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

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Abstract

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

Keywords

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

Introduction

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

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

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

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

Material and Methods

Soil and sediment samples

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

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

Microcosms Setup

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

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

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

Figure ***1***B and C). Thus, six different experimental conditions were compared. In the HC spiked conditions, soil and sediment (1/10 of the soil and sediment as dry weight) received a mix 1:1 (W:W) of deuterated n-hexadecane (D34, 98%, Cambridge Isotope Laboratories, Inc, USA) and phenanthrene (D10, 98%, Euriso-top, France), dissolved in hexane solvent. A stock solution was prepared in order to add each HC at a concentration of 1000 mg/kg dry soil or sediment. For the unspiked conditions, the same volume of hexane was added alone without addition of HC stock solution. After total solvent evaporation, 9:10 of crude soil and sediment were mixed with spiked fractions to have a contamination at 100 mg/kg. Soils were watered to reach 60% of their water holding capacity. *Catapodium marinum*, a grass identified *in situ*, was sown in soil with 25 seeds (seed bank of the Muséum National d'Histoire Naturelle, Paris, France) per microcosm. For the sediment compartment, 200 mL of seawater was added on the top of the sediment. After an aging period of 4 days at 4 °C, allowing the sorption of the HC into soil and sediment matrices, microcosms were installed in a phytotronic chamber with controlled conditions (22 °C/18 °C day/night, 80% relative humidity, c.a. 250 µmol photons m^{-2} s^{-1}, 16 h photoperiod). Microcosms were incubated for 39 days, the estimated time necessary for plant growth and HC degradation (Ben Said et al., 2015; Bourceret et al., 2017; Duran et al., 2015b). Soil compartments were watered five consecutive days per week by means of a syringe dispensing 73 mL mineral water (Volvic®) to mimic rainfall and produce soil runoff and in turn terrigenous inputs. After seed germination, 16 plants were kept per device.

Both in land-sea continuum and in control microcosms, peristaltic pumps helped to simulate a 12 h tidal cycle. In this way, the seawater was renewed twice a day maintaining sediment covered by 3 cm of seawater during the low tide ensuring conditions close to those prevailing in natural environment.

Sampling

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

DNA extraction and rRNA gene sequencing

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

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

Sequence processing and ASV delimitation

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

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

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

Alpha and beta-diversity of the core microbial communities

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

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

Venn diagram, microbial source tracking and indicator species analyses

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

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

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

Results and discussion

Partitioning the microbial community into core and satellite groups

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

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

Diversity of the core microbial community

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

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

Microbial composition within the land-sea continuum compartments

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

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

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

Comparison of microbial communities

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

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

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

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

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

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

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

Identification of community coalescence microbial indicators

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

Conclusion

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

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Declaration of Competing Interest

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

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Table 1. ASV indicators of coalescence identified by the indicator value index (IndVal). ASV indicators specifically associated to sediment with runoff (SedR tf) were identified by an indicator analysis performed among conditions in the sediment compartment. In a second step, the IndVal of each ASV indicator was calculated among soil, runoff and sediment compartments. IndVal value range from 0 (no association) to 1 (perfect association). Only 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	*Hypocreales*	0.850	0.015	SedR tf	0.779	0.005	Soil
2716	Bacteria	Alphaproteobacteria	*Rhodobacteraceae*	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	*Cyclobacteriaceae*	0.857	0.01	SedR tf	0.707	0.005	Sed

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; ^{2}D:
887 Inverse Simpson index; Faith's PD: Faith's phylogenetic diversity index; Hill ^{2}PD:
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, Omnitrophicaeota, Latescibacteria,
900 Armatimonadetes, Patescibacteria, Spirochaetes, Calditrichaeota, Rokubacteria,
901 Marinimicrobia (SAR406 clade), Tenericutes, Dadabacteria, Dependentiae, 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

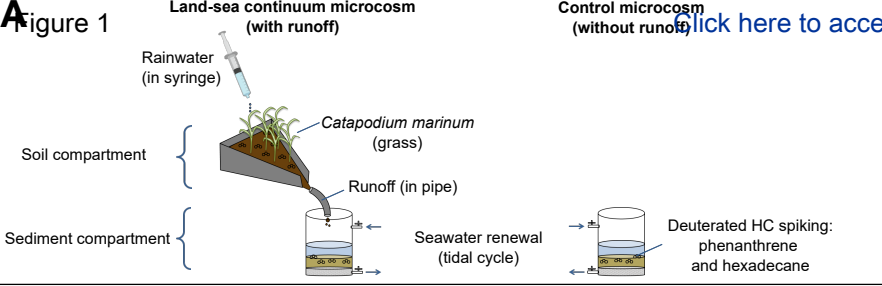
906 **Figure 4.** NMDS analysis based on the weighted UniFrac metrics presenting the differences
907 observed in the prokaryotic (A) and in the fungal (B) community composition of soil, runoff
908 and sediment compartments. Coloured segments connect samples with the same plant condition
909 and sampling 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

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

Figure 1



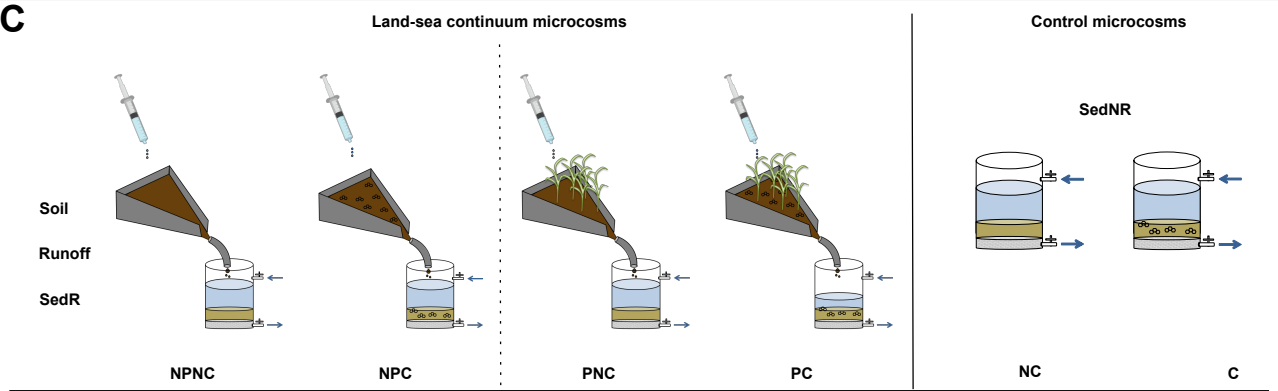


Figure 2

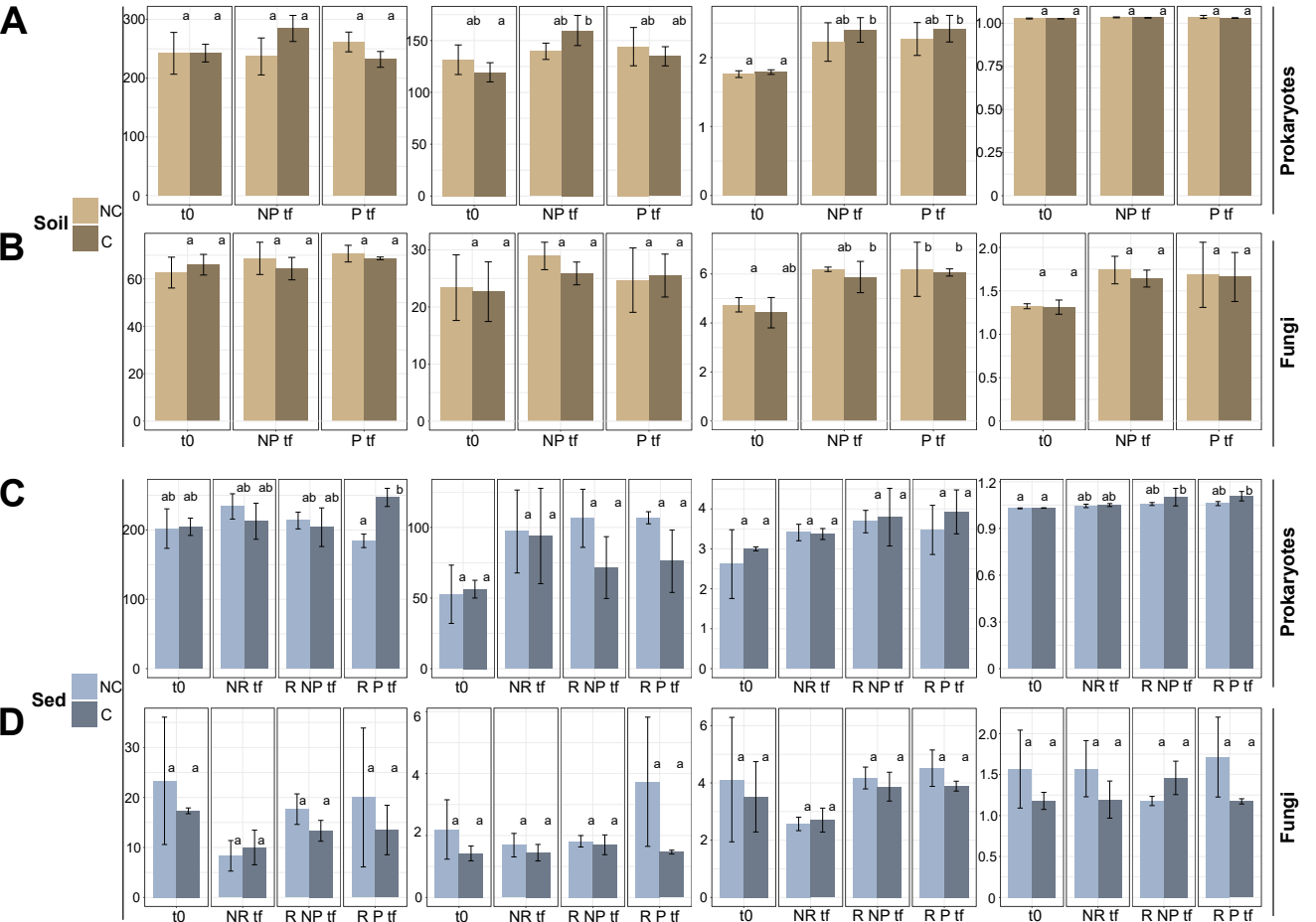


Figure 3

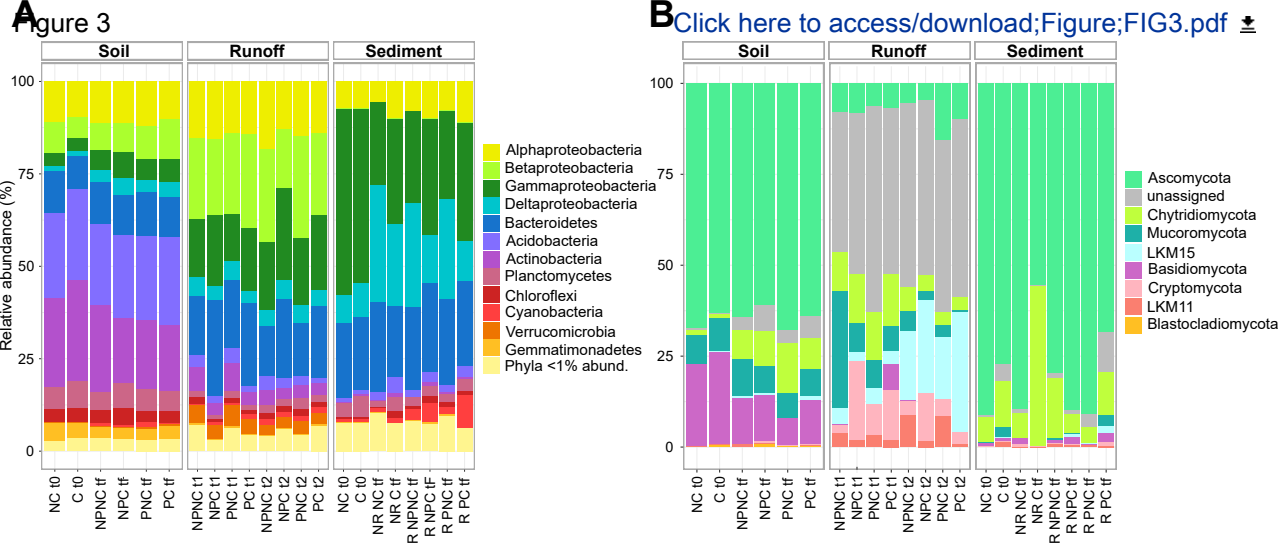

A
Soil
Runoff
Sediment
Relative abundance (%)
100
75
50
25
0
NC t0
C t0
NPNC tf
NPC tf
PNC tf
PC tf
NPNC t1
NPC t1
PNC t1
PC t1
NPNC t2
NPC t2
PNC t2
PC t2
NC t0
C t0
NR NC tf
NR C tf
R NPNC tf
R NPC tF
R PNC tf
R PC tf
Alphaproteobacteria
Betaproteobacteria
Gammaproteobacteria
Deltaproteobacteria
Bacteroidetes
Acidobacteria
Actinobacteria
Planctomycetes
Chloroflexi
Cyanobacteria
Verrucomicrobia
Gemmatimonadetes
Phyla <1% abund.
B
Click here to access/download;Figure;FIG3.pdf
Soil
Runoff
Sediment
100
75
50
25
0
NC t0
C t0
NPNC tf
NPC tf
PNC tf
PC tf
NPNC t1
NPC t1
PNC t1
PC t1
NPNC t2
NPC t2
PNC t2
PC t2
NC t0
C t0
NR NC tf
NR C tf
R NPNC tf
R NPC tf
R PNC tf
R PC tf
Ascomycota
unassigned
Chytridiomycota
Mucoromycota
LKM15
Basidiomycota
Cryptomycota
LKM11
Blastocladiomycota

Figure 4

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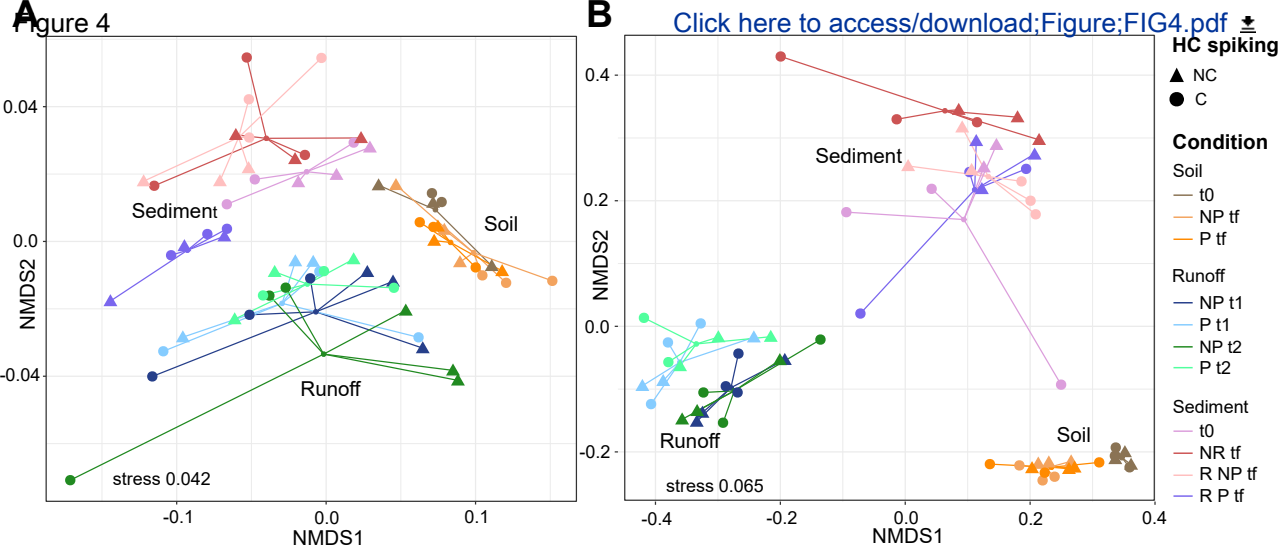

Figure 5

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