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Title

Linking multiple facets of biodiversity and ecosystem functions in a coastal reef habitat

Short title

Reef biogeochemical fluxes and biodiversity

Authors

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1. INTRODUCTION

Ecosystems worldwide are experiencing increasing rates of biodiversity loss mainly caused by land and sea use changes, direct resource exploitation and climate change (IPBES 2019). This biodiversity crisis triggered in the 1990s a new line of work investigating the links between biodiversity and ecosystem functioning and the mechanisms underpinning these relationships, known today as BEF research (Hooper and Vitousek, 1997; Tilman, 1997). Focusing first on terrestrial autotrophic ecosystems, many experimental studies found that an increase in plant species richness led to an increase in ecosystem functions, such as primary production and nutrient cycling (Cardinale et al., 2011; Hector et al., 1999; Naeem et al., 1996). Nonetheless, species richness is not the unique driver of ecosystem functioning and considering the diversity of functions performed by species (*i.e.* functional diversity) is also key when studying BEF relationships (Hooper et al., 2005). For example, functional identity of species and functional diversity among grassland species, rather than species diversity per se, together promote primary production and decomposition (Mouillot et al., 2011). More generally, ecosystem functioning can be promoted by a higher diversity of species and their functional traits through mechanisms like resource partitioning and niche complementarity, as stated by the diversity hypothesis (Tilman, 1997). Among species assemblages, dominant species and their traits can also promote an ecosystem's functioning through a selection effect linked to competitive differences (Cadotte, 2017), as stated by the mass ratio hypothesis (Grime, 1998).

In aquatic ecosystems, sediments and microorganisms are key in regulating biogeochemical functions like organic matter remineralization and nutrient cycling (Jones et al., 1985). Larger benthic fauna able to rework sediments (bioturbation) and/or to transfer solutes (bioirrigation) also influence strongly these functions (Kristensen, 1988; Stief, 2013). High densities of sediment-reworking species (*e.g.* fiddler crabs *Uca* spp. in Kristensen (2008)) modify the sediment resource through various biological activities like feeding, burrowing or

ventilation and can be considered as allogenic ecosystem engineers (Jones et al., 1994). Conversely, autogenic ecosystem engineers like mangrove trees or salt marsh plants "change the environment via their own physical structures", often creating new habitats (Jones et al., 1997, 1994). Many different organisms engineer marine habitats, from mollusks (*e.g. Crassostrea virginica*) and polychaetes (*e.g. Phragmatopoma caudata*) to cnidarians (*e.g.* scleractinian corals) and plants (*e.g. Zostera marina*) (Goldberg, 2013). These engineers often have a positive effect on local species richness through the reduction of abiotic and biotic pressures like thermal stress and predation (Romero et al., 2015; Stachowicz, 2001) and could also promote, through their density, the functioning of the engineered ecosystem, a potential role called the engineer effect.

Classically, BEF studies in aquatic ecosystems focused on soft sediments, considering biogeochemical fluxes as the response variable while controlling for macrofauna species richness and/or functional group richness. Such studies generally reported positive BEF relationships, while stressing the role of the species' functional identity and density (Covich et al., 2004; Gamfeldt et al., 2015). In such controlled experiments, interspecific interactions like resource use complementarity are limited by the manipulation of low diversity levels that represent only a fraction of the local species pool (Brose and Hillebrand, 2016; Thrush and Lohrer, 2012). Conversely, observational *in situ* studies can consider natural multi-trophic communities along environmental gradients (Godbold and Solan, 2009) helping for example, to tease apart the effects of abiotic and biotic factors on ecosystem processes (Brose and Hillebrand, 2016). More generally, new hypothesis and "a more integrated empirical approach to BEF research" can stem from observational studies (Thrush and Lohrer, 2012).

We aimed at bringing new insights on BEF relationships drawn from observations of a temperate reef ecosystem built by a primary consumer, the honeycomb-worm *Sabellaria alveolata*. Despite their ubiquity and the many ecosystem services they provide (IPBES, 2019;

Romero et al., 2015), bivalve and polychaete reefs are rarely investigated in the context of BEF research. Studies measuring functions like respiration or calcification, mainly focus on the engineer species, overlooking the role the associated organisms could have in regulating these functions (Kellogg et al., 2013; Lejart et al., 2012; Newell et al., 2002; Smyth et al., 2016). Natural diversity gradients often occur in ecosystems dominated by an engineer species (*e.g.* mussels, oysters, tubiculous worms), giving us the opportunity to investigate how this particular species and the associated fauna influence functions like biogeochemical fluxes (Bouma et al., 2009; Jones et al., 2018; Norling and Kautsky, 2007).

Sabellaria alveolata is an intertidal ecosystem engineer distributed along the European Atlantic coast from Scotland to Morocco (Muir et al., 2016). Once settled on the seabed, this polychaete builds a tube using mostly bioclastic particles (Le Cam et al., 2011). When environmental conditions are favorable, *S. alveolata* can form bioconstructions on rocky shores or on soft sediments (Dubois et al., 2002; Gruet, 1972; Holt et al., 1998), where a diverse and abundant fauna establishes (Dias and Paula, 2001; Jones et al., 2018; Porta and Nicoletti, 2009). These habitats undergo natural cycles of growth (progradation) and decline (retrogradation) (Curd et al. 2019) forced by abiotic factors like particle availability (Le Cam et al., 2011) and hydrodynamic forces (Gruet, 1986) and by biotic factors like recruitment strength (Ayata et al., 2009; Dubois et al., 2007a) and interspecific competition (Dubois et al., 2007b). These cycles are mostly characterized by modifications of the reef's physical structure (Curd et al., 2019) and by changes in the associated fauna in terms of richness, abundance and composition (Dubois et al., 2002). Anthropogenic disturbances like trampling and coastal modifications can also modify the reef's structure and the associated fauna (Desroy et al., 2011; Dubois et al., 2006; Jones et al., 2018; Plicanti et al., 2016).

In this study, we investigated the biogeochemical functioning of a reef habitat engineered by *S. alveolata* and evaluated the relative support of the engineer effect hypothesis, the diversity

hypothesis, and the mass-ratio hypothesis on driving key benthic processes taking place in the sediments glued into bioconstructions by the tube-building activity of *S. alveolata* (*i.e.* engineered sediments). First, we measured and compared the sediment-water fluxes (*i.e.* oxygen, ammonium, nitrate, and nitrite) in the engineered sediments and in the surrounding soft sediments. Then, using a multiple linear regression approach (model selection and effect size calculation), we investigated the relative importance of the engineer itself (engineer effect hypothesis) and of the macrofauna associated to the engineered sediments, in terms of taxonomic or functional diversity (diversity hypothesis) and in terms of biological trait dominance (mass-ratio hypothesis) on the different biogeochemical fluxes.

2. MATERIAL AND METHODS

2.1. Study area

The bay of Mont-Saint-Michel is a macrotidal bay located in the English Channel between Brittany and Normandy, characterized by an intertidal zone covering over 250 km² and a mean spring tide range of 14.5 m (Bonnot-Courtois et al., 2004). In its central part, the Sainte-Anne reef (48°38'700N and 1°40'100W) is the largest bioconstruction in Europe, built by the gregarious and tubiculous polychaete *S. alveolata* (Gruet, 1972; Holt et al., 1998). This part of the bay is characterized by a high proportion of bioclastic sediments with increasing medium grain size from the intertidal to the subtidal zone (Bonnot-Courtois et al., 2004). The Sainte-Anne reef is located in the lower intertidal zone (between the -2 and -4 m isobaths), parallel to the coastline, perpendicular to the dominant tidal currents and *ca.* 3 km from the shoreline (Dubois et al., 2006; Noernberg et al., 2010). Because *S. alveolata* bioconstructions occur in systems where this species finds soft sediment material to build its tube and hard substrata to settle on (Curd et al. 2019), the Sainte-Anne reef is composed of a mosaic of structures built by

150 the engineer species (hereafter called engineered sediment, 32 ha in 2014, pers. obs.)
151 surrounded by soft sedimentary features (Jones et al., 2018).
152
153 *2.2. Field sampling and experimental set-up*
154 We sampled four dominant sediment typologies according to Curd et al. (2019): (1)
155 engineered sediment in prograding phase, identified by growing and expanding tubes, without
156 epibiontes (hereafter called Undisturbed Engineered Sediment or UES), (2) engineered
157 sediment in retrograding phase, identified by tubes lacking apertures, often covered by biofilm
158 and epibiontes (hereafter called Disturbed Engineered Sediment or DES), (3) soft sediment
159 composed of coarse sand (CS) with bioclastic elements and (4) soft sediment composed of fine
160 and muddy sand (MS). We sampled these four typologies 3 times over a year, according to a
161 temperature gradient: in winter (February, water temperature = 8°C), in spring (April, water
162 temperature = 12°C) and in summer (September, water temperature = 17°C). During each
163 sampling period, we randomly extracted four cores – at low tide – across a surface of *ca.* 100
164 m^2 of each sediment typology using either a toothed metal corer (15 cm diameter) for the
165 engineered sediment cores or 35-cm long Perspex tubes (15 cm diameter) for the soft sediment
166 cores. We immediately transferred the engineered sediment cores into 35-cm long Perspex
167 tubes (15 cm diameter), sealed all the tubes and transported them to the laboratory where we
168 placed them inside a dark refrigerated room. Prior to the coring, we collected 40 liters of
169 seawater next to the reef - during high tide - using inflatable bags to avoid bubbles that we
170 stored in a dark room at the *in situ* water temperature.
171 In the laboratory, we filled the Perspex tubes with the collected water, sealed them with
172 caps equipped with small magnetic stirrers, connected them *via* a tube to the inflatable water
173 reserve tank and incubated them respecting the *in situ* water temperature. We started the
174 incubations *ca.* 2 hours after the sampling and incubated the 16 cores sampled during each

campaign between 3 and 15 hours, until a loss of 30% of the initial dissolved oxygen concentration measured in each core. During the incubations, we sampled 6 to 8 times both the water overlying the sediment and the water from the reserve tank (control water) using a 60 ml plastic syringe (see Denis et al. (2001) for further details on the incubation set up). Finally, we measured the oxygen, ammonium, nitrate, and nitrite concentrations in all the water samples, and we used the difference between concentration changes in the overlying water of each core and control water to calculate the sediment-water fluxes.

2.3. Flux measurements and calculations

To determine oxygen concentration, we gently transferred the required volume from the 60 ml plastic syringe into a 10 ml glass flask using a tubing and allowing overflow from the flask to avoid air bubbles. We then measured oxygen concentration using an oxygen Clark-type microsensor (Revsbech, 1989) characterized by a 90 % response time of <8s, a stirring sensitivity of <1.5 % and a current drift of <1 % h^{-1} (Unisense A/S, Aarhus, Denmark, 100µm tip diameter). Linear two-point calibration of each microelectrode was systematically performed before and after each series of measurements. Zero oxygen current was measured in the anoxic zone of an additional sediment core with muddy sediments while a 100% oxygen level was calibrated using air-bubbled water. To determine the other concentrations, we filtered the volume remaining in the syringe through GF/F Whatman glass fiber filters before transferring them into a 20 ml polyethylene flask for ammonium analysis and a 10ml polyethylene tube for nitrate and nitrite analysis. We immediately carried out the ammonium analysis following the indophenol-blue method (Solórzano, 1969). We froze the remaining samples and measured later on the nitrate and nitrite concentrations using a Seal autoanalyzer, following the protocol of Tréguer & Le Corre (1975). We determined the fluxes by regressing the change in overlying water concentration versus time and considered fluxes as null when

non-significant regressions (Pearson correlation, $p > 0.05$) based on changes over time were less than the analytical variability. For all fluxes, we systematically applied a correction for water replacement. We measured a significant oxygen consumption during all the incubations ($p < 0.05$). We considered the ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-) fluxes (from the sediment to the overlying water) from the following cores as null; two spring CS cores for the NH_4^+ fluxes, all the summer MS cores for the NO_3^- fluxes and two spring MS cores, one summer MS core and one summer CS core for the NO_2^- fluxes. Finally, we expressed the nitrate and nitrite fluxes of each core as a sum we called nitrate + nitrite flux (NO_{2+3}) and considered the oxygen flux as going from the overlying water to the sediment, hereafter called the sediment oxygen demand (SOD).

2.4. Macrofauna taxonomic and functional diversity

At the end of each incubation, we fixed the sediment cores using a 5 % formaldehyde solution, before sieving them through a 1-mm square mesh. We sorted the macrofauna (>1 mm) and identified it to the lowest taxonomic level, often species level (except for Nemerteans, Nematodes and Tubificoides, see Table S1). For each core, we measured the abundance and the ash-free dry weight (AFDW – 4 hours at 550°C) of each taxonomic group including the engineer species *S. alveolata* and then standardized the different measurements taken for each core (fluxes, macrofauna abundance and biomass) to unit surface. First, we characterized the macrofauna according to each species taxonomic identity, before calculating Hill's indices (*i.e.* the number equivalents of three diversity indices), always including *S. alveolata* (Hill, 1973): the species richness (SR), the exponential of Shannon-Wiener ($\log_e$) calculated using either the abundance ($N1_{ab}$) or the biomass ($N1_{biom}$) and the inverse of Simpson's dominance calculated using either the abundance ($N2_{ab}$) or the biomass ($N2_{biom}$). Hill's indices are recommended for

224 the study of benthic communities (Gray, 2000) and have the "doubling" property, making their
225 interpretation more straightforward than the raw Shannon-Wiener and Simpson dominance
226

227 **Table 1.** Macrofauna biological traits and associated modalities used to calculate the functional
228 diversity indices. For each trait, we indicated the macrofauna processes linked to organic matter
229 remineralization and nutrient cycling, along with the macrofauna processes linked to the
230 ecosystem functions via microorganism processes.

Trait and associated modalities	Direct macrofauna processes	Via microorganism processes	References
Maximum size (literature, mm): <10 [10-50[[50-100[[100-200[>200	respiration, excretion of DIN	egestion of POM via remineralization, transport of solutes and O_2 via nitrification, denitrification	Hildrew et al. (2007); Kristensen (1988); Shumway (1979); Vanni (2002)
Daily movement capacity: No movement Low (<1 m) Medium (1-10 m) High (>10 m)	respiration, excretion of DIN	transport of solutes and O_2 via nitrification, denitrification, remineralization	Kristensen (1988); Queirós et al. (2013); Shumway (1979)
Sediment reworking: Epifauna Surficial modifiers Upward and downward conveyors Biodiffusors Regenerators		transport of solutes and O_2 via nitrification, denitrification, remineralization	Janson et al. (2012); Queirós et al. (2013); Solan et al. (2004); Thrush et al. (2006)
Feeding mode: Suspension feeder Surface deposit feeder Sub-surface deposit feeder Predator-scavenger Grazer	respiration, excretion of DIN, ingestion of POM	egestion of POM via remineralization	Janson et al. (2012); Kristensen (1988); Thrush et al. (2006)
Bathymetric preference: Intertidal Subtidal		informs indirectly on the engineered sediment's thermal properties which can mediate microorganism processes	Gutiérrez and Jones (2006)

231 DIN: dissolved inorganic nitrogen, POM: particulate organic matter

232 indices (Hill, 1973). The indices N1 and N2 both increase when the sample diversity increases
233 but N1 is sensitive to the abundance or biomass variations of rare or uncommon species while
234 N2 is sensitive to the variations of the most common species. Then, we characterized the
235 macrofauna according to a set of biological traits (five categorical traits each divided into
236 modalities) known to directly or indirectly affect individual processes ("effect traits" *sensus*
237 Lavorel & Garnier (2002)), such as aerobic respiration, which themselves affect benthic
238 ecosystem functions such as nitrogen cycling and organic matter remineralization (Table 1).
239 These ecosystem functions are estimated by measuring oxygen and solute fluxes (*i.e.* NH_4^+,
240 NO_3^-, NO_2^-) between the sediment and the overlying water. We used the two main components
241 of the bioturbation potential (Queirós et al., 2013), mobility and sediment reworking, rather
242 than the bioturbation potential per se because both components are influenced by habitat
243 structure (Godbold et al., 2011), a characteristic differing between UES and DES zones of the
244 reef (Curd et al., 2019; Jones et al., 2018). Furthermore, transferring bioturbation potential
245 across space and time is only possible if the species body size is constant (Queirós et al., 2013),
246 which was not the case since we sampled across three different periods.
247 Some species present different modalities for certain traits like *Carcinus maenas*, which can
248 behave as a grazer and as a predator-scavenger (2 modalities in the feeding mode trait). To take
249 into account this intraspecific variability, we fuzzy coded the categorical traits by assigning a
250 value between 0 (no affinity) and 3 (strict affinity) to each modality of a given trait depending
251 on the species affinity for the modality, with 1 and 2 indicating intermediate affinities (Chevenet
252 et al., 1994). The sum of the values attributed to all the modalities of a given trait was always
253 equal to three except for the tidal position, which could be equal to four if the species had an
254 equal affinity for the intertidal and subtidal modalities. We recovered most of the information
255 on polychaete feeding mode and daily movement capacity from Fauchald & Jumars (1979) and
256 Jumars et al. (2015). The rest was recovered from peer-reviewed journals

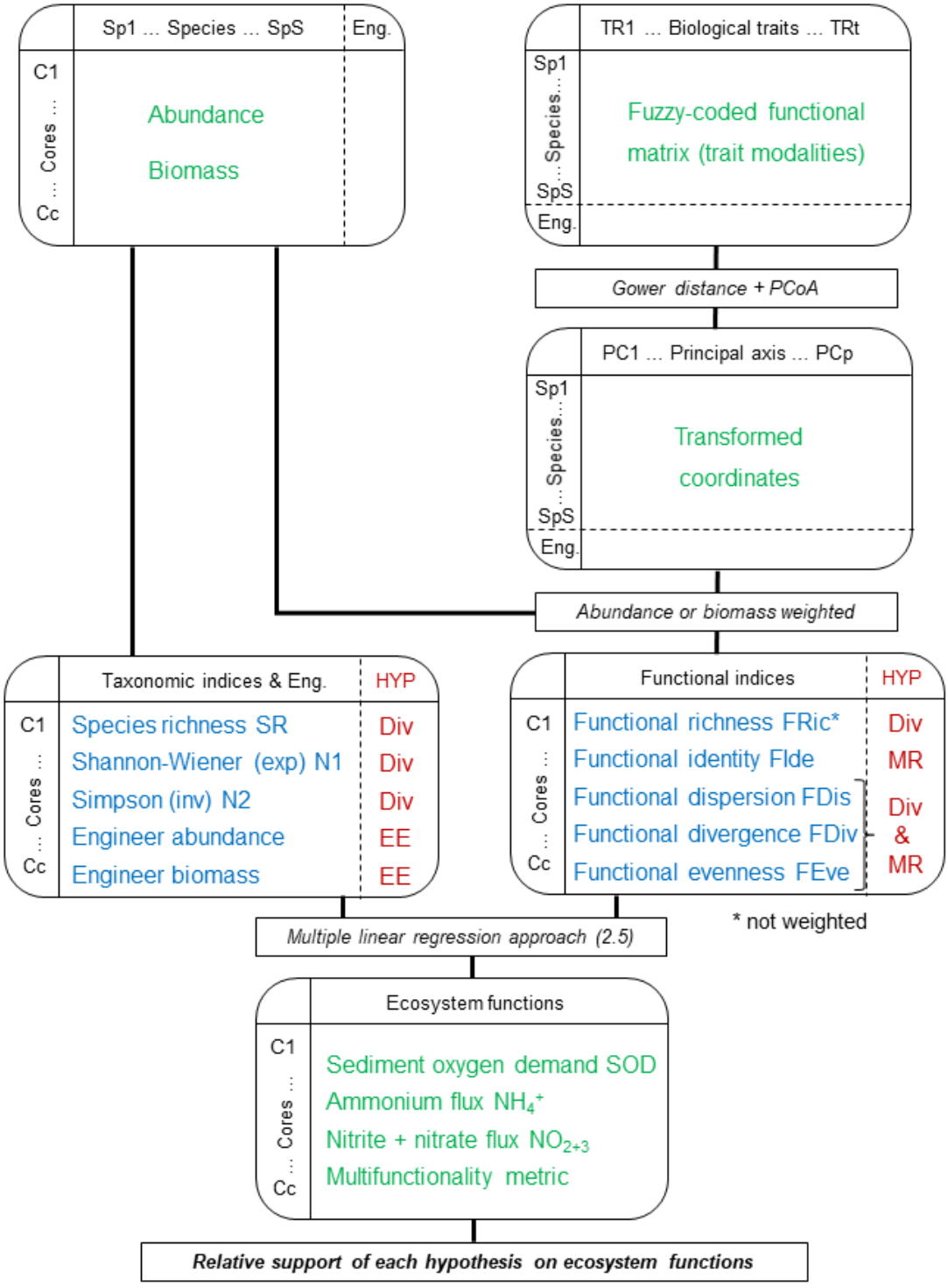


Figure 1. Framework used to study the relative support of the diversity hypothesis (Div), the mass ratio hypothesis (MR) and the engineer effect hypothesis (EE) on ecosystem functions (here biogeochemical fluxes) in the context of a community structured by an ecosystem engineer (Eng.). Each index in blue is used to test a specific hypothesis (HYP) in red and all the indices along with the water temperature, were first considered as explanatory variables in the multiple linear regression approach detailed in part 2.5. Adapted from Villéger et al. (2008).

(Guerra-García et al., 2014; Navarro-Barranco et al., 2013) and biological trait databases (Marine species identification portal, BIOTIC).

Using the biological traits matrix defined for the 43 species identified in the UES and DES cores (n = 24), we calculated several functional indices following the framework detailed in Figure 1 and using the R packages presented in Table 2. We used the Gower distance to calculate the functional distance between each pair of species and then performed a principal coordinate analysis (PCoA) on the distance matrix (Laliberté and Legendre, 2010; Villéger et al., 2008) to represent each species in a multidimensional functional space, each dimension (PCoA axis, 42 axes in total) being a combination of traits. Finally, we calculated for each core, several functional diversity and identity indices using different data types (Table 2) and weighted each index (except functional richness) by species relative abundance (ab in subscript) or relative biomass (biom in subscript) (Fig. 1). *Sabellaria alveolata* was always included in the data sets used to calculate the indices. Functional richness was standardized by the 'global' functional richness (including all species recorded in the UES and DES cores) to constrain it between 0 and 1 (Laliberté and Legendre, 2010).

2.5. Statistical analyses

First, we tested the effect of sediment typology (four levels: CS, MS, UES and DES), sampling period (three levels: spring, summer and winter) and their interaction on the different fluxes (SOD, NH_4^+ and NO_{2+3}) using an analysis of variance (ANOVA) with a two-way crossed balanced design. If the interaction term was significant for a flux, we performed Tukey HSD post-hoc tests to disentangle which sediment typology x sampling period cores presented significantly higher or lower fluxes than others. After running the ANOVAs, we checked each model's residuals for normality using a histogram and for homoscedasticity by plotting them against the predicted values (Zuur et al., 2010).

289 **Table 2.** Definition and associated information (data type, key references, R functions and weighting procedure) on the five functional indices
290 (diversity and identity). The first four PCoA axes represent 60% of the total inertia. See Figure 4 for a graphical illustration of each index.

Functional indices	Name	Definition	Data type	Unweighted or weighted	Key references	R function
Functional identity	FIde	Weighted average position on the selected functional space axis (PCoA axis)	PCoA axis 1, 2 or 3	Weighted by abundance or biomass	Mouillot et al. (2013)	multidimFD
Functional richness	FRic	Multidimensional functional space filled by all species in a community	PCoA axes 1 to 4	Unweighted	Villéger et al. (2008); Laliberté and Legendre (2010)	dbFD
Functional dispersion	FDis	Weighted average distance to the weighted average mean trait values of the community	Uncorrected functional distance matrix	Weighted by abundance or biomass	Laliberté and Legendre (2010)	dbFD
Functional divergence	FDiv	Weighted average deviation of the Euclidian distance between the position of all the species in the functional space and the unweighted center of gravity of the vertices of the convex hull	PCoA axes 1 to 4	Weighted by abundance or biomass	Villéger et al. (2008)	dbFD
Functional evenness	FEve	Regularity of abundance or biomass distributions in the functional space along the shortest minimum spanning tree linking all the species	PCoA axes 1 to 42	Weighted by abundance or biomass	Villéger et al. (2008); Laliberté and Legendre (2010)	dbFD

sediment core a multifunctionality metric using the mean of the four standardized fluxes (mean = 0 and SD = 1), to give them the same weight (Mouillot et al., 2011).

Then, to estimate the importance of macrofauna *vs* meiofauna + microorganisms in organic matter processing, we calculated the macrofauna-normalized SOD (mmol O_2. day^{-1}.g $AFDW^{-1}$) for each core by dividing the daily oxygen consumption (mmol O_2. day^{-1}) by the total macrofauna biomass (g AFDW). Values inferior to 1 indicate processes are predominantly driven by macrofauna whereas values superior to 1 indicate processes are predominantly driven by meiofauna and microorganisms (Stenton-Dozey et al., 2001 in Clough et al., 2005). A multifunctionality metric was also calculated for each engineered sediment core as the mean of the four fluxes after standardizing each of them (mean of 0 and standard deviation of 1) to give them the same weight (Mouillot et al., 2011).

Finally, we implemented a multiple linear regression approach (ordinary least-square regressions) to determine the relative importance of (1) water temperature, (2) the engineer *S. alveolata* (engineer effect hypothesis), (3) macrofauna diversity in terms of species or biological traits (diversity hypothesis) and (4) the functional traits of the dominant species (mass-ratio hypothesis) on the four ecosystem functions measured in the engineered sediments. Each index presented in Figure 1 is used to test one hypothesis, except FDis, FDiv and FEve, which are used to test the diversity and mass-ratio hypotheses (Mokany et al., 2008), as their values are driven by macrofauna traits and macrofauna abundance or biomass. We considered the 24 incubated engineered sediment cores as statistically independent replicates because the cores were physically isolated from each other during the flux measurements (independent incubations) and the processes we measured take place at spatial scales inferior to the *in situ* distance separating two cores (Hewitt et al., 2005). Indeed, the cores sampled in the UES and DES sediment typologies were extracted from different engineered sediment patches across a surface of *ca.* 100 m² and most of the engineered sediment benthic macrofauna being sessile or

316 presenting a low mobility, their movements are constrained to a given engineered sediment
317 patch (Table 1, Fig. 4 and 5).

318 First, we reduced the number of explanatory variables, previously standardized (Schielzeth,
319 2010), to consider in the multiple linear regressions by removing variables that were highly
320 correlated ($|r| > 0.8$, Spearman correlations) (Godbold and Solan, 2009). We removed $N2_{ab}$ and
321 $N2_{biom}$ as they were highly correlated with $N1_{ab}$ ($r = 0.98$) and $N1_{biom}$ ($r = 0.98$), respectively,
322 $FIde2_{ab}$ and $FIde2_{biom}$ as they were highly correlated with $FIde1_{ab}$ ($r = -0.97$) and $FIde1_{biom}$ ($r =$
323 -0.87), respectively and $FDiv_{ab}$ and $FDiv_{biom}$ as they were highly correlated with $FDis_{ab}$ ($r = -$
324 0.85) and $FDis_{biom}$ ($r = -0.90$), respectively. After this step, we had one environmental variable
325 (temperature), two variables associated to the engineer effect hypothesis (*S. alveolata*
326 abundance and biomass), four variables associated to the diversity hypothesis (SR, $N1_{ab}$, $N1_{biom}$
327 and FRic), four variables associated to the mass-ratio hypothesis ($FIde1_{ab}$, $FIde1_{biom}$, $FIde3_{ab}$
328 and $FIde3_{biom}$) and four variables associated to the diversity and mass ratio hypotheses ($FDis_{ab}$,
329 $FDis_{biom}$, $FEve_{ab}$ and $FEve_{biom}$).

330 Secondly, we built first and second-degree polynomial regressions between each
331 explanatory variable and each ecosystem function, as preliminary inspections of the biplots
332 indicated the presence of quadratic relations (Thrush et al., 2017). Prior to this second step, we
333 squared the 15 remaining explanatory variables to build raw second-degree polynomial
334 regressions and the second-degree terms were standardized to improve the interpretability of
335 the multiple linear regression coefficients (Schielzeth, 2010). Regarding temperature, we only
336 considered first-degree linear regressions, as water temperature inside small ranges (here 9°C)
337 will have positive effects on biogeochemical fluxes such as SOD, according to the Q10 of 2
338 general relation (Herbert, 1999; Hildrew et al., 2007; Thamdrup et al., 1998).

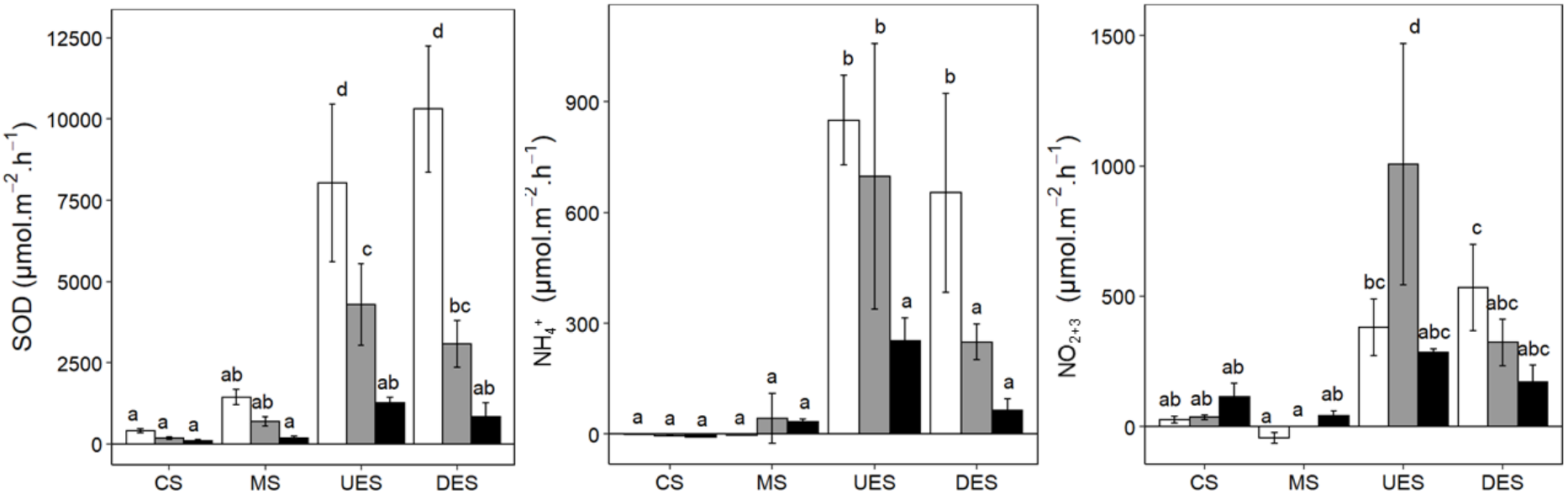
339 Thirdly, the variable associated to each hypothesis that had a significant effect on a given
340 ecosystem function ($p < 0.05$) and explained the highest amount of ecosystem function

341 variability (adjusted R^2) was included in the four initial multiple linear models. The following
342 explanatory variables were considered in each initial multiple linear model: for SOD,
343 temperature, *S. alveolata* biomass (first-degree), $FIde1_{ab}$ (second-degree) and $FDis_{ab}$ (second-
344 degree); for NH_4^+, temperature, *S. alveolata* biomass (first-degree), SR (first-degree), $FIde1_{ab}$
345 (first-degree) and $FDis_{ab}$ (second-degree); for NO_{2+3}, temperature, *S. alveolata* abundance
346 (first-degree), $N1_{ab}$ (first-degree) and $FEve_{ab}$ (second-degree); for the multifunctionality metric,
347 temperature, *S. alveolata* biomass (first-degree), SR (first-degree), $FIde1_{biom}$ (first-degree) and
348 $FDis_{ab}$ (second-degree).

349 Finally, to determine the minimal adequate models (final multiple linear models), we
350 selected the subset of predictors that minimized the Akaike information criterion (AIC) using
351 the 'ols_step_best_subset' function from the 'olsrr' package. If two models had AIC differences
352 of less than 2, we chose the one with the lowest Mallow's Cp to select the most parsimonious
353 model (Godbold and Solan, 2009). Before running the model selection procedure, we removed
354 the explanatory variables that presented high levels of collinearity based on a threshold of the
355 variance inflation factor of 10. For SOD and NH_4^+, we removed $FIde1_{ab}$, which was highly
356 correlated with $FDis_{ab}$ ($r = 0.99$) and defined reduced multiple linear models. After running each
357 model (initial, reduced, and final multiple linear regressions), we checked the residuals for
358 normality using a histogram and for homoscedasticity by plotting them against the predicted
359 values (Zuur et al., 2010). To estimate the independent effect of each selected predictor on a
360 given ecosystem function, we calculated the standardized partial regression coefficients and
361 represented this independent effect using partial linear regression plots (Schielzeth, 2010). We
362 considered a significance level of 0.05 for all the tests.
363

364 **3. RESULTS**

365 *3.1. Effect of sediment typology and sampling period on the different fluxes*



366

367 **Figure 2.** Sediment oxygen demand (SOD), ammonium flux (NH_4^+) and the sum of nitrate and nitrite fluxes (NO_{2+3}) measured for the four sediment
368 typologies (mean ± SD, n = 4), coarse sand (CS), muddy sand (MS), undisturbed engineered sediments (UES) and disturbed engineered sediments
369 (DES) in spring (white), summer (grey) and winter (black). The results of the post-hoc tests performed after the two-way crossed ANOVA
370 (sediment typology x sampling period) are presented as letters above each barplot, considering a p-value of 0.05.

Visually, the SOD, NH_4^+ and NO_{2+3} fluxes appeared higher in the undisturbed (UES) and disturbed (DES) engineered sediments compared to the coarse (CS) and muddy (MS) sediments across the three sampling periods. The engineered sediment fluxes appeared maximal in spring (Fig. 2 and Table S2). The mean SOD ranged from a minimum of 105 $\mu mol.m^{-2}.h^{-1}$ in winter for the CS cores to a maximum of 10 309 $\mu mol.m^{-2}.h^{-1}$ in spring for the DES cores. Sediment typology ($F(3,36) = 68.83$, $p < 0.001$), sampling period ($F(2,36) = 81.95$, $p < 0.001$) and their interaction ($F(6,36) = 20.96$, $p < 0.001$) had statistically significant effects on the SOD. The CS cores and the winter MS cores had the lowest SOD while the spring UES and DES cores and the summer UES cores had, respectively the first and second highest SOD. The spring and summer MS cores, the winter UES and DES cores and the summer DES cores had intermediate SOD (spring and summer MS and winter UES and DES ≤ summer DES ≤ summer UES, Fig. 2).

The mean NH_4^+ fluxes ranged from slightly negative (between -7.9 and -0.8 $\mu mol.m^{-2}.h^{-1}$) for all the CS cores and for the MS cores in spring to above 200 $\mu mol.m^{-2}.h^{-1}$ for all the UES cores and for the spring and summer DES cores with the maximum values measured in the spring UES cores (850.40 ± 121.79 $\mu mol.m^{-2}.h^{-1}$). Sediment typology ($F(3,36) = 51.14$, $p < 0.001$), sampling period ($F(2,36) = 17.72$, $p < 0.001$) and their interaction ($F(6,36) = 7.26$, $p < 0.001$) had statistically significant effects on the NH_4^+ fluxes. All the CS, MS, the winter UES and the spring and winter DES cores had significantly lower NH_4^+ fluxes than the spring and summer UES cores and the spring DES cores (Fig. 2).

All the NO_{2+3} fluxes were on average positive except in the spring MS cores (-43.7 $\mu mol.m^{-2}.h^{-1}$). The summer MS cores had mean NO_{2+3} fluxes near zero (0.2 $\mu mol.m^{-2}.h^{-1}$) while the rest of the soft sediment cores had mean fluxes between 26.0 and 114.2 $\mu mol.m^{-2}.h^{-1}$. All the engineered sediment cores had mean fluxes above 170.6 $\mu mol.m^{-2}.h^{-1}$ with the maximum values measured in the summer UES cores (1 006.9 ± 463.8 $\mu mol.m^{-2}.h^{-1}$). Sediment typology ($F(3,36)$

396 = 35.89, $p < 0.001$), sampling period (F(2,36) = 6.41, $p = 0.004$) and their interaction (F(6,36)
397 = 9.17, $p < 0.001$) had statistically significant effects on the NO_{2+3} fluxes. The spring and
398 summer MS cores presented the lowest NO_{2+3} fluxes while the summer UES and the spring
399 DES cores presented, respectively the first and second highest NO_{2+3} fluxes. The rest of the
400 cores presented intermediate NO_{2+3} fluxes (winter CS and MS ≤ winter UES and DES and
401 spring DES ≤ spring UES, Fig. 2).

402 Calculation of the macrofauna-normalized SOD for each core indicated that meiofauna and
403 microorganisms predominantly drove organic matter processing in the CS and MS
404 (macrofauna-normalized SOD >> 1). Differently, macrofauna was the principal driver of
405 organic matter processing in the UES and DES (Fig. 3).

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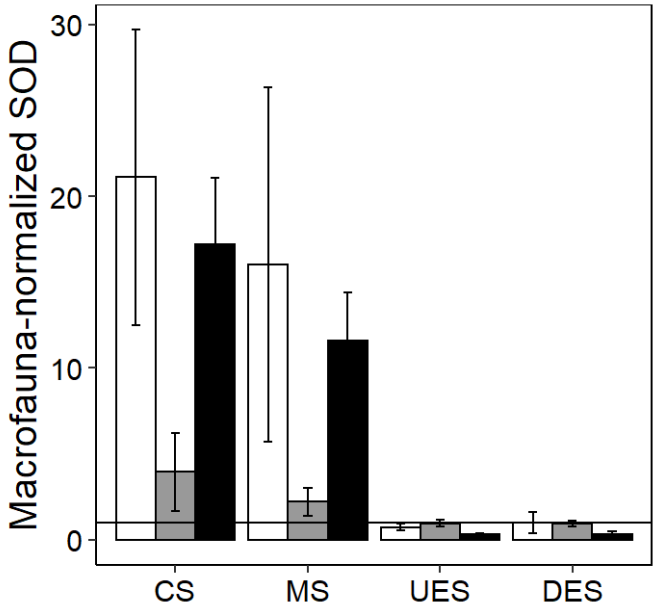

407

408 **Figure 3.** Macrofauna-normalized sediment oxygen demand (SOD) in mmol O_2. day^{-1}.g
409 $AFDW^{-1}$ (mean ± SD, n = 4) calculated for the four sediment typologies, coarse sand (CS),
410 muddy sand (MS), undisturbed engineered sediments (UES) and disturbed engineered
411 sediments (DES) in spring (white), summer (grey) and winter (black). The horizontal line
412 represents a macrofauna-normalized SOD value of one. To improve readability, we removed
413 one winter CS core with a macrofauna-normalized SOD above 30 (140.5 mmol O_2. day^{-1}.g
414 $AFDW^{-1}$).

3.2. Functional diversity and identity indices

Each functional index weighted by biomass was significantly and positively correlated with its abundance-weighted version, except FEve. Functional richness, FDis, FDiv, FIde1 and FIde2 weighted by biomass and abundance presented values intricately linked to the engineered sediment types (UES *vs* DES). The other functional indices appeared to be completely independent from the engineered sediment type (FEve) or weakly linked to it (FIde3).

As an illustration (Fig. 4), we calculated the different functional indices using the mean macrofauna biomass across all the DES (n = 12) and all the UES cores (n = 12). The mean DES core had a higher FRic (0.98) than the mean UES core (0.86) indicating there were more functionally dissimilar species in DES than in UES. Functional dispersion followed the same pattern with a higher value in the mean DES core (0.14) than in the mean UES core (0.04). If a species dominates an assemblage (*e.g. S. alveolata* in UES, Table S1), it will attract the weighted-mean position of the assemblage and the FDis will be small. Differently, if two species have high abundances or biomasses and are distant in the functional space (*i.e.* functionally dissimilar), like *S. alveolata* and the crustacean *Porcellana platycheles* in the DES cores (Fig. 5 and Table S1), both will attract the weighted-mean position of the assemblage and the FDis will be higher. Functional divergence was higher in the mean UES (0.98) than in the mean DES core (0.84) because *S. alveolata*, which presents trait modalities very different from the "average species" represented by the unweighted center of gravity of the convex hull vertices (Fig. 5), dominates the UES cores while it dominates less the DES cores (Table S1).

The mean UES core was characterized by negative FIde1 (-0.24) and positive FIde2 (0.19) while the mean DES core was characterized by higher and negative FIde1 (-0.20) and by lower and positive FIde2 (0.13). The first PCoA axis is mainly associated to a daily movement capacity gradient with negative values corresponding to species presenting none to low movement capacities (*e.g. Sabellaria alveolata*) and higher values corresponding to

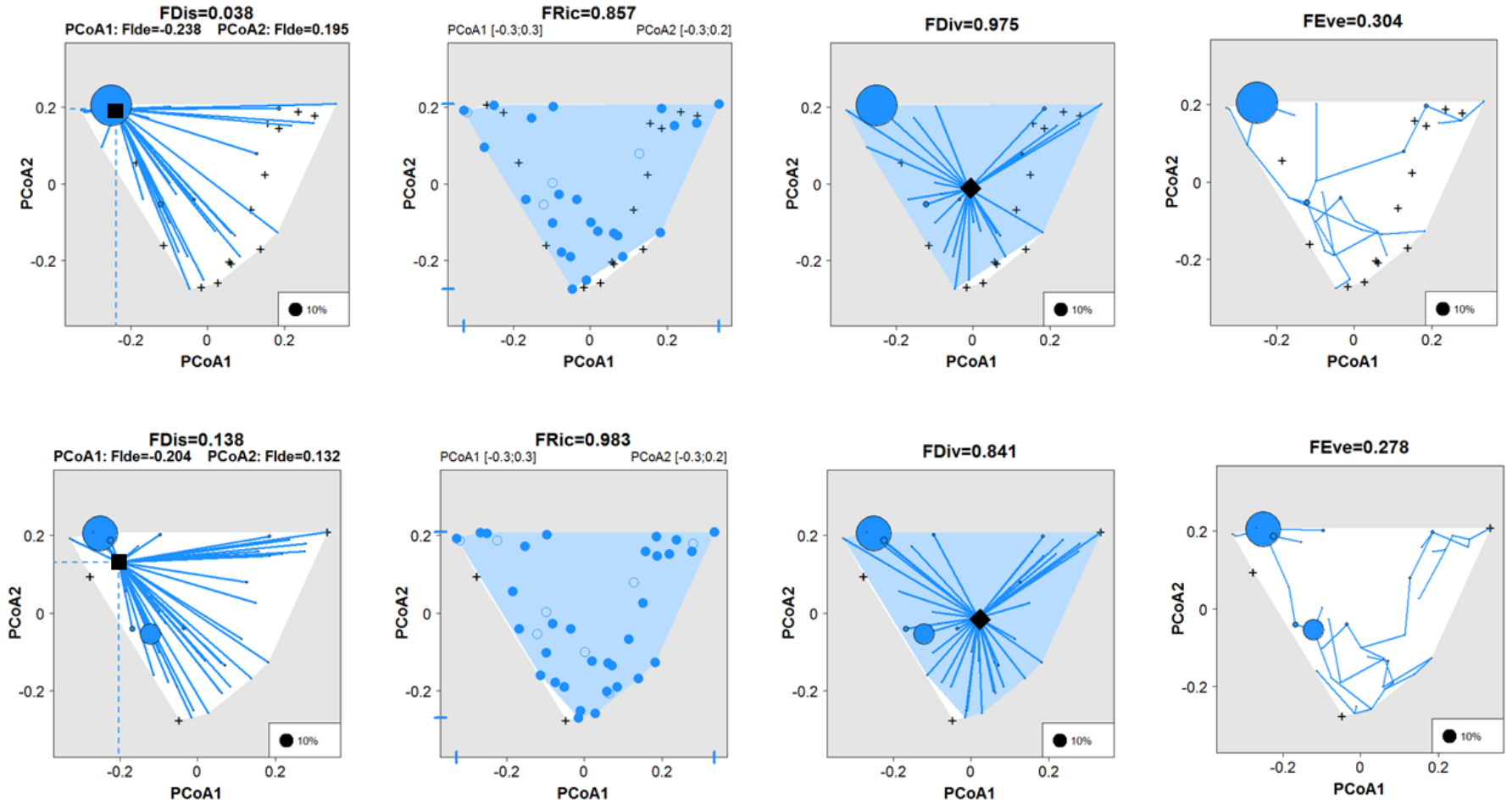

Figure 4. Two-dimensional illustration of the five functional indices (functional dispersion = FDis, functional identity = FIde, functional richness = FRic, functional divergence = FDiv, functional evenness = FEve) based on the species identified in the 12 undisturbed (top line) and 12 disturbed (bottom line) engineered sediment cores. The black crosses indicate species absent from an engineered sediment type but present in the global pool of species. Except for FRic, the dots are proportional to each species' mean biomass. In the FDis panels, the black squares and dashed lines represent

the weighted-mean position of the species in the multidimensional space and the weighted-mean positions of the species on the first and second axis (FIde1 and FIde2), respectively. In the FRic panels, the colored convex polygons represent the projection of the multidimensional convex hull in 2D, the filled symbols represent the species used as vertices in the multidimensional space and the bold bars on the axes represent the minimum and maximum values on each axis. In the FDiv panels, the black diamonds represent the center of gravity of the vertices. In the FEve panels, the blue lines represent the minimum spanning tree linking all species in the multidimensional space.

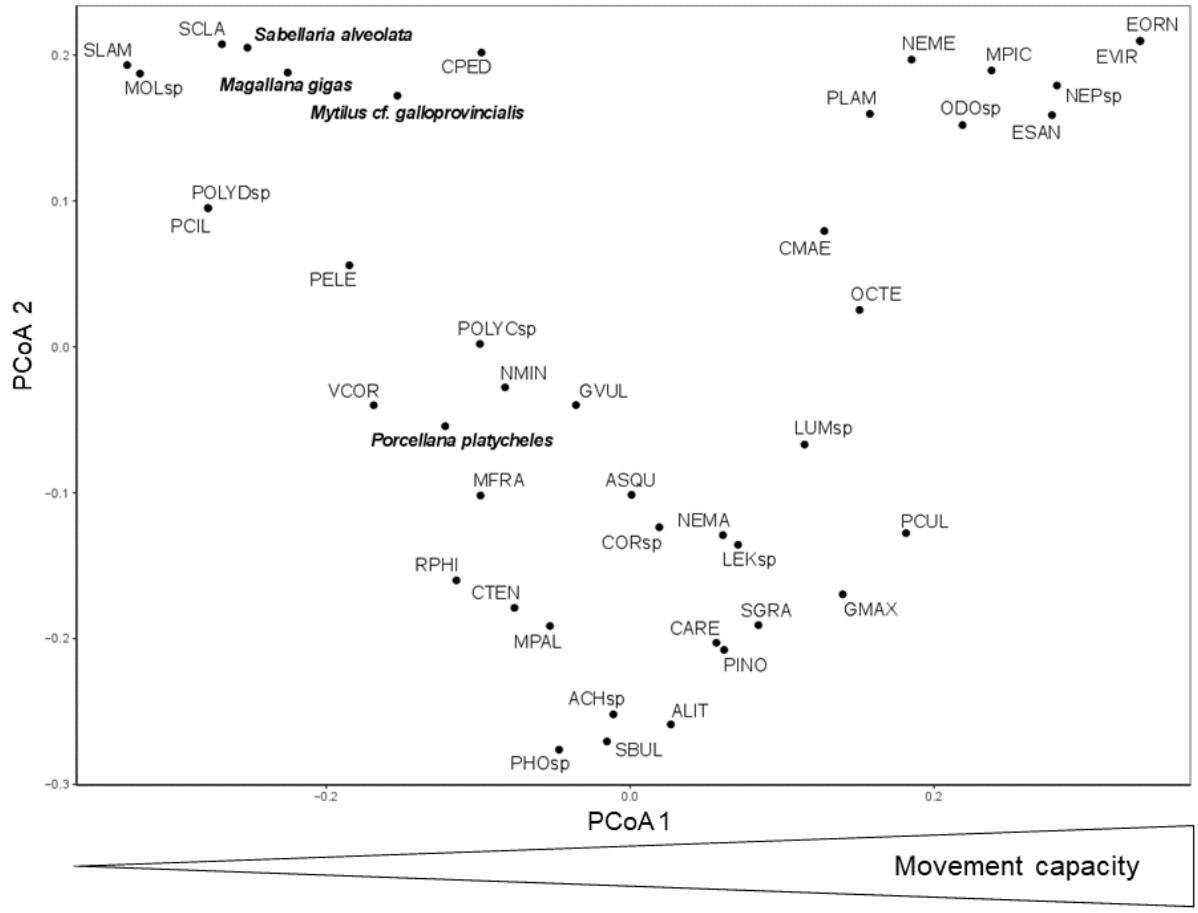

Figure 5. Position, on the first two axes of the functional space, of all the species present at the global engineered sediment level and identified by their full or abbreviated names (see Table S1). *Sabellaria alveolata* is the engineer species while *Porcellana platycheles* is the second dominant species in the disturbed engineered sediment cores. *Magallana gigas* and *Mytilus* cf. *galloprovincialis* are two other engineer species present as epibionts on the engineered sediments.

increasingly mobile species (*e.g.* errant polychaetes such as *Eulalia viridis*, EVIR) (Fig. 5). The second PCoA axis is mainly associated to the sediment reworking trait with positive values generally corresponding to epifauna (*e.g. Magallana gigas*) and biodiffusors (*e.g.* Nemerteans, NEME), values close to 0 corresponding to upward and downward conveyors (*e.g. Mediomastus fragilis*, MFRA and *Pygospio elegans*, PELE) and negative values corresponding to surficial modifiers (*e.g. Lekanesphaera* sp., LEKsp) (Fig. 5). Consequently, functional identity values on the first two PCoA axes can bring direct indications on which modalities are

key in driving the different ecosystem functions. The other biological traits (size, feeding mode and bathymetric preference) were not associated with a specific PCoA axis.

3.3. Relative importance of macrofauna and temperature on the engineered sediment biogeochemical functioning

The minimal adequate models contained three or four predictors and explained *ca.* 70% of the ecosystem function variability (Table 3). All the models contained water temperature, a predictor associated to the engineer effect hypothesis (*S. alveolata* biomass or abundance) and a predictor associated to both the diversity and mass-ratio hypotheses ($FDis_{ab}$ or $FEve_{ab}$). Furthermore, $FDis_{ab}$ and $FIde1_{ab}$ appeared correlated at 0.99 (Spearman correlation) indicating that when $FDis_{ab}$ increases, the abundance of species with medium to high movement capacities also increases (Figure S3). One UES core sampled in summer was closer to the summer DES cores than to the other summer UES cores because of a higher $FDis_{ab}$ and a lower engineer abundance. Nonetheless, the fluxes of this unexpectedly different core in terms of macrofauna characteristics were in line with the partial linear regressions (Fig. 6), which seems to indicate our minimal adequate models are not the result of an UES/DES dichotomy.

a. Engineer effect hypothesis

Based on the standardized slopes also called standardized partial regression coefficients or effect sizes (β), the engineer had a positive effect on the four functions (Fig. 6). Engineer biomass (mean = 125, SD = 94) was the predictor with the strongest effect on the SOD (mean = 4640, SD = 3750) and NH_4^+ (mean = 462, SD = 330) fluxes, holding all the other predictors of each model statistically constant. An increase by one population SD of *S. alveolata* biomass increases the SOD and NH_4^+ fluxes by 0.63 and 0.59 population SD, respectively (Table 3). Considering the multifunctionality metric model, engineer biomass had an effect of comparable magnitude to $FDis_{ab}$ (Table 3). Finally, engineer abundance (mean = 4765, SD = 13 936) was

Table 3. Minimal adequate models (ordinary least-square regressions) explaining the standardized ecosystem functions (sediment oxygen demand (SOD), ammonium flux (NH_4^+), sum of nitrate and nitrite fluxes (NO_{2+3}) and the multifunctionality metric). We expressed the slope estimates as effect sizes (β) to compare their relative effects on each function.

	df	RSE	F statistic	β	P
SOD adjusted R^2 = 0.73					
Model	3		21.3		< 0.001
Error	20	0.52			
Biomass				0.63	< 0.001
$FDis_{ab}^2$				-0.31	0.025
Temperature				0.23	0.048
NH_4^+ adjusted R^2 = 0.69					
Model	3		18.4		< 0.001
Error	20	0.55			
Biomass				0.59	< 0.001
Temperature				0.45	0.001
$FDis_{ab}$				-0.35	0.011
NO_{2+3} adjusted R^2 = 0.70					
Model	3		19.0		< 0.001
Error	20	0.55			
Abundance				0.62	< 0.001
Temperature				0.30	0.031
$FEve_{ab}$				-0.25	0.076
Multifunctionality metric adjusted R^2 = 0.73					
Model	4		17.0		< 0.001
Error	19	0.51			
Temperature				0.52	< 0.001
Biomass				0.37	0.021
$FDis_{ab}$				-0.38	0.008
$FDis_{ab}^2$				-0.32	0.035

df: degree of freedom, RSE: Residual standard error, Abundance: *S. alveolata* abundance, Biomass: *S. alveolata* biomass, FEve: functional evenness, FDis: functional dispersion. The subscripts ab indicates that the index was weighted using species abundance.

the predictor with the strongest effect on the NO_{2+3} fluxes (mean = 450, SD = 334), holding all the other predictors of the model statistically constant (Table 3).

500 b. Diversity and mass-ratio hypotheses

501 Two functional indices weighted by abundance were retained in the minimal adequate
502 models, FDis (mean = 0.18, SD = 0.11) and FEve (mean = 0.61, SD = 0.11), and both predictors
503 always presented negative standardized slopes (Fig. 6). The functional dispersion displayed a
504 simple linear effect on the NH_4^+ fluxes, a simple quadratic effect (concave form) on the SOD
505 and a more complex quadratic effect on the multifunctionality metric (*i.e.* concave form with
506 low values of $FDis_{ab}$ eliciting higher values of the multifunctionality metric than high values of
507 $FDis_{ab}$). It was the predictor with the weakest effect on the NH_4^+ fluxes and with the second
508 strongest effect on the SOD. The functional evenness displayed a simple linear effect on the
509 NO_{2+3} fluxes and was the predictor with the weakest effect, holding all the other predictors of
510 the model statistically constant (Table 3).

511 c. Water temperature

512 Based on the standardized partial regression coefficients, the water temperature (mean =
513 12.33, SD = 3.76) had a positive effect on the four ecosystem functions, all other predictors of
514 each model being held statistically constant (Table 3). It was the predictor with the strongest
515 effect on the multifunctionality metric, with the second strongest effect on the NH_4^+ and NO_{2+3}
516 fluxes and with the smallest effect on the SOD (Fig. 6). Increasing the water temperature by
517 one population SD increases the different functions by 0.23 (SOD) to 0.52 (multifunctionality,
518 SD = 0.83) population SD (Table 3).

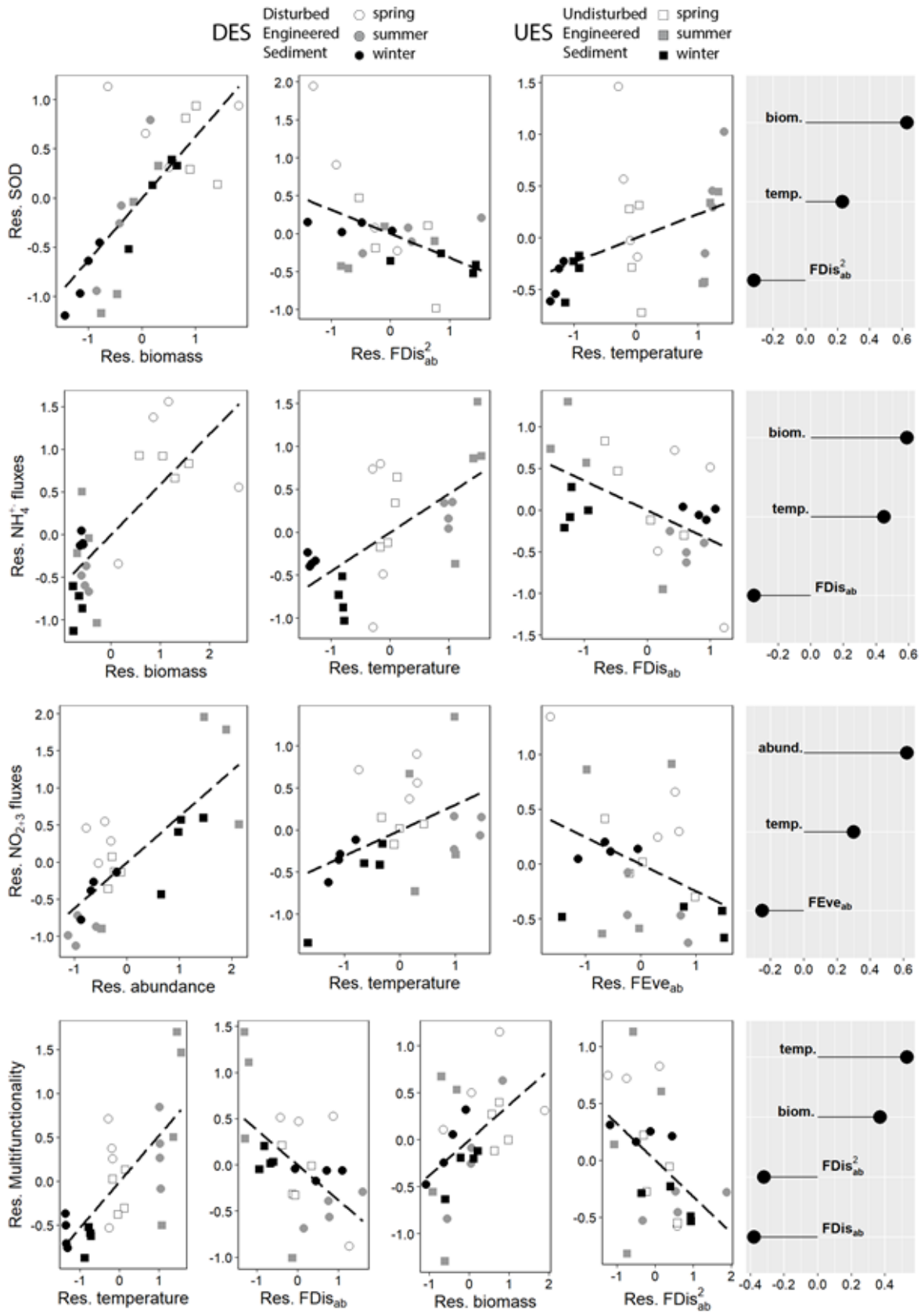

Figure 6. Partial linear regression plots (left) and standardized partial regression coefficients (effect sizes, right) of the predictors retained in the minimal adequate models explaining the

standardized ecosystem functions (sediment oxygen demand (SOD), ammonium flux (NH_4^+), sum of nitrate and nitrite fluxes (NO_{2+3}) and the multifunctionality metric). Abundance (abund.) and biomass (biom.) refer to the engineer *S. alveolata* abundance and biomass, respectively. $FDis_{ab}$ and $FEve_{ab}$ refer to the functional dispersion and functional evenness, respectively, both weighted by species abundance.

4. DISCUSSION

The study of the link between taxonomic diversity, functional diversity and ecosystem functions is complex but crucial if we are to understand in a more holistic way ecosystem functioning and the impact of disturbances on this functioning (Brose and Hillebrand, 2016; Gamfeldt et al., 2015). Using *Sabellaria alveolata* reefs as a study case, we started to fill the gap relative to the role played by biodiversity in the functions performed by tubiculous structural engineers (Berke, 2010), building upon studies on the biogeochemical functioning of bivalve reefs (see Stief (2013) and references therein). This study is a necessary first step towards conceiving more controlled *in situ* experiments by removing potentially key species such as highly mobile biodiffusors (*e.g. Eulalia viridis*) or manipulating the physical disturbance of the reef by clearing out small *S. alveolata* tube patches.

4.1. Biogenic structures promote biogeochemical fluxes in coastal waters

Microorganisms and meiofauna were probably the main drivers of the oxygen and solute fluxes measured in the soft sediments surrounding the engineered sediments along with physico-chemical mechanisms such as diffusion and advection. Indeed, solutes transfer mechanisms inside the first 10 cm of these soft sediments are probably dominated by advection in the highly permeable CS sediments and by diffusion in the less permeable MS sediments (Huettel et al., 2003). Macroinvertebrates were also relatively scarce with average abundances between 226 ind.m^{-2} (winter) and 4145 ind.m^{-2} (spring) in the MS, 636 ind.m^{-2} (winter) and

549 1556 ind.m^{-2} (spring) in the CS. Consequently, macrofauna was probably not a driving force in
550 these sediments, either in terms of solute transfer via bioturbation or in terms of oxygen uptake
551 as indicated by a macrofauna-normalized SOD above 1 (Clough et al., 2005). Conversely,
552 macrofauna was across the three periods the main driver of the engineered sediment oxygen
553 uptake, as indicated by a macrofauna-normalized SOD close or below 1 (Clough et al., 2005).
554 Since, we did not measure microbial respiration or biomass during our study, we focused on
555 the engineered sediments for which we had information on what appeared to be the driving
556 force of its biogeochemical functioning, the macrofauna.

557 Across the three periods, we measured higher SOD, NH_4^+ and NO_{2+3} fluxes in the
558 engineered sediments compared to the CS and MS, a difference we attribute at least partly to
559 the 8 (summer) to 1000 (winter) times higher macrofauna biomass in the UES and DES
560 compared to the CS and MS. Indeed, community biomass and oxygen consumption are often
561 strongly correlated (Braeckman et al., 2010; Clough et al., 2005; Norkko et al., 2013) through
562 the positive link between individual body mass and respiration rate (Gillooly et al., 2001;
563 Hildrew et al., 2007). Macrofauna can also account for 10 to 70% of community NH_4^+ fluxes
564 from the sediment through ammonium excretion (Kristensen, 1988; Vanni, 2002). Despite
565 representing between 45 and 97% of the macrofauna abundance in the engineered sediments,
566 *Sabellaria alveolata* creates, through the structures it builds and its biological activity, an
567 environment favorable to other macroinvertebrates (Dubois et al., 2002; Jones et al., 2018) and
568 probably also to a community of meiofauna and microorganisms (Ataide et al., 2014;
569 Kristensen and Kostka, 2005; Passarelli et al., 2014). Indeed, meiofauna and especially
570 nematodes are often more diverse and abundant inside biogenic structures such as *Sabellaria*
571 *wilsoni* reefs compared to neighboring bare sediments (Ataide et al., 2014). Furthermore, the
572 colonization of macrofauna tubes by prokaryotic communities is known to be stimulated by the
573 host's organic secretions that represent a food source for these organisms, probably affecting

574 global biogeochemical processes (Kristensen and Kostka, 2005; Passarelli et al., 2014). For
575 example, burrows built by polychaetes like *Hediste diversicolor*, that penetrate the anaerobic
576 subsurface sediment, promote microbial abundance and activity, increasing O_2 consumption
577 and nutrient release from the sediment (Mermillod-Blondin et al., 2004; Reise, 1981).
578 Consequently, meiofauna and even more so microorganisms surely play an important part in
579 the engineered sediments biogeochemical fluxes, mainly through aerobic respiration, dissolved
580 inorganic nitrogen excretion, particulate organic nitrogen remineralization, ammonium
581 assimilation, nitrification and denitrification (Herbert, 1999; Kristensen, 1988; Vanni, 2002).
582 Overall, oxygen consumption, ammonium and oxidized nitrogen release were enhanced in
583 the sediments engineered by *S. alveolata* compared to bare substratum, as reported for bivalve
584 reefs (Kellogg et al., 2013; Norling and Kautsky, 2007). The mechanisms promoting
585 biogeochemical fluxes in *S. alveolata* reefs and other polychaete reefs are probably the same as
586 in bivalve reefs and involve the dense macrofauna and the associated microorganisms
587 (Passarelli et al., 2014; Stief, 2013). First, the engineered structures (bivalve shells or
588 polychaete tubes) extend the surface available for colonization by nitrifying and denitrifying
589 microorganisms, which benefit from the metabolic waste products excreted by the engineer
590 species (ammonium and carbon dioxide). Second, microorganisms can use the large amounts
591 of biodeposits, including large quantities of extracellular polymeric substances such as mucus,
592 produced by bivalves and polychaetes (*i.e.* egestion of particulate organic matter), as a source
593 of labile organic matter (Gutiérrez et al., 2003; Heisterkamp et al., 2013).
594
595 *4.2. Biogeochemical fluxes in engineered habitats: a comparison*
596 We compared our results with fluxes measured in a polychaete reef built by the invasive
597 serpulid polychaete *Ficopomatus enigmaticus* (Keene, 1980), in a restored subtidal *Crassostrea*
598 *virginica* reef (Kellogg et al., 2013) and in a mudflat structured by *Upogedia pugettensis*, a

599 bioirrigating shrimp (D'Andrea and DeWitt, 2009) (Table 4). The two polychaete reefs had
600 close community respiration rates (between the spring DES values and the early March values)
601 and maximal NO_{2+3} fluxes (between the summer UES values and the November values) while
602 maximal NH_4^+ fluxes were two folds higher in our study (spring DES) compared with the
603 November values. For close water temperatures (12°C in this study and 14.5°C in Kellogg et
604 al. (2013)), the respiration rates measured in the *S. alveolata* and *C. virginica* reefs were close.
605 The maximal NH_4^+ and NO_{2+3} fluxes measured for the *S. alveolata* reef were comparable to the
606 ones measured respectively in April and June at the restored oyster reef. Finally, maximal daily
607 community respiration rates and NH_4^+ fluxes in this study were like the ones reported for the
608 high *U. pugettensis* density plots (Table 4). Differently, maximal NO_{2+3} fluxes measured in the
609 engineered sediments were two folds greater than the ones recorded in high *U. pugettensis*
610 density plots.

611 This comparison highlights a few interesting points on biogeochemical fluxes and
612 ecosystem engineers. First, the extend and the shape of the polychaete reefs seems to affect
613 NH_4^+ fluxes probably via the amount of organic matter trapped inside and between the
614 engineered structures. Indeed, *S. alveolata* reefs are composed of coalescent hummock
615 structures that completely recover the initial substrate (Jones et al., 2018) whereas *F.*
616 *enigmaticus* reefs are discontinuous structures between which water can pass and flush out the
617 accumulated organic matter (Bruschetti et al., 2011). Second, structural engineers like *S.*
618 *alveolata* and oysters that build coalescent structures, enhance in similar amounts sediment
619 oxygen demand, ammonium, and nitrates + nitrites fluxes. Finally, habitats built by reef-
620 forming species such as bivalve and tubiculous structural engineers could have a higher
621 potential as organic nitrogen recyclers than burrowing and bioturbating infauna like *U.*
622 *pugettensis* in engineered soft sediments (Berke, 2010).

623 **Table 4.** Sediment oxygen demand (SOD), ammonium (NH_4^+) and nitrate + nitrite fluxes (NO_{2+3}) measured in engineered habitats built by
624 polychaetes, bivalves and crustaceans and reported in this study and three others. D'Andrea & DeWitt (2009) measured fluxes in a mudflat
625 colonized by low, medium, and high densities of *Upogedia pugettensis*.

Engineered habitat	Study location and reference	Type of flux reported	SOD	NH_4^+	NO_{2+3}
***Sabellaria alveolata* (polychaete) reef**	English Channel coast (bay of Mont-Saint-Michel, France), this study	Min – max across spring (12°C), summer (17°C) and winter (8°C)	0.03 (winter DES) – 0.33 (spring DES) g $O_2.m^{-2}.h^{-1}$	0.06 (winter DES) – 0.85 (spring UES) $mmol.m^{-2}.h^{-1}$	0.17 (winter DES) – 1.01 (summer UES) $mmol.m^{-2}.h^{-1}$
		Min – max in spring and summer (daily values)	Spring: 8.03 (193) – 10.31 (247) Summer: 3.08 (74) – 4.24 (102) mmol $O_2.m^{-2}.h^{-1}$	Spring: 0.65 (15.6) – 0.85 (20.4) Summer: 0.25 (6) – 0.70 (16.8) $mmol.m^{-2}.h^{-1}$	Spring: 0.38 (9.12) – 0.53 (12.72) Summer: 0.32 (7.68) – 1.01 (24.24) $mmol.m^{-2}.h^{-1}$
***Ficopomatus enigmaticus* (polychaete) reef**	Mediterranean Sea (Tunisia), Keene 1980	exact temperature unknown	0.24 (early March) – 1.17 (late March) g $O_2.m^{-2}.h^{-1}$	0.40 (November) $mmol.m^{-2}.h^{-1}$	1.05 (November) $mmol.m^{-2}.h^{-1}$
Restored *Crassostrea virginica* (bivalve) reef	Maryland coast (USA), Kellogg et al. 2013	Comparable values	12.87 mmol $O_2.m^{-2}.h^{-1}$ (November, 14.5°C)	0.8 $mmol.m^{-2}.h^{-1}$ (April, 15.1°C)	0.46 $mmol.m^{-2}.h^{-1}$ 1.3 $mmol.m^{-2}.h^{-1}$ (June, 25.7°C)
Mudflat colonized by bioirrigating shrimp *Upogedia pugettensis* (crustacean)	Oregon coast (USA), D'Andrea & DeWitt 2009	Summer (17.1°C)	97.4 (low density) – 225.7 (high density) mmol $m^{-2}.d^{-1}$	7.11 (low density) – 16.37 (high density) mmol $m^{-2}.d^{-1}$	1.16 (medium density) – 11.38 (high density) mmol $m^{-2}.d^{-1}$

627 *4.3.* Sabellaria alveolata *and water temperature are the main drivers of the engineered*
628 *sediment biogeochemical functioning*

629 What we termed the engineer effect (*i.e.* the engineer *S. alveolata* promotes, through its
630 density, the biogeochemical functioning of the engineered sediments) mainly results from the
631 combined biological activity of the engineer species *S. alveolata per se*, as well as the
632 meiofauna and microorganisms associated to each individual and its tube, a community likely
633 specific to complex structures like polychaete tubes (Mermillod-Blondin et al., 2004; Reise,
634 1981; Tout et al., 2014) with a temperature-dependent activity (Herbert, 1999; Thamdrup et al.,
635 1998). This study based on observational data helped us to determine some of the main drivers
636 of the biogeochemical functioning of a *S. alveolata* reef; the engineer, the water temperature
637 and the associated macrofauna through their biological traits, strongly supporting the engineer
638 effect hypothesis and giving some support to the diversity hypothesis but only at relatively low
639 levels of functional diversity. The use of terms like “effect” or “driver” are somehow abusive
640 since real causality between predictors and response variables can only be determined through
641 controlled experiments. Nonetheless, we believe this study is a first step towards better
642 understanding the functioning of these complex habitats, helping us to better conserve and
643 manage them.

644 In sediments engineered by *S. alveolata*, the number one driver of community respiration,
645 was *S. alveolata* biomass. Water temperature was not the main driver of SOD like we expected
646 according to the Q10 of 2 relation (Hildrew et al., 2007) and subtidal studies on soft sediments
647 and oyster reefs (Janson et al., 2012; Kellogg et al., 2013). Nonetheless, temperature still had a
648 small positive effect on the SOD. We measured the highest SOD values in spring (12°C) and
649 not in summer (17°C), a difference we mainly attribute to the 2-3 times higher engineer biomass
650 in spring compared to summer, but also to the ripe and heavy individuals ready to spawn in
651 spring (Dubois et al., 2007a). Biomass can have a strong influence on respiration rates at the

individual and community level, a biomass effect we observed here which clearly surpassed the effect of temperature on the SOD (Braeckman et al., 2010; Clough et al., 2005; Hildrew et al., 2007; Norkko et al., 2013). Structural ecosystem engineers such as *S. alveolata* can also act as agents of biogeochemical heterogeneity through the structural changes they cause, affecting heat transfer processes and temperature dependent microbial activity (Gutiérrez et al., 2003). Temperature loggers placed inside the reefs revealed that the engineered sediments present lower heat transfers than the surrounding coarse sediments (Jones, pers. obs.), indicating water temperature variations could be buffered inside these sediments, probably reducing temperature-dependent aerobic respiration (Thamdrup et al., 1998; Woodin et al., 2010).

Sabellaria alveolata biomass was also the number one driver of the NH_4^+ fluxes, a result probably caused by two processes positively correlated to the engineer biomass and stronger in spring than in summer: excretion and egestion. First, the engineer biomass has a positive effect on the NH_4^+ fluxes probably because of higher excretion rates of *S. alveolata* in spring when its mean biomass is the highest, a seasonality also recorded for the gastropod *Crepidula fornicata* (Martin et al., 2006). *Sabellaria alveolata* probably also egests more feces and pseudofeces (Dubois et al., 2006) in spring during the phytoplankton bloom and the main reproductive season, as recorded for *Modiolus modiolus* (Navarro and Thompson, 1997). These biodeposits are rapidly remineralized by associated bacteria, producing NH_4^+ (Stief, 2013) and linking the engineer biomass and NH_4^+ fluxes. Temperature was the second most important driver of the NH_4^+ fluxes, an effect probably linked to the temperature-dependent metabolic rates of the meio and macrofauna (excretion and egestion) and associated bacteria (nitrogen remineralization) (Gillooly et al., 2001; Magni et al., 2000).

The first and second most important drivers of NO_{2+3} fluxes were *S. alveolata* abundance and water temperature, respectively, probably through the promotion of nitrification by the engineer and its tube and the temperature-dependent activity of nitrifying bacteria. The

677 transformation of NH_4^+ into NO_2^- and then NO_3^- requires ammonium, oxygen, and the presence
678 of aerobic nitrifying microorganisms, more active at higher water temperatures (Herbert, 1999).
679 First, a diverse community of microorganisms including nitrifying bacteria are probably
680 directly associated to the surface of *S. alveolata* as shown for other polychaetes, amphipods and
681 bivalve soft tissues (Welsh and Castadelli, 2004). Secondly, *S. alveolata* density is also an
682 indirect measure of tube density, tubes that are home to nitrifying bacteria (D'Andrea and
683 DeWitt, 2009) and act as vectors allowing oxygen to penetrate deeper into the engineered
684 sediment, ultimately promoting nitrification. Finally, the vertical movements of *S. alveolata* in
685 its tube increases the oxygen fluxes from the overlying water to the deeper engineered sediment
686 layers further promoting nitrification, as reported in the burrows of many soft sediment
687 organisms (Woodin et al., 2010).
688
689 *4.4. Biological traits of associated macrofauna is a secondary driver of the engineered*
690 *sediments biogeochemical functioning*
691 Using a multiple linear regression approach, we never detected a significant effect of indices
692 only used to test the diversity hypothesis (SR, N1 and FRic) or the mass-ratio hypothesis (FIde1
693 and FIde3), on a flux. If there is an effect of a higher associated macrofauna diversity or
694 biological trait dominance on the fluxes, it is mostly accounted for by *S. alveolata* abundance
695 or biomass (engineer effect hypothesis) and by functional dispersion (FDis) or functional
696 evenness (FEve) (diversity and mass ratio hypotheses). Indeed, a decrease in the abundance of
697 *S. alveolata* is linked to an opposite increase in the abundance and richness of associated
698 macrofauna (Dubois et al., 2002; Jones et al., 2018). Furthermore, 75% of the species richness
699 variability can be explained by *S. alveolata* biomass (negative effect) and $FDis_{ab}$ (positive
700 effect). Finally, $FDis_{ab}$ and $FIde1_{ab}$ have a 0.99 correlation indicating $FDis_{ab}$ increases with an

abundance increase of higher mobility species (movement capacity trait) and this index can also be used to test the mass-ratio hypothesis.

Functional dispersion, only weighted by abundance, was the second most important driver of the SOD and multifunctionality metric, displaying in both cases a concave form (second degree polynomial form with a negative effect size), a form also detected in sandy sediments when relating benthic species richness and ammonium fluxes (Thrush et al., 2017). Maximal values of the two functions were detected for $FDis_{ab}$ values of *ca.* 0.19 for SOD and *ca.* 0.16 for the multifunctionality metric, corresponding to the middle of the disturbance continuum present in the engineered sediments (slightly disturbed reefs). Bumped-shaped relationships seem to be relatively common in cross community studies possibly because the explanatory variables are more variable and have a wider range of values in these studies than in a single community type helping to detect these functional forms (Mittelbach et al., 2001; Thrush and Lohrer, 2012). We deliberately sampled two different engineered sediment typologies characterized by different communities dominated by the engineer species but with a large diversity gradient, favoring the detection of this concave functional form.

Mechanisms linked to the diversity hypothesis such as resource partitioning and niche complementarity (Tilman, 1997) or non-additive interactions among species through trait redundancy (insurance hypothesis, Yachi and Loreau (1999)) probably explain the positive effect low functional diversity has on the SOD and the global biogeochemical functioning (Brose and Hillebrand, 2016). The presence of species with modalities like *S. alveolata,* especially regarding their mobility (*e.g. Magallana gigas*, *Mytilus* cf. *galloprovincialis*), limit the functional loss due to the increasing disturbance and the resulting decrease of the engineer species abundance (Dubois et al., 2006, 2002). Other species with no to low movement capacities and with modalities complementary to *S. alveolata* (*e.g. Venerupis corrugata*)

725 regarding other traits (*e.g.* sediment reworking) enhance the global biogeochemical functioning
726 of the engineered sediments (Bruno et al., 2003; Stachowicz, 2001).

727 In a second phase, interferences between species' modalities (*i.e.* interference competition)
728 seem to limit biogeochemical processes like organic matter remineralization, leading to the
729 negative effect of high functional diversity on biogeochemical fluxes (Brose and Hillebrand,
730 2016). Indeed, structural engineers such as *S. alveolata* likely build habitats where the local
731 environmental conditions are optimal for them and where they are likely the best performing
732 species of the assemblage for most ecosystem functions, including biogeochemical fluxes
733 (Gamfeldt et al., 2015). Consequently, a functional dispersion above 0.16-0.19 could translate
734 into a stronger spatial and/or trophic competition between the associated macrofauna and *S.*
735 *alveolata* (Dubois et al., 2006; Jones et al., 2018), potentially leading to lower metabolic rates
736 of the engineer species (*e.g.* respiration) and to lower global fluxes. Functionally dissimilar
737 species could also disrupt the local conditions created by the engineer, for example through the
738 destruction of *S. alveolata* tubes (*e.g. Carcinus maenas* excavate *S. alveolata* tubes), decreasing
739 nutrient cycling.

740 Furthermore, functional dispersion weighted by abundance had a strictly negative effect on
741 the NH_4^+ fluxes. Considering the strong correlation between $FDis_{ab}$ and $FIde_{ab}$, this result
742 supports the mass-ratio hypothesis and is probably linked to the same mechanisms as the ones
743 explaining the negative effect of higher functional diversity levels on the SOD and
744 multifunctionality. Even at low functional diversity levels, we did not detect a positive effect
745 of increasing diversity on the NH_4^+ fluxes. The loss of *S. alveolata* type species in terms of
746 mobility and the addition of species with different modality combinations seems to rapidly
747 impair NH_4^+fluxes, probably through the loss of sessile bivalves and polychaetes, organisms
748 that strongly influence these fluxes through excretion and biodeposit production (Stief, 2013).

749 Finally, functional evenness (abundance weighted only), an index informing on the
750 regularity of the abundance distribution in the functional space, had a weak negative effect on
751 the NO_{2+3} fluxes. A high value of FEve indicates a homogenous distribution of the species and
752 of their abundance in the functional space with similar distance between species (Villéger et
753 al., 2008). Consequently, NO_{2+3} fluxes seem to be promoted by the presence of several clumps
754 of species with similar trait combinations, indicating that a certain level of biological trait
755 redundancy associated to a certain level of species richness (*ca.* 10 species), is necessary for an
756 optimal nitrogen cycling in the reef.
757
758 *4.5. Global biogeochemical functioning of the engineered sediments*
759 Overall, the biogeochemical functioning of the sediments engineered by *S. alveolata* was
760 much more intense than that of the soft sediments surrounding the engineered sediments, a
761 difference likely linked to the abundant and diversified macrofauna, meiofauna and
762 microorganisms promoted by the reef structures and the engineer itself. Focusing on the
763 engineered sediments, we found that water temperature is the main driver of their global
764 biogeochemical functioning, followed by *S. alveolata* biomass and the macrofauna functional
765 dispersion weighted by abundance. Consequently, tubiculous structural engineers such as *S.*
766 *alveolata* have biomass-dependent effects on biogeochemical fluxes as do burrowing and
767 bioturbating infauna (Braeckman et al., 2010; D'Andrea and DeWitt, 2009; Norkko et al., 2013;
768 Thrush et al., 2017), suggesting this could be a general property of many marine ecosystem
769 engineers. Furthermore, the concave effect $FDis_{ab}$ has on the multifunctionality metric brings
770 support to the diversity hypothesis at low levels of functional dispersion (0.01-0.16), when
771 sessile species with complementarity modalities for other traits dominate the engineered
772 sediments. When functional dispersion is higher (0.16-0.36), the biogeochemical functioning
773 of the engineered sediments is promoted by higher abundances of species with no to low

movement capacities (higher $FIde1_{ab}$), bringing support to the mass-ratio hypothesis, as found in autotrophic terrestrial systems (Díaz et al., 2007; Garnier et al., 2004; Mokany et al., 2008) and across field studies on soil fauna (Gagic et al., 2015). The concave effect of $FDis_{ab}$ on the multifunctionality metric also indicates an intermediate macrofauna trait diversity could maximize the global biogeochemical functioning of a *S. alveolata* reef through trait redundancy and niche complementarity.

Maintaining a high abundance and biomass of the engineer species appears paramount if we wish to further maintain ecosystem processes performed by this habitat such as organic matter remineralization and nitrogen cycling; indeed, our results evidence that a good physical status of the reef structure (prograding areas with high tube density) leads to a good ecological functioning of the reef. Local disturbances (reef degradation) can increase species number (Dubois et al., 2020) and possibly enhance functional diversity, which does not appear, at first, as detrimental in terms of biogeochemical fluxes. However, anthropogenic disturbances such as trampling should be limited as much as possible, as they could alter *S. alveolata* biomass in the long term (Desroy et al., 2011; Plicanti et al., 2016). Complementary studies should aim at manipulating disturbance levels and/or species composition, measuring other functions such as primary and secondary production or consumption and studying other *S. alveolata* reefs to test if engineer biomass and functional dispersion weighted by abundance could be used as indicators of *S. alveolata* reef functioning.

CONCLUSION

In a conservation goal, identifying indices that inform us on the global functioning of ecosystems and its evolution is paramount. In the case of *S. alveolata* reefs, our study indicates the two most important parameters to measure are the biomass and abundance of the engineer species. In a second step, estimating the abundance of the associated species (and not their

biomass) and focusing on their respective movement capacities, a trait associated to a species' sediment reworking abilities (Queirós et al., 2013) and known to affect many biogeochemical fluxes (Braeckman et al., 2010; Ieno et al., 2006; Mermillod-Blondin et al., 2005; Michaud et al., 2005), can help to evaluate more precisely the reef's biogeochemical functioning. Biomass is often considered as more functionally relevant than abundance especially when the process is size-based (Gagic et al., 2015; Mouillot et al., 2011) and large macrofauna have been shown to play a prominent role in soft sediment biogeochemical fluxes (Norkko et al., 2013; Thrush et al., 2006). Nonetheless, soft sediments engineered into hard substrata by *S. alveolata* act as an environmental filter and only relatively small organisms can establish between the engineer tubes and affect biogeochemical fluxes (Jones et al., 2018). Consequently, in this highly size-constrained habitat, abundance appears to be more important than biomass in explaining biogeochemical fluxes.

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Supplementary material

Table S1. Mean (n = 12) abundance and biomass (ash-free dry weight in mg) of all the species identified in the undisturbed and disturbed engineered sediments. The mean was calculated over the three seasons and the four cores sampled for each engineered sediment type.

Species name	**Abbreviated name**	**Undisturbed engineered sediment**		**Disturbed engineered sediment**	
		Density (ind .m^{-2})	Biomass (AFDW mg.m^{-2})	Density (ind .m^{-2})	Biomass (AFDW mg.m^{-2})
***Achelia* sp.**	ACHsp	38	4	599	61
Axelsonia littoralis	ALIT	0	0	47	0
Amphipholis squamata	ASQU	9	5	156	32
Corophium arenarium	CARE	0	0	5	0
Carcinus maenas	CMAE	71	858	61	631
***Corophium* sp.**	CORsp	33	5	207	34
Cereus pedunculatus	CPED	439	67	104	846
Cirriformia tentaculata	CTEN	5	1	28	8
Eulalia ornata	EORN	170	65	0	0
Eumida sanguinea	ESAN	24	17	24	38
Eulalia viridis	EVIR	71	168	52	517
Gnathia maxilaris	GMAX	0	0	5	20
Golfingia vulgaris	GVUL	85	813	156	1 369
***Lekanesphaera* sp.**	LEKsp	179	313	269	541
***Lumbrinereis* sp.**	LUMsp	0	0	5	1
Magallana gigas	MGIG	0	0	9	4 347
Mytilus* cf. *galloprovincialis	McfGAL	47	89	132	251
Mediomastus fragilis	MFRA	24	1	85	15
***Molgula* sp.**	MOLsp	14	80	5	32
Melita palmata	MPAL	28	5	137	47
Mysta picta	MPIC	0	0	10	2
***Nematoda* spp.**	NEMA	726	185	1 151	103
Nemertean	NEME	231	1 637	278	1 311
***Nephtys* sp.**	NEPsp	0	0	5	2
Nephasoma minutum	NMIN	250	71	189	47

Odontosyllis ctenostoma	OCTE	0	0	118	28
***Odontosyllis* sp.**	ODOsp	42	9	42	5
Polydora ciliata	PCIL	9	9	0	0
Perinereis cultrifera	PCUL	47	207	141	209
Pygospio elegans	PELE	0	0	28	12
***Photys* sp.**	PHOsp	24	0	0	0
Pholoe inornata	PINO	0	0	9	6
Phyllodoce laminosa	PLAM	0	0	38	269
***Polycirrus* sp.**	POLYCsp	5	1	38	8
***Polydora* sp.**	POLYDsp	5	1	0	0
Porcellana platycheles	PPLA	236	3 916	2 415	35 303
Ruditapes philippinarum	RPHI	0	0	9	325
Sabellaria alveolata	SALV	25 734	151 178	7 036	99 177
Sphaerosyllis bulbosa	SBUL	0	0	9	1
Styela clava	SCLA	0	0	19	130
Syllis gracilis	SGRA	5	4	14	4
Spirobranchus lamarcki	SLAM	5	11	52	76
Venerupis corrugata	VCOR	14	30	52	3 004
Total macrofauna including *S. alveolata*		28 532	159 746	13 140	148 751
Total macrofauna excluding *S. alveolata*		2 798	8 568	6 104	49 574
***S. alveolata* dominance (%)**		90.19	94.64	53.55	66.67

5

Table S2. Mean (± SD, n = 4) sediment oxygen demand (SOD), ammonium fluxes (NH_4^+) and the sum of nitrate and nitrite fluxes (NO_{2+3}) measured during the spring, summer and winter campaigns for the four different sediment types, coarse sediments (CS), muddy sediments (MS), undisturbed engineered sediments (UES) and disturbed engineered sediments (DES).

	Spring				**Summer**				**Winter**			
	CS	*MS*	*UES*	*DES*	*CS*	*MS*	*UES*	*DES*	*CS*	*MS*	*UES*	*DES*
SOD	414.7 ±	1445.4 ±	8032.65 ±	10308.9 ±	181.1 ±	693.8 ±	4294.6 ±	3083.8 ±	105.2 ±	178.5 ±	1276.0 ±	843.8 ±
($\mu mol.m^{-2}.h^{-1}$)	60.2	238.5	2426.51	1939.1	45.6	144.0	1259.2	718.8	33.3	62.9	166.9	429.3
NH_4^+	-0.8 ±	-2.4 ±	850.40 ±	653.9 ±	-4.4 ±	42.4 ±	698.2 ±	249.7 ±	-7.9 ±	32.8 ±	252.7 ±	65.2 ±
($\mu mol.m^{-2}.h^{-1}$)	1.0	0.6	121.79	269.0	1.2	67.2	359.2	49.1	1.3	8.8	62.1	31.0
NO_{2+3}	26.0 ±	-43.7 ±	381.87 ±	534.2 ±	35.6 ±	0.2 ±	1006.9 ±	322.8 ±	114.2 ±	42.8 ±	284.9 ±	170.6 ±
($\mu mol.m^{-2}.h^{-1}$)	13.4	20.3	108.61	166.2	8.8	0.7	463.8	89.0	51.3	17.3	14.2	64.3

Figure S3. Relation between the functional dispersion weighted by macrofauna abundance ($FDis_{ab}$) and the functional identity 1 weighted by macrofauna abundance ($FIde1_{ab}$) considering the 24 engineered sediment cores. An increase of the $FIde1_{ab}$ index is associated to an increase in the relative abundance of species with medium to high movement capacities.