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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 (NH_4^+) was determined using the
157 spectrophotometric indophenol blue method according to NF T 90-015-2. Nitrite (NO_2^-) was
158 determined by colorimetric method according to NF EN 26777. Nitrate (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 μm 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 μL containing a $10 \times$ *Taq* reaction buffer (GE Healthcare),

180 1.5 mM MgCl_2 , 200 μM of each deoxynucleotide, 0.2 μM of each primer, bovine serum

181 albumin (Sigma, 0.3 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 KNO₃ (2.16
202 g.L⁻¹) solution (denitrification). For the measurements of CO₂ production (aerobic
203 respiration), incubation was conducted under aerobic conditions. For the measurements of
204 N₂O 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 (C₂H₂, 10% v/v final volume) was added to inhibit N₂O 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 CO₂ and N₂O (g of sediment dry weight (DW))⁻¹ h⁻¹, 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 (NH₄)₂SO₄.

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_x (NO₂⁻
219 + NO₃⁻) 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 NO₂⁻ and NO₃⁻ 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_x (g of sediment DW)⁻¹ h⁻¹.

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)⁻¹ h⁻¹.

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-r², 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 μm , pH, Specific conductance, Temperature, DOC, DO, NH_4^+ , NO_2^- , 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 log₁₀-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 μ 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⁻¹. 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 ± 3 ($n=108$) in average
325 and ranged between 8 and 25 per sample. Shannon-Weaver index averaged 2.62 ± 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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785

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
Sediment characteristics												
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
Water characteristics												
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 ⁻¹)	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 ⁻¹)	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 ⁻¹)	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 ⁻¹)	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 ⁻¹)	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 ⁻¹)	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:**

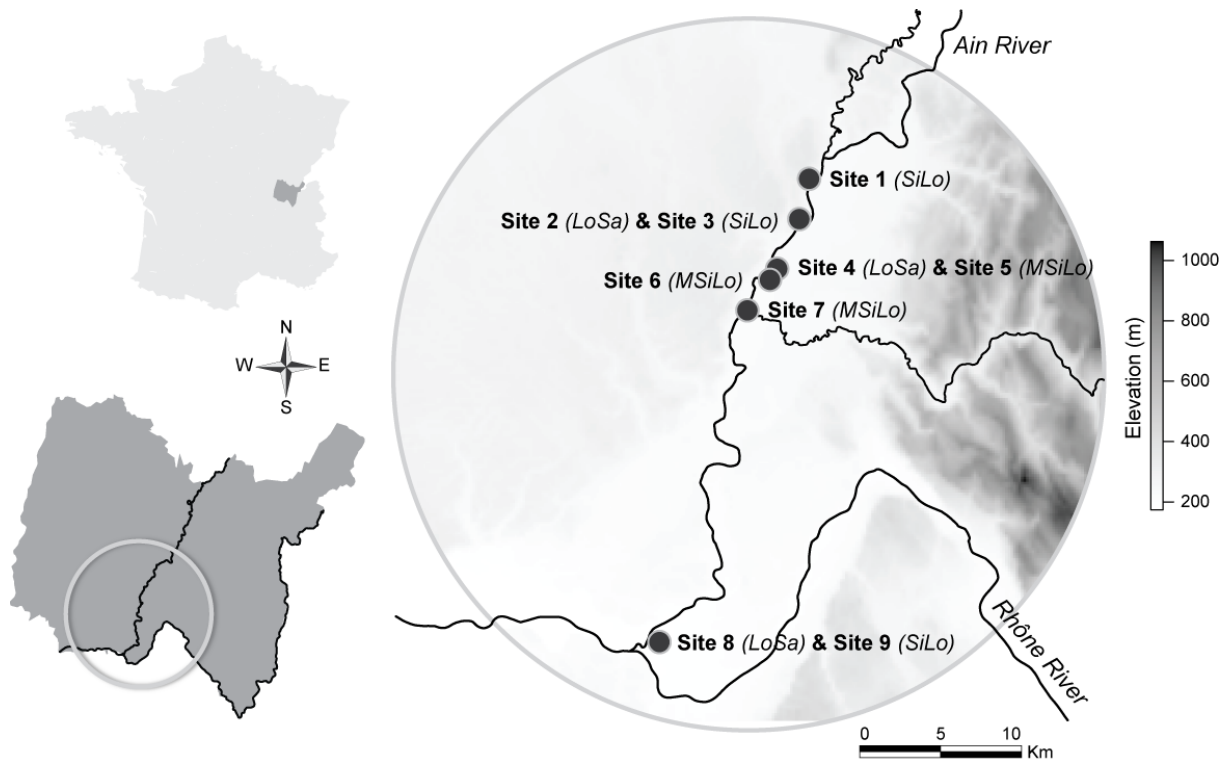
	Sediment Type		Hydrological Regime		Depth		Sediment Type × Hydrological Regime		Sediment Type × Depth		Hydrological Regime × Depth		Sediment Type × Hydrological Regime × Depth	
	F(2,6)	p-value	F(1,6)	p-value	F(1,12)	p-value	F(2,6)	p-value	F(2,12)	p-value	F(1,12)	p-value	F(2,12)	p-value
Sediment characteristics														
Organic matter content	31.38	0.001	0.00	0.949	33.02	<0.0001	3.18	0.115	0.70	0.515	0.07	0.801	0.38	0.689
Nitrogen content	20.79	0.002	0.13	0.729	38.25	<0.0001	1.89	0.230	0.02	0.980	0.07	0.801	0.84	0.454
C:N ratio	8.15	0.019	0.00	0.979	43.42	<0.0001	0.23	0.797	7.32	0.008	0.00	0.970	0.25	0.784
Water content	25.67	0.001	1.10	0.335	49.86	<0.0001	1.90	0.230	0.70	0.514	0.13	0.725	0.60	0.566
Fine particles < 50µm	112.39	<0.0001	0.00	0.974	0.14	0.715	2.63	0.151	1.54	0.253	2.33	0.153	2.81	0.100
Water characteristics														
pH	3.46	0.100	0.01	0.909	18.80	0.001	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	0.006	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	0.001	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	<0.0001	0.60	0.580	6.63	0.012	2.84	0.118	1.68	0.227
Dissolved Oxygen	0.93	0.443	6.93	0.039	111.06	<0.0001	0.47	0.644	7.29	0.008	7.70	0.017	2.68	0.109
Ammonium	2.76	0.141	5.09	0.065	17.36	0.001	3.79	0.086	3.49	0.064	4.69	0.051	3.51	0.063
Nitrites	5.53	0.043	0.23	0.648	8.30	0.014	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	0.002	1.28	0.345	10.02	0.003	0.99	0.339	0.26	0.773
Microbial activities														
Aerobic respiration	11.49	0.009	2.78	0.147	62.50	<0.0001	1.77	0.249	1.41	0.282	0.18	0.677	0.12	0.892
Denitrification	9.29	0.015	0.33	0.589	88.74	<0.0001	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	0.037	3.12	0.118	0.62	0.556	0.06	0.814	1.28	0.313
Glucosidase	54.99	<0.0001	0.71	0.431	49.82	<0.0001	0.56	0.596	3.71	0.056	0.09	0.771	0.39	0.687
Xylosidase	69.38	<0.0001	0.10	0.760	76.62	<0.0001	0.98	0.428	0.81	0.469	0.03	0.867	0.50	0.617
Leucine Aminopeptidase	12.18	0.008	0.27	0.622	50.86	<0.0001	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
Sediment Type	2	19.67	0.001
Hydrological Regime	1	6.08	0.001
Depth	1	1.31	0.225
Sediment Type × Hydrological Regime	2	3.00	0.002
Sediment Type × Depth	2	0.95	0.497
Hydrological Regime × Depth	1	1.10	0.359
Sediment Type × Hydrological Regime × Depth	2	0.63	0.892
Residuals	96		

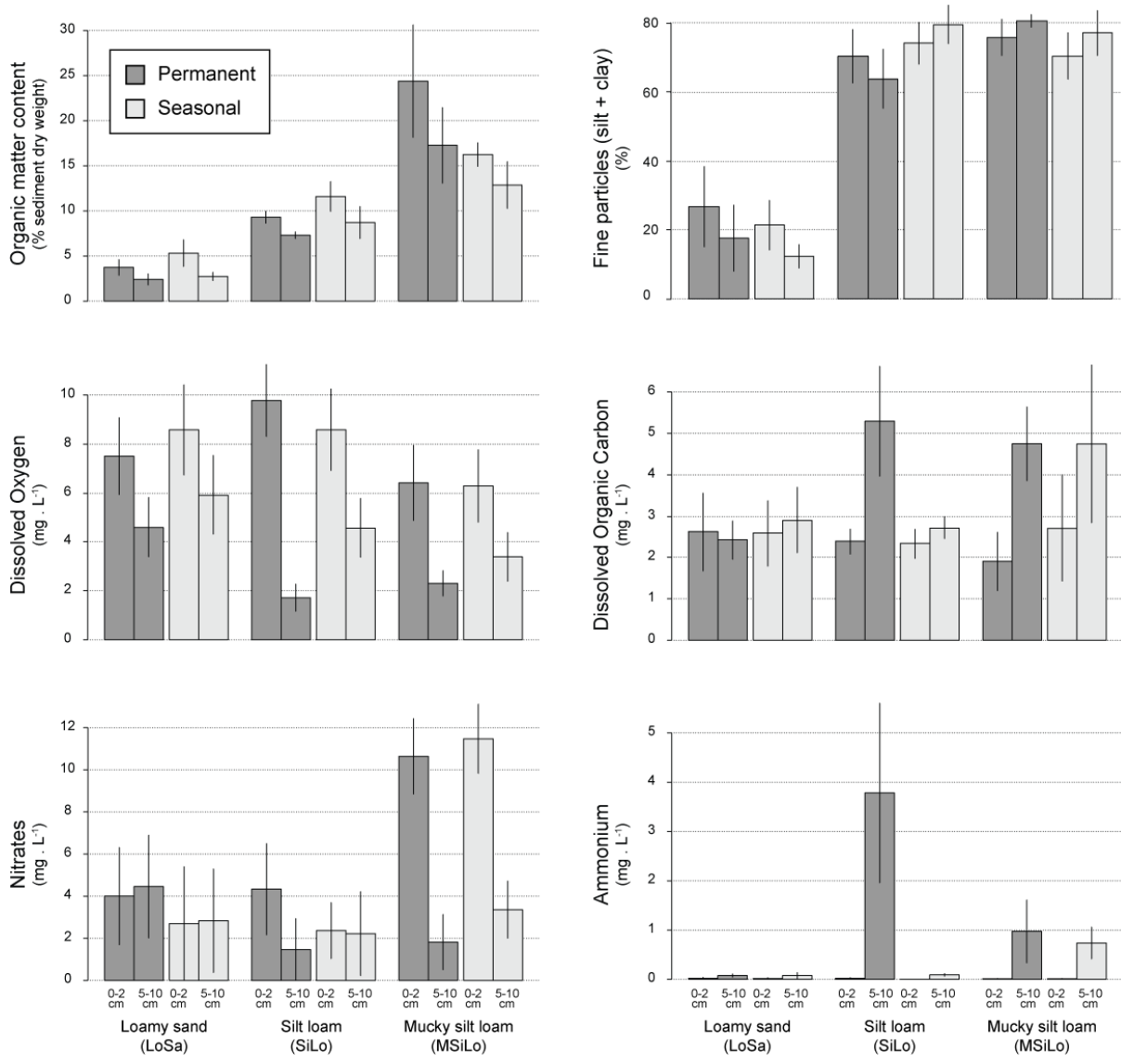
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826 **Figure 01:**



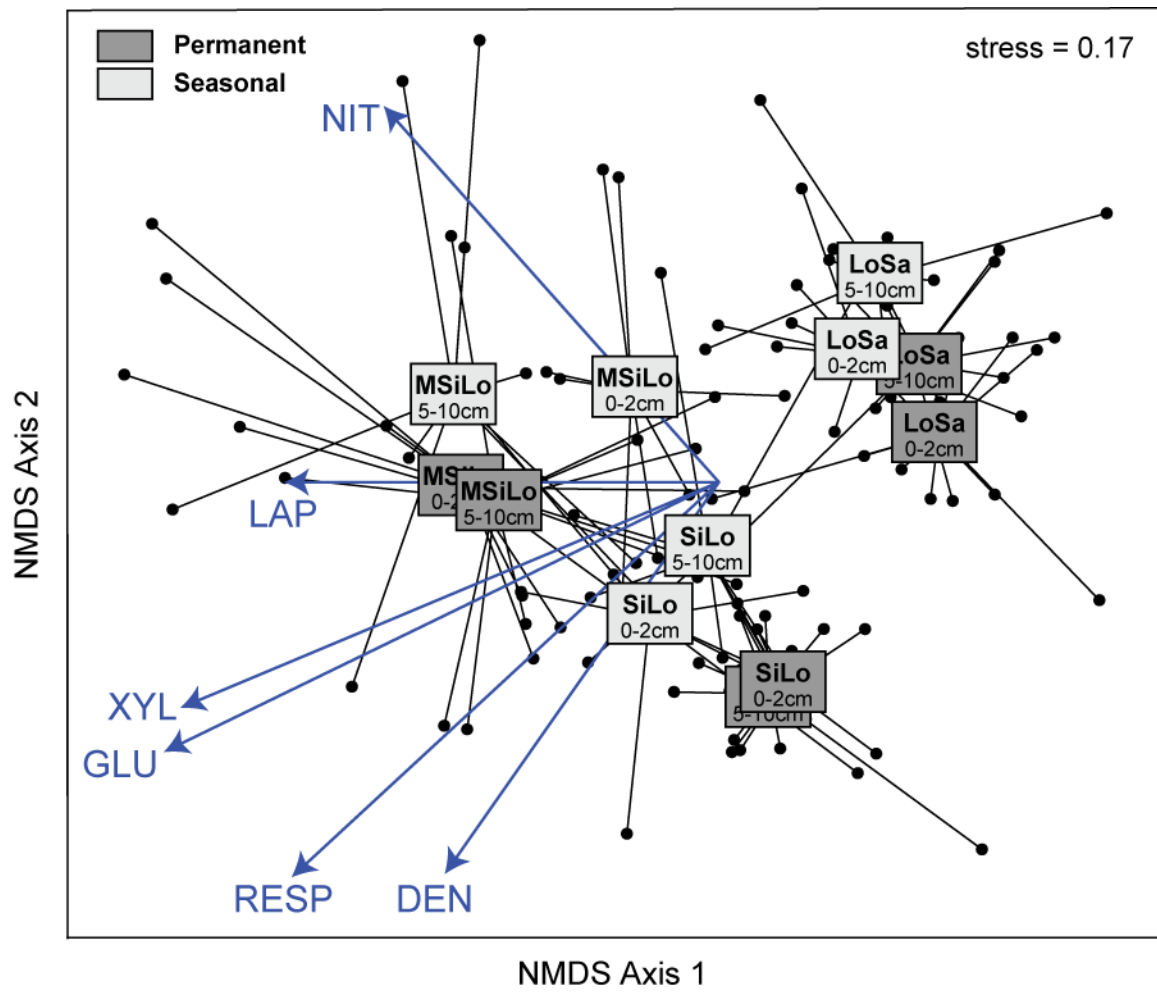
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828 **Figure 02:**



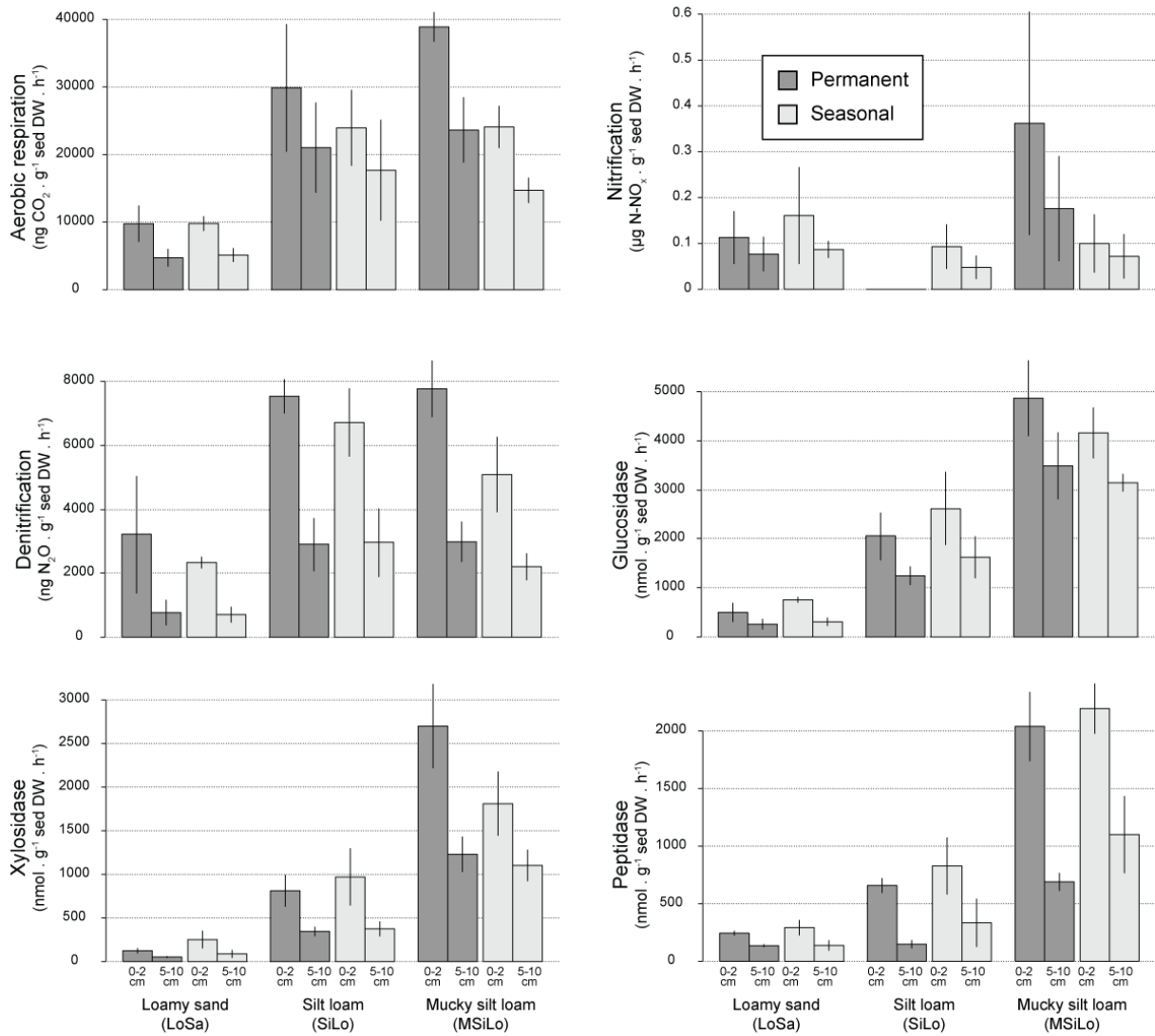
829

830 **Figure 03:**



831

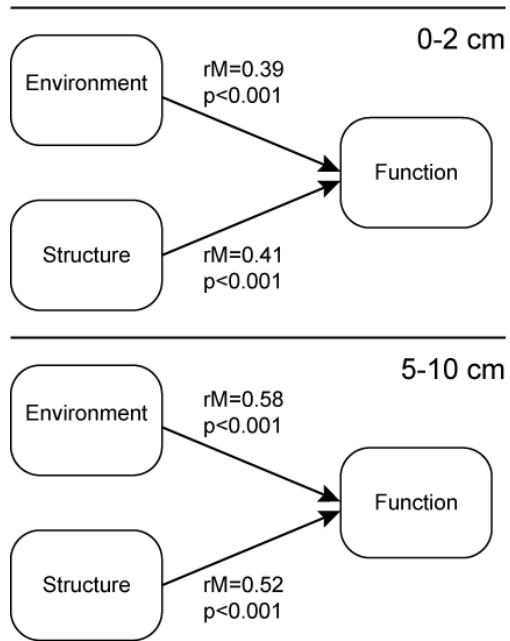
832 **Figure 04:**



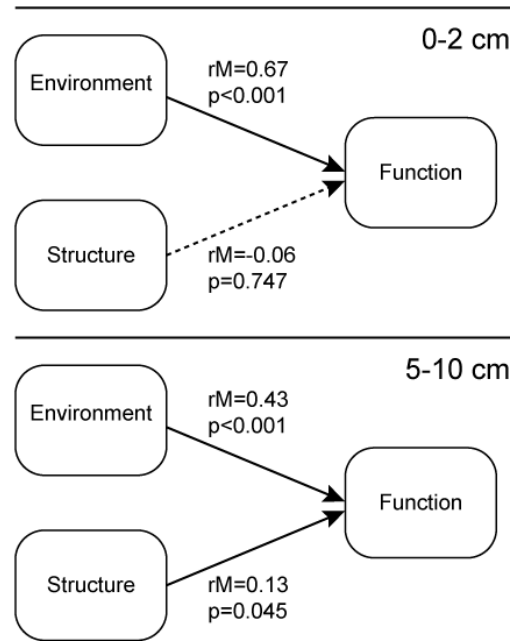
833

834 **Figure 05:**

Permanent



Seasonal



835