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► **To cite this version:**

Elise Châtillon, Robert Duran, François Rigal, Christine Cagnon, Aurélie Cébron, et al.. New insights into microbial community coalescence in the land-sea continuum. *Microbiological Research*, 2023, 267, pp.127259. 10.1016/j.micres.2022.127259 . hal-03884564

HAL Id: hal-03884564

<https://univ-pau.hal.science/hal-03884564v1>

Submitted on 28 Jun 2023

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1 **New insights into microbial community coalescence in the land-sea**
2 **continuum**

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14

15 **Abstract**

16 The land-sea continuum constitutes a mixing zone where soil microbial communities encounter,
17 via runoff, those inhabiting marine coastal sediment resulting in community coalescence. Here,
18 we propose an experimental approach, mimicking the land-sea continuum, to study the
19 microbial community coalescence events in different situations, by 16S and 18S rRNA genes
20 metabarcoding. The microbial community structure of sediment diverged with the soil inputs.
21 For prokaryotes, phylogenetic enrichment and amplicon sequence variants (ASVs)
22 replacements characterized the community changes in sediment receiving soil inputs. For fungi,
23 despite phylogenetic enrichment was not observed, the fungal ASVs richness was maintained
24 by soil inputs. Comparison of microbial communities revealed ASVs specific to sediment
25 receiving soil inputs, and also ASVs shared with soil and/or runoff. Among these specific
26 ASVs, four bacterial and one fungal ASVs were identified as indicators of coalescence. Our
27 study provides evidences that coalescence involves the mixing of microorganisms and of the
28 environment.

29

30 **Keywords**

31 microcosm, community coalescence, soil runoff, marine coastal sediment, indicator value,
32 microbial indicator

33 **Introduction**

34 The land-sea continuum is a transition zone mixing terrestrial and marine coastal ecosystems,
35 through diverse forms of connections, including direct inputs via rivers and flows from soil
36 runoff. Inputs from the riverine network into marine environment have been shown to
37 significantly change environmental parameters (e.g. nutrients and suspended particulate matter,
38 salinity, pH) (Brannock et al., 2016; Jeffries et al., 2016) and also transport microorganisms
39 (Halliday et al., 2014; Yakirevich et al., 2013), resulting in community coalescence. Thus,
40 community coalescence corresponds not only to the blending of previously separated
41 communities but also includes the mixing of their respective environments (Bandelj et al., 2012;
42 Rillig et al., 2015). Studies of coalescence in marine environment have only considered the
43 direct inputs via rivers in estuaries (Campbell and Kirchman, 2013; Crump et al., 2004, 1999;
44 Fortunato and Crump, 2015; Mansour et al., 2018; Webster et al., 2015) while the inputs from
45 soil runoff have been neglected within land-sea continuum. However, soil runoff, generated by
46 rainfall, is widespread among coastal areas representing an important upload of terrigenous
47 materials (plant debris, organic matter, mineral particles material and pollutants (Duran and
48 Cravo-Laureau, 2016; Hoffman et al., 1984; Montgomery et al., 2000)) that reaches directly the
49 sea without dilution in river. It is likely that microbial communities transported by these
50 terrigenous materials coalesce with marine microbial communities, which remains to be
51 demonstrated. The content of terrigenous materials depends on the vegetation cover that modify
52 water flow (Nagase and Dunnett, 2012; Wenzel, 2009) and control the soil microbial
53 communities. Therefore, it is worth considering the contribution of soil runoff to microbial
54 community structure in marine coastal sediment. Additionally, land-based activities
55 dramatically alter microbial processes (Fredston-Hermann et al., 2016) by disrupting microbial
56 communities influenced by biotic and abiotic factors (Cravo-Laureau and Duran, 2014; Duran
57 et al., 2015a; Pischedda et al., 2008), probably affected by terrigenous inputs from soil runoff.

58 Several studies have shown the influence of terrigenous inputs in the organization of microbial
59 communities in water column (Crump et al., 2004, 1999; Logares et al., 2009; Paver et al.,
60 2018; Wisnoski et al., 2020), but information is missing for marine sediment. Microbial
61 communities play a pivotal role in the biogeochemical processes influencing ecosystem
62 services (Falkowski et al., 2008; Graham et al., 2016; Nelson et al., 2016). For instance, the
63 activity of microbial communities has been shown to be crucial in mitigating the effect of
64 pollutants (Grizzetti et al., 2019), particularly hydrocarbons (HC) (McGenity et al., 2012) that
65 accumulate in marine coastal sediment (Tolosa et al., 2004).

66 We hypothesize that soil runoff contributes to shape microbial communities inhabiting HC
67 contaminated marine coastal sediment by the concomitant transfer of microorganisms and their
68 environment (community coalescence), despite an asymmetric contribution due to dilution of
69 soil runoff into marine habitat. In addition, the contribution of soil runoff depends on the soil
70 vegetation cover and the presence of HC. In order to test this hypothesis, an experimental
71 ecology approach was set up to mimic soil runoff within land-sea continuum in microcosm.
72 This experiment was specifically designed to consider the effect of plant and HC influencing
73 potentially the runoff, and in turn modulate the coalescence events.

74 Changes in marine sediment microbial community across experimental conditions were
75 revealed by quantifying shifts in community diversity and composition for both prokaryotic and
76 fungal assemblages. Microbial communities were characterized by Illumina sequencing of the
77 16S and 18S rRNA genes allowing their comparison in the different situations.

78 **Material and Methods**

79 **Soil and sediment samples**

80 Soil (10 kg) and sediment (2 kg) were collected in the same geographical area, in southeast of
81 France, in October 2017. Soil came from the surroundings of the Berre Pond (43°29'6.9"N

82 5°11'18.53"E, France) and sediment from the Canal Vieil Cove (43°23'20.3"N 4°59'31.8"E,
83 France). Both sites are close to petroleum refinery and constitute a model of a realistic HC
84 contaminated land-sea continuum. Prior to microcosms setup, soil and sediment were sieved to
85 <4 mm and <1 mm, respectively, to homogenize, remove coarse gravels, plant debris and
86 macroorganisms. The whole soil sample and a part of the sediment sample were air dried under
87 a cupboard. The rest of the sediment was stored at 4 °C in a 5 L bottle completely covered with
88 *in situ* seawater and with continuous aeration through an aquarium pump. Soil and sediment
89 characteristics were determined on dry samples at the Laboratoire d'Analyses des Sols - LAS
90 (INRAe, Arras, France). The soil had a loamy and sediment a sandy texture (23.4% and 4.7%
91 clay, 38.5% and 4.5% silt, 38.1% and 90.8% sand, for soil and sediment, respectively). Both
92 soil and sediment showed basic pH (8.4 and 9.1 for soil and sediment, respectively). The C/N
93 ratio was about 30.0 and 46.6 for soil and sediment, respectively. The organic carbon content
94 and the total nitrogen were higher in soil than in sediment (35.4 and 18.6 g C/kg, 1.2 and 0.4 g
95 N/kg). The cation-exchange capacity estimated by cobaltihexamine method is higher in soil
96 than in sediment (15.9 and 1.4 cmol+/kg).

97 **Microcosms Setup**

98 An original microcosm system was set up under controlled conditions at the laboratory (

99 Figure 1). The experimental design was drawn with the aim to test the hypothesis that the soil
100 runoff influences the structure and the composition of microbial communities in downstream
101 sediment depending on the presence of plants and/or on HC. For this purpose, two kinds of
102 microcosms were set up (

103 Figure *IA*): the land-sea continuum microcosms (R) that simulated the soil runoff to marine
104 coastal sediment connecting soil and sediment compartments; and the control microcosms (NR)
105 without runoff of soil consisting of single sediment compartment. Briefly, the microcosms were
106 composed of glass devices (1 L beaker equipped with an inlet and outlet) containing the
107 equivalent of 100 g of dry sediment covered with seawater (Salt Instant Ocean, Aquarium
108 systems, concentration 35 g/L). For the land-sea continuum microcosm, these devices were
109 connected through Teflon pipes to stainless steel devices containing 600 g of dry soil moistened
110 at 60% water holding capacity. Different conditions were applied in triplicate combining the
111 presence of plant (P) or not (NP) in soil with the spiking of deuterated HC (C) or not (NC) in
112 soil and sediment (

113 Figure *IB* and C). Thus, six different experimental conditions were compared. In the HC spiked
114 conditions, soil and sediment (1/10 of the soil and sediment as dry weight) received a mix 1:1
115 (W:W) of deuterated n-hexadecane (D34, 98%, Cambridge Isotope Laboratories, Inc, USA)
116 and phenanthrene (D10, 98%, Euriso-top, France), dissolved in hexane solvent. A stock
117 solution was prepared in order to add each HC at a concentration of 1000 mg/kg dry soil or
118 sediment. For the unspiked conditions, the same volume of hexane was added alone without
119 addition of HC stock solution. After total solvent evaporation, 9:10 of crude soil and sediment
120 were mixed with spiked fractions to have a contamination at 100 mg/kg. Soils were watered to
121 reach 60% of their water holding capacity. *Catapodium marinum*, a grass identified *in situ*, was
122 sown in soil with 25 seeds (seed bank of the Muséum National d'Histoire Naturelle, Paris,
123 France) per microcosm. For the sediment compartment, 200 mL of seawater was added on the
124 top of the sediment. After an aging period of 4 days at 4 °C, allowing the sorption of the HC
125 into soil and sediment matrices, microcosms were installed in a phytotronic chamber with
126 controlled conditions (22 °C/18 °C day/night, 80% relative humidity, c.a. 250 $\mu\text{mol photons}$
127 $\text{m}^{-2} \text{s}^{-1}$, 16 h photoperiod). Microcosms were incubated for 39 days, the estimated time
128 necessary for plant growth and HC degradation (Ben Said et al., 2015; Bourceret et al., 2017;
129 Duran et al., 2015b). Soil compartments were watered five consecutive days per week by means
130 of a syringe dispensing 73 mL mineral water (Volvic®) to mimic rainfall and produce soil
131 runoff and in turn terrigenous inputs. After seed germination, 16 plants were kept per device.
132 Both in land-sea continuum and in control microcosms, peristaltic pumps helped to simulate a
133 12 h tidal cycle. In this way, the seawater was renewed twice a day maintaining sediment
134 covered by 3 cm of seawater during the low tide ensuring conditions close to those prevailing
135 in natural environment.

136 **Sampling**

137 Samples of the different compartments (soil, runoff, sediment) and of seawater were collected
138 at different times: at the beginning, at the end, and during the incubation for subsequent
139 biomolecular analysis. Soil and sediment samples (ca. 10-12 g) were collected in triplicates at
140 the beginning and end of the experiment (t₀ and t_f, respectively) for the DNA extraction. Soil
141 samples were collected using a little stainless steel corer (diameter: 14 mm; height: 40 mm, 31)
142 and sediment samples using a spatula. At t₀, three soil samples (each being the mixture of 3
143 cores) were collected from two additional soil devices, one with HC spiking and one without
144 HC spiking, so as not to alter soil structure or disturb plant germination in devices that continued
145 the incubation. Three sediment samples (each being the mix of 3 subsamples) were collected
146 from the sediment batch prepared for sediment devices with HC spiking (NPC, PC, NRC
147 conditions) and from the one prepared for sediment devices without HC spiking (NPNC, PNC,
148 NRNC conditions). Runoff samples were collected from each land-sea microcosms, by mixing
149 runoff from three consecutive days, at t₁ (days 16, 17 and 18 of incubation) and at t₂ (days 31,
150 32 and 33 of incubation). Runoff samples (45 mL) and 45 mL of Volvic water (rainwater) as
151 control were filtered at 0.22 µm (Millex). At t_f (after 39 days of incubation), *Catapodium*
152 *marinum* were cut at the collar before soil sampling. Soil samples were collected in triplicate
153 from each land-sea continuum microcosm using a template (three notches per row and three per
154 column) as a guide for the corer. The cores from the same column were mixed and formed one
155 sample. Sediment samples were collected from each microcosm after mixing of sediment. Soil,
156 runoff (filters) and sediment samples were stored at -80°C.

157 **DNA extraction and rRNA gene sequencing**

158 DNA was extracted from 250 mg of soil or sediment sample and from the filter of runoffs using
159 the PowerSoil DNA Isolation Kit (MoBio Laboratories) according to the manufacturer's
160 recommendations. PCR amplification of the V4-V5 hypervariable region of the 16S rRNA gene

161 was performed using the Archaea/Bacteria primers 515F (5'-GTG-YCA-GCM-GCC-GCG-
162 GTA-3') and 928R (5'-CCC-CGY-CAA-TTC-MTT-TRA-GT-3') (Parada et al., 2016; Wang
163 and Qian, 2009). Likewise, 18S rRNA gene was also amplified using the eukaryotic primers
164 FF390 (5'-CGA-TAA-CGA-ACG-AGA-CCT-3') and FR1 (5'-AIC-CAT-TCA-ATC-GGT-
165 AIT-3') targeting the V7-V8 region (Chemidlin Prévost-Bouré et al., 2011; Vainio and Hantula,
166 2000). The reverse and forward primers included Illumina adapters. Before amplification, the
167 concentration of DNA was determined with a Quant-It kit in microplate in order to normalize
168 the following amplification. Amplifications were performed in triplicate in a total volume of 25
169 μ L reaction mixture containing 0.8 μ M or 0.4 μ M of each primer for Archaea/Bacteria and
170 Eukaryote respectively, 2 ng or 4 ng of DNA for Archaea/Bacteria and Eukaryote respectively,
171 12.5 μ L of AmpliTaq Gold 360 Master Mix (Applied Biosystems). The final volume was
172 adjusted with distilled water. Cycling conditions were: an initial denaturation step at 95 °C for
173 10 minutes, followed by 35 cycles with denaturation step at 95 °C for 30 s, hybridization step
174 at 60 °C for 30 s or at 50 °C for 45 s (for Archaea/Bacteria primers and Fungi primers,
175 respectively), and elongation step at 72 °C for 40 s or 30 s (for Archaea/Bacteria primers and
176 Fungi primers, respectively), after which a final elongation step at 72 °C for 10 minutes was
177 performed. The 2 \times 250 paired-end sequencing was carried out at the Genotoul platform
178 (Toulouse, France) with Illumina-MiSeq. Raw sequence data for the amplicon data were
179 deposited in the Sequence Read Archive (SRA) of the National Center for Biotechnology
180 Information (NCBI) and is available under the assigned Bioproject PRJNA803214
181 (<https://dataview.ncbi.nlm.nih.gov/object/PRJNA803214>).

182

183 **Sequence processing and ASV delimitation**

184 The open source software Qiime2 (Bolyen et al., 2019) was used for 16S and 18S rRNA gene
185 read analysis. Sequencing resulted in 3 735 622 and 3 716 691 raw reads for prokaryotic and

186 eukaryotic datasets, respectively (Table S1). The rarefaction curves (Fig. S1) showed that most
187 of the diversity was captured during the sequencing. The two datasets were first demultiplexed
188 and dada2 (Callahan et al., 2016) was used to control reads quality and infer amplicon sequence
189 variants (ASVs) (Callahan et al., 2017). Default settings were used except that reverse reads
190 were truncated to 230 base pairs before merging. This denoising step resulted in 6 988 and 2
191 488 ASVs for prokaryotic and eukaryotic datasets, respectively (Table S1). The taxonomy was
192 assigned to the ASVs with a fixed sequence similarity threshold of 97 % using the SILVA
193 database release 132 for 16S and 18S rRNA gene sequences (Quast et al., 2013). Then, ASVs
194 assigned to mitochondria and chloroplasts and ASVs unassigned at the domain level were
195 further removed from the datasets resulting in 6 748 prokaryotic ASVs (Table S1). For
196 Eukaryotes, only ASVs affiliated to Fungi were retained resulting in 705 fungal ASVs (Table
197 S1). Phylogenetic trees were constructed using FastTree (Price et al., 2010) in the Qiime2
198 phylogeny plugin. The phylogenetic tree was made ultrametric (i.e. all tips equidistant from the
199 root) for the following analyses using the “chronos” function in the R package ape (Paradis and
200 Schliep, 2019) with branch lengths representing relative time (root at 1 and tips at 0). The
201 number of reads for each sample was rarefied to the same number corresponding to the
202 minimum read number per sample (7 578 sequences) for prokaryotic dataset (Fig. S1). The
203 same procedure was carried out for the fungal dataset (i.e. with a minimum read number per
204 sample of 1 027 sequences), after having removed two samples with too low read number
205 (Runoff PC t2-3 and SedR PNC tf-1) (Fig. S1). The rarefaction was performed with R software
206 using phyloseq package (McMurdie and Holmes, 2013). These thresholds are trade-offs
207 reflecting the need to maximize sampling effort while preserving most of the samples according
208 to the rarefaction curves (Fig. S1). The prokaryotic dataset encompassed 66 samples whereas
209 fungal datasets 64 samples. The following statistical analyses were implemented within the R
210 programming environment (R Core Team, 2021).

211 Metabolic and ecological functions of prokaryotic and fungal communities were predicted
212 using FAPROTAX (Louca et al., 2016) and FUNGuild (Nguyen et al., 2016) respectively.

213 **Alpha and beta-diversity of the core microbial communities**

214 Prior to the diversity analyses, the ASVs were partitioned into core (abundant and widely
215 distributed) and satellite (low abundant and limited distribution) groups. It has been shown that
216 the interpretation of biodiversity patterns reacting to environmental change was improved by
217 combining abundance and occurrence of taxa (Jeanbille et al., 2016; Lindh et al., 2017). The
218 core community has been demonstrated to be high sensitive to environmental changes and the
219 presence of contaminants while the distribution of the satellite group has been shown to be
220 mostly random (Jeanbille et al., 2016). The core and satellite groups were identified as follow:
221 first, the correlation between the relative abundance and the occurrence of each ASV was
222 calculated throughout the dataset. Then, the index of dispersion of each ASV was calculated as
223 the ratio of the variance to the mean abundance multiplied by the occurrence (Jeanbille et al.,
224 2016). The ASVs were partitioned into core (abundant and widely distributed) and satellite (low
225 abundant and limited distribution) groups (Hanski, 1982; Hu et al., 2017; Magurran and
226 Henderson, 2003; Ulrich and Zalewski, 2006). The ASVs were considered as core if their index
227 of dispersion deviated from a random Poisson distribution fall outside the 95% confidence
228 interval of the χ^2 distribution (Jeanbille et al., 2016; Unterseher et al., 2011; van der Gast et al.,
229 2011). In order to characterize the core and the satellite groups according to the level of the
230 habitat specialization, the Levins' niche breadth index (Levins, 1968) was calculated using
231 levins.Bn function in the R package MicroNiche (Finn et al., 2020). A Wilcoxon rank sum test
232 was performed to compared the niche breadth index of the core and the satellite groups.
233 Therefore, the subsequent analyses were focused on the core group. Alpha and beta-diversity
234 were quantified at both taxonomic and phylogenetic level. For alpha-diversity, the indices ASV
235 richness and Inverse Simpson index (i.e. the Hill number of order 2, 2D) were selected as well

236 as their phylogenetic equivalents namely the Faith's phylogenetic diversity index (Faith's PD)
237 and the Hill2 phylogenetic diversity index (2 PD) respectively. In order to identify changes in
238 alpha-diversity among conditions, two-way analyses of variance (ANOVA) were performed
239 using two factors, HC spiking (NC, C), and a factor grouping the other conditions (t0, NP tf
240 and P tf for soil; t0, NR tf, R NP tf and R P tf for sediment), and their two-ways interactions.
241 When factors were significant, post hoc tests (Tukey's HSD test) were performed to identify
242 conditions that were significantly different from each other. Beta-diversity between all pairs of
243 samples were quantified using the weighted Jaccard dissimilarity index for ASV and weighted
244 UniFrac for phylogenetic (branches) beta-diversity (Lozupone and Knight, 2005). Prior to the
245 analyses, the abundances were square root transformed. Following Cardoso et al. (2015), the
246 total beta-diversity (β_{tot}) for both Jaccard and UniFrac was partitioned into its replacement
247 (β_{repl}) and richness difference (β_{rich}) components in order to decipher the different process
248 underlying the change in community assembly; β_{repl} reflects true turn-over and β_{rich} quantifies
249 the loss and gain of ASV between communities. Beta partitioning was implemented with R
250 package BAT (Cardoso et al., 2015). Patterns of beta-diversity were visualized using a non-
251 metric multidimensional scaling (NMDS). PerMANOVA (permutational multivariate analysis
252 of variance) based on 9 999 permutations were implemented using adonis2 function from vegan
253 R package (Oksanen et al., 2013) to test the effect of the different conditions in each
254 compartment (soil, runoff, sediment). Post-hoc tests were conducted using pairwise
255 comparisons to identify conditions that were significantly different from each other.

256 **Venn diagram, microbial source tracking and indicator species analyses**

257 The web-based tool InteractiVenn (Heberle et al., 2015) was used to analyse and visualize the
258 shared presence of prokaryotic and fungal ASVs among soil, runoff and sediment according to
259 runoff treatment.

260 An indicator analysis was performed to identify ASVs that were associated with a specific
261 condition or a combination of conditions using the Dufrene and Legendre indicator value (ie.
262 IndVal) (Dufrière and Legendre, 1997) in the R package indicpecies (Caceres and Legendre,
263 2009). IndVal index quantifies the strength of the association by combining information on
264 ecological specificity and fidelity for each ASV. IndVal value range from 0 (no association) to
265 1 (perfect association). Significance of IndVal values were assessed using permutation tests (N
266 = 9 999) under the null hypothesis of no association.

267 Microbial source tracking analysis was conducted using SourceTracker2 (version 2.0.1;
268 Knights et al., 2011) to identify the contribution of soil and runoff microbial communities as
269 source for those of sediment with runoff.

270 **Results and discussion**

271 **Partitioning the microbial community into core and satellite groups**

272 The experiment was specifically designed to investigate the microbial coalescence in a land-
273 sea continuum i.e. the contribution of soil and soil microbial community inputs (via soil runoff)
274 in shaping the marine coastal sediment microbial community. For this purpose, the microbial
275 community composition of the different compartments (soil, runoff, and sediment), collected
276 at the beginning and at the end of the experimental incubation, was determined by high
277 throughput sequencing. For the prokaryotic and eukaryotic communities, 3 735 622 and 3 716
278 691 raw reads were respectively obtained (Table S1). The observed richness rarefaction curves
279 (Fig. S2) reached a plateau suggesting the sampling depth was sufficient to capture the diversity.
280 After trimming and rarefaction, 7 578 and 1 027 sequences were respectively affiliated to 6 064
281 prokaryotic and 638 fungal ASVs (Table S1). The ASVs abundance distribution showed that
282 the microbial communities were distributed into core and satellite ASVs groups, the mean
283 ASVs abundance being positively linked to the occurrence (Fig. S2A), as already evidenced

284 (Hu et al., 2017; Jeanbille et al., 2016; Lindh et al., 2017). The core and satellite ASVs were
285 identified by examining the relationship between the index of dispersion and occurrence of each
286 ASV (Fig. S2B). Most of the microbial ASVs (4 462 prokaryotic and 465 fungal ASVs; Table
287 S1) fitted a random distribution (Poisson model) defining the satellite ASVs. In contrast, 1 602
288 prokaryotic and 173 fungal ASVs formed the non-randomly distributed core ASVs (Table S1).
289 This core microbial community contained less than 30 % of the total ASVs, accounting for
290 more than 80 % of the total reads. The core microbial community had a significantly wider
291 (Wilcoxon test: $W = 68\,363$ $p < 0.001$, Fig. S3) niche breath than the satellite community. This
292 feature suggests that the microbial core community includes generalists able to use widespread
293 resources (Brown, 1984). In addition, studies showed that the core microbial community brings
294 information reporting the effect of the environmental factors (Jeanbille et al., 2016; Magurran
295 and Henderson, 2003; Ulrich and Zalewski, 2006) which allow us to focus on the core microbial
296 community in order to characterize the microbial communities inhabiting mixing zone
297 influenced by soil runoff.

298 **Diversity of the core microbial community**

299 Using ASV and phylogenetic alpha-diversity indices, the effects of plant, HC spiking and soil
300 runoff were investigated in the core microbial communities inhabiting soil and sediment (Fig.
301 2). Prokaryotic and fungal soil richness (R) and the inverse Simpson (2D) indices remained
302 stable along the course of the experiment while the Faith's PD increased (ANOVA 16S: $F =$
303 5.07 , $p < 0.05$; ANOVA 18 S: $F = 12.65$, $p < 0.05$), irrespective of the presence of plants (NP,
304 P), with a significant additional increase (Tukey's test: Soil C t0 – Soil C tf, $p < 0.05$) in HC
305 spiking samples (Fig. 2A and B). It was surprising to observe that the presence of plants was
306 not affecting the soil microbial diversity although plant roots exudates have been shown to
307 provide nutrients (Van Hecke et al., 2005) and promote the development of microorganisms
308 carrying HC degrading genes (Cébron et al., 2011; Toyama et al., 2011). Regarding the

309 sediment microbial diversity, similar trends were observed for the prokaryotic communities
310 with a significant temporal increase of ²PD (ANOVA 16S: F = 6.79, p < 0.05) irrespective of
311 the condition, while the fungal diversity was not affected (Fig. 2C and D). Sediment receiving
312 terrigenous inputs and with HC spiking had the highest prokaryotic ²PD, showing increased
313 phylogenetic enrichment due to both runoff and HC spiking (Tukey's test: Sed t0 - SedR C tf,
314 p < 0.05; Fig. 2C). Such HC effect on prokaryotic community was consistent with previous
315 studies showing i/ modification of microbial communities after petroleum addition (Bordenave
316 et al., 2004; Chronopoulou et al., 2013; Stauffert et al., 2014), and ii/ an increase of microbial
317 diversity, especially in historically HC contaminated sediments (Duran et al., 2015b; Jeanbille
318 et al., 2016; Paissé et al., 2008). The diversity increase was explained by the legacy effect of
319 previously exposed microbial communities to pollutants (Ben Salem et al., 2019) and
320 environmental disturbances (Jurburg et al., 2017; Nunes et al., 2018). In our study, the observed
321 increase of phylogenetic enrichment due to both runoff and HC spiking suggested that runoff
322 transferred microorganisms from soil to sediment, which probably resulted in microbial
323 community coalescence as reported for river sediment (Mansour et al., 2018), relating
324 modifications in the microbial community composition.

325 **Microbial composition within the land-sea continuum compartments**

326 In order to have an overview of the composition of the microbial community within the land-
327 sea continuum, the relative abundance of the phyla in the different compartments (soil, runoff,
328 sediment) was examined. Overall, most ASVs were affiliated to twelve bacterial and eight
329 fungal phyla (Fig. 3). ASVs affiliated to Archaea belonged to Nanoarchaeota and
330 Thaumarchaeota phyla with relative abundance less than 1% of prokaryotes. Proteobacteria
331 dominated the prokaryotic communities (21±7%, 60±14% and 60±22% in soil, runoff and
332 sediment, respectively; Fig. 3A and Table S2) while the Ascomycota dominated the fungal
333 communities, except in runoff in which most fungi were unassigned (65±7% and 80±17% of

334 Ascomycota in soil and sediment, respectively, and $47 \pm 12\%$ of unassigned fungi in runoff; Fig.
335 3B and Table S3). As expected, the compartments along the continuum (soil, runoff, and
336 sediment) exhibited different microbial community composition. Soil was characterized by the
337 presence of Acidobacteria, Actinobacteria and Betaproteobacteria (23 %, 21 % and 8 %,
338 respectively). In runoff and sediment, Proteobacteria (60%) and Bacteroidetes (~20%)
339 predominated (Fig. 3A). As in soil, the runoff was dominated by Betaproteobacteria (23%),
340 whereas in sediment Gammaproteobacteria and Deltaproteobacteria (32 and 19%, respectively)
341 prevailed, which is in accordance with previous studies showing that Gammaproteobacteria and
342 Deltaproteobacteria are abundant in HC contaminated coastal sediments (Acosta-González and
343 Marqués, 2016; Stauffert et al., 2015). Regarding the fungal community (Fig. 3B), Ascomycota
344 was the dominant phylum in soil and sediment (65 and 80 %, respectively), followed by
345 Basidiomycota (15 %) in soil and Chytridiomycota (14 %) in sediment, which is consistent with
346 the fact that these phyla have been found in diverse ecosystems (Amend et al., 2019; Bahram
347 et al., 2018; Comeau et al., 2016; Kohlmeyer and Kohlmeyer, 1979). In runoff, most fungi were
348 unassigned (almost 50 %), showing that a large part of soil fungal diversity transported by soil
349 runoff remains unknown and corresponds to the low abundant soil fungal taxa. Thus, simulated
350 soil runoff represents a way to reveal undescribed soil fungal diversity. The difference between
351 compartments was also observed at the functional level using predictive FAPROTAX (Figure
352 S4) and FUNGuild (Figure S5) tools. A total of 478 functional assignments for 1602
353 prokaryotic ASVs were obtained, revealing that sediment is characterized by the presence of
354 metabolisms involved in the sulfur cycle. Only 13.9% of the fungal ASVs (24 out of the 173)
355 were assigned to guilds, mostly represented in soil by plant parasite-saprotroph fungi, runoff
356 dominated by endophyte- saprotroph fungi while the sediment was characterized by unassigned
357 guilds highlighting the lack of data about marine fungi. The use of more powerful techniques
358 as metagenomic or functional DNA arrays is required to reveal similarities and differences

359 between the three compartments and under the different conditions. Nevertheless, overall,
360 distinct microbial communities were identified in each compartment consistent with the alpha-
361 diversity analysis. Thus, the experimental design allows the study of coalescence by mixing
362 different microbial communities.

363 **Comparison of microbial communities**

364 In order to characterize the coalescence, further comparisons between microbial communities
365 were performed, particularly the detection of shift in microbial community composition (ASV
366 and phylogenetic) due to terrigenous inputs using betadiversity partitioning. Overall, the
367 comparison of the microbial community composition between samples by NMDS based on the
368 weighted UniFrac metric showed three clusters corresponding to the three compartments (soil,
369 runoff and sediment) for both prokaryotes and fungi (Figure 4A and B respectively). Significant
370 differences in the ASV and phylogenetic microbial composition between the compartments
371 (Figure 4) were observed (ASV and phylogenetic β_{tot} , PerMANOVAs: all p-values < 0.001
372 Table S2). Such observations highlighted that each compartment contained specific ASVs and
373 lineages, in accordance with the presence of habitat filtering mechanisms (Lozupone and
374 Knight, 2007). The fact that runoff microbial communities (prokaryotic and fungal) were
375 distinct from those of soil (ASV and phylogenetic β_{tot} , Post-hoc tests: all p-values < 0.001,
376 Table S2, Figure 4) showed that the microbial component of the terrigenous inputs represented
377 only part of the soil diversity. This result suggests that only a subset of soil microorganisms and
378 soil aggregates was able to flow in runoff, which depends on the microbial lifestyle and the soil
379 properties allowing more or less their detachment from the matrix (Holmsgaard et al., 2011).
380 In both soil and runoff (Fig. 4), the microbial ASV composition changed with time and with
381 the HC spiking (ASV β_{tot} , PerMANOVAs: time: all p-values < 0.001, HC spiking: all p-values
382 < 0.05, Tables S3, S4), irrespective of the presence of plant (ASV β_{tot} , PerMANOVAs: all p-
383 value > 0.05, Tables S3, S4). In sediment, the prokaryotic community behaviour was different

384 to that of the fungal community. Two clusters separated the prokaryotic community according
385 to time (Figure 4A) while the fungal community was separated into two clusters according to
386 runoff treatment (Figure 4B). For prokaryotes, the replacement of ASVs explained the
387 differences between clusters observed at the beginning and at the end of the experiment (ASV
388 β repl, PerMANOVA and Post-hoc tests: all p-values<0.001, Table S5). The effect of the
389 terrigenous inputs was not observed, despite that alpha diversity showed an enrichment,
390 probably hidden by the effect of time. For fungi, the clusters contained different ASVs
391 corresponding to lineage richness modifications, explained by the loss of richness in sediment
392 without terrigenous inputs (SedNR tf) (phylogenetic β rich, PerMANOVA and Post-hoc tests:
393 all p-values < 0.01, Table S5) reflecting that the compartments were not connected. In contrast,
394 the fungal phylogenetic richness was maintained by terrigenous inputs, suggesting that the lack
395 of runoff affect the fungal community. It is likely that the terrigenous inputs simulated in our
396 experiment mimicking *in situ* coalescent event explained the resilience of the fungal community
397 in sediment observed only with runoff.

398 The microbial communities from the three compartments were further compared by Venn
399 diagrams in order to identify the shared and specific microbial ASVs (Figure 5). No ASVs
400 shared by the compartments was identified for the prokaryotic communities (Figure 5A), while
401 five shared ASVs were identified for the fungal communities (Figure 5 B). This result
402 corroborates the structuration of the microbial communities in different compartments. Soil and
403 runoff shared the highest number of prokaryotic and fungal ASVs (336 ASVs and 27 ASVs
404 respectively; Figure 5A and B), as expected since beta-diversity analysis showed that runoff is
405 a subset of soil. Interestingly, runoff was mostly constituted of specific prokaryotic ASVs (408
406 ASVs, Figure 5A), supporting the hypothesis that a large part of soil microbial diversity
407 transported by soil runoff corresponded to the low abundant soil taxa. The sediment receiving
408 terrigenous inputs exhibited 48 prokaryotic (Figure 5A) and three fungal specific ASVs (Figure

409 5B), which indicates that these ASVs were below the detection threshold in both soil and
410 sediment at the beginning of the experiment (Soil t0 and Sed t0), they emerged in the sediment
411 receiving terrigenous inputs during the experiment (SedR tf). We hypothesize that these specific
412 ASVs correspond to i/ sediment taxa benefiting from the terrigenous inputs, and ii/ soil taxa
413 transferred to sediment. It is likely that terrigenous inputs favoured the development of specific
414 ASVs because sediment without terrigenous inputs (Sed NR tf) exhibited only eight specific
415 ASVs. These results are in accordance with previous studies showing the loss of specialists and
416 the emergence of taxa during coalescence event (Logares et al., 2009; Paver et al., 2018; Rocca
417 et al., 2020; Wisnoski et al., 2020). Focusing on the ASVs shared by soil, runoff and sediment
418 receiving terrigenous inputs, 4 prokaryotic (Figure 5A) and 13 fungal (Figure 5B) ASVs were
419 identified, indicating the potential transfer of ASVs within the soil and marine coastal sediment
420 continuum. Consistently, the microbial source tracking analysis conducted with
421 SourceTracker2 identified terrigenous inputs as minor sources for fungal communities in
422 sediment at the end of the experiment, irrespective of the runoff treatment (soil or runoff
423 estimated fungal contributions ranged between 0.01% and 3.18% except for two sediment
424 without runoff samples for which these contributions were null; Table S8). Soil and runoff
425 fungal contributions were especially increased in sediment with runoff (Wilcoxon tests:
426 $W=57$, $p\text{-value}<0.01$ for soil; $W=66$, $p\text{-value}<0.001$ for runoff) compared to sediment without
427 runoff. In contrast, soil and runoff were not reported by the analysis as sources for prokaryotic
428 communities in sediment at the end of the experiment except for three samples out of 18
429 (exclusively sediment with runoff samples) for which soil or runoff prokaryotic contributions
430 were less than 1% (Table S8). The low number of shared microbial ASVs and the low
431 contributions of soil and runoff as source show that many microbial taxa present in runoff did
432 not persist in the sediment they entered. They probably do not have the capacity to deal with
433 the new conditions (salinity, pH, oxygen) and niche competition, prevalent in sediment. They

434 may have been diluted or washed away during the renewal of seawater. Among the 4 shared
435 prokaryotic ASVs, two were affiliated to Gammaproteobacteria (*Legionella* and *Massilia*), one
436 to Bacteroidia (*Terrimonas*) and one to Actinobacteria (*Williamsia*). The fungal ASVs were
437 affiliated to Dikarya (Ascomycota), LKM15 group, Chytridiomycota (Chytridiomycetes),
438 Mucoromycota (Mucoromycotina, Mucorales) and Cryptomycota. It is likely that these
439 transferred microorganisms characterized the microbial community coalescence event. The
440 distribution of the prokaryotic transferred ASVs in the land-sea continuum showed that
441 *Legionella* (ASV1184) and *Massilia* (ASV1436) were found at low abundance in soils,
442 enriched in runoff, and detected only in HC spiked sediment receiving terrigenous inputs from
443 unplanted soil (SedR NPC tf; Figure 5C). Microorganisms affiliated to these taxa are found in
444 various ecosystems (Engleberg, 2009; Ofek et al., 2012), including HC contaminated
445 environments (Gu et al., 2016), and characterized by motile capacity (Engleberg, 2009; Ofek et
446 al., 2012) explaining their enrichment in the runoff. *Terrimonas* (ASV4242) was present in soil
447 compartment in the different microcosms and poorly represented in runoff and sediment
448 receiving terrigenous inputs, which is consistent with the fact that it is a non-motile soil
449 microorganism (Board, 2015). *Williamsia* (ASV6220) was not specific to a compartment
450 (Figure 5C). Environmental members from this genus have been isolated from oil-contaminated
451 soil and deep-sea sediments (Pathom-Aree et al., 2006; Stach et al., 2004; Yassin et al., 2007).

452 Among the 14 fungal transferred ASVs, four ASVs were the most abundant, showing a
453 particular distribution (Figure 5D). Noteworthy, Cryptomycota (ASV234) and LKM15 (ASV4
454 and ASV15) were enriched in runoff. Recent studies revealed the importance of these early
455 diverging lineages in freshwater lakes and marine environments (Rojas-Jimenez et al., 2017).
456 In particular, they produce motile aquatic spores (Money, 2016) and are able to parasitize the
457 phytoplankton, which are advantages for inhabiting aquatic ecosystems (Rojas-Jimenez et al.,
458 2017), supporting their enrichment in runoff. *Hypocreales* (ASV525) was present in soil, runoff

459 and sediment receiving terrigenous inputs, irrespective of the condition (Figure 5D).
460 *Hypocreales* are common in terrestrial and marine (seawater and sediment) environments
461 (Jones et al., 2015; Torres and White, 2009). Their particle associated lifestyle (Pang et al.,
462 2019; Torres and White, 2009) may explain their persistence along the land-sea continuum.
463 These results, based on the presence/absence of ASVs, indicate that sediment with runoff
464 owned specific microbial population, either coming from or favoured by terrigenous inputs,
465 supporting the microbial community coalescence between compartments.

466 **Identification of community coalescence microbial indicators**

467 In order to deeper characterize the ASVs participating in the coalescence, the identification of
468 indicators, based on ASV relative abundances, was performed in sediment receiving terrigenous
469 inputs by runoff (SedR). The ASV indicator value analysis, comparing the distribution of
470 microbial population in the sediment compartment under the different conditions, revealed three
471 bacterial ASVs and one fungal ASV significantly associated (p value <0.05) to the sediment
472 with runoff (SedR) (Table 1). Interestingly, the distribution of these bacterial and fungal ASV
473 SedR indicators among all compartments showed that the three bacterial ASVs were associated
474 with sediment, in particular at the end of the experiment (Sed tf) while the fungal ASV was
475 associated with soil (Table 1), which was in accordance with the Venn analysis (Figure 5).
476 These results further support that specific bacterial ASVs correspond to sediment taxa
477 benefiting from the terrigenous inputs while the specific fungal ASV corresponds to soil taxa
478 transferred to sediment, showing the biotic and abiotic transfers resulting in community
479 coalescence. Although the community coalescence, involving biotic and abiotic transfers,
480 showed by Rocca et al. (2020) in laboratory experiment, have been suspected in field
481 investigations (Crump et al., 2004, 1999; Logares et al., 2009; Paver et al., 2018; Wisnoski et
482 al., 2020), our experimental ecology approach provide a set of evidences that coalescence in
483 land-sea continuum involves the mixing of both microorganisms and the environment.

484 **Conclusion**

485 Our experimental ecology approach mimicking the land-sea continuum revealed that soil runoff
486 modified the microbial communities inhabiting HC contaminated marine coastal sediment. The
487 comparison of microbial communities, based on high throughput sequencing, identified
488 bacteria and fungi taxa specific to sediment receiving soil inputs via soil runoff. The in-depth
489 analysis of these specific taxa distinguished two ways of community coalescence: i/ the transfer
490 of soil microorganisms, and ii/ the development of sediment taxa favoured by soil inputs. The
491 community coalescence may result in the modification of the ecological niches constraining the
492 functional organization of microbial communities and their role in biogeochemical cycles. In
493 order to obtain a comprehensive view of microbial communities in coastal marine sediment, we
494 advocate considering coalescence events, particularly for the monitoring and management of
495 HC contaminated areas.

496 **Acknowledgments**

497 We thank the TOTEM project team for discussions and technical assistance. The seed bank of
498 the Muséum National d'Histoire Naturelle de Paris - DGD MJZ is acknowledged for providing
499 seeds of *Catapodium marinum*. Authors thank Manon Runza and Pauline Latour for setting up
500 the experimental devices, and members of the Experimental phytotronic platform of Lorraine
501 (PEPLor) at the Université de Lorraine (Site FST, Vandoeuvre-les-Nancy) for technical
502 assistance and access to plant growth facilities.

503 **Funding**

504 This work was supported by the French national programme EC2CO-LEFE (TOTEM project).
505 EC was supported by E2S-CCLLO grant.

506

507 **Declaration of Competing Interest**

508 The authors declare that they have no known competing financial interests or personal
509 relationships that could have appeared to influence the work reported in this paper.

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- 866

867 **Table 1.** ASV indicators of coalescence identified by the indicator value index (IndVal). ASV
868 indicators specifically associated to sediment with runoff (SedR tf) were identified by an
869 indicator analysis performed among conditions in the sediment compartment. In a second step,
870 the IndVal of each ASV indicator was calculated among soil, runoff and sediment
871 compartments. IndVal value range from 0 (no association) to 1 (perfect association). Only
872 ASVs indicators with significant IndVal index are presented (p for p-value).

Indicator analysis				Sediment compartment's conditions			Soil, runoff and sediment compartments		
ASV	Taxonomic affiliation			IndVal	p	association	IndVal	p	association
525	Fungi	Pezizomycotina	<i>Hypocreales</i>	0.850	0.015	SedR tf	0.779	0.005	Soil
2716	Bacteria	Alphaproteobacteria	<i>Rhodobacteraceae</i>	0.764	0.045	SedR tf	0.540	0.005	Sed
635	Bacteria	Deltaproteobacteria	NA	0.844	0.025	SedR tf	0.707	0.005	Sed
3543	Bacteria	Bacteroidia	<i>Cyclobacteriaceae</i>	0.857	0.01	SedR tf	0.707	0.005	Sed

873

874 **Figure 1.** Experimental design. Schema of the land-sea continuum microcosm (A) mimicking
875 the terrigenous inputs to marine coastal sediment by soil runoff (left). Control microcosm (right)
876 corresponds to sediment without soil runoff. Photo of the experiment (B). Schematic
877 representation of the microcosms (C) with the different conditions applied to the soil and
878 sediment compartments: Soil: soil; Runoff: runoff water (with terrigenous inputs); Sed:
879 sediment; SedR: sediment receiving runoff; SedNR: Sed without runoff; NP: non-planted; P:
880 planted; NC: without HC spiking; C: HC spiking. Each condition was performed in triplicate.

881

882 **Figure 2.** Microbial alpha-diversity in soil and in sediment. Taxonomic (left) and phylogenetic
883 (right) alpha-diversity indices for the prokaryotic (A) and the fungal (B) communities in soil,
884 and for the prokaryotic (C) and the fungal (D) communities in sediment, in the different
885 experimental conditions. Error bars represent standard deviation of three replicates for each
886 condition. Letters represent pairwise contrasts ($p < 0.05$) of sample conditions. R: richness; ²D:
887 Inverse Simpson index; Faith's PD: Faith's phylogenetic diversity index; Hill ²PD:
888 phylogenetic diversity index based on Hill 2 number; Soil: soil; Sed: sediment; R: with runoff;
889 NR: without runoff; NC: without HC spiking; C: with HC spiking; P: planted; NP: non-planted;
890 t0: beginning of the experiment; tf: end of the experiment (after 39 days of incubation).

891

892 **Figure 3.** Composition of the prokaryotic (A) and the fungal (B) communities in soil, runoff
893 water and sediment, in the different conditions (NC: without HC spiking; C: with HC spiking;
894 NP: non-planted; P: planted; NR: without runoff; R: with runoff; t0: beginning of the
895 experiment; t1 and t2: 16 and 30 days of incubation; tf: end of the experiment, after 39 days
896 incubation). The analysis was performed at the phylum level with Proteobacteria split into
897 classes. Phyla <1% abund.: phyla with total relative abundance less than 1% ranked by

898 decreasing relative abundance, including unassigned, Thaumarchaeota, Firmicutes,
899 Fibrobacteres, Fusobacteria, Nitrospirae, Omninitrophicaeota, Latescibacteria,
900 Armatimonadetes, Patescibacteria, Spirochaetes, Calditrichaeota, Rokubacteria,
901 Marinimicrobia (SAR406 clade), Tenericutes, Dadabacteria, Dependuntiae, Elusimicrobia,
902 Zixibacteria, Nanoarchaeaeota, unassigned Proteobacteria, Epsilonproteobacteria, candidate
903 phylum WPS-2 (or Eremiobacterota), Deinococcus-Thermus, Cloacimonetes, Abditibacteriota
904 (previously known as FBP candidatus).

905

906 **Figure 4.** NMDS analysis based on the weighted UniFrac metrics presenting the differences
907 observed in the prokaryotic (A) and in the fungal (B) community composition of soil, runoff
908 and sediment compartments. Coloured segments connect samples with the same plant condition
909 and sampling date to their average point while shapes indicate if samples were HC spiked
910 (circle) or not (triangle). NR: without runoff (control); R: with runoff; NP: non-planted; P:
911 planted; NC: without HC spiking; C: with HC spiking; t0: beginning of the experiment; t1: 16
912 days of incubation; t2: 30 days of incubation; tf: end of the experiment.

913

914 **Figure 5.** Venn diagrams of prokaryotic (A) and fungal (B) core communities from the different
915 compartments and the distribution of transferred prokaryotic (C) and fungal (D) ASVs in soil,
916 runoff and sediment. Soil (t0&tf): ASVs present in soil at the beginning (t0) and at the end of
917 the experiment (tf); Runoff (t1&t2): ASVs present in runoff after 16 (t1) and 30 (t2) days of
918 incubation; Sed t0: ASVs in sediment at the beginning of the experiment (t0); SedR tf: ASVs
919 in sediment with runoff at the end of the experiment (tf); SedNR tf, ASVs present in sediment
920 without runoff at the end of the experiment (tf). The total number of ASVs in each compartment
921 is indicated in parenthesis. The microbial ASVs exclusively shared between soil, runoff and
922 sediment with runoff was coloured in red and were probably transferred from soil to sediment

923 by runoff. In C and D, the data represent the mean of three biological replicates ($n = 3$). R:
924 sediment with runoff; NR: sediment without runoff; NP: non-planted; P: planted; NC: without
925 HC spiking; C: with HC spiking.

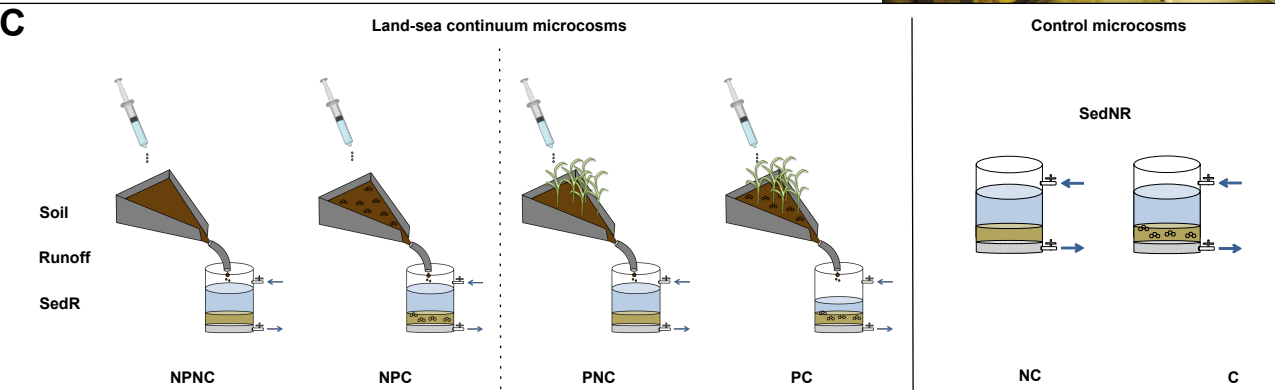
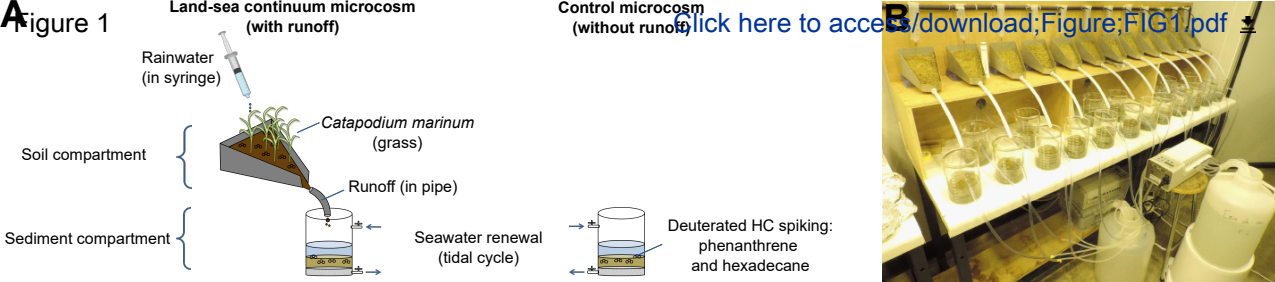
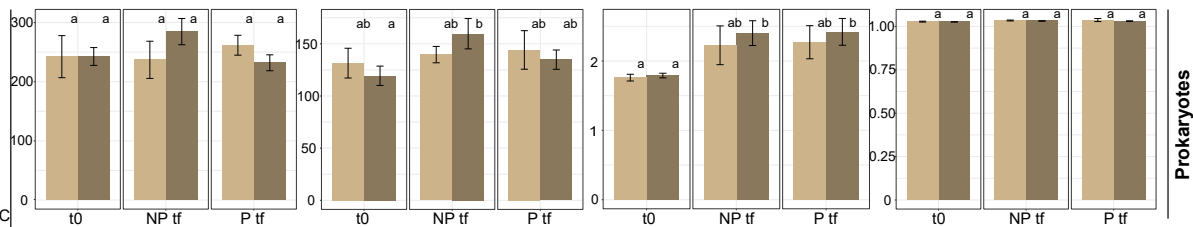


Figure 2

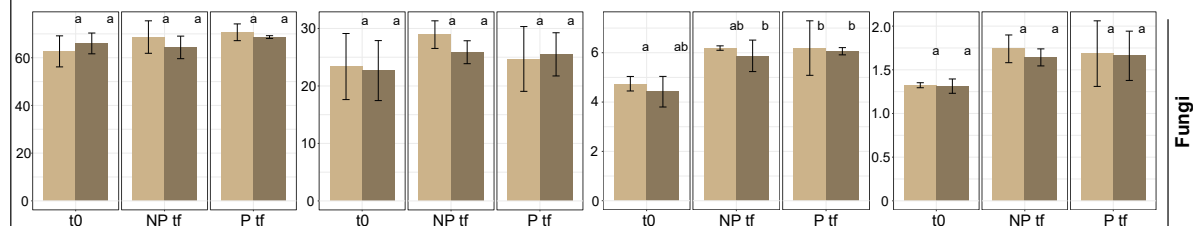
ASV alpha-diversity

Phylogenetic alpha-diversity
Faith's PD

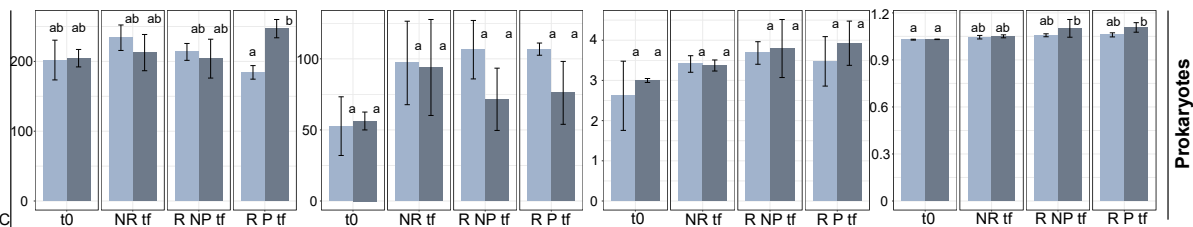
A



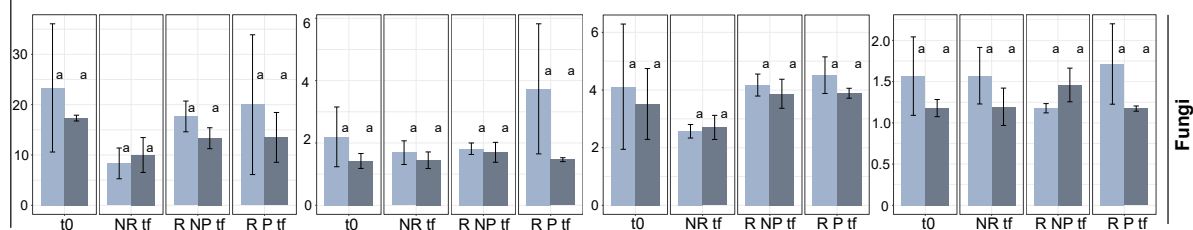
B



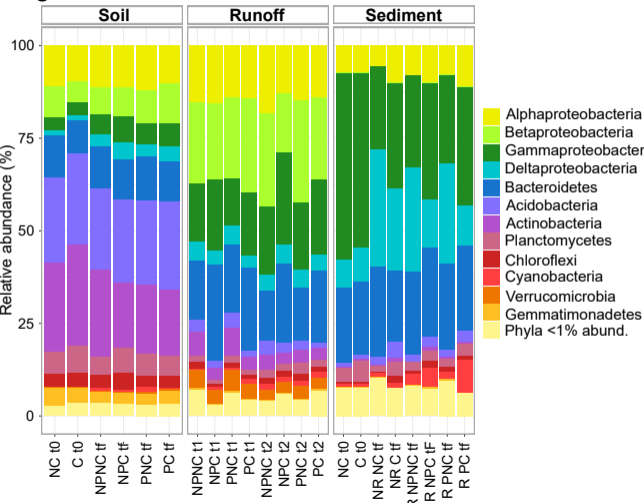
C



D



A Figure 3



B [Click here to access/download;Figure;FIG3.pdf](#)

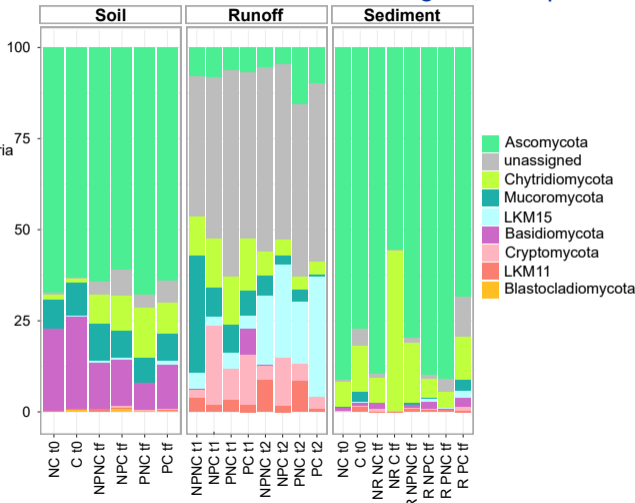
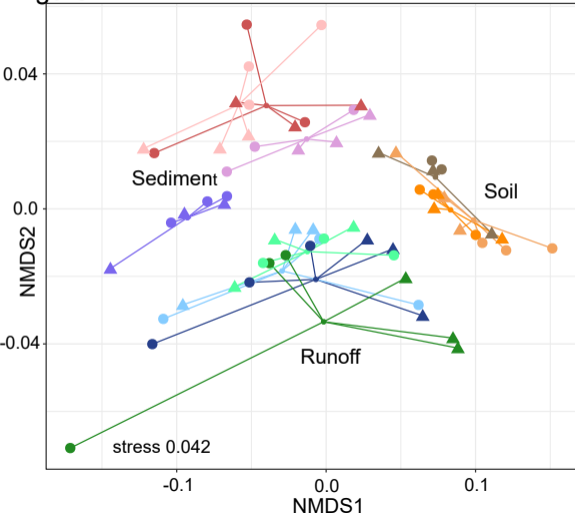
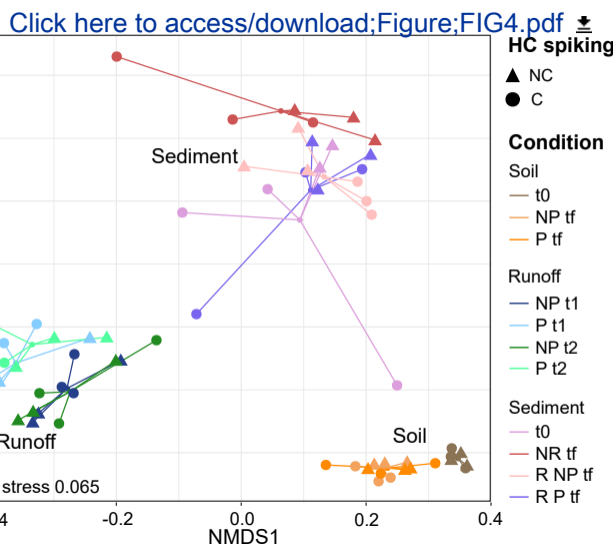


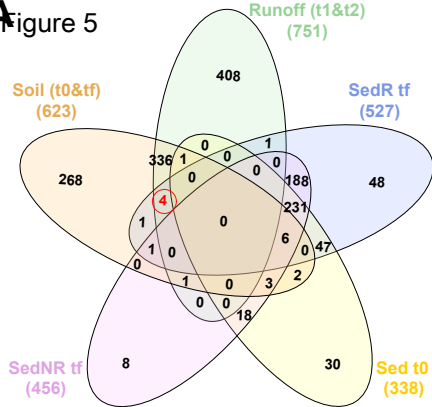
Figure 4



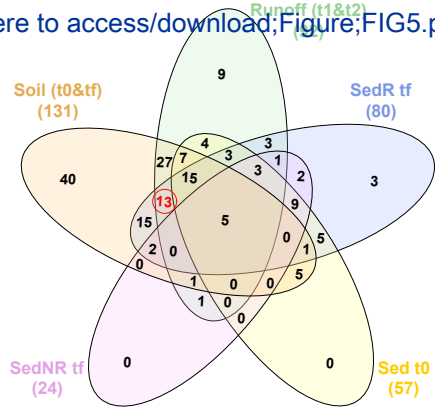
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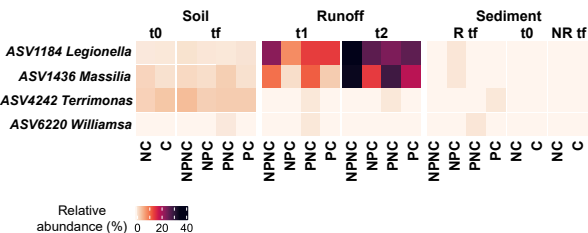
A Figure 5



B [Click here to access/download;Figure;FIG5.pdf](#)



C



D

