

1 **Carbon dioxide release driven by organic carbon in minerogenic**
2 **salt marshes**

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13 **Abstract**

14 Coastal wetlands play an important role in the global carbon cycle by sequestering carbon (referred to as
15 “blue carbon”). At the same time, organic carbon (OC) in the subsurface is decomposed, releasing greenhouse gases
16 (GHGs) such as carbon dioxide (CO₂) and methane (CH₄). To predict how this carbon balance in salt marshes will
17 change under future climate scenarios (e.g., higher temperatures, sea level rise), it is essential to understand the controls
18 on OC decomposition in these systems. Here, we investigated OC turnover and CO₂ release in a minerogenic salt marsh
19 at the Wadden Sea, Germany. We first characterized the porewater and sediment of a pioneer marsh and adjoining
20 intertidal flat to identify key biogeochemical processes. We then performed an in situ experiment by injecting two OC
21 sources (labile (acetate)/complex (humic acid)) and subsequently monitored GHG release over four injection cycles
22 along with subsurface geochemistry. Overall, we found that the microbially mediated CO₂ release was likely limited
23 by OC availability and composition, and electron acceptor availability was unlikely to be the primary limiting factor,
24 as evidenced by the presence of aqueous sulfate (SO₄²⁻) at all tested depths and the lack of detectable CH₄. Following
25 the addition of labile OC, CO₂ release in the pioneer marsh increased by up to 47.4 ± 36.4 % compared to the control,
26 with a generally similar trend in the intertidal flat. The CO₂ release from the complex OC treatment was similar to the
27 control. The results of our work improve understanding of minerogenic salt marsh OC dynamics in temperate zones
28 and enable better prediction of future changes.

29 1 Introduction

30 Vegetated coastal wetlands, located at the interface between land and the open sea, occur along all continental
31 coastal zones except Antarctica and comprise mangroves, seagrass, and salt marshes (Nellemann et al., 2009; Pendleton
32 et al., 2012; Tan et al., 2025). Salt marshes, including the seaward adjoining intertidal flats, sequester high amounts of
33 carbon primarily in the sediment (Mcleod et al., 2011; Nellemann et al., 2009; de Vlas et al., 2013). Globally, around
34 60.4-70 Tg yr⁻¹ of carbon is buried in vegetated salt marshes (Duarte et al., 2005; Nellemann et al., 2009). The
35 sequestration of carbon is disproportional in vegetated coastal areas, with around half of the total organic carbon in
36 ocean sediment (often referred to as “blue carbon”) buried in these areas which only account for 0.2 % of the ocean
37 surface (Duarte et al., 2013; Nellemann et al., 2009). As the rate of carbon input into the sediment exceeds its rate of
38 decomposition (especially for allochthonous carbon), salt marshes are characterized by high carbon sequestration rates
39 (Mueller et al., 2019; Temmink et al., 2022; Van de Broek et al., 2018). Simultaneously, salt marshes release
40 greenhouse gases (GHGs) due to organic carbon (OC) decomposition: carbon dioxide (CO₂) at 0.02-0.24 Pg CO₂ yr⁻¹
41 (Pendleton et al., 2012) and methane (CH₄) at 0.142 ± 0.02 Mg carbon ha⁻¹ yr⁻¹ (Alongi, 2020). Therefore,
42 understanding carbon turnover in coastal wetlands is crucial for predicting how these ecosystems will respond to
43 climate change, such as temperature increase, sea level rise, and eutrophication of coastal waters. This is especially
44 important given the annual 1-2 % loss of salt marshes due to land-use change and their vulnerability to climate impacts
45 (Duarte et al., 2008).

46 In coastal wetlands, microbial respiration pathways couple OC as an electron donor with terminal electron
47 acceptors (TEAs), especially oxygen (O₂), ferric iron (Fe(III)) and sulfate (SO₄²⁻) (Tan et al., 2025; Tobias and
48 Neubauer, 2019). Oxygen, the thermodynamically most favourable TEA, exhibits fluctuating penetration depth into
49 the sediment due to tides, bioturbation or root-mediated O₂ transport (de Beer et al., 2005; Huettel et al., 2014; Maricle
50 and Lee, 2002). In deeper sediment layers, where anoxic conditions can dominate, microorganisms utilize Fe(III), from
51 iron minerals, or SO₄²⁻, which infiltrates the sediment through inundation of seawater, as alternative TEAs (Jørgensen
52 et al., 2019; Tobias and Neubauer, 2019). Upon full depletion of TEAs, OC is further decomposed to CH₄ (Schlesinger
53 and Bernhardt, 2013b). Microbial decomposition of OC may be further influenced by its chemical composition.
54 Chemically simpler e.g., short chain aliphatic OC may be substantially favoured for decomposition compared to
55 complex OC, such as natural organic matter (Gunina and Kuzyakov, 2022; Lipczynska-Kochany, 2018; Schlesinger
56 and Bernhardt, 2013a).

57 The primary controls on GHG release in salt marshes, as interfaces between land and open ocean, are not
58 fully understood. Specifically, it is unclear whether OC turnover is primarily controlled by the availability of the
59 electron acceptors – as observed in organogenic marshes and consistent with studies in terrestrial wetlands (Schlesinger
60 and Bernhardt, 2013b) – or by the organic matter itself, as suggested for marine sediment in general (Arndt et al.,
61 2013). Past studies on OC dynamics (including GHG release) in salt marshes have largely concentrated on the eastern
62 coast of the US (Capooci et al., 2024; Kostka et al., 2002b; Lowe et al., 2000; Seyfferth et al., 2020), which is dominated
63 by organogenic peat marshes. Organogenic marshes are generally low energy, microtidal wetlands, characterized by a
64 high organic matter deposition via autochthonous pathways that results in high TOC contents (Logemann et al., 2025).
65 For example, Lowe et al. (2000) and Kostka et al. (2002a) observed that OC oxidation was controlled by SO₄²⁻ and

66 Fe(III) reduction in salt marshes in Georgia, USA. Further, CH₄ fluxes were detected in salt marshes in Delaware,
67 suggesting a co-occurrence of methanogenesis and SO₄²⁻ reduction (Capooci et al., 2024; Seyfferth et al., 2020).
68 European salt marshes, in contrast, are primarily minerogenic, i.e., contain high fractions of mineral sediment due to
69 high sedimentation rates, resulting in comparably lower TOC content (Nolte et al., 2013). Studies conducted in
70 European salt marshes have focused on the TEA turnover (e.g., SO₄²⁻ respiration rates) and not GHG emissions (de
71 Beer et al., 2005; Bosselmann et al., 2003; van Erk et al., 2023). These studies showed that O₂ penetrates down the
72 sediment, Fe(III) is available and SO₄²⁻ reduction occurs. Hence, these studies have provided indirect links between
73 belowground biogeochemistry, especially in the context of available TEA, and the release of GHGs in minerogenic
74 salt marshes; however, a direct investigation of the determining factor(s) of OC degradation from these ecosystems is
75 missing. By understanding the controls on GHG release, we can better predict how climate impacts such as higher
76 temperatures and sea level rise will affect OC turnover and thereby GHG release in minerogenic salt marshes.

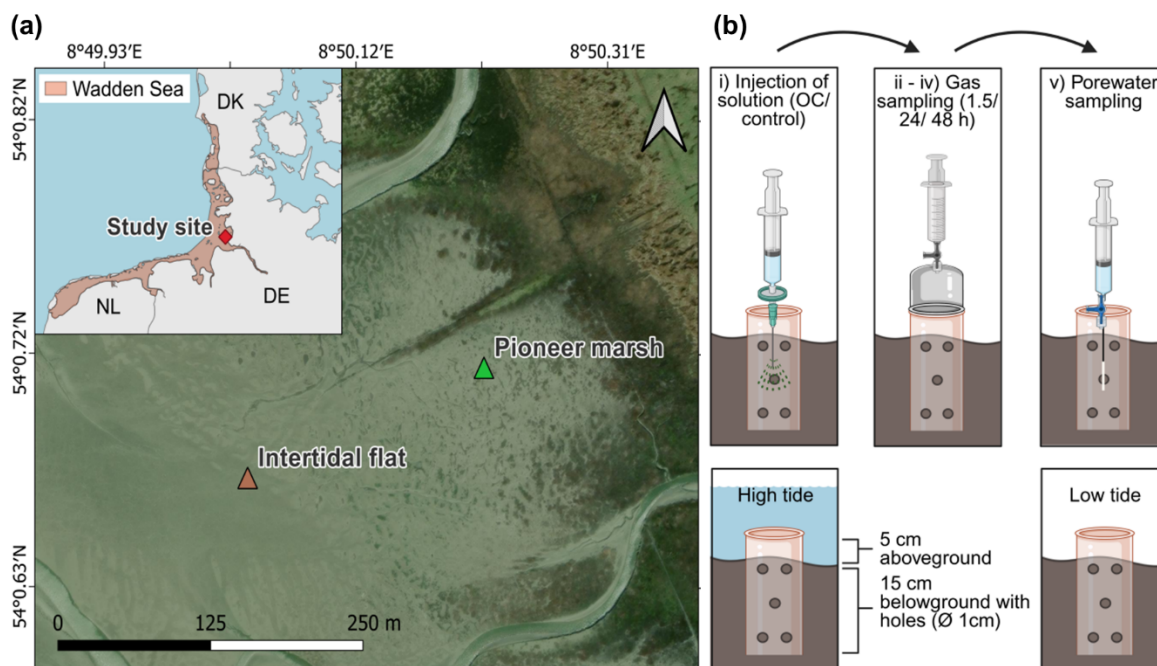
77 To investigate the in situ carbon dynamics in minerogenic salt marshes, we chose a representative field site
78 at the Wadden Sea coast. Our goals were (i) to identify the key microbial processes (O₂, Fe(III) and/or SO₄²⁻ reduction)
79 that control the release of OC as CO₂ and/or CH₄, and (ii) to determine the role of OC (concentration and composition)
80 in the release of GHGs. To this end, we first characterised the primary geochemical parameters from a minerogenic
81 pioneer marsh and intertidal flat at the German Wadden Sea. Building on those results, we conducted an in situ
82 manipulation experiment investigating the impact of two contrasting OC sources (acetate, humic acid) on GHG
83 emissions. We hypothesized that (i) the high energy and sediment inputs in minerogenic salt marshes result in low
84 TOC supply and high TEA availability. (ii) We further hypothesize that this leads to the likely limitation of electron
85 donor and not acceptor on OC decomposition and (iii) the composition of OC plays a more important role than the
86 concentration in CO₂ release from a minerogenic salt marsh. These hypotheses were tested in two successional zones
87 of a salt marsh, a pioneer marsh with sparse pioneer vegetation and a non-vegetated intertidal flat.

88 2 Materials and Methods

89 2.1 Study site

90 This study was conducted at the Altfelder Koog by Friedrichskoog (54°01'02.4"N 08°51'17.09"E), an area
91 that consists of a salt marsh with different successional zones in the Wadden Sea National Park (Schleswig-Holstein)
92 in northern Germany at the mouth of the Elbe estuary (Fig. 1a). The Wadden Sea is a UNESCO World Heritage Site
93 and the largest continuous salt marsh (including tidal flats) in Europe (Common Wadden Sea Secretariat, 2017). The
94 tidal range at the study area is 3.59 m, defined as the difference between mean height of high water and approximately
95 the lowest astronomical tide. The mean high tide is 1.56 m higher than the mean sea level (BSH, 2025).

96 At the Wadden Sea, different successional zones of salt marshes are developing as a result of the ongoing
97 process of sediment transportation by waves and tides (Esselink et al., 2017; de Vlas et al., 2013). The two successional
98 zones which are of interest in our study are the pioneer marsh and the intertidal flat (Fig. 1a). Pioneer species such as
99 *Salicornia* spp. and *Spartina anglica* occur in the pioneer marsh, promoting further sediment trapping (Esselink et al.,
100 2017; de Vlas et al., 2013). The intertidal flat (seaward of a pioneer marsh) is an area with no plants to buffer incoming
101 waves and is therefore subject to a strong tidal influence (Esselink et al., 2017). In general, both the pioneer marsh and
102 intertidal flat are inundated daily during high tide, with the pioneer marsh experiencing less and shorter inundation (<
103 3 h fully inundated) compared to the intertidal flat (> 3 h fully inundated) (de Vlas et al., 2013). During a spring tide,
104 which occurs twice a month, the magnitude of high and low tide is amplified leading to stronger exposure of the pioneer
105 marsh to tides (Gao, 2019; Kvale, 2006).



106

107 **Figure 1. Study site at the Wadden Sea including the successional zones of a salt marsh and a schematic representation of**
 108 **the in situ experimental design.** (a) Wadden Sea, in light red in the inset with a red marker indicating our study site in northern
 109 Germany (Friedrichskoog, Elbe estuary). Gradient of salt marsh successional zones, beginning with the intertidal flat, followed by
 110 the pioneer marsh and more developed successional zones extending further inland. Map information: Reference system WGS 1984,
 111 UTM 32N, data imagery ESRI 2025. (b) Experimental design: experimental procedure (top) and cylinder setup in sediment (below).
 112 Each sampling plot consisted of a 20 cm long cylinder (diameter 16 cm), drilled with 1 cm diameter holes along the length of the
 113 cylinder. The cylinder was inserted 15 cm deep in the sediment to define the injection area. The top 5 cm was used to mount a gas
 114 chamber during gas sampling. The cylinder stayed in the sediment over the course of the experiment including high and low tide.
 115 Numbers i-v) indicate the experimental procedure: i) injection of solution (acetate or humic acid, only NaCl for control), ii) 1.5 h
 116 after injection, the first gas measurement was done, iii) followed by the second gas measurement after 24 h of injection, and iv) the
 117 final gas measurement after 48 h of injection, followed by the final step of v) porewater sampling. Each treatment (acetate, humic
 118 acid) and the control consisted of spatial triplicates.

119 2.2 Porewater and sediment sampling for general geochemistry

120 In August 2022 and 2023, sediment cores were collected from the pioneer marsh and intertidal flat to analyse
 121 the general geochemistry of the sediment and porewater. The sampling was performed during low tide. Push cores
 122 were collected using core liners (UWITEC, polyvinyl chloride PVC) with an inner diameter of 8.6 cm (outer diameter
 123 9 cm) and a length of 60 cm. To minimize compression, we used open push cores and only capped them when the core
 124 liner was fully in the sediment. Furthermore, the inside wall of the cores was plain and clean to smoothly insert the
 125 core liner in the sediment. To further minimize disturbance, the sampled cores were immediately closed, vertically
 126 transported, and stored in the dark. At depth intervals of 5 cm, porewater samples (Rhizon sampler CSS, 0.12-0.18 μm
 127 pore size, Rhizosphere Research, Netherlands) and sediment samples (using a cut-off syringe) were taken through
 128 pre-drilled holes which had been covered with isolation tape during coring. We made sure to not take sediment or

129 porewater samples at the edges but rather from the middle of the cores, where the sediment is likely undisturbed.
130 Porewater samples were analysed for dissolved organic carbon (DOC), iron speciation, SO_4^{2-} , and dissolved CH_4 , and
131 sediment samples for total organic carbon (TOC). Detailed method for dissolved CH_4 sampling is given in Supplement,
132 S1.1.

133 We collected further sediment cores for fine scale O_2 profiles. For this, sediment push cores (inner diameter
134 2.5 cm, length 10 cm) were collected and immediately sealed. Shortly after sampling, O_2 profiles were taken with a
135 depth resolution of 500 μm using Clark-type O_2 microsensors (Unisense, Denmark) with a 100 μm tip, following
136 Revsbech (1989). Before measurement, a two-point calibration was done using air-saturated seawater and 0.1 M
137 sodium ascorbate in 0.1 M NaOH solution. Profiles were recorded with the Unisense software SensorTrace Suite
138 (version 2.8.200.21688, Unisense, Denmark).

139 **2.3 Physicochemical characteristics of the sediment**

140 For a general physicochemical characterization, bulk sediment was collected from a depth up to 15-20 cm in
141 sterile sample bags with puncture proof tabs (Nasco, Whirl-pak, USA), and stored at 4 °C in the dark. Stones and
142 macrofauna were removed prior to further analysis. We determined grain density, bulk porosity, moisture content, and
143 particle size (details in Supplement, S1.2).

144 **2.4 In situ experiment: Enhanced organic carbon input**

145 **2.4.1 In situ experiment design**

146 An in situ OC addition experiment was conducted in August and September 2023 to test the response of
147 pioneer marsh and intertidal flat systems to elevated inputs of OC with different compositions. We choose acetate, a
148 chemically simple organic compound that has been detected at other salt marshes (Hyun et al., 2007; Kostka et al.,
149 2002a) and at a site nearby (Llobet-Brossa et al., 2002), and humic acid (in the form of Pahokee Peat humic acid), a
150 more complex OC source, as a proxy for natural organic matter. The two OC sources were chosen, knowing their
151 thermodynamical difference from previous studies (Gunina and Kuzyakov, 2022), to present a fermentation product
152 (acetate) and a proxy for terrestrial organic matter (in addition to the difference with respect to complexity). Studying
153 both labile and complex OC additions is ecologically relevant as salt marshes receive OC from multiple sources
154 (Howard et al., 2023; Temmink et al., 2022). Eutrophication of coastal waters and/or root exudates can supply readily
155 degradable OC to salt marshes, while increased organic matter load in rivers can deliver more complex OC compounds
156 to salt marshes. The applied OC compounds in our study, therefore, represent environmental scenarios and allows us
157 to investigate how these OC sources influence GHG release under realistic conditions. The injection solutions were
158 prepared in the laboratory prior to use in the field. Solutions of 1 g OC L^{-1} were prepared with either acetate or humic
159 acid as a carbon source. For the preparation of the solutions, sodium acetate or Pahokee Peat humic acid (obtained
160 from the International Humic Substances Society (IHSS), Table S1) were dissolved in deionized water (Barnstead MQ
161 system, Thermo Fisher Scientific, Germany), the pH was adjusted to 7.07-7.81 and NaCl was added (20 g L^{-1}). The
162 solution for the control only contained NaCl. Additionally, 25 mM bromide (Br^-) (in the form of NaBr) was added into

163 the carbon and control solutions as an inert tracer in the field. All solutions were purged with nitrogen and stored at 4
164 °C in the dark until used in the field. Details of the preparation process are provided in Supplement, S1.3.

165 The in situ experiment was performed in the pioneer marsh (54°00'43.14"N 08°50'12.9"E) and intertidal flat
166 (54°00'40.45"N 08°50'02.27"E) (Fig. 1a), with the same setup in both zones. The assigned plots in the field were
167 selected as visually similar triplicates (spatial triplicates), at a distance of ~5 m between plots of the same treatment
168 and ~10 m between different treatments and the control plots. In the pioneer marsh, plots were placed outside of
169 vegetated areas, i.e., the actual plot area of injection and sampling were free of vegetation although vegetation was
170 present in the vicinity (Figs. S1a/b). For the intertidal flat, no vegetation was present, neither in the surroundings nor
171 inside of the plots (Figs. S1c/d). Each plot consisted of a 16 cm diameter PVC cylinder with both ends open which
172 was pushed 15 cm deep into the sediment (Fig. 1b). Holes (diameter 1 cm) were drilled in the cylinder wall to allow
173 underground water movement. A porewater sampler (Rhizon sampler CSS, 0.12-0.18 µm pore size, Rhizosphere
174 Research, Netherlands) was inserted in the middle of each plot at a depth of 5-10 cm and remained in the sediment
175 over the duration of the experiment. The cylinder reached 5 cm out of the sediment, allowing a gas flux chamber to be
176 mounted gastight for gas measurements. During the experiment, the cylinder stayed in the field. To decrease the
177 influence of disturbances due to the setup of the experiment, we waited at least three days between setting up and the
178 first measurements. Apart from the incubation time for gas sampling, the sediment within the cylinder was exposed to
179 the atmosphere (low tide) or covered with seawater (high tide) (Fig. 1b).

180 The experiment was conducted similarly in both zones, the pioneer marsh and intertidal flat, using spatial
181 triplicates and comprising four injection cycles (Fig. 1b). One injection cycle consisted of i) the injection of the anoxic
182 sterile solution (OC or control solution), followed by ii) the first gas sampling 1.5 h after the injection. Gas sampling
183 was repeated iii) 24 h after the injection and iv) 48 h after the injection. After the 48 h gas sampling, v) porewater was
184 collected. Injection of the solutions and sampling was done during low tide. The solution for the different treatments
185 was slowly injected in step i) with a bent needle at a depth of approximately 5-10 cm in the middle of each plot into
186 the sediment. The injected solution was filtered (PES filter, pore size 0.22 µm, pre-rinsed with double deionized water)
187 during injection to ensure that the solutions were sterile.

188 In each injection cycle, the native OC was increased by 12.0 mg C L⁻¹ in the pioneer marsh and 12.6 mg C L⁻¹
189 in the intertidal flat, assuming an even distribution across the experimental cylinder (calculation Supplement, S1.4).
190 After one cycle was completed, the system had three days to recover before the next injection. At the end of the four
191 injection cycles, sediment samples were collected (details below). The applied approach allowed us to assess short-
192 term OC process response in minerogenic salt marshes, rather than long-term responses.

193 **2.4.2 In situ experiment sampling**

194 **Gas sampling**

195 Gas sampling was conducted using an opaque, static, non-flow gas chamber made of polypropylene (chamber
196 volume 3000 cm³). The gas chamber was placed on the cylinder and gas samples were collected at 20-minute intervals
197 over an incubation period of 1 hour using a 50 mL gastight syringe with a three-way valve. For sampling, the chamber

198 gas was gently mixed by pumping the syringe plunger three times before withdrawing 35 mL gas. The first 5 ml were
199 used to flush the attached needle, and the rest was transferred immediately into a pre-evacuated 12 mL Exetainer® vial
200 (Labco, UK). The samples were measured with a Greenhouse GC equipped with two Pulsed Discharge Detector (PDD)
201 (ThermoFisher Scientific TRACE™ 1310 GC-Analyzer, USA – custom designed by S+H-Analytik) and two column
202 structure (first structure 30 m long, 0.53 mm ID TGBondQ column, second structure 30 m long, 0.53 mm ID Molsieve
203 column (for CH₄) and 30 m long 0.32 mm ID TGBondQ+ column (for CO₂, N₂O)). Calculation for the gas fluxes and
204 cumulative CO₂ emissions are given in Supplement, S1.5.

205 **Porewater sampling**

206 Porewater samples were collected via the pre-installed porewater sampler. The pH (Mettler Toledo SevenGo,
207 Germany) and salinity (refractometer) were measured in the field. The collected porewater was fixed for DOC
208 (acidification with 2 M HCl), iron speciation (acidification with 1 M HCl), and total sulfide (S(II)_{tot}) (alkalinization
209 with zinc acetate). Dissolved inorganic carbon (DIC) samples were transferred into vials without headspace
210 immediately after sampling and capped. The remaining porewater was anoxically stored in nitrogen flushed bottles in
211 the dark at 4 °C for Br⁻, SO₄²⁻ and chloride (Cl⁻) measurements.

212 **Sediment sampling**

213 At the end of the experiment, sediment samples were collected for geochemical analysis (TOC, solid iron
214 speciation, sulfide species) and microbial analysis. For this, push cores (inner diameter of 2.5 cm, and a length 10 cm)
215 were taken from the middle of each plot at the same positions as the porewater samples and immediately frozen until
216 further analysis. Sediment samples for the molecular biology analysis were stored at -80 °C upon bringing them back
217 to the laboratory.

218 **2.5 Geochemical analysis**

219 **2.5.1 Porewater analysis**

220 DOC (as non-purgeable OC) and DIC (as the difference of total carbon and OC) was determined by a TOC
221 analyser (multi N/C 2100S, Analytik Jena GmbH, Germany). To analyse the iron speciation in the porewater, the
222 ferrozine assay (Stookey, 1970) was used. The S(II)_{tot} was quantified by the Cline assay (Cline, 1969). Sulfate, Br⁻,
223 and Cl⁻ were analysed by an ion chromatograph (Metrohm 930 Compact IC Flex, Switzerland).

224 **2.5.2 Sediment analysis**

225 For all sediment analyses, sampled cores were thawed in an anoxic glovebox to prevent oxidation (UNILab
226 plus Glovebox, MBRAUN, Germany), sliced in two depths (0-5 and 5-10 cm), and each depth fraction was
227 homogenized by hand.

228 **Iron extraction**

229 To target the poorly and higher crystalline iron phases in the sediment samples, parallel iron extractions were
230 performed under anoxic conditions, adapted from Moeslundi et al. (1994) and Lueder et al. (2020). From each depth

231 (0-5 and 5-10 cm) ~0.2 g wet sediment sample (in triplicates) were added into an Eppendorf tube. To extract poorly
232 crystalline iron minerals, we used an extraction with anoxic 0.5 M HCl (Heron et al., 1994). We expect that poorly
233 crystalline iron (oxyhydr)oxides as well as ferrous iron (Fe(II)) phases such as carbonates and sulfides (e.g., FeCO₃ or
234 FeS) would be extracted by this acidification. One mL of anoxic 0.5 M HCl was added to the sediment, vortexed, and
235 incubated for 2 h in the dark at room temperature in the glovebox. For the extraction of iron minerals of higher
236 crystallinity, targeting more crystalline Fe(II) (except pyrite) and Fe(III) phases (Cornwell and Morse, 1987; Heron et
237 al., 1994), 1 mL of anoxic 6 M HCl was added to the sediment, and the sediment was vortexed and vertically rotated
238 for 24 h under anoxic conditions at room temperature (30 rpm, dark). For both HCl extractions, the samples were then
239 centrifuged (5 min, 13400 rpm), the supernatant was diluted with 1 M HCl, and iron speciation and concentration of
240 the supernatant was determined using the ferrozine assay (Stookey, 1970). Total iron and Fe(II) concentrations of the
241 supernatant were measured directly, and Fe(III) was determined by subtracting Fe(II) from total iron. To obtain the
242 higher crystalline fraction separately, the poorly crystalline fraction (0.5 M HCl extract) was subtracted from the 6 M
243 HCl fraction. We acknowledge that the weaker acid extraction extracted Fe(II) from carbonates and sulfides in addition
244 to iron (oxyhydr)oxides. We therefore used this approach to determine the crystallinity of iron minerals and call it
245 poorly (extracted by 0.5 M HCl) and higher (extracted by 6 M HCl) crystalline iron minerals (and not (oxyhydr)oxides).

246 **Acid volatile sulfide**

247 To determine the mass of acid volatile sulfide (AVS) in the sediment similar to Burton et al. (2007), ~2 g of
248 wet sediment was weighed in centrifuge tube in a glovebox. A smaller tube filled with anoxic 1 M zinc acetate + anoxic
249 2 M NaOH (v/v 15:85) was placed into the sediment-filled centrifuge tube. To the sediment, 10 mL anoxic 6 M HCl
250 + 2 mL anoxic 1 M L-ascorbic acid was added and immediately closed. The double tubes were placed in an ultrasonic
251 bath for 30 seconds, followed by horizontal shaking overnight (150 rpm). The sulfide released from the sediment was
252 captured in the zinc acetate solution and was analysed according to Cline (1969).

253 **Total organic carbon**

254 To quantify sediment TOC, samples collected in 2023 were dried under anoxic conditions, while those from
255 2022 were dried under oxic conditions, at room temperature until constant weight was reached. Sediments from both
256 years were milled and analysed by a TOC analyser (SoliTOC Cube Elementar, Germany).

257 **2.6 Molecular biology analysis**

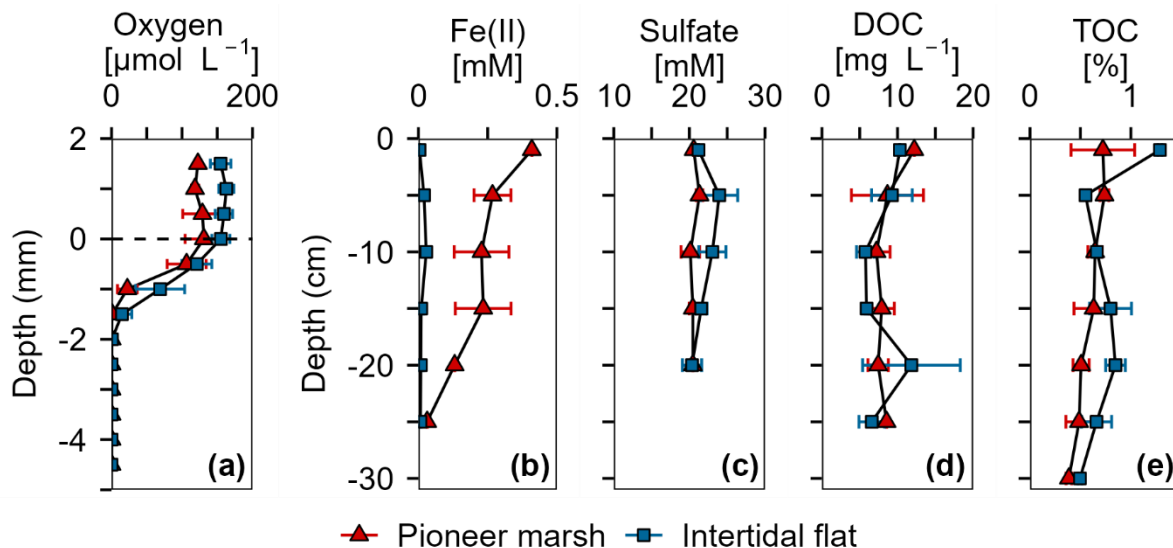
258 The co-extraction of DNA and RNA was performed according to Lueders et al. (2004). Quantitative
259 polymerase chain reaction (qPCR) for DNA and complementary DNA (cDNA) was done to quantify total bacterial
260 16S rRNA gene copies using the primer 341F and 797R. Functional genes were also targeted: *Geobacter* spp. (involved
261 in Fe(III) reduction) using the primer Geo 577F and Geo 822R, and *dsrA* (involved in SO₄²⁻ reduction) using the primer
262 DSR_1F and DSR_1R. Quantitative polymerase chain reaction was done using SsoAdvanced SYBR Green Supermix
263 (Bio-Rad) on the C1000 Touche Thermal Cycler (CFX96™ Real-Time System, Bio-Rad, Germany). Data analysis
264 was performed by the software Bio-Rad CFX Maestro 1.1 (version 4.1.2433.1219). Further details are given in
265 Supplement, S1.6 and Table S2.

266 **2.7 Statistical analysis**

267 For statistical analysis RStudio (R version R-4.4.3) was used. The significance level for all tests was set at p
268 < 0.05. Normal distribution of the data and homogeneity of variances were tested by Shapiro-Wilk test and Levene
269 test, respectively. Correlations between parameters was tested with the relevant tests (Pearson's correlation test or
270 Spearman's rank correlation test depending on the normality of the data). Statistical differences between two groups
271 were tested with a t-test and for more than two groups with a one-way Analysis of Variance (ANOVA) or Kruskal-
272 Wallis rank sum test. For differences in the CO₂ release, a linear mixed model was applied. More details on the chosen
273 tests and model are given in Supplement, S1.7. We reported the p-value in the text; further relevant statistical test
274 results and parameters are shown in the corresponding sections in the SI. The variability of the geochemistry analysis
275 is represented by the standard deviation of triplicates/duplicates. For the in situ experiment, the variability is reflected
276 in the standard error of triplicates. For duplicate analyses, variability reflects the range of the two samples.

277 **3 Results**

278 **3.1 Geochemistry at the study site**



279
 280 **Figure 2. Overview of porewater and sediment biogeochemistry in terms of electron acceptors (O_2 , Fe(III) , SO_4^{2-}) and**
 281 **electron donor (DOC, TOC) from in situ push cores in the pioneer marsh (red triangles) and intertidal flat (blue squares).**
 282 (a) Oxygen concentration profiles measured in intact cores using microsensors. Note that these cores were collected in 2022, separate
 283 from the push cores used for analysis shown in (b-e). Two cores were collected from each zone and two to four profiles were taken
 284 from each core, shortly (within hours) after sampling. (b) Ferrous iron in the porewater, as an indicator of Fe(III) reduction. (c)
 285 Sulfate concentrations in the porewater. (d) Dissolved organic carbon in the porewater. (e) Total organic carbon in the sediment.
 286 For (b-d), push cores were taken in triplicates in both zones to a depth of 25 cm in 2023. Duplicate push cores for (e) the TOC were
 287 sampled in 2022. For all sub-figures, markers denote mean \pm standard deviation (due to limited sample mass, some depth values
 288 only show mean and the range of two samples, or only a single value). All cores were sampled during low tide.

289 Porewater and solid phase measurements from the push and microsensor cores analysis show availability of
 290 electron acceptors (O_2 , Fe(III) , and SO_4^{2-}) over depth in both the pioneer marsh and intertidal flat (Fig. 2). In the pioneer
 291 marsh, O_2 decreased from $131.02 \pm 26.49 \mu\text{mol L}^{-1}$ at the sediment-water interface to $0.18 \pm 0.12 \mu\text{mol L}^{-1}$ over 2 mm
 292 and was depleted beyond this depth. We observed a similar trend for the intertidal flat, with $155.17 \pm 12.71 \mu\text{mol L}^{-1}$
 293 at the sediment-water interface, and a decrease to $0.62 \pm 1.10 \mu\text{mol L}^{-1}$ at 2 mm depth before it was fully depleted (Fig.
 294 2a). Aqueous Fe(II) (as an indicator of Fe(III) reduction) showed a decreasing trend in both zones, with higher
 295 concentration in the pioneer marsh of $267.49 \pm 66.77 \mu\text{M}$ at 5 cm depth and $31.41 \mu\text{M}$ at 25 cm, and 19.93 ± 16.15
 296 μM at 5 cm decreasing to $7.20 \pm 2.89 \mu\text{M}$ at 25 cm in the intertidal flat (Fig. 2b). Sulfate was detected in the porewater
 297 at all sampled depths (1.5 to 20 cm) in both zones (Fig. 2c). In the pioneer marsh, it ranged in the upper 20 cm from a
 298 minimum of 20.12 ± 1.23 to a maximum of 21.34 ± 0.43 mM and in the intertidal flat from 20.35 ± 1.27 to $23.95 \pm$
 299 2.44 mM. We observed a slight decrease in SO_4^{2-} concentration over depth which was more pronounced in the intertidal
 300 flat. This is further supported by the ratio of sulfate:chloride (Fig. S2a). The ratio remained constant in the pioneer
 301 marsh, while a slight decrease was measured in the intertidal flat. We also measured SO_4^{2-} at lower depths (up to 50

302 cm) in cores taken in 2022 and observed similar SO_4^{2-} concentrations (Fig. S2b). To complement the porewater Fe(II),
303 we measured the 0.5 M HCl extractable Fe(III) from the bulk sediment from a depth up to 15-20 cm: $1.30 \pm 1.08 \mu\text{mol}$
304 Fe(III) g^{-1} dry sediment in the pioneer marsh and $1.00 \pm 0.51 \mu\text{mol}$ Fe(III) g^{-1} dry sediment in the intertidal flat. The
305 resulting Fe(II) to total iron ratio was 0.98 ± 0.02 and 0.98 ± 0.01 respectively.

306 Organic carbon as the likely electron donor was measured in the porewater as non-purgeable organic carbon
307 and in the sediment as TOC. The DOC and TOC decreased slightly over depth (Fig. 2d/e) in both zones. In the pioneer
308 marsh, the DOC was $12.21 \text{ mg C L}^{-1}$ at the top (1 cm deep) and decreased over depth to 8.55 mg C L^{-1} at 25 cm. For
309 the intertidal flat, the DOC at the top (1 cm deep) was $10.31 \text{ mg C L}^{-1}$ and decreased to $6.60 \pm 1.69 \text{ mg C L}^{-1}$ at 25 cm.
310 The TOC decreased from $0.7 \pm 0.3 \%$ at the top to $0.5 \pm 0.1 \%$ at a depth of 25 cm in the pioneer marsh and from 1.3%
311 to $0.7 \pm 0.2 \%$ in the intertidal flat (Fig. 2e). Concentrations at lower depths are shown in Supplement, Fig. S2c, and
312 are in a similar range. In both the pioneer marsh and intertidal flat, no CH_4 release, neither as fluxes or in the porewater
313 up to a depth of 50 cm, was detected (detection limit: 0.28 and 0.53 ppm respectively; Table S3).

314 Particle size analysis indicated that sediment from the pioneer marsh was dominated by fine particles, whereas
315 the intertidal flat sediment was coarser. In the sediment of the pioneer marsh, we determined $41.7 \pm 9.1 \%$ sand,
316 $38.7 \pm 2.5 \%$ silt, and $19.7 \pm 8.1 \%$ clay. For the sediment of the intertidal flat, a higher sand fraction ($61.5 \pm 0.5 \%$),
317 less silt ($29.0 \pm 5.0 \%$), and notably lower clay content ($9.5 \pm 5.5 \%$) was measured. For more details on the size
318 fractions, see Supplement, Table S4.

319 **3.2 In situ organic carbon manipulation experiment**

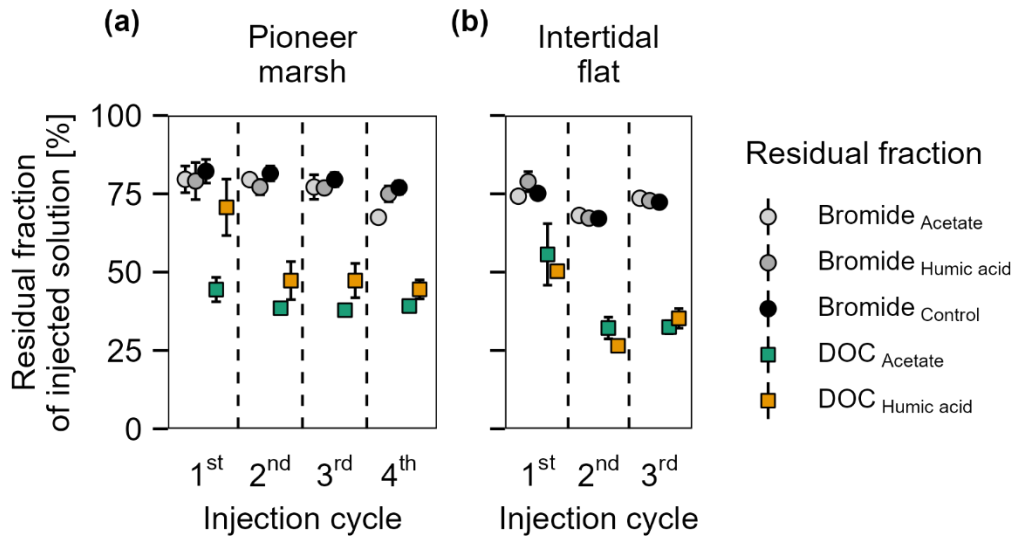
320 **3.2.1 Distribution of bromide tracer and dissolved organic carbon in the sediment**

321 Bromide was used in the in situ experiment as an inert tracer to test the washing out of the injection solution
322 from the experimental plot over the sampling time of one injection cycle (48 h). The native Br^- concentration was
323 $0.66 \pm 0.02 \text{ mM}$ in the pioneer marsh and $0.63 \pm 0.01 \text{ mM}$ in the intertidal flat. Assuming an equal distribution of the
324 injected solution in the experimental cylinder, we expected the Br^- concentration to increase by 0.30 mM to a final
325 concentration of 0.99 mM in the plots of the pioneer marsh and by 0.32 mM to a final concentration of 0.97 mM for
326 the plots in the intertidal flat (calculations Supplement, S1.4 – expected Br^- concentration). Throughout a test injection
327 cycle with the same sampling intervals as the experimental injection cycles, the Br^- concentration remained above the
328 background level with a gradual decrease over time in both zones (Figs. S3a/b). Overall, after 48 h (one injection
329 cycle), Br^- levels in the porewater remained elevated in each cycle for both zones. In the pioneer marsh, an average of
330 $77.5 \pm 5.9 \%$ of the expected level of Br^- remained in the porewater of the experimental cylinder. The intertidal flat
331 had a slightly lower average residual fraction of $72.1 \pm 4.4 \%$ of the expected Br^- level across all injection cycles (Fig.
332 3). Here, residual fraction is defined as the ratio between the Br^- concentration measured in the porewater 48 h post
333 injection and the expected total Br^- concentration in an experimental cylinder (Eq. (1); details in S1.4). The expected
334 total Br^- concentration includes both the native Br^- and the added Br^- during the experiment (expected Br^-) after
335 accounting for dilution in the sediment. Details on the calculation of the Br^- residual fraction are provided in
336 Supplement, S1.4.

337

$$\frac{\overline{\text{Br}^- \text{ concentration at the end of an injection cycle}}}{\overline{\text{Br}^- \text{ expected}}} = \text{residual fraction} \quad (1)$$

338 The residual fraction of DOC is defined in the same way as for Br⁻, representing the proportion of measured
 339 DOC after 48 h to the expected DOC (native DOC + added acetate/humic acid) and was calculated analogously to Br⁻
 340 , with DOC concentrations used instead (Eq. (1) and S1.4). Comparing the average residual fraction of DOC and Br⁻
 341 (Fig. 3) across all injection cycles, the DOC fraction was significantly lower in both the pioneer marsh and intertidal
 342 flat (Br⁻ vs. acetate and Br⁻ vs. humic acid) ($p \leq 0.001$, Table S5). In the pioneer marsh, 40.0 ± 1.2 % of the injected
 343 DOC in the acetate treatment remained, on average across all injection cycles, while the corresponding value for the
 344 humic acid treatment was 52.9 ± 4.5 %. In the intertidal flat, relatively less carbon remained, with a smaller difference
 345 between the carbon sources. Here, the mean residual fraction was 38.2 ± 4.8 % for the acetate treatment and 37.3 ± 3.6
 346 % for the humic acid treatment.

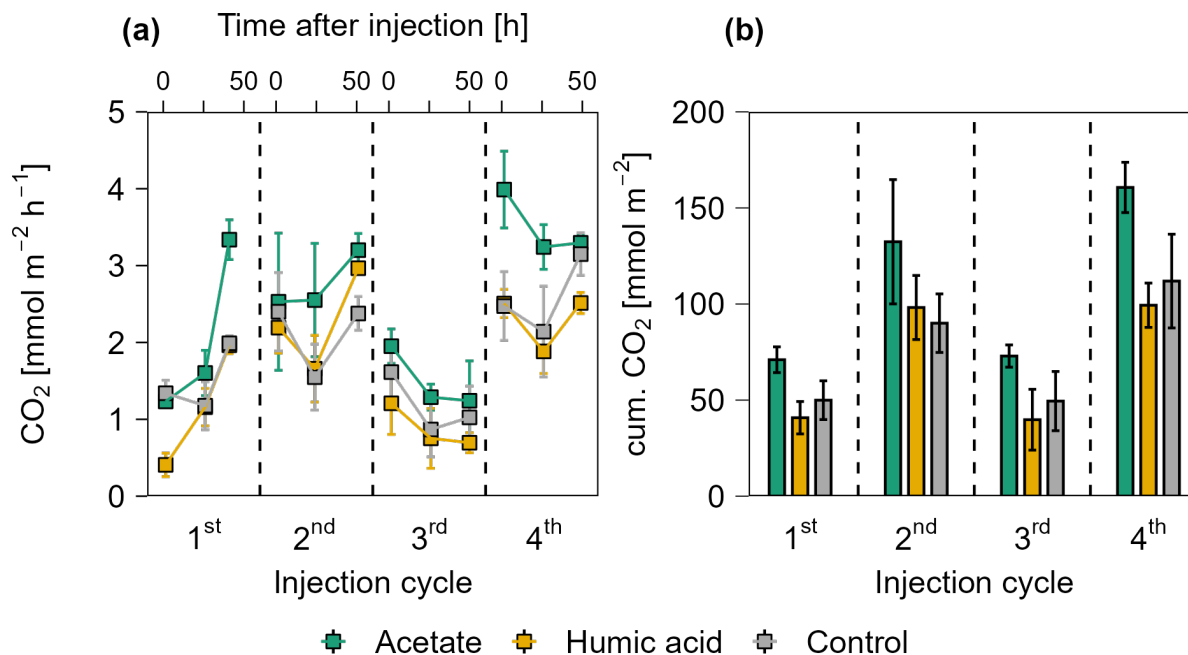


347

348 **Figure 3. Residual fraction of injected solutions (Br^- and DOC) in percentage after 48 h for treatments (acetate, humic acid)**
349 **and control plots in the (a) pioneer zone (over four injection cycles) and (b) intertidal flat (over three injection cycles).**
350 Coloured squares show the residual fraction of injected DOC (acetate in green and humic acid in orange). The grey shaded circles
351 represent the residual of Br^- from the different treatments and the control. The values were calculated based on the ratio between
352 the measured DOC or Br^- concentration (porewater concentration 48 h post injection) and the expected DOC or Br^- concentration
353 (native + added). Markers represent the mean of the triplicates, with error bars indicating the corresponding standard error for
354 treatments and control in both zones for DOC and Br^- across all injection cycles.

355 **3.2.2 Effect of organic carbon input in the pioneer marsh**

356 **Carbon dioxide release**



357
 358 **Figure 4. CO₂ release over four OC injection cycles for the acetate, humic acid, and control plots in the pioneer marsh.** The
 359 dashed lines separate the individual injection cycles. (a) presents individual measured CO₂ fluxes 1.5, 24, and 48 h after injection
 360 in CO₂ mmol m⁻² h⁻¹. Acetate (green), humic acid (orange), and NaCl for the control (grey) were injected into the sediment and
 361 GHG fluxes were measured directly above the injection spot at the aforementioned time intervals. (b) shows the cumulative CO₂
 362 emissions in CO₂ mmol m⁻² over one injection cycle for each treatment and control. We note here that some variability in the fluxes
 363 based on factors such as day/night could not be captured in our sampling approach; we therefore aimed to use a consistent approach
 364 and report relative changes rather than emphasize absolute values. For (a/b), markers represent mean ± standard error of triplicates
 365 for all treatments and the control across injection cycles. For the 1st and 3rd injection cycle for the acetate treatment (both 1.5 h
 366 values) were based on duplicate measurements, which is thus also the case for the (b) cumulative CO₂ emission of these cycles.

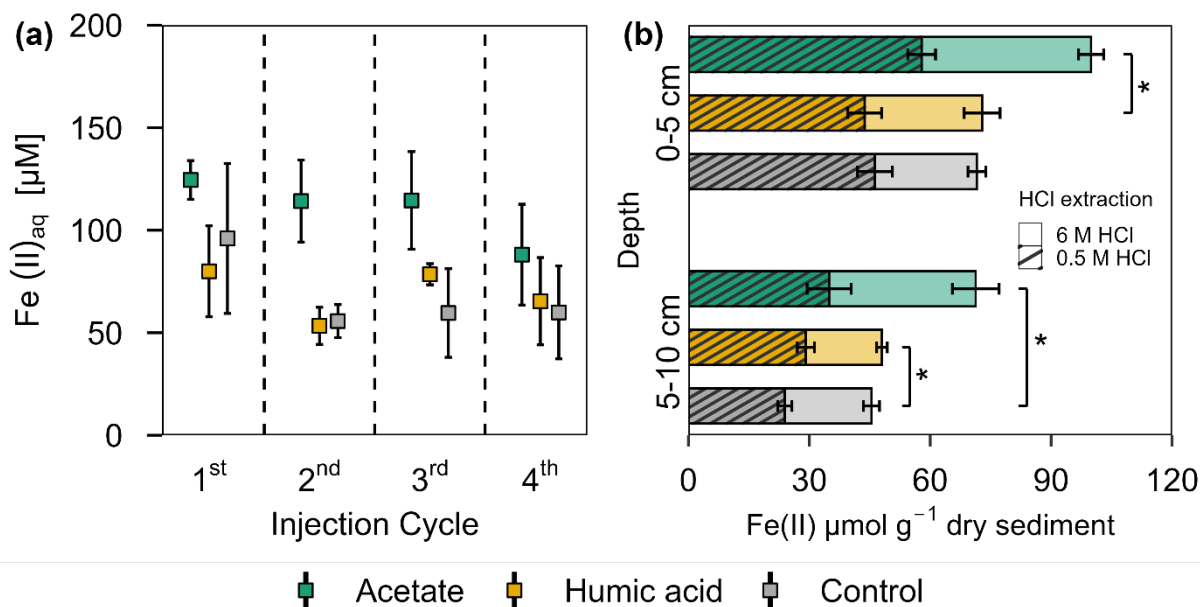
367
 368 Figure 4 presents the CO₂ release for each injection cycle with the individual CO₂ fluxes 1.5, 24, and 48 h
 369 post injection (Fig. 4a) and the cumulative CO₂ emissions (Fig. 4b) in the pioneer marsh. For all four injection cycles,
 370 the CO₂ fluxes of the acetate treated plots exceeded the CO₂ fluxes of the humic acid and control plots (Fig. 4a). For
 371 the first injection cycle, the acetate treatment was significantly higher compared to the humic acid treatment ($p < 0.05$,
 372 Table S6) and slightly above the threshold for statistical significance ($p = 0.08$, Table S6) compared to the control. In
 373 the following injection cycle, the CO₂ fluxes of the acetate treatment were also higher compared to the humic acid and
 374 control plots but not significantly ($p > 0.05$). Hence, the acetate treated plot consistently exhibited the highest fluxes.
 375 The difference between the humic acid and control plots was statistically negligible ($p > 0.05$). Similarly, the
 cumulative CO₂ emissions from the acetate treated plots were the highest while the emissions from the humic acid and

376 control plots were in a similar range for all four injection cycles (Fig. 4b). The CO₂ emitted from the acetate treated
377 plots was up to 83.2 ± 53.7 % higher than for the humic acid treated plots. Similarly, the emissions of the acetate plots
378 were up to 47.4 ± 36.4 % higher relative to the control plots. No statistical differences were measured between the
379 cumulative CO₂ emission of the acetate treated plots and the control or humic acid treatment. Overall, these differences
380 were smaller than those seen at individual CO₂ fluxes at specific time points (Fig. 4a), likely due to high variability in
381 fluxes that resulted in variable cumulative CO₂ emissions. In all treatments and the control, no CH₄ as a flux was
382 detected (lower than detection limit (0.28 ppm); Table S3).

383 The CO₂ fluxes showed a positive correlation with air temperature and a moderate positive correlation with
384 the tidal cycle in the pioneer marsh (Table S7). Specifically, CO₂ fluxes were found to be higher as the spring tide
385 receded. Lower CO₂ fluxes were measured during the first and third injection cycles, which occurred close to spring
386 tides.

387 Further differences between the treatments and control were observed in the DOC concentrations (Fig. S4)
388 and the residual fraction of DOC (Fig. 3a) in the pioneer marsh. Over all four injection cycles, the average DOC
389 concentration in the acetate treated plots did not significantly differ from the control ($p > 0.05$), while the DOC
390 concentrations of the humic acid treated plots were significantly higher than the concentrations of acetate treated plots
391 and the control plots ($p < 0.05$, Table S8). These differences are consistent with the residual fraction of DOC (Fig. 3a).
392 Across all four injection cycles, the average residual fraction in the humic acid treatment was significantly higher
393 compared to the acetate treatment but significantly lower than the Br⁻ residual fraction ($p < 0.002$, $p < 0.001$
394 respectively, Table S5). No difference in the TOC content was found between treatments and control in both depths.
395 The content ranged from 0.9 ± 0.1 % to 1.2 ± 0.1 % in the upper 5 cm, with a slight decrease at lower depth (Table S9).

396 In addition to the gas fluxes, we also measured DIC and pH of the porewater for each treatment and control
397 for each injection cycle (Fig. S5). As the differences in the CO₂ fluxes were more pronounced and our focus was on
398 GHG release, we only present and later discuss these data.



400
 401 **Figure 5. Ferrous iron in (a) porewater and (b) solid phase from acetate and humic acid treated plots and the control plots**
 402 **in the pioneer marsh.** (a) Aqueous ferrous iron (Fe(II)_{aq}) [µM] sampled after each injection cycle (cycles are separated by the
 403 dashed line). Triplicates for each treatment and control for each injection cycle were collected and mean ± standard error is shown.
 404 (b) HCl extractable Fe(II) content [µmol g⁻¹ dry sediment] at two different depths (0-5 and 5-10 cm) sampled at the end of all four
 405 injection cycles. Different colour coding was used for contrasting treatments: acetate treatment (green), humic acid treatment
 406 (orange), and control (grey). Striped bars represent poorly crystalline Fe(II) (0.5 M HCl extraction) and solid bars higher crystalline
 407 Fe(II) (6 M HCl extraction). The 0.5 M HCl extract was subtracted from the 6 M HCl extracted fraction to separate poorly and
 408 higher crystalline Fe(II). Significance is denoted for the 0.5 M HCl extraction. Statistical details are given in the SI (Table S11),
 409 significance level $p < 0.05$ *. For each treatment and control, each spatial triplicate ($n = 3$) was analyzed in triplicate (total $n = 9$)
 410 for each depth (0-5 and 5-10 cm); results are presented as mean ± standard error.

411 In the pioneer marsh, acetate treated plots had significantly higher aqueous Fe(II) concentrations compared
 412 to humic acid and control plots when considering the average concentration across all injection cycles (acetate vs.
 413 humic acid $p = 0.007$ and vs. control $p = 0.002$, Table S10). Although the differences were not always statistically
 414 significant for the individual cycles, the Fe(II) concentration in the porewater of the acetate treated plots was
 415 consistently higher (Fig. 5a): 1st cycle 124.52 ± 9.44 µM, 2nd cycle 114.20 ± 19.98 µM, 3rd cycle 114.54 ± 23.80 µM,
 416 and 4th cycle 88.08 ± 24.58 µM. Humic acid treated plots and the control plots showed similar aqueous Fe(II)
 417 concentrations. For humic acid treated plots the aqueous Fe(II) concentration ranged between 53.36 ± 9.05 µM
 418 (2nd cycle) and 79.96 ± 22.16 µM (1st cycle), and for the control between 55.69 ± 8.04 (2nd cycle) and 96.01 ± 36.61
 419 µM (1st cycle) (Fig. 5a).

420 A similar trend can be seen in the solid phase for the HCl extractable Fe(II), for both extractions approaches
 421 (0.5 M and 6 M HCl) (Fig. 5b). Comparing the poorly crystalline Fe(II) fraction, the acetate treatment had the highest

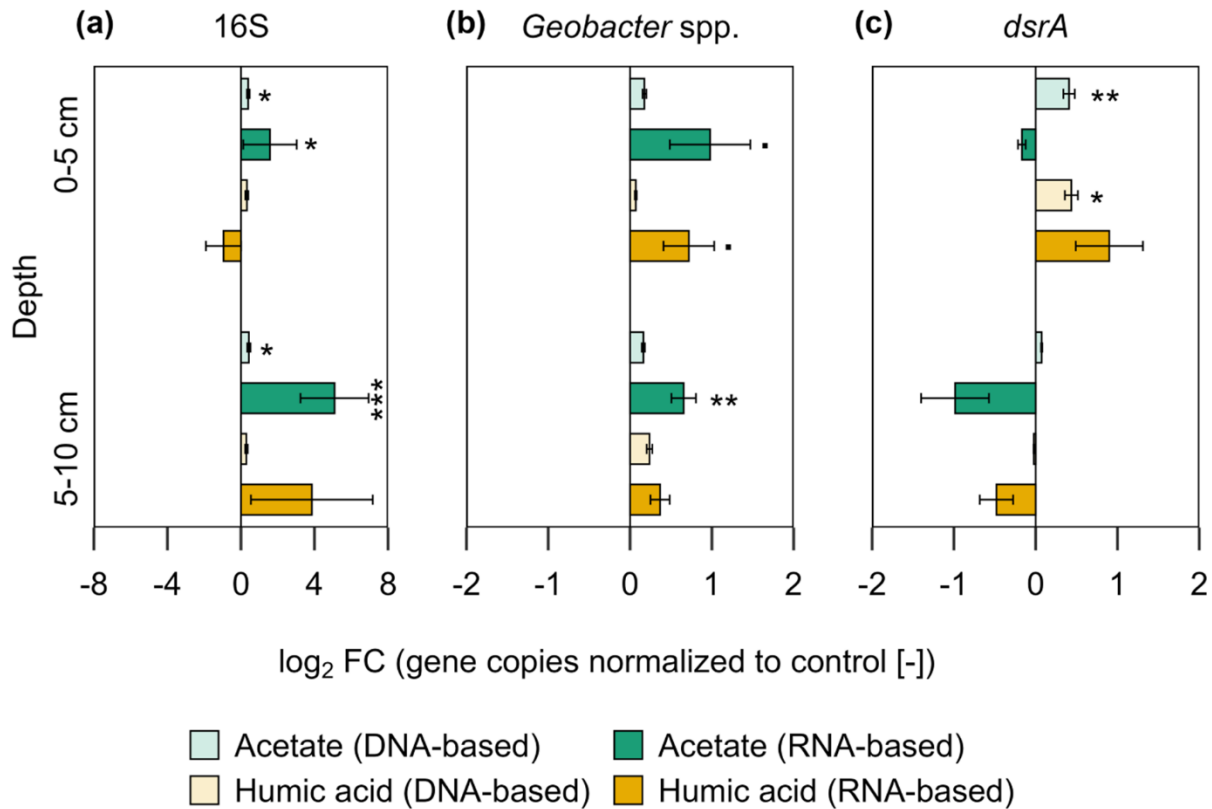
422 Fe(II) content compared to the humic acid treatment and the control at both depths. Acetate treated plots showed an
423 Fe(II) content of $57.87 \pm 3.44 \mu\text{mol g}^{-1}$ sediment in the upper 5 cm and $34.91 \pm 5.45 \mu\text{mol g}^{-1}$ sediment from 5-10 cm.
424 Humic acid and control plots had similar levels of Fe(II): for the humic acid plots, the content in the upper 5 cm was
425 $43.74 \pm 4.18 \mu\text{mol g}^{-1}$ sediment and from 5-10 cm, it was $29.13 \pm 2.12 \mu\text{mol g}^{-1}$ sediment. The control plots showed
426 $46.28 \pm 4.32 \mu\text{mol g}^{-1}$ sediment in the upper 5 cm and $23.93 \pm 1.75 \mu\text{mol g}^{-1}$ sediment between 5 to 10 cm. We observed
427 the same trend for the higher crystalline Fe(II) content. The acetate treatment had the highest contents with 42.04 ± 3.12
428 $\mu\text{mol g}^{-1}$ sediment (0-5 cm) and $36.38 \pm 5.79 \mu\text{mol g}^{-1}$ sediment compared with humic acid or control plots. For both
429 depth and crystallinities, the acetate treatment showed significantly the highest content, in nearly all comparisons to
430 the humic acid or control plots (Table S11). Except for poorly crystalline Fe(II) at 5-10 cm depth, humic acid and
431 control plots did not differ significantly (Table S11).

432 No consistent difference was detected in $S(\text{II})_{\text{tot}}$ in the porewater of the pioneer marsh (Fig. S6a). The $S(\text{II})_{\text{tot}}$
433 concentrations were in the same range: acetate from $3.16 \pm 0.01 \mu\text{M}$ (4th cycle) to $5.59 \pm 1.21 \mu\text{M}$ (1st cycle), humic
434 acid from $3.0 \pm 0.11 \mu\text{M}$ (4th cycle) to $6.34 \pm 1.56 \mu\text{M}$ (1st cycle) and control from $3.63 \pm 0.34 \mu\text{M}$ (1st cycle) to
435 $4.39 \pm 1.13 \mu\text{M}$ (4th cycle). Also, statistical analysis did not reveal a difference between the different treatments and
436 control $S(\text{II})_{\text{tot}}$ averaged over all cycles ($p > 0.05$). Similarly, AVS measurements of the solid sulfide species showed
437 no difference between treatments and the control (Fig. S6b). In the upper 5 cm, contents were similar (acetate:
438 6.13 ± 1.40 , humic acid 3.89 ± 1.19 , and control $7.37 \pm 1.76 \mu\text{mol g}^{-1}$ sediment). Similar contents were measured at
439 5-10 cm depth, with no coherent trend between the layers.

440 **Effect of organic carbon input on microbial growth and metabolic activity**

441 The impact of the added OC on the bacterial community was analysed by qPCR. The analyses were based on
442 DNA (microbial abundance) and RNA (metabolically active microorganisms). The results show the gene copies of
443 both treatments normalized to the control as \log_2 fold change (\log_2 FC) (Fig. 6). Statistics are based on the absolute
444 gene copy numbers (Fig. S7). For the acetate treated plots a significantly higher bacterial 16S rRNA gene copy number
445 (DNA- and RNA-based) was measured compared to the control plots across all analysed depths (Fig. 6a; $p < 0.05$). In
446 comparison to the control, DNA-based bacterial 16S rRNA gene copies increased by a factor of 0.4 ± 0.07 (\log_2 FC)
447 under acetate treatment and their potential activity, indicated by RNA, increased by $1.58 \pm 1.46 \log_2$ FC in the upper 5
448 cm. This remained similar at the depth of 5-10 cm, with an increase in DNA-based 16S rRNA gene copies by $0.43 \pm$
449 $0.09 \log_2$ FC and an increase in activity (RNA) by $5.09 \pm 1.86 \log_2$ FC. For the comparison between plots amended
450 with humic acid and the control, variations were observed but no significant differences were measured ($p > 0.05$).
451 Microbial activity (RNA) of *Geobacter* spp., were higher in the acetate and humic acid treatment compared to the
452 control in the upper 5 cm, however, slightly over the significance criterion (Fig. 6b; $p = 0.051$, $p = 0.057$, respectively).
453 For the acetate treated plots, the activity (RNA-based) of *Geobacter* spp. was higher compared to the control by a
454 factor of 0.98 ± 0.49 . The humic acid treatment also had upregulated activity by a factor of 0.72 ± 0.31 . The higher
455 microbial activity of *Geobacter* spp. remained significantly enhanced ($p = 0.008$) for the acetate treatment compared
456 to the control at the lower depth (RNA-based: \log_2 FC: 0.66 ± 0.15), too. The addition of OC did not affect the microbial
457 activity (RNA) of *dsrA* genes at both depths (Fig. 6c) in the pioneer marsh. However, the abundance (DNA) of *dsrA*

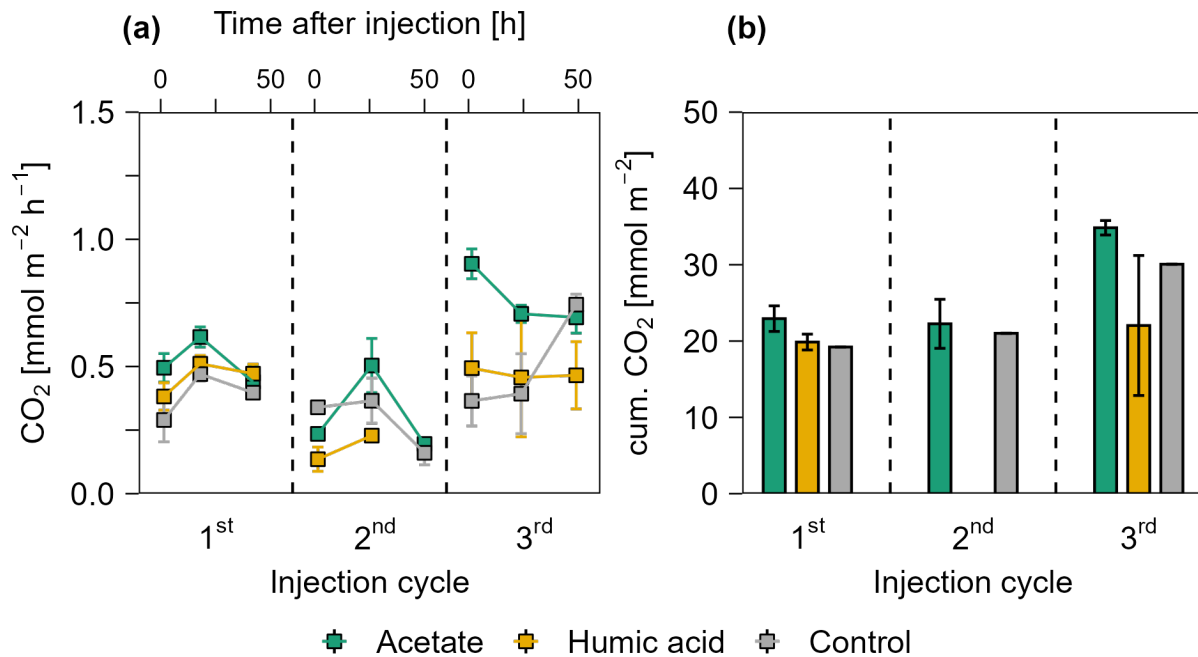
458 genes in the upper layer was significantly higher for both treatments (acetate $p = 0.006$, humic acid $p = 0.015$). Absolute
 459 gene copy numbers are given in Supplement, Fig. S7 and statistical details in Table S12.



460
 461 **Figure 6. Bacterial gene copy numbers of (a) 16S rRNA (16S), (b) *Geobacter* spp., and (c) *dsrA* for acetate and humic acid**
 462 **treatment normalized to the control in the pioneer marsh.** The values are represented as log₂ fold change (FC). Values > 0
 463 indicate an upregulation while values < 0 indicate downregulation of the genes compared to the control (acetate in green, humic
 464 acid in orange). DNA-based numbers are given in lighter colours and RNA-based in darker colours. Statistical differences in the
 465 absolute gene copy numbers are indicated as stars in the figure: significant codes are $p = 0.05$., $p \leq 0.05$ *, $p \leq 0.01$ **, and
 466 $p \leq 0.001$ ***. Absolute gene copy numbers given in Supplement, Fig. S7. Sample sizes include triplicates of each treatment and
 467 control at both depths, represented as mean \pm standard error (exception of duplicate measurements for 16s RNA-based humic
 468 substances (5-10 cm) and 16s RNA-based control (0-5 cm)).

469 **3.2.3 Effect of organic carbon input in the intertidal flat**

470 **Carbon dioxide release**



471
 472 **Figure 7. CO₂ release over three injection cycles for the acetate and humic acid treated plots and the control plots in the**
 473 **intertidal flat.** (a) CO₂ fluxes after 1.5, 24, and 48 h after injection in CO₂ mmol m⁻² h⁻¹ over three injection cycles. The dashed
 474 lines separate the individual injection cycles. In the 2nd injection cycle, fluxes in the humic acid treatment are only displayed at 1.5
 475 and 24 h post injection due to missing data. Acetate (green), humic acid (orange), and NaCl for the control (grey) were injected into
 476 the sediment and GHG fluxes were measured directly above the injection spot at the aforementioned time intervals. (b) presents the
 477 cumulative CO₂ release in mmol CO₂ m⁻² over one injection cycle for each treatment and control. Due to missing values for humic
 478 acid amended plots in the second injection cycle, cumulative emissions could not be calculated. For the same reason, standard errors
 479 of the control plots are also not available. For (a/b), markers represent the mean ± standard error of triplicates for all treatments and
 480 the control across injection cycles, except where missing values for CO₂ release occurred due to nonlinear CO₂ release during the
 481 gas sampling incubation time. (a) duplicate measurements are reflected for the 1st injection cycle for the control (1.5 and 24 h), for
 482 the 2nd injection cycle for the acetate treatment and control (48 h), and the 3rd injection cycle for the acetate treatment and control
 483 (1.5, 24, and 48 h). Single measurement values are shown for the control in the 1st (48 h) and 2nd (1.5 h) injection cycle. For (b),
 484 cumulative CO₂ emissions, the acetate treatment shows duplicate measurements for the 2nd and 3rd injection and for the control,
 485 only single values are reflected.

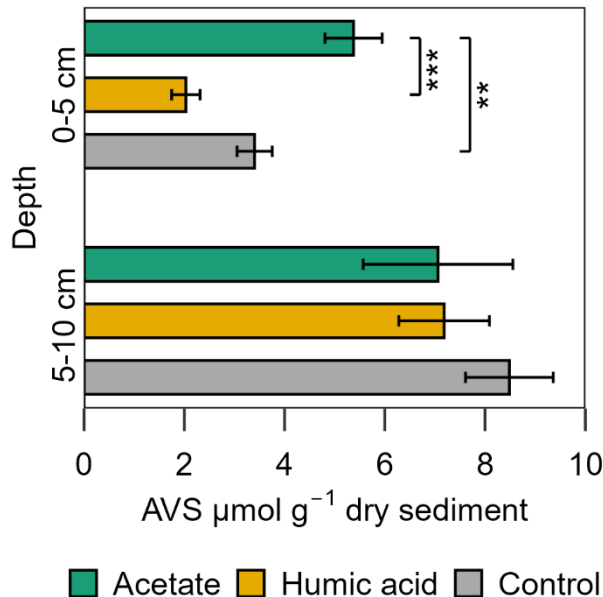
486 Figure 7a presents the CO₂ release from the intertidal flat over three injection cycles 1.5, 24, and 48 h post
 487 injection. Acetate treated plots released the highest CO₂ in all three injection cycles compared to the humic acid and
 488 the control plots. Similar to the pioneer marsh, no strong differences were observed between humic acid treated plots
 489 and the control plots. Consistently, the maximum cumulative CO₂ emissions were observed in the acetate treated plots
 490 (Fig. 7b). Due to nonlinearity of CO₂ release over the incubation time of gas sampling, some data points are missing;

491 therefore, statistical comparison of CO₂ release between treatments and the control was not done. Nevertheless, plots
 492 amended with acetate consistently showed higher CO₂ releases across all injection cycles. Methane was not detected
 493 in the fluxes of any treatment in the intertidal flat plots (lower than detection limit (0.28 ppm); Table S3). Similar to
 494 the pioneer marsh, we focus here on CO₂ data although DIC and pH were measured (Fig. S8).

495 No difference in the DOC concentrations between the treatments and the control were measured (Fig. S9).
 496 Similarly, no difference was measured between the residual fraction (recovery of injected DOC) between acetate and
 497 humic acid treatments (Fig. 3b). The TOC content among the treatments and the control was also in the same range
 498 (0.4-0.5 %) (Table S9).

499 Effect of organic carbon input on the geochemistry of porewater and sediment

500 In the intertidal flat, aqueous Fe(II) concentrations ranged from 9.25 ± 0.21 to 24.82 ± 4.50 μM in both
 501 treatments and the control, with no significant differences ($p > 0.05$) (Fig. S10a). Additionally, no difference between
 502 the treatments and the control was detected in the solid phase for both crystallinities (0.5 and 6 M HCl extraction) and
 503 depths. In the upper 5 cm, the content of the poorly crystalline Fe(II) ranged from 18.28 ± 1.28 to 19.60 ± 0.88 $\mu\text{mol g}^{-1}$
 504 sediment among all treatments and control, while in the deeper layer, the range was from 18.11 ± 0.71 to 24.59 ± 1.22
 505 $\mu\text{mol g}^{-1}$ sediment. The content of the higher crystalline Fe(II) ranged from 11.68 ± 0.99 to 20.06 ± 3.64 $\mu\text{mol g}^{-1}$
 506 sediment in the upper 5 cm and from 12.98 ± 1.03 to 17.50 ± 2.75 $\mu\text{mol g}^{-1}$ sediment at a depth of 5-10 cm (Fig. S10b).



507
 508 **Figure 8. Acid volatile sulfide (AVS) in the solid phase sampled at the end of the experiment for the acetate and humic acid**
 509 **treated plots and the control plots in the intertidal flat.** AVS [$\mu\text{mol g}^{-1}$ dry sediment] content of the solid phase from the different
 510 treatments (acetate in green, humic acid in orange) and control (grey). Significance is denoted for the upper sediment layer (0-5
 511 cm), deeper layer no statistically significant difference occurred. Statistical details are given in the SI (Table S13), significance level

512 $p < 0.05$ *, $p < 0.01$ **, and $p < 0.001$ ***. Each spatial triplicate (n=3) was analyzed in triplicates (total n = 9) for each treatment
513 and the control at both depths; results are presented as mean \pm standard error.

514 For porewater $S(II)_{tot}$, no large differences were measured between the treatments and control in the intertidal
515 flat. The concentrations of both treatments and the control were in a similar range over all injection cycles, 0.62 ± 0.01
516 to $1.73 \pm 0.67 \mu M S(II)_{tot}$ (Fig. S11). In contrast, the AVS in the solid phase exhibited a significant difference between
517 the treatments and the control (Fig. 8). Higher AVS contents were measured in the acetate plots. This difference was
518 strongly pronounced in the upper 5 cm in the acetate plots relative to the setups amended with humic acid and the
519 control ($p < 0.001$ and $p = 0.007$, respectively, Table S13). AVS content in the upper 5 cm was $5.38 \pm 0.57 \mu mol g^{-1}$
520 sediment from the acetate plots, $2.03 \pm 0.28 \mu mol g^{-1}$ sediment from the humic acid plots, and $3.40 \pm 0.35 \mu mol g^{-1}$
521 sediment from the control. In the deeper layer (5-10 cm), the differences between treatments and control were
522 statistically negligible ($p > 0.05$).

523 **Effect of organic carbon input on microbial growth and metabolic activity**

524 In the intertidal flat, an increase in DNA- and RNA-based gene copy numbers of the bacterial 16S rRNA gene
525 was detected in the acetate treatment compared to the control at both depths (0-5 and 5-10 cm) (Fig. S12a). This
526 increase was significant for DNA and RNA in the upper layer and remained significant for RNA in the lower layer (p
527 = 0.008, $p = 0.01$, and $p = 0.008$, respectively). The acetate treatment showed a $3.62 \pm 2.41 \log_2 FC$ increase in the
528 metabolic activity (RNA) of the total microbial community compared to the control in the upper layer and an increase
529 of $2.73 \pm 1.41 \log_2 FC$ from 5-10 cm. For *Geobacter* spp. (Fig. S12b) the RNA-based gene copies were significantly
530 higher compared to the control ($p < 0.001$) by a factor of 0.6 ± 0.10 in the upper 5 cm. No significant increase in the
531 RNA-based copy numbers of *dsrA* genes in both depths (Fig. S12c) were observed; however, we detected slightly
532 higher RNA-based *dsrA* gene copies in the acetate treatments ($0.33 \pm 0.06 \log_2 FC$) compared to the control in the
533 upper layer. Absolute gene copy numbers are presented in Fig. S13 and statistical details in Table S14.

534 4 Discussion

535 4.1 Geochemistry at the study site

536 Porewater and solid phase measurements from the push cores showed availability of electron acceptors (O_2 ,
537 $Fe(III)$, and SO_4^{2-}) at different depths in both the pioneer marsh and intertidal flat. Based on microsensor measurements
538 during low tide, we observed O_2 concentrations in the top 2 mm decreasing with depth, from 131.02 ± 26.49 to $0.18 \pm$
539 $0.12 \mu\text{mol L}^{-1}$ in the pioneer marsh, and in the intertidal flat from 155.17 ± 12.71 to $0.62 \pm 1.10 \mu\text{mol L}^{-1}$, reaching 0
540 μM below that depth. This finding directly affects which biogeochemical processes occur below this depth. Other
541 studies conducted in comparable ecosystems have indicated that during high tide and/or daytime, O_2 penetrates deeper
542 into the sediment (de Beer et al., 2005; Bosselmann et al., 2003), but reducing conditions may prevail underneath and
543 that the depth of O_2 penetration might be influenced by sediment grain size. Both zones in our study showed a high
544 proportion of fine particles (silt: 29.0 ± 5.0 to $38.7 \pm 2.5 \%$ and clay: 9.5 ± 5.5 to $19.7 \pm 8.1 \%$). Such a size distribution
545 retains more water (Novák and Hlaváčiková, 2019), resulting in water-filled pore spaces even during low tide, which
546 limits gas exchange. We suggest that the lack of O_2 penetration beyond 2 mm at our study site results from the presence
547 of fine particles. Despite differences in the duration and magnitude of inundation between the zones, the depth of O_2
548 penetration remained similar, indicating that these factors do not influence O_2 penetration depth and that reducing
549 conditions prevail beyond the upper millimetres during both tidal conditions. We do not exclude that the presence of
550 sparse vegetation in the pioneer marsh compared to no vegetation in the intertidal flat may cause differences in the
551 intrusion of O_2 into the sediment (Koop-Jakobsen et al., 2017; Maricle and Lee, 2002). However, we did not detect
552 this difference in our O_2 measurements. In addition to plants, benthic organisms such as worms may introduce O_2 into
553 the sediment and influence the biogeochemical cycling in the sediment (Huettel et al., 2014). As worms were present
554 in both zones, it is likely that they play a role in O_2 penetration and re-oxidizing of reduced $Fe(II)$ or sulfide species
555 (Figs. S14a-d). We expect that this effect is not substantially different for the two zones, as no large qualitative
556 difference in the presence of worms was observed visually.

557 Below the oxic zone, alternative electron acceptors were present. We used $Fe(II)$ porewater data as an
558 indicator of $Fe(III)$ reduction. A decrease in the aqueous $Fe(II)$ from 267.49 ± 66.77 to $31.41 \mu\text{M Fe(II)}$ in the pioneer
559 marsh and from 19.93 ± 16.15 to $7.20 \pm 2.89 \mu\text{M Fe(II)}$ in the intertidal flat was measured over 25 cm. Based on the
560 presence of aqueous $Fe(II)$, we assumed that $Fe(III)$ reduction is likely occurring in both zones, which is less
561 pronounced in the intertidal flat. The observed decreasing trend over depth has been commonly seen in other studies
562 of coastal sediment (Moeslundi et al., 1994; Lowe et al., 2000). It suggests a depletion of bioavailable $Fe(III)$ with
563 depth and/or removal of aqueous $Fe(II)$. Aqueous $Fe(II)$ can precipitate with sulfide, which forms through SO_4^{2-}
564 reduction deeper in the sediment when more thermodynamically favourable electron acceptors are exhausted
565 (Jørgensen et al., 2019). The $Fe(II)$ porewater concentrations are in the range of other studies from salt marshes,
566 especially for the pioneer marsh (0-800 μM) (Kostka et al., 2002b; Seyfferth et al., 2020). Concentrations of the
567 intertidal flat are on the lower end of the studies mentioned above. Ferrous iron was the predominant iron species in
568 the solid fraction extracted by 0.5 M HCl in both zones. Manganese(IV) as an electron acceptor was not further
569 considered as the total manganese concentration from the study site is $5 \mu\text{mol g}^{-1}$ sediment (Kubeneck et al., 2025),
570 and thus relatively low in comparison to the total iron concentration.

571 Sulfate has a major role in the oxidation of OC as an important electron acceptor in coastal wetlands due to
572 its frequent supply via the incoming seawater. We observed a slight decrease in SO_4^{2-} over a depth of 20 cm which
573 was more distinct in the intertidal flat, as seen in the sulfate to chloride ratio (Fig. S2a). This suggests some SO_4^{2-}
574 reduction in the upper 20 cm. A similar pattern was observed at a comparable site where Fe(II) predominates over total
575 iron and porewater SO_4^{2-} concentration decreases with depth, albeit with slightly higher SO_4^{2-} concentrations (Kostka
576 et al., 2002b). The relatively high levels of SO_4^{2-} at all tested depths (>50 cm), supported the absence of detectable
577 CH_4 dissolved in the porewater or as an efflux. This is consistent with past studies such as Martens and Berner (1974)
578 who stated that if more than ~10 % of seawater SO_4^{2-} is still present, CH_4 is not produced, as a thermodynamically
579 more favourable electron acceptor is available (Schlesinger and Bernhardt, 2013b). We examined different possible
580 explanations for the lack of detected CH_4 as we could not entirely exclude that CH_4 was produced further down in the
581 sediment and oxidized via anaerobic methane oxidation (AOM), as observed in some coastal wetlands (Capooci et al.,
582 2024; La et al., 2022; Wang et al., 2019), or by lateral transport to surrounding tidal channels (Trifunovic et al., 2020).
583 We did not measure any CH_4 as an efflux or in the porewater over multiple field campaigns, similar to a study conducted
584 at the same study site by Kubeneck et al. (2025). Furthermore, the absence of an observed decrease in SO_4^{2-}
585 concentration, particularly in the pioneer marsh, suggest a lack of AOM until 50 cm, as CH_4 and SO_4^{2-} are consumed
586 in a 1:1 stoichiometric ratio during sulfate AOM. The few other studies that have detected CH_4 in the Wadden Sea were
587 at depths where SO_4^{2-} was largely depleted (Røy et al., 2008; Wu et al., 2015), which is not the case in our study. Thus,
588 our results indicate that CH_4 production and consumption is unlikely until 50 cm, and could occur, if at all, below these
589 depths. Further analysis using microbial analysis and/or CH_4 injection experiments is needed to fully exclude
590 methanogenesis and AOM at lower depths. Collectively, due to the occurrence of Fe(III) reduction (especially in the
591 upper sediment layers) and the availability of SO_4^{2-} throughout the sediment, we suggest that electron acceptor
592 availability likely did not limit microbial OC decomposition in our study.

593 We also considered the OC sources in the system: porewater DOC and solid phase TOC. The TOC content
594 was ~1 % and decreased with depth in both zones. A decreasing trend over depth was also seen in the DOC
595 concentrations. The decrease of OC with depth indicates decomposition and has been commonly observed in other
596 studies (Hansen et al., 2017; Mueller et al., 2019). The range in TOC and DOC concentrations are at the lower end of
597 comparable ecosystems with the main differences in the upper centimetres (Gribsholt and Kristensen, 2003; Hansen et
598 al., 2017; Mueller et al., 2023).

599 Based on the availability of electron acceptors (e.g., SO_4^{2-}) at all depths and the lack of detectable CH_4 , we
600 hypothesize that at our field site and other comparable coastal sites, OC is likely the constraint on microbially mediated
601 CO_2 release and that electron acceptors are likely not a limiting factor. To our knowledge, this is rarely reported for
602 coastal wetlands and not commonly expected for terrestrial ecosystems. Hence, we performed an in situ experiment to
603 test this hypothesis.

604 **4.2 In situ organic carbon manipulation experiment**

605 **4.2.1 Validation of the experimental setup**

606 Bromide, as an inert tracer, was injected along with the OC/control solution into each experimental cylinder
607 for each injection cycle. This allowed us to follow the distribution and retention time of the injected solution over one
608 injection cycle. The Br⁻ concentration over each injection cycle was higher than the background Br⁻ concentration (Fig.
609 3/S3a/b), indicating that the injected solution was partially retained within the experimental cylinder over one injection
610 cycle. The observed decrease in Br⁻ concentration over one injection cycle, more pronounced in the intertidal flat (Fig.
611 S3b), was likely due to flushing out by tidal water and belowground water movement. We observed a slightly lower
612 retention of Br⁻ in the intertidal flats compared to the pioneer zone. We attribute this difference to the higher sand
613 fraction in the intertidal flats, which likely increased permeability and led to stronger tidal flushing of the injected
614 solution as well as subject to greater tidal inundation.

615 As the Br⁻ concentrations and the respective calculated residual fractions were similar for each cycle (Fig. 3),
616 we infer that there was no residue of Br⁻ and thus no injected OC was carried over between cycles. Furthermore, the
617 retained Br⁻ was similar between the plots of a treatment within one zone, indicating similar belowground conditions
618 within one zone and thereby validating the experimental setup. By placing the experimental plots outside of vegetated
619 areas in the pioneer marsh, we tried to avoid geochemical influence on the sediment by plants. However, it is possible
620 that benthic organisms such as worms may have influenced the biogeochemistry in both the pioneer marsh and
621 intertidal flat, causing some variability.

622 **4.2.2 Effect of organic carbon input in the pioneer marsh**

623 **Carbon dioxide fluxes**

624 To test our hypothesis that that microbially mediated CO₂ release is OC limited in the pioneer marsh, we
625 injected two different OC sources into the sediment and monitored the subsequent release of CO₂ 1.5, 24, and 48 h post
626 injection. We observed that acetate treated plots emitted the highest CO₂ throughout the experiment (Fig. 4). No
627 difference in the CO₂ release was measured between the humic acid treatment and the control despite the additional
628 availability of OC. This is supported by the work of Gunina and Kuzyakov (2022) who showed that reduced and
629 complex organics in soils are predominantly thermodynamically preserved due to insufficient energy yield upon
630 decomposition. Humic acid, as complex OC, may be thus preserved in our study, as reflected in higher DOC
631 concentrations. In contrast, acetate, with a simpler chemical structure, is favourable for microbial decomposition even
632 under reducing conditions (Boye et al., 2017; LaRowe and Van Cappellen, 2011) and thus could be readily utilized
633 and oxidized to CO₂. Notably, plots treated with humic acid received the same OC concentrations as the acetate plots,
634 indicating that OC composition is crucial for the CO₂ release from minerogenic pioneer marshes. Based on the
635 geochemistry at the field site, which suggested that the ecosystem is limited by the availability of OC, the results from
636 the in situ experiment further support our hypothesis, while simultaneously highlighting the importance of OC
637 composition. This is contrasting to other terrestrial wetlands, which are characterized by a depletion of TEAs
638 (Schlesinger and Bernhardt, 2013b).

639 The increased turnover of acetate to CO₂ relative to humic acid is also evidenced in the DOC concentrations
640 (Fig. S4) and the retention fraction of both DOC sources (Fig. 3a). Although the same mass of OC was added to both
641 treatments, the DOC concentrations in the acetate plots were significantly lower than that in the humic acid plots,

642 suggesting that more acetate was utilized, reflected in higher CO₂ release. However, this result does not explain the
643 lower retention of DOC relative to the retention of Br⁻ from the humic acid plots (Fig. 3a). This suggests that in addition
644 to flushing out, adsorption likely occurred. Previous studies have shown that minerals within the subsurface adsorb
645 organic compounds (Kahle et al., 2003; Kleber et al., 2021). This adsorption may be preferential, favouring more
646 aromatic and high molecular weight compounds, particularly when metal (oxyhydr)oxides and clay minerals are
647 present (Kaiser and Guggenberger, 2000; Lv et al., 2016; Voggenreiter et al., 2024). Based on the results of our study
648 and a previous study conducted at the same site (Kubeneck et al., 2024), both iron(oxyhydr)oxides and clay minerals
649 are present. As adsorption suppresses the decomposition of OC (Kleber et al., 2021), we speculate that the lower
650 retention fraction of humic acid compared to Br⁻ was primarily due to adsorption onto the sediment rather than
651 decomposition. This is consistent with the CO₂ fluxes: humic acid treated plots showed lower retention fractions
652 compared to the Br⁻ retention fractions, however, the CO₂ fluxes were comparable to the control. This suggests that
653 little to no decomposition occurred and that adsorption was the dominant process. It is worth noting that anoxic
654 decomposition of humic acid is generally possible but the turnover time would have exceeded the duration of the
655 experiment (Lipczynska-Kochany, 2018). These results highlight that it is not only the presence of OC that affects
656 short-term OC release from coastal wetlands; the composition of OC is the primary determining factor.

657 Furthermore, it is important to note that the OC concentrations used in this experiment are higher than those
658 expected for naturally occurring OC inputs, such as root exudates, which are typically released at lower concentrations
659 with a continuous input. Thus, upscaling the enhanced CO₂ fluxes measured in our study might result in overestimation
660 of CO₂ release from minerogenic salt marshes. Our findings rather reveal, on a process level, that the addition of labile
661 OC stimulates microbially mediated CO₂ release. Enhanced CO₂ release from the acetate amended plots was measured
662 at nearly all sampling time points (1.5, 24, and 48 h) without a clear trend, while the concentration of the inert tracer
663 showed a slight decrease over the same period (Fig. S3) – indicating slight dilution and flushing of the injected OC.
664 This suggest that the elevated CO₂ release was driven by enhanced availability of labile OC independently of its
665 concentration. These findings allow us to generalize that the system is likely limited by labile OC availability,
666 regardless of the concentration; however, further work should quantify how the magnitude of CO₂ promotion
667 corresponds to OC concentration, particularly under low, naturally sustained OC input rates. In conclusion, we can
668 reliably predict the direction of increased OC inputs to minerogenic salt marshes, but further studies are needed to
669 predict the specific long-term magnitude of changes in the carbon cycle in these ecosystems.

670 **Enhanced microbial Fe(III) reduction leads to higher CO₂ release**

671 This section combines the observed effect of OC input on the geochemistry of the porewater and sediment
672 with the microbial growth and metabolic activity and links them to the CO₂ release from the pioneer marsh. The
673 bacterial 16S rRNA gene copy number, an indicator of the total bacterial abundance, was significantly higher in the
674 acetate treatment compared to the control for both DNA and RNA at both depths. This suggests greater bacterial
675 abundance and metabolic activity, which likely led to higher CO₂ fluxes from these plots. No significant difference
676 was noticeable in the 16S rRNA gene copy number between plots amended with humic acid and the control. Overall,
677 the 16S rRNA gene copy numbers (DNA) are in the range of other studies from coastal wetlands and marine sediment
678 (Petro et al., 2019; Zhou et al., 2017).

679 The enhanced metabolic activity in the acetate treated plots is further reflected in the elevated aqueous and
680 solid phase Fe(II). The acetate treatment showed higher aqueous Fe(II) concentrations in all four injection cycles, while
681 no significant difference was observed between the humic acid and control plots. In the solid phase, the Fe(II) content
682 was the highest in the acetate treatment. Thus, the higher expression of *Geobacter* spp. in the acetate treated plots
683 corresponds well to our geochemical observations. *Geobacter* spp. have been shown to use acetate as a carbon source
684 to gain energy (Coates et al., 1996). The higher Fe(II) levels observed in both aqueous and solid phase of acetate treated
685 plots along with elevated *Geobacter* spp. gene copies indicate that Fe(III) reduction was stimulated by increased
686 availability of labile OC.

687 Ferric iron and SO_4^{2-} reduction have been reported as OC decomposition processes in salt marshes (Hyun et
688 al., 2007; Kostka et al., 2002a; Lowe et al., 2000). Sulfide concentrations in the porewater as well as in the solid phase
689 gave evidence that SO_4^{2-} reduction occurred; however, no differences between the treatments and controls were seen.
690 The functional gene analysis provided further evidence for this, as sulfate-reducing bacteria (SRB) were present
691 (absolute gene copy numbers in Supplement, Fig. S7); however, none of the treatments led to an increase in their
692 metabolic activity compared to the control (Fig. 6). Thus, we speculate that the higher CO_2 release from the acetate
693 treatment was mainly driven by the enhanced Fe(III) reduction and not by SO_4^{2-} reduction. Our finding that acetate is
694 utilized follows the conventional thermodynamic sequence of iron reduction being more favorable than SO_4^{2-} reduction
695 (Schlesinger and Bernhardt, 2013b) – even if the concentrations and availability of SO_4^{2-} were much higher.
696

697 **4.2.3 Effect of organic carbon input in the intertidal flat**

698 **Carbon dioxide fluxes**

699 Adding OC to the intertidal flat, a zone more influenced by tides than the pioneer marsh, resulted in CO₂
700 trends similar to the pioneer marsh. Acetate addition led to a noticeable increase in CO₂ fluxes. In contrast, the CO₂
701 fluxes from the humic acid and control plots were similar. This supports our hypothesis that the electron donor limits
702 CO₂ release from the ecosystem. Moreover, it highlights that irrespective of tidal influence, the system is limited by
703 the availability and composition of OC.

704 **Enhanced microbial activity leads to higher CO₂ release**

705 Total microbial 16S gene copies were significantly higher in the acetate treated intertidal flat plots compared
706 to the control at both depths (RNA-based), whereas plots amended with humic acid showed no significant difference
707 from the control plots (Fig. S12a). In contrast to the significant increase in *Geobacter* spp. gene copies, no difference
708 in the aqueous Fe(II) or in the Fe(II) content in the upper sediment layer (0-5 cm) was measured for the acetate
709 treatment, except for a higher Fe(II) content in the deeper sediment layer. Conversely, we measured higher AVS
710 contents in the upper layer for the acetate treatment, but this is not reflected in higher *drrA* copies numbers. Based on
711 these mixed results, we consider two hypotheses: (i) acetate promoted increased Fe(III) reduction, which is supported
712 by higher gene copies of *Geobacter* spp.. However, this is not clearly reflected in the Fe(II) data. Furthermore, with
713 increased Fe(III) reduction and a constant SO₄²⁻ reduction rate, we would have expected a depletion of S(II)_{tot} in the
714 porewater of the acetate treatment due to iron-sulfur mineral formation; however, this was not observed. Thus, we
715 consider a second hypothesis that (ii) acetate promoted SO₄²⁻ reduction, supported by increased AVS content in the
716 acetate treatment in the upper sediment layer. In contrast, the number of *drrA* gene copies was not higher in the acetate
717 treatment. Although a small increase (RNA-based) in the gene copies of *drrA* was observed in the upper layer, this
718 was not statistically significant. Additionally, no differences were observed in the S(II)_{tot} concentrations, which were
719 generally low and should therefore be interpreted with caution. Based on our data, we cannot clearly reject either
720 hypothesis. We therefore suggest Fe(III) and SO₄²⁻ reduction both lead to higher CO₂ release, stimulated by higher
721 supply of labile OC in the intertidal flat.

722 **5 Conclusion and Implications**

723 Our study demonstrated that the composition in combination with the concentration of OC determines the
724 CO₂ release from minerogenic salt marshes typical of the Wadden Sea. Initial porewater and sediment geochemical
725 characterization indicated that microbially mediated CO₂ release is likely not limited by the availability of electron
726 acceptors in both the pioneer marsh and intertidal flat, contrary to what is generally observed in terrestrial wetlands.
727 We caution here that we did not directly measure TEA reduction rates. Future studies should investigate turnover rates,
728 potentially utilizing isotopes to confirm this finding. Overall, our results indicate that the OC composition, rather than
729 the concentration alone, controlled CO₂ release in both succession zones. This suggests that OC composition likely
730 plays a limiting role in microbially mediated CO₂ release from minerogenic salt marshes. The higher CO₂ release
731 observed in the acetate treated plots within the pioneer marsh was accompanied by higher levels of reduced iron. This
732 pattern also corresponded with greater activity of Fe(III)-reducing bacteria in these plots, indicating that microbially
733 mediated CO₂ release resulted from Fe(III) reduction driven by increased labile OC input. The addition of the complex
734 OC (humic acid) did not exceed the CO₂ release of the control, showing that complex OC was not decomposed. Overall,
735 our results indicate that the OC composition, rather than the concentration alone, limits the CO₂ release from
736 minerogenic salt marshes. Similar trends in CO₂ release were measured for the intertidal flat, further indicating that
737 OC (both in terms of composition and concentration) is the key driver of microbial decomposition of OC to CO₂ for
738 salt marsh systems. We expect that this is particularly relevant in salt marshes similar to ours with a high proportion
739 of fine particles (muddy marshes) relative to marshes with larger particles (sandy marshes).

740 The results of this in situ study contribute to our understanding of short-term carbon dynamics in minerogenic
741 temperate salt marshes. Labile OC inputs such as root exudates may enhance CO₂ release from minerogenic salt
742 marshes, while complex OC inputs, such as plant fragments, might be sequestered in the sediment rather than degraded
743 and released as CO₂. The controls on OC turnover observed here should be considered when accounting for these
744 ecosystems as carbon sinks and stocks. Also, our results show that the link between OC composition and the release
745 of CO₂, independent of electron acceptor concentrations, is crucial and should be included in process-based modelling
746 of carbon fluxes in these ecosystems (Brown, 2025; Regnier et al., 2013). This will contribute to more accurate
747 predictions of the response of salt marshes to climate change. Further, the in situ experiment simulated a potential
748 increase of short-term OC inputs to the ecosystem, reflecting scenarios associated with climate change such as
749 inundation of previously unflooded areas due to sea level rise and storm surges or eutrophication (van Beusekom,
750 2005; Esselink et al., 2017; Woth et al., 2006). For example, eutrophication may result in an input of organic matter
751 into the Wadden Sea that is eventually washed onto the coastal sediment. Our study thus provides valuable insight into
752 the consequences of such short-term scenarios for GHG release and highlights that the input of labile OC (e.g., primary
753 production during eutrophication, root exudates) into the sediment of a minerogenic salt marsh results in higher CO₂
754 releases.

755 **CRedit authorship contribution statement**

756 **NK:** Investigation, Methodology, Formal Analysis, Visualization, Writing – Original Draft Preparation,
757 Conceptualization. **FR:** Investigation, Writing – Review & Editing. **LJK:** Methodology, Writing – Review & Editing.
758 **RK:** Methodology, Writing – Review & Editing. **AK:** Writing – Review & Editing, Funding Acquisition. **PJ:**
759 Conceptualization, Funding Acquisition, Supervision, Project Administration, Writing – Review & Editing.

760 **Competing interests**

761 The authors declare that they have no conflict of interest.

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776 **Data availability statement**

777 Data are publicly available at Zenodo via doi.org/10.5281/zenodo.17136252 (Kainz et al., 2025)

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