Biogeochemical and plant trait mechanisms drive enhanced methane emissions in response to whole-ecosystem warming

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Abstract

Climate warming perturbs ecosystem carbon (C) cycling, causing both positive and negative feedbacks on greenhouse gas emissions. In 2016, we began a tidal marsh field experiment in two vegetation communities to investigate the mechanisms by which whole-ecosystem warming alters C gain, via plant-driven sequestration in soils, and C loss, primarily via methane (CH_4) emissions. Here, we report the results from the first four years. As expected, warming of 5.1 °C more than doubled CH_4 emissions in both plant communities. We propose this was caused by a combination of four mechanisms: (i) a decrease in the proportion of CH_4 consumed by CH_4 oxidation, (ii) more C substrates available for methanogenesis, (iii) reduced competition between methanogens and sulfate reducing bacteria, and (iv) indirect effects of plant traits. Plots dominated by *Spartina patens* consistently emitted more CH_4 than plots dominated by *Schoenoplectus americanus*, indicating key differences in the roles these common wetland plants play in affecting anerobic soil biogeochemistry and suggesting that plant composition can modulate coastal wetland responses to climate change.

1. Introduction

Methane (CH_4) is a potent greenhouse gas that contributes to 15-19 % of total greenhouse gas radiative forcing (IPCC, 2013) and has a sustained-flux global warming potential that is 45 times that of CO_2 on a 100-year timescale (Neubauer & Megonigal, 2015). Wetlands are the largest natural source of CH_4 to the atmosphere and were recently identified as the largest source of uncertainty in the global CH_4 budget (Saunois et al., 2016). Recent estimates calculate that CH_4 emissions from vegetated coastal wetlands offset 3.6 of the 12.2 million metric tons (MMT) of CO_2 equivalents accumulated by these ecosystems each year (EPA, 2017). Despite this, there is still a substantial knowledge gap regarding how global change factors, such as climate warming, will alter coastal wetland CH_4 emissions (Mcleod et al., 2011) even though these feedbacks have the potential to shift coastal wetlands from being a net sink of C to a net source (Al-Haj & Fulweiler, 2020; Bridgham et al., 2006).

The net flux of CH_4 to the atmosphere from any ecosystem represents the balance between the amount of CH_4 produced (methanogenesis), the amount of CH_4 oxidized (methanotrophy), and the rate of CH_4 transport from the soil. ~~Rates of methanogenesis are driven by low redox conditions and substrate availability, while aerobic CH_4 oxidation requires both O_2 and CH_4 as substrates. Roots and rhizomes in wetland ecosystems influence methane-related substrates through at least two mechanisms: (i) deposition of organic compounds that support multiple pathways of heterotrophic microbial respiration, including methanogenesis, and (ii) release of O_2 that simultaneously promotes CH_4 oxidation (Philippot et al., 2009; Stanley & Ward, 2010) and regeneration of competing electron acceptors such as Fe(III) and SO_4. Root exudates, which typically include low molecular~~ In coastal wetlands, methanogenesis occurs through three pathways: (i) hydrogenotrophic methanogenesis (i.e. CO_2 reduction) in which H_2 is the electron donor and CO_2 is the electron acceptor, (ii) acetoclastic methanogenesis, in which acetate (CH_4COOH) is split into CH_4 and CO_2 and (iii) methylotrophic methanogenesis in which methylated compounds are converted to CH_4 and CO_2 (Conrad, 2020; Oremland et al., 1982; Schlesinger & Bernhardt, 2020). Rates of methanogenesis are driven by low redox conditions and substrate availability, while aerobic CH_4 oxidation requires both O_2 and CH_4 as substrates. Roots and rhizomes in wetland ecosystems influence methane-related substrates through at least two mechanisms: (i) deposition of organic compounds that support multiple pathways of heterotrophic microbial respiration, including methanogenesis, and (ii) release of O_2 that simultaneously promotes CH_4 oxidation and regeneration of competing electron acceptors such as Fe(III) and SO_4 (Philippot et al., 2009; Stanley & Ward, 2010). Root exudates, which typically include low-molecular-weight compounds, may either be more readily used by microbes than existing soil C ~~(Kayranli et al., 2010; Megonigal et al., 1999)~~(Kayranli et al., 2010; Megonigal et al., 1999) or may prime microbial use of soil C ~~(Basiliko et al., 2012; Philippot et al., 2009; Robroek et al., 2016; Waldo et al., 2019)~~(Basiliko et al., 2012; Philippot et al., 2009; Robroek et al., 2016; Waldo et al., 2019). Root exudates can also decrease CH_4 oxidation by stimulating use of O_2 by other aerobic microbes (Lenzewski et al., 2018; Mueller et al., 2016). Consequently, wetland CH_4 emissions are strongly linked to a wide variety of plant traits that govern the supply of reductive (organic carbon) and oxidative (O_2) substrates to soils (Moor et al., 2017; Mueller et al., ~~in press~~2020).

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Although it is understood that wetland plants are a primary control on CH_4 emissions and that much of their influence is mediated through conditions in the rhizosphere (Waldo et al., 2019), there are surprisingly few data, especially from coastal wetlands, that couple plant responses to the dynamics of electron donors (organic C), electron acceptors (O_2, SO_4), and the rates of competing (sulfate reduction vs methanogenesis) or opposing (CH_4 production vs CH_4 oxidation) microbial processes. The general lack of process data on wetland CH_4 cycling makes it difficult to forecast ecosystem responses to climate change. For example, the well-documented observation that warming increases wetland methane emissions can be either amplified or dampened depending on changes in plant activity (e.g. primary production) or plant traits (e.g. community composition) ~~(Mueller et al., in press).~~(Mueller et al., 2020). Vegetation composition has been shown to be a stronger control on CH_4 emissions than ~1 °C of warming in northern peatlands (Ward et al., 2013) and ~~Chen et al. (2017)~~Chen et al. (2017) proposed that warming effects on plant functional types can drive C flux responses that cannot otherwise be explained by abiotic conditions. In freshwater marshes, plant species and growth trends have also been linked to seasonal shifts in pools of dissolved CH_4 and DIC ~~(Ding et al., 2005; Stanley & Ward, 2010)~~(Ding et al., 2005; Stanley & Ward, 2010) and methanogenesis dynamics ~~(Sorrell et al., 1997)~~(Sorrell et al., 1997).

Tidal wetlands are particularly good model systems for determining the mechanisms by which warming alters CH_4 emissions. Not only will the CH_4 cycle respond to the direct effects of warming, but the temperature effects on the outcome of competition for electron acceptors is relatively easily observed because of the abundance of SO_4. Thermodynamic theory in which terminal electron acceptors (TEAs) are used in order of decreasing thermodynamic yield is commonly interpreted to mean that a system will support only one form of anaerobic respiration at time, with ~~methanogenesis occurring only when pools of more energetically favorable TEAs have been depleted.~~acetoclastic and hydrogenotrophic methanogenesis occurring only when pools of more energetically favorable TEAs have been depleted (Conrad, 2020; Schlesinger & Bernhardt, 2020). However, in real systems with spatial and temporal variability in the supply of electron donor substrates and TEAs, all forms of anaerobic metabolism occur simultaneously (Megonigal et al. 2004, Bridgham et al., 2013). Much of this spatial and temporal variation arises from the distribution and activity of roots and rhizomes as mediated by the rhizosphere (Neubauer et al., 2008). Global change factors such as warming will further affect the spatial distribution of key metabolic substrates. In addition, the relatively~~-~~-limited species diversity in saline tidal wetlands allows species-level effects on CH_4 cycling to be delineated more easily than in diverse freshwater wetlands.

Methane flux measurements are a metric of broader shifts in redox potential and biogeochemical cycling, as they are sensitive to virtually all processes that regulate availability of electron donors and electron acceptors. Emissions are commonly predicted to increase with future climate warming, including from coastal wetlands (Al-Haj & Fulweiler, 2020), but there is minimal prior understanding of the underlying mechanisms, which was the focus of this study. Our objectives were to explore the mechanisms that drive enhanced CH_4 emissions under warming. To accomplish this, we measured monthly CH_4 emissions from 2016 through 2019 and coupled these flux measurements with analysis of porewater biogeochemistry and vegetation biomass and composition.

2. Materials and Methods

2.1 Site Description and Experimental Design

The Salt Marsh Accretion Response to Temperature eXperiment (SMARTX) was established in the Smithsonian's Global Change Research Wetland (GCReW) in 2016. GCReW is part of Kirkpatrick Marsh, a microtidal, brackish high marsh on the western shore of the Chesapeake Bay, USA (38°53' N, 76°33' W). Soils are organic (>80 % organic matter) to a depth of 5 m, which is typical of high marshes in the Chesapeake Bay~~. The marsh is typically saturated to within 5-15 cm of the soil surface, but inundation frequency varies across the site, from 10-20 % of high tides in high elevation areas to 30-60 % of~~ and elsewhere. The very low mineral content (<20%) affects methane dynamics because negligible competition between methanogens and iron-reducing bacteria for electron donors is expected in the absence of a significant pool poorly crystalline iron oxides (Roden & Wetzel, 1996), as has been documented previously at this site (Weiss et al., 2004) (Weiss et al. 2004). Soil bulk density in the upper 60 cm averages 0.124 g cm^3 and ranges from 0.079 to 0.180 g cm^3. The relatively uniform bulk density of the soil profile reflects the uniform soil organic matter content and the fact that bulk density becomes largely independent of organic matter and mineral content once organic matter content exceeds 50% (Holmquist et al., 2018). The marsh is typically saturated to within 5-15 cm of the soil surface, but inundation frequency varies across the site, from 10-20 % of high tides in high elevation areas to 30-60 % of high tides in low elevation areas.

SMARTX consists of six replicate transects, three located in each of the two dominant annual plant communities (Fig. S1). In the C_3-dominated community (herein the ‘C_3 community’) the C_3 sedge *Schoenoplectus americanus* (herein *Schoenoplectus*) composes more than 90 % of the aboveground biomass (Table 1). In the C_4-dominated community (herein the ‘C_4 community’), 75 % of the aboveground biomass was initially composed of two C_4 grasses (*Spartina patens* and *Distichlis spicata*, herein *Spartina* and *Distichlis*, respectively). However, by 2019, *Spartina* and *Distichlis* declined to 56 % of the aboveground biomass (Table 1).

Table 1. Relative contribution to total aboveground biomass from C_3 sedges (*Schoenoplectus americanus*) and C_4 grasses (*Spartina patens* and *Distichlis spicata*) in each plant community. Values are means and SE (n = 12).

	C_3 community		C_4 community	
Year	% C_3	% C_4	% C_3	% C_4
2016	93 (3)	8 (3)	8 (2)	76 (6)
2017	91 (3)	9 (3)	10 (3)	64 (4)
2018	95 (1)	5 (1)	15 (4)	65 (7)
2019	93 (2)	4 (1)	23 (5)	56 (6)

Each transect is an active warming gradient consisting of unheated ambient plots and plots that are heated to 1.7 °C, 3.4 °C, and 5.1 °C above ambient. All plots are 2 x 2 meters with a 20 cm-wide buffer around the perimeter. Aboveground plant-surface temperature is elevated via infrared heaters and soil temperature is elevated via vertical resistance cables ~~(Rich et al., 2015)~~(Rich et al., 2015). Soils are heated to a depth of 1.5 m, which is the depth most vulnerable to climate or human disturbance (Pendleton et al., 2012). ~~Aboveground and belowground temperature variation are assessed via~~

~~thermocouples embedded in acrylic plates at plant canopy level and inserted into the soil, respectively, and the temperature gradient is maintained by integrated microprocessor-based feedback control (Rich et al., 2015)~~Aboveground and belowground temperature variation are assessed via thermocouples embedded in acrylic plates at plant canopy level and inserted into the soil, respectively, and the temperature gradient is maintained by integrated microprocessor-based feedback control (Rich et al., 2015). Noyce et al. (2019) provides additional details of the heating system. Warming began on 1 Jun 2016 and has continued year-round.

2.2 Methane flux measurements

Methane emissions were measured monthly year-round from May 2016 to Dec 2019 using a static chamber system. One permanent 160 cm^2 aluminum base was inserted 10 cm into the soil in each plot in Apr 2016. On each measurement date, clear chambers (40 x 40 x 40 cm) were gently placed on top of each base and secured with compression clips. Chambers consisted of an aluminum frame with transparent sides made of polychlorotrifluoroethylene film (Honeywell International) and closed-cell foam on the base. Depending on the height of the vegetation at the time of measurement, chambers were stacked up to four high (total height of 40 to 160 cm) (Fig. S2). The advantage of this stacking method is that it uses the minimal chamber volume necessary, while also allowing for plant growth. After placement, the chambers were left open for at least 10 minutes, to minimize disturbance effects and allow air inside the chamber to return to ambient conditions. During data collection, chambers were covered with a transparent polycarbonate top equipped with sampling tubes, a fan to circulate air inside the chambers, a PAR sensor, and thermocouples. The sealed chamber was covered with a foil shroud to block out all light and to minimize changes in temperature and relative humidity during the measurement period. An UltraPortable Greenhouse Gas Analyzer (Los Gatos Research, CA) was used to measure headspace CH_4 concentrations for 5 min. Plots were accessed from permanent boardwalks elevated 15 cm above the soil surface to avoid compressing the surrounding peat and altering diffusive CH_4 emissions. Fluxes were calculated as the slope of the linear regression of CH_4 concentration over time. The 40 fluxes where $p > 0.05$ were assigned a value of ½ the limit of detection of the system (Wassmann et al., 2018;

Table S1). This was 1 % of fluxes during the growing season and 4.5 % of fluxes over the remaining months. For 2017-2019, monthly measurements were scaled to annual estimates by regressing CH_4 emissions against daily mean soil temperature and day of year (as a proxy for phenological status). Annual estimates were not calculated for 2016 because flux measurements did not start until May.

2.3 Porewater sampling and analysis

Porewater samples were collected in May, Jul, and Sep of each year using stainless steel ‘sippers’ permanently installed in each plot. Each sipper consisted of a length of stainless-steel tubing, crimped and sealed at the end, with several slits (approximate width 0.8 mm) cut in the bottom 2 cm. The aboveground portion of each sipper was connected to Tygon Masterflex® tubing capped with a 2-way stopcock. In May 2016, duplicate clusters of sippers were installed in each of the 30 plots at 20, 40, 80, and 120 cm below the soil surface. An additional set of 10 cm-deep sippers was installed in 2017. In this study we defined samples from 10-20 cm as “rooting zone” samples and samples from 40-120 cm as "deep peat" samples. On sampling dates, porewater sitting in the sippers was drawn up and discarded, after which 60 mL of porewater from each depth (30 mL from each sipper) was withdrawn and stored in syringes equipped with 3-way stopcocks. A 10 mL-aliquot of each sample was filtered through a pre-leached 0.45 µm syringe-mounted filter, preserved with 5 % zinc acetate and sodium hydroxide, and frozen for future SO_4 and Cl analysis. Dissolved CH_4 was extracted from 15 mL of porewater in the syringe by drawing 15 mL of ambient air and shaking vigorously for 2 min to allow the dissolved CH_4 to equilibrate with the headspace. Headspace subsamples were then immediately analyzed on a Shimadzu GC-14A gas chromatograph equipped with a flame ionization detector. 3 mL of porewater was used to measure pH using a Fisher Scientific accumet electrode (13-620-290). The remaining porewater was used to measure ~~pH,~~ H_2S, and NH_4; those data are not reported here.

SO_4 and Cl were measured on a Dionex ICS-2000 ion chromatography system (2016-2018) or a Dionex Integrion (2019). On the Dionex ICS-2000 samples were separated using an ~~AA11~~A11 column with 30 mM of KOH as eluent; on the Dionex Integrion samples were separated using an ~~AA11~~A11-4µm-fast column with 35 mM KOH. Sulfate depletion ($Sulfate_{Dep}$) was calculated based on measured porewater concentrations of SO_4 (SO_{4pw}) and Cl (Cl_{pw}) and the constant molar ratio of Cl to SO_4 in surface seawater (R_{sw} = 19.33; ~~Bianchi 2006) using the following equation: Sulfate~~$\cancel{_{Dep} = Cl_{pw} / R_{sw} – SO_{4pw}}$~~.~~ ~~Based only on~~Bianchi, 2006) using the following equation: $Sulfate_{Dep} = Cl_{pw} / R_{sw} - SO_{4pw}$. If driven only by seawater inputs, the ratio of Cl to SO_4 would remain constant, but under anaerobic conditions SO_4 can be reduced by sulfate reducing bacteria, altering this ratio. As a result, SO_4 depletion can be used as a proxy for SO_4 reduction rates.

2.4 Plant biomass measurements

Measurements of *Schoenoplectus, Spartina,* and *Distichlis* biomass were conducted during peak biomass of each year (29 Jul – 2 Aug) as described by Noyce et al. (2019). *Schoenoplectus* biomass was estimated using non-destructive allometric techniques (Lu et al., 2016) in 900-cm^2 quadrats, and *Spartina* and *Distichlis* biomass were estimated through destructive harvest of 25-cm^2 subplots.

2.5 Data analysis

Statistics were conducted in R (version 3.6.3). ~~ANOVA tests were used to compared means between warming treatments and plant communities, with Tukey's HSD test for *post hoc* analyses. The 'growing season' was defined as May through Sep, based on *Schoenoplectus* growth trends (see Fig. S3). Due to the non-normal distribution of the~~ ~~CH_4~~ ~~flux (Fig. S4) and porewater data, values were log transformed prior to calculating~~Methane flux (Fig. S3) and porewater data were log transformed to become normally distributed prior to statistical analyses. The 'growing season' was defined as May through Sep based on *Schoenoplectus* growth trends (Fig. S4). Pearson's correlations were used to test the relationships between CH_4 flux and soil temperature, and CH_4 flux and plant biomass. Responses of CH_4 emissions to vegetation type and warming treatment were analyzed using linear mixed models with vegetation community and warming treatment as categorial variables, and plot and year as random effects. P-values were calculated using Satterthwaite's method and Tukey's post-hoc tests were used to compare individual means. Porewater data was averaged per year and then analyzed using one-way ANOVAs to determine the effects of warming treatment or plant community, applying Tukey's HSD test for post-hoc analyses.

3. Results

3.1 Environmental conditions, site characteristics, and experiment performance

The growing season of 2016 was the hottest of the four years, with growing season temperatures averaging >1 °C above the other three years (Table 2). While 2017 through 2019 had similar summer temperatures, they had very different precipitation regimes; 2018 was much wetter on average and 2019 was slightly drier (Table 2). During all years, temperatures in the experimental plots were successfully shifted by the target differentials of +1.7, +3.4, and +5.1 °C above the ambient plots (Fig. 1; Noyce et al., 2019). Porewater pH ranged from 6.4 to 6.8 across the measurement period, with no effect of temperature treatment ($p > 0.1$; data not shown). There was no difference in soil bulk density between the ambient and +5.1 °C plots after 4.5 years of warming ($p = 0.54$; data not shown).

~~Year~~	~~Mean aboveground temperature (°C)~~	~~Mean soil temperature (°C)~~	~~Total precipitation (cm)~~
~~2016~~	~~24.7 (0.3)~~	~~22.4 (0.2)~~	~~51.0~~
~~2017~~	~~22.0 (0.3)~~	~~20.7 (0.2)~~	~~51.1~~
~~2018~~	~~23.7 (0.3)~~	~~20.8 (0.2)~~	~~86.4~~
~~2019~~	~~23.6 (0.3)~~	~~20.9 (0.2)~~	~~43.7~~

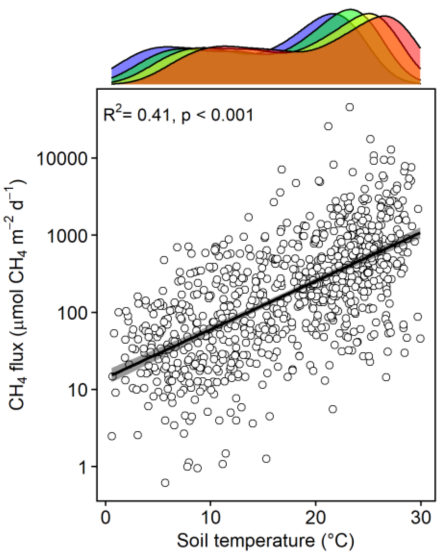
Table 2. Growing season (May-Sep) temperature and precipitation. Temperature data are means (SE) of daily averages from ambient plots and precipitation is total from May through September.

Year	Mean aboveground temperature (°C)	Mean soil temperature (°C)	Total precipitation (cm)
2016	24.7 (0.3)	22.4 (0.2)	51.0
2017	22.0 (0.3)	20.7 (0.2)	51.1
2018	23.7 (0.3)	20.8 (0.2)	86.4
2019	23.6 (0.3)	20.9 (0.2)	43.7

3.2 Methane fluxes

Methane emissions increased with soil temperature ($R^2 = 0.41$, $p < 0.001$) (Fig. 1). Emissions from all treatments had strong seasonal trends; fluxes were highest in the C_3 community in Jun through Aug and peak fluxes in the C_4 community were shifted about a month later to Jul through Sep (Fig. ~~S4~~S3). Whole-ecosystem warming increased CH_4 emissions throughout the growing season ($F_{3,}$~~$_{439}$ = 3.7~~$_{400}$ = 5.1,

p = 0.~~012~~002; Fig. 2). Across all four years, 5.1 °C of warming more than doubled growing season emissions, from 624 to 1413 μmol CH_4 m^{-2} d (p_{adj} = 0.~~01~~02; Fig. 2).



~~Figure 1. CH4 emissions from each plot versus the soil temperature at the time of measurement. Density plot shows the range of soil temperatures in each treatment.~~

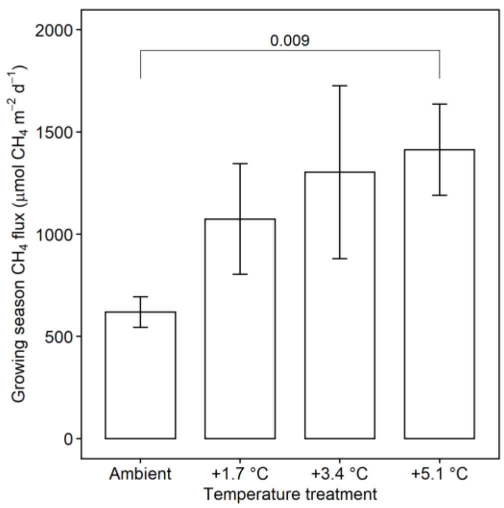


Figure 2. Comparison of CH_4 emissions from each warming treatment during the growing season (May-Sep). Means include both the C_3 and C_4 community and all years of measurement. Error bars indicate SE. Horizonal bars indicate means that are significantly different and the corresponding p_{adj}.

Mean CH_4 emissions were higher from the C_4 community than from the C_3 community both during the growing season ($F_{1,}$~~$_{70}$ =~~$_{22}$~~.0~~ = 13.6, *p* ~~<~~= 0.001; Fig. 3a) and on an annual basis ($F_{1,}$~~$_{70}$~~ ~~= 10.2~~$_{22}$ = 8.5, *p* = 0.~~002~~008; Fig. 3b). Mean annual CH_4 emissions ranged from 58 mmol CH_4 m^{-2} yr^{-1} (ambient) to 343 mmol CH_4 m^{-2} yr^{-1} (+5.1 °C) in the C_3 community and from 55 mmol CH_4 m^{-2} yr^{-1} (ambient) to 879 mmol CH_4 m^{-2} yr^{-1} (+5.1 °C) in the C_4 community (Table S2). Under ambient conditions, growing season CH_4 fluxes were almost twice as large from C_4 plots, whereas under low warming (1.7~~-~~ to 3.4 °C) this difference increased to more than three times as large (Fig. 3a). From 2017-2019, CH_4 emissions were positively related to *Spartina* and *Distichlis* aboveground biomass across all warming treatments and negatively related to *Schoenoplectus* biomass (Fig. 4a,b). In 2016, however, the direction of those relationships in both plant communities were the exact opposite, with *Spartina* and

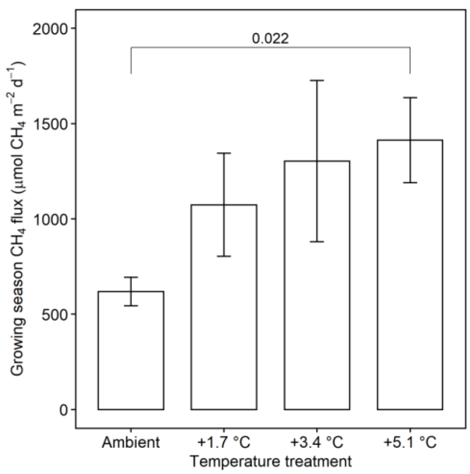


Figure 1. Bottom: CH_4 emissions from each plot versus the soil temperature at the time of measurement. Top: Density plot depicting the range of soil temperatures in each treatment, delineated by color: ambient (blue), +1.7°C (green), +3.4°C (yellow), +5.1°C (red).

Distichlis biomass negatively related, and *Schoenoplectus* biomass positively related, to CH_4 emissions (Fig. 4a,b).

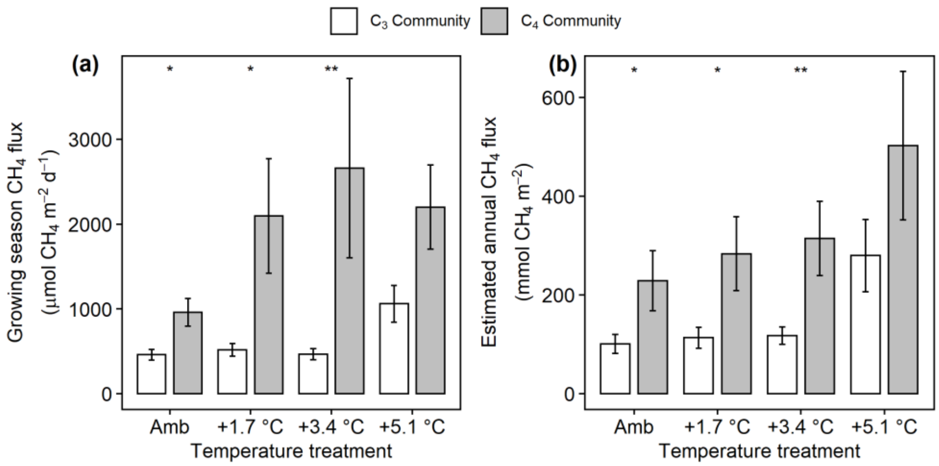


Figure 3. Comparison of CH_4 emissions from the C_3 community dominated by *Schoenoplectus* (open bars) and the C_4 community dominated by *Spartina* and *Distichlis* (grey bars). (a) During the growing season (May-Sep) and (b) scaled to a year. Means are averaged across all sampling dates for 2017 – 2019. Error bars indicate SE. Asterisks indicate significant differences between C_3 and C_4 means at a given temperature (* p_{adj} <0.05, ** p_{adj} < 0.01).

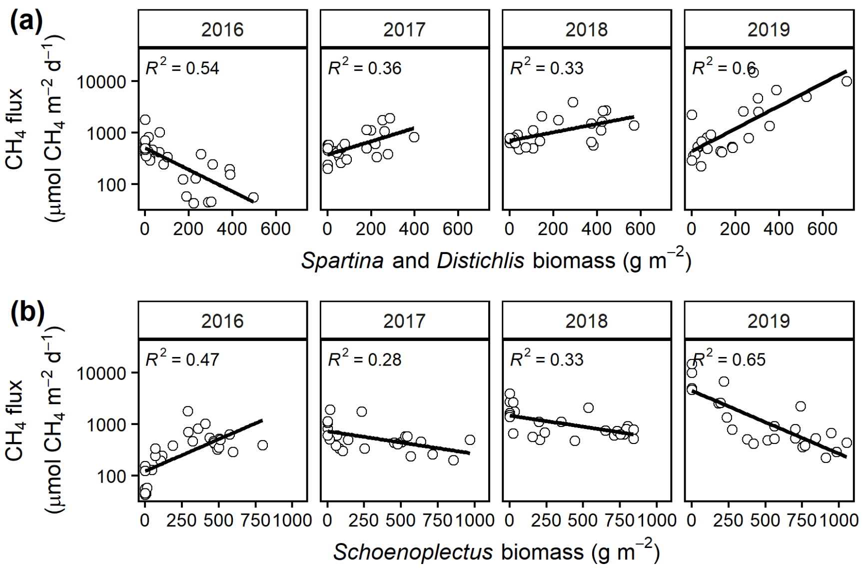


Figure 4. Mean growing season (May-Sep) CH_4 emissions from each plot versus the biomass of (a) C_3 (*Schoenoplectus*) and (b) C_4 (*Spartina* and *Distichlis*) plants. All regressions are significant at p = 0.05.

3.3 Porewater chemistry

Under ambient conditions, porewater collected from the C_4 community had ~~lower salinity ($F_{1,315}$ = 15.5, p < 0.001),~~ more dissolved CH_4 ($F_{1,}$~~$_{315}$ = 45.0~~$_{22}$ = 18.4, p < 0.001; Fig. 5a,b), ~~and~~ less SO_4 ($F_{1,}$~~$_{315}$ = 61.5~~$_{22}$ = 29.1, p < 0.001; Fig 6a~~) than~~), and similar salinity (p = 0.068) compared to the C_3 community. In the C_3 community, warming increased dissolved CH_4 in both the rooting zone porewater (~~i.e.~~ 10-20 cm) ($F_{3,}$~~$_{225}$ = 5.45~~$_{44}$ = 2.85, p = 0.~~001~~048; Fig. 5a) and in the deep peat (40-120 cm) ($F_{3,}$~~$_{368}$ = 13.~~$_{44}$ = 6.23, p ~~<~~= 0.001; Fig. 5b). Dissolved CH_4 concentrations were relatively similar in the ambient, +1.7 °C, and +3.4 °C treatments, but more than doubled with +5.1 °C of warming in both the rooting zone (59 to 125 µmol CH_4 L^{-1}, p_{adj} ~~=~~ < 0.001) and the deeper porewater (43 to 1254 µmol CH_4 L^{-1}, p_{adj} < 0.001). In the C_4 community there was minimal effect of warming treatment on porewater in the rooting zone ($F_{3,}$~~$_{230}$ = 5.45~~$_{44}$ = 0.442, p = 0.~~67~~72; Fig. 5a), but all levels of warming decreased dissolved CH_4 below 40 cm

($F_{3,\cancel{379}44} \cancel{= 39} = 129.3$, $p < 0.001$), with concentrations in the +3.4 and +5.1 plots less than a third of the concentrations in the ambient plots (155 vs 56 and 40 µmol CH_4 L^{-1}, $p_{adj} < 0.001$; Fig. 5b).

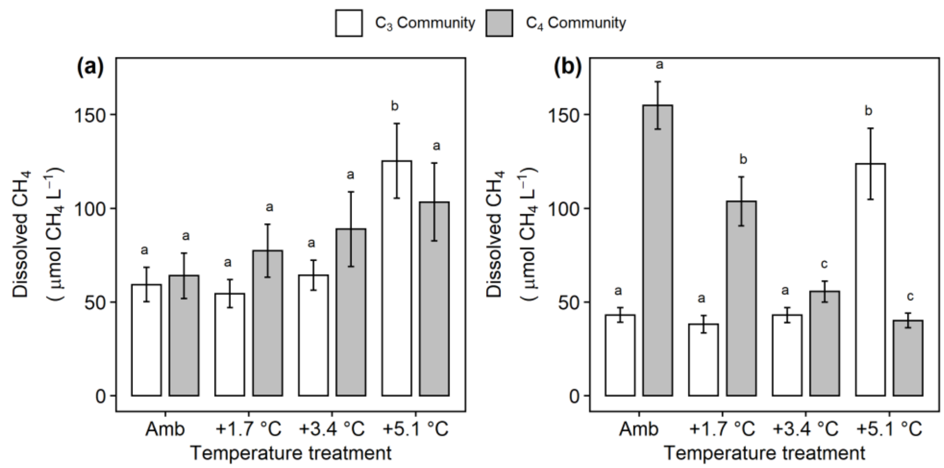


Figure 5. Comparison of dissolved CH_4 from the C_3 community dominated by *Schoenoplectus* (open bars) and the C_4 community dominated by *Spartina* and *Distichlis* (grey bars). (a) In the dominant rooting zone (10-20 cm) and (b) below the rooting zone (40-120 cm). Means are averaged across all sampling dates for 2016 – 2019. Error bars indicate SE. Letters indicate temperature treatments that are ~~significant~~significantly different from each other (p_{adj} <0.05) within the same plant community.

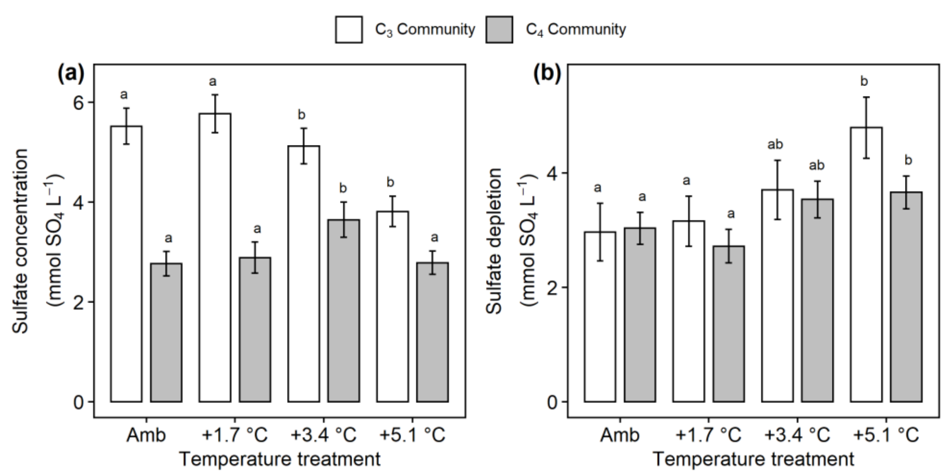


Figure 6. Comparison of sulfate concentrations and estimated sulfate depletion from the C_3 community dominated by *Schoenoplectus* (open bars) and the C_4 community dominated by *Spartina* and *Distichlis* (grey bars). (a) Sulfate ~~in~~availability throughout the entire soil profile and (b) sulfate depletion in the rooting zone. Means are averaged

across all sampling dates for 2016 – 2019. Error bars indicate SE. Letters indicate temperature treatments that are significant different from each other (p_{adj} <0.05) within the same plant community.

In the C_3 community, ~~warming of +3.4 and +5.1 °C reduced~~ SO_4 concentrations decreased with warming ($F_{3,}$~~$_{597}$ = 11.7~~$_{44}$ = 3.76, p ~~<~~= 0.~~001~~017), but warming effects on SO_4 cycling in the C_4 community were more mixed with +3.4 °C increasing SO_4 (p_{adj} = 0.~~013~~048) but no other treatments having large effects (Fig. 6a). In all plots, the measured concentrations of rooting~~-~~-zone SO_4 were lower than expected based on salinity (Fig. 6b), indicating that SO_4 reduction occurred. In both plant communities, the +5.1 °C treatments increased this SO_4~~-~~-depletion effect compared to ambient~~ (~~, though the effect was stronger in the C_3~~: $F_{3,349}$ = 3.96,~~ community (p ~~=~~≤ 0.~~008; C_3: $F_{3,358}$ = 3.04,~~ 001) than the C_4 community (p = 0.~~029)~~04). (Fig. 6b). ~~In~~Dissolved CH_4 was highest in both plant communities~~, dissolved CH_4 was highest~~ when SO_4 concentrations were ~~below~~≤ 5 mmol SO_4 L^{-1} (Fig. S5).

4. Discussion

Soil temperature (both seasonal and experimental) and plant traits were both strong drivers of CH_4 emissions from this site. This follows prior field, mesocosm, and incubation studies across a variety of wetlands, in which temperature has been shown to be a strong predictor of CH_4 emissions (e.g. ~~Al-Haj and Fulweiler, 2020; van Bodegom and Stams, 1999; Christensen et al., 2003; Dise et al., 1993; Fey and Conrad, 2000; Liu et al., 2019; Ward et al., 2013; Yang et al., 2019; Yvon-Durocher et al., 2014)~~Al-Haj and Fulweiler, 2020; van Bodegom and Stams, 1999; Christensen et al., 2003; Dise et al., 1993; Fey and Conrad, 2000; Liu et al., 2019; Ward et al., 2013; Yang et al., 2019; Yvon-Durocher et al., 2014) and in which plant functional type has an interacting effect (e.g. Chen et al., 2017; Duval & Radu, 2018; ~~L.~~ Liu et al., 2019; Mueller et al., ~~in press~~2020; Ward et al., 2013). Methane emissions are a function of the balance between methanogenesis, CH_4 oxidation, and CH_4 transport, so explaining these results requires some combination of stimulation of methanogenesis, reduction of CH_4 oxidation, or increase in CH_4 transport.

Prior data from brackish wetlands are limited, but incubation studies ~~on~~of freshwater wetland soils typically show large increases in CH_4 fluxes with warming (Duval & Radu, 2018; Hopple et al., 2020; Inglett et al., 2012; Sihi et al., 2017; van Bodegom & Stams, 1999; Wilson et al., 2016), indicating that

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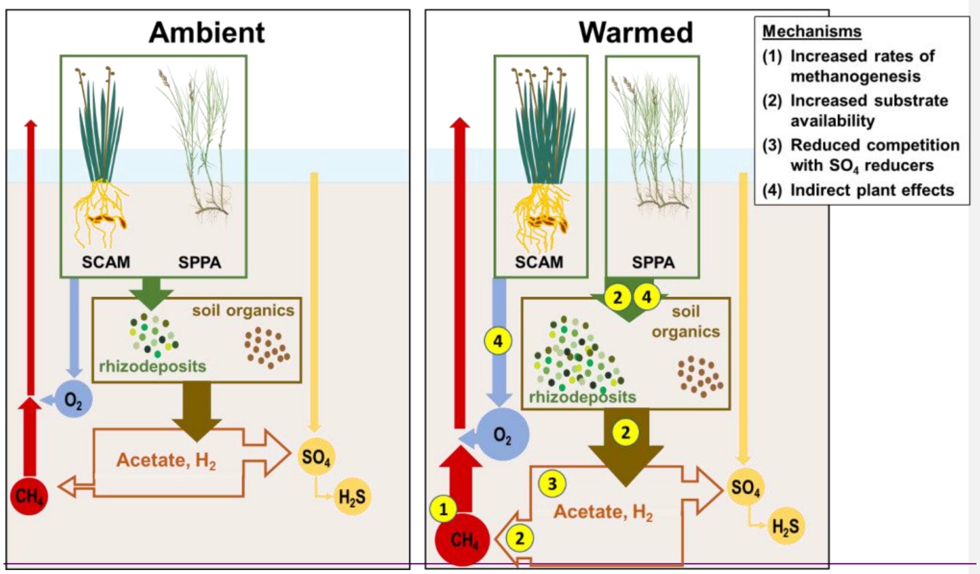
warming alters belowground processes. Though there is some evidence that rhizosphere temperature alters CH_4 transport through rice aerenchyma (Hosono & Nouchi, 1997), any transport-driven effects in this ecosystem would be transient unless there was a simultaneous increase in net CH_4 production (i.e. an increase in methanogenesis that was not completely offset by methanotrophy). Instead, we observed a sustained increase in CH_4 emissions, suggesting large shifts in anaerobic metabolism, especially with +5.1 °C of warming. We propose four potential and non-exclusive mechanisms to explain the temperature-driven increase in CH_4 emissions: (1) shifted ratios of CH_4 production to oxidation, (2) increased substrate availability, (3) reduced competition with sulfate reducers for H_2 and organic C, and (4) indirect plant trait effects (Fig. 7).



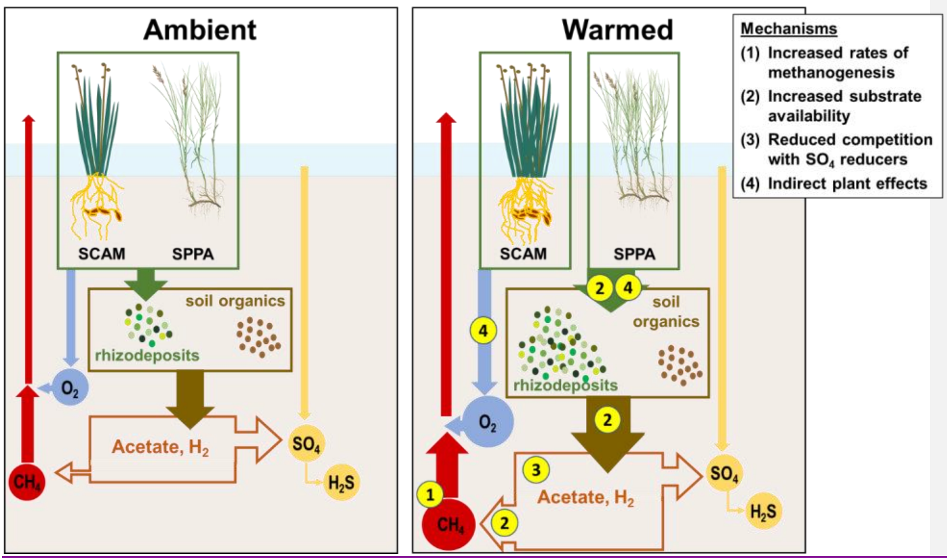


Figure 7. Schematic of mechanisms driving enhanced CH_4 emissions in response to warming. SCAM = *Schoenoplectus americanus*. SPPA = *Spartina patens*. Left: Processes under ambient conditions. Plants add organic compounds to the soil, which are transformed into other low-molecular-weight organic compounds. This pool, and processed soil organic matter, support terminal respiration processes dominated by SO_4 reduction over CH_4 production in organic-rich brackish marsh soils. Plants also transport O_2 which supports oxidation of a fraction of the CH_4 before it can be transported out of the soil. Right: Processes under warmed conditions. 1) Rates of CH_4 production increase more than rates of CH_4 oxidation. 2) Substrate availability increases as plants add more rhizodeposits and organic matter is more rapidly fermented to low-molecular-weight organic compounds and H_2. 3) The pool of electron donors available to methanogens increases as SO_4 reducers become SO_4 limited. 4) The dominant plant species have different effects on these process with *S. americanus* driving a net increase in O_2 transport and *S. patens* driving a net increase in rhizodeposits.

4.1 Whole-ecosystem warming promotes methanogenesis over CH_4 oxidation

Holding the supply of substrates and transport properties of the system constant, warming is expected to increase rates of CH_4 production relative to CH_4 oxidation due solely to differences in the temperature dependence of each process ~~(Megonigal et al., 2016).~~(Megonigal et al., 2016). In wetland soils, the average Q_{10} of methanogenesis is 4.1 compared to 1.9 for aerobic CH4 oxidation ~~(Segers, 1998),~~(Segers, 1998), which means that a system starting with a given initial ratio between the two processes will become increasingly dominated by methanogenesis as soils warm. A corollary to this expected pattern is that the ratio of the two processes should be constant if the Q_{10} responses are similar, an outcome that was supported with *in situ* measurements of the two processes in a tidal freshwater forested wetland (Megonigal & Schlesinger, 2002). We did not quantify the temperature dependence of CH_4 production and oxidation in the present study, but based on the literature (Segers, 1998) it is likely that methanogenic activity increased more than aerobic methanotrophic activity in direct response to warming (Fig. 7, mechanism 1). Evidence for this is that rhizosphere pools of porewater CH_4 were highest in the warmest treatment (Fig. 5a); because this occurred despite either no change or an increase in aboveground biomass (Noyce et al., 2019) which would by itself have lowered porewater CH_4 due to venting (plant transport), it indicates that CH_4 production increased relative to the sum of aerobic and anaerobic methane oxidation.

4.2 Whole-ecosystem warming increases substrate availability for methanogens

Methanogenesis can be the terminal step of anaerobic decomposition, but a consortium of microbes is required to break down soil organic matter to electron donor substrates that methanogens can metabolize. The final step in any decomposition pathway involves the flow of electrons from organic matter (electron donors) to a TEA. Under anaerobic conditions, this is accomplished by microbes that tend to specialize in one TEA and compete for organic C as an electron donor (Megonigal et al., 2004). Consequently, the supply of both electron donors and TEAs ~~regulate~~regulates the multi-step process of anaerobic decomposition and thus ultimately control CH_4 emissions. ~~Methanogenic~~For all pathways, methanogenic activity is typically limited by the supply of electron donors, including low~~-~~-molecular~~-~~-weight organic compounds (e.g. acetate, Neubauer & Craft, 2009) and H_2, a product of organic matter fermentation. We propose that whole-ecosystem warming increases the availability of previously limited C substrates ~~through~~in two ~~pathways~~aspects (Fig. 7, mechanism 2).

First, warming may directly influence C availability through biochemical kinetics. Even if organic inputs remained constant, warming likely accelerates fermentation of soil organic matter, ~~presumably~~ increasing substrate availability for methanogens. Second, the warmed plots had longer growing seasons than the unheated controls (Noyce et al., 2019). This ~~increases~~presumably increased inputs of root exudates and fresh detritus, accelerating all forms of heterotrophic microbial respiration by providing organic material that ~~can be broken down~~is decomposed into ~~acetate, H_2,~~low-molecular-weight organic C compounds and ~~other electron donors~~H_2 ~~(Philippot et al., 2009) and stimulating CH_4 emissions from warmed plots, particularly during the growing season as seen here. In 2017, we measured GPP at the same time as CH_4 emissions and observed that CH_4 emissions were positively correlated with GPP and that this effect increased with warming (Fig.~~(Philippot et al., 2009), stimulating growing season CH_4 emissions from warmed plots. In 2017, we observed that gross primary production was positively correlated with CH_4 emissions and that this effect increased with warming (Fig. S6). Prior studies have also linked CH_4 production or emissions to rates of photosynthesis (Vann & Megonigal, 2003), periods of active growth ~~(Chen et al., 2017; Ward et al., 2013)~~(Chen et al., 2017; Ward et al., 2013), and plant senescence which coincides with a pulse input of labile C from plants to soils (Bardgett et al., 2005).

Temperature-accelerated biochemical kinetics and increased electron-donor supply are mechanisms that can increase methanogenesis without necessarily shifting methanogenic pathways. However, shifts in the balance between hydrogenotrophic, acetoclastic, and methylotrophic methanogenesis pathways can be expected with warming. For example, in Arctic permafrost, methylotrophic methanogenesis was found to be more sensitive to warming than the other pathways (de Jong et al., 2018). Such shifts can be quantified with future analyses of H_2 and low-molecular-weight organic compounds (e.g. Bridgham et al., 2013; Yang et al., 2016), isotopic tracing of specific methanogenic pathways (e.g. Blaser & Conrad, 2016; Conrad, 2005; Neumann et al., 2016; Whiticar, 1999) and molecular community analyses (e.g. Bridgham et al., 2013; He et al., 2015; Wilson et al., 2016).

4.4 Whole-ecosystem warming reduces competition with sulfate reducers

While ~~acetate and other~~ low-molecular-weight organic compounds are ~~important~~ electron donors for acetoclastic methanogenic respiration, they are also ~~a key substrate~~substrates for other microbial groups ~~including~~such as SO_4 reducers (Megonigal et al., 2004; Ye et al., 2014). As a result, consumption of the limited ~~acetate~~organic carbon supply by SO_4 reducers should (and often does) limit methanogenic activity, such that terminal microbial respiration is typically dominated by SO_4 reduction in brackish marshes (Sutton-Grier et al., 2011).

~~We did not measure rates of SO_4 reduction in this study,~~Similarly, SO_4 reducers are more efficient than methanogens at competing for the H_2 required for CO_2 reduction (Kristjansson et al., 1982). We did not measure rates of SO_4 reduction in this study but can use SO_4 depletion as a proxy; more SO_4 depletion indicates that more SO_4 reduction has occurred. Warming generally increased SO_4 depletion, especially in the plots dominated by *Schoenoplectus* (Fig. 6b). Differences in SO_4 depletion between plots is not driven by SO_4 inputs because the only supply of SO_4 is the tidal flow, which is the same for all plots in each community of the experiment. Instead, higher rates of SO_4 reduction are most likely driven by some combination of electron donor supply and kinetics. While SO_4 reducers likely benefited from the increased availability of electron donors, as described above, the kinetics of SO_4 reduction also respond strongly to temperature (Weston & Joye, 2005).

When SO_4 concentrations drop below a threshold concentration, SO_4 reduction becomes SO_4-limited, rather than electron donor-limited (Megonigal et al., 2004). A review of the coastal wetland CH_4 literature estimated this threshold at 4 mmol SO_4 (Poffenbarger et al., 2011), a value that is consistent with patterns of porewater ~~[~~CH_4~~]~~ and ~~[~~SO_4~~]~~ at the GCReW site (Keller et al. 2009). As SO_4 and O_2 are the dominant electron-accepting compounds that suppress methanogenesis in this organic soil, this drawdown then releases the methanogens from substrate competition (Fig. 7, mechanism 3). Here, we show that ~~[~~SO_4~~]~~ is typically below 4 mmol in the +5.1 plots in the C_3 community and in all plots in the C_4 community (Fig. 6, Fig. S5). The drawdown of SO_4 may also reduce rates of anaerobic CH_4 oxidation (Hinrichs & Boetius, 2003). Van Hulzen et al. (1999) proposed a multi-phase system in a warming incubation experiment, observing that first methanogens are out-competed for substrates by other microbes, next CH_4 production increases as the supply of inhibiting TEA decreases, and finally ~~[TEA] decreases~~TEA availability is reduced to the point that methanogenesis is controlled only by the supply of electron donors. Warming in this study decreased the time required for the system to pass through the first two phases (van Hulzen et al., 1999). In our ~~study~~experiment, this final phase of increased methanogenic activity occurs when SO_4

concentrations dip below 4 mmol SO_4 L^{-1}, which occurs most often in the +5.1 °C plots, especially in the C_3 community. This interpretation is also supported by the long-term record of porewater chemistry from an allied experiment at the site, demonstrating that porewater CH_4 concentrations increase as SO_4 concentrations decrease (Keller et al., 2009).

Methanogens may also have a competitive advantage over SO_4 reducers for electron donor consumption at warmer temperatures (van Hulzen et al., 1999). Sulfate reducers and methanogens have very similar K_M values for acetate, but the K_M for acetoclastic methanogenesis may decrease with temperature whereas K_M values for SO_4 reducers increase with temperature (van Bodegom & Stams, 1999). If this is the case in our system then warming would allow methanogens to use a greater proportion of the available ~~acetate and other organic compounds~~substrates.

4.5 Plant traits modify warming effects on CH_4 cycling

The three biogeochemical mechanisms we propose to explain a warming-induced increase in CH_4 emissions should interact strongly with plant responses to warming. Relationships between plant functional groups and CH_4 emissions have been demonstrated through field studies in other wetland ecosystems such as peatlands (Bubier et al., 1995; Ward et al., 2013) ~~(Bubier et al., 1995, Ward et al., 2013) and in tidal wetland mesocosms (L. Liu et al., 2019; Martin & Moseman-Valtierra, 2017; Mueller et al., in press). We provide field evidence that two species with distinct plant traits – *Schoenoplectus* and *Spartina* – have strikingly different effects on CH_4 emissions from brackish wetlands. *Spartina*-dominated communities had consistently higher CH_4 emissions under both ambient and warmed conditions (Fig. 3). In most years, *Schoenoplectus* biomass was negatively correlated with CH_4 emissions, while *Spartina*/*Distichlis* biomass was positively correlated. Vegetation effects are typically strongest during the growing season, when the plants are actively altering rhizosphere biogeochemistry (F. J. W. A.~~

~~van der Nat & Middelburg, 1998; Ward et al., 2013), which is consistent with our observations in this study.~~

~~As with warming effects, plant-driven shifts in CH_4 emissions are the result of differing rates of CH_4 production, oxidation, transport, or a combination of these processes, but sustained differences in emissions cannot be attributed only to transport, as discussed previously. Instead, the stimulation of CH_4 emissions is likely due to changes in the plant-mediated supply of electron acceptors and electron donors. In a field environment, differentiating between species-specific effects and underlying environmental conditions can be difficult, but mesocosm studies that control all environmental factors have also found species-specific effects on CH_4 cycling (e.g. (D. Liu et al., 2014). Plants can alter CH_4 cycling by adding O_2 (electron acceptor) or C substrates (electron donors) to the rhizosphere, altering the redox state. We propose that *Schoenoplectus* is a net oxidizer of the rhizosphere and that *Spartina* is a net reducer, and thus their presence and productivity have opposing effects on CH_4 emissions (Fig. 7, mechanism 4).~~

~~*4.5.1 Schoenoplectus oxidizes the rhizosphere, increasing CH_4 oxidation*~~

~~Species vary in their capacity to support aerobic CH_4 oxidation (van der Nat & Middelburg, 1998)~~ and in tidal wetland mesocosms (Liu et al., 2019; Martin & Moseman-Valtierra, 2017; Mueller et al., 2020). We provide field evidence that two species with distinct plant traits -- *Schoenoplectus* and *Spartina* -- have strikingly different effects on CH_4 emissions from brackish wetlands. *Spartina*-dominated communities had consistently higher CH_4 emissions under both ambient and warmed conditions (Fig. 3). In most years, *Schoenoplectus* biomass was negatively correlated with CH_4 emissions, while *Spartina*/*Distichlis* biomass was positively correlated. Vegetation effects are typically strongest during the growing season, when the plants are actively altering rhizosphere biogeochemistry (van der Nat & Middelburg, 1998; Ward et al., 2013), which is consistent with our observations in this study.

As with warming effects, plant-driven shifts in CH_4 emissions are the result of differing rates of CH_4 production, oxidation, transport, or a combination of these processes, but sustained differences in emissions cannot be attributed only to transport, as discussed previously. Instead, the stimulation of CH_4

emissions is likely due to changes in the plant-mediated supply of electron acceptors and electron donors. In a field environment, differentiating between species-specific effects and underlying environmental conditions can be difficult, but mesocosm studies that control all environmental factors have also found species-specific effects on CH_4 cycling (e.g. Liu et al., 2014). Plants can alter CH_4 cycling by adding O_2 (electron acceptor) or C substrates (electron donors) to the rhizosphere, altering the redox state. We propose that *Schoenoplectus* is a net oxidizer of the rhizosphere and that *Spartina* is a net reducer, and thus their presence and productivity have opposing effects on CH_4 emissions (Fig. 7, mechanism 4).

4.5.1 Schoenoplectus oxidizes the rhizosphere, increasing CH_4 oxidation

Species vary in their capacity to support aerobic CH_4 oxidation (van der Nat & Middelburg, 1998) and *Schoenoplectus* appears to support higher rates of aerobic CH_4 oxidation than *Spartina* ~~(Mueller et al., in press).~~(Mueller et al., 2020). *Scirpus lacustris* is morphologically similar to *Schoenoplectus americanus* studied here and has been demonstrated to have substantial ~~rhizospheric~~rhizosphere oxidation capacity, especially during the growing season ~~(van der Nat & Middelburg, 1998)~~(van der Nat & Middelburg, 1998). Consequently, these plants likely exert stronger control on rates of CH_4 oxidation than rates of methanogenesis (van der Nat & Middelburg, 1998). We hypothesize that the relatively high capacity of *Schoenoplectus* to transport O_2 held the CH_4 emissions stimulation caused by modest levels of warming (+1.7 to +3.4 °C) to rates similar to under ambient conditions (Fig. 3). At high warming (+5.1 °C), however, *Schoenoplectus* community CH_4 emissions drastically increase (Fig. 3). We suggest that this is due to the combined effects of the three mechanisms discussed previously, namely the differences in the Q_{10}-values of CH_4 production and CH_4 oxidation, the increased supply of organic substrate through plant productivity, and the decrease in competition for electron donors due to SO_4 depletion. Collectively, when the ecosystem is warmed above current ambient conditions by 5 °C or more, enhanced stimulation of CH_4 production starts to offset some of the *Schoenoplectus* oxidation effect. This also offers an explanation for the positive correlation between *Schoenoplectus* biomass and CH_4 emissions observed in 2016 as that was the hottest of the four years in this study.

4.5.2 Spartina reduces the rhizosphere, increasing CH_4 production

The variability in quality and quantity of root exudates between plant functional types is well known to affect microbial community composition and activity (Deyn et al., 2008). Methanogenesis responses to warming in incubation studies are related to the lignin and cellulose content of the peat, which in turn depends on the plant functional type from which the peat developed (Duval & Radu, 2018). Although warming is likely increasing substrate availability across the whole experiment, the production ~~rate~~ of labile, low~~-~~-molecular~~-~~-weight C substrates through fermentation ~~does not increase as rapidly~~is less sensitive to temperature above 25 °C than below this threshold ~~(Scott C Neubauer & Craft, 2009; Weston & Joye, 2005). Microbes may also preferentially use root exudates as their C sources~~(Neubauer & Craft, 2009; Weston & Joye, 2005). Microorganisms may also preferentially use freshly produced (i.e. labile) organic carbon compounds as electron donors ~~(Delarue et al., 2014)~~(DeLaune et al., 2014) and consequently warming effects on CH_4 production should be strongest in a system where ~~the plants~~rates of root exudation and turnover are ~~directly releasing key C substrates.~~most rapid. We propose ~~this explains the patterns~~that root exudation and turnover explain the positive correlation between plan t biomass and CH_4 emissions that we observed in the C_4 community. Multiple years of porewater chemistry at this site show that *Spartina*-dominated communities have higher DOC and dissolved CH_4 than adjacent *Schoenoplectus* communities ~~(Keller et al., 2009; Marsh et al., 2005).~~(Keller et al., 2009; Marsh et al., 2005). Though we did not directly measure root exudation, porewater DOC is partially derived from root ~~exudation~~exudates and has been used as a proxy to understand the responses of root exudates to global change factors ~~(Dieleman et al., 2016; Fenner et al., 2007; Jones et al., 2009).~~(Dieleman et al., 2016; Fenner et al., 2007; Jones et al., 2009).

We observed a simultaneous increase in dissolved CH_4 at the soil surface and a decrease in dissolved CH_4 at depth in the warmed C_4 plots. As with the observed trends in CH_4 emissions, there are multiple mechanisms that could cause a shift in porewater CH_4 concentrations. Of the four mechanisms outlined above, perhaps the simplest explanation is an increase in labile C at shallow depths and a decrease in deeper soil. This is consistent with DOC depth profiles from this the C_4 community in which porewater

DOC increases with warming in shallow samples but decreases with warming in deep samples (Fig. S7). This shallowing of peak DOC concentrations could be due to a warming-induced increase in evapotranspiration, leading to slower downward hydrologic transport of DOC-rich surface porewater to lower depths, or a warming-induced shallowing of the root system, leading to a shift in the location of root exudates.

In most years, *Spartina* biomass was positively correlated with CH_4 emissions, supporting our hypothesis that *Spartina* favors net CH_4 production. However, in 2016 *Spartina* biomass and CH_4 emissions were negatively correlated. Prior work at this site has indicated that *Spartina*/*Distichlis* biomass is more negatively affected by hot and dry growing conditions than *Schoenoplectus* (Noyce et al., 2019) due in part because the *Spartina*/*Distichlis* (C_4) communities are less frequently inundated. The 2016 growing season was substantially warmer than average (Table 2) and the heating treatments were initialized on 1 Jun of that year, after the annual plants had already established and may have developed adaptations to ambient, rather than elevated, temperature conditions. The combination of these two effects likely led to heat stress, reducing the root exudates supplied to the rhizosphere microbial community (Heckathorn et al., 2013) and thus minimizing the *Spartina* stimulation effect.

4.6 Comparisons with prior data

Methane emissions have been measured at the GCReW site previously, but this study represents the most comprehensive dataset collected to date, and is thus particularly useful for advancing the process-based understanding needed to improve prognostic models. Overall, our flux estimates are lower than those reported previously. The earliest CH_4 fluxes were measured in a single month (July) in *Schoenoplectus*-dominated plots and reported to be 331 to 6883 µmol m^{-2} d^{-1} (Dacey et al., 1994), much higher than our range of 359 to 1651 µmol m^{-2} d^{-1} for ambient temperature *Schoenoplectus* plots in July. Similarly, ~~Marsh et al. (2005)~~Marsh et al. (2005) reported mean growing season (May-Oct) CH_4 emissions from this site of 846 ± 111 µmol CH_4 m^{-2} d^{-1}, whereas we measured 656 ± 79 µmol CH_4 m^{-2} d^{-1} over the same months. Finally, Pastore et al. (2017) estimated average annual fluxes in their *Schoenoplectus*-dominated ambient CO_2 plots as 3.1 ± 1.7 g CH_4 m^{-2} yr^{-1}, compared to our estimates of 1.6 ± 0.3 g CH_4 m^{-2} yr^{-1} for

Schoenoplectus plots. The different estimates by these studies may be partly due to interannual variability as demonstrated in our data where 2018 had substantially higher fluxes than any of the surrounding years (Table S2).

The annual estimates reported here for ambient temperature plots trended lower than published mean CH_4 emissions for mesohaline tidal marshes. Our plots ranged from 0.7 to 9.3 g CH_4 m^{-2} yr^{-1} (mean = 9.3), compared to the range of 3.3 to 16.4 g CH_4 m^{-2} yr^{-1} (mean = 16.4) reported by Poffenbarger et al. (2011). This difference may be explained by the fact that there was significant within-class variation in the oligohaline and mesohaline salinity classes that was unexplained and their assessment was based on too few data points to fully capture the variation that is expected to exist in the mesohaline class. Indeed, subsequent studies have documented fluxes well below 3 g CH_4 m^{-2} yr^{-1} (Krauss & Whitbeck, 2012), and even negative fluxes (Al-Haj & Fulweiler, 2020). We hypothesize that the low fluxes measured at our site reflect *Schoenoplectus americanus* traits that favor CH_4 oxidation more than CH_4 production, and that the high end of our range was limited by the high soil elevation (i.e. deep water table) of areas dominated by *Spartina patens*, off-setting the influence of *S. patens* traits that favor CH_4 production.

4.7 Implications for tidal wetland carbon cycling

Warming accelerates rates of CH_4 emissions from brackish marshes, especially during the growing season. This is driven by both direct and indirect warming effects and mediated by soil biogeochemistry, but the magnitude of the warming effect is also dependent on traits of the plant species that dominate the plant community. Communities dominated by *Spartina patens* increase net CH_4 emissions in response to smaller increments of warming than communities dominated by *Schoenoplectus americanus*. *Spartina*-dominated sites may thus have a higher likelihood of shifting from a net C sink to a net C source under future warming conditions, due to this increased loss of C as CH_4. However, this effect could be mitigated if these high-elevation *Spartina* marshes become dominated by *Schoenoplectus* in response to predicted accelerated sea-level rise (Kirwan & Guntenspergen, 2012). In addition, *Spartina* traits are plastic and influenced by factors such as soil redox conditions ~~(Kludze & DeLaune, 1994)~~(Kludze & DeLaune, 1994), salinity (Crozier & DeLaune, 1996), and water level ~~(Liu et al., 2019)~~(Liu et al., 2019), all of which can be expected to change plant-mediated effects on CH_4 biogeochemistry. Further studies are needed to thoroughly assess the range of environmental conditions under which *Spartina* is a net reducer and *Schoenoplectus* is a net oxidizer as proposed by the present study.

Data availability

All data is available from the corresponding author upon request.

Author contributions

GLN and JPM designed the study, GLN collected and analyzed the data, and GLN and JPM wrote the paper.

Competing interests

The authors declare that they have no conflict of interest.

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