Plants, microbes and soil-redox in salt marshes: Intricate interactions and responses to global warming

Dissertation

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vorgelegt von

Julian Johannes Mittmann-Götsch

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Erstgutachter: Prof. Dr. Kai Jensen

Zweitgutachter: Prof. Dr. Peter Müller

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„Now Suzanne takes your hand and she leads you to the river”

– Leonard Cohen

List of publications and contributions

Chapter 2:

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Authors affiliations: Julian Mittmann-Goetsch[1], Monica Wilson[1], Kai Jensen[1], Peter Mueller[2]

[1] Institute of Plant Science and Microbiology, Universität Hamburg, Hamburg, Germany

[2] Institute of Landscape Ecology, University of Münster, Münster, Germany

Author contributions

Julian Mittmann-Goetsch, Peter Mueller and Kai Jensen designed the field experiment. **Julian Mittmann-Goetsch** and Monica Wilson set up the tidal tank mesocosm. **Julian Mittmann-Goetsch** conducted the IRIS study in both field and mesocosm. **Julian Mittmann-Goetsch** measured all ancillary parameters (below- and aboveground biomass, organic matter content, pH). **Julian Mittmann-Goetsch** analysed the data and created the figures. Monica Wilson conducted the planar optode study. **Julian Mittmann-Goetsch** and Peter Mueller wrote the manuscript with input by all co-authors.

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Prof. Dr. Kai Jensen (first supervisor)

Chapter 3:

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Authors affiliations: Hao Tang[1,2], Stefanie Nolte[3,4], Kai Jensen[2], Roy Rich[5], Julian Mittmann-Goetsch[2] and Peter Mueller[5,6]

[1] Key Laboratory of Land Resources Evaluation and Monitoring in Southwest, Ministry of Education, Sichuan Normal University, Chengdu, 610068, China

[2] Institute of Plant Science and Microbiology, Universität Hamburg, Hamburg, 22609, Germany

[3] School of Environmental Sciences, University of East Anglia, Norwich, NR47TJ, UK

[4] Centre for Environment, Fisheries and Aquaculture Science, Pakefield Rd, Lowestoft, UK

[5] Smithsonian Environmental Research Center, Edgewater, MD 21037, United States

[6] Institute of Landscape Ecology, Münster University, 48149 Münster, Germany

Author contributions

HT, SN, KJ, and PM designed the TBI decomposition study. SN, KJ, and RR designed the field experiment. HT conducted the TBI assays and analyzed the resulting data. **JM** conducted the study on soil reduction. HT and PM wrote the original draft with input from all co-authors.

_____

Prof. Dr. Kai Jensen (first supervisor)

Chapter 4:

Mittmann-Goetsch, J.[1], Mueller, P.[2,3], Jensen, K.[1], Liebner, S.[4,5], Thomsen, S.[1], Rich, R.[6], Bartholomäus, A.[4], Jaitner, J.[1], Unger, V.[1] (in revision). Hydrology Masks Warming Effects on Microbial Communities in Salt Marsh Soils. FEMS Microbiology Ecology

[1] Institute of Plant Science and Microbiology, University of Hamburg, Hamburg, Germany

[2] Institute of Landscape Ecology, Universität Münster, Münster, Germany

[3] Institute for Environmental Sciences, Rheinland-Pfälzische Technische Universität, Kaiserslautern Landau, Germany

[4] GFZ Helmholtz Centre for Geosciences, Geomicrobiology, Potsdam, Germany

[5] Institute for Biochemistry and Biology, Universität Potsdam, Potsdam, Germany

[6] Smithsonian Environmental Research Center, Edgewater, MD, USA,

CRediT authorship contribution statement

Julian Mittmann-Goetsch: Writing – original draft, formal analysis, data curation, investigation, conceptualization, visualization. Peter Mueller: Funding acquisition, supervision, conceptualization, writing – review & editing, project administration. Kai Jensen: Funding acquisition, supervision, conceptualization, writing – review & editing, project administration. Susanne Liebner: Conceptualization, writing – review & editing. Simon Thomsen: Methodology, writing – review & editing, project administration. Roy Rich: Methodology, data curation, writing – review & editing, project administration Alexander Bartholomäus: Formal analysis, writing – review & editing. Johann Jaitner: Formal analysis, investigation, writing – review & editing. Viktoria Unger Writing – review & editing, co-supervision investigation, conceptualization, project administration

Chapter 5:

Goesele, C.[1]* & **Mittmann-Goetsch, J**.[1]*, Unger, V.[1], Jensen, K.[1], Liebner, S.[2,3], Thomsen, S.[1], Rich, R.[4], Kutzbach, L.[5], Cheng, C.[1], Bartholomäus, A.[2], Mueller, P.[6] (in prep) Warming drives soil reduction and methane cycling in salt marshes

[1] Institute of Plant Science and Microbiology, Universität Hamburg, Hamburg, Germany

[2] GFZ Helmholtz Centre for Geosciences, Geomicrobiology, Potsdam, Germany

[3] Institute for Biochemistry and Biology, Universität Potsdam, Potsdam, Germany

[4] Smithsonian Environmental Research Center, Edgewater, MD, USA

[5] Institute of Soil Science, Center for Earth Research and Sustainability (CEN), Universität Hamburg, Hamburg, Germany

[6] Institute for Environmental Sciences, Rheinland-Pfälzische Technische Universität, Kaiserslautern Landau, Germany

* These authors contributed equally

CRediT authorship contribution statement

Clarisse Goesele: Writing – original draft, formal analysis, data curation, investigation, conceptualization, visualization. **Julian Mittmann-Goetsch:** Writing – original draft, formal analysis, data curation, investigation, conceptualization, visualization. Viktoria Unger: Writing – review & editing, co-supervision, investigation, conceptualization, project administration. Kai Jensen: Funding acquisition, supervision, conceptualization, writing – review & editing, project administration. Susanne Liebner: Conceptualization, writing – review & editing. Simon Thomsen: Methodology, writing – review & editing, project administration. Roy Rich: Methodology, writing – review & editing, project administration. Lars Kutzbach: Writing – review & editing, conceptualization. Chen (Caroline) Cheng: Writing – review & editing, investigation. Alexander Bartholomäus: Formal analysis, writing – review & editing. Dirk Granse: project administration. Peter Mueller: Funding acquisition, supervision, conceptualization, writing – review & editing, project administration

Box B:

Goesele, C.[1]* & **Mittmann-Goetsch, J**.[1]*, Hessler, L.[1], Cheng, C.[1], Unger, V.[1], Jensen, K.[1], Liebner, S.[2,3], Mueller, P.[4], Täumer, J.[2] (in prep) Hidden methane oxidation processes within salt marsh plant tissues.

[1] Institute of Plant Science and Microbiology, University of Hamburg, Hamburg, Germany

[2] GFZ Helmholtz Centre for Geosciences, Geomicrobiology, Potsdam, Germany

[3] Institute for Biochemistry and Biology, Universität Potsdam, Potsdam, Germany

[4] Institute for Environmental Sciences, Rheinland-Pfälzische Technische Universität, Kaiserslautern Landau, Germany

* These authors contributed equally

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Mason, V.G., Stoorvogel, M. M., Fivash, G. S., Willemsen, P. W. J. M., van IJzerloo, L., **Mittman-Goetsch, J.**, Borsje, B. W., van de Koppel, J., Bouma, T. J. (in preparation). Contrasting responses of high and low macrotidal salt marsh to sea-level rise: impact on ecosystem services.

Abstract

As part of blue carbon ecosystems, salt marshes exert outsized leverage on global carbon cycling. Their soils act as highly effective carbon sinks, with substantial rates of carbon sequestration and long-term storage capacity. However, the low redox potentials that underpin this sequestration also create favourable conditions for microbial methanogenesis. Bidirectional interactions between both plant-soil and microbe-soil regulate the processes that determine soil redox conditions in salt marshes. However, the understanding of these regulative processes remains limited. Further, we lack fundamental insight into how these plant-soil and microbe-soil redox interactions will respond to global warming and in turn mediate warming effects on carbon cycling. To address these research gaps, I investigated these interactions under both controlled conditions and *in situ* warming, leveraging the MERIT (Marsh Ecosystem Response to Increased Temperatures) whole-ecosystem warming experiment. This thesis is structured into six chapters: an introduction to the study context (**Chapter 1**), four studies that address the research gaps (**Chapters 2-5**), and a unifying synthesis that discusses the results from previous chapters (**Chapter 6**).

The first study (**Chapter 2**), assesses plant-soil redox interactions combining mesocosm and field study with high resolution oxygen profiling using planar optodes. Results highlight that, roots can act both as net reducers and net oxidizers in wetland soils, and that the direction of this plant effect is inversely correlated with background redox conditions. I find that plant effects on soil reduction are net reducing, due to the comparably well aerated soils of the study system, a minerogenic Wadden Sea salt marsh.

The second study (**Chapter 3**), examines early-stage (1-2 years) warming effects on decomposition processes, using the Tea-Bag Index approach. Results show that, increased temperature accelerated decomposition rates. However, warming effects on litter stabilization were restricted to higher elevated zones and soil layers. This suggests that the reducing soil conditions suppress the response of belowground litter stabilization processes to warming.

The third study (**Chapter 4**), shows results from mid-stage (5 years) warming effects on microbial functioning (i.e., exo-enzymatic activities) and putatively active microbial community structure (i.e., 16S sequencing on total RNA). Results indicate that, exo-enzymatic activities tend to decrease with warming. Additionally, microbial community structure remains largely stable under warming, however shifts towards phyla with capacities to degrade complex carbon compounds occur in the higher elevated zones. These findings suggest, that warming can induce drought stress in higher elevated zones, causing subtle shifts with implications for carbon cycling.

The fourth study (**Chapter 5**), addresses warming effects on soil redox conditions and links them to methane fluxes and activity of methanogenic and methanotrophic potential processes. Results reveal that, soils become more reducing with warming. In the pioneer zone, this effect is accompanied by increasing methane fluxes and a higher ratio of methanogenic to methanotrophic potential processes.

Abstract

Findings from this study challenge the common hypothesis that hydrology, especially in the lower elevated marsh zones, outweighs warming effects in salt marshes.

Overall, this work emphasizes that interactions between plants and soil and between microbes and soil influence soil redox conditions, and that soil redox conditions are of central importance for the global carbon cycle. It shows that hydrological constraints frequently outweigh direct warming effects, but that sustained warming ultimately shifts microbial functioning and redox dynamics toward enhanced methanogenesis and methane release. This thesis demonstrates that salt marsh vulnerability to climate change is best understood through the lens of bidirectional plant-soil and microbe-soil redox interactions.

Zusammenfassung

Als Teil der Blue-Carbon-Ökosysteme haben Salzmarschen einen überproportional großen Einfluss auf den globalen Kohlenstoffkreislauf. Ihre Böden wirken als hochwirksame Kohlenstoffsenken mit erheblich hohen Kohlenstoffbindungsraten und langfristiger Speicherkapazität. Die niedrigen Redoxpotenziale, die diesen Prozessen zugrunde liegen, schaffen jedoch auch günstige Bedingungen für die mikrobielle Methanogenese. Wechselwirkungen zwischen Pflanzen und Boden sowie zwischen Mikroorganismen und Boden regulieren Prozesse, die die Redoxbedingungen in Salzmarschböden bestimmen. Das Verständnis dieser regulierenden Prozesse ist jedoch begrenzt. Zudem fehlen grundlegende Erkenntnisse darüber, wie diese Redox-Wechselwirkungen zwischen Pflanzen und Boden sowie zwischen Mikroorganismen und Boden auf die globale Erwärmung reagieren und wiederum die Auswirkungen der Erwärmung auf den Kohlenstoffkreislauf beeinflussen. Um diese Forschungslücken zu schließen, habe ich die genannten Wechselwirkungen sowohl unter kontrollierten Bedingungen als auch unter in situ Erwärmungsbedingungen untersucht und dabei das MERIT-Experiment (Marsh Ecosystem Response to Increased Temperatures) zur Erwärmung des gesamten Ökosystems genutzt. Diese Arbeit gliedert sich in sechs Kapitel: eine Einführung in den Forschungskontext (**Kapitel 1**), vier Studien, die sich mit den Forschungslücken befassen (**Kapitel 2–5**), und eine zusammenfassende Synthese, in der die Ergebnisse der vorangegangenen Kapitel diskutiert werden (**Kapitel 6**).

Die erste Studie (**Kapitel 2**) untersucht die Redox-Wechselwirkungen zwischen Pflanzen und Böden, wobei Mesokosmos- und Feldstudien mit hochauflösenden Sauerstoffprofilen unter Verwendung planarer Optoden kombiniert werden. Die Ergebnisse zeigen, dass Wurzeln in Feuchtgebieten sowohl als Netto-Reduzierer als auch als Netto-Oxidierer wirken können und dass die Richtung dieses Pflanzeneffekts umgekehrt proportional zu den Hintergrund-Redoxbedingungen ist. Ich stelle fest, dass die Auswirkung der Pflanzen auf die Böden des von mir untersuchten Systems, netto reduzierend ist. Dies lässt sich auf die vergleichsweisen gut durchlüfteten Böden der minerogenen Salzmarsch des Wattenmeers zurückführen.

Die zweite Studie (**Kapitel 3**) untersucht die Auswirkungen von kurzzeitiger Erwärmung (1–2 Jahre) auf Zersetzungsprozesse unter Verwendung der Tea-Bag-Index-Methode. Die Ergebnisse zeigen, dass erhöhte Temperaturen die Zersetzungsraten beschleunigten. Die Auswirkungen der Erwärmung auf die Streustabilisierung beschränkten sich jedoch auf höher gelegene Zonen und Bodenschichten. Dies deutet darauf hin, dass die reduzierenden Bodenbedingungen die Reaktion der Stabilisierungsprozesse von organischem Material auf die Erwärmung unterdrücken.

Die dritte Studie (**Kapitel 4**) zeigt Auswirkungen von mittelfristiger Erwärmung (5 Jahre) auf die mikrobielle Funktion (d. h. exo-enzymatische Aktivitäten) und die vermutlich aktive Struktur der mikrobiellen Gemeinschaft (d. h. 16S-Sequenzierung der Gesamt-RNA). Die Ergebnisse zeigen, dass die exo-enzymatischen Aktivitäten mit Erwärmung tendenziell abnehmen. Darüber hinaus bleibt die Struktur der mikrobiellen Gemeinschaft unter Erwärmung weitgehend stabil, jedoch kommt es in den

höher gelegenen Zonen zu einer Verschiebung hin zu Phyla mit der Fähigkeit, komplexe Kohlenstoffverbindungen abzubauen. Diese Ergebnisse deuten darauf hin, dass die Erwärmung in höher gelegenen Zonen zu Trockenstress führen kann, was eine subtile Verschiebung der mikrobiellen Gemeinscahften, mit Auswirkungen auf den Kohlenstoffkreislauf zur Folge hat.

Die vierte Studie (**Kapitel 5**) befasst sich mit den Auswirkungen von Erwärmung auf die Redoxbedingungen im Boden und setzt diese in Zusammenhang mit Methanflüssen und der potenziellen Aktivität methanogener und methanotropher Prozesse. Die Ergebnisse zeigen, dass Böden mit zunehmender Erwärmung reduzierender werden. In der Pionierzone geht dieser Effekt mit steigenden Methanflüssen und einem höheren Verhältnis von potentiellen methanogenen zu methanotrophen Prozessen einher. Die Ergebnisse dieser Studie stellen die gängige Hypothese in Frage, dass die Hydrologie, insbesondere in den tiefer gelegenen Zonen der Marschen, Erwärmungseffekte unterdrückt.

Insgesamt unterstreicht diese Arbeit, dass die Interaktion zwischen Pflanzen und Boden und zwischen Mikroben und Boden Boden-Redoxbedingungen beeinflussen und dass Boden-Redoxbedingungen von zentraler Bedeutung für den globalen Kohlenstoffkreislauf sind. Sie zeigt, dass ein starker hydrologischer Einfluss häufig die direkten Erwärmungseffekte übersteuert, dass aber eine anhaltende Erwärmung letztendlich die mikrobielle Funktion und die Redoxdynamik in Richtung einer verstärkten Methanogenese und Methanfreisetzung verschiebt. Diese Arbeit zeigt, dass die Anfälligkeit von Salzmarschen gegenüber dem Klimawandel am besten durch die Betrachtung der bidirektionalen Wechselwirkungen zwischen Pflanzen und Boden sowie zwischen Mikroben und Boden verstanden werden kann.

Contents

Chapter 1 | General Introduction

Julian Mittmann-Goetsch

„It's just the way it changes, like the shoreline and the sea"

– Leonard Cohen

1.1 | Global relevance and ecosystem services of salt marshes

Wetlands, including coastal blue carbon ecosystems (salt marshes, mangroves, and seagrass beds) and peatlands, are disproportionately efficient carbon sinks, storing approximately 20% of global terrestrial organic carbon despite covering just 1% of the Earth's surface (Temmink et al., 2022). These outsized carbon stocks are driven by the imbalance between high plant primary productivity and suppressed microbial decomposition (Kirwan & Megonigal, 2013; Temmink et al., 2022). In oxygen-depleted wetland soils, microbial decomposition is energetically constrained by the lack of high-yield electron acceptors (e.g. oxygen) and inhibited by phenol oxidase exo-enzymes (Freeman et al., 2001; Keiluweit et al., 2016). Such anaerobic environment, reflected in low soil redox potential, slows organic matter turnover and increases long-term carbon storage (Sutton-Grier et al., 2011; Almahasheer et al., 2017). However, methanogenesis in anoxic zones generates methane (CH_4), a greenhouse gas 45 times higher in global warming potential than CO_2 (Neubauer & Megonigal, 2015), which can offset the climate benefits of carbon sequestration (Rosentreter et al., 2018; Eyre et al., 2023). Thus, understanding the interplay between carbon storage, redox-driven decomposition of organic matter, and methane emissions is critical for predicting the stability of wetland carbon cycling and greenhouse gas emission under future climate scenarios (Zhu et al., 2025).

Among different wetland ecosystems, vegetated coastal ecosystems like salt marshes have received increasing attention in the past decades for their various ecosystem services. They provide critical nurseries for multiple fish species (MacKenzie & Dionne, 2008), breeding grounds for various bird species (Zedler & Kercher, 2005), and habitats for rare plant species (Wanner et al., 2014). Because of their wave attenuation abilities, they are effective natural measures for coastal protection (Möller et al., 2014). In the aftermath of the Hurricane Sandy which hit the east coast of the US in October 2012, it was estimated that coastal wetlands prevented damages as high as 625 million USD (Narayan et al., 2017). According to Narayan et al. (2017), salt marshes can reduce annual flood losses by 16 %. This adds to a growing body of research that assesses salt marsh ecosystem services directly linked to global change factors like sea level rise and potential for global change mitigation by these ecosystems (Kirwan et al., 2010; IPCC, 2023).

Like other wetlands, salt marshes are well-known for their outsized capacity to sequester carbon. In salt marshes and other coastal ecosystems, the carbon sequestration rate is further accelerated by the input of allochthonous carbon rich sediments through flooding with seawater (Mueller et al., 2019). Salt marshes account for nearly 50 % of marine sediment organic carbon burial (Duarte et al., 2013; Spivak et al., 2019). A recent study on soil organic carbon estimated that 1.22 ± 0.20 Pg carbon is buried in the top meter of tidal marsh soils (Maxwell et al., 2023). This strong leverage over the global carbon cycle gives salt marsh ecosystems an important role in nature-based climate change mitigation (Fink & Ratter, 2025).

Inland wetlands are major contributors to global methane emissions, with natural wetlands accounting for approximately 20-39% of the total methane flux to the atmosphere (Laanbroek, 2010). Atmospheric methane is responsible for approximately 16-25% of observed global warming (Etminan et al., 2016; IPCC, 2021). In contrast, coastal wetlands typically exhibit comparatively low methane emissions. This is largely due to the continuous input of sulfate from seawater inflow (Huertas et al., 2019), which stimulates sulfate-reducing bacteria that outcompete methanogenic microorganisms (Schorn et al., 2022). Nevertheless, methane fluxes can still occur under high salinity, such as when sulfate is locally depleted, or when plants supply non-competitive substrates that favour methylotrophic methanogens (Yuan et al., 2019). This balance between carbon storage and methane release arises from waterlogged conditions, which create low-oxygen (i.e. low redox potential) environments: while oxygen limitation slows decomposition and enhances carbon burial, low oxygen environment also support microbial pathways that generate methane (Rosentreter et al., 2018; Temmink et al., 2022, Eyre et al., 2023).

1.2 | Soil redox potential: The biogeochemical central variable for carbon cycling in salt marshes

Soil redox potentials can be seen as the central variable in wetland soils, which explains much of the variation observed in both carbon sequestration and methane cycling (Zhang & Furman, 2021). Redox potentials have long emerged as a reliable measurement of reduction-oxidation states of soils. Oxygen diffusion through water is about 8400 times slower (at 25°C) than through air, making frequently waterlogged wetlands fundamentally different from upland environments in terms of soil chemistry and biology (Chapman et al., 2019). This slow diffusion results in rapid oxygen depletion in the soils through the metabolism of plant roots and microorganisms, and through chemical reactions, leading to a sharp drop in soil redox potential (Pezeshki & Delaune, 2012). In aerobic soils (Eh > 300 mV), oxygen is readily available to support rapid organic matter decomposition and aerobic respiration. In contrast, the low redox conditions typical of saturated wetland soils (Eh often < 100 mV) limit oxygen-dependent processes and favour anaerobic pathways using alternative electron acceptors (aTEAs) like NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-} and CO_2 (Fig. 1.1). Soil redox potentials are influenced by the abundance of both electron acceptors and electron donors, soil pH and soil temperature. The quantitative relationship can be calculated based on theoretical redox half-reactions (Reddy & DeLaune, 2008; Zhang & Furman, 2021):

$$E_h = E_h^0 + 2.3\frac{RT}{nF}log\frac{\{Ox\}}{\{Red\}} + 2.3\frac{mRT}{nF}pH$$

Where E_h is the redox potential (V) measured against a normal hydrogen electrode, E_h^0 (V) is the redox potential under standard conditions, R is the gas constant (8.314 J * mol^{-1} * K^{-1}), T is the temperature (K), m is the number of protons exchanged, n is the number of electron exchanged, F is the Faraday constant (96,490C * mol^{-1}), Ox / Red is the ratio of oxidized to reduced redox species (Zhang & Furman, 2021).

Soil redox processes have a strong leverage over the distribution and adaptation of wetland plants (Davy et al., 2011), nutrient cycling (Crowley & Bedford, 2011), greenhouse gas emissions (Lee et al., 2025). They are also predictors of the carbon storage potential of soils (Keiluweit et al., 2017). Most of the redox processes are driven by microbial metabolisms (Candry et al., 2023).

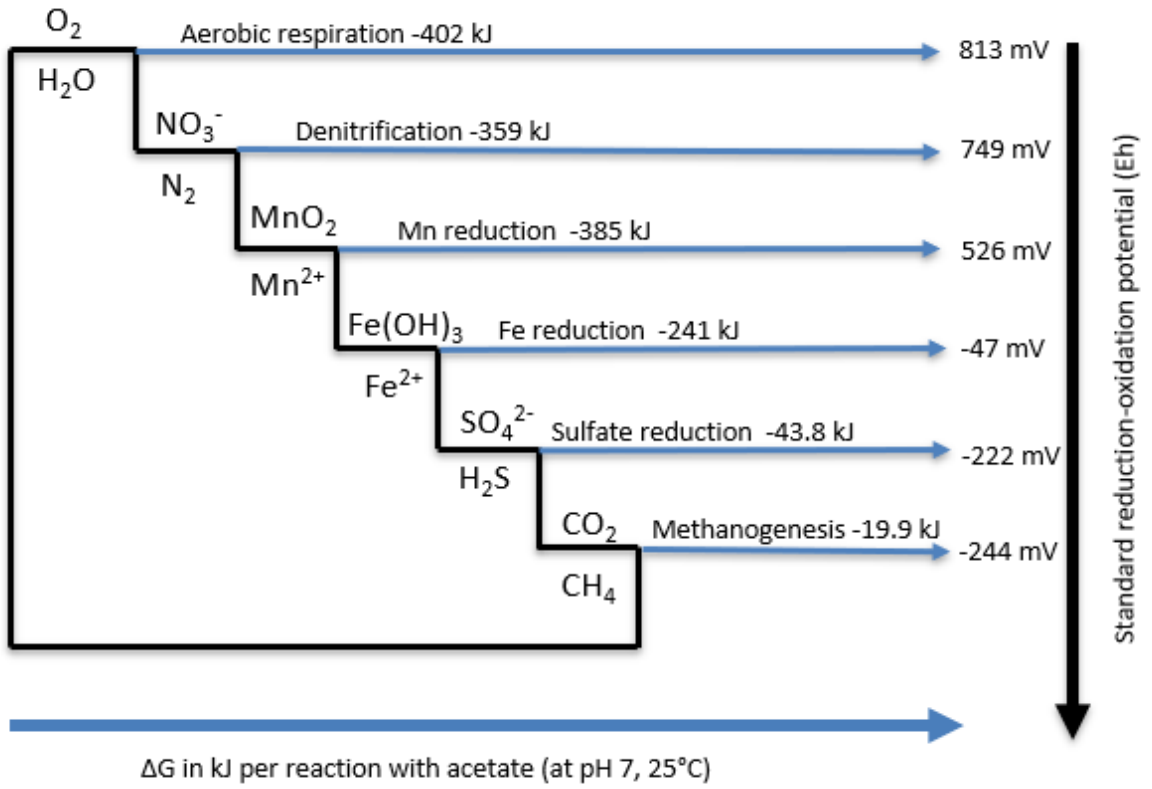

Figure 1.1: Schematic overview of the redox ladder, showing all relevant redox reactions occurring in wetland soils. Shown are the redox couples with the respective free energy yield ΔG in kJ per reduction reaction with acetate at pH 7 at 25°C. Sources: Redox ladder (Sapkota et al., 2022), free energy yield (Canfield & Thamdrup, 2009), standard reduction-oxidation potentials (Schlesinger & Bernhardt, 2020).

1.3 | Exo-enzymatic activities: The rate limiting step in microbial-driven decomposition of soil organic matter

Exo-enzymatic hydrolysis is an essential step in the degradation of soil organic matter and a predecessor of both aerobic and anaerobic microbial respirational processes, linked to various redox reactions (Fig. 1) (Candry et al., 2023). Exo-enzymes therefore play a pivotal role in organic matter decomposition processes (Skujins, 1978), and are often described as the rate-limiting step in the decomposition of soil organic matter (Sinsabaugh & Shah, 2011). Hydrolysis involves the breakdown of organic polymers into monomers, which can then be taken up by microbial cells (Bacteria, Archaea, Fungi) for their respirational processes (Nikaido & Vaara, 1985; Schimel & Schaeffer, 2012; Abs et al., 2020; Conrad, 2023). Hydrolysis is only performed by some members of soil microbial community, but it is for the benefit of all members and the general process of soil organic matter decomposition (Folse & Allison, 2012; Abs et al., 2020). Due to the mixed composition of soil organic matter from carbon, nitrogen and phosphorus sources, the breakdown of organic matter polymers requires a synergistic combination of

enzymes (Sinsabaugh et al., 2009). Among the hydrolases found in soils, ß-Glucosidase and Cellobiosidase have been widely studied as the main carbon acquiring enzymes, involved in the breakdown of cellulose and further ß-1,4 glucans (Marx et al., 2005; Sinsabaugh et al., 2008, 2009; Rietl et al., 2016). The most important nitrogen acquiring enzymes are Leucine-Aminopeptidase and Chitinase (ß-*N*-acetyl-glucosaminidase), which breakdown leucine, as well as other hydrophobic amino acids and chitin (Sinsabaugh et al., 2008; German et al., 2011; Sinsabaugh & Shah, 2011). Phosphatases are important for the estimation of microbial-driven soil phosphorus acquisition, as they are involved in the hydrolyzation of phosphomonoesters (Sinsabaugh et al., 2008). Taken together, the carbon, nitrogen and phosphorus hydrolases activities link soil organic matter decomposition with ecosystem nutrient availability and microbial community composition (Sinsabaugh et al., 2008).

Oxidases, including phenol oxidase and peroxidase, are key regulators of carbon cycling in upland soils, because of their ability to break down refractory organic compounds such as lignin and polyphenols (Toberman et al., 2008; Duan et al., 2021). They are equally important for decomposition processes in wetland soils. However, compared to in well aerated upland soils (e.g., heathlands, croplands), the activities of oxidases are suppressed in wetland soils. The enzymatic latch hypothesis, first proposed by Freeman et al. (2001), states that oxidase activity is supressed under persistent waterlogged and anoxic conditions, leading to an accumulation of phenolic compounds that inhibits hydrolases and thereby decelerates organic matter decomposition. Thus, while oxidases act as major regulators of decomposition in upland soils, their suppression in wetlands is indirectly (enzymatic latch hypothesis) controlling carbon preservation under anoxic conditions.

1.4 | Fermentation processes: A key intermediate process for downstream decomposition pathways

Fermentation is a crucial metabolic process in the anaerobic decomposition of organic matter in wetland soils, including salt marshes. In these environments, oxygen is rapidly depleted due to water saturation, restricting aerobic respiration and making anaerobic pathways predominant (Reddy & DeLaune, 2008). While aerobic respirational pathways rely on the hydrolysed monomers, anaerobic respirational pathways are dependent on fermentation as an essential intermediary step in the decomposition of soil organic matter (Candry et al., 2023). During fermentation, microbial fermenters convert hydrolysed monomers, such as sugars and amino acids, into smaller molecules like organic acids, alcohols, hydrogen, and carbon dioxide (Reddy & DeLaune, 2008). These fermentation products provide substrates for terminal anaerobic processes, with sulfate reduction being particularly dominant in salt marshes because seawater intrusion leads to high sulfate concentrations, while methanogenesis plays a comparatively minor role (Wang et al., 2019; Frates et al., 2023).

Fermentation and these downstream pathways (i.e. sulfate reduction, methanogenesis) shape carbon cycling and greenhouse gas emissions in salt marsh ecosystems. Microbial community composition and environmental factors such as salinity and inundation strongly influence the rates and efficiency of

fermentation and subsequent anaerobic respiration (Zhang et al., 2023). Thus, fermentation is not only of importance for the anaerobic microbial food web, but also drives key biogeochemical transformations under the anoxic conditions of salt marsh soils.

1.5 | Microbial respiration processes: Bidirectional feedbacks with soil redox conditions

By transferring electrons from electron donors to electron acceptors, microbes are the principal agents controlling soil redox potentials. In wetland soils, it is generally assumed that microbial communities are capable of utilizing all of the electron acceptors (O_2, NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-} and CO_2) (He et al., 2015). While aerobic respiration and heterotrophic denitrification are widespread processes performed by a diverse array of microbial taxa (Sanford et al., 2012; Candry et al., 2023), the use of other respiratory pathways are restricted to specialised microorganisms. For example, dissimilatory manganese and iron reduction can be carried out by bacteria like *Shewanella putrefaciens* and *Geobacter metallireducens* (Lovley et al., 1993; Nealson & Saffarini, 1994; Hernandez & Newman, 2001), while members of the genus *Desulfuromonas* are specialised for manganese reduction (Wunder et al., 2024). Sulfate reduction is primarily mediated by sulfate-reducing bacteria, such as *Desulfovibrio* and *Desulfobacter*, which possess the dsrAB genes - key functional markers that are widely used as phylogenetic indicators of sulfate-reducing microorganisms (Rosenberg et al., 2013). Methanogenesis, the terminal step in anaerobic carbon mineralization, is performed by methanogenic archaea, which harbor the mcrA gene (Liu & Whitman, 2008; Vaksmaa et al., 2017). There are three known methanogenesis pathways, which all use different substrates as electron donors (Capooci et al., 2024). Acetoclastic and hydrogenotrophic methanogens use the same competitive substrates as sulfate reducers, which is acetate and H_2 + CO_2 (Le Mer & Roger, 2001; Yuan et al., 2019). Methylotrophic methanogens use non-competitive substrates, like trimethylamine and methionine and can co-occur with sulafe reducers in soils (Oremland et al., 1982; Oremland & Polcin, 1982; Yuan et al., 2019). Methanotrophs, capable of oxidizing methane, are also present in wetland soils and play a crucial role in mitigating methane emissions (Knief, 2015). Assessing methanotrophic bacteria is possible by the pmoA gene, which encodes the particulate methane monooxygenase (Bourne et al., 2001). While metal reduction (of both manganese and iron) cannot be attributed to a single gene and is distributed across various taxa (Rosenberg et al., 2013), the existence of function-specific genes in sulfate reducers, methanogens, and methanotrophs suggests evolutionary specialization within these pathways.

Most of these respiratory processes are microbially mediated (Candry et al., 2023). However, abiotic reactions also play a role, particularly in the regeneration (oxidation) of alternative electron acceptors such as Mn^{2+} (Yu & Leadbetter, 2020), Fe^{2+} (Hedrich et al., 2011) and H_2S (Trojan et al., 2016). The regeneration of electron acceptors can also be a part of biotic processes and is sometimes performed by microorganisms that are also involved in the reduction pathways. For example a strain (MIZ03) of the *Rhodoferax* bacterium can both oxidize and reduce iron (Kato & Ohkuma, 2021). For the reduction of both Fe^{3+} and Mn^{4+} some abiotic pathways exist alongside the biological, microbial mediated pathways (Luther et al., 1997, 2011).

Collectively, these diverse microbial and abiotic mechanisms build the complex redox dynamics observed in wetland soils. The relationship between soil microbes and redox potential in salt marshes is governed by a dynamic feedback system in which both microbes and chemical conditions continuously co-regulate each other. Microbial communities set soil redox potentials through their metabolic electron transfer activities, determining which electron acceptors are consumed within different soil zones (Candry et al., 2023). At the same time, the prevailing redox conditions and the availability of electron acceptors shape the composition and activity of microbial communities (Pett-Ridge & Firestone, 2005). Changes in the redox conditions thus indirectly regulate plant functioning as well (Pezeshki & Delaune, 2012).

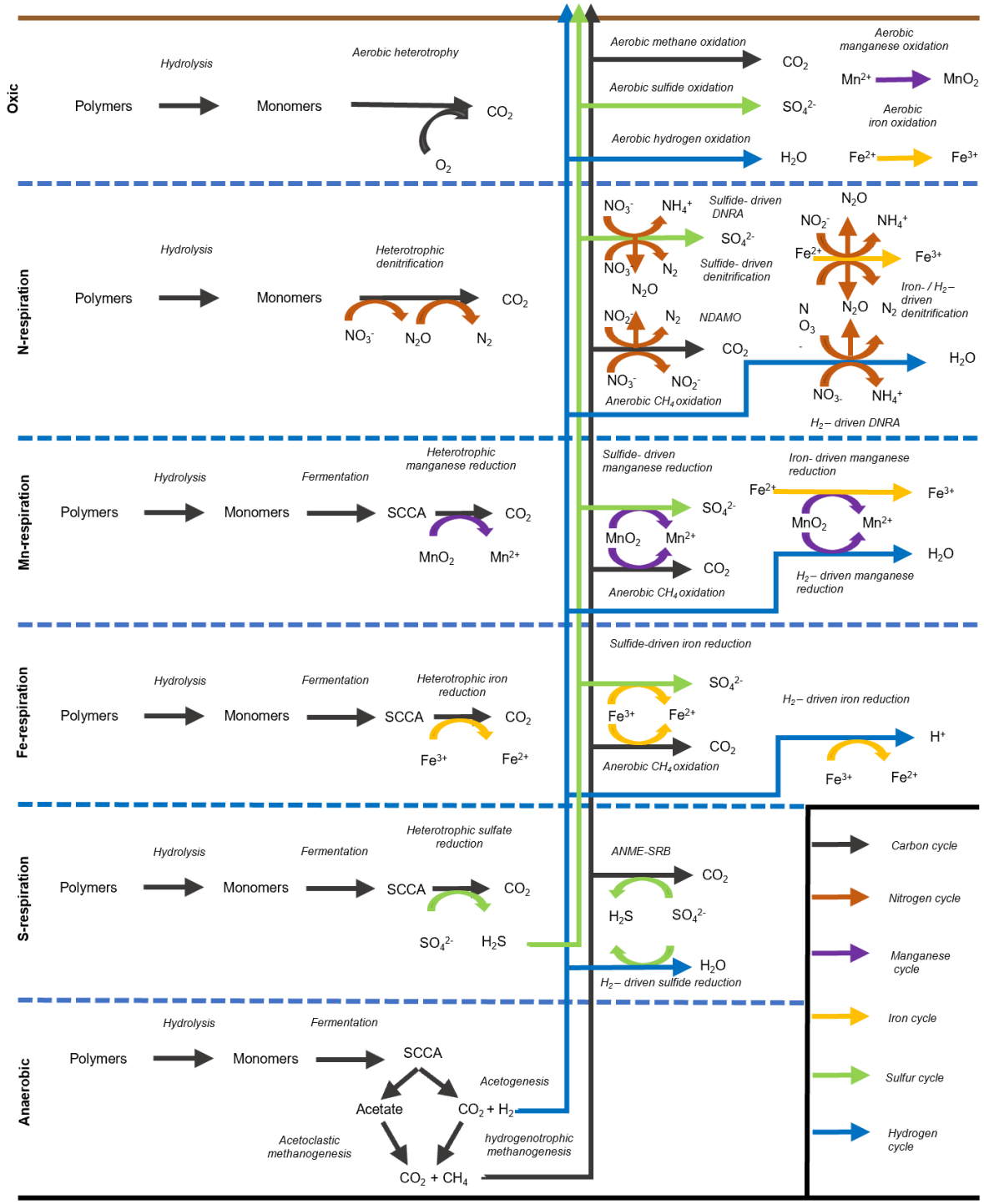

Figure 1.2: Simplified schematic of redox relevant processes (catabolic, abiotic, biotic) in wetland soils related to greenhouse gas fluxes. Shown are processes involved in the carbon cycle (black), nitrogen cycle (red), manganese cycle (violet), iron cycle (orange), sulfur cycle (green) and hydrogen cycle (blue). Reactions are written in italics. Adapted from Candry et al., (2023).

1.6 | Microbe-soil redox and plant-soil redox interactions: Key drivers in salt marsh carbon cycling

Soil microbes act as “double-agents”, participating in the sequestration and long-term storage of carbon, while simultaneously driving the ecosystem carbon efflux through their respiration activities (Rui et al., 2016). The microbial carbon pump involves anabolic processes that convert plant-derived carbon into new organic compounds, which are stabilized in soils through the "entombing effect" (Liang, 2020). Additionally, microbes can leverage the carbon cycling in wetland soils, by producing methane during the reductive process of methanogenesis (Rosentreter et al., 2018). The balance between carbon storage and release is regulated by microbe-soil redox interactions under waterlogged conditions. Low oxygen availability lowers redox potential, which suppresses aerobic decomposition and promotes the accumulation and burial of organic carbon. At the same time, these reducing conditions enable anaerobic microbial pathways, such as methanogenesis, which convert part of the stored carbon into methane (Rosentreter et al., 2018; Temmink et al., 2022; Eyre et al., 2023).

Plant-soil interactions are fundamental to the functioning of wetland ecosystems, particularly through their influence on soil redox processes (plant-soil redox interactions). Wetland plants function as key drivers of soil biogeochemistry by simultaneously providing electron acceptors and donors to the rhizosphere. Through radial oxygen loss, plant roots supply oxygen as an energetically favorable electron acceptor, while root exudates and litter contribute organic matter that serves as electron donors (Megonigal et al., 2004; Sutton-Grier et al., 2011; Gardiner & James, 2012). The magnitude and spatial pattern of radial oxygen loss can vary substantially between plant species and environmental conditions, with some species releasing oxygen primarily at root tips and others along the entire root surface (Koop-Jakobsen & Wenzhöfer, 2015; Koop-Jakobsen et al., 2021). Conversely, the addition of organic matter through plant roots increases electron donor availability, promoting microbial respiration and soil reduction (Blagodatskaya & Kuzyakov, 2008; Gardiner & James, 2012; Keiluweit et al., 2017). The net effect of plants on soil redox potential is determined by the balance between their oxidative and reductive influences, which are themselves shaped by plant traits, species composition, and hydrological context (Mueller et al., 2020a).

These plant-mediated rhizosphere dynamics directly influence soil microbial communities by modifying their growth (Haney et al., 2015) and metabolic activities (Hinsinger et al., 2009), thereby controlling biogeochemical cycling throughout wetland soils (Haviland & Noyce, 2024). The oxygen released into the rhizosphere by plant roots supports aerobic microbial respiration in otherwise anoxic soils, thereby enabling nutrient uptake (Bradley & Morris, 1990) and protecting roots from toxic reduced compounds (Pezeshki, 2001). Plant-mediated gas transport of oxygen into the soil can have a positive priming effect, by increasing rates of microbial-driven organic matter decomposition (Wolf et al., 2007). Moreover, recent studies have shown that the oxygen priming effects can also lead to decreased methane emissions (Noyce et al., 2023). This highlights the importance of soil microbes for C-cycling in wetlands, as well as their dependence on redox conditions, determined by plant-driven processes. Together, plant-soil and

microbe-soil interactions are the key drivers of the balance between oxidative and reductive products, which ultimately determine the fate of carbon in salt marshes.

1.7 | Global warming and hydrological controls on plant-soil-microbe interactions

Human-induced global warming (Forster et al., 2024) is expected to increase soil microbial respiration rates across terrestrial ecosystems (Kirschbaum, 2006; Bradford et al., 2008; Bond-Lamberty & Thomson, 2010). As salt marshes store substantial amounts of carbon in their soils, warming induced increases in microbial activity raise concerns about the potential for positive ecosystem-climate feedbacks if warming accelerates soil organic matter decomposition and carbon loss (Kirwan & Blum, 2011). However, the response of salt marsh ecosystem functioning to warming is complex and influenced by multiple interacting factors (Buschbaum et al., 2024).

A growing body of research suggests that both above- and belowground biomass is stimulated by moderate warming in terrestrial ecosystems (Wan et al., 2023). Similar results are found for salt marsh plants where both aboveground (Noyce et al., 2019) and belowground net primary production (Charles & Dukes, 2009; Smith et al., 2022) persist or even increase under moderate warming. These positive feedbacks could offset potential losses of carbon from salt marsh soils. Yet, our understanding of how warming affects soil organic matter decomposition processes in salt marshes is still limited, primarily due to a lack of well-controlled field experiments that simulate realistic warming across entire soil profiles (Rich et al., 2023). The few whole-soil warming experiments conducted in wetland ecosystems to date indicate that warming can indeed enhance carbon loss, but these effects are strongly mediated by hydrological conditions and substrate composition (Smith et al., 2022). For instance, in a micro-tidal, organic-rich coastal marsh, moderate warming actually stimulated belowground carbon accumulation, with declines only occurring at higher temperatures (Smith et al., 2022). Moreover, warming effects are mediated by plant traits, which alter redox conditions in soils (Noyce et al., 2023).

Hydrology and redox conditions exert a strong influence on these warming effects. Anoxic soil environments may effectively “lock away” carbon, as the accumulation of enzyme-inhibiting phenolic compounds can suppress organic matter decomposition even under elevated temperatures (Freeman et al., 2001). A recent study has underscored the strong effects of hydrology in salt marshes, where both soil elevation and depth acted as the strongest predictors for soil organic carbon stocks (Maxwell et al., 2024). These site-specific factors can outweigh the impact of temperature, with studies showing that spatial heterogeneity in hydrology often has a greater effect on soil organic matter decomposition than seasonal warming (Rinke et al., 2022; Tebbe et al., 2022). Evidence from peatland warming experiments reinforces this view, revealing that subsoil decomposition is less responsive to warming compared to topsoil layers (Wilson et al., 2016; Hopple et al., 2020). There is strong evidence that hydrological factors are the dominant drivers of salt marsh ecosystem functioning (Tebbe et al., 2022; Maxwell et al., 2024) . There is also a growing body of studies that indicate stimulating effects of warming on plant biomass (Noyce et al., 2023; Wan et al., 2023). Yet, we currently lack the understanding of how these

plant responses to global warming affect soil-borne processes like carbon sequestration or methane emissions. Additionally, current findings rely on data from organic rich systems (i.e., peatland, organic-rich coastal marsh), we cannot assume that minerogenic salt marshes, with a larger body of soil inorganic carbon, will respond the same to global change factors (Mueller et al., 2023; Logemann et al., 2025). Here, carbon sources are fundamentally different than in organic rich systems, and rely to a large fraction on inorganic carbons (Mueller et al., 2023). Furthermore, mineral sediments can lead to a protection of carbon from microbial decomposition processes (Unger et al., 2016).

1.8 | Study context: Wadden Sea salt marshes

The entirety of studies carried out for this thesis was situated within minerogenic salt marshes of the World Heritage Wadden Sea area. The Wadden Sea area hosts over 42,000 hectares of salt marshes, accounting for approximately 20% of all European salt marshes and representing one of the largest contiguous salt marsh systems worldwide (Elschot et al., 2024). Research in this region has provided detailed insights into vegetation zonation and management impacts (Suchrow & Jensen, 2010; Wanner et al., 2014), as well as the biophysical properties of salt marshes in relevance to their role in coastal protection (Schulze et al., 2019).

In terms of carbon cycling, studies have quantified both the long-term carbon sequestration potential and the origins of organic carbon in these marshes, highlighting the significant storage capacity of semi-natural salt marshes and the complex interplay between autochthonous and allochthonous carbon sources (Mueller et al., 2019). Research on microbial communities has revealed pronounced spatial and seasonal patterns, with strong zonation and soil depth effects shaping bacterial and archaeal community compositions (Rinke et al., 2022; Tebbe et al., 2022). Despite these advances, uncertainties remain regarding the response of carbon turnover and storage to global change, particularly warming. While the fundamental role of Wadden Sea salt marshes in blue carbon storage and ecosystem functioning is well established, there is still limited understanding of how rising temperatures and associated shifts in microbial communities will affect long-term carbon dynamics in these critical coastal systems (Fink & Ratter, 2025).

1.9 | Objectives and Hypotheses

Soil redox conditions represent a fundamental baseline for assessing soil biogeochemical cycles (Zhang & Furman, 2021; Burgin & Loecke, 2023). In coastal wetlands such as salt marshes, soil redox conditions regulate the balance between carbon storage and release and exhibit strong spatial and temporal variability (Freeman et al., 2001; Mansfeldt, 2003a; Reddy & DeLaune, 2008). Given the importance of redox conditions in regulating soil carbon storage, understanding the processes that alter redox conditions in salt marsh soils is critical, especially in the context of climate warming. The overarching aim of this thesis is to uncover how plant-soil and microbe-soil interactions regulate redox conditions (hereafter plant-soil redox and microbe-soil redox interactions) and carbon cycling in the minerogenic soils of Wadden Sea salt marshes in times of global warming.

I hypothesize that both plant-soil and microbe-soil interactions modulate the effects of global warming on soil carbon cycling in salt marshes, primarily by influencing the soil redox conditions, and that the magnitude and direction of warming effects on organic matter decomposition and carbon stabilization depend on the dynamic balance between oxidative and reductive processes. I therefore want to test the hypothesis that plant-soil redox and microbe-soil redox interactions mediate warming effects on carbon cycling in salt marshes of the Wadden Sea area.

In **Box A** I present a novel approach for the analysis of Indicator of Reduction in Soils (IRIS) sticks, using a supervised classification tool. This method is used throughout **chapter 2-5** to assess soil reduction as the central variable for salt marsh soil carbon cycling. In **chapter 2** I present a study in which the effects of plants and individual plant-roots on soil redox conditions (Plant-soil redox interactions) were assessed. In **chapter 3** I assess early-stage warming effects on organic matter decomposition parameters and relate them to soil reduction (Microbe-soil redox interactions). In **chapter 4** I study mid-term warming effects on soil microbial communities and functioning related to carbon cycling (decomposition of soil organic matter). In **chapter 5** I address the effects of warming on soil redox processes and the implications for methanogenesis and methanotrophy. In **Box B** I present novel findings of hidden methane oxidation locations within salt marsh plant tissues, which could play a pivotal role in understanding methane fluxes in salt marsh ecosystems. In **chapter 6** I summarise all findings and discuss their implications for carbon cycling in salt marsh ecosystem in times of global warming.

Box A | Novel Analysis of Indicator of Reduction in Soils Sticks

Julian Mittmann-Goetsch

„Then at home on a branch

In the highest tree

A songbird sings out

So suddenly

Ah the sun is warm

And the soft winds ride

On the willow trees

By the river side "

- Leonard Cohen

BA.1 | Introduction

Indicator of reduction in soils (IRIS) has emerged as an effective measurement technique to assess soil reduction (Jenkinson, 2002; Castenson & Rabenhorst, 2006; Rabenhorst, 2013). The cost-effective alternative to common redox potential measurements using pt-tipped electrodes has been advanced in the past years (Sapkota et al., 2022). Next to Fe(III) coatings, recent advances in the field introduced Mn(IV) coatings (Dorau et al., 2016) and analysis of FeS precipitations on sticks (Duball et al., 2023). The use of flat PVC carrier sticks has made the scanning process substantially more effective (Mueller, et al., 2020b). The analysis however remains a crucial step which possesses risks for biases introduced by manually set thresholds (Rabenhorst et al., 2010; Mueller et al., 2020b). Here I want to introduce and evaluate a novel random forest driven analyse method.

BA.2 | Material & Methods

Image analysis of IRIS sticks was performed using a custom-developed automated processing pipeline implemented in R Studio version 4.5.0 (R Core Team, 2024). The tool employs supervised machine learning through Random Forest classification to differentiate between reduced and non-reduced areas based on RGB-color characteristics. Raw scanned images undergo standardized preprocessing including rotation correction and geometric standardization. The analysis tool allows for flexible depth segmentation, allowing for custom depth increments for systematic evaluation of reduction patterns along the vertical soil-profile.

Classification is based on a training dataset of manually annotated pixels extracted from representative IRIS stick images, resulting in four distinct classes: not reduced pixels, reduced pixels, as well as scanning artifacts (green and black pixels). The trained Random Forest model classifies all image pixels and computed reduction indices as the proportion of reduced pixels among valid pixels, explicitly excluding artifact classes.

$$Reduction\ index = \frac{P_r}{(P_t - P_g - P_b)}$$

Where P_r are the reduced pixels, P_t are the total pixels, P_g and P_b are green and black pixels respectively.

The analytical pipeline generates both quantitative reduction metrics and visual prediction maps with customizable depth boundaries, providing a comprehensive assessment tool for soil redox condition analysis that can be adapted to various study requirements and sampling depths.

BA.3 | Results

The Random Forest classifier achieved 95.45 % overall accuracy (95% CI: 94.76-96.07 %) when classifying IRIS stick segments into four classes: non-reduced sediment (Class 0), reduced sediment (Class 1), scanning artifacts from green background (Class 2), and black background (Class 3). Predicted maps show coherent spatial patterns of paint loss (Fig. B.1), and the computed RI increases where visually apparent reduction dominates. Segments heavily affected by artifacts are automatically flagged and excluded from RI summaries, improving robustness.

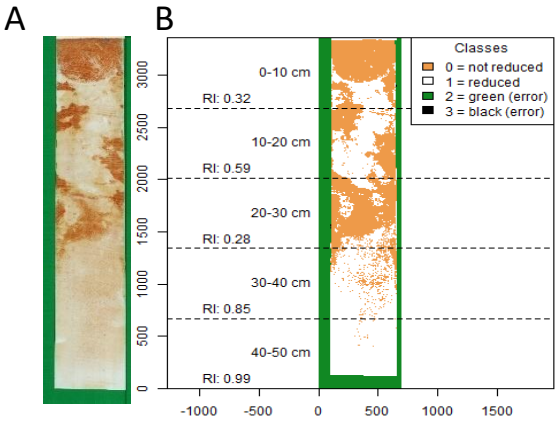

Figure BA.1: IRIS image analysis [A] scanned image of the stick [B] predicted image output, based on supervised classification model calculations. Shown are calculated Reduction indices for the assessed depth segments (0-50 cm in 10 cm increments).

BA.4 | Discussion

Replacing manual thresholding with a trained classifier improves reproducibility, reduces operator bias, and enables scalable batch processing of IRIS images. Currently many labs are still using visual estimation approaches

(Sapkota et al., 2022). Using the random-forest based approach allows for unbiased analysis of IRIS sticks and yield predicted images to the operator which allow for a visual control of the conducted analysis (Fig. BA.1).

The demonstrates a very strong performance, yet it also underscores important methodological considerations. Much of the remaining error stems from confusion between Classes 0 and 1, reflecting the limits of RGB color space in distinguishing subtle spectral differences between reduced and non-reduced iron states. This is a challenge not only for automated approaches but also for manual assessments, since the Fe(III)/Fe(II) color transitions—especially in partially reduced zones are inherently gradual. Such boundaries make strict binary classification problematic. However, the Random Forest model probabilistic output can help identify these uncertain areas, offering a more robust interpretation than simple thresholding. Adopting automated, operator-independent image analysis is in line with broader developments in the field, where advanced machine learning models are increasingly recognized for their ability to handle complex and heterogeneous field datasets (Kaplan et al., 2024).

Overall, the tool advances IRIS analysis by providing a transparent, scriptable workflow that delivers consistent classification maps and standardized RI metrics suitable for monitoring and comparative studies. The tool can be accessed through the open access software R Studio (R Core Team, 2024).

BA.5 | Acknowledgments

I want to acknowledge Andreas Dahlkamp for his support during the development of the analysis script.

Chapter 2 | Root-Driven Soil Reduction in Wadden Sea Salt Marshes

Julian Mittmann-Goetsch, Monica Wilson, Kai Jensen, Peter Mueller

Published in Wetlands (2024)

„Well, you asked how much I love you

Why do the ships with sails love the wind?"

- The Doors

2.1 | Abstract

The soil redox potential in wetlands such as peatlands or salt marshes exerts a strong control over microbial decomposition processes and consequently soil carbon cycling. Wetland plants can influence redox by supplying both terminal electron acceptors (i.e. oxygen) and electron donors (i.e. organic matter) to the soil system. However, quantitative insight into the importance of plant effects on wetland soil redox and associated plant traits are scarce. In a combined mesocosm and field study we investigated the impact of plants on soil reduction using IRIS (Indicator of Reduction in Soils) sticks. Vegetated plots were compared to non-vegetated plots along an elevational gradient in a salt marsh of the Wadden Sea and along an artificially created gradient in a tidal tank mesocosm experiment. Our findings from the mesocosm experiment demonstrated that vegetation both enhanced and suppressed soil reduction relative to non-vegetated control pots. The direction of the plant effect (i.e., net oxidizing or net reducing) was inversely correlated with background redox conditions. Insights from high-resolution oxygen profiling via planar optode imaging corroborated these findings. In the field study, vegetation consistently reduced the comparatively well-aerated Wadden Sea salt marsh soil. Reduction correlated positively with soil organic matter content and belowground biomass, indicating that greater availability of plant-derived electron donors, in the form of organic matter, increased soil reduction. Challenging the dominant paradigm that wetland plants primarily act as soil oxidizers, our study reveals their potential to exert a net reducing effect. The documented impact of these plant-induced changes in soil redox conditions suggests a previously overlooked role in shaping the stability of soil organic carbon stocks in wetland ecosystems with variable water tables.

2.2 | Introduction

Wetland plants act as sources of both electron acceptors (e.g. oxygen) and electron donors (i.e. organic matter, such as root exudates and litter) to the soil, thereby controlling the soil redox potential (Sutton-Grier et al., 2011). Wetland plants increase the availability of electron acceptors via root or radial oxygen loss (ROL), diffusive oxygen release into the rhizosphere. This process supports microbial aerobic respiration of soil organic matter (SOM) in an otherwise anoxic soil environment (Wolf et al., 2007; Mueller et al., 2016). ROL allows plants to maintain nutrient uptake (Bradley & Morris, 1990; Mendelssohn & Morris, 2002; Lai et al., 2012) protects plant roots from reduced phytotoxins often present in wetland soils (Pezeshki, 2001). In several wetland plants, ROL increases at low redox potentials (Kludze & DeLaune, 1994). The amount of oxygen released by wetland plants can also differ strongly between species. For instance, planar optode measurements showed that in the flooding-adapted salt-marsh grass *Spartina anglica*, only a small amount of oxygen is leaking from a restricted area at the root tip into the soil (Koop-Jakobsen & Wenzhöfer, 2015; Koop-Jakobsen et al., 2018), while the less flooding-adapted salt-marsh grass *Elymus athericus* shows ROL along the entire root-surface under anoxic soil conditions (Koop-Jakobsen et al., 2021).

Organic matter input to soils enhances electron donor availability (Gardiner & James, 2012), a prerequisite for soils to turn anoxic (Jenkinson, 2002). Organic matter input by both root exudation and litter input (Megonigal et al., 2004) fuels microbial respiration and therefore increases soil reduction (Gardiner & James, 2012; Keiluweit et al., 2017). On a conceptual level, the net effect of plants on soil redox should depend on the balance between oxidation through ROL and reduction through organic matter input to the soil system (Mueller, et al., 2020a). However, quantitative insight into the importance of plant effects on wetland soil redox and associated plant traits are scarce.

This study aims to develop a deeper quantitative and mechanistic understanding of plant effects on wetland soil redox. Our study system was a salt marsh on the European Wadden Sea coast. In recent years, salt marshes and other coastal blue carbon ecosystems have been studied intensively due to their high carbon sink potential (Chmura et al., 2003; McLeod et al., 2011). In salt marshes, soil redox potentials are predominantly hydrologically driven. Daily inundations lead to periods of water saturation, that are accompanied by a limited oxygen availability, which is reflected in a lower redox potential (Mansfeldt, 2003). These redox dynamics vary along an elevation gradient, representing a flooding-frequency gradient, and in relation to soil depth (Rich et al., 2023; Tang et al., 2023). Wadden Sea salt marshes typically show a distinct vegetation zonation along the elevation gradient. The pioneer zone is flooded twice a day, the low marsh during spring-tides occurring twice per months, and the high marsh only during storm tides, usually less than ten times a year (Butzeck et al., 2015; Jensen et al., 2018). Soil redox can be expected to be lowest either in the pioneer zone, due to frequent flooding, or in the low marsh, due to combined effects of waterlogging and greater organic matter (i.e. electron donor) availability (Mueller, et al., 2020a). To assess the interaction of plant processes and hydrology

on soil redox dynamics, we conducted mesocosm and field experiments including vegetated and non-vegetated treatments along flooding-frequency gradients.

We hypothesized that plant effects on soil redox conditions are controlled by the hydrology-driven background redox conditions (i.e., the redox conditions outside the rhizosphere). With increasing background soil reduction, the net plant effect on the soil redox becomes increasingly positive, i.e., oxidizing. Conversely, with decreasing background reduction, the net plant effect becomes increasingly negative, i.e., reducing. Specifically, we hypothesize that plants act as net reducers in the rarely flooded and well-drained zones and as net oxidizers in frequently flooded and waterlogged zones of the salt marsh.

2.3 | Material and methods

Our study combined a full-factorial mesocosm experiment with a field study conducted in a Wadden Sea salt marsh. We used IRIS (Indicator of Reduction in Soils) sticks to quantify soil reduction in both the mesocosm and the field study. To support findings on differences in soil reduction derived from IRIS sticks, we conducted planar optode measurements on an exemplary set of salt-marsh plants.

2.3.1 | Full-factorial mesocosm experiment

A mesocosm experiment was set up to analyse plant effects on soil redox under controlled hydrological conditions (Fig. 2.1). The mesocosm experiment was conducted using a tidal tank facility at the Institute for Plant Science and Microbiology, Universität Hamburg, Germany. Tidal tanks had a volume of 6750 L (300 cm x 150 cm x 150 cm) and were connected to a storage tank (9000 L). An automatic pump was used to move water between storage and tidal tanks. Different flooding frequencies, representing salt marsh-zone-specific inundation regimes, were realized by placing mesocosms at different elevations of a staircase situated inside the tidal tank (Fig. 2.1). The lowest level, representing the pioneer zone was flooded twice a day for two hours. The second level was flooded once a week, and the highest level was flooded twice a month, simulating low- and high-marsh. Salinity was set and held at 20 psu using synthetic sea salt (Aqua Medic GmbH). To create a full-factorial design, each planting treatment (see below) was realized for each flooding treatment in five replicates. During the experiment, mesocosms were moved randomly within each flooding treatment to exclude position effects.

Plant individuals of dominant species from each zone (*Spartina anglica, Atriplex portulacoides, Elymus athericus*) were collected in June 2021. Plants were thoroughly rinsed to remove soil and weighed. The plants were then potted individually into opaque plastic pots (d = 16 cm, h = 21 cm). Experimental soil was a mix part of salt-marsh soil from the Hamburger Hallig site (20 % of the total soil volume), sand (40 %), and standard potting soil (40 %). Unplanted pots containing only mixed soil were also included as a control planting treatment. Five replicates of each planting treatment were established for each flooding treatment for a total of 60 samples (3 zones x 4 planting treatments x 5 replicates).

2.3.2 | Field experiment

The field experiment was conducted in a salt marsh on the Wadden Sea coast of Germany, at Hamburger Hallig (54°36'06.2"N, 8°49'00.1"E). Three salt-marsh zones (pioneer zone, low marsh, high marsh) were identified based on the dominant vegetation. Three plots were created within each zone, consisting of a non-vegetated and a vegetated subplot (Fig. 2.1). To create non-vegetated subplots, soil was removed down to a depth of 20 cm in a 20 cm x 20 cm area using a shovel, cleared of roots or rhizomes, and placed back. Plastic pots (diameter = 20 cm, height = 20 cm) were inserted into these non-vegetated areas to function as a root-barrier. Each pot had two holes (d = 9.5 cm) in the lower third, which were covered with a fine mesh, to minimize effects on hydrology. Three tidal flat positions were included as references in the experimental design. Due to the lack of vegetation in tidal flats, these plots were only included for some analysis (i.e., OM and pH).

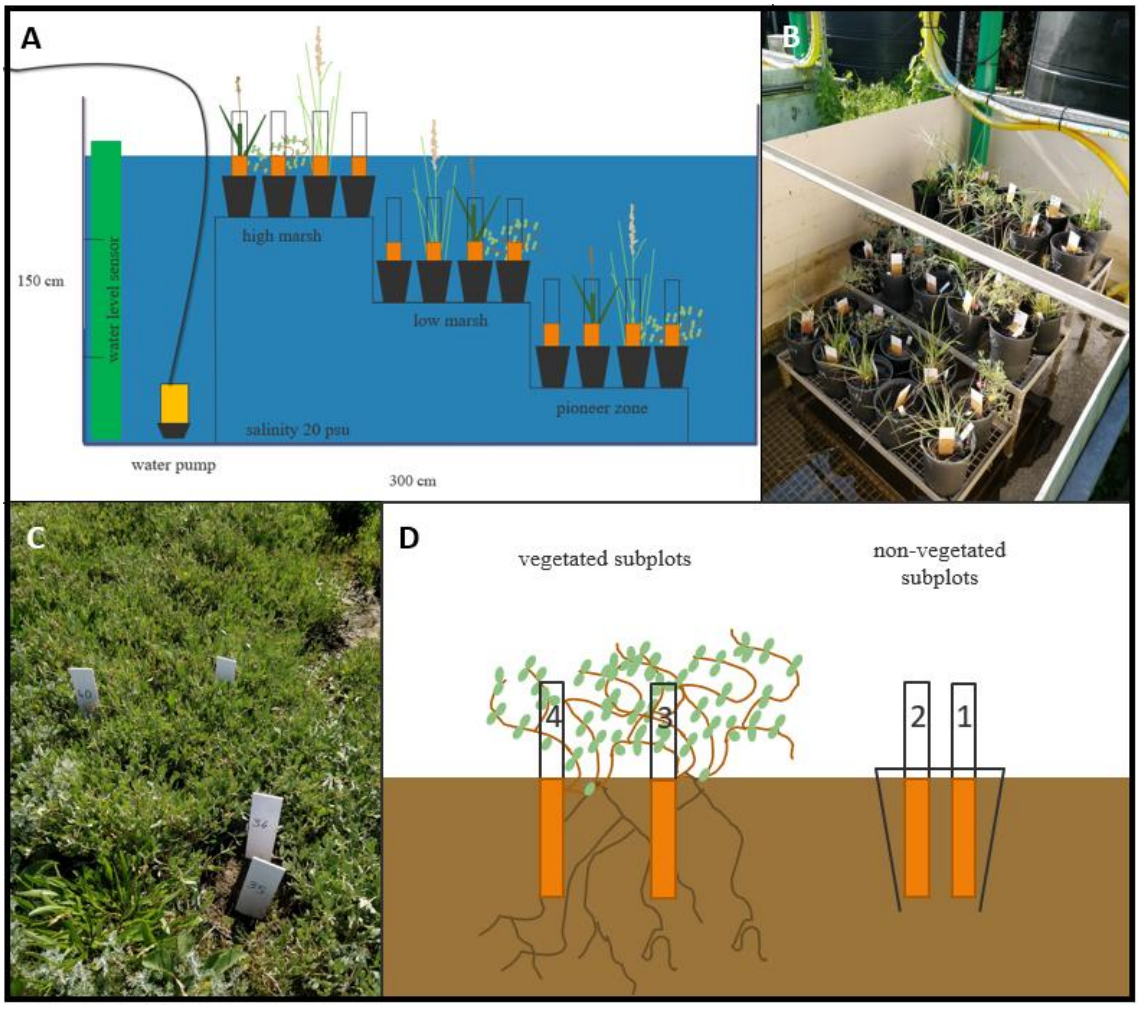

Figure 2.1: Overview of both study set-ups (mesocosm and field experiment). [A, B] The tidal tank experiment. At each of the three flooding levels, four planting treatments were realized: *Elymus athericus* from the high marsh; *Atriplex portulacoides* from the low marsh; *Spartina anglica* from the pioneer zone; non-vegetated control (n = 5 mesocosms per planting treatment). Flooding treatments were set to values that simulate the flooding-frequency of Wadden Sea salt marshes along elevation gradients, i.e., pioneer zone, low marsh, high marsh. [C, D] The complementary field experiment at the Hamburger Hallig (54°36'06.2"N, 8°49'00.1"E). At each of the three elevational zones (pioneer zone, low marsh, high marsh) three non-vegetated subplots were created, allowing for a plant vs. non-vegetated comparison as in the tidal tank experiment.

2.3.3 | Soil properties and reduction index

Indicator of Reduction in Soil (IRIS) has emerged as a practicable approach to get an insight into the redox dynamics of hydric soils (Jenkinson, 2002; Castenson & Rabenhorst, 2006). The IRIS method, following (Rabenhorst & Burch, 2006; Rabenhorst, 2013) utilizes a Fe oxide paint which is applied to PVC tubes. To prepare the Fe oxide paint, anhydrous $FeCl_3$ is dissolved in distilled water, and 1 M KOH is added in a second step. The reddish-brownish precipitate is centrifuged with distilled water, to remove the ions from the Fe oxide cake. The PVC-sticks were sanded using an orbital grinder with fine sanding paper (grid 180). Afterwards the Fe oxide paint was applied to the PVC-sticks (300 mm x 50 mm x 3 mm) in circular movements using a sponge (For more details see supplement S2.1). The capacity of the Fe oxide paint to be reduced from insoluble Fe (III) to soluble Fe (II) under anoxic conditions and in presence of microbial Fe-reducers allows for the determination of soil reduction (Rabenhorst 2013). The area of the removed paint functions as a proxy for soil redox conditions (reduction index), integrated over a 4-week period. Higher amounts of paint removal indicate higher soil reduction. It has been shown that IRIS correlates well with soil redox potentials (Mueller, et al., 2020b). Compared to redox potential measurements, IRIS sticks are less susceptible to the high variability of soil redox (Bansal et al., 2023). In this study, the method was modified according to Mueller, et al. (2020b) by using flat PVC sticks instead of tubes to simplify the scanning process. Upon removal, sticks were cleaned carefully with cold tab water to remove soil particles. Each stick was scanned to create digital images for further processing. Using a snipping tool (ShareX), which allows pixel-wise cutting, the individual IRIS images were cut to a standardized size of 115 x 700 pixels. Image analysis was conducted applying a supervised classification on randomly chosen sticks from different field campaigns. Classification was done using the software ArcGIS Pro. In total 4300 points were classified as either reduced, not reduced or errors (background, scanning effects). RGB colour values (0-255) of classified point were retrieved using the *Extract Multi values to Points* function. The classification was included in a Random Forest model (confusion matrix 1.5 %) using the software R. This model allowed for a pixel-wise classification of the scanned IRIS sticks (Fig. 2.2). Sticks were analysed in increments of 5 cm, covering a depth gradient from 0 to 30 cm. Reduction index was calculated as an unitless value ranging from 0 to 1 based on the share of reduced pixel from the total pixels.

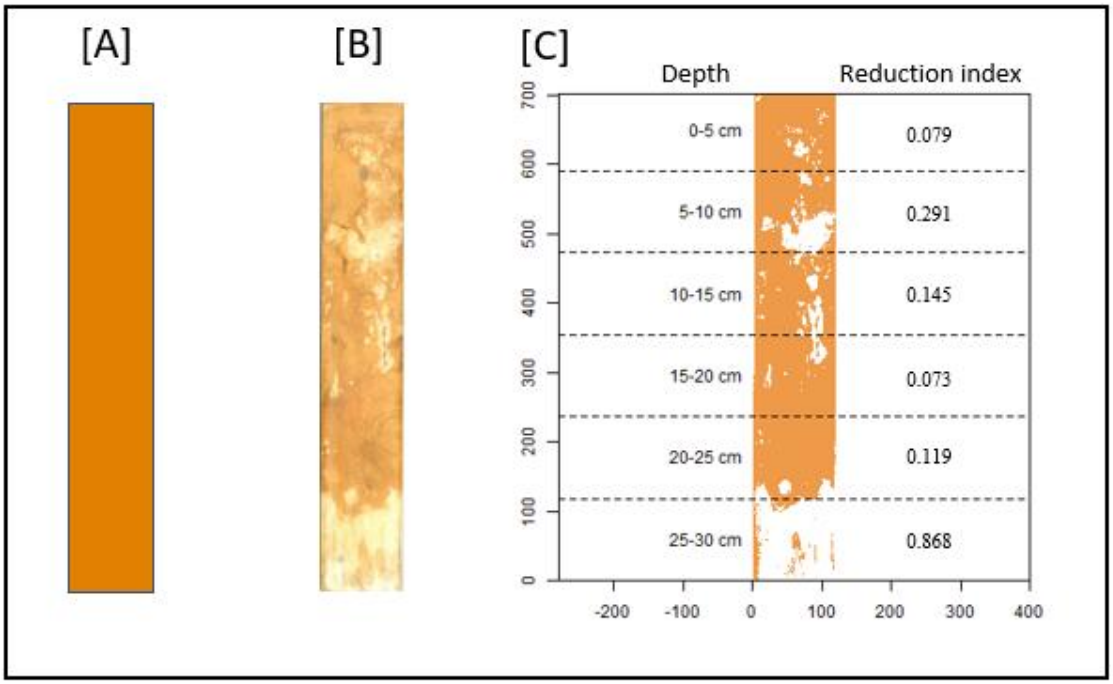

Figure 2.2: Images of an IRIS stick [A] schematic prior to installation with Fe (III) coating. [B] Post installation in the field for 4 weeks. [C] Predicted images after analyzation. Predicted images show not reduced areas (orange), reduced areas (white), errors during scanning are either green or black. Classes were defined based on RGB color values of 4300 randomly set points on test sticks. The reduction index is calculated per depth increment.

In the tidal tank experiment, there was one stick in each mesocosm (N = 60). Sticks were removed after six weeks and replaced with new sticks for a total of two consecutive IRIS campaigns. The first campaign spanned from beginning of August until mid-September 2021, the second campaign spanned from mid-September until end of October 2021.

In the field study, IRIS sticks were collected and replaced at the field site every four weeks beginning in June 2021. Before inserting the sticks into the soil, a pilot hole of 30 cm depth was created using a machete. This step prevents the sticks from scratches and paint removal not attributable to reduction processes. Each plot (N = 18) had two IRIS sticks in vegetated and non-vegetated subplots, resulting in 36 IRIS sticks per 4-week cycle. A total of four campaigns were conducted from June until October 2021.

The organic matter (OM) content of soils, as important electron donor source, was determined via loss on ignition following standard protocols (Dean, 1974; Heiri et al., 2001). Soil cores (volume = 100 cm^3) from every field plot (including the tidal-flat) were taken in October 2023. Samples were dried at 105°C in ceramic crucibles. After the samples cooled to room temperature inside a desiccator, they were weighed on a fine scale. Samples and crucibles were then placed in a muffle furnace operating at 550°C. Samples were removed after 2.5 h and placed in a desiccator for cooling. Samples were weighed again to calculate OM contents based on the weight loss following ignition.

Soil pH, as integral part of the soil redox chemistry, was determined for soil samples from both mesocosm experiment pots (N = 60) and field study plots (N = 9). Soil samples were taken at the end of

the experiments, in October 2021 and November 2021, respectively. 5 g of air-dried soil was incubated in a 0.01 M solution of $CaCl_2$ for one hour, and pH was measured using a pH-meter (Multi 9310 IDS).

2.3.4 | Plant biomass

Plant biomass was harvested in the field experiment in early October 2021. Aboveground and belowground biomass were quantified as potentially important plant traits associated with plant-mediated changes in soil redox. Aboveground biomass was collected in a 20 cm x 20 cm square. Squares were determined around the IRIS stick in each plot. Belowground biomass was collected to a soil depth of 10 cm using a PVC ring (A = 314.15 cm^2). Aboveground biomass was cleaned from remaining soil using tap water and dried for 48 hours at 50°C in a drying oven. Belowground biomass was cleaned from remaining soil using tap water and a fine sieve (2 mm) and dried at 50°C for 48 hours. Aboveground biomass and belowground biomass were weighed using a fine scale (FH-2000 Gram).

2.3.5 | Planar optodes

We conducted planar optode measurements to analyse plant effects on soil redox at the single-root scale. Planar optode measurements were conducted on an exemplary set of roots (2-3) from individuals of *Spartina anglica* (pioneer zone) and *Atriplex portulacoides* (low marsh). The set-up for planar optode investigations followed standard protocols (Wang et al., 2010, Koop-Jakobsen et al., 2018) The planar optode set-up consisted of a VisiSens TD imaging system (combined camera and excitation light source) facing a rhizobox containing soils and the sample roots. The rhizobox was situated in an aquarium filled with non-sterile water covering the sediment and continuously illuminated by a LED growth lamp. A custom Arduino-controlled, relay switch circuit system ensured regular dark intervals during photography. Roots and root-free soil compartments (i.e. bulk soil), were covered with a luminescent, 10 x 10 cm O_2-sensitive foil. The VisiSens™ ScientifiCalsoftware detects and evaluates oxygen signals on the sensor foils captured for each frame over a given time series.

Roots were carefully arranged on a freshly re-wetted sand substrate inoculated with soil from the field site. Oxygen concentration of the bulk soil decreased over time (0-24 h) from fully oxic to anoxic driven by increasing microbial respiration upon re-wetting and reduced oxygen diffusion under waterlogged conditions of the rhizobox. Changes in oxygen concentration over time were compared between root vicinity and bulk soil and plotted over 24 hours upon re-wetting.

2.3.6 | Statistical analyses

A mixed-model ANOVA was conducted to test for differences in reduction index between planting treatments (non-vegetated, *Spartina anglica*, *Atriplex portulacoides*, *Elymus athericus*), flooding treatments (pioneer zone, low marsh, high marsh) and their possible interaction effect within the tidal tank mesocosm experiment. There were no differences between treatments in the upper 15 cm of the sticks (Fig. S2.1). Therefore, only the bottom 5 cm section of each stick was considered in the statistical analysis (Fig. 2.3). A similar ANOVA was used to test for effects of vegetation presence, marsh zone,

and soil depth on the reduction index in the field experiment. A random factor (stick ID) was included to account for statistical dependency of depth segments. Equal sample size was assured and allowed for robust parametric testing using factorial ANOVAs despite moderate deviations from homogeneity of variance (McGuinness, 2002). Normality of residuals was checked visually for each ANOVA. Tukey´s HSD tests were used for pairwise comparison following significant ANOVA tests. Linear regressions were used to test for relationships between reduction index and different environmental parameters measured in the field study (i.e. above- and belowground biomass, organic matter content, soil pH). All statistical analyses were conducted with the software R Studio version 4.4.1 (R Core Team, 2024). Data were modified using psych (Revelle, 2024), dplyr (Wickham et al., 2023) and rstatix (Kassambara, 2023) R packages. All plots were created using ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2020), ggpmisc (Aphalo, 2024) and gridExtra (Auguie & Antonov, 2017) R packages. Mixed model ANOVA was conducted using R package afex (Singmann et al., 2024). Tukey´s HSD post hoc test were conducted using the emmeans (Lenth et al., 2024) R package.

2.4 | Results

2.4.1 | Mesocosm experiment

Soil reduction differed significantly by flooding treatment ($F = 6.45$, $p < 0.01$). The high marsh flooding treatment led to significantly less reduction than the pioneer zone and low marsh flooding treatments (Fig. 2.3a). In planted treatments, reduction was greatest in the pioneer zone. By contrast, background reduction in non-vegetated controls was greatest in the low marsh treatment (Fig. 2.3b). While there was no significant main effect of the planting treatment ($F = 0.75$, $p = 0.53$), reduction was significantly affected by the interaction of flooding and planting treatment ($F = 2.33$, $p < 0.05$). Planting treatment had an effect on soil reduction, but not across all flooding treatments. Magnitude and direction of plant effects differed between flooding treatments (Fig. 2.3c): the change in reduction index in relation to the non-vegetated control was positive in pioneer zone, negative in low marsh and both positive and negative in the high marsh flooding treatment depending on the plant species (Fig. 2.3c).

pH was 7.42 ± 0.23 and did not differ across planting and flooding treatment combinations (Fig. S2.2).

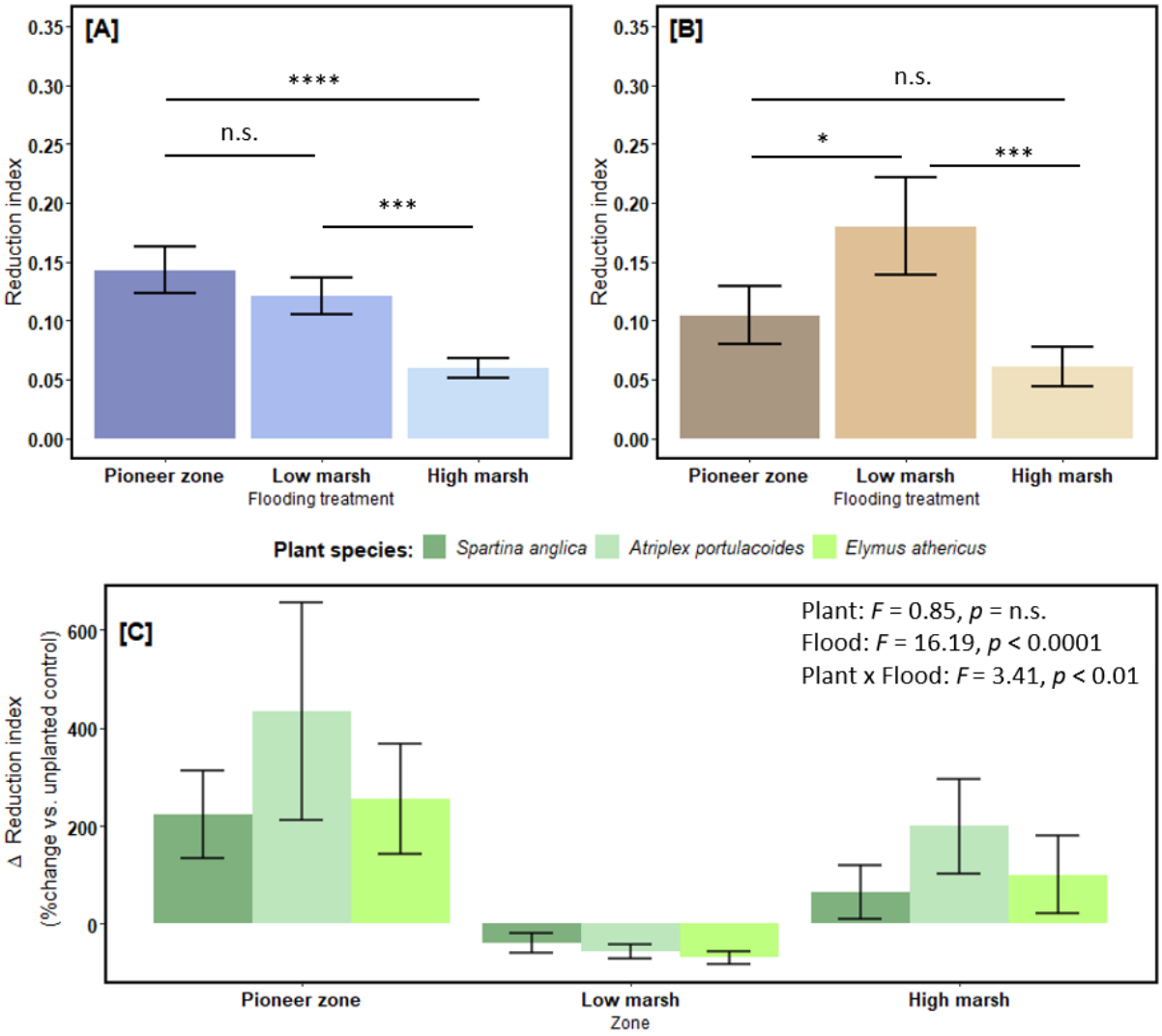

Figure 2.3: Reduction index, i.e., the fraction of reduced Fe paint from IRIS campaigns in the tidal tank experiment across the flooding frequency gradient (pioneer zone, low marsh, high marsh). [A] With all planting treatments across the flooding frequency gradient. [B] Only non-vegetated control planting treatments across the flooding frequency gradient. [C] Δ Reduction index as % change vs. the non-vegetated control, for all plant species (*Spartina anglica*, *Atriplex portulacoides*, *Elymus athericus*) across the three flooding treatments (pioneer zone, low marsh, high marsh). Barplots show mean ± se values. Main effects of mixed model ANOVA are presented in the subpanel [C]. Significant differences based on Tukey pairwise comparisons between all vegetated and all non-vegetated subplot are indicated as follows * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

2.4.2 | Planar optode results

Both *Spartina anglica* and *Atriplex portulacoides* roots initially showed lower oxygen concentrations compared to the bulk soil (Fig. 2.4). After 17 hours and 21 hours, respectively, two of the three *Spartina anglica* roots had a higher oxygen concentration compared to the bulk soil (Fig. 2.4a inlet). For *Atriplex portulacoides*, oxygen concentration remained lower in direct root vicinity compared to bulk soil throughout the entire experiment (Fig. 2.4b).

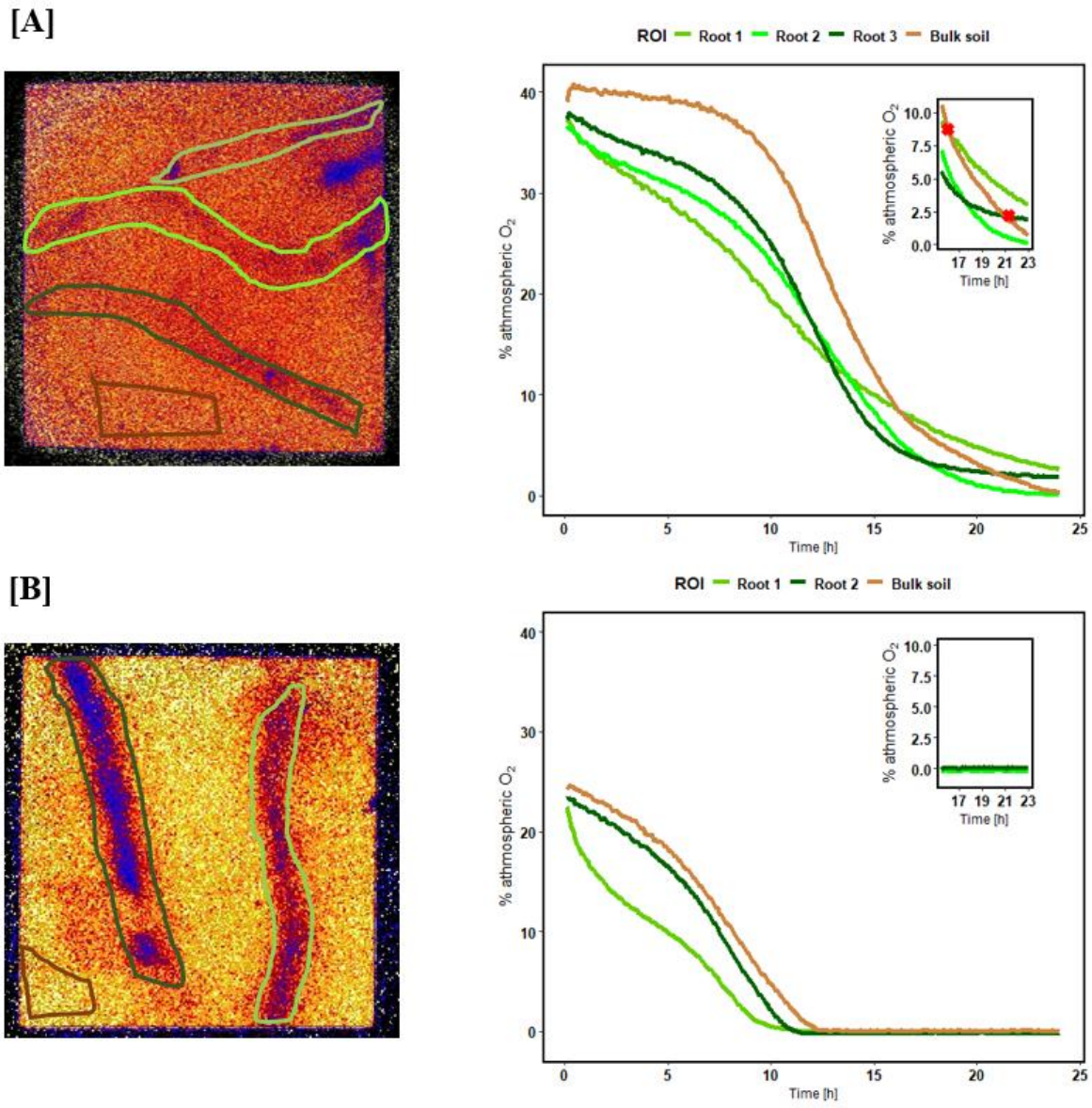

Figure 2.4: Planar optode images of the soil oxygen concentration around roots from [A] *Spartina anglica* and [B] *Atriplex portulacoides*. Different regions of interest (ROI) were selected for roots (green) and a root-free bulk soil control (brown) and tracked over 24 hours. Inlets show timeframe where some roots showed higher oxygen concentrations than bulk soil, crossing points are indicated by red x marks.

2.4.3 | Field experiment

Soil reduction differed significantly between zones along the flooding-frequency gradient (F = 73.95, p < 0.001). Reduction across all IRIS sticks was higher in the pioneer zone (0.204 ± 0.011 mean ± se) than in the low marsh (0.046 ± 0.003) and high marsh (0.034 ± 0.004). Zones affected reduction similar for both subplots (vegetated, non-vegetated) and only control subplots (non-vegetated). Reduction increased significantly with soil depth (F = 12.46, p < 0.0001) and was maximized at the deepest section assessed, i.e., 25-30 cm below soil surface. Here, the highest reduction index was 0.342 ± 0.028 in the pioneer zone, 0.088 ± 0.01 in the low marsh and 0.123 ± 0.023 in the high marsh. The soil-depth effect on reduction differed between zones as indicated by the significant zone x depth interaction term of the ANOVA (F = 3.68, p < 0.001). While soil depth lead to a linear increase in reduction in the pioneer zone there were less consistent depth trends in both low marsh and high marsh (Fig. S2.3). Soil reduction was significantly higher in vegetated subplots compared to non-vegetated controls (F = 4.34, p < 0.05). In both pioneer zone and low marsh, vegetated subplots were significantly more reduced than non-vegetated subplots (Fig. 2.5c). In the pioneer zone, this effect was detected from 0 to 10 cm and in the low marsh from 0 to 25 cm depth (Fig. 2.5c). In the high marsh, this effect was present from 20 to 25 cm depth (Fig. 2.5c).

pH in vegetated subplots was lower compared to non-vegetated subplots across all zones (Fig. S2.2). pH was 7.31 ± 0.15 in vegetated subplots and 7.69 ± 0.48 in the non-vegetated subplots (p = 0.05).

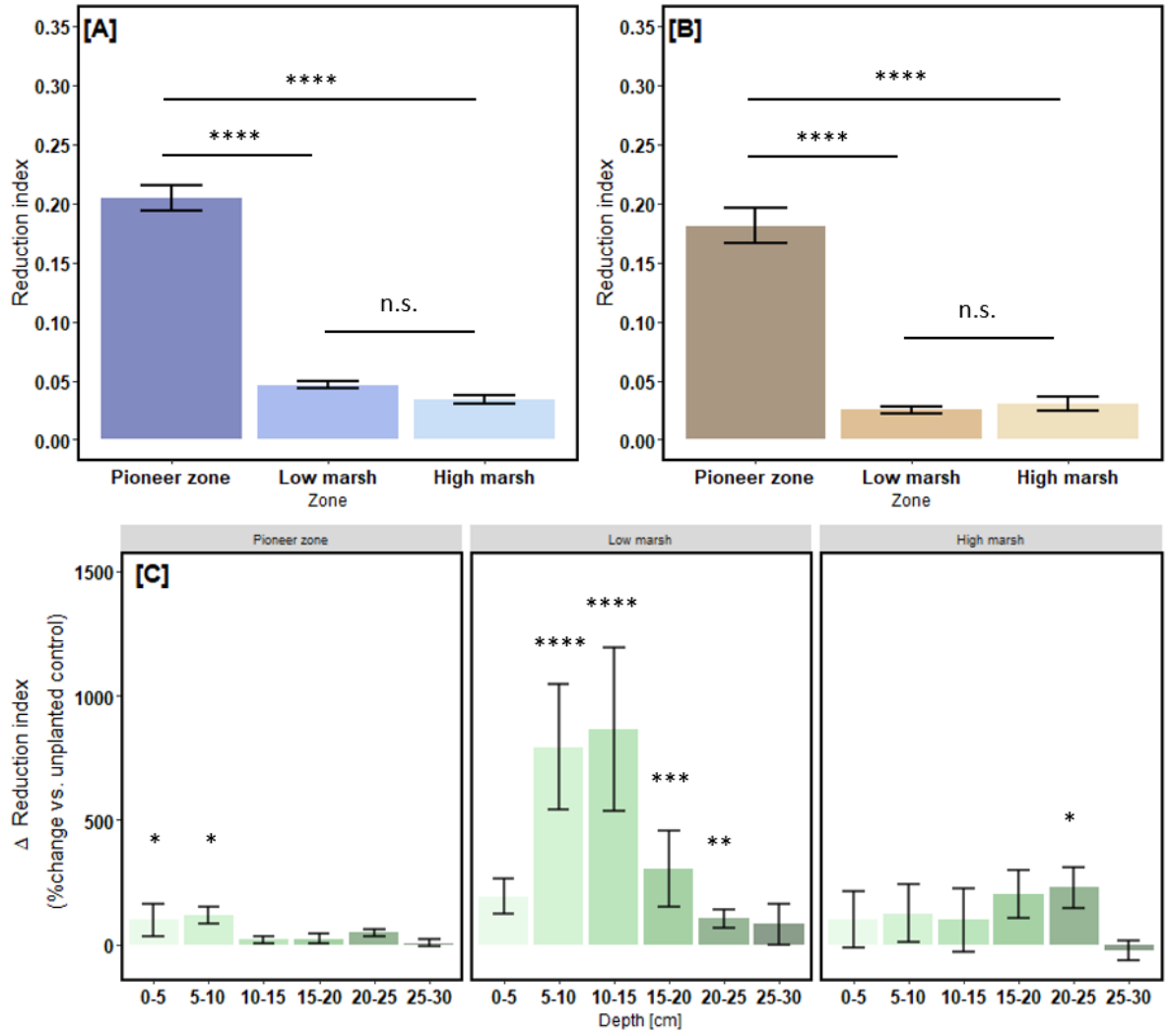

Figure 2.5: Reduction index, i.e., the fraction of reduced Fe paint from IRIS campaigns in the field experiment across the flooding frequency gradient (pioneer zone, low marsh, high marsh). [A] With all planting treatments across the flooding frequency gradient. [B] Only non-vegetated subplots across the flooding frequency gradient. [C] Δ Reduction index as % change vs. the non-vegetated control, for all depths (0-30 cm) across the flooding frequency gradient (pioneer zone, low marsh, high marsh). Barplots show mean ± se values. Significant differences based on Tukey pairwise comparisons between vegetated and non-vegetated subplot are indicated as follows * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

Field experiment belowground biomass ($p = 0.001$; $R^2 = 0.8$) and soil organic matter content ($p = 0.026$; $R^2 = 0.21$) had positive effects on soil reduction (Fig. 2.6). There were no effects by aboveground biomass and soil pH (Fig. 2.6).

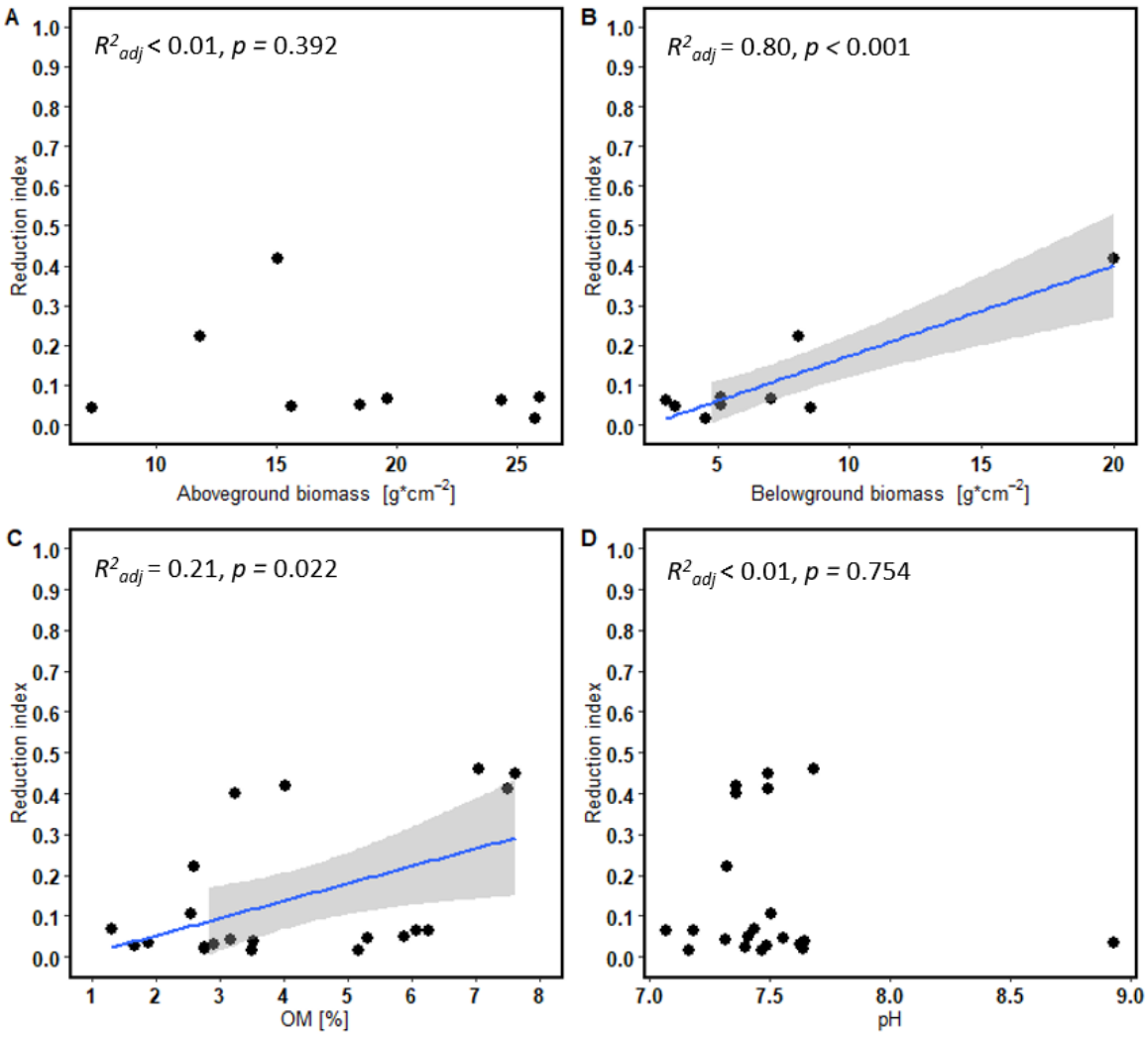

Figure 2.6: Field experiment reduction index, i.e., the fraction of reduced Fe paint, as means across the entire depth (0-30 cm), in relationship to [A] aboveground biomass in g*cm^{-2}, [B] belowground biomass in g*cm^{-2}, [C] organic matter content in % and [D] soil pH values. Plotted lines indicate a significant linear trend ($p < 0.05$). Compare Fig.S4 for more details.

2.5 | Discussion

2.5.1 | Mesocosm experiment

Using IRIS sticks as proxy for redox potentials, we found wetland plants to act as both net reducers and net oxidizers of soils. Our data suggest that background levels of soil reduction drove the observed plant effects. Plants acted as net oxidizers in the most reducing flooding treatment, the low marsh treatment, and as net reducers in the less reducing treatments of the pioneer zone and high marsh (Fig. 2.3c). Maximized soil reduction in the low marsh (Fig. 2.3b), despite lower flooding frequency than the pioneer zone, seems counterintuitive but is in line with results from field investigations in hydrologically unaltered Wadden Sea marsh sites (Mueller et al., 2020b; Fig. S2.5). It is possible that the observed net oxidizing effect of the planting treatment in the most reducing flooding treatment is the result of root oxygen loss from plants, a process known to increase with decreasing redox potential of the rhizosphere environment (Kludze & DeLaune, 1994).

While no significant differences between plant species could be found, low-marsh derived *Atriplex portulacoides* tended to induce the greatest reduction compared to non-vegetated controls, while high-marsh derived *Elymus athericus* tended to induce the greatest oxidizing effect compared to non-vegetated controls (Fig. 2.3c). The capacity of the grasses *Elymus athericus* and *Spartina anglica* to oxidize soils has previously been shown using planar optodes (Koop-Jakobsen & Wenzhöfer, 2015; Koop-Jakobsen et al., 2021). By contrast, oxygenation capacity of salt marsh shrubs such as *Atriplex portulacoides* have never been investigated. It is also possible that species tend to differ in their potential to oxidize or reduce soils because they differ in their capacity to release electron donors in the form of organic matter. However, our insight into exudation dynamics of wetland plants is scarce.

2.5.2 | Planar optode results

Planar optode investigations support findings from IRIS sticks showing that plant roots can act as both net reducers and net oxidizers of soils: roots from *Spartina anglica* acted as both oxygen sinks and oxygen sources to the soil. Planar (Koop-Jakobsen & Wenzhöfer, 2015; Koop-Jakobsen et al., 2018) and multi-fiber (Koop-Jakobsen et al., 2017) optode systems have previously been used to measure in situ sediment oxygenation in *Spartina anglica* rhizospheres and well as other wetland vascular species, e.g., *Elymus athericus* (Koop-Jakobsen et al., 2021), *Juncus spp.* (Blossfeld et al., 2011), and most extensively by Lai et al. (2012). In our study roots were oxygen sinks when background (bulk soil) oxygen concentration was high and (Fig. 2.4a) at lower oxygen concentration of the bulk soil, some of the roots became net sources of oxygen (net oxidizers). These findings are in line with the mesocosms results, showing net oxidizing effects at high background reduction. *Atriplex portulacoides* roots did not show the reducer-oxidizer shift observed for *Spartina anglica*. Instead, roots remained an oxygen sink over the entire 24 hours of the experiment. Koop-Jakobsen et al. (2017) found that different sediment types led to a different extend of oxic root zones, indicating that the background reduction plays an important role in determining the plant effects on soil reduction. Our findings now suggest that soils can

have a tipping point of background reduction, which ultimately can lead to net reducing effects of the plants.

2.5.3 | Field experiment

Plants consistently acted as net reducers of the soil system throughout all zones (Fig. 2.4c). This finding contrasts from the mesocosm results, indicating more variable plant effects on soil redox. Conditions differed between the two experiments regarding hydrology, plant traits and soil characteristics. Especially differences in alternative terminal electron acceptors as well as electron donors might have led to contrasting findings.

Wadden Sea salt marshes are situated relatively high in the tidal frame, leading to well aerated, oxidizing soil conditions (Erchinger et al., 1996; Mueller et al., 2017). In close agreement with our IRIS data, continuous soil redox records from the nearby low-marsh site at Dieksanderkoog demonstrated frequent oxidizing conditions (Eh > 400 mV) to a soil depth of 15 cm during the growing season (Mueller, et al., 2020b). We argue that these oxidizing conditions are a precondition for plants to function as strong reducers of the soil system.

Plant-driven reduction in the field experiment was particularly pronounced in the low marsh. We observed highest % change in soil reduction compared to non-vegetated control areas in the low marsh (Fig. 2.4c) at more oxidizing background soil redox compared to pioneer zone (Fig. 2.4b). We attribute the observed net reduction to the dominance of *Atriplex portulacoides*, which showed the greatest net reducing effect in the mesocosm in pioneer zone and high marsh treatments with low background soil redox (Fig. 2.3c). These findings are in line with a study conducted English salt marshes, where *Atriplex portulacoides* stands showed increased carbon stocks, possibly by their comparable high belowground productivity (McMahon et al., 2023).

We show that soil reduction scaled positively with plant belowground biomass and SOM (Fig. 2.6b, Fig. 2.6c). These findings suggest that greater input of organic matter either via root exudates or belowground root litter input depleted soil oxygen and thus led to greater soil reduction (Gardiner & James 2012). Studies from other wetland ecosystems (i.e. mangroves) showed that plant roots can reduce the activity of the oxygen-dependent enzyme phenol oxidase (Luo et al., 2018). This finding might be linked to the here described capacity of wetland plants to decrease soil oxygen availability in soils. Further studies are needed to better understand the potential consequences for soil microbial functioning and ultimately soil carbon stability.

2.5.4 | Methodological considerations

Soil pH and redox are not independent and need to be studied together in order to understand plant effects on the overall redox chemistry of the soil system. We observed a tendency of lower pH in planted treatments (Fig. S2.2). This effect was pronounced in the field experiment, but negligible in the mesocosms. We attribute this effect to the root release of protons and organic acids (Jones, 1998) as

well as increased levels of soil CO_2 through plant and microbial respiration (Koop-Jakobsen et al., 2018). IRIS sticks have proven robust against pH changes at pH > 4.5 (Loffredo et al., 2023). Soil pH was > 7 in both mesocosm and field. We therefore consider the plant effects on iron reduction observed here to be independent of plant mediated pH dynamics. Root exclosures are a useful technique to create *in-situ* control plots without vegetation. However, the installation is destructive and could possibly lead to changes in hydrology. After installation of root exclosures, we allowed the soil to stabilize for four weeks to account for the destructiveness of the installation. To avoid alterations in hydrology, we drilled two holes in each root exclosure, allowing for horizontal water exchange. Remaining artefacts of root exclosures on hydrology cannot be entirely excluded. However, we show that belowground biomass correlated positively with reduction index indicating that differences in reduction between planting treatments were indeed driven by plant effects and not by hydrology artifacts of the installation.

2.5.5 | Conclusion

Contrary to the prevailing notion that wetland plants generally act as oxidizers of the soil system, we show that wetland plants can have a net reducing effect on the soil system (Fig. 2.3c, Fig. 2.4c). While the mesocosm experiment revealed plants acting as oxidizers and reducers based on the background soil redox conditions (Fig. 2.3b-c), we found plants to consistently act as net reducers in the field setting. We argue that no net oxidizing effect was observed in the field study due to the comparably well aerated soils of the Wadden Sea salt marshes (Mueller et al., 2020b). The here described plant effects on soil redox might play an overseen role in shaping the soil redox conditions and thus the stability of soil carbon stocks in wetland ecosystems with fluctuating water tables such as peatlands (C. D. Evans et al., 2021) or seasonal wetlands (Bansal et al., 2018). Previous studies have indicated shifts in plant communities being closely related to the carbon-sink potential of wetlands (Ward et al., 2013; Robroek et al., 2016). Wetland plants may protect old SOC stocks by providing fresh electron donors, such as low molecular organic compounds, which soil microbial communities preferentially use over old SOC (Robroek et al., 2016). Yet these plant-microbe interactions in wetlands are still poorly understood. Revealing these interactions might require a combination of plant trait and microbial analysis.

2.6 | Competing interests

The authors declare no conflict of interest.

2.7 | Data availability

Data and code are available at https://github.com/JulianMiGoe/iris_optode_2024

2.8 | Acknowledgments

We would like to thank Tom Kamin and Jörn Ehlers for helping with the technical set-up and maintenance of the tidal tank experiment, Maren Winnacker for her support with the plants in the greenhouse and Claudia Mählmann for her organizational support.

2.9 | Supporting information

2.9.1. | Fe-oxide paint protocol

Procedure: (For approx. 200ml)

1. For one litre of 1 M KOH, fill a 1 L glass bottle with 56 g KOH and 1 L of distilled water (DW). Let the KOH dissolve.
2. Fill a 2 L glass beaker with 500 ml DW. Place the glass beaker on a magnetic stirrer, install and calibrate a pH-meter. Weigh 16 g of $FeCl_3$ (anhydrous) and let it dissolve in the DW. The pH value should be between 1.2-2.0.
3. Start the magnetic stirrer and slowly add 1M KOH up to 370 mL. In this process the pH-value should rise to 12. Continuously measure the pH-value and stop adding KOH when it reaches pH 12. The suspension is getting thicker as you add KOH. Let the suspension rest for 30 min.
4. After 30 min start the magnetic stirrer and check the pH-value, if it hast dropped below 12, slowly add KOH until it reaches pH 12 again.
5. Then transfer the suspension into two 1000 mL centrifuge glass bottles. Centrifuge at approx. 1000 rpm for 5 min, this should lead to a separation of the Fe-cake on the bottom and the KOH as the supernatant. Remove the KOH supernatant.
6. Add distilled water to the Fe-cake until the volume is doubled. Centrifuge five times at 1000 rpm for 5 min. Remove the supernatant after each centrifugation and refill the glass bottle again. This process helps removing ions from the Fe-cake.

- After the last centrifugation remove the supernatant and carefully fill the whole glass bottles with DW (make sure that the Fe-cake remains on the bottom of the bottle, otherwise centrifuge again). Fill a basin with about 2.5L DW, slowly place the bottles in the basin. Add more DW until the bottles are submerged by DW.

7. The paint should stay in the water basins for 3 days. Using a conductivity meter allows you to check if the Fe-cake is losing Ions. If the value raises above 60 µS the water should be replaced. The Fe-cake should keep its dark red brownish colour.
8. After 3 days the glass bottles can be removed from the basin. Remove the supernatant above the Fe-cake. Add DW and centrifuge at 1000rpm for 5 min and remove the supernatant. The paint is than stored at 4°C for 2 weeks prior to painting.
9. Clean the PVC sticks with acetone than sand both sides of the sticks with a fine sandpaper (grit 180).
10. Fill some paint into a petri dish, put the flat side of the sponge into the paint. Paint the PVC-Sticks with the sponge doing circular movements. The paint should be evenly distributed.

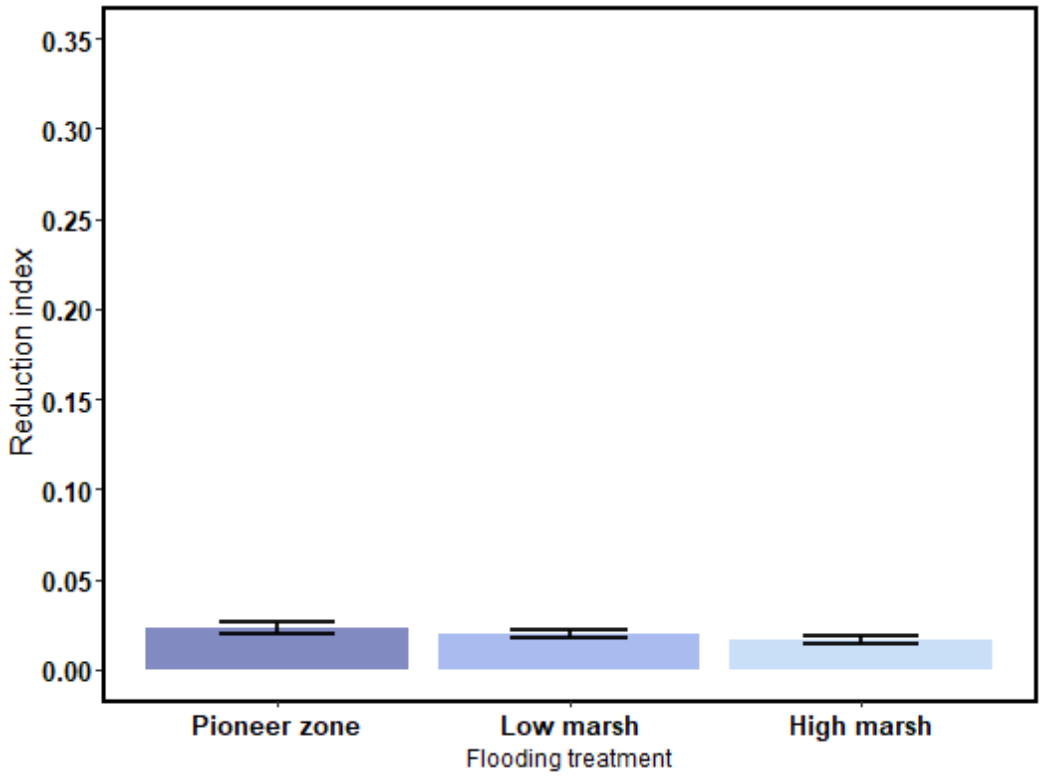

Figure S2.1: Top-soil reduction index, i.e., the fraction of reduced Fe paint across the three flooding treatments in the tidal tank experiment. Shown are values from IRIS stick segments above 15 cm depth. Barplots show mean ± se values.

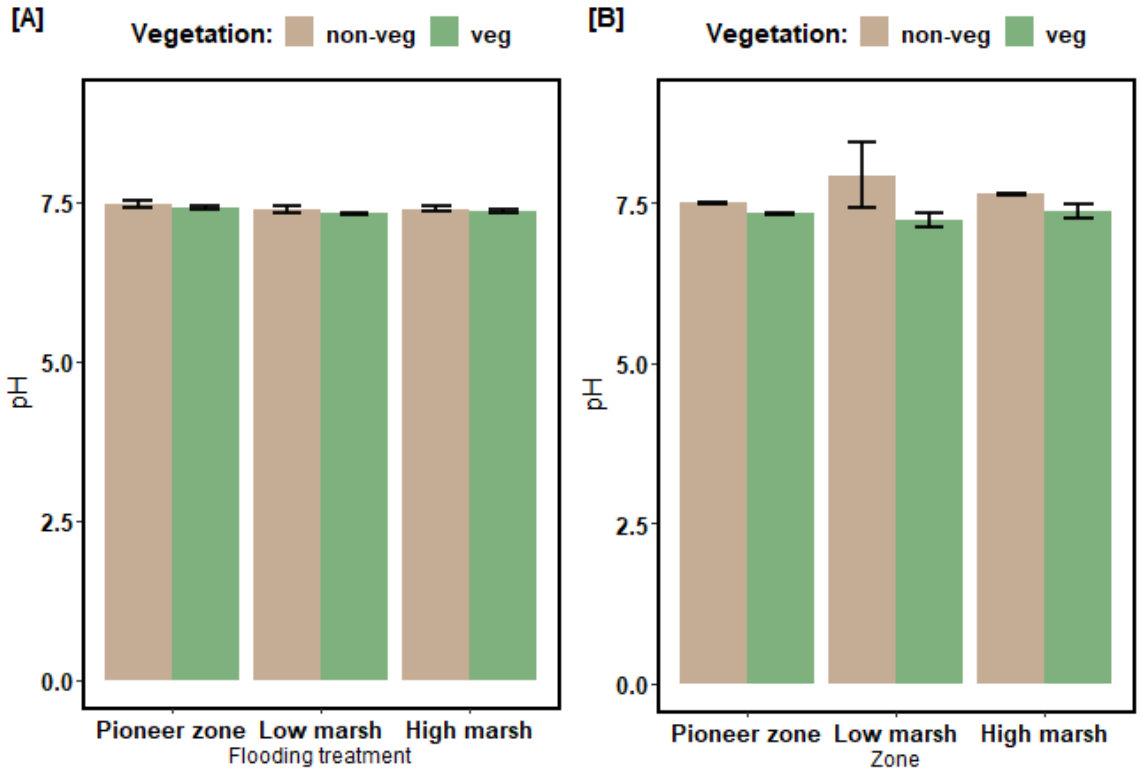

Figure S2.2: pH values of vegetated and non-vegetated subplots across the flooding frequency gradients (pioneer zone, low marsh, high marsh) in both [A] mesocosm experiment in tidal tank and [B] field-study site at the Hamburger Hallig.

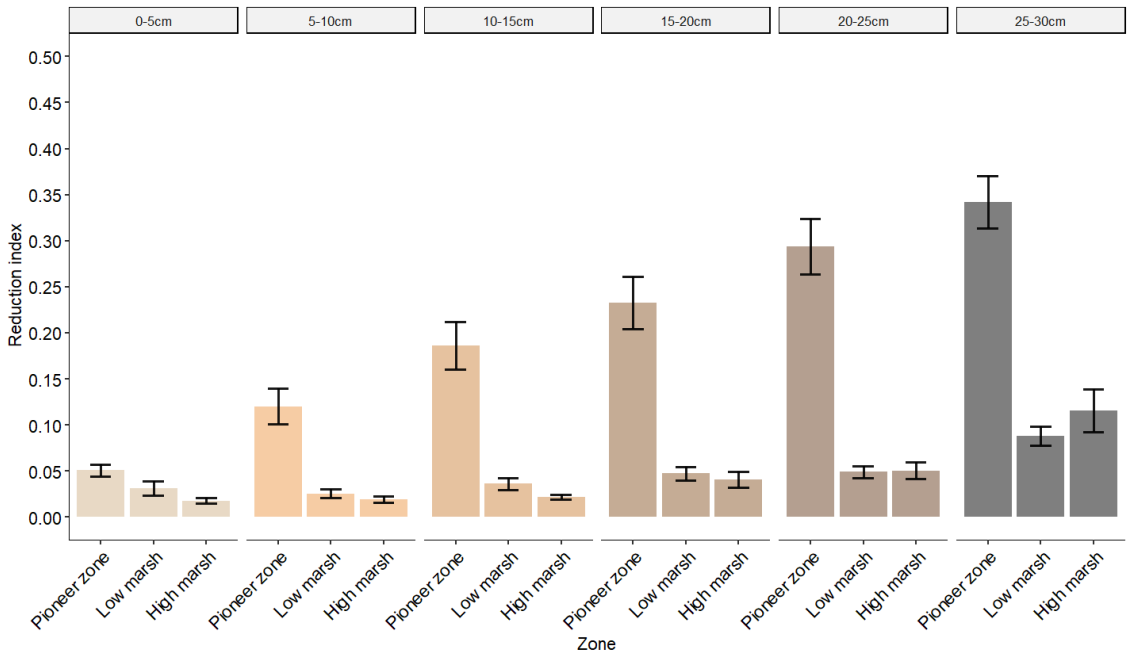

Figure S2.3: Reduction index, i.e., the fraction of reduced Fe paint along the elevational (pioneer zone, low marsh, high marsh) and depth gradient (0-30 cm in 5 cm increments) of the field study. Barplots show mean ± se values.

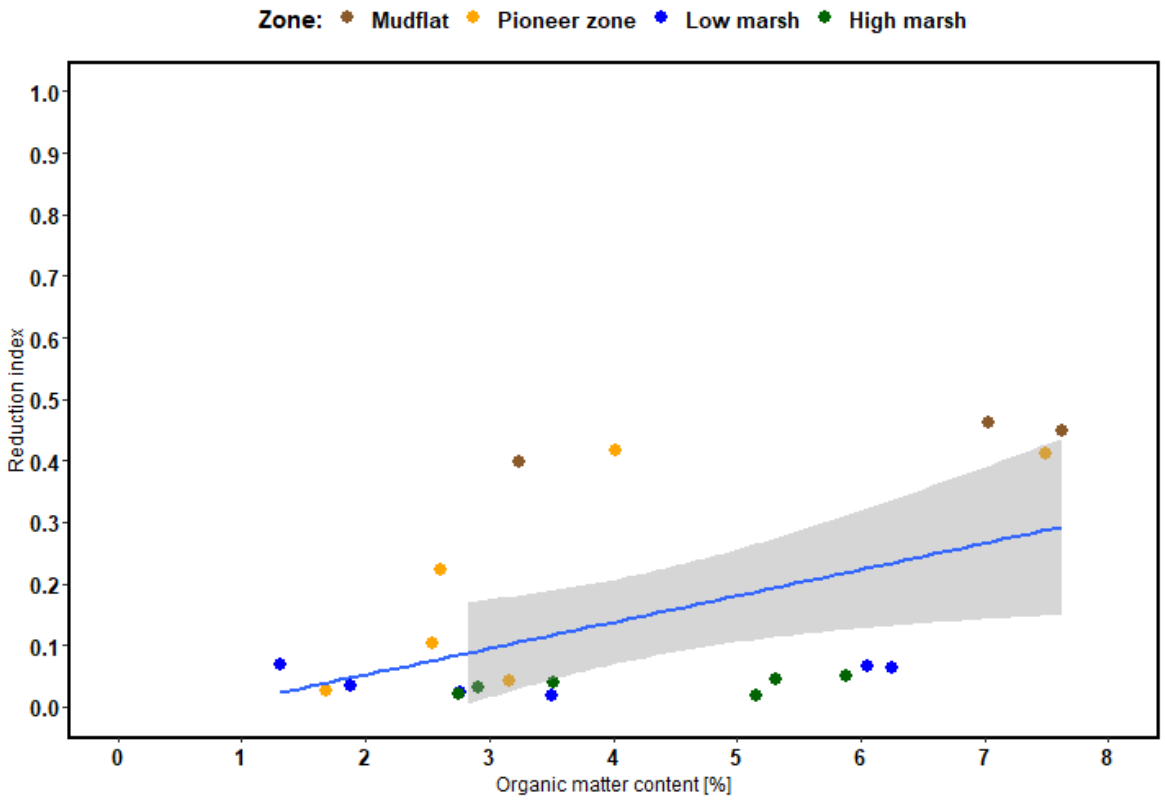

Figure S2.4: Reduction index, i.e., the fraction of reduced Fe paint, in relationship to organic matter content in % across the elevational gradient (tidal flat, pioneer zone, low marsh, high marsh).

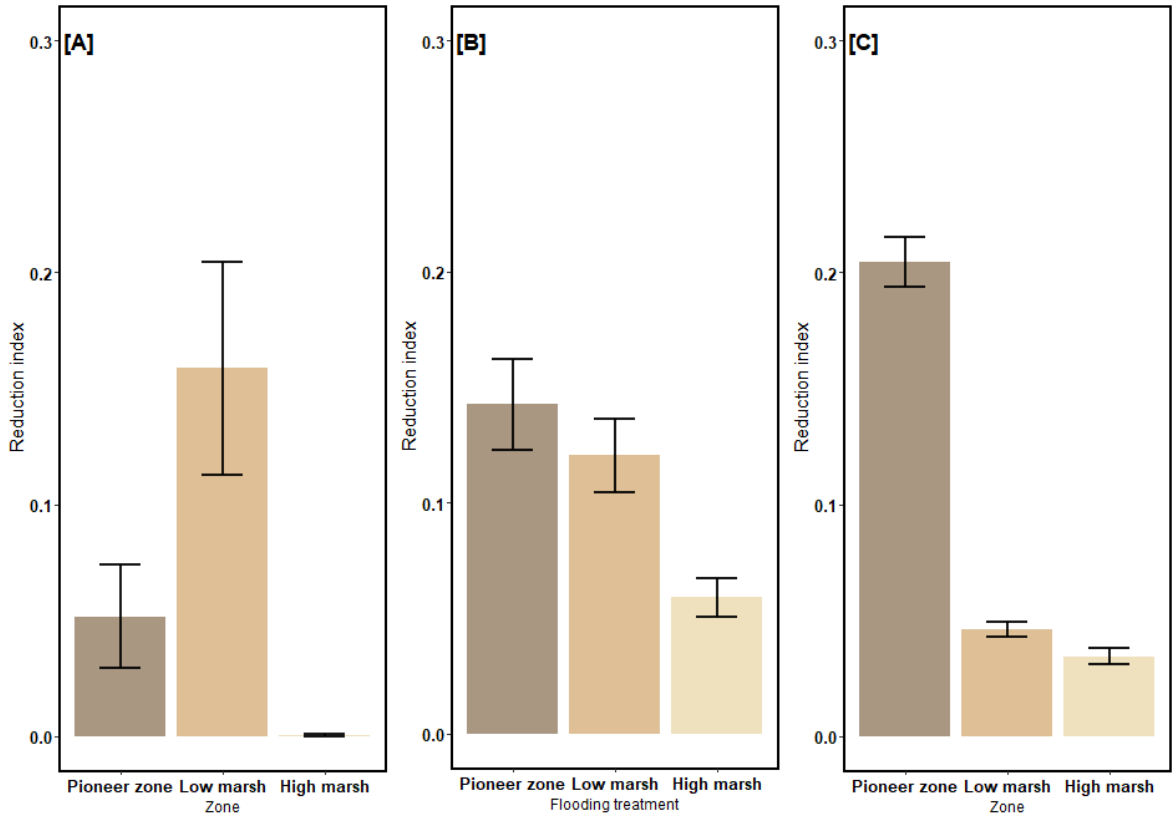

Figure S2.5: Reduction index, i.e., the fraction of reduced Fe paint from IRIS campaigns across the flooding frequency gradient (pioneer zone, low marsh, high marsh) in [A] Natural salt marsh located at Dieksanderkoog (data from Mueller et al., 2020b). [B] The tidal tank mesocosm experiment. [C] The field experiment at the Hamburger Hallig.

Chapter 3 | Warming accelerates belowground litter turnover in salt marshes - insights from a Tea Bag Index study

Hao Tang, Stefanie Nolte, Kai Jensen, Roy Rich, **Julian Mittmann-Goetsch** and Peter Mueller

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„The water is wide and I can't cross over

Neither have I wings that I could fly

Build me a boat that could carry two

And both shall row my love and I”

– Bob Dylan

3.1 | Abstract

Salt marshes play an important role in the global carbon (C) cycle due to the large amount of C stored in their soils. Soil C input in these coastal wetland ecosystems is strongly controlled by the plant primary production and initial decomposition rates of plant belowground biomass and litter. This study used a field warming experiment to investigate the response of belowground litter breakdown to rising temperature (+1.5°C and +3.0°C) across whole-soil profiles (0-60 cm soil depth) and the entire intertidal flooding gradient ranging from pioneer zone via low marsh to high marsh. We used standardized plant materials, following the Tea Bag Index approach, to assess the initial decomposition rate (*k*) and the stabilization factor (*S*) of labile organic matter (OM) inputs to the soil system. While *k* describes the initial pace at which labile (= hydrolyzable) OM decomposes, *S* describes the part of the labile fraction that does not decompose during deployment in the soil system and stabilizes due to biochemical transformation. We show that warming strongly increased *k* consistently throughout the entire soil profile and across the entire flooding gradient, suggesting that warming effects on the initial decomposition rate of labile plant materials are independent of the soil aeration (i.e., redox) status. By contrast, negative effects on litter stabilization were less consistent. Specifically, warming effects on *S* were restricted to the aerated topsoil in the frequently flooded pioneer zone, while the soil depth to which stabilization responded increased across the marsh elevation gradient via low to high marsh. These findings suggest that reducing soil conditions can suppress the response of belowground litter stabilization to rising temperature. In conclusion, our study demonstrates marked differences in the response of initial decomposition rate vs. stabilization of labile plant litter to rising temperature in salt marshes. We argue that these differences are strongly mediated by the soil redox status along flooding and soil-depth gradients.

3.2 | Introduction

Salt marshes provide a multitude of ecosystem services, such as wildlife conservation, flood protection, and water quality improvement (Barbier et al., 2011; Kirwan & Megonigal, 2013). Recently, salt marshes have additionally been recognized for their ability to store large amounts of organic carbon (C) in their soils, which has been acknowledged by the now common use of the term *blue carbon* (McLeod et al., 2011; Chmura, 2013). Global warming yields the potential to influence C sequestration in salt marshes by affecting the balance between organic matter (OM) input to the soil system, through plant primary production, and output, through microbial decomposition of plant OM inputs (Kirwan & Mudd, 2012). Most of the current debate regarding the temperature sensitivity of the salt-marsh C balance is dealing with aboveground processes, i.e. plant primary production (Kirwan & Blum, 2011; Noyce et al., 2019) and aboveground or surface litter breakdown (Charles & Dukes, 2009), whereas the effects on belowground processes remain largely unexplored (but see Mueller et al., 2018; Noyce et al., 2019). Belowground litter input and turnover often are more important drivers of soil C sequestration than aboveground processes, because aboveground litter gets deposited in an oxic environment and is subject to fast decomposition, whereas belowground litter can get stabilized under reducing soil conditions (Langley & Megonigal, 2010; Kirwan & Megonigal, 2013; Mueller et al., 2018)

Litter decomposition dynamics are commonly quantified using litter-bag techniques. Litter bags are mesh bags filled with native plant litter of variable quality (e.g., with respect to C:N ratio or labile vs. recalcitrant fractions) that get deployed in the ecosystem or soil system in question. Initial decomposition rates are calculated based on litter mass loss over time. However, the mechanistic insight into climate change effects that can be gained from it is often limited owing to the challenge of separating climate from litter-quality effects (Prescott, 2010). Litter decomposition is controlled by complex interactions between litter-quality and climate parameters (Zhang et al., 2008). To separately assess climate effects on litter decomposition, it has proven useful to standardize litter quality. The Tea Bag Index *sensu* Keuskamp et al. (2013) represents a widely used standardized litter bag approach. It allows for the quantification of two key litter-breakdown parameters: the initial decomposition rate, k, and the stabilization factor, S.

Warming effects on litter breakdown in coastal wetlands may be strongly controlled by hydrology and resulting soil redox gradients. For instance, warming studies conducted in boreal peatlands demonstrated a dramatic reduction of warming effects on soil decomposition processes in waterlogged, and thus strongly reducing subsoils compared to less reducing topsoil (Wilson et al., 2016; Hopple et al., 2020). The authors suggest that the absence of oxygen can inhibit warming effects on soil microbial activity because phenolic compounds accumulate under anoxic conditions and inhibit microbial hydrolytic enzyme activity via the “enzymic latch” mechanism (Freeman et al., 2001). In order to understand warming effects on litter breakdown in coastal wetland ecosystems, it is therefore necessary to use a standard substrate to study temperature effects across gradients in both flooding frequency (i.e. along the marsh elevation gradient) and in relation to soil depth.

The present study uses a unique field experiment to assess the effects of rising temperatures on litter breakdown in relation to soil depth and across the marsh elevation gradient ranging from pioneer zone via low marsh to high marsh. The MERIT (Marsh Ecosystem Response to Increased Temperature) experiment operates in a NW European salt marsh and induces active temperature manipulation to 1 m soil depth. We investigated litter breakdown for two consecutive growing seasons during the growing season of year 1 and year 2 of the experiment. We hypothesized (1) that warming will increase litter initial decomposition rate, *k*, and decrease the ability of litter to stabilize, *S*, in soil, and (2) that warming effects on *k* and *S* will be inhibited by reducing soil conditions and thus, vary along gradients of both flooding frequency and soil depth.

3.3 | Material and Methods

3.3.1 | Site description

The MERIT ecosystem warming experiment is located in a NW European salt marsh at Hamburger Hallig, Germany (54°36'06.2"N, 8°49'00.1"E) and has operated since spring 2018. The site is located on the coast of the Schleswig-Holstein Wadden Sea (Fig. 3.1a, Fig. 3.1c) and has been protected as part of a National Park since 1985. This area is exposed to a temperate maritime climate; the annual mean temperature and mean precipitation are 10°C and 850 mm, respectively. The site is exposed to a tidal range of 3.4 m, with floodwater salinity ranging from 25 to 29 ppt (Mueller et al., 2023). The vegetation shows a zonation typical for Wadden Sea salt marshes: *Spartina anglica* is dominant in the pioneer zone, *Artiplex portulacoides* and *Puccinellia maritima* are dominant in the low marsh, and *Elymus athericus* is dominant in the high marsh (Esselink, 2017; Mueller et al., 2020b). The mean elevation of the pioneer zone, low marsh, and high marsh are 136 cm, 174 cm, and 212 cm (NHN, German standard ordnance datum), respectively. The pioneer zone is a typical feature of NW European salt marshes and is defined as the area where pioneer vegetation covers ≥ 5 % (Peterson et al., 2014). In the Wadden Sea region its average surface elevation is below mean high tide. Thus, the pioneer zone is typically flooded twice daily (Esselink, 2017). Soil pH (measured in $CaCl_2$) at the site ranges between 7.0 and 7.5 without pronounced differences between zones (Mueller et al., 2023). Both organic and inorganic carbon stocks increase from pioneer zone to high marsh (Mueller et al., 2023). ^{13}C signatures of the soil organic matter demonstrate a strong decrease in allochthonous marine-derived vs. autochthonous vascular plant-derived organic contributions along the flooding gradient from pioneer zone to high (Mueller et al., 2023).

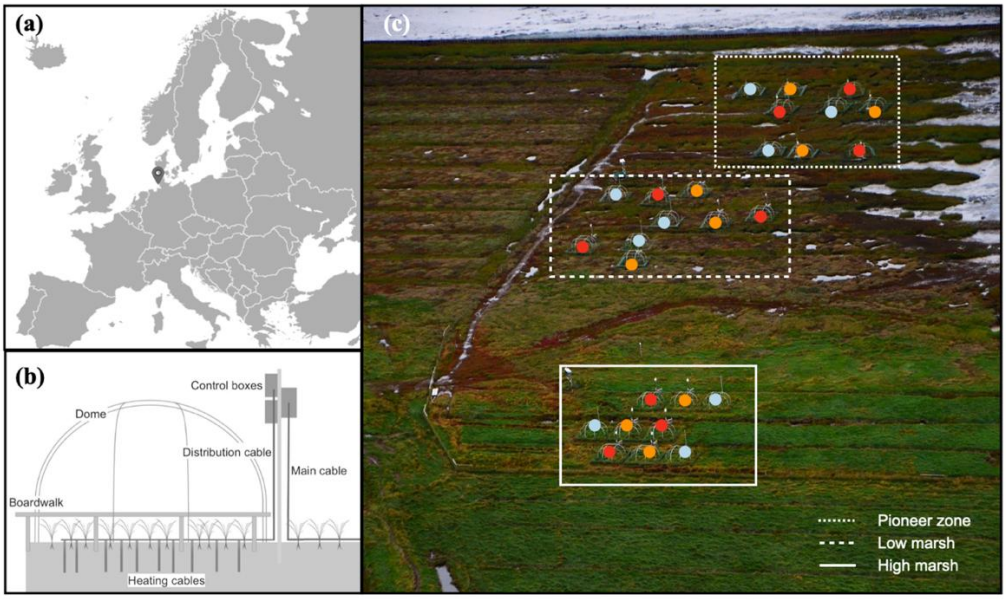

Figure 3.1. Location of the MERIT experimental site (a), diagram of belowground and aboveground heating (b), and plot distribution in the pioneer zone, low marsh, and high marsh (c, aerial photo of the experimental site, courtesy of Norbert Kempf). Color points, i.e., blue, orange, and red, accordingly present the ambient, + 1.5°C and + 3°C treatments in different plots and marsh zones.

3.3.2 | Experimental design

MERIT consists of N = 27 experimental plots, each with an area of approx. 7 m^2. Belowground active temperature manipulation is conducted using 31 heating cables (GX 088L3100, 9.8 Ω/m, Danfoss, Denmark) per plot, inserted into the ground vertically to 1.0 m soil depth. Aboveground and soil-surface temperature manipulation is achieved using a combination of passive open-top chambers and surface heating cables with a length of 52 m per plot sinuously deployed at the soil surface (GX 088L3100, 9.8 Ω/m, Danfoss, Denmark) (Fig. 3.1b). The experiment is conducted across three hydrological zones (pioneer zone, low marsh, and high marsh) and applies three temperature treatments (ambient, +1.5°C, and +3°C) in a full factorial design (3 zones x 3 temperature treatments x 3 replicates) (Fig. 3.1d).

Belowground temperature was monitored continuously and logged at 5-min intervals using custom made thermistors and dataloggers. To control the heating rate evenly throughout the soil profile, sensors were placed at -5, -25, and -75 cm depth below the soil surface. At -5 cm, the highest variation in mean temperature difference across all marsh zones and plots ranged from 1.43° to 1.67°C for the +1.5° treatment, and 2.54° to 2.99°C for the +3.0° treatment. At -25 cm depth, the mean temperature difference values ranged from 1.51° to 1.55°C for the +1.5° treatment and 2.87° to 3.02° for the +3.0°C treatment. At -75 cm, temperature difference values ranged from 1.14° to 1.43°C for the +1.5° treatment and 1.92° to 2.36°C for the +3.0°C treatment (Rich et al., 2023).We selected the belowground temperature data from -10 cm to -60 cm for the deployment times in 2018 and 2019 to calculate the average belowground ambient temperature per zone. Mean ambient temperature during the deployment time in 2018 (pioneer

zone = 16.45°C; low marsh = 15.99°C; high marsh = 14.54°C) was higher compared to 2019 (pioneer zone = 13.55°C; low marsh = 12.95°C; high marsh = 12.46°C).

3.3.3 | Decomposition of standardized plant litter

The initial decomposition rate (*k*) and stabilization factor (*S*) were assessed following the Tea Bag Index (TBI) protocol (Keuskamp et al., 2013). *k* describes the rate at which the labile (here defined as hydrolysable) fraction of the plant material decomposes. *S* describes the part of the labile fraction that did not decompose during deployment in the soil system and stabilized. Twelve polypropylene tea bags, six green tea (EAN: 8714100770603; Lipton, Unilever) and six rooibos tea bags (EAN: 8711200 875665; Lipton, Unilever), were put into the salt marsh soil using two solid PVC-posts per plot, perforated with six holes between 10 and 60 cm soil depth (Fig. 3.2). Posts contained either green or rooibos tea and were placed at a distance of 20 cm to each other (Fig. 3.2). The initial weight of the tea bag content was determined by subtracting the mean content weight of 5 empty bags from the total tea bag weight (green tea: 1.592 ± 0.004 g; rooibos tea: 1.801 ± 0.006 g). Tea bags were deployed in two consecutive growing seasons. In 2018 (year 1 of the experiment), tea bags were deployed from 19 June to 20 September (= 93 days). In 2019 (year 2), tea bags were deployed from 14 May to 17 July (= 93 days). Following deployment, tea bags were removed from the soil, and the tea material was carefully separated from roots and soil, dried for 48 h at 70°C, and weighed. The calculation of *k* and *S* followed Mueller et al. (2018), who used a different extraction protocol than the original Keuskamp et al. (2013) publication, yielding slightly higher values for the hydroloyzable (= labile) fractions of green and rooibos tea.

(1) $W_r(t) = a_r e^{-kt} + (1 - a_r)$,

(2) $S = 1 - \frac{a_g}{H_g}$,

(3) $a_r = H_r(1 - S)$.

$W_r(t)$ refer the weight of the rooibos substrate after the incubation time (t in days); a_r refers the labile fraction substrate and $1\text{-}a_r$ refers the recalcitrant fraction of the rooibos substrate, respectively; *k* is the initial decomposition rate; *S* is the stabilization factor; a_g represents the labile fraction of green tea substrate, and H_g represents the hydrolysable fraction of the green tea substrate. The labile fraction of the rooibos substrate is calculated in Eq. (3) based on the hydrolysable fraction (H_r) and the stabilization factor *S*. H_g and H_r values are taken from Tang et al. (2021), because the same tea materials were used.

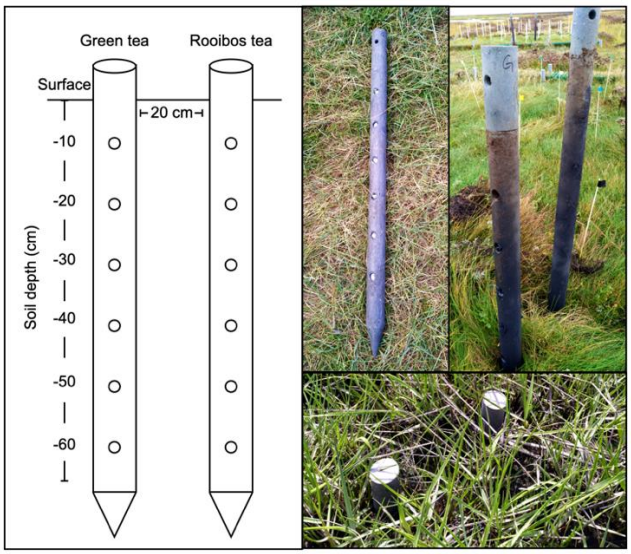

Figure 3.2. Procedure for measuring standardized litter breakdown under in-situ warming. In each plot, two posts with six holes at a distance of 10 cm to -60 cm were put into the soil. One post contained six green tea bags, the other six rooibos tea bags.

3.3.4 | Characterization of soil redox conditions

A soil reduction index was determined based on the *Indicator of Reduction in Soils* technique (IRIS *sensu* Jenkinson, 2002; Rabenhorst, 2015; Mueller et al., 2020b). $FeCl_3$-coated PVC sticks were inserted to a soil depth of 30 cm in three zones along the marsh elevation gradient. There were 6 sticks per zone (n = 6), and 18 (N = 6 x 3) sticks per campaign, in total N = 72 (n = 4 campaigns x 18) sticks were analyzed. These measurements were conducted along a transect directly adjacent to the experimental plots. The Reduction Index describes the fraction of $FeCl_3$ paint that is removed from the PVC stick after four weeks of deployment in the field. The IRIS method utilizes the property of the ferrihydrite paint to be reduced from solid-phase Fe(III) to soluble Fe(II) under anoxic soil conditions and in presence of microbial Fe-reducers. The area of removed paint from PVC sticks is used as a proxy for soil reduction (reduction Index). Upon the 4-wk deployment phase, sticks were removed from the soil and cleaned carefully with tap water to remove soil particles. Each stick was scanned to create digital images for further processing. Image analysis was conducted applying a supervised classification using the software ArcGIS Pro. RGB color values (0-255) of 4300 randomly set points on a test set of sticks were determined. Points were classified as either reduced, not reduced or errors (background, scanning effects). The classification was included in a Random Forest model (confusion matrix 1.5%) using the software R. This model allowed for a pixel-wise classification of the scanned IRIS sticks. Sticks were analyzed in increments of 5 cm, covering a depth gradient from 0 to 30 cm. Reduction Index was calculated as an unitless value ranging from 0 to 1 based on the share of reduced pixels from the total pixels.

3.3.5 | Statistical analyses

Two-way repeated-measures ANOVA were used to test the effects of warming treatment (ambient, +1.5°C and +3°C), ecosystem zone (pioneer zone, low marsh, and high marsh), and soil depth (within subject / repeated measure) on TBI parameters for each year separately. Because we were not primarily interested in year-to-year differences, ANOVAs were used separately for each year to better understand the interactions between warming, zone, and soil depth. Pairwise comparisons were performed using Tukey's HSD tests. The normal distribution of residuals and homogeneity of variance were assessed visually and met ANOVA assumptions.

The temperature-induced change in k and S was calculated relative to the ambient controls (k_0) for each marsh zone separately: Δk (%) = (k_t/k_0 - 1) x 100 and ΔS (%) = (S_t/S_0 - 1) x 100, t represents the value under different warming treatments (i.e., +1.5 and +3.0 ° C). Linear regression was used to analyze the relationships of Δk and ΔS with soil depth.

These analyses were conducted using the statistical software STATISTICA, version 12 (StatSoft Inc, Tulsa, Oklahoma, USA).

3.4 | Results

3.4.1 | Decomposition and stabilization dynamics

Initial decomposition rate (*k*) was increased by warming in both year 1 and year 2 of the experiment (Fig. 3.3, Fig. 3.4). The effect of the +3.0°C treatment (+158.6% in year 1; +234.6% in year 2) was more pronounced than that of the 1.5°C treatment (+162.3% in year 1; +170.39% in year 2). Overall, positive warming effects on *k* appear to be consistent across marsh zones and soil depths (Fig. 3.3a-c, Fig. 3.4a-c), despite a significant depth x zone x warming interaction in year 2, as indicated by ANOVA ($p < 0.01$, Tab. 3.1). We ascribe this significant three-way interaction term to inconsistent depths trends of the warming responses between the marsh zones (Fig. 3.4a-c). That is, the magnitude of the +3.0°C warming effect on *k* decreases linearly with increasing soil depth in pioneer zone and high marsh, whereas the warming effect in the low marsh was maximized at an intermediate soil depth (Fig. 3.4a-c).

The stabilization factor (*S*) was not affected by the warming treatment as a single factor, but by the depth x zone x warming interaction in year 2 of the experiment (Tab. 3.1). Negative effects of warming on *S* were pronounced throughout the whole soil profile of the high marsh (on average -13.6% at +3.0°C; -8.6% at +1.5°C), but were restricted to the upper soil layers in the pioneer zone and low marsh (Fig. 3.4d-f). The soil depth to which *S* responded to warming treatments increased across the marsh elevation gradient from pioneer zone via low to high marsh (Fig. 3.4). While the magnitude of negative warming effects decreased with soil depth in both pioneer zone and low marsh, the opposite was true for the high marsh (Fig. 3.5).

Table 3.1 Results of two-way repeated-measures ANOVA testing for effects of warming (W), marsh zone (Z), soil depth (D), and their interactions on TBI parameters (*k* = initial decomposition rate and *S* = stabilization factor) in year 1 (2018) and year 2 (2019) of the experiment. Significant effects ($p \leq 0.05$) are shown in bold.

		Between subject						Within-subject							
		W		Z		W x Z		D		D x Z		D x W		D x Z x W	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Year 1	*k*	10.67	**0.00**	3.05	0.08	0.89	0.50	10.00	**0.00**	0.48	0.90	1.02	0.44	0.39	0.99
	S	0.00	1.00	56.11	**0.00**	0.71	0.60	32.74	**0.00**	5.39	**0.00**	1.02	0.44	0.84	0.66
Year 2	*k*	36.32	**0.00**	0.17	0.85	0.58	0.68	10.92	**0.00**	1.77	0.10	1.76	0.10	2.23	**0.01**
	S	2.64	0.10	35.67	**0.00**	0.45	0.77	68.87	**0.00**	5.33	**0.00**	0.45	0.89	2.06	**0.02**

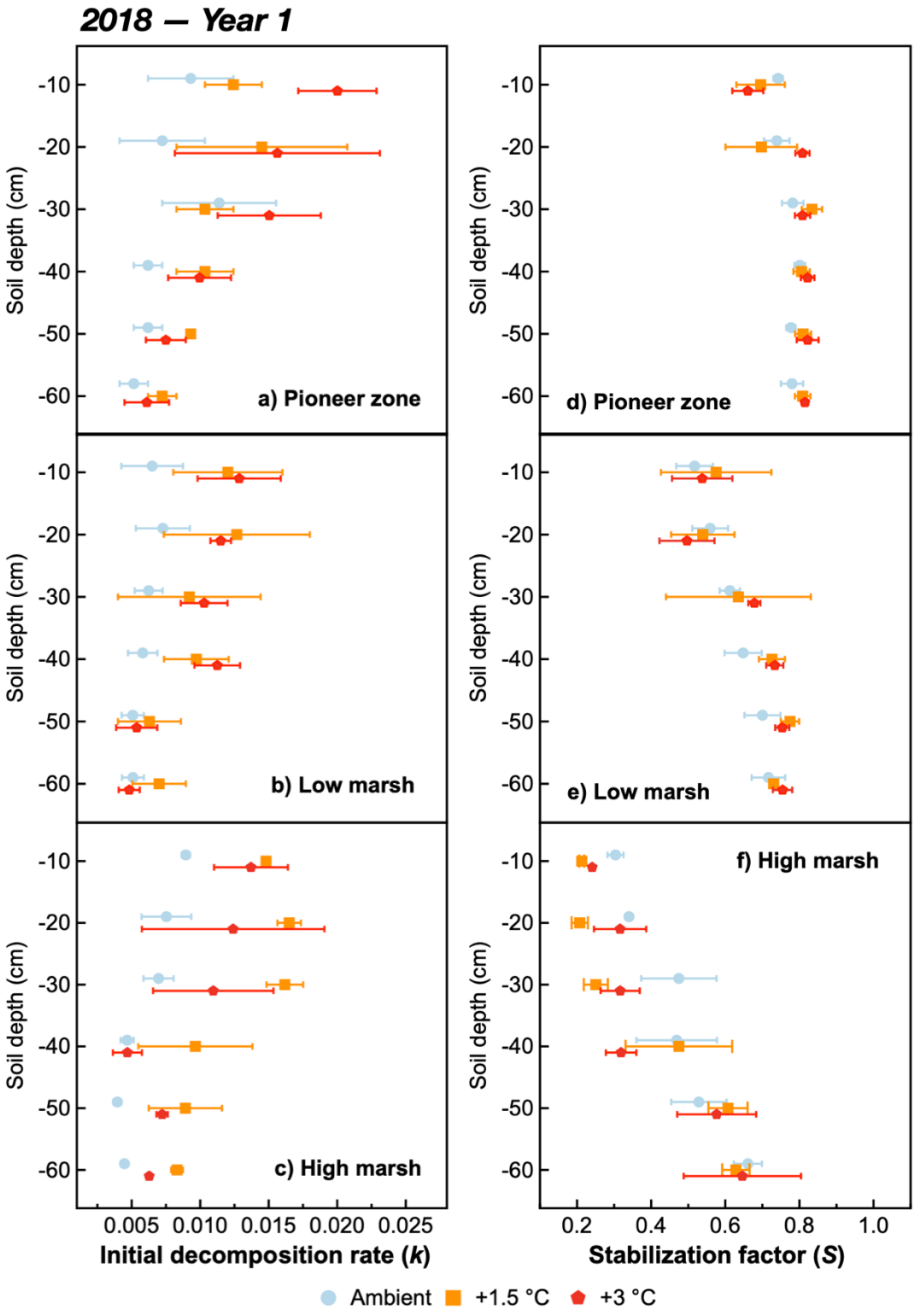

Figure 3.3 The initial decomposition rate (*k*) (a, b, c) and stabilization factor (*S*) (d, e, f) at different soil depths of the pioneer zone, low marsh, and high marsh zones under three temperature treatments (ambient, + 1.5°C and + 3°C) in year 1 (2018). Values are means ± SE (n =3). *k* describes the labile fraction which is decomposed in the deployed material, and *S* presents the part of the labile fraction that did not decompose which stabilized in the soil.

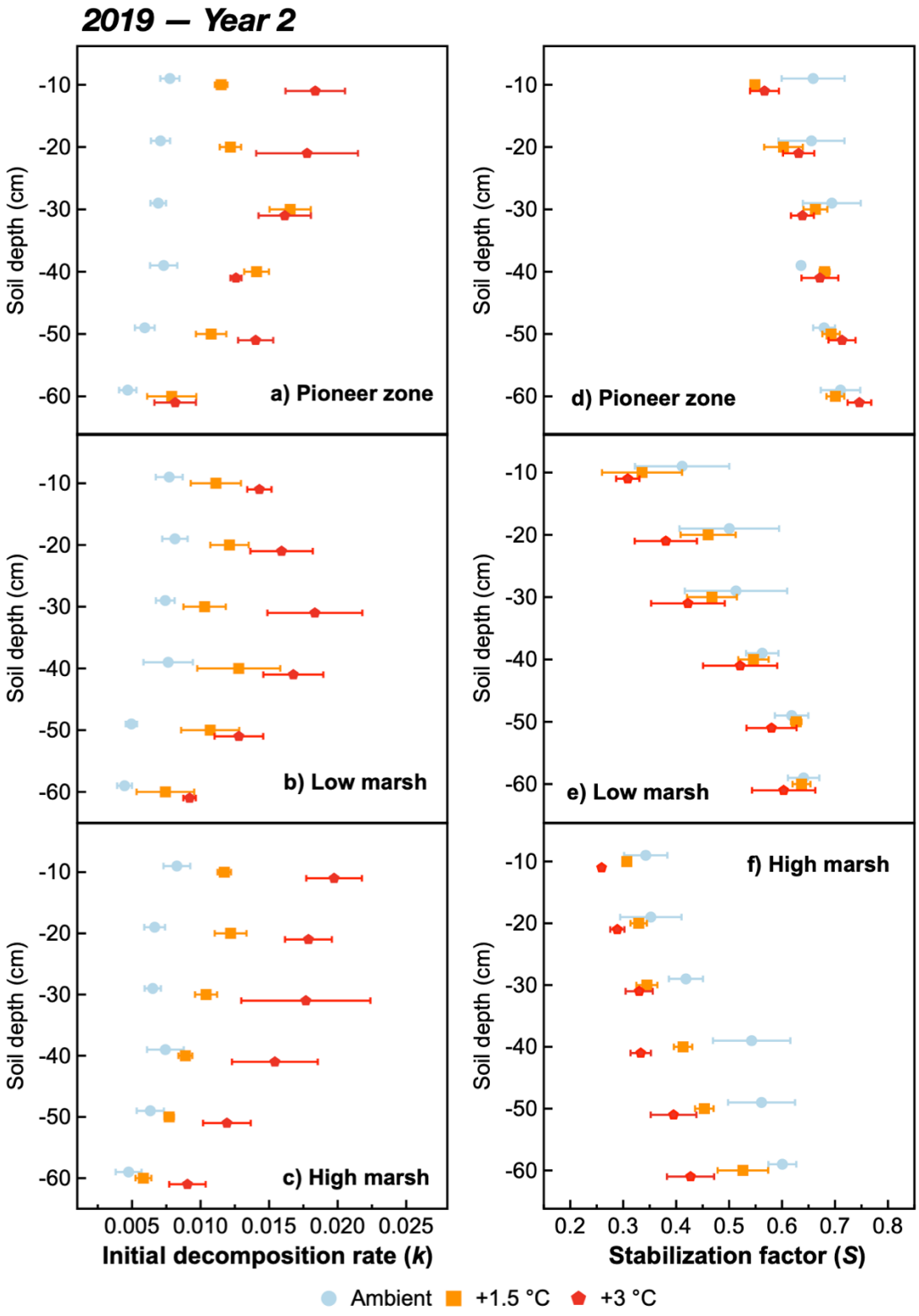

Figure 3.4 The initial decomposition rate (a, b, c) and stabilization factor (d, e, f) at different soil depths of the pioneer zone, low marsh, and high marsh zones under three temperature treatments (ambient, + 1.5°C and + 3°C) in year 2 (2019). Values are means ± SE (n =3). *k* describes the labile fraction which is decomposed in the deployed material, and *S* presents the part of the labile fraction that did not decompose which stabilized in the soil.

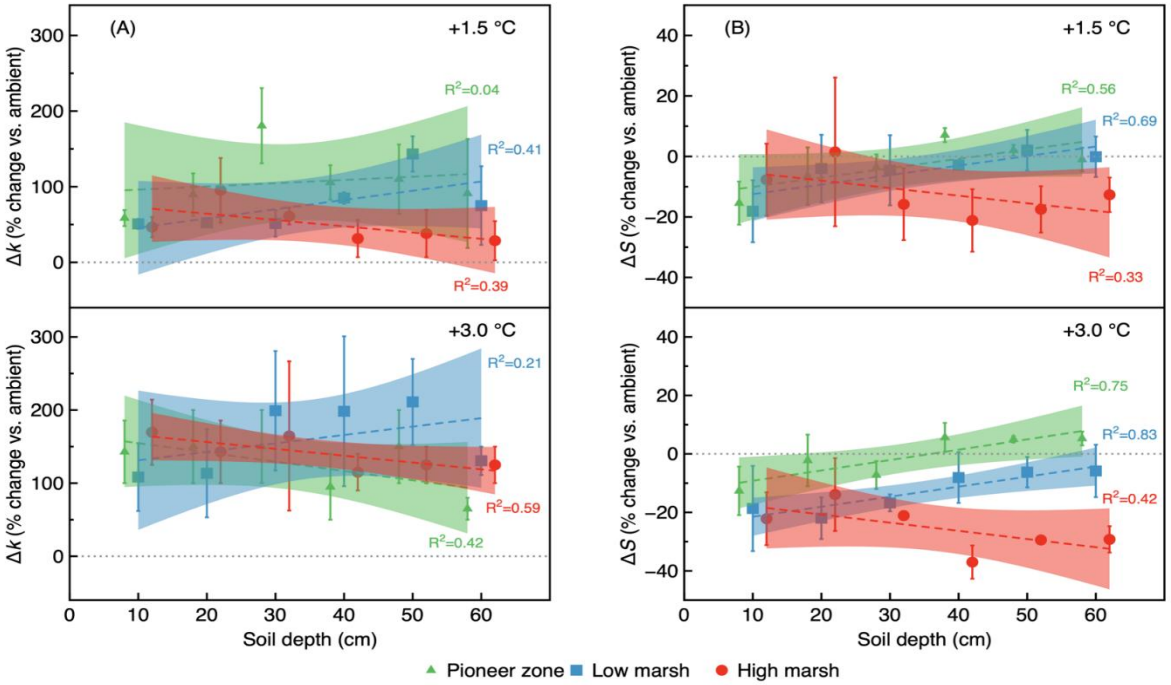

Figure 3.5 Warming-treatment effect size (% change vs. ambient) as a function of soil depth and marsh zone, shown for the initial decomposition rate, Δ*k* [A] and the stabilization factor, Δ*S* [B] in year 2 (2019). Linear regression was used to analyze the relationships of *Δk* and *ΔS* with soil depth.

3.4.2 | Soil redox conditions

Pronounced soil redox gradients both with respect to soil depth and flooding frequency exist at the study site (Fig. 3.6). Reducing soil conditions markedly increase with soil depth and along the flooding gradient from high marsh to pioneer zone. In the frequently flooded pioneer zone, reducing soil conditions are reached closer to the soil surface than in the high marsh (Fig. 3.6).

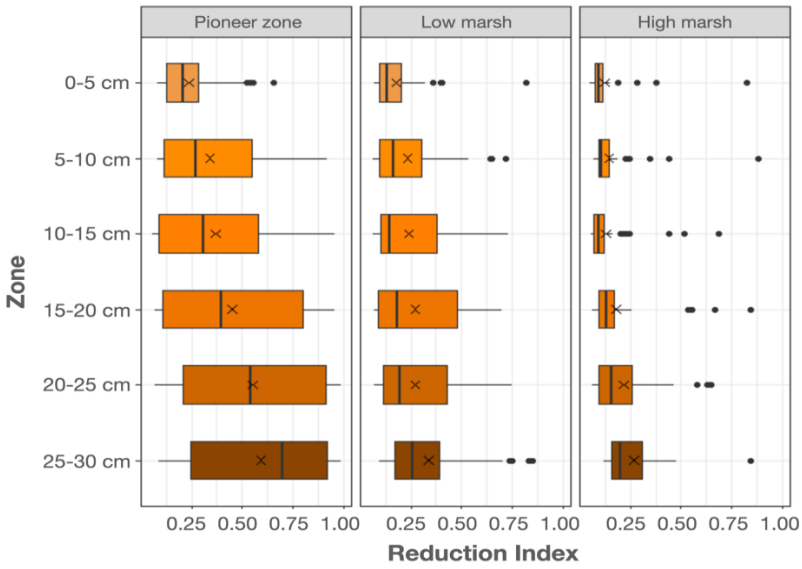

Figure 3.6. Soil reduction in relation to marsh zone and soil depth at the Hamburger Hallig salt marsh site. Shown are median- (black bar) and mean values (black x). The box is giving the interquartile range, and potential outliers are depicted as black points. Data are based on n = 6 observations per zone, deployed over four consecutive deployment campaigns (July-October). The reduction index (0-1) describes the fraction of $FeCl_3$ paint that is removed from the PVC stick after four weeks of deployment in the field.

3.5 | Discussion

3.5.1 | Litter breakdown parameters response to rising temperature

The initial decomposition rate (*k*) was strongly increased by warming across all marsh zones in two consecutive years (Tab. 3.1). By contrast, warming effects on stabilization (*S*) were less consistent and only present in year 2. This finding agrees with an large number of studies, from a range of ecosystems, demonstrating that *k* and *S* can be de-coupled, rather than strictly inversely related (Sarneel & Veen, 2017; Elumeeva et al., 2018; Fanin et al., 2020; Ochoa-Hueso et al., 2020; Sarneel et al., 2020; Tang et al., 2020, Mori et al., 2022).

Our results suggest that the decoupling of warming responses in *k* and *S* is controlled by hydrology or – more specifically – the soil redox status. Soil depth and marsh zone had no effects on *k* (two-way ANOVA, $p > 0.1$), which shows that the initial decomposition rate of labile plant inputs is not influenced by hydrology or the soil redox status. This finding agrees with previous studies demonstrating the effects of oxygen availability on OM decomposition depends on OM quality, and that labile materials decompose at similar rates in oxic and anoxic environments (Benner et al., 1984; Kristensen et al., 1995). By contrast, *S* increased with flooding frequency (i.e., from high marsh to pioneer zone) and with soil depth, indicating that the stabilization of labile materials does depend on the soil redox status. Flooding and soil depth were also the primary constraints of warming effects on *S*. Specifically, warming effects on *S* were restricted to the topsoil in the pioneer zone, but the soil depth to which *S* responded to warming treatments increased across the marsh elevation gradient via low to high marsh (Fig. 3.4d-f).

The here observed redox constraints on warming effects resemble the findings of the SPRUCE (Spruce and Peatland Responses Under Changing Environments) warming experiment operating in a boreal peatland ecosystem in Minnesota, United States. Research in SPRUCE demonstrated a dramatic reduction of warming effects on soil OM decomposition in strongly reducing waterlogged subsoils compared to less reducing topsoils (Wilson et al., 2016; Hopple et al., 2020). It is possible that oxygen constraints on phenol-oxidase activity, following the enzymic-latch hypothesis (Freeman et al., 2001), are responsible for the redox control of warming effects on both the labile OM stabilization observed in our study and soil OM decomposition observed in SPRUCE. The enzymic-latch hypothesis states that phenolic substances accumulate under anoxic conditions, as phenol-oxidase activity requires oxygen, and inhibit the activity of hydrolases responsible for the breakdown of the majority of organic compounds supplied to the soil system. For blue carbon ecosystems, the phenolic-driven reduction of OM decomposition has recently been confirmed for the breakdown of sucrose in seagrass sediments (Sogin et al., 2022), demonstrating that even the breakdown of short-chained and labile sugars can be affected by the enzymic latch. The application of the enzymic latch hypothesis to the findings of the present study is not straightforward, because it is unclear how an accumulation of phenolics could increase the stabilization of labile OM, as well as the warming sensitivity of this process, but not their initial decomposition rate. It is however possible that initial microbial processing increased the

secondary chemical recalcitrance of originally labile OM (Lützow et al., 2006; Prescott, 2010) thereby increasing the sensitivity to phenolic inhibition of downstream enzymatic processes.

The current state of science lacks a mechanistic understanding of labile OM processing and stabilization in wetland soils, so that we cannot easily build hypotheses to explain the here observed redox control. For terrestrial soil systems, an increasing number of studies highlighted the importance of labile OM stabilization for long-term soil C storage (e.g., Lützow et al., 2006; Cotrufo et al., 2013). Along with this, the prevailing concept of terrestrial soil OM formation was called into question stating that primarily recalcitrant OM inputs (i.e., non-hydrolysable compounds, such as phenolics) stabilize in the soil matrix and build the soil OM pool (e.g., Lützow et al., 2006; Schmidt et al., 2011). The Microbial Efficiency-Matrix Stabilization (MEMS) framework hypothesizes that labile plant inputs are the primary source for soil OM formation. Specifically, the MEMS framework considers labile plant inputs as the dominant microbial substrate source and thus, the dominant source of microbial decomposition products. Microbial decomposition products, in turn, are the main precursors of stabilized soil OM, which forms through aggregation or strong chemical bonding to the mineral matrix in terrestrial soils (Cotrufo et al., 2013). It is questionable if MEMS or related frameworks can be applied to wetland soils, because here physical protection through mineral armoring is largely absent in organic soils and hypothesized to be of little consequence in tidal mineral soils, which often lack aggregates owing to low fungal activity and wet–dry cycles (Kirwan and Megonigal, 2013; but see Spivak et al., 2019). We therefore hypothesize that secondary recalcitrance of originally labile organic compounds via microbial processing (Lützow et al., 2006) plays a larger role for the stabilization of labile OM inputs in many wetland soils than do aggregation and other interactions of OM with the mineral matrix.

Our data suggest that warming effects on litter breakdown are not necessarily linear. In year 1 of the experiment, 1.5°C warming had a stronger positive effect on the initial decomposition rate than 3.0°C warming in the high marsh. We doubt that potential warming-induced drought effects in the soil surface were the responsible driver of this pattern, because higher k under +1.5°C vs. +3.0°C warming was relatively consistent throughout the 60-cm soil profile. Instead, it is possible that plant-microbe interactions caused the observed pattern. For instance, warming-stimulated nutrient demands and belowground trait responses in plants could have negatively affected microbial communities via competition for nutrients (Noyce et al., 2019).

While qualitatively, warming effects on k and S were often similar between year 1 and 2, and effects were generally much more pronounced in year 2 compared to year 1 (Fig. 3.3, Fig. 3.4). The experimentally achieved temperature difference values were consistent between years (Tab. S3.1); however, differences in the actual temperature (not temperature difference) and the seasonal shift of 13 weeks between the two incubation periods of year 1 and 2 deployment phases could have affected the magnitude of warming effects. Absolute soil temperatures were lower in year 2 than 1 (Fig. S3.1), which could have resulted in the amplified warming effect. It is also possible that changes in the microbial

community with increased treatment duration and/or greater microbial biomass as warming stimulated plant growth and substrate input to the soil system contributed to the observed effect amplification over time.

3.5.2 Methodological considerations

The use of PVC posts may have affected drainage and thus redox conditions of the deployed litter materials after flooding events. This could have amplified the redox differences between frequently and rarely flooded vegetation zones we observed. However, we argue that this potential effect on drainage is unimportant for the interpretation of our results, because our study was primarily designed to gain qualitative insight, not to capture actual rates of litter breakdown.

Compared to most previous studies which used the TBI to investigate litter breakdown in surface (approx. 5 cm depth) soils according to the original TBI protocol (e.g., Mueller et al., 2018; Marley et al., 2019; Sarneel et al., 2020; Fanin et al., 2020), our present study used the TBI to assess litter breakdown in whole-soil profiles (10 – 60 cm depth) in order to improve the mechanistic understanding of belowground carbon turnover. One important caveat in this respect is that we do not know how TBI materials relate to the quality and microbial accessibility of native belowground inputs, namely root litter and rhizodeposits such as exudates. Warming and other climate change drivers are expected to induce changes in the quality of plant litter and other organic matter inputs accumulating in salt-marsh soils, for instance through shifts in the plant community composition that can potentially counterbalance or amplify the effects on decomposition processes described here (Mueller et al., 2018, 2020a) Future research within the MERIT project will therefore address litter quality-feedback effects on decomposition processes in order to gain a more complete understanding of warming effects on salt-marsh soil carbon cycling.

While the quality of TBI materials is likely to somewhat resemble the quality of root litter, it is questionable if this study can be used to infer anything about the turnover dynamics of root exudates – known to represent a considerable belowground carbon flux (Canarini et al., 2019). In this context, it is also important to note that the TBI, as well as native-litter bag techniques, likely reduce the influence of aggregate protection in relation to plant inputs under natural conditions. It is therefore possible that important stabilization mechanisms of terrestrial soils, relying on aggregation or chemical interactions with the mineral matrix, cannot be adequately captured by the method. The importance of these stabilization mechanisms in wetlands soils, however, remains to be evaluated (Kirwan & Megonigal, 2013; Spivak et al., 2019).

A number of recent studies have highlighted the importance of dissolved organic carbon (DOC) and nutrient leaching during early litter breakdown in the context of the TBI (Marley et al., 2019; Lind et al., 2022). Because leaching is a rapid process, particularly in wetlands, we assume that, in the present study, leaching was complete and thus, did not contribute to the observed variability in k and S. Indeed,

k did not increase, and *S* did not decrease with flooding (elevation gradient) or soil moisture (depth gradient) suggesting that leaching did not (overly) affect the variability of the data presented here.

3.5.3 | Conclusion

Our results show that warming can strongly increase the initial rate of labile litter decomposition, but has less consistent effects on the stabilization of this material. This finding suggests that warming may accelerate carbon and nutrient cycling through stimulated initial decomposition rates, whereas soil organic matter formation and carbon sequestration through stabilization may be less consistently affected. We argue that the differential outcome of warming effects on initial decomposition rate and stabilization factor were mediated by the soil redox status, with redox conditions constraining the warming response of litter stabilization but not its initial decomposition rate. Because belowground organic matter turnover is a key determinant of surface elevation gain and carbon sequestration in blue carbon ecosystems, our findings may yield important implications for our understanding of climate change effects on ecosystem stability and carbon sequestration in the coastal zone.

3.6 | Competing interests

The authors declare that they have no conflict of interest.

3.7 | Data availability

All data presented in this paper are available upon reasonable request.

3.8 | Acknowledgements

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3.9 | Supporting information

Table S3.1 Mean soil temperature differences (°C) between ambient and warmed treatments in year 1 and year 2.

Year	Treatment	Pioneer zone	Low marsh	High marsh
Year 1 (2018)	+ 1.5°C	1.21	0.99	1.66
	+ 3°C	1.61	2.08	2.81
Year 2 (2019)	+ 1.5°C	1.82	1.26	1.43
	+ 3°C	2.81	2.06	2.07

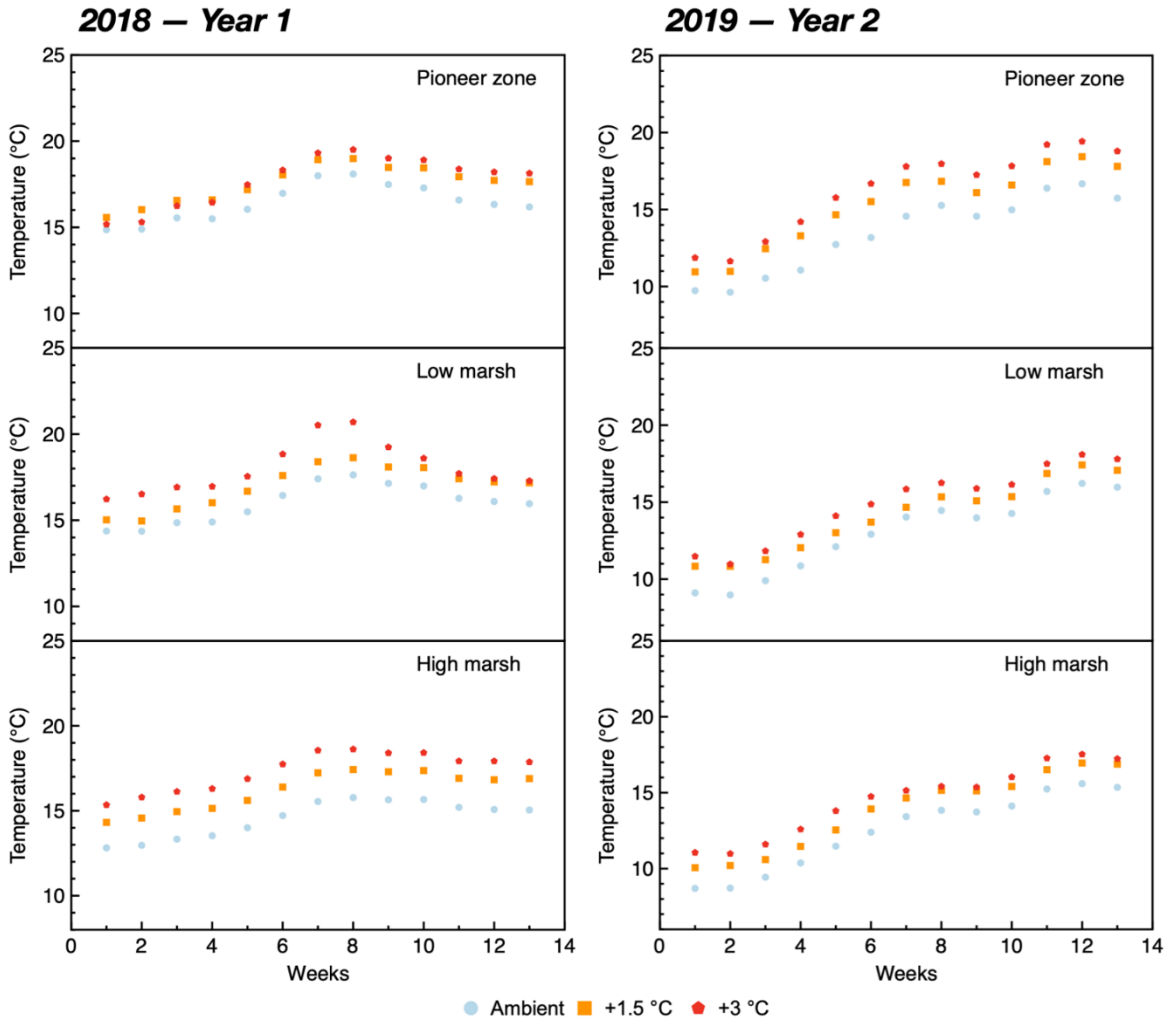

Figure S3.1 Soil temperature across marsh zones and warming treatments during the incubation phases of year 1 and year 2. Shown are means across all soil depths.

Chapter 4 | Hydrology Masks Warming Effects on Microbial Communities in Salt Marsh Soils

Julian Mittmann-Goetsch, Peter Mueller, Kai Jensen, Susanne Liebner, Simon Thomsen, Roy Rich, Alexander Bartholomäus, Johann Jaitner, Viktoria Unger

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„El agua canta siempre bajo el temblor del bosque"

– Federico García Lorca

4.1 | Abstract

Soil microbial communities play a pivotal role in salt marsh ecosystem functioning, driving processes such as organic matter decomposition and greenhouse gas cycling. Despite their importance, it remains unclear how climate warming will affect the diversity and activity of salt marsh soil microbial communities, limiting our ability to predict the fate of the vast stores of soil organic carbon in these so-called blue carbon ecosystems. Here, we leveraged the Marsh Ecosystem Response to Increased Temperature (MERIT) experiment to investigate the effects of sustained warming on the structure and function of the putatively active microbial community, as assessed by rRNA transcripts, alongside measurements of exo-enzymatic activities involved in carbon and nitrogen acquisition. Our results reveal that, after five years of experimental warming by +1.5 and +3 °C, the overall structure of the active microbial community remains remarkably stable, suggesting a high degree of resilience to elevated temperatures in this dynamic environment. However, warming selectively promoted drought-tolerant phyla, particularly Actinobacteriota and Firmicutes, which are known for their ability to degrade complex organic compounds and withstand desiccation. These findings suggest that while the active microbial community is broadly resistant to warming, subtle compositional shifts may enhance decomposition of recalcitrant soil carbon.

4.2 | Introduction

Salt marshes — semi-terrestrial wetlands that primarily occupy the intertidal zone at temperate latitudes — are important sinks for greenhouse gases. They are highly efficient at capturing and converting carbon dioxide to plant biomass and ultimately soil organic carbon (McLeod et al., 2011). Despite covering only a small fraction of the global ocean's surface, salt marshes, along with other blue carbon ecosystems such as mangroves and seagrass beds, account for approximately 50% of total organic carbon burial in marine soils and sediments (Duarte et al., 2013; Spivak et al., 2019). High rates of carbon accumulation in salt marsh ecosystems are the result of an imbalance in plant primary production and microbial decomposition of organic matter (Kirwan & Megonigal, 2013; Temmink et al., 2022). Microbial decomposition is inhibited by the lack of more energy efficient electron acceptors (i.e. oxygen), reducing overall soil carbon turnover (Almahasheer et al., 2017).

Salt marshes are characterised by hydrology-driven gradients (e.g. salinity, soil redox), which are strongly reflected in gradients of biotic communities (e.g. plants, animals, microbes) (Suchrow & Jensen, 2010; Klink et al., 2016; Dinter et al., 2019). Both elevation and soil-depth gradients are characterised by strong differences in soil redox potential (Rich et al., 2023; Tang et al., 2023; Mittmann-Goetsch et al., 2024). While soil redox does not always decrease with soil depth or decreasing surface elevation, the measurement of both parameters serves as an effective predictor for plant community composition (Davy et al., 2011). Many studies have shown that changes in abiotic conditions such as hydrology are reflected in changes in the microbial communities (Hernández et al., 2020, 2021; Unger et al., 2021; Kim et al., 2022). Microbial abundances and functioning (exo-enzymatic activities) were shown to have clear responses to hydrology (Mueller, et al., 2020b; Tang et al., 2021). Similarly, salinity can alter both organic matter decomposition rates (Luo et al., 2019) and microbial community composition (Neubauer et al., 2018; Dang et al., 2019). While hydrology-driven factors, such as salinity and soil redox are strong predictors for biotic communities and their functioning, the combined influence of hydrology and warming have rarely been studied *in situ*.

Along with other global change factors, temperature rise is expected to alter carbon cycling (i.e. carbon sequestration) in salt marshes (Buschbaum et al., 2024). While salt marshes are highly effective carbon sinks, higher temperatures can accelerate soil respiration and potentially offset gains in carbon storage in these ecosystems (Bond-Lamberty & Thomson, 2010). Yet, several studies highlight that salt marsh plants are resilient to moderate warming. This has been found for both aboveground- (Noyce et al., 2019) and belowground plant net primary production (Charles & Dukes, 2009; Smith et al., 2022). The response of organic matter decomposition to warming in salt marsh soils is still poorly understood, however the substantial carbon reservoir stored in salt marsh soils presents a risk of positive feedbacks to global warming (Kirwan & Blum, 2011). This is due to the lack of salt marsh warming experiments involving well-controlled and realistic warming treatments across whole-soil profiles (Rich et al., 2023).

First results from two existing field experiments employing whole-soil warming in coastal marshes reveal a potential for greater carbon loss (as respiration) with warming; this effect, however, is strongly mediated by hydrology and substrate composition (Smith et al., 2022; Tang et al., 2023). While in a micro-tidal, organic-rich salt marsh, belowground carbon accumulation was stimulated by moderate warming, and decreased only with higher warming (Smith et al., 2022) organic matter decomposition rates were consistently higher with moderate and strong warming in a minerogenic, organic-poor salt marsh (Tang et al., 2023). This positive feedback can offset the carbon sequestration potential of salt marshes (Kirwan & Blum, 2011). Hydrology and soil redox have strong leverage over warming effects. Anoxic conditions might "lock" carbon stocks away from warming effects, due to the accumulation of enzyme-inhibiting phenolic compounds (Freeman et al., 2001; but see Urbanová & Hájek, 2021). Differences in site conditions across the elevational gradient of a salt marsh have been found to outweigh temperature effects (i.e. seasonal), to a large extent (Rinke et al., 2022; Tebbe et al., 2022). Studies from a peatland warming experiment corroborate these findings, showing a supressed response of subsoil organic matter decomposition to warming compared to topsoil decomposition (Wilson et al., 2016; Hopple et al., 2020).

It has been posited that certain soil microbial groups are likely to thrive under warmed conditions. In particular, warming may enhance the ability of microbes to degrade more recalcitrant organic matter. Both Actinobacteriota and Firmicutes are well known for their ability to degrade complex organic compounds (P. Chen et al., 2016; Ni et al., 2024) and are expected to respond positively to increased temperatures given their resistance to desiccation (Oliverio et al., 2017; Wu et al., 2022). However, studies on the effects of warming on the soil microbial community structure in salt marshes are scarce, and even fewer examine the putatively active microbial pool. Limitations in commonly applied methods such as DNA-based amplicon sequencing, may obscure our ability to detect changes. For example, extracellular DNA can persist in soils outside of living cells, masking shifts in community composition (Schnecker et al., 2024). Additionally, 16S rRNA gene sequencing of DNA includes dormant microbes, which are particularly abundant in salt marsh systems (Kearns et al., 2016). While approaches that separate extracellular DNA from intracellular DNA offer a promising way to better distinguish living microbial communities from relic DNA, these methods are technically challenging and require optimization tailored to specific soil types to yield reliable results (Alawi et al., 2014; Medina Caro et al., 2023). To overcome these challenges, total RNA analysis has emerged as a more precise approach for assessing changes in active microbial communities in salt marshes (Emery et al., 2019).

This study aims to assess the combined effects of climate warming and hydrology on microbial community structure and functioning in salt marsh soils. The study was conducted in a whole-ecosystem warming experiment, situated in a highly dynamic minerogenic salt marsh on the mainland coast of the German Wadden Sea, characterized by steep abiotic gradients in both salinity and soil redox (Rich et al., 2023). Both gradients are predominantly hydrology driven and vary along both elevation (marine-

terrestrial) and soil-depth gradients. To our knowledge, this is the first study examining the effect of active belowground soil warming on the structure and function of salt marsh soil microbes *in situ*.

We hypothesized that (1) warming would increase microbial exo-enzymatic activity and (2) alter the community composition of putatively active microbes, characterized by higher relative abundances of microbes with the ability to degrade complex carbon compounds. We further hypothesized that (3) warming effects would be more pronounced in areas with less extreme hydrological conditions.

4.3 | Material & Methods

4.3.1 | Site-description and experimental design

The MERIT (Marsh Ecosystem Response to Increased Temperature) experiment was established in 2018 in a Wadden Sea salt marsh on the Hamburger Hallig (54°36′06.7″N 8°48′57.4″E) in Germany, where tidal amplitude averages 3.4 m and accretion rates range from 3.0 to 12.9 mm yr^{-1} (Nolte et al., 2013). MERIT is a whole-ecosystem warming experiment with passive aboveground and active belowground warming to a depth of 100 cm. Aboveground warming is applied by open-top chambers that trap heat and incoming radiation. Active belowground warming is accomplished by a combination of horizontal (GX-088L3106 GX, 9.8 Ω/m, 240 V) and vertical heating cables (GX 088L3100, 9.8 Ω/m, Danfoss, Denmark). MERIT consists of three 8 m^2 replicate plots in three elevational marsh zones located along the marine-terrestrial ecotone (pioneer zone, low marsh, high marsh) with three temperature treatments (ambient, +1.5°C, +3.0°C) leading to a total of 27 plots. The zones are characterized by differences in hydrology, soil redox conditions, and vegetation. The pioneer zone lies at the lowest elevation and is inundated almost daily during high tide. Here, soils remain waterlogged for extended periods, favoring strongly reduced conditions. Vegetation is sparse and dominated by *Spartina anglica* and *Salicornia europaea* with a low canopy height (~24 cm) (Nolte et al., 2013; Rich et al., 2023). The low marsh is inundated less frequently, mainly during spring tides, resulting in a shorter hydroperiod and somewhat less reducing soil conditions compared to the pioneer zone. Vegetation is more diverse, forming a patchy community dominated by *Puccinellia maritima*, *Atriplex portulacoides*, and *Limonium vulgare* with a mean canopy height of ~22 cm (Nolte et al., 2013; Rich et al., 2023). At the highest elevation, the high marsh (HM) is flooded only occasionally, typically during storm tides in autumn and winter. Soils here drain more rapidly and are less frequently reduced. Vegetation is dominated by tall *Elymus athericus* stands (mean canopy height ~30 cm), forming dense monocultures that contrast with the more heterogeneous vegetation of the lower zones (Nolte et al., 2013; Rich et al., 2023). A detailed description of the experimental facility and its performance is given in Rich et al. (2023).

4.3.2 | Soil sampling and processing

Soil sampling was conducted in September 2022. Sampling positions were chosen to have a similar distance to deep heating cables (d = 5cm), sampling in close proximity without coring directly next to the heating cables, to avoid artificial effects of heating cables. Four replicate soil cores (100 cm deep)

were taken from each of the N = 27 plots, using a 2.5-cm diameter gouge auger. The auger was rinsed with ethanol and DI water after each sampling to avoid microbial cross-contamination. Cores were cut into depth increments (0-5 cm, 5-10 cm, 20-30 cm, 40-50 cm, 80-100 cm) resulting in five samples per core. These samples were then stored at -20°C until further analysis. Subsamples for RNA analysis were taken during sampling, from one of the four replicate cores, using a sterilized spatula, carefully scratching of material from the entire depth segment and storing it in a 5 ml Eppendorf tube. All tools used to cut and subsample increments were rinsed after every sample. RNA subsamples were immediately stored on dry ice in the field and during transport to the lab and were stored at -80°C until RNA extraction. The organic matter content was determined for every sample following standard loss on ignition protocols (Heiri et al., 2001).

4.3.3 | Exo-enzymatic activity

Fluorometric exo-enzyme assays were conducted to measure activities of five hydrolytic enzymes involved in microbial carbon (ß-Glucosidase, GLU) and nitrogen acquisition (Chitinase, CHI; Leucine Aminopeptidase, LEU). Frozen field samples were homogenized and a 2 g subsample was transferred into a 50-ml Falcon Tube. Soil slurries were prepared by adding 20 ml deionized water and mixing thoroughly. Exo-enzyme assays followed a standard protocol by Mueller et al. (2017). Assays were conducted in 96-well plates on a Multi-Detection Microplate Reader (Bio-tek Synergy ^{TM} HT, Winooski, USA). Substrate concentrations were at 1.6 mmol/L. Plates were incubated in the dark for 16-24 hours at 20°C. Emission and excitation wavelengths were set to 460 nm and 365 nm, respectively. Due to the high carbonate buffer potential of the samples, assays were not buffered beforehand.

4.3.4 | Soil RNA extraction and 16S rRNA amplicon sequencing

Total RNA was extracted from soil samples using the GeneMATRIX Environmental DNA & RNA Purification Kit (Roboklon, Germany) according to the manufacturer´s protocol. Extracted RNA was purified using the Turbo DNA-free kit (Thermo Fisher, Germany). Reverse Transcriptase PCR was performed to convert single-stranded RNA into complementary DNA (cDNA). In a PCR tube placed on ice, the following components were combined to a total volume of 13 µl: 10 µl of sterile distilled water, 1 µl of 10 mM dNTP mix (Invitrogen, USA), 1 µl of $pd(N)_6$ random hexamer primers (GE Healthcare, USA), and 1 µl of RNA sample. The mixture was heated at 65°C for 5 minutes in a PCR machine (Bio-Rad, USA) to denature secondary structures, then immediately cooled on ice. After a brief centrifugation, the following reagents were added: 1 µl of sterile distilled water, 1 µl of 0.1 M DTT, 1 µl of SuperScript III Reverse Transcriptase (Thermo Fisher, Germany) and 4 µl of 5 x First-Strand Buffer. The reaction mixture was gently mixed by pipetting. To facilitate primer annealing, the reaction was incubated at 25°C for 5 min, followed by a 60 min incubation at 50°C for reverse transcription. The reaction was terminated by heating at 70°C for 15 min to inactivate the enzyme. cDNA concentrations were quantified using a Qubit 2.0 Flurometer (Invitrogen, USA) with the dsDNA HS and BR assay kits (Thermo Fisher, Germany). Amplicon libraries' preparation was done by using in-house barcoded

primer pairs targeting the V3-V4 hypervariable regions of the 16S rRNA (Uni515-F: GTGTGYCAGCMGCCGCGGTAA; Uni806-R: CCGGACTACNVGGGTWTCTAAT). PCR reactions (25 µl) consisted of 10x Pol Buffer C (Roboklon, Germany), 0.5 µM of each primer, 0.2 mM dNTP mix (Thermo Fisher, Germany), 2 mM $MgCl_2$, 1.25 U Optitaq Polymerase (Roboklon, Germany), PCR water and 1 µl of template cDNA. PCR water and RNA extract were used as negative controls. The PCR program was set as follows: initial denaturation (5 min, 95°C), 32 cycles of denaturation (30 sec, 95°C), annealing (30 sec, 56°C), elongation (1 min, 72°C) and a final elongation (7 min, 72°C). Purification of PCR product was done using the HighPrep™ PCR clean-up-reagents (Magbio Genomics inc, USA) according to manufacturer protocol. Concentrations of recovered PCR products were equilibrated and pooled together with positive and negative controls. The pool was sent for sequencing to Eurofins Genomics (Germany). The library preparation was done by PCR-free adapter ligation. Sequencing was done on the Illumina MiSeq platform using 2 x 300 bp paired end mode using the V3 chemistry.

4.3.5 | Processing of 16S rRNA amplicon data

Sequencing data was demultiplexed using cutadapt version 3.4 (Martin, 2011) with the parameters -e 0.2 -q 15,15 -m 150 --discard-untrimmed. Amplicon sequence variants (ASVs, a proxy for phylogenetic species) were generated with trimmed reads and the DADA2 package version 1.20 (Callahan et al., 2016) in R version 4.1. For this, the pooled approach with the filtering parameters maxN=10, truncQ=20, rm.phix=TRUE and minLen=150 were used. Read pair merging was done using function “mergePairs” provided by the DADA2 package. Taxonomic assignment of the ASVs was done using DADA2 and the SILVA database version 138.1 (Quast et al., 2013). Further data processing was performed in R (version 4.4.2, R Core Team, 2024) with the help of RStudio (version 2024.09.1+394, Posit team, 2024) and the packages ggplot2 (Wickham, 2016), phyloseq (McMurdie & Holmes, 2013), plyr (Wickham, 2011), and vegan (Oksanen et al., 2025). ASVs that were assigned to chloroplasts or mitochondria and singletons were removed before rarefaction to 5000 reads per sample. To assess the metabolic potential of the assigned ASVs, we used the Functional Annotation of Prokaryotic Taxa (FAPROTAX) (Louca et al., 2016).

4.3.6 | Quantification of 16S rRNA gene copy numbers

Quantitative polymerase chain reaction (qPCR) was employed to assess bacterial 16S rRNA gene abundance in soil samples collected in May 2023. Soil samples were collected to a depth of 30 cm using a gouge auger (d = 1.2 cm). The cores were sectioned into two depth increments (0-10 cm and 20-30 cm). DNA was extracted using the NucleoSpin® Soil Kit (NucleoSpin, Germany) according to manufacturer’s protocol, with the exception that elution was carried out using autoclaved, ultrapure water. For the plasmid standard curve, *E. coli* DH5α cells transformed with the 16S rRNA gene were cultured, and their plasmid DNA was extracted using the Presto™ Mini Plasmid Kit (Geneaid, Taiwan). DNA concentrations of both the soil samples and *E. coli* DH5α cells eluate were quantified at 280 nm

using a NanoDrop 2000 spectrophotometer (Thermo Scientific, USA). The *E. coli* plasmid eluate was diluted to 30 ng/µl and used to create a five-step dilution series up to a dilution of 1:100000, while the eluate from the soil samples was diluted once to 1:10. qPCR was carried out using the Eub341F and Eub534R primers (Muyzer et al., 1993) and SsoAdvanced™ Universal SYBR® Green Supermix on a Bio-Rad CFX96 system (Bio-Rad, USA). Cycling conditions included an initial denaturation at 98 °C for 180 s, followed by 40 cycles of 95 °C for 15 s, 60 °C for 30 s, and 72 °C for 15 s, followed by melt curve analysis. A melt curve analysis was performed from 60 °C to 94 °C with a ramp rate of 0.56 °C per second. A standard curve was generated from the dilution series, relating measured Ct values to $\log_{10}$-transformed copy numbers calculated from known plasmid (pDrive: 3851bp) and vector length (194bp) as well as measured DNA-concentrations. Gene abundance were calculated as $\log_{10}$ copies per gram organic matter.

4.3.7 | Soil reduction, soil temperature and elevation data

IRIS-sticks (Indicator of Reduction in Soils) were used to determine a soil reduction index. The method followed Rabenhorst & Burch (2006) and was adapted by using flat PVC-sticks, to simplify the scanning process (Mueller et al., 2020b). Fe oxides were applied to white PVC-sticks (80 cm length) and deployed into the soils for six weeks. The capacity of solid-phase Fe (III) oxides to be reduced, by microbial Fe reducers, to soluble Fe (II) under anoxic conditions is used to assess soil-reduction in soils. After six weeks of deployment, sticks were carefully taken out of the soil and rinsed with tap-water. After drying, sticks were scanned using an overhead scanner (Viisan, China). Using a supervised classification, white areas on the sticks were determined (Mittmann-Goetsch et al., 2024). Reduction index was calculated as the share of white pixels from total pixels. Two consecutive campaigns, with duplicate 80 cm long IRIS sticks per plot, were conducted in 2023, spanning from six weeks prior to the soil sampling days in the previous year, until six weeks after. Depth increments were pooled together, to align with the soil layers from the microbial analysis (see 2.8 Statistical analysis). Per plot duplicate measurements of marsh surface elevation were conducted in 2024 using a DGPS device (ppm GmbH, Germany). Marsh surface elevations were calibrated to calculate elevation above mean high tide (MHT). Belowground temperatures were measured continuously in all plots using thermistors at 25 cm and 75 cm depth (Rich et al., 2023). Mean monthly temperatures were calculated per plot using temperature data ranging back one month before the soil-sampling date on 11th of September in 2022.

4.3.8 | Statistical analyses

Rooting depth patterns at our sites guided the definition of two soil depth intervals. For microbial analyses, soil samples were pooled into a topsoil layer (0–30 cm) with strong live root influence and a subsoil layer (40–100 cm) with minimal live root influence. For redox characterization, reduction indices derived from IRIS sticks were pooled over the same topsoil layer (0–30 cm) but only down to 80 cm depth in the subsoil (40–80 cm), reflecting the installation depth of the probes. For all analyses the enzymes Leucine-Aminopeptidase and Chitinase were combined into nitrogen acquiring enzymes,

to allow for a comparison with the carbon acquiring enzyme ß-Glucosidase. We used nested mixed effect ANOVA models with fixed effects (zone, layer, temperature) and random effects (core ID, Plot ID), to test for differences in microbial exo-enzymatic activities between the three elevational zones (pioneer zone, low marsh, high marsh), the soil-layers (topsoil 0-30 cm, subsoil 40-100 cm) and the temperature treatments (ambient, +1.5°C, +3.0°C). A similar model was used to test for differences in alpha diversity (Shannon index) of microbial communities without random effect for core ID. The qPCR data were analysed with a nested mixed effect ANOVA model for differences in abundance of bacteria (EUB primer pairs) between zones and warming treatments. Prior to calculating mixed effect ANOVA models, we visually inspected residuals for normal distribution and assessed the homogeneity of variances across groups. Given the fully balanced design of the study, potential moderate deviations from variance homogeneity were considered negligible for the validity of the ANOVA results (McGuinness, 2002; Schielzeth et al., 2020). A non-metric multidimensional scaling (NMDS) was performed based on Bray-Curtis distances from the microbial communities. Permutational multivariate analysis of variance (PERMANOVA) was performed, with Bray-Curtis distances to estimate the effect of experimental factors (zone, treatment, layer) on the microbial communities assed by rRNA transcripts. A correlation matrix between all metric environmental variables (soil elevation, soil reduction, soil temperature) and microbial response variables (exo-enzyme activities, alpha diversity) was calculated using Pearson correlations. Correlations were adjusted using the Holm correction. A Distance-decay analysis was performed using the Bray-Curtis distances and Δ values of environmental variables (Δ soil elevation, Δ soil reduction, Δ soil temperature). All statistical analyses were conducted with the software R Studio version 4.4.1 (R Core Team, 2024). Data was prepared using R packages dplyr (Wickham et al., 2023), broom (Robinson et al., 2025) and lubridate (Spinu et al., 2024). All plots were created using R package ggplot2 (Wickham, 2016) with extensions ggpubr (Kassambara, 2020) and ggpmisc (Aphalo, 2024). Nested mixed effect ANOVA models were calculated using R package, lme4 package (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2023). Tukey´s pairwise comparisons were performed using the R package emmeans (Lenth et al., 2024). PERMANOVA was calculated using the R package vegan (Oksanen et al., 2025), pairwise comparison was performed using pairwiseAdonis (Arbizu, 2020).

4.4 | Results

4.4.1 | Exo-enzymatic activity

Exo-enzymatic activity of the carbon acquiring enzyme ß-Glucosidase differed significantly between elevational zones ($F = 14.79$, $p < 0.001$) and between soil layers ($F = 90.75$, $p < 0.001$, Fig. 4.1a). Both factors also showed a significant interaction effect ($F = 4.16$, $p < 0.05$). High marsh soils showed significantly higher carbon acquisition enzyme activity than samples from both pioneer zone and low marsh. Carbon acquisition enzyme activities were significantly higher in the topsoil layer compared to the subsoil layer ($p < 0.001$). While carbon acquisition enzyme activities did not significantly differ between the three warming treatments (ambient, +1.5°C, +3.0°C), there was a significant interaction

effect between warming treatment and layer ($F = 6.03$, $p < 0.01$). Though not statistically significant, simple linear regression of carbon acquisition enzyme activities with mean plot temperature data (20 cm depth) showed a negative trend in activity with higher temperatures in the high marsh (Fig. S4.1a). This trend was only apparent in the topsoil layer (0-30 cm soil depth) and showed an opposite trend in the subsoil layer (40-100 cm soil depth).

The nested mixed-effects ANOVA revealed significant differences in combined nitrogen acquiring enzymes Chitinase and Leucine-Aminopeptidase among elevational zones ($F = 9.03$, $p < 0.01$, Fig. 4.1b). Tukey HSD post-hoc showed that high marsh samples were significantly higher in nitrogen acquisition activity than pioneer zone samples. There were significantly lower nitrogen acquisition activities in subsoil samples (40-100 cm soil depth) than in topsoil samples (0-30 cm soil depth). Factors zone and layer had a significant interaction effect ($F = 3.06$, $p < 0.05$). There was no effect of warming treatment on the nitrogen acquisition enzyme activities. Across all zones and layers, the nitrogen acquisition enzymes did not relate to increased mean temperatures at the respective depths (Fig. S4.1b). However, there was a negative trend with higher temperatures in the activity of nitrogen acquiring enzymes in high marsh soil across all layers, though this trend was not statistically significant (Fig. S4.1b).

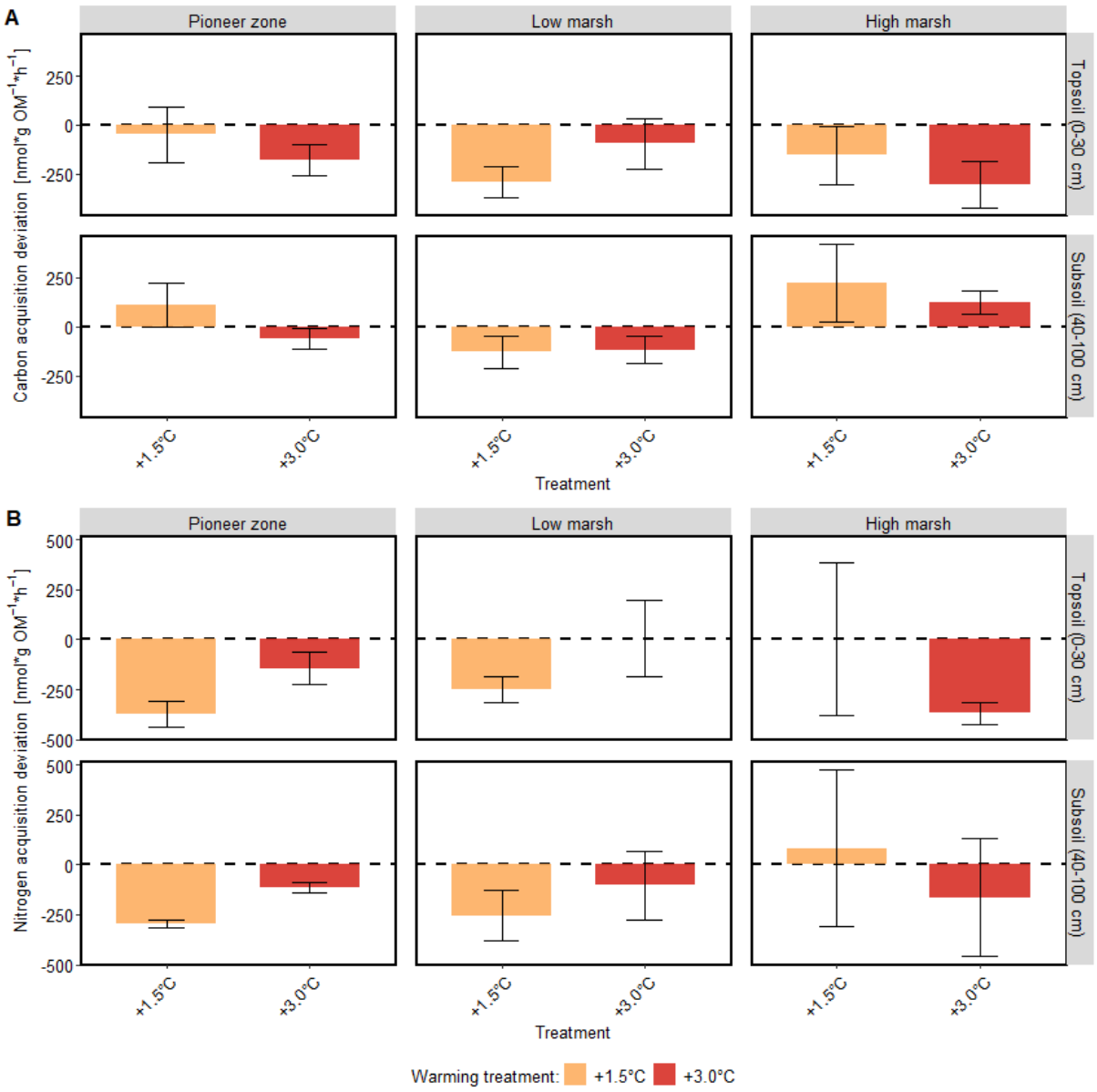

Figure 4.1: Exo-enzymatic activity deviations (mean ± SE) in nmol * g OM-1 * h-1 from ambient baseline of [A] carbon acquiring enzyme β-Glucosidase, [B] nitrogen acquiring enzymes Leucine aminopeptidase and Chitinase across the elevational gradient (pioneer zone, low marsh, high marsh), between soil layers (topsoil 0-30 cm, subsoil 40-100 cm) and between warming treatments (+1.5°C, +3.0°C). Dashed line at 0 represents ambient baseline. Deviations show warming treatment effects relative to ambient control for each zone × layer combination.

4.4.2 | Microbial diversity, community composition and abundance

Alpha diversity (Shannon index of rRNA transcripts) differed significantly between soil-layers, with higher diversity in the topsoil layer than in the subsoil layer (F = 26.56, p < 0.001). Zone had no significant effect on alpha diversity (F = 3.03, p = 0.07). Warming treatment showed no significant effects on Shannon index for samples from top- and subsoil (Fig 4.2a, Tab 4.1). Though not significant, the alpha diversity within the high marsh showed a negative trend from ambient to +3.0°C samples (Fig. 4.2a). Similarly, there was a non-significant positive trend in the low marsh, where alpha diversity increased toward the +3.0°C treatment in the subsoil layer (Fig. 4.2a).

PERMANOVA showed that community composition, as assessed via rRNA transcripts, was significantly affected by both zone (F = 11.97, p < 0.001) and layer (F = 13.83, p < 0.001) (Tab. 4.1, Fig. 4.2b). Post hoc pairwise comparisons revealed that community compositions differed between all elevational zones and the two depth layers. There is a gradual change in community composition from pioneer zone to high marsh as well as from topsoil to subsoil (Fig. 4.2b). Both factors (zone, layer) also showed a significant interaction effect on microbial community composition (F = 4, p < 0.001). Warming treatment did not significantly alter the community composition (F = 1.25, p = 0.121).

The most abundant phyla, as assessed via rRNA transcripts, across all samples were Proteobacteria (27 %), Chloroflexi (15 %) and Firmicutes (11 %), which represented more than half of the detected ASVs (53%). The next most abundant groups were Desulfobacterota (9%), Acidobacteriota (7%), Planctomycetota (7%), Actinobacteriota (5%), Myxococcota (3%), Gemmatimonadota (2%). All other phyla accounted for less than 1 % of all ASVs and were pooled together in the group “others” (13 %). Analysis of taxonomic groups on phyla level revealed differences between zones and warming treatments (Fig. 4.3). While Firmicutes and Actinobacteriota increased from pioneer zone, to the low marsh, and to high marsh, there was an opposite trend for Desulfobacterota and Chloroflexi which both decreased toward the higher elevated zones. Differences between warming treatments were especially pronounced in high marsh. For Firmicutes, there was an increase in abundance between ambient and +3.0°C treatments of 9 % in the high marsh zone. This effect was especially pronounced in the subsoil layer, where Firmicutes increased by 15 %, while the topsoil layer showed an increase by 5 %. The effect was reversed in low marsh where abundance decreased about 7% from +3.0°C to ambient (Fig. 4.3). In the pioneer zone, the changes in abundance of Firmicutes were comparably small (about 2%). Warming induced changes in Actinobacteriota were found in the high marsh where the abundance from ambient to +3.0°C treatments increased about 4%. This increase in Actinobacteriota with warming was especially strong in the subsoil layer (8%) compared to the topsoil (1%).

FAPROTAX-based functional guild analysis revealed distinct differences among marsh zones and soil depths (Fig. 4.4a-b). In the topsoil (0–30 cm), warming was associated with increased relative abundances of taxa linked to aromatic compound degradation and hydrocarbon degradation, particularly in the high marsh plots. In contrast, subsoil communities (40–100 cm) showed stronger responses in

fermentation-related functional potential, which increased under both warming levels across all zones (Fig. 4.4a). While functional group patterns in the pioneer zone and low marsh remained relatively stable, high marsh soils showed the strongest warming-related shifts, with enhanced functional potential for the breakdown of complex organic compounds. Deviation plots revealed differences in the most relevant functional guilds in temperature treatments (+1.5°C, +3.0°C) in %-change to the ambient controls (Fig. 4.4b). In the high marsh topsoil (0-30 cm) layer hydrocarbon degradation showed a strong increase in the +3.0°C temperature treatments. In the subsoil (40-100 cm) of the high marsh both temperature treatments (+1.5°C, +3.0°C) led to increases in hydrocarbon degradation.

qPCR analysis on samples from 2023 (topsoil 0-10 cm, 20-30 cm) were tested using nested mixed-effects ANOVA. The analysis revealed that microbial abundance (16S rRNA gene copy number) was significantly affected by *zone* ($F = 3.61$, $p < 0.05$), low marsh samples showed significantly higher microbial abundance than pioneer zone ($p < 0.05$). Both temperature *treatment* ($F = 0.79$, $p = 0.46$) and the interaction of temperature treatment and zone ($F = 0.33$, $p = 0.86$) had no significant effect on total the microbial abundance (Fig S4.3).

Linear regressions between dissimilarities (Bray-Curtis Distances) and Δ elevation revealed positive significant effects for both topsoil and subsoil samples, where higher difference in elevation resulted in higher dissimilarities (Fig. 4.5a-b, both $p < 0.001$). A similar trend was found for Δ reduction index in the topsoil (Fig. 4.5c, $p < 0.001$), but not for the subsoil samples (Fig. 4.5d). For Δ mean monthly temperature both topsoil and subsoil samples showed non-significant negative trends in dissimilarities. Higher differences in temperature between samples led to smaller dissimilarities (Fig 4.5e-f, $p = 0.061$). This negative trend, however, might be largely driven by the strongly diverging community in one plot of the low marsh (Fig. 4.2b).

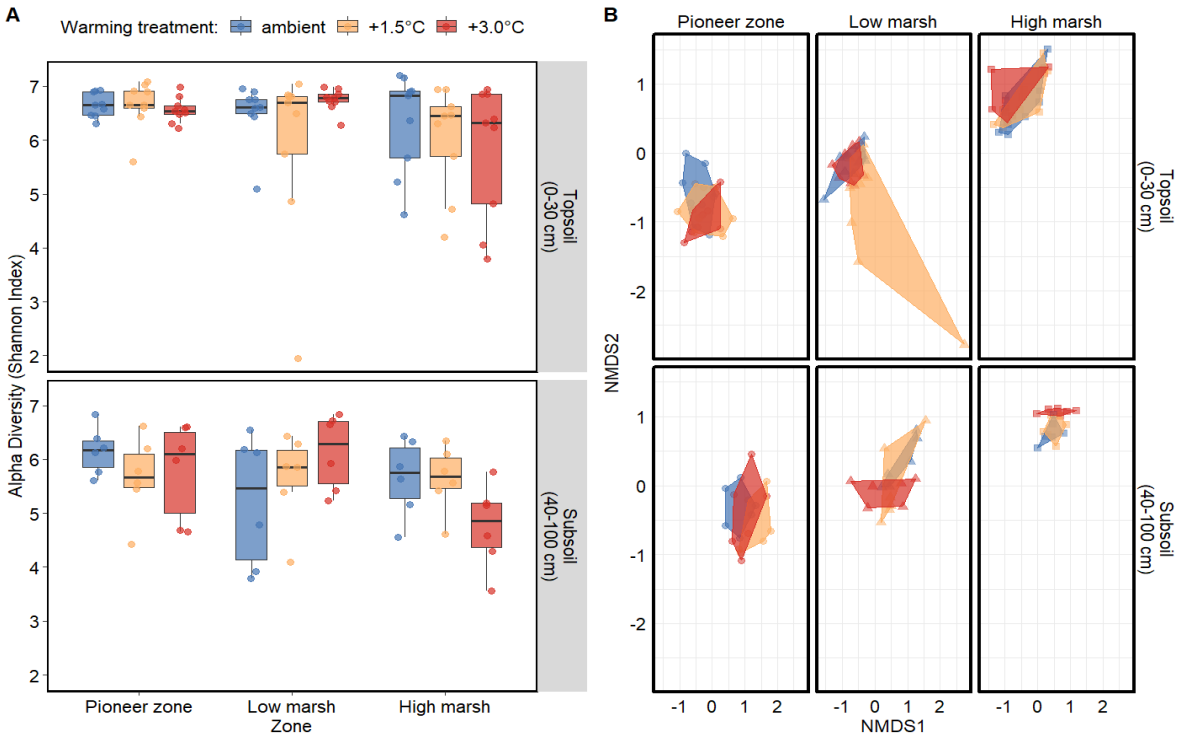

Figure 4.2: [A] Alpha diversity, assessed using the Shannon diversity index, is compared across the elevational gradient (pioneer zone, low marsh, high marsh), between the three warming treatments (ambient, +1.5°C, +3.0°C), and between soil layers (topsoil 0–30 cm, subsoil 40–100 cm) using boxplots. [B] Microbial community composition is visualized with non-metric multidimensional scaling (NMDS) plots based on Bray-Curtis distances between bacterial communities (16S rRNA sequenced as cDNA), illustrating patterns of beta diversity across the same environmental gradients. The subpanels show the results of one singular NMDS and share the same axis.

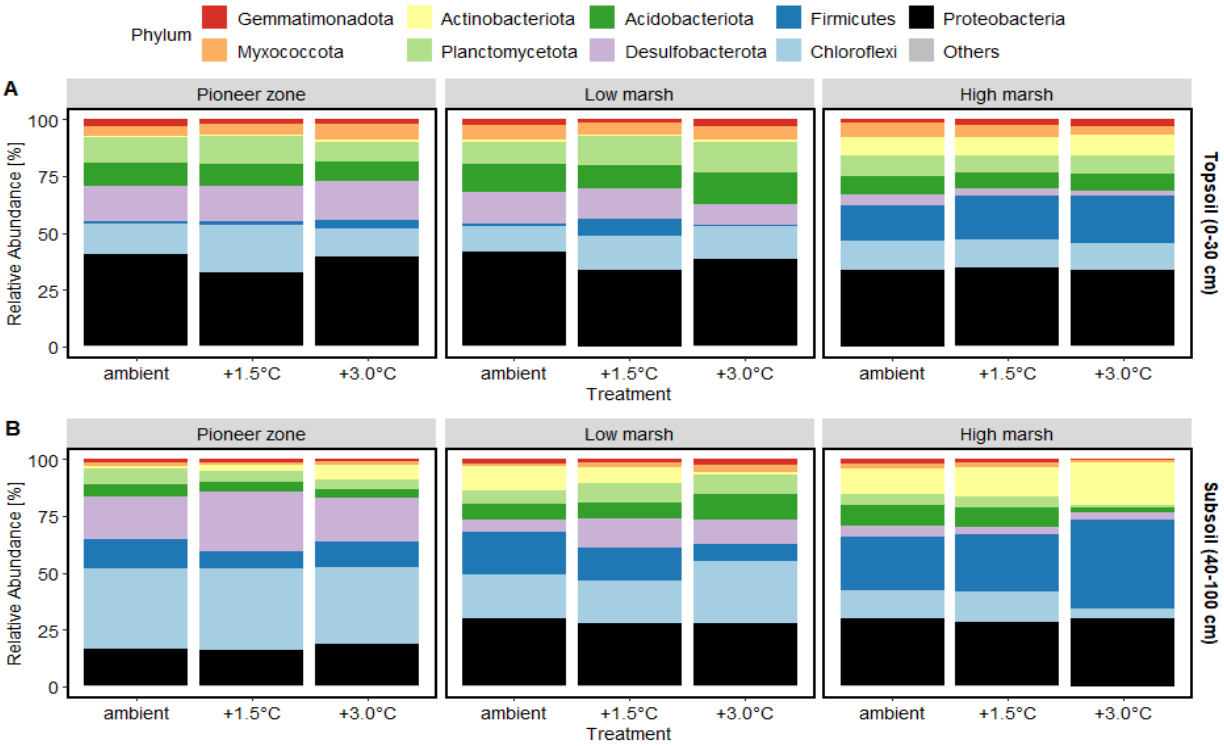

Figure 4.3: Stacked bar plots showing the relative abundance of the most abundant phyla, based on total transcribed RNA (16S rRNA sequenced as cDNA), in all samples across elevational zones (pioneer zone, low marsh, high marsh) between different warming treatments (ambient, +1.5°C, +3.0°C), based on total transcribed RNA. Shown are the top nine most abundant phyla and all remaining phyla in category others.

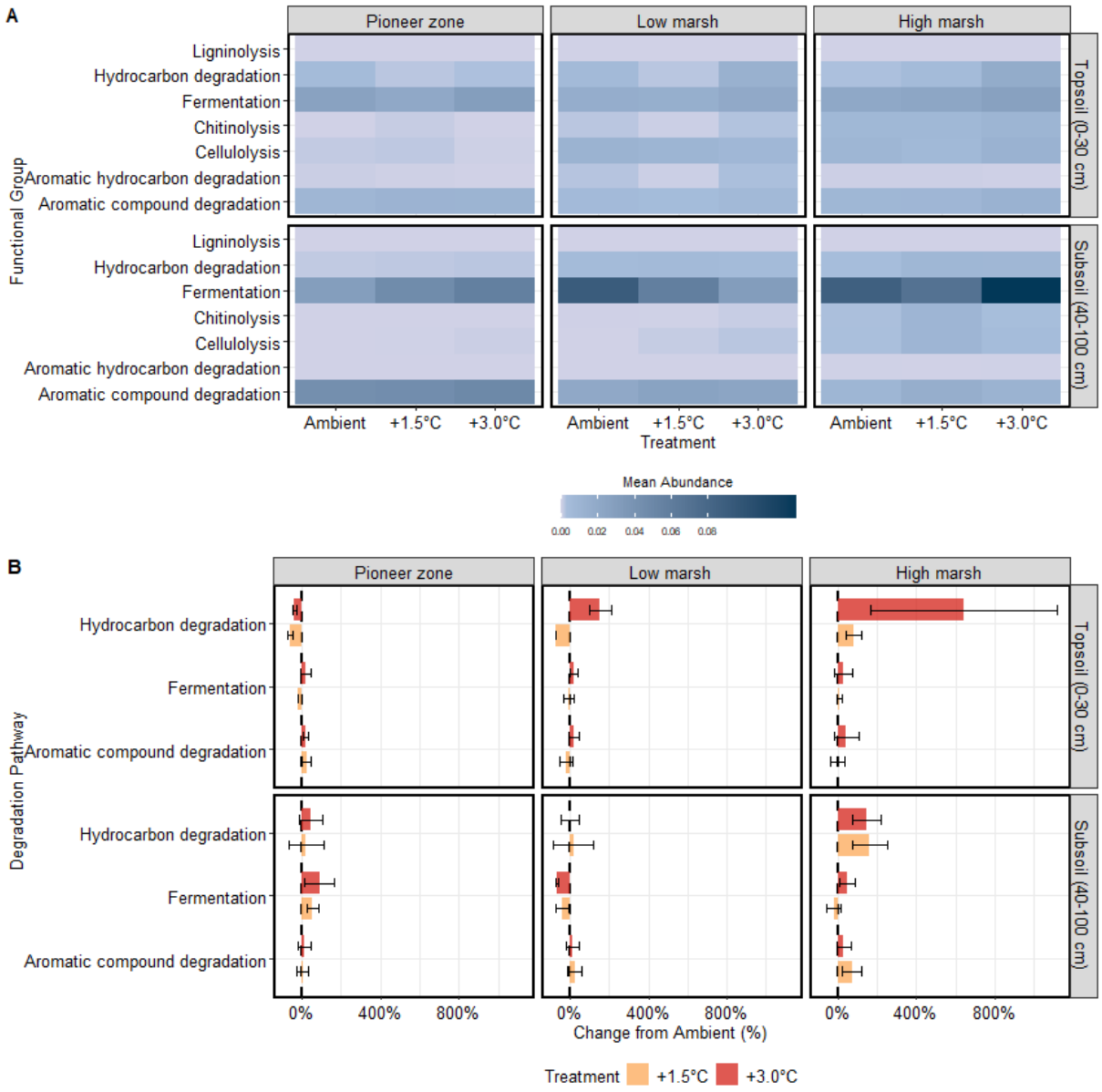

Figure 4.4: Microbial degradation pathway abundances and warming responses across the elevational gradient. [A] Heatmap showing mean abundances of degradation pathways across warming treatments (ambient, +1.5°C, +3.0°C) between soil layers (topsoil 0-30 cm, subsoil 40-100 cm) and across the elevational gradient (pioneer zone, low marsh, high marsh). Functional predictions based on FAPROTAX database. [B] Percentage changes (mean ± SE) of key degradation pathways (hydrocarbon degradation, fermentation, aromatic compound degradation) relative to ambient conditions (dashed line at 0%) for +1.5°C (orange) and +3.0°C (red) treatments. Only pathways with sufficient data coverage (>50% non-zero values) were included in the analysis. For more detailed information see Fig. S4.2

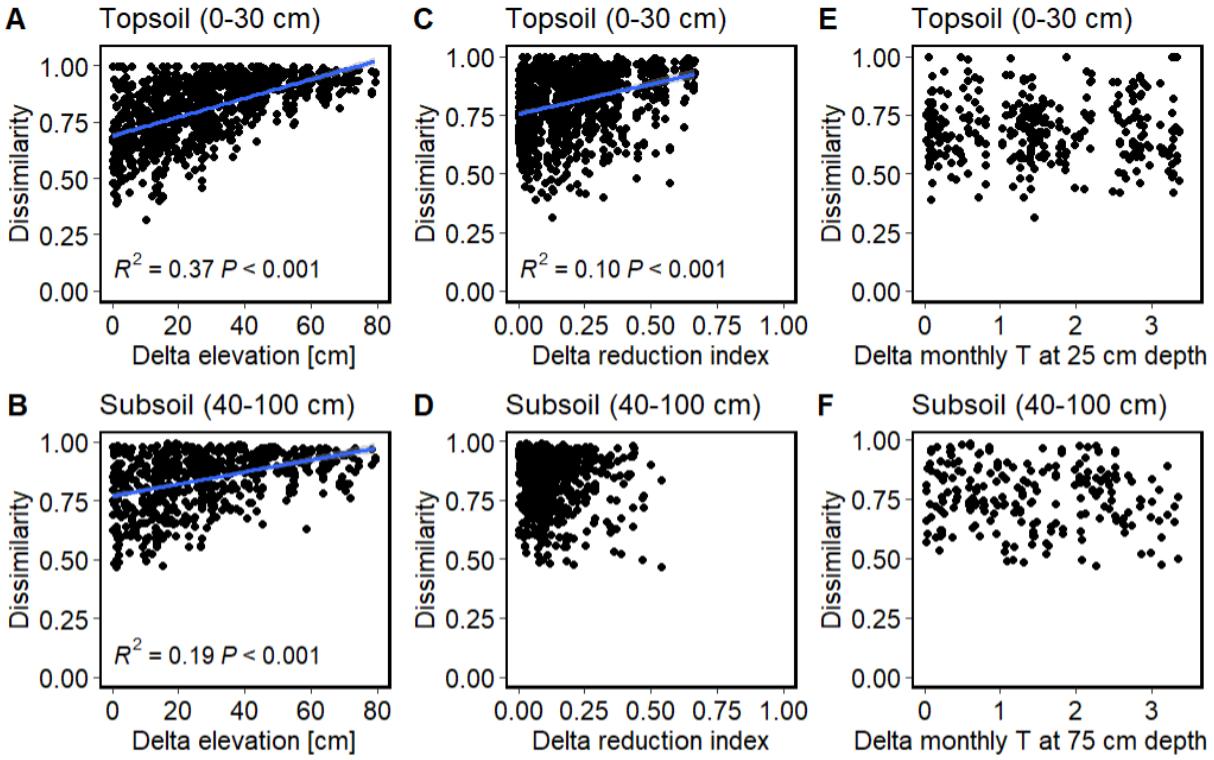

Figure 4.5: Bray-Curtis distances between microbial communities based on total bacterial 16S rRNA (sequenced as cDNA) as a function of differences in elevation [A, B], in reduction index [C, D] and mean soil temperature [E, F]. All differences are calculated for pairwise comparisons of the 27 plots of the MERIT experiment. Top panels [A, B, C] show samples from topsoil layer (0-30 cm) and bottom panels [D, E, F] show samples from subsoil layer (40-100 cm). R^2 and p-values are shown based on linear regression models. Blue regression lines are shown for significant linear regressions ($p < 0.05$).

Table 4.1: Summary table of statistical analyses reporting differences in microbial functioning variables (Carbon and nitrogen acquiring enzymes) and microbial community variables from 16S rRNA sequencing (alpha- and beta-diversity) on soil samples taken in September 2022. Nested mixed effect models (PERMANOVA for Bray-Curtis distances), were used to test for differences between factors: zones (pioneer zone, low marsh, high marsh), layers (topsoil 0-30 cm, subsoil 40-100 cm) and warming treatments (ambient, +1.5°C, +3.0°C). For the abundance data (log_{10} copies * g OM $^{-1}$), a nested mixed effect model was used to test for differences between factors zone and treatment on soil samples taken in May 2023. Shown are *p*-values, significant differences are highlighted in bold.

Factor/ Parameter	Carbon acquisition	Nitrogen acquisition	Alpha diversity (Shannon)	Beta diversity (Bray-Curtis Distances)	Abundance (log_{10} copies)
Factorial Approach					
Zone	***p* < 0.001**	***p* < 0.01**	*p* = 0.072	***p* < 0.001**	***p* < 0.01**
Layer	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**	/
Treatment	*p* = 0.686	*p* = 0.562	*p* = 0.759	*p* = 0.118	*p = 0.459*
Zone x Treatment	*p* = 0.538	*p* = 0.774	*p* = 0.175	*p* = 0.151	*p = 0.059*
Zone x Layer	***p* < 0.05**	*p* = 0.094	*p* = 0.991	***p* < 0.001**	/
Treatment x Layer	***p* < 0.01**	*p* = 0.764	*p* = 0.673	*p* = 0.636	/
Treatment x Layer x Zone	*p* = 0.154	*p* = 0.97	*p* = 0.395	*p* = 0.726	/

4.4.3 | Soil parameters Soil reduction index

Across the elevational gradient, marsh surface elevation increased from the pioneer zone (−30.4 ± 3.6 cm) to the low marsh (−7.1 ± 2.4 cm) and was highest in the high marsh (26.2 ± 2.4 cm). Soil temperature showed little variation among zones, with values ranging from 18.9 ± 0.2°C in the low marsh to 19.5 ± 0.1°C in the pioneer zone, while the high marsh was slightly cooler at 19.4 ± 0.1°C. In contrast, the reduction index (RI) decreased with elevation, being highest in the pioneer zone (0.76 ± 0.07), intermediate in the low marsh (0.70 ± 0.06), and lowest in the high marsh (0.60 ± 0.07).

Reduction index showed a strong negative correlation with marsh surface elevation in topsoil samples ($p < 0.05$). Reduction index was lower in plots with lower marsh surface elevation. This relationship was not significant in the bottom soil samples (Fig. 4.6). Correlation analysis showed that the activity of the carbon and nitrogen acquiring enzymes was positively correlated with soil elevation ($p < 0.05$). For carbon acquiring enzymes, there was a negative correlation with soil reduction ($p < 0.05$). Mean monthly temperature did not correlate with any of the microbial parameters (Fig. 4.6). The nested mixed-effects ANOVA revealed no significant differences in reduction index between the temperature treatments ($p > 0.05$).

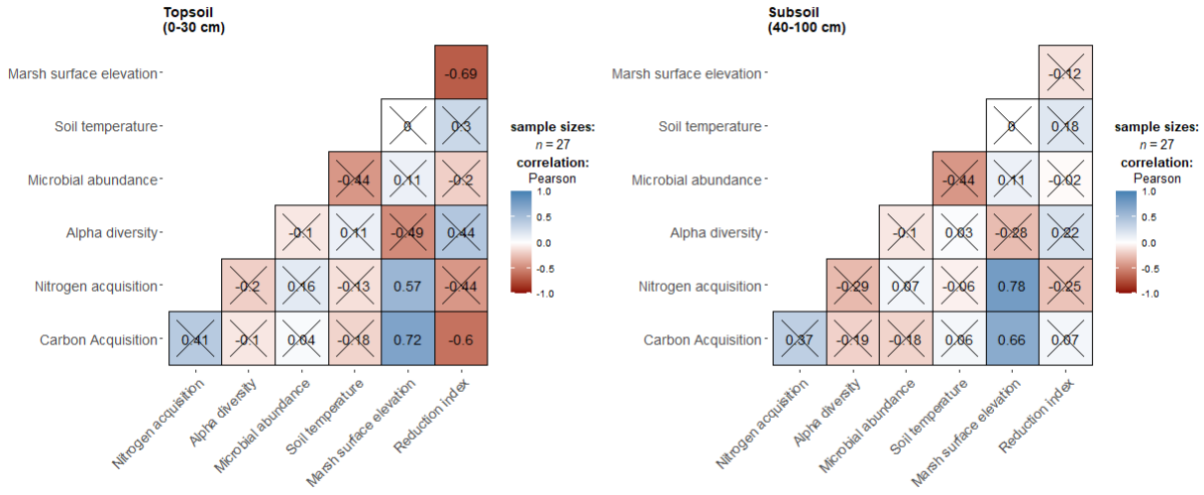

Figure 4.6: Pearson correlation matrix of environmental parameters: Reduction index, marsh surface elevation (m), soil temperature) and microbial variables (Carbon acquisition, Nitrogen acquisition, Alpha diversity (Shannon index), Abundance (log_{10} copies * g OM^{-1})). Shown are two separately calculated matrixes for topsoil (0-30 cm) and subsoil (40-100 cm) samples. Significant correlations ($p < 0.05$) are highlighted and non-significant correlations ($p > 0.05$) are crossed out. Correlations were adjusted using the Holm correction.

4.5 | Discussion

4.5.1 | Warming effects on microbial exo-enzymatic activity are limited to the high marsh

Contrary to our first hypothesis, warming did not increase microbial exo-enzymatic activity in our study (Fig. 4.1a-b). In contrast, we see negative deviations in exo-enzymatic activities for both temperature treatments across the zones (Fig 4.1a-b). Differences compared to the ambient plots were most pronounced in the high marsh for carbon acquiring enzymes, while nitrogen acquiring enzymes were most affected by the +1.5°C treatments in the pioneer zone (Fig 4.1a-b). Interestingly, in the high marsh both carbon and nitrogen acquiring enzymes showed a negative trend in response to higher monthly temperature in topsoil layer (Fig. S4.1a, Fig. S4.1c), while subsoil samples in the high marsh responded with higher activity of carbon acquiring enzymes with warming (Fig. S4.1b). This finding contrasts general catalytic assumptions and previous work in the MERIT experiment (Tang et al., 2023). In an early stage of the MERIT experiment (year 1 & 2 of experimental warming), Tang et al. (2023) showed that warming increases the initial organic matter decomposition rate across the three elevational zones. The results of this study (year 5 of experimental warming) can potentially be explained by [1] acclimation of microbial communities to warming and/or [2] substrate depletion over a longer time frame of warming. Both factors have been shown to cause a return to lower microbial activities after an initial warming-induced increase (Bradford et al., 2008; Romero-Olivares et al., 2017; Walker et al., 2018).

Acclimation of microbial communities after initial warming has been suggested as an important mechanism in terrestrial ecosystems (Luo et al., 2001; Crowther & Bradford, 2013). Acclimation describes a widespread down-regulation of microbial respiration across species adapted to warmer temperatures in response to warming (Crowther & Bradford, 2013). This mechanism would explain why there were no longer significant differences in microbial exo-enzymatic activity among temperature treatments in our study after five years of warming. We argue that substrate depletion also plays an important role in salt marshes in this study, as has been shown in other ecosystems (Walker et al., 2018). This is supported by the documented trend of decreasing C acquisition activity with higher temperatures (Fig. 4.1a & Fig. S4.1a). Additionally, organic matter content has continuously decreased in the high marsh from 2019 to 2022 (Fig. S4.4). While there are no significant differences in organic matter content between the warming treatments, it is likely that through higher temperatures and dryer soil conditions in the high marsh, resources are becoming limited (Schimel, 2018; Metze et al., 2023). According to climate data, the sampling year 2022 has been among the driest and hottest in the past twenty years (Fig. S4.5), this can in fact cause drought conditions in less frequently flooded zones of salt marshes and accompanied changes in root distribution (Menzel et al., 2025).

4.5.2 | Indication of drought stress within the putatively active microbial community structure of the high marsh

In this study, we present novel insights from 16S amplicon sequencing conducted on rRNA transcripts (sequenced as cDNA) from an *in-situ* salt marsh warming experiment. Previous findings from other studies showed that microbial community composition in salt marshes (based on 16S amplicon sequencing of DNA) changes little under experimental warming (Duchesneau et al., 2025). However, it remained unclear if changes in microbial communities might be obscured by extracellular DNA (see Schnecker et al., 2024), which can have comparably long retention times, if the DNA is protected (Bartholomäus et al., 2024). Contrary to our second hypothesis, we demonstrate that overall the putatively active microbial community composition changed little after five years of experimental warming. Nevertheless, there were some notable trends with regards to changes in relative abundances of indicator groups, as well as the functional potential of the communities according to FAPROTAX analysis (Fig. 4.3a-b & Fig. 4.4a-b).

Recent studies from the same experiment suggested that the high marsh zone is particularly vulnerable to drought stress (Ostertag et al., 2023; Menzel et al., 2025). Here, we observed higher abundances of Actinobacteriota and Firmicutes, phyla well-documented for their drought and heat tolerance due to their spore-forming capabilities (Oliverio et al., 2017; Wu et al., 2022). Actinobacteriota are well known for their ability to degrade complex, relatively recalcitrant soil organic matter compounds (P. Chen et al., 2016; Ni et al., 2024). Our FAPROTAX analysis reveals an increase in both aromatic carbon and hydrocarbon degradation functional abundance in the warmed high marsh plots (Fig. 4.4a-b). This effect is especially pronounced in the topsoil layer, while the increasing temperatures in the subsoil lead to an increase in fermentation processes. It has previously been suggested that organic matter is especially vulnerable to warming effects in the high marsh (Tang et al., 2023). The enrichment of these dry-adapted groups in the high marsh suggests that drought conditions are already exerting selective pressure on the microbial community, or that such conditions are likely to occur. We see this further supported by the declining trend in alpha diversity with warming in the high marsh (Fig. 4.2a). Studies from upland ecosystems have shown sensitive negative responses of microbial alpha diversity to warming (Li et al., 2025). We argue that the declining alpha diversity is the result of a selection process towards more heat-tolerant taxa, a mechanism well known from upland ecosystems (Nottingham et al., 2022; Wu et al., 2022). It is also possible that the observed trend is due to a selection for microbial groups that can use carbon more efficiently when resources are limited. In August 2022—the month before sampling—there was an extreme drought, with the lowest rainfall and third highest temperature recorded since 2002 (Fig. S4.5). These dry conditions may have altered soil chemistry, making more electron acceptors available (Knorr & Blodau, 2009). This could have supported microbes that break down more complex forms of carbon. Therefore, we cannot say for sure if the decline in microbial diversity was caused directly by higher temperatures or indirectly by changes in soil conditions due to drought.

Due to the lack of warming experiments in high energy coastal systems like salt marshes (Rich et al., 2023), we so far had no evidence regarding effects of warming on microbial diversity in these systems. To our knowledge, we report for the first time results demonstrating that high marsh zones respond to warming in a manner similar to upland ecosystems with respect to microbial diversity, whereas microbial diversity in low marsh and pioneer zones with more reducing conditions remain stable under warming (Fig 4.2a & b, Fig 4.3a). Overall, the high marsh harbors conditions which could promote a positive feedback of soil organic matter decomposition (i.e., exo-enzymatic activities, hydrocarbon degradation) to global warming.

4.5.3 | Hydrology (zonation & soil layer) as the main driver of salt marsh microbial functioning and community structure

In line with our third hypothesis, we report that, salt marsh zone and soil layer are main predictors for composition and functioning of microbial communities in Wadden Sea salt marshes (Fig. 4.1, Fig. 4.2b). Given the strong relation between marsh surface elevation and reduction index (Fig. 4.6) we argue that hydrology is the main driver in determining composition and functioning of microbial communities. Both zonation (position along the marine-terrestrial ecotone) as well as marsh surface elevation of individual plots showed significant effects on exo-enzymatic activities, and on alpha and beta diversity (Fig. 4.5, Tab. 4.1). Our findings are in line with other studies from wetland ecosystems, showing strong redox constraints on decomposition processes, with no indication of warming effects in permanently waterlogged (reducing) soil layers (Wilson et al., 2016; Hopple et al., 2020; Tang et al., 2023). Maxwell et al. (2024) showed that soil depth and elevation are the strongest predictors for SOC stocks in tidal marshes. Studies from the Wadden Sea area, where bacterial communities showed a clear zonation, further support our findings (Tebbe et al., 2022). This zonation is especially characterised by an increase in Firmicutes and Actinobacteriota from the pioneer zone to the high marsh, while Desulfobacterota and Planctomyceota decreased with increasing elevation (Fig. 4.3a).

We show that microbial activities were highest for both carbon and nitrogen acquisition in the high marsh (Fig. 4.1a-b). In addition, carbon enzyme activities were negatively correlated with soil reduction in the topsoil and nitrogen enzyme activities showed a negative trend with soil reduction in the topsoil (Fig. 4.6). In the least reduced zone (high marsh) organic matter breakdown is likely promoted. The high marsh zone is characterised by a low flooding frequency resulting in dryer soils (Rich et al., 2023). We see, that in areas with low reduction the activity of exo-enzymes was higher (Fig. 4.6). These findings are in line with the enzymatic latch hypothesis, stating that hydrolase enzymes are negatively affected by the accumulation of phenols in anoxic soils (Freeman et al., 2001). Our data suggest that the high marsh zone is distinct in its hydrology from lower elevated pioneer zone and low marsh and thus especially vulnerable to the influence of global warming.

4.5.4 | Conclusion

In this study we investigated how soil microbes are affected by both hydrology (i.e., zonation, soil layers) and climate (experimental warming). The study was conducted within the whole-ecosystem warming experiment MERIT located in a Wadden Sea salt marsh. Previously, litter decomposition was found to increase with warming in the early stages of the MERIT experiment (Tang et al., 2023). We find that five years after warming was initiated, hydrological conditions (i.e., zonation, soil layer) are the main drivers for both microbial functioning (i.e., carbon and nitrogen acquisition) and microbial community composition (i.e., alpha- and beta-diversity). Warming effects on the parameters investigated in this study are strictly limited to the higher-elevated, more terrestrial areas of the ecosystem. An additional reason for the unexpected finding that warming did not have significant effects on microbial community structure and functioning, is because in our experiment we only employ passive aboveground warming, meaning plant-driven effects may be less prominent than in experiments with active aboveground warming. We show with our study that, in wetland ecosystems the effect of hydrology (here soil reduction and marsh surface elevation) is of overriding power, masking changes in microbial functioning and community structure through warming.

4.6 | Competing interests

The authors declare no conflict of interest.

4.7 | Data availability

Data and code are available at https://github.com/JulianMiGoe/merit_microbes_repo. The raw sequencing data is publicly available on the European Nucleotide Archive (ENA) under project accession number PRJEB91652 (https://www.ebi.ac.uk/ena/browser/view/PRJEB91652).

4.8 | Acknowledgments

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4.9 | Supporting information

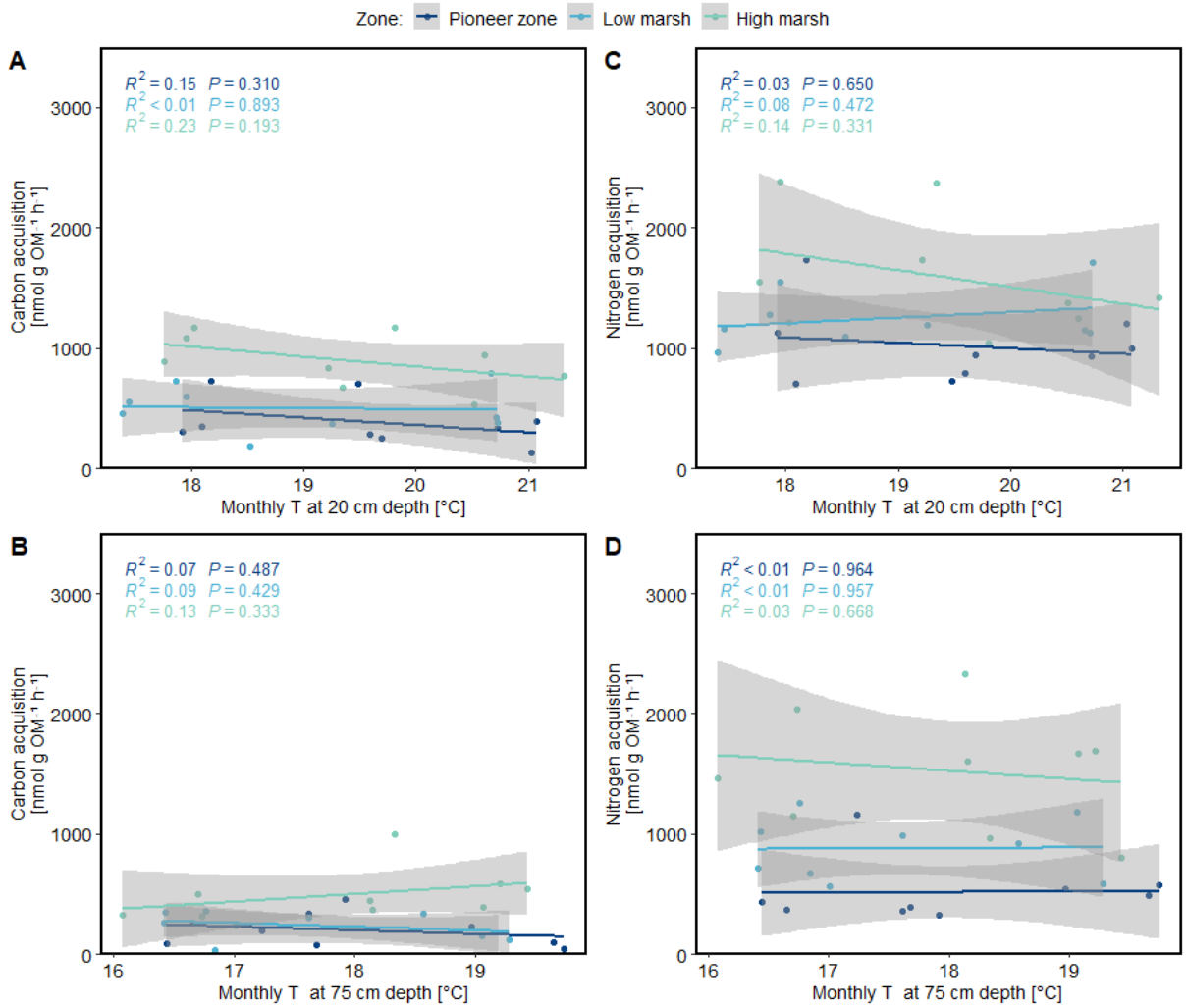

Figure S4.1: Response of exo-enzymatic activity (mean ± se) in nmol * g OM^{-1} * h^{-1} to MAT measured at 20 cm and 75 cm depth respectively. (A) carbon acquiring enzyme ß-Glucosidase in topsoil samples (0-30 cm) (B) in subsoil samples (40-100 cm). (C) nitrogen acquiring enzymes Leucine aminopeptidase and Chitinase in topsoil samples (0-30 cm). (D) in subsoil samples (40-100 cm). Colours represent different elevational zones (pioneer zone, low marsh, high marsh).

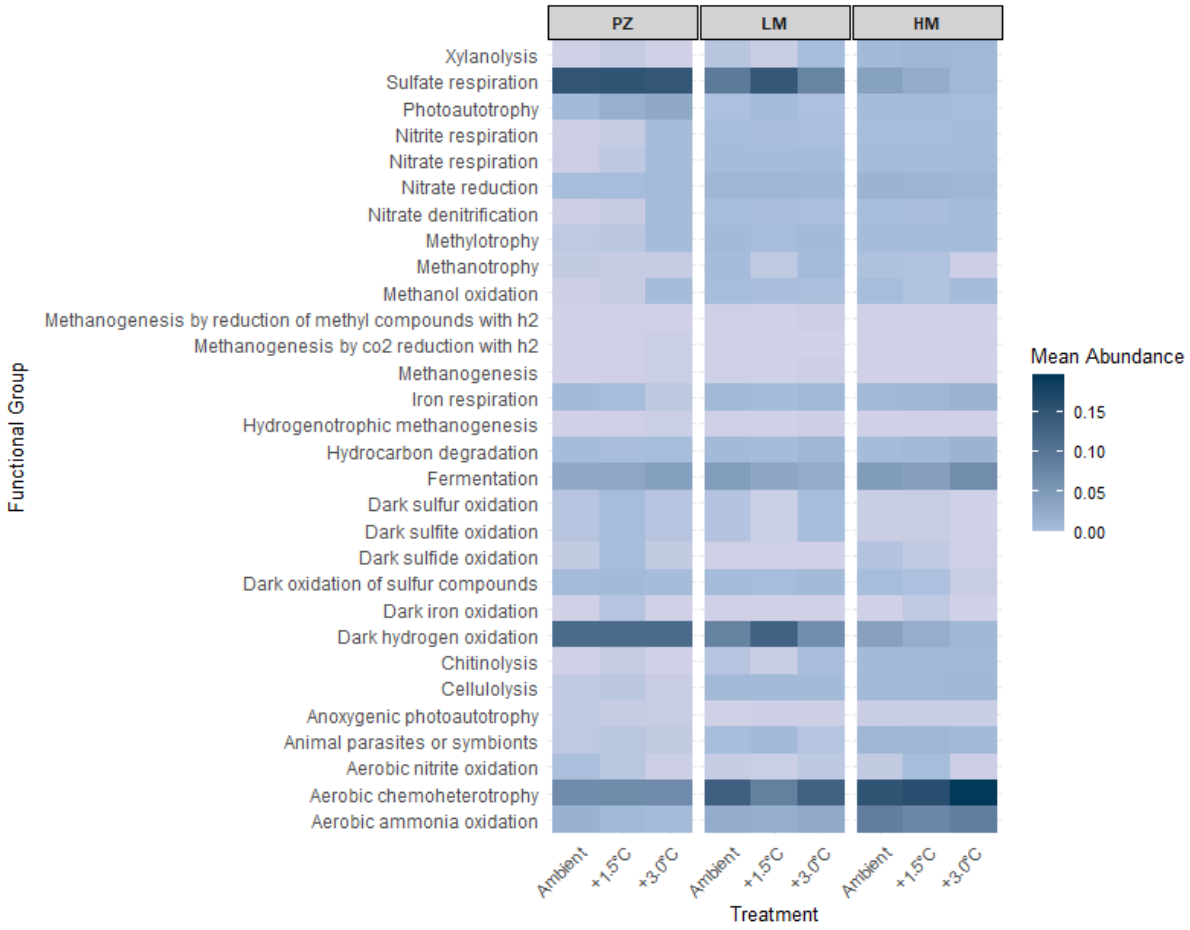

Figure S4.2: Heatmap plot showing Functional Annotation of Prokaryotic Taxa (FAPROTAX) analysis. All functional profiles of bacteria are compared between temperature treatments (ambient, +1.5°C, +3.0°C) and zones (pioneer zone, low marsh, high marsh).

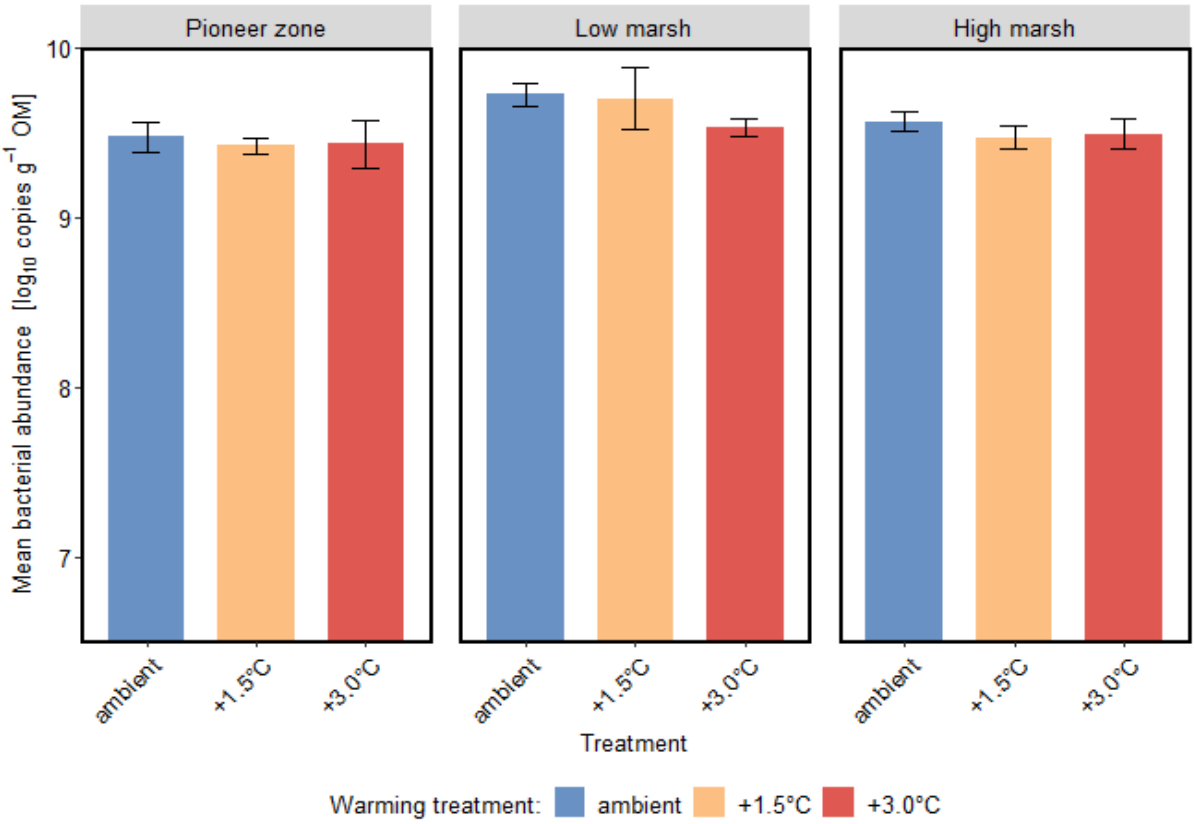

Figure S4.3: Mean bacterial abundance (log_{10} copies g^{-1} OM) across warming treatments (ambient, +1.5°C, +3.0°C) in three salt marsh zones (pioneer zone, low marsh, high marsh). Bars with errorbars represent means ± se.

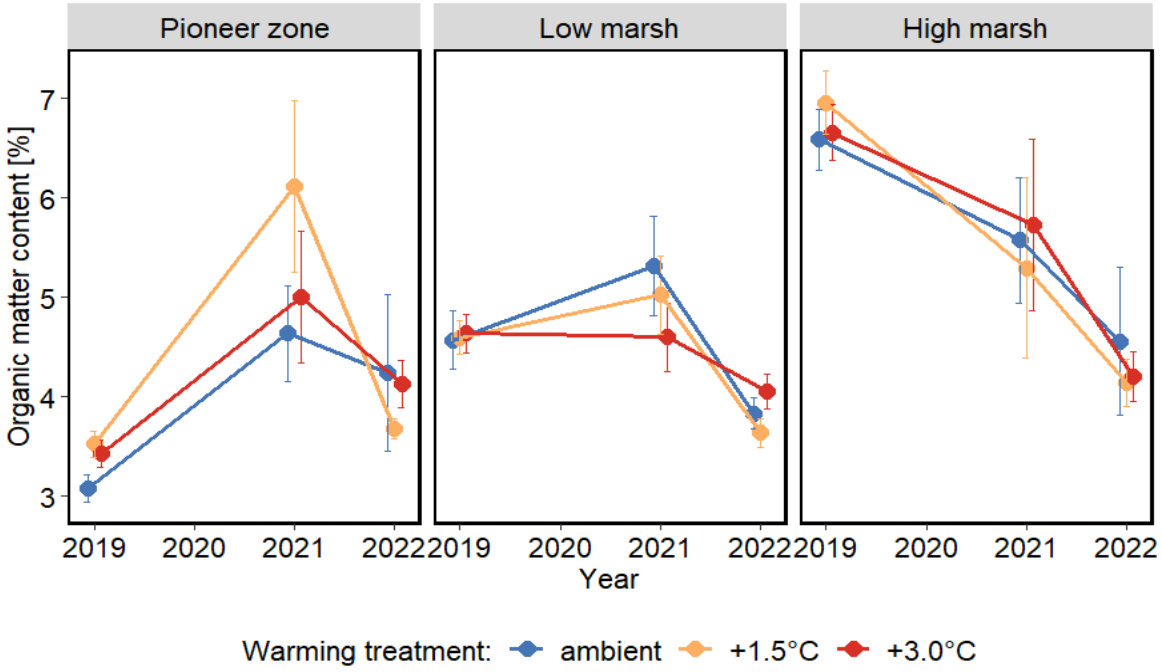

Figure S4.4: Soil organic matter content (%), acquired from loss on ignition. Points show mean soil organic matter content across the elevational gradient (pioneer zone, low marsh, high marsh) and between the warming treatments (ambient, +1.5°C, +3.0°C). Standard errors are indicated as lines with whiskers.

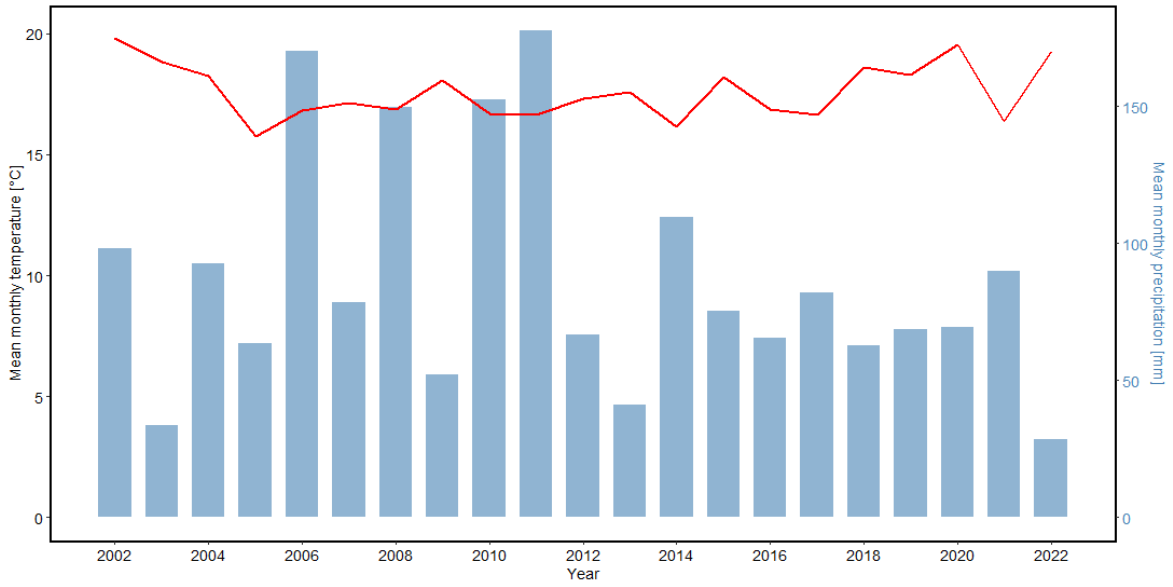

Figure S4.5: Mean precipitation (blue bar plots in mm) and temperature (red line in °C) of the sampling month August for the timeframe 2002 until 2022. Climate data were provided by the DWD (Deutscher Wetterdienst) and are available online at http://www.dwd.de.

Chapter 5 | Warming stimulates soil reduction and methane cycling in salt marshes

Clarisse Goesele & **Julian Mittmann-Goetsch**, Viktoria Unger, Kai Jensen, Susanne Liebner, Simon Thomsen, Roy Rich, Lars Kutzbach, Chen (Caroline) Cheng, Alexander Bartholomäus, Peter Mueller

In preparation

„Momentan ist richtig

Momentan ist gut

Nicht ist wirklich wichtig

Nach der Ebbe kommt die Flut"

\- Herbert Grönemeyer

5.1 | Abstract

Coastal wetlands are globally significant carbon sinks, but their oxygen depleted soils also produce methane, a greenhouse gas with a 45 times higher warming potential than CO_2. Carbon storage and methane fluxes are governed by the redox potential, which reflects the balance between electron acceptors and electron donors. Climate warming is expected to shift these processes since reductive pathways are generally more temperature sensitive than oxidative ones. Since the common hypothesis is that hydrology is the dominant control in lower elevated zones in salt marshes, warming effects are expected to increase along the marine-terrestrial gradient. Yet responses in salt marshes remain largely unknown. We investigated redox dynamics (continuous redox-potentials, reduction index), methane fluxes and the composition of the active microbial community through 16S sequencing (on rRNA transcripts), in a whole-ecosystem warming experiment (MERIT) in a salt marsh of the European Wadden Sea. In line with our hypothesis, warming decreased redox potentials, with most pronounced effects in the high marsh. However, warming effects on the reduction index were most pronounced in the pioneer zone, where methane fluxes also increased in line with our second hypothesis. These unexpected patterns—stronger warming responses at the marine end of the marine–terrestrial gradient—can be explained by methanogenic microbes responding to warming primarily in the pioneer zone, thereby lowering redox potentials and enhancing methane emissions. We suggest that the higher temperature sensitivity of methanogenesis relative to methanotrophy underlies these dynamics. Overall, our findings challenge the prevailing assumption that hydrology outweighs warming effects in salt marshes and advance the understanding of salt marsh biogeochemistry and its vulnerability to global warming.

5.2 | Introduction

Coastal wetlands rank among the most effective natural systems for long-term carbon storage (McLeod et al., 2011; Temmink et al., 2022), simultaneously they act as sources of methane (CH_4) (Rosentreter et al., 2018), a greenhouse gas with 45 times the warming potential of CO_2 (Neubauer & Megonigal, 2015). This balance between carbon storage and methane release arises from waterlogged conditions, which create low-oxygen (i.e. low redox potential) environments: while oxygen limitation slows decomposition and enhances carbon burial, it also supports microbial pathways that generate methane (Rosentreter et al., 2018; Temmink et al., 2022; Eyre et al., 2023). Therefore, redox potential has emerged as an important variable, providing a basis for predicting the climate change mitigation potential of coastal wetlands under future warming (Lee et al., 2025; Zhu et al., 2025).

Redox potentials are reflecting the availability of electron acceptors and donors, that strongly influence microbial-driven decomposition processes (Sutton-Grier et al., 2011; Z. Zhang & Furman, 2021). Climate warming exerts a strong control on redox sensitive microbial processes, with reduction processes generally showing greater increases with warming than oxidation processes (Bullock et al., 2013; Lee et al., 2025). This differential sensitivity extends to methane metabolism, where methanogenesis (reductive process) is expected to be favored over methanotrophy (oxidative process) under warmed conditions (Segers, 1998; Noyce & Megonigal, 2021). Incubation studies support this prediction, consistently showing that microbial methanogenesis is strongly stimulated by elevated temperature (Inglett et al., 2012; Yvon-Durocher et al., 2014; Chen et al., 2020). However, robust field experimental insight is yet scarce.

Results from a peatland whole-ecosystem warming experiment suggest that indeed methanogenic processes are favored under warming (Hopple et al., 2020; Wilson et al., 2021). These findings are partly supported by findings from a brackish coastal wetland whole ecosystem warming experiment, where warming led to higher methane emissions (Noyce et al., 2023). However, we currently lack the understanding of how coastal marshes with higher salinities respond to global warming. Here, enhanced sulfate concentration can lead to sulfate-reducing microbes outcompeting methanogenic microbes (Kristjansson & Schönheit, 1983), and strong increases in methane emissions have been associated with decreases in salinity and hereby sulfate concentrations (Bartlett et al., 1987).

In salt marshes the common hypothesis is that hydrology is the dominant control in lower elevated zones in salt marsh ecosystems, largely outweighing the effects of warming. Accordingly, warming effects are expected to increase following the marine-terrestrial gradients (Rich et al., 2023). This study was carried out in the in-situ whole-ecosystem warming experiment (MERIT: Marsh Ecosystem Response to Increased Temperatures) in a salt marsh on the European Wadden Sea coast of Schleswig-Holstein, Germany. A recent MERIT study found that soil redox potential is strongly shaped by flooding frequency and soil depth (Tang et al., 2023), and is expected to decrease with warming under which reductive processes are favored processes (Bullock et al., 2013; Lee et al., 2025). A similar overriding

role of hydrology has been observed for plant belowground biomass (Menzel et al., 2025) and microbial communities (Mittmann-Goetsch et al., 2025, *in revision*), where warming effects were most evident in the high marsh. We therefore hypothesize [1] that warming will decrease soil redox potentials, with most pronounced effects in the high-elevation zones. We further hypothesize that [2] decreasing redox potentials, caused by warming effects, will lead to higher methane emissions.

5.3 | Material & Methods

5.3.1 | Site-description

The MERIT (Marsh Ecosystem Response to Increased Temperature) experiment, initiated in 2018, is located in a salt marsh on Hamburger Hallig in the German Wadden Sea (54°36′06.7″N, 8°48′57.4″E). This whole-ecosystem warming study combines passive aboveground and active belowground heating, with soil warming to 100 cm soil depth. Aboveground warming is achieved using open-top chambers that trap heat and solar radiation, while belowground warming is delivered via a system of horizontal (GX-088L3106 GX, 9.8 Ω/m, 240 V) and vertical (GX 088L3100, 9.8 Ω/m, Danfoss, Denmark) heating cables. The experiment comprises three replicate plots of 8 m² within each of three distinct marsh zones along the marine–terrestrial gradient: the pioneer zone, low marsh, and high marsh. Each zone includes three temperature treatments (ambient, +1.5°C, and +3.0°C) resulting in a total of 27 plots. Soil temperatures are continuously measured at 5 cm, 25 cm, 75cm depth. A detailed description of the experimental setup and its operation can be found in Rich et al. (2023).

5.3.2 | Soil redox

Soil redox potentials were constantly measured using an automated redox system, consisting of 96 sensors, with two measurement depths respectively (15 cm, 75 cm). A combination of 36 sensors (Sander Smits, Netherlands) and 60 sensors (built using in-house protocol) were installed in spring 2023 and 2024, respectively. Redox potentials were measured against 3 M KCl (Ag/AgCl) reference electrodes. Values were recorded using a combination of CR1000X Data loggers (Campbell Scientific, USA), and AM 16/32 Multiplexer (Campbell Scientific, USA). Redox data were corrected to the standard hydrogen electrode by adding +207 mV to the values (Mansfeldt, 2003b).

IRIS (Indicator of Reduction in Soils) sticks were used to determine a soil reduction index. Sticks were installed in six consecutive campaigns, each spanning a six-week period during 2023. The method followed standard protocols (Rabenhorst & Burch, 2006). Iron (Fe) oxides were applied to white PVC sticks and deployed. The capacity of solid-phase Fe (III) oxides to be reduced, by microbial Fe reducers, to soluble Fe (II) under anoxic conditions is used to assess soil-reduction in soils. After retrieval, sticks were carefully rinsed with tap water. After drying, sticks were scanned using an overhead scanner (Viisan, China). White pixels on the images were determined using a supervised classification tool (Mittmann-Goetsch et al., 2024). Reduction index was calculated as the share of white pixels from total pixels, where high amounts of paint removal are reflected in high reduction indices.

5.3.3 | Methane fluxes

Methane fluxes were determined in all 27 plots employing a closed chamber method. Measurements were conducted in regular intervals of six weeks from March 2023 to October 2023. In total six campaigns were carried out. Flux measurements were conducted around low tide, i.e., when soil surfaces were not flooded.

For CH_4 flux measurements, a flexible (i.e. height-adjustable) portable closed chamber (max height of 100 cm in height) as described by Yang et al. (2025), adapted by Goesele et al. (2025) and permanently installed collars were used. The chamber was equipped with fans on the inside for air circulation. During each flux measurement, air temperature and relative humidity inside the chamber were measured. Photosynthetically active radiation (PAR) was measured outside with a sensor installed on top of the chamber.

Two types of portable laser-based trace-gas analyzers – a Micro Portable Greenhouse Gas Analyzer (ABB GLA131 Series Microportable Analyzers, ABB Inc. Measurement & Analytics, Quebec, Canada) and a portable $CH_4/CO_2/H_2O$ Trace Gas Analyzer (LI-7810, LI-COR Environmental, Lincoln, NE, US)) – were used to quantify CH_4 concentration changes inside the chamber headspaces during 6-min flux measurements. The CH_4 fluxes were calculated based on linear regression slopes of CH_4 concentration change over time. After visual inspection of each individual flux measurement, 5 % of all CH_4 fluxes were excluded from the dataset due to analyzer errors or chamber leakage. For further flux evaluation, a combination of the root mean square error (RMSE; threshold at 5 ppb) and coefficient of determination (R^2; threshold at 0.85) of the linear regressions was used (adapted from Kutzbach et al. (2007)) following Goesele et al. (2025)). Flux-calculation statistics were conducted in R (version 4.5.0 (2025-04-11)).

5.3.4 | Soil microbes

Soil sampling was carried out in September 2022. From each of the 27 plots, a single soil core (100 cm deep) was collected using a 2.5-cm diameter gauge auger. To prevent microbial cross-contamination, the auger was thoroughly rinsed with ethanol and deionized water after each sampling. Each core was sectioned into four depth intervals (5–10 cm, 20–30 cm, 40–50 cm, and 80–100 cm), resulting in five samples per core. Immediately after collection, samples were placed on dry ice in the field and during transport, and subsequently stored at –80°C in the laboratory until RNA extraction.

Total RNA was extracted from soil samples using the GeneMATRIX Environmental DNA & RNA Purification Kit (Roboklon, Germany) following the manufacturer's instructions. The RNA was further purified with the Turbo DNA-free kit (Thermo Fisher, Germany). For cDNA synthesis, reverse transcription PCR was performed to convert single-stranded RNA into complementary DNA (cDNA). In a PCR tube on ice, 10 µl sterile distilled water, 1 µl 10 mM dNTP mix (Invitrogen, USA), 1 µl pd(N)6 random hexamer primers (GE Healthcare, USA), and 1 µl RNA sample were combined (total volume 13 µl). This mixture was heated at 65°C for 5 minutes in a PCR machine (Bio-Rad, USA) to denature secondary structures, then immediately cooled on ice. After brief centrifugation, 1 µl sterile distilled

water, 1 µl 0.1 M DTT, 1 µl SuperScript III Reverse Transcriptase (Thermo Fisher, Germany), and 4 µl 5× First-Strand Buffer were added. The reaction was gently mixed by pipetting. Primer annealing was performed at 25°C for 5 minutes, followed by reverse transcription at 50°C for 60 minutes. The reaction was terminated by heating at 70°C for 15 minutes to inactivate the enzyme. cDNA concentrations were measured using a Qubit 2.0 Fluorometer (Invitrogen, USA) with dsDNA HS and BR assay kits (Thermo Fisher, Germany).

Amplicon libraries were prepared using in-house barcoded primer pairs targeting the V3–V4 hypervariable regions of the 16S rRNA gene (Uni515-F: GTGTGYCAGCMGCCGCGGTAA; Uni806-R: CCGGACTACNVGGGTWTCTAAT). PCR reactions (25 µl) contained 10× Pol Buffer C (Roboklon, Germany), 0.5 µM of each primer, 0.2 mM dNTP mix (Thermo Fisher, Germany), 2 mM $MgCl_2$, 1.25 U Optitaq Polymerase (Roboklon, Germany), PCR-grade water, and 1 µl template cDNA. Negative controls included PCR water and RNA extract. The PCR program was: initial denaturation (5 min, 95°C); 32 cycles of denaturation (30 sec, 95°C), annealing (30 sec, 56°C), elongation (1 min, 72°C); and a final elongation (7 min, 72°C). PCR products were purified using HighPrep™ PCR clean-up reagents (Magbio Genomics, USA) per manufacturer's protocol. PCR product concentrations were normalized and pooled with controls. The pool was sent for sequencing to Eurofins Genomics (Ebersberg, Germany). The library preparation was done by PCR-free adapter ligation. Sequencing was done on the Illumina MiSeq platform using 2 x 300 bp paired end mode using the V3 chemistry. Sequencing data were demultiplexed using cutadapt v3.4 with parameters -e 0.2 -q 15,15 -m 150 --discard-untrimmed. Amplicon sequence variants (ASVs) were generated using DADA2 (Callahan et al., 2016) v1.20 in R v4.1 with pooled approach and filtering parameters maxN=10, truncQ=20, rm.phix=TRUE, and minLen=150. Read pair merging was done using function "mergePairs" provided by the DADA2 package. Taxonomic assignment used DADA2 and the SILVA database v138.1 (Quast et al., 2013). Further data processing was performed in R (v4.4.2) with RStudio (v2024.09.1+394) and the packages ggplot2 (Wickham, 2016), phyloseq (McMurdie & Holmes, 2013), and vegan (Oksanen et al., 2025). ASVs assigned to chloroplasts or mitochondria and singletons were removed before rarefaction to 5000 reads.

Functional annotation of prokaryotic taxa was performed using the Tax4Fun2 R package (Wemheuer et al., 2020). Genes involved in methane oxidation (https://www.kegg.jp/module/M00174), and methylotrophic- (https://www.kegg.jp/kegg-bin/show_module?M00356), acetoclastic- (https://www.kegg.jp/kegg-bin/show_module?M00357), and hydrogenotrophic- (https://www.kegg.jp/kegg-bin/show_module?M00567) methanogenesis respectively, were included using the KEGG (Kyoto Encyclopedia of Genes and Genomes) database (Kanehisa & Goto, 2000). The balance between methanogenic and methanotrophic processes was analyzed using rRNA-based functional predictions (Tax4Fun2) across three salt marsh zones (pioneer zone, low marsh, high marsh) and three temperature treatments (ambient, +1.5°C, +3.0°C). Methylotrophic, Acetoclastic and hydrogenotrophic methanogenesis were pooled together, to represent all methanogenic processes. This

approach provided information on the putatively active methane-cycling microbial community along the marine-terrestrial gradient of the marsh. A ratio of methanogenic to methanotrophic predicted functional potential was calculated, based on normalized counts per copy number of Tax4Fun2 prediction on the 16S rRNA transcripts.

Rooting depth patterns at our sites were used to define two soil intervals. For microbial analyses, samples were pooled into a topsoil layer (10–30 cm), strongly influenced by live roots, and a subsoil layer (40–100 cm), where live root influence was minimal. For redox characterization, reduction indices from IRIS sticks were pooled over the same topsoil layer (10–30 cm), but only down to 60–80 cm in the subsoil, reflecting the installation depth of the sticks.

5.3.5 | Statistical analyses

The automated redox potential data was summarized on hourly mean values and plotted for the entire warming period. Due to insufficient replication of the respective warming treatments, we refrained from calculating statistics with the redox potential data. We therefore included reduction index data, assessed using IRIS sticks.

For the reduction index, distributions for both topsoil and subsoil were first assessed visually. Since both reduction index datasets followed a beta distribution, we fitted generalized linear mixed models (GLMMs) using the beta_family (link = "logit"). Reduction index values were aggregated per plot and campaign within each depth increment (topsoil: 10, 20, 30 cm; subsoil: 60, 70, 80 cm). Fixed effects included zone, temperature treatment, and season, while depth nested within plot ID was specified as a random effect to account for repeated measurements across campaigns and depth. In addition, reduction index (0-80 cm) and temperature data (5 cm, 25 cm, 75 cm) were averaged at the plot level and then linear regressions were calculated to assess the relationships between reduction index and soil temperature.

For methane emissions, data were normally distributed and therefore analyzed using a GLMM with Gaussian error distribution. Methane fluxes were measured once per plot in each campaign, resulting in five values per plot (March, May, June, August, September). The model included zone, temperature treatment, and season as fixed effects and plot ID as a random effect to account for repeated measurements. In addition, methane fluxes, reduction index (10-30 cm) and temperature data (5 cm) were averaged at the plot level and then linear regression were calculated to assess the relationship between methane fluxes and both reduction index and soil temperature.

To test whether warming affected methanogenic activity relative to methanotrophic activity, we calculated the ratio between methanogenic and methanotrophic potential processes. Microbial ratio data were separated into topsoil (5-10, 20-30 cm) and subsoil (40-50, 80-100 cm). After visual inspection, abundances were found to be non-normally distributed and were therefore log-transformed. Data were aggregated by plot ID and depth. GLMMs were then fitted with zone and temperature treatment as fixed

effects and plot ID as a random effect, accounting for repeated measurements across depths. In addition, reduction index (0-30 cm) and the ratio between methanogenic and methanotrophic potential processes (0-100 cm) were averaged at the plot level and then linear regression were calculated to assess the relationship between reduction index and the ratio between methanogenic and methanotrophic potential processes.

For all models, the significance of main effects (zone, temperature treatment, and season, where applicable) and their interactions was tested using Type-III Wald χ^2 tests (car::Anova). Pairwise comparisons were performed using Tukey's HSD tests.

All statistical analyses were conducted with the software R Studio version 4.4.1 (R Core Team, 2024). Data was prepared using R packages dplyr (Wickham et al., 2023), broom (Robinson et al., 2025) and lubridate (Spinu et al., 2024). All plots were created using R package ggplot2 (Wickham, 2016) with extensions ggpubr (Kassambara, 2020) and ggpmisc (Aphalo, 2024). GlmmTMB (Brooks et al., 2025). Tukey´s paiwise comparisons were performed using the R package emmeans (Lenth et al., 2024).

5.4 | Results

5.4.1 | Soil redox conditions

Across all temperature treatments, the strongest differences in redox potentials were observed among zones (Fig. 5.1a). Values increased along the marine-terrestrial gradient, from the pioneer zone (–112.1 ± 0.8 mV) to the low marsh (–43 ± 3 mV) and the high marsh (192.2 ± 4 mV). Variation was generally lowest in the pioneer zone, moderate in the low marsh, and highest in the high marsh topsoil (Fig. 5.1a). Redox potentials were lower in the subsoil compared to the topsoil, with differences between the marsh zones (Fig. 5.1a). In the high marsh, redox potentials were consistently lower in the topsoil (15 cm) compared to the subsoil (75 cm). In the low marsh and pioneer zone, depth-related differences were smaller and less consistent. Differences in redox potentials with warming treatments differed among zones and depths. In the high marsh topsoil, both temperature treatments (+1.5°C, +3.0°C) lowered redox potentials relative to ambient conditions, while in the subsoil +3.0°C plots were lower than ambient but the +1.5°C plots showed slightly higher values. In the low marsh topsoil, +3.0°C plots showed slightly higher redox potentials compared to ambient, while +1.5°C plots were lower. In the low marsh subsoil, both warming levels generally resulted in higher redox potentials than ambient. In the pioneer zone, redox potentials showed little variability overall and no consistent warming response was detected (Fig. 5.1a).

Reduction index (assessed using IRIS sticks) increased significantly with soil temperature across the entire soil profile from 0–80 cm ($R^2 = 0.26$, $p < 0.01$; Fig. 5.1b, Tab. 5.1). In topsoil (0–30 cm) and subsoil layers (60–80 cm), values were significantly higher in summer than in spring ($p < 0.001$, Fig. 5.1c, Tab. 5.1). In the topsoil, neither zone nor temperature treatment had a significant effect on reduction index, whereas in the subsoil, reduction index was significantly affected by zone ($p < 0.05$),

temperature treatment ($p < 0.001$), and season ($p < 0.001$). Because zone interacted significantly with temperature treatment ($p < 0.01$), season ($p < 0.001$), and their interaction effect ($p < 0.01$), main effects must be interpreted with caution. Interaction patterns showed that in the pioneer zone subsoil, reduction index increased significantly in spring under +1.5°C warming ($p < 0.05$; Fig. 5.1c). In the low marsh subsoil, reduction index increased significantly under both +1.5°C ($p < 0.05$) and +3.0°C ($p < 0.01$) temperature treatments (Fig. 5.1c). In the pioneer zone topsoil, reduction index also tended to increase with warming in both spring and summer ($p > 0.05$, Fig. 5.1c).

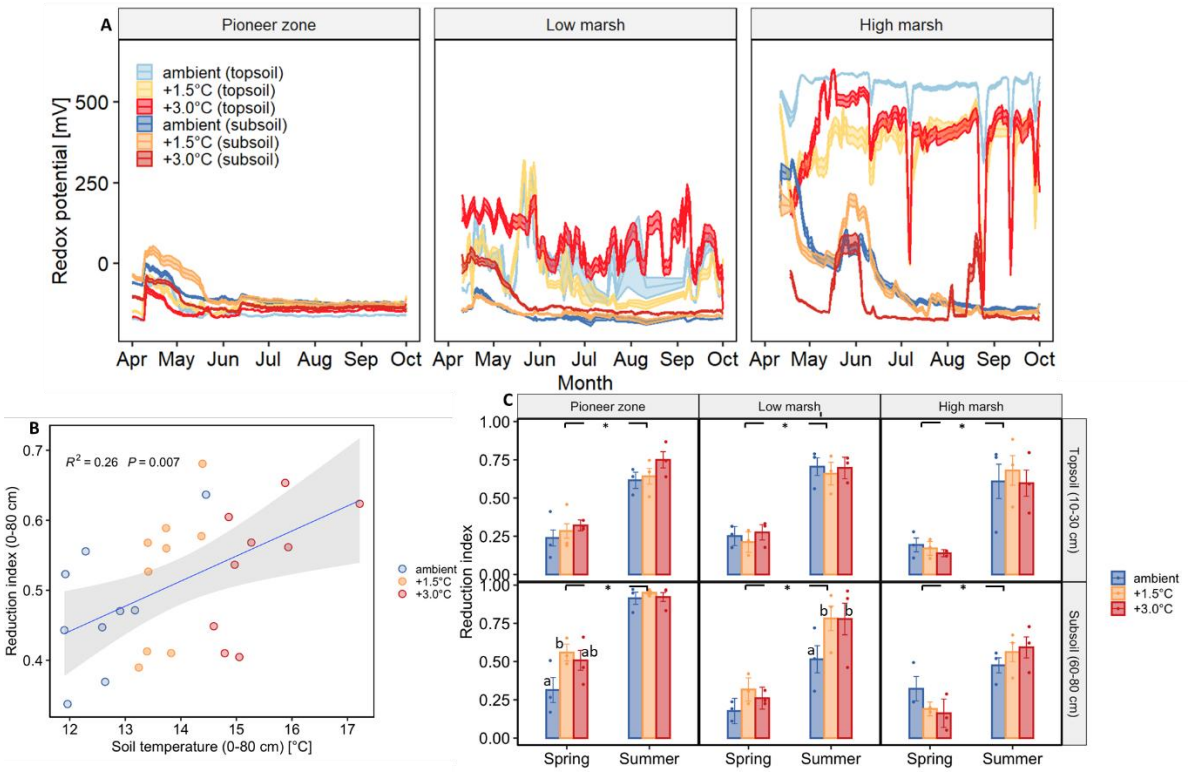

Figure 5.1: [A] Soil redox potentials (mV) from automated redox system (Apr 2024 – Oct 2024). [B] Linear regression between plot mean soil temperature and mean reduction index for vegetation period of 2023. Soil temperatures were averaged for the entire vegetation period (Mar-Oct 2023), at plot level across continuous temperature measurements at 5 cm, 25 cm and 75 cm soil depth. Reduction index (Mar-Oct 2023) was averaged at plot level across 0-80 cm depth. Shown are linear regression coefficient R^2 with corresponding *p*-values, linear fit, and 95% confidence intervals. [C] Reduction index data from vegetation periods (Mar-Sep 2023) in topsoil (10-30 cm) and subsoil (60-80 cm) layers across the marsh zones (pioneer zone, low marsh, high marsh) and the temperature treatments (ambient, +1.5°C, +3.0°C). Differences between zones are indicated as follows: * $p < 0.05$. Significant differences between temperature treatments within each zone and season are indicated with letters based on Tukey HSD pairwise comparison ($p < 0.05$).

5.4.2 | Methane fluxes

Methane fluxes were generally low (mean -1.34 ± 4.51 µmol m^{-2} d^{-1}) and ranged from -288.4 µmol m^{-2} d^{-1} to 172.09 µmol m^{-2} d^{-1}. Methane fluxes increased significantly with increasing reduction index (R^2 = 0.19; $p < 0.05$; Fig. 5.2a, Tab. 5.1) and with increasing soil temperature at 5 cm depth (R^2 = 0.17; $p < 0.05$; Fig. 5.2b, Tab. 5.1). Both temperature treatment and season had a significant effect on methane fluxes (both $p < 0.001$). As revealed by the two significant interaction effects between temperature treatment and zone ($p < 0.05$) and zone and season ($p < 0.01$), the effect of warming on methane fluxes depends on the context. During spring, methane fluxes in the pioneer zone were significantly higher in the +1.5°C temperature treatment compared to the ambient controls ($p < 0.05$; Fig. 5.2c, Tab. 5.1). In summer, temperature treatments did not differ with respect to methane fluxes (Fig. 5.2c).

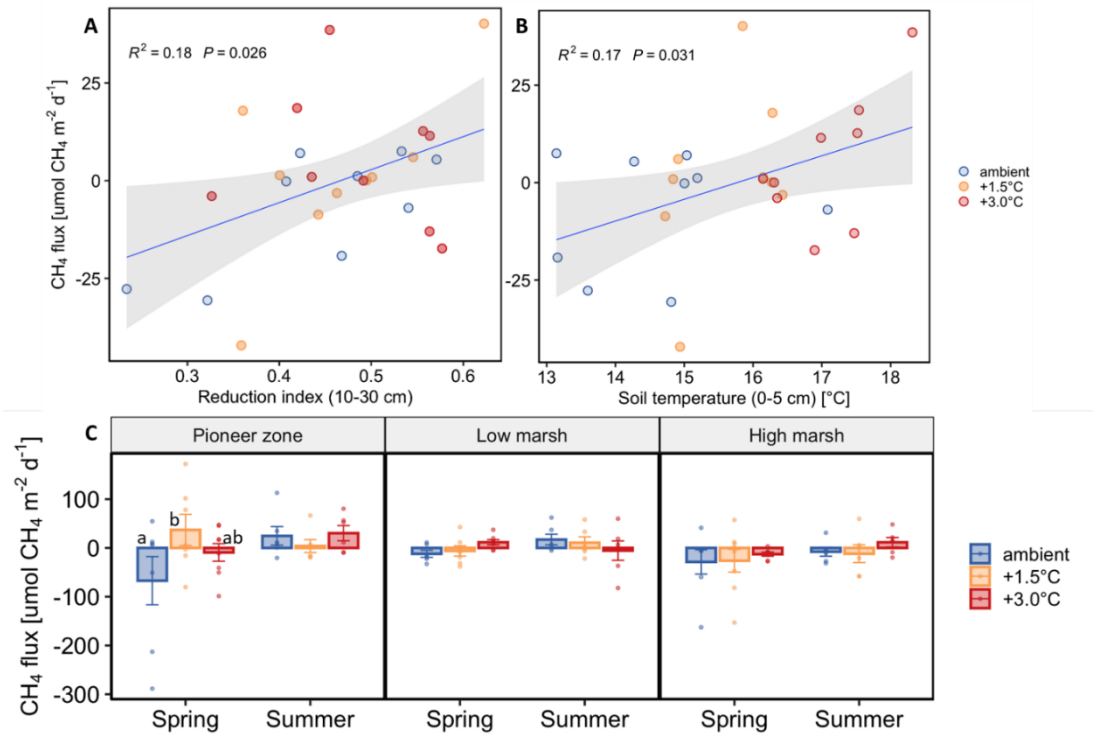

Figure 5.2: Methane flux data: [A] Linear regression between reduction index (Mar-Oct 2023) and methane fluxes (Mar-Oct 2023) Shown are linear regression coefficient R^2 with corresponding *p*-values, linear fit, and 95% confidence intervals. [B] Linear regression between plot surface temperature (Mar-Oct 2023) and methane fluxes (Mar-Oct 2023). Shown are linear regression coefficient R^2 with corresponding *p*-values, linear fit, and 95% confidence intervals. [C] Differences in methane fluxes (µmol m^{-2} d^{-1}) between the three temperature treatments (ambient, +1.5°C, 3.0°C), in two seasons (spring, summer), in the three marsh zones (pioneer zone; low marsh, high marsh). Significant differences between temperature treatments within each zone and season are indicated with letters based on Tukey HSD pairwise comparison ($p < 0.05$).

5.4.3 | Microbial methanogenesis and methanotrophy (Tax4Fun2)

The ratio of methanogenic to methanotrophic microbial potential processes increased significantly with increasing reduction index (R^2 = 0.30; p < 0.01; Fig. 5.3a, Tab. 5.1). Zone had a significant main effect on the ratio of methanogenic to methanotrophic potential processes). In the topsoil (10-30 cm), the ratio was significantly higher in the pioneer zone compared to both low marsh (p < 0.01) and high marsh (p < 0.01). In the subsoil (50-100 cm), the ratio differed significantly between all zones (Fig. 5.3b). In the subsoil, the methanogenic to methanotrophic ratio tended to decrease in response to warming (p = 0.13). The +1.5°C temperature treatment shows higher ratios compared to ambient plots, while the ratio is lower in the +3.0°C temperature treatments (Fig. 5.3b).

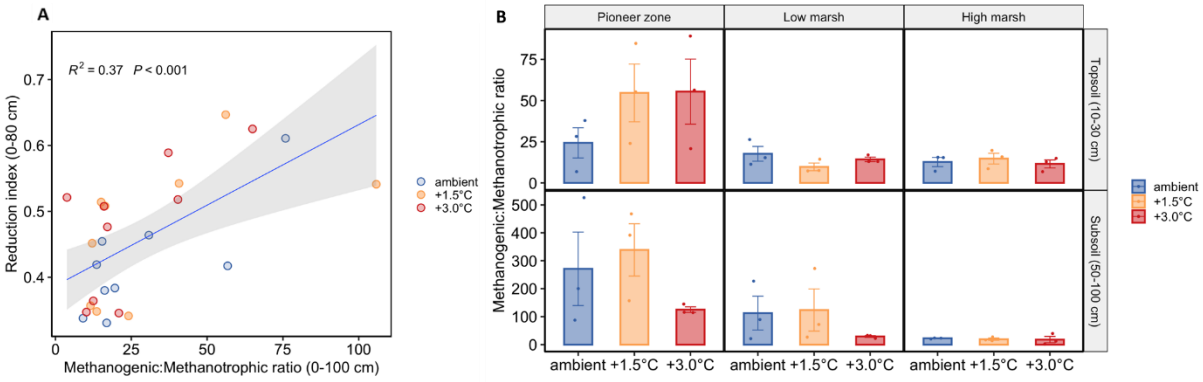

Figure 5.3: [A] Linear regression between reduction index (Mar-Oct 2023) across the entire measurement depth (0-80 cm) and the ratio between methanogenic and methanotrophic microbial potential processes, across the entire soil depth (0-100 cm). Shown are linear regression coefficient R^2 with corresponding p-values, linear fit, and 95% confidence intervals. [B] Differences in the ratio of methanogenic to methanotrophic microbial potential processes between the three temperature treatments (ambient, +1.5°C, 3.0°C) in the three marsh zones (pioneer zone, low marsh, high marsh), within the topsoil layer at 10-30 cm soil-depth and subsoil layer at 50-100 cm. Shown are barplots with errorbars (mean ± se). Functional groups were assigned from 16S rRNA transcript data using Tax4Fun2.

Table 5.1: Results of the generalized linear mixed models (GLMMs) testing for differences between marsh zones (pioneer zone, low marsh, high marsh), temperature treatment (ambient, +1.5°C, +3.0°C), seasons (spring, summer) conducted for both topsoil samples (10-30 cm depth) and subsoil samples (IRIS: 60-80 cm, Ratio methanogenesis:methanotrophy: 50-100 cm depth). Methane fluxes were testes on plot level (N= 27). Significant effects are indicated in bold ($p < 0.05$).

Factor / Parameter	**Reduction index**		**Methane fluxes**	**Ratio methanogenic to methanotrophic microbial potential processes**	
	Topsoil (10-30 cm)	Subsoil (60-80 cm)	Plot	Topsoil (10-30 cm)	Subsoil (40-100 cm)
Zone	$\chi^2 = 1.55$, $p = 0.46$	$\chi^2 = 6.57$, $\mathbf{p < 0.05}$	$\chi^2 = 4.34$, $\mathbf{p = 0.11}$	$\chi^2 = 18.46$, $\mathbf{p < 0.001}$	$\chi^2 = 42.39$, $\mathbf{p < 0.001}$
Treatment	$\chi^2 = 1.96$, $p = 0.38$	$\chi^2 = 16.27$, $\mathbf{p < 0.001}$	$\chi^2 = 15.63$, $\mathbf{p < 0.001}$	$\chi^2 = 0.45$, $p = 0.8$	$\chi^2 = 4.16$, $p = 0.13$
Season	$\chi^2 = 24.16$, $\mathbf{p < 0.001}$	$\chi^2 = 85.09$, $\mathbf{p < 0.001}$	$\chi^2 = 11.18$, $\mathbf{p < 0.001}$		
Zone x Treatment	$\chi^2 = 2.92$, $p = 0.57$	$\chi^2 = 15.99$, $\mathbf{p < 0.01}$	$\chi^2 = 9.83$, $\mathbf{p < 0.05}$	$\chi^2 = 5.6$, $p = 0.23$	$\chi^2 = 0.91$, $p = 0.92$
Zone x Season	$\chi^2 = 0.22$, $p = 0.89$	$\chi^2 = 22.78$, $\mathbf{p < 0.001}$	$\chi^2 = 3.96$, $p = 0.14$		
Treatment x Season	$\chi^2 = 0.47$, $p = 0.79$	$\chi^2 = 4.81$, $p = 0.09$	$\chi^2 = 10.44$, $\mathbf{p < 0.01}$		
Zone x Treatment x Season	$\chi^2 = 1.23$, $p = 0.89$	$\chi^2 = 16.27$, $\mathbf{p < 0.01}$	$\chi^2 = 7.33$, $p = 0.12$		

5.5 | Discussion

The automated redox potential measurements data is supportive of our first hypothesis, in which we predicted that warming would decrease soil redox potentials, with most pronounced effects in higher elevated zones. We observed warming effects on redox potentials primarily in the topsoil high marsh and topsoil low marsh zones, while the pioneer zone showed no clear trends (Fig. 5.1a). This result aligns with previous findings that warming can negatively influence redox-sensitive processes in wetland soils (Lee et al., 2025; Noyce et al., 2023). This pattern further supports our hypothesis that high-elevation zones would be most responsive to warming, as these areas experience the greatest baseline redox variability and are less poised by constant tidal inundation. This is in line with other studies from a peatland warming experiment, where warming effects on decomposition processes were restricted to top-soil layers (Hopple et al., 2020; Wilson et al., 2016). Previously reported results from the MERIT experiment demonstrated that these hydrology driven limitations of warming effects are also present in salt marshes, here both microbial functioning (Mittmann-Goetsch et al., *in revision*) and belowground biomass (Menzel et al., 2025) were only responsive to warming in the high marsh.

Reduction index and redox potential were negatively correlated (Fig. S5.2), but warming effects differed between methods (Fig. 5.1a & 5.1c). IRIS sticks may register brief reducing events in frequently flooded zones that are missed or averaged out by electrode data due to rapid re-oxidation during drainage (A. E. Evans et al., 2021). Thus, IRIS films could be more sensitive to changes in microbially mediated reduction in wet zones, while electrodes better capture warming responses in drier zones with higher mean redox values (Gotoh & Patrick Jr., 1974). In the high marsh, mean redox potentials were at 264.6 ± 6.6 mV across the entire soil profile, which is not within the range of iron reduction measured with the IRIS method (Z. Zhang & Furman, 2021). However, redox potential measurements at 75 cm depth in the high marsh were at −77.8 ± 2.8 mV; in subsoils, warming also led to more reduction on IRIS sticks, though not statistically significant (Fig. 5.1c). Importantly, IRIS is only responsive under strongly reducing conditions where Fe(III) reduction actively dissolves the coating (Jenkinson & Franzmeier, 2006; Rabenhorst et al., 2008). Such conditions are largely absent from high marsh topsoils, which typically remain well-aerated (Tang et al., 2023), meaning that IRIS and electrode data partly reflect different ranges of the redox spectrum. Taken together, the here presented IRIS sticks and automated redox potential measurements yield very strong evidence for warming effects on soil redox conditions.

The IRIS reduction index data revealed a more complex picture. That is, the data clearly showed that temperature (both season and temperature treatment) is a strong driver of soil reduction (Fig. 5.1b). However, against our first hypothesis warming effects were most pronounced in the top- and subsoil layers in the pioneer zone (Fig. 5.1c). Our second hypothesis stated that increases in reduction index (i.e., decreases in redox potential) would increase methanogenesis and methane emissions. Indeed, we found a significant increase of reduction index with warming in the pioneer zone subsoil, along with strong trends in topsoil in spring, while we simultaneously find a significant increase of methane emissions with warming in the pioneer zone in spring. The second hypothesis is further supported by the significant positive relationship between reduction index and methane fluxes (Fig. 5.2a), which demonstrates the fundamental coupling between redox conditions and methane dynamics in salt marshes. This relationship aligns with the established biogeochemical theory that low redox potentials favor methanogenic over methanotrophic processes (Hirano et al., 2013).

This interpretation is supported by the functional prediction analysis using Tax4Fun2, which revealed that the ratio of methanogenic to methanotrophic potential processes increased in moderate warming treatments (+1.5°C) in the pioneer zone (Fig. 5.3b) and limited to the topsoil also in the strong warming treatment (+3.0°C). Although these effects were not statistically significant, the trend mirrors the observed increase in methane fluxes (Fig. 5.2c) and aligns with evidence that even relatively small methanogenic populations can exert disproportionate functional activity (Cai et al., 2022). Increasing methanogenic activity over methanotrophy can also be explained by the higher Q10 of methanogenesis (4.1) compared to methanotrophy (1.9) and sulfate reduction (1.6) (Segers, 1998; Bodegom & Stams, 1999). Mean ambient surface soil temperatures at our site range between 13.6°C and 15.3°C (Rich et al., 2023), which is below the temperature optima for methanogenesis of approximately 25-30°C

(Conrad, 2023; Metje & Frenzel, 2005). However, rapid increases of methanogenesis with warming have previously been reported for temperatures below the temperature optima (Arnosti et al., 1998; Yvon-Durocher et al., 2014). Interestingly, the temperature increase by +3.0°C in the pioneer zone did not lead to increasing methane fluxes compared to ambient temperatures (Fig. 5.2c). Our findings are in line with studies from other wetland ecosystems (i.e. peatlands), where warming has shown to drive soils to become more methanogenic (Hopple et al., 2020; Wilson et al., 2021). Contrary to findings from a low-salinity coastal wetland where methane fluxes increased at warming of +5.1°C (Lee et al., 2025; Noyce et al., 2023; Noyce & Megonigal, 2021), at our site stimulating effects of warming were limited to the moderate temperature treatment of +1.5°C (Fig. 5.2c).

This moderate warming effect in a salt marsh on methane cycling is suprising, since methanogenesis in salt marshes is expected to be suppressed due to competition from sulfate-reducing bacteria (SRB), which preferentially use hydrogen or acetate under high sulfate conditions (Oremland & Polcin, 1982; Poffenbarger et al., 2011). This relationship makes the observed increase in methane fluxes in the pioneer zone especially interesting, since the pioneer zone is the most frequently flooded zone with high sulfate inputs (Rich et al., 2023). Studies show, that indeed methanogenesis can be favored over sulfate reduction (Noyce & Megonigal, 2021), when sulfate depletion occurs at faster rates due to temperature increase (Weston & Joye, 2005). This temperature driven mechanism is further supported by Van Hulzen et al. (1999), showing competitive advantage of methanogens over sulfate reducers.

However, the suppression of methanogenesis by sulfate reducers is not always of importance. Yuan et al. (2019) showed that the salt marsh plant *Spartina alterniflora* can increase the methane production potential by providing non-competitive substrates, beneficial for methylotrophic methanogens. We argue, that *Spartina anglica,* the dominant species in the pioneer zone at our site, may provide similar substrates that enable methanogenesis to respond strongly to warming in the pioneer zone (Fig. 5.2c). While this relationship can be supported by the general significant positive relationship between fine root biomass and soil reduction (Fig. S5.1), it fails to explain the warming effects on methane fluxes. This is consistent with previous results from this site showing that belowground biomass is not stimulated by warming (Menzel et al., 2025).

However, we find a strong positive relationship between the ratio of methanogenic to methanotrophic microbial processes and reduction index (Fig. 5.3a). Although not statistically significant, the observed differences in this ratio (Fig. 5.3b) between temperature treatments suggest that warming effects on redox and methane fluxes are predominantly microbially driven, likely because reductive processes show greater temperature sensitivity than oxidative (Bullock et al., 2013; Lee et al., 2025). Finally, we stress that this study did not measure methanogenesis or methanotrophy rates, and therefore does not provide direct links between microbial activity and methane fluxes. To get a deeper understanding on warming effects on these rates and their interactions with microbial activity and methane fluxes, these processes should be addressed simultaneously in future studies.

5.5.1 | Conclusion

Taken together, our findings highlight that salt marsh methane dynamics are responsive to warming. The results provide evidence that microbe–soil redox interactions, rather than plant-mediated effects, are the dominant drivers of warming responses in minerogenic marshes. Importantly, the results underscore that even under sulfate-rich, tidally influenced conditions, methanogenesis can be stimulated by moderate warming. This work therefore advances the understanding of salt marsh biogeochemistry and responses to global warming.

Our study shows that warming alters redox dynamics and methane cycling in salt marsh soils, with effects varying across seasons, zones and soil depths. While high marsh soils confirmed our first hypothesis of reduced redox potentials under warming, the reduction index revealed the strongest warming effects in the pioneer zone, where moderate warming (+1.5°C) significantly increased methane fluxes. These responses suggest that methanogenesis can be stimulated even under high salinity and sulfate availability, likely due to the higher temperature sensitivity of reductive processes compared to oxidative ones.

5.6 | Competing interests

The authors declare no conflict of interest.

5.7 | Data availability

Data and code are available at https://github.com/JulianMiGoe/merit_response_repo. The raw sequencing data is publicly available on the European Nucleotide Archive (ENA) under project accession number PRJEB91652 (https://www.ebi.ac.uk/ena/browser/view/PRJEB91652).

5.8 | Acknowledgments

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We thank Claudia Mählmann for her support with organizational issues.

5.9 | Supporting information

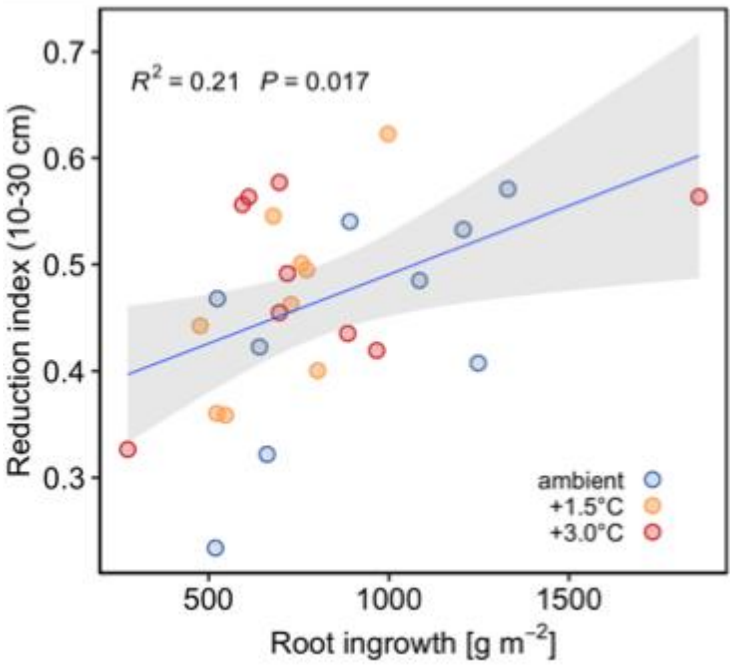

Figure S5.1: Regression analysis with reduction index data from 2023 and ratio of methanogenic to methanotrophic microbial processes, as assessed via 16S Sequencing of rRNA transcripts in 2022.

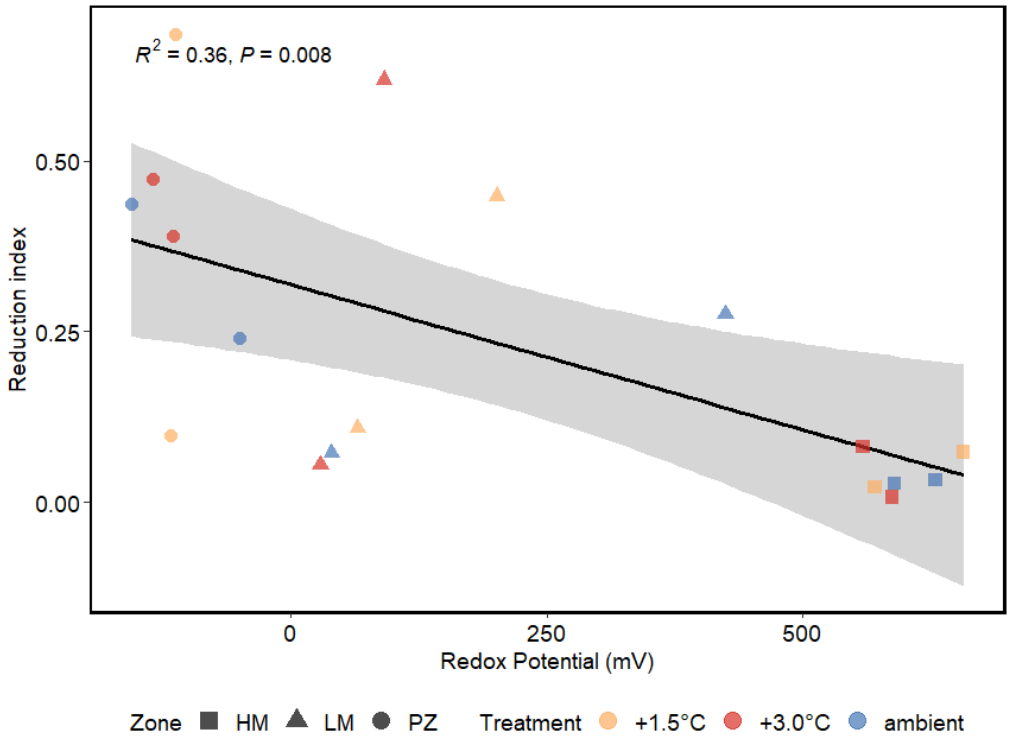

Figure S5.2: Redox potential measurements from automated redox system and reduction index measurements from IRIS sticks campaigns in 2024.

Box B | Hidden methane oxidation processes within salt marsh plant tissues

Clarisse Goesele & **Julian Mittmann-Goetsch**, Lena Hessler, Chen (Caroline) Cheng, Viktoria Unger, Kai Jensen, Susanne Liebner, Peter Mueller, Jana Täumer.

In preparation

„Let's meet tomorrow, if you choose, upon the shore, beneath the bridge

That they are building on some endless river"

- Leonard Cohen

BB.1 | Introduction

Salt marshes are highly productive wetland ecosystems in terms of carbon sequestration and long-term storage (Temmink et al., 2022). Additionally, salt marshes play a crucial role in global methane dynamics, serving as significant sources of atmospheric methane through anaerobic methanogenesis in waterlogged sediments (Al-Haj & Fulweiler, 2020; Krause & Treude, 2021; Capooci et al., 2024). Despite the influence of high saline sulfate rich water, that inhibit methanogenesis, a recent study has revealed unexpectedly high methane concentrations in salt marsh soils, reaching up to 145,000 μmol mol^{-1}, primarily through methylotrophic methanogenesis pathways (Capooci et al., 2024). While methane oxidation by aerobic methanotrophic bacteria has been extensively documented in terrestrial and freshwater ecosystems, particularly in association with Sphagnum mosses where endophytic methanotrophs can reduce methane emissions by 30-35% (Raghoebarsing et al., 2005; Liebner et al., 2011), the potential for similar plant-associated methane oxidation in salt marsh vegetation remains largely unexplored. Given that endophytic methane-oxidizing bacteria have been identified within plant tissues of upland species, where they were detected in tree-barks (Jeffrey et al., 2021), as well as in wetland species, including rice roots and peat moss (Kip et al., 2012; Minamisawa et al., 2016), the question arises whether salt marsh plants similarly harbor methanotrophic bacterial communities within their tissues, potentially representing a previously overlooked methane sink in these greenhouse gas-active ecosystems. In this study we hypothesize that [1] tissues of salt marsh plant species harbor methanotrophic microbes, that [2] effectively decrease atmospheric methane concentrations.

BB.2 | Material & Methods

Genomic DNA was extracted from soil and plant samples using the NucleoSpin® Soil Kit (Macherey-Nagel, Germany) following manufacturer instructions, with adaptations for plant tissues and modified centrifugation and elution steps. Eluates were stored at –20 °C. Plasmid DNA containing target genes (pmoA, mcrA) was isolated from transformed E. coli DH5α strains using the Presto™ Mini Plasmid Kit (Geneaid, Taiwan), with similar modifications to drying and elution steps, and stored at –20 °C.

Quantitative PCR (qPCR) was performed to quantify methanotrophic (pmoA) and methanogenic (mcrA) microbes using specific primers (pmoA 189 -F/pmoA661-R; mcrA:mlas-F/mcrA-R). Plasmids carrying 16S rRNA gene sequences were cloned and serially diluted to provide standards for absolute quantification. DNA concentrations were measured with a NanoDrop spectrophotometer (Thermo Scientific, USA). qPCR reactions were conducted in 10 µL volumes using SYBR Green master mix (5 µL SYBR Green Master Mix, 0.25 µL forward primer, 0.25 µL reverse primer, 3.5 µL distilled water, 1 µL DNA template) on a CFX96 Touch Real-Time PCR Detection System (Bio-Rad, USA). The qPCR program consisted of an initial denaturation (98°C, 180 s), followed by 40 cycles of 95°C (15 s), 60°C (30 s), and 72°C (30 s), and a final melt curve from 65°C to 94°C at 0.56°C s^{-1}.

Methane emissions from plant tissues were quantified by incubation experiments. Fresh plant stems and leaves (≥2.5 g) were sealed in headspace bottles, initially injected with 1.0 mL CH_4; on day 4 bottles were vented and reinjected with 1.5 mL CH_4. Methane concentrations were measured over 11 days by extracting 350 µL headspace gas per sample and analyzing 250 µL aliquots by gas chromatography (Agilent 7890A GC System).

BB.3 | Results

Abundance of methanotrophic microbes (pmoA gene) was detected in all plant compartments (roots, stems, leaves) and surrounding soil for both plant species *Spartina anglica* and *Elymus ahtericus* (Fig. BB1). With *Spartina anglica* consistently showing higher copy numbers compared to *Elymus athericus* (Fig. BB1). Incubation experiments revealed a clear reduction of headspace methane concentration over time in both species (Fig. BB2). Initial methane concentration was adjusted to 100%, and decreases were observed over 11 days.

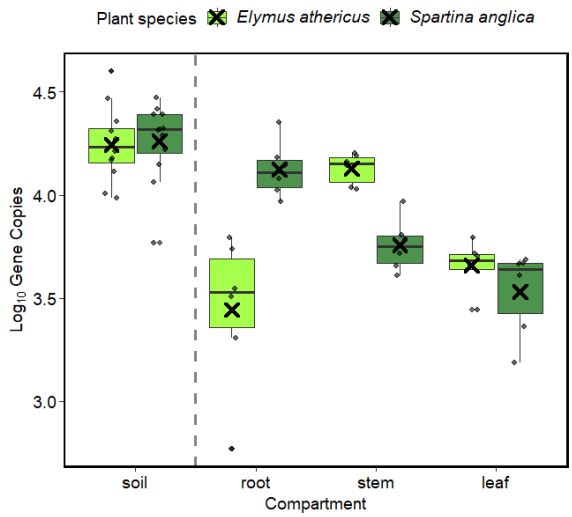

Figure BB.1: pmoA gene copies, assessed using qPCR, across the four compartments (soil, root, stem, leaf) in the two plant species *Spartina anglica* (dark green) and *Elymus athericus* (light-green). Shown are boxplots with medians as black lines and means as black x.

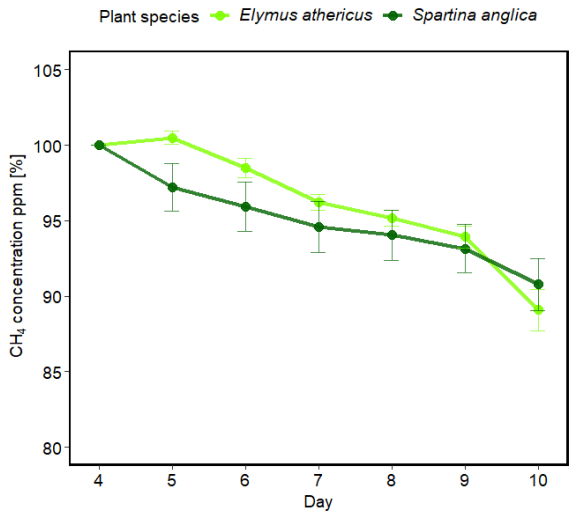

Figure BB.2: Temporal profile of methane concentration from incubation study in *Spartina anglica* (dark green) and *Elymus athericus* (light-green). Shown are days since equilibrium and methane concentration in parts per million (ppm) [%]. Initial methane concentration was calibrated as 100%.

BB.4 | Discussion

These results demonstrate that methanotrophic bacteria are not confined to salt marsh soils but are also present in plant tissues (both aboveground and belowground), supporting the first hypothesis. These findings are supported by previous findings from terrestrial and freshwater species (Jeffrey et al., 2021; Kip et al., 2012; Liebner et al., 2011). The observed methane decrease in incubation experiments (Fig. BB2) confirms these tissues are sites of methane oxidation, implying a previously overlooked methane sink in salt marsh ecosystems. This supports the second hypothesis, that methane oxidizers, within plant tissues can effectively decrease atmospheric methane concentrations.

Further work should characterize the diversity and activity of endophytic methanotrophs in different plant species and environmental contexts, and evaluate the contribution of these pathways to net ecosystem methane fluxes under changing climate and hydrological conditions.

Chapter 6 | Synthesis

Julian Mittmann-Goetsch

„Das Meer besitzt den Zauber der Dinge, die auch nachts nicht schweigen, die unserem unruhigen Leben erlauben zu schlafen"

- Marcel Proust

6.1 | Synthesis introduction

The synthesis is structured into six sections (Fig. 6.1), beginning with a brief review of the research rationale, overarching aims, and main hypothesis (6.1). This section concludes with a summary of specific aims, objectives and key findings from **chapters 2-5** (Tab. 6.1). In the second section, I discuss the bidirectional plant-soil redox interactions in wetland soils (6.2). In the third section, I discuss microbe-soil redox interactions and their relevance for carbon cycling in salt marshes under global warming (6.3). The fourth section discusses the effects of hydrology and climate, individually and their interaction, on salt marsh biogeochemical processes (6.4). The fifth section will delve into the time dependence of these plant-soil-microbe interactions and warming effects (6.5). The final section offers an outlook on the thesis research field and provides recommendations for future studies (6.6)

Salt marshes occupy a small fraction of the Earth's surface but disproportionately shape the global carbon balance (Temmink et al., 2022). Low redox potentials in salt marshes contribute to their exceptional capacity for carbon accumulation and storage, but also promote conditions favourable for methane production (Rosentreter et al., 2018; Temmink et al., 2022). In coastal salt marshes, redox dynamics, driven by complex plant-soil redox and microbe-soil redox interactions, regulate the balance between carbon sequestration and loss through decomposition of organic matter and greenhouse gas emissions. Yet, as these systems face a warming climate, our understanding of how these processes mediate the ecosystem response remains elusive. This thesis tests the hypothesis that plant-soil redox and microbe-soil redox interactions mediate the effects of global warming on soil carbon cycling.

Through the work of this thesis, I find strong support for the hypothesis that the interactions of both plants and microbes with the soil redox environment, are crucial for our understanding of global warming effects on carbon cycling in salt marshes.

Table 6.1: Overview of the chapters of this thesis and their respective objectives, methods and key findings.

Study	Objectives	Methods	Key Findings
Chapter 2: Root-Driven Soil Reduction in Wadden Sea Salt Marshes	• Assess how plants influence soil redox along hydrological gradients. • Test if background redox conditions determine plant effects. • Evaluate whether plants act as reducers in dry zones and oxidizers in wet zones.	• IRIS sticks • Planar optodes • Plant biomass • Soil organic matter content	• Plants act as net reducers in well-aerated minerogenic marshes of the Wadden Sea • Background level of soil reduction drives plant-effects • Plants were net oxidizers in most reduced soils and net reducers in less reducing soils
Chapter 3: Warming accelerates belowground litter turnover in salt marshes - insights from a Tea Bag Index study	• Assess how rising temperatures affect litter breakdown in salt marsh soils. • Test whether warming increases decomposition rate (k) and decreases litter stabilization (S). • Examine how warming effects on k and S vary with soil depth and marsh elevation • Determine if reducing soil conditions inhibit warming effects on litter decomposition.	• Tea Bag Index • IRIS sticks	• Rising temperatures significantly increased decomposition rate (k) across all zones and soil-depths • Warming effects on litter stabilization (S) were inconsistent and limited compared to effects on k. • Negative effects of warming on S occurred mainly in aerated topsoil of the pioneer zone, with effects extending deeper in soils from low to high marsh. • Reducing soil conditions suppressed the response of litter stabilization (S) to warming, but not the response of decomposition rate (k).

Chapter 4: Hydrology Masks Warming Effects on Microbial Communities in Salt Marsh Soils	• Assess how climate warming and hydrology shape microbial community structure and functioning in salt marsh soils. • Examine if warming alters microbial community composition toward microbes capable of degrading complex carbon compounds. • Test whether warming increases microbial exo-enzymatic activity. • Evaluate whether warming effects are stronger under less extreme hydrological conditions.	• 16S rRNA transcript sequencing • Exo-enzymatic assays (Carbon- and nitrogen acquisition) • IRIS sticks	• Overall microbial community structure remained stable under warming, indicating resilience • Subtle shifts occurred, with warming promoting drought-tolerant phyla (e.g., Actinobacteriota, Firmicutes) capable of degrading complex organic matter. • Warming effects on exo-enzymatic activities were not significant, but tend to decrease with warming in the high marsh. • Warming effects were most pronounced in the highest elevated zones.
Chapter 5: Warming stimulates soil reduction and methane cycling in high saline coastal wetlands	• Test whether warming decreases soil redox potential, especially in the high marsh. • Assess if warming-induced decreases in redox enhance methanogenesis and increase methane emissions.	• Automated redox potential measurements • IRIS sticks • Predicted potential microbial processes (Tax4Fun2) • Methane flux measurements	• Warming decreased soil redox potential, especially in high- and low-marsh topsoils. • Moderate warming (+1.5 °C) in the pioneer zone increased reduction index and methane fluxes. • Warming effects on methane fluxes were linked to microbially driven redox changes, even under high salinity and sulfate.

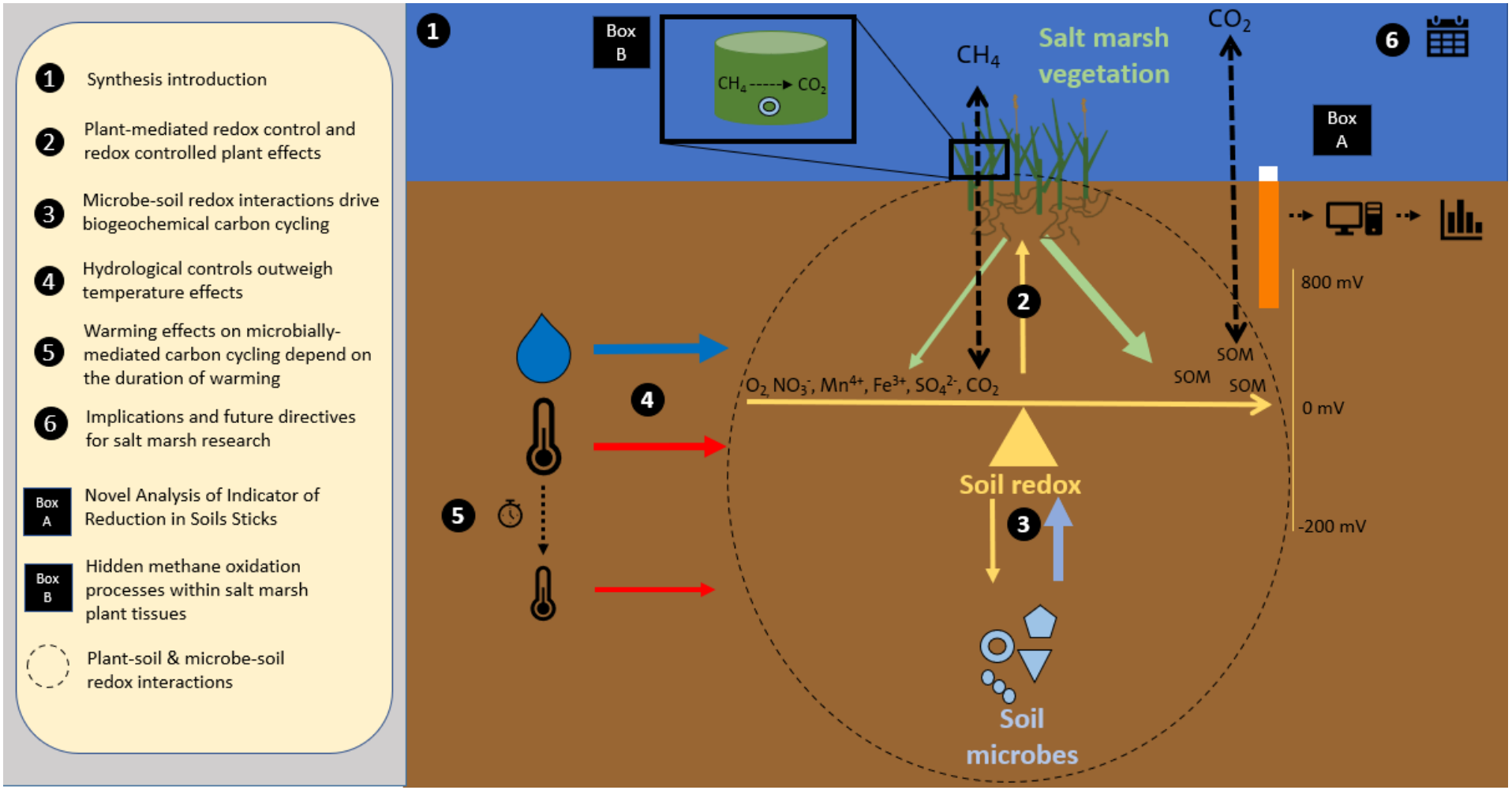

Figure 6.1: Schematic overview of the synthesis structure: [1] Synthesis introduction [2] Plant-mediated redox control and redox controlled plant effects [3] Microbe-soil redox interactions drive biogeochemical carbon cycling [4] Hydrological controls outweigh temperature effects [5] Warming effects on microbially-mediated carbon cycling depend on the duration of warming [6] Implications and future research directives for salt marsh research. Numbers correspond to sections of the synthesis.

6.2 | Plant-mediated redox control and redox controlled plant effects

The reciprocal relationship of wetland plant-soil redox interactions have gained increasing attention in the past decades due to the importance of redox potentials for the biogeochemistry of ecosystems with fluctuating water tables (Zhang & Furman, 2021). Soil redox potential is known to affect plant processes, such as photosynthesis, via reduced stomatal conductance in anoxic soils (Pezeshki, 2001), and root growth when redox potentials fall below certain thresholds (Davy et al., 2011). Redox potentials, linked to the hydrological regime, can also be used to determine the occurrence of different salt marsh plant species (Caçador et al., 2007; Davy et al., 2011). Plant-soil redox interactions are bidirectional and encompass both the effects of redox conditions on plant behavior as well as plant-driven processes that affect soil redox potentials.

The common hypothesis is that under the prevalent anoxic conditions of wetlands, plants are forced to transport oxygen, through their aerenchyma tissues into the roots to support their respiration. This process can result in the leakage of oxygen into the rhizosphere (Reddy & DeLaune, 2008; Schlesinger & Bernhardt, 2020), which in turn affects redox-sensitive reactions like the oxidation of sulfide (Lee, 1999). Recent studies report on these positive priming effects (e.g., oxygen priming) and their impacts on salt marsh carbon cycling (Noyce et al., 2023; Haviland & Noyce, 2024). For example, Koop-Jakobsen et al. (2021) demonstrated a positive correlation between plant activity and increased redox potentials in the rhizosphere, which likely stimulated SOM decomposition.

The second important plant-driven process that exerts a strong control over redox conditions in wetland soils is the input of electron donors into soils in the form of root exudates or plant litter (Sutton-Grier et al., 2011; Haviland & Noyce, 2024). These inputs of soluble organic compounds can be used directly by microbes for their respirational processes and thus lead to decreasing redox potentials and therefore supressed SOM decomposition, which is referred to as negative priming effects (Haviland & Noyce, 2024; Mueller & Megonigal, 2024; Krüger et al., 2025).

The work of **chapter 2** indicates that plant species of the minerogenic Wadden Sea salt marshes act primarily as electron donors. Results from both mesocosm and field-site studies show salt marsh plants act as net reducers of the soil (Fig. 2.3 & 2.5). My findings suggest that these reducing effects, assessed using the IRIS method (see **Box A**), are caused by root-driven inputs of litter and exudates. This view is supported by the positive correlation between organic matter content and reduction index (Fig. 2.6c). These findings contrast the prevailing notion that wetland plants act primarily as net oxidizers. I argue that the observed effects are facilitated by the relatively well aerated soils of the Wadden Sea salt marshes compared to other wetland ecosystems, as it has previously been suggested by other authors (Erchinger et al., 1996; Mueller et al., 2017). **Chapter 2** also shows that plant mediated redox controls are inversely related to background redox conditions. A planar-optode study indicates that roots acted as oxygen sinks when bulk soil oxygen concentrations were high. As soil oxygen declined, roots maintained relatively higher oxygen concentrations than the surrounding soil, acting as net oxygen

sources (Fig. 2.4). These observations suggest that the apparent shift from sink to source is a consequence of the relative difference between root and soil oxygen levels.

Chapter 2 further demonstrates that soil redox potential is a central variable for understanding biogeochemical feedbacks in wetland ecosystems (Husson, 2013; Zhang & Furman, 2021). Plants influenced soil conditions through redox interactions, exerting net reducing or oxidizing effects (Fig. 2.3). Conversely, background soil redox conditions also shaped plant activity determining the directions of the plant effects on soil redox conditions (Fig. 2.4). This study, also did not directly investigate plant-soil microbe interactions and it remains elusive how these interconnected processes respond to global warming. Previous studies have shown that plants can mediate the effects of global change factors such as sea level rise on soil microbial communities (Mueller, et al., 2020a; Tang et al., 2021). Taken together, these findings highlight the critical role of plant-driven processes in maintaining salt marsh ecosystem functioning under changing environmental conditions. Currently, the effect of global warming on these plant-driven processes remains elusive.

Studies from organic-rich coastal marshes and peatlands suggest that moderate warming stimulates plant productivity (Noyce et al., 2019; Smith et al., 2022; Hanson et al., 2025). This increased productivity was found to increase oxygen availability in soils, creating a net oxidizing effect on redox conditions and indirectly regulating methane dynamics (Noyce et al., 2023). This indicates that with increasing temperatures, the plant-soil redox interactions could be altered when plant productivity is stimulated. Since **chapter 2** clearly indicated that plant effects on soil redox conditions can be expected to be net reducing in Wadden Sea salt marshes, it could be anticipated that soils become more reducing under warming. Findings from the MERIT site, a minerogenic salt marsh, indicate little evidence that warming enhanced plant productivity (Menzel et al., 2025). This may be explained by the limited warming effects on microbial activity (**Chapter 4**), which in turn could have constrained nutrient availability for plants (Hanson et al., 2025). Instead, warming directly drives microbial-mediated changes: enhanced fermentation in high marsh soils increases soil reduction (Fig. 5.1, S4.2). The increase in soil reduction is reflected in increased methane fluxes in the pioneer zone (**Chapter 5**). Thus, compared to organic-rich marshes and peatlands, where plant productivity is the primary mediator of warming effects on soil redox and greenhouse gas fluxes (Wilson et al., 2021; Noyce et al., 2023; Hanson et al., 2025), soil redox and greenhouse gas fluxes in minerogenic marshes are strongly microbially controlled, with soil redox and methane dynamics largely decoupled from plant productivity.

6.3 | Microbe-soil redox interactions drive biogeochemical carbon cycling

Microbe–soil redox interactions in salt marsh ecosystems form complex, bidirectional feedbacks that fundamentally regulate carbon cycling and overall ecosystem functioning. Soil redox conditions are recognized as a central variable in wetland soils, fundamentally controlled by microbial respiration processes through the sequential usage of terminal electron acceptors following thermodynamic laws (Heimann et al., 2010; Candry et al., 2023). This creates a distinct redox zonation where oxygen

depletion drives the sequential reduction of NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-} and ultimately CO_2 for methanogenesis. While some microbial groups are specialized for specific redox processes, many are facultative and can utilize multiple electron acceptors depending on environmental conditions to the present redox conditions (Lovley & Phillips, 1987; Candry et al., 2023). At the same time, microbial communities are highly sensitive to immediate changes in the soil redox potential, creating dynamic feedback system in which microbes both control and are regulated by soil redox potential (Pett-Ridge & Firestone, 2005, **Chapter 4**). Here, I discuss microbe-soil redox and soil redox-microbe bidirectional interactions in salt marsh soils and how they affect carbon cycling.

Findings from **chapter 3** underscored the strong leverage of redox potentials over microbial functioning (i.e., stabilization / decomposition of organic matter). That is, in areas with high soil reduction (i.e., pioneer zone), warming effects are comparably small, while in areas with low soil reduction (i.e., high marsh) effects of warming on stabilization and partly on decomposition of organic matter are more pronounced. These findings are in line with results from the peatland whole-ecosystem warming experiment SPRUCE, where redox constraints limited warming effects to top-soil layers, while in subsoil layers warming effects were absent (Wilson et al., 2016).

Extending the insights of redox constraints, **chapter 4** demonstrates that microbe-soil redox interactions are in fact bidirectional. Microbial communities both respond to and actively control soil redox, creating a dynamic feedback system. This relationship is exemplified by the spatial distribution of key microbial taxa along redox gradients, where sulfate-reducing bacteria (Desulfobacterota) dominate in more reduced, frequently flooded zones, while aerobic decomposers like Actinobacteriota and Firmicutes increase towards well-aerated, higher elevated areas (Fig. 4.3). The distance-decay analysis (Fig. 4.5) shows a clear effect and demonstrates that, greater differences in soil reduction, between samples is significantly related to greater differences between microbial communities. At the same time, there are greater abundances of putatively active microbes related to fermentation processes in warmed high marsh plots as well as in the pioneer zone (Fig. 4.4). This pattern aligns well with findings from **chapter 5** showing a higher prevalence of methanogenic processes relative to methanotrophic processes (Fig. 5.3), which are reflected in lower redox potentials (Fig. 5.2). Here, microbes drive the redox conditions and not-vice versa (Megonigal et al., 2004). The dominance of heat-tolerant taxa in the warmed high marsh soils is accompanied by a greater functional potential to degrade complex carbon compounds (Fig. 4.4a-b). This finding aligns with the constraints of warming on the stabilization of labile materials in **chapter 3** (Fig. 3.3, Fig. 3.4).

Chapter 5 further illustrates the link between soil redox potentials and activity of methanogenic and methanotrophic microbes. Automated redox potential measurements showed clear differences between marsh zones, with increasing redox potentials along the elevational gradient (Fig. 5.1a). This increase in redox potentials was inversely related to methane fluxes. The pioneer zone exhibited the highest methane emissions, whereas the high marsh generally acted as a net methane sink (Fig. 5.2).

6.4 | Hydrological controls outweigh temperature effects

Hydrology plays a central role in wetland ecosystems. In salt marshes, hydrology is largely determined by marsh surface elevation, which drives the distinct zonation patterns observed in both vegetation (Bockelmann et al., 2002; Engels & Jensen, 2010; Pennings & Callaway, 1992) and microbial communities (Tebbe et al., 2022). Variation in hydrology is often directly reflected in redox dynamics (Niedermeier & Robinson, 2007). Consequently, the main components (plant, soil redox, microbe) of this thesis are known to be heavily controlled by hydrology. At the same time, numerous studies have reported that salt marshes and other wetland ecosystems also respond to global warming. Stimulating effects of warming have been found for both plant above- and belowground biomass (Noyce et al., 2019; Smith et al., 2022), and microbial decomposition of soil organic matter (Wilson et al., 2016). However, soil redox conditions can mediate these warming effects. Anoxic or reducing soils, particularly in low-elevation and wetter zones, may buffer against warming-induced carbon loss by limiting decomposition processes in subsoils (Wilson et al., 2016). In such environments, litter and organic matter can be stabilized under persistently low redox potentials (Hatton et al., 2015; Lajtha et al., 2018b; Poirier et al., 2018). Here I want to discuss the controls of hydrology in salt marshes, where they outweigh temperature effects and how microbe-soil redox and plant-soil redox interactions leverage the directions and magnitudes of these effects.

Chapter 3 demonstrates how hydrology mediates warming effects on carbon stabilization. While warming accelerates the initial decomposition rate (k) of labile organic matter across all zones and depths, its impact on long-term stabilization (S) is suppressed by reducing soil conditions, particularly in deeper or wetter zones (Fig. 3.3, Fig. 3.4). The study suggests that soil redox potentials, here reduction index assessed using IRIS sticks (**Box A**), control the magnitude of warming effects on stabilization of organic matter. Moreover, the study showed that the leverage of hydrology over the initial decomposition rate (k) was not significant. Similar findings have previously been reported, where labile organic matter has been shown to decompose at similar rates in oxic and anoxic environments (Kristensen et al., 1995).

Chapter 4 emphasizes that marsh zonation and soil depth, driven by hydrological conditions, are the primary predictors for microbial community composition and functioning, often masking direct warming effects. While the study shows clear differences in microbial communities between the marsh zones, corresponding with their respective hydrological regime, the study could not identify clear warming effects on the microbial community composition (Fig. 4.2). This is in line with other studies that reported on the strong control of hydrology over temperature effects on microbial community composition (Tebbe et al., 2022) as well as the microbial-driven initial decomposition of organic matter (Mueller et al., 2018). While **chapter 4** underscored the overriding effect of hydrology, there is indications of shifts in microbial communities in the high marsh, that could favour the degradation of complex carbon compounds (Fig. 4.3, Fig. 4.4). These findings are in-line with the findings of Mueller et al. (2018), which showed that while initial decomposition is not temperature sensitive, the overall

stabilization is indeed reduced by warming. Findings of **chapter 4** highlight the stability of the overall microbial community structure to warming where hydrological control is strong.

These findings are only partly corroborated by **chapter 5**, where the MERIT experiment was leveraged to assess the effects of global warming on soil redox itself and linking these changes to the emissions/uptake of greenhouse gases. Findings from **chapter 5** reveal that despite microbial communities being resilient to warming (**Chapter 4**), methanogenic activities might, in fact, be stimulated by warming (Fig. 5.3). This is in line with findings from the SPRUCE warming experiment, where soils became more methanogenic with warming (Hopple et al., 2020; Wilson et al., 2021). Interestingly, this effect was most pronounced in the pioneer zone. This finding contrasts the general assumption, and findings from **chapter 3-4**, which showed, the high marsh to be most vulnerable to warming effects. Notably, it is surprising that the pioneer zone responded in this way, as the common assumption is, that in the pioneer zone, continuous input of sulfate allows sulfate-reducing microbes to outcompete methanogens (Kristjansson & Schönheit, 1983). This has been shown to be reflected in strong decreases in methane (Bartlett et al., 1987).

Nevertheless, the main findings from **chapters 3-5** support the common hypothesis, that hydrology in fact is the dominant factor controlling biogeochemical processes in salt marshes (Rich et al., 2023). This finding is in line with recent meta-study findings that show environmental constraints to dominate over temperature responses in wetlands (Zhang et al., 2025, *preprint*). However, as reported in **chapter 2** the Wadden Sea salt marshes have shown to be comparably well aerated and "dry". In the high marsh, the highest elevated zone and least frequently flooded area of salt marshes (Harvey et al., 1987) the effect of warming was expected to be most pronounced. Results of **chapters 3-5** showed that in the highest elevated zone (high marsh), there is strong evidence of warming effects on salt marshes. Here, warming decreased the organic matter stabilization (**Chapter 3**), increased several heat-tolerant microbial phyla (**Chapter 4**), and decreased overall soil redox potentials, partly reflected in a reduced capacity of the marshes to oxidize methane (**Chapter 5**). I argue that the conditions of the high marsh zone in the Wadden Sea area often resemble upland ecosystems, where warming effects are known to stimulate microbial decomposition processes (Cheng et al., 2017). However, there is evidence for temperature responses of methane cycling to be especially pronounced in the pioneer zone. This finding is contrasting the previously reported findings. Since methanogenesis is a process that only occurs in highly reducing soils (Reddy & DeLaune, 2008), I argue that warming effects on methane fluxes (i.e. emissions) can only be expected in zones that harbor conditions favorable for methanogens. I suggest, that the higher elevated zones are less affected by warming, with regards to methane fluxes, due to the well-oxygenated soils, which would generally not allow for methanogenesis or rather promote methanotrophy. This view is supported by higher elevated zones showing net uptake of methane (Fig. 5.2c).

6.5 | Warming effects on microbially-mediated carbon cycling depend on the duration of warming

Warming effects on microbial respiration rate have been found in several upland ecosystems (Nissan et al., 2023). It is generally assumed that rising temperatures stimulate microbial metabolism and enzyme activity, leading to increased decomposition of soil organic matter and thus higher respiration rates.

Warming experiments across different ecosystems suggest that warming induced changes to carbon cycling are temporally dependent. Short-term (< 2 years) warming experiments in both upland and wetland ecosystems yield uniform results with regards to warming effects on soil respiration. That is, both in upland- and wetland- ecosystems, short-term warming increases soil respiration (Wilson et al., 2016; Romero-Olivares et al., 2017; Chen et al., 2022). With longer duration of warming, however, the effect of warming on soil respiration decreases significantly (Romero-Olivares et al., 2017). At the same time many studies agree, that warming effects on microbial community structure are rare in short to mid-term warming experiments (Bai et al., 2025; Duchesneau et al., 2025). Detecting effects of warming on microbial community structure is often only possible in long-term (> 2 years) experiments (Deslippe et al., 2012; DeAngelis et al., 2015). It has been found that alpha-diversity responds negatively to warming after 3-6 years, while ß-diversity increases after 6 years of warming, according to recent findings (Wang et al., 2025). Based on these contrasting findings, there is a growing body of research that calls for long-term studies on warming effects, because the magnitude and even the direction of warming effects can shift over years. Here, I want to elucidate short- to mid- to long-term warming effects within the whole ecosystem warming experiment MERIT and to test if these trends also apply to other coastal marshes.

The earliest study (year 1 & 2) presented in this thesis (**Chapter 3**) from the MERIT experiment showed very clear warming effects on microbial decomposition of organic matter, here assessed using the Tea-Bag Index method. This initial response to warming is in line with various other studies and the general finding of stimulating effect of early-stage on the decomposition of soil organic matter (Romero-Olivares et al., 2017). While studies from upland systems reported that warming effects on soil respiration become more pronounced with increasing duration of warming (Chen et al., 2022), I find contrasting results in **chapter 4**. Here I show that after a prolonged period of warming within the MERIT experiment (year 5), exo-enzymatic activities, involved in the decomposition of soil organic matter, are not increased by warming. While other studies reported that long-term effects of warming might be manifested in altered microbial community structures (Deslippe et al., 2012; DeAngelis et al., 2015), again the results of **chapter 4** yield a different picture. The putatively active microbial community (16S rRNA transcripts) has not altered with 5 years of warming. Recent findings from Duchesneau et al. (2025) support the observation from the MERIT experiment, for a peatland ecosystem where microbial community assemblages are resilient to short-term (<3 years) warming durations, stating that changes in activities might prevail over community changes. Other authors have reported on warming effects in coastal wetlands after 50 years of warming, suggesting that changes in the community assemblage at

the MERIT site can be expected in the future (Seidel et al., 2023). In the data presented in this thesis, the results from **chapter 4** show an increase in Actinobacteriota with warming, taxa positively associated with higher respiration rates (Xie et al., 2025), as well as FAPROTAX-based indications of enhanced microbial potential for degrading complex carbon compounds in the high marsh zone (Fig. 4.4). Together with the findings from **chapter 5**, where methane fluxes significantly increased after six years of moderate warming in the +1.5 °C plots (Fig. 5.3b), these patterns suggest that while the microbial community structure at the MERIT site appears stable, early signs of functional and biogeochemical responses are emerging. This supports the view that functional shifts may precede compositional changes under sustained warming, as it has been reported collectively for the SPRUCE peatland warming experiment (Wilson et al., 2016; Hopple et al., 2020; Duchesneau et al., 2025).

Here I present additional results from *Schwarzer & Logemann et al., (in prep)* (see further contributions and manuscripts), where we leveraged a short-term (1.5 years) salt marsh mesocosm warming experiment (NordSalt), to investigate microbial community composition and functioning. This study contrasts the findings from **chapters 3 + 4**, showing that short-term warming effects can in-fact alter microbial community composition (Fig. 6.2), while also affecting the specific enzyme activity (Fig. 6.3). Notably, specific enzyme activity (ß-Glucosidase) showed a nearly significant decrease in the +6.0°C treatment ($R^2 = 0.38$, $p < 0.1$) with rising organic matter content, suggesting that microbial acclimation played a substantial role (Fig. 6.3). This is supportive of prior studies showing that microbial communities respond to warming not only by changing their community composition, but also through functional adaptations such as increased enzyme affinity for substrates (Bradford et al., 2008; Romero-Olivares et al., 2017; Fanin et al., 2022). Such acclimation mechanisms can offset the direct stimulatory effects of higher temperatures, leading to reduced enzyme production per substrate and maintaining ecosystem stability under ongoing climate change. (Razavi et al., 2015; Fanin et al., 2022).

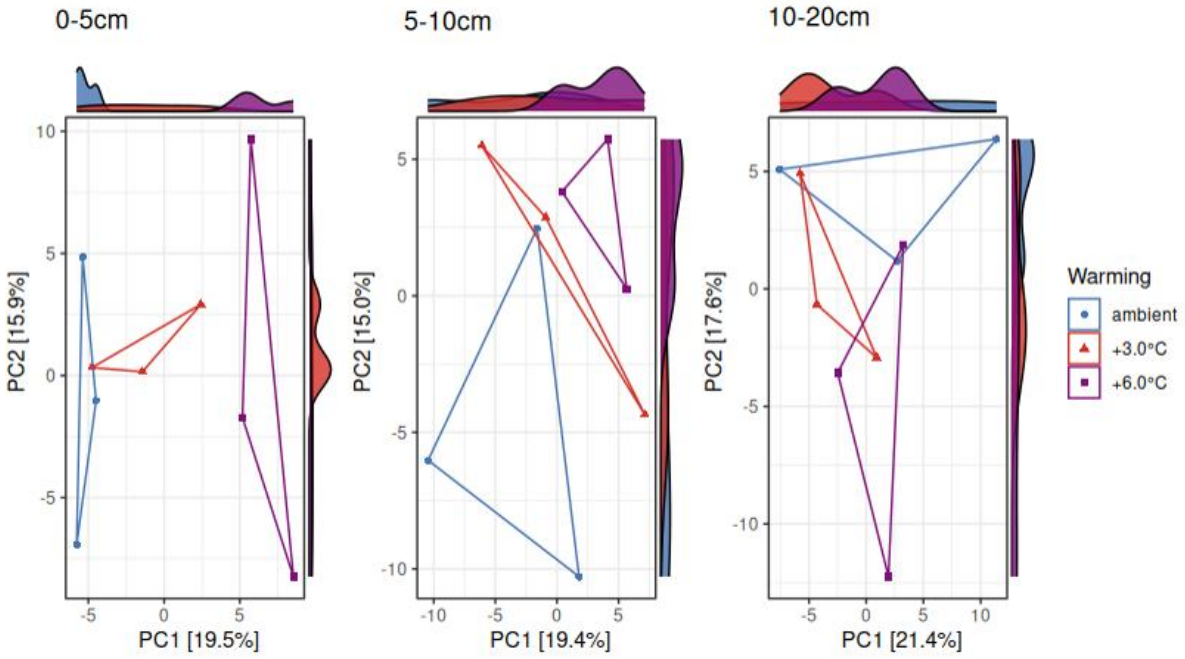

Figure 6.2: Principal Component Analysis (PCA) of center log-ratio transformed 16S rDNA microbial community composition for sample subsets from different soil depths (0-5 cm, 5-10 cm, 10-20 cm. Warming treatment triplicates are connected by lines (blue: ambient, red: +3.0°C, purple: +6.0°C). Source: Schwarzer & Logemann et al., (in prep). Colors were adapted for this thesis for clarity.

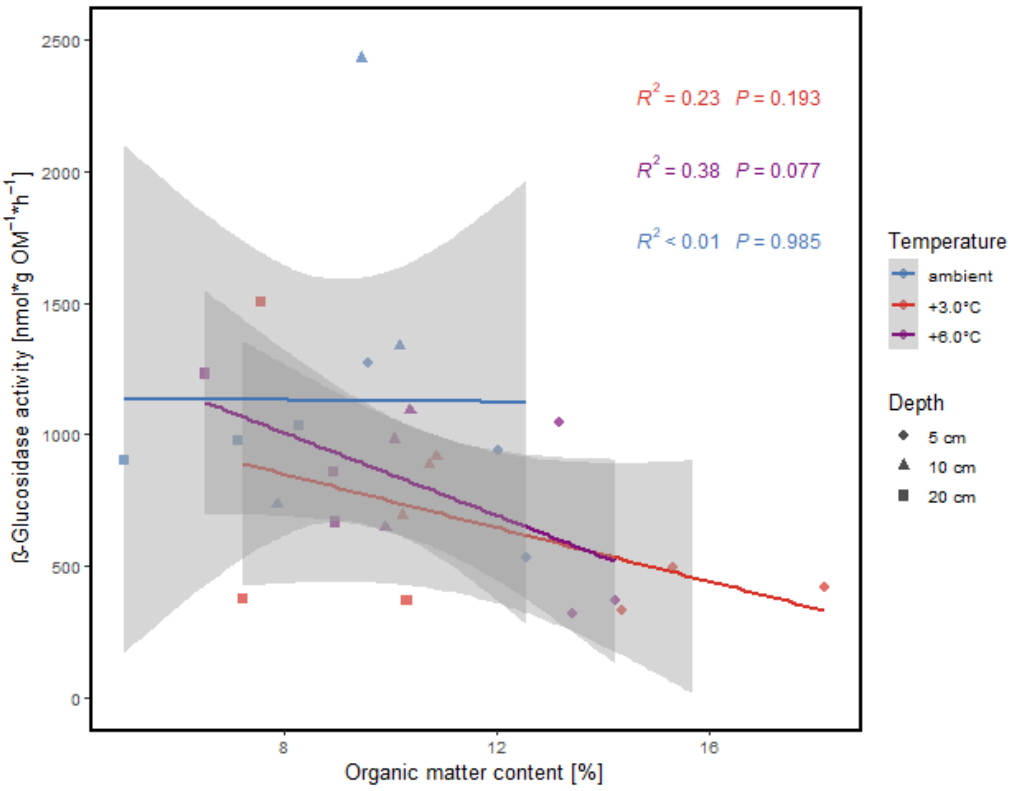

Figure 6.3: Linear regressions of specific exo-enzymatic activities [nmol * g OM^{-1} * h^{-1}] of ß-Glucosidase to organic matter content of marsh mesocosms of the NordSalt experiment. Regressions are displayed for three different warming treatments (blue: ambient, red: +3.0°C, purple: +6.0°C). Source: Schwarzer & Logemann et al., (in prep). Colors were adapted for this thesis for clarity.

These findings add an additional perspective to the results from **chapter 4**. To assess whether exo-enzymatic activities in salt marsh soils at the MERIT site responded to warming in a manner similar to Schwarzer et al. (in prep), I incorporated additional unpublished data from **chapter 4** (Fig. 6.4). Unlike the findings from Schwarzer et al., which showed decreasing specific enzyme activities in warmed plots (+3.0°C, +6.0°C) with increasing organic matter (Fig. 6.3), MERIT samples displayed increasing ß-glucosidase activities with increasing organic matter content (Fig. 6.4). This contrasting response likely reflects the generally low organic matter levels at the MERIT site on the North Sea Coast. While findings from the NordSalt mesocosm suggest an acclimation of microbes via reduction of enzyme affinity (Fig. 6.3), this strategy plays a subordinate role in salt marshes of the Wadden Sea which are poor in organic matter (Fig. 6.4). Here, both ambient and warmed plots showed increasing specific enzyme activities with higher organic matter content. These effects were statistically significant for the ambient treatment ($R^2 = 0.58$, $p < 0.001$) and the moderate warming treatment (+ 1,5°C; $R^2 = 0.24$, $p < 0.05$), while the strong temperature treatments show a weaker non-significant relationship (+ 3,0°C; $R^2 = 0.20$, $p > 0.05$). This could be indicative of acclimation processes, under strong warming treatments (+3.0°C), in the microbial communities exhibiting less enzymes per unit of substrate.

Overall, these outcomes highlight that warming-induced changes in microbial community composition and enzyme activities are highly dynamic and strongly context-dependent, reflecting site-specific differences in substrate availability and organic matter content. The contrasting responses observed between the NordSalt mesocosm and the MERIT field experiment emphasize that microbes adjust their functional strategies differently depending on local resource constraints. A recent study supports this view, showing that soil organic matter contents are comparably low at the study site of the MERIT experiment (Logemann et al., 2025). Collectively, these findings underscore that [1] the temporal dimension is central to understanding microbial responses to warming in the studied system (minerogenic salt marsh). [2] Here microbial communities show little indication of ongoing acclimation processes; [3] Such mechanism is not applicable to coastal marshes with higher substrate availabilities (i.e., soil organic matter contents), where microbial communities are altered in their structure and their functioning after short periods of strong warming

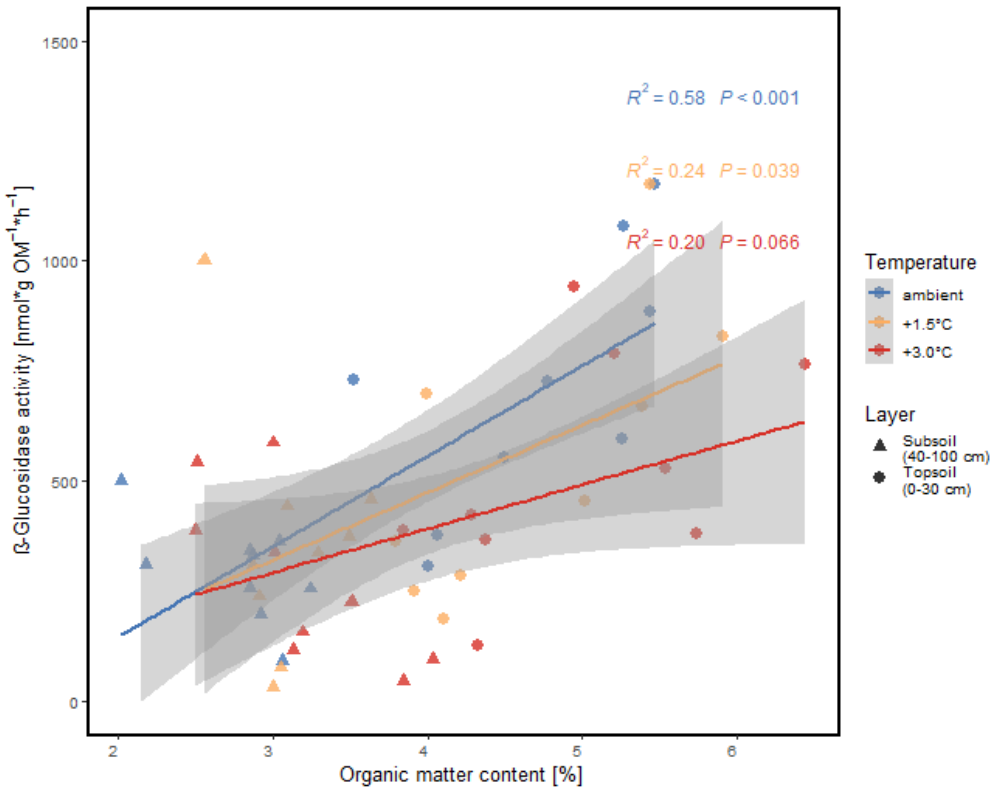

Figure 6.4 Linear regressions of specific exo-enzymatic activities [nmol * g OM^{-1} * h^{-1}] of ß-Glucosidase to organic matter content of marsh mesocosms of the MERIT experiment. Regressions are displayed for three different warming treatments (blue: ambient, orange: +1.5°C, red: +3.0°C).

6.6 | Implications and future directives for salt marsh research

This dissertation demonstrates that plant-soil and microbe-soil redox interactions are the principal drivers of carbon cycling responses to warming in salt marsh ecosystems. Through a comprehensive examination of the Wadden Sea salt marshes, this work reveals that the sensitivity of carbon cycling to global warming is fundamentally controlled by the bidirectional interactions of plant-soil and microbe-soil, with soil redox conditions serving as the central variable.

Collectively, the thesis findings highlight the overriding influence of hydrology and plant-soil and microbe-soil redox interactions in shaping the fate of blue carbon and greenhouse gas emissions in salt marshes providing a foundation for informed management and conservation of this ecosystem in a changing climate. The here presented results underpin the importance of soil redox conditions for addressing hypotheses about biogeochemical processes in salt marshes. I show remarkable links between the redox conditions and processes related to the carbon cycling (decomposition of soil organic matter, methanogenesis, methanotrophy). While other authors highlighted the importance of redox processes for biogeochemical processes, direct measurements and predictions are often not representative of the total capacity of ecosystems to accept and donate electrons (De Laune & Reddy, 2005; Burgin & Loecke, 2023). This thesis succeeded in predicting biogeochemical processes by applying state-of the art automated redox measurements (**chapter 5**) combined with an improved IRIS stick assessments a high-frequency method (**Box A**). Taken together, this allowed for nuanced

assessments of soil redox conditions. Due to the high temporal and spatial variability of redox potentials (Mansfeldt, 2003; Fiedler et al., 2007), future research should implement a combination of methods to assess redox potentials in ecosystem with fluctuating water-tables. Recent advances in the field of IRIS sticks have suggested the implementation of Mn(IV) IRIS sticks, to assess less reduced soils in addition to the commonly used Fe(III) coated IRIS sticks (Dorau et al., 2016; Rabenhorst & Post, 2018).

While this thesis has extensively addressed the effects of warming on salt marshes, we currently lack understanding of how elevated atmospheric CO_2 concentrations will affect the ecosystem in combination with elevated temperatures. Former studies on elevated atmospheric CO_2 concentrations revealed that effects on methane fluxes in wetlands might be neglectable (Chen et al., 2025). The combined effects of elevated CO_2 and elevated temperatures can, however, often be different in direction and magnitude from single effects of both global change factors (Noyce et al., 2023; Chen et al., 2025). Future research should address this knowledge gap, ideally by conducting long-term experiments, where elevated CO_2 and elevated temperature treatments are applied in a full factorial design. The few in-situ experiments applying both elevated temperature and CO_2 have shown that taken together these global change factors induce synergistic effects on plant productivity (Noyce et al., 2023). This increase in belowground biomass effectively reduced methane emissions, by increasing net oxidizing effects of plants on the soil redox conditions (Noyce et al., 2023; Lee et al., 2025). I hypothesize, that the minerogenic salt marshes of the Wadden Sea would experience opposite effects by possible increases in plant productivity. Here, plant-soil redox interactions have shown to net reduce the soils (**Chapter 2**), this effect would be amplified by higher root-productivity, induced by warming and elevated atmospheric CO_2. However, other studies suggest, that the effect of elevated CO_2 on plant productivity and ultimately methane cycling will differ between C3 and C4 species (Mueller et al., 2020a; Noyce & Megonigal, 2021), as C4 plants show little response to elevated atmospheric CO_2 concentrations (Drake, 2014). This should inform hypothesis formation for the system studied in this thesis, where both C4 (*Spartina anglica*, pioneer zone) and C3 (*Elymus athericus*, high marsh) species occur.

While microbial community structure remained largely resilient to five years of experimental warming, functional shifts towards enhanced fermentation and methanogenesis indicate that microbial processes are acclimating to warming in ways that may not be immediately apparent from taxonomic analyses (**Chapters 4-5**). The increase in methanogenic activity with warming, particularly in the pioneer zone, suggests a potential shift in these ecosystems from carbon sinks to greenhouse gas sources under continued warming. At the same time, results of **chapter 5** (Goesele & Mittmann-Goetsch et al., *in prep*), show the remarkable capacity of salt marshes to act as methane sinks. While wetlands are generally considered as methane sources (Laanbroek, 2010; Rosentreter et al., 2018), salt marshes were previously found to exhibit low emissions, due to the continuous input of sulfate from the seawater (Schorn et al., 2022). Recent advances in the field have reported the methane sink possibility of salt marshes (Rosentreter et al., 2021), which aligns well with the findings of this thesis. Findings from **Box B** contribute to the process understanding of the methane cycling in salt marshes, with methane oxidizing

communities within plant tissues. Collectively, these findings advance the mechanistic understanding of salt marsh functioning and can inform natural climate mitigation solutions. They also highlight substantial research potential to further disentangle the drivers and controls of methane dynamics in salt marsh ecosystems.

Microplastic pollution is another increasingly recognized research field. Recently, microplastic pollution has been identified as a factor that could alter methane dynamics in salt marshes, complementing the warming-driven functional shifts observed in this study. Salt marsh sediments are effective sinks for microplastics, which accumulate primarily in surface layers where microbial activity is highest (Lloret et al., 2021). Recent research in salt marsh ecosystems has linked microplastic contamination to increased methanogenic activity by favouring methanogenic archaea and disrupting methane oxidation, thereby potentially enhancing methane emissions (An et al., 2024). These findings suggest that microplastics could amplify the shift from methane sink to source by interacting with redox-dependent microbial communities responsible for methane cycling. Other studies report alterations of bulk density, soil aggregation, water holding capacity and microbial activity caused by microplastic pollution (De Souza MacHado et al., 2018; Liang et al., 2021).

Recent advances in viral ecology have exemplified that viruses can affect carbon cycling in oceans by complex interactions with microbial communities (Suttle, 2007). While. the role of soil viruses in carbon cycling is understudied, the few published studies reveal that soil viruses predate carbon cycling microorganisms linked to methanogenesis and methanotrophy and influence carbon degradation processes (Dalcin Martins et al., 2018; Emerson et al., 2018). Given the disproportionate leverage of coastal wetland over the carbon cycle, future research should account for virus-mediated effects on carbon cycling.

This work contributes to a growing recognition that coastal wetland responses to global change are highly context-dependent and mediated by complex biogeochemical feedbacks (Rich et al., 2023). The finding that minerogenic salt marshes respond differently to warming than organic-rich systems (Smith et al., 2022; Duchesneau et al., 2025; Hanson et al., 2025), underlines the need for ecosystem specific approaches to climate change mitigation and management strategies.

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Acknowledgments

Julian Mittmann-Goetsch

„Think of the words as science, not as art. They are a report. You are speaking before a meeting of the Explorers´ Club of the National Geographic Society. These people know all the risks of mountain climbing. They honor you by taking this for granted. If you rub their faces in it that is an insult to their hospitality. Tell them about the height of the mountain, the equipment you used, be specific about the surfaces and the time it took to scale it. Do not work the audience for gasps and sighs. If you are worthy of gasps and sighs it will not be from your appreciation of the event but from theirs. It will be in the statistics and not the trembling of the voice or the cutting of the air with your hands. It will be in the data and the quiet organization of your presence."

- Leonard Cohen

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„ After all is said and done

Gotta move while it's still fun

Let me walk before they make me run”

\- Keith Richards

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Hiermit versichere ich an Eides statt, die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen benutzt zu haben. Sofern im Zuge der Erstellung der vorliegenden Dissertationsschrift generative Künstliche Intelligenz (gKI) basierte elektronische Hilfsmittel verwendet wurden, versichere ich, dass meine eigene Leistung im Vordergrund stand und dass eine vollständige Dokumentation aller verwendeten Hilfsmittel gemäß der Guten wissenschaftlichen Praxis vorliegt. Ich trage die Verantwortung für eventuell durch die gKI generierte fehlerhafte oder verzerrte Inhalte, fehlerhafte Referenzen, Verstöße gegen das Datenschutz- und Urheberrecht oder Plagiate.

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