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Dormant season warming amplifies daytime CO₂ emissions from a temperate urban salt marsh

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Salt marshes provide many important ecosystem services, key among them being carbon sequestration. However, a large degree of uncertainty remains in salt marsh carbon budgets, particularly during colder months of the year when salt marsh microbial and vegetative activity is assumed to dormant. We also lack data on urban systems. In this study, we used an easily portable carbon dioxide sensor package to directly measure net carbon dioxide (CO₂) fluxes throughout the winter in a temperate, urban salt marsh. We sampled across the dormant season both on normal (cold) temperature days and on days that were anomalously warm (defined here as air temperatures 2.8°C above the long-term average). We demonstrated that median (\pm mad) daytime CO₂ fluxes doubled on the warm days, compared to cold days (1.7 ± 2 mmol m⁻² h⁻¹, 0.7 ± 1.3 mmol m⁻² h⁻¹, respectively). We also show that net CO₂ emissions scaled with soil temperature. The high day-to-day variability, however, implies that infrequent or sparse measurements cannot sufficiently capture the temporal dynamics of dormant season salt marsh net CO₂ fluxes. The magnitude of the net CO₂ source from our sampling during the dormant season leads us to hypothesize that, as mean annual temperatures continue to increase, dormant season CO₂ emissions from salt marshes will increasingly offset growing season carbon dioxide uptake. This change compromises the carbon sequestration capacity, and therefore the climate mitigation potential of these ecosystems. Future studies should focus on quantifying the impact of dormant season CO₂, and other greenhouse gases on salt marsh carbon budgets.

KEYWORDS

winter biogeochemistry, blue carbon, climate change, portable sensors, greenhouse gas, carbon dioxide

1 Introduction

Salt marshes are important ecosystems which deliver a wealth of services such as critical habitat provision, storm surge protection, and pollution filtration (e.g., [De Groot et al., 2012](#)). Compared to other coastal wetlands and forested terrestrial ecosystems, salt marshes also have the highest global average carbon accumulation rate of ~ 250 g C m⁻² y⁻¹ ([Ouyang and Lee, 2014](#)). Despite their importance, these are some of the most degraded systems on earth, with approximately half of all salt marshes having been lost in the last ~ 200 years worldwide ([Silliman et al., 2009](#), [Campbell et al., 2022](#)). Salt marsh degradation is driven by

TABLE 1 Examples of dormant season carbon dioxide fluxes as measured with chambers from temperate salt marshes. Note that the method and frequency of sampling differs across studies.

Month(s)	Carbon dioxide flux (mmol m ⁻² h ⁻¹)	Location	Method	Study
Monthly (November to March)	3.5–5.0	Southport, United Kingdom	Chamber, Light	Ford et al. (2012)
January, February	0–2.3	Massachusetts, United States	Chamber, Light	Emery and Fulweiler (2014)
November, March	2.04–4.18	New Brunswick, Canada	Chamber, Dark	Chmura et al. (2016)
December, January	–5.11–11.99*	Washington, United States	Chamber, Dark and Light	Diefenderfer et al. (2018)
November, December	–11.2–3.1	Delaware, United States	Chamber, Light	Hill and Vargas (2022b)
February–March	–1.85–33.36**	Massachusetts, United States	Chamber, Light	This Study

*Only control fluxes are included here. **Note included in this range of two statistical outliers of 11.57 and 36.36 mmol m⁻² h⁻¹.

a variety of human activities including major hydrological alterations, such as ditching and draining, as well as pollution exposure from excess nutrients and heavy metals (Bergbäck et al., 2001; Verhoeven et al., 2006; Davidson et al., 2010; Mitsch and Hernandez, 2013). Additionally, salt marshes are losing their ability to migrate in response to sea level rise because they are increasingly bounded by impervious human infrastructure (Fitzgerald and Hughes, 2019). This is especially true for urban salt marshes, which are even more heavily impacted and degraded. Further, urban marshes are vastly understudied relative to their rural counterparts, so the impacts of anthropogenic stressors on urban marshes remain poorly understood (Macreadie et al., 2013; Doroski et al., 2019).

Over the last decade, renewed attention has focused on salt marshes as part of a major push to understand coastal blue carbon capacity, that is the ability of marine ecosystems to capture and store carbon (e.g., Macreadie et al., 2013; Crooks et al., 2018; Bertram et al., 2021). Marshes have the potential to sequester and store large quantities of carbon from the atmosphere. In fact, vegetated coastal ecosystems (e.g., salt marshes, mangroves, and seagrasses), account for 50% of the total carbon buried in marine sediments (Duarte et al., 2013). The carbon sequestration capacity of a salt marsh is the result of a combination of various processes. There is the carbon stored within the salt marsh which includes carbon taken up through photosynthesis and stored as biomass as well as captured allochthonous organic carbon, the carbon released from the marsh to the atmosphere (as carbon dioxide (CO₂) or methane), riverine carbon input, and any lateral flux out of the marsh into surrounding water. It is the balance of these processes that determines if a salt marsh is a net sink or net source of carbon. However, the magnitudes of these fluxes remain an area of uncertainty due to the highly variable nature of salt marsh systems and the difficulty in capturing high spatial or temporal resolution data (McLeod et al., 2011; Rosentreter J. A. et al., 2021; Gallagher et al., 2022).

Most of our understanding of greenhouse dynamics in temperate salt marshes is based on measurements made during the growing season (e.g., Emery and Fulweiler, 2014; Al-Haj and Fulweiler, 2020; Rosentreter J. et al., 2021). In temperate salt marshes, the growing season is between May and October (or

October to March in the Southern hemisphere), and for a variety of ecological and logistical reasons, we tend to collect fluxes of CO₂ and other greenhouse gases during this period. Ecologically, these decisions are based on the idea that metabolism scales with temperature, thus little respiration activity is expected in the colder winter months (e.g., Thamdrup et al., 1998; Kostka et al., 2002). Further, the lack of living salt marsh vegetation and the weak winter sun also means minimal photosynthetic activity. Logistically, sampling in colder months can be challenging for many of reasons, for example, where this study took place, ice and snow cover may limit access to the salt marsh surface. Thus, few studies of dormant season CO₂ fluxes from salt marshes have been published. However, despite preconceptions, the few existing studies highlight the potential for salt marshes to be a source of CO₂ during this period (Table 1).

While the prevailing view is that little metabolic activity occurs in salt marshes outside of the growing season, there is reason to think this is not always the case. Over 40 years ago Teal and Teal (1983) noted that warm winter days can increase the temperature of the surface of the salt marsh up to 27°C. Terrestrial studies highlight the insulating power of snowpack and increased respiration under it, allowing a buildup of CO₂ (Bubier et al., 2002; Lupascu et al., 2018). The snow itself may also act as a barrier impeding the escape of CO₂ to the atmosphere, keeping emissions low when snow cover is intact (Pedron et al., 2022). Today, climate change is leading to warming temperatures throughout the year, with many temperate areas experiencing disproportionately more warming in the winter months (NOAA, 2023). Additionally, in the northeast United States winter temperatures are becoming more variable with cold days often followed by multiple warm days, thus increasing the potential CO₂ generation during a season we normally consider metabolically dormant (Fan et al., 2015).

The goal of this study was to quantify daytime CO₂ fluxes from an urban temperate salt marsh during the dormant season and to examine how the marsh responds to warm days during this otherwise cold period. We hypothesized that in general daytime CO₂ fluxes from the dormant marsh would be low, but not zero, and that they would increase as the salt marsh warmed. To test these hypotheses, we conducted a series of closed chamber flux measurements on an urban salt marsh in Boston, MA (United States) between February and April 2022.

2 Materials and methods

2.1 Study site

This study was conducted at the Belle Isle Marsh Reserve in Boston, MA, United States of America. Belle Isle is the largest remaining salt marsh in the city of Boston, where over 80% of native salt marshes have been lost (Bromberg and Bertness, 2005). Here we use the U.S. census definition of “urban” meaning within the boundaries of a city or town with a population of 50,000 or more. This marsh falls within the boundaries of the city of Boston, population ~650,000 (census.gov). This is an urban ecosystem that is bounded by dense human development, and approximately 30% of the marsh area has been restored from industrial and commercial use since the late 1970s (Massachusetts Department of Conservation and Recreation, Supplementary Figure S1). To capture the impact of warming winters on marsh CO₂ dynamics, we took daytime flux measurements roughly twice weekly from the beginning of February through the beginning of April 2022, totaling 15 sampling days.

According to NOAA, the winters in this study region were, on average, 5°F warmer than normal in 2021. We therefore used this as the threshold for “warm days” and have converted it to degrees Celsius to meet scientific notation standards. Sample days were evenly distributed between normal temperature days, or days which fell within the 1981–2010 average temperature range (National Weather Service, 2021), and warm days which were at least 2.8°C (i.e., 5°F) warmer than the 1981–2010 average. We used the daily air temperatures from the National Weather Service station at Boston Logan International Airport, which is located within Boston Harbor, and is just 3.3 km away from the study site. We measured salt marsh soil temperature at 5 cm depth using a soil temperature probe (Sunleaves).

Triplicate carbon dioxide fluxes were measured in two marsh zones, high marsh (42° 23'20"N, 70° 59'29"W) and low marsh (42° 23'18"N, 70° 59'22"W). In the high marsh *Spartina patens* was the dominant vegetation species, whereas the low marsh was dominated by *Distichlis spicata* interspersed with *Spartina alterniflora* (short form). The high marsh site is approximately 1.1 m above sea level, while the low marsh is approximately 0.6 m above sea level. The mean tidal range is range 2.9 m, therefore at high tide the low marsh is fully flooded, while the high marsh site only flood during spring tides. We chose representative high and low marsh sites for this research, and haphazardly chose chamber placement within these zones each sampling trip. We also took flux measurements in the middle of the day between 10 a.m. and 3 p.m. All sampling took place when the salt marsh was exposed and not inundated with tidal water. On average sampling took place within 6.5 h of last high tide, though this ranged from 1 to 11 h.

2.2 CO₂ sensor

We measured CO₂ concentrations in this study using an affordable, easily portable (<0.8 kg) sensor package (Supplementary Material) similar to those used previously for experimental CO₂ monitoring (Bastviken et al., 2015; Chen and

Markham, 2020). Briefly, a small, non-dispersive infrared CO₂ sensor (K30, Sensair) and a weather-proof temperature and humidity sensor (SHT-30, Adafruit) were coupled to a microcontroller (Uno Rev3, Arduino) with data logging shield (1,141, Adafruit) and programed to record CO₂ concentration, temperature, and humidity every 3 s. The sensor system was housed in a waterproof container and internal pumps pulled air in from the outside over the CO₂ sensor. We calibrated the sensor before each deployment with a two-point calibration by connecting the sensor inflow to helium and 400 ppm CO₂ standard tanks per manufacturer specifications (SenseAir). The digital sensors were then adjusted to calibration data using GasLab software (CO2meter.com). These sensors were ground-truthed against the more widely used cavity ringdown mass spectrometer (G2508, Picarro) and found to have good agreement (Supplementary Information, Supplementary Figure S2).

2.3 Data analysis

To measure CO₂ fluxes, sensor packages were placed inside domed, acrylic chambers (25.4 cm diameter by 20.3 cm tall). Chambers were pushed approximately 1 cm into the marsh surface (or snow surface if there was consistent snow cover), sealing off 9.4 L of air. Sensors then recorded the CO₂ concentration, temperature, and humidity every 3 s during 10-min incubations. Multiple incubations were conducted each day as our objective was to deploy triplicate samples in the high and low marsh during each sampling event. CO₂ concentrations were consistently linear with time throughout the study, allowing us to use a linear regression to calculate net CO₂ fluxes. We calculated net CO₂ flux using the rate of change in CO₂ concentration over the course of the incubation, temperature corrected and normalized to chamber volume and surface area, yielding fluxes in mmol m⁻² h⁻¹. The slope of this linear relationship was used in the flux calculation, provided that $p > 0.05$ (Brannon et al., 2016; Eq. (1)). If $p < 0.05$, the flux was reported as net zero. The minimum detectable flux for these sensors was found to be 0.072 mmol m⁻² h⁻¹ (Supplemental Information) and any flux smaller than this (absolute value) was designated as non-detect (ND). These are net fluxes and are equivalent to net ecosystem exchange (NEE): positive fluxes are indicative of net CO₂ release (respiration) while negative fluxes indicate net CO₂ uptake (photosynthesis).

All data analysis was done in R v.4.3.2 (R Core Team, 2023). We considered statistical tests significant when $p \leq 0.05$. Packages *EnvStats* (Millard, 2013), *outliers* (Komsta, 2022), *ggpmisc* (Aphalo, 2024), and *ggplot2* (Wickham, 2016) were used for statistical analyses and data visualization.

3 Results

Temperatures during the sampling period (February 2–4 April 2022) were highly variable and often much warmer than 1981–2010 normals (National Weather Service, 2021; Figure 1). Soil temperature on sampling days were also variable with air and soil temperatures ranging from –7–19°C and –1–13°C, respectively. Sensor package temperature measured outside the sample chambers

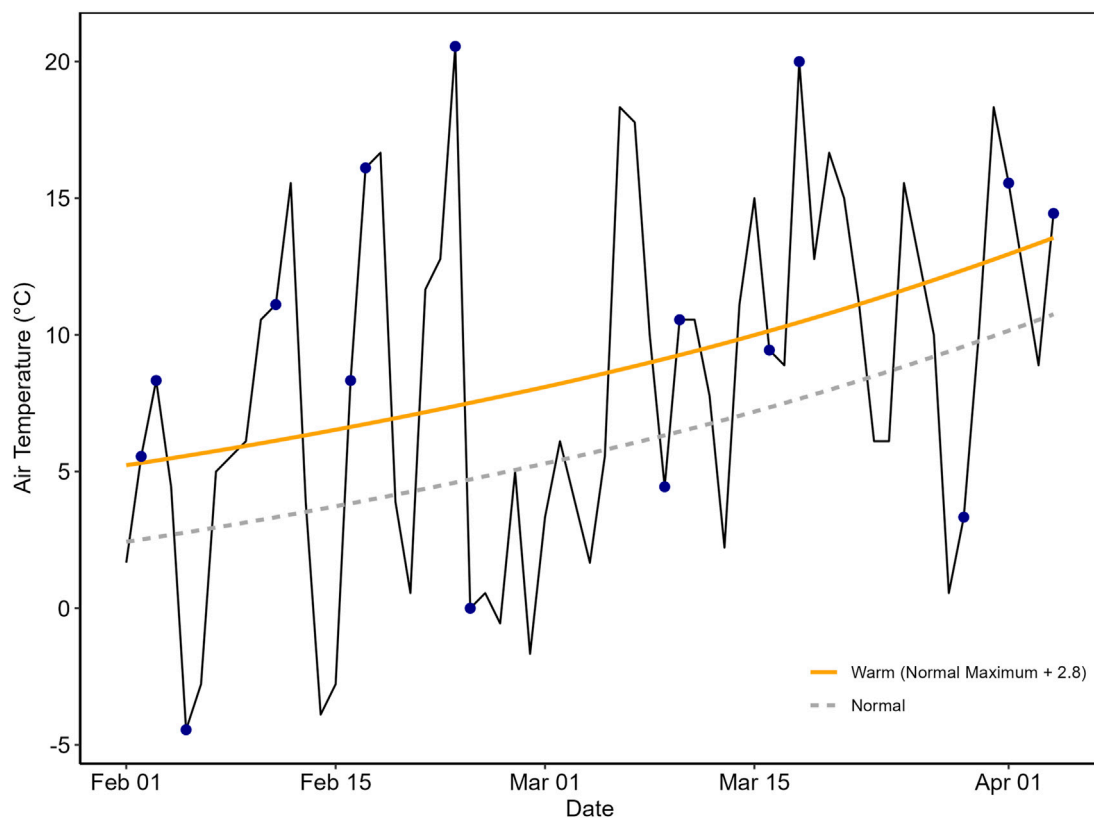


FIGURE 1
Air temperature variation over the course of this study showing daily high temperature (solid black line), average normal high temperature (1981–2010, dashed grey line), warm days which we defined here as at least 2.8°C warmer than the 1981–2010 average (yellow line), and sampling dates (blue circles). Dates are listed as day of year (2022). In this study 10 out of the 15 sampling events occurred on days that were above long-term average temperatures.

was significantly correlated with the mean daily air temperature recorded at the National Weather Service station at Boston Logan International Airport ([Supplementary Figure S3](#)). Sensor package temperature was on average 4°C higher than the maximum recorded daily temperature at Boston Logan International Airport. We are unsure of the reason for the discrepancies between the two air temperature sensors. We suspect it may be due to the location of the temperature probes—where the weather station is recording air temperature above the ground, while the sensor package temperature sensors are measuring at the ground level. Regardless the strong correlation suggests the data are comparable.

Soil temperature was strongly correlated to maximum daily air temperature as recorded at the National Weather Service station at Boston Logan International Airport ($r = 0.80$, $p = 0.0005$) and to the sensor package temperature outside the sample chambers ($r = 0.73$, $p = 0.003$).

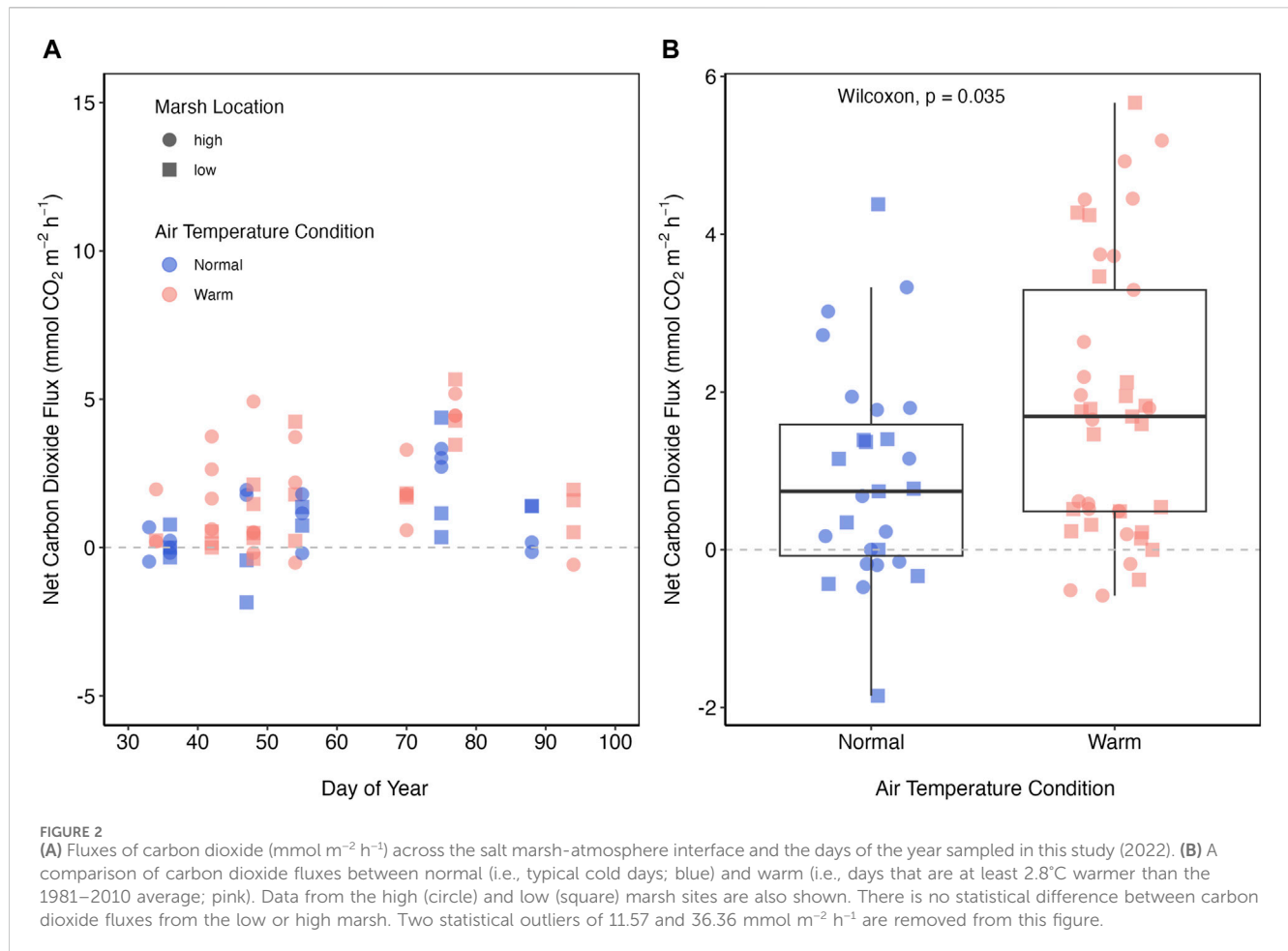
Net CO₂ fluxes across the salt marsh soil-air interface in this study ranged from -1.85 – 36.61 mmol m⁻² h⁻¹, and fluxes from the high and low marsh were not significantly different ($p = 0.4958$) from each other ([Figure 2A](#)). On one occasion (March 29), we measured two high CO₂ fluxes of 11.57 and 36.61 mmol m⁻² h⁻¹. A Rosner test and the interquartile range method identified these values as outliers, so we removed them from further analysis. However, we note that although these points were a statistical outliers, we have no reason to think they are necessarily

measurement errors so we have retained these values in the dataset and provide them in the figure and table captions.

We captured CO₂ fluxes on both normal and warm days throughout this study period and typically within a few days of each other ([Figure 2A](#)). We observed that median (\pm mad) CO₂ fluxes from normal days were more than 2x lower than those from the warm days (0.74 (± 1.3) mmol m⁻² h⁻¹, 1.69 (± 2.0) mmol m⁻² h⁻¹, respectively; [Figure 2B](#)). We also observed a significant positive linear relationship between soil temperature and CO₂ flux ([Figure 3A](#); $R^2 = 0.33$, $p < 0.001$). This relationship appears slightly stronger for the low marsh compared to the high marsh ([Figure 3B](#)).

4 Discussion

Given the gaps in our understanding of salt marsh carbon dynamics, we examined daytime CO₂ fluxes during the dormant season in an urban, temperate marsh using a chamber and a low-cost portable sensor package. We found that net CO₂ fluxes were dominated by net emissions, regardless of sampling location (i.e., high or low marsh, [Figure 2A](#)). We also found that, as hypothesized, net CO₂ fluxes were lower on normal (i.e., cold) days compared to the anomalous warm days ([Figure 2B](#)). The range of fluxes observed in this study are comparable to those reported for nearby salt marshes ([Emery and Fulweiler, 2014](#); [Forbrich and Giblin, 2015](#); [Emery et al.,](#)

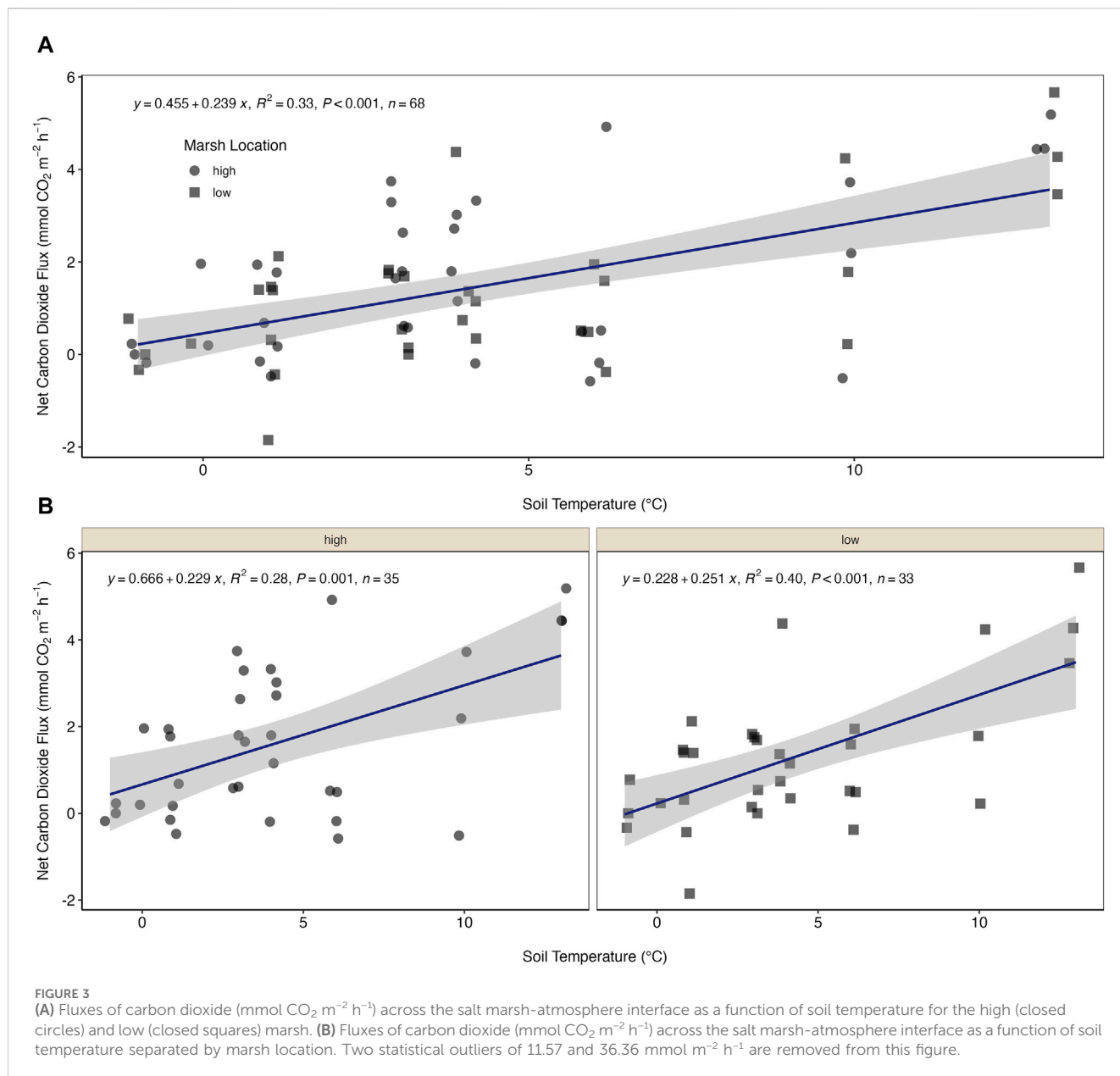


2019), and to other dormant season salt marsh CO_2 fluxes measured using similar methods (Table 1). They are also on par with dormant season CO_2 fluxes reported from salt marsh eddy co-variance measurements across a variety of conditions (Tonti et al., 2018; Huang et al., 2020; Arias-Ortiz et al., 2021; Chu et al., 2021; Vázquez-Lule and Vargas, 2021). Eddy co-variance measurements offer an excellent way to measure long-term, continuous CO_2 fluxes, however they are expensive, and require significant expertise to maintain and conduct the data analysis (Rosentreter et al., 2023). Here we demonstrate that chambers equipped with low-cost sensor package can also capture dormant season CO_2 fluxes. Additionally, this study contributes to mounting evidence that non-growing season months have a quantifiable and relevant impact on salt marsh net carbon budgets.

The current marsh sampling paradigm heavily biases salt marsh greenhouse gas data toward the growing season carrying over the assumption that, due to low temperatures and correspondingly low respiration rates, winter and early spring greenhouse gas fluxes are negligible. The result is a limited understanding of carbon and greenhouse gas dynamics in salt marshes, with snapshots often being used as representatives for an entire season. However, this study illustrates that, while dormant season CO_2 fluxes are highly variable, they are larger and more dynamic than the existing paradigm would suggest (Table 1; Figure 2). Further, we have demonstrated that the timing and frequency of sampling matters. Single or scattered

sampling is insufficient to capture these dynamics and thus understand how they impact carbon storage and budgets.

To illustrate the potential impact on a salt marsh carbon budget we can compare the median daytime carbon dioxide uptake during the active growing season (June to August) from a nearby salt marsh (median = $-10.96 \text{ mmol m}^{-2} \text{h}^{-1}$, Emery and Fulweiler, 2014), to the median normal ($0.74 \pm 1.3 \text{ mmol m}^{-2} \text{h}^{-1}$) and warm ($1.69 \pm 2.0 \text{ mmol m}^{-2} \text{h}^{-1}$) fluxes observed here. There are 92 days in this period, and if we assume that CO_2 uptake occurs in the 12 daylight hours of those days, then we would estimate a net, daytime carbon dioxide uptake of $12,100 \text{ mmol m}^{-2}$ for those 3 months. If we similarly assume a non-growing season period of 92 days, 12 daylight hours, and normal temperatures we estimate a release of 817 mmol m^{-2} , or under warm conditions a release of 1866 mmol m^{-2} per dormant season. This back of the envelope calculation demonstrates that even during the normal dormant season the marsh is source of carbon dioxide that would decrease growing season, daytime carbon dioxide uptake by $\sim 7\%$. However, under warm conditions, like those we anticipate seeing increasingly in the future, dormant season carbon dioxide release would decrease carbon dioxide uptake during the growing season by 15% . Of course, this is a simplistic calculation that does not account for numerous variables across space and time—including the full-time range of the growing season, nighttime respiration, carbon dioxide fluxes during other parts of the year, or when the marsh is inundated. However, it does illustrate the importance of quantifying carbon



dioxide fluxes across the whole year. Additionally, it is important to note that these percentages would change drastically on any given day we sampled—from augmenting growing season CO_2 uptake by ~1% to reducing it by >100% (Figure 2). These natural variations in carbon dioxide flux are substantial, and clearly underscore the need for higher temporal resolution sampling to adequately assess the carbon dynamics in salt marshes during the entire year.

Further, in this study we clearly demonstrate that the relationship between temperature and respiration holds through the dormant season for both the high and low marsh (Figure 3). We hypothesize then that warming temperatures in winter and early spring can be expected to further increase carbon emissions from temperate salt marshes. The variability and scarcity of cold weather data leaves a gap in our ability to model and predict the consequences of continued warming. However, our work and others suggest that, among its many known consequences,

climate change is also likely to change and limit the dormant season carbon storage capacity of temperate blue carbon ecosystems such as salt marshes. Increasing temperatures lead to increased microbial respiration, resulting in increased carbon emissions as well as accelerated depletion of soil organic carbon stocks (Campbell et al., 2022). This shift could not only potentially change marshes from net sinks to net sources of carbon, but also diminish their capacity for long-term carbon storage in their anoxic sediments, as has been observed in other systems (Natali et al., 2019; Pedron et al., 2022). Additionally, it is worth noting that the predictive power of the CO_2 flux versus soil temperature is low, indicating that there are other factors driving these fluxes. Anomalously warm winter events and warmer dormant seasons in general are happening in concert with many other changes to salt marshes including rising sea level, increased atmospheric CO_2 concentrations, and nutrient pollution. The combined impact of

these stressors will alter salt marsh production in the growing season, and very likely the dormant season response to temperature. For example, [Koop-Jakobsen and Dolch \(2023\)](#) recently used mesocosms to demonstrate that increased temperature and CO₂ concentration alters above and below ground biomass differently, and that the response varied with both vegetation type and marsh location. All together it is clear that capturing the blue carbon capacity of salt marshes, and other blue carbon systems, is complicated and dynamic ([Gallagher, 2023](#)), but higher temporal resolution data throughout the year will certainly help fill the existing knowledge gaps.

As temperate and polar regions continue to experience disproportionately warmer winters ([NOAA, 2023](#)), a climate induced change in marsh carbon storage may result in reduced natural climate change mitigation potential. A recent study estimated the current, global carbon storage of blue carbon ecosystems, such as salt marshes, to be worth $\$190.7 \pm 30$ bn USD annually, with the United States having the second largest blue carbon storage potential in the world ([Bertram et al., 2021](#)). Therefore, the diminishing capacity of temperate marshes to sequester and store carbon will not only have devastating ecological effects but can also have both national and global economic consequences.

Annual temperatures within the last decade are the hottest on record worldwide ([Lenssen et al., 2019](#); [NASA and GISTEMP, 2023](#); [NOAA, 2023](#)). This unprecedented warming is having a range of impacts on ecological systems. Here we show that CO₂ fluxes from a temperate urban salt marsh ecosystem responds rapidly to short-term warming events. This study also demonstrates that in addition to needing more and higher resolution dormant season measurements for better salt marsh carbon budgets, we now must also take in account the impact winter and early spring warming will have on the blue carbon capacity of salt marshes, and by extension their ability to help mitigate the devastating effects of climate change. Additionally, while we focused on carbon dioxide here, we anticipate nitrous oxide and methane, two other powerful greenhouse gases may also exhibit similar responses to warming temperatures ([Gallagher, 2023](#)). For example, laboratory incubation studies revealed that increased temperature caused a dramatic rise in salt marsh N₂O fluxes ([Comer-Warner et al., 2024](#)). We anticipate methane emissions would also increase with temperature but to what degree likely depends on site specific conditions like water levels and carbon to nitrogen content of soils ([Al-Haj and Fulweiler, 2020](#); [Hu et al., 2024](#)). Overall, this study highlights that dormant season may no longer be metabolically quiet. We hope this study motivates future research on salt marsh greenhouse gas cycling in non-growing season months.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AV: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Visualization, Writing–original draft,

Writing–review and editing. PG: Funding acquisition, Writing–review and editing. RF: Funding acquisition, Writing–review and editing, Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing–original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2024.1340416/full#supplementary-material>

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