
297 the estimated regression coefficients (Sheather, 2009). A total of 1000 permutations of the reduced  
298 model were computed to assess the significance of marginal effects.

299 Using the same procedure described above, two different models were built to further decorticate the  
300 collinearity of our data, since an increase of TOC is often correlated to an increase in microbial  
301 biomass, WEOC, and thus respiration rates. The first model (identified as “PE-DW”) was run using  
302 PE and explanatory variables expressed on unit per gram of dry weight soil; the second model was run  
303 using PE and some explanatory variables (WEOC, microbial biomass, and respiration rates)  
304 normalized to TOC and identified as “PE/TOC”.

305 To simplify the discussion of the manuscript, only the parameters selected as significant descriptors by  
306 the two models were graphically represented and discussed within the text. Boxplots were generated  
307 using “ggplot2” (Wickham, 2009) packages in R. Data normality was checked before pairwise  
308 comparisons among land-use classes with a Shapiro-Wilk’s test. The significant differences for the  
309 analyzed parameters between land-use classes were assessed by non-parametric Kruskal-Wallis tests  
310 and the Dunn’s multiple pairwise comparisons. This step allows to interpret how land-use affects PE  
311 descriptors and thus the susceptibility of agroecosystems to PE. Due to the non-normal distribution of  
312 most of the values, two different levels of significance were used,  $p=0.05$  was evidenced by lowercase  
313 letters, while uppercase letters were used when significance satisfied the Bonferroni’s correction for  
314 10 hypotheses (significance level  $p=0.005$ ). No letters were used in case of the lack of significance  
315 between land-use classes.

316

### 317 **3. Results**

#### 318 3.1. Soil physical and chemical parameters

319 The correlation heatmap in figure 2 highlights a strong and diffuse correlation network between the  
320 investigated variables.

321 The contents of TOC were significantly higher only for permanent grassland soils, whereas no  
322 significant differences were found between the other land-uses (Fig. 3A). TOC and TN were highly

323 correlated ( $\rho^2 = 0.926$ ,  $p$ -value  $< 0.0001$ , Fig. 2) leading to the absence of significant differences  
324 among land-uses for C/N ratios (10.1 to 10.2 for all treatments, Table S1). Hereafter, the variables TN  
325 and TOC/TN will be omitted from the discussion, using TOC contents as the unique reference  
326 parameter.

327 More WEOC was extracted from samples with higher frequency of grassland, the amount of extracted  
328 C normalized to TOC content showed significant differences between cropland and permanent  
329 grassland samples only, with larger amounts extracted from the latest (Fig. 3B).

330 The stability of soil aggregates increased with grassland frequency and the MWD was generally higher  
331 for permanent grassland, as well as for HI compared to cropland (Fig. 3D). Texture of analyzed soils  
332 evidenced how samples classified as permanent and high-frequency grassland were shifted through a  
333 slightly higher presence of clay, compensated by a relative decrease in silt content (Fig. 3E).  
334 Concomitantly, permanent grassland samples showed lower and more dispersed pH values compared  
335 to other treatments, even if no significant differences were detected (Fig. 3F). Olsen's P content was  
336 higher for cropland than for HI and permanent grassland (Fig. 3G).

337 The quantity of crop litter returned yearly to soil differed according to land-use. HI samples received  
338 significantly higher inputs of crop litter than MI, even if data dispersion was high (Fig. 3H).

339

### 340 3.2. Qualitative indicators of soil OM obtained from EEM fluorescence and PARAFAC 341 decomposition of water-extractable OM

342 The components identified from the EEM fluorescence and PARAFAC decomposition are shown in  
343 figure 1. The  $CP1_{(Fluo)}$  most intense peak corresponds to fluorophores defined as "terrestrial humic-  
344 like" material and negatively correlated with DOM bioavailability (Lambert et al., 2017; Romero et  
345 al., 2017), whereas the  $CP1_{(Fluo)}$  secondary peak is similar to fluorophores correlated to biological  
346 activity in freshwater DOM (CP3 and CP5 in Lambert et al., 2017). The spectra obtained for  $CP2_{(Fluo)}$   
347 resemble those of  $CP1_{(Fluo)}$  with a shift towards longer wavelengths, previously described as  
348 "terrestrial humic-like" compounds (Stedmon and Markager, 2005) with greater aromaticity, higher  
349 molecular weight, and a larger degree of conjugation. Thus,  $CP2_{(Fluo)}$  is interpreted as a pool of organic  
350 compounds that have undergone more processing and transformation within the soil than  $CP1_{(Fluo)}$ .

351 These characteristics and the strong correlations among CP1<sub>(Fluo)</sub> and CP2<sub>(Fluo)</sub> ( $r^2 = 0.953$ ;  $n = 253$ )  
352 suggest their common sources, probably related to lignin breakdown during plant litter decomposition  
353 (Cory and McKnight, 2005).

354 The emission spectra of CP3<sub>(Fluo)</sub> presented a secondary peak with a “terrestrial humic-like” profile  
355 similar to the main peaks of the other two components. The primary peak is, however, found at longer  
356 wavelengths for excitation, similar to peaks found for biologically processed organic substrate (Coble,  
357 1996; Søndergaard et al., 2003). Such spectrum is less common in the literature and suggests an even  
358 higher degree of aromaticity with extensive and conjugated chemical complexes and low  $\delta^{13}\text{C}$   
359 signatures, indicating a scarce contribution of molecules from microbial origin (Dainard et al., 2015;  
360 Osburn et al., 2012; Yamashita et al., 2011). Bernard-Jannin et al. (2018) showed that such component  
361 is present in soil pore water of a peatland and tends to concentrate during dry period and Lambert et al.  
362 (2017) demonstrated its contribution to total fluorescence in rivers during high-water period.  
363 Therefore, these fluorescent compounds assigned to CP3<sub>(Fluo)</sub> likely correspond to highly processed  
364 organic material that tends to be preserved in soils, such as biodegraded tannins (Maie et al. 2007), or  
365 degradation products inherited from plant litter and swine manure (Hunt and Ohno, 2007; Wheeler et  
366 al., 2017). Fluorescence signal of CP3 (Fluo) decreased with higher frequencies of grassland ( $p < 0.05$ ,  
367 Fig. 3C), whereas the other fluorophores showed no significant differences among treatment.

368

### 369 3.3. Carbon fluxes, measured PE and soil microbial communities

370 Soil respiration of control microcosms, considered as the potential basal respiration of soil and  
371 expressed as mg of CO<sub>2</sub> emitted per gram of TOC, increased with grassland frequency, leading to  
372 significantly higher values for permanent grassland when compared with cropland (Fig. 4A). On the  
373 contrary, for the respiration of amended microcosms, permanent grassland shows significantly lower  
374 CO<sub>2</sub> emissions compared to HI, LO, and cropland (Fig. 4B). Calculated values of PE-DW were  
375 significantly higher ( $p < 0.05$ ) for HI than for MI and cropland, and permanent grassland presented  
376 huge data dispersion (Fig. 4C). The amount of wheat litter mineralized ranged between the 29.5 and  
377 the 42.9% of the total litter-<sup>13</sup>C added (Table 1), no significant differences between treatments were  
378 highlighted. PE was responsible of the mineralization of a portion of TOC ranging between 1.7 and

379 3.2 mg g<sup>-1</sup> TOC (Fig. 4D) during the incubation experiment; as a comparison term, basal respiration of  
380 soils mineralized between 6.3 and 10.4 mg g<sup>-1</sup> of TOC (Fig. 4B). At a  $p<0.05$  significance level, soils  
381 under LO and HI showed the highest values of PE, permanent grassland the lowest ones.

382 The influence of legume plants in some temporary and permanent grassland was tested by splitting  
383 grassland-only samples into two groups (with and without legumes). Soils from farms with legume  
384 crops showed slightly higher PE potential ( $2.40\pm 0.70$  vs.  $2.60\pm 0.95$  mg g<sup>-1</sup> TOC) than those without  
385 legumes, but with high data dispersion ( $p=0.363$ ). Running the same test excluding the samples from  
386 permanent grassland reduced the data dispersion, but differences between the two groups were still not  
387 significant ( $p=0.187$ ).

388 The quantities of DNA extracted per g of TOC showed an increasing trend with frequency of  
389 grassland, but only HI had significantly higher values ( $p<0.05$ ) when compared with Cropland (Fig.  
390 4E). LO and MI showed significantly higher values ( $p<0.05$ ) of bacterial Pielou's indexes of evenness  
391 (Eve\_B) than permanent grassland (Fig. 4F).

#### 392 3.4. Variance partitioning models rank variables related to the priming effect potentials

393 The complete statistical description of analyzed parameters is presented in table 1. Priming effect per  
394 unit of dry weight soil (PE-DW) and priming effect per TOC unit (PE/TOC) were selected as  
395 dependent variables to build two separate models, and the variance explained by each one of the  
396 independent variables was calculated with the variance partitioning models (Fig. 5). The PE-DW and  
397 PE/TOC models explained 53.62 and 49.04% of the total variance, respectively, but a part of it  
398 consisted of interactions, i.e. co-variance that cannot be assigned unequivocally to one descriptor. This  
399 is a common issue when several independent variables present a co-linearity pattern. For the PE-DW  
400 model, the variance assigned to interactions was negative (-6.33%). This value is due to the use of  
401 adjusted R<sup>2</sup> values as fitting parameters by the function `ordiR2step`, combined with a low sample to  
402 variable ratio. The negative interactions would lead to a lower percentage of total variance explained,  
403 but the value is small enough not to invalidate our analysis, and it may be approximated to zero  
404 (Tabachnick and Fidell, 2007). As for positive value of interactions, this percentage of variance cannot  
405 be subtracted to the descriptors selected. Among the selected descriptors for this model, frequency of



406 grassland was selected as a numeric variable, describing 5.24% ( $p < 0.001$ ) of the variance and with a  
407 positive relationship with measured PE.

408 The significant variables explaining the PE-DW variations corresponded to water-soluble organic  
409 matter chemical composition ( $CP3_{(Fluo)}$ ), P availability, microbial biomass, soil pH and land-use  
410 characteristics (grasslands frequency and crop residues). The WEOC amount and clay content were  
411 also significant but explained much smaller part of variance. All the variables had a positive effect on  
412 the PE-DW with the exception of soil microbial biomass and crop residues.

413 In the case of PE/TOC model, despite the high contribution of interactions (16.52%), a large part of  
414 PE variance (53.62%) was explained by a set of only four significant variables with the following  
415 hierarchy: MWD, grassland frequency (selected as land-use categories, not numeric), Biomass/TOC  
416 and bacterial evenness. Among the different explanatory variables, soil microbial biomass promoted  
417 PE/TOC, whereas higher aggregation and bacterial evenness impeded it. The effect of the frequency of  
418 grassland on PE/TOC was land-use dependent, indeed PE/TOC was higher at low and high frequency  
419 of grasslands in comparison to cropland and lower for samples under mid and permanent grassland.

420

## 421 **4. Discussion**

### 422 4.1. Priming effect in a mosaic of land-uses

423 The average  $CO_2$  production attributed to PE for cropped soils ranged between 2 and 3  $mg\ g^{-1}$  TOC, a  
424 value equal to half of the basal respiration of soils for some treatments. Soil is the source for 60-90%  
425 of the total  $CO_2$  fluxes of an ecosystem (Longdoz et al., 2000), and Guenet et al. (2018) showed how  
426 prediction on C sequestration may be halved if PE is integrated into global C models. Yet, the  
427 mechanisms impacting the C balance of PE are still under debate, since they may co-occur at the same  
428 time, vary from site to site, and be land-use dependent (Chen et al., 2014; Kuzyakov et al., 2000;  
429 Razanamalala et al., 2018). In fact, the frequency of grassland in the rotation was selected as a  
430 significant descriptor of PE by both variance partitioning models, implying that susceptibility of  
431 agroecosystems to PE is partially related to the adopted land-use.

432 Introduction of grassland into crop rotations results in changes in type and quantity of litter returned to  
433 the soil, and potentially supports the establishment of more diverse roots-soil interactions modifying

434 soil physical properties and promote the stabilization of roots-derived C (Cambardella and Elliot,  
435 1992; Panettieri et al., 2017). Most of the soils from permanent grassland received no manuring,  
436 aboveground litter was mowed and we could not estimate the quantitative information about  
437 rhizodeposition.

438 The PE-DW model selected the frequency of grassland as a positive descriptor. In the same time, we  
439 found positive correlation of TOC and WEOC amounts, as well as clay content with the frequency of  
440 grassland. Considering these results together, we hypothesized that the higher TOC contents  
441 accumulated under permanent grassland support larger C mineralization fluxes and strongly influence  
442 the PE differences between our land-use classes, as highlighted by the model. This observation  
443 justifies our approach consisting of running a second model after normalization of PE fluxes to TOC  
444 contents in the soil samples.

445 For PE/TOC model, the increase of PE was land-use dependent: a positive relationship was found for  
446 LO and HI, whereas the effect of MI and permanent grassland were negative. These results add key  
447 information to the results for PE-DW model, suggesting that, in our system, PE is triggered by specific  
448 frequencies in the occurrence of grassland within crop rotation cycles.

449 These observations suggest that alternation of cropland and grassland can create favorable conditions  
450 for PE. We observed that short-term conversion of agricultural fields into grassland (LO), or short-  
451 term cultivation of prairies (HI), both resulted in increased values of PE/TOC. The similarity between  
452 these two situations is that the ecosystem functioning under the dominant land-use is destabilized by  
453 the land-use conversion during one to three years per ten years. The mechanisms triggering the PE,  
454 however, are likely to differ between the two situations.

455 If for LO we can hypothesize that frequent tillage and a C-limited environment may change the  
456 composition of microbial communities and create biogeochemical conditions prone to PE. The  
457 conversion to grassland is likely resulting in changes of SOM composition with more belowground  
458 biomass inputs (Jackson et al., 1996) compared to cropland, as well as preservation of organic  
459 compounds entering soils through root exudation or root litter (Panettieri et al., 2017). We think that  
460 these pools of OM may present a different decomposition stage, and be more easily mineralized by  
461 microorganisms than SOM under cropland causing the increased PE under LO land-use (Shahbaz et

462 al., 2018). The low C contents and high N and P availability are both favorable conditions for PE in  
463 these soils (Kuzyakov, 2010).

464 For HI samples, soils are principally devoted to grassland, with higher SOM levels and root inputs.  
465 The occasional ploughing of these soils dominated by grassland use is altering soil structure, as shown  
466 by lower MWD of aggregates and could promote PE compared to permanent grassland. Indeed, the  
467 microbial decomposers in these soils are more likely adapted to the decomposition of SOM made  
468 available by the loss of physical protection after ploughing (Kuzyakov, 2010). However, a further  
469 characterization of the agricultural practices is necessary to understand this result.

470 Interestingly, we did not find any increase in PE/TOC for MI land-use class compared to soil under  
471 permanent cropland or grassland land-uses. While the processes underlying the different responses of  
472 soils under various frequencies of temporary grassland use are hard to demonstrate, MI samples  
473 supports the idea that the frequency of switches between land-uses alter soil susceptibility to PE in a  
474 non-linear way. Increase or decrease with respect to MI frequency resulted in higher PE values. It is  
475 noteworthy that MI soils showed more evenly distributed microbial communities. This result has been  
476 related to a greater adaptation and resilience potential of the soil subjected to “intermediate  
477 perturbation” (Acosta-Martínez et al., 2008; Shange et al., 2012; Tardy et al., 2015).

478

#### 479 4.2. Influence of land-use on the descriptors of PE-DW model

480 The amount of crop litter returned to soil was selected by PE-DW model, showing that a soil with  
481 lower input of labile C represents an energy-limited environment prone to PE when labile C is  
482 occasionally added (Hamer and Marschner, 2005; Razanamalala et al., 2018). Among the  
483 microbiological variables measured, only the quantity of microbial biomass was selected as a predictor  
484 of PE-DW, with a negative relation. Higher content of biomass is normally found in soils of “high  
485 quality” and microbial interactions are more devoted to mineralization of fresh substrates rather than  
486 degradation of physically or chemically protected SOM (Blagodatskaya and Kuzyakov, 2008).

487 Soil pH was selected as a positive descriptor of PE-DW, indicating that among the studied soils, those  
488 with slightly higher pH were more prone to PE. In general, soils with slightly higher pH have higher  
489 biomass, higher respiration rates, and faster degradation of SOM. In a single soil type with a similar

490 pH gradient of our study, Aciego Pietri and Brookes (2009) found that pH and substrate availability  
491 affected the structure of microbial community during the decomposition of wheat straw via the  
492 succession of litter degradation activities assigned to specific microbial groups. For their study, the  
493 increase in soil respiration after straw addition was positively correlated with pH. Taking into account  
494 our results, we can therefore assume that a part of the respiration measured by Aciego Pietri and  
495 Brookes (2009) at higher pH was originated by priming effect. No differences in mean pH were found  
496 between land-use classes (Fig. 3F), suggesting that the pH effect on PE is independent from our  
497 classification.

498 Further interesting results are the positive relations of WEOC, CP3<sub>(fluor)</sub> and clay with PE-DW. For this  
499 study, WEOC per TOC unit increased with frequency of grassland, and is a common early indicator of  
500 changes in SOM chemical and biochemical composition (Bongiorno et al., 2019; Panettieri et al.,  
501 2014) that increases with the amount of microbial biomass and root exudation (Kalbitz et al., 2000).  
502 On one hand, microbial biomass is larger for HI compared to cropland ( $p < 0.05$ , Fig. 4C), and a trend  
503 towards higher values of WEOC at higher frequencies of grassland was detected. On the other hand,  
504 grassland has higher root density than the cereal crops of the study area, especially for surface soils  
505 (Jackson et al., 1996), resulting in larger inputs by rhizodeposition and higher microbial activity (van  
506 Eekeren et al., 2008).

507 The component of WEOC fluorescence CP3<sub>(fluor)</sub> is the variable explaining the largest part of variance  
508 in the PE/DW model. It corresponds to a highly processed form of SOM with a high degree of  
509 aromaticity, therefore not an ideal source of C for microbes (Coble, 1996; Søndergaard et al., 2003).

510 The relative contribution of CP3<sub>(fluor)</sub> decreased with the increase of grassland frequency, indicating  
511 differences in WEOC composition between land-uses. This result may be explained by larger inputs of  
512 fresh and labile organic matter, larger microbial biomass content, and different composition of  
513 microbial communities under grassland, while cropland soils generally receive larger quantities of  
514 exogenous OM, especially swine manure in the study area. Hunt and Ohno (2007) identified CP3<sub>(Fluor)</sub>  
515 as being conserved during biodegradation of swine manure. It should be taken into account that the  
516 measured CP3<sub>(fluor)</sub> represents a group of fluorescent compounds referenced as resistant to microbial  
517 degradation and co-varying with PE-DW. Each fluorophore identified in WEOC and dissolved organic

518 matter is likely accompanied with a consortium of non-fluorescent soluble organic compounds  
519 (Stubbins et al., 2014). Deciphering the high molecular complexity of WEOC, e.g. using high-  
520 resolution mass spectrometry (Guigue et al., 2016; Roth et al., 2014), could allow to investigate  
521 organic molecules (e.g. easily degradable ones, N-rich molecules, or organic acids) directly or  
522 indirectly related to PE fluxes. The positive relation of CP3<sub>(fluor)</sub> with PE-DW may be due to: (i) the  
523 dynamics of co-metabolism of the compounds forming the consortium with CP3<sub>(fluor)</sub> in presence of  
524 fresh litter (Chen et al., 2014), or (ii) to the temporary stabilization of the consortium with CP3<sub>(fluor)</sub> via  
525 adsorption on clay surfaces and short-range order minerals investigated in recent works (Finley et al.,  
526 2018; Keiluweit et al., 2015), most probably a combination of both. This adsorption of highly aromatic  
527 compounds can be reversed by input of organic acids from root exudates, manure (Hamer and  
528 Marschner, 2005), or produced during the degradation of new litter inputs (Blagodatskaya and  
529 Kuzyakov, 2008).

530 The texture of some of the permanent grassland and, to a minor extent, HI samples shifted through a  
531 more clayey texture (Fig. 3E). Since a lower water drainage is often associated with higher clay  
532 contents, rotations with higher frequency of grassland may have been established in higher wetness  
533 areas, to avoid crop losses due to flooding. The positive effect of clay content on PE could be  
534 attributed to an increase of carbon content in these soils.

535 Olsen P explained the second highest percentage of variance of PE-DW model. High frequencies of  
536 grassland were characterized by lower amounts of organic amendment per year and lower available P  
537 contents. In the study area, differences in soil available P contents are attributable mostly to the  
538 spreading of swine manure derived from the widely developed husbandry farms in the area of study  
539 (Matos-Moreira et al. 2017). However, the absence of correlation between Olsen P and PE-DW ( $\rho^2 =$   
540 0.035, p-value 0.7) highlight that the variance explained may be due to intragroup variability and/or by  
541 different P speciation, not investigated in this study. The fact that P is mainly derived from swine  
542 manure and that CP3, the descriptor explaining the higher percentage of variance, was also found in a  
543 swine manure degradation experiment (Hunt and Ohno, 2007) points towards the importance of  
544 manure degradation in PE dynamics, even if further experiments are needed to corroborate these  
545 findings.

546

#### 547 4.3. Influence of land-use on the descriptors of PE/TOC model

548 The selected descriptors for PE/TOC model were MWD, microbial C normalized to TOC and bacterial  
549 evenness. MWD, a proxy of aggregation, represents a physical protection of SOM from degradation.  
550 Thus, the negative relation with PE is easily understandable by the limited access to the protected  
551 SOM (Six et al. 1999). The MWD of the water-stable aggregates increased with frequency of  
552 grassland, thus lower PE is expected at higher frequencies of grassland. Consistent with literature,  
553 temporary and permanent grassland are reported to provide a better protection of aggregates due to  
554 two main factors: (i) a lower number of tillage operations which physically disrupt soil aggregates (Six  
555 et al. 1999; Panettieri et al. 2015) and (ii) a higher contribution of aggregation factors, such as root  
556 exudates and extracellular polymeric substances (Redmile-Gordon et al. 2014) proceeding from a  
557 more extended and dense root network (Tisdall and Oades 1982; Jackson et al. 1996; Six et al. 1998;  
558 Panettieri et al. 2017). However, the higher PE/TOC measured for HI (Fig. 4D) contrasts this  
559 interpretation, suggesting that PE regulation is dependent of other co-occurring factors.

560 The other two descriptors are related with microbial communities. A higher value of microbial  
561 biomass per TOC unit represents the paradigm of a higher microbial growth with higher respiration,  
562 but also a more energy limited environment, in which more microorganisms compete for the SOM  
563 substrate. The PE/TOC model selected this descriptor as a trigger for PE, and the bacterial evenness as  
564 a descriptor with a negative relationship with PE. In a substrate limited environment, competition and  
565 predation may increase, inducing a shift of microbial communities through a less even distribution of  
566 species (Banerjee et al., 2016; Fontaine et al., 2003). This reduce the resilience of the communities and  
567 the capacity of degradation of SOM, limiting the colonization of specific niches and, consequently,  
568 making the soil more prone to PE when fresh energy sources are added during incubation (Chen et al.,  
569 2014; Razanamalala et al., 2018). Bacterial evenness had a positive correlation with two descriptors of  
570 SOM quality ( $CP3_{(fluor)}$  and TOC/TN ratio). SOM with a more complex and diverse chemical structure  
571 promote the development of a higher bacterial evenness and increase the capacity of microbial  
572 communities to degrade substrates (Goldfarb et al., 2011), resulting in a more efficient cycling of the  
573 whole pool of allochthonous fresh-C molecules, rather than triggering PE from autochthonous pools of

574 SOM. The trend to higher microbial biomass per TOC unit at higher frequency of grassland (Fig. 4C)  
575 is consistent with literature for soils under grassland (Baumann et al., 2013; Potthoff et al., 2005),  
576 since a higher microbial activity is found in rhizosphere and grasslands have a denser and  
577 interconnected root architectures, especially for upper soil layers (Jackson et al., 1996; Panettieri et al.,  
578 2017; Rasse et al., 2005; Sparling, 1992).

579 Regarding the composition of soil microbial communities, Le Guillou et al. (2018) conducted a study  
580 on the same area using the theory of intermediate perturbation, or hump-backed curve (Acosta-  
581 Martínez et al., 2008; Shange et al., 2012; Tardy et al., 2015) to relate their metagenomics results with  
582 land-use classes. Maximum bacterial diversity occurs at an optimum of soil perturbation, in which  
583 more diverse species can proliferate. Considering the classification adopted for the present study,  
584 higher values for bacterial richness (Table S1) and evenness (Fig 4E), found for LO and MI  
585 confirming that slight modifications in crop rotation led to slightly but significant modification of  
586 bacterial richness and evenness. This explanation is in line with the fact that MI soils, corresponding to  
587 the ecosystems with the most equal distribution between time under cropland and under grassland,  
588 tend to have a higher evenness  $J'$  index and a lower potential for PE than LO and HI. It suggests that  
589 this frequency of disturbances (tillage and changes in land-use) stimulate the adaptation of microbial  
590 communities that become more resilient and are thus able to sustain ecosystem functions better than in  
591 agroecosystems where lower frequencies of disturbances had a more negative impact regarding SOM  
592 decomposition and PE, i.e. in LO and HI.

593

## 594 **Conclusions**

595 Unveiling the dynamics of priming effect (PE) at landscape scale and on soil samples from real farms  
596 is an extremely complex operation, especially for such study area (5 km<sup>2</sup>) with little heterogeneities in  
597 climate, soil types and agricultural management. Chemical and physical interactions with soil mineral  
598 phases are fundamental parts of the environmental context in which living organisms are developing.  
599 PE represents an indicator of SOM turnover and nutrient cycling, but particular attention must be paid  
600 to high values of PE per TOC unit (PE/TOC), a clear indication that C losses may occur. Targeted  
601 land-uses may help to mitigate PE/TOC or at least reduce the susceptibility of soils to PE/TOC. For

602 the studied area, SOM contents with lower PE potentials are attained for temporary grassland at an  
603 optimum of 40-60% of time devoted to grassland, corresponding to the intermediate frequency in  
604 grassland use (MI), while a change in the frequency of grassland seems to create conditions favorable  
605 to over-mineralization of soil C through PE. The MI frequency also represents a microbiological  
606 *optimum* with higher values of bacterial richness and evenness. Higher frequencies of grassland (HI)  
607 may tend to increase SOM contents, whereas lower frequency may be uninfluential for this purpose,  
608 when compared with permanent cropland. However, HI samples were also intensively prone to PE,  
609 and the newly stored SOM may be unstable in the long-term. Interestingly, a pool of specific water  
610 soluble organic compounds identified by fluorescence analyses was selected among the descriptors for  
611 the susceptibility of soils to PE, highlighting that the composition of soil organic matter in both solid  
612 and dissolved phases are potential indicators of PE dynamics, thus offering new possibilities for future  
613 research aiming to refine prediction models of C cycle.

614

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619

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915

916 **Table 1** Descriptive statistic of environmental parameters for the 88 soil samples from MOSAIC  
 917 project.

Variable	Units	Minimum	1 <sup>st</sup> Quartile	Median	Mean	3 <sup>rd</sup> Quartile	Maximum
<b>Priming Effect DW soil</b> <sup>a</sup>	$\mu\text{g C g}^{-1} \text{ DW soil}$	7.97	48.0	56.5	59.6	66.8	147.5
<b>Priming Effect/TOC</b> <sup>a</sup>	$\text{mg C g}^{-1} \text{ TOC}$	0.24	1.98	2.48	2.50	2.96	4.96
<b>Control Soil CO<sub>2</sub></b> <sup>a</sup>	$\mu\text{g C-CO}_2 \text{ g}^{-1} \text{ DW soil}$	86	128	154	182	191	726
<b>Amended Soil CO<sub>2</sub></b> <sup>a</sup>	$\mu\text{g C-CO}_2 \text{ g}^{-1} \text{ DW soil}$	808	915	969	995	1048	1522
<b>Control Soil CO<sub>2</sub> Norm TOC</b> <sup>a</sup>	$\text{mg C-CO}_2 \text{ g}^{-1} \text{ TOC}$	4.0	5.6	6.7	7.1	8.2	15.7
<b>Amended Soil CO<sub>2</sub> Norm TOC</b> <sup>a</sup>	$\text{mg C-CO}_2 \text{ g}^{-1} \text{ TOC}$	21.9	35.0	41.3	41.8	45.7	78.1
<b>Mineralized litter C<sub>org</sub></b>	$\% \text{ of litter C}_{\text{org}} \text{ added}$	29.5	33.6	34.9	35.5	37.4	42.9
<b>TOC</b>	$\text{mg C g}^{-1} \text{ DW soil}$	13.4	21.0	23.8	25.2	26.0	69.6
<b>TN</b>	$\text{mg N g}^{-1} \text{ DW soil}$	1.6	2.1	2.3	2.5	2.5	6.4
<b>TOC/TN</b>		8.64	9.61	10.1	10.2	10.8	11.6
<b>Soil <math>\delta^{13}\text{C}</math> signature</b>	$\%$	-29.5	-27.0	-26.1	-26.3	-25.3	-24.2
<b>WEOC DW soil</b>	$\text{mg WEOC g}^{-1} \text{ DW soil}$	0.25	0.41	0.48	0.52	0.53	1.60
<b>WEOC/TOC</b>	$\text{mg WEOC g}^{-1} \text{ TOC}$	8.1	18.3	20.4	20.9	22.1	36.9
<b>WEOC <math>\delta^{13}\text{C}</math> signature</b>	$\%$	-29.9	-26.0	-25.2	-25.2	-23.8	-22.7
<b>SUVA</b>	$\text{l mg C}^{-1} \text{ m}^{-1}$	0.013	0.021	0.023	0.023	0.025	0.045
<b>Fluo CP1</b>	$\text{RU mg}^{-1} \text{ WEOC}$	0.93	1.62	1.84	1.91	2.18	3.22
<b>Fluo CP2</b>	$\text{RU mg}^{-1} \text{ WEOC}$	0.73	1.22	1.42	1.50	1.77	2.68
<b>Fluo CP3</b>	$\text{RU mg}^{-1} \text{ WEOC}$	0.26	0.51	0.58	0.57	0.64	0.91
<b>Microbial biomass DW soil</b>	$\text{mg DNA g}^{-1} \text{ DW Soil}$	13.3	35.7	51.4	58.1	71.4	251.7
<b>Microbial biomass/TOC</b>	$\text{mg DNA g}^{-1} \text{ TOC}$	0.56	1.46	2.21	2.32	2.83	6.055
<b>Richness_b</b>	<i>Number of OTUs</i>	573	730	754	755	786	853
<b>Evenness_b</b>	<i>J' Index</i>	0.80	0.86	0.86	0.86	0.88	0.89
<b>Richness_f</b>	<i>Number of OTUs</i>	235	419	462	473	527	742
<b>Evenness_f</b>	<i>J' Index</i>	0.55	0.64	0.67	0.66	0.69	0.74
<b>MWD</b>	<i>mm</i>	0.51	1.20	1.73	1.83	2.33	3.37
<b>Bulk Density</b>	$\text{g cm}^{-3}$	0.52	1.05	1.14	1.148	1.26	1.53
<b>Clay</b>	$\text{mg g}^{-1} \text{ soil}$	135	165	172	178	181	356
<b>Silt</b>	$\text{mg g}^{-1} \text{ soil}$	511	643	673	668	702	744
<b>Sand</b>	$\text{mg g}^{-1} \text{ soil}$	77	128	148	154	173	255
<b>Altitude</b>	<i>M</i>	80.7	113.0	123.4	121.1	131.5	137.6
<b>Hydromorphy</b>		0	0	0	0.24	0	1.00
<b>Beven's Index</b>		2.10	3.20	3.80	4.10	4.30	17.0
<b>Soil pH</b>		4.80	5.82	6.04	6.02	6.25	7.23
<b>Olsen P</b>	$\text{mg g}^{-1} \text{ soil}$	0.02	0.16	0.14	0.15	0.195	0.33
<b>Cu</b>	$\text{mg kg}^{-1} \text{ soil}$	1.15	3.51	4.92	5.48	7.33	14.30
<b>Si</b>	$\text{mg kg}^{-1} \text{ soil}$	0.03	0.04	0.05	0.05	0.06	0.09
<b>Al</b>	$\text{mg kg}^{-1} \text{ soil}$	0.16	0.25	0.30	0.31	0.37	0.49
<b>Fe</b>	$\text{mg kg}^{-1} \text{ soil}$	0.34	0.47	0.50	0.54	0.58	1.31
<b>Grassland Frequency</b>		0	0	0.10	0.28	0.60	1.00
<b>No. cropped species</b> <sup>b</sup>		1.00	3.00	3.00	3.61	4.25	8.00
<b>Crop Litter</b>	$\text{Mg C ha}^{-1} \text{ y}^{-1}$	0	2.71	3.16	3.15	4.18	4.83
<b>Manure</b>	$\text{Mg C ha}^{-1} \text{ y}^{-1}$	0	0.34	0.61	0.63	0.88	1.78

918 <sup>a</sup> Cumulative values obtained after 80 days of soil incubation in microcosms

919 <sup>b</sup> For permanent grassland, number of cropped species was assumed to be 1, not taking into account species  
 920 diversity within prairie.

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923 **Figure Captions**

924 **Figure 1** Representation of WEOM fluorescence PARAFAC components in excitation-emission  
925 matrices. All components were previously described as humic-like components in the literature and  
926 identified in soil DOM, as well as in natural waters. (see the text for details)

927

928 **Figure 2** Correlation heatmap of Spearman's correlation of all measured parameters. Size and color of  
929 the circles are proportional to the  $r_s$  coefficient of correlation

930

931 **Figure 3** Box and whisker plots of the chemical and edaphological parameters of sampled soils.  
932 Cropland (n=42); LO: low frequency grassland (n=13); MI: mid-frequency grassland (n=13); HI:  
933 high-frequency grassland (n=13); Permanent Grassland (n=7). Treatments with identified by different  
934 letters are significantly different. Capital letters are used to highlight significance levels satisfying  
935 Bonferroni's correction ( $p < 0.005$ ). Lowercase letters indicate significance levels at  $p < 0.05$ . Circles  
936 represent outliers

937

938 **Figure 4** Box and whisker plots of the priming effect and biological parameters of sampled soils.  
939 Cropland (n=42); LO: low frequency grassland (n=13); MI: mid-frequency grassland (n=13); HI:  
940 high-frequency grassland (n=13); Permanent Grassland (n=7). Treatments with identified by different  
941 letters are significantly different. Capital letters are used to highlight significance levels satisfying  
942 Bonferroni's correction ( $p < 0.005$ ). Lowercase letters indicate significance levels at  $p < 0.05$ . Circles  
943 represent outliers

944

945 **Figure 5** Outputs of the two variance partitioning models for (i) priming effect per g of soil (PE-DW)  
946 and (ii) priming effect per g of TOC (PE/TOC). HI: high-frequency grassland; MI: mid-frequency  
947 grassland; LO: low-frequency grassland. Significance levels: \*\*  $p < 0.001$ , \*  $p < 0.05$ , °  $p < 0.1$ . (+)  
948 and (-) represent positive or negative coefficients of relation between modeled variables and  
949 descriptors.

950 df: degrees of freedom.

951 ‡ :variance assigned to interactions for Priming Effect/DW soil model had a negative value of -6.33%,

952 see text for more details

**Table 1** Descriptive statistic of environmental parameters for the 88 soil samples from MOSAIC project

Variable	Units	Minimum	1 <sup>st</sup> Quartile	Median	Mean	3 <sup>rd</sup> Quartile	Maximum
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<b>Amended Soil CO<sub>2</sub></b> <sup>a</sup>	$\mu\text{g C-CO}_2 \text{ g}^{-1}$ DW soil	808	915	969	995	1048	1522
<b>Control Soil CO<sub>2</sub> Norm TOC</b> <sup>a</sup>	$\text{mg C-CO}_2 \text{ g}^{-1}$ TOC	4.0	5.6	6.7	7.1	8.2	15.7
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<b>Mineralized litter C<sub>org</sub></b>	% of litter C <sub>org</sub> added	29.5	33.6	34.9	35.5	37.4	42.9
<b>TOC</b>	$\text{mg C g}^{-1}$ DW soil	13.4	21.0	23.8	25.2	26.0	69.6
<b>TN</b>	$\text{mg N g}^{-1}$ DW soil	1.6	2.1	2.3	2.5	2.5	6.4
<b>TOC/TN</b>		8.64	9.61	10.1	10.2	10.8	11.6
<b>Soil <math>\delta^{13}\text{C}</math> signature</b>	‰	-29.5	-27.0	-26.1	-26.3	-25.3	-24.2
<b>WEOC DW soil</b>	$\text{mg WEOC g}^{-1}$ DW soil	0.25	0.41	0.48	0.52	0.53	1.60
<b>WEOC/TOC</b>	$\text{mg WEOC g}^{-1}$ TOC	8.1	18.3	20.4	20.9	22.1	36.9
<b>WEOC <math>\delta^{13}\text{C}</math> signature</b>	‰	-29.9	-26.0	-25.2	-25.2	-23.8	-22.7
<b>SUVA</b>	$\text{l mg C}^{-1} \text{ m}^{-1}$	0.013	0.021	0.023	0.023	0.025	0.045
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<b>Evenness_f</b>	J' Index	0.55	0.64	0.67	0.66	0.69	0.74
<b>MWD</b>	mm	0.51	1.20	1.73	1.83	2.33	3.37
<b>Bulk Density</b>	$\text{g cm}^{-3}$	0.52	1.05	1.14	1.148	1.26	1.53
<b>Clay</b>	$\text{mg g}^{-1}$ soil	135	165	172	178	181	356
<b>Silt</b>	$\text{mg g}^{-1}$ soil	511	643	673	668	702	744
<b>Sand</b>	$\text{mg g}^{-1}$ soil	77	128	148	154	173	255
<b>Altitude</b>	M	80.7	113.0	123.4	121.1	131.5	137.6
<b>Hydromorphy</b>		0	0	0	0.24	0	1.00
<b>Beven's Index</b>		2.10	3.20	3.80	4.10	4.30	17.0
<b>Soil pH</b>		4.80	5.82	6.04	6.02	6.25	7.23
<b>Olsen P</b>	$\text{mg g}^{-1}$ soil	0.02	0.16	0.14	0.15	0.195	0.33
<b>Cu</b>	$\text{mg kg}^{-1}$ soil	1.15	3.51	4.92	5.48	7.33	14.30
<b>Si</b>	$\text{mg kg}^{-1}$ soil	0.03	0.04	0.05	0.05	0.06	0.09
<b>Al</b>	$\text{mg kg}^{-1}$ soil	0.16	0.25	0.30	0.31	0.37	0.49
<b>Fe</b>	$\text{mg kg}^{-1}$ soil	0.34	0.47	0.50	0.54	0.58	1.31
<b>Grassland Frequency</b>		0	0	0.10	0.28	0.60	1.00
<b>No. cropped species</b> <sup>b</sup>		1.00	3.00	3.00	3.61	4.25	8.00
<b>Crop Litter</b>	$\text{Mg C ha}^{-1} \text{ y}^{-1}$	0	2.71	3.16	3.15	4.18	4.83
<b>Manure</b>	$\text{Mg C ha}^{-1} \text{ y}^{-1}$	0	0.34	0.61	0.63	0.88	1.78

<sup>a</sup> Cumulative values obtained after 80 days of soil incubation in microcosms<sup>b</sup> For permanent grassland, number of cropped species was assumed to be 1, not taking into account species diversity within prairie.

**Table S1** Means and standard deviations of the measured parameters not selected as PE descriptors for each land-use

Variables	Units	Cropland		LO		MI		HI		Permanent Grassland	
		Mean	Std. deviation	Mean	Std. deviation	Mean	Std. deviation	Mean	Std. deviation	Mean	Std. deviation
TN	mg N g <sup>-1</sup> DW soil	2.238 <b>a</b>	0.272	2.115 <b>a</b>	0.321	2.369 <b>a</b>	0.170	2.485 <b>a</b>	0.555	4.600 <b>b</b>	1.130
TOC/TN		10.2	0.7	10.2	0.8	10.1	0.6	10.1	0.5	10.2	0.8
Soil δ <sup>13</sup> C signature	‰	-25.68	0.78	-25.44	0.60	-26.71	0.70	-27.42	0.68	-28.78	0.63
SUVA	l mg C <sup>-1</sup> m <sup>-1</sup>	2.269	0.242	2.631	0.750	2.285	0.316	2.262	0.491	2.129	0.718
WEOC δ <sup>13</sup> C signature	‰	-24.44	1.01	-24.04	0.84	-25.70	0.91	-26.76	0.73	-27.65	2.08
CP1 <sub>(fluor)</sub>	RU mg <sup>-1</sup> WEOC	1.868	0.328	2.106	0.498	1.832	0.359	2.024	0.592	1.683	0.590
CP2 <sub>(fluor)</sub>	RU mg <sup>-1</sup> WEOC	1.480	0.295	1.632	0.447	1.420	0.343	1.574	0.565	1.374	0.485
Richness_b	Number of OTUs	757 <b>A</b>	38	773 <b>AB</b>	25	770 <b>AB</b>	36	742 <b>AB</b>	48	697 <b>A</b>	68
Richness_f	Number of OTUs	451 <b>a</b>	90	457 <b>ab</b>	63	508 <b>b</b>	91	494 <b>ab</b>	79	527 <b>ab</b>	107
Evenness_f	J' Index	0.654 <b>A</b>	0.035	0.648 <b>A</b>	0.025	0.670 <b>AB</b>	0.030	0.697 <b>B</b>	0.023	0.693 <b>B</b>	0.025
Silt	g kg <sup>-1</sup> soil	679.0 <b>B</b>	32.1	667.3 <b>B</b>	56.8	676.1 <b>B</b>	14.7	669.7 <b>B</b>	60.5	583.7 <b>A</b>	37.8
Sand	g kg <sup>-1</sup> soil	148.9	29.1	164.4	46.3	152.2	13.8	144.4	32.2	181.6	66.4
Bulk Density	g cm <sup>-3</sup>	1.122	0.179	1.212	0.127	1.108	0.165	1.234	0.161	1.101	0.197
Si	mg kg <sup>-1</sup> soil	0.502	0.100	0.538	0.171	0.438	0.087	0.431	0.085	0.443	0.113
Al	mg kg <sup>-1</sup> soil	3.29	0.75	3.20	0.69	2.95	0.74	2.66	0.62	2.71	0.69
Fe	mg kg <sup>-1</sup> soil	5.29	1.03	5.28	0.70	5.05	1.05	5.16	0.59	7.37	3.42
Cu	mg kg <sup>-1</sup> soil	5.88	3.06	5.34	1.69	5.45	2.64	5.14	3.02	4.02	2.90
Altitude	m	122.1 <b>AB</b>	9.9	116.9 <b>AB</b>	9.8	125.0 <b>AB</b>	8.0	127.4 <b>B</b>	8.3	103.8 <b>A</b>	21.1
Beven's index		4.21	2.36	4.01	0.73	4.11	1.44	3.62	0.78	4.86	2.94
Manure	Mg C ha <sup>-1</sup> y <sup>-1</sup>	0.725 <b>B</b>	0.330	0.513 <b>AB</b>	0.286	0.785 <b>B</b>	0.387	0.585 <b>AB</b>	0.176	0.136 <b>A</b>	0.269
No. cropped species*		3.86 <b>B</b>	1.07	4.46 <b>B</b>	1.85	3.92 <b>B</b>	0.49	2.92 <b>AB</b>	0.64	1.00 <b>A</b>	

Significant differences at  $p < 0.05$  are marked with different lowercase letters. Significant differences at  $p < 0.005$  are marked with different capital letters.

LO: low-frequency grassland; MI: mid-frequency grassland; HI: high-frequency grassland;

\*For permanent grassland, number of cropped species was assumed to be 1, not taking into account species diversity within prairie.

Figure 1

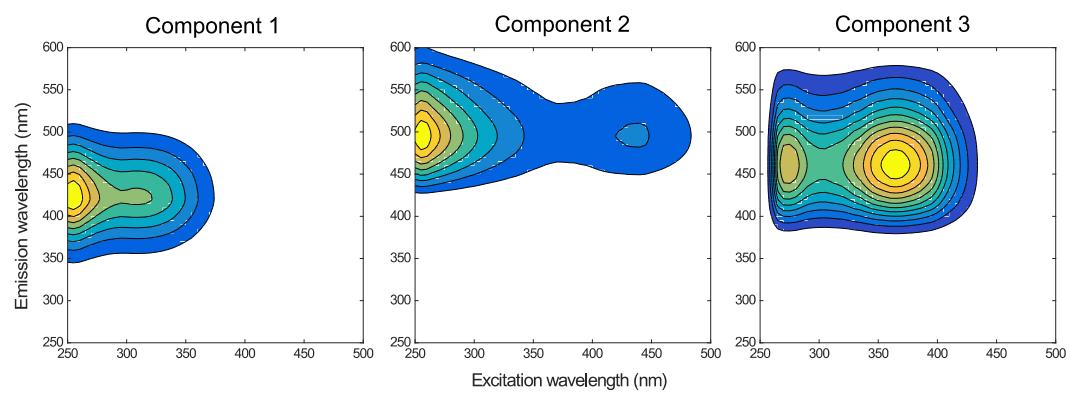
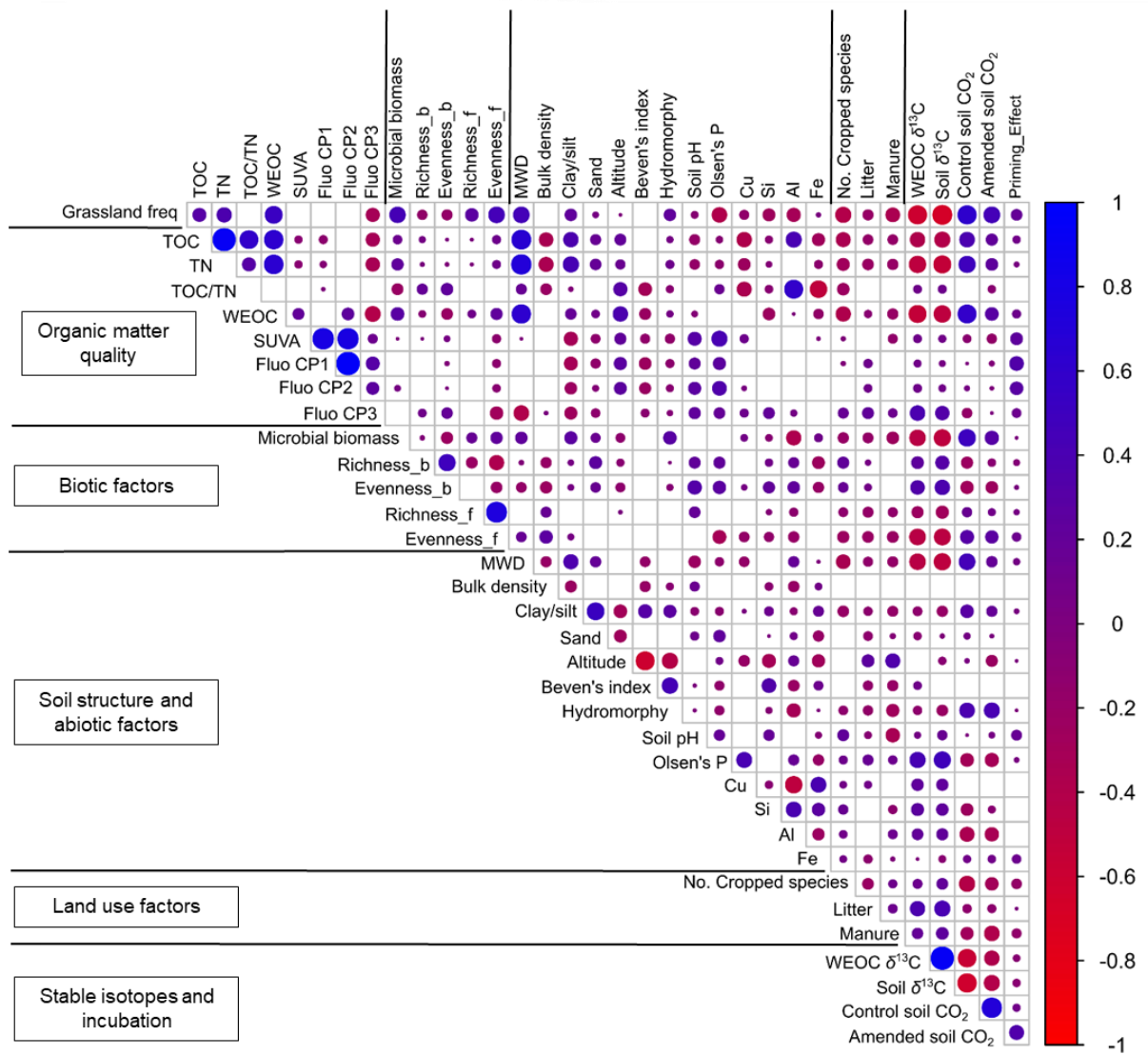


Figure 2

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Figure 2



**Figure 3**  
[Click here to download Figure: Figure 3REV\\_d.pdf](#)

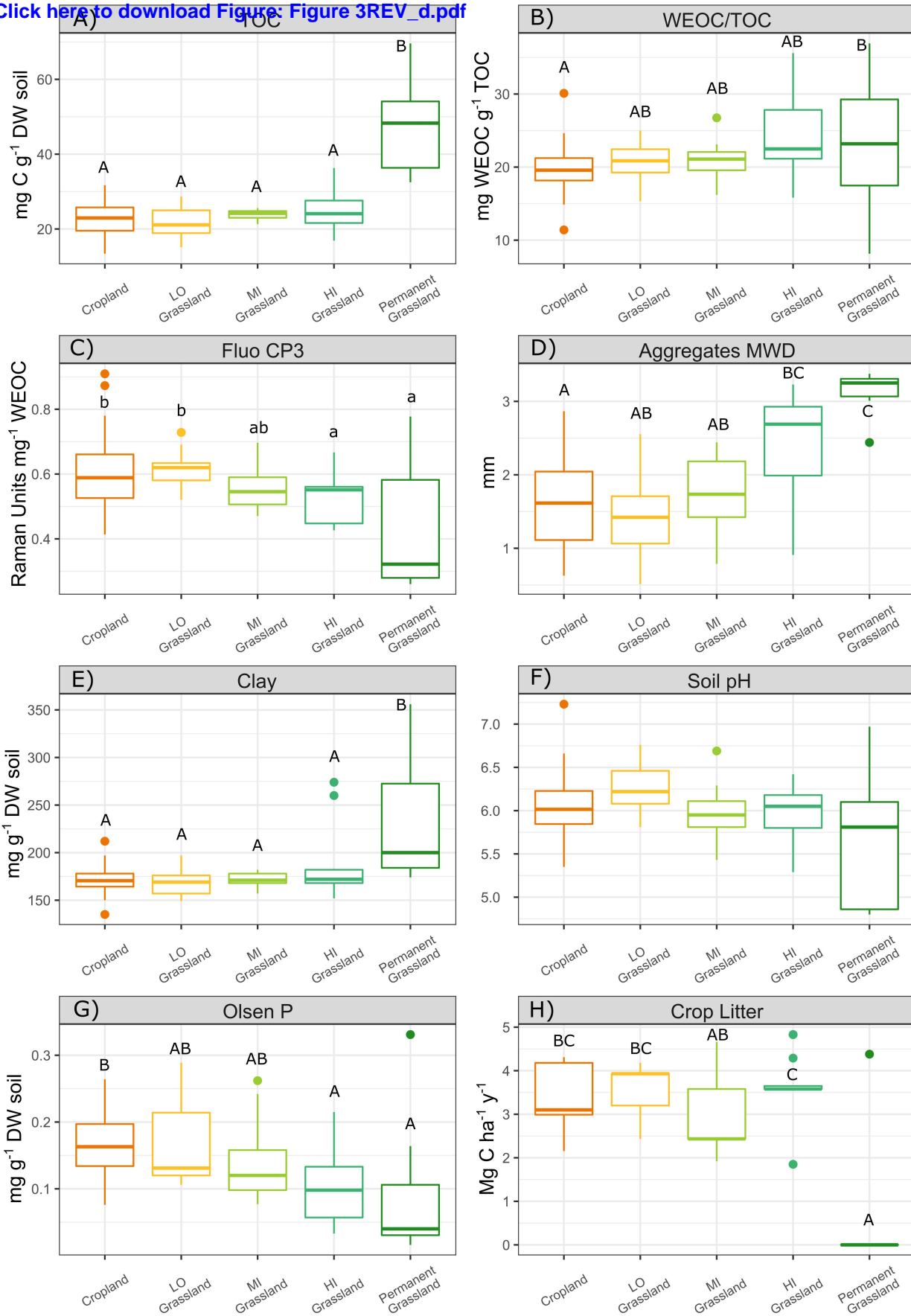


Figure 4

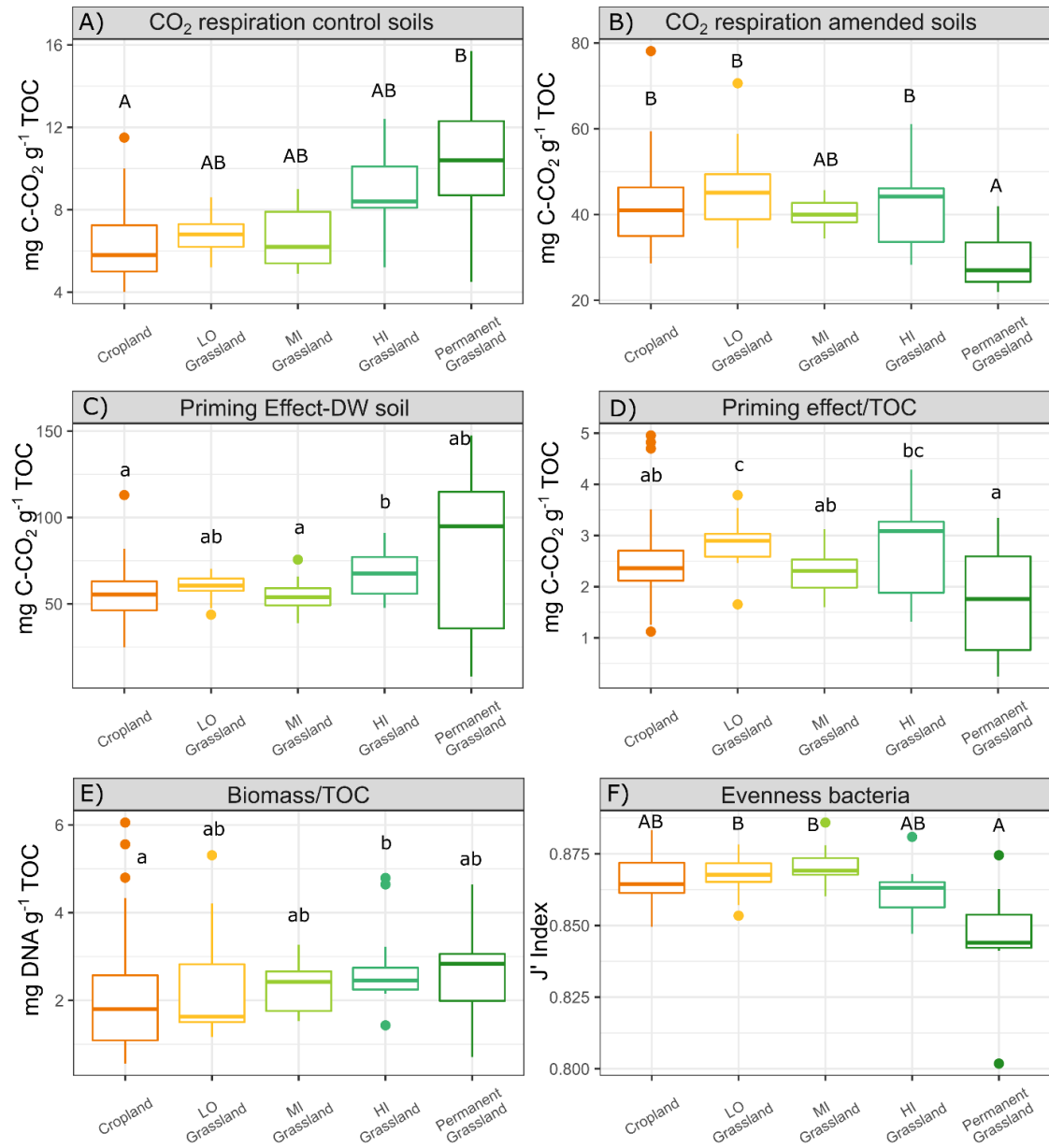




Figure 5

