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1 **Long-term impact of hydrological regime on structure and functions of**  
2 **microbial communities in riverine wetland sediments.**

3 Running title: Impact of hydrology on wetland microbial communities  
4

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22 **ABSTRACT**

23 In a context of global change, alterations of the water cycle may impact the structure and  
24 function of terrestrial and aquatic ecosystems. Wetlands are particularly at risk because  
25 hydrological regime has a major influence on microbially-mediated biogeochemical processes  
26 in sediments. While the influence of water availability on wetland biogeochemical processes  
27 has been comprehensively studied, the influence of hydrological regime on microbial  
28 community structure has been overlooked. We tested for the effect of hydrological regime on  
29 the structure and functions of microbial communities by comparing sediments collected at  
30 multiple sites in the Ain département (Eastern France). Each site consisted of two plots, one  
31 permanently and one seasonally inundated. At the time of sampling, all plots were  
32 continuously inundated for more than 6 months but still harbored distinct bacterial  
33 communities. This change in community structure was not associated with marked  
34 modifications in the rates of microbial activities involved in the C and N cycles. These results  
35 suggest that the observed structural change could be related to bacterial taxa responding to the  
36 environmental variations associated with different hydrological regimes but not strongly  
37 associated with the biogeochemical processes monitored here.

38

39 **KEYWORDS**

40 bacterial community structure, drying, environmental stress, hydrological regime, sediment,  
41 structure-function relationships, wetlands

42

## 43 INTRODUCTION

44 In a context of climate change, the intensification of the global water cycle is predicted to  
45 modify precipitation patterns and increase the frequency of extreme events such as floods and  
46 droughts in many parts of the world (Arnell 1999; Huntington 2006; Coumou & Rahmstorf  
47 2012). Such modifications may severely impact the structure and function of terrestrial and  
48 aquatic ecosystems (Bunn & Arthington 2002; Weltzin et al. 2003; Langhans & Tockner  
49 2006; Knapp et al. 2008; Poff & Zimmerman 2010). This impact is likely to be particularly  
50 marked in wetland ecosystems where hydrological regime controls their ability to regulate the  
51 fluxes of matter and energy between terrestrial and aquatic ecosystems (Andersen et al. 2003;  
52 Mitsch & Gosselink 2007; Pitchford et al. 2012). Sediment microorganisms are key drivers of  
53 organic matter (OM) decomposition and nutrient recycling in aquatic ecosystems.  
54 Consequently, their response to altered hydrological regime will likely condition changes in  
55 ecosystem processes. Indeed, even though sediment OM content and temperature are key  
56 drivers of microbial activity, hydrological regime, by regulating gas exchange between  
57 atmosphere and sediments, has a major influence on the rates of biogeochemical processes  
58 occurring within wetland sediments (Hefting et al. 2004; Reddy & Delaune 2008; Siljanen et  
59 al. 2011). Under permanent flooding, water-saturated conditions limit the diffusion of oxygen  
60 in the sediment profile, and generally promote anaerobic processes (denitrification, sulfate  
61 reduction, methanogenesis) over the aerobic processes (aerobic respiration, nitrification,  
62 aerobic methane oxidation), that remain limited to the very upper sediment layers. During  
63 water level drawdown, the enhanced diffusion of oxygen in the sediment profile can lead to  
64 the reverse pattern (promotion of aerobic processes over anaerobic processes) (Baldwin &  
65 Mitchell 2008; Knorr et al. 2008).

66

67 There is an extended body of research on how water availability affects the rates of wetland  
68 biogeochemical processes (Qiu & McComb 1996; Venterink et al. 2002), but much less  
69 attention has been given to how it affects microbial community structure (Boon et al. 1996;  
70 Bossio et al. 2006; Kim et al. 2008; Juanjuan Wang et al. 2012). Soil texture and OM content  
71 are recognized as important drivers of microbial community structure (Johnson et al. 2003),  
72 but the impact of drying/wetting cycles on the structure of microbial communities in wetlands  
73 has been poorly investigated (Boon et al. 1996; Sundh et al. 1997; Bossio et al. 2006). Most  
74 of the available knowledge has arisen from studies focusing on terrestrial soil microbial  
75 communities (Fierer et al. 2003a; Mikha et al. 2005; Xiang et al. 2008). These studies suggest  
76 that while drying and rewetting events represent an immediate physiological stress for  
77 microorganisms, repeated dry-wet cycles might have long-term effects at community level  
78 through the selection of taxa able to cope with the high temporal variability in environmental  
79 conditions (Fierer et al. 2003a; Schimel et al. 2007). Fierer et al. (2003a) found that the  
80 decrease in soil respiration rates six weeks after the end of a series of dry-wet stress cycles  
81 was associated with changes in microbial community composition. Despite this example, the  
82 cost of such adaptations to environmental stress in terms of the rates of ecosystem processes  
83 remains largely unknown. Due to the supposedly high functional redundancy in microbial  
84 communities, parameters such as community structure and composition are not classically  
85 considered as limiting factors to biogeochemical functioning. However, a growing body of  
86 literature suggests that rates of microbial processes are not only driven by environmental  
87 conditions, such as water content or substrate and electron acceptor availability, but may also  
88 depend on bacterial community structure in a range of ecosystems (Strickland et al. 2009;  
89 Langenheder et al. 2010). Consequently, changes in community structure in response to a  
90 varying hydrological regime may affect the rates of biogeochemical processes (Schimel et al.  
91 2007; Allison & Martiny 2008; Wallenstein & Hall 2011). Indeed, the tolerance to various

92 environmental conditions may come at a cost of bacterial functions because of a lower  
93 metabolic capacity due to physiological trade-offs (Schimel et al. 2007). As a consequence,  
94 ecosystem functioning could be affected by repeated cycles of drying and rewetting (Mikha et  
95 al. 2005).

96  
97 The main objective of this study was therefore to measure the influence of hydrological  
98 regime on microbial activities and bacterial community structure in riverine wetland  
99 sediments. We compared sediments collected at multiple sites ranged along a gradient of  
100 sediment OM content. Each site consisted of two plots, one permanently and one seasonally  
101 (from about October to May) inundated. At the time of sampling, all plots had been inundated  
102 for an extended period of time (> 6 months). Our second objective was to evaluate the relative  
103 influence of environmental conditions and bacterial community structure on sediment  
104 microbial activities.

105 Our first hypothesis was that the structure of bacterial communities under dry-wet cycles  
106 would differ from those found under permanently inundated conditions. Our second  
107 hypothesis was that rates of microbial functions would be persistently affected in seasonally-  
108 dewatered plots compared to permanently-inundated plots.

109

## 110 **MATERIALS AND METHODS**

### 111 *Study Sites*

112 Sediment and water samples were collected in riverine wetlands corresponding to cut-off  
113 channels of the Ain river (South Eastern France) (Figure 1). The ecosystems are cut-off  
114 braided channels abandoned by the natural river dynamics. As the river substrate is very  
115 coarse (pebbles, gravels), the bed-load grain size in the floodplain is coarse, maintaining a  
116 high connectivity between the floodplain wetlands and 1) seepage water coming from the

117 river, and 2) water that may come from the surrounding hillslope aquifer (Bornette et al.  
118 1998; Bravard et al. 1997). As a consequence, any variation in the groundwater table affects  
119 immediately the water level in the wetlands. The wetlands drain seepage and groundwater,  
120 and function as phreatic streams. When the water-levels decrease, the water stop flowing in  
121 the wetlands, and it results in the occurrence of very closely located (a few meters) dry and  
122 inundated zones along the upstream downstream continuum of the channels, depending on the  
123 soil elevation above groundwater table. We studied three types of wetlands that differed in  
124 sediment OM content: Loamy Sand (LoSa), Silt Loam (SiLo) and Mucky Silt Loam (MSiLo).  
125 In all the wetlands, the vegetation consists in oligo-mesotraphent aquatic plant communities  
126 with a preponderance of *Potamogeton coloratus* in MSiLo sediments and a preponderance of  
127 *Juncus articulatus* and *Mentha aquatica* in SiLo and LoSa sediments. Samples were  
128 collected at three independent sites for each sediment type, leading to a total of 9 sites. Each  
129 site consisted of two plots, one permanently inundated and one seasonally dewatered (from  
130 about May to September). Within each plot, water and sediment samples were collected in  
131 triplicate at three random sampling locations separated by a minimum distance of three meters  
132 from each other.

133

#### 134 *Water and sediment sampling*

135 Water and sediments were collected once at the 9 sites ( $n = 108$  samples) to test the effect of  
136 sediment type, hydrological regime and depth below the sediment surface on (1)  
137 environmental characteristics, (2) microbial activity, and (3) bacterial community structures.  
138 Sampling was carried out over a 15-day period from 4 to 18 April 2011 to enable  
139 microbiological parameters to be measured on freshly collected sediment samples. At the time  
140 of sampling, all plots (permanent and seasonal) were inundated for more than 6 months  
141 (previous fall). A sediment corer was used to collect the top 10 cm of sediments. The

142 uppermost layer (0–2 cm) and deeper layer (5-10 cm) was sampled and immediately sieved  
143 by a 2-mm mesh in the field. The sieved fraction (at least 0.5 L of sediment) was stored in  
144 polypropylene containers and kept refrigerated (4°C) until analysis within 24 h. Surface water  
145 samples were collected directly from the flowing water. Interstitial water was sampled with a  
146 syringe connected to a flexible tube and a mini-piezometer (length: 1 m, inner diameter: 1.7  
147 cm, screen length: 3 cm) pushed to a 10 cm depth into sediment using an internal metallic rod  
148 (Boulton 1993; Marmonier et al. 2010). Water pH, dissolved oxygen, specific conductance  
149 and temperature were measured in the field using portable meters (WTW, Germany). Water  
150 samples (100 mL) were taken in glass vials to determine inorganic nutrient (ammonia, nitrate  
151 and nitrite) and dissolved organic carbon (DOC) concentrations.

152

### 153 *Water and sediment chemical analyses*

154 Water chemical analyses were performed according to standard procedures based on the  
155 French, European or ISO standard methods. DOC concentration was determined by persulfate  
156 oxidation according to NF EN 1484. Ammonium ( $\text{NH}_4^+$ ) was determined using the  
157 spectrophotometric indophenol blue method according to NF T 90-015-2. Nitrite ( $\text{NO}_2^-$ ) was  
158 determined by colorimetric method according to NF EN 26777. Nitrate ( $\text{NO}_3^-$ ) was  
159 determined by ion chromatography according to NF EN ISO 10 304. Sediment water content  
160 was measured on a subsample of wet sediments that was weighed and then dried at 60°C to  
161 constant weight. Sediment water content was calculated as the difference between wet and dry  
162 weight divided by wet weight, and expressed as a percentage. OM content was determined on  
163 a subsample of dry sediment as loss on ignition at 550°C for 8 hours, and expressed as a  
164 percentage. Sediment nitrogen content (Kjeldahl) was determined according to NF EN 25663.  
165 Sediment OM content was converted to organic carbon content using a conversion factor of  
166 0.58 (DW Nelson & Sommers 1982) before the C:N ratio was calculated for each sediment



167 sample. The proportion of fine particles (silt + clay) was determined on a subsample of  
168 sediments by manual sieving through a 50  $\mu\text{m}$  mesh sieve, and expressed as a percentage.

169

#### 170 *Microbiological analyses*

##### 171 - Bacterial community structure

172 Genomic DNA was extracted from 0.5 g of sediment using the UltraClean Soil DNA Kit

173 (MoBio Laboratories, Ozyme, France) according to the manufacturer's instructions.

174 Automated Ribosomal Intergenic Spacer Analysis (ARISA) was performed as described in

175 (Ranjard et al. 2001). Amplification of the 16S-23S intergenic spacer region from the

176 bacterial rRNA operon was performed using the primers S-D-Bact-1522-b-S-20 (eubacterial

177 rRNA small subunit, 5'-TGC GGC TGG ATC CCC TCC TT-3') and L-D-Bact-132-a-A-18

178 (eubacterial rRNA large subunit, 5'-CCG GGT TTC CCC ATT CGG-3'). PCR reactions were

179 carried out in a total volume of 25  $\mu\text{L}$  containing a  $10 \times$  *Taq* reaction buffer (GE Healthcare),

180 1.5 mM  $\text{MgCl}_2$ , 200  $\mu\text{M}$  of each deoxynucleotide, 0.2  $\mu\text{M}$  of each primer, bovine serum

181 albumin (Sigma, 0.3  $\text{mg ml}^{-1}$  final concentration), 2.5 U *Taq* DNA polymerase (GE

182 Healthcare) and 3 ng of template DNA. PCR reactions were run in a Thermal Cycler

183 *Tpersonal* (Biometra, Göttingen, Germany) under the following conditions: initial

184 denaturation at 94°C for 3 min, followed by 25 cycles of denaturation (1 min at 94°C),

185 annealing (30 s at 55°C), and extension (1 min at 72°C), and a final extension at 72°C for 5

186 min. Amplified fragments were separated and quantified by capillary electrophoresis on an

187 Agilent 2100 bioanalyzer using a DNA 1000 kit (Agilent Technologies, Massy, France)

188 according to the manufacturer's instructions. Fluorescence data were converted into 2-D gel

189 images using 2100 Expert Software (Agilent Technologies, Santa Clara, CA). Sample patterns

190 were normalized with an internal standard and external ladder included in each gel using the

191 GelCompar II version 4.6 software (Applied Maths, Ghent, Belgium). The intensity and

192 length of each fragment were determined, and fragments with the same length were grouped  
193 into an operational taxonomic unit (OTU). An abundance matrix based on the abundance of a  
194 given OTU in each sample was constructed. A community distance matrix was calculated  
195 between all pairs of samples using the Bray-Curtis dissimilarity index after the Hellinger  
196 transformation was applied to the OTU abundance matrix (Ramette 2007).

197

#### 198 - Aerobic respiration, denitrification and nitrification measurements

199 Aerobic respiration and denitrification rates were measured on sediments using the slurry  
200 technique (Furutani et al. 1984). About 15 g of wet sediment were placed in 150 mL flasks  
201 supplemented with 10 mL of distilled water (aerobic respiration) or 10 mL of a KNO<sub>3</sub> (2.16  
202 g.L<sup>-1</sup>) solution (denitrification). For the measurements of CO<sub>2</sub> production (aerobic  
203 respiration), incubation was conducted under aerobic conditions. For the measurements of  
204 N<sub>2</sub>O production (denitrification), incubation was conducted under anaerobic conditions under  
205 an He atmosphere. Incubation flasks assigned to denitrification measurements were purged  
206 three times with He to achieve anaerobiosis, and internal pressure was then adjusted to  
207 atmosphere. After removal of 15 mL of He from the incubation flasks, 15 mL of acetylene  
208 (C<sub>2</sub>H<sub>2</sub>, 10% v/v final volume) was added to inhibit N<sub>2</sub>O reductase. All samples were  
209 incubated at 20°C in the dark under a gentle shaking. At t = 3 h and t = 6 h, gases were  
210 collected and measured by gas chromatography on a MTI 200 microcatharometer (MTI  
211 Analytical Instruments, Richmond, CA). For each flask, dry weights of incubated sediments  
212 were determined after drying at 65°C for 48 h. Aerobic respiration and denitrification were  
213 expressed as ng of CO<sub>2</sub> and N<sub>2</sub>O (g of sediment dry weight (DW))<sup>-1</sup> h<sup>-1</sup>, respectively.  
214 Potential nitrification rate was determined using a protocol slightly modified from (Norton &  
215 Stark 2011). About 15 g of wet sediment were placed in a 250-mL Erlenmeyer flask  
216 supplemented with 100 mL of a phosphate buffer (1mM, pH 7.2) and 3 mM (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>.

217 Incubations were performed in the dark at 25°C under gentle shaking (to maintain aerobiosis)  
218 for 26 hours. At  $t = 2$  and  $t = 26$  h, 10 mL of suspension was sampled to measure NO<sub>x</sub> (NO<sub>2</sub><sup>-</sup>  
219 + NO<sub>3</sub><sup>-</sup>) concentration. These samples were centrifuged (5 min at 4300 g) and the supernatant  
220 was filtered through a 0.2 µm-pore cellulose acetate filter and stored at 4°C until analysis.  
221 Analyses of NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup> were performed using an automatic Easychem Plus analyzer  
222 (Systea, Italia) based on standard colorimetric methods (Grasshoff et al. 1999). The 24-h  
223 accumulation of nitrite and nitrate was used to estimate potential nitrification rate. Results  
224 were expressed as nmol of NO<sub>x</sub> (g of sediment DW)<sup>-1</sup> h<sup>-1</sup>.

225

#### 226 - Exo-enzymatic activities

227 Potential activities of β-glucosidase (EC 3.2.1.21), β-xylosidase (EC 3.2.1.37) and leucine  
228 aminopeptidase (EC 3.4.11.1) were measured on wet sediments (1 g) by fluorimetry using a  
229 constant volume of fluorescent-linked artificial substrates: 4-methylumbelliferyl-β-D-  
230 glucoside (MUF-glu; 1,000-2,500 µM, 2 mL), 4-methylumbelliferyl-β-D-xyloside (MUF-xyL;  
231 1,000-2,000 µM, 2 mL) and L-leucine-4-methyl coumarinyl-7-amide HCl (AMC-leu; 1,000-  
232 3500 µM, 2 mL), respectively. The optimal substrate concentration was determined for each  
233 activity and sediment type prior to the experiment. Incubation at 20°C (30 min) in the dark on  
234 a shaker was stopped by adding glycine buffer (pH 10.4) before centrifugation (10,000 g,  
235 10 min). Fluorescence was measured using a microplate reader (Synergy HT Biotek  
236 Instruments, USA) with excitation wavelength set to 360 nm and emission wavelength set to  
237 460 nm. Enzymatic activity was quantified using standard curves of the reference compounds:  
238 MUF (for β-glucosidase and β-xylosidase) and AMC (for leucine aminopeptidase) (Sigma-  
239 Aldrich, Steinheim, Germany). For each sample, values were corrected by the fluorimetric  
240 signal obtained with formaldehyde-killed sediments (reaction blanks). Sediment DW was

241 determined at the end of analysis to express results as nanomoles of hydrolysed compound (g  
242 of sediment DW)<sup>-1</sup> h<sup>-1</sup>.

243

#### 244 *Statistical analysis*

245 Mixed-model analysis of variance (ANOVA) was used to test the effects of sediment type,  
246 hydrological regime and depth below the sediment surface on water and sediment physical-  
247 chemical and microbial activities. Models were fitted by the restricted maximum likelihood  
248 (REML) method using the “lme” function from the “nlme” package (Pinheiro et al. 2012) in  
249 R version 2.15.0 (R Development Core Team 2012). Sediment type, hydrological regime and  
250 depth were fixed effects and the random error structure was specified as Site/Hydrological  
251 regime/Depth to account for the stratified structure of the data (Crawley 2005). When a  
252 significant effect was observed, post-hoc comparisons of means were conducted with a  
253 Tukey’s test and p-values were adjusted for multiple comparisons using the Holm procedure.  
254 A non-parametric multivariate analysis of variance (PERMANOVA, Anderson 2001) was  
255 performed on the community distance matrix based on Bray-Curtis dissimilarity index to test  
256 the null hypothesis of no difference in the structure of bacterial communities among sediment  
257 types, hydrological regimes and depths below the sediment surface, using the “adonis”  
258 function of the “vegan” package (Oksanen et al. 2012) in R. The “adonis” function also  
259 computes a partial-r<sup>2</sup>, which measured the percentage of total variability in bacterial  
260 community structure that could be accounted for by the effects of sediment type, hydrological  
261 regimes and depths. Patterns in bacterial community structure were visualized using non-  
262 metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrix. A stress  
263 function (which ranges from 0 to 1) was used to assess the goodness-of-fit between the  
264 ordination and the original data. Stress values below 0.2 suggest that the ordination accurately  
265 represents the dissimilarity among samples. Microbial activities were fitted as vectors onto

266 the NMDS ordination of bacterial communities with the “envfit” function of the “vegan”  
267 package. This method allowed us to determine which microbial activities were significantly  
268 correlated with the NMDS ordination of bacterial communities. The “envfit” function returns  
269 a goodness of fit statistic (squared correlation coefficient) and the significance of fitted  
270 vectors is assessed by a permutation test (Oksanen et al. 2012). Fitted vectors were plotted  
271 onto the NMDS ordination of bacterial community structure. The correlation between  
272 sediment OM content and rates of microbial activities was calculated via Pearson’s  
273 correlation coefficients.

274 The links between water and sediment physical-chemistry, microbial activities and bacterial  
275 community structure were examined via Mantel correlation tests between distance matrices.  
276 The main objective was to determine whether these links were modified between permanent  
277 or seasonal flooding and with depth below the sediment surface. Partial Mantel tests were  
278 performed to evaluate whether a significant relationship could be observed (i) between  
279 bacterial community structure and microbial activities after removing the effect of  
280 environmental conditions and (ii) between environmental conditions and microbial activities  
281 after removing the effect of bacterial community structure. The partial Mantel analysis tests  
282 for the correlation between two distance matrices while controlling for the effect of a third  
283 matrix, and is analogous to a partial correlation. The significance of correlation coefficients  
284 was assessed using a permutation procedure. The environmental distance matrix was  
285 calculated as Euclidean distances computed from the table comprising the variables  
286 describing water and sediment physical-chemistry (OM content, Water content, Fine particles  
287 < 50  $\mu\text{m}$ , pH, Specific conductance, Temperature, DOC, DO,  $\text{NH}_4^+$ ,  $\text{NO}_2^-$ ,  $\text{NO}_3^-$ ). The  
288 microbial activity distance matrix was calculated as Euclidean distances computed from the  
289 table comprising the rates of microbial activities (aerobic respiration, denitrification,  
290 nitrification, glucosidase, xylosidase, leucine aminopeptidase). Data were log<sub>10</sub>-transformed

291 or arcsine-transformed (data expressed as percentages) and normalized before the Euclidean-  
292 distance matrices were computed. The community distance matrix was the Bray-Curtis  
293 distance matrix based on the banding pattern obtained by ARISA.

294

## 295 **RESULTS**

### 296 *Water and sediment characteristics*

297 At the time of sampling, no significant effect of hydrological regime was observed on  
298 sediment OM, water content, C:N ratio or percentage of fine particles (<50 $\mu$ m) between  
299 permanent and seasonal plots (Table 1 and 2). OM content increased significantly between  
300 each sediment type (post-hoc Tukey test,  $p < 0.05$ ) in the following order: LoSa < SiLo <  
301 MSiLo. Sediment water content and percentage of fine particles did not significantly differ  
302 between SiLo and MSiLo sediments but were significantly lower in LoSa sediments. OM and  
303 water content decreased with depth in the sediment.

304 Except for dissolved oxygen concentration, water characteristics did not vary significantly  
305 between permanent and seasonal plots (Table 2). ANOVA indicated significant differences  
306 between surface and interstitial waters corresponding to an increase in specific conductance,  
307 nitrite and ammonium concentrations and a decrease in pH with increasing depth in the  
308 sediment. Compared to surface water, the increase in interstitial water DOC concentrations  
309 was only significant in SiLo and MSiLo sediments (Sediment type  $\times$  Depth interaction, post-  
310 hoc Tukey test,  $p < 0.05$ ). Interstitial nitrate concentrations were only significantly lower than  
311 in surface water in MSiLo sediments. Although dissolved oxygen concentrations in surface  
312 water were not different between permanent and seasonal plots, post-hoc Tukey tests  
313 (Hydrological regime  $\times$  Depth interaction) revealed that interstitial waters were more  
314 deoxygenated in permanent than in seasonal plots, but the difference was less than 1 mg  
315 DO.L<sup>-1</sup>. The decrease in dissolved oxygen concentrations between surface and interstitial

316 waters was more pronounced in SiLo and MSiLo sediments (Sediment type  $\times$  Depth  
317 interaction, post-hoc Tukey test,  $p < 0.05$ ). The significant increase in ammonium  
318 concentration with depth in the sediment was more pronounced in permanent SiLo plots  
319 (Figure 2).

320

### 321 *Bacterial community structure*

322 Estimators of OTU richness (number of OTU per sample) and diversity (Shannon-Weaver  
323 index) did not vary significantly among sediment types, hydrological regimes or depths below  
324 the sediment surface (ANOVA,  $p > 0.05$ ). The number of OTU was  $16 \pm 3$  ( $n=108$ ) in average  
325 and ranged between 8 and 25 per sample. Shannon-Weaver index averaged  $2.62 \pm 0.20$   
326 ( $n=108$ ) and ranged between 2.00 and 3.09. NMDS plot and PERMANOVA indicated that  
327 sediment type and hydrological regime had a significant influence on bacterial community  
328 structure (Table 3, Figure 3), with these factors explaining 25% and 4% of total variability  
329 (PERMANOVA), respectively. No significant influence of depth could be detected, but note  
330 that in SiLo and MSiLo sediments, samples collected at the surface layer (0-2cm) and at depth  
331 (5-10cm) clustered together more in permanent plots than seasonal plots.

332

### 333 *Microbial activities*

334 No difference in microbial activities was detected between permanent and seasonal plots  
335 (hydrological regime effect,  $p > 0.05$ , Table 2). We did not detect any effect of hydrological  
336 regime on nitrification potential, but this activity was not observed in SiLo sediments that  
337 were permanently flooded (Figure 4). Excluding nitrification potential, sediment type had a  
338 significant effect on all measured microbial parameters. All microbial parameters decreased  
339 significantly with depth in the sediment (Figure 4). Post-hoc comparisons indicated that  
340 aerobic respiration and denitrification were significantly lower in LoSa sediments, but that

341 both SiLo and MSiLo sediments exhibited comparable values for these parameters.  
342 Glucosidase and xylosidase activities differed significantly between each sediment type, and  
343 increased from LoSa to SiLo and from SiLo to MSiLo sediments (sediment type effect, post-  
344 hoc Tukey test,  $p < 0.05$ ). Post-hoc tests revealed that leucine aminopeptidase activity was  
345 significantly higher in MSiLo than in LoSa sediments (sediment type effect, post-hoc Tukey  
346 test,  $p < 0.05$ ). Rates of leucine aminopeptidase activity in SiLo sediments did not differ  
347 significantly from those of the other sediment types. Rates of aerobic respiration ( $r^2 = 0.72$ ,  $p$   
348  $< 0.001$ ), denitrification ( $r^2 = 0.53$ ,  $p < 0.001$ ), nitrification ( $r^2 = 0.10$ ,  $p = 0.001$ ), glucosidase  
349 activity ( $r^2 = 0.85$ ,  $p < 0.001$ ), xylosidase activity ( $r^2 = 0.87$ ,  $p < 0.001$ ), and leucine  
350 aminopeptidase activity ( $r^2 = 0.55$ ,  $p < 0.001$ ) were significantly correlated to sediment OM  
351 content.

352

353 *Influence of environmental conditions and bacterial community structure on microbial*  
354 *functions*

355 When data from permanent and seasonally inundated conditions were considered together,  
356 results of the vector-fitting procedure (Fig.3) indicated that all microbial activities were  
357 significantly correlated to bacterial community structure (envfit,  $p$ -value  $< 0.001$ ) in the  
358 following order : Glucosidase ( $r^2 = 0.59$ ) > Xylosidase ( $r^2 = 0.53$ ) > Respiration ( $r^2 = 0.52$ ) >  
359 Nitrification ( $r^2 = 0.38$ ) > Denitrification ( $r^2 = 0.35$ ) > Leucine aminopeptidase ( $r^2 = 0.29$ ).  
360 When data from permanent and seasonal inundated conditions were analyzed separately,  
361 results of the partial Mantel analysis indicated that microbial activities were significantly  
362 influenced by environmental conditions under both permanent ( $rM = 0.35$ ,  $p < 0.001$ ) and  
363 seasonal ( $rM = 0.32$ ,  $p < 0.001$ ) inundated conditions. Microbial activities were significantly  
364 influenced by the structure of bacterial communities only in the permanently inundated plots  
365 ( $rM = 0.50$ ,  $p < 0.001$ ), whereas no such relationship was found in the seasonal plots ( $rM =$



366 0.05,  $p = 0.23$ ). The pattern observed in permanently inundated plots remained unchanged  
367 when the two depths within the sediment were considered separately (Figure 5). However, the  
368 analysis indicated that in seasonal plots, microbial activities were significantly influenced by  
369 bacterial community structure at depth within the sediment (5-10 cm,  $rM = 0.13$ ,  $p = 0.04$ ) but  
370 not at the sediment surface (0-2 cm,  $rM = -0.06$ ,  $p = 0.75$ ) (Fig. 5).

371

## 372 **DISCUSSION**

### 373 *Influence of hydrological regime on bacterial community structure*

374 Our first hypothesis stipulating that bacterial community structure would be persistently  
375 impacted by hydrological regime was supported by our results. At the time of sampling,  
376 seasonal plots had been continuously inundated for more than 6 months but still harbored  
377 bacterial communities distinct from those found in permanently inundated plots. This is  
378 consistent with other reports that variations in hydrological regime can drive long-lasting  
379 changes in sediment microbial community structures (Boon et al. 1996; Mentzer et al. 2006;  
380 Rees et al. 2006). For example, Rees et al. (2006) reported that microbial communities in  
381 stream sediments submitted to a 2-month drought had not fully returned to their pre-drought  
382 structure up to one month after rewetting. In our case, one would have expected that an  
383 extended time of sediment submersion and exposure to similar environmental conditions  
384 would allow a convergence of bacterial community structures between permanently and  
385 seasonally inundated plots. Several authors suggest that the increased environmental  
386 variability associated with dry-wet cycles constitutes a physiological stressor for  
387 microorganisms through, among other things, changes in water potential or the alternation of  
388 aerobic and anaerobic conditions within the sediment profile (Sundh et al. 1997; Schimel et  
389 al. 2007). The persistent change in community structure observed in the present study  
390 suggests that seasonal dry-wet cycles could have favored the growth of a portion of the

391 bacterial community able to cope with the associated environmental stress. However, despite  
392 a long-standing influence of hydrological regime, sediment type was found to account for the  
393 greatest part of the variability in bacterial community structure. In addition, among the  
394 environmental parameters measured in this study, sediment OM content emerged as a key  
395 driver of bacterial community structure. Through their influence on colonizable surface and  
396 substrate availability, soil type and OM content have been reported as major determinants of  
397 microbial community structure in terrestrial ecosystems (Bossio et al. 1998; Sessitsch et al.  
398 2001; Girvan et al. 2003; Johnson et al. 2003; Marschner et al. 2003). Our results suggest that  
399 the primary drivers of microbial community structure in sediment could be the same as those  
400 observed in soils, and that hydrological variations could have less profound effect than the  
401 variations induced by sediment composition and structure. It is unclear whether plant species  
402 composition in wetlands and riparian areas can influence microbial community structure in  
403 wetland sediments (Gutknecht et al. 2006). Changes in plant community structure driven by  
404 variations in hydrological regime could modify the composition of organic matter inputs to  
405 sediment microbial communities and indirectly result in a change in bacterial community  
406 structure. C:N ratio varied between sediment types, but not between between permanent and  
407 seasonal plots, suggesting that changes in bacterial community structure between permanent  
408 and seasonal plots reflected differences in hydrological regime rather than a change in organic  
409 matter composition resulting from a change in plant community composition.

410 In contrast with other studies in soil (Fierer et al. 2003b; Bossio et al. 2006), depth in the  
411 sediment was not found to be a strong determinant of bacterial community structure. Fierer et  
412 al. (2003b) suggested that decreasing C availability with depth selected for different microbial  
413 groups along soil profiles. However, these authors also suggested that the frequent variations  
414 in water availability such as those occurring at the soil surface could be an important control  
415 on the composition of microbial communities through the selection of microbial groups able

416 to cope with moisture stress. In the present study, despite a lack of interaction between depth  
417 and sediment type, the NMDS plot indicated that changes in bacterial community structure  
418 with depth in the sediment were apparently more marked in seasonally-inundated sediments.  
419 In comparison with the stable environmental conditions associated with permanent inundated  
420 conditions, it is likely that the increase in environmental variability induced by dry-wet cycles  
421 was more pronounced at the sediment surface than at depth in the sediment profile in seasonal  
422 plots. This mechanism could have resulted in a stronger divergence between bacterial  
423 community structures found at sediment surface than those observed at depth in the sediment  
424 profile and submitted to relatively more stable environmental conditions.

425

#### 426 *Influence of hydrological regime on microbial functions*

427 Contrary to what we expected, rates of microbial activities were not related to hydrological  
428 regime, whatever the microbial activity considered, indicating that microbial communities in  
429 seasonal plots exhibited equivalent metabolic capacities to microbial communities found in  
430 permanently inundated plots. Most studies evaluating the impact of drying events on  
431 microbial metabolism have reported equivocal results, with some but not all reporting a rapid  
432 recovery of microbial activities upon sediment rewetting (Larned et al. 2007; Austin &  
433 Strauss 2010; Fromin et al. 2010; Marxsen et al. 2010). For example, Marxsen et al. (2010)  
434 showed that rates of bacterial production and extracellular enzymatic activities in previously-  
435 dried sediments of a Central European stream exhibited comparable rates to those in  
436 permanently wet sediments within 4 days after rewetting, whereas sediments from a  
437 Mediterranean stream were unable to recover during this time interval. Here, the extended  
438 inundated period since the previous drying event was probably long enough to observe  
439 equivalent metabolic capacities between permanent and seasonal plots. The only argument in  
440 favor of an influence of hydrological regime on microbial activities was the lack of

441 nitrification activity in permanently inundated SiLo sediments, possibly because a low level  
442 of oxygen inhibited the aerobic processes. Even though potential nitrification was measured  
443 in aerobic conditions, it is also possible that SiLo sediments maintained anaerobic micro-sites  
444 where active denitrifying communities would have consumed products of nitrification.  
445 However, permanently inundated MSiLo sediments exhibited the highest rates of potential  
446 nitrification measured in this study and had similar interstitial oxygen concentration and  
447 denitrification rates than in SiLo sediments. Further research should explore whether the lack  
448 of measurable nitrification activity in permanently inundated SiLo sediments reflected a lower  
449 abundance of nitrifiers than in seasonal SiLo sediments.  
450 In the present study, the rates of biogeochemical processes implicated in OM decomposition  
451 and nutrient recycling were strongly correlated to sediment type and depth, which may reflect  
452 the positive influence of sediment OM content on heterotrophic activities. Indeed, Findlay et  
453 al. (2003) showed that OM availability was an important determinant of sediment microbial  
454 activities. In contrast with the other microbial parameters measured in this study, potential  
455 nitrification did not vary significantly with sediment type or depth, and was poorly correlated  
456 with sediment OM content. This finding likely reflects the fact that under high levels of OM,  
457 the benefit of increased ammonium availability through mineralization can be counteracted by  
458 a limited oxygen availability resulting from increased activities of heterotrophic  
459 microorganisms under conditions of high carbon availability.

460

461 *Links between environmental conditions, bacterial community structure and microbial*  
462 *activities*

463 Few studies have attempted to simultaneously examine the structure and functioning of  
464 bacterial communities in wetland sediments (Gutknecht et al. 2006; Kjellin et al. 2007; Ruiz-  
465 Rueda et al. 2009). The results obtained here contribute to the long-standing debate on the

466 relative importance of environmental factors and microbial community structure on  
467 ecosystem functioning (Ekschmitt & Griffiths 1998). The high degree of functional  
468 redundancy within microbial communities is usually considered to limit the coupling between  
469 structure and function (Allison & Martiny 2008), which implies that rates of biogeochemical  
470 processes would mainly be driven by environmental factors. However, a previous study  
471 conducted in a wetland mitigation bank reported that general bacterial community structure  
472 assessed by molecular fingerprint (16S rRNA-based T-RFLP) accounted for 40% of the  
473 variation in potential denitrification rates (Peralta et al. 2010). Without denying the  
474 importance of environmental conditions, the present results add to an increasing body of  
475 literature suggesting that the structure of bacterial communities can at least partially drive  
476 biogeochemical functioning. Multivariate analyses revealed that all microbial activities,  
477 including denitrification and nitrification rates, were significantly correlated to bacterial  
478 community structure. The detection limit of ARISA ranges theoretically between 0.1 and 1%  
479 (Fuhrman 2009) but, as other molecular fingerprinting methods, ARISA can not provide  
480 taxonomic identification and it is unknown whether OTUs belonging to denitrifiers or  
481 nitrifiers were detected in the present study. Based on the cumulated abundance of nirK and  
482 nirS nitrite reductase gene copy number, recent studies reported denitrifiers to make up to 5 %  
483 of the total bacterial community in soils (Henry et al. 2006; Baudoin et al. 2009). A growing  
484 body of data suggests that freshwater sediments are enriched with nitrite-oxidizing bacteria  
485 belonging to *Nitrospira* (Wang et al. 2012) that could represent up to 10 % of the total  
486 bacterial community (Altmann et al. 2003; Tamaki et al. 2005). Although such values would  
487 theoretically allow the detection of nitrifiers and denitrifiers by ARISA, it can not be  
488 concluded whether the correlation of denitrification and nitrification rates with bacterial  
489 community structure reflected the occurrence of OTUs belonging to denitrifying or nitrifying

490 groups, or whether it reflected cooperative activities (such as cross-feeding) or common  
491 environmental preferences with OTUs belonging to other bacterial groups (Fuhrman 2009).  
492 Our results indicate that the increased environmental variability associated with drying-  
493 rewetting cycles in seasonal wetlands could attenuate, especially in the upper layer of  
494 sediment, the link between the structure and the functioning of bacterial communities.  
495 Langenheder et al. (2005) suggest that the presence of generalist species that are able to cope  
496 with a wide range of environmental conditions may explain the decoupling between bacterial  
497 community structure and functioning in aquatic ecosystems. In the present study, we  
498 demonstrated that the stable environmental conditions prevailing in permanently inundated  
499 situations could strengthen the link between the structure and the functioning of sediment  
500 bacterial communities. However, the observed difference in bacterial community structure  
501 between permanent and seasonal plots was not associated with a marked contrast in the rates  
502 of biogeochemical processes. A possible explanation may be that the moderate change in  
503 bacterial community structure was not strong enough to induce a marked shift in  
504 biogeochemical functioning. Another explanation would be that the observed structural  
505 change was related to bacterial taxa responding to the variations in environmental conditions  
506 during dry-wet cycles but that these taxa were not strongly associated with the  
507 biogeochemical processes that were monitored here. While no OTUs were exclusively related  
508 to permanent or seasonal plots, multivariate analyses indicated that the relative abundance of  
509 a few OTUs increased in permanently inundated sediments. A further step of 16S rDNA  
510 sequencing may help to identify the ecological role of the bacterial groups responsible for the  
511 differences in bacterial community structure under varying hydrological regimes.  
512

## 513 **CONCLUSIONS**

514 This study revealed a persistent change in bacterial community structure between  
515 permanently inundated sediments and sediments submitted to seasonal dewatering. However,  
516 this compositional shift was not related to a marked change in the microbial functions  
517 involved in the C and N cycles. This finding suggested that bacterial taxa responding to  
518 dewatering were not necessarily implicated in the biogeochemical processes monitored in this  
519 study. Our conclusions raise the question of whether this observed structural change would  
520 confer a better resistance to subsequent drying stress for microbial communities in seasonally  
521 dewatered sediments. Indeed, microbial communities that are regularly exposed to drying  
522 events appear to be more resistant to this stress than communities that have never experienced  
523 this stress (Lundquist et al. 1999; Schimel et al. 2007). A next important step will be to assess  
524 the relative resistance to drying stress of bacterial communities found in permanently  
525 inundated sediments and those found in seasonally dewatered samples.

526

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534

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786 **TABLE LEGENDS**

787 **Table 01:** Physical-chemistry of water and sediment in permanent and seasonal plots. Values  
788 are expressed as means  $\pm$  SE of three independent sites.

789 **Table 02:** Results of mixed-model ANOVA testing the effects of sediment type, hydrological  
790 regime and depth below the sediment surface on water and sediment physical-chemistry and  
791 rates of microbial activities.

792 **Table 03:** Results of a non-parametric multivariate analysis of variance (MANOVA) testing  
793 the effects of sediment type, hydrological regime and depth below the sediment surface on  
794 bacterial community structure.

795 **FIGURE LEGENDS**

796 **Figure 01:** Location of the Ain département in France (left panel), and description of the  
797 study area showing location of sampling sites (right panel). Sediment type is indicated for  
798 each site.

799 **Figure 02:** Sediment organic matter content, percentage of fine particles, dissolved organic  
800 carbon, dissolved oxygen, nitrates and ammonium concentrations measured at the sediment  
801 surface and at depth in the sediment on permanent and seasonal plots in three sediment types.  
802 Values are expressed as means  $\pm$  SE of three independent sites.

803 **Figure 03:** Non-metric multidimensional scaling ordination plot comparing bacterial  
804 community structure between sediment type, hydrological regime and depths below the  
805 sediment surface. Stress value indicates the concordance between the distance among samples  
806 in the plot and the actual Bray-Curtis distance among samples. Stress values below 0.2  
807 suggest that the ordination accurately represents the dissimilarity among samples. Rates of  
808 microbial activities were incorporated in the analysis with a vector-fitting procedure. The  
809 length of the arrow is proportional to the correlation between the corresponding activity and  
810 bacterial community structure. RESP (aerobic respiration) – DEN (denitrification) – NIT  
811 (nitrification) – GLU (glucosidase) – XYL (xylosidase) – LAP (leucine aminopeptidase).

812 **Figure 04:** Rates of aerobic respiration, nitrification, denitrification, glucosidase, xylosidase  
813 and peptidase activities measured at two depths below the sediment surface for permanent and  
814 seasonal plots in three sediment types. Values are expressed as means  $\pm$  SE of three  
815 independent sites.

816 **Figure 05:** Partial Mantel analysis showing the relationships between environmental  
817 conditions, bacterial community structure and microbial activities in permanent (left panel)  
818 and seasonal (right panel) plots. Partial Mantel correlation coefficients (rM) and p-values are  
819 indicated. A broken line indicates a non-significant relationship.

820 **Table 01:**

	Loamy Sand (LoSa)				Silt Loam (SiLo)				Mucky Silt Loam (MSiLo)			
	Permanent		Seasonal		Permanent		Seasonal		Permanent		Seasonal	
	0-2 cm	5-10 cm	0-2 cm	5-10 cm	0-2 cm	5-10 cm	0-2 cm	5-10 cm	0-2 cm	5-10 cm	0-2 cm	5-10 cm
<b>Sediment characteristics</b>												
Organic Matter content (%)	3.7 ± 0.8	2.4 ± 0.6	5.3 ± 2	2.7 ± 0.5	9.3 ± 1.2	7.3 ± 0.4	11.6 ± 2.3	8.7 ± 1.9	24.4 ± 5.7	17.3 ± 4.6	16.2 ± 2	12.9 ± 2.5
Nitrogen content (%)	0.12 ± 0.05	0.05 ± 0.02	0.17 ± 0.07	0.06 ± 0.02	0.42 ± 0.07	0.26 ± 0.05	0.47 ± 0.12	0.30 ± 0.11	0.89 ± 0.19	0.55 ± 0.12	0.61 ± 0.07	0.47 ± 0.12
Water content (%)	37.7 ± 7.8	27.7 ± 4.7	40.5 ± 8.7	25.6 ± 5.9	68.8 ± 2.6	56.2 ± 5.3	70.7 ± 4.2	56.9 ± 6.7	81.4 ± 2.9	72.3 ± 4.5	71.7 ± 2.7	64.6 ± 4.8
Fine particles < 50µm (%)	26.7 ± 10.1	17.5 ± 8.3	21.4 ± 6.2	12.4 ± 3	70.4 ± 6.7	63.9 ± 7.3	74.2 ± 5.2	79.6 ± 4.8	75.9 ± 4.6	80.7 ± 1.6	70.4 ± 5.9	77.2 ± 5.6
<b>Water characteristics</b>												
pH	7.85 ± 0.21	7.61 ± 0.06	7.76 ± 0.09	7.60 ± 0.15	7.74 ± 0.05	7.11 ± 0.13	7.67 ± 0.09	7.45 ± 0.07	7.59 ± 0.07	7.48 ± 0.09	7.6 ± 0.05	7.33 ± 0.16
Temperature (°C)	18.0 ± 3.5	17.0 ± 1.7	10.8 ± 1.1	15.2 ± 1.1	14.2 ± 1.7	15.9 ± 1.8	12.2 ± 1.3	14.9 ± 0.7	13.2 ± 1.5	16.5 ± 1.2	13.8 ± 1.1	17.8 ± 0.7
Specific Conductance (µS.cm <sup>-1</sup> )	453.3 ± 33.3	527.1 ± 34.8	471.3 ± 15.9	562.8 ± 41.5	490.7 ± 44.2	695.7 ± 94.6	529.7 ± 61.9	515.4 ± 27.1	531 ± 16.1	577.1 ± 36.5	543 ± 18.7	634.7 ± 94.1
Dissolved Organic Carbon (mg L <sup>-1</sup> )	2.62 ± 0.82	2.42 ± 0.48	2.58 ± 0.69	2.91 ± 0.76	2.39 ± 0.27	5.29 ± 2.28	2.33 ± 0.31	2.72 ± 0.28	1.9 ± 0.61	4.75 ± 0.97	2.72 ± 1.12	4.75 ± 2.33
Dissolved Oxygen (mg L <sup>-1</sup> )	7.51 ± 1.36	4.61 ± 1.13	8.58 ± 1.59	5.92 ± 1.46	9.78 ± 1.27	1.71 ± 0.51	8.59 ± 1.44	4.58 ± 1.52	6.42 ± 1.33	2.3 ± 0.69	6.3 ± 1.28	3.38 ± 1.18
Ammonium (mg L <sup>-1</sup> )	0.02 ± 0.02	0.08 ± 0.07	0.02 ± 0.01	0.08 ± 0.06	0.02 ± 0.01	3.78 ± 2.39	0.00 ± 0.00	0.09 ± 0.06	0.01 ± 0.01	0.97 ± 0.6	0.01 ± 0.01	0.74 ± 0.59
Nitrites (mg L <sup>-1</sup> )	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.01	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.03 ± 0.02	0.02 ± 0.01	0.04 ± 0.03	0.01 ± 0.01	0.06 ± 0.03
Nitrates (mg L <sup>-1</sup> )	4.00 ± 2.00	4.46 ± 2.19	2.70 ± 2.34	2.83 ± 2.14	4.33 ± 1.88	1.47 ± 1.35	2.37 ± 1.15	2.22 ± 1.74	10.64 ± 1.55	1.82 ± 2.11	11.47 ± 1.42	3.36 ± 2.25

822 **Table 02:**

	Sediment Type		Hydrological Regime		Depth		Sediment Type × Hydrological Regime		Sediment Type × Depth		Hydrological Regime × Depth		Sediment Type × Hydrological Regime × Depth	
	F(2,6)	p-value	F(1,6)	p-value	F(1,12)	p-value	F(2,6)	p-value	F(2,12)	p-value	F(1,12)	p-value	F(2,12)	p-value
<b>Sediment characteristics</b>														
Organic matter content	31.38	<b>0.001</b>	0.00	0.949	33.02	<b>&lt;0.0001</b>	3.18	0.115	0.70	0.515	0.07	0.801	0.38	0.689
Nitrogen content	20.79	<b>0.002</b>	0.13	0.729	38.25	<b>&lt;0.0001</b>	1.89	0.230	0.02	0.980	0.07	0.801	0.84	0.454
C:N ratio	8.15	<b>0.019</b>	0.00	0.979	43.42	<b>&lt;0.0001</b>	0.23	0.797	7.32	<b>0.008</b>	0.00	0.970	0.25	0.784
Water content	25.67	<b>0.001</b>	1.10	0.335	49.86	<b>&lt;0.0001</b>	1.90	0.230	0.70	0.514	0.13	0.725	0.60	0.566
Fine particles < 50µm	112.39	<b>&lt;0.0001</b>	0.00	0.974	0.14	0.715	2.63	0.151	1.54	0.253	2.33	0.153	2.81	0.100
<b>Water characteristics</b>														
pH	3.46	0.100	0.01	0.909	18.80	<b>0.001</b>	1.15	0.379	1.69	0.225	0.70	0.418	1.81	0.206
Specific Conductance	1.66	0.267	0.00	0.989	10.98	<b>0.006</b>	1.46	0.305	0.19	0.833	1.14	0.306	2.22	0.151
Temperature	0.22	0.806	1.53	0.263	18.02	<b>0.001</b>	1.44	0.308	0.39	0.683	3.38	0.091	1.30	0.308
Dissolved Organic Carbon	0.19	0.831	0.12	0.744	26.14	<b>&lt;0.0001</b>	0.60	0.580	6.63	<b>0.012</b>	2.84	0.118	1.68	0.227
Dissolved Oxygen	0.93	0.443	6.93	<b>0.039</b>	111.06	<b>&lt;0.0001</b>	0.47	0.644	7.29	<b>0.008</b>	7.70	<b>0.017</b>	2.68	0.109
Ammonium	2.76	0.141	5.09	0.065	17.36	<b>0.001</b>	3.79	0.086	3.49	0.064	4.69	0.051	3.51	0.063
Nitrites	5.53	<b>0.043</b>	0.23	0.648	8.30	<b>0.014</b>	0.11	0.895	1.26	0.318	0.40	0.540	0.15	0.859
Nitrates	0.72	0.524	0.24	0.640	16.12	<b>0.002</b>	1.28	0.345	10.02	<b>0.003</b>	0.99	0.339	0.26	0.773
<b>Microbial activities</b>														
Aerobic respiration	11.49	<b>0.009</b>	2.78	0.147	62.50	<b>&lt;0.0001</b>	1.77	0.249	1.41	0.282	0.18	0.677	0.12	0.892
Denitrification	9.29	<b>0.015</b>	0.33	0.589	88.74	<b>&lt;0.0001</b>	0.19	0.832	0.98	0.404	0.17	0.687	0.08	0.925
Nitrification	1.04	0.410	0.18	0.684	5.52	<b>0.037</b>	3.12	0.118	0.62	0.556	0.06	0.814	1.28	0.313
Glucosidase	54.99	<b>&lt;0.0001</b>	0.71	0.431	49.82	<b>&lt;0.0001</b>	0.56	0.596	3.71	0.056	0.09	0.771	0.39	0.687
Xylosidase	69.38	<b>&lt;0.0001</b>	0.10	0.760	76.62	<b>&lt;0.0001</b>	0.98	0.428	0.81	0.469	0.03	0.867	0.50	0.617
Leucine Aminopeptidase	12.18	<b>0.008</b>	0.27	0.622	50.86	<b>&lt;0.0001</b>	0.07	0.934	2.81	0.100	0.02	0.884	0.12	0.889

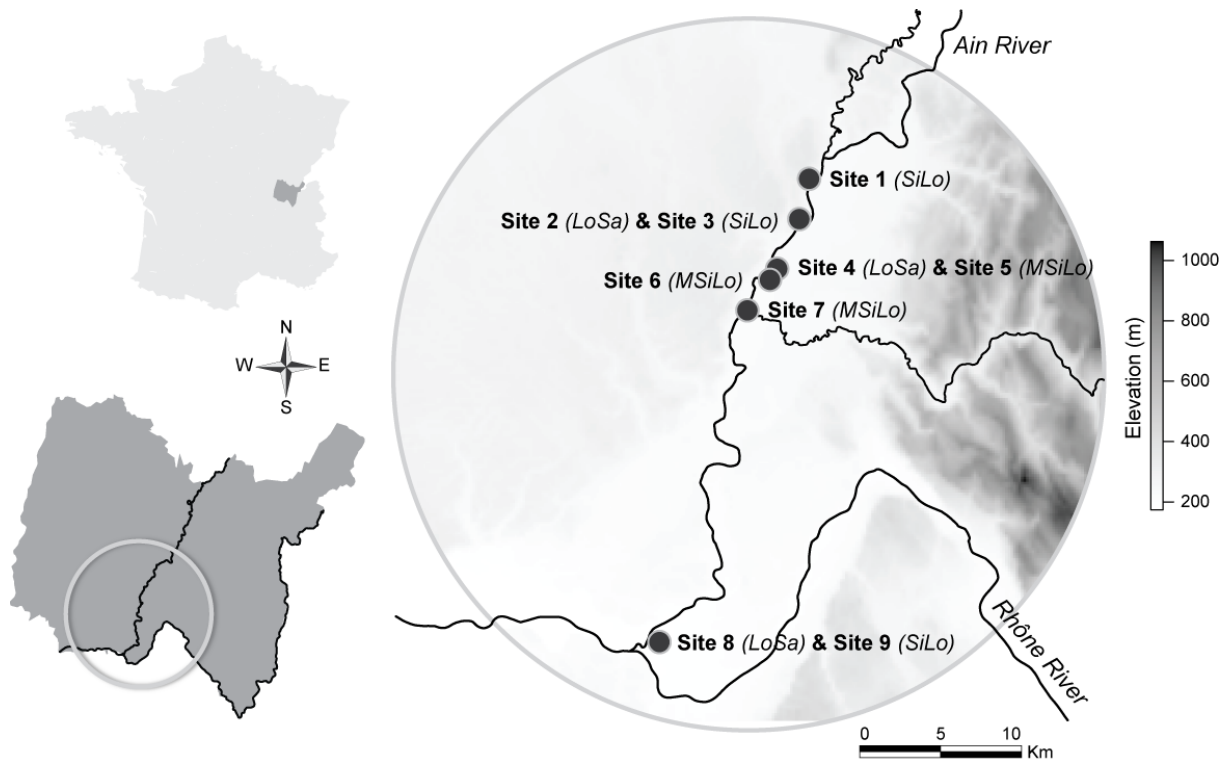


824 **Table 03:**

	Bacterial community structure		
	df	F	p
<b>Sediment Type</b>	2	19.67	<b>0.001</b>
<b>Hydrological Regime</b>	1	6.08	<b>0.001</b>
<b>Depth</b>	1	1.31	0.225
<b>Sediment Type × Hydrological Regime</b>	2	3.00	<b>0.002</b>
<b>Sediment Type × Depth</b>	2	0.95	0.497
<b>Hydrological Regime × Depth</b>	1	1.10	0.359
<b>Sediment Type × Hydrological Regime × Depth</b>	2	0.63	0.892
<b>Residuals</b>	96		

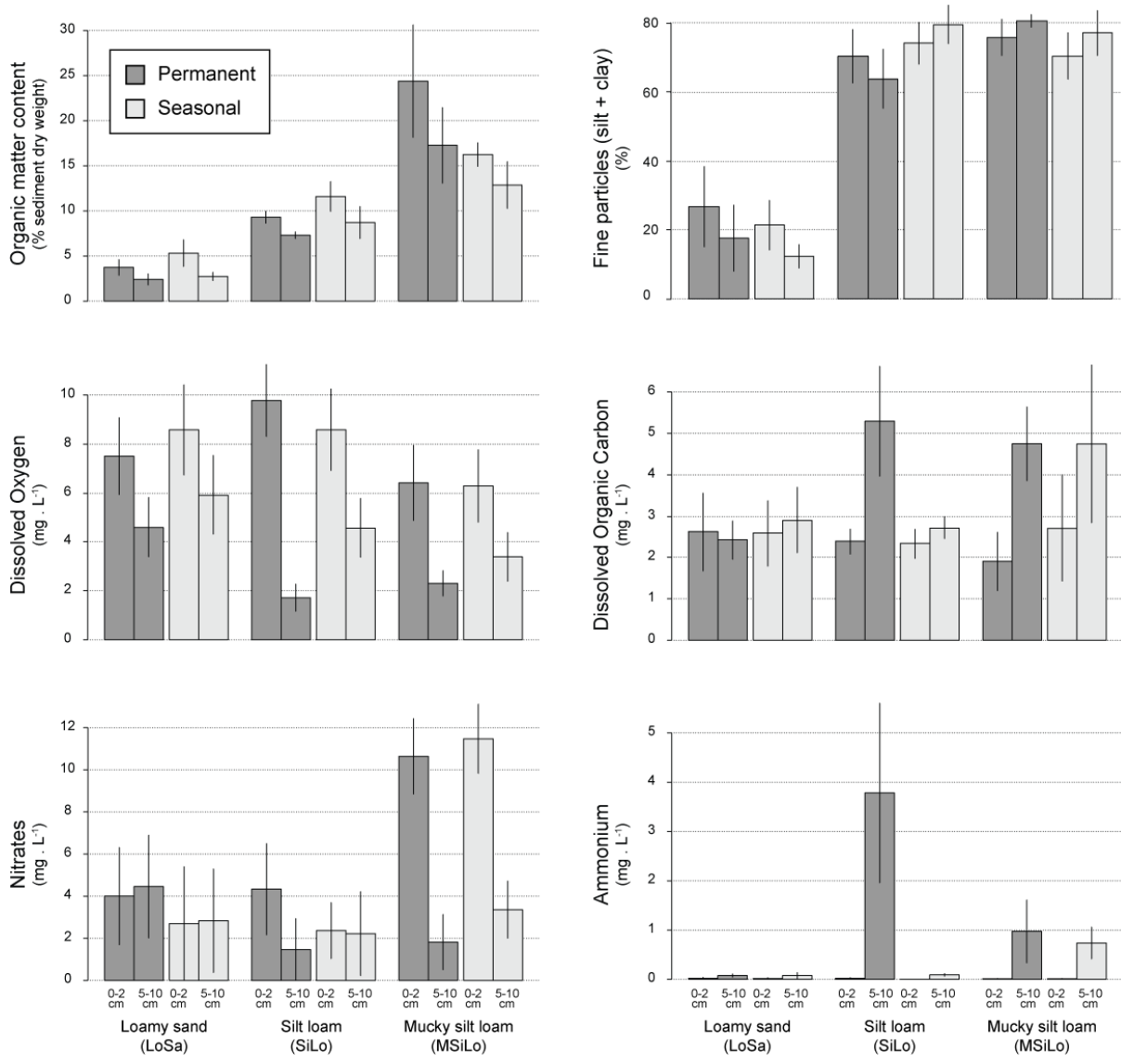
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826 **Figure 01:**



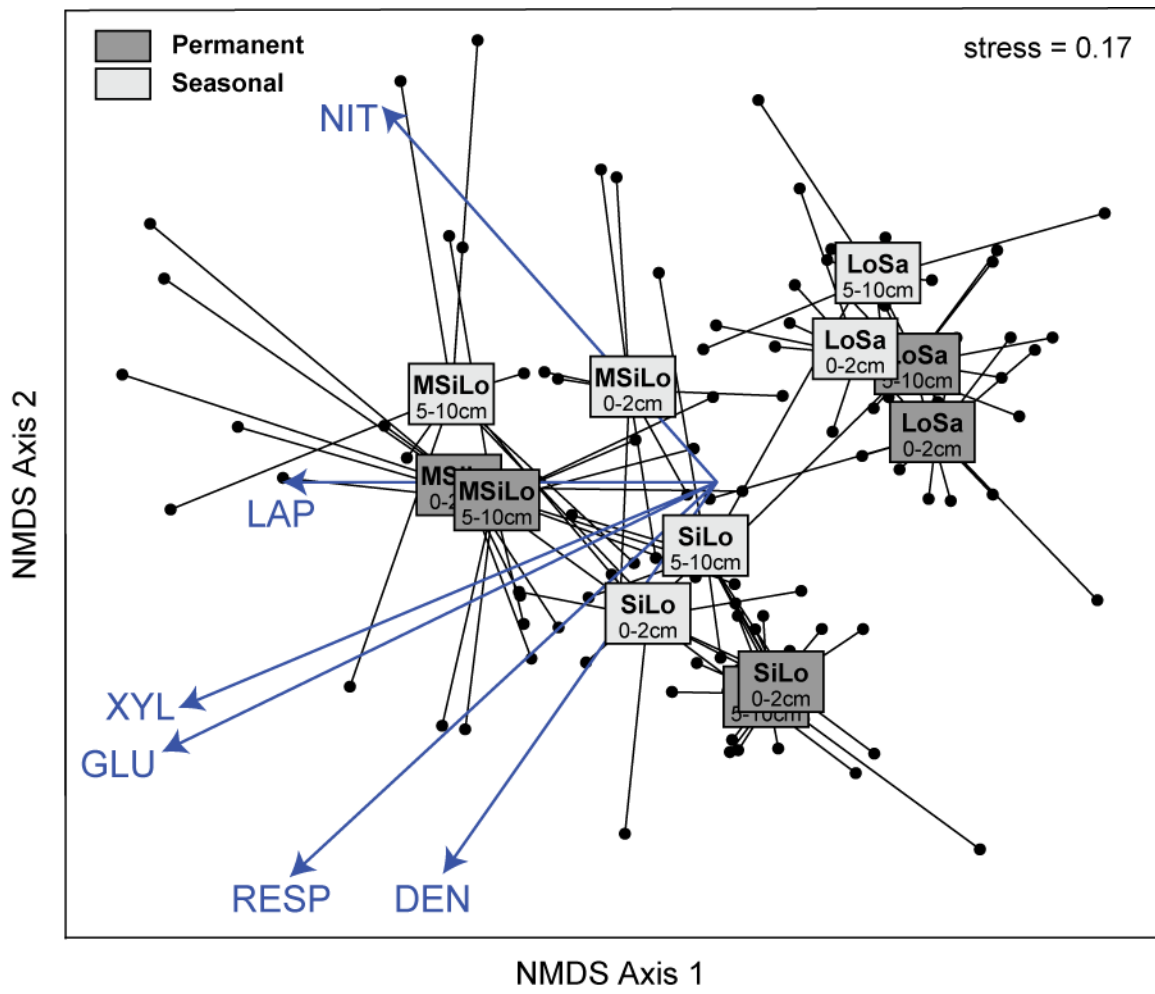
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828 **Figure 02:**

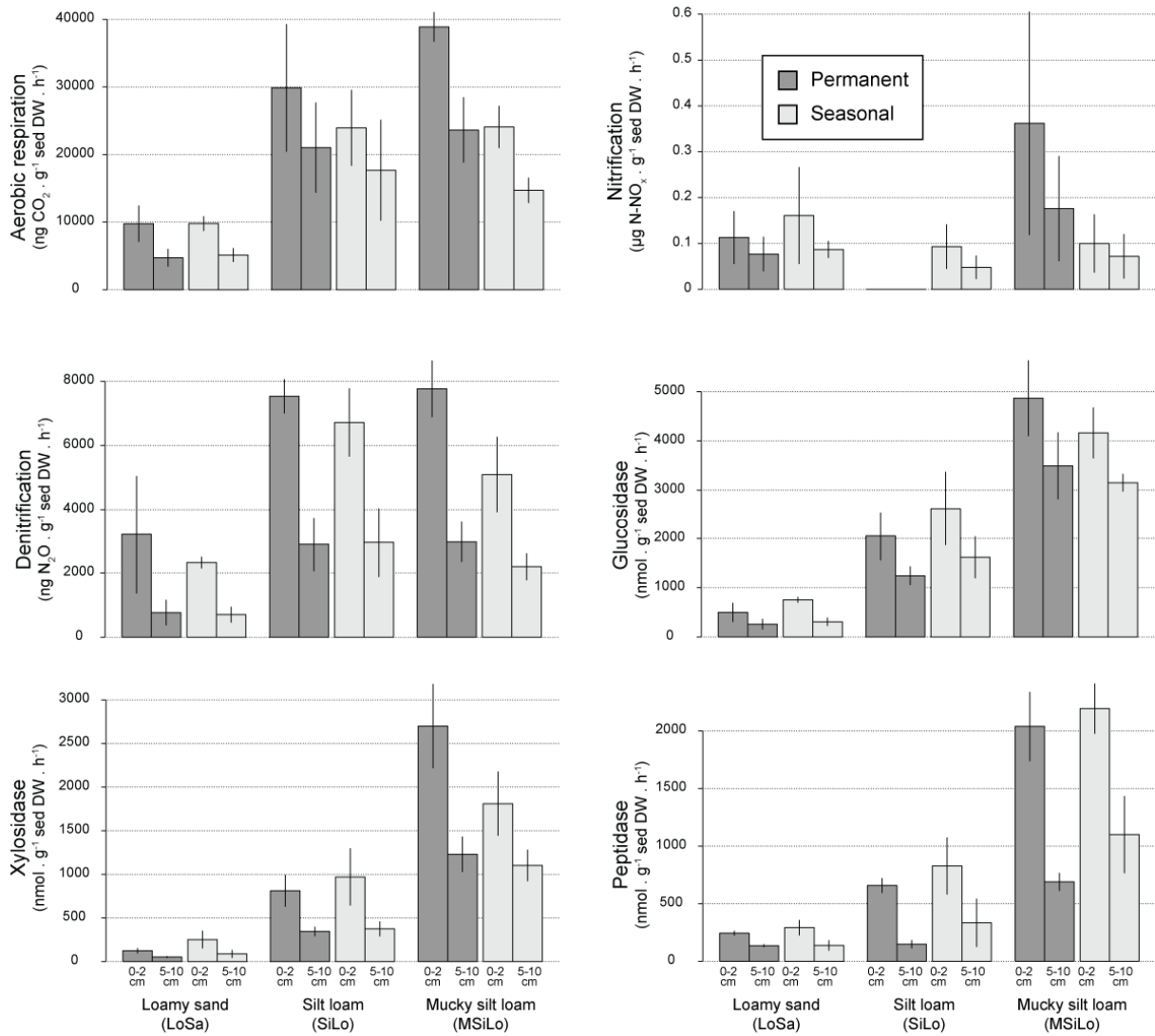


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830 **Figure 03:**



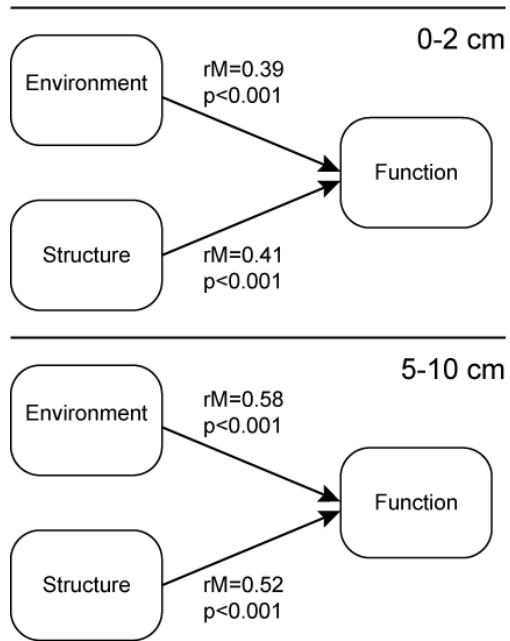
832 **Figure 04:**



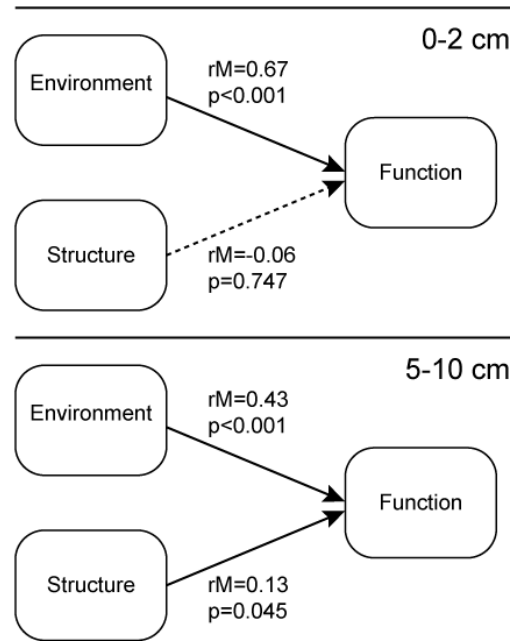
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834 **Figure 05:**

### Permanent



### Seasonal



835