The Role of Plant-Soil Interactions for Carbon Cycling in Baltic and North Sea Coastal Wetlands

Dissertation

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Abstract

Plants in coastal wetlands act as ecosystem engineers, as they shape ecosystem development through bio-geomorphic feedbacks and exert strong control over carbon cycling in these dynamic systems and globally important carbon sinks. High primary productivity supplies large amounts of organic matter to the soil, while water saturation slows soil organic matter (SOM) decomposition. The fate of the sequestered carbon further depends on plant-soil interactions, as plants modify soil conditions such as redox potential and pH - key drivers of microbial activity. In addition, plants influence microbial decomposition by supplying substrates of differing quality. Compared to upland ecosystems, plant-mediated control over microbial activity is particularly pronounced in wetlands, where roots not only provide organic inputs but also release oxygen, altering redox conditions through radial oxygen loss. These interactions are particularly important for methane dynamics - a greenhouse gas with greater radiative forcing potential than carbon dioxide - which can be high in wetlands due to the waterlogged soils.

Despite their disproportionate role as carbon sinks, the effects of global warming on ecosystem carbon responses in wetlands remain poorly understood. The net climate-carbon feedback of wetlands is strongly dependent on plant-soil interactions and their warming-induced alterations, as both plant carbon assimilation (inputs) and SOM decomposition (outputs) are temperature-sensitive. Warming-driven increases in SOM decomposition are likely to enhance plant-available nitrogen, potentially alleviating nitrogen limitation and promoting greater biomass production and carbon retention. However, if decomposition outpaces plant carbon inputs, this will result in substantial SOM loss, creating a positive climate-carbon feedback accelerating climate change.

This thesis investigates carbon cycling and storage under current and warmer climate conditions in coastal wetlands of the North Sea and Baltic Sea, with a particular focus on plant-soil interactions. Four complementary studies were conducted. First, carbon stocks (chapter 2) and methane emissions (chapter 3) were quantified across German coastal wetlands, addressing both large-scale differences (between coasts) and small-scale variation (within sites and plant communities). Second, two studies (chapter 4 and 5) were conducted in a mesocosm warming experiment and investigated warming effects on transplanted vegetated soil-sods originating coastal wetlands from Denmark, Sweden, and Finland spanning distinct soil morphologies and plant communities. Here we assessed warming effects on aboveground biomass, soil organic matter (SOM), and microbial communities.

Across these studies, several key findings emerged. Low-energy Baltic Sea salt marshes contained higher soil organic carbon (SOC) stocks than high-energy North Sea marshes. Livestock grazing increased SOC stocks in the North Sea by enhancing soil compaction but showed mixed effects in the Baltic, driven by changes in plant biomass. Contrary to expectations, grazing effects on soil compaction and plant communities did not increase methane emission but varied strongly among sites. Grazing-induced shifts in plant community composition and subsequent alterations in belowground biomass and hence redox potentials explained methane emission. Grazing often excluded high-emission species such as *Phragmites australis*, highlighting complex underlying plant-soil interactions that vary between species and connected functional traits.

The studies conducted in the mesocosm warming experiment revealed that elevated temperatures increased plant-available nitrogen and enhanced aboveground biomass especially in SOM-rich systems, though systems with nitrogen-fixing plants and lower SOM content showed weaker responses. SOM losses occurred in soils initially rich in SOM, suggesting that ecosystem carbon responses to warming depend strongly on initial resource status. Warming also induced significant restructuring of soil microbial communities in SOM richer tall-grass communities but not in the SOM-poorer tall-grass community, likely reflecting differences in successional stage and microbial specialization. Taxa that increased under warming were linked to nutrient cycling and organic matter breakdown, whereas those that decreased under warming were associated with cold and low-oxygen adaptation.

Together, these studies demonstrate the pivotal role of plant-soil-microbe interactions in regulating carbon dynamics in coastal wetlands under both current and future climate conditions. Future research should prioritize two key pathways: (1) developing a mechanistic understanding of plant-soil interactions and how they are altered under warming, understanding particularly the influence of plant traits such as radial oxygen loss and root exudation on microbial activity and SOM decomposition; and (2) assessing SOM as a central variable in ecosystem carbon responses to warming, supported by further experimental studies to test the generality of this pattern.

Zusammenfassung

Pflanzen in Küstenfeuchtgebieten wirken als Ökosystemingenieure, da sie durch bio-geomorphologische Rückkopplungen die Entwicklung dieser Systeme prägen und zugleich den Kohlenstoffkreislauf in diesen dynamischen und global bedeutenden Kohlenstoffsenken stark beeinflussen. Die hohe Primärproduktion führt zu einem erheblichen Eintrag organischer Substanz in den Boden, während die Wassersättigung die Zersetzung von Bodenorganischer Substanz (SOM; von „soil organic matter“) verlangsamt. Das Schicksal des gebundenen Kohlenstoffs hängt von Pflanze-Boden-Interaktionen ab, da Pflanzen Bodenbedingungen wie Redoxpotenzial und pH-Wert verändern - zentrale Faktoren für mikrobielle Aktivität. Darüber hinaus steuern Pflanzen den mikrobiellen Abbau, indem sie organische Substrate unterschiedlicher Qualität bereitstellen. Im Vergleich zu terrestrischen Ökosystemen ist die Kontrolle der Pflanze über mikrobielle Aktivität in Feuchtgebieten besonders ausgeprägt: Hier liefern Wurzeln nicht nur organische Substanz, sondern geben auch Sauerstoff in den Wurzelraum ab und verändern so die ansonsten reduzierende Bodenbedingungen. Diese Prozesse sind besonders relevant für die Methandynamik - ein Treibhausgas mit deutlich höherem Strahlungsantrieb als Kohlenstoffdioxid -, die in Feuchtgebieten aufgrund der Wassersättigung im Boden sehr hoch sein können.

Trotz ihrer herausragenden Bedeutung als Kohlenstoffsenken sind die Auswirkungen der globalen Erwärmung auf den Kohlenstoffhaushalt von Feuchtgebieten weitgehend unerforscht. Die Netto-Klima-Kohlenstoff-Rückkopplung hängt entscheidend von Pflanze-Boden-Interaktionen und deren Erwärmungs-induzierten Veränderungen ab, da sowohl die pflanzliche Kohlenstoffassimilation (Eintrag) als auch der mikrobiell vermittelte SOM-Abbau (Austrag) temperaturabhängig sind. Ein durch Erwärmung gesteigerter SOM-Abbau kann den pflanzenverfügbaren Stickstoff erhöhen, somit eine potenzielle Stickstofflimitierung verringern und so das Biomassewachstum und den damit verbundenen Kohlenstofffeintrag fördern. Übersteigt jedoch der Abbau den Kohlenstoffeintrag, führt dies zu erheblichen SOM-Verlusten und damit zu einer positiven Klima-Kohlenstoff-Rückkopplung, die den Klimawandel weiter verstärkt.

Diese Dissertation untersucht den Kohlenstoffkreislauf sowie die Kohlenstoffspeicherung in Küstenfeuchtgebieten der Nord- und Ostsee mit einem besonderen Fokus auf Pflanze-Boden-Interaktionen im Ist-Zustand und unter zukünftiger globaler Erwärmung. Vier komplementäre Studien wurden durchgeführt. Zunächst wurden Kohlenstoffvorräte (Kapitel 2) und Methanemissionen (Kapitel 3) in deutschen Küstenfeuchtgebieten quantifiziert, wobei sowohl großräumige Unterschiede (zwischen Küsten) als auch kleinräumige Variationen (innerhalb von Standorten und Pflanzengemeinschaften) betrachtet wurden. Anschließend wurde in zwei Studien, die in einem Erwärmungs-Mesokosmos-Experiment durchgeführt wurden (Kapitel 4 und 5), Bodensoden mit

Pflanzengemeinschaften aus Küstenfeuchtgebieten aus Dänemark, Schweden und Finnland in einer kontrollierten Erwärmungsanlage untersucht, um Effekte erhöhter Temperaturen auf pflanzliche Biomasseproduktion, SOM-Dynamik und mikrobielle Gemeinschaften zu erfassen.

Die Ergebnisse zeigen: Ostsee- Salzmarschen wiesen höhere Vorräte an Bodenorganischem Kohlenstoff (SOC; soil organic carbon) auf als die meso-tidalen Nordsee-Salzmarschen. Beweidung erhöhte die SOC-Vorräte an der Nordsee durch Verdichtung des Bodens, zeigte jedoch in der Ostsee uneinheitliche Effekte, die durch Veränderungen der unterirdischen Pflanzenbiomasse bedingt waren. Entgegen den Erwartungen führten Beweidungseffekte auf Boden und Pflanzengemeinschaften nicht zu höheren Methanemissionen, sondern variierten stark zwischen den Standorten. Beweidungs-induzierte Veränderungen in der Pflanzengemeinschaft und der damit verbundenen Wurzelbiomasse und deren Einfluss auf Boden-Redoxpotentiale, erklärten die Unterschiede in den Methanemissionen. Häufig wurden hoch emittierende Arten wie *Phragmites australis* durch Beweidung ausgeschlossen, was die komplexen und artspezifischen Pflanzen-Boden-Interaktionen unterstreicht.

Die Studien aus dem Mesokosmos-Experiment zeigten, dass Erwärmung den pflanzenverfügbaren Stickstoff erhöhte und vor allem in SOM-reichen Systemen die oberirdische Biomasse steigerte, während Systeme mit stickstofffixierenden Pflanzen und geringerem SOM-Gehalt schwächer auf Erwärmung reagierten. SOM-Verluste traten in ursprünglich SOM-reichen Böden auf, was darauf hindeutet, dass die Reaktion von Feuchtgebietsökosystemen auf Erwärmung stark vom Ausgangszustand abhängt. Zudem führte Erwärmung zu einer signifikanten Umstrukturierung der mikrobiellen Gemeinschaften in SOM-reicheren Böden, aber nicht in SOM-ärmeren Böden - vermutlich aufgrund unterschiedlicher Sukzessionsstadien und mikrobieller Spezialisierung. Taxa, die unter Erwärmung in Abundanz zunahmen, waren mit dem Abbau komplexer organischer Substanzen und dem Nährstoffkreislauf verbunden. Im Gegensatz dazu nahmen Abundanzen von Taxa ab, die vor allem an kalte, sauerstoffarme Bedingungen angepasst sind.

Zusammenfassend verdeutlichen diese Studien die zentrale Rolle von Pflanze-Boden-Mikroben-Interaktionen für die Steuerung des Kohlenstoffkreislaufs in Küstenfeuchtgebieten unter aktuellen Bedingungen und zukünftigen Klimaszenarien. Zukünftige Forschung sollte zwei Schwerpunkte verfolgen: (1) ein detailliertes mechanistisches Verständnis der Pflanze-Boden-Interaktionen und der Erwärmungseffekt auf diese, wobei insbesondere die Rolle spezifischer Pflanzeneigenschaften wie radialem Sauerstoffverlust und Wurzelexsudation für mikrobielle Aktivität und SOM-Abbau untersucht werden sollte; sowie (2) die Betrachtung von SOM als zentrale Variable für die Kohlenstoffdynamik unter Erwärmung in Küstenfeuchtgebieten, ergänzt durch experimentelle Studien, um die Allgemeingültigkeit dieses Musters zu prüfen.

Manuscripts related to this Dissertation

Chapter 2

Logemann E. L., Goesele C., Jensen K., & Mueller P. (2025). Soil Organic Carbon Stocks of German Salt Marshes: A Comparative Study Along Low-and High-Energy Coastlines. *Journal of Geophysical Research: Biogeosciences*, *130*(7), e2025JG008797.

Conceptualization: **EL,** CG, PM, KJ; *Methodology*: **EL**, PM; *Data curation:* **EL**, CG; *Investigation:* **EL**; *Formal analysis:* **EL**; *Supervision*: PM, KJ; *Funding acquisition*: PM, KJ; *Visualization*: **EL**; *Resources:* **EL***,* CG; *Writing – original draft*: **EL**; *Writing – review & editing*: **EL**, CG, PM, KJ

Chapter 3:

Mittmann-Goesele C., **Logemann E.L.,** Chen C.C.; Kutzbach L., Jensen K., & Mueller P. (in preparation). Plant Control On Soil Redox State Determines Grazing Effects On Methane Emissions From Coastal Wetlands

Conceptualization: CG, **EL,** PM, KJ; *Methodology*: CG, LK, PM; *Software*: CG; *Data curation:* CG; *Investigation:* CG, **EL**, PM; *Formal analysis:* CG; *Supervision*: PM, KJ; *Funding acquisition*: PM, KJ; *Visualization*: CG; *Resources:* CG, CC; *Writing – original draft*: CG; *Writing – review & editing*: CG, **EL**, CC, PM, LK, KJ

Chapter 4:

Logemann E.L., Mueller P., Banta G., Boström C., Eklöf J.S., Krause-Jensen D., Lanari M., Leiva-Dueñas C., Quintana C. O., Rich R., Thomsen S. & Jensen K. (in preparation). Plant-Soil Interactions Determine Coastal Wetland Carbon Cycle Response to Rising Temperatures.

Conceptualization: **EL,** PM, GB, CB, JE, DK, RR, ST, KJ; *Methodology*: **EL**, PM, GB, CB, JE, DK, ST, KJ; *Software*: RR; *Data curation:* **EL**; *Investigation:* **EL**, PM, KJ; *Formal analysis:* **EL**; *Supervision*: PM, KJ; *Funding acquisition*: PM, GB, CB, JE, DK, KJ; *Visualization*: **EL**, ST; *Project administration:* **EL**, PM, GB, ST, KJ; *Resources:* **EL**, GB, CB, JE, DK, ML, CL, CQ, ST, KJ; *Writing – original draft*: **EL**; *Writing – review & editing*: **EL**, PM, GB, CB, JE, DK, ML, CL, CQ, RR, KJ

Chapter 5:

Schwarzer J.*, **Logemann E.L.*,** Mittmann-Goesele J., Brodehl A., Bartholomäus A., Jensen K., Mueller P. & Liebner S. (in preparation). Warming Effects Microbial Community Composition in Nordic Coastal Wetland Soils.

Conceptualization: JS, JM, PM, **EL**; *Methodology*: JS, **EL**, JM, PM, SL; *Data curation:* JS, JM, **EL**; *Investigation:* JS, **EL**, JM, ABr, ABa, PM, SL; *Formal analysis:* JS; *Supervision*: PM, KJ, SL; *Funding acquisition*: PM, KJ, SL; *Visualization*: JS, **EL**, JM; *Project administration:* **EL**, KJ; *Resources:* **EL**, JM, JS, ABr; *Writing – original draft*: JS; *Writing – review & editing*: JS, **EL**, SL, PM, JM

* equal contribution

Further Contributions to Manuscripts

Koplin, J., Peter, C., Bischof, K., Böttcher, M. E., Kuhn, A., **Logemann, E**., ... & Pogoda, B. (2025). Blue Carbon potential in Germany: Status and future development. *Estuarine, Coastal and Shelf Science*, *323*, 109354.

Graversen, A. E. L., Lønborg, C., Addamo, A. M., Pedersen, S. G., Chemello, S., Alejo, I., ..., **Logemann, E.**, … & Jensen, D. K. (2025). A marine and salt marsh sediment organic carbon database for European regional seas (EURO-CARBON). *Data in brief*, *60*, 111595.

Leiva-Dueñas, C., Banta, G.T., Boström, C., Eller, F., Eklöf, J., Holm Andersen, L.,..., **Logemann, E**., ..., Krause-Jensen, D. (under review). Low climate benefit of Nordic coastal marshes. *Global Change Biology.*

CHAPTER ONE

GENERAL INTRODUCTION

1.1. Carbon cycling in coastal wetlands

Coastal wetlands deliver a range of critical ecosystem services, such as serving as nesting habitat for breeding avifauna, facilitating nutrient cycling, providing nursery ground for fish, supporting recreational activities, offering coastal protection, and storing substantial amounts of carbon (Friess et al. 2020). Notably, the role of coastal wetlands as carbon sink has gained increasing attention over the past decade (Mcleod et al.; Lovelock and Duarte 2019; Macreadie et al. 2021). Carbon sequestration results from the imbalance between buried organic matter as carbon input into soils and the decomposition of organic compounds through microbial activity as carbon output (Duarte et al. 2005; Lovelock and Reef 2020). The decomposition rate of organic compounds is relatively slow in coastal wetlands compared to upland soils, primarily due to waterlogged soil conditions that lead to lower redox potentials (Neubauer and Megonigal 2021). Simultaneously, coastal wetlands are characterized by high net primary productivity, which is fostering carbon cycling. The high primary productivity in coastal wetlands contributes not only to positive plant-soil interaction by increasing the physical accretion of coastal wetlands through forming both soil volume and sediment deposition rates but also to the accumulation of soil organic matter (SOM) via vegetation-derived plant litter (Kirwan and Megonigal 2013; Morris et al. 2016). Consequently, plant productivity serves as a critical determinant of the resilience and long-term carbon sequestration capacity of coastal wetlands in times of climate change (Kirwan and Megonigal 2013; Spivak et al. 2019). The persistence of soil organic carbon is an emergent property shaped by the interplay of plant-soil interactions, including biological processes (e.g., litter input quantity and quality versus microbial decomposition), environmental conditions, and chemical as well as physical stabilization mechanisms (Schmidt et al. 2011; Dungait et al. 2012; Cotrufo et al. 2013; Neiske et al. 2025). The balance between plant-derived carbon inputs versus respiration-mediated carbon output is strongly influenced by bio-geomorphological factors as well as by biotic interactions. Microbial respiration and activity are tightly linked to both the quantity and quality of organic plant inputs, highlighting the central role of biotic feedbacks in controlling carbon persistence. Understanding plant-soil-microbe interactions, particularly in wetland ecosystems, is crucial for predicting future carbon-climate feedback and the climate mitigation potential of these blue carbon ecosystems under global change (Schmidt et al. 2011; Ren et al. 2022; Haviland and Noyce 2024). The following sections discuss the range of abiotic and biotic factors influencing the carbon cycle dynamics (Fig. 1) in coastal wetlands, with particular emphasis on plant productivity and plant-mediated processes.

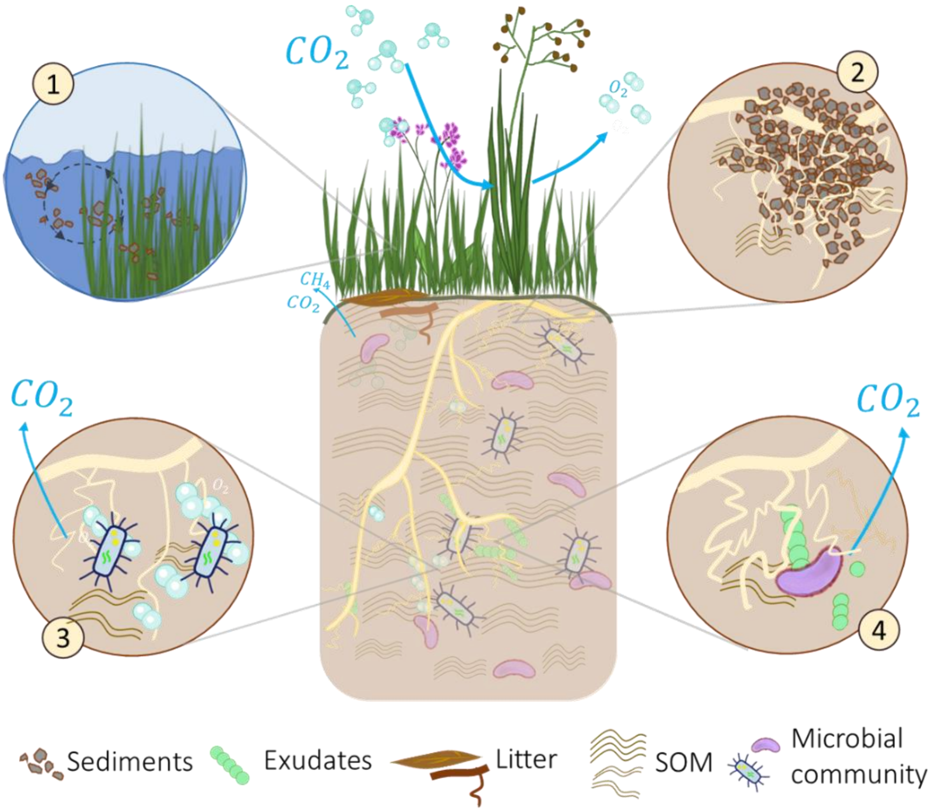

Figure 1. Coastal wetland plants act as ecosystem engineers by controlling carbon inputs and outputs while interacting with both aboveground and belowground environments. Specifically, they (1) slow water flow, trapping sediments and allochthonous carbon; and (2) stabilize soils through their roots, which also contribute to the SOM pool, together supporting vertical marsh accretion. Belowground, plants further influence microbial communities by (3) releasing oxygen through radial oxygen loss (ROL), providing microbes a highly efficient terminal electron acceptor and creating hotspots of microbial respiration; and (4) releasing exudates, low-molecular-weight carbon compounds that are readily metabolized by microbes. Both oxygen inputs and exudates can enhance SOM decomposition.

1.1.1. Environmental challenges and plant adaptation

Coastal wetlands occur at the interface between land and sea and withstand extreme conditions, forging the development of dynamic systems shaped by regular tidal and/or irregular wind-driven inundation. These dynamic processes create systems adapted to rapidly changing environments which often are also able to withstand extremes. Plant adaptations to environmental challenges such as flooding, hypoxic or anoxic soils, and increased salinities involve morphological changes, such as the development of specific tissues, altered growth strategies, and osmotic regulation (Adam 1990). To cope with mechanical stresses from water movement and wind, wetland plants have evolved structural adaptations like increased stem flexibility, variation in stem height, and enhanced anchoring through well-developed root systems (Schoutens et al. 2021). Salt intrusion into the soil during tidal inundation induces a physiological drought by inducing osmotic stress, leading to water deficit conditions and ion toxicity within plant tissues (Parida and Das 2005; Munns and Tester 2008). The accumulation of salt ions constitutes as a further stress factor that potentially disrupts critical physiological processes, including protein synthesis, photosynthesis, and lipid metabolism.

Additionally, the accumulation of salt ions in the rhizosphere can impair nutrient uptake by interfering with the absorption and transport of essential minerals (Parida and Das 2005; Lambers and Oliveira 2019). Consequently, coastal wetland plants have developed various adaptations to cope with osmotic stress. These strategies include active salt excretion through specialized structures such as salt glands, salt accumulation within tissues, and salt dilution via succulence, allowing plants to store water in specific tissues to reduce salt concentrations in physiologically more active plant parts (Munns and Tester 2008). Additionally, the waterlogged conditions induce metabolic stress in the rhizosphere by affecting root respiration and nutrient availability (Bradley and Morris 1990). As a response, many wetland plants develop high stem and root porosity through the formation of aerenchyma, which facilitate oxygen transport within the plant (Armstrong 1980; Pedersen et al. 2021). This allows plants to oxygenate the rhizosphere which in turn enables root respiration and nutrient uptake in waterlogged soils (Lai et al. 2012; Pedersen et al. 2021).

1.1.2. Coastal wetland plants as ecosystem engineers

Coastal wetlands are complex ecosystems continuously shaped by the force of tides and/or periodic flooding. These dynamic hydrological processes drive intricate biogeochemical interactions and establish feedback loops between pioneer plants establishing on bare intertidal flats and sediment properties (Fagherazzi et al. 2012; Nolte et al. 2013a; Fig. 1). In this context, wetland plants function as ecosystem engineers: they slow water flow and trap sediments during inundation, thus promoting vertical accretion of the soil (Allen 2000; Bouma et al. 2005). This interaction ultimately fosters the self-sustaining development and succession of coastal wetlands on tidal flats within the intertidal zone (Olff et al. 1997; Fagherazzi et al. 2012). In coastal areas where tidal influence and sedimentation rates are limited (e.g. in the Baltic Sea), wind-driven periodic inundation can play a similar role in shaping these systems (Adam 1990; Dijkema 1990). Beyond trapping sediments, plants also contribute to vertical soil accretion through their belowground growth and the deposition of organic matter such as root litter (Kirwan and Megonigal 2013; Allen 1990; Fig. 1). Based on the prevailing mechanisms driving vertical growth, coastal wetlands can be classified into two main types: organogenic and minerogenic systems. In minerogenic systems, vertical accretion is primarily controlled by sediment deposits of sand, clay or mud, often linked to tidal range (Nolte et al. 2013; Allen 1990). In contrast, organogenic systems typically exhibit slower vertical accretion, which is strongly driven by organic matter accumulation (Allen 1990; Kirwan and Megonigal 2013).

1.1.3. Effects of wetland soil properties on primary productivity

In coastal wetlands, plant community composition and primary productivity exhibit a direct and highly variable response to various environmental parameters, including sediment type, salinity, and elevation, as well as to the interactions among these factors (Willis and Hester 2004; Howard 2010;

Suchrow and Jensen 2010; Wilburn et al. 2024). Besides the important role of inundation itself in determining plant community composition along elevational gradients (Suchrow and Jensen 2010), plant productivity is constrained by environmental stressors associated with inundation, among which increased salinity plays a prominent role (Naidoo and Kift 2006). Physiological disruptions due to stressful environmental conditions can induce alterations in plant community composition, by selectively disadvantaging salt-sensitive species (Więski et al. 2010). Previous studies along estuarine gradients (thus along salinity gradients) have demonstrated a reduction in overall plant productivity with increasing salinity (Hansen et al. 2017; Neiske et al. 2025).

Sediment and soil texture, often linked to the flooding regime (Temmerman et al. 2003), plays a critical role in shaping plant responses to interacting abiotic factors (Chapman et al. 2012; Pezeshki and DeLaune 2012). Soil characteristics such as grain size distribution and soil porosity determine water and nutrient availability, as well as soil redox conditions, all of which directly influence plant productivity (Pezeshki and DeLaune 2012; Haque et al. 2018; Feng et al. 2020). Plant responses to changes in soil properties are species-specific (Liu et al. 2023) and vary across spatio-temporal scales (Contreras-Cruzado et al. 2017). Furthermore, soil texture is a key determinant of carbon persistence, primarily due to the reduced bioavailability of organic compounds, either through adsorption onto mineral surfaces or through encapsulation within soil aggregates of humic substances (Schmidt et al. 2011; Dungait et al. 2012; Cotrufo et al. 2013; Neiske et al. 2025).

1.1.4. Plant-microbe interactions

The fate of organic carbon inputs into soils largely depends on microbial activity, as microbes re-mineralize organic carbon by secreting extracellular enzymes to fuel their metabolism. Microbial communities play a central role in ecosystem functioning, as they provide essential nutrients to plants, enhance plant performance through multitrophic interactions, and contribute to overall soil fertility (Fierer 2017; Banerjee and van der Heijden 2023). The composition and activity of soil microbial communities are shaped by a range of abiotic factors in soils, including pH, redox potential, water content, temperature, and the availability of nutrients and organic carbon, as well as by biotic interactions with plants (Philippot et al. 2013; Fierer 2017).

Plant-microbe interactions occur through multiple pathways. Indirectly, plants modify the rhizosphere and soil environment by altering chemical properties such as pH and redox conditions (Fig. 1), thereby influencing microbial habitats (Hinsinger et al. 2006; Wang and Kuzyakov 2024). These effects are especially pronounced in wetland ecosystems, where species-specific plant-soil interactions play a crucial role in shaping microbial processes (Robroek et al. 2016). Moreover, plants directly affect microbial communities through the release of root exudates, rhizodeposits, and litter (Fig. 1). Root exudates are low-molecular-weight organic compounds exuded into the rhizosphere that provide easily accessible substrates for microbial metabolism (Megonigal et al. 1999; Oburger and Jones 2018). In addition to supplying organic carbon, wetland plants also transport oxygen into the rhizosphere, particularly plant species with extensive aerenchyma tissues (Armstrong 1980; Lai et al. 2012). The ability of plants to oxidize their rhizosphere depends also on background redox state of the wetland soil and varies among species, therefore shifts in plant species composition can alter their sediment redox conditions in different directions (Lai et al. 2012; Koop-Jakobsen et al. 2021; Mittmann-Goetsch et al. 2024). The combined input of labile organic compounds and of oxygen can trigger a priming effect, whereby microbial activity is stimulated, potentially accelerating the decomposition of existing SOM and potentially leading to increased carbon losses (Kuzyakov 2010; Lei et al. 2023; Mueller and Megonigal 2024).

1.1.5. Effect of wetland soil properties on soil organic matter decomposition

In water-saturated soils, oxygen availability becomes a key limiting factor for microbial activity, as oxygen is rapidly depleted, creating anoxic conditions. The efficiency of microbial degradation of organic compounds is strongly influenced by the availability of terminal electron acceptors. Under aerobic conditions, microbes utilize oxygen, the most energy-yielding terminal electron acceptor, enabling enhanced oxidation of organic compounds. This results in high SOM decomposition rates and rapid carbon turnover, with CO_2 produced as a byproduct of aerobic respiration (Pezeshki and DeLaune 2012). Under more reducing conditions, microbial metabolism shifts to rely on alternative electron acceptors with lower Gibbs free energy yields (e.g., nitrate, manganese(IV), iron(III), sulfate, and carbon dioxide), resulting in slower SOM decomposition rates (Pezeshki and DeLaune 2012). In the absence of oxygen, SOM decomposition further slows down, and microbial communities transition to fermentative pathways (Chapman et al. 2019).

1.1.6. Methane production in anaerobic soils

During anaerobic metabolism, the activity of methanogens may increase methane production in coastal wetlands, depending on the availability of terminal electron acceptors (Chapman et al. 2019). Elevated methane production and finally emissions may counteract the climate mitigation potential of these carbon sinks, as methane is a more potent greenhouse gas than CO_2 in terms of radiative forcing (Rosentreter et al. 2021b; Forster et al. 2024). However, methane production is governed by a range of environmental and biological factors. Different microbial communities, employing distinct metabolic strategies, compete for available electron donors. In the absence of oxygen and other high-energy-yielding terminal electron acceptors, methanogenic archaea can mineralize organic carbon via hydrogenotrophic, acetoclastic or methylotrophic methanogenesis, producing methane as a byproduct (Conrad 2020). Further, methanogenesis relies on the availability of labile organic matter as an electron donor, and is therefore closely linked to plant activity, which supplies easily degradable organic carbon compounds to rhizospheres (Oburger and Jones 2018; Haviland and Noyce 2024). In the presence of more beneficial terminal electron acceptors, methanogens are readily outcompeted by microbial communities that utilize the more energetically favorable terminal electron acceptors, such as sulfate. Sulfate availability is positively correlated with increasing salinity and is thus typically abundant in coastal tidal wetlands. As a result, sulfate-reducing bacteria often dominate under these conditions, thereby suppressing methanogenesis and reducing methane emissions in coastal wetlands (Bridgham et al. 2006; Poffenbarger et al. 2011).

Once methane is produced in the soil, it needs to pass the soil matrix to be emitted into the atmosphere. This occurs via three primary pathways: diffusion, ebullition, and plant-mediated transport. Diffusion is driven by concentration gradients between methane-rich zones (e.g., soil pores or sediment layers) and the surrounding environment (e.g., overlying water column or atmosphere). Due to the slow rate of diffusion through soils, methane “transported” via this pathway is often oxidized by methanotrophic bacteria before it reaches the soil surface (Bridgham et al. 2013; Neubauer and Megonigal 2021). Ebullition, by contrast, is a rapid release of methane gas via bubbles that form and escape due to changes in hydrostatic pressure, typically driven by temperature fluctuations, atmospheric pressure changes, or shifts in water levels (Neubauer and Megonigal 2021). Plant-mediated transport occurs through aerenchyma, which facilitate both passive and convective gas flow between the soil to the atmosphere. This pathway allows methane to bypass oxidative zones in the soil, reducing the likelihood of microbial consumption and thus potentially increasing methane emissions. However, the same tissues that transport methane also deliver oxygen to the rhizosphere, enabling aerobic methane oxidation or outcompeting methanogens by promoting aerobic respiration and partially offsetting methane emissions from plant roots (Noyce et al. 2023; Haviland and Noyce 2024). Accordingly, plants can both increase methane emissions by supplying labile organic compounds to rhizospheres and by facilitating gas transport from the soil, and decrease methane emissions by enhancing methane oxidation through oxygen release into the soil (Waldo et al. 2019; Haviland and Noyce 2024; Määttä and Malhotra 2024).

1.2. Global change in coastal wetlands

Coastal wetlands face numerous challenges in the context of global change. As described previously, carbon cycling in coastal wetlands is governed by complex plant-soil interactions, which remain poorly understood. This complexity is further amplified as coastal wetlands face multiple challenges, including global warming, increased atmospheric CO_2 concentrations, accelerated rates of sea-level rise, and increasing storminess (Spivak et al. 2019; Macreadie et al. 2021; Lovelock et al. 2022). These environmental shifts may alter carbon inputs, microbial activity, and decomposition dynamics in unpredictable feedbacks (Reich et al. 2020). For instance, Noyce et al. (2023) reported that elevated atmospheric CO_2 unexpectedly reduced methane (CH_4) emissions. This finding contrasts with earlier studies, which demonstrated increased CH_4 emissions under elevated CO_2, largely due to greater inputs of labile organic compounds to rhizospheres fueling methanogenesis. Noyce et al. (2023) suggest that the reduction in methane emissions they observed may reflect a legacy effect: long-term CO_2 enrichment increased the accumulated stem density of the dominant grass species, which in turn enhanced oxygen priming to the rhizosphere. These changes suppressed the activity of methanogens or promoted methanotrophy, thereby mitigated the anticipated rise in CH_4 emissions. This study alone underscores the intricate plant-soil interactions among various environmental variables, even when considering only a single global change driver. Additionally, the resilience of wetlands in the face of accelerated rates of rising sea levels is closely linked to interacting abiotic and biotic factors such as accommodation space and plant growth (Rogers et al. 2019; Kirwan and Mudd 2012). Aboveground plant structures interact with sediments during inundation (Bakker et al. 1993; Fagherazzi et al. 2012), while belowground productivity contributes to soil stability (Ford et al. 2016; Battisti et al. 2019), both of which are essential for vertical accretion - a crucial mechanism for coping with accelerated rates of sea level rise (Allen 2000; Kirwan and Megonigal 2013; Mudd et al. 2009). How plants may acclimate or adapt and how plant community composition may shift in response to accelerated rates of sea-level rise is further influenced by other global change factors, such as elevated CO_2 and temperature, complicating the plant-soil feedback loops. Despite the recognized importance of coastal wetlands in climate change mitigation, the impacts of global environmental change on their carbon cycling processes remain insufficiently explored. Few existing studies, such as Noyce et al. (2023) highlight the complexity of ecosystem responses, emphasizing the need for more integrated research to understand how these vital ecosystems will function under future climate scenarios. In this thesis, I investigated the effects of warming on the carbon dynamics of coastal wetlands. To disentangle the individual and interactive effects of warming on carbon cycling, I explore the impacts of warming on various ecosystem properties and their interrelations in the following sections.

1.2.1. Warming effects on plant-soil interactions

One of the key abiotic consequences of warming for terrestrial and coastal ecosystems is a reduction in soil moisture via higher evapotranspiration, often coupled with a precipitation deficit, which affects multiple soil properties with direct implications for biotic processes. The decreasing soil moisture potentially leads to increased soil salinity in coastal regions, especially in times of reduced precipitation (Lorrain-Soligon et al. 2023). Moreover, shifts in soil moisture influence the redox conditions of the soil, with drier conditions favoring more aerobic states and likely increasing SOM decomposition and thus carbon turnover in wetland soils (Pezeshki and DeLaune 2012). These changes alter microbial community composition and plant-microbe interactions, affecting ecosystem functioning (Philippot et al. 2013; Jansson and Hofmockel 2020; Philippot et al. 2024). Reduced soil moisture can also impair nutrient availability and uptake by plants and microbes, further influencing productivity and carbon cycling (Pezeshki and DeLaune 2012; Jansson and Hofmockel 2020). Furthermore, drought can impose significant water stress on plants. To maintain water flow, plants rely on stomatal transpiration, which drives the upward movement of water from roots to leaves. However, under water-limited conditions, plants close their stomata to conserve water (Lambers and Oliveira 2019). Since stomata are also essential for CO_2 uptake, this closure often leads to a reduced primary productivity (Boeck et al. 2008; Hoeppner and Dukes 2012). In response to reduced water availability, plants can further adapt physiologically by increasing water use efficiency, adjusting osmotic pressure, or developing succulence (Lambers and Oliveira 2019). Additionally, plants may reallocate biomass to root growth to enhance water and nutrient acquisition (Eziz et al. 2017; Noyce et al. 2019).

1.2.2. Warming effects on plants

As all biological processes are temperature-sensitive, warming is expected to positively affect various kinetic reactions, such as enzymatic activity (including carbon assimilation by RuBisCo), CO_2 diffusion rates, tissue and cell growth, and nutrient uptake (Bassirirad 2000; Sage and Kubien 2007; Crous 2019). Ultimately, the increased reaction rates at elevated temperatures are anticipated to enhance primary productivity (Rustad et al. 2001; Sage and Kubien 2007). Plant species and microbial communities have adapted to different climatic zones and thus exhibit specific temperature optima for their metabolic processes (Mendelssohn and Morris 2002; Münzbergová et al. 2017). However, extreme warming may surpass the optimal temperature ranges for individual species, potentially leading to thermal stress and reduced biomass production. Plants adapted to greater temperature fluctuations, such as those found in higher latitudes, are likely to have a greater capacity to acclimate their photosynthetic thermal optimum upwards (Crous 2019).

Temperature is a key driver of plant phenology in terrestrial ecosystems, and warmer temperatures are likely to extend the growing season by promoting earlier spring greening and delaying senescence in the fall (Menzel 2013). This extension provides plants with a longer period for photosynthesis, which could lead to increased annual primary productivity (Wang et al. 2022; Liu et al. 2025). However, the extension of growing season varies across ecosystems, and in some cases may result in shifts rather than in an elongation of the growing season. For instance, Liu et al. (2022a) found in their meta-analysis that the growing season was primarily delayed in herbaceous communities, with both later greening and senescence observed. Additionally, it is likely that warming has a stronger effect on elongating the growing season in higher compared to lower latitudes (Liu et al. 2025).

Lastly, productivity-diversity theory suggests that longer growing seasons may favor a few highly productive plant species, outcompeting subdominant species and potentially reducing overall community diversity (Pärtel et al. 2007; Fridley et al. 2016). Previous studies investigating the effects of warming in wetlands have shown shifts in plant community structure, often accompanied by a loss in species richness (Weltzin et al. 2003; Charles and Dukes 2009; Baldwin et al. 2014). Plant diversity can be positively associated with increased plant productivity (Duffy et al. 2017) and has been shown to enhance soil organic carbon storage across ecosystems (Lange et al. 2015; Chen et al. 2020). Consequently, warming-induced shifts in the diversity of plant communities may exert a significant influence on future carbon cycling.

1.2.3. Warming effects on plant-microbe interactions

Microbial communities can demonstrate resilience against disturbances depending on different community properties such as spore dormancy, growth strategies, and the taxonomic composition (Philippot et al. 2021). Microbial activity will directly respond to warming through enhanced metabolic processes until a certain threshold driven by faster kinetic reactions (Luo 2007). Additionally, microbial communities will be indirectly affected by changes in environmental conditions, such as soil moisture, pH, and redox potential, as well as by complex feedbacks with associated plant communities (Philippot et al. 2021; Philippot et al. 2024). In terrestrial ecosystems, a warming-induced reduction in soil moisture is expected to limit microbial activity due to a lower accessibility of substrates and nutrients (Schimel 2018). In contrast, decreased soil moisture in wetland ecosystems may lead to increased oxygen availability, potentially boosting microbial activity and accelerating SOM decomposition rates (Charles and Dukes 2009; Noyce et al. 2023; Haviland and Noyce 2024). Warming-driven shifts in plant community composition and structure are likely to have concurrent effects on microbial activity and community composition, though the outcome remains challenging to predict due to the various potential biotic feedbacks (Philippot et al. 2013). Generally, increased primary productivity (under warmer temperatures) is expected to enhance microbial activity, potentially leading to the decomposition of previously sequestered carbon stored in SOM (Kuzyakov 2002; Mueller and Megonigal 2024). This priming effect is because higher primary productivity is associated with increased exudation, thereby providing more input of labile carbon compounds to the soil (Fu and Cheng 2002; Mueller et al. 2016; Dijkstra et al. 2006). If plant communities shift in composition, it is likely that corresponding changes will also alter microbial community composition and activity (Philippot et al. 2013). Previous studies in terrestrial ecosystems have reported significant shifts in microbial community composition with warming (Luo et al. 2014; Nottingham et al. 2022b; Li et al. 2024a), with some studies highlighting a more profound warming-induced shift in organic soils rather than in minerogenic systems (Deslippe et al. 2012; DeAngelis et al. 2015). However, other studies show ambiguous or negligible warming effects on microbial community composition (Castro et al. 2010; Contosta et al. 2015; Cheng et al. 2017).

While plants play a critical role in mediating microbial responses to temperature increases, the feedback loop under climate change is further complicated by bidirectional effects from plant-microbe interactions. On the one hand, increased SOM turnover driven by microbial activity could accelerate nutrient mineralization, potentially improving nutrient availability for plants and enhancing productivity (van der Heijden et al. 2008; Dijkstra et al. 2010; Bai et al. 2013). On the other hand, microbial immobilization of nutrients potentially reduces nutrient availability for plants e.g. Jiang et al. (2025) who found higher ammonium immobilization under warming, thereby exacerbating plant stress and potentially diminishing productivity.

Plant-soil-microbe dynamics under future climate scenarios have crucial implications for the overall functioning of coastal wetlands as carbon sinks as the net balance of these reciprocal interactions determines whether warming will shift the ecosystem carbon balance towards a net-positive or net-negative carbon-climate feedback (Melillo et al. 2002b; Davidson and Janssens 2006; Charles and Dukes 2009; Kirwan and Blum 2011; Smith et al. 2022). As laid out above, these dynamics are highly variable and require a deeper understanding of plant-soil interactions as driver of carbon cycling.

1.3. Framework of this study

The studies that are part of this thesis were conducted in coastal wetlands along the North Sea and Baltic Sea coasts. The Wadden Sea and Baltic Sea coastal wetlands are relatively young ecosystems, having developed over the past 8,000 years following the last glacial period (Elschot et al. 2024; HELCOM 2018). Over the past ~500 years, human activity has significantly influenced the development and morphology of these ecosystems, particularly through cultivation and agricultural land-use, which continue to shape the structure of most European coastal wetlands (Dijkema 1990; Rupprecht et al. 2023).

Despite their comparable geological age and shared history of anthropogenic influence, coastal wetlands of Wadden Sea and Baltic Sea shorelines differ substantially. These differences are primarily driven by distinct hydrological regimes, which strongly influence plant community composition, sediment deposition, and small-scale distribution along elevation gradients in Wadden Sea wetlands and affect the large-scale distribution of plant community composition along landscape gradients in Baltic Sea wetlands. A more detailed description of these contrasting hydrological and ecological characteristics is provided in the following sections.

1.3.1. Coastal wetlands of the North Sea

Europe and more specifically its North Sea coast is home to the world's largest tidal flat, the Wadden Sea. The Wadden Sea ranges from Denmark to the Netherlands with 11,456 km² being listed as a UNESCO world heritage site (CWSS 2017). Furthermore, within this unique landscape, about 42,500 ha are covered by minerogenic coastal wetlands, namely salt marshes (Elschot et al. 2024). Cultivation and diking resulted in a loss of 80 % of Wadden Sea salt marshes in the past 400 years (Dijkema 1987). In Germany, the largest share of the Wadden Sea is protected by national parks, which has led to a stagnation in salt marsh loss and a recent increase of total salt marsh area (Elschot et al. 2024). Nonetheless, most of the Wadden Sea salt marshes at the mainland are still heavily impacted by former land use, often resulting in low plant diversity (Kleyer et al. 2003; Rupprecht et al. 2023; Elschot et al. 2024).

The North Sea coast in Germany is characterized by meso- to macrotidal dynamics, resulting in strong tidal influence on Wadden Sea salt marshes. These high tidal amplitudes create pronounced small-scale hydrological gradients, where even slight differences in elevation lead to clearly distinguishable plant communities along an elevational gradient reflecting succession (Olff et al. 1997; Suchrow and Jensen 2010). Salt marsh species occur across an elevational gradient spanning about 2.5 meters (-63 cm below to +198 cm above mean high tide in Schleswig-Holstein, Germany; Suchrow and Jensen 2010). The pioneer zone, closest to the water edge, is inundated during high tide and dominated by the highly adapted *Salicornia europaea* agg. and *Spartina anglica.* The highest diversity can be found in the low marsh with species as e.g. *Puccinellia maritima* and *Atriplex portulacoides*. *Elymus athericus* and *Festuca rubra* dominated-communities indicate the peak of saltmarsh succession in the high marsh and experience event-based inundation during storm floods (Suchrow and Jensen 2010; Leuschner and Ellenberg 2018).

1.3.2.Coastal wetlands of the Baltic Sea

The Baltic Sea is characterized by several environmental gradients mostly due to its semi-enclosed nature. Sea water enters through the Kattegat, whereas freshwater influx from river run-off is more pronounced in the inner parts (Weisse et al. 2021). With increasing distance to the Kattegat, salinity and tidal influence on coastal wetlands decreases. Tidal amplitude of the Baltic Sea close to the Kattegat is about 20 to 30 cm while it ranges only between 2 and 5 cm in the inner Baltic (Weisse et al. 2021). Overall, inundation in Baltic coastal wetlands is mostly driven by irregular events such as storm surges (Dijkema 1990). These dynamics lead to a high variability in soil salinity along the latitudinal gradient of the Baltic Sea as well as within individual coastal wetland sites (Kniebusch et al. 2019). In drier periods, patches located at higher elevations can display much higher soil salinity due to dominating evapotranspiration compared to low laying areas (Dijkema 1990). The high heterogeneity of soil salinity, water saturation and soil texture within sites and along the latitudinal gradient shape differences in plant community composition (Hulisz et al. 2016; Vehmaa et al. 2024). Therefore, plant communities tend to display a patchiness instead of a clear zonation, as observed in their Wadden Sea counterparts (Dijkema 1990; Pätsch et al. 2019). Furthermore, the latitudinal gradient of the Baltic Sea is associated with changes in climatic conditions and isostatic land uplift (Dijkema 1990). Isostatic uplift is particularly high in the Gulf of Bothnia with annual land rise of 5-9 mm (Schwarzer et al. 2008). Being microtidal, low-saline systems, Baltic coastal wetlands are often dominated by tall-growing plants with low salinity tolerance as e.g. *Phragmites australis.* In these systems, the establishment of halophytes is facilitated by livestock grazing. Here, trampling by grazers increases soil compaction and salinity, thereby promoting the growth of salt-tolerant plants as e.g. *Agrostis stolonifera* and *Juncus gerardii* (see Dijkema 1990; Jutila 1999; Dupré and Diekmann 2001).

1.4. Objectives of this study

To investigate both current and possible future carbon cycling and carbon storage potential, and to evaluate the role of vegetation in mediating these processes, I conducted and participated in four complementary studies in coastal wetlands of the North Sea and Baltic Sea. In the study presented in chapter 2, current standing carbon stocks were quantified in both North Sea and Baltic Sea coastal wetlands in Germany, while the study presented in chapter 3 focused on current methane emissions and its drivers in a subset of the same sites. These two studies examined both larger scale variation (across coasts and sites) and small-scale differences (within sites, based on plant community composition). In the two following studies presented in chapter 4 and 5, soil-sods from Baltic Sea coastal wetlands with different origin (Denmark, Sweden, Finland) were transplanted into a controlled warming mesocosm facility at University of Hamburg. The different origins captured a wide range of soil morphologies and two different plant community types (tall-grass vs. small-grass community) were collected in each country. This study design, spanning the large-scale gradient of the Baltic Sea, allowed us to address carbon cycling and carbon storage potentials in times of climate change across distinct, yet similar coastal wetlands. Within this experimental setup, the study presented in chapter 4 assessed the effects of warming on aboveground biomass and soil organic matter (SOM) dynamics, while chapter 5 investigated warming-induced shifts in microbial community composition. Together, these studies provide novel insights into the role of plant-soil interactions in regulating carbon fluxes under current environmental conditions, as well as under projected future warming scenarios.

CHAPTER TWO

SOIL ORGANIC CARBON STOCKS OF GERMAN SALT MARSHES: A COMPARATIVE STUDY ALONG LOW- AND HIGH-ENERGY COASTLINES

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2.1. Abstract

Blue carbon ecosystems, such as salt marshes, store comparably large amounts of organic carbon in their soils and function more effectively as carbon sinks than most other terrestrial ecosystems. Here we provide the first comprehensive study, quantifying soil organic carbon (SOC) stocks in grazed and non-grazed German salt marshes. In Germany, salt marshes are found along the low-energy, microtidal coastline of the Baltic Sea as organogenic ecosystems and along the high-energy, mesotidal coastlines of the North Sea as minerogenic ecosystems. One-meter soil cores were taken across 14 sites covering three distinct salt marsh types: Baltic Sea, North Sea mainland and North Sea island. Baltic salt marshes held on average the greatest SOC stocks with 221±56.3 (mean±SE) Mg SOC/ha followed by North Sea mainland salt marshes with 187±24.9 Mg SOC/ha and North Sea island salt marshes with 78±9 Mg SOC/ha. Our findings indicate that livestock grazing resulted in a 1.5-fold increase in SOC density. The microtidal Baltic salt marshes store more SOC in their topsoil than mesotidal North Sea salt marshes, most likely due to the higher sediment deposition rates in North Sea mainland salt marshes causing SOC dilution through mineral inputs. We conclude greater aeration in high-marsh soils might counterbalance SOC accumulation under proceeding succession. Positive livestock grazing effects were relatively consistent within North Sea salt marshes, likely caused by trampling-induced changes in soil biogeochemistry. By contrast, grazing had variable effects on SOC in Baltic Sea salt marshes, with belowground plant productivity identified as the primary driver.

2.2. Introduction

Salt marshes and other blue carbon ecosystems, such as seagrass meadows and mangroves, are characterized by high rates of organic carbon sequestration in soils and function more effectively as carbon sinks than many other terrestrial and aquatic ecosystems (Mcleod et al. 2011; Lovelock and Duarte 2019; Macreadie et al. 2021). Blue carbon ecosystems globally cover less than 0.2 % of the ocean surface but account for 50 % of the marine SOC burial. At the same time, the global area of blue carbon ecosystems declines at a rapid rate, with an estimated annual decline of 1-2 % for salt marshes (Duarte et al. 2013). Soil carbon sequestration is the outcome of organic matter input to the soil and its microbial decomposition as output (Duarte et al. 2005; Lovelock and Reef 2020). The fate of organic matter inputs to the soil depends on various variables influencing carbon persistence. Flooding leads to waterlogged soils that reduce decomposition through shifts in microbial functioning towards anaerobic metabolism (Neubauer and Megonigal 2021). SOC stocks of blue carbon ecosystems are fed by both autochthonous and allochthonous organic inputs. Autochthonous organic matter is derived from *in-situ* primary productivity, while allochthonous organic matter stems from external sources, such as aquatic primary production, and is deposited in the salt marshes through sedimentation (Needelman et al. 2018).

Salt marshes cover approximately 5.5 million ha globally (Mcowen et al. 2017) estimating a global total of ~862 to 1,350 Tg SOC (157-245 Mg/ha) (Macreadie et al. 2021). Studies assessing the global SOC stocks of salt marshes show large variability (Alongi 2020; Macreadie et al. 2021; Maxwell et al. 2023), emphasizing the need of regional studies for estimating national blue carbon stocks. In Europe, national budgets of salt marsh SOC stocks were compiled recently for UK (Mason et al. 2022) and Denmark (Leiva-Dueñas et al. 2024). In Germany, salt marshes are widespread along the North Sea coast and to a lesser extent along the coast of the Baltic Sea. Blue carbon stocks have only been assessed in a handful of case studies (Mueller et al. 2019b; Buczko et al. 2022; Mueller et al. 2023). A comprehensive study describing carbon storage in salt marshes along both German coastlines of North Sea and Baltic Sea is still missing.

Salt marshes of the North Sea and the Baltic Sea coast greatly differ with respect to geomorphology and other abiotic conditions (Elschot et al. 2024; Dijkema 1990). North Sea salt marshes along the mainland coast form in front of dikes and are exposed to strong hydrodynamics and mesotidal conditions. Island salt marshes of the North Sea coast form under less exposed conditions in the lee of back-barrier islands (Elschot et al. 2024). The Baltic salt marshes differ in morphology and hydrodynamic exposure due to the semi-enclosed nature of the Baltic Sea, resulting in microtidal to non-tidal conditions and a salinity of 5-10 psu which is much lower than at the North Sea coast with 32-34 psu (Dijkema 1990). The mesotidal conditions at the North Sea coast lead to clearly distinguishable vegetation zones along an elevation gradient, where the highest zone reflects the oldest stages in succession (Olff et al. 1997; Suchrow and Jensen 2010). In contrast to the fast-accreting minerogenic salt marshes of the North Sea, the microtidal Baltic salt marshes are characterized by low sediment deposition rates and slow-accreting organogenic soils (Dijkema et al. 2010; Nolte et al. 2013a).

Salt marsh SOC stocks can show strong variability in response to sedimentation, vertical accretion rate and succession. Higher SOC stocks are generally connected to progressing influence of vegetation e.g. in later successional stages (Connor et al. 2001; Spohn et al. 2013; Ouyang and Lee 2014; Hansen et al. 2017).

The majority of salt marshes in Germany have been impacted by anthropogenic activity over the past centuries. This is primarily due to land reclamation and agricultural practices. Even today, livestock grazing remains a prevalent activity in many salt marshes (Rupprecht et al. 2023). Livestock grazing can have variable effects on salt marsh SOC stocks due to a variety of mechanisms. First, grazing can increase root:shoot ratios by partially removing the aboveground biomass (Davidson et al. 2017), which can decrease sediment trapping (Schulze et al. 2021). Second, grazing can increase root productivity leading to greater belowground organic matter input to the soil (Elschot et al. 2015). Third, grazers compact the soil via trampling (Nolte et al. 2015) thereby reducing oxygen availability through increased water-logging (Keshta et al. 2020), which ultimately may slow down organic matter decomposition (Schrama et al. 2013; Elschot et al. 2015; Mueller et al. 2017). For salt marshes in the Netherlands and Denmark, an increase in the SOC stock under grazing has been reported (Elschot et al. 2015; Leiva-Dueñas et al. 2024).

The objective of this study is to provide a comprehensive overview of salt marsh SOC stocks along the North Sea and Baltic Sea coasts of Germany. Our study is based on SOC assessments in 14 marsh sites comprising a total of 146 soil cores. We aim to identify geomorphological and land-use factors affecting salt marsh SOC stocks along the German coasts by addressing the following hypotheses: 1) Baltic salt marshes have a greater SOC stock than North Sea salt marshes due to predominantly organogenic soil formation; 2) In North Sea salt marshes, SOC density increases with succession and is greatest in mature high-marsh zones; 3) Livestock grazing increases SOC density via soil biogeochemical changes and 4) decreases the proportion of allochthonous SOC via reduced plant-mediated sediment trapping.

2.3. Materials and Methods

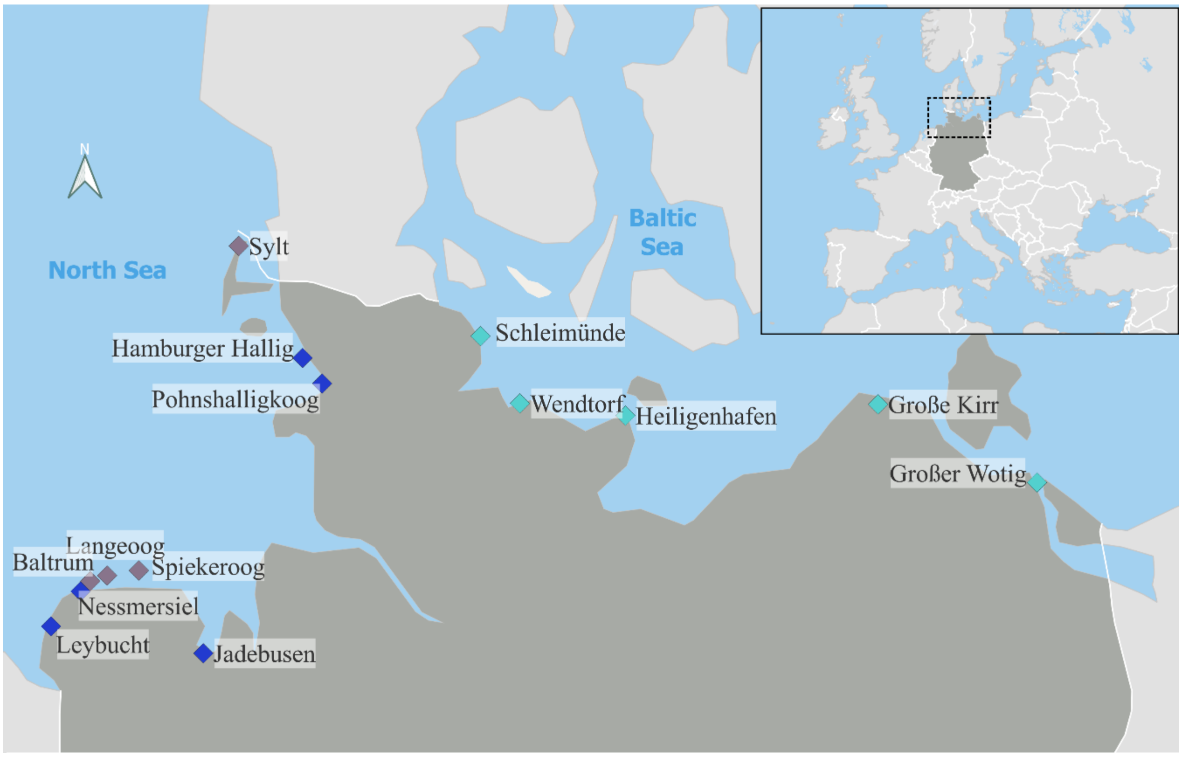

Figure 1: Overview map of study sites in Germany. Three distinct salt marsh types were sampled. Baltic Sea, North Sea mainland and North Sea island salt marshes indicated by different colors.

In order to assess the differences in SOC stocks between contrasting geomorphological settings of salt marshes in Germany, three distinct salt marsh types were sampled: Baltic Sea salt marshes, North Sea mainland salt marshes and North Sea island salt marshes. In North Sea salt marshes, sampling plots were arranged along transects on the elevation gradient representing pioneer, low marsh, and high marsh vegetation zones. Effects of livestock grazing on SOC storage were assessed in an additional campaign.

2.3.1. Field site description

Located along the SE North Sea coastline, the Wadden Sea stretches from Denmark, via Germany to the Netherlands. Here, minerogenic salt marshes cover about 42,500 ha from which 25,060 ha are located along the German North Sea coast (Elschot et al. 2024). North Sea mainland salt marshes are developing along the mainland coast, mostly in front of dikes. Most salt marshes of this type developed through land-reclamation activities along the coast over past centuries. Today, these salt marshes are hydrologically disturbed by artificial drainage ditches or their remnants. Furthermore, management practices like livestock grazing and mowing still apply to approximately 50 % of all North Sea salt marshes (Elschot et al. 2024). Typically, grazed North Sea mainland salt marshes are located closer to the dike than non-grazed areas. This consequently entails that these grazed salt-marsh soils tend to be older (Elschot et al. 2024). North Sea island salt marshes cover approximately 25 % of the German

North Sea salt marshes and form in lee of barrier islands. This sheltered geomorphic setting leads to lower sediment deposition rates compared to the more exposed mainland salt marshes (Olff et al. 1997; Elschot et al. 2024). North Sea island salt marshes have a larger share of hydrologically undisturbed relief, and they can be described as mostly natural (Elschot et al. 2024). The German North Sea coast as high-energy coast with mesotidal ranges constitutes salt marshes with clearly distinguishable vegetation communities across the elevation gradient (Olff et al. 1997; Suchrow and Jensen 2010). The gradual increase of elevation results in different flooding frequencies which are then reflected by three vegetation zones: pioneer zone, low marsh, and high marsh. The low-energy coasts of the Baltic Sea lead to salt marshes that often lack a clear vegetation zonation as flooding is mostly due to irregular wind-driven water-level changes (Dijkema 1990). In contrast to the extensive North Sea salt marshes, Baltic salt marshes usually do not exhibit a clear elevation gradient but rather show small-scale vegetation heterogeneity representing different abiotic conditions and/or successional stages. In comparison to North Sea salt marshes as prograding systems, Baltic salt marshes are often smaller and most likely older. Today, they cover a total of 8,050 ha in Germany of which about half is grazed by livestock (Wanner 2009). Baltic salt marshes typically develop in the shelter of dunes and lagoons and do not differentiate morphologically between mainland and island coasts. Due to storm floods, marine sediments occasionally deposit on the marsh surface (Dijkema 1990). Under non-grazed conditions, Baltic salt marshes mostly develop into tall-grass communities dominated by *Phragmites australis*. In contrast, livestock grazing promotes small-stature vegetation and the establishment of halophytes (Dijkema 1990).

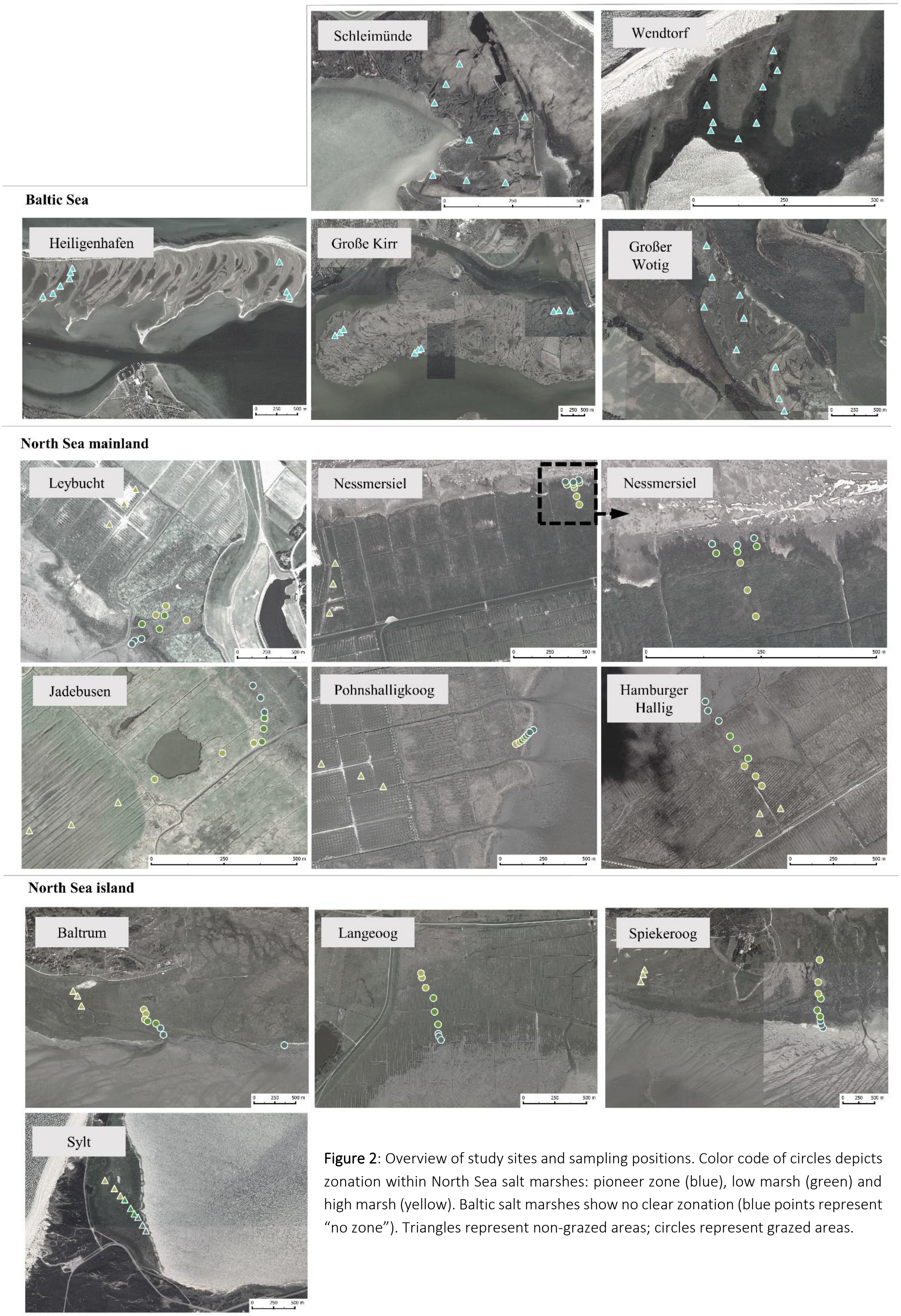

Figure 2: Overview of study sites and sampling positions. Color code of circles depicts zonation within North Sea salt marshes: pioneer zone (blue), low marsh (green) and high marsh (yellow). Baltic salt marshes show no clear zonation (blue points represent "no zone"). Triangles represent non-grazed areas; circles represent grazed areas.

2.3.2. Study design for assessing SOC stocks and density of different salt marsh types and vegetation zones

By including salt marshes of the North Sea mainland coast, the North Sea islands and the Baltic Sea coast, all three relevant salt marsh types based on extent along the German coastlines are represented in this study (Fig. 1,2). The 14 study sites were sampled using a transect design to cover gradients of different plant communities and management types. The sampled transects of the North Sea salt marshes spanned this gradient in elevation and included all three vegetation zones, i.e. high marsh, low marsh and pioneer zone. Based on previous ground truthing, transects at the Baltic coast were laid to capture small-scale vegetation heterogeneity. Soil cores from all 14 study sites were taken between November 2021 and September 2022 (Table S. 1a).

2.3.3. Soil sampling and vegetation analysis

In each of the 14 study sites, 8-12 plots (Table S. 1a) were sampled. For assessing vegetation composition and structure, plant species composition and coverage, as well as the percentage of bare soil and dead plant matter were recorded for each plot within a 100 x 100 cm square. Vegetation height was measured at five points within each plot. To quantify aboveground biomass, plants were cut 2 cm above the soil on a 25 x 25 cm square centered in each plot. Biomass samples were put into paper bags, transported to the laboratory, and weighed after drying at 60°C for a minimum of three days.

For the quantification of SOC content, soil bulk density, SOC $\delta^{13}C$ signature, and nitrogen content, a single 1-m soil core was taken from the center of each plot (Fig. 2). An Eijkelkamp peat sampler was used for taking soil cores, which allowed compaction-free sampling of a half-cylindrical core with a diameter of 5 cm. The use of the peat sampler for mineral soils required pre-coring with a narrow (3-cm diameter) gouge auger to reduce friction resistance during coring (Mueller et al. 2023). Each core was sliced into 10 cm increments, transferred into plastic bags and transported to the laboratory for further processing.

2.3.4. Analysis of soil parameters

Fresh soil samples were homogenized and weighed before and after being air dried at 60°C for at least five days. Dry soil bulk density was calculated from sample dry weight and volume. Gravimetric water content was calculated from the ratio of sample fresh weight to dry weight. Prior to elemental and isotope analysis, macroscopic root residues were removed using tweezers.

Electrical conductivity, pH and sand content were measured in subsamples. For electrical conductivity, 5 g of milled dry soil was dissolved in 25 mL of deionized water, and measured with a benchtop conductivity meter (Cond 7310). Soil pH was measured by dissolving 2 g of milled dry soil in 5 mL 0.01 M $CaCl_2$ solution. The samples were shaken regularly for a period of 1 h and afterwards measured with a benchtop pH meter (Multi 9310 IDS). Mud and sand contents were approximated by passing subsamples of 2-5 g through a 0.06-mm test sieve.

To remove inorganic carbon (carbonate minerals) from soil samples, we applied the following acidification procedure: A fraction of all soil samples was milled and acidified with 10% HCl until no visible effervescence was observed. The acidified samples were weighed before and after acidification and the difference in dry weight was used as a correction factor before elemental (carbon and nitrogen) analysis. For quantifying carbon and nitrogen contents, 2-35 mg of acidified dry soil was weighted into tin capsules and analyzed with an element analyzer (EURO EA 3000, Euro Vector, Italy). The evolved CO_2 was further passed to a coupled isotope ratio mass spectrometer (nu Horizon, Nu Instruments Limited, UK) for assessing the $\delta^{13}C$ signature. Obtained nitrogen data were used for calculating the C/N ratio of samples. C/N and $\delta^{13}C$ signatures were used to examine SOC origin (i.e. allochthonous vs. autochthonous) (Khan et al. 2015; Mueller et al. 2019a).

SOC data with carbon contents below 0.1% lack precision. Nevertheless, these SOC measurements, which account for 19.1 % of the total dataset, were retained in subsequent statistical analyses rather than being discarded or set to zero. However, carbon contents were occasionally too low for accurate $\delta^{13}C$ assessments, leading to the exclusion of these isotopic data from further analysis.

SOC density (g C / cm^3) was calculated from soil bulk density (g dry soil / cm^3) and SOC content (g C / g dry soil). SOC stock (Mg C/ha) was calculated in two steps. First, for each 100-cm core, the SOC density values of all 10-cm increments were averaged to determine the mean SOC density per core. Second, the mean SOC stock per site was calculated across all cores and converted to a per-hectare basis. Missing values in individual 100-cm cores (5.2% of the total dataset) were estimated through interpolation. Interpolated values were only used for SOC stock calculation. The upscaled total German salt marsh SOC stock (Tg SOC) was calculated by multiplying the mean, standard error, median and interquartile range (IQR) of type-specific salt marsh SOC stock with the areal extent of the respective salt marsh type. The data regarding the areal extent were taken from Wanner (2009) for Baltic salt marshes and Elschot et al. (2024) for North Sea salt marshes. In addition to the North Sea island and mainland salt marshes, Elschot et al. (2024) reports on Hallig marshes and summer polders, which collectively account for approximately 12% of the potential total salt-marsh extent of German salt marshes. However, Hallig marshes and summer polders are strongly hydrologically altered due to dikes and revetments that impair natural flooding. They were not sampled in the present study and are excluded from the calculation of the total German salt-marsh SOC stock.

2.3.5. Additional study for assessing effects of livestock grazing on SOC stocks

Livestock grazing effects on SOC stocks were additionally assessed in a separate campaign, that followed a parallel design (instead of a transect design) and allowed comparison of grazed vs non-grazed plots in similar successional stages/ marsh ages (Fig. 3). The additional campaign was carried out in four of the study sites (North Sea mainland: Pohnshalligkoog, Nessmersiel; Baltic Sea: Schleimünde, Heiligenhafen). These assessments were restricted to the top 30 cm of soil because grazing histories vary across sites, making it difficult to accurately attribute any effects on the deeper soil layers to grazing.

Sampling took place in October to November 2023. Four or five cores each were taken from grazed and non-grazed areas in each of the four selected study sites resulting total in 38 cores (Table S. 1b). Samples were processed as described for the SOC stocks. Loss on ignition was used to determine soil organic matter (SOM). Carbon and nitrogen content, δ^{13}C signature, pH and electrical conductivity were measured in samples of 0-10 cm and 20-30 cm depth and interpolated for the 10-20 cm section (text S. 1.2).

Aboveground and belowground biomass was harvested in September 2023. Aboveground plant samples were cut from a 30 x 30 cm square, dried at 60°C for 5 days and weighed. Belowground biomass was retrieved with an Edelman corer (diameter 5 cm; depth 20 cm) centered within the aboveground biomass square. The belowground biomass samples were washed free from soils, and dried at 60°C for 5 days and weighed.

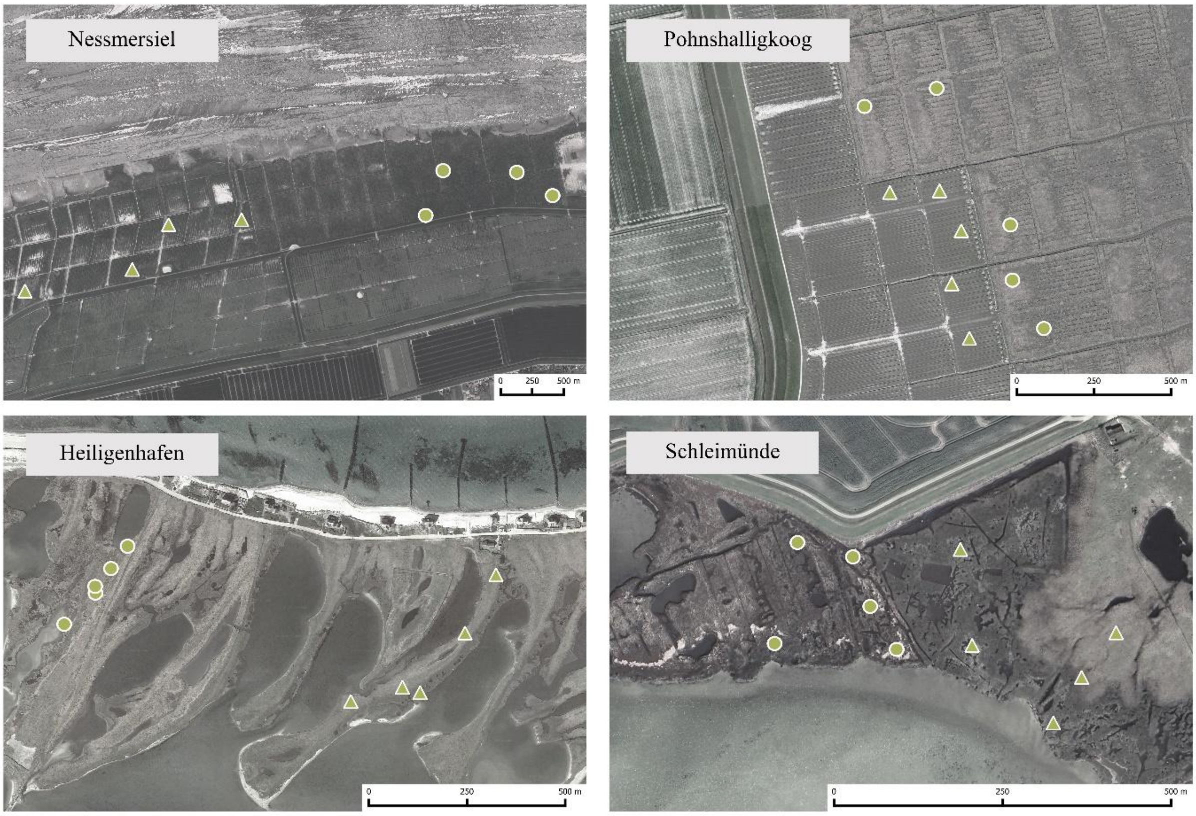

Figure 3: Overview of study sites with additional plots to compare grazed (triangle) and non-grazed (circle) areas.

2.3.6. Data analysis

This study distinguishes soil properties between topsoil (0-30 cm) and subsoil (30-100 cm) core sections, and calculated average δ^{13}C, SOC, soil bulk density and electrical conductivity, sand content and pH for these soil sections. For analyzing effects of vegetation zone, only data from non-grazed North Sea salt marshes were included, because only for these salt-marsh types vegetation zonation was clearly discernable. In order to investigate livestock grazing effects, the dataset comprised data from the additional livestock grazing campaign, as well as from high marsh grazed and non-grazed plots in Jadebusen, Leybucht, Baltrum and Spiekeroog (Fig. 2, yellow points). The analysis of the grazing effect on δ^{13}C was constrained to data from the uppermost 10 cm, as the grazing effect on vegetation is expected to decrease with increasing depth.

As most data was not normally distributed, Kruskal-Wallis tests were used to test for the effect of vegetation zone (pioneer zone, low marsh, high marsh) and grazing (grazed, non-grazed) on SOC, δ^{13}C, soil bulk density, aboveground and belowground biomass, sand content and gravimetric water content. Prior to running the statistical tests and creating the graphs, the mean of these measures was calculated as follows: SOC stock graphs display the mean of top- and subsoils of the respective salt marsh type and site. In order to display and test the zonation effect on non-grazed North Sea salt marshes, mean values for each vegetation zone-site combination were calculated for both topsoil (0-30 cm) and subsoil (30-100 cm) and used in separate Kruskal-Wallis and Dunn's test for pairwise comparison. When displaying and testing for grazing effects, mean values for each grazing treatment-site combination were calculated for the topsoil and used in Kruskal-Wallis tests.

Data has been processed using Rstudio (Version 2024.04.2).

2.4. Results

2.4.1. Salt marsh SOC stocks of the German Baltic and the North Sea

In German salt marshes, approximately 5.40 ± 0.928 Tg SOC were stored (Table 1.b). On average, the German salt marshes stored 168±26.2 Mg SOC/ha within the top 100 cm of soil (Table 1.b). Based on single cores, the SOC stock ranged from 12 to 695 SOC Mg/ha across the 0–100 cm profile. Baltic salt marshes displayed greatest average SOC stock (Fig. 4, Table 1.b), caused primarily by high SOC contents within the topsoil (Fig. 4, Table 1.a), whereas the high average subsoil SOC content in the Baltic salt marshes was strongly excelled by the high subsoil content of the study site Schleimünde (Fig. 4). North Sea mainland and island salt marshes had similar SOC contents in their topsoil (Fig. 4, Table 1.a). However, the North Sea island salt marshes stored the least SOC within the entire one-meter soil profile (Fig. 4, table 1 b). North Sea mainland sites exhibited the highest SOC stock within the subsoil, with a SOC stock exceeding more than twice that of the topsoil (Fig. 4, Table 1 a). North Sea island salt marshes showed the least variability in SOC stocks, whereas Baltic Sea salt marshes had the highest variability in SOC stocks (Fig. 4, Table 1 b).

Table 1: Salt marsh-type specific a) mean values of SOC stock, SOC density, SOC content and δ^{13}C in SOC for topsoil (0-30 cm) and subsoil (30-100 cm) b) mean, median and sum values of total area in ha that is covered by salt marshes, SOC in Mg/ ha and SOC in Tg. ± SE – Standard Error. [1] Wanner (2009). [2] Elschot et al. (2024)

a)

Saltmarsh type	Depth-profile	SOC stock (Mg/ha)	±SE	SOC density (g/cm³)	± SE	SOC content (%)	±SE	SO^{13}C signature (‰)	±SE
Baltic Sea	subsoil	116	53.5	0.016	0.00	2.34	1.4	-24.45	0.97
	topsoil	106	30.2	0.035	0.01	7.86	2.1	-27.34	0.49
North Sea island	subsoil	22	5.1	0.003	0.00	0.21	0.1	-24.31	0.18
	topsoil	57	6.8	0.017	0.00	2.19	0.2	-24.38	0.03
North Sea mainland	subsoil	130	18.9	0.018	0.00	1.53	0.3	-23.73	0.16
	topsoil	57	6.1	0.017	0.00	2.05	0.3	-23.94	0.22

b)

	total area in ha	SOC (Mg/ha)				Tg SOC	
		mean	±SE	median	±IQR	Upscaling based on mean	±SE
Baltic Sea	8050 [1]	221	56.3	240	118	1.78	0.453
North Sea island	5370 [2]	78	9.0	84	13	0.42	0.048
North Sea mainland	17120 [2]	187	24.9	171	41	3.20	0.426
total	**30540**	**168**	**26.2**	**154**	**143**	**5.40**	**0.928**

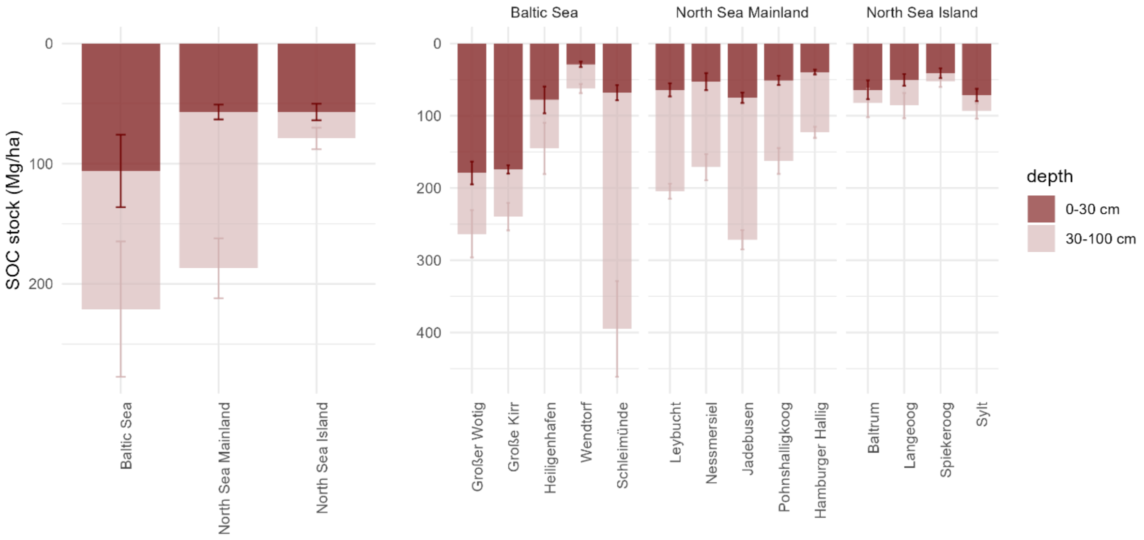

Figure 4: SOC stocks (Mg/ha) of different salt marsh types (left) and the individual study sites (right) across the top 30 cm and 100 cm. Shown are means ± standard error.

2.4.2. Vegetation zone effects in North Sea salt marshes

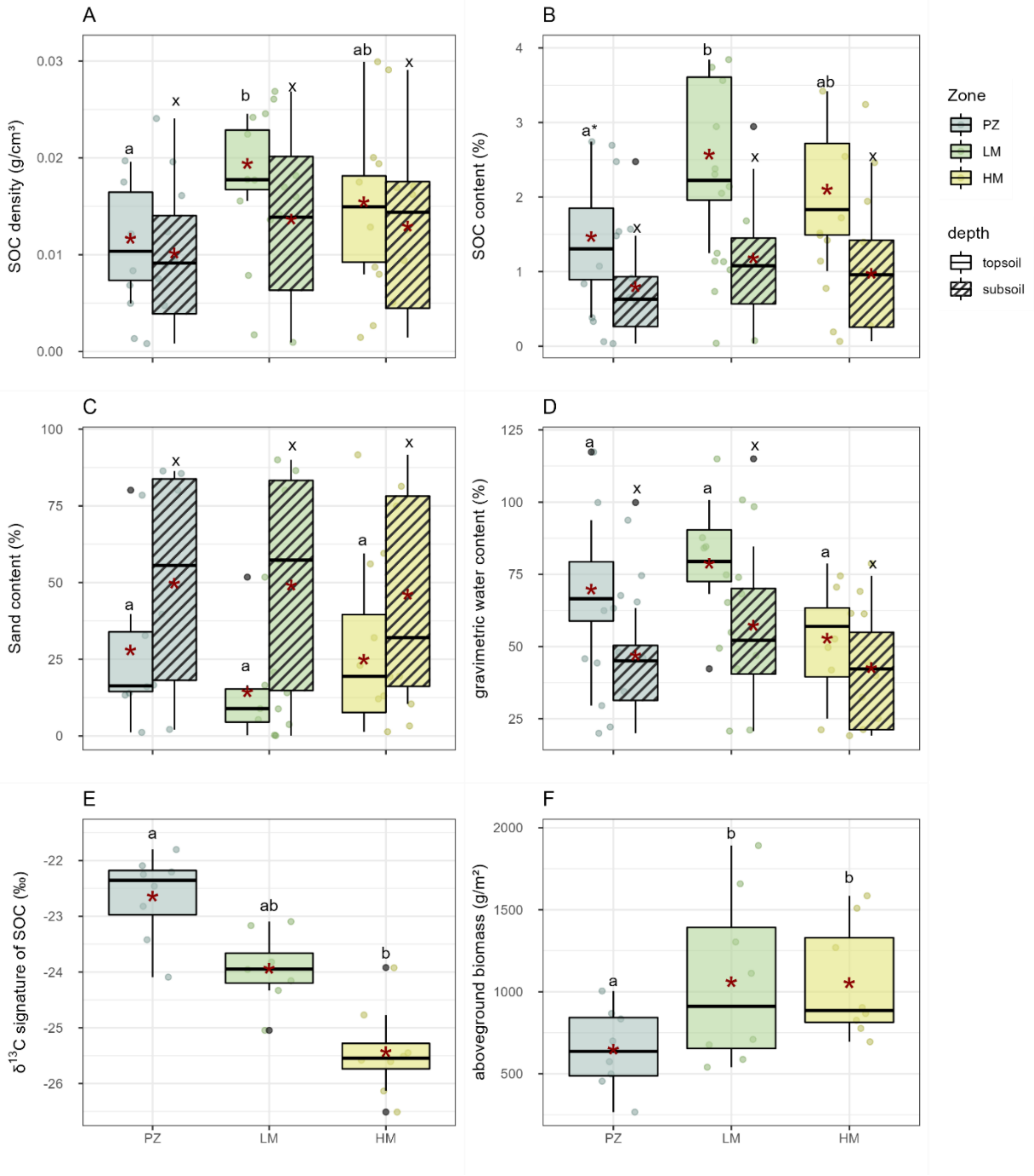

Figure 5: SOC content (%) **A**, SOC density (g/cm³) **B**, sand content (%) **C**, gravimetric water content (%) **D**, $\delta^{13}C$ signature of SOC (‰ VPDB) **E**, and aboveground biomass AGB (g/m²) **F** across vegetation zones reflecting progressing succession from pioneer zone (PZ), via low marsh (LM) to high marsh (HM) in North Sea salt marshes. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Red stars display mean values of each site. Shaded boxplots display subsoil, not shaded boxplots display the topsoil. Single data points (means of each site-by-zone combination) are overlaid. Small letters indicate statistical significance (p-value < 0.05; * p-value <0.1) between zones based on Dunn test. Differences between topsoil and subsoil were not tested.

Table 2: Mean vegetation height (cm), aboveground biomass (dry weight (DW, g/m²)), δ^{13}C signature of SOC, SOC density (g/cm³) and SOC content (%) in the topsoil and subsoil for non-grazed North Sea salt marshes. ± SE – Standard error

Zone	Mean height (cm)	DW AGB (g/m²)	Depth-profile	SOC δ^{13}C signature (‰)	±SE	SOC density (g/cm³)	±SE	SOC content (%)	±SE
pioneer zone	28.04	649.95	topsoil	-22.64	0.29	0.012	0.0017	1.47	0.26
			subsoil	-23.26	0.19	0.010	0.0014	0.80	0.12
low marsh	29.43	1080.42	topsoil	-23.89	0.38	0.019	0.0042	2.52	0.74
			subsoil	-23.49	0.27	0.014	0.0018	1.23	0.16
high marsh	26.52	1054.11	topsoil	-25.43	0.23	0.015	0.0033	2.10	0.76
			subsoil	-24.70	0.22	0.013	0.0021	0.97	0.14

In non-grazed North Sea salt marshes, the SOC density peaked in the low marsh with a mean of 0.019±0.0042 g/cm³ in the topsoil. SOC density was lower in the high marsh and lowest in the pioneer zone (Fig. 5 A, Table 2). Despite a similar trend in SOC density was observed in the subsoil, no significant difference between zones were identified in the subsoil (Fig. 5 A, Table 2). Topsoil δ^{13}C in SOC decreased with succession from pioneer zone, via low marsh to high marsh (Fig. 5 E, Table 2). This effect was less pronounced in the subsoil (Table 2). Sand content was lowest and gravimetric water content was highest in the topsoil of the low marsh (Fig. 5 C, D). Aboveground biomass was lowest in the pioneer zone and did not differ between low marsh and high marsh (Fig. 5 F, Table 2).

2.4.3. Livestock grazing effects

Livestock grazing increased the topsoil SOC density (Fig. 6 A) by approximately 50%. Grazing effects were more pronounced in the top 10 cm compared to deeper soil depths (Fig. S. 4.1.). Soil bulk density (g/cm²) slightly increased with livestock grazing (Fig. 6 C). A slight decrease in the δ^{13}C signatures was observed under grazing (Fig. 6 D). Grazing did not increase belowground biomass and significantly decreased aboveground biomass (Fig. 6 E, F).

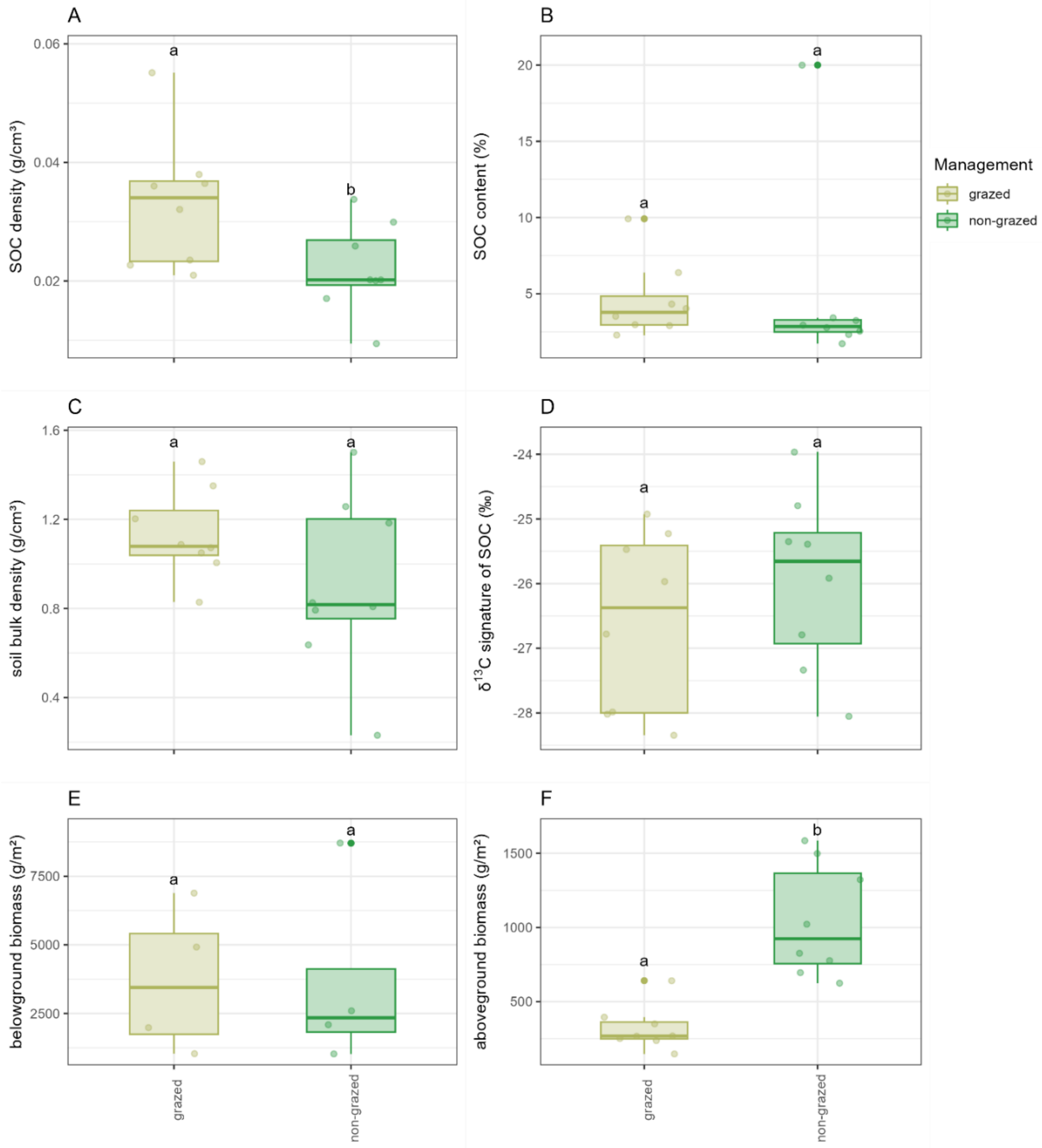

Figure 6: Livestock grazing effects on SOC density (g/cm²) **A**, SOC content (%) **B,** soil bulk density (g/cm²) **C,** the δ^{13}C signature of SOC in the topsoil **D**, the belowground biomass (g/m²) **E** and the aboveground biomass (g/m²) **F**. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Single datapoints (site means) are overlaid. Boxes not connected by the same letter are significantly different at $p < 0.05$ based on Kruskal-Wallis test. Note: Data from North Sea pioneer zones and low marshes are excluded.

2.5. Discussion

2.5.1. Salt marsh SOC stocks of the German Baltic and North Sea

We found an average SOC stock of 168±26.2 Mg SOC/ha (mean±SE), which is comparable to global averages of 162±259 Mg/ha for salt marshes reported by Duarte et al. (2013), and approximately half compared to values reported in more recent meta-studies (Alongi 2020 with 317.2 ± 19.1 Mg SOC/ha (mean±SE); Maxwell et al. 2023 with 231±134 Mg SOC/ha (median ± median absolute deviation); this study with 154±143 (median±IQR)). Previous studies from the North Sea region (Elschot et al. 2015; Mueller et al. 2019b; Mueller et al. 2023; Leiva-Dueñas et al. 2024) and Baltic Sea region (Buczko et al. 2022; Leiva-Dueñas et al. 2024) indicate similar SOC stocks as reported here. SOC stocks of North Sea island salt marshes, which is 78±9 Mg SOC/ha, are below the German average of 168±26.2 Mg/ha whereas salt marshes located on the North Sea mainland coast and at the Baltic Sea, 187±24.9, 221±56.3 respectively, exceed the German average SOC stock.

The topsoil SOC stock of the North Sea salt marshes is approximately half that of the topsoil SOC observed in Baltic Sea salt marshes. The difference in topsoil SOC stock between North Sea mainland and islands salt marshes are rather small. Nonetheless, North Sea island salt marshes exhibit the lowest carbon stock, primarily due to the underlying sandy parent material, that dominated the one-meter profile of this salt marsh type. It can be assumed that this sandy foundation has not been significantly influenced by the salt marsh vegetation (Elschot et al. 2015; Pollmann et al. 2021), resulting in little to no additional carbon input and thus SOC content steeply declines down-core resulting in the lowest SOC stocks in North Sea island salt marshes. In contrast, the high-energy North Sea mainland salt marshes are characterized by high rates of fine-grained sediment deposition (Allen 2000; Elschot et al. 2024). High rates of sediment deposition lead to a fast rates of minerogenic vertical accretion and enables rapid soil formation in these relatively young systems. The low-energy Baltic Sea salt marshes, on the other hand, form highly organic topsoils due to microtidal conditions that promote peat formation (Dijkema et al. 2010; Nolte et al. 2013a). The topsoil SOC stock of Baltic Sea salt marshes are greater than the one of North Sea mainland salt marshes. Despite the highly organic topsoils, Baltic Sea and North Sea mainland salt marshes SOC stocks are comparable across the whole one-meter depth profile. The high sediment deposition rate in North Sea mainland salt marshes leads to a dilution of the SOC with minerals (Granse et al. 2024) while simultaneously allowing for fast vertical accretion, resulting in the formation of thicker salt marsh soils with less organic-rich topsoil compared to that found in slow-accreting Baltic Sea and North Sea island salt marshes (see also Kirwan and Megonigal 2013). Consequently, 1-m SOC stocks are comparable between low-energy Baltic Sea and high-energy North Sea mainland salt marshes.

This study and previous research on North Sea and Baltic Sea salt marshes (e.g. Buczko et al. 2022; Leiva- Dueñas et al. 2024) reveal considerable spatial variability in SOC stocks both between different types of salt marshes and within the same type, emphasizing the necessity for regional assessments. Variability between sites both in topsoil and one-meter soil profiles was found to be the highest in Baltic Sea salt marshes, where we also found the highest variability in plant community composition (Fig. S. 2). Numerous studies emphasize the strong control of plant community composition on SOC dynamics (Langley et al. 2009; Langley and Megonigal 2010; Saintilan et al. 2013), therefore it is likely that the high variability in SOC stocks in Baltic Sea salt marshes is driven by larger variability in plant community composition and associated plant traits. Nevertheless, the differences in plant communities also indicate varying environmental settings at the different sites (Hulisz et al. 2016). For instance, sites in the southeastern Baltic (Große Kirr & Großer Wotig) had the highest topsoil SOC. Both sites lay within a lagoon which entails reduced water exchange, riverine inflow and shallow waters which provides protection from storm surge deposits and erosion (Hulisz et al. 2016). Moreover, the resulting lower salinity and flooding increase plant productivity which in turn increases the organic carbon input into the soil (van de Broek et al. 2016; Hansen et al. 2017).

In contrast, the northern Baltic marsh sites (Schleimünde, Wendtorf, and Heiligenhafen) are less sheltered as they are situated behind beach ridges and dunes. These locations are more prone to storm surges, which can lead to erosion and increased salinity (Hulisz et al. 2016), resulting in low SOC stocks, as observed in Wendtorf. Additionally, storm surges can cause the redeposition of sand over the marshes (Dijkema 1990), which may lead to the burial of marshes, an occurrence suggested for Schleimünde. In this location, we found inconsistent presence of an organic layer in the topsoil, while denser peat layers were identified at greater depths. This phenomenon has been observed previously where reed peat layers were found under beach ridges in Heiligenhafen (Wanner 2009).

In German salt marshes (excluding Hallig and summer polder salt marshes) approximately 5.40 ± 0.928 Tg SOC are stored. This is somewhat higher than the value estimated in the review by Macreadie et al. (2021) (3.41-4.9 Tg SOC in German salt marshes). This is most likely due to the lower areal extent that has been used as the basis by Macreadie et al. (2021). The amount of 5.40 ± 0.928 Tg is proportionate with approximately 20 Tg CO_2 equivalents ($eCO_{2)}$.

2.5.2.Zonation effects on North Sea salt marsh SOC

We hypothesized that SOC would increase from pioneer zone, via low marsh to high marsh under proceeding “terrestrial” influence (Connor et al. 2001; Spohn et al. 2013; Ouyang and Lee 2014; Hansen et al. 2017; Mueller et al. 2020a). Indeed, we found the high marsh topsoils to be most depleted in ^{13}C which is to be expected given the persistent influence of C_3- dominated plant communities along soil development and proceeding succession (Suchrow and Jensen 2010; Whitaker et al. 2015). However, despite the increasing terrestrial influence with proceeding succession from pioneer zone, via low to high marshes, this study found the SOC peaks in the low marsh, decreasing significantly towards the pioneer zone and slightly towards the high marsh. The high marsh as the oldest successional stage with highest elevation entails reduced tidal influence and thus augmented aeration of the soil enhances oxidation of organic matter (Hemminga and Buth 1991; Mueller et al. 2016). Furthermore, the highest SOC content in the low marsh is associated with the lowest sand and highest water content. It has previously been shown that water content correlates positively and sand content correlates negatively with SOC content in salt marshes (Kelleway et al. 2016; Stagg et al. 2017; Leiva-Dueñas et al. 2024), through reducing microbial remineralization of SOC by decreasing oxygen availability (Kelleway et al. 2016; Chapman et al. 2019) and higher mineral association of SOC with fine sediments (Baldock and Skjemstad 2000).

Plant community composition and associated plant traits control soil biogeochemistry and SOC dynamics in coastal wetlands (Saintilan et al. 2013; Mueller et al. 2016; Granse et al. 2024; Mittmann-Goetsch et al. 2024; Mueller and Megonigal 2024). In North Sea salt marshes, plant communities clearly differ between vegetation zones (Fig. S. 4). Non-grazed high marsh and pioneer zone were found to have the lowest plant species richness with mono-dominant plant communities. On the contrary, the low marsh exhibited comparatively high plant species richness. Plant diversity has been shown to increase SOC across different ecosystems (Lange et al. 2015; Chen et al. 2020). This is primarily driven by the increasing plant trait functionality of the more diverse plant community (Deyn et al. 2008; Ford et al. 2016), which is associated with increased plant productivity (Duffy et al. 2017). At any rate, in this study the SOC peak in the low marsh cannot be explained by the aboveground biomass. Likewise, plant diversity increases belowground productivity through root space partitioning by functionally different species (Loreau and Hector 2001; Steudel et al. 2011). Thereby it can be assumed, that direct belowground inputs through root productivity and root exudation are highest in the low marsh. This is also emphasized by Redelstein et al. (2018) who found the highest fine root biomass in the low marsh for both island and mainland North Sea salt marshes. Furthermore, Granse et al. (2024) found a greater sediment-trapping capacity in high marsh compared to low marsh plant communities, resulting in greater dilution of SOC with mineral sediments in the high marsh. Conclusively, we suggest that the higher SOC quantity in the low marsh is potentially caused by shifts in plant productivity and SOC decomposition or stabilization processes linked to low oxygen-availability (as a result of fine soil texture and more regular inundation). Furthermore, SOC is likely lost and diluted in the high marsh soil as a consequence of soil aeration and higher sediment trapping, respectively.

2.5.3. Livestock grazing effects on salt marsh SOC density

In line with our third hypothesis, we found an overall increase in SOC density under livestock grazing in the topsoil across Baltic and North Sea salt marshes. This effect is strongest in the top 10 cm and vanishes with soil depth (Fig. S. 5). Similar effects of livestock grazing on SOC density were reported by Elschot et al. (2015) and Leiva-Dueñas et al. (2024) for salt marshes in the Netherlands and Denmark, respectively. Conversely, a global meta-analysis with most observations from European sites revealed no consistent effect of livestock grazing on SOC (Davidson et al. 2017). Livestock grazing affects vegetation and soil processes related to SOC decomposition (Elschot et al. 2015; Davidson et al. 2017; Mueller et al. 2017). Trampling associated with grazing increases bulk density by compacting soils (Nolte, 2013) and alters pore connectivity (Keshta et al. 2020). These changes increase water saturation in the soil and subsequently decrease soil oxygen availability and microbial activity (Mueller et al. 2017; Keshta et al. 2020). In North Sea salt marshes, we confirm a raise in soil bulk density with livestock grazing, whereas this effect was not found in Baltic Sea salt marshes. Baltic Sea salt marshes have higher sand content than North Sea salt marshes (Fig. S. 1 D) which has been shown to alleviate possible grazing effects on soil compaction (Schrama et al. 2013; Keshta et al. 2020).

Most consistency in the SOC-density response towards grazing is found in North Sea mainland salt marshes, whereas responses in Baltic Sea salt marshes remain variable (Fig. S. 6 A; Fig. S. 7 A). Under grazing, the removal of the aboveground biomass can additionally cause a shift in carbon allocation towards belowground biomass, directly increasing the belowground carbon inputs (Elschot et al. 2015). Belowground biomass responses to grazing varied from positive to negative among sites. In Baltic Sea salt marshes, we observed an increase in SOC under grazing in one site (Heiligenhafen), which could be explained by increased belowground biomass (Fig. S. 7 A, E). The other Baltic site (Schleimünde) did not show a difference in SOC density between grazed and non-grazed areas despite increased soil bulk density in grazed plots. Here we found belowground biomass to be higher in non-grazed plots (Fig. S. 7 E). Therefore, we argue that, within Baltic Sea salt marshes, compaction effects through trampling are mitigated by changes in belowground productivity.

The reduction of aboveground biomass as a result of livestock grazing decreases sediment trapping, which consequently reduces the deposition of marine sediments (Schulze et al. 2021). Here, we propose that the SOC dilution through mineral sediments (Granse et al. 2024) is a direct consequence of non-grazing on plant-sediment interactions. This phenomenon results in a higher dilution of SOC with allochthonous mineral sediment under non-grazed conditions. Indeed, our results show in line with our fourth hypothesis, that grazing leads to a higher share of autochthonous carbon sources in the SOC pool by displaying more depletion of $\delta^{13}C$ signatures (Khan et al. 2015). Elschot et al. (2015) argue that grazing increases the belowground biomass which in return could cause an increased autochthonous carbon input. However, we do not find a consistent increase of belowground biomass with grazing and therefore suggest that the increase of $\delta^{13}C$ in non-grazed salt marshes is the outcome of less sediment trapping resulting in higher dilution with allochthonous carbon sources (Mueller et al. 2019b; Granse et al. 2024).

2.6. Conclusion and implications

Throughout this study we propose sedimentary properties to be a key driver for differences in SOC stock and density between salt marsh types and within zonation. Lower sediment deposition rates in Baltic salt marshes, North Sea low marsh vegetation and salt marshes under livestock grazing are associated with higher SOC densities. Sedimentation dynamics are controlled by plant community composition and associated traits, whereas plant community composition is controlled by grazing or flooding regime. The higher sediment deposition rates in North Sea mainland salt marshes presumably allow them to keep pace with accelerated rates of sea-level rise (Kirwan et al. 2016; Elschot et al. 2024) bearing higher potential for future climate change mitigation. Baltic Sea salt marshes store considerable amounts of SOC underscoring the necessity to protect these ecosystems to prevent potential carbon emission as a consequence of marsh loss (e.g. marsh edge erosion).

Acknowledgement

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2.7. Supporting Information

Table S. 1: detailed overview of the sampling design. In total 14 sites were sampled that are categorized into three different salt marsh types: North Sea island, North Sea mainland and Baltic Sea. Number of cores and sampling date are listed for the respective sites

Salt marsh type	Site	Number of cores taken		Sampling date
a) Main dataset		in **non-grazed**	in **grazed**	
North Sea island	Baltrum	8	3	11.08.2022
	Langeoog	9	-	08.08.2022
	Spiekeroog	9	3	17.08.2022
	Sylt	-	9	05.09.2022
North Sea mainland	Leybucht	9	3	10.08.2022
	Nessmersiel	9	3	16.08.2022
	Jadebusen	9	3	09.08.2022
	Pohnshalligkoog	9	3	06.09.2022 (grazed) 09.11.2021 (ungrazed)
	Hamburger Hallig	9	3	06.09.2022 (grazed) 08.11.2021 (ungrazed)
Baltic Sea	Schleimünde	-	9	25.08.2022
	Wendtorf	-	9	24.08.2022
	Heiligenhafen	-	9	23.08.2022
	Große Kirr	-	9	30.08.2022
	Großer Wotig	-	9	31.08.2022
b) Additional dataset (Management)				
North Sea mainland	Nessmersiel	4	4	17.10.2023
	Pohnshalligkoog	5	5	24.20.2023
Baltic Sea	Schleimünde	5	5	03.11.2023
	Heiligenhafen	5	5	07.11.2023

Text S. 1: Calculation of SOC in additional management campaign

To estimate the SOC content for the 10-20 cm depth interval, an interpolation approach was applied, as follows: This involved calculating the ratio of SOC to OM for the neighboring depth intervals (0-10 cm and 20-30 cm), and then averaging these ratios for the respective sample. The resulting mean value was multiplied by the OM content of the 10-20 cm layer to derive the estimated SOC for this segment, as follows:

$$SOC_{10-20} = \left(\frac{SOC_{0-10}}{OM_{0-10}} + \frac{SOC_{20-30}}{OM_{20-30}}\right) \times \frac{1}{2} \times OM_{10-20}$$

The final management dataset comprises high marsh topsoil data from the SOC stock dataset collected at Jadebusen, Leybucht, Baltrum, and Spiekeroog, as well as the additional data collected from Pohnshalligkoog, Nessmersiel, Schleimünde, and Heiligenhafen.

Figure S. 1 Abiotic variables in comparison between salt marsh types

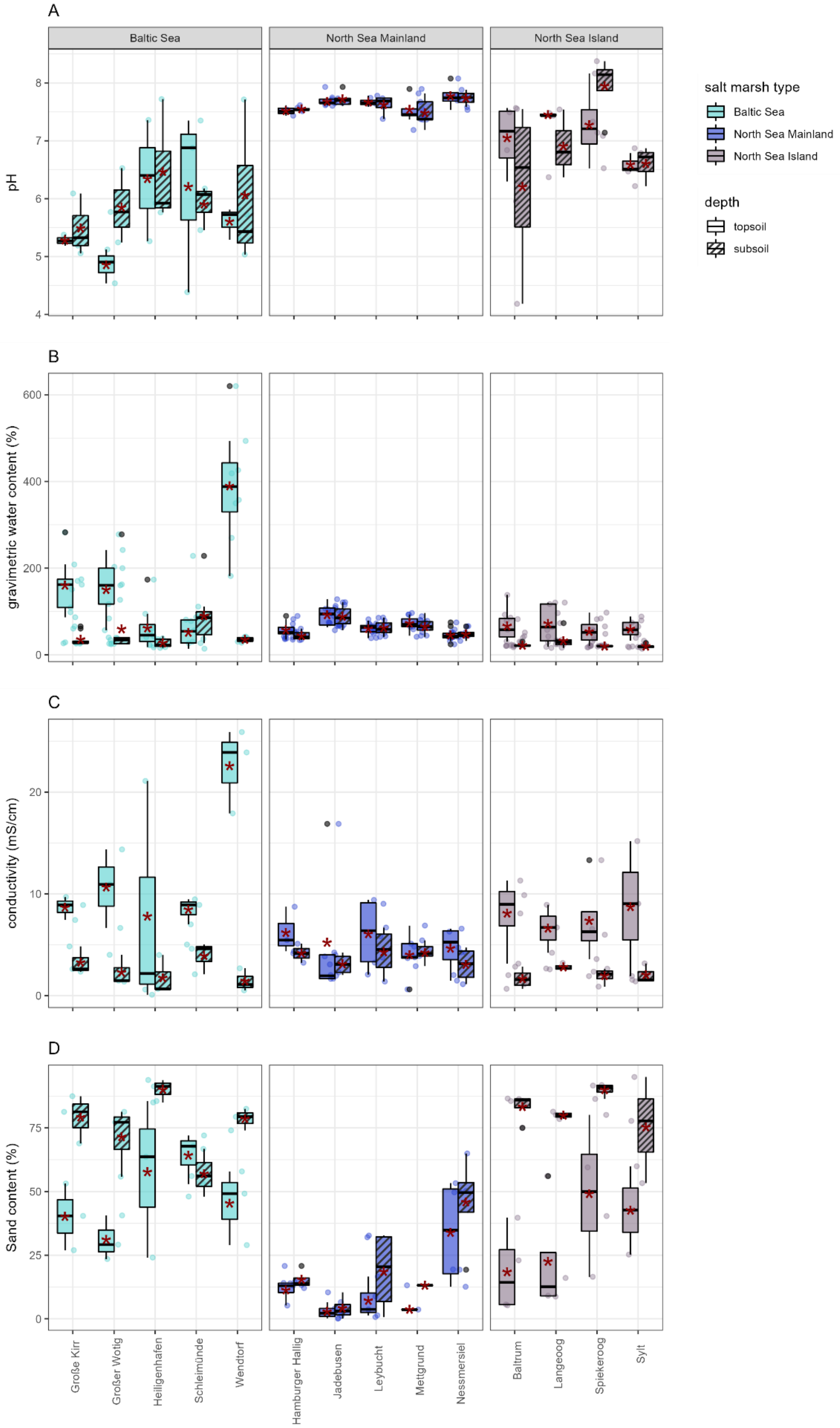


Figure S.1: pH **A**, gravimetric water content (%) **B**, conductivity (mS/cm) **C**, sand content (%) **D** measured in individual sites, ordered by salt marsh type. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Red stars display mean values of each site. Shaded boxplots display subsoil, not shaded boxplots display the topsoil. Single data points (means of each plot) are overlaid.

Figure S. 2 Plant communities of salt marsh types and individual

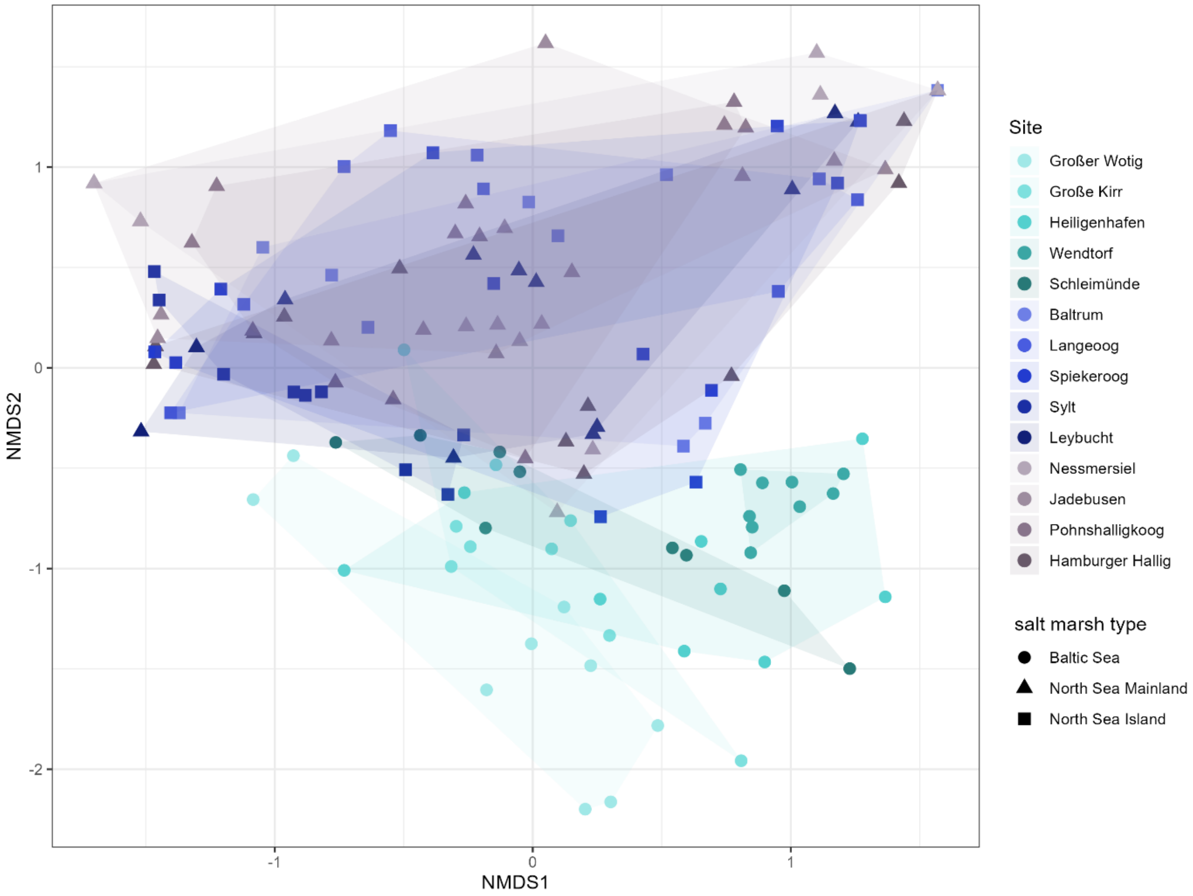


Figure S. 2: NMDS representation of plant community across sites (polygon colour) and salt marsh types (shapes). Ordination was based on Bray-Curtis dissimilarities.

Figure S. 3 effects of successional stages in North Sea salt marshes on abiotic variables

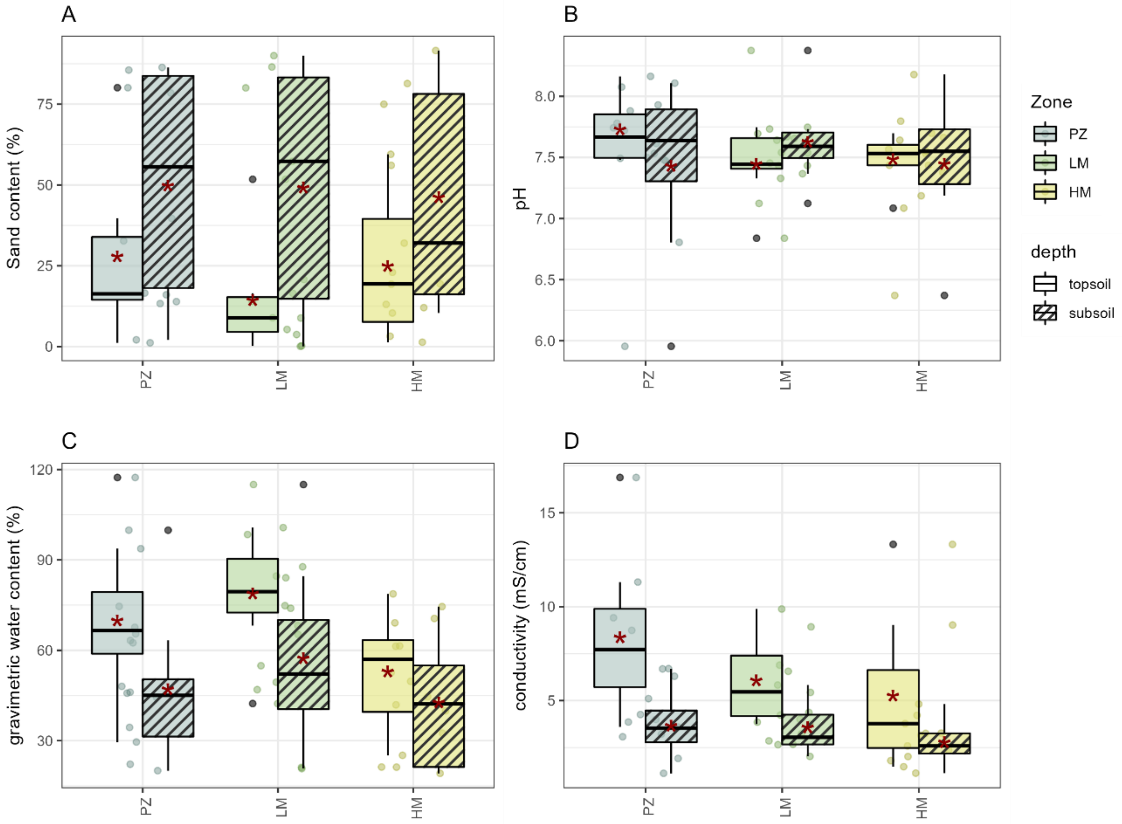


Figure S. 3: sand content (%) **A**, pH **B**, gravimetric water content (%) **C**, conductivity (mS/cm) **D** across vegetation zones reflecting progressing succession from pioneer zone (PZ), via low marsh (LM) to high marsh (HM) in North Sea salt marshes. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Red stars display mean values of each site. Shaded boxplots display subsoil, not shaded boxplots display the topsoil. Single data points (means of each site-by-zone combination) are overlaid.

Figure S. 4 plant communities (NMDS) of different successional stages in North Sea salt marshes

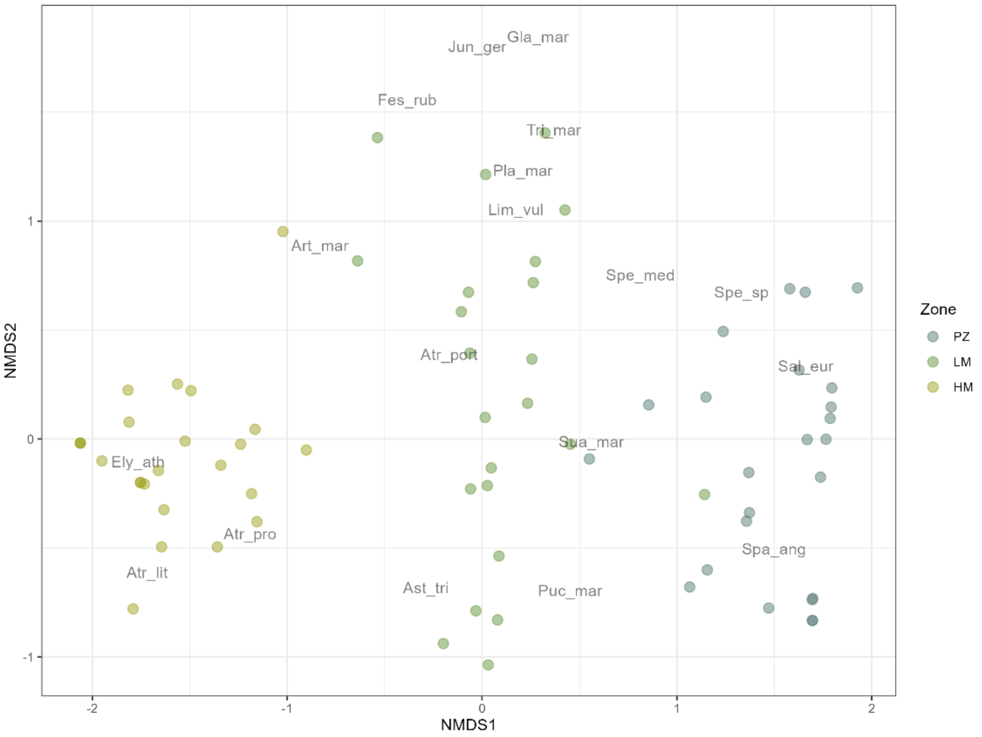


Figure S. 4: NMDS representation of plant community across vegetation zones reflecting progressing succession from pioneer zone (PZ), via low marsh (LM) to high marsh (HM) in North Sea salt marshes. Ordination was based on Bray-Curtis dissimilarities. Plant speceis (S. 3.3) are indicated by the first three letters of genus and species epithet.

List S. 1: Plant species found in North Sea salt marshes (excluding grazed salt marshes)

Artriplex maritima
Aster trifolium
Atriplex prostrata
Artiplex portulacoides
Atriplex littoralis
Elymus athericus
Festuca rubra
Juncus geradii
Glaux maritima
Limonium vulgare
Plantago maritima
Puccinelia maritima
Spergularia media
Spergularia sp.
Suaeda maritima
Salicornia europaea
Spartina anglica
Triglochin maritima

Figure S. 5: Management effect on SOC density across different depths

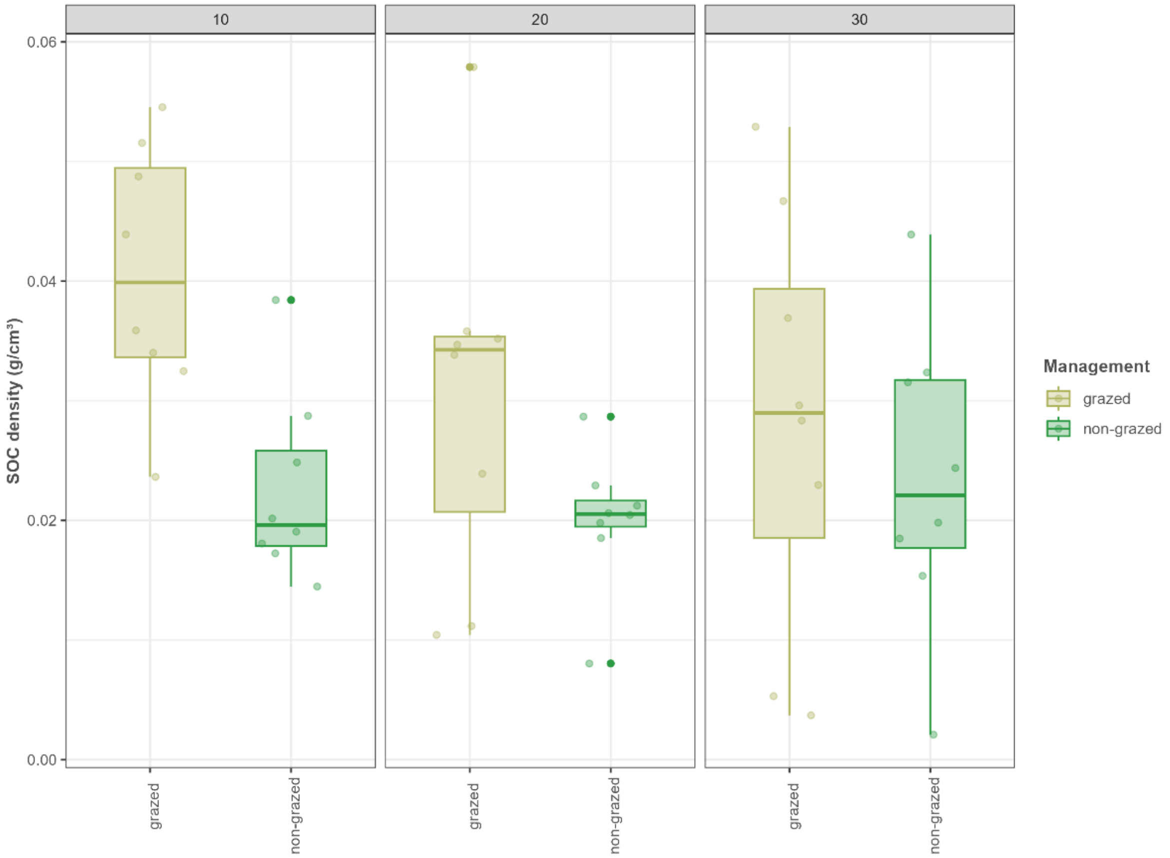


Figure S. 5: Management effect on all salt marsh types along the depth gradient. 10= 0-10 cm; 20= 10-20 cm; 30= 20-30 soil depth. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Single data points (means of each site-by-management combination) are overlaid.

Figure S. 6: Effect of management on OC density on Salt marsh type level

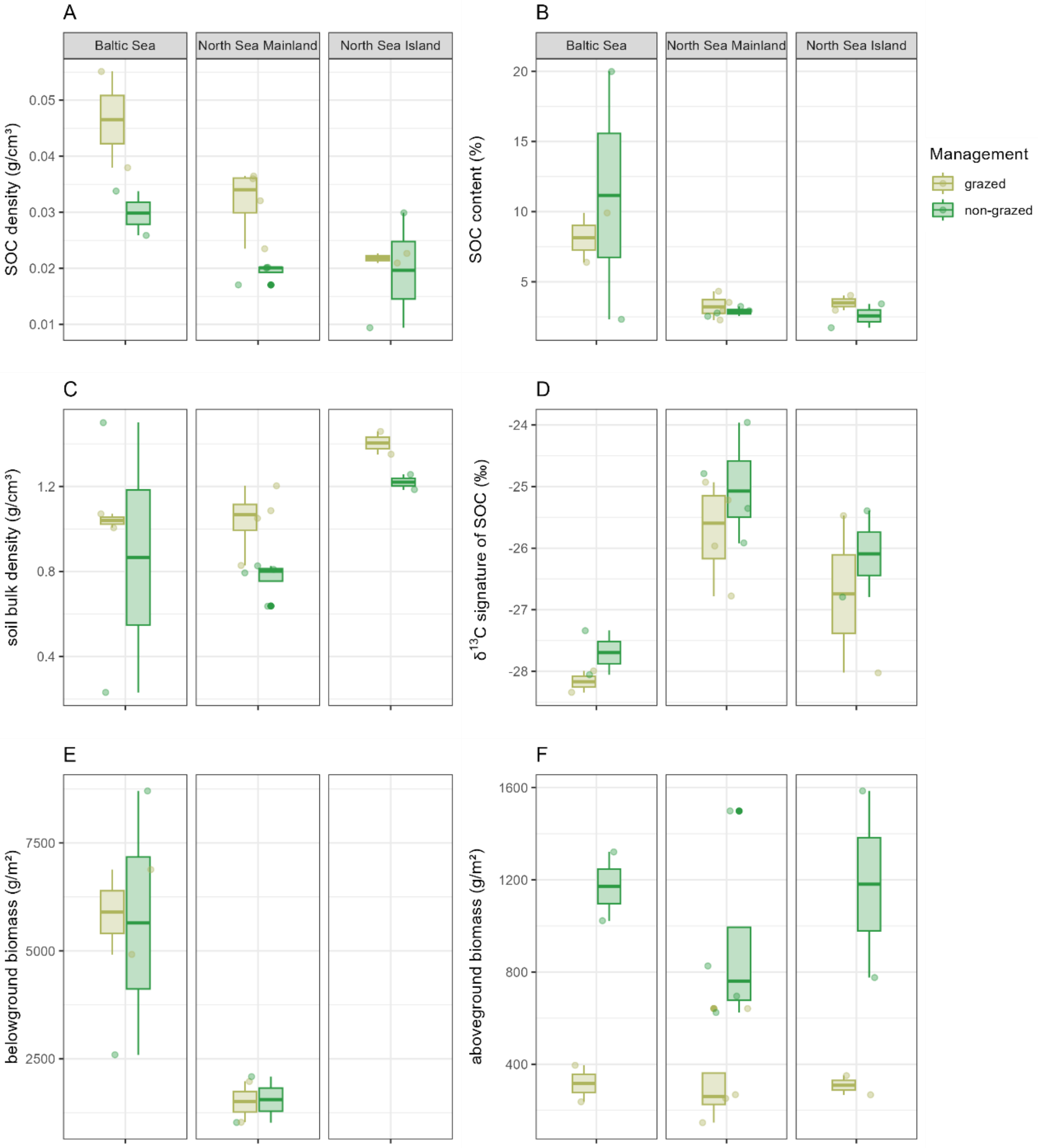


Figure S. 6: Livestock-grazing effects on salt marsh type level on SOC density (g/cm²) **A**, SOC content (%) **B**, soil bulk density (g/cm²) **C**, the δ^{13}C signature of SOC in the topsoil **D**, the belowground biomass (g/m²) **E** and the above-ground biomass (g/m²) **F**. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Single data points (means of each site-by-management combination) are overlaid. Note: Data from North Sea pioneer zones and low marshes are excluded.

Figure S. 7: Effects of management on OC density on site level

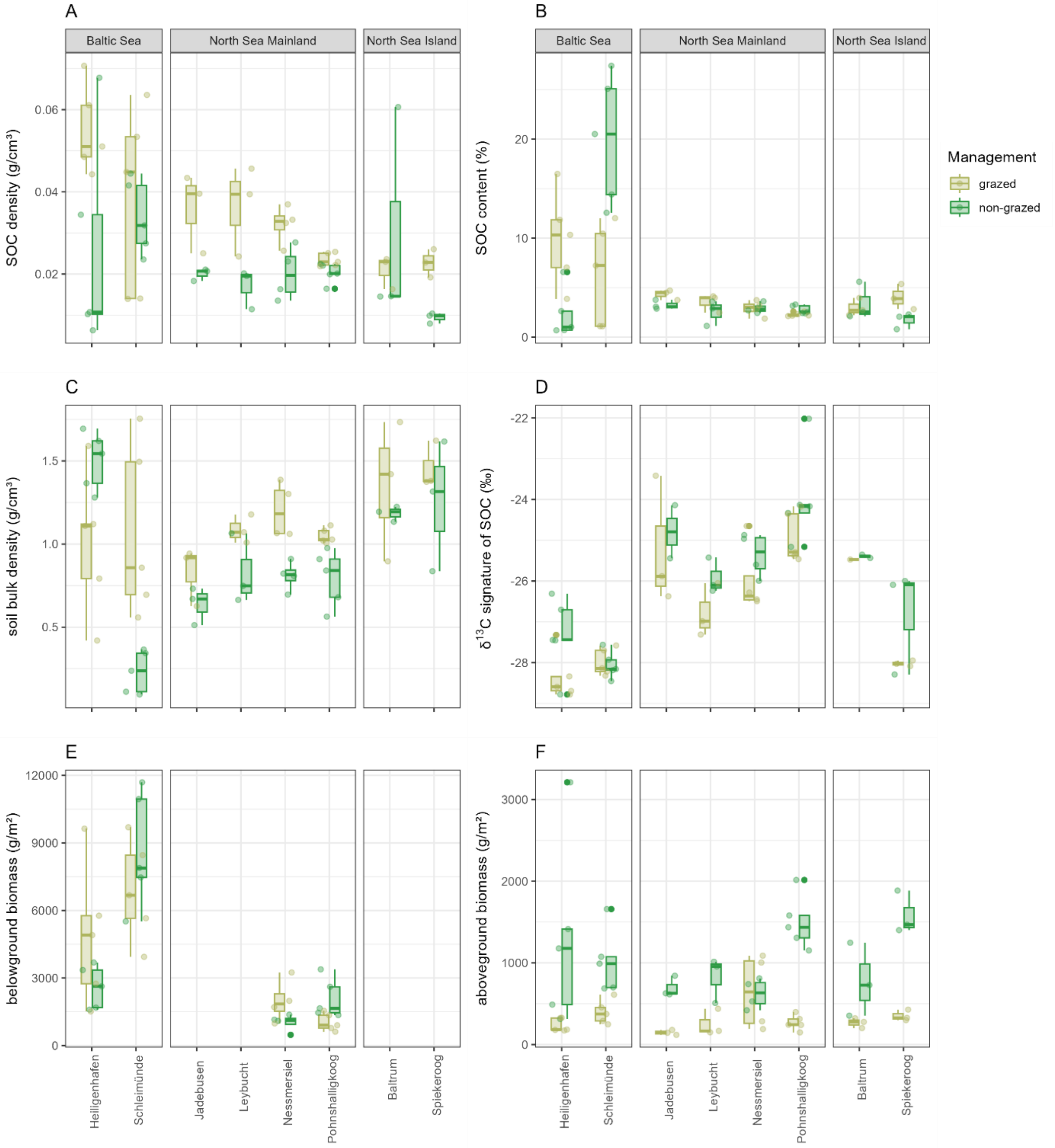


Figure S. 7: Livestock-grazing effects on site level on SOC density (g/cm²) **A**, SOC content (%) **B**, soil bulk density (g/cm²) **C**, the δ^{13}C signature of SOC in the topsoil **D**, the belowground biomass (g/m²) **E** and the above-ground biomass (g/m²) **F**. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Single data points (means of each site-by -management combination) are overlaid. Note: Data from North Sea pioneer zones and low marshes are excluded.

CHAPTER THREE

PLANT CONTROL ON SOIL REDOX STATE DETERMINES GRAZING EFFECTS ON METHANE EMISSIONS FROM COASTAL WETLANDS

In preparation

Clarisse Mittmann-Goesele, Ella Logemann, Cheng Caroline Chen,
Lars Kutzbach, Kai Jensen, Peter Mueller

3.1. Abstract

Coastal wetlands store carbon effectively, but their anoxic soils can promote methane emissions potentially offsetting their negative carbon-soil feedback. Given the widespread use of coastal wetlands for livestock grazing, it is crucial to understand how land-use practices influence CH_4 emissions and thereby affect the role of coastal wetlands in climate change mitigation. In this study, we compare CH_4 emissions between grazed and ungrazed coastal wetlands along the German North and Baltic Sea coastlines, with the aim to identify ecological and biogeochemical drivers that control potential grazing effects on CH_4 emissions. On average, livestock grazing had decreasing effects on CH_4 emissions (grazed: 0.29 ± 0.07 mg CH_4 m^{-2} day^{-1}; ungrazed: 4.36 ± 1.12 mg CH_4 m^{-2} day^{-1}, mean ± standard error (SE)), but this effect was not consistent across sites. Variable CH_4 emission responses to grazing across study sites could be attributed to differences in belowground biomass, soil organic carbon and soil redox potentials responses to grazing. Significant correlations among variables – belowground biomass positively with soil organic carbon, soil organic carbon negatively with soil redox potential, and soil redox potential negatively with CH_4 emissions - suggest that grazing influences CH_4 emissions by altering belowground biomass, which in turn modifies redox potential through plant-mediated processes. Furthermore, grazing led to lower CH_4 emissions by diminishing grazing-intolerant plant species associated with higher CH_4 emissions, e.g. *Phragmites australis*. Understanding these plant-mediated mechanisms is essential for improving predictions of CH_4 emissions under different global change scenarios including land-use and for informing coastal wetlands management strategies aimed at maximizing climate change mitigation benefits.

3.2. Introduction

Wetlands cover 4-6% of global land area, yet they are the largest natural source of methane (CH_4), contributing up to 53% of global CH_4 emissions (Rosentreter et al. 2021b). CH_4 emissions from coastal wetlands are, however, often lower compared to other upland wetland (Bridgham et al. 2006) because regular flooding with sulfate-rich seawater enables sulfate-reducing bacteria to outcompete CH_4 producers (i.e., methanogenic archaea; King and Wiebe 1980; Poffenbarger et al. 2011; Davidson et al. 2021). Nevertheless, there is also evidence that many coastal wetlands can act as strong emitters of CH_4 (Zhang et al. 2017; Rosentreter et al. 2021a). CH_4 is produced during the terminal step of organic matter decomposition, when oxygen and all other alternative electron acceptors have been depleted (Segers 1998). Hence, CH_4 emissions are highly dependent on the soil redox state of the wetland soils, which is in turn highly sensitive to both abiotic and biotic factors (Mueller et al. 2020b; Sulman et al. 2022).

Abiotic factors such as salinity (as indicator of marine water chemistry) and hydrological dynamics are key drivers of CH_4 emissions in coastal wetlands (King and Wiebe 1980; Poffenbarger et al. 2011; Davidson et al. 2021). While wetlands with organic-rich soils generally emit more CH_4 than organic-poor ones (Sutton-Grier et al. 2011), salinity is the primary factor predicting CH_4 emissions from coastal wetlands. Coastal wetlands with high-salinity harbor sulfate-reducing bacteria that outcompete methanogens for substrates, thereby suppressing methane production (King and Wiebe 1980; Poffenbarger et al. 2011; Davidson et al. 2021). Salinity and hydrology both govern biotic parameters such as species composition of vegetation and primary productivity, which in turn influence CH_4 emissions (Mueller et al. 2016).

Wetland plants play a critical role in shaping CH_4 emissions, by functioning both as soil oxidizers and reducers (Turner et al. 2020; Koop-Jakobsen et al. 2021; Mittmann-Goetsch et al. 2024). Through their aerenchyma tissues, they facilitate a bi-directional gas exchange, releasing oxygen (O_2) into the rhizosphere and transporting CH_4 from the soil to the atmosphere (Dacey and Klug 1979; Armstrong 1980; Vroom et al. 2022). In addition, plants release organic substrates via root litter and root exudates to the soil. Thus, they act as soil reducers (Bhullar et al. 2014; Waldo et al. 2019; Girkin et al. 2018), increasing the availability of electron donors for microbial methanogenesis (Mueller et al. 2020b; Turner et al. 2020; Määttä and Malhotra 2024; Girkin et al. 2025). Certain plant species, such as *Phragmites australis* and *Spartina alterniflora*, have been shown to enhance CH_4 emissions (van der Nat and Middelburg 2000; Brix et al. 2001; Comer-Warner et al. 2022), likely due to their extensive belowground biomass and efficient internal gas transport mechanisms (Cheng et al. 2007; Fuchs et al. 2025).

Building on the role of abiotic and biotic factors in shaping CH_4 emissions, land-use, particularly livestock grazing, emerges as an additional driver that can influence soil-redox conditions and, consequently, carbon cycling in coastal wetlands (Mueller et al. 2017; Keshta et al. 2020). Globally, coastal wetlands are commonly used for livestock grazing including South America (Di Bella et al. 2015; Sica et al. 2016), East Asia (Suzuki and Suzuki 2011; He et al. 2015; Ning et al. 2019), and Europe (Tessier et al. 2003; Nolte et al. 2015; Barr and Bell 2017). Grazing alters soil and vegetation properties, often with important consequences for soil organic carbon (SOC) cycling (Davidson et al. 2017; Ford et al. 2019; Harvey et al. 2019; Leiva-Dueñas et al. 2024; Logemann et al. 2025). Despite its clear relevance for SOC dynamics, potential effects of livestock grazing on CH_4 emissions in coastal wetlands remain poorly understood (Ford et al. 2012). However, based on the established mechanistic insight into grazing effects on coastal wetlands SOC dynamics, we propose two pathways by which grazing may increase CH_4 emissions from coastal wetlands (Fig. 1).

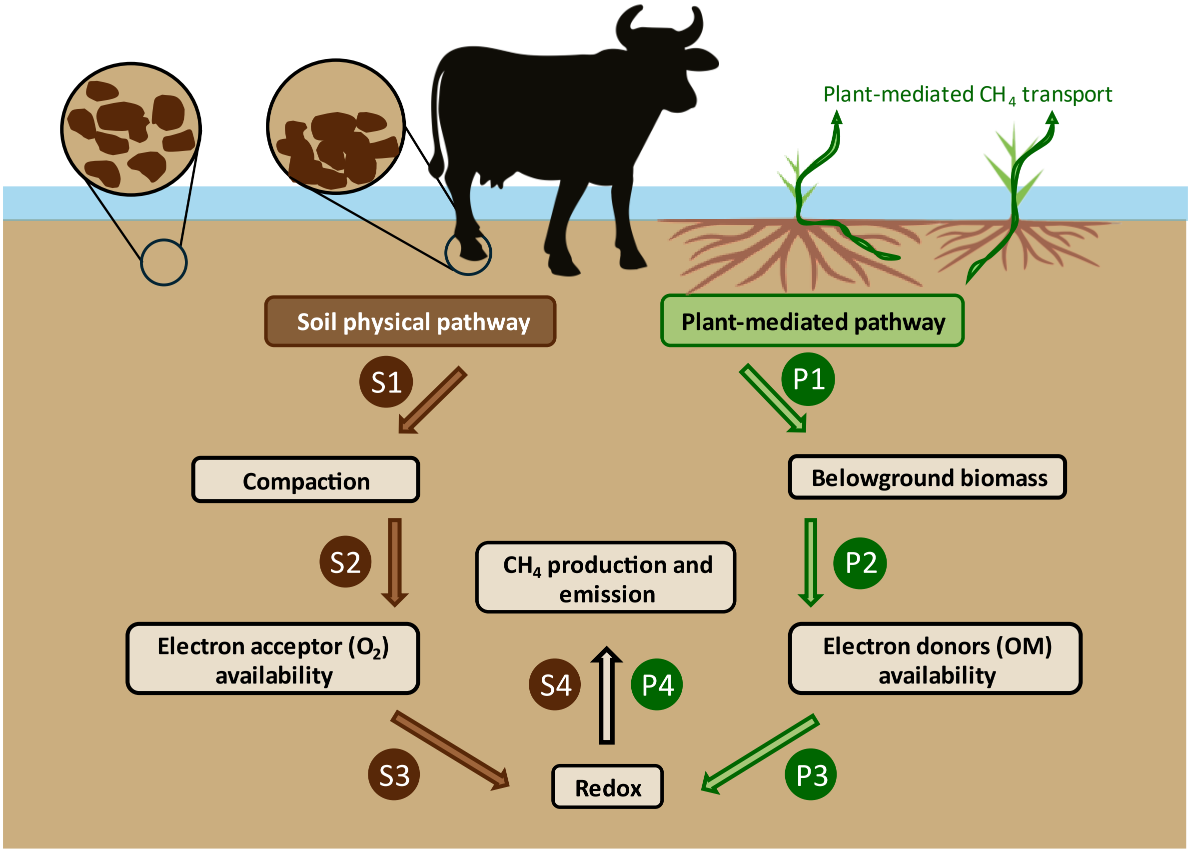


Figure 1 Conceptual framework of livestock-grazing effects on CH_4 emissions from coastal wetlands via the soil physical pathway (S) and the plant-mediated pathway (P). Arrows and the associated driving mechanisms illustrate a causal chain expected to ultimately increase CH_4 emission. The soil physical pathway predicts that (S1) trampling-driven soil compaction, which (S2) increases soil bulk density, leading to (S3) reducing soil conditions and (S4) CH_4 production and emission. The plant-mediated pathway predicts that (P1) grazing increases belowground biomass allocation and thus (P2) organic matter input to the soil, leading to (P3) reducing soil conditions and (P4) CH_4 production and emission. In addition, the potential for a direct plant-mediated transport of CH_4 from soil to the atmosphere is illustrated.

The soil-physical pathway predicts that trampling by livestock grazing increases soil compaction (Nolte et al. 2013b) and reduces drainage, leading to lower soil oxygen availability (Elschot et al. 2015; Bakker et al. 2020), enhancing methane production and consequently emissions. The plant-mediated pathway predicts that livestock grazing increases belowground biomass allocation (Elschot et al. 2015; Graversen et al. 2022), enhancing organic-matter input to the soil and thereby promoting reducing conditions that favor methane production (Turner et al. 2020; Girkin et al. 2025). Both pathways therefore predict increased CH_4 emissions in response to livestock grazing in coastal wetlands.

In this study, we aimed to determine whether livestock grazing indeed increases CH_4 emissions across multiple sites along two coastal regions in Northern Germany, namely the North Sea and the Baltic Sea coast. Along both coastlines, livestock grazing has been carried out on large areas of coastal wetlands for centuries (Elschot et al. 2024). Due to the semi-enclosed feature of the Baltic Sea with little exchange of seawater with the Atlantic, salinity levels are much lower in coastal wetlands at the Baltic Sea (5–10 psu) compared to those along the North Sea coast (32–34 psu; Dijkema 1990). By comparing these coastal regions, we aimed to conduct a comprehensive assessment of the effects of livestock grazing on CH_4 emissions in coastal wetlands. We hypothesized that (1) CH_4 emissions will be higher in grazed compared to ungrazed coastal wetlands due to trampling-driven soil compaction and increased soil reduction (soil-physical pathway hypothesis). We further hypothesized that (2) this grazing effect is more pronounced in Baltic Sea than in North Sea coastal wetlands, due to the higher CH_4 production potential of the less saline Baltic Sea coastal wetlands. Finally, we hypothesized that (3) additional site-specific variation in the CH_4 emission response to grazing is explained by plant-community-specific grazing effects on belowground biomass allocation (the plant-mediated pathway hypothesis).

3.3. Material and Methods

3.3.1. Study sites and sampling design

Study sites were identified along the North Sea and Baltic Sea coastlines of Germany based on clear grazed-ungrazed contrasts within sites (Fig. 2). The study design included two coastal wetland sites at the North Sea coast, Pohnshalligkoog (N1) and Nessmersiel (N2), and two at the Baltic Sea coast, Schleimünde (B1) and Heiligenhafen (B2) (Fig. 2 b-e). At each site, the grazed and ungrazed areas were selected based on similar elevation ranges and equal distances to the shoreline. To further keep environmental factors other than grazing as constant as possible, five plots per site and treatment were distributed randomly within the grazed and ungrazed areas (Fig. 2).

3.3.2. Methane flux measurements

Five plots per study site and per grazing treatment (N = 40 plots) were investigated for CH_4 fluxes. Flux measurements by a closed chamber method were conducted in regular intervals of six weeks from February 2023 to December 2023. In total, six campaigns were carried out. Flux measurements were conducted around low tide, i.e. when soil surfaces were not flooded.

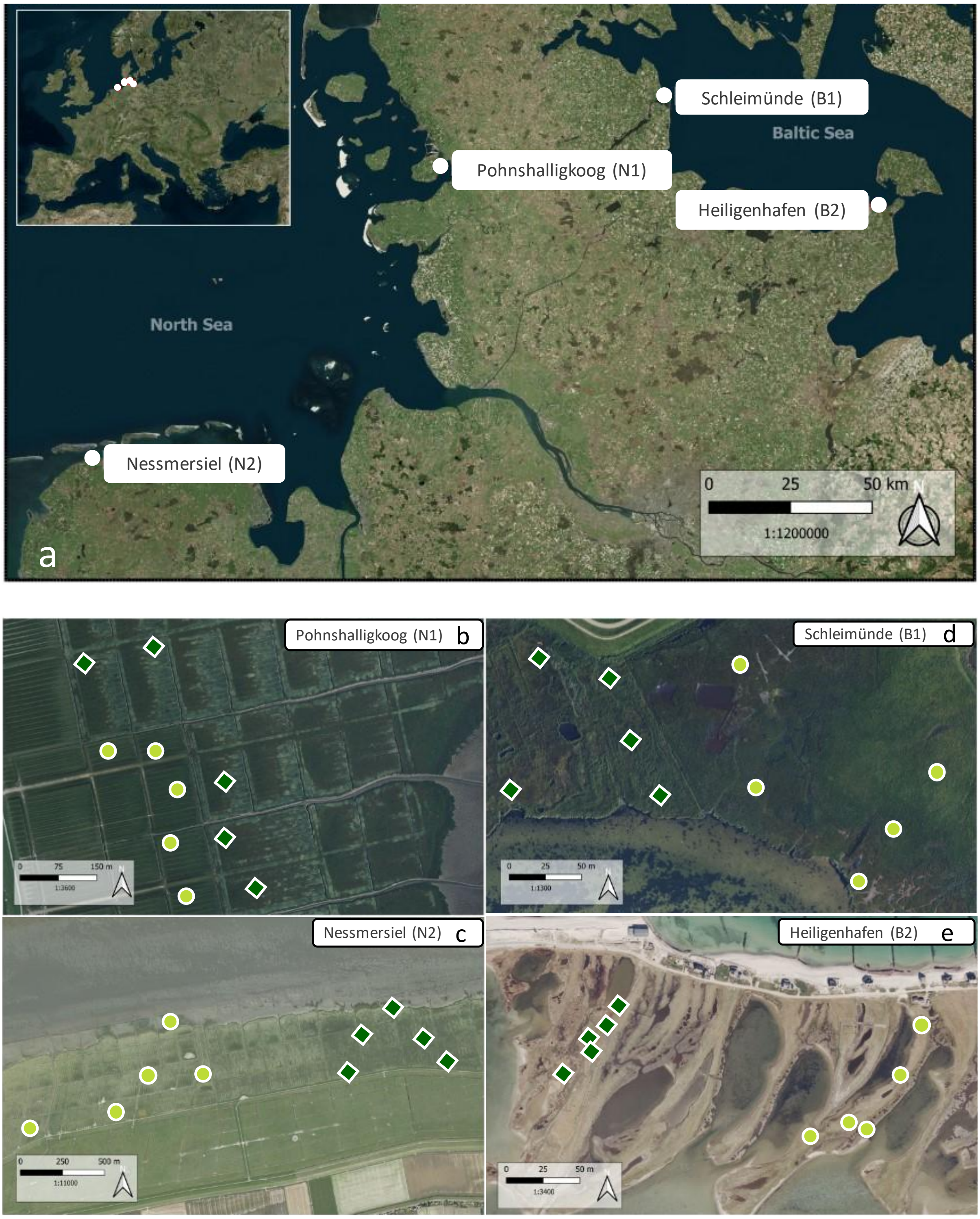


Figure 2: [a] Overview of the four study sites across Northern Germany. [b-e] Plot locations within the study sites Pohnshalligkoog (N1) and Nessmersiel (N2) at the North Sea coast, and within the study sites Schleimünde (B1) and Heiligenhafen (B2) at the Baltic Sea coast. Circles indicate grazed and squares indicate ungrazed plots.

For CH_4 flux measurements, we used flexible (i.e. height-adjustable) portable closed chambers and permanently installed collars as described by Yang et al. (2024). One of two chamber types (50 cm and 100 cm in height) were chosen depending on vegetation height. Chambers were 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) or 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, 5.6% 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). This method ensured the inclusion of high-quality flux measurements close to zero, which would have been excluded if considering the R^2 threshold alone. CH_4 flux measurements were considered acceptable if either the RMSE of the linear regression of the concentration-over-time-data was below the threshold of 5 ppb or the R^2 of this linear regression was above 0.85. A satisfactory RMSE could therefore offset a sub-threshold R^2, and conversely, a strong R^2 could justify accepting a flux despite an elevated RMSE (see Fig. S. 3). Flux-calculation statistics were conducted in R (version 4.5.0 (2025-04-11)).

3.3.3.Vegetation properties

Vegetation composition and structure were assessed in September 2023 by recording plant species composition and percent cover, along with percent cover of bare soil and standing dead plant matter, within each plot inside the flux collar. During the field campaign, it was not possible to reliably distinguish between *Festuca rubra* and *Juncus gerardii*, therefore, these species were combined and treated as a single taxonomic group for analysis. Vegetation height was measured for five random individuals, along with the tallest and shortest plant within each flux collar. To quantify aboveground biomass, plants were cut 2 cm above the soil surface in 30 cm x 30 cm squares approx. 50 cm adjacent to the flux collars. Biomass samples were transported to the laboratory in plastic bags and weighed after drying at 60 °C for five days. Belowground biomass was sampled using an Edelmann corer (diameter 5 cm; depth 20 cm) within the aboveground biomass sampling square. The belowground biomass samples were washed free from soils, dried at 60 °C for five days and then weighed.

3.3.4.Soil properties

Soil bulk density was quantified as a proxy to assess trampling-driven soil compaction. Single 50 cm deep soil cores were taken from each of the aboveground biomass sampling squares in September 2023, using an Eijkelkamp peat sampler (5 cm diameter). Bulk density was calculated based on sample dry weight and soil volume from the upper 20 cm of the soil core. To assess grazing effects on substrate (organic matter) availability for soil microbial communities, SOC content was quantified in the same soil samples following protocols outlined in Logemann et al. (2025).

To understand grazing effects on soil redox conditions, two complementary assessments were carried out. Redox potential measurements [mV] at 5-10 cm soil depth adjacent to the flux collar were carried out every six weeks during each flux measurement using a handheld Pt-tipped redox electrode and an Ag/AgCl reference electrode (3 M KCl solution) connected to a portable, high impedance redox potential meter (Model No.: 4612; Serial No.: 33402563, ecoTech Umwelt-Messsysteme GmbH, Bonn, Germany). The readings were corrected to the redox potential of the standard hydrogen electrode (+207 mV) (Mansfeldt 2003). Redox measurements were complemented by the Indicator-of-Reduction-In-Soils (IRIS) technique (Rabenhorst and Burch 2006; Rabenhorst 2013), which allowed us to calculate a Reduction Index [RI; %] integrated over the 6-week periods between single campaigns of redox potential and CH_4 flux measurements. The IRIS method is based on the reduction of Fe (III) to Fe (II) under anoxic soil conditions via the microbial respiration of Fe-reducing microorganisms. Since Fe (II) is soluble, the area of removed paint indicates the oxygen concentrations in the soil, where lower oxygen concentrations result in more paint removal. Hence a more positive RI indicates more reducing soil conditions. The IRIS protocols and RI calculation followed Mittmann-Goetsch et al. (2024). Each flux collar was equipped with two IRIS sticks reaching to 60 cm soil depth each 10 cm adjacent to the flux collar. To make the reduction index comparable with the redox potential measurements and to account for the topsoil layer that is directly impacted by grazing, only the root zone (0-20 cm) was considered during data analysis.

Soil temperature and volumetric water content were measured 10 cm adjacent to the flux collar during each CH_4 flux measurement. To account for salinity as an influencing factor across sites, a water sample was collected from the adjoining seawater body during each campaign, as wetland soil salinity often reflects that of the adjacent water body (Mitsch et al. 2013). Seawater salinity was then determined using a handheld refractometer (Model No.: 282030, Sybon Meerwasser Refractometer; aquaristic.net, Babenhausen, Germany).

3.3.5. Statistical analysis

CH_4 flux data were not normally distributed and therefore log-transformed. Since the dataset included negative values, log-transformation required adding a constant of +10 to each value.

To test if grazing affected methane emissions via the soil physical pathway (hypothesis 1), grazing effects on soil bulk density and CH_4 emissions were tested using paired t-tests (N = 4). Then bulk density, redox parameters (redox potential and reduction index, RI), further environmental parameters, and CH_4 emissions were tested for correlations, statistical significance was assessed with two-sided t-tests. To further understand grazing effects on environmental variables, paired t-tests (N=4) were conducted across all sites for all assessed parameters. To test whether grazing effects on methane emissions differed between coasts and sites (hypothesis 2), site-specific linear mixed models, with livestock grazing treatment and its interaction with month as fixed effects and plot-id as random effect, were conducted.

To test if grazing affected CH_4 emissions via increases in belowground biomass allocation and soil organic carbon (hypothesis 3), the grazing effect on belowground biomass and soil organic carbon per site was assessed using t-tests (N=5), and then correlations between belowground biomass and soil organic carbon, redox potentials and CH_4 emissions were calculated.

To assess the relationship between plant species composition and CH_4 emissions, plant species were categorized based on their association with CH_4 flux categories (high or low fluxes). First, the dataset was split into one high and one low CH_4 flux category using the average of 2.31 CH_4 [mg CH_4 m^{-2} day^{-1}] CH_4 flux of the total dataset as threshold value (low flux < mean, n = 217; high flux > mean, n = 42). Next, plant species that served as indicators for one of the two flux categories were identified. Finally, non-metric multidimensional scaling (NMDS) was used to further explore potential grazing effects operating via changes in plant species composition. Specifically, NMDS was used to assess compositional variation among plots and to examine relationships between plant species composition and plant relevant parameters, including belowground biomass, aboveground biomass, soil redox potential, and CH_4 emissions. Species were visually distinguished in the ordination plot according to their association with high or low CH_4 flux categories, as identified in the indicator species analysis.

Statistics were conducted in R (version 4.5.0 (2025-04-11)). All LMMs were performed using the *lmer* function from the *lme4* R package (Douglas Bates 2018). Correlations were calculated using the *rcorr* function from the *Hmsic* R package (Table 1) or the cor.test function from the *stats* R package (Fig. 5i-k). The *indicspecies* R package was used to categorize plant species in CH_4 categories. This method identified indicator species based on a permutation test of the point-biserial correlation coefficient. Environmental variables were fitted post-hoc to the ordination using the *envfit* function from the *vegan* R package.

3.4. Results

3.4.1.Abiotic controls of CH4 emissions

Annual CH_4 emissions were 0.97 ± 0.39 mg CH_4 m^{-2} day^{-1} (mean ± standard error (SE)) at the North Sea wetland sites and 3.76 ± 1.10 mg CH_4 m^{-2} day^{-1} at the Baltic Sea wetland sites. Annual CH_4 emissions correlated significantly negatively with soil redox potential (Fig. 5k, Table 1), and soil bulk density, and significantly positively with reduction index, belowground biomass, SOC, and volumetric water content (Table 1). No significant correlations were found between CH_4 emissions and aboveground biomass, salinity, air and soil temerature, relative humidity of air, and photosynthetically active radiation (Table 1).

3.4.2.Grazing and environmental predictors of CH_4 emissions

Soil bulk density was higher in grazed (0.94 ± 0.07 g cm^{-3}) areas than in ungrazed (0.74 ± 0.11 g cm^{-3}) areas (Fig. 3b, Table 2). All other parameters including aboveground biomass, soil temperature, relative humidity of air, SOC, belowground biomass, redox potential, reduction index, volumetric water content, salinity, air temperature did not differ significantly ($p > 0.05$) between grazing treatments, except for radiation ($p = 0.04$; Table 2).

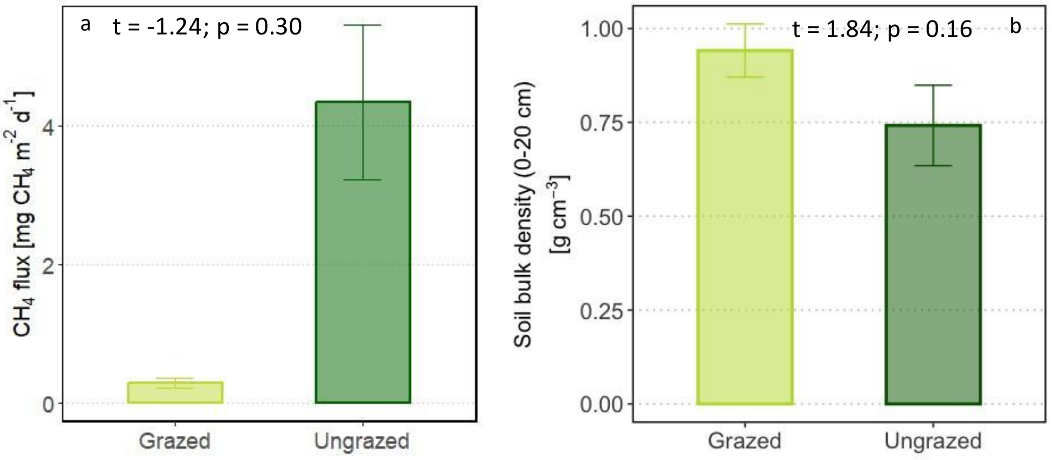
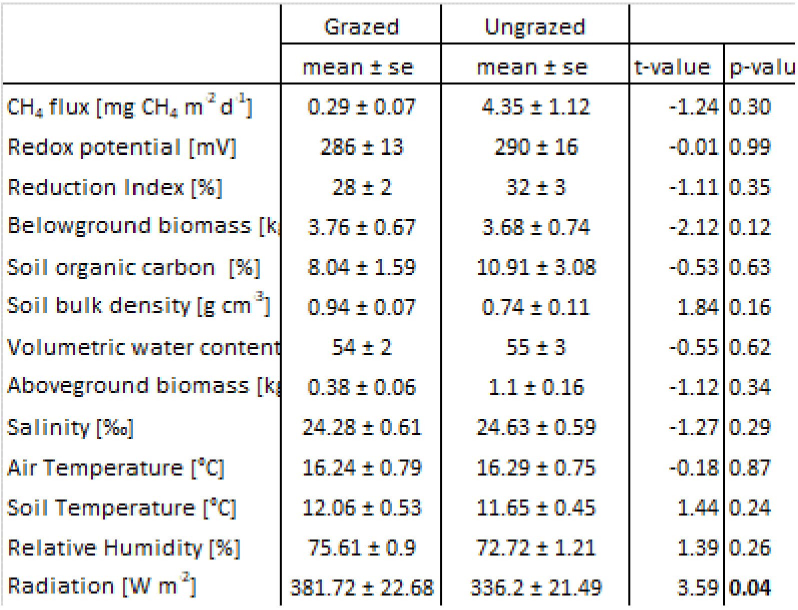


Figure 3: Average annual CH4 emissions (a) and soil bulk density (b) in grazed and ungrazed treatments across all sites. Error bars represent SE. For statistical comparison of grazed and ungrazed treatments, paired t-tests were conducted using site-level means, with site as the pairing factor. Values indicate t-statistics. For CH_4 emissions, means are shown on the original scale, while statistical testing was performed on log-transformed values.

	log CH_4 flux	Redox potential	Reduction Index	Belowground biomass	Soil organic carbon	Dry bulk density	water content	Aboveground biomass	Salinity	Temperature	Temperature	Relative Humidity
Redox measurements	**-0.59** ***											
Reduction Index	**0.52** ***	**-0.72** ***										
Belowground biomass	**0.59** ***	**-0.67** ***	**0.62** ***									
Soil organic carbon	**0.58** ***	**-0.62** ***	**0.55** ***	**0.67** ***								
Dry bulk density	**-0.59** ***	**0.45** **	**-0.53** ***	**-0.50** ***	**-0.78** ***							
Volumetric water conte	**0.42** **	**-0.36** *	**0.49** **	**0.33** *	**0.35** *	-0.25						
Aboveground biomass	0.19	0.07	-0.07	-0.05	-0.06	0.03	-0.08					
Salinity	-0.22	**0.52** ***	-0.27	**-0.60** ***	**-0.43** **	0.07	0.03	-0.03				
Air Temperature	-0.16	**0.31** *	-0.16	**-0.40** *	**-0.31** *	0.03	-0.15	0.16	**0.59** ***			
Soil Temperature	-0.14	0.07	-0.12	-0.19	-0.15	0.03	**-0.32** *	-0.11	**0.39** *	**0.75** ***		
Relative Humidity	-0.14	-0.17	0.06	0.19	0.10	0.14	0.08	**-0.43** **	-0.24	**-0.59** ***	-0.22	
Radiation	-0.07	-0.05	-0.01	-0.11	-0.13	0.00	-0.10	-0.13	0.20	**0.68** ***	**0.56** ***	**-0.39** ***

Table 3: Pearson correlations, based on plot-level means, between CH4 emissions and potential environmental predictor variables. Values represent Pearson correlation coefficients (r) and corresponding significance levels ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***).

Table 4: Paired t-test using site-level means, with site as paring factor, for CH_4 emissions and environmental parameters. Values represent group means ± SE including all sites. For CH_4 emissions, means are shown on the original scale, while statistical testing was performed on log-transformed values.



	Grazed	Ungrazed		
	mean ± se	mean ± se	t-value	p-valu
CH_4 flux [mg CH_4 m^{-2} d^{-1}]	0.29 ± 0.07	4.35 ± 1.12	-1.24	0.30
Redox potential [mV]	286 ± 13	290 ± 16	-0.01	0.99
Reduction Index [%]	28 ± 2	32 ± 3	-1.11	0.35
Belowground biomass [k	3.76 ± 0.67	3.68 ± 0.74	-2.12	0.12
Soil organic carbon [%]	8.04 ± 1.59	10.91 ± 3.08	-0.53	0.63
Soil bulk density [g cm^{-3}]	0.94 ± 0.07	0.74 ± 0.11	1.84	0.16
Volumetric water content	54 ± 2	55 ± 3	-0.55	0.62
Aboveground biomass [k	0.38 ± 0.06	1.1 ± 0.16	-1.12	0.34
Salinity [‰]	24.28 ± 0.61	24.63 ± 0.59	-1.27	0.29
Air Temperature [°C]	16.24 ± 0.79	16.29 ± 0.75	-0.18	0.87
Soil Temperature [°C]	12.06 ± 0.53	11.65 ± 0.45	1.44	0.24
Relative Humidity [%]	75.61 ± 0.9	72.72 ± 1.21	1.39	0.26
Radiation [W m^{-2}]	381.72 ± 22.68	336.2 ± 21.49	3.59	**0.04**

3.4.3. Direct grazing effects on CH_4 emissions

On average, annual CH_4 emissions were lower in grazed (0.29 ± 0.07 mg CH_4 m^{-2} day^{-1}) compared to ungrazed areas (4.35 ± 1.12 mg CH_4 m^{-2} day^{-1}; Fig. 3a, Table 2). However, grazing effects on CH_4 emissions differed among sites, while within each site the direction of the effect was consistent across all sampling months (Fig. 4). At site B2, CH_4 emissions were significantly lower in grazed (0.22 ± 0.1 mg CH_4 m^{-2} day^{-1}) than in ungrazed (13.37 ± 3.70 mg CH_4 m^{-2} day^{-1}) coastal wetlands (Estimate = -0.59; p = 0.001; Fig. 4d), with significant differences observed in three months (May, June, August). Similarily, at site N2 grazed areas emitted less CH_4 (0.11 ± 0.14 mg CH_4 m^{-2} day^{-1}) compared to ungrazed areas (3.45 ± 1.54 mg CH_4 m^{-2} day^{-1}; Estimate = -0.14; p = 0.39; Fig. 4b), while a significant difference occurred in March. In contrast, at site B1 CH_4 emissions were consistently higher in grazed areas (grazed: 0.65 ± 0.24 mg CH_4 m^{-2} day^{-1}; ungrazed: 0.07 ± 0.05 mg CH_4 m^{-2} day^{-1}; Fig. 4c). At site N1, no significant differences in CH_4 emissions were observed between treatments (grazed: 0.12 ± 0.06 mg CH_4 m^{-2} day^{-1}; ungrazed: 0.23 ± 0.13 mg CH_4 m^{-2} day^{-1}; Fig. 4a).

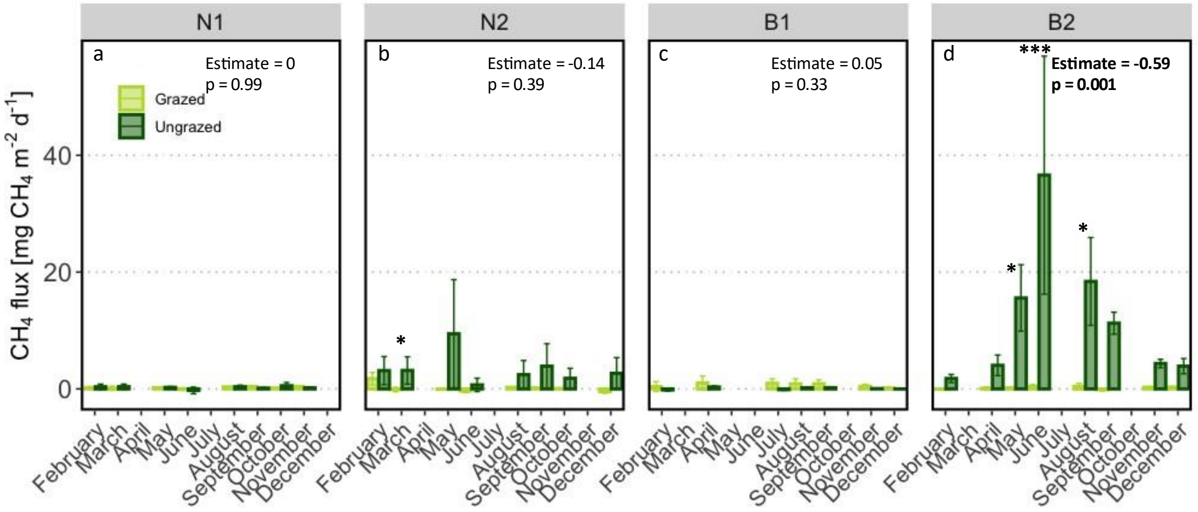


Figure 4: Seasonal pattern of CH4 emissions [a-d] in grazed (light green bars) and ungrazed coastal wetland areas (dark green bars) in the four study sites (N1 and N2 at the North Sea, B1 and B2 at the Baltic Sea; see Figure 2). Bars represent mean CH_4 fluxes per sampling campaign based on measurements from five plots per grazing treatment and site; error bars represent SE. Values above bars indicate model estimates (β) from linear mixed-effects models with grazing treatment and its interaction with month as fixed effects and plot ID as random effect. Stars denote significance levels per campaign ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***. For CH_4 emissions, means are shown on the original scale, while statistical testing was performed on log-transformed values.

3.4.4.Grazing effects on biotic controls of redox potentials and CH4 emissions

Grazing effects on belowground biomass were not consistent across sites. At N2 and B2, belowground biomass was lower in grazed (N2: 1.3 ± 0.18 kg m^{-2}; B2: 6.89 ± 1.02 kg m^{-2}) than in ungrazed (N2: 2.09 ± 0.39 kg m^{-2}; B2: 8.70 ± 1.15 kg m^{-2}) areas (Fig. 5b, 5d). N1 and B1 exhibited the opposite pattern, with higher belowground biomass in grazed (N1: 2.19 ± 0.42 kg m^{-2}; B1: 4.91 ± 1.40 kg m^{-2}) compared to ungrazed areas (N1: 1.35 ± 0.36 kg m^{-2}; B1: 2.59 ± 0.42 kg m^{-2}; Fig. 5a, 5c). SOC showed the same patterns where at N2 and B2, SOC was significantly lower in grazed (N2: 3.57 ± 0.18 %; B2: 8.33 ± 2.87 %) compared to ungrazed areas (N2: 4.42 ± 0.31 %; B2: 31.82 ± 5.43 %; Fig. 5f, 5h). B1 had significantly lower SOC contents in grazed than in ungrazed areas (grazed: 3.57 ± 0.17 %; ungrazed: 4.42 ± 0.31 %; Fig. 5g), while in N1 there were no significant differences within treatments (grazed: 3.99 ± 1.00 %; ungrazed: 4.13 ± 0.74 %; Fig. 5e). Belowground biomass correlated significantly positively with SOC ($r = 0.67$; $p < 0.001$; Fig. 5i), SOC correlated significantly negatively with redox potentials ($r = 0.58$; $p < 0.001$; Fig. 5j), and redox potentials correlated significantly negatively with CH_4 emissions ($r = 0.59$; $p < 0.001$; Fig. 5k).

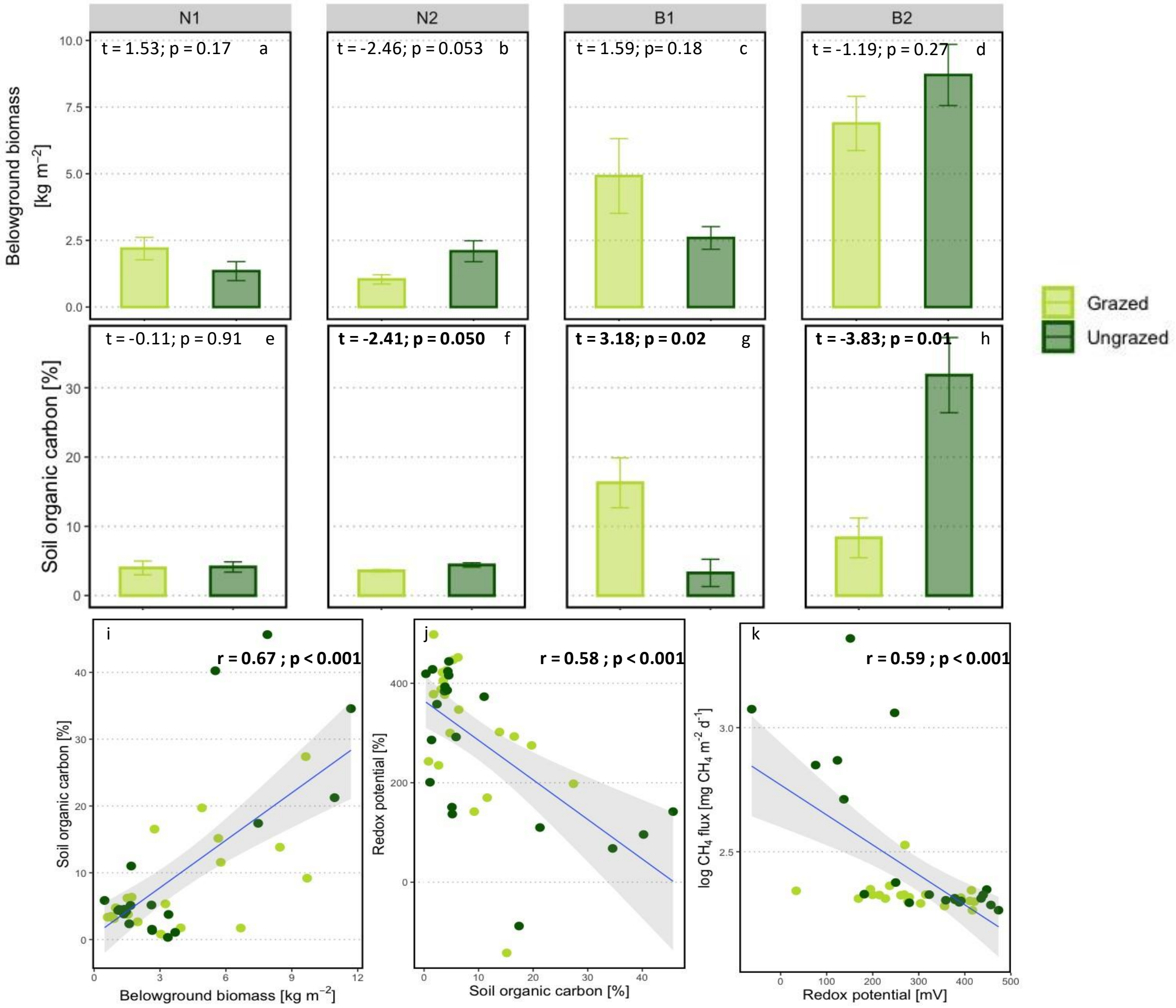


Figure 5: Belowground biomass [a–d] and SOC [e-h] in grazed and ungrazed treatments within each site. Bars represent site-level treatment means ± SE, and values indicate t-statistics from independent t-tests. Panel [i] shows the correlation between belowground biomass and SOC, panel [j] displays the correlation between SOC and redox potential, and panel [k] shows CH4 emissions in relation to redox potentials. Panels [i-k] include Pearson correlation coefficients (r) with corresponding p-values, linear fit, and 95% confidence intervals.

3.4.5. Plant species as driver in plot-based methane emission

A total of 17 plant species was identified (Fig. S. 4). Vegetation of grazed areas was mostly dominated (single species cover > 60%) by *Puccinellia maritima* in N1, N2 and B1, while *Juncus geradii/Festuca rubra* and *Puccinellia maritima* dominated B2. Vegetation of the ungrazed areas on the North Sea coast was predominantly a mix of non-dominant species (all single species covers < 60%), often with high cover of *Elymus athericus* and either *Atriplex prostrata* or *Sueda maritima* (see Fig. S. 4 for detailed plant distribution).

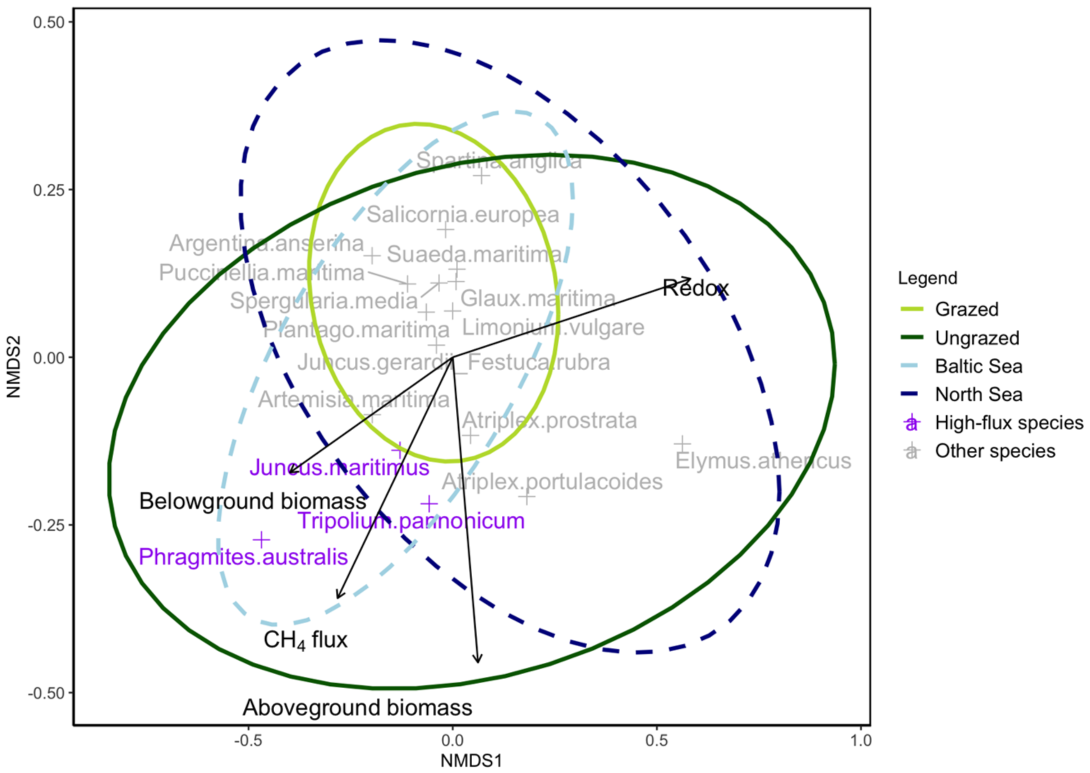


Figure 6: Non-metric multidimensional scaling (NMDS) ordination (Euclidean distance, stress = 0.15) of plant species composition in relation to grazing treatment, coast, and environmental vectors. The plant species are grouped by CH_4-flux category: high-flux species (purple) and other species (grey). Grazing treatments and coasts are represented by ellipses: grazed (light green), ungrazed (dark green), Baltic Sea (light blue) and North Sea (dark blue). Environmental vectors represent correlations with key variables: CH_4 emissions (CH_4 flux) and belowground biomass align positively with high-flux species, the Baltic Sea and the ungrazed treatment, while redox potential diverges in the opposite direction of belowground biomass, indicating a strong negative correlation. The ungrazed ellipse extends beyond coastal ellipses, driven by species such as Phragmites australis that is dominant in ungrazed coastal wetlands of Baltic Sea and Elymus athericus that is dominant in ungrazed coastal wetlands of the North Sea coast.

Based on the categorization of plant species into “high” and “low” CH_4-flux groups, three plant species were significantly associated with the “high-flux” category ($p < 0.05$): *Phragmites australis*, *Tripolium pannonicum*, and *Juncus maritimus*. *Plantago maritima* tended toward the “high-flux” category, although not significantly ($p = 0.08$). Six plant species were (not significantly) associated with the “low-flux” category: *Elymus athericus*, *Artemisia maritima*, *Limonium vulgare*, *Glaux maritima*, *Atriplex portulacoides*, and *Argentina anserina* ($p > 0.05$). All remaining species could not be assigned to either flux category. The NMDS ordination (based on Euclidean distance; Fig. 6) revealed clear grouping patterns based on grazing treatment and coastal location, with distinct environmental gradients. All environmental vectors were significant at $p < 0.05$. The three high-flux species aligned with vectors representing CH_4 emissions and below- and aboveground biomass and were generally associated with the ungrazed treatment. *Tripolium pannonicum* and *Juncus maritimus* occurred in sites on both coasts, whereas *Phragmites australis* was only present in the Baltic Sea sites. In contrast, *Elymus athericus*, was restricted to the North Sea sites and similarly occurred exclusively within the ungrazed ellipse. Belowground biomass and soil redox potential pointed in the opposite directions, reflecting strong negative correlation. The grazed treatment ellipse was mostly nested within both coastal ellipses, indicating more similar plant communities between coasts under grazing. Ungrazed plant communities were less similar between coasts, mostly driven by two plant species: *Elymus athericus* and *Phragmites australis*.

3.5. Discussion

Contrary to our first hypothesis, CH_4 emissions were on average not higher but lower in grazed than in ungrazed treatments. As expected, grazing led to an overall increase in soil bulk density, aligning with the proposed soil physical pathway by which trampling (i.e. soil compaction) could lower soil redox potential and consequently stimulate CH_4 emissions (Fig. 1). However, soil bulk density was significantly positively correlated with redox potential (and negatively with the reduction index) and significantly negatively with CH_4 emissions. Specifically, in sites N2 and B2, grazing increased bulk density but decreased CH_4 emissions, while in site B1, grazing decreased bulk density but increased CH_4 emissions (Fig. S. 2a-d for site-level soil bulk density), contradicting the proposed mechanistic links of the soil physical pathway. Additionally grazing effects on soil moisture varied across sites, with both increased and decreased soil water content (Fig. S. 2 e-h). However, we did not find the expected link between water content and CH_4 in all sites. That is, in site B1, grazing decreased water content on average but increased CH_4 emissions, while in site N1, grazing increased water content on average but showed no effect on CH_4 emissions. Overall, these results indicate that grazing effects on CH_4 emissions cannot be explained by the proposed soil physical pathway.

We further hypothesized that grazing effects on CH_4 emissions would be more pronounced in Baltic Sea than North Sea wetlands (hypothesis 2), due to the greater CH_4 production potential in the less saline Baltic Sea wetlands. While CH_4 emissions were indeed higher in B2 of the Baltic Sea wetlands and sea water salinity was lower compared to the North Sea (Fig. S. 5), there was no evidence that grazing changed CH_4 emissions in Baltic Sea wetlands more pronounced or more consistently compared to the North Sea wetlands. Instead, the CH_4 response to grazing varied qualitatively across all sites, with either higher, lower, or similar emissions observed in grazed relative to ungrazed treatments independent of the situation at the North Sea vs-Baltic Sea coasts. These multidirectional responses suggest more complex grazing effects on soil biogeochemistry and CH_4 emissions than those predicted by the soil-physical pathway hypothesis or by salinity differences alone.

Our third hypothesis proposed that site-specific variation in CH_4 responses to grazing would be explained by the plant-mediated pathway, predicting that grazing effects on belowground biomass determines soil redox conditions and ultimately CH_4 emissions. Indeed, belowground biomass was identified a key driver influencing redox conditions by determining SOC contents and, in turn, CH_4

emissions across all sites. Belowground biomass was significantly positively correlated with SOC, which was significantly negative correlated with redox potentials, following a significant negative correlation of redox potentials with CH_4 emissions, supporting the hypothesis that belowground biomass stimulates CH_4 production by reducing the soil via electron donor (i.e. organic matter) input. Grazing effects on belowground biomass (i.e. SOC) were inconsistent across sites, while the bi-directional (either increasing or decreasing) influence of grazing on belowground biomass and SOC continuously predicted the ecosystem CH_4 response. That is, at site B1, grazing was associated with higher belowground biomass and SOC and increased CH_4 emissions compared to the ungrazed areas while at sites N2 and B2 grazing was associated with lower belowground biomass and SOC and decreased CH_4 emissions compared to the ungrazed areas. These results highlight a consistent plant-mediated pathway via which grazing influences CH_4 emissions in coastal wetlands, as grazing-induced changes in belowground biomass shape redox conditions and ultimately control CH_4 emissions.

While our data provide evidence that belowground biomass shapes CH_4 emissions mostly by reducing the soil via organic matter deposition such as root litter or exudation (Mittmann-Goetsch et al. 2024), there are additional important mechanisms by which roots affect CH_4 emissions in wetlands (Määttä and Malhotra 2024). This is reflected in high variability in CH_4 emissions under low soil redox potential conditions. Wetland plant species can facilitate CH_4 transport to the atmosphere via aerenchyma, bypassing the oxic soil layer where CH_4 would otherwise be oxidized to CO_2 (Vroom et al. 2022). This process is closely linked to root architecture, as lateral roots and root tips have been identified as key features in mediating CH_4 transport (Henneberg et al. 2012). Furthermore, wetland plants can reduce CH_4 emissions through aerobic methanotrophy, by oxidizing the rhizosphere (Segers 1998; Wang et al. 2018; Capooci et al. 2024). Since plant species have different effects on soil redox conditions and consequently CH_4 emissions (Sutton-Grier and Megonigal 2011), it is possible that shifts in plant community- or species-specific functional traits associated with root architecture contributed to the observed grazing effects on CH_4 emissions.

Our plant-mediated and species-dependent interpretation aligns with findings by Ford et al. (2012), the only other study to date that directly examined the effect of livestock grazing on CH_4 emissions in coastal wetlands. They compared grazed and ungrazed plots within a single coastal wetland site and suggested that plant species identity exerted a stronger influence on CH_4 emissions than direct effects of grazing on soil conditions. Our findings further support this conclusion, as grazing-driven shifts in plant species composition, and consequently in plant-associated traits, are likely to contribute to the observed differences in CH_4 emissions. In our study, all species significantly associated to the “high-flux” category occurred exclusively in ungrazed areas of the coastal wetlands, independent of coast. While studies have shown that *Phragmites australis* (as one of the identified “high-flux “species) can stimulate CH_4 emissions (van den Berg et al. 2020, Vroom et al. 2022), plant trait-based CH_4 emission predictions remain limited. For example, Ge et al. (2025) reported large regional variation in CH_4 emissions from *Phragmites australis* and *Spartina* species, suggesting that focusing on species identity alone without considering the environmental context is insufficient to predict CH_4 emissions. Our study expands the perspective of Ford et al. (2012) by incorporating a multi-site, broad-scale approach across diverse coastal wetlands, capturing a wider range of environmental conditions, and plant communities. This broader spatial scope allowed us to provide more generalizable insights into the (plant-mediated) pathways driving CH_4 emissions. However, understanding how species-specific traits influence CH_4 cycling remains a key knowledge gap and was beyond the scope of our non-manipulative study design.

3.6. Conclusion

This study provides supporting evidence that plant-mediated soil redox conditions, driven by belowground biomass, are the primary control on CH_4 emissions from coastal wetlands. Grazing effects did not consistently affected CH_4 emission, but rather induced plant community changes that resulted in either higher or lower belowground biomass compared to ungrazed areas. Higher belowground biomass consistently - regardless of grazing treatment or coast - promoted CH_4 emissions through its positive effect on SOC, which in turn reduced soil conditions. Moreover, we found that this plant-mediated effect may be further reinforced when grazing-induced shifts in plant community exclude species that enhance CH_4 emissions, such as *Phragmites australis*. Understanding these plant-mediated mechanisms is essential for improving predictions of CH_4 emissions under different land-use types and for strengthening coastal wetland management strategies aimed at maximizing climate change mitigation benefits.

3.7. Supporting Information

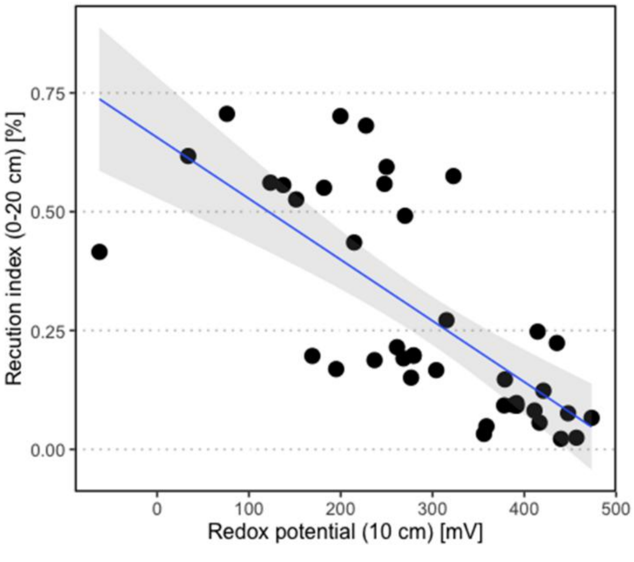


Figure S. 1 The redox measurements (mV) using the Pt-tipped electrode are backed up by the reduction index (%) from the root zone (0-20cm). With a decreasing redox potential, the reduction index increases, which reflects an increase in reduced areas on the IRIS stick (R^2= 0.51, $p < 0.001$).

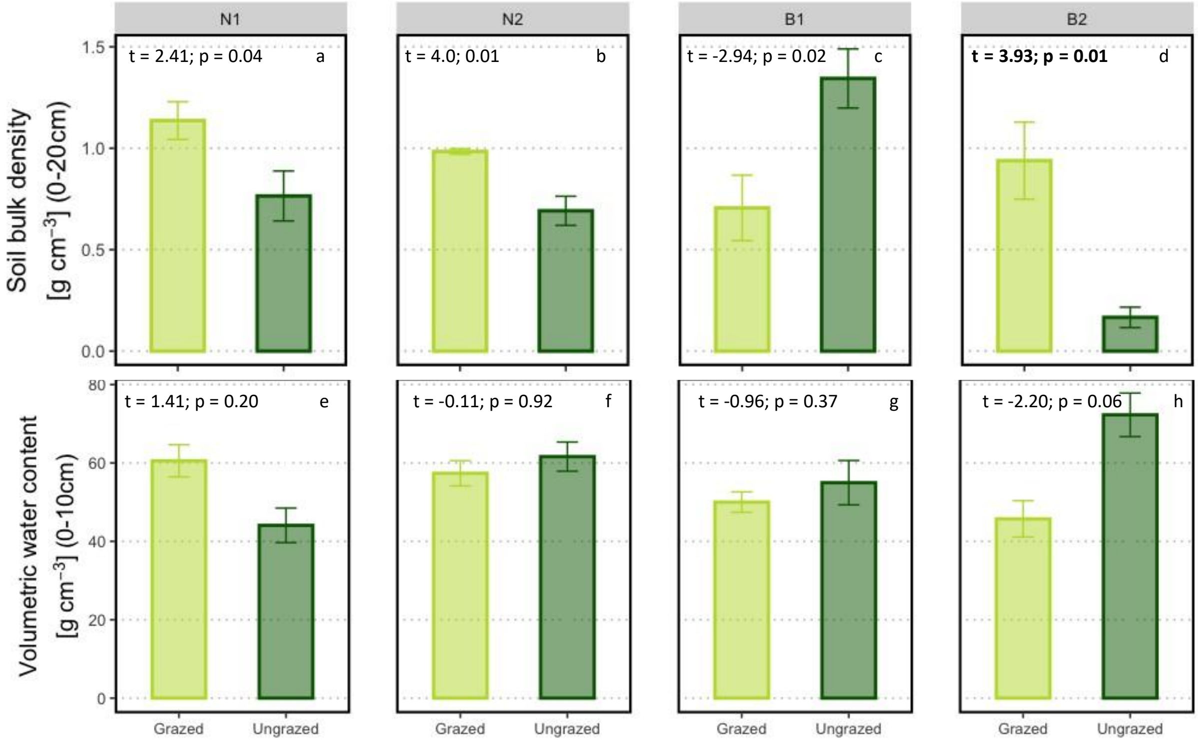


Figure S. 2 Soil bulk density [a-d] and volumetric water content [e-h] in grazed and ungrazed treatments within each site. Bars represent site-level treatment means ± SE, and values indicate t-statistics from independent t-tests.

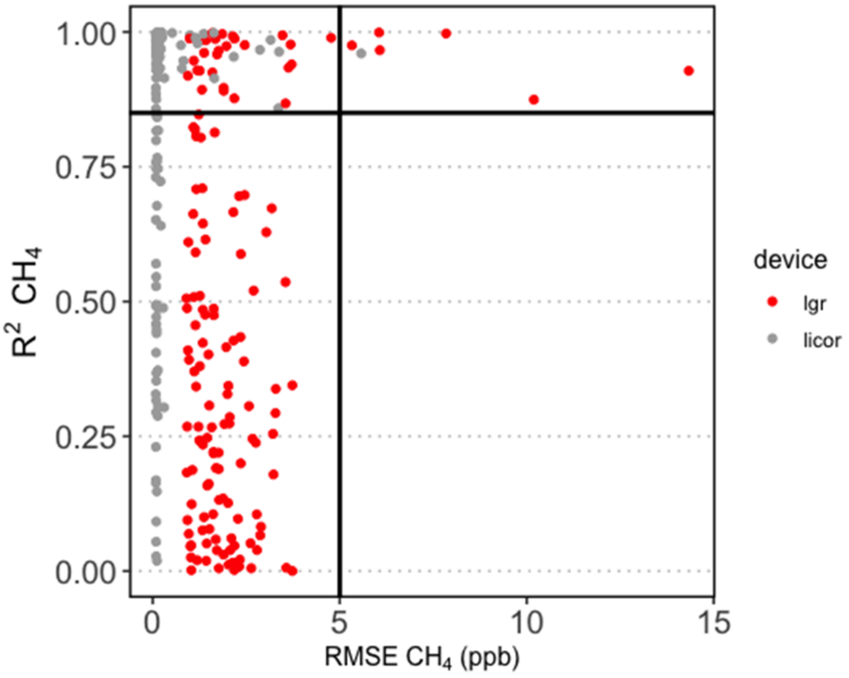


Figure S. 3 Combination of R^2 and RMSE as criteria for flux quality control of linear regression results. CH_4 flux measurements were considered acceptable if either the RMSE of the linear regression of the concentration-over-time-data was below the threshold of 5ppb or the R^2 of this linear regression was above 0.85.

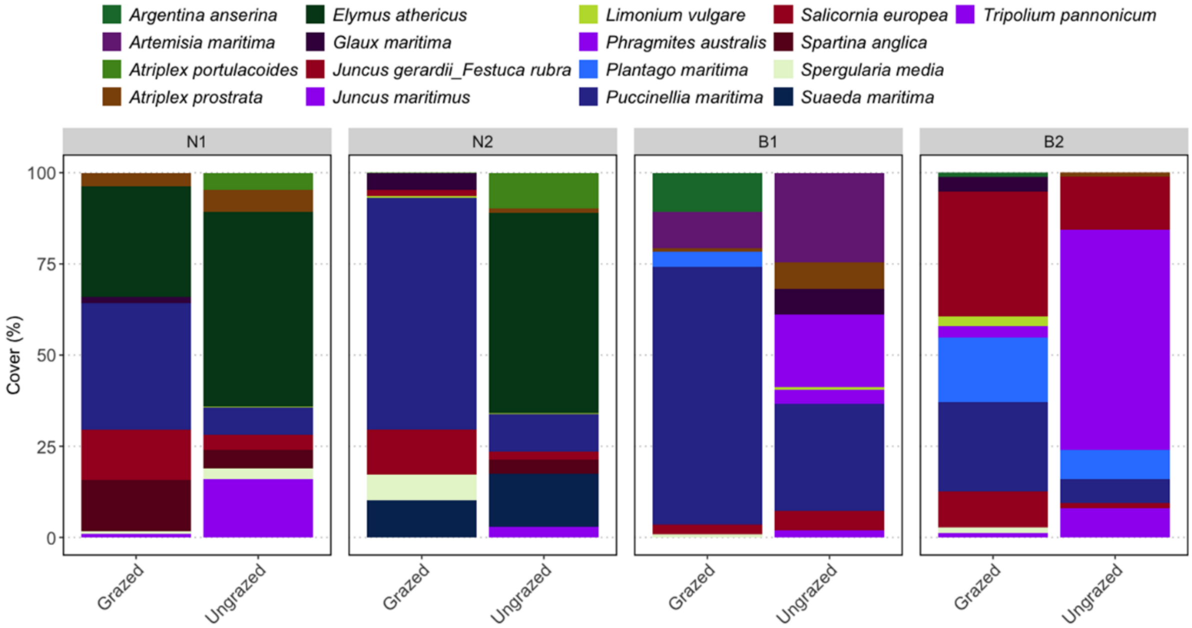


Figure S. 4 Mean species cover in grazed and ungrazed coastal wetlands at each site. Panels show plant species cover standardized to 100% per treatment within each site. “High-flux” species are indicated in purple.

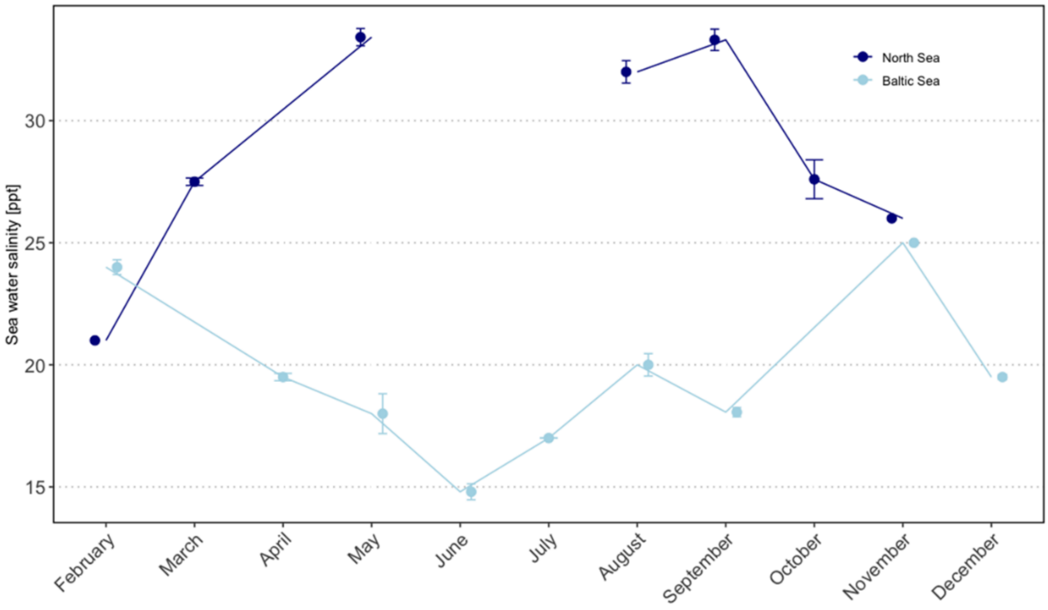


Figure S. 5 Seawater salinity measured in the North and Baltic Sea across sampling campaigns. Values represent measurements from water samples collected from the adjoining seawater body during each campaign, as wetlands soil salinity often reflects the adjacent water body.

BOX A

UNRAVELING PLANT-SOIL INTERACTIONS BY IMPLEMENTING AN EXPERIMENTAL APPROACH: EFFECTS OF DIVERSITY AND HYDROLOGY ON CARBON CYCLING IN COASTAL WETLANDS

Ella Logemann, Julian Mittmann-Goesele, Kai Jensen, Peter Mueller

A. Introduction

Global change is associated with a decline in global plant diversity, likely decreasing terrestrial carbon storage (Spohn et al. 2023; Weiskopf et al. 2024). However, the role of biodiversity in wetlands remains insufficiently understood, despite their disproportionate role as carbon sinks. First studies suggest that plant diversity may enhance carbon storage in coastal wetlands (e.g. Bai et al. 2021; Liu et al. 2024a), yet the mechanistic basis of this relationship has not been fully explored. Coastal wetlands are particularly affected by climate change, as they are exposed not only to rising atmospheric CO_2 concentrations and elevated temperatures but also to accelerating sea-level rise (SLR). Plant-soil interaction under changing inundation are critical for ecosystem resilience and carbon cycling dynamics (Kirwan and Megonigal 2013; Spivak et al. 2019). For example, as plants supply oxygen and root exudates that can stimulate soil organic matter decomposition - known as rhizosphere priming (Mueller and Megonigal 2024). Consequently, it is essential to understand how altered interactions between plant-soil dynamics by changing hydrological regimes and shifts in plant diversity and plant community structure shape the carbon storage potential of wetlands.

According to the biodiversity-productivity relationship, more diverse plant communities generally exhibit higher productivity, as species complement one another through differential niche use (Ford et al. 2016; Duffy et al. 2017; Chen et al. 2020). This enhanced productivity translates into greater carbon inputs to soils. In wetlands, however, the mechanisms governing carbon dynamics are more complex, as plant-soil interactions play a particularly intricate role in determining carbon ‘fate’. For example, increased productivity may intensify soil priming effects to a greater extent than in terrestrial systems (Mueller and Megonigal 2024), thereby exerting strong control over decomposition processes. Oxygen priming, in particular, has profound implications for wetland carbon cycling, as improved soil oxygenation can stimulate microbial activity and enhance SOM decomposition (Mueller and Megonigal 2024). Consequently, the expected positive effect of higher diversity on carbon inputs potentially be offset by priming-induced SOM losses.

Furthermore, (Mueller et al. 2020b) demonstrated species-specific effects on carbon cycling in tidal wetlands, showing that plots dominated by *Schoenoplectus americanus* emitted less methane than those dominated by *Spartina patens*. Such differences likely arise from contrasting functional types: *S. americanus* enhances soil oxygenation through radial oxygen loss, whereas *S. patens* releases higher amounts of root exudates into the soil (Mueller et al. 2020b). These findings highlight the need to further investigate biotic interactions, both plant-plant and plant-microbe, to better understand their role in regulating carbon dynamics in blue carbon ecosystems (Ren et al. 2022).

Within this framework I raise the following questions: (I) Does higher primary productivity resulting from increased plant diversity amplify aerobic decomposition of organic matter? (II) How are these plant-soil interactions shaped by contrasting hydrological regimes? (III) And to what extent are such effects driven by specific functional groups or traits associated with particular plant species?

I address these questions using a full-factorial marsh organ mesocosm experiment approach with manipulated inundation and diversity levels (Fig. 1). In this tidal basin experiment, the effects of hydrological regime and plant diversity on carbon turnover are investigated. The tidal basin experiment has been running since four consecutive vegetation periods and started in July 2022. The marsh organs were filled with sediment collected from tidal creeks, which was homogenized, sieved to remove shells, roots, and coarse organic matter, and subsequently mixed with organic-free sand and clay. The programmed inundation treatment simulates daily tidal dynamics by flooding the lower 10 cm of each plot during high tide treatment twice a day. Inundation treatments differ in the frequency of storm flood events, which replace the second daily high tide and inundate plots approximately 20 cm above the soil surface. In the ‘high’ inundation treatment, storm floods are applied daily, whereas in the ‘low’ inundation treatment they occur once every two weeks (Fig. 2). The species pool consists of ten typical low marsh species from North Sea coastal wetlands. From this species pool, monocultures of each species were established, alongside assembled two-species and five-species mixtures. This design allows for the assessment of plant diversity effects on carbon fluxes, while also disentangling the selection and complementarity effects associated with species-specific functional traits.

A. Methods:

- Methane fluxes were assessed using a Micro Portable Greenhouse Gas Analyzer (ABB GLA131) connected to a transparent chamber system.
- Plant aboveground biomass was harvested in December 2024 and dried at 60°C.
- Reduction index was assessed during vegetation period 2024 based on the "IRIS" method see Mittmann-Goetsch et al. 2024.

A. Study Design and Setup

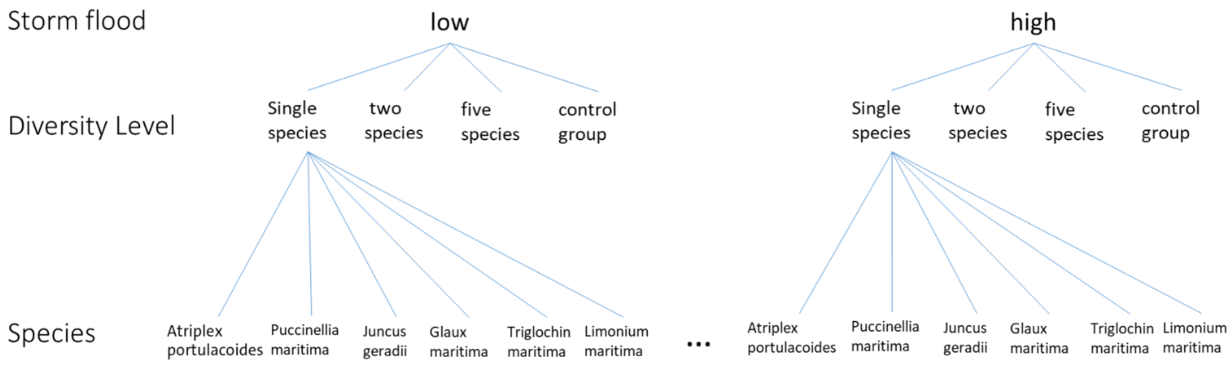


Figure 1: Full-factorial study design of the tidal basin experiment investigating responses and interaction effects of different diversity levels under two different inundation treatments. Five individuals were planted into each plot in different species composition depending on the diversity level.

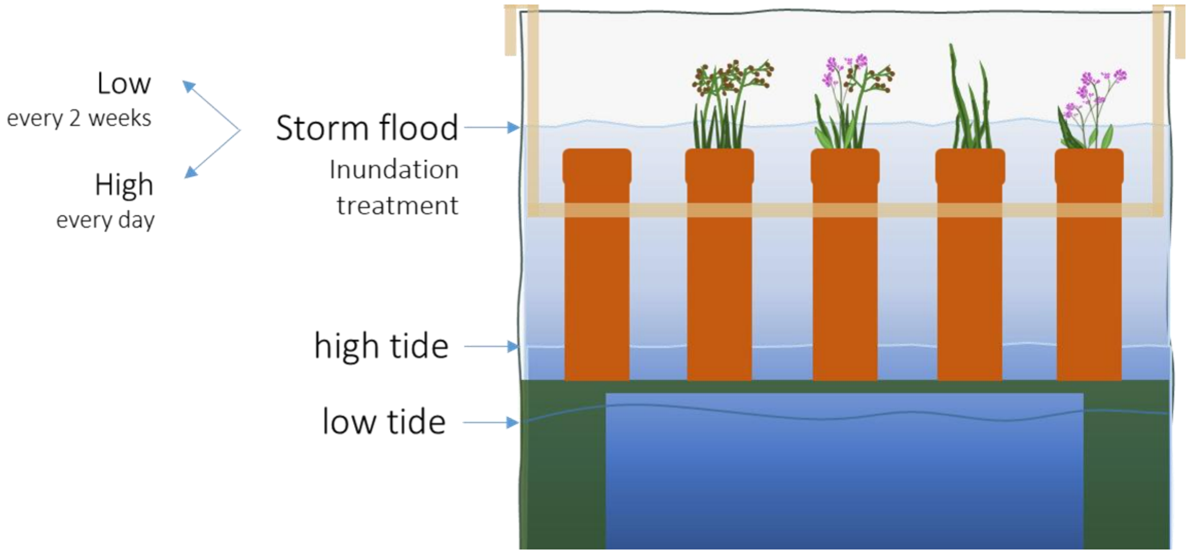


Figure 2: Schematic cross-section of the tidal basin setup representing one row of plots. One plot comprises a 50 cm long PVC pipe (orange) with a diameter of 15 cm filled with sediment from a tidal creek. The PVC pipes stand on a plastic construction (green) and are stabilized by wooden frames (beige). The lower 10 cm of each plot are inundated twice a day imitating high tide. Depending on the inundation treatment storm flood happens daily (inundation: high) or every two weeks (inundation: low) during the second high tide of a day.

A. Preliminary results and discussion:

- Complementary effect might offset methane emission from high-emitting species such as *Triglochin maritima*, that displayed increasing methane emission in monoculture but no change in methane emission could be detected when growing with four other species (Fig. 3).
- Plots with the highest diversity treatment had slightly higher aboveground biomass (Fig. 4 B) but no difference in reduction index was detected between diversity levels (Fig. 5 A).
- Inundation treatment did not affect overall aboveground biomass though there are species-specific differences in most species in response to inundation treatment (Fig. 4).
- Soil reduction index was slightly higher (more reduced) in “drier” inundation treatment (storm flood low).
- Plants had a net-oxidizing effect in the inundation treatment that had more reduced soils (storm flood low) but were highly net-reducing in the more oxidized soils (storm flood high; Fig. 5; in line with Mittmann-Goetsch et al. 2024).
- Soil reduction index significantly differed between species (Fig. 5).
- Reduction depth profile differed between plant species in the wetter treatment (storm flood high) likely reflecting different belowground strategies and functional traits between species. Namely, *Plantago maritima* and *Puccinellia maritima* did not follow the “typical” (increasing with depth) reduction depth profile and consistently reduced top- and deeper soil layers (Fig 6).

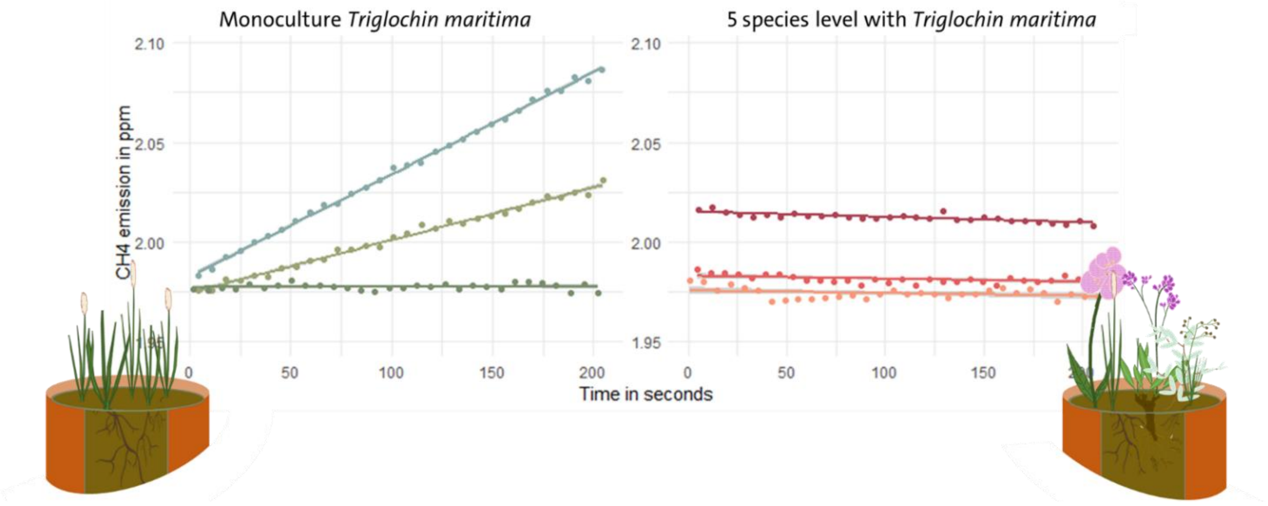


Figure 3: Preliminary methane (CH_4) measurements are presented as concentration slopes (ppm) over time. Each colored line represents three-minute measurement *from one individual plot* conducted with a transparent-chamber system connected to a Micro Portable Greenhouse Gas Analyzer. Measurements were carried out in April 2023 only in the “high” inundation treatment on two vegetation types: monocultures of *Triglochin maritima* (left) and mixed plots containing five species, including *Triglochin maritima* (right).

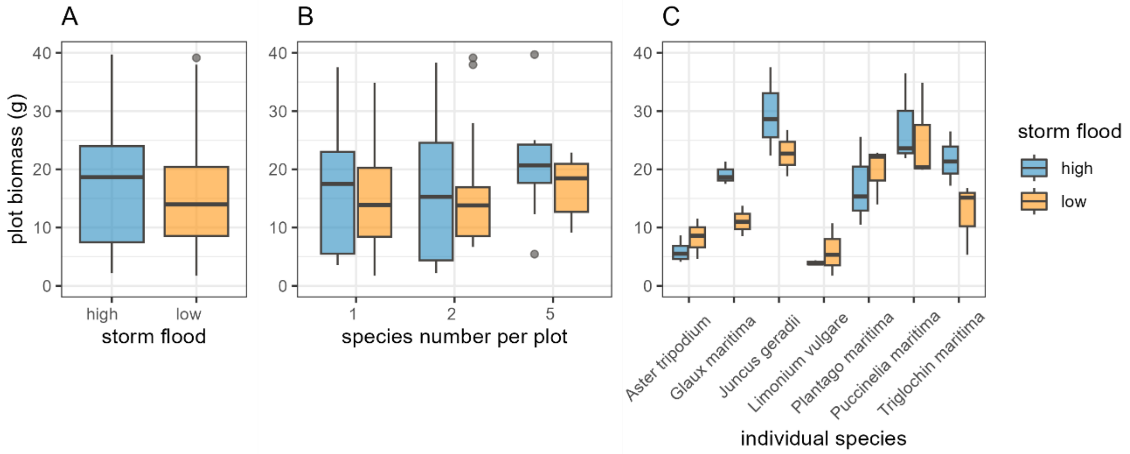


Figure 4: Plot-based aboveground biomass (dry weight in g). Aboveground biomass was harvested in December after the third vegetation period in 2024. Displayed are storm flood treatment (A); diversity level (B) and species-specific monocultures (C). Colours indicate storm flood treatment (blue: daily storm flood; orange: biweekly storm flood). *Atriplex portulacoides* not displayed as it is sensitive to cutting and was therefore not harvested. Boxplots display the median (centered line), 25-quatrile and 75- quartile.

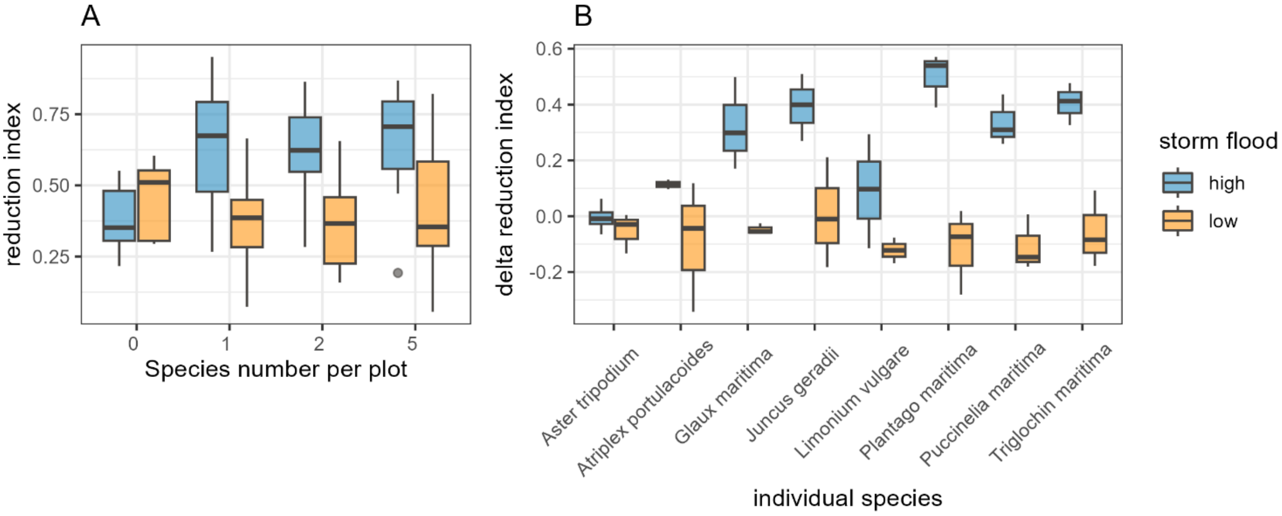


Figure 5: Reduction index (RI) based on IRIS stick method. Higher values indicate higher reduction of the soil. (A) RI displayed based on storm flood treatment and plot diversity level (0= control/ non-vegetated). (B) Species-specific (monoculture) RI as delta change vs. the non-vegetated controls. Lower values indicate net-oxidizing effects on background condition (control plots of respective inundation treatment); Higher values indicate net-reducing effects. Data based on one IRIS campaign (six-week incubation) during the third consecutive vegetation period in 2024. Colours indicate storm flood treatment (blue: daily storm flood; orange: biweekly storm flood). Boxplots display the median (centered line), 25-quatrile and 75- quartile.

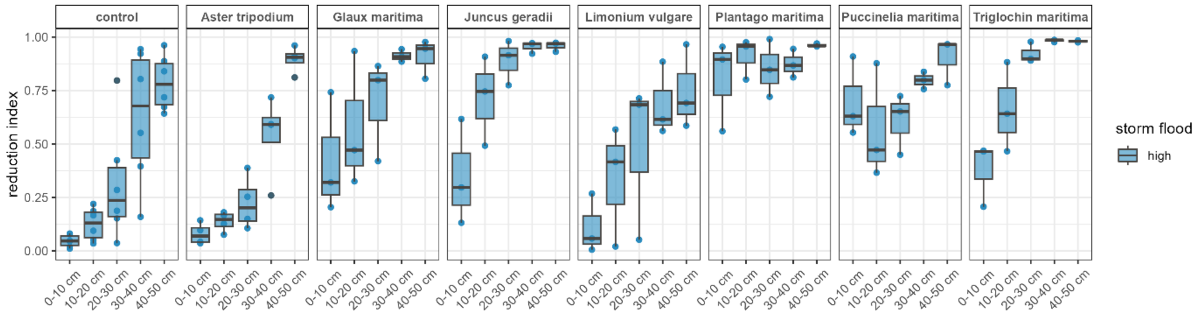


Figure 6: Reduction index of marsh organs with individual plant species (monoculture) and unplanted control group along the depth gradient (cm). Higher values indicate high reduction. Data based on one IRIS campaign (six-week incubation) during the third vegetation period in 2024 displaying only high storm flood treatment (daily storm flood). Boxplots display the median (centered line), 25-quatrile and 75- quartile.

CHAPTER
FOUR

PLANT-SOIL INTERACTIONS DETERMINE COASTAL WETLAND CARBON CYCLE RESPONSE TO RISING TEMPERATURES

In preparation

Ella Logemann, Peter Mueller, Gary Banta, Christoffer Boström, Johan Eklöf, Dorte Krause-Jensen, Marianna Lanari, Carmen Leiva-Dueñas, Malina Oelze, Cintia Quintana, Roy Rich, Simon Thomsen, Kai Jensen

4.1. Abstract

Wetlands are globally important carbon sinks, combining high plant productivity with water-saturated soils that slow down soil organic matter (SOM) decomposition. Yet, their carbon-climate feedbacks under global warming remain uncertain. Warming accelerates SOM decomposition, which can release nitrogen, potentially alleviating nitrogen limitation, and stimulating plant growth. Whether warming leads to net positive or negative climate-carbon feedback depends on warming effects on plant-soil interactions.

We tested warming effects on carbon dynamics in Baltic coastal wetlands using a mesocosm experiment with feedback-controlled and continuous warming up to +6 °C. Mesocosms contained intact vegetated coastal soil-sods from three Baltic countries (Denmark, Sweden, Finland) and two plant community types (tall-grass and short-grass). We predicted that warming would increase aboveground biomass by enhancing nitrogen supply, and decrease SOM through enhanced decomposition.

Overall, warming did not alter biomass or SOM significantly. However, in Danish short-grass communities, biomass rose by 52% (+4.5 °C) while SOM declined by 12% (+6.0 °C). Aboveground biomass strongly increased with the abundance of nitrogen-fixing plants; when excluding individual mesocoms with nitrogen-fixing plants, warming tended to enhance biomass across sites (except one). Aboveground biomass also rose with nitrogen availability (foliar $\delta^{15}N$), which itself responded significantly to warming in interaction with country or species. SOM losses were most pronounced in soils with high baseline SOM content, and biomass responses to warming srongly correlated with baseline SOM across sites.

Overall, the study highlights the complexity and relevance of plant-soil interactions in the context of climate-carbon feedbacks of wetlands. The results provide strong evidence that warming-induced ecosystem carbon responses depend on the ecosystems baseline resource status such as SOM and nutrient availability.

4.2. Introduction

Wetlands, including coastal welands, peatlands and mangroves, cover only 1-2 % of Earth's surface but store about 20% of the global organic carbon (Davidson 2018; Temmink et al. 2022). Their important role in the global organic carbon budget results from an imbalance between high rates of organic matter input through primary production and low rates of microbial decomposition of soil organic matter (SOM; (Duarte et al. 2005; Lovelock and Reef 2020; Temmink et al. 2022). Rates of SOM decomposition in wetlands are low compared to most upland environments, primarily due to waterlogged soil conditions with lower redox potentials (Neubauer and Megonigal 2021; Temmink et al. 2022). In coastal wetlands and other blue carbon ecosystems, plants not only support high rates of primary production, they also function as ecosystem engineers (Schwarz et al. 2018) by trapping sediments and external carbon sources (Needelman et al. 2018), resulting in higher rates of carbon sequestration in relation to most inland wetlands (Mcleod et al. 2011; Temmink et al. 2022). Despite their crucial role to store carbon as SOM, coastal wetlands face high rates of areal loss driven by multiple (human-made) global change factors, such as warming-induced accelerated rates of sea-level rise or increasing storminess (Duarte et al. 2005; Campbell et al. 2022).

Rising temperatures affect various interconnected ecosystem properties and processes through both direct and indirect pathways, ultimately altering plant-soil interactions. As biogeochemical reactions are temperature-dependent, it is expected that metabolic activities (such as carbon assimilation, nutrient uptake and cell growth) of plants and soil microbes typically increase with rising temperatures (Bassirirad 2000; Sage and Kubien 2007; Crous 2019). For instance, warming typically enhances microbial remineralization of SOM which in turn releases plant-available nitrogen into the soil (Hobbie et al. 2002; Dijkstra et al. 2010; Li et al. 2024b). Such increases in nitrogen availability often underlie the positive biomass responses to rising temperatures in various upland ecosystems, where water availability is not the primary limiting factor (Terrer et al. 2019; Liu et al. 2022c; Zhou et al. 2022). Further, meta-analyses on warming effects on biomass in terrestrial ecosystems revealed that warming-induced responses are weaker in nitrogen-rich systems or when nitrogen is experimentally supplemented indicating a negligible role of direct warming effects on plant biomass (Song et al. 2019; Liu et al. 2022c; Zhou et al. 2022). In wetland ecosystems, however, our understanding of the extent to which such plant-soil feedbacks mediate warming responses is limited (Noyce et al. 2019). As nitrogen is often the primary growth-limiting nutrient for plants in coastal wetlands (Kiehl et al. 1997; Delaune et al. 2005; Herbert et al. 2020), a key-role of nitrogen availability on warming responses of biomass can be expected also in these ecosystems. Notably, Noyce et al. (2019) found in coastal wetlands that plant biomass responses to warming were strongly linked to porewater nitrogen availability, suggesting that particularly microbial nitrogen remineralization is a key driver of biomass responses in these environments.

Plant and SOM responses to warming are likely coupled because SOM creates conditions that stimulate plant productivity by stabilizing water availability and increasing nutrient availability as inorganic nutrients are released during SOM decomposition (Schimel and Weintraub 2003; Li et al. 2019; Liu et al. 2022c). Warming may also accelerate microbial SOM decomposition, which enhances microbial nitrogen mineralization, potentially alleviating nutrient limitations and enabling positive plant biomass responses (Melillo et al. 2002a; Liu et al. 2022b; Liu et al. 2022c). In turn, SOM accumulation is largely driven by plant inputs, such as litter and root exudates, highlighting the feedback between plant growth and SOM dynamics (Kirwan and Megonigal 2013; Morris et al. 2016). Depending on the balance of warming-induced changes in plant primary production and microbial SOM decomposition, warming can therefore shift the carbon balance towards a positive or negative ecosystem-climate feedback (Davidson and Janssens 2006; Kirwan and Mudd 2012; van Gestel et al. 2018; Smith et al. 2022).

Experimental data allowing us to predict net changes in ecosystem carbon stocks in response to global warming are scarce, and the few results available for wetlands are equivocal. Previous warming studies in wetlands provide evidence for both enhanced decomposition as carbon output (Charles and Dukes 2009; Hanson et al. 2020) and primary productivity as carbon input (Charles and Dukes 2009; Baldwin et al. 2014; Noyce et al. 2019), which may result in stable SOM pools (Wilson et al. 2016). Studies that reported increased carbon output through accelerated litter decomposition (Charles and Dukes 2009; Kirwan and Blum 2011) and reduced to negative surface elevation change (Hanson et al. 2020; Smith et al. 2022) suggest that carbon release may offset carbon input. However, changes in SOM were not quantified in these studies. Only recently, Sun et al. (2025) provided first evidence for net SOM loss from wetlands with warming. Given that changes in SOM have crucial implications for both wetland function as carbon sinks and determining coastal wetland stability against accelerating sea-level rise (Kirwan et al. 2016; Spivak et al. 2019; Temmink et al. 2022), it is crucial to better understand SOM dynamics under climate change.

Recent climate projections suggest that warming will likely exceed 1.5°C above pre-industrial levels in 2030 and projections for 2100 range from +1.4°C to +4.4°C (Lee et al. 2023). Meanwhile, few experiments have tested the effects of excessive warming on plant and soil processes in wetlands (Noyce et al. 2019; Rich et al. 2023b). As a result, most of our understanding comes from open-top chamber studies that typically apply a single level of warming (e.g. Carey et al. 2018; reaching average warming effect of 1.1-1.6 °C). Because such studies rarely achieve high levels of warming, they may overlook potential nonlinear responses (Noyce et al. 2019). Consequently, we lack experimental data on how wetland ecosystems respond to more extreme warming scenarios, limiting our ability to predict the full range of climate change impacts.

The Baltic Sea is a unique brackish water body characterized by several environmental gradients (e.g. salinity, climate, tides, rate of isostatic land-uplift). As an outcome, a large variety of coastal wetlands with distinct plant communities and soil types occurs along the shorelines of the Baltic Sea (Dijkema 1990; Vehmaa et al. 2024). These wetlands have undergone centuries of different management practices that have significantly altered vegetation composition and structure resulting in tall-grass and short-grass communities differing in plant diversity and soil morphology (Dijkema 1990; Jutila 2001; Vehmaa et al. 2024). This mosaic of environmental and historical variation makes Baltic coastal wetlands an excellent model system for exploring if ecosystem carbon balances in response to warming are generalizable across differently structured plant communities and distinct soil morphologies.

The aim of this study was to examine ecosystem carbon responses under four warming scenarios, assess potential differences across distinct coastal wetland plant communities and soil morphologies, and investigate how plant-soil feedbacks may mediate these responses. We hypothesize that i) warming indirectly increases aboveground biomass via increased nitrogen availability and ii) warming results in a net loss of SOM, because warming-induced SOM decomposition through stimulated soil microbial activity will not be compensated by increased organic matter input through accelerated primary production. Furthermore, we explore which site-specific factors, such as plant community composition and soil characteristics, may lead to distinct aboveground biomass responses to warming across different ecosystem origins. To do so, we actively warmed soil-sods in 1.5°C intervals from Baltic coastal wetlands with heterogenic soil morphologies from three Baltic countries (Denmark, Sweden, and Finland) and two different wetland plant communities types (short-grass and tall-grass).

4.3. Material and Methods

4.3.1. Baltic Sea as the model system and study sites characteristics

The Baltic Sea is characterized by climate, salinity and tidal gradients that determine soil morphology and plant community composition of its coastal wetlands (Dijkema 1990; Pätsch et al. 2019). Along these gradients, we sampled intact soil-sods from short-grass and tall-grass communities at three study sites in Denmark, Sweden, and Finland. Livestock-grazing of coastal wetlands is a common management practice in the Baltic region and promotes the growth of small-stature vegetation (hence short-grass community) and the establishment of halophytes (Dijkema 1990; Jutila 1997; Jutila 2001). In the absence of livestock-grazing, the mostly oligohaline water conditions favor tall-grass communities dominated by species as e.g. *Phragmites australis* (Dijkema 1990; Jutila 2001). Livestock-grazing can change the soil characteristics due to trampling induced compaction, mostly altering oxygen availability (Elschot et al. 2013; Keshta et al. 2020). Grain size distribution did not significantly differ between grazed (short-grass) and non-grazed (tall-grass) study sites (Leiva-Duenas et al. submitted; Fig. S. 1).

The three study sites span a range of climatic regions, from temperate and Atlantic climates in Denmark (North of Ajstrup Bugt, "Als" – short-grass community: 56°45'00.9"N 10°18'03.8"E – tall-grass community: 56°44'46"N 10°18'14.9"E) to boreal and sub-continental climates in Sweden (South of Stockholm – short-grass community: 58°59'27.6"N 17°37'14.9"E – tall-grass community: 58°59'12.7"N 17°36'58.4"E), and Finland (South of Turku – short-grass community: 60°14'26.6"N 22°12'54.7"E – tall-grass community: 60°14'34.5"N 22°11'50.8"E). Swedish and Finnish sites are non-tidal coastal wetlands and inundation is here mainly caused by wind-driven storm floods. Along the Danish coast the tidal amplitude mostly ranges between 10 to 30 cm (Weisse et al. 2021). The ambient seawater salinity at the Danish, Swedish and Finnish sites was 16-18, 5-6 and 4-5, respectively, based on on-site measurements in soil-sod pits (accumulated water in pits after excavating soil sods was used for assessing salinity with a refractometer). Soil morphology differed in terms of grain size distribution and SOM content (Fig. S. 1; mineral data taken *in situ*; adapted to top 30 cm from Leiva-Duenas et al. submitted) with the highest clay and lowest SOM content in Finnish sites, followed by Swedish sites and lowest clay and highest SOM content in Danish sites.

4.3.2. Plant community in transplanted soil-sods

Tall-gras communities differed in species composition between countries and were clearly distinguishable from short-gras plant communities (Fig. S. 2). In Danish tall-gras communities, *Phragmites australis* and *Elymus repens* were found in similar abundance (mean cover: 39% and 49% respectively). In Swedish tall-gras communities *Phragmites australis* was the most abundant species (32 %) followed by *Agrostis stolonifera* (19 %) and *Betula pubescens* (17 %) (Fig. S. 2 & 3). In Finnish tall-grass communities *Potentilla anserina* (62 %) and *Agrostis stolonifera* (20 %) were most prevalent (Fig. S. 2). Short-gras communities were more similar in community composition between countries though still distinct (Fig. S. 3). Short-gras communities primarily included *Plantago maritima, Juncus gerardii, Festuca rubra*, and *Glaux maritima* as the most common species across all countries (Fig. S. 2).

4.3.3. Experimental system overview

The warming experiment was carried out in the Climate Change Marsh Mesocosm Facility (CCMMF; Pic. S. 1) at the Institute of Plant Science and Microbiology of University of Hamburg (53°33´39.0"N 9°51´31.5"E; Pic. S. 1) and consisted of a total of 90 mesocosms with transplanted soil-sods. The soil-sods were experimentally warmed with above- and belowground feedback-controlled systems in 1.5 °C intervals up to +6°C above ambient conditions over two consecutive vegetation periods. Belowground warming was achieved by heating pins placed in the soil and aboveground warming using infrared radiation heaters (Fig. 1 A). A detailed description of the technical implementation of the CCMMF, temperature control, data processing and achieved warming is provided in the Supporting Information (Text S. 2 & 3; Fig. S. 3).

4.3.4.Setup of mesocosm experiment

Intact soil-sods consisting of soils and vegetation were obtained from both short-grass and tall-grass communities from each of the three study sites (Denmark, Sweden, Finland). Soil-sods were collected from the low marsh zone, with *Juncus gerardii* serving as identifier plant in short-grass community. In tall-grass community sampling sites, distance to the marsh edge and depth of the water table was used to identify the low marsh zone. The sampling campaigns took place in October and November 2021. Soil-sods were sampled using a custom-built square sediment corer (20 x 20 x 35 cm), which was pushed into the ground to cut square sods to 35 cm soil depth (Pic. S. 2). For each experimental unit, six soil-sods were sampled, cut to a length of 30 cm and directly transferred to a single plastic container (H: 32 cm; L: 60 cm; W: 40 cm). These containers served as our experimental units, in the following referred to as mesocosms. The base of each mesocosm was perforated with 12 holes (diameter 2 cm) to later allow hydrological exchange during the experiment and was lined with plant fleece to prevent the plants from rooting out from underneath.

The 90 mesocosms were transported from their sampling locations to Hamburg and kept outside until they were placed into the 6 m by 12 m water basin of the CCMMF in January 2022. The salinity of the water was kept at approximately 6, which corresponds to the average low-salinity / brackish water of the inner Baltic (Stockmayer and Lehmann 2023). The water table was kept at a constant level, with only minor fluctuations after periods of severe precipitation or drought. Approximately, the lower 10 cm of soil within the mesocosms was permanently inundated, leaving 20 cm of soil above the water table. This corresponds to the relative position to average sea level at the sites, where the soil-sods were procured. To simulate grazing effects, aboveground biomass in short-grass communities was clipped 2-3 cm above surface once per year during the vegetation period (19.07.2022; 19.06.2023).

One mesocosm of each site (country x plant community) was placed together as an individual experimental plot (therefore each plot contains six mesocosm). Each plot was separated into two rows (subplots) distinct by plant community type (tall-grass and short-grass). The mesocosms in each individual plot were subjected to one of six temperature treatments: ambient, and +1.5 °C, +3.0 °C, +4.5 °C or +6.0 °C above the ambient temperature. The five plots with six mesocosms each were arranged in three blocks (total of 90 mesocosm). The plot-based temperature treatments were randomly distributed within each block. One plot in each block served as a control without any warming (“ambient”; Fig. 1 B). Warming commenced on June 10, 2022, and concluded on November 6, 2023, thereby spanning two consecutive vegetation periods. Due to safety measures, aboveground warming was turned off while working in the experiment. In winter 2022/2023, aboveground warming was deactivated from beginning of December 2022 to end of March 2023 due to energy saving measures in the wake of the German energy crisis.

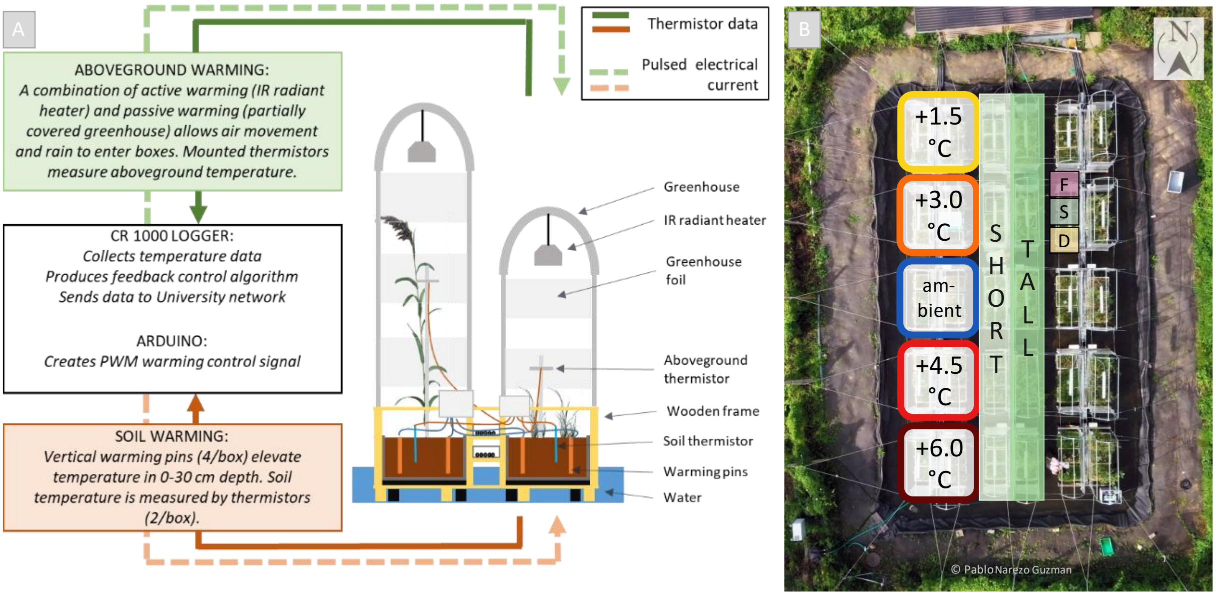


Figure 1: Experimental setup of the mesocosm warming experiment. **A** Schematic diagram of the feedback control system of one experimental unit. Each plot consisted of a tall and a short greenhouse for the tall-grass and the short-grass communities, of which each subplot housed three mesocosms (one per country). Solid lines visualize the data flow of measured aboveground and soil temperatures; dotted lines show the pulsed electrical current of the active warming system. **B** Aerial view of the facility showing the three independently controlled blocks (vertical direction). In addition to the control (= ambient), each block contains four temperature treatments (+1.5 °C, +3.0 °C, +4.5 °C, +6.0 °C), two plant community types (short-grass, tall-grass) and three countries (S=Sweden, D= Denmark, F= Finland). The temperature treatments were randomly distributed within each block. Detailed information about the technical set-up of the CCMMF can be found in the Supporting Information (Text S. 2).

4.3.5. Vegetation and soil analyses

Vegetation was assessed during peak-season in the second year (Aug 2023) and involved evaluating cover and plant species composition, as well as the percentage of bare soil. Plant species that associate with nitrogen-fixing bacteria (hereafter “nitrogen-fixing plants”), including *Vicia cracca*, *Alnus glutinosa* and various species from the genus *Trifolium,* were grouped separately as “nitrogen-fixing plants” for further analysis. Species diversity was quantified using the Simpson and Shannon indices, and evenness was expressed as Pielou’s J (Simpson diversity divided by the logarithm of species richness). To quantify aboveground biomass, the entire aboveground biomass of each mesocosm was cut at the soil surface during end-of-season of the second year (final deconstruction of the experiment in Nov 2023). Aboveground biomass for the short-grass community was calculated from the sum of the peak-season harvest (see above) and the end-of-season harvest. Plant biomass was dried at 60°C for a minimum of five days before weighing.

In addition to total aboveground biomass quantification, leaves of one to three individuals per mesocosm of the common and consistently present plant species *Phragmites australis* (tall-grass community; sampled end-of-season) and *Plantago maritima* (short-grass community; sampled during peak season) were sampled for stable isotope analysis (nu Horizon, Nu Instruments Limited, UK). Per mesocosm, one mean stable isotope value was used for further analysis. No individuals of *Phragmites australis* were present in three Finnish tall-grass community mesocosms (one in ambient, one in "+1.5°C" and one in "+4.5°C) and therefore stable isotope data is missing here. No individual of *Plantago maritima* was present in one Danish short-grass community ("+6.0°C"). Foliar δ^{15}N signatures serve as proxies for nitrogen availability, as foliar δ^{15}N scales positively with nitrogen availability relative to plant nitrogen demand across natural ecosystems (Craine et al. 2009; Craine et al. 2018).

To quantify belowground biomass, 2.5-cm diameter soil cores were collected from each mesocosm end-of-season in Nov 2023, using a gouge auger. Belowground biomass was washed free of soil using a 1-mm mesh sieve, collected with tweezers, dried at 60°C for five days, and weighed. Core lengths varied between 7 cm and 35 cm (with 8/90 cores being shorter than 20 cm) due to variability in soil depth between mesocosms and core loss during sampling, therefore the root biomass was corrected based on root distribution derived from site specific field data (correction see text S. 3). The belowground biomass was then scaled to grams dry weight per square meter (g/m^2) for the top 30 cm.

For soil analysis, two soil cores were collected from each mesocosm end-of-season in Nov 2023 and each core was sliced into the following depth intervals: 0-5, 5-10, 10-20, and 20-30 cm. Soil samples were weighed before and after air drying at 60°C for at least five days. Dry soil bulk density was calculated based on sample dry weight and volume while gravimetric water content was determined from the ratio of fresh weight to dry weight. SOM contents (% of dry weight) were determined via loss on ignition (LOI; 550°C for 2 hours). Carbon and nitrogen contents (% of dry weight) were determined using a dry combustion elemental analyzer ("vario MAX cube"; Elementar Analysensysteme GmbH, Langenselbold, Germany) and used to calculate C:N ratios. Prior to LOI and elemental analysis, the samples were manually milled, and macroscopic root residues ~5 mm were removed using tweezers. Soil samples were acidified on test-basis (50/360 samples) on randomly chosen samples. As no effervescence was revealed, no acidification was applied prior to elemental analysis. Eight out of 360 samples had too little sample material for both analyses and were used up for loss on ignition. The eight missing values of carbon and nitrogen content were estimated based on established relationships with SOM content derived from LOI.

4.3.6.Statistical analysis

As a first step, we performed a three-way ANOVA to test the main effects and interactions of country, plant community type, and warming level on aboveground biomass, belowground biomass, foliar δ^{15}N, and soil organic matter (SOM) content (0–30 cm depth). The significance level was set to the default value of $\alpha = 0.05$.

While ANOVA allowed us to test for overall treatment effects, it was not sufficient to capture the complexity of site-specific aboveground biomass responses. Therefore, we additionally applied generalized linear models (GLMs) to better explain mesocosm-level variation in aboveground biomass and to explore which factors, beyond the experimental treatments, accounted for this variation.

In this approach, warming treatment was tested by using the real temperature data from each mesocosm (soil sensors; see text S. 2). Temperature mean values were calculated based on temperatures measured between 01.05.2023 and 01.10.2023 (representing vegetation period). Using continuous temperature data in the GLM and following regression analysis allowed for a more detailed analysis of the relationship between warming intensity and ecological responses, better reflecting the actual temperature gradient experienced in the experiment. To identify the best-fitting GLM, we tested a range of explanatory variables, including the manipulated factors country, plant community type, and warming (real temperature) as fixed effects. To refine the model, we first assessed multicollinearity using Variance Inflation Factors (VIFs) and then applied the Akaike Information Criterion (AIC) for model selection. The final model included the fixed factors (country, plant community type, warming) along with foliar $\delta^{15}N$, the cover of nitrogen-fixing plants, the Simpson diversity index, and the soil C:N ratio, based on model selection criteria (Table S. 1). The final model explained 79.8% of the variance in aboveground biomass (pseudo-R^2), suggesting a strong predictive fit based on both experimental treatments and ecosystem properties.

Given that experimental origin (i.e. individual sites or the combination of country and plant community type) is associated with distinct ecological characteristics such as differences in soil morphology and plant community composition, we explored site-specific responses of aboveground biomass and SOM to warming in a second analytical step. For each site (country × plant community combination), we applied linear regressions to assess warming (real temperature) effects on SOM content and soil C:N ratio. In the case of aboveground biomass, we used both linear and second-degree polynomial regression models to test for potential nonlinear effects of warming. Polynomial and linear models were compared using R^2 values and the Akaike Information Criterion (AIC). Across most sites, model comparison showed no meaningful difference ($\Delta AIC < 2$) between linear and quadratic fits for aboveground biomass, with the exception of the Danish short-grass communities, where the polynomial model provided a better fit.

Following the GLM, which revealed a significant increase in aboveground biomass associated with the presence of nitrogen-fixing plants, we further examined their influence on warming-induced total plant community biomass both above- and belowground. To isolate potential nitrogen-mediated warming effects on plant biomass, we treated the presence of nitrogen-fixing plants as confounding factor for exploring potential indirect warming responses on plant biomass. We therefore ran a second regression model, excluding mesocosms with more than 5% cover of nitrogen-fixing plants. This approach was intended to better capture biomass responses to warming driven by increased soil nitrogen availability rather than by the presence of nitrogen fixing plants (biological nitrogen fixation).

In a final step, we explored the drivers underlying the differing aboveground biomass responses to warming across sites (country x plant community). The factors country and plant community type serve primarily as proxies for ecological variation and are not themselves explanatory. To test whether plant responses to warming were related to ecological differences among sites, we examined the relationship between the maximum slope of aboveground biomass change with warming and baseline site (resource) conditions (Table S. 2). The slope of aboveground biomass response was calculated from the maximum increase of the regression line that excluded mesocosms with more than 5% cover of nitrogen-fixing plants. Tested baseline (resource) variables included SOM content (%), soil nitrogen content (%), gravimetric water content (%), soil C:N ratio, Shannon index, Evenness, aboveground biomass (g/m²) and belowground biomass (g/m²), all calculated as mean values from ambient sites (Table. S. 2).

Data have been processed using Rstudio (R Version R 4.2.2).

4.4. Results

Table 1: F and p-values of the main and interaction effects of Country, Plant community and Warming tested with a three-way ANOVA on aboveground biomass (AGB; g/m²), belowground biomass (BGB; g/m²), the root:shoot ratio, soil organic matter (SOM; %), and foliar $\delta^{15}N$ (‰). For foliar $\delta^{15}N$ analysis, different plant species were used depending on the plant community type: *Plantago maritima* in short-grass communities and *Phragmites australis* in tall-grass communities. ns = non-significant.

	AGB		BGB		root:shoot		SOM		$\delta^{15}N$	
	F	p	F	p	F	p	F	p	F	p
Country (C)	124.7	<0.001	13.9	<0.001	9.1	<0.001	259.5	<0.001	192.5	<0.001
Plant community (PC)	0.05	ns	0.7	ns	1.6	ns	1.5	ns	238.6	<0.001
Warming (W)	0.3	ns	0.6	ns	0.1	ns	0.7	ns	1.1	ns
C × PC	32.3	<0.001	2.5	<0.1	5.7	<0.01	68.8	<0.001	38.7	<0.001
C × W	1.2	ns	0.5	ns	0.6	ns	1.4	ns	3.7	<0.005
PC × W	1.2	ns	1.2	ns	0.7	ns	0.9	ns	2.6	<0.05
C × PC × W	0.9	ns	1.9	<0.1	0.7	ns	1.4	ns	1.3	ns

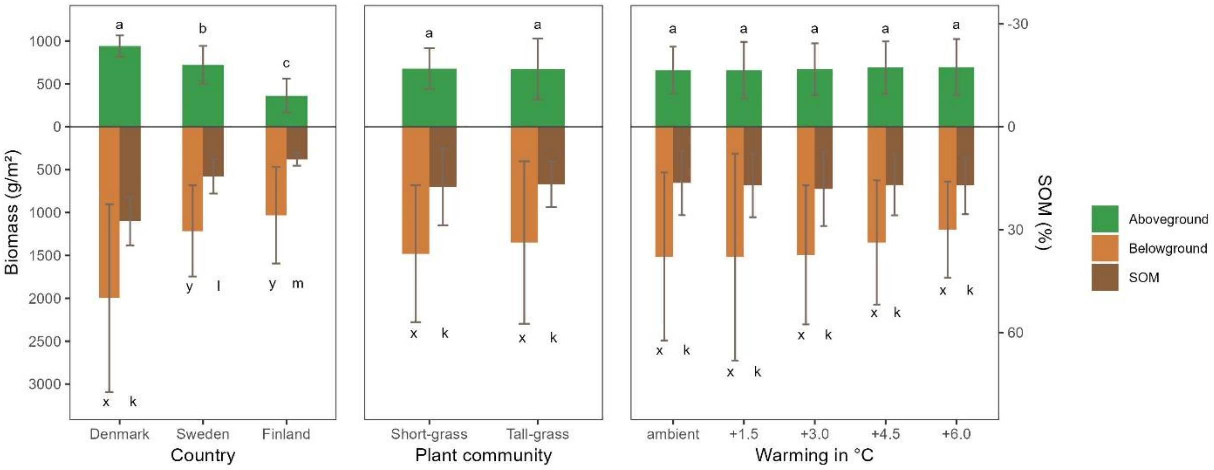


Figure 2: Soil organic matter (SOM) content (%, 0-30 cm) and aboveground and belowground plant biomass (g/m²) by country, plant community type and warming treatment. Different letters indicate significant differences ($p < 0.05$) based on Tukey's HSD test. a-c for aboveground biomass; k-m for SOM; x-y for belowground biomass.

4.4.1. Plant biomass response

Biomass differed significantly between countries (Fig. 2; Table 1), with the highest biomass in Danish mesocosms (above: 941.1±124.7 g/m²; below: 1997.8±1094.6; mean ± SD), and lowest in Finnish mesocosms (above: 363.1±198.6 g/m²; below: 1031.6±562 g/m²).

Plant community types did not consistently differ in biomass (Fig. 2), but aboveground biomass was significantly affected by the interaction between plant community type and country (Table 1). In Finnish short-grass communities, aboveground biomass was higher than in tall-grass communities, in short-grass communities from Sweden it was lower and in Demark aboveground biomass did not differ between plant community types.

Warming did not significantly affect above- or belowground biomass (Table 1), although belowground biomass decreased slightly with severe warming (+4.5 and +6.0 °C; Fig. 2) and warming was found to be marginally non-significant ($p<0.1$) in interaction with country and plant community type (Table 1).

GLM revealed that aboveground biomass was altered by country, plant community type, and significantly increased with warming (real temperature), the presence of nitrogen-fixing plants, diversity (Simpson index) while it significantly decreased with soil C:N ratio (Fig. S. 5, Table S. 1).

At most sites, the effect of warming on aboveground biomass tested individually for each site (country x plant community), was not significant except for Danish short-grass communities ($R^2=0.47$; $p=0.023$; Fig. 3 A). In this site, warming increased aboveground biomass by 39 % on average, peaking in the +4.5 °C warming treatment with an additional 52 % aboveground biomass. Meanwhile, in this site the belowground biomass response was inverted to the aboveground biomass response with the lowest biomass in the +3.0°C warming treatment (Fig. S. 6).

The proportion of explained variation of the temperature effect on total aboveground and belowground biomass increased when mesocosms with more than 5% cover of nitrogen-fixing plants were excluded (higher R², Fig. 3 A, Fig. S.6 compare grey to blue regression), although regressions remained non-significant. The exclusion of nitrogen-fixing plants increased the explanatory power of the regression for aboveground biomass responses to warming for all sites except for Finnish short-grass communities (Fig. 3 A). The explanatory power for belowground biomass was increased for all sites (except for Danish short-grass communities where there was no to little cover of nitrogen-fixing plants therefore the model was unaffected; Fig. S. 6).

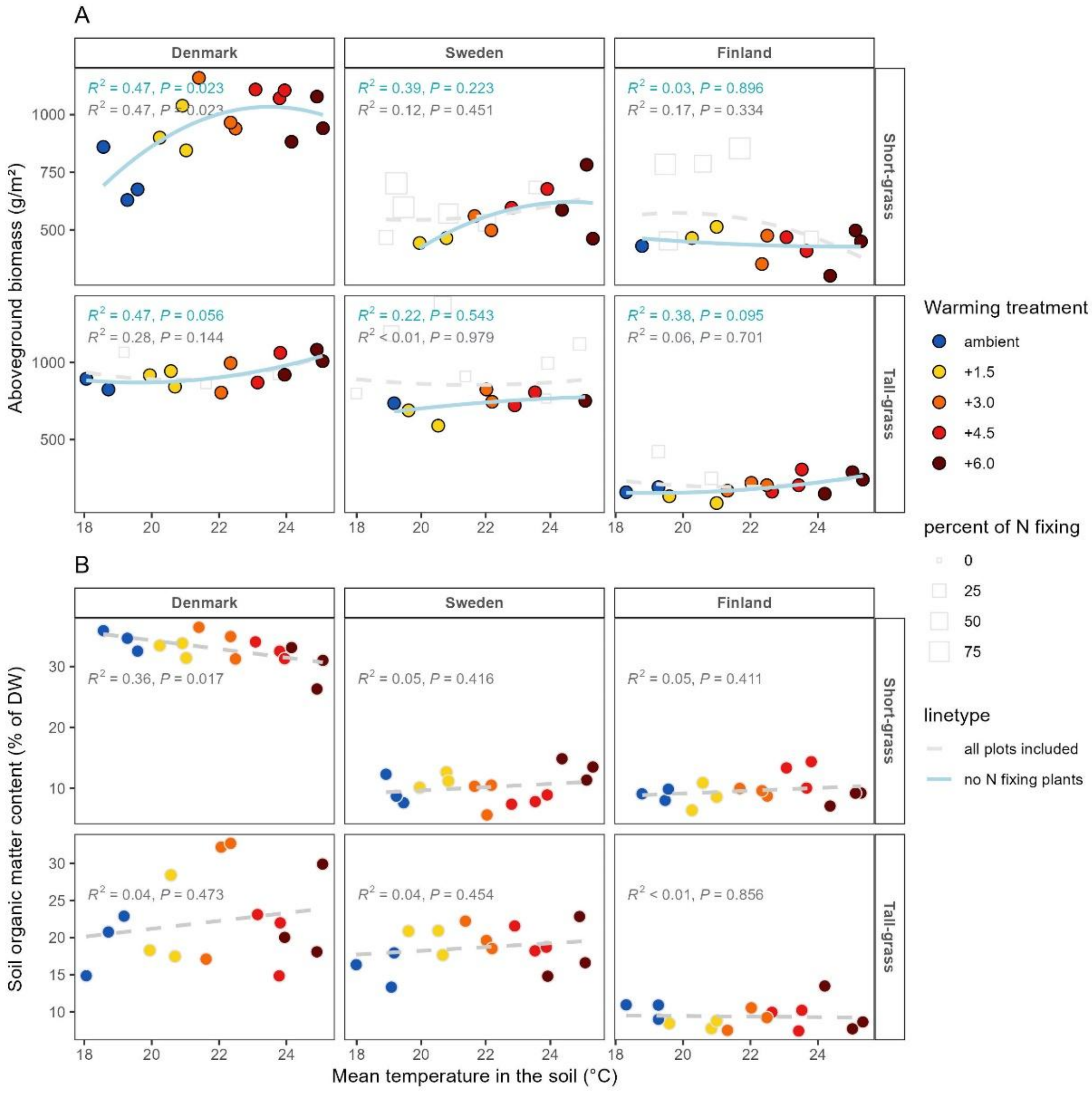


Figure 3: **A** Aboveground biomass, **B** soil organic matter in response to warming (mean temperature between 01.05.-01.10.2023). Regression based on all mesocosms (grey dashed line; including grey squares) and on mesocosms with less than 5 % cover of nitrogen-fixing plants (blue solid line; excluding grey squares).

Based on the (non-significant) regression trends from the model excluding mesocosms with nitrogen-fixing species, aboveground biomass in the Swedish mesocosms increased slightly and consistently across all levels of the warming treatment. In the Danish and Finnish tall-grass communities, aboveground biomass did not change under lower levels of warming but slightly increased under stronger warming treatments. In the Finnish short-grass communities, aboveground biomass did not increase with warming; instead, aboveground biomass marginally declined with higher temperatures (Fig. 3 A).

4.4.2. Foliar δ^{15}N signature

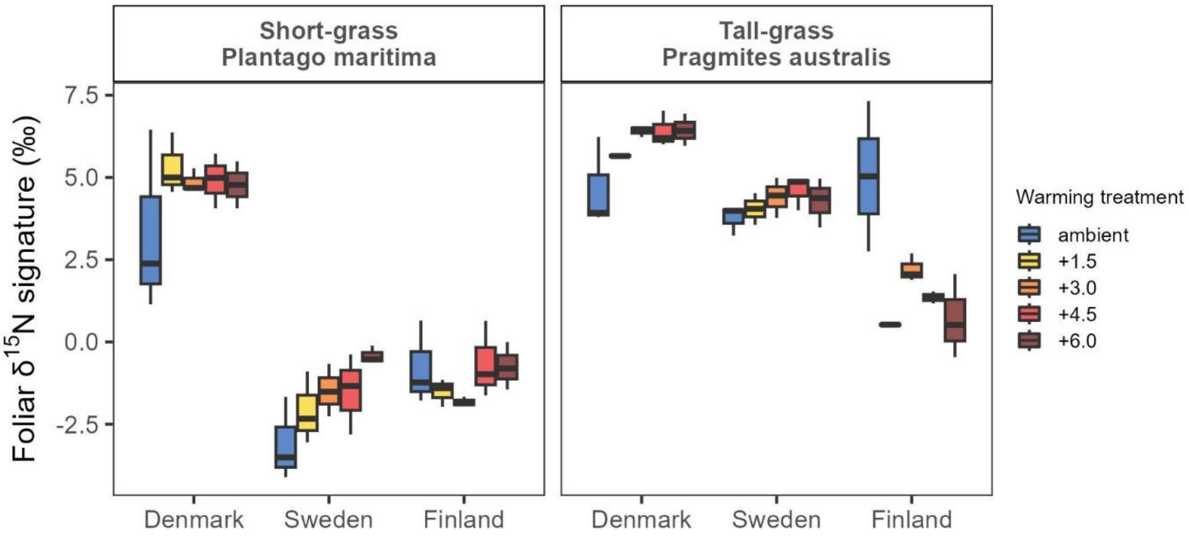


Figure 4: Foliar δ^{15}N signature (‰) per site and across warming (indicated by colours). Leaves of Plantago maritima were measured from short-grass communities and leaves of Phragmites australis were measured from tall-grass communities. The mean of mesocosm was used as 1-3 three individuals were sampled per mesocosms. Boxplots display the median (centered line), 25-quatrile and 75-quartile. Note: due to low occurrence of Phragmites australis in Finnish tall-grass communities and Plantago maritima in Danish short-grass communities a total of four data points are missing leading to fewer replicates than three (see methods).

Based on the three-way ANOVA, foliar δ^{15}N differed significantly between the plant species from mesocosms representing tall-grass (*Phragmites australis*) and short-grass *(Plantago maritima)* communities (Table 1). δ^{15}N signature was highest in Denmark for both species. *Phragmites australis* had higher foliar δ^{15}N values than *Plantago maritima*. Foliar δ^{15}N also significantly differed between countries. Warming had a significant effect on foliar δ^{15}N in two-way interactions with both country and plant community type. Warming shifted the foliar δ^{15}N signature towards more positive values in Danish and Swedish mesocosm (Fig. 4). No clear shift in δ^{15}N was observed with warming in Finnish short-grass communities and a decline occurred in Finnish tall-grass communities (Fig. 4).

Soil organic matter response

SOM content differed significantly between countries with the highest SOM content (including all warming treatments) in Denmark (27.5±7.1%), followed by Sweden (14.4±5.0%), and Finland

(9.5±1.9%; Table 1, Fig. 2). There was no significant difference in SOM between plant community types but the interaction between country and plant community type significantly affected SOM (Table 1). In Danish mesocosms, SOM content was higher in short-grass compared to tall-grass communities. By contrast, in Swedish mesocosms SOM content was lower in short-grass communities, while no significant difference was recorded between plant community types in Finland (Fig. 3 B).

SOM was not significantly affected by warming, neither as main factor nor in interaction with plant community type or country (Table 1, Fig. 3 B). Danish short-grass communities had the highest SOM content, and these were the only communities showing a significant negative regression between temperature and SOM (R^2=0.36; p=0.017; Fig. 3 B) and between temperature and soil C:N ratio (R^2=0.37; p=0.017; Fig. S. 7).

4.4.3. SOM and plant biomass response to warming

The linear regression between baseline SOM content and aboveground biomass response to warming was marginally non-significant (p=0.070) but explained 60% of the variation in aboveground biomass responses across sites (R^2=0.6; Fig. 5 A; Table S. 3). Baseline soil nitrogen content also non-significantly correlated with aboveground biomass responses to warming (R^2=0.39; p=0.182; Table S. 3) but was strongly linked with SOM (Fig. 5 B). Other tested variables had weaker relationship with the warming-induced aboveground biomass response (R^2< 0.6; p>0.1; Table S. 3).

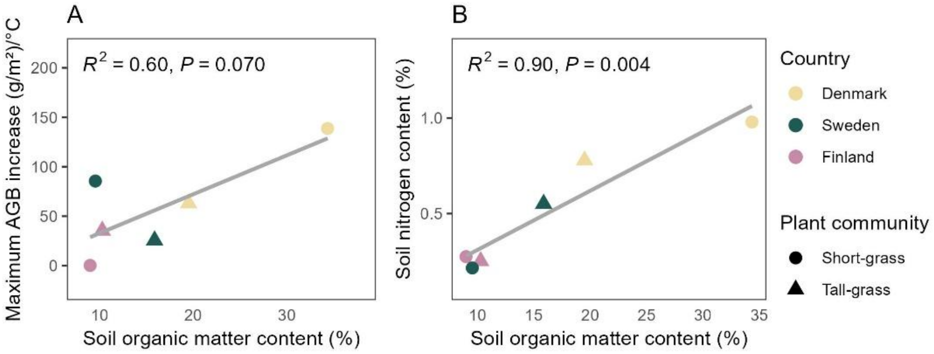


Figure 5: Linear regression between maximum slope of aboveground biomass response ((g/m²)/°C) and SOM content of each site. SOM content based on mean of ambient SOM content (%) representing the "initial" conditions of each site **(A)**. Linear regression between SOM and soil nitrogen content (%). Mean site values calculated based on ambient mesocosms only **(B)**. Colour indicates country; shape indicates plant community type.

4.5. Discussion

4.5.1. Warming-induced aboveground biomass responses are obscured by the presence of nitrogen-fixing plants

We found no clear support for our initial hypothesis that aboveground biomass would increase with warming. Instead, we observed significant variation in biomass between sites, highlighting the importance of site-specific analyses. Site-specific regressions revealed that warming-induced biomass responses were nonlinear and varied between sites, with significant increases in aboveground biomass and decreases in belowground biomass at short-grass Danish communities while above- and belowground biomass at Swedish and Finnish communities responded equivocal. However, we found that the presence of nitrogen-fixing plants significantly increased overall aboveground biomass (see Table S.1; Fig. S. 5 A), hence corroborating that nitrogen-fixing plants can enhance ecosystem biomass (Ortiz and Wolf 2024).

Particularly, in Swedish tall-grass communities, we found an overall "neutral" aboveground biomass response to warming (Fig. 3 A, grey regression) and higher aboveground biomass with increasing nitrogen-fixing plant cover, but also shifts between different functional groups in response to warming (Fig. S. 9). Specifically, warming decreased the cover of nitrogen-fixing *Alnus glutinosa*, while the cover of *Phragmites australi*s increased. *Phragmites australis* is known for its broad nitrogen acquisition strategy (Cott et al. 2018) and potentially experiences a higher benefit from warming-induced increases in nitrogen availability (Bedford et al. 1999; Langley and Megonigal 2010). Simultaneously, the enhanced productivity of the "favored" species may diminish the competitive advantage of nitrogen-fixing plants as e.g. *Alnus glutinosa* (Fig. S. 9 B), which subsequently lose their ecological benefit with (warming-induced) higher nitrogen availability (Xia and Wan 2008; Qin et al. 2023).

We conclude that due to shifts in plant community composition, warming-induced changes in aboveground biomass can be "masked" (increased biomass in ambient and moderately warmed mesocosms governed by nitrogen-fixing plants versus warming-induced biomass increase via higher availability of alternative nitrogen sources), therefore warming may not lead to changes in overall aboveground biomass (Liu et al. 2018). However, warming-induced shifts in plant community composition and as a consequence also in functional traits (such as rooting depth and exudate or oxygen release rates) may have crucial implications for future soil carbon cycling (e.g. Liu et al. 2018; Noyce et al. 2023; Sun et al. 2025).

4.5.2. Plant available nitrogen increased with warming

As part of our first hypothesis, we proposed that warming-induced increases in aboveground biomass would be mediated by enhanced nitrogen availability. This hypothesis is partially supported by our findings, as aboveground biomass was significantly affected by foliar δ^{15}N (GLM; Fig. S. 5 D) which, in turn, was significantly influenced by warming in two-way interaction with country or species. Notably, aboveground biomass responses to warming (excluding nitrogen-fixing plants as potential confounding factor) showed modest to strong increases at Danish and Swedish sites, all of which were associated with elevated foliar δ^{15}N. In nitrogen-limited systems such as wetlands (Delaune et al. 2005; Herbert et al. 2020; Kiehl et al. 1997; Simpson et al. 2013), warming can exert a positive feedback on plant growth by alleviating nitrogen limitation (Melillo et al. 2002a; Dijkstra et al. 2010; Liu et al.

2022c). These positive warming effects predominantly occur if nitrogen limitation is present, as warming tends to influence plant responses indirectly through plant-soil feedbacks (Zhou et al. 2022). Accordingly, it is likely that warming enhanced nitrogen mineralization in the soil-sods, resulting in higher nitrogen availability for plants (Bai et al., 2010, Dijkstra et al., 2010; Noyce et al., 2019) and enabling positive biomass responses to warming (Melillo et al. 2002a; Liu et al. 2022b).

Similar to other wetland studies that applied continuous warming gradients (e.g. Norby et al. 2019; Noyce et al. 2019; Smith et al. 2022), our study design allowed us to capture nonlinear biomass responses (Luo 2007; Sage and Kubien 2007), which manifested as plateaus, latencies, or declines in biomass across the warming gradient. Particularly, Danish short-grass communities were characterized by a strong aboveground biomass peak at +4.5 °C warming, beyond which biomass gains leveled off. It is likely that warming-induced shifts in plant-microbe interactions, that enable positive biomass responses with moderate warming mediated by increased nitrogen availability for plant uptake (Bai et al. 2013; Dijkstra et al. 2010; Noyce et al. 2019) may also impose stress or resource depletion with continued warming (e.g. Danish short-grass communities) or in low resource systems (e.g. Finnish short-grass communities). This depletion could occur due to different mechanisms: 1) by exceeding temperature thresholds to which microbes can profit (Luo 2007); 2) by accelerating microbial mineralization rates beyond plant nitrogen demand (Bai et al. 2013; Noyce et al. 2019), leading to leaching of excessive nitrogen thus inducing progressive nitrogen limitation (Fang et al. 2023; Luo et al. 2004); and 3) through warming-induced microbial nitrogen immobilization (Jiang et al. 2025) thus competing with microbes for nitrogen.

4.5.3. Warming-induced SOM loss in SOM-rich soil

In accordance with our second hypothesis, stating that warming would result in a net loss of SOM, because warming-induced SOM decomposition through stimulated soil microbial activity will not be compensated by increased organic matter input, we observed decreasing SOM contents with increasing warming for Danish short-grass communities. Interestingly, clear negative effects of warming on SOM content were only observed in the site that was characterized by the highest SOM content (Danish short-grass communities). No clear response was seen for the other sites with lower initial SOM contents. The observed SOM loss aligns with previous research on North American coastal wetlands, suggesting greater warming-stimulation of litter breakdown than of primary production (Kirwan and Blum 2011) and marsh elevation loss associated with decreasing productivity (Smith et al. 2022). Moreover, Hanson et al. (2020) found soil carbon loss in response to warming in a northern peatland. More recently, Sun et al. (2025) found a net-loss in SOM after three years of warming in estuarine wetlands, which was associated with shifts in plant species composition leading to higher belowground biomass and priming of SOM. In contrast, we found that sites with lower initial SOM content did not exhibit SOM loss, which is consistent with the common – though debated – hypothesis for upland soils that warming-induced SOM losses are proportional to the existing SOM stocks (Crowther et al. 2016; van Gestel et al. 2018). Our results provide further evidence that warming induces a net loss of SOM (e.g. Sun et al. 2025), but this effect appears to occur primarily in SOM-rich soils and may therefore depend on the existing SOM stocks (e.g. Crowther et al. 2016).

Warming-induced SOM loss could be driven by a combination of interacting abiotic and biotic factors. First, warming stimulates soil microbial activity, therefore stimulating microbial decomposition (Charles and Dukes 2009; Kirwan and Blum 2011; Smith et al. 2022). Microbial activity may be further affected by warming-induced changes in abiotic conditions, such as soil moisture (Charles and Dukes 2009; Bai et al. 2013; Davidson and Janssens 2006) or changes in biotic interactions, for instance via plant activity and traits controlling SOM decomposition via so-called rhizosphere priming effects (Liu et al. 2022b; Mueller and Megonigal 2024). Second, warming may lead to lower SOM contents via reduced SOM formation due to a decline in belowground organic matter inputs (Langley and Megonigal 2010). In this study, the net SOM loss with rising temperature was associated with reduced belowground organic matter input (i.e., lower root biomass). Nonetheless, the warming-driven reduction in belowground biomass was not consistently found across rising temperatures. While warming up to +3°C strongly reduced belowground biomass, this negative effect lessened at higher warming levels (Fig. S. 6). Further, the reduction in SOM was associated with decreasing soil C:N ratio (Fig. S. 7), suggesting enhanced SOM decomposition due to increased microbial activity (Hobbie et al. 2002). We therefore suggest SOM loss was primarily driven by accelerated microbial decomposition of SOM. However, the potential role of rhizosphere priming, where plant-responses driven by higher nitrogen demands under warmer conditions may accelerate SOM decomposition (Noyce et al. 2023; Mueller and Megonigal 2024), cannot be ruled out or conclusively tested with our data.

4.5.4. Initial resource status mediates plant response to warming

Lastly, we explored the site-dependent variability in aboveground biomass responses and our results suggest that warming-induced changes in aboveground biomass are controlled by soil resource availability, given the observed strong positive relationship between SOM content and aboveground biomass responses to warming. Warming caused the most pronounced positive biomass response in the Danish short-grass communities, which is characterized by the highest SOM content. Conversely, Finnish soils, with the lowest SOM content, exhibited the lowest overall aboveground biomass, and their response to warming was the least pronounced or tended to be negative. SOM serves as integrative factor in plant ecology as it serves as reservoir for nutrients and also stabilizes water availability (Tiessen et al. 1994; Falkowski et al. 2000; Herrick and Wander 2018). We found strong positive correlations of SOM with soil nitrogen content (%), soil organic carbon (%), water content, and reducing soil conditions (Fig. 5 B & Fig. S. 8). Soil nitrogen content itself is, however, sensitive to various ecological processes and therefore SOM is a better overarching ecological variable regulating nutrient provision for plants. Systems with low SOM content are limited in nutrient mineralization and nutrient export, and thus immobilization or uptake by competing organisms can constrain plant growth (Temmink et al. 2022). Previous studies reporting warming-induced increases in aboveground biomass investigated coastal wetlands characterized by highly organic soils (Charles and Dukes 2009; Kirwan and Blum 2011; Noyce et al. 2019; Smith et al. 2022). These systems can therefore be categorized as productivity-stimulating systems and thus expected to respond differently compared to the clay-rich, minerogenic and nutrient limited Finnish marshes of the current study.

4.6. Conclusion

We were able to show that SOM content can determine the magnitude of aboveground biomass responses to warming in coastal wetlands. In the SOM-richest soils, warming caused the strongest plant biomass increases. This was accompanied by a net loss of SOM, as microbial decomposition of SOM overcompensated for plant input through increased biomass production. These results yieldimportant implications for blue barbon ecosystems, which have received increasing attention in recent decades (Mcleod et al. 2011; Lovelock and Duarte 2019; Macreadie et al. 2021). Systems with higher stocks of sequestered carbon and thus high SOM may be at higher risk to substantial losses of soil organic carbon under warming. Furthermore, our results suggest that SOM content determined nitrogen availability to plants via microbial mineralization, thus controlling the degree to which plant growth can be stimulated by warming. Nitrogen dynamics appear to be key to understanding the observed plant–SOM interactions in response to warming. Importantly, in some mesocosms aboveground biomass increased through the presence of nitrogen-fixing plants, which thereby masks or counteracts the plant response to warming via SOM-microbial interactions. These findings highlight the critical role of plant-soil interactions in driving ecosystem-climate feedbacks.

While mesocosm studies inherently introduce certain disturbances (e.g. sod transplantation and environmental manipulation) they also offer valuable advantages. In this case, our study design uniquely enabled comparison of different coastal wetland communities and their ecosystem carbon responses to warming, offering valuable insights into how plant-soil interactions under warming depend on initial resource status and plant community. Despite some limitations, the experiment revealed that ecosystems – often treated uniformly – can show heterogeneous responses, emphasizing the importance of local variability and background conditions in shaping climate change impacts.

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4.7. Supporting Information

Picture S. 1: Overview of the experimental setup

Picture S. 1: Aerial picture of the CCMMF located at the Institute of Plant Science and Microbiology of University of Hamburg (53°33´39.0´´ N; 009°51´31.5´´ E). Photo: Pablo Narezo Guzman.

Picture S. 2: Sampling of soil-sods

Picture S.2: Overview of the sampling procedure of individual soil sods. A shows the tailor-made square corer (20 x 20 x 35 cm). B inserted into the marsh soil. C showing the clean cut and D one idividual core before cutting it to 30 cm length. Photos: Simon Thomsen (A), Ella Logemann (B-D)

Figure S. 1: Soil characteristics of each site

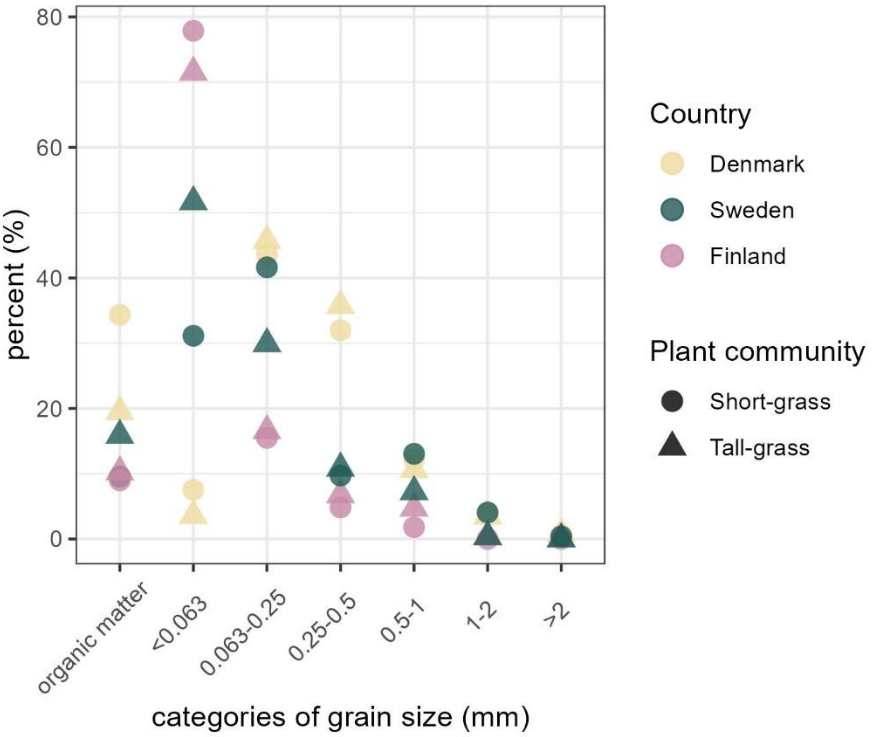


Figure S.1: Distribution of mean grain sizes in percent (%; 0-30 cm). Mineral content was assessed in Leiva-Duenas et al. (submitted) based on single cores taken in the field. Organic matter content is mean ambient SOM (0-30 cm). Each point represents a site indicated by colour and shape.

Figure S. 2: Plant community composition of study sites

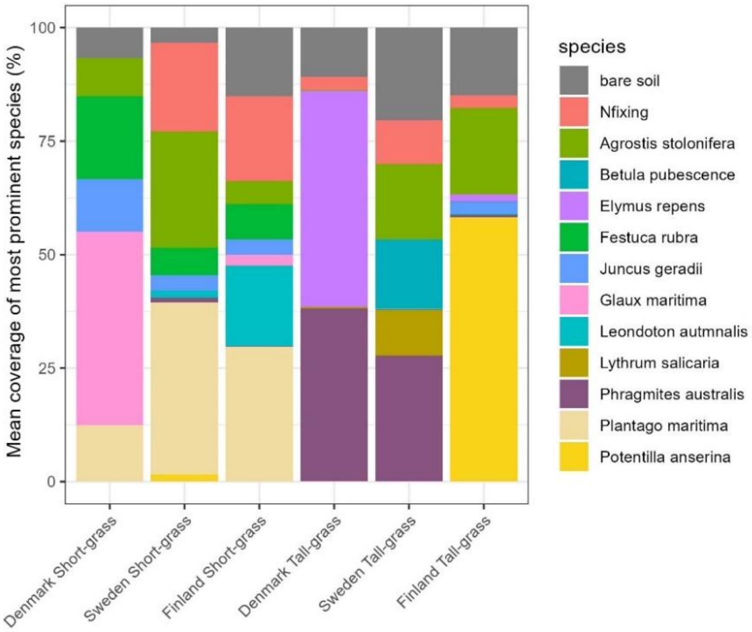


Figure S. 2: Most prominent plant species (species were selected when mean cover was higher than 10 % across all sites) and bare soil in percent (%) per site based on mean coverage (left). Nitrogen-fixing plant species were grouped and include *Vicia cracca*, *Alnus glutinosa* and various species from the genus *Trifolium*.

Figure S. 3: Variation in site-specific composition of plant communities

Figure S. 3: Non-Metric Multidimensional Scaling (NMDS) plot based on Bray-Curtis dissimilarity, illustrating the differences and similarities in plant species compositions between sites (indicated by colours).

Text S. 1: Climate data

Based on 1971–2000 climate data, mean annual minimum and maximum temperatures were 5.00 and 11.08 °C in Copenhagen, 4.96 and 11.26 °C in Stockholm, 1.48 and 9.02 °C in Turku, and 5.24 and 12.74 °C in Hamburg (data derived from WMO 2025). Mean annual precipitation was 525 mm in Copenhagen, 546 mm in Stockholm, 698 mm in Turku and 773 mm in Hamburg (data derived from WMO 2025).

Text S. 2: Detailed description of technical implementation of warming

Aboveground Warming

In the CCMMF, aboveground warming was a combination of active and passive warming. Active warming was generated by infrared radiation heaters. Each heater consisted of three ceramic radiators (FFE 400 W, Friedr. Freek GmbH, Germany), installed in a stainless-steel housing (Projektor PAS 3, Friedr. Freek GmbH, Germany), and was supplied with 230 V. One heater per subplot (short-grass vs. tall-grass) was placed centrally on a height-adjustable suspension approx. 1 m above the vegetation. In addition, passive warming was provided by semi-open foil greenhouses (906468, Biber Umweltprodukte Versand GmbH, Germany), each of which was installed above a subplot aiming to partially trap solar radiation and retain heat. To allow precipitation and wind to enter the mesocosms, four 15 cm high segments were cut out of the foil on the back and the foil roof was removed. The greenhouses of the tall-grass subplot with tall-grass communities were 1 m higher than the greenhouses of the short-grass subplots with short-grass communities. Accordingly, the infrared radiation heaters were placed higher in the tall-grass subplots, but the distance to the aboveground temperature sensors was kept the same as in the short-grass communities (~1 m). Each subplot was warmed to the assigned warming treatment based on ambient temperatures of the short-grass or tall-grass subplot in that block.

Active Belowground Warming

Each mesocosm soil was heated with four vertically installed heating pins, installed in the middle of each of the four quadrants for the best possible heat distribution. The 30 cm long heating pins were built from serial resistance heating cables (89846002, 9,36 Ω/m, Danfoss, Denmark) as described by Rich et al. (2023). To match incoming voltage (12 v) with cable resistance and maximize heating pin capacity, pairs of pins were operated in series within each mesocosm resulting in approximately 50 W per mesocosm. Additionally, all mesocosm were insulated externally using Styrofoam panels. Each soil mesocosm was heated independently based on the ambient soil mesocosm in that block from the same site because soil textural differences may affect heating rates.

Placement and type of temperature sensors

All temperature sensors used were manufactured in-house based on the Therm109 sensor specification (Campbell Scientific, USA), using 10 kΩ NTC-thermistors (GA10K3A1IA, TE Connectivity, Ireland). Plate sensors were used for measuring aboveground temperature (Noyce et al. 2019; Reich et al. 2018; Rich et al. 2023a). In this experiment, the aboveground temperature of each subplot was monitored by a plate sensor consisting of a thermistor embedded with epoxy in a 100 x 100 x 8 mm acrylic plate (Plexiglas XT, Röhm GmbH, Germany) and located in the upper third of the vegetation.

Belowground temperature sensors were built by embedding thermistors with epoxy in 20 cm long CFK tubes (2009070, CG TEC GmbH, Germany) with a diameter of 9 mm. To control soil warming, a belowground sensor was installed in each mesocosm at a depth of 15 cm and 2 cm from one of the four heating pins. A second sensor was installed in the center of each mesocosm and thus furthest away from the heating pins to measure the spatial expansion of the warming.

Measurement methodology and temperature control

Warming feedback control operated independently for aboveground and belowground heating systems and generally follows established methods (Noyce et al. 2019; Reich et al. 2018; Rich et al. 2023a; Rich et al. 2015) using the following operating code (SI-Github share). Each block had a separate control system to accommodate independent control for the 90 total soil mesocosms and over 180 belowground and 30 aboveground temperature sensors. Heating control and data collection was coordinated via CR1000X each with three AM16/32B multiplexers (Campbell Scientific, USA). Temperature data were collected, and feedback heating control parameters were calculated at 30 second intervals. As has been done in other experiments, power to the heating system turned on and off for portions of a 10 second interval to modulate heating and the duration was determined for each cycle by the control program. Aboveground heating was based on a three-minute projection of ambient aboveground temperature and belowground heating was based on a five-minute projection of ambient soil temperature. Heated elements were limited to ~70% power to prevent overheating. Feedback control signals were routed through an Arduino MEGA and through optically isolated relays to provide sufficient digital control signals for each of the 90 mesocosms to have independent control. Feedback control systems ‘borrowed’ data within treatment neighboring subplots or mesocosms to maintain treatments if sensor failures were detected. The control system interface allowed technicians to bypass sensors in the feedback control if errors were observed in daily checks.

Data Processing

For this paper, we averaged data to hourly intervals to report basic treatment temperature data by employing methods developed for other feedback controlled warming experiments ((Noyce et al. 2019; Reich et al. 2018; Rich et al. 2023a; Rich et al. 2015). Algorithmic processing was used to identify data points that fell out of range due to sensor failure or electronic noise; values outside of -10 to 50˚ C for aboveground and values outside of 0 to 30 ˚C for soil temperature data were removed. Further checking compared hourly data from each individual mesocosm to the overall block mean for that hourly increment and values were removed if individual mesocosm was ± 5˚C for soil data or ±10 ˚C for aboveground data from the overall block mean of each. Lastly, to identify erratic or noisy sensor values, the standard deviation of each sensor value over a rolling four-hour window was calculated and removed if data value fell outside the 95% quantile. Because the feedback control system used neighboring values to maintain the heating, we used plot average data to backfill missing data when we calculated treatments. Altogether, cleaning removed and filled < 0.8 % of data for aboveground data and < 1.2% of belowground data. In data processing, we excluded data from one aboveground sensor for April to October 2023 (tall-grass plots in block two at heating level +4.5°C). This sensor exhibited a data offset indicative of a faulty thermistor. We determined that heating was working based on the heating signal that this plot was receiving and comparing the magnitude and its deviation of that signal to the heating signals from other subplots. These malfunction data are not included in figures or overall treatment analysis.

Text S. 3: Experimental warming data

Aboveground and belowground temperature tracked diurnal and seasonal temperature cycles. The mean ambient soil temperature during the second vegetation period 2023 (01 May–01 October) was 18.9 ± 3.1 °C, while the mean air temperature was 17.8± 6.4 °C. Soil warming was implemented in 1.5 °C steps and achieved with high accuracy, deviating on average by only 0.06 °C across treatments, with the largest deviations observed in the strongest warming levels. In tall-grass communities, soil temperatures in the warming treatments were slightly higher than targeted (except in the +6 °C treatment), whereas in short-grass communities, achieved soil warming was slightly lower than anticipated. In contrast, aboveground warming was less consistent: on average, air temperatures were 0.61 °C lower than targeted, with the shortfall increasing at higher warming levels. This discrepancy is likely attributable to the regular shutdown of the aboveground heating system during maintenance and data collection. Aboveground warming in short-grass mesocosms more closely matched the target levels than in tall-grass mesocosms, where tall-growing grasses likely interfered with the uniform distribution of heating energy, leading to greater shortfall.

Figure S. 4: Experimental warming data

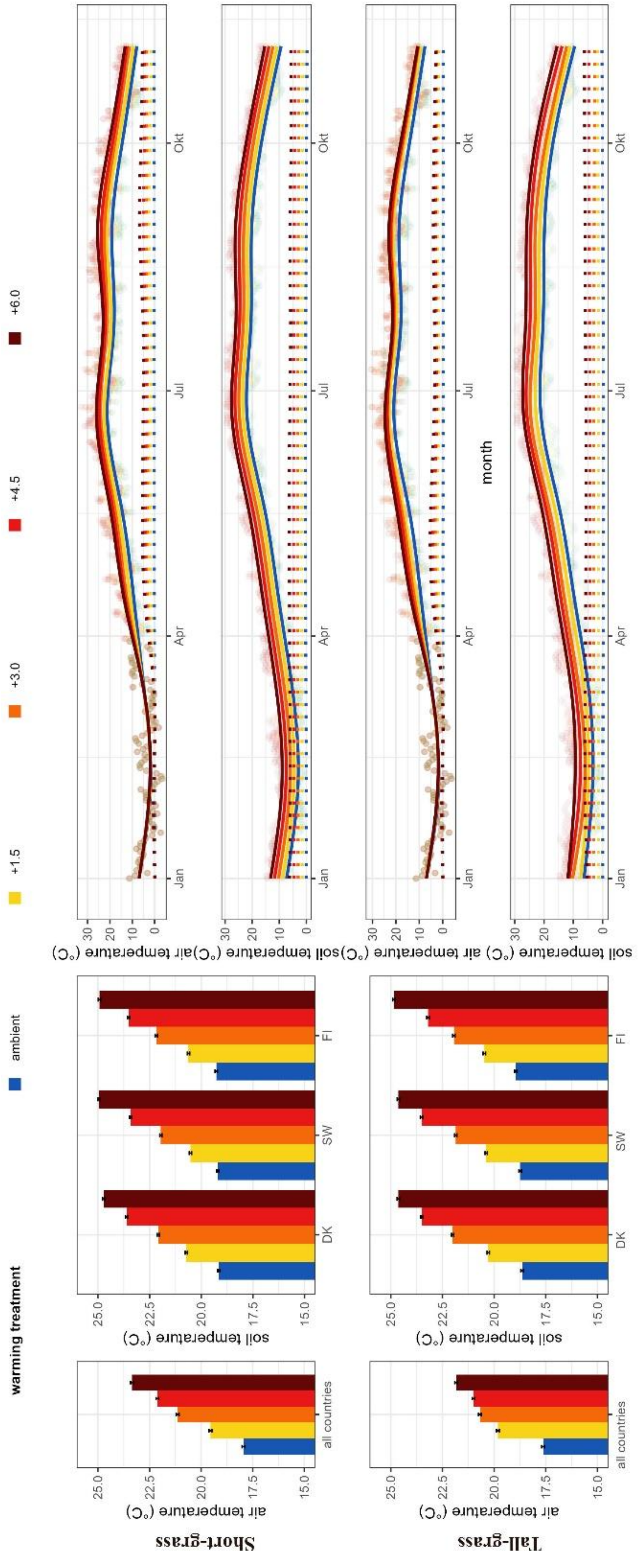


Figure S. 4: Achieved warming (°C) across countries and plant community types (short-grass vs. tall-grass). Bar plots show mean temperatures per treatment, with error bars representing 95% CI bars during vegetation period (01.05.2023-01.10.2023). Aboveground air temperature was measured at the subplot level and is not country-specific (see methods for details). Soil temperature was recorded in each mesocosm, and values represent the mean across countries: Denmark (DK), Sweden (SW), and Finland (FI). Line plots depict smoothed seasonal temperature fluctuations from 01.01.2023 to 05.11.23, with solid lines indicating the real temperature and dotted lines showing the temperature delta from ambient conditions. Aboveground warming was deactivated in winter 2022/2023. Overlaid points display daily mean of each sensor. Each color represents a different warming treatment.

Text S. 3: Interpolated belowground biomass

The soil cores collected for assessing belowground biomass vary in length due to some soil loss during the sampling process. Unfortunately, these cores were not divided into different depth increments for analysis. Instead, all cores were assumed to represent the total belowground biomass, even when parts of the core were missing. The entire depth of the mesocosms is approximately 30 cm, with many cores ranging from 20 to 30 cm in length, and a smaller proportion not reaching 20 cm. This approach neglects the significant variation in root distribution at different soil depths, which can lead to inaccuracies in estimating total belowground biomass. Simply correcting for the length of the cores without considering root distribution along a depth gradient can either underestimate or overestimate the belowground biomass. Therefore, extrapolating the overall belowground biomass to a total length of 30 cm may result in misleading conclusions.

To address these issues, we utilized root distribution from cores collected in the field and divided the root distribution into segments of 10 cm. Based on these increments each core for belowground biomass taken in the CCMMF was corrected. Thus, we standardized belowground biomass estimates by adjusting for missing or extra core sections using site-specific root distributions derived from field data.

This method allows for better interpolation of root biomass, taking into account the variations among different sites. However, it is important to note that this approach is still subject to sampling error. Therefore, we recommend using this data only for internal comparisons within the experiment and not for comparisons with other studies.

Table S. 1: p- values and estimate output from generalized mixed model

GLM testing for explanatory variables for aboveground biomass (AGB). All tested explanatory variables (country, plant community type, warming treatment, foliar δ^{15}N (‰), cover of nitrogen-fixing plants (%), Simpson index and soil C:N ratio were tested significant.

	AGB	
	p	Estimate
Country: Sweden	<0.05	-128.4
Country: Finland	<0.001	-322.5
Plant community	<0.05	-113.8
Warming	<0.05	16.3
foliar δ^{15}N	<0.001	45.9
nitrogen fixing	<0.001	4.3
Simpson	<0.05	343.8
soil C:N ratio	<0.05	-33.0

Figure S. 5: Variables that significantly influence aboveground biomass

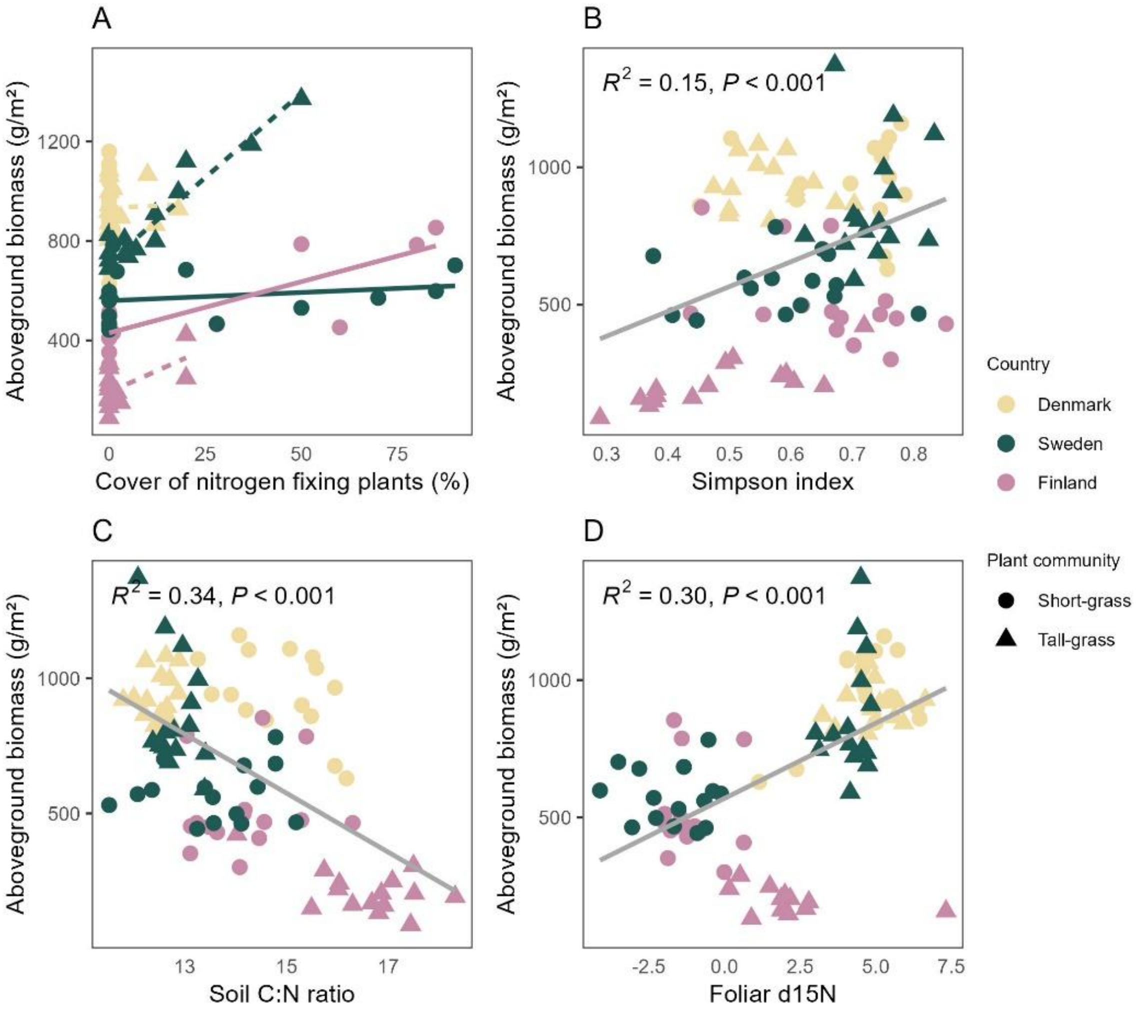


Figure S. 5: The GLM revealed the displayed explanatory variables that significantly relate to aboveground biomass. Aboveground biomass (g/m²) was positively correlated with the cover of nitrogen fixing plants, though correlations varied between sites (**A**), with increasing diversity, here Simpson index (**B**), with decreasing soil C:N ratio (**C**) and with increasing nitrogen availability, here foliar δ^{15}N (**D**). Colour indicates country; shape indicates plant community type.

Table S. 2: Baseline differences between sites (country x plant community). Mean values based on mesocosm that were not treated with warming (ambient)

Country	**Plant community**	**SOM (%)**		**soil nitrogen (%)**		**soil C:N ratio**		**gravimetric water (%)**		**aboveground biomass (g/m²)**		**belowground biomass (g/m²)**		**Shannon index**		**Simpson index**		**Evenness**	
		mean	±SD	mean	±SD	mean	±SD	mean	±SD	mean	±SD	mean	±SD	mean	±SD	mean	±SD	mean	±SD
Denmark	Short-grass	34.35	1.70	0.98	0.10	15.9	0.4	210.9	13.3	721.8	121.7	3157.0	885.2	1.34	0.34	0.65	0.17	0.36	0.07
Denmark	Tall-grass	19.50	4.16	0.78	0.19	12.7	0.2	169.4	27.6	928.7	124.2	1381.1	445.7	0.96	0.16	0.57	0.06	0.37	0.06
Sweden	Short-grass	9.54	2.45	0.22	0.11	14.1	1.3	59.6	11.5	589.2	117.7	770.9	226.7	1.47	0.31	0.66	0.14	0.30	0.07
Sweden	Tall-grass	15.87	2.35	0.55	0.06	12.7	0.1	153.3	32.6	908.1	244.7	1354.6	690.6	1.73	0.22	0.78	0.04	0.35	0.03
Finland	Short-grass	8.99	0.93	0.27	0.07	14.0	1.2	56.5	2.0	555.8	198.3	1577.0	976.1	1.59	0.40	0.71	0.13	0.33	0.04
Finland	Tall-grass	10.28	1.11	0.25	0.06	16.4	2.2	85.4	7.8	257.7	143.5	960.6	447.5	1.01	0.44	0.48	0.20	0.23	0.07

Table S. 3: R² and p-values (p) of linear regressions of aboveground biomass response (slope of each response per site) against different predicting factors. All predictors were calculated based on ambient means representing "initial" site conditions. Tested predictors: soil organic matter (SOM), soil nitrogen content, gravimetric water content, soil C:N ratio, aboveground biomass (AGB), belowground biomass (BGB), Shannon index and Evenness.

predictor	R²	p
SOM (%)	0.60	0.070
Soil nitrogen (%)	0.39	0.182
water content (%)	0.34	0.222
soil C:N ratio	0.11	0.512
AGB (g/m²)	0.03	0.727
BGB (g/m²)	0.36	0.210
Shannon	0.06	0.654
Evenness	0.09	0.567

Figure S. 6: Site-specific belowground biomass responses to warming

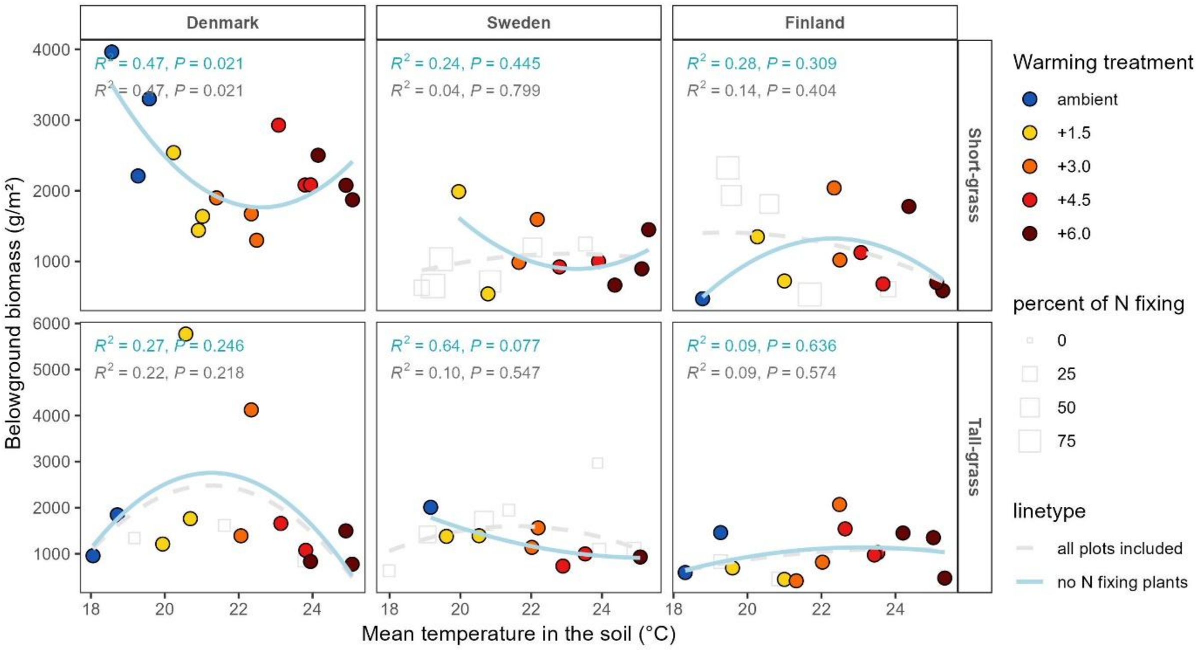


Figure S. 6: Belowground biomass in response to warming (mean soil temperature between 01.05.-01.10.2023). Regression based on all mesocosms (grey dashed line) and on mesocosms with less than 5 % cover of nitrogen-fixing plants (blue solid line; excluding grey squares).

Figure. S. 7: Linear regression of soil C:N ratio to mean soil temperature

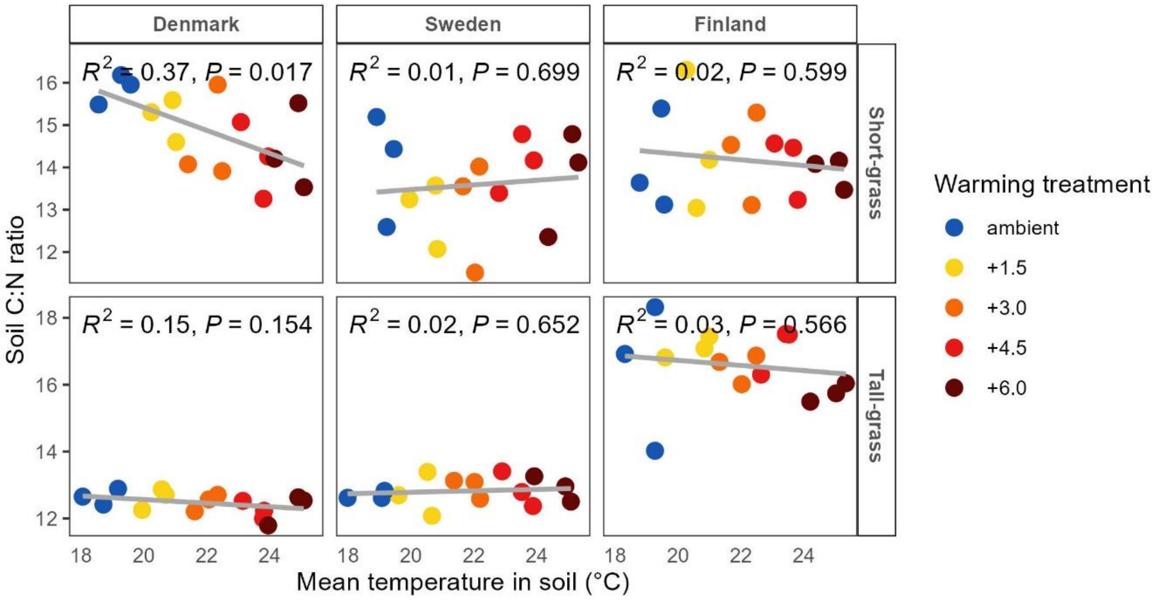


Figure S.7: Linear regression between mean soil temperature (°C) and soil C:N ratio for all tested sites. Colours indicating warming treatments.

Figure S. 8: SOM as "master variable" for ecosystem properties

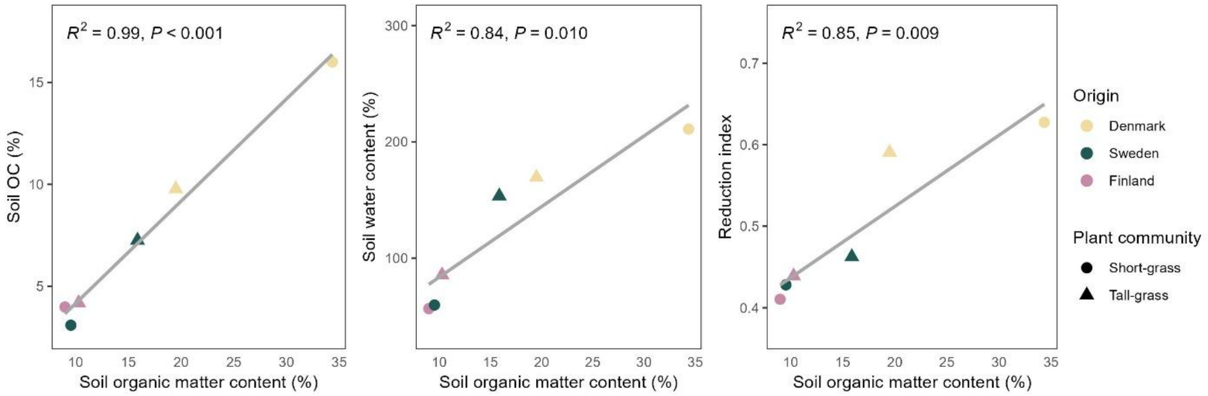


Figure S. 8: Linear regression between SOM and soil organic carbon content (%), gravimetric water content (%), and reduction index (based on IRIS sticks; method see Mittmann-Goetsch et al. 2024)). Mean site values calculated based on ambient mesocosms only. Colour indicates country; shape indicates plant community type.

Figure S. 9: Temperature effect on different plant functional groups and species

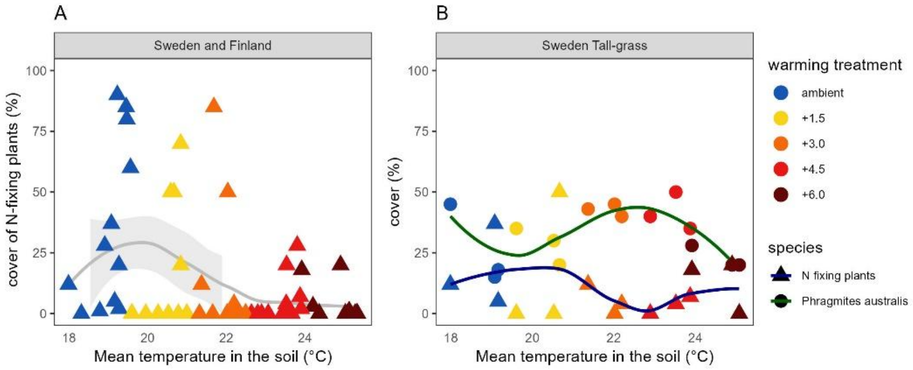


Figure S. 9: **A** Cover of nitrogen-fixing plants along warming across Swedish and Finnish mesocosms. Denmark was excluded as nitrogen-fixing plants had a lower abundance. **B** cover of the nitrogen-fixing plant *Alnus glutinosa* and of Phragmites australis in mesocosms originating from tall-grass Swedish marshes (%).

BOX B

LIMITED PHYSIOLOGICAL RESPONSES OF PHRAGMITES AUSTRALIS TO WARMING

Ella Logemann, Lisa Däbler, Lia Ruhrus, Kai Jensen, Peter Mueller, Christoph Reisdorff

Plants are directly affected by warming, as higher kinetic energy of molecules accelerates numerous physiological processes, due to higher metabolic rates and increased enzymatic activity (Bassirirad 2000; Sage and Kubien 2007; Crous 2019). The activity of Ribulose-1,5-bisphosphate-carboxylase/-oxygenase (RuBisCO), the most abundant protein in photosynthetically active plant organs and the enzyme responsible for CO_2 fixation, is a key determinant of photosynthetically mediated carbon assimilation (Andersson and Backlund 2008). Consequently, temperature exerts strong control over instantaneous rates of photosynthesis. However, because plants are generally adapted to specific climate regimes, their thermal optima can be exceeded by high temperatures, leading to declines in photosynthetic performance and, ultimately, reduced primary productivity (Mendelssohn and Morris 2002; Luo 2007; Münzbergová et al. 2017).

Plants take up CO_2 through diffusion from the atmosphere into intercellular spaces via stomata. The uptake and upward transport of water compensates the inevitable water loss (during CO_2 uptake) which would otherwise impair vital physiological functions of cells with progressing loss of turgescence (Lambers and Oliveira 2019). When water availability becomes limited, plants reduce transpiration by decreasing their stomatal conductance. This, however, restricts CO_2 diffusion into the intercellular spaces leading to a reduction of assimilation. In terrestrial systems one crucial global-warming effect is the increased evapotranspiration potentially inducing drought stress for plants and microbes (Sherwood and Fu 2014; Schimel 2018). Therefore, it is shown for various terrestrial ecosystems that warming decreased carbon assimilation (Boeck et al. 2008; Hoeppner and Dukes 2012; Hatfield and Dold 2019). Under drier conditions and reduced stomatal conductance, the intercellular CO_2 partial pressure is lowered and the share of $^{13}CO_2$ increases due it's discrimination by RuBisCO, which finally results in greater incorporation of the heavier isotope ($^{13}CO_2$) into assimilates. As a result, leaves become relatively less deprived in ^{13}C, which is reflected in less negative $\delta^{13}C$ values of the biomass (O'Leary 1981).

To test whether *Phragmites australis* - representing one prominent species of the tall-grass communities experimentally warmed in the CCMMF (see chapter 4) - exhibits physiological responses to warming, we measured stomatal conductance and foliar δ^{13}C as proxy for water-use-efficiency. To see whether higher temperatures cause acclimation of photosynthetic capacity, V_{cmax} (the maximum rate of carboxylation) was determined using gas exchange measurements. Contrary to our expectations, that warming would cause physiological reactions and acclimation of physiological traits we did not detect significant responses in *Phragmites australis* to warming as:

- Water-use-efficiency (stomatal conductance and foliar δ^{13}C; Fig. 1 & 2 B) was not increased and
- Photosynthetic capacity (V_{cmax}; Fig. 2 B) was not decreased under warming.

I therefore conclude that the applied warming treatment in the CCMMF, despite being relatively strong, did not induce detectable drought stress in the tall-grass communities (namely, *Phragmites australis*) nor caused a physiological acclimation.

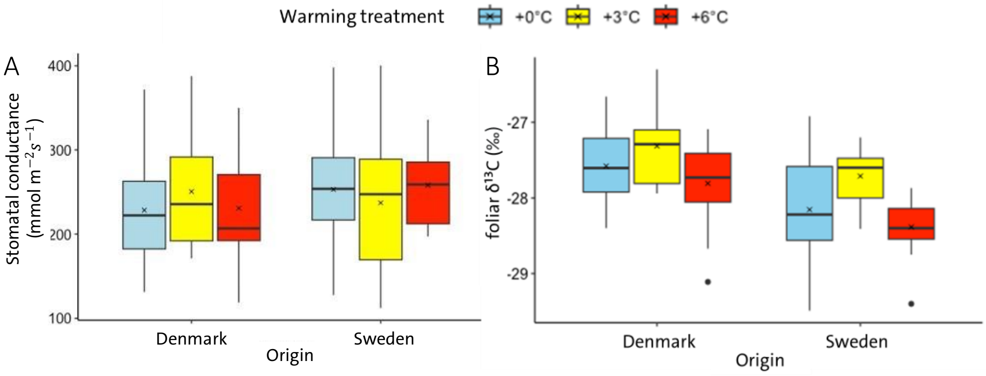


Figure 1: Stomatal conductance (A) and foliar δ^{13}C (B) in Danish and Swedish mesocosm measured in *Phragmites australis* leaves originating Danish and Swedish mesocosm warmed in the CCMMF. Measurement took place in July and August 2022. Boxplots display the median (centered line), 25-quatrile, 75-quartile.

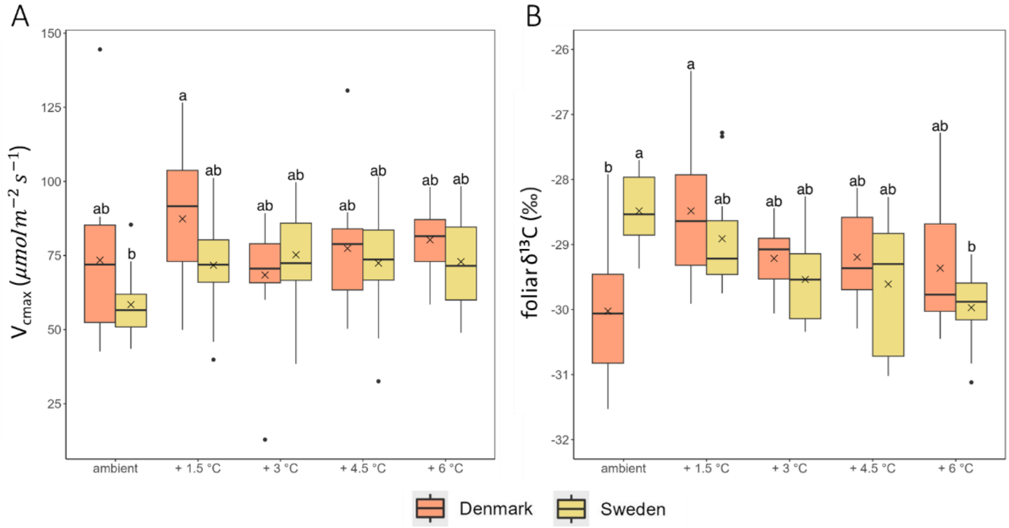


Figure 2: the maximum carboxylation rate (V_{cmax} standardized to 25°C; A) and foliar δ^{13}C (B) in Danish and Swedish mesocosm measured in *Phragmites australis* leaves originating Danish and Swedish mesocosm warmed in the CCMMF. Measurements took place in September and October 2023. Boxplots display the median (centered line), 25-quatrile, 75-quartile.

CHAPTER FIVE

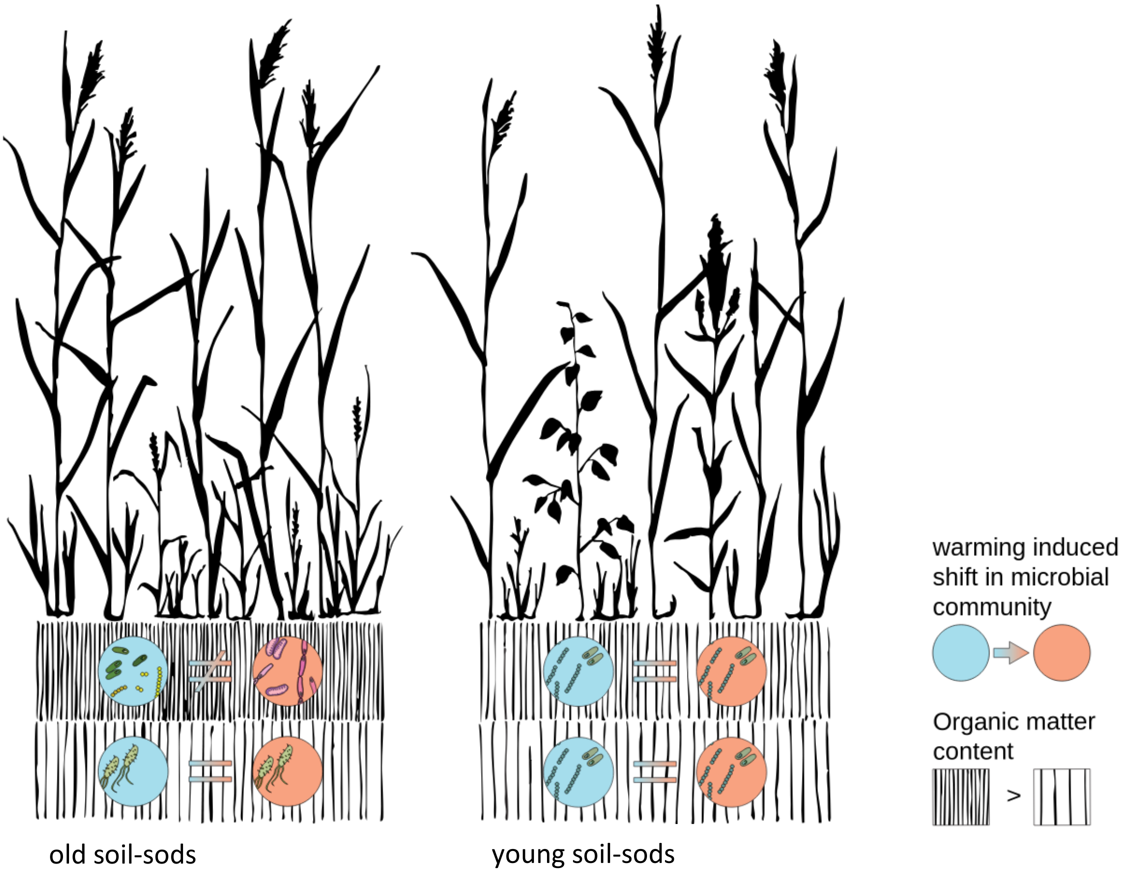
WARMING EFFECTS ON MICROBIAL COMMUNITY COMPOSITION IN NORDIC COASTAL WETLAND SOILS

Accepted

iScience

Johanna Schwarzer*, Ella Logemann*, Julian Mittmann-Goesele, Alexander Brodehl, Alexander Bartholomäus, Kai Jensen, Peter Mueller, Susanne Liebner

Graphical abstract



Graphical abstract: old soil-sods from Denmark (left panel) were dominated by two grasses, young soil-sods from Sweden (right panel) had a more diverse plant community. The organic matter content for every analyzed sampling depth (0 - 10 cm and 10 - 20 cm) is indicated by vertical lines. Magnifiers show temperature induced changes in the rare biosphere after 1.5 years of warming**.**

5.1. Abstract

Coastal wetlands are efficient carbon sinks, yet it remains unclear how climate change will affect their net carbon balance. Plants and microbes engage in complex, interconnected relationships that significantly promote growth and subsequently carbon balance of wetlands. However, how these microbial communities respond to warming in natural, vegetated wetland soils is poorly understood.

To investigate responses in microbial community composition to warming in the rhizosphere, we took soil-sods from two different coastal wetlands along the Baltic coast and transferred them to a state-of-the-art warming mesocosm facility applying active above- and belowground heating of +3°C, +6°C and ambient conditions as control for two subsequent vegetation periods.

Our study shows that after 1.5 years of active warming, a clear shift in the soil microbial community composition can be identified, depending on the soil marsh origin. While microbial community composition was altered in the older soil-sods derived from Denmark, the microbial response in soil-sods from a less mature coastal wetland originating Sweden was hardly detectable. Here we demonstrate that warming-induced shifts in soils microbial community composition are detectable, even after short periods of time. We argue that the magnitude of warming-induced changes depends on baseline conditions, such as plant composition, and successional stage. These divergent responses in microbial community composition to warming differentially regulate carbon dynamics, carrying important implications for carbon sequestration in coastal wetlands under warmer conditions.

5.2. Introduction

Global warming-driven changes in carbon fluxes between soils and the atmosphere are still poorly understood. Warming has the potential to mobilize large amounts of the global soil organic carbon (SOC) stock, thereby causing a release of greenhouse gases (CO2, CH4) into the atmosphere and reinforcing a positive soil-climate feedback (Melillo et al. 2017). The conversion of SOC to greenhouse gases is driven by soil microbial respiratory processes, which have been shown to increase globally over recent decades (Lei et al. 2021; Sáez-Sandino et al. 2023).

The primary source of SOC is plant derived organic matter, and as microbial communities drive biogeochemical processes (Wu et al. 2024), the fate of SOC is ultimately determined by soil microbial communities (Schmidt et al. 2011; Crowther et al. 2019; Nottingham et al. 2022b). Plants steer microbial functioning and composition by the quality of their litter as well as by releasing exudates and leachates that either enhance or inhibit microbial activity (Högberg and Read 2006; Hartmann et al. 2009). In turn, the soil microbiome modifies biotic and abiotic soil conditions and supports the ability of plants to adapt to their environment (Philippot et al. 2013; Philippot et al. 2024). Microbes make nutrients available to plants, but they also compete with plants for nutrients or are pathogenic (Bardgett et al. 2008; van der Heijden et al. 2008). Yet, our current understanding of how climate warming influences soil microbial functioning and respiration remains limited, partly, because the complex biotic interactions between plants and soil microbes are difficult to assess (Dal Bello and Abreu 2024; Mueller and Megonigal 2024).

Despite the importance of plant-microbe interactions in shaping biogeochemical dynamics, many studies rely on soil incubations at varied temperatures. Only few studies assess microbial community compositions in vegetated soils under warming. So far research in this field has focussed on upland terrestrial ecosystems, such as forests, grasslands and arctic tundra. Results range from significant warming induced changes in prokaryotic community composition after 10 years or longer (Deslippe et al. 2012; Luo et al. 2014; DeAngelis et al. 2015; Liu et al. 2024b), or functional gene adaptations without shifts in community structure (Cheng et al. 2017), to studies with shorter warming periods of few years, where warming had no detectable effect on microbial communities, particularly when compared to other factors (Castro et al. 2010; Contosta et al. 2015; DeAngelis et al. 2015). Known factors that were identified to control prokaryotic community composition shifts following rising temperatures are soil depth and site (Contosta et al. 2015; DeAngelis et al. 2015), as well as precipitation (moisture), seasonality and the availability of nitrogen (Castro et al. 2010; Contosta et al. 2015).

A key ecosystem type regarding SOC storage in the context of climate change mitigation are wetlands. They play an important role in the global carbon cycle, as they represent the largest terrestrial soil organic carbon pool (Köchy et al. 2015; Mitra et al. 2005). Their capacity to sequester and store carbon results from waterlogged conditions that slow down microbial activity (Candry et al. 2023). The interacting roles of microbial communities and plant functioning in wetlands are even more complex compared to upland ecosystems, as the influence of plants is particularly relevant: Roots do not only provide the soil environment with organic matter but also with oxygen, thus altering an otherwise reducing environment via root oxygen loss (Koop-Jakobsen et al. 2021; Philippot et al. 2013).

Research on warming effects on microbial communities in wetlands is concentrated on studies conducted in Sphagnum dominated peatlands. Here it was shown that plant-microbe interactions modulate greenhouse gas emission, an interaction strongly influenced by warming (Jassey et al. 2013; Ward et al. 2013). A study simulating strong climate warming (up to +9°C) in a peat bog revealed no temperature effect on microbial communities after one year (Wilson et al. 2016). In a follow-up publication after prolonged temperature treatment of 5 years, authors argue that, although they did not see a change in microbial composition, the observed increase in methane fluxes are a result of changes in microbial activity (Hopple et al. 2020).

Despite their importance for climate change mitigation, coastal wetlands are rarely considered in studies of microbial responses to active warming in vegetated systems. A coastal wetland study with open top chambers for passive experimental warming (up to +0.6°C) found microbial community composition to be largely unaffected, and divergent effects on the complexity of microbial co-occurrence networks (Pei et al. 2024). Plants have been shown to strongly influence microbial community composition, highlighting the importance of experiments including plant-microbe interactions and their feedback on carbon dynamics in coastal wetlands (Haviland and Noyce 2024; Pei et al. 2024).

The effect of warming on soil microbial community composition and activity has yet to be clarified, particularly in wetland ecosystems. Furthermore, it is unclear to what extent insights from upland soils can be applied to wetlands. Therefore, we aimed to address the following research questions: I) Do factors known to influence the warming response in upland soils, such as sample origin and soil depth, also play a role in coastal wetlands? II) Can we identify a shift in microbial community composition with increased warming? and if so, III) Can we identify generalizable patterns across different sample origins?

In order to investigate these factors, we use an ecosystem-transplant approach with vegetated soil-sods from two Nordic coastal wetlands of different ages and successional stages. These sods were transferred to a state-of-the-art warming mesocosm experiment for two consecutive vegetation periods.

5.3. Materials and Methods

5.3.1. Experimental mesocosm set-up

The Climate Change Marsh Mesocosm Facility (CCMMF) is a state-of-the-art experimental setup designed to simulate future climate warming scenarios through active, feedback- controlled warming both above- and belowground. A detailed description of the CCMMF can be found in Logemann et al. (submitted). Coastal wetland soil-sods from the Baltic coast were transplanted into mesocosms at Institute of Plant Science and Microbiology at the University of Hamburg, in winter 2021/22. The present study is focused on a selected subset of the experiment, specifically tall-grass communities from Denmark and Sweden, subjected to ambient, +3°C, and +6°C warming treatments. The two selected coastal wetland differ in ecosystem age: the Danish site emerged about 125 years ago, whereas the Swedish site is only 35 years old (Leiva-Dueñas et al. 2026).

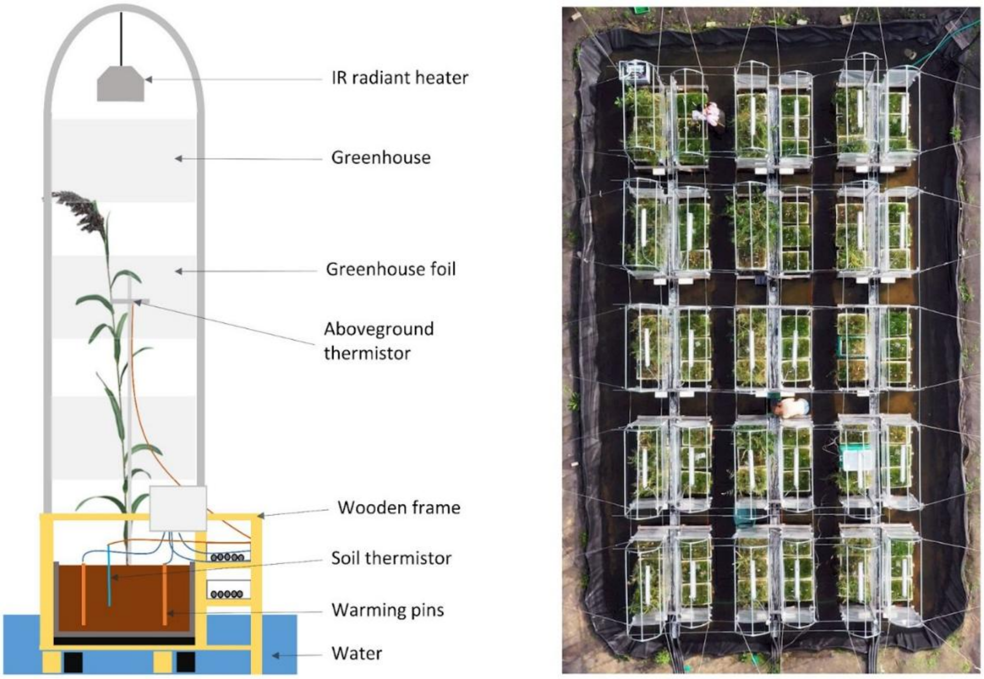


Figure. 1: Schematic overview of the CCMMF experimental setup at the University of Hamburg. Vegetated soil-sods were transplanted into mesocosms subjected to active above- and belowground warming (ambient, +3°C and +6°C) using soil heating pins and infrared heaters. Mesocosms were partially submerged in a brackish water basin (6 ‰) to simulate natural water table conditions (graphic adapted from Logemann et al., submitted).

5.3.2. Soil sampling and vegetation assessment

Vegetation composition was assessed two months before destructive sampling during the vegetation period in August 2023. Individual plant species cover and bare soil was estimated in percent. After 1.5 years of active warming, soil samples were collected during destructive harvesting in November 2023. Triplicate soil cores were collected from each mesocosm using a gouge auger with a diameter of 2.5

cm. Each core was sectioned into depth increments of 0–5 cm, 5–10 cm, and 10–20 cm, which were then pooled into composite samples. Samples were stored at -20°C after sampling until further processing.

5.3.3. Exoenzyme activity assays

Fluorometric exoenzyme assays were performed to quantify the activities of five hydrolytic enzymes involved in microbial nutrient acquisition, targeting carbon- (β-glucosidase, cellobiosidase), nitrogen- (chitinase, leucine aminopeptidase), and phosphorus- acquisition (phosphatase). Frozen soil samples were homogenized, and a 2 g subsample was transferred into a 50-ml Falcon tube. Soil slurries were prepared by adding 20 ml of deionized water and mixing thoroughly. Enzyme activities were measured following the standard fluorometric protocol described by (Mueller et al. 2017). Assays were conducted in black 96-well microplates using a Multi-Detection Microplate Reader (BioTek Synergy™ HT, Winooski, USA). Substrates corresponding to each enzyme were added at a final concentration of 1.6 mmol/L (Table S. 1). Plates were incubated in the dark at 20 °C for 18–24 hours. Fluorescence was measured with excitation and emission wavelengths set at 365 nm and 460 nm, respectively. Due to the high buffer capacity of the carbonate-rich soils, no additional buffering was applied before incubation. Exoenzymatic activities were normalized to the soil organic matter content (Mueller et al. 2017). Soil organic matter was determined by loss on ignition (550°C for 2 hours).

5.3.4. 16S rRNA-based microbial community composition of bacteria and archaea

Soil DNA was extracted using the DNeasy PowerSoil Kit (QIAGEN) according to the manufacturer's instructions. Approximately 250 mg of soil per sample was used for extraction. Extracted DNA was quantified with a fluorometer (DeNovix DS-11) with the Qubit™ dsDNA BR Assaykit (Invitrogen), checked for size through gel electrophoresis and stored at 4°C until further processing.

For amplification of the 16S rRNA gene, samples were first diluted 1:10 with nuclease free water to dilute PCR inhibitors that are commonly found in soil samples. Amplicon libraries were prepared using the barcoded universal primers Uni515-F and Uni806-R (Caporaso et al. 2011) targeting the V4 region of the prokaryotic 16S rRNA gene. The barcoded amplicons were purified with a magnetic bead clean-up step using HighPrep PCR – DX (MagBio Genomics Inc., Gaithersburg (Maryland), USA) according to the manufacturer's protocol. The barcoded amplicons were pooled in equal quantities. Sequencing was performed by Novogene (Munich, Germany) using Illumina 2x250bp paired end sequencing.

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 pseudo-pooled approach with the filtering parameters maxN=10, truncQ=2, rm.phix=TRUE and minLen=80 were used. Taxonomic assignment of the ASVs was done using DADA2 and the SILVA database version 138.1 (Quast et al. 2013). ASVs that were assigned to chloroplasts, eukaryotes or mitochondria were removed.

5.3.5.Statistical Analysis

Statistical analysis was performed in R version 4.5.1 and RStudio. All graphs were produced using ggplot2 and the tidyverse packages, with figure layouts arranged using patchwork.

For the 16S rRNA microbial community composition, beta diversity was assessed using principal component analysis (PCA) of centered log-ratio (clr)–transformed 16S rRNA gene count data with the R- packages phyloseq and microViz.

Community composition was also analyzed using PERMANOVA to test the influence of environmental factors on microbial community composition with the function adonis2 of the R-package vegan. Following the same clr transformation applied for PCA (see above), community dissimilarities were quantified using the Aitchison distance, i.e. Euclidean distance on clr-transformed 16S rRNA gene count data. PERMANOVA tests were performed with 9999 permutations, using a fixed random seed (seed = 1) to ensure reproducibility. For the full dataset, we tested the effects of soil-sod origin, depth, and warming treatment (as continuous variable) on community composition. In addition, we repeated PERMANOVA analyses on stratified datasets to assess the isolated influence of warming treatment within each subset.

Differentially abundant taxa in relation to the warming treatment (again modeled as continuous variable), were identified using DESeq2 (Love et al. 2014; McMurdie and Holmes 2014). DESeq2 accounts for differences in sequencing depth across samples, stabilizes variability in the data, and adjusts p-values for multiple testing using the Benjamini–Hochberg procedure (Love et al. 2014; McMurdie and Holmes 2014). The midpoint rooted Cladogram was produced by aligning the 16S rRNA sequences with the following tools: Biostrings, seqinr, msa, ape and ggtree.

We tested enzyme activities for effects of warming, soil-sod origin, and their interaction using mixed effect ANOVAs. Post-hoc tests were performed following significant main effects of the ANOVA. We included mesocosm replicates and sampling depth of the composite samples as a random factor into the model. Mixed effect ANOVAs were conducted using lme4 R package. Post-hoc pairwise comparisons were performed using the emmeans R package.

5.4. Results

5.4.1. Microbial community composition

Prokaryotic community composition was strongly clustered by soil-sod origin and sampling depth. Microbial community composition differences between soil-sod origin explained 40% of variance in community composition (Fig. 2). Sampling depth was separated along the second principal component, explaining 12 % of the total variance in microbial composition. Soil-sods from Denmark showed a stronger depth differentiation than soil-sods from Sweden (Fig. 2). The effect of soil-sod origin and depth on microbial community composition is significant ($p < 0.0001$; Table S. 2).

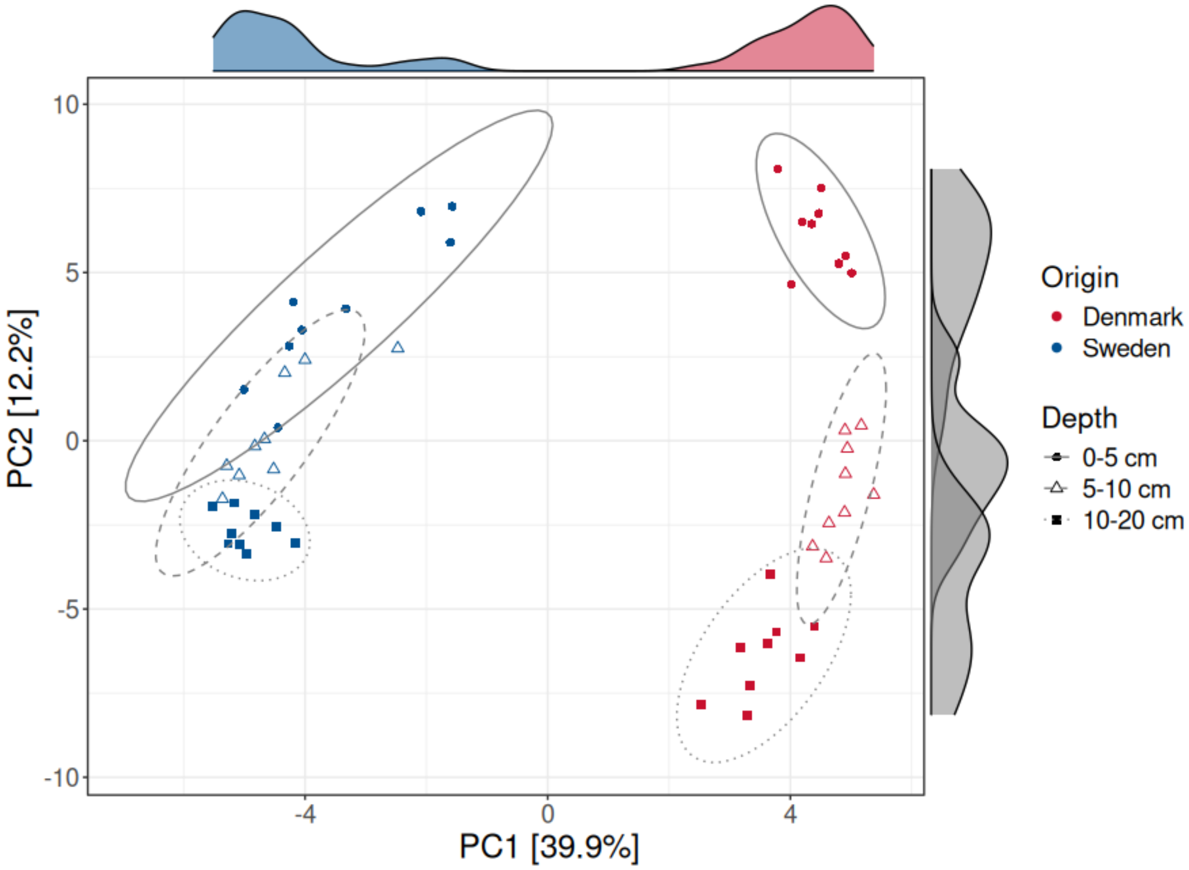


Figure 2: Principal Component Analysis (PCA) of center log-ratio transformed 16S rDNA community composition across all samples. Sample origin (red: Denmark, blue: Sweden); Sampling depth (circles and straight-lined hull: 0–5 cm, triangles and dashed-lined hull: 5–10 cm, squares and dotted-line hull: 10–20 cm). Site density distribution along the x-axis represents wetland origin, site density distribution along the y-axis sampling depth.

When samples were stratified according to the PCA-derived main clusters soil-sod origin and sampling depth (Fig. 2), a warming pattern was identified (Fig. 3). In the uppermost Danish soil layers (0-5 cm), warming led to distinct clustering with a linear trend along the first principal component. This effect is significant (PERMANOVA $p < 0.001$, Table S. 3). With increasing depth this trend becomes less apparent and non-significant.

In contrast, microbial community compositions in Swedish soil-sods did not cluster clearly with warming treatment. Waming-clusters of samples from 5-10 cm depth overlap, but a distinction between warming treatments is apparent (Fig. 3). Uppermost soil communities from the Swedish wetlands distinctly clustered along the third and fourth PC (supplement Fig. 1).

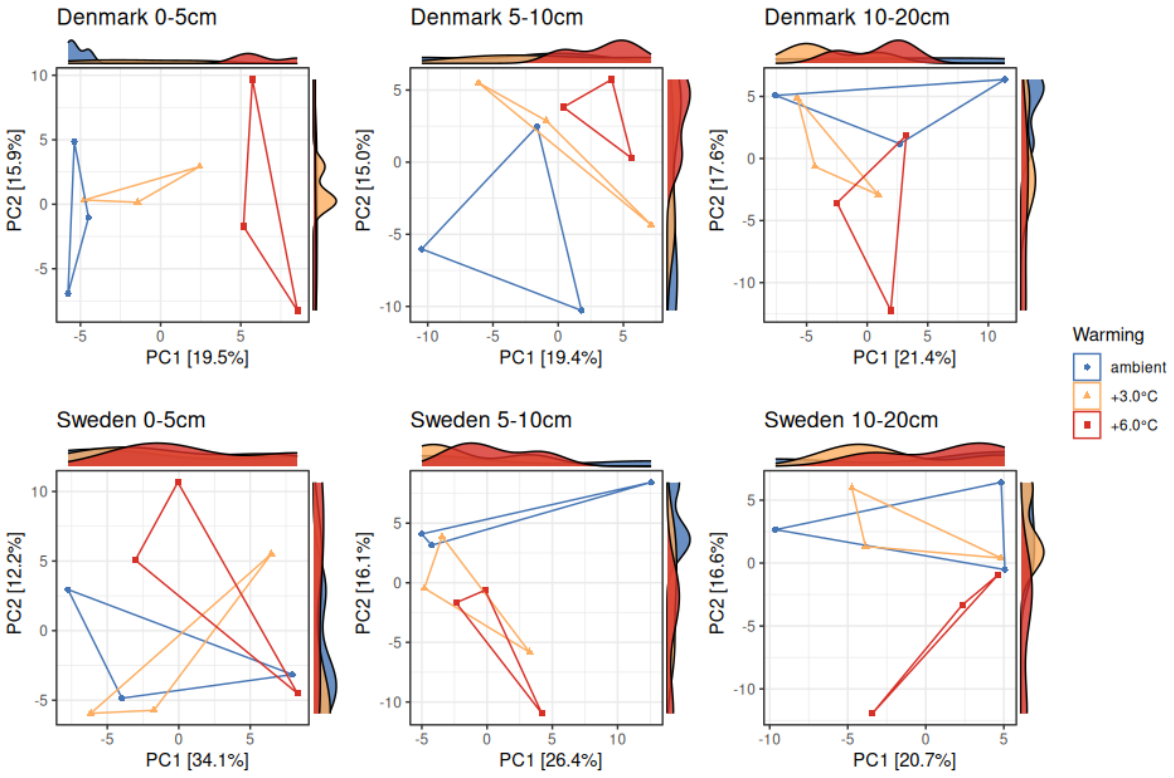


Figure 3: Principal Component Analysis (PCA) of center log-ratio transformed 16S rDNA community composition for sample subsets corresponding to the identified significant clusters (soil-sod and depth; Fig. 2). Soil-sods from Denmark are displayed in the top row, soil-sods from Sweden in the bottom row; sampling depths increase from left to right. Warming treatment triplicates are connected by lines (blue: ambient, orange: +3 °C, red: +6 °C).

5.4.2.Vegetation cover

Plant community composition varied strongly between Danish and Swedish mesocosms (Fig. S. 2). Danish soil-sods were dominated by the grasses *Phragmites australis* and *Elymus repens*; other species, such as *Viccia cracca* covered less than 10%. Swedish soil-sods had higher plant diversity, grasses, such as *Phragmites australis* and *Agrostis stolonifera* were present, but less abundant as in Danish soil-sods. During the experiment tree shoots of *Alnus glutinosa* and *Betula pubescence* emerged from inherent seed banks, covering up to 45% in individual mesocosms.

5.4.3.Exoenzyme activity

Swedish mesocosms consistently showed higher variation in exoenzymatic activity compared to Danish mesocosms (Fig. 5 A & B). According to the mixed effect ANOVA, Carbon- (ß-glucosidase + cellobiosidase, $p < 0.001$), nitrogen- (leucine-aminopeptidase + chitinase, $p < 0.01$) and phosphorous-

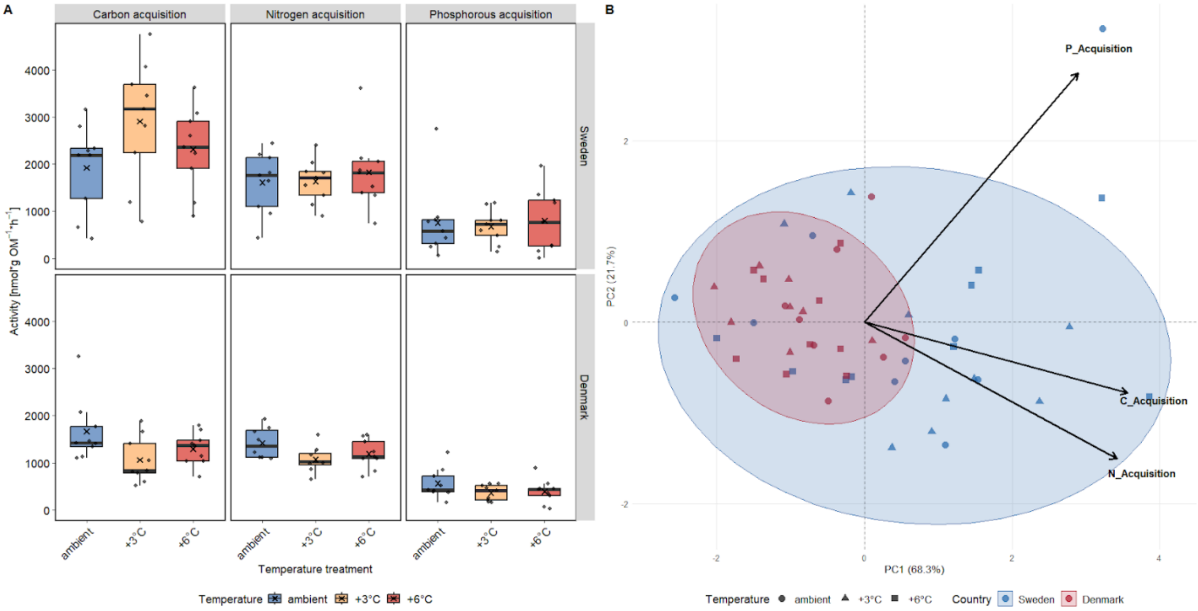


Figure 5: Exo-enzymatic activities of carbon- (ß-glucosidase + cellobiosidase), nitrogen- (leucine-aminopeptidase + chitinase) and phosphorus- (phosphatase) acquiring enzymes, across three temperature treatments (ambient, +3.0°C, +6.0°C), two soil-sod origins (Denkmark, Sweden) and three soil depths (0-5 cm, 5-10 cm, 10-20 cm). A: boxplots for individual marsh origin and warming treatments, B: PCA of carbon-, phosphorus- and nitrogen acquiring Enzymes.

(phosphatase, $p < 0.05$) acquiring enzymes were all significantly lower in soil-sods from Denmark compared to soil-sods from Sweden (Fig. 4 A). Depth led to significantly lower carbon- ($p < 0.001$) and nitrogen- ($p < 0.01$) acquisition, phosphorus acquisition did not differ significantly between depths ($p = 0.22$). While temperature treatment did not significantly affect the exo-enzymatic activities (all enzymes $p > 0.05$), there was a significant interaction effect of temperature treatment and country for the carbon acquiring enzymes ($p < 0.01$). Intermediate warming (+3.0°C) increased the microbial carbon acquisition in Swedish soil-sods, the effect is oppositely directed in soil-sods from Denmark (Fig. 5 A). When exoenzymatic activity is correlated with soil organic matter content, the two origins show diverging effects with negative and positive relationships between exoenzymatic activity and soil organic matter in Danish and Swedish origins, respectively (Fig. S. 3)

5.4.4. Differential abundance of microbial taxa

1% of overall relative abundances of individual taxa significantly changed in abundance with warming treatment, which was highest in uppermost soil layers from Danish mesocosms. A few additional taxa were also identified for sampling depths of 5-10 cm in Danish and Swedish soil-sods (Fig.6). All identified taxa that changed with warming are displayed in the Cladogram (Fig. 7). Approximately half of the warming-responsive taxa increased in relative abundances with warming.

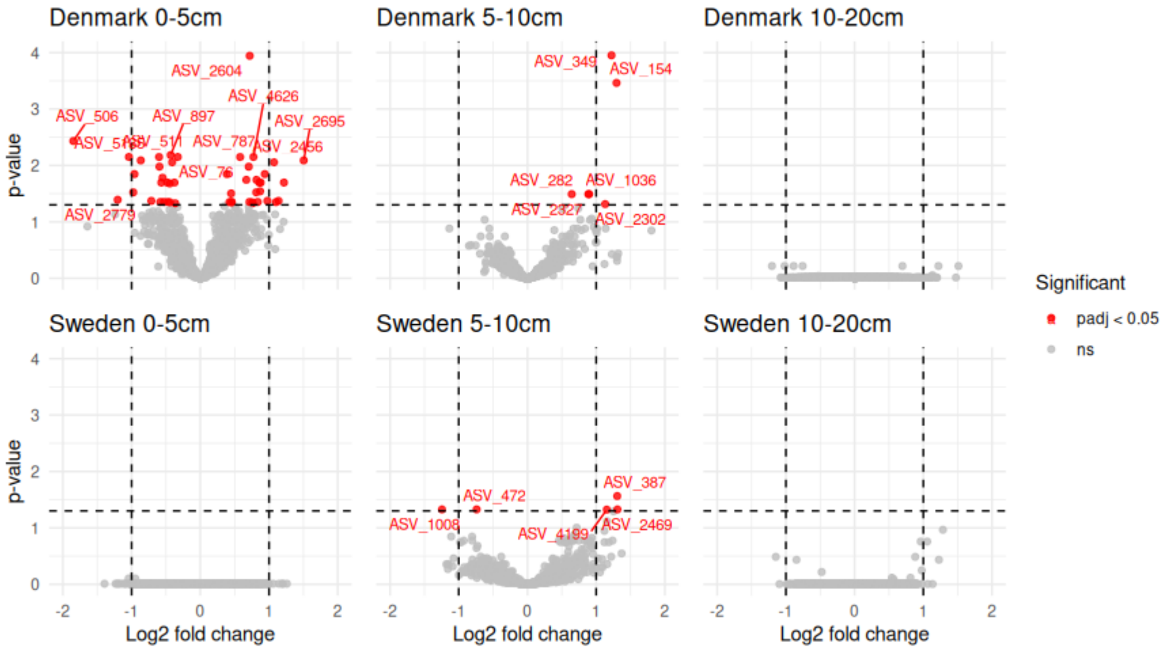


Figure 6: Differential abundance analysis for sample subsets corresponding to the identified warming clusters (Fig. 3). Volcano plots display log2 fold changes (x-axis) in Amplicon sequence variants (ASV) abundance in response to warming, with adjusted p-values on the y-axis. Each point represents an individual ASV; red points indicate statistically significant changes in ASV (benjamini-hochberg-adjusted p-value < 0.05). Positive fold changes indicate increased abundance and negative values indicate decreased abundance under warming.

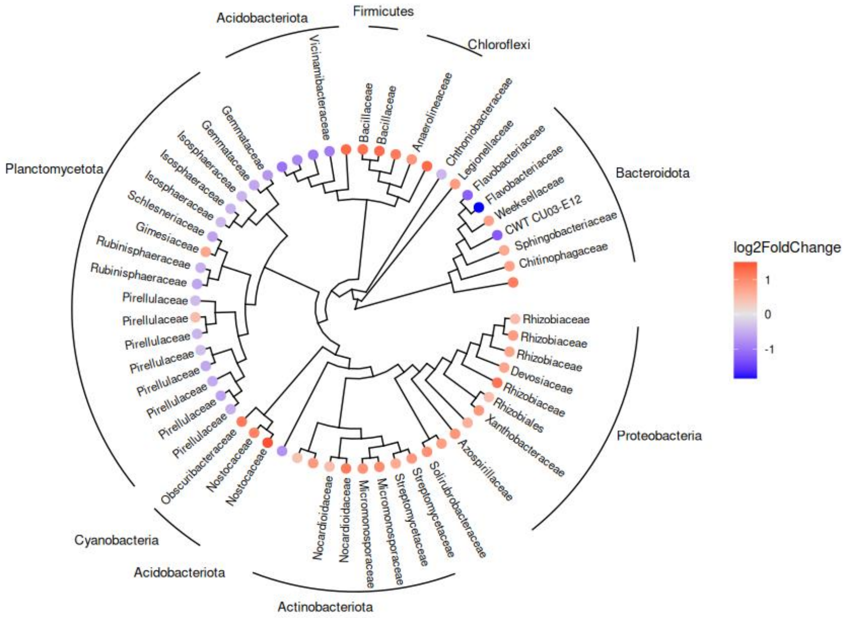


Figure 7: 16S rRNA based cladogram of taxa that changed significantly in response to the warming treatment (compare Fig. 6). Tip color indicates direction of change: red for increased abundance and blue for decreased abundance in response to warming. Tip labels are family, site labels are phylum.

5.5. Discussion

Our study demonstrates that warming can alter the prokaryotic soil community composition of Nordic coastal marsh soils within two vegetation periods - an effect not previously reported. So far, warming experiments across various ecosystems did not identify shifts in microbial community composition within five or less years of warming (DeAngelis et al. 2015; Wilson et al. 2016; Pei et al. 2024). This may seem surprising, considering that temperature is a fundamental environmental variable for microorganisms (Dal Bello and Abreu 2024). It has been argued that potential short-term warming effects on soil microbial communities are minor compared to the control of ecosystem type and vegetation composition, vertical stratification with soil depth and seasonality (Wilson et al. 2016; Pei et al. 2024). Instead, a high degree of functional redundancy within microbial communities can result in a short-term adaptation of microbial activity and metabolism in response to warming without detectable community shifts (DeAngelis et al. 2015). An exception from this absence of changes in microbial community composition to warming is the SWELTER experiment in the moist lowland tropical forest, Panama, where a large shift towards thermotolerant species with warming (up to +8°C) was identified after 2 years (Nottingham et al. 2022b), supporting the notion that the sensitivity of soil microbial communities to warming is more pronounced in the tropics, where temperatures are already close to their physiological optimal temperatures (Nottingham et al. 2022a; Nottingham et al. 2022b; Dal Bello and Abreu 2024).

In general, findings of the present study follow results of previous studies (DeAngelis et al. 2015; Wilson et al. 2016; Naylor et al. 2022), with microbial community composition being shaped firstly by soil-sod origin and secondly by soil depth (Fig. 2). However, when microbial community composition is stratified by origin and soil depth (Fig. 3), warming related shifts in the community composition become apparent particularly in surface samples derived from Denmark. A reason for the distinct finding compared to previous studies may be the higher soil temperatures compared to our study, obtaining up to +6°C, whereas previous findings from Pei et al. (2024) achieved relatively modest aboveground warming with open top chambers (+0.6 °C). However, even in studies employing active warming, effects on microbial community composition have not been observed within 2 years. For instance, in a forest ecosystem, a shift was only detected after 20 years of continuous warming of +5 °C (DeAngelis et al. 2015). In a deep peat heating experiment with warming treatments of up to +9 °C, no shift in microbial community composition was observed after 13 months of treatment (Wilson et al. 2016).

The absence of temperature-related shifts in microbial community composition in active warming experiments is unlikely a true absence of microbial response. It is often argued that physiological adaptations outweigh compositional changes, or that the variability in microbial communities is too high to detect a consistent shift (DeAngelis et al. 2015; Wilson et al. 2016; Hopple et al. 2020). This argument is supported by a peatland warming experiment where a strong increase of temperature related methane emissions for the upper peat layers was observed (Wilson et al. 2016; Hopple et al. 2020).

The warming effect on soil microbial community composition was determined by wetland origin, being pronounced in the soil-sods from Denmark, but hardly detectable in the soil-sods from Sweden. We argue that at least two non-exclusive mechanisms explain the origin-specific response to warming: differences in ecosystem age (or successional stage) and plant community composition.

Differences in the successional stage between sites might explain the contrasting community response to warming. The Danish marsh site is approximately 125 years old, whereas the Swedish site is only 35 years old (Leiva-Dueñas et al. 2026). This contrast in ecosystem age is particularly relevant in the context of microbial succession theory, predicting that the initial establishment of microbial communities in the early phase of ecosystem development is mainly driven by stochastic processes, meaning that the microbial community composition is formed at random. With time the community is increasingly structured by environmental filters, to finally form a mature strongly structured community (Dini-Andreote et al. 2015). In support of this concept, our data demonstrates a much clearer differentiation of microbial community composition with soil depth in the Danish than Swedish mesocosms. Soil-sods that originated from the younger Swedish site exhibit the structure of an intermediate succession stage, where microbial communities are not yet thoroughly structured by sampling depth, but a depth pattern emerges. Samples from the older Danish marsh are well stratified by depth, with distinct community compositions for each sampling depth (compare Fig.2).

Based on this framework, we interpret the differing responses to warming as an additional environmental filter, at the two sampling sites as follows (Dini-Andreote et al. 2015; Guo et al. 2018): In soil sods originated from the mature, well-structured Danish coastal wetland, the warming treatment introduces a relatively strong “disturbance”. The more specialized community might be forced into a stronger restructuring, which we can identify as a warming response, especially in the upper soil layers. In contrast, samples from an earlier successional stage, such as the Swedish coastal wetlands, harbor microbial communities that are still in the process of adapting to the environmental conditions. As a result, these communities may initially accommodate warming-induced disturbance without observable shifts due to their greater ecological flexibility and functional redundancy. The greater physiological range in microbial communities from Sweden is also reflected in the higher variability of exoenzymatic activities (Fig. 5). However, it is likely that in both coastal wetlands, experimental warming will ultimately act as a deterministic environmental filter that imposes strong selective pressure on microorganisms (Guo et al. 2018; Seidel et al. 2023).

Given the well-established bi-directional interactions between plants and microbes, the observed differences in plant diversity and community variation between mesocosm origins likely plays a key role in shaping microbial responses to warming (Mueller et al. 2020a; Tang et al. 2021; Haviland and Noyce 2024; Pei et al. 2024). In the Swedish mesocosms we observed higher plant diversity and compositional variability with a larger share of early- and mid-successional species but also *Phragmites australis* (Fig. 4). The higher plant diversity in the soil-sods from Sweden is likely associated with a wider range of plant traits affecting the soil microbial community, such as species-specific differences in rooting depth, root exudation quantity and profile or radial oxygen loss (Mueller and Megonigal 2024). As a result, the soil microbial community may be adapted to a more diverse set of soil environmental conditions, with a wide range of physiological traits, and possibly a higher degree of functional redundancy (Guo et al. 2023; Schmid et al. 2021). We suggest that this may also lead to a more generalist microbial community capable to better adapt to temperature changes without inducing detectable shifts in microbial community composition. The comparably low plant diversity (*Phragmites australis* and *Elymus repens as* two dominating grass species) in Danish communities thereby reinforce the rather stable and mature community. *Phragmites australis* is typical for later successional stages of coastal wetlands (Packer et al. 2017), and *Elymus repens* is a highly competitive colonizing plant on a wide range of soil conditions (Ringselle et al. 2020). Here the lower diversity in vegetation may be accompanied by a lower degree of functional redundancy in the microbial community. However, the experimental design of this study and the obtained data, are not sufficient to directly assess the relationship between plant community composition and diversity and soil microbial responses to warming. These interactions remain poorly understood, and future research will require targeted experimental approaches to disentangle the complex links between vegetation composition, successional stage, and microbial community dynamics under changing temperature regimes.

An origin-specific warming response was also observed in exoenzymatic activities. Similar to the variances in vegetation composition, exoenzymatic activities were more variable in mesocosms from Sweden compared to the ones from Denmark (Fig. 5). The higher variability in exoenzymatic activities in Sweden further emphasizes the effect of younger successional stages of these mesocosms. An origin-specific warming response was also observed in carbon-acquiring exoenzyme activities. Carbon acquisition rates tend to increase with warming for soil-sods derived from Sweden, but in contrast tend to decrease in soil-sods from Denmark. This may be related to the organic matter content, which is lower in the younger soil-sods from Sweden. Here, the availability of carbon may be limited with increased temperatures, so carbon acquiring enzymes are increased.

Additional considerations for differences in microbial community responses to warming between sample origins: Successional stage and vegetation composition are closely linked: ecosystems in earlier successional stages typically host more generalist plant communities, while late-successional systems tend to be dominated by a few well-adapted species. In addition, soil microbial communities themselves steer plant diversity, thus the described effects are bidirectional (van der Heijden et al. 2008). Another important factor, not discussed, are soil physicochemical properties, as strong environmental filters that determine the composition of microbial communities and likely have contributed to the observed differences (Xia et al. 2020; Schmid et al. 2021; Naylor et al. 2022). These plant-soil-microbe interactions highlight the need for additional manipulative experiments to disentangle the relative contributions of individual factors on microbial community responses.

5.5.1. Warming responses of individual microbial taxa

In addition to community-level responses, we identified microbial taxa that showed significant changes in relative abundance in response to warming, comprising approximately 1% of the total detected taxa. Most of these were from soil-sods from Denmark, and derived from the upper 5 cm (compare Fig.4). These findings indicate that specific prokaryotic taxa do respond to elevated temperatures, even within a relatively short experimental timeframe of two vegetation periods (Fig. 4 and 5).

Increased temperatures led to a consistent rise in Actinobacteriota abundance, in line with previous long-term warming studies (Deslippe et al. 2012; Oliverio et al. 2017; Wu et al. 2022). This response likely reflects their metabolic capacity to utilize complex carbon and nitrogen sources such as chitin and chitosan (Lacombe-Harvey et al. 2018). This is in line with an increase in leaf $\delta^{15}N$ isotopic signature data, pointing towards microbial mobilization of nitrogen in response to warming, supporting aboveground biomass (Logemann et al. submitted). Enriched families included Micromonosporaceae, Nocardioidaceae, and Streptomycetaceae, all known for their ability to degrade complex organic compounds and contribute to nutrient cycling, particularly nitrogen and phosphorus (Evtushenko et al. 2015; Ma et al. 2023; Montes-Montes et al. 2024). These functional traits may have a competitive advantage under warming while outcompeting other taxa better adapted to nutrient poor conditions and lower temperatures.

Similarly, we identified increased relative abundance of the phylum Proteobacteria, which was also found in long-term warming studies (DeAngelis et al. 2015; Oliverio et al. 2017). The family Rhizobiacea is closely associated with the rhizosphere, not only as symbiotic nitrogen-fixer in legume root nodules, but also as free-living nitrogen-fixers in non-legumes (Garrido-Oter et al. 2018; Burghardt and diCenzo 2023). The only identified legume growing in our soil-sods is *Viccia cracca*, which occurred only in low coverage in those soil-sods from Denmark where the strongest microbial temperature response was observed. The coverage of *Viccia cracca* does not follow a temperature pattern (data not shown), thus the increased relative abundance of Rhizobiales is probably linked to free living taxa. Unlike in our study, host-specific Rhizobiales decreased in abundance under warming in a study investigating

Sphagnum moss, indicating that host-microbe interactions may modulate warming responses differently compared to bulk soil and depending on ecosystem and location (Carrell et al. 2019). Taxa of the family Azospirillaceae, also belonging to the phylum of Proteobacteria, are known to be beneficial for plants, for example through phytohormone production that help plants to tolerate stress or associative nitrogen-fixation and are often closely associated with grasses (Fukami et al. 2018; Li et al. 2021). Nitrogen-fixation is characteristic for the free-living Cyanobacteria (Stal 2015), among which we identified three warm-responsive taxa. The family Obscuribacteraceae was recently affiliated with the Cyanobacteria phylum although they were described as anaerobic and non-phototrophs (Soo et al. 2014). However, this group was associated with metabolic versatility and potentially with phosphate metabolism (Soo et al. 2014) and may, thus, also contribute to higher carbon turnover in response to rising temperatures. Two taxa of the family Bacillaceae in the phylum Firmicutes increased in abundance with warming, which is consistent with other long-term studies (Oliverio et al. 2017; Wu et al. 2022). Their ability to grow rapidly when conditions are favourable, and their plant growth promoting traits, may be advantageous under warmer conditions (Mandic-Mulec et al. 2015). Warm responsive taxa among the phylum Chloroflexi, are related to soil nitrogen and phosphate cycling. Chloroflexi can ferment complex polymers, and the family Anaerolineae is known as thermophylic (Yamada et al. 2006; Speirs et al. 2019). Despite mixed results in the literature, these functional capabilities may explain their higher abundance under warming in our system (Oliverio et al. 2017; Dahl et al. 2023; Liu et al. 2024b).

Within Bacteroidota, responses were variable. Some taxa, particularly within Chryseobacterium (Weeksellaceae), increased under warming. This group is known for nitrogen and phosphorus cycling and for plant interaction (Jung et al. 2023). Others, including Flavobacteriaceae, decreased, suggesting functional divergence within this phylum. Additional warm-responsive taxa within Sphingobacteriales and Chitinophagaceae may also contribute to enhanced nutrient turnover under elevated temperatures as reported before (Campos et al. 2023; Jia et al. 2024).

Plantomycetota generally declined in response to warming, potentially reflecting their known adaptation to cold, low-oxygen environments (Kulichevskaya et al. 2007; Kulichevskaya et al. 2016; Kulichevskaya et al. 2017; Kulichevskaya et al. 2020). This trend aligns with observations from long-term warming experiments, where similar decreases were reported (Jia et al. 2024; Wu et al. 2022). Although members of this phylum play important roles in nitrogen and phosphorus cycling, only two taxa showed an increase under elevated temperatures, indicating that most Plantomycetota may be outcompeted in warmer conditions (Wiegand et al. 2018; Dedysh et al. 2020).

Acidobacteriota were also predominantly decreasing in relative abundance, aligning with previous findings that many members of this diverse phylum prefer colder conditions (Luo et al. 2014; Huber and Overmann 2018; Wu et al. 2022). Still, also within Acidobacteria the temperature response was not fully consistent since one warm-responsive taxon within this group was also observed. This taxon may reflect functional heterogeneity, as members of Acidobacteriota were enriched in other long-term warming experiments as well (DeAngelis et al. 2015; Sikorski et al. 2022; Liu et al. 2024b).

Overall, warming favored taxa with traits supporting plant growth and nutrient cycling, particularly nitrogen and phosphorus mobilization. This shift may be induced directly through warming, as well as through plant mediated selection of microbes (Hartmann et al. 2009). Conversely, declines in cold-adapted, slow-growing taxa suggest a loss of functional groups tied to more oligotrophic, low-energy systems. Despite relying on a single time-point sampling, we detected prokaryotic community responses to warming, aligning with patterns observed in long-term experiments. However, warming effects were only clearly evident in soil-sods from Denmark, not Sweden, highlighting the importance of local ecosystem context and successional stage. While our snapshot study captures meaningful responses to environmental warming, long-term, seasonal monitoring will be critical to fully capture microbial dynamics under climate change.

5.6. Conclusion

Our study demonstrates that warming has an effect on soil microbial community composition in Nordic coastal wetland within just two vegetation periods. However, this effect depends strongly on wetland origin and possibly successional stage. A mature microbial community composition may inherit less functional redundancy and therefore are more prone to react to ecosystem changes such as global warming. These findings highlight the importance of local context in predicting microbial responses to climate change and underscore the importance of manipulative experiments to disentangle the relative contributions of individual global change drivers and plant-soil interaction. Further research is needed to assess the implications for the carbon-soil feedbacks under climate change.

5.7. Supporting Information

Table S. 1: Overview of the substrates and fluorophore standard used for exoenzyme assays

Enzyme	Substrate	Fluorophore standard (100 µmol/L)
Cellobiosidase (CEL)	4-MUF-ß-D-4-cellobioside	methylumbelliferone
β-Glucosidase (GLU)	4-MUF-ß-D- glucopyranoside	4-methylumbelliferone
Leucine-Aminopeptidase (LEU)	L-leucine-7-AMC	7-amido-4-methylcoumarin-hydrochloride
Chitinase (CHI)	4-MUF-N-acetyl-ß-D-glucosaminide	4-methylumbelliferone
Phosphatase (PHO)	4-methylumbelliferyl-phosphate	4-methylumbelliferone

Table S. 2. Permanova result

Factor	R2	p-value	Significance level
soil-sod origin	0.385	0.0001	***
Depth	0.126	0.0001	***
Warming	0.014	0.1501	

Table S. 3. Permanova results for Warming for stratified datasets

Dataset	R2	p-value	Significance level
Denmark 0-5 cm	0.183	0.0014	**
Denmark 5-10 cm	0.148	0.0833	
Denmark 10-20 cm	0.133	0.3073	
Sweden 0-5 cm	0.117	0.4382	
Sweden 5-10 cm	0.140	0.2256	
Sweden 10-20 cm	0.135	0.3241	

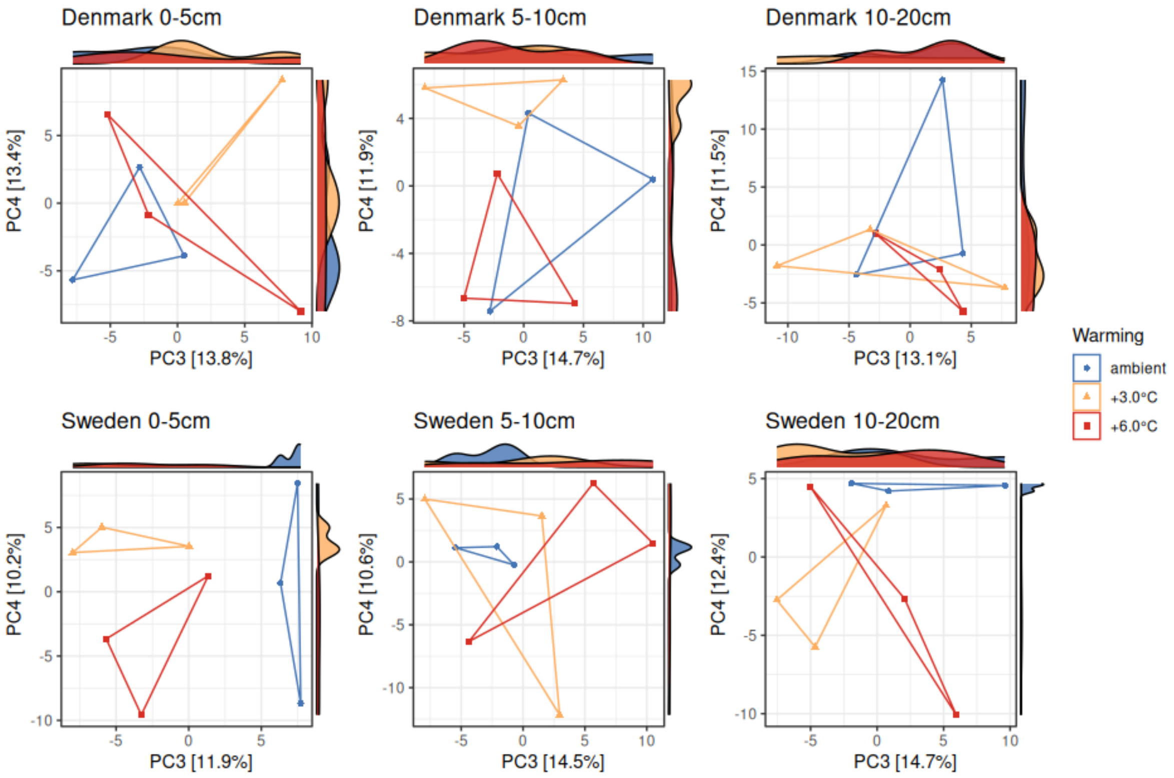


Figure S. 1: Principal Component Analysis (PCA) of center log-ratio transformed 16S rDNA community composition for sample subsets corresponding to the clusters shown in Fig. 1. PC3 and 4 are shown Samples from Denmark are displayed in the top row, those from Sweden in the bottom row; sampling depths increase from left to right. Warming treatment (blue: ambient, orange: +3 °C, red: +6 °C).

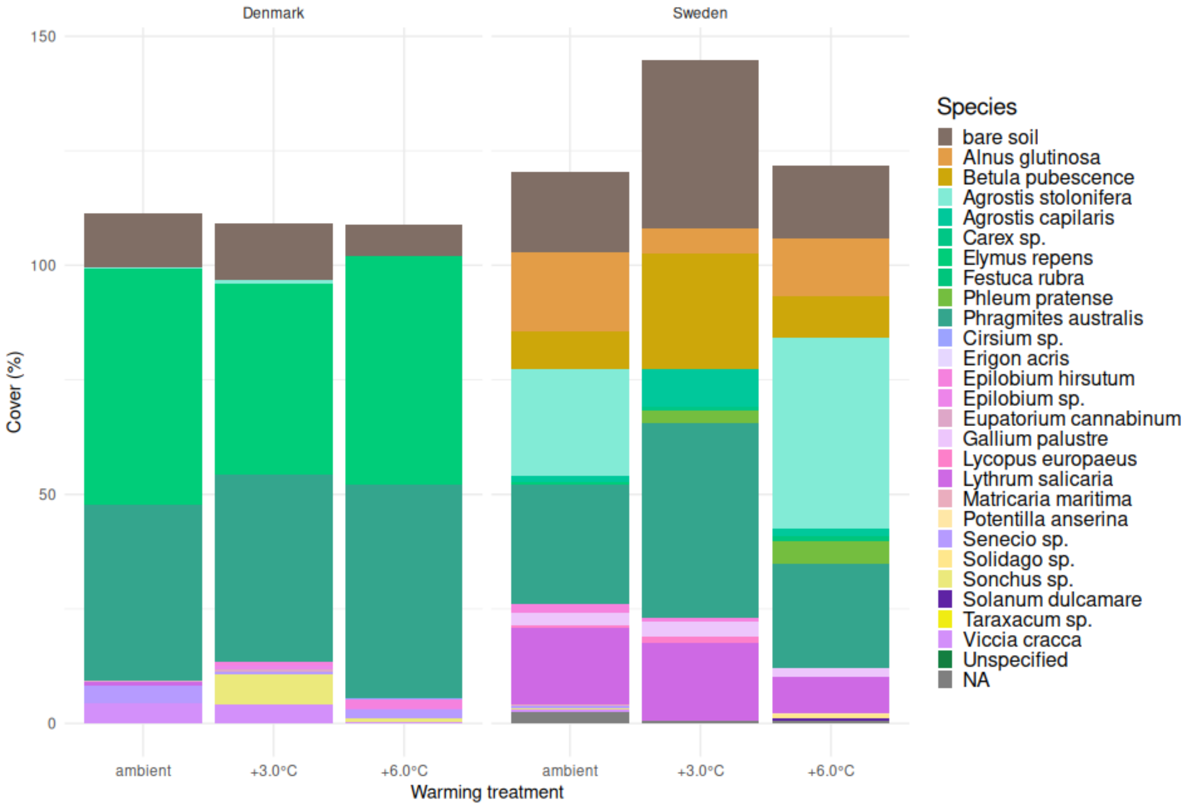


Figure S. 2: Average plant community composition for marsh soil sods separated by origin (Denmark left, Sweden right) and warming treatment. Plant species are distinct by color; grasses are in greens, trees in shades of brown and flowering herbs in pink and yellow shades.

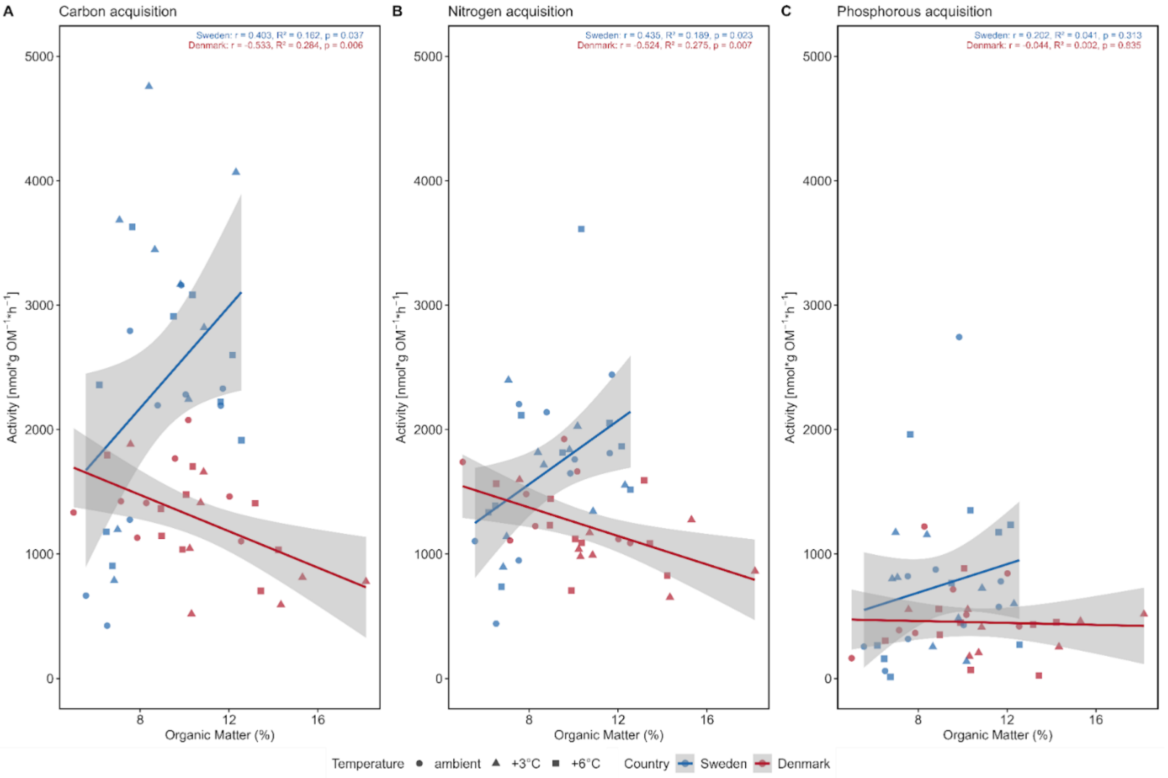


Figure S. 3: Exo-enzymatic activities of C,N, P- acquiring enzymes, for all temperature treatments against organic matter content for the two soil-sod origins Denmark (red) and Sweden (blue).

CHAPTER SIX

SYNTHESIS

6.1. Key points of all chapters

Chapter 2: Soil Organic Carbon Stocks Of German Salt Marshes: A Comparative Study Along Low- And High-Energy Coastlines

- Low-energy Baltic Sea salt marshes store more SOC on average than high-energy North Sea salt marshes.
- Grazing increased SOC density by enhancing soil compaction and thereby consistently increased SOC stocks in North Sea salt marshes. In contrast, grazing effects on SOC density in Baltic Sea salt marshes were equivocal and could be explained by induced changes in plant productivity.
- In North Sea salt marshes, the highest SOC density was found in the low marsh, most likely as increased aeration and associated SOM decomposition led to lower SOC density in high marsh soils.

Chapter 3: Plant Control On Soil Redox State Determines Grazing Effects On Methane Emissions From Coastal Wetlands

- Although livestock grazing was expected to increase methane emissions by lowering soil redox conditions through trampling, it instead decreased methane emissions across all sites.
- Methane emissions and grazing effects on methane emission varied strongly among sites, indicating that grazing alone was a weak predictor for methane emission.
- The underlying drivers for methane emission were grazing-induced shifts in plant community composition and structure, which altered soil redox conditions through changes in belowground biomass.
- Lower methane emissions in grazed areas may be explained by the exclusion of grazing-intolerant “high-flux” plant species such as *Phragmites australis*.

Box A: Unraveling Plant-Soil Interactions By Implementing An Experimental Approach: Effects Of Diversity And Hydrology On Carbon Cycling Of Coastal Wetlands

- Aboveground biomass was not significantly increased with higher plant diversity and did not differ between inundation treatments.
- Responses to inundation differed in aboveground biomass and in ability to reduce the soil on species level.
- Plants oxidized the soil under oxygen depleted soil conditions and reduced the soil in the less oxygen depleted soil.

Chapter 4: Plant-Soil Interactions Determine Coastal Wetland Carbon Cycle Response To Rising Temperatures

- Active feedback-control warming in a marsh mesocosm facility increased plant-available nitrogen and enhanced aboveground biomass in Baltic coastal wetlands.
- Plant communities with nitrogen-fixing plants were able to counteract the warming-induced biomass response likely due to alternative nitrogen acquisition strategies.
- During 16 months of warming, SOM decreased in systems with soils initially rich in SOM, associated with strong warming-induced increases in aboveground biomass.

- Wetland ecosystem carbon (biomass and SOM) responses to warming depend on the initial resource status of the ecosystem.

Box B: Physiological traits of *Phragmites australis* under warming

- Physiological traits of *Phragmites australis* of two tall-grass communities (Denmark and Sweden) were assessed in the CCMMF.
- Photosynthetic capacity (V_{cmax}), water use efficiency (stomatal conductance and foliar $\delta^{13}C$) remained unchanged under warming.
- Together, these results indicate that warming did not induce physiological acclimation in *Phragmites australis*.

Chapter 5: Warming Effects On Microbial Community Composition In Nordic Coastal Marsh Soils

- Soil microbial communities differed between Baltic tall-grass marsh communities originating from Denmark and from Sweden and were significantly stratified along the soil depth profile.
- Active warming applied to marsh mesocosms induced clear shifts in microbial communities within the uppermost soil layers (0–5 cm; 5–10 cm) of the Danish tall-grass marsh community, but not in Swedish microbial communities of the tall-grass community.
- The contrasting responses to warming between marsh origins are likely explained by their different successional stages: the Danish marsh represents an older, more mature system with lower plant diversity, where the more specialized microbial community experienced stronger restructuring under warming.
- Approximately 1% of all identified taxa showed either higher or lower relative abundances. Taxa with increased relative abundance included those known to promote nutrient cycling, plant growth, and the breakdown of complex organic molecules, whereas taxa with decreased relative abundances were primarily associated with adaptation to cold and low-oxygen environments.

6.2. Blue Carbon in Northern European Coastal Marshes

6.2.1. Potential of Northern European Coastal Marshes in Climate-Change Mitigation

There is a growing interest among decision-makers in developing strategies for managing blue carbon ecosystems, such as coastal wetlands, in order to optimize their carbon sequestration potential (Macreadie et al. 2021; Koplin et al. 2025). However, this management interest has progressed more rapidly than (i) the scientific process understanding on carbon cycling in coastal wetlands and (ii) the regional quantifications of carbon stocks and sequestration rates. While numerous studies on carbon stocks in coastal systems have been conducted in North America (Chmura et al. 2003; Bridgham et al. 2006; Kirwan and Mudd 2012; Holmquist et al. 2018), Australia (Owers et al. 2020; Navarro et al. 2021; Young et al. 2021; Lovelock et al. 2022) and in some tropical regions (Thorhaug et al. 2020), the national quantification of carbon stocks in European coastal marshes has only recently begun (Mason et al.

2022; Leiva-Dueñas et al. 2024). Studies that were conducted in the framework of this thesis, namely chapter 2-4, as well as three additional co-authored studies (Graversen et al. 2025; Koplin et al. 2025; Leiva-Dueñas et al. 2026) have substantially contributed to the advancements to regional quantifications of the blue carbon potential of Northern European Coastal Marshes. The following section compares the blue carbon potential of different Northern European coastal marshes and synthesizes findings from this thesis (Chapters 2–4), Leiva-Dueñas et al. (2026; same study sites as investigated in chapter 4) and published data to derive an integrated assessment of their (future) carbon sequestration potential.

Globally, coastal wetlands/marshes store an average of 83 Mg C/ha in their top 30 cm (Maxwell et al. 2023). We found German Baltic Sea marshes to be on average above (106 Mg C/ha) and German North Sea marshes were on average below (57 Mg C/ha) this global value. In Leiva-Dueñas et al. (2026), we assessed carbon stocks of Nordic salt marshes (Denmark, Sweden, Finland, Norway) and found a (lower) median of 69 Mg C/ha across all sites. This study uses the method established by Smeaton et al. (2023) to calculate carbon stocks, in which only the marsh SOC stock is considered by subtracting the “background” OC stock from the ‘underlying’ marine sediments. Consequently, soil depth was not standardized and varied between 15 and 35 cm (Leiva-Duenas et al., under review). Within this study, Danish marshes had the highest carbon stock (78 Mg C/ha), whereas Swedish, Finnish and Norwegian marshes had carbon stocks that were much lower than the global average (25, 38 and 43 Mg C/ha, respectively). Overall, we demonstrate that southern Baltic salt marshes (Germany and Denmark) had the highest SOC stock, followed by German and Norwegian North Sea marshes and lastly northern Baltic marshes (Sweden and Finland; see chapter 2 and Leiva-Duenas et al., 2026).

Methane emissions of salt marshes differed between the German coastlines with higher emissions in Baltic marshes than in North Sea marshes (chapter 2). Within the Nordic sites at the Baltic Sea investigated by Leiva-Dueñas et al. (2026), methane emissions were higher in Finnish marshes than in Danish marshes (only those two sites were sampled within this study). Baltic marshes in Germany and Denmark showed similar emission levels (chapter 2 and Leiva-Dueñas et al. 2026). These findings further support the well-established knowledge that increasing salinity (specifically sulfate) leads to lower methane emissions (Poffenbarger et al. 2011; Davidson et al. 2021; Arias-Ortiz et al. 2024), with methane emissions following a clear salinity gradient (chapter 3 and Leiva-Dueñas et al. 2026): highest emissions in the oligohaline Finnish marshes (4-5 psu), intermediate emissions in the mesohaline German and Danish Baltic marshes (8-18 psu), and negligible emissions in the polyhaline German North Sea marshes (about 30 psu).

Table 1: Overview of blue carbon function and potential of different Northern European coastal marsh types in relation to morphological characteristics. The table synthesizes results of studies included in this thesis (chapter 2 -4), the study of Leiva-Duenas et al. (2026) and considers other relevant studies (mentioned in the text). Leiva-Dueñas et al. (2026) conducted carbon stock and accumulation rate assessments at the sites from which soil-vegetation sods were taken for the mesocosm experiment presented in chapters 4 & 5; SLR = sea level rise

	North Sea marshes	**Southern Baltic marshes**	**Central Baltic marshes**
Soil morphology	Mineral marsh with high silt deposition	Organic marsh with highly organic (top)soils	Mineral marshes with highly organic and shallow topsoils on top of glacial clay
Tidal influence	Meso-tidal	Micro-tidal	Non-tidal
Salinity	High	Medium	Low
Vertical marsh accretion	Fast	Medium	Low
SOC stock	Slightly below global average	Above global average	Below global average
Methane emissions	Negligible emissions	Low emissions	High emissions
Current climate benefit	Medium	Low-medium	Low
Future risk	Expected persistence under SLR; Consistent and stable carbon burial; Warming effect likely neutral for SOC stock	Uncertain persistence Risk of SOC loss due to erosion and warming	Potentially stable SOC stock under SLR (due to land uplift) and under warming but negligible overall SOC sink

Within the framework of this thesis, I propose the broad-scale differentiation of three marsh types for evaluating their Blue Carbon potential of northern European marshes: (1) North Sea marshes with mineral soils due to high tidal influence and high sediment deposition, where organic carbon is frequently sequestered but substantially diluted by mineral inputs; (2) southern Baltic marshes with highly organic soils with low sedimentation rates and low vertical accretion; and (3) central Baltic marshes as mostly mineral systems with organic and shallow top soils in which the mineral fraction of the soil is primarily derived from glacial clay as subsoils.

Nevertheless, the current and future climate benefit of southern Baltic marshes is likely low and potentially negative, as they are increasingly threatened by erosion (Weisse et al. 2021, personal communication by local managers). In the future, this risk is expected to increase further with sea-level rise (SLR), particularly in systems with low vertical accretion (Kirwan et al. 2016) such as coastal marshes along the Southern Baltic Sea. In these marshes, external sediment supply is limited, as deposition occurs predominantly during extreme events (Dijkema 1990), which prevents consistent vertical growth. Methane emissions - although comparable to the global average for salt marshes (Rosentreter et al. 2021b) - further diminish their overall climate-change mitigation potential (chapter 2; Leiva-Dueñas et al. 2026). The mesocosm warming experiment carried out in this thesis (chapter 4) additionally revealed an overall SOM loss in SOM-rich soils (short-grass communities from Denmark;

southern Baltic), highlighting the high vulnerability of stored carbon to environmental change. Taken together, the higher risk of carbon loss in Southern Baltic coastal marshes compared to Central Baltic or North Sea marshes can be attributed to high erosion and SOC decomposition potential under SLR and warming, and thus potentially turn these systems into a carbon source. Accordingly, I recommend prioritizing the protection of these old coastal marshes (often older than 250 years) in the southern Baltic Sea, rather than expanding efforts to artificially promote marsh establishment.

The same conclusion applies to coastal wetlands in the central Baltic, where both SOC stocks and SOC accumulation rates are much lower than the global average (Mcleod et al. 2011; Maxwell et al. 2023; Leiva-Dueñas et al. 2026), while methane emissions exceed global averages (Rosentreter et al. 2021b; Leiva-Dueñas et al. 2026). In the mesocosm warming experiment carried out for this thesis (Chapter 4), no significant SOM loss or gain was observed for these coastal wetlands originating from the central Baltic Sea coastlines (Sweden and Finland). I therefore conclude that although high methane emissions likely offset much of the carbon storage potential, the relatively small carbon stocks in central Baltic coastal wetlands (Sweden and Finland) appear stable under future warming. However, coastal wetlands in the central Baltic are likely to be transient systems, since land uplift currently outpaces sea-level rise (Weisse et al. 2021). As they gradually transition into uplands, the consequences for their carbon stocks remain unclear.

In the mineral North Sea (Wadden Sea) marshes examined in this thesis, organic carbon stocks are lower than the global average. This is largely because sequestered carbon is diluted with mineral sediments and because these systems are comparatively young, owing to extensive land reclamation and diking of mature marshes that continued into the twentieth century (Dijkema 1990; Elschot et al. 2024). However, considering their young age, the organic carbon stocks are relatively high, in many sites approaching or even exceeding those of the Baltic Sea marshes, which are often more than twice as old. Mueller et al. (2019b) measured carbon accumulation rates at three sites and reported values near the global average (Mcleod et al. 2011). Young marshes generally accumulate carbon rapidly, with rates stabilizing as they mature (Miller et al. 2022). North Sea salt marshes, however, may maintain an elevated carbon sink potential in the near future owing to their accommodation space and regressive dynamics, enabling vertical growth with SLR and continued carbon stock increases through both aging and new marsh formation (Rogers et al. 2019; Miller et al. 2022; Elschot et al. 2024). Although organic carbon is comparatively diluted in these stocks, I expect stable, broadly average future carbon sequestration potential. Future climate change impacts on mineral marshes of the North Sea were not tested within the framework of this study. However, another investigation at one of the sampled North Sea marshes (Hamburger Hallig; chapter 2) found only marginal belowground biomass responses to warming and concluded that soil-stabilizing functions are likely to persist under future warmer conditions across the different salt marsh zones (Menzel et al. 2025). Furthermore, I suggest that potential positive aboveground biomass responses to warming could additionally enhance plant-sedimentation feedbacks, thereby enabling the marsh platform to keep pace with accelerated rates of SLR (Fagherazzi et al. 2012; Nolte et al. 2013a; Kirwan et al. 2016). Even in the absence of strong bio-geomorphic feedbacks, North Sea salt marshes have a high likelihood of persistence under accelerated rates of SLR, supported by ample accommodation space and rapid vertical accretion (Suchrow et al. 2012; Mueller et al. 2019b; Rogers et al. 2019; Elschot et al. 2024). Collectively, these factors indicate a strong potential for North Sea marshes to function as reliable, long-term carbon sinks.

6.2.2.Grazing in Northern European Coastal Marshes: Implications for Blue-Carbon Potential

Livestock grazing and mowing for hay making as management tools have a long-lasting tradition in European marshes. Moreover, diking has been carried out over centuries both for coastal protection and for turning coastal (tidal) wetlands into agricultural fields without tidal inundation. Diking also resulted in strong alterations of the coastline (Jutila 2001; Tessier et al. 2003; Barr and Bell 2017; Elschot et al. 2024). Management implications for blue carbon cycling - particularly in European contexts - represent a relatively recent field, and there is an emerging need to address knowledge gaps in management strategies for implementing these systems as nature-based carbon solutions (Koplin et al. 2025).

Results of chapter 2 show that grazing has an overall positive effect on salt-marsh carbon storage. The mechanism aligns with prior work that demonstrated how grazing-induced trampling leads to soil compaction, which increases bulk density (Nolte et al. 2013b) and alters pore connectivity (Keshta et al. 2020). These physical changes increase water saturation and soil moisture, thereby reducing soil oxygen availability and suppressing microbial activity (Mueller et al. 2017; Keshta et al. 2020). In North Sea salt marshes, our data corroborate this pathway - livestock grazing increased soil bulk density and, in turn, enhanced carbon storage. By contrast, neither the Baltic Sea marshes in Germany analyzed in chapter 2 nor our *in-situ* study on Baltic marshes in Finland, Sweden, and Denmark (Leiva-Dueñas et al. 2026) exhibited a detectable grazing effect on bulk density or soil carbon storage, underscoring the context dependence of grazing outcomes (Ford et al. 2021).

Surprisingly, grazing was a weaker determinant than anticipated, as it did not exert uniform effects on either SOC stocks or methane emissions, nor did it consistently control the (increasing or decreasing) direction of SOM or aboveground biomass responses to warming (chapter 2-4). In chapter 2, I argue that the effects of grazing-induced trampling in Baltic Sea salt marshes are largely negligible because they tend to have higher sand content compared to the fine-grained soils of the North Sea salt marshes. This higher sand content has been shown to mitigate the potential impact of trampling on soil compaction (Schrama et al. 2013; Keshta et al. 2020). However, despite this, we did observe bidirectional grazing-induced effects in the two Baltic sites presented in chapter 2 as grazing increased

SOC stock in one site and decreased the SOC stock in the other site. These effects can be explained by variation in plant response to grazing, specifically changes in belowground biomass. Consistent with these equivocal SOC responses under grazing presented in chapter 2, the role of grazing-induced shifts in plant community structure and related traits is further emphasized in chapter 3. Rather than exerting a uniform effect on methane emissions, grazing influenced methane emissions indirectly through changes in belowground biomass and the resulting shifts in soil redox conditions and substrate availability. Lastly, across different Baltic sites, aboveground biomass and SOM content did not show clear responses to management in the experimental mesocosm warming experiment (chapter 4). Instead, SOM quantity emerged as a stronger predictor of warming responses in aboveground biomass rather than grazing itself. While SOM itself can be altered by grazing, as discussed previously, our results did not reveal clear directional effects of grazing on SOM in this warming study. In summary, our findings laid out here, emphasize the importance of plant-mediated pathways in shaping grazing effects on SOC, rather than revealing a consistent direct grazing effect. For future management practices, it is important to recognize that the direction of change in SOC storage and ecosystem warming responses under grazing are strongly contingent on initial plant species composition and geomorphological context. Consequently, grazing cannot be considered a universal management tool with predictable outcomes for carbon storage and climate mitigation.

6.3. Identifying plant traits as mediators of carbon dynamics

Plant traits mediating SOC dynamics in wetlands can be primarily categorized into two functional aspects: gas transport through plant tissues and organic matter input into soils. Aerenchyma facilitate bidirectional gas transport through the plant, serving a dual function with regard to greenhouse gas emissions and carbon cycling of coastal wetlands: they act as conduits for methane from deeper soil layers to the atmosphere (Armstrong 1980; Waldo et al. 2019) and they also enable oxygen transport into the rhizosphere, increasing oxygen concentration in the soil and potentially accelerating SOM decomposition and enabling methane oxidation (Lai et al. 2012; Koop-Jakobsen et al. 2021; Haviland and Noyce 2024; Mittmann-Goetsch et al. 2024). Organic matter input quantity and quality have been identified as significant predictors explaining local *in-situ* variability of methane emissions (Girkin et al. 2018; Al-Haj and Fulweiler 2020), though these inputs are highly plant species-dependent (Ström et al. 2003; Ström and Christensen 2007; Koelbener et al. 2010). Alongside aboveground and belowground litter that serve as input, plants excrete low-molecular-weight exudates (Megonigal et al. 1999; Oburger and Jones 2018) that are preferentially utilized by microbes as readily degradable organic compounds. This stimulation of microbial activity via plant-derived inputs not only generates a higher production of CO_2 and methane (Ström and Christensen 2007; Kayranli et al. 2010; Waldo et al. 2019; Goud et al. 2022), but may potentially influence the decomposition of SOM, also known as the priming effect (Kuzyakov 2002, 2010; Mueller et al. 2016; Mueller and Megonigal 2024).

In order to systematically characterize different plant functional types in their ecological and carbon turnover strategies, plant species can be classified based on the plant economic spectrum, which range from either fast-growing/acquiring to slow-growing/conservative species (Wright et al. 2004; Reich 2014). Fast-growing or acquiring species exhibit high carbon turnover rates and are characterized by rapid growth, higher exudation, elevated nutrient content in tissues, higher litter decomposition and short life cycles (Freschet et al. 2012; Henneron et al. 2020; Goud et al. 2022). In contrast, conservative or slow-growing species display lower carbon turnover due to investment in structural biomass, resulting in higher C:N ratios in tissues, slower growth rates, and reduced competitiveness in nutrient-rich environments (Lambers and Poorter 1992) potentially forming “low-flux” species.

In chapter 4, we demonstrate that methane emissions are mediated by plant traits, as equivocal shifts in belowground biomass under grazing influence soil redox conditions. We were able to identify some plant species to be associated with low (“low-flux”) or high (“high-flux”) methane emission (Table 2). These categories were derived from individual plots that exhibited consistently low or high methane emissions, and where the occurrence/dominance of certain plant species correlated with emission rates. Building on this concept, I aim to further discuss “high-flux” and “low-flux” species in the following sections by examining how plant traits modulate these distinct carbon fluxes. This approach integrates the plant economic spectrum with the findings presented in chapters 2 and 3, as well as in Box A.

Species from both functional categories (‘low-flux’ and ‘high-flux’; see Chapter 3) develop aerenchyma, a tissue type known to both enhance and suppress methane emissions. Consequently, the presence of aerenchyma alone cannot account for the contrasting directions of methane flux observed between these groups, indicating that additional plant-related drivers linked to species-specific carbon fluxes must be considered. One likely explanation lies in the plasticity of plants functioning as either net soil oxidizers or reducers, a dynamic strongly influenced by background redox conditions (Määttä and Malhotra 2024; Mittmann-Goetsch et al. 2024, Box A). Moreover, radial oxygen loss from roots can be restricted by anatomical barriers such as suberization or lignification, which reduce oxygen diffusion into the surrounding soil and instead facilitate oxygen transport toward the root tip (Ejiri and Shiono 2019; Pedersen et al. 2021). The extent and expression of these barriers vary considerably among species (Koop-Jakobsen et al. 2021; Pedersen et al. 2021; Mittmann-Goetsch et al. 2024). Taken together, these considerations demonstrate that aerenchyma formation alone is insufficient to explain microscale variation in methane emissions. Rather, they underscore the necessity of integrating species-specific traits related to carbon turnover into future investigations of plant-mediated methane fluxes in wetlands.

I propose that species combining aerenchyma formation with high resource-acquisition traits represent 'high-flux' species, as they couple the conduit effect with increased organic substrate inputs, thereby promoting net soil reduction, methane production and gas transport. In contrast, species that possess aerenchyma but follow a more conservative strategy exert a net oxidizing influence on their soils and are therefore more likely to represent 'low-flux' species.

Table 2: Classification of plant species as high- or low-flux species to methane emissions (Chapter 3). *Notes:* * indicates a statistically significant effect; other entries have p-values < 0.4. Plant Economic Spectrum (PES) categories are synthesized from literature (reference); species-specific evidence is limited and PES should be interpreted with caution.

	Species	**PES**	**PES comment**	**aerenchyma**	**reference**
high flux	*Phragmites australis**	fast / acquisitive	clear evidence	yes	Armstrong 2000; Mozdzer et al. 2013
	*Aster tripolium**	fast / acquisitive		yes	Minden et al. 2012; Ludwiczak et al. 2024
	*Juncus maritimus**	intermed	high belowground biomass	yes (genus)	Visser and Bögemann 2006; Sousa et al. 2017
	Plantago maritima		Data from Box A suggests fast/ acquisitive strategy (high biomass and high soil reduction)	yes	Minden et al. 2012 ; Box A
low flux	*Elymus athericus*	fast / acquisitive		yes	Koop-Jakobsen et al. 2021; Reents et al. 2021; Elschot et al. 2024
	Glaux maritima	intermed	weak data	yes	Minden et al. 2012; Box A
	Limonium vulgare	slow/ conservative	weak data	No	Minden et al. 2012; Box A

Interestingly, all species identified as 'high-flux' in chapter 3 develop aerenchyma and exhibit traits typical of fast-growing, resource-acquisitive species (Table 2). These characteristics likely enable them to function both as effective conduits for methane transport and as net soil-reducers as they supply a greater quantity of low-molecular-weight organic compounds to microbial communities. For instance, *Phragmites australis* combines substantial exudation rates (Haviland and Noyce 2024) with deep rooting capacity (>3m depth; Mozdzer et al. 2013; Mozdzer et al. 2016), potentially reaching soil layers that harbor methane reservoirs that otherwise remain trapped or oxidize while diffusing through upper soil layers. Although detailed trait data are limited for other species, similar patterns may apply to *Aster tripolium*, for which roots were observed at depths of up to one meter (visual observation; see Pic. 1).

Picture 1. Soil core from a marsh dominated by *Aster tripolium*. The core section shown here represents the depth interval between approximately 50 to 60 cm. Root structures are visible through the formation of iron plaques, illustrating radial oxygen loss (ROL) in an otherwise anoxic (black) soil matrix. Photo: Ella Logemann.

To further explore these relationships of species-specific effects on carbon turnover, I analyzed SOC correlations with plant species cover using data from chapter 2 (Fig. 1). Among the identified flux species, only those plant species with acquisitive traits (*Phragmites australis, Aster tripolium, Plantago maritima; Juncus maritmus was not assessed in chapter 2*) correlated positively with plant cover (%) and SOC content (0–30 cm). This further emphasizes the conceptual framework developed here, as these high-acquisition strategist contribute substantial carbon inputs that favor SOC accumulation under water-saturated conditions.

By contrast, most 'low-flux' species identified in chapter 3 are characterized by conservative, slow-growing strategies, which are expected to support more stable organic carbon pools with slower turnover due to substrates of higher C:N ratios (Freschet et al. 2012; Spohn et al. 2023). An exception is *Elymus athericus*, which is categorized as a methane 'low-flux' species despite exhibiting traits of the fast-growing, resource-acquisitive spectrum (Table 2). This apparent mismatch suggests that *Elymus athericus* does not fit neatly into the proposed concept and may require closer consideration of its environmental context. In contrast to the acquisitive and 'high-flux' plant species - that all correlated positively with SOC - *Elymus athericus* cover correlated negatively with SOC (Fig. 1). This negative relationship can be interpreted in two ways: (i) *Elymus athericus* indicates environmental conditions that promote SOC loss or inhibit SOC accumulation (e.g. high soil aeration in the high marsh where it is dominant), (ii) and it likely contributes to SOC decline through bio-geomorphic feedbacks through oxygen and exudate priming. As an acquisitive species with high root porosity, it likely supplies both oxygen (Koop-Jakobsen et al. 2021) and substantial amounts of low-weight organic carbon compounds to relatively aerated soil environment, *Elymus athericus* may not stimulate methanogenesis but instead enhance aerobic SOM decomposition via positive priming, ultimately leading to SOC loss.

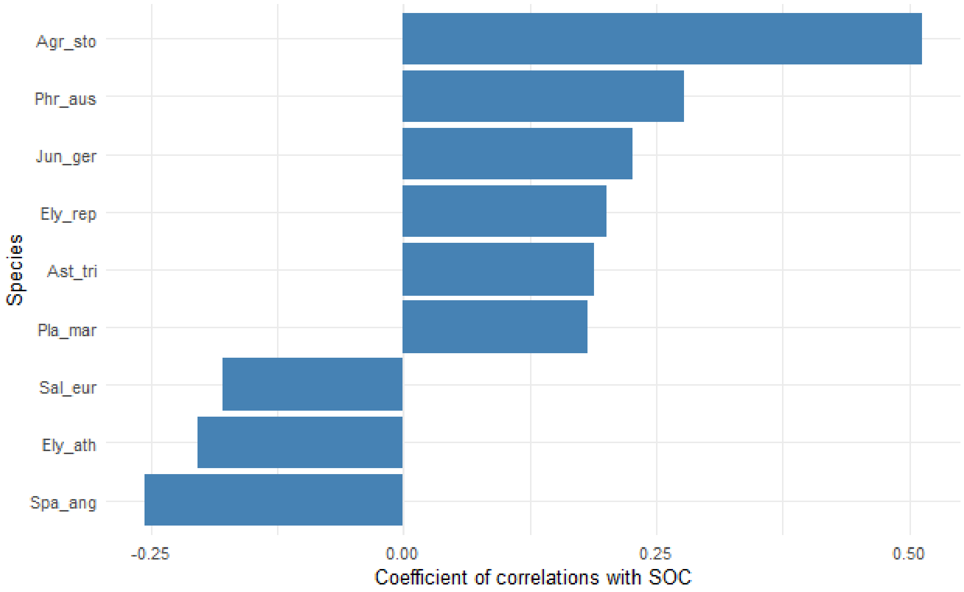


Figure 1: Coefficient of correlation of individual species cover with SOC content (%; 0-30 cm). Data derived from carbon stock assessment form chapter 2. Displayed are only species for which correlation coefficient deviate more than 0.125 from 0. Species are listed from top as follows: *Agrostis stolonifera, Phragmites australis, Juncus gerardii, Elymus repens, Aster tripolium/ Tripolium pannonicum, Plantago maritima, Salicornia europaea, Elymus athericus, Spartina anglica*

Mechanistic understanding of drivers of carbon fluxes at the plant-soil interface remain largely uncertain, and the perspectives developed in this thesis further emphasize the need for empirical investigations into how carbon cycling is shaped by species-specific plant traits, particularly those related to roots. At broader spatial scales, e.g. between the saline North Sea and the brackish Baltic Sea coast, environmental factors such as salinity remain reliable predictors of methane emissions (chapter 3; Poffenbarger et al. 2011; Davidson et al. 2021; Arias-Ortiz et al. 2024). However, even at this broad scale we observed substantial differences between two grazing treatments (chapter 3), which could not be explained solely by biogeochemical pathways but were strongly influenced by plant community composition. This highlights the need to assess carbon dynamics at fine, region-specific scales and to mechanistically disentangle the plant traits that drive these processes.

6.4. Resource availability controls shifts in plant-soil-microbe interactions under warming

6.4.1. SOM quantity can be linked to ecosystem carbon responses under warming

A central question in global change research has been for several decades the uncertainty surrounding soil carbon-climate feedbacks. Predicting future trajectories of soil organic carbon dynamics remains challenging, as previous studies have yielded conflicting and sometimes controversial results (Davidson and Janssens 2006; Zhou et al. 2012; Karhu et al. 2014; Hicks Pries et al. 2017; van Gestel et al. 2018; Song et al. 2019). At the core of these ambiguous dynamics lies the complex interplay between plants and microbes, which governs the fate of SOM. SOM functions not only as a critical reservoir of carbon and nutrients (Tiessen et al. 1994; Falkowski et al. 2000; Herrick and Wander 2018), but also as a foundation for diverse biotic processes (Jackson et al. 2017). Consequently, SOM should be regarded as an essential ecosystem function, critical for soil fertility, plant growth, and substantially overall ecosystem productivity.

A key finding of this thesis is that resource availability - mostly related to SOM and its breakdown providing available nitrogen - mediates ecosystem carbon responses to warming. In chapter 4, we demonstrate that the availability of SOM influences the magnitude of carbon-cycle responses to warming. Specifically, pronounced SOM loss and the strongest aboveground biomass responses were observed in soils with high SOM content. In contrast, aboveground biomass responses were either diminished or negligible in soils with lower SOM levels. While many studies have emphasized nitrogen as the main driver of aboveground biomass responses under warmer conditions (Zhou et al. 2022; Fang et al. 2023; Li et al. 2024b) and of plant-microbe interactions and priming effects (Chen et al. 2014; Craine et al. 2007; Mau et al. 2018), other work highlight SOM as a critical determinant of ecosystem nutrient cycling (Tiessen et al. 1994; Schimel and Weintraub 2003; Brzostek et al. 2013). To my knowledge, however, no previous research has explicitly identified SOM as a mechanistic control that links SOM quantity with nitrogen mobilization under warming, thereby regulating aboveground biomass responses and carbon cycling dynamics.

Furthermore, in chapter 5, warming responses in microbial communities from tall-grass communities were only observed in one of the two soil origins analyzed - namely, the SOM-rich soil originating from Denmark. Previous studies that found long-term warming effects on microbial communities show more pronounced warming effects in the upper organic layer compared to subsoil layers (Deslippe et al. 2012; DeAngelis et al. 2015). Deslippe et al. (2012) attributed this to the more effective warming achieved in the organic layer under passive warming, whereas DeAngelis et al. (2015) who applied active soil warming explained the stronger responses in the organic horizon by its higher resource availability and faster turnover dynamics, in contrast to the mineral layer, where greater physical protection reduces microbial responsiveness. In the microbial study presented in chapter 5, active soil warming was successfully applied across different soil types that differed in grain size composition and SOM content, yet we still observed only in the SOM richer soil type and soil layer short-term microbial responses to warming. This differential microbial responses between distinct soils observed in this and previous studies suggest that SOM content may play a central role in mediating both microbial and plant responses to warming ultimately altering plant-microbe interactions. Our findings underscore the potential of SOM as a master variable that could be readily incorporated into future carbon-climate feedback models. However, while findings of this study highlight potential mechanisms on how SOM influences plant and microbial community dynamics under changing climatic conditions, further work across broader scales is essential to fully establish generality.

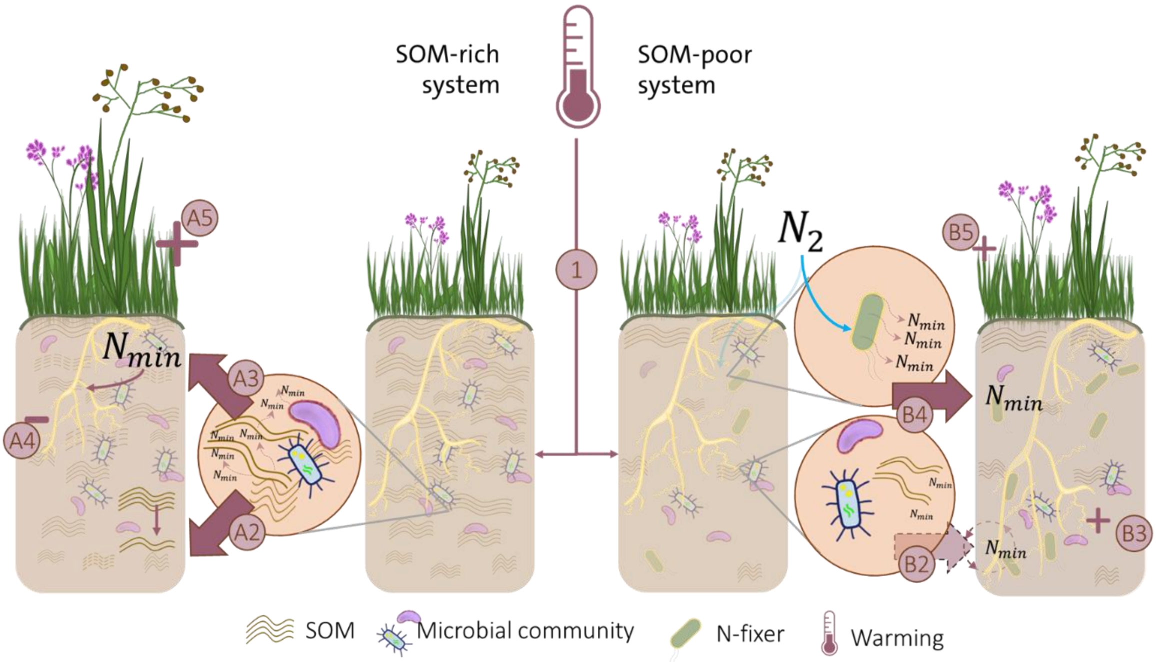


Figure 2. Conceptual diagram illustrating how warming alters plant-soil interactions depending on the initial resource status in SOM-rich (e.g., Denmark short-grass communities) versus SOM-poor coastal wetlands (e.g., Denmark tall-grass community; for simplicity, differences in plant community composition are not displayed). In **SOM-rich systems**, warming (1) enhances microbial activity, which accelerates SOM decomposition and loss (A2). This process increases nitrogen remineralization and plant-available nitrogen (A3), leading to reduced belowground biomass (A4) but an increase in aboveground biomass (A5). In **SOM-poor systems**, warming (1) also stimulates microbial activity (B2 and B4); however, nitrogen remineralization from SOM is constrained by limited SOM accessibility (B2). As a result, plants allocate more resources to belowground biomass (B3), potentially supporting growth of plant-associated microbes involved in nutrient cycling (B2) and/or free-living nitrogen fixers (B4). This subsequently increases plant-available nitrogen, ultimately enhancing aboveground biomass (B5).

6.4.2.What drives SOM dynamics under warming – temperature sensitivity vs. priming

The different responses in SOM under warming (chapter 4) are likely driven by multiple interacting factors. In the following section, I introduce and examine the extent to which the theoretical frameworks of temperature sensitivity and rhizosphere priming can explain altered plant-soil interactions under warming and their control over SOM dynamics observed in chapters 4 and 5.

Within the concept of temperature sensitivity, the degradation of SOM is understood to be driven by the temperature dependence of enzymatic processes, as described by the Arrhenius equation (Davidson and Janssens 2006). This framework is further refined by the Carbon-Quality Temperature Sensitivity (CQT) hypothesis, which proposes that more stable and recalcitrant organic carbon compounds exhibit higher temperature sensitivity, whereas labile organic carbon compounds are already readily decomposable and therefore require lower activation energy (Davidson and Janssens 2006; Lefèvre et al. 2014; Wang et al. 2019). However, the applicability of the CQT hypothesis is limited, as temperature sensitivity is also strongly influenced by other environmental factors, including SOM availability, accessibility, and nutrient status (Davidson and Janssens 2006; Lefèvre et al. 2014; Reynolds et al. 2017; Wang et al. 2019). Wang et al. (2019) conducted a global meta-analysis and found that temperature sensitivity of SOM decomposition varied among terrestrial ecosystems, with croplands exhibiting the highest sensitivity and wetlands the lowest.

The rhizosphere priming effect (RPE) refers to short-term changes - either positive or negative - in the turnover rate of SOM in the presence of roots (Kuzyakov 2002, 2010). Such plant-presence effects can be triggered by alterations in the abiotic soil environment, for instance through drying or changes in pH or redox conditions (Kuzyakov 2002, 2010; Mueller and Megonigal 2024; Wang and Kuzyakov 2024). In wetlands, RPEs are further complicated by the strong influence of plants on redox conditions due to potentially high rates of root oxygen loss, thereby altering SOM decomposition processes and potentially amplifying both positive and negative RPEs compared to terrestrial RPE (Haviland and Noyce 2024; Mueller and Megonigal 2024). However, evidence from terrestrial ecosystems suggests that biological factors, such as root exudation and microbial activity, are the more important drivers of the RPE (Kuzyakov 2002, 2010). Taken from terrestrial systems, the main biological mechanisms underlying RPE include: (a) competition between microbes and plants for mineral nitrogen, where root uptake reduces SOM decomposition because microbes become strongly nutrient-limited; (b) preferential utilization of rhizodeposits as easily available organic compounds as microbial substrates, which decreases SOM decomposition; and (c) microbial activation by fresh inputs of organic compounds, which stimulates the decomposition of otherwise less favorable SOM (Kuzyakov 2002, 2010; Mueller and Megonigal 2024).

Priming is regarded as a central concept in nutrient cycling between plants and microbes (Craine et al. 2007; Chen et al. 2014), as it directly links plant organic carbon inputs to microbial activity and SOM decomposition. Within the framework of RPE, I draw the focus on priming effects that activate microbes to enhance nitrogen mineralization. Either plant-derived exudation or oxygen loss into the rhizosphere can stimulate extracellular enzyme activity, which in turn accelerates SOM breakdown and releases nitrogen into the rhizosphere (Brzostek et al. 2013; Dijkstra et al. 2013; Pausch et al. 2024). Therefore, ultimately increases nitrogen availability for plant uptake, and several studies emphasize the role of plants in facilitating beneficial microbial communities (Fontaine et al. 2024; Yang et al. 2025).

Within the scope of these two main concepts (temperature sensitivity and RPE), enhanced SOM decomposition under warming can be integrated for chapter 4 and 5 in different ways. From a temperature-sensitivity perspective, warming can increase substrate availability by making recalcitrant SOM enzymatically degradable once higher activation energy thresholds are met, suggesting that SOM degradation is primarily temperature-limited. However, if SOM is otherwise protected, it may remain undecomposed despite its abundance. Indeed, in chapter 4, we found primarily support for temperature sensitivity as the main driver of SOM loss (in the SOM-richest soils of the short-grass community from Denmark). This is evidenced by the concurrent declines in SOM content, C:N ratio, and belowground biomass. Together, these findings point to a temperature sensitivity of SOM (Davidson and Janssens 2006), which indirectly increased aboveground plant growth by enhancing nitrogen remineralization previously locked in SOM (Melillo et al. 2002b; Dijkstra et al. 2010), rather than through a plant-driven priming effect. In contrast, in tall-grass communities from the same origin (chapter 4) we found a slight though non-significant increase in SOM and belowground biomass associated with a non-significant decrease in soil C:N ratio with warming. Combining these findings indicates microbial decomposition of SOM and plant-induced priming. Microbial community data from the same soils revealed a warming-induced increase in relative abundance of taxa associated with nutrient cycling and plant-beneficial functions (chapter 5). Notably, nitrogen-fixing Rhizobiales and various other nitrogen-fixing families from the phyla Proteobacteria increased in relative abundance as well as several families linked to nutrient mineralization and the breakdown of complex organic compounds. Together, the selective increase of plant-beneficial microbial taxa and indicators from chapter 4 (slightly increasing SOM and belowground biomass; decreasing C:N ratio) potentially highlight the active role of plants in shaping their microbial communities enabling plants to better exploit soil resources under warming (Fontaine et al. 2024; Yang et al. 2025).

Temperature sensitivity of SOM and priming through plant presence are not mutually exclusive but likely act together. In this thesis, evidence suggests that temperature sensitivity of SOM exerts a stronger influence than plant-induced effects, particularly in SOM-rich soils where substantial SOM losses occurred under warming (chapter 4). In these soils, high microbial activity generates strong bottom-up nutrient supply, reducing the need for plant investment into stimulating microbial communities by increasing root exudation. This favors aboveground biomass while limiting allocation to belowground biomass under warming, further amplifying the SOM loss. By contrast, in tall-grass communities with weaker nutrient supply, plants appear to stimulate SOM degradation through greater investment into the soil, resulting in top-down control of microbial activity and nutrient availability. In both cases, it is likely that RPEs interact with temperature sensitivity, underscoring the complexity of plant-microbe-soil feedbacks under warming and the need for further mechanistic understanding of SOM dynamics.

6.4.3.SOM as resource for nitrogen mineralization

SOM plays a central role in regulating carbon cycling as it functions as a key provider of essential resources for plant growth, particularly nutrients and water (Tiessen et al. 1994; Herrick and Wander

2018; Falkowski et al. 2000). In terrestrial ecosystems, numerous studies highlight both water and nutrient availability as limiting factors that can constrain biotic growth responses (Elmendorf et al. 2012; Bai et al. 2013; Carey et al. 2016; Reich et al. 2018; Song et al. 2019; Zhou et al. 2022). According to the law of the minimum (Liebig 1841), it is reasonable to assume that in wetlands, water is not the primary limiting growth factor. Instead, recent research from terrestrial ecosystems has made substantial progress in disentangling the relative roles of nitrogen and water availability in shaping plant responses to warming, increasingly emphasizing the central role of nitrogen in mediating these responses (Terrer et al. 2019; Liu et al. 2022b; Zhou et al. 2022). In (Baltic) coastal wetlands, overcoming nitrogen limitation appears to be key for enhancing ecosystem productivity. In this study, we identified multiple mechanisms facilitating increased nitrogen availability for plants, which varied across different soil origins: (a) association of plants with nitrogen-fixing microbes (regardless of warming); (b) enhancement of free-living nitrogen fixing microbes with warming; and (c) higher mineralization of SOM with warming.

Nitrogen limitation was alleviated through warming-induced shifts in plant-soil interactions (chapter 4 and 5), by warming-induced increases in nitrogen availability through either higher microbial nitrogen fixation or higher nitrogen remineralization. Interestingly, it is likely that warming primarily influenced plant growth indirectly through alterations in these plant-soil interactions (Fig. 2), as the warming-induced plant growth responses occurred in the absence of any direct physiological reaction of plants to warming (Box B). Consistent with the findings of this thesis, nitrogen availability is increasingly recognized as a key regulator of plant responses to environmental change (Fontaine et al. 2024; Yang et al. 2025), potentially overriding direct effects of warming on plant metabolism. Both nitrogen acquisition pathways - microbial nitrogen fixation and mineralization - contributed to alleviating nitrogen limitation under warming, at least in tall-grass communities from Denmark and Sweden, where the microbial communities were investigated. Evidence includes the higher relative abundance of free-living nitrogen fixing Proteobacteria (chapter 5), the higher relative abundance of Actinobacteriota (known to contribute to nutrient cycling; chapter 5) and shifts in foliar $\delta^{15}N$ (chapter 4) indicating greater mineral nitrogen availability in plants. We argue that the observed higher relative abundance of nitrogen-fixing microbes does not primarily reflect plant-associated taxa but is instead driven by free-living nitrogen fixers (Burghardt and diCenzo 2023), which is further supported by the increase in soil nitrogen content under warming across both soil origins (Fig. 2).

In low-SOM systems such as the coastal wetland mesocosms originating from Finland, biological nitrogen fixation (which we observed in Danish soils) and its stimulation under warming may play a more central role in biomass production. In Finland, where microbial data were lacking, aboveground biomass responses were less straightforward (chapter 4 Fig. 3): warming increased *Phragmites australis* biomass but coincided with declining foliar $\delta^{15}N$ values indicating lower mineral nitrogen availability. A likely explanation, supported by the previously described results from Denmark and Sweden (chapter 5), is a warming-induced increase in free-living microbial nitrogen-fixing taxa with warming. This would also account for the declining $\delta^{15}N$ signature, which shifts towards zero when plants depend more on biologically fixed nitrogen (Wang et al. 2021). Overall, these findings suggest that warming enhances nitrogen availability through different pathways depending on SOM content: free-living microbial nitrogen fixation in low-SOM soils and mostly SOM mineralization in SOM-rich soils. This further highlights the importance of plant-soil-microbe interactions in mediating ecosystem responses to warming.

6.5. Future research perspective

6.5.1. Plant-soil interactions and ecosystem carbon dynamics in coastal wetlands

Numerous studies have demonstrated that plants exert significant control over carbon fluxes, particularly methane emissions, which are of special interest given methane's substantially higher global warming potential compared to carbon dioxide (Joabsson et al. 1999; Ström et al. 2003; Al-Haj and Fulweiler 2020; Mueller et al. 2020b; Haviland and Noyce 2024; Määttä and Malhotra 2024). Nonetheless, substantial uncertainties remain at the micro-scale, particularly the mechanistic understanding of how specific root traits regulate methane emissions requires further investigation (Määttä and Malhotra 2024). Species-specific root architecture and the degree of radial oxygen loss (ROL) are likely important root traits controlling methane (and carbon dioxide) emissions (Joabsson et al. 1999; Laanbroek 2010; Määttä and Malhotra 2024; Haviland and Noyce 2024). In addition, the quantity and quality of rhizodeposits strongly influence carbon dynamics at fine spatial scales (Girkin et al. 2018; Al-Haj and Fulweiler 2020).

The composition of root exudates is of particular interest, as it can differently influence carbon fluxes, exemplified here by their role in regulating methane emissions. Simple sugars such as glucose can be rapidly fermented to organic acids and hydrogen, indirectly fueling methane production (Le Mer and Roger 2001; Vizza et al. 2017; Määttä and Malhotra 2024). Exuded low-molecular-weight acids such as acetate directly increase methane emissions, whereas amino acids tend to suppress methane emissions (Haviland and Noyce 2024). Phenolic compounds can inhibit microbial exoenzyme activity that generates organic acids and hydrogen, thereby indirectly suppressing methane production (Freeman et al. 2001; Limpens et al. 2008; Toberman et al. 2008; Määttä and Malhotra 2024). The exudation profile of these different organic compounds is highly species-specific (Ström et al. 2003; Ström and Christensen 2007; Koelbener et al. 2010; Kim et al. 2018; Haviland and Noyce 2024).

In addition, links to morphological traits - particularly aerenchyma development and the regulation of radial oxygen loss (ROL) - are essential, as the extent of these tissues strongly influences microbial activity and carbon fluxes (Armstrong 1980; Waldo et al. 2019). Depending on whether plant-soil interactions result in net-reducing or net-oxidizing conditions, these traits may ultimately shift emissions toward either higher or lower fluxes (Haviland and Noyce 2024). Therefore, advancing a mechanistic understanding of species-specific patterns of radial oxygen loss (ROL) and rhizodeposition (in particular root exudation), and integrating these processes across different soil morphologies, is essential for improving predictions of plant-soil feedbacks under changing environmental conditions. Addressing these knowledge gaps will require experiments that assess species-specific carbon fluxes. Such assessments should combine measurements of plant biomass (above- and belowground) with detailed evaluations of functional traits which link to rhizodeposition and gas transport, including root architecture, aerenchyma development, and rates and barriers of ROL as important belowground traits, and plant height, biomass, and leaf area as traits characterizing primary productivity. In parallel, greenhouse gas fluxes should be quantified while simultaneously monitoring the effects of plant species on soil redox conditions. Finally, these experiments should integrate analyses of microbial community composition (e.g. 16S rRNA) and assessments of soil carbon quality, including plant tissue and carbon compounds in the porewater. To complement this, hydroponic cultivation could be used to quantify species-specific exudation rates and exudation profile (e.g. LC-MS profiling; e.g. (Haviland and Noyce 2024; Ritter et al. 2025). Combining these approaches would provide a more comprehensive understanding of how plant traits, and microbial processes interact in shaping carbon cycling in coastal wetlands.

6.5.2. Plant soil interactions and carbon cycling under climate change

Despite the important role of priming in regulating carbon cycling, studies explicitly investigating priming effects in wetlands under global change drivers are scarce. Incubation studies using wetland soils indicate that after addition of analogue carbon substrates (to mimic root exudation), temperature sensitivity of SOM decomposition and the priming effect can either enhance, reduce, or even negate (Zhang et al. 2021; Wei et al. 2021; Jiang et al. 2025). Similar ambiguous results are drawn from terrestrial incubation studies (Zhu and Cheng 2011; Mau et al. 2018; Tao et al. 2024), though warming studies assessing RPE and temperature sensitivity of SOM *in-situ* remain scarce. Noyce and Megonigal (2021) found in a coastal wetland increased methane emission under *in-situ* warming and suggest increased substrate availability for methanogens modified by shifts in plant traits, thus highlighting the importance of plant-soil interactions in mediating carbon dynamics in a warmer world.

As highlighted by Mueller and Megonigal (2024), RPEs are likely to be amplified in wetlands compared to terrestrial upland ecosystems, and this amplification may be further intensified under global change drivers. Therefore, RPEs should be explicitly considered in future studies on how warming affects wetland ecosystem functioning. Such studies should employ active above- and belowground heating and disentangle root-derived from SOM-derived CO_2 fluxes, for example by applying ^{13}C labeling (Kuzyakov 2002). I further suggest conducting these experiments *in-situ* in vegetated soils rather than incubation studies, as this allows plants to play an active role in shaping rhizosphere processes.

6.5.3. SOM as a key factor controlling ecosystem responses to warming

The results of this thesis suggest that SOM plays a central role in mediating biotic responses of coastal ecosystems to warming. Specifically, SOM availability appears to modulate the pathways through which nitrogen becomes accessible under warming, underscoring its importance in ecosystem nutrient dynamics (Dijkstra et al. 2009; Ni et al. 2024). However, further research is needed to test the generalizable applicability of these findings, and I recommend manipulative experiments applying active warming that examine plant and microbial responses in soils with different levels of SOM. Ideally, SOM should be labeled with $\delta^{15}N$ to trace nitrogen fluxes in both plants and microbes (e.g. Bengtson et al. 2012). Since priming is a crucial mechanism in nutrient cycling, it would also be valuable to incorporate ^{13}C labeling into this experimental approach, which would enable us to distinguish between decomposition driven solely by temperature sensitivity and decomposition mediated by plant activity (RPE) potentially shaping microbial processes to optimize nutrient supply according to plant demand (Fontaine et al. 2024; Yang et al. 2025).

Taken together, future research should focus on several key pathways. First, a more detailed mechanistic understanding of plant-soil interactions is essential for predicting future carbon-climate feedbacks from wetlands. In particular, the roles of specific plant traits, such as ROL and root exudation, in shaping microbial activity and SOM decomposition require further investigation. Second, SOM should be regarded as a central variable for understanding ecosystem carbon dynamics under warming in coastal wetlands; however, further experimental studies are required to evaluate the generality of this pattern.

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