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Key Points:

- Tidal marsh net ecosystem exchange can vary by 3-fold annually and 2-fold across a single species canopy gradient
- Drought, temperature, precipitation, and river discharge affect spatially explicit net ecosystem exchange
- Inclusion of within-footprint habitat zones can reduce uncertainties in scaling up net ecosystem exchange

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

P. A. Hawman,
pete36@uga.edu

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Author Contributions:

Conceptualization: P. A. Hawman
Data curation: D. L. Cotten
Funding acquisition: D. R. Mishra
Methodology: P. A. Hawman
Project administration: D. R. Mishra
Supervision: D. R. Mishra
Visualization: P. A. Hawman
Writing – original draft: P. A. Hawman, D. R. Mishra
Writing – review & editing: P. A. Hawman, D. L. Cotten, D. R. Mishra

Canopy Heterogeneity and Environmental Variability Drive Annual Budgets of Net Ecosystem Carbon Exchange in a Tidal Marsh

P. A. Hawman[1], D. L. Cotten[2], and D. R. Mishra[1]

[1]Department of Geography, University of Georgia, Athens, GA, USA, [2]Oak Ridge National Laboratory, Oak Ridge, TN, USA

Abstract Tidal salt marshes are important ecosystems in the global carbon cycle. Understanding their net carbon exchange with the atmosphere is required to accurately estimate their net ecosystem carbon budget (NECB). In this study, we present the interannual net ecosystem exchange (NEE) of CO_2 derived from eddy covariance (EC) for a *Spartina alterniflora* salt marsh. We found interannual NEE could vary up to 3-fold and range from -58.5 ± 11.3 to -222.9 ± 12.4 g C m^{-2} year^{-1} in 2016 and 2020, respectively. Further, we found that atmospheric CO_2 fluxes were spatially dependent and varied across short distances. High biomass regions along tidal creek and estuary edges had up to 2-fold higher annual NEE than lower biomass marsh interiors. In addition to the spatial variation of NEE, regions of the marsh represented by distinct canopy zonation responded to environmental drivers differently. Low elevation edges (with taller canopies) had a higher correlation with river discharge ($R^2 = 0.61$), the main freshwater input into the system, while marsh interiors (with short canopies) were better correlated with in situ precipitation ($R^2 = 0.53$). Lastly, we extrapolated interannual NEE to the wider marsh system, demonstrating the potential underestimation of annual NEE when not considering spatially explicit rates of NEE. Our work provides a basis for further research to understand the temporal and spatial dynamics of productivity in coastal wetlands, ecosystems which are at the forefront of experiencing climate change induced variability in precipitation, temperature, and sea level rise that have the potential to alter ecosystem productivity.

Plain Language Summary Salt marshes are dynamic coastal wetlands where frequent tidal flooding in conjunction with elevation gradients create plant zonation. In tidal marshes found in the southeastern United States, the species of marsh grass *Spartina alterniflora* dominates much of the marsh area. This species' canopy height, density, and biomass vary along an elevation gradient and because of this, their productivity is spatially dependent. In this paper, we used measurements of carbon dioxide exchange between the marsh surface and the atmosphere to estimate the interannual ecosystem carbon budgets. We found that across years, ecosystem carbon fluxes could vary up to 3-fold. This variability year-to-year could be explained by drought conditions, specifically temperature, precipitation, and river discharge. We also found that the magnitude of carbon fluxes and its response to environmental drivers were spatially dependent. Taller canopies with higher biomass found along tidal creeks had higher rates of carbon uptake and were more sensitive to river discharge. While shorter canopies with low biomass found in the marsh interiors were more sensitive to precipitation. Our findings suggest the atmospheric carbon dynamics in salt marshes are spatially dependent and scaling these estimates to larger areas requires careful consideration of habitat zones and local environmental drivers.

1. Introduction

Tidal marshes are highly productive ecosystems that are important in the carbon (C) cycle because of their high burial rates of soil organic carbon (Hinson et al., 2019), known as blue carbon (Mcleod et al., 2011). However, their geographic position at the interface between marine and terrestrial ecosystems makes them vulnerable to human induced forcings such as rapid sea level rise (Holmquist et al., 2021), direct human impacts from uncontrolled land conversion and urbanization (Murray et al., 2022), and a changing climate where rainfall patterns and storm intensity alters freshwater input and sediment supplies (Cherry & Battaglia, 2019). It is, therefore, vital to understand the drivers and variance in tidal marsh carbon dynamics across space and time to better understand, monitor, and assess their resiliency and vulnerability to climate change.

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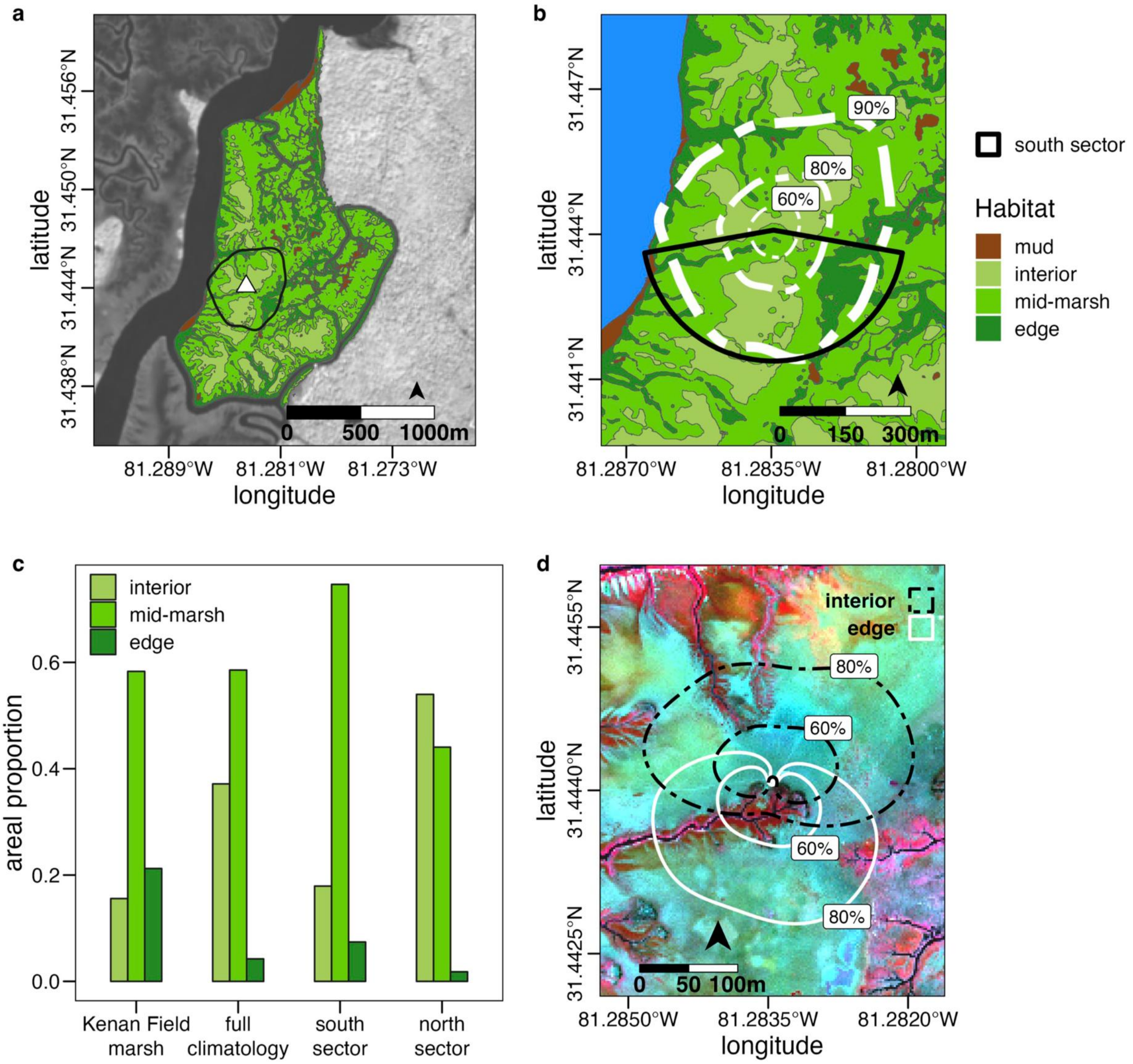

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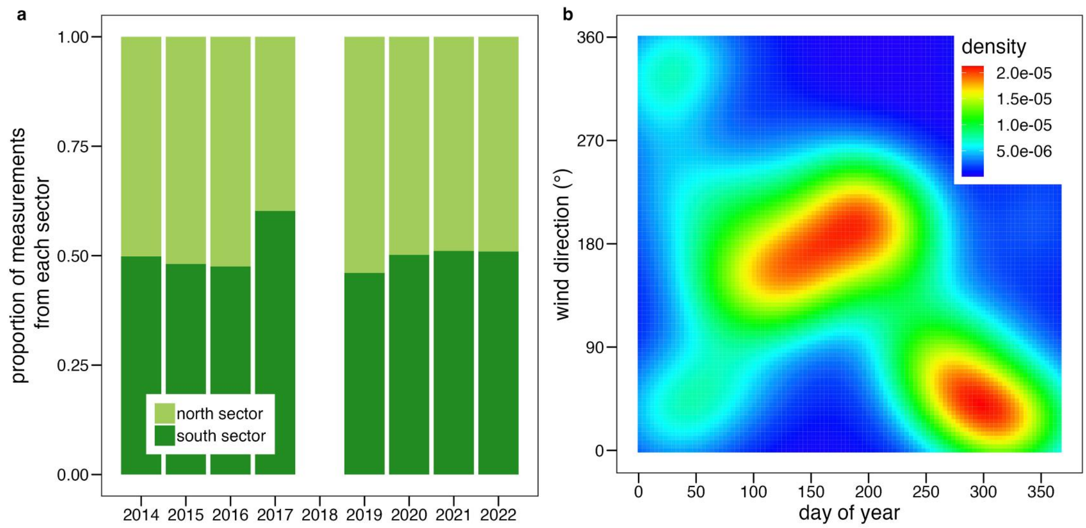

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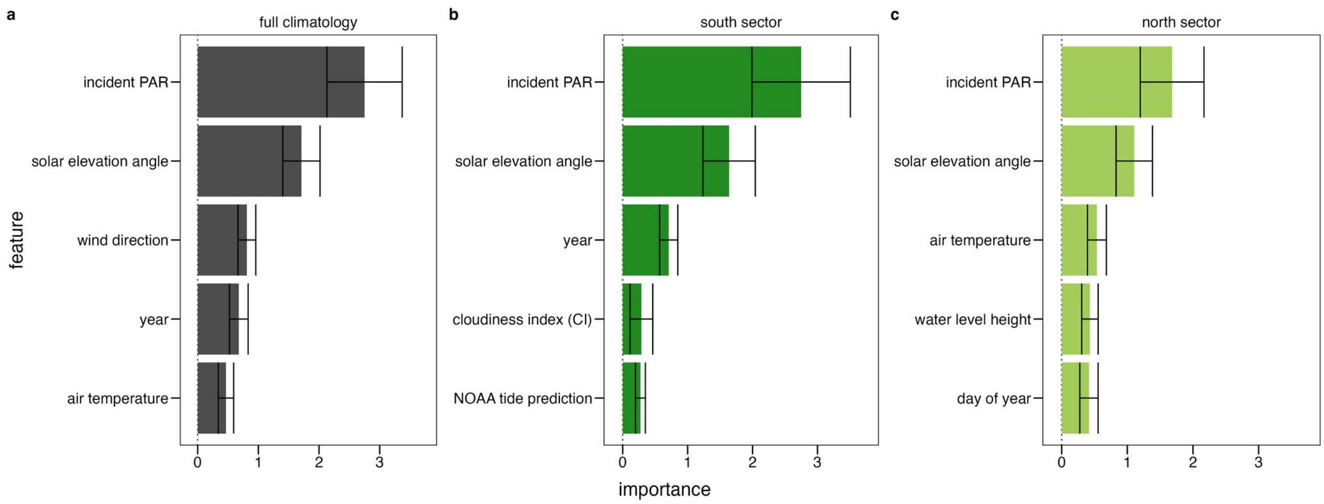

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Table 1
Interannual Net Ecosystem Exchange (NEE) Budgets for the Full Climatology, the Creek Sector, and the Marsh Sector

year	Full climatology	South sector	North sector
2014	−145 ± 9.6	−170.2 ± 9.5	−158.1 ± 8.7
2015	−119.7 ± 9.9	−160.5 ± 8.1	−132.5 ± 12.3
2016	−58.5 ± 11.3	−90.9 ± 20.8	−107.5 ± 9.7
2017	−186.4 ± 13	−160 ± 13.1	−202.2 ± 28.3
2018	–	–	–
2019	−141.6 ± 10.2	−186.2 ± 9.2	−135.5 ± 11.6
2020	−222.9 ± 12.4	−310.1 ± 14.8	−169.6 ± 11.5
2021	−203.2 ± 11.1	−297.7 ± 15	−135.9 ± 17.4
2022	−168.7 ± 21.1	−244.8 ± 25	−128.4 ± 21.3

Note. Annual budgets are in $gCm^{-2}y^{-1}$ with 95% confidence intervals.

north sector had no relationship ($R^2 = 0.007$; p-value = 0.8) and the full climatology had a small but nonsignificant one ($R^2 = 0.21$; p-value = 0.1).

3.4. Environmental Drivers

The environmental conditions at the GCE-LTER site from 2014 to 2022 showed considerable variability in terms of precipitation measured using river discharge and in situ precipitation, number of days each year air temperatures exceeded 34°C, and droughtiness using PDSI. The growing season mean Altamaha River discharge ranged from 153 to 384 m^3s^{-1} with the lowest discharge occurring in 2019 and the highest in 2020 (Figure S7a in Supporting Information S1). 2019 was also the year with the lowest in situ precipitation (797 mm) while 2020 and 2017 were the wettest, 1158 and 1042 mm, respectively. The hottest years were 2016 and 2019, when air temperature exceeded 34°C for 14 days (Figure S7c in Supporting Information S1). In terms of droughtiness using the PDSI, over the entire study period, PDSI ranged from −1.24 (2016) to 1.96 (2020) (Figure S7d in Supporting Information S1).

For the annual growing season (April-September) mean river discharge, the south sector showed a significant correlation ($R^2 = 0.61$; p-value <0.01), while the north sector did not show a relationship ($R^2 = 0.05$; p-value = 0.60) and the full climatology was somewhat correlated ($R^2 = 0.43$; p-value = 0.08) (Figures 5a and 5b). Growing season total precipitation was only significantly correlated with north sector interannual NEE ($R^2 = 0.53$; p-value <0.01) (Figures 5d–5f). We found that years with more days that reached maximum air temperatures >34°C were well correlated with full climatology annual NEE ($R^2 = 0.63$; p-value <0.01) but not NEE from the south sector ($R^2 = 0.36$; p-value = 0.12) or the north sector ($R^2 = 0.36$; p-value = 0.12) (Figures 5g–5i). Lastly, annual mean PDSI explained the highest proportion of the variation in full climatology interannual NEE ($R^2 = 0.89$; p-value <0.001) and the south sector ($R^2 = 0.78$; p-value <0.01), but no trend for the north sector ($R^2 = 0.28$; p-value = 0.18) (Figures 5f–5l).

3.5. Marsh-Wide NEE

We compared scaling annual NEE to the wider Kenan Field marsh (area = 1,763,600 m^2) using the full climatology NEE versus a habitat-corrected scaling approach using the south and north sector annual estimates to account for proportional differences in marsh habitat zones. Maps of annual NEE based on a habitat map (Hladik & Alber, 2014) and IDW interpolation show the spatial distribution of NEE across Kenan Field marsh (Figure 6b; Figure S8 in Supporting Information S1).

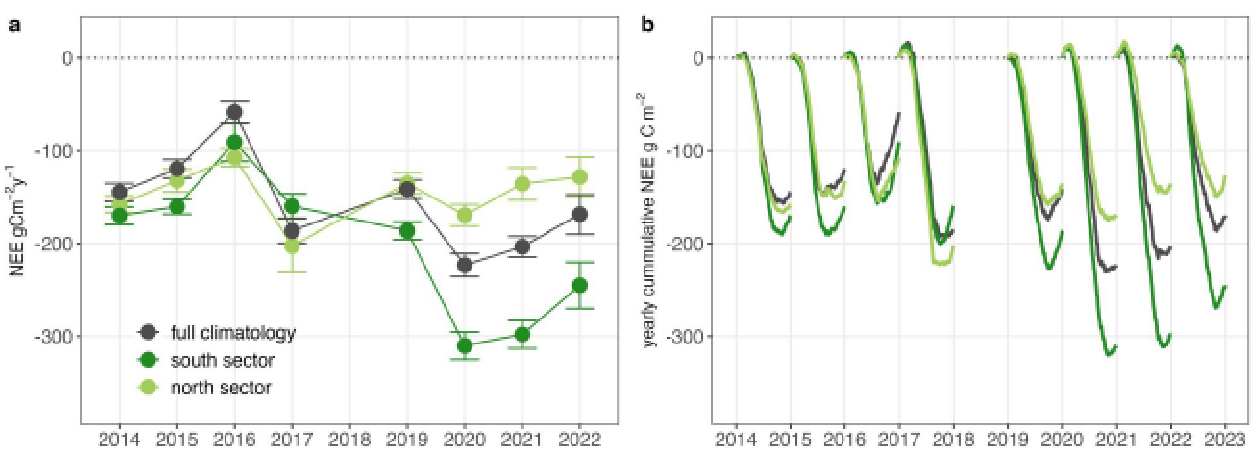
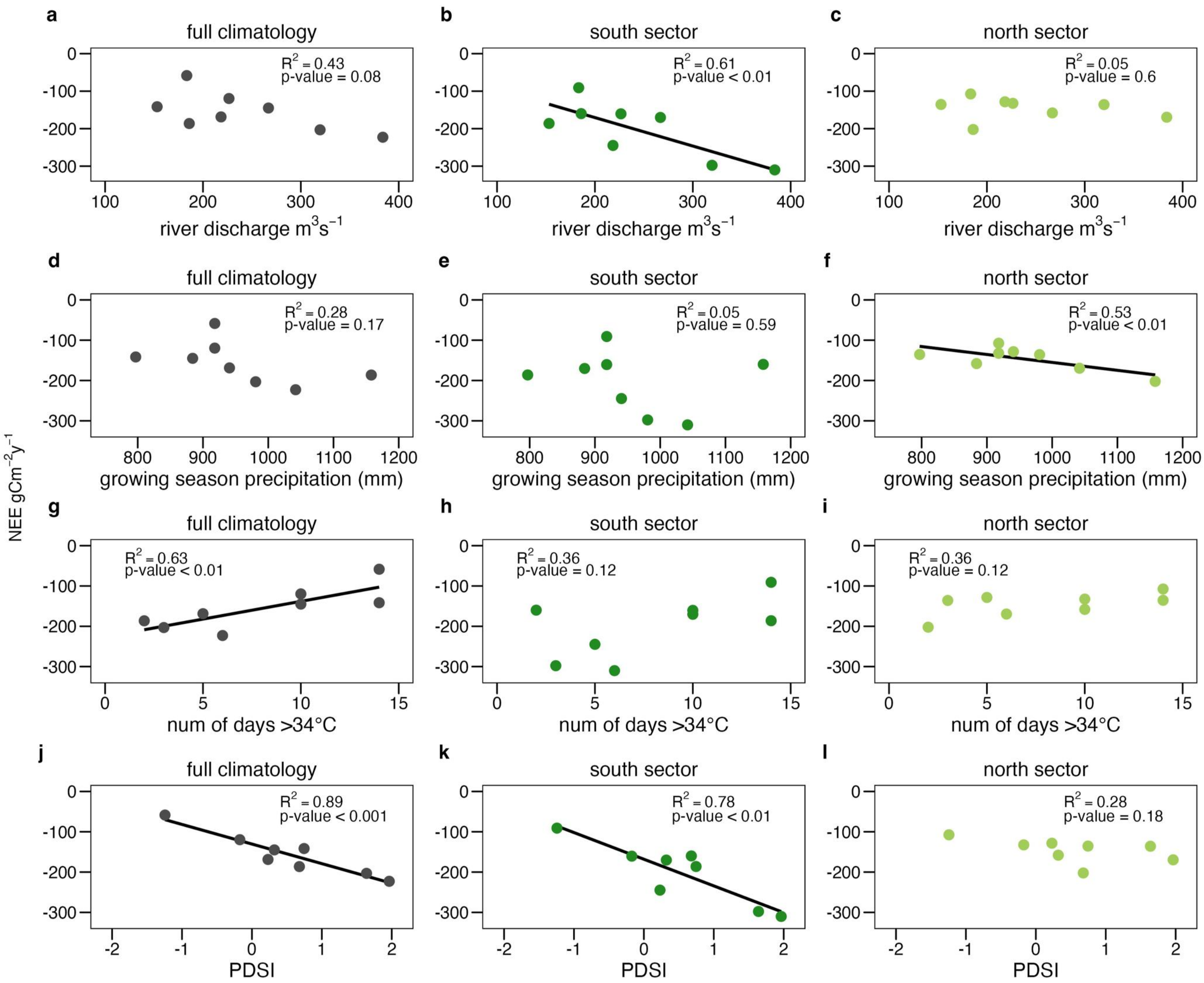


Figure 4. (a) Interannual net ecosystem exchange (NEE) from the GCE flux tower for years 2014–2022 for the full climatology (gray), the south sector (dark green), and the north sector (light green). Error bars indicate 95% confidence intervals. (b) Cumulative annual NEE for the full footprint, the south sector, and the north sector.



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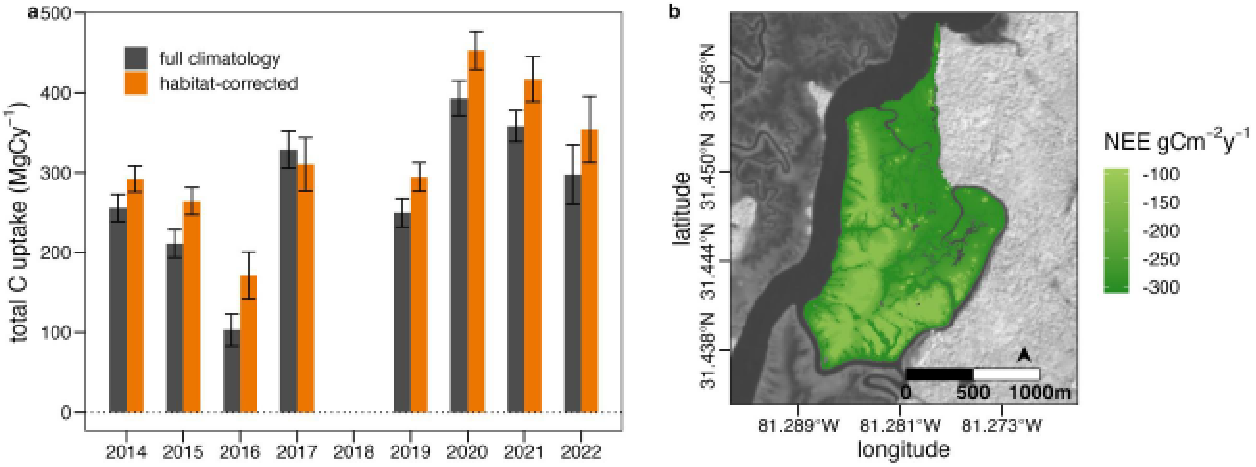

Figure 6. (a) Total carbon uptake for Kenan Field marsh based on the flux tower climatology NEE budgets (dark gray) and habitat-corrected estimates (orange). Error bars show the 95% confidence intervals. (b) Map showing spatially explicit annual NEE for Kenan Field marsh for 2021. Darker greens show marsh areas where carbon uptake was higher.

The south sector had a higher proportion of tall (high) biomass canopies found along the tidal creek marsh edge. These taller canopies have up to 3-fold higher LAI compared to the shorter canopies found in interior zones in the north sector (Hawman et al., 2023). Tall canopies of *S. alterniflora* have also shown higher rates of photosynthesis compared to shorter canopies, up to 45% (Giurgevich & Dunn, 1979). Therefore, differences in canopy LAI, biomass, and productivity rates around the flux tower altered the importance of features in the gap-filling models for the south and north sectors and the combined full climatology (Figure 3; Figure S5 in Supporting Information S1).

Differences in canopy density also impacted NEE across sectors. The south sector NEE was more sensitive to the proportion of diffuse and direct radiation captured through the cloudiness index. During cloudy days with more diffuse radiation, light use efficiency (the ratio of productivity to incoming radiation) increases because more of the canopy interior is illuminated due to increased scattering (Hawman et al., 2021). Shorter canopies with lower LAI found in the interiors and the north sector may not have benefited from the increased diffuse radiation. Variation in canopy leaf area may have also have impacted responses to tidal flooding. Though the taller canopies experience more tidal flooding because of the proximity to tidal creeks and their lower position within the tidal frame (Hladik & Alber, 2014), tidal flooding did not have as high a feature importance as the north sector models. This could be because of the differences in vertical distribution of leaf area within the canopy profiles. The taller

Table 2
Total Carbon Uptake (gCm^{-2}y^{-1}) for Kenan Field Marsh (1,763,600 m^2) With 95% Confidence Intervals

year	Flux tower based total C (MgCy^{-1})	Habitat-corrected total C (MgCy^{-1})
2014	255.70 ± 17.01	292.07 ± 16.25
2015	211.02 ± 17.42	264.36 ± 17.06
2016	103.15 ± 19.88	171.38 ± 29.27
2017	328.73 ± 22.94	310.34 ± 33.23
2018	–	–
2019	249.71 ± 17.96	294.54 ± 17.79
2020	393.09 ± 21.89	453.07 ± 23.93
2021	358.28 ± 19.5	417.09 ± 28.13
2022	297.56 ± 37.19	354.03 ± 41.57

Note. Values labeled as "full climatology" were based on the flux tower full climatology annual budgets. Values labeled "habitat-corrected" used the south and north sector budgets mapped to marsh habitat zones and inverse distance weighting (IDW).

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9 : 5 5 P @@ D 4 . . 03 14 5
KL8%& 8/ & ; ; B & ; K ' 4 7 & /
& 2' 4 ? 44@411 D
4 4 2 4 ? 44@411
KL8%& 8/ & K ' 4 * #
455 41. 42 D 4 4 5 9 4 4 41. 42
K ; ' 22@] & &# '
0 '. 0 P0 5 D 4 @) 0 4/43 5' 22@4 3 40 D)) 6 B 4) G
K) ;) ; ? ' 4 . ; & /
) 35' 1 P 23 D 4 44@ 44 @4 / 4@5/0
- - H ?) * * & ; B & ; ' 445) &# & #
D & ' D 4 4 2 440? 44442.
- (H B , & ' 214) &# & & &
G 53' 33@ 10P 44 D 4 44 %932@ 4533@4@
- I H B) ' 4 3) & ' 2'. 3@P313
D 4 44@ 44 /4 . /2@ /5

- 8 ? ; B ' 44 ' @P 04
D 4 4 . D4 1255 43350
- & 6 B)) &8 ? 6 - ; ; ' 4 & D7 /
& & 9 ' B 32' D 4 44 15@
- & - * B ; ' 4 4 / &
& 0 0 8 ' 2 : . @1 D 4 4 5 9 4 4 . @1
M - M T -] M - 7 ? ? ' 4 &
& # &) ' ' 2 04 D 4 . . 24 3 204