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Microbial communities from different soil types respond differently to organic waste input

Sophie Sadet-Bourgeteau[a,b,*], Sabine Houot[c], Battle Karimi[a], Olivier Mathieu[d], Vincent Mercier[c], Denis Montenach[e], Thierry Morvan[f], Valérie Sappin-Didier[g], Françoise Watteau[h], Virginie Nowak[a], Samuel Dequiedt[a], Pierre-Alain Maron[a]

[a]INRA, UMR01347, Agroécologie, Dijon, France

[b]AgroSup Dijon, Dijon, France

[c]INRA, UMR1402, Écologie fonctionnelle et écotoxicologie des agroécosystèmes, Thiverval-Grignon, France

[d]CNRS, UMR 6282 Biogéosciences, Dijon, France

[e]INRA, UE 0871 Service d'expérimentation Agronomique et Viticole, Colmar, France

[f]INRA, UMR1069, Sol Agro et hydrosystème Spatialisation, Rennes, France

[g]INRA, UMR 1391, Interaction Sol Plante Atmosphère, Villenave d'Ornon, France

[h]Laboratoire Sols et Environnement, Université de Lorraine, INRA, Nancy, France

*Corresponding Author:

E-mail address: sophie.bourgeteau-sadet@agrosupdijon.fr

Permanent Postal address : Sophie Sadet-Bourgeteau, INRA, UMR 1347 Agroecologie, 17 rue de Sully, 21000 Dijon

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Abstract

Using organic waste products (OWP) in agriculture has been reported to impact both the activity and composition of soil microbial communities. However, little information is available on how the response of a soil microbial community to a given OWP may depend on the physicochemical and microbial properties of the soil receiving the input. Here, we performed a microcosm experiment to compare the effect of 2 different OWPs (GWS: co-compost of Green Wastes and Sewage sludge or FYM: FarmYard Manure), each applied to 5 different soils, on the activity, abundance and diversity of the soil microbial communities. Soils were selected to represent a range of physicochemical and climatic characteristics. CO_2 and N_2O emissions, microbial biomass and taxonomic diversity were monitored for 28 days following OWP input. The five soils presented different prokaryotic and fungal communities structures before OWP application. During the 28 days of incubation, those control soils (without OWP) harboring the highest organic matter contents released the greatest CO_2 and N_2O emissions, and had the highest soil microbial biomass. The impact of organic amendments on soil activity and microbial diversity differed with the nature of the OWP. FYM application increased CO_2 emissions 2-fold and delayed N_2O emissions compared to GWS. Major changes in prokaryotic genetic structures were also observed when GWS was applied. The effect of OWPs was dependent on soil type and the five soils exhibited distinct patterns of CO_2 and N_2O emission after a given input. This accorded with the fact that the structure and composition of the microbial communities harbored by each soil type responded differently to a given OWP application. To conclude, our results show that different soil types, harboring distinct microbial community structures, responded differently to OWP application, leading to different patterns and rates of greenhouse gas emissions. This response was also OWP-dependent.

Keywords: soil microbes; soils incubation; CO_2; N_2O; high throughput sequencing approach.

1. Introduction

Organic waste products (OWP) resulting from human activities (*e.g.,* sewage sludge, municipal solid waste composts or farmyard manure) are being increasingly applied to soils because they facilitate the recycling of nutrients and improve soil fertility. Indeed, organic amendment is known to enhance (i) physical soil fertility by improving soil porosity, aggregation and structure stability, bulk density and water holding capacity (Abiven et al., 2009; Annabi et al., 2011; Eden et al., 2017) and (ii) chemical fertility through pH regulation, as well as increased CEC and availability of nutrients (Diacono and Montemurro, 2010; Chalhoub et al., 2013). Organic amendment also improves the biological components of soil, especially the soil microbial communities. Application of organic materials led to an increase of soil microbial biomass (Ros et al., 2006; Chaudhry et al., 2012; Francioli et al., 2016) and changes in prokaryotic and fungal community structures (Ros et al., 2006; Chaudhry et al., 2012; Francioli et al., 2016; Sadet-Bourgeteau et al., 2018). The effect of OWP on soil microbial communities may depend on: (i) the duration of repeated OWP application, (ii) the rate of OWP applied, (iii) the delay between OWP application and soil sampling, (iv) the quality of the different OWP applied and (v) the soil type (Pérez-Piqueres et al., 2006; Sadet-Bourgeteau et al., 2018). In parallel to these microbial changes, several incubation studies revealed an increase of CO_2, N_2O and CH_4 emissions (Saison et al., 2006; Pezzolla et al., 2013; Pezzolla et al., 2015; Ho et al., 2017). Thus, the use of organic materials on agricultural soils may also have unwanted side effects, such as increased greenhouse gas (GHG) production.

Soil microorganisms (prokaryote and fungi) are key actors in ecosystem processes (Wagg et al., 2014; Werling et al., 2014). Changes in the microbial community and biotic interactions may therefore affect the processes mediated by soil microbes, with consequences on GHG emission. In order to maximize the benefits of OWP by reducing soil GHG emissions, it is therefore important to better characterize the impact of amendments on soil microbial

community composition and activity. Most studies have focused on the importance of the quality of the applied OWP and very few have taken the importance of soil type into consideration. However, soil type is the main driver of soil microbial abundance and diversity (Dequiedt et al., 2011; Thomson et al., 2015).

Ho et al. (2017) and Pezzolla et al. (2013) investigated the impact of different organic materials on several soil types and GHG emission in laboratory incubation experiments. Pezzolla et al. (2013) assessed the effect of OWPs on soil microbial community response by using Phospholipid Fatty Acid Analysis (PLFA) analysis, and CO_2 emission only. Ho et al. (2017) targeted the soil bacterial community using high throughout sequencing techniques (16S rRNA gene), and measured both CO_2 and N_2O emissions. According to these authors, the CO_2 and N_2O emission patterns and rates were amendment-dependent even though the soils possessed different physicochemical parameters, textures and bacterial community compositions and structures. To our knowledge, these two studies are the only ones to have examined the impact of different organic materials on several soil types and GHG emission in the same experiment. However, only two different soil types were assessed, and different methodological tools (PLFA *vs* 16S rRNA gene Ion Torrent amplicon sequencing) were used in each study which makes general conclusions difficult.

The objective of the present study was to assess the effect of the application of different types of organic material on five different soil microbial communities. Based on previous studies, we hypothesized that whatever the soil microbial community considered, the respond was amendment dependent. This work was performed using a laboratory microcosm experiment involving the application of two different types of organic amendments to five soils each containing different microbial communities. The soils were sampled from five field sites representing contrasted pedo-climatic conditions (especially soil type and climate). The sampled plots had never received any organic amendments. The organic amendments applied to the microcosms differed mainly in their organic matter content and stability. One of the

100 novel point of this work was to assess in the same experiment the responses of prokaryotic
101 and fungal communities to these organic amendments by a high throughput sequencing
102 approach respectively targeting the 16S and 18S ribosomal genes. This approach is
103 appropriate to characterize the vast microbial diversity of soil and monitor microbial
104 communities' composition changes after amendment. Soil CO_2 and N_2O emission were also
105 measured in parallel.

106

107 **2. Materials and methods**

108 *2.1. Soils and Organic waste products*

109 The soil samples used in this experiment were collected in March 2015 from the
110 ploughed horizon (0-20 cm) of five french long-term observatories belonging to the SOERE-
111 PRO-network (http://www6.inra.fr/valor-pro/SOERE-PRO-Presentation-de-l-
112 observatoire/SOERE-PRO-Les-sites): QualiAgro (Qa; at Feucherolles), PROspective (Co; at
113 Colmar), Efele (Ef; at Rennes), Couhins (Ch; at Bordeaux) and La Bouzule (LB; at Nancy).
114 Choice of using these sites were to characterize the agronomic value of regular organic
115 residue application and their environmental impacts, in a long-term field experiments. The
116 main soils properties are given in Table 1.

117 For each observatory, a composite soil sample was made from a pool of five sub-samples
118 (Ø 7 cm) in the diagonal section of plots that never received organic waste products. Samples
119 were then mixed and homogenized by passing them through a 4 mm sieve to remove above-
120 ground plant debris, roots and stones. A portion of each soil was air-dried at room
121 temperature for physico-chemical analysis. Particle size distribution, pH, soil organic matter,
122 soil organic carbon, soil total nitrogen (N), soil C/N ratio, Olsen P and Cation Exchange
123 Capacity (CEC), were determined by the Soil Analysis Laboratory at INRA Arras, France
124 (http://www.lille.inra.fr/las; Table 1). The rest of the sieved soils, was used for incubation.

125 The organic amendments used in the experiment included a farmyard manure (FYM) and
126 a compost issued from the co-composting of green wastes with sewage sludge (GWS). pH,
127 organic carbon, phosphorus and total N contents were determined for each of these two
128 organic waste products (OWP). Before analysis, the organic amendments were dried and
129 ground to 1 mm. The total N and organic C contents were measured by elemental analysis
130 (NA 1500, Fison Instrument, San Carlos, CA, USA) after additional grinding to 200 µm
131 (Retsch SM 2000, Haan, Germany). The mean OWP characteristics measured are represented
132 in Table 2. The index of residual organic carbon (I_{ROC}) that represents the proportion of
133 organic matter potentially incorporated into soil organic matter after OWP application
134 (Lashermes et al., 2009) was also determined (Table 2).

135

136 *2.2. Microcosms set up and Incubation*

137 The experimental design consisted of a factorial arrangement with five soils (Qa, Co, Ef,
138 Ch and LB), two amendments (a farmyard manure (FYM) and a co-compost of sewage
139 sludge, green wastes and wood chips (GWS)) plus unamended control for each soil (CON).
140 For each treatment, a series of 9 sterile plasma flasks (150 mL) were filled with 30 g of dried
141 and sieved soil to allow for 3 destructive samplings at 0 (d0), 7 (d7) and 28 (d28) days of
142 incubation. These microcosms were supplemented with sterile water to attain 60 % soil water-
143 holding capacity. After 2 weeks of pre-incubation (20°C), FYM or GWS were thoroughly
144 mixed with soil samples in their dry form (5 and 6.9 mg g^{-1} of soil respectively). The
145 sampling time d0 was considered immediately after amendment. The rest of plasma flasks
146 were then incubated for 7 and 28 days in the dark at 20°C and always 60 % water-holding
147 capacity to ensure good biomass activation. Every week, plasma flasks were aerated by
148 flushing with air and at the same time, the water content was adjusted to correct for any soil
149 moisture lost through evaporation. At d0, d7 and d28, for each treatment, soil from
150 corresponding plasma flasks were sacrificed for molecular analyses. After sampling, each

151 sample was lyophilized and stored at -40 °C until use for molecular analyses based on soil
152 DNA extraction.

153

154 *2.3. CO2 and N2O emissions*

155 At 0, 3, 7, 14, 21 and 28 days of incubation, the gaseous phase was sampled in 10 mL
156 pre-vacuumed airtight flasks exetainers, to measure the CO_2 and N_2O concentrations using an
157 Agilent 7890B GC coupled to an automatic sampler (Agilent HS7697A Headspace). The
158 concentrations were measured on a thermal conductivity detector for CO_2 and on a plasma
159 emission detector (LDetek) for N_2O. The GC system was calibrated using multipoint CO_2 and
160 N_2O gas standards prepared by a GasMix (Alytech, France). Since the microcosms were
161 hermetically-sealed and aerated by flushing with air at each sampling date, the concentrations
162 measured corresponded to the CO_2 and N_2O accumulated in the microcosm headspace
163 between two sampling dates.

164

165 *2.4. DNA Extraction and purification*

166 Microbial DNA was extracted from 1 g (dry weight) of soil from the 135 microcosms,
167 GWS (n=3) or FYM (n=3), using a single procedure standardized by the GenoSol platform
168 (INRA, Dijon, France, www.dijon.inra.fr/plateforme_genosol) (Terrat et al., 2012). Since a
169 highly positive linear relationship has been shown between soil DNA recovery and C-biomass
170 measurement (Marstorp et al., 2000; Dequiedt et al., 2011), DNA concentrations of crude
171 extracts were determined by electrophoresis in 1% agarose gel stained with ethidium bromide
172 using a calf thymus DNA standard curve, and used as estimates of microbial biomass
173 (Dequiedt et al., 2011). After quantification, nucleic acids were separated from the residual
174 impurities, particularly humic substances, by centrifuging through two types of minicolumn.
175 Aliquots (100 µL) of crude DNA extract were first loaded onto polyvinyl polypyrrolidone

minicolumns (BIORAD, Marne-la-Coquette, France) and centrifuged at 1000 × g for 4 min at 10 °C. The eluates were then purified using the Geneclean turbo kit (Mp Biomedicals, Illkirch, France) (Ranjard et al., 2003). Purified DNA concentrations were finally measured using the Quantifluor (Promega, Lyon, France) staining kit, according to the manufacturer's instructions.

2.5. High throughput sequencing of 16S and 18S rRNA gene

For prokaryotic (bacterial-archaeal) diversity, a 440-base 16S rRNA gene fragment was amplified from each DNA sample with the following primers: F479 (5'-CAG CMG CYG CNG TAA NAC-3') and R888 (5'-CCG YCA ATT CMT TTR AGT-3') as previously described (Tardy et al., 2014). For each sample, 5 ng of DNA were used for a 25 µL PCR conducted under the following conditions: 94 °C for 2 min, 35 cycles of 30 s at 94 °C, 52 °C for 30 s and 72 °C for 1 min, followed by 7 min at 72 °C.

For fungal diversity, a 350-base 18S rRNA gene fragment was amplified from each DNA sample with the following primers: FF390 (5'-CGA TAA CGA ACG AGA CCT-3') and FR1 (5'-ANC CAT TCA ATC GGT ANT-3') (Chemidlin Prévost-Bouré et al., 2011). For each sample, 5 ng of DNA were used for a 25 µL PCR conducted under the following conditions: 94 °C for 3 min, 35 cycles of 30 s at 94 °C, 52 °C for 1 min and 72 °C for 1 min, followed by 5 min at 72 °C. Prokaryotic and fungal PCR products were purified using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano) and quantified with the Quantifluor (Promega, Lyon, France) staining kit according to the manufacturer's instructions.

A second PCR was performed with the purified PCR products (7.5 ng of DNA for bacteria and archaea, and 5 ng of DNA for fungi), with 10-bp multiplex identifiers added to the 5′ end of the primers for the specific identification of each sample and the prevention of PCR biases. For bacteria and archaea, the second PCR conditions were the same as previously

described but with only seven cycles. For fungi, the second PCR conditions were optimized, with the number of cycles being reduced to seven and the denaturation step processed at 94 °C during 1 min. PCR products were purified with the MinElute PCR purification kit (Qiagen NV) and quantified with the Quantifluor (Promega, Lyon, France) staining kit according to the manufacturer's instructions. Equal amounts of each sample were pooled and then cleaned with the SPRI (Solid Phase Reverse Immobilization Method) using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano). The pooled samples was finally sequenced with a MiSeq Illumina instrument (Illumina Inc, San Diego, CA) operating with V3 chemistry and producing 250 bp paired-reads.

2.6. Bioinformatic analysis of 16S and 18S rRNA gene sequences

Bioinformatic analyses were done using the GnS-PIPE, which was initially developed by the Genosol platform (INRA, Dijon, France) (Terrat et al., 2012). Data from soils and OWP were treated independently. First, all the 16S and 18S raw reads were sorted according to the multiplex identifier sequences. The raw reads were then filtered and deleted based on their length, their number of ambiguities (Ns), and their primer(s) sequence(s). More precisely, all raw sequences were checked and discarded if: (i) they contained any ambiguous base (Ns), (ii) if their length was less than 350 nucleotides for 16S reads or 300 nucleotides for 18S reads, (iii) if the exact primer sequences were not found (for the distal primer, the sequence can be shorter than the complete primer sequence, but without ambiguities). A PERL program was then applied for rigorous dereplication (i.e. clustering of strictly identical sequences). The dereplicated reads were then aligned using Infernal alignment (Cole et al., 2009), and clustered into operational taxonomic units (OTU) using a PERL program that groups rare reads to abundant ones, and does not count differences in homopolymer lengths with a threshold of 95% of sequence similarity. A filtering step was then carried out to check all singleton (reads detected only once and not clustered, which might be artifacts, such as PCR

chimeras) based on the quality of their taxonomic assignments. Finally, in order to compare the datasets efficiently and avoid biased community comparisons, the reads retained were homogenized by random selection (soils: 9 600 and 8 420 reads for 16S and 18S rRNA gene sequences, respectively; Organic Waste Products (OWP): 5 080 and 8 420 reads for 16S and 18S rRNA gene sequences, respectively).

The retained high-quality reads were used for: (*i*) taxonomy-independent analyses, determining several biodiversity indexes (Shannon, richness and evenness) using the OTU dataset and defining global OTU matrices, and (*ii*) taxonomy-based analysis using similarity approaches against dedicated reference databases from SILVA (Quast et al., 2012). The raw data sets are available in the EBI database system under project accession number PRJEB31513.

2.7. Statistical analyses

All statistical analyses were achieved with R studio (RStudio, Version 0.98.501, RStudio Inc., Boston, Massachusetts, USA) with the free statistics software R (R version 3.0.2). A three-way analysis of variance (ANOVA) was used to compare the CO_2 and N_2O cumulative fluxes and microbial community indicators. The statistical model included soil type, OWP type, incubation time, soil type × OWP type and soil type × OWP type × incubation time. For all parameters, all significant effects were assessed by Tukey's Honestly Significant Difference (HSD) *post hoc* test ($P < 0.05$). All the variables were tested for normality using Shapiro-Wilk test. The prokaryotic and fungal communities from all samples were also compared by using taxonomical abundance matrix. Principal Component Analysis (PCA) was then used to graphically depict any differences in the microbial structure at phylum level between the samples. For each sample, the coordinates of both principal axes were analyzed by calculating the Euclidean distance (Eudist) between the treatment and the corresponding controls for each incubation time and OWP type. This genetic distance was interpreted as the

magnitude of genetic structure modifications induced by OWP application and was calculated as follows. Magnitude of modifications, example of calculation for one OWP type and each incubation time = [Average of Inter Eudist (treated microcosms/control microcosms)]-[((Average of Intra Eudist treated microcsms) + (Average of Intra Eudist control microcosms))/2] (Bressan et al., 2008).

3. Results

3.1. CO2 emissions

Variations in the cumulative emissions of CO_2 in unamended and amended soils are shown in Fig. 1. Basal respiration differed significantly between the five control soils, the greatest cumulative emissions of CO_2 being observed with LB (94.1 µg C g^{-1} of soil), and the lowest with Co (34.2 µg C g^{-1} of soil, $P < 0.001$). Addition of organic amendment (GWS or FYM) resulted in greater cumulative emissions of CO_2 in all five soils with respect to the unamended controls (Fig.1, $P < 0.001$). Regardless of the soil, GWS application led to lower cumulative emissions of CO_2 (on average 156.9 µg C g^{-1} of soil) than FYM (on average 304.8 µg C g^{-1} of soil, $P < 0.001$), particularly at the end of incubation (from day 14 to 28). In amended soils (GWS or FYM), the cumulative emissions of CO_2 also differed according to the soil type, greater values being observed for soil from Ch (188.1 and 369.7 µg C g^{-1} of soil for GWS and FYM respectively) and the lowest values being observed for soil from Co (104.9 and 217.1 µg C g^{-1} of soil for GWS and FYM respectively, $P < 0.001$).

3.2. N2O emissions

Variations in the cumulative emissions of N_2O in unamended and amended soils are reported in Fig. 2. Only control soil from LB, Ch and Ef soils showed a significant N_2O release throughout the incubation period (from 0 to 3.7 ng N g^{-1} of soil in average, $P<0.001$).

The addition of organic amendment (GWS or FYM) resulted in greater cumulative emissions of N_2O in all five soils with respect to unamended controls ($P < 0.001$). Regardless of the soil, GWS and FYM application induced equivalent cumulative emissions of N_2O (23.6 and 26.4 ng N g^{-1} of soil respectively). GWS led to more rapid N_2O emission (until day 3) than FYM. In amended soils, the cumulative emissions of N_2O differed according to the site considered. For GWS, the highest cumulative emissions of N_2O were observed for Co (35.9 ng N g^{-1} of soil, $P < 0.001$). LB and Ef soils emitted significantly less (~1.3 fold) N_2O than Co (23.7 and 30.3 ng N g^{-1} of soil respectively). Still compared to Co soil, Qa emitted ~2 fold less (17.5 ng N g^{-1} of soil, $P < 0.001$) and Ch ~4 fold less (10.3 ng N g^{-1} of soil, $P < 0.001$). The soil emission classification after FYM application differed from that observed with GWS, the lowest emission rates of N_2O being observed for Co and Qa soils (4.5 and 16.2 ng N g^{-1} of soil respectively). Ch emitted ~5 fold more N_2O (22.1 ng N g^{-1} of soil, $P < 0.001$) than Co. Soils Ef and LB emitted ~10 fold more N_2O than Co (52.2 and 36.9 ng N g^{-1} of soil respectively, $P < 0.001$).

3.3. Microbial biomass

The dynamics of the microbial biomass during incubation of unamended and amended soils are shown in Fig. 3. The microbial biomass in control soils generally remained constant throughout the incubation ($P > 0.05$). The LB soil had the highest biomass (on average 73.6 µg DNA g^{-1} of dry soil) and Ch the lowest (on average 16.9 µg DNA g^{-1} of dry soil; $P < 0.001$). The biomass values for Co, Qa and Ef soils were similar and significantly lower than LB, and greater than Ch (on average 29.8 µg DNA g^{-1} of dry soil; $P < 0.001$). Addition of GWS or FYM enhanced the microbial biomass only in LB soil, from 7 days of incubation (106.7 and 123.7 µg DNA g^{-1} of dry soil respectively; $P < 0.001$). A significantly greater amount of microbial biomass was observed when FYM was applied on LB soil with respect to GWS (123.7 and 106.6 µg DNA g^{-1} of dry soil respectively; $P < 0.001$).

304

305 *3.4. Prokaryotic and fungal diversity indices*

306 The dynamics of the microbial diversity indices during incubation of unamended and
307 amended soils are shown in Fig. 4. In general, the control soils did not show any variations in
308 prokaryotic and fungal diversity indices (richness and Shannon) throughout the study period.
309 Only the control soils from LB showed, at 28 days of incubation, an increase in fungal
310 richness and microbial Shannon indices ($P < 0.001$). The effect of organic amendment on
311 microbial diversity indices was dependent on the soil and the type of amendment. Thus, the
312 addition of GWS led to a decrease of prokaryotic richness and Shannon index in Qa soil after
313 7 days of incubation ($P < 0.001$), and an increase of the prokaryotic Shannon index in LB soil
314 after 28 days of incubation ($P < 0.001$). Concerning fungal diversity indices, the addition of
315 GWS led to a decrease of richness and Shannon index in Co and Ch soils ($P < 0.001$), after 7
316 days of incubation, but an increase of richness in Ef soil ($P < 0.001$). The addition of FYM
317 increased the prokaryotic richness in Ch soil and the fungal richness in Co soil after 7 days of
318 incubation ($P < 0.001$). For Co soil, from day 7 to 28, the fungal Shannon index decreased to
319 reach, at the end of incubation, a value lower than that observed before the application ($P <$
320 0.001). This suggests that the fungal community from Co soil would be resilient 28 days after
321 FYM application. The addition of FYM also led to a decrease of the fungal Shannon index in
322 Ef soil throughout the entire incubation ($P < 0.001$).

323

324 *3.5. Prokaryotic and fungal community structures and taxonomic composition*

325 Principal Component Analysis (PCA) achieved on phyla taxonomical abundance matrix
326 revealed that before the OWP application, the microbial community structures in the five soils
327 differed significantly from each other (Supplementary Fig. S1A and B). The addition of GWS
328 or FYM induced, from 7 days of incubation, a change in the prokaryotic and fungal (Fig. 5A
329 and B, Supplementary Fig. 1A and 1B) community structure in all the soils. Same results

were obtained on genera taxonomical abundance matrix (data not shown). OWP (FYM or GWS) application impacted prokaryotic community structure whatever the sampling site, as evidenced by the Euclidian distances calculated at D7 and 28 (Fig. 5). However, the amplitude of the modifications depended on the type of OWP applied, with major changes observed when GWS, rather than FYM, was used (Fig. 5). The prokaryotic genetic structures seemed to be more impacted in Ch than in the other soils, 28 days after OWP application (FYM or GWS) ($P < 0.05$). Analysis of the taxonomic composition, following FYM application to Ch soil, revealed that the observed changes in prokaryotic genetic structures were mainly due to an increase in the relative abundance of *Firmicutes* and a decrease of *Acidobacteria* and *Planctomycetes* groups ($P < 0.05$). GWS led only to a decrease of the *Planctomycetes* group in that soil. Twenty-eight days after GWS application, the prokaryotic genetic structure showed resilience in the Ef, LB and Qa soils, but not in the Ch and Co soils (Fig. 5). This was also observed after FYM amendment, but only in Co soil (Fig. 5). OWP (FYM or GWS) application also impacted the fungal community structure whatever the sampling site (Fig. 5). Fungal genetic structure changes were due to a decrease of *Chytridiomycota* in Ef soil 28 days after FYM application ($P < 0.05$). FYM input also led to an increase of *Glomeromycota* in Ch soil 28 days after application ($P < 0.05$). A decrease of *Chytridiomycota* was observed in LB soil 28 days after GWS application ($P < 0.05$). Twenty-eight days after GWS application, the fungal genetic structure in Ch, Co and Qa soils showed resilience (Fig. 5). This was not observed after amendment with FYM (Fig. 5). Interestingly, in the present study, the prokaryotic and fungal communities appeared more resilient after GWS application than after FYM application.

4. Discussion

The addition of OWP (FYM or GWS) led to a rapid increase of CO_2 emission in all the soil samples tested. This confirmed the role of labile C (provided by OWP) in inducing a

rapid increase of soil microbial respiration after amendment application. Among the different soil types studied, those with the greatest basal respiration (Ch, LB and Ef) were also the greatest emitters when OWPs were applied. Soil CO_2 emissions were not correlated with any of the soil physicochemical characteristics measured in the present study. From 14 days of incubation, and whatever the type of soil considered, CO_2 emission was ~50 % greater in soils amended with FYM than in those amended with GWS. As previously observed by Brenzinger et al. (2018), this could be explained by the quality of OWP applied. In the present study, the different OWP varied in their organic matter quality. FYM was characterized by a lower potential ability to increase soil stable pool of exogenous organic matter - total organic carbon, as shown by its smaller I_{ROC} (66.6 %), compared to GWS (77.6 %) (Lashermes et al., 2009). This suggests that FYM was subjected to a greater biodegradability of organic carbon and a greater CO_2 emission compared to GWS.

The addition of OWP (FYM or GWS) led to an increase of N_2O emission. Twenty-eight days after application, both OWP led to equivalent cumulative emissions of N_2O. However, the trend of N_2O emission differed according to the amendment applied. Indeed, whatever the type of soil considered, the application of GWS led to earlier N_2O emission with ~50 % of the total N_2O emission observed after 3 days of incubation. After the same period of incubation, FYM application had induced only 10 % of the total N_2O emission. Increased N_2O emission from soil is commonly reported after organic fertilization (Shah et al., 2016; Ho et al., 2017); however, the effect of the type of OWP amendment on the kinetics of N_2O emission is poorly documented (Shah et al., 2016). According to Shah et al. (2016), the kinetics of N_2O emission would depend on the C/N ratio of the applied OWP. More precisely, a high C/N ratio means that N will be exhausted before the C has been digested by the bacteria as an energy source, hence leading to a lower N_2O emission. Conversely, a low C/N ratio results in high $NH4^+$ concentrations and finally a greater emission of N_2O (Shah et al., 2016). Thus, the lower C/N ratio measured for GWS (13.2 ± 0.5), as compared to FYM (18.1± 0.1), could explain the earlier N_2O emission observed with this amendment.

Interestingly, an effect of soil type on N_2O emission was also observed. Soil with the highest pH before amendment (Co; pH=8.51) emitted the greatest amount of N_2O after amendment with GWS, but the lowest after amendment with FYM. As previously mentioned, the cumulative emissions of N_2O from other soil types were equivalent after GWS and FYM applications. According to the literature, the relationship between soil pH and denitrification remains unclear. In the present study, soil pH had not been measured throughout the incubation. However, based on previous study (Shah et al. 2016), for a same soil type, the dynamic of soil pH would be different according to the quality of OWP applied. Some authors indicated that the N_2O fraction could be larger at low soil pH (Focht, 1974; Goodroad and Keeney, 1984; Eaton and Patriquin, 1989; Brumme and Beese, 1992; Thomas et al., 1994), whereas others reported lower N_2O emissions in acidic compared to neutral or slightly alkaline soils (ŠImek and Cooper, 2002). Thus, it is difficult to explain the effect of soil type on N_2O emission as being determined by soil pH and other interpretations are needed.

In the present work, before the amendments, the prokaryotic and fungal community structures and compositions of the five soils were distinctly different (Supplementary Fig. S2). Moreover, as previously observed by Ho et al. (2017), the application of OWP led to changes in the microbial community that were dependent on the soil type and the quality of OWP applied (Fig. 5 and Supplementary Fig. S1). Nitrous oxide (N_2O) is mainly generated *via* microbial processes of nitrification and denitrification in soils (Pajares and Bohannan, 2016). Thus, as proposed by Ho et al. (2015), we hypothesized that, in the case of Co soil, GWS application stimulated the soil-borne microbes involved in denitrification (resulting in earlier N_2O emission), whereas FYM favored those involved in the nitrification process (leading to later N_2O emission). The effect of OWP quality on N_2O emission was not so marked for the other soil types probably due to the differences between the soil-borne microbial communities.

From 7 to 28 days of incubation, and only in LB soil, the addition of OWP (FYM or GWS) led to a ~40 % increase in microbial biomass. Previous soil incubation studies had already highlighted an increase in microbial biomass within 10 days after the addition of OWP (Saison et al., 2006; Pezzolla et al., 2013; Pezzolla et al., 2015). However, in the present study, OWP had an effect on microbial biomass in only one soil (LB), which is surprising. As proposed by Marschner et al. (2003), this could be due to the higher organic carbon content (17.9 g kg^{-1}) of LB soil before OWP application. Indeed, the organic carbon content is known to determine the response of microbial communities to external inputs, soils with higher organic carbon being more prone to an increase in microbial biomass and changes in the microbial community (Marschner et al., 2003). Further studies also reported a correlated increase of soil CO_2 emission and microbial biomass in the first days after OWP application (Saison et al., 2006; Pezzolla et al., 2013). This was not observed in the present study, except for the LB soil. As proposed by other studies, this suggests that the modifications in activity highlighted would more likely be due to a modification in microbial community structure and composition, rather than in its size (Zogg et al., 1997; Zhang et al., 2005).

No overall tendency was observed regarding the effect of OWP on soil microbial diversity indices. However, changes in microbial richness and diversity occurred depending both on the type of soil and OWP. The effects of OWP on microbial diversity reported in the literature are often ambiguous, mainly due to great variations between the experimental systems and management definitions (Chaudhry et al., 2012; Hartmann et al., 2015; Chen et al., 2016; Sadet-Bourgeteau et al., 2018). As reported by several authors (Saison et al., 2006; Pezzolla et al., 2013; Pezzolla et al., 2015; Federici et al., 2017), OWP addition (GWS or FYM) led to a rapid shift in microbial community structure, in all soils, within 7 days. The observed changes in microbial structure were dependent on the soil type and the quality of OWP applied. It cannot be excluded that these early changes might be due to microorganisms present in the organic materials applied (Supplementary Fig. S3). This hypothesis is reinforced by the different microbial genera composition present in unamended soils and OWPs

435 (Supplementary Fig. S2 and S3). However, as mentioned by Saison et al. (2006), the OWP
436 microbiota added to soil is rapidly outcompeted by the soil-derived microorganisms and its
437 effect on community structure is likely to be marginal. In addition, as proposed by Ho et al.
438 (2016), the changes in microbial community structure observed in the present study is more
439 likely due to the stimulation of soil-borne microbes by chemical composition of OWP
440 applicated than microbes present in the organic materials applied. The early shift in structure
441 of the soil microbial community seems in close agreement with the initial increase of
442 microbial respiration observed immediately after applying the amendments and could be
443 ascribed to the stimulation of microbial populations with great ability to rapidly metabolize
444 the labile organic C provided by OWP (Blagodatskaya et al., 2007). This was corroborated by
445 the fact that, in the present study, the application of FYM led to a stimulation of *Firmicutes* in
446 Ch soil and also the highest CO_2 emission. Carbon additions appear to strongly stimulate
447 organisms within the *Firmicutes* clades (Cleveland et al., 2007). The dominance of organisms
448 within the *Firmicutes* groups, and their relative increase in abundance in response to C
449 additions, suggested that members of these groups quickly respond to the addition of organic
450 material to the soil, leading to rapid increases in soil respiration (Cleveland et al., 2007). In
451 parallel, the decrease of *Acidobacteria* and *Planctomycetes*, suggested that these organisms
452 exhibit poor competitiveness and colonization ability, which could explain their decrease in
453 the present experiment. The impact on these *phyla* generally becomes apparent 3 days after
454 amendment and has already been highlighted in previous studies of the impact of digestate
455 application on soil microbial communities (Fierer et al., 2007; Cruz-Martínez et al., 2009;
456 Pezzolla et al., 2015). Interestingly, contrary to FYM, the addition of GWS to soils only led to
457 a decrease in *Planctomycetes* 3 to 28 days after the application. As mentioned above, the lack
458 of increase in the proportion of *Firmicutes* in GWS-amended soils may help to explain the
459 lower CO_2 emissions, as compared to FYM.

460 The fungal community also responded by a decrease of *Chytridiomycota* 28 days after
461 FYM or GWS application, and an increase in *Glomeromycota* 28 days after FYM application.

462 *Chytridiomycota* have been recovered as saprophytes and can degrade polymers from a
463 variety of plant and animal debris (Czeczuga and Mazalska, 2000; Czeczuga et al., 2005).
464 This fungal phylum is probably included within the group of k-strategists, which could
465 explain its decrease in the present experiment. It has been reported in the literature that 4
466 months after the last application, OWP tended to increase *Basidiomycota*, one of the main soil
467 decomposers (Ma et al., 2013; Weber et al., 2013) and to decrease *Glomeromycota* (Chen et
468 al., 2016; Sadet-Bourgeteau et al., 2018). This did not occur in the present study, where no
469 effect on *Basidiomycota* was apparent and an increase of *Glomeromycota* was observed 28
470 days after OWP application. As mentioned in a previous study, this emphasizes the
471 importance of taking the delay between OWP application and soil sampling into account
472 when studying the effect of OWP on the soil microbial community (Sadet-Bourgeteau et al.,
473 2018).

474 Despite the above-described overall response of soils to OWP application, in the present
475 work, the microbial communities of some soils responded differently. This concords with
476 observations by Pérez-Piqueres et al. (2006) that the changes in microbial community
477 structure induced by amendments were related both to the soil and to the type of OWP used.
478 The particular behavior of the prokaryotic community in response to OWP application in the
479 Ch soil could be related to the soil's physico-chemical characteristics. Indeed, Ch soil has a
480 sandy loam texture, unlike the other soils in the present study (silty clay loam or silty loam
481 texture). In a recent study, Ho et al. (2017) highlighted that the composition of the bacterial
482 community from sandy loam soil responded differently to a same type of OWP application
483 than a bacterial community from clay soil. Thus, we suggest that, contrary to the other soils in
484 this study, the sandy loam texture of Ch soil would be an important determinant of its
485 microbial community composition, and lead to a different impact of the amendment on soil
486 prokaryotic community composition. As previously observed by Procter et al. (2014), the
487 effect of OWP on the fungal community was also soil type-dependent. Some of the microbial
488 communities impacted by OWP application, tended to revert to their initial structure (before

amendment). This resilience was dependent on soil type, and globally more marked after GWS input. This accords with reports by Saison et al. (2006) that the resilience of the soil microbial community was OWP-quality dependent.

5. Conclusions

The present study indicated that soils with different physico-chemical properties and microbial community structures responded differently to organic fertilization. This response appeared to depend on the type of OWP and suggests that GHG emission could be modulated by spreading specific types of amendment on specific types of soil. Further analyses are needed to best determine which type of amendment should be applied to which type of soil in order to limit soil GHG emission.

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Table 1

Soil physico-chemical parameters from control plots of different Long-Term observatories

Item	Long-Term Observatories				
	QualiAgro (Qa)	PROspective (Co)	EFELE (Ef)	La Bouzule (LB)	Couhins (Ch)
Location	Feucherolles	Colmar	Rennes	Nancy	Bordeaux
	North West of France	Est of France	North West of France	North Est of France	South West of France
Geographical coordinates	48°53′49”N, 1°58′21”E	48°03′33”N, 7°19′41”E	48°05′35.9”N, 1°48′53.1”W	48°44’23.64”N, 6°19′20.16”E	44°45′06.45”N, 0°33′34.37”W
Clay (<2 µm) g kg^{-1}	199	243	181	359	83
Fine silt (2/20 µm) g kg^{-1}	263	292	241	398	45
Coarse silt (20/20 µm) g kg^{-1}	442	353	423	127	21
Fine sand (50/200 µm) g kg^{-1}	87	69	103	44	64
Coarse sand (200/2000 µm) g kg^{-1}	9	43	52	72	787
Organic Carbon g kg^{-1}	9.11	13.4	11.3	17.9	9.33
Total N g kg^{-1}	0.87	1.18	1.17	1.76	0.64
C/N	10.4	11.4	9.64	10.2	14.6
Organic Matter g kg^{-1}	15.8	23.1	19.6	31	16.1
pH	6.88	8.51	6.4	6.93	6.06
CEC cmol+kg^{-1}	8.26	10.8	6.79	14.3	2.78
P_2O_5 g $100g^{-1}$	0.13	0.23	0.25	0.35	0.06

510 **Table 2**

511 Main characteristics of the different organic waste products (OWP) used

Treatment		FYM	GWS
Dry Matter (DM†)	%	33.9 ± 0.7	67.2 ± 1.3
Organic Carbon	$g.kg^{-1}$ DM	355 ± 14	257 ± 2
Total N	$g.kg^{-1}$ DM	19.7 ± 0.6	22.5 ± 0.5
P_2O_5 (Olsen)	$g.kg^{-1}$ DM	2.6 ± 0.1	0.8 ± 0.1
C:N		18.1 ± 0.1	13.2 ± 0.5
pH (water)		8.8 ± 0.3	7.7 ± 0.1
I_{ROC}‡	(% organic C)	66.6 ± 7.5	77.6 ± 9.3
Microbial Biomass	µg of $DNA.g^{-1}$ of OWP	515.5 ± 87.0	54.9 ± 19.1

512 †DM: Dry Matter; FYM: farmyard manure; GWS: green wastes with sewage sludge

513 ‡I_{ROC}: index of residual organic carbon

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522 **Fig 1.** The dynamics of cumulative emission of CO_2 from five different types of soils
523 (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB))
524 amended or not (control) with two different organic materials (FYM: farmyard manure or
525 GWS: green wastes with sewage sludge).

526 **Fig. 2.** The dynamics of cumulative emission of N_2O from five different types of soils
527 (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB))
528 amended or not (control) with two different organic materials (FYM: farmyard manure or
529 GWS: green wastes with sewage sludge).

Fig. 3. The dynamics of microbial biomass from five different types of soils (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB)) amended or not (control) with two different organic materials (FYM: farmyard manure or GWS: green wastes with sewage sludge).

Fig. 4. The dynamics of Prokaryotic (A) and fungal (B) diversity indices from five different types of soils (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB)) amended or not (control) with two different organic materials (FYM: farmyard manure or GWS: green wastes with sewage sludge).

538 **Fig. 5.** Magnitude of the prokaryotic and fungal genetic structure of five different types of
539 soils (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB))
540 modifications during 28 days after amendment with two different organic materials: (A)
541 farmyard manure or (B) green wastes with sewage sludge.

Supplementary Figure S1

Principal Component Analysis of the evolution of microbial community composition over time (A: Prokaryote and B: Fungi) of five different types of soils (QualiAgro (Qa), PROspective (Co), Efele (Ef), Couhins (Ch) and La Bouzule (LB)) amended or not (CON) with two different organic materials (FYM: farmyard manure or GWS: green wastes with sewage sludge).

548 **Supplementary Figure S2**

549 Relative abundances of prokaryotic (A) and fungal (B) *phyla* and prokaryotic (A') and fungal
550 (B') *genera* in the different sampling sites (QualiAgro (Qa), PROspective (Co), Efele (Ef),
551 Couhins (Ch) and La Bouzule (LB)) before the application of organic waste products (T0).

552 **Supplementary Figure S3**

553 Relative abundances of prokaryotic (A) and fungal (B) *phyla* and prokaryotic (A') and fungal

554 (B') *genera* in the two organic waste products applied on soils (GWS and FYM).

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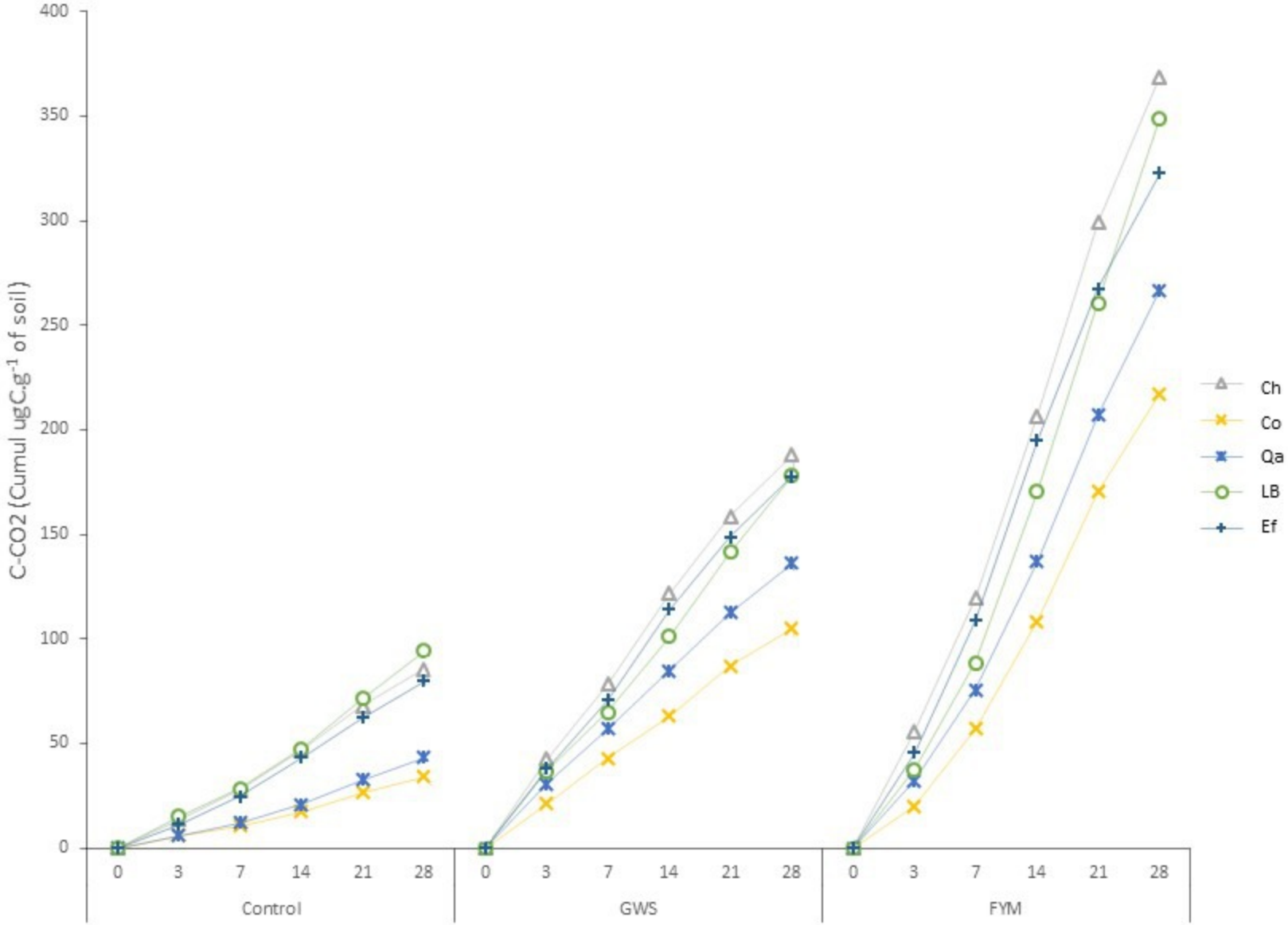
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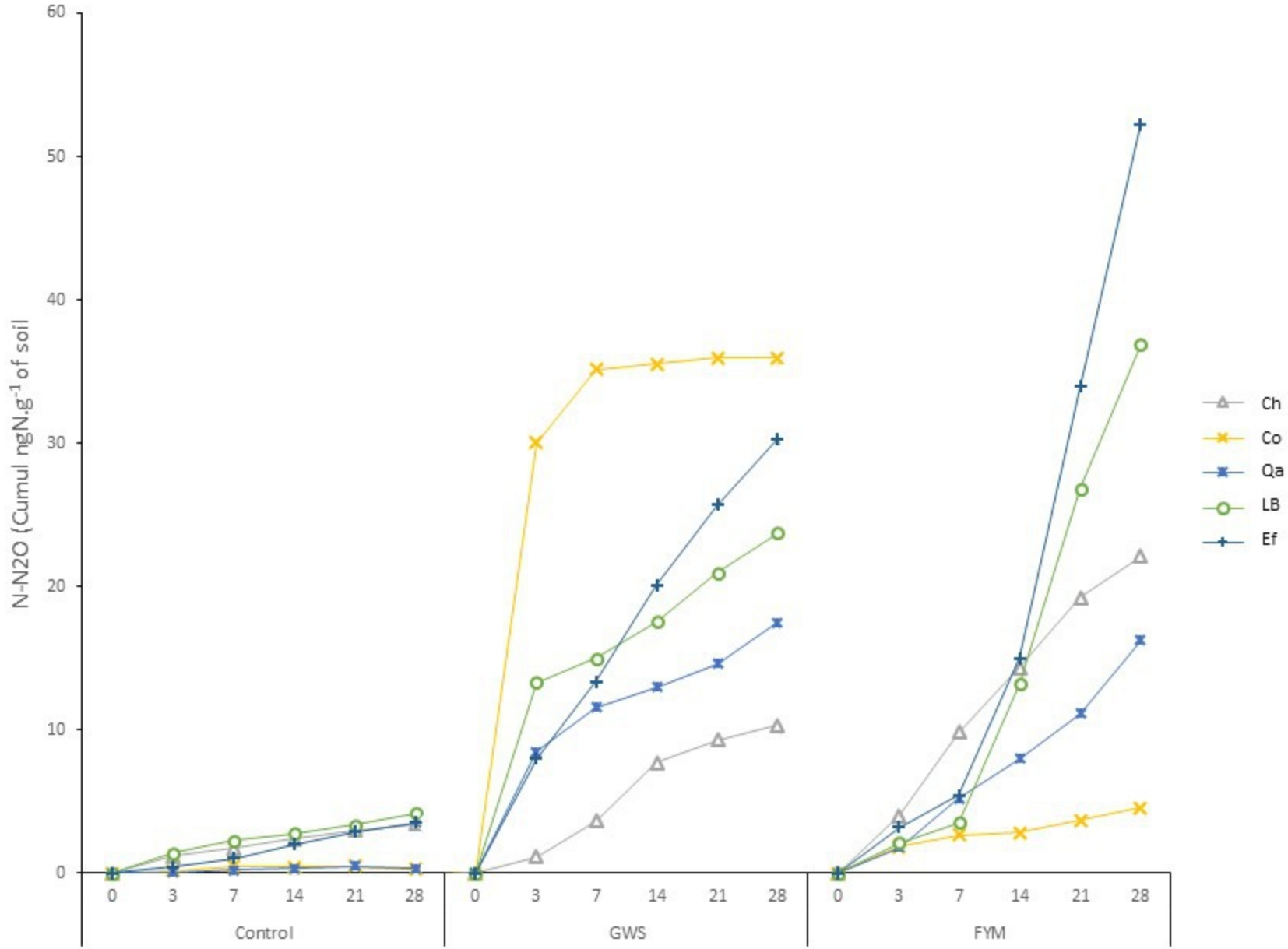
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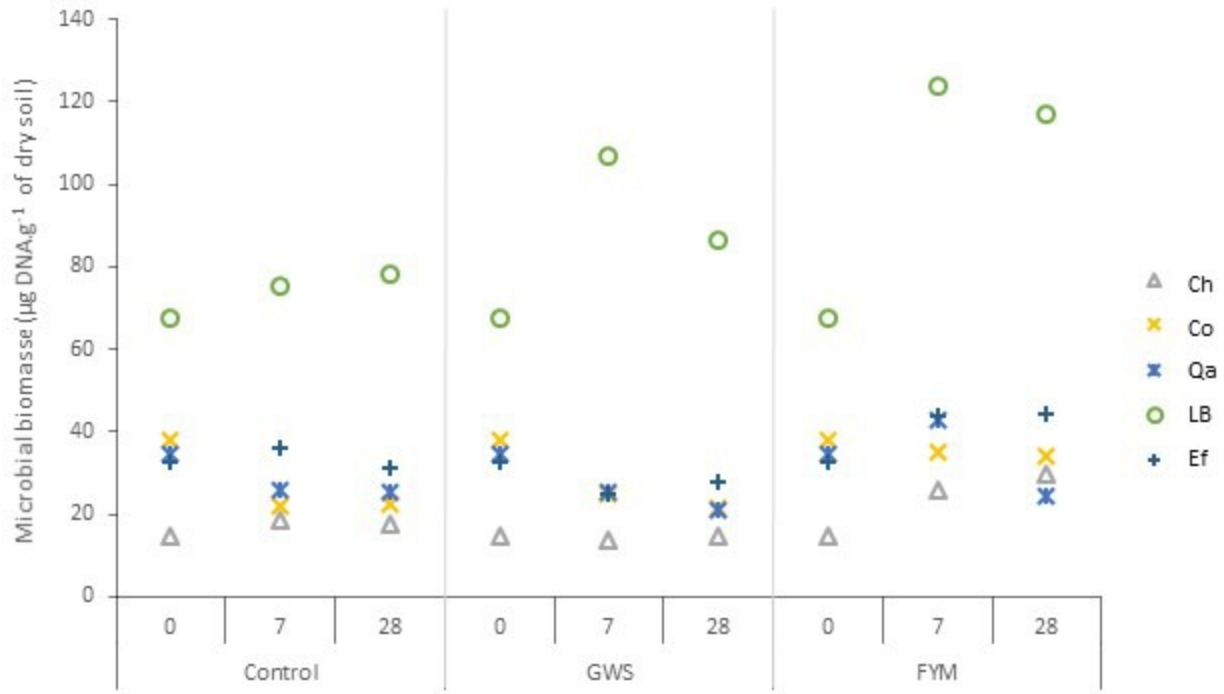
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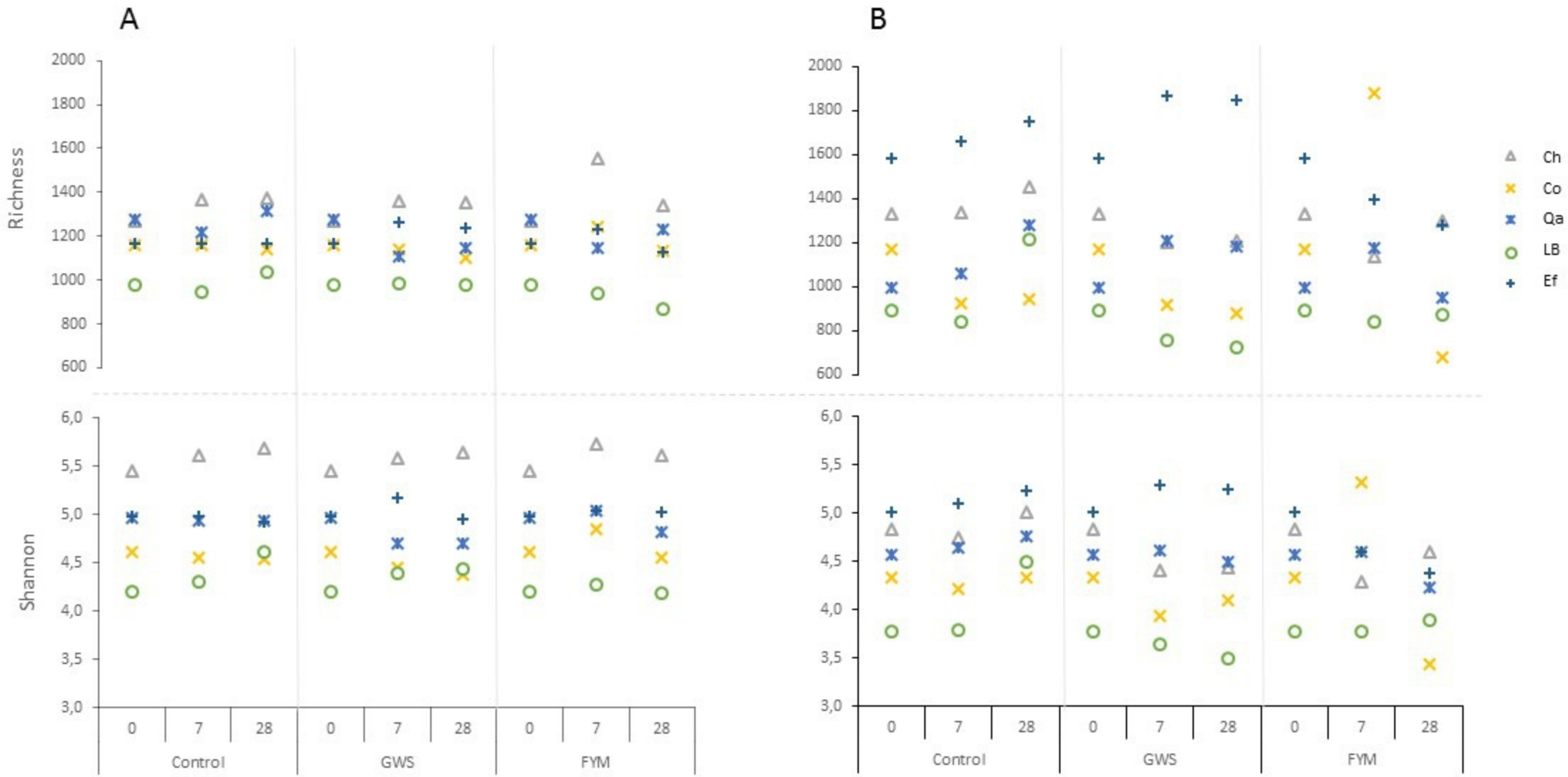
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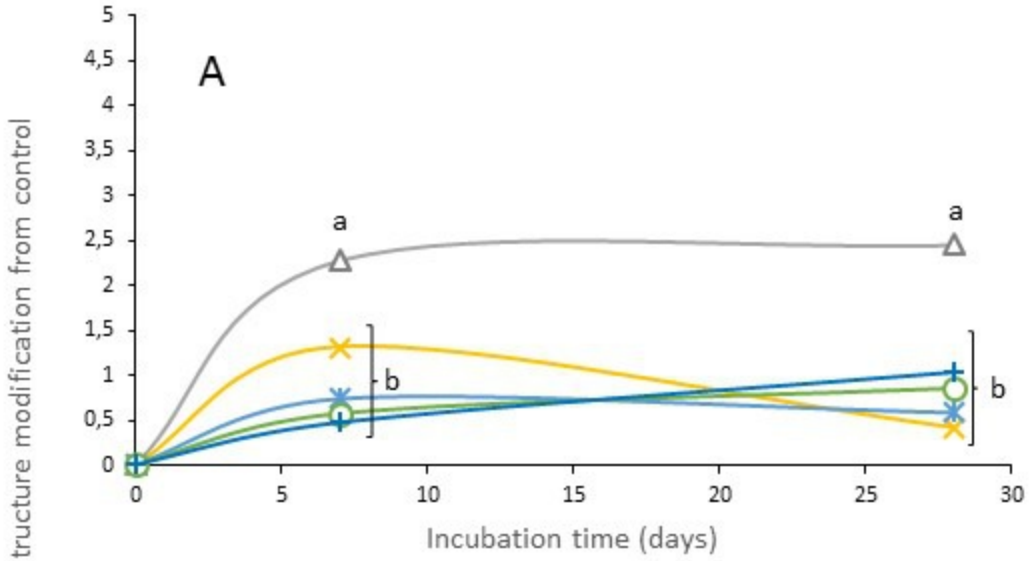
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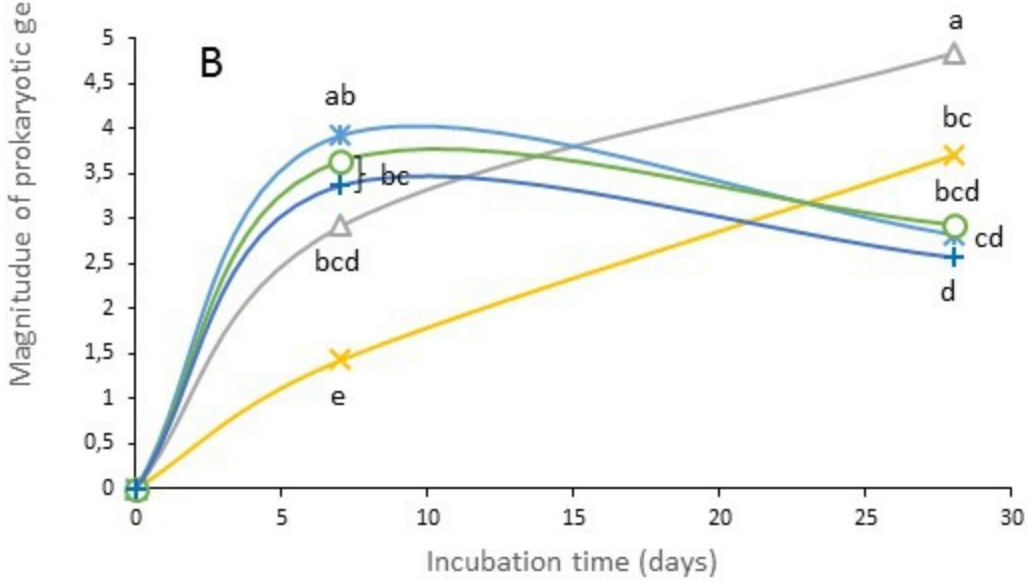

400
350
300
250
200
150
100
50
0
C-CO2 (Cumul ugC.g-1 of soil)
0
3
7
14
21
28
Control
GWS
FYM
Ch
Co
Qa
LB
Ef

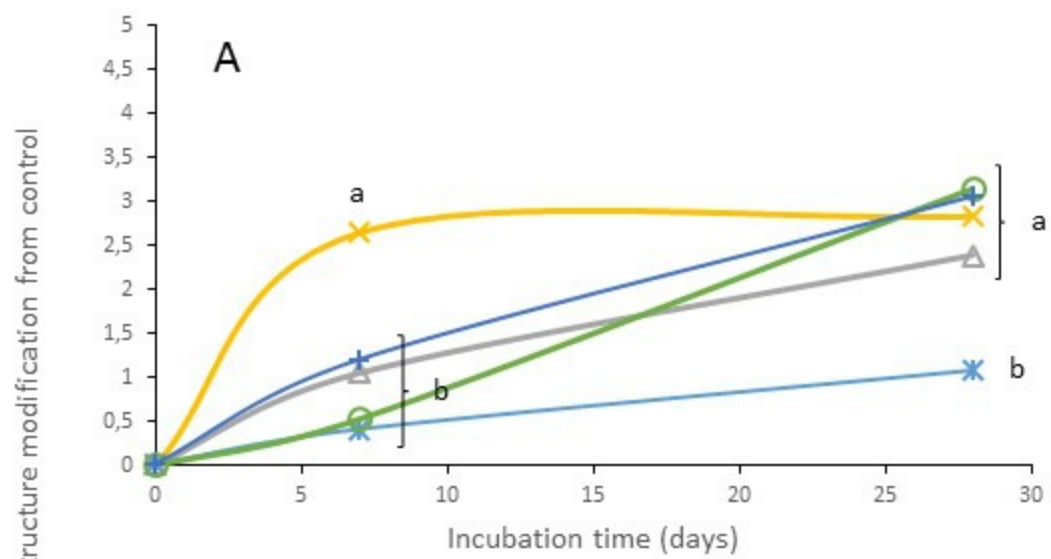

60
50
40
30
20
10
0
N-N2O (Cumul ngN.g-1 of soil
0
3
7
14
21
28
Control
GWS
FYM
Ch
Co
Qa
LB
Ef

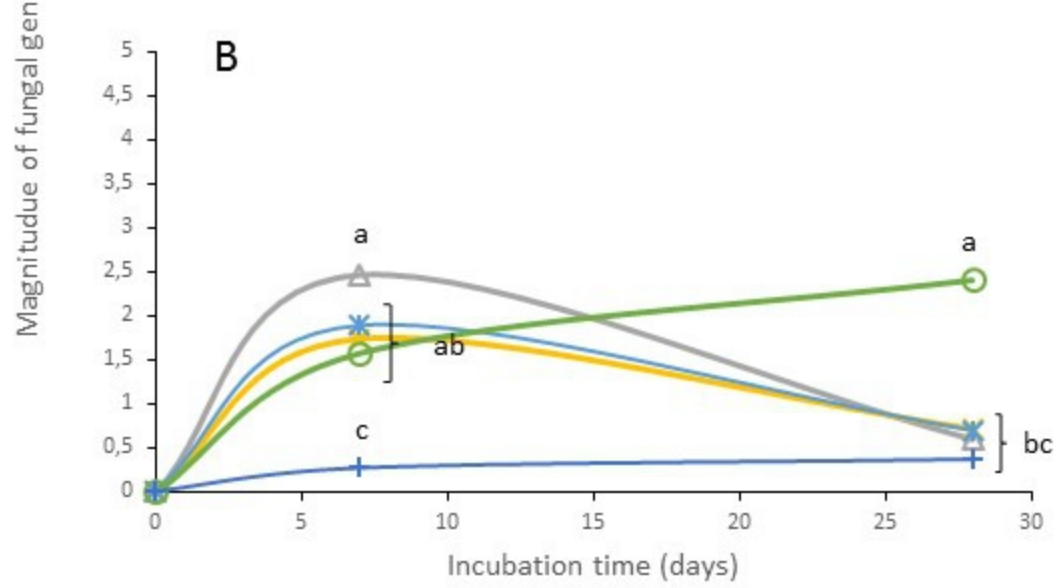

Microbial biomasse (µg DNA.g-1 of dry soil)
140
120
100
80
60
40
20
0
0
7
28
0
7
28
0
7
28
Control
GWS
FYM
Ch
Co
Qa
LB
Ef


A
B
Richness
Shannon
2000
1800
1600
1400
1200
1000
800
600
6,0
5,5
5,0
4,5
4,0
3,5
3,0
0
7
28
Control
GWS
FYM
Ch
Co
Qa
LB
Ef

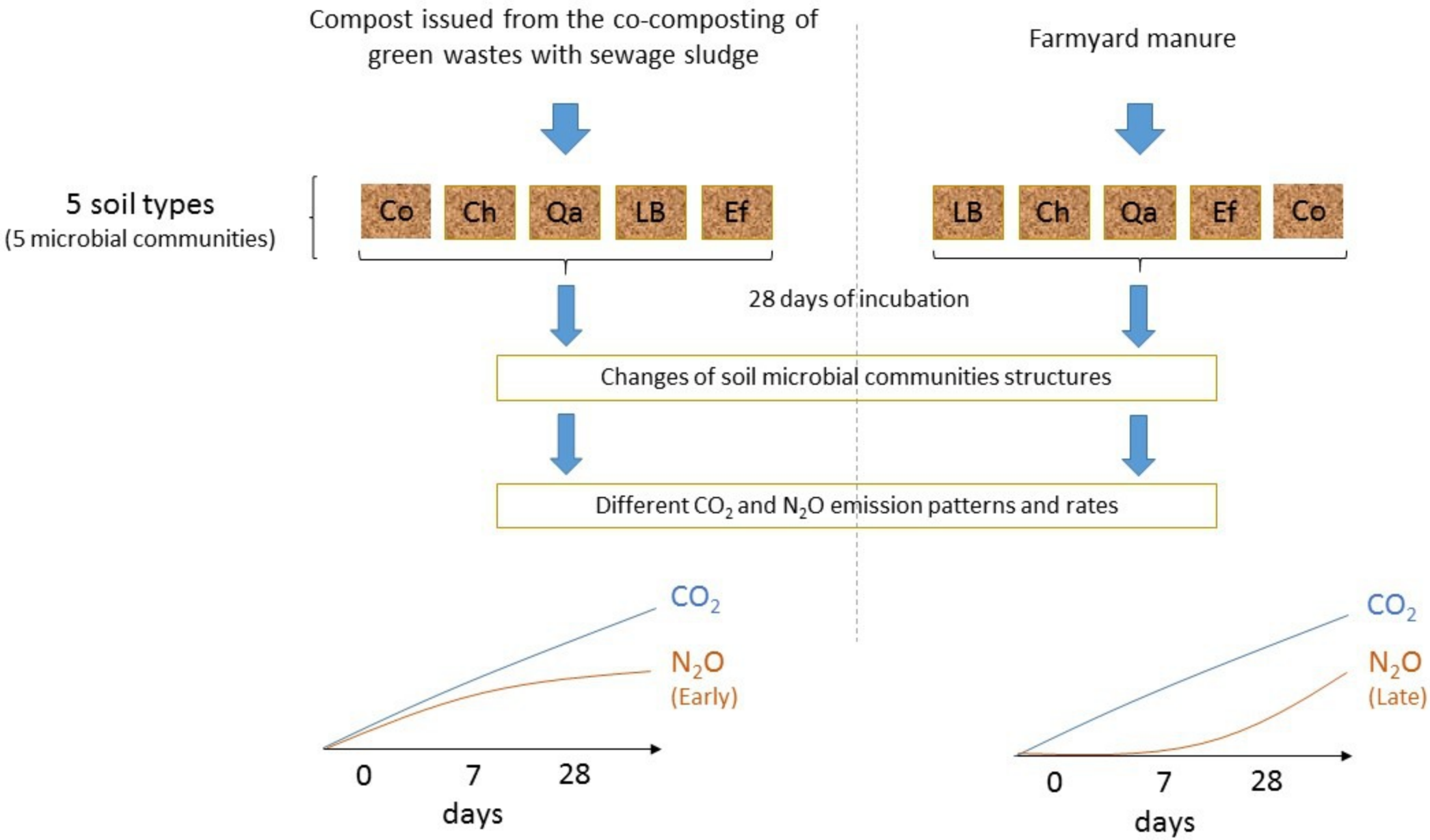

A
Magnitudue of prokaryotic genetic structure modification from control
Incubation time (days)
a
a
b
b


B
Incubation time (days)
a
ab
bc
bc
bcd
cd
bcd
d
e


A
Magnitudue of fungal genetic structure modification from control
Incubation time (days)
a
a
b
b


B
Incubation time (days)
a
a
ab
c
bc


Ch
Co
Qa
LB
Ef


Compost issued from the co-composting of green wastes with sewage sludge
Farmyard manure
5 soil types
(5 microbial communities)
Co
Ch
Qa
LB
Ef
LB
Ch
Qa
Ef
Co
28 days of incubation
Changes of soil microbial communities structures
Different CO_2 and N_2O emission patterns and rates
CO_2
N_2O
(Early)
0
7
28
days
CO_2
N_2O
(Late)
0
7
28
days