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Landscape-scale spatial variability of blue carbon stocks and fluxes in tropical seagrass meadows

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Abstract. Seagrass meadows are emerging natural ~~climate~~ solutions for climate change mitigation through their high potential for organic carbon sequestration and storage, also known as blue carbon. However, the variability in current blue carbon stock and flux estimates is high, particularly at landscape scales. This knowledge gap highlights the need for evaluating blue carbon at spatial scales that are both locally robust and globally relevant. We quantified the magnitude of variability in blue carbon stocks and fluxes in tropical intertidal seagrass meadows at the landscape scale. We sampled six intertidal seagrass meadows representing three geomorphic settings, including reef-associated settings, estuaries and lagoons, across Singapore. Across these sites, we measured soil organic carbon (C_{org}) stocks and greenhouse gas fluxes using the static chamber method. We found that tropical intertidal seagrass meadows stored 132 ± 78 Mg C_{org} ha^{-1} (mean ± SD) in the top 100 cm of soil, which varied significantly within sites and geomorphic settings (min-max: 19-303 Mg C_{org} ha^{-1}), and were positively associated with salinity. Seagrass fluxes averaged 660 ± 695 mg m^{-2} d^{-1} of CO_2 and 12 ± 484 µg m^{-2} d^{-1} of CH4, which, unlike stocks, did not appear to vary significantly across geomorphic settings. However, we identified redox (positive) and bulk density (negative) as independent drivers of CO_2, and C_{org} as an independent, strong predictor of CH_4 after accounting for spatial hierarchy and geomorphic setting. Spatially explicit stock assessments and inclusion of greenhouse gas fluxes are important to inform robust coastal carbon budgeting and support the inclusion of seagrass in national climate mitigation frameworks.

1 Introduction

Seagrass meadows have a high capacity for storing organic carbon, also known as blue carbon, and are therefore widely recognised as emerging natural ~~climate~~ solutions for climate change mitigation (Unsworth et al., 2022; Duarte et al., 2025; Do Amaral Camara Lima et al., 2023). Yet seagrasses globally face a high risk of degradation, which could lead to ~ 1,154 Tg CO_2 emissions with a social cost of $213 billion USD (Krause et al., 2025). Therefore, there is a global interest in incorporating the conservation and restoration of seagrass meadows into climate change mitigation schemes and policies, such as a country's Nationally Determined Contribution (NDC) to the Paris Agreement and associated Nationally Appropriate Mitigation Actions

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(NAMAs) (Macreadie et al., 2021). However, policies and management decisions should be guided by a robust evidence base, including credible estimates of the extent, drivers and patterns of organic carbon storage (Dahl et al., 2025).

Although knowledge and understanding of the magnitude and drivers of variation in organic carbon (C_{org}) storage in seagrass meadows has greatly increased recently at the global scale (Gomis et al., 2025; Krause et al., 2025), there are still challenges in quantifying blue carbon at site-specific or landscape scales, which is essentially an ecosystem and its surrounding biophysical environment, hindering global efforts to establish them as reliable natural climate solutions (Williamson et al., 2022; Stankovic et al., 2023). Variability in seagrass C_{org} and carbon budgets is driven by biotic and abiotic factors at various spatial scales (Krause et al., 2025; Gomis et al., 2025; Mazarrasa et al., 2021; Mazarrasa et al., 2023). At the intra-site scale, extrapolating standard 100 cm C_{org} stocks from shallower cores is a major caveat, potentially leading to 1.5- to 10-fold underestimation (Dahl et al., 2025; Stankovic et al., 2023). Local or site-scale variability of C_{org} is generally attributed to grain size (Miyajima et al., 2015), species composition (Gomis et al., 2025), the contribution of sources of organic matter, i.e. autochthonous and allochthonous (Ricart et al., 2020; Serrano et al., 2019), water depth, and hydrodynamic energy, etc. (Lavery et al., 2013; Ndhlovu et al., 2024; York et al., 2018). However, our understanding of how these factors scale to broader landscape contexts remains incomplete.

At larger landscape scales, the coastal geomorphic setting has emerged as a key control on seagrass C_{org} variability (Kennedy et al., 2022; Mazarrasa et al., 2021); however, it is not known how the geomorphic setting would influence GHG emissions from seagrasses. Estuarine meadows generally inhabit the intertidal interface and shallower depths, receive large inputs of terrigenous organic material, and experience low hydrodynamic energy, creating a depositional environment (Ricart et al., 2020), potentially facilitating high accumulation of allochthonous carbon (Capece et al., 2025). Sheltered coastal settings—such as lagoons or back-reef meadows—can maintain higher surface-soil C_{org} due to reduced sediment resuspension and wave energy (Guerra-Vargas et al., 2020; Alemu et al., 2022). However, typical anoxic conditions and high organic matter inputs in seagrasses that promote high C burial and sequestration can also favour the production and emission of greenhouse gases such as methane (CH_4) (Rosentreter et al., 2021). Seagrass meadows appear to be negligible to moderate CH_4 sources, ranging from 0.3 to 378 µg m^{-2} h^{-1} and potentially offsetting ~12–78 times the CO_2 equivalents of their carbon accumulation rates (Asplund et al., 2022; Burkholz et al., 2020). Thus, geomorphic environmental gradients are expected to affect GHG emissions such that GHG emissions could be elevated in estuarine or sheltered seagrass meadows where C_{org} stocks are potentially higher. Kirwan et al. (2023) proposed that GHG emissions in coastal wetlands would be governed by local-scale factors plant productivity and electron acceptor availability compared to landscape-scale geomorphic processes, yet this hypothesis has not been explicitly tested across geomorphic settings in seagrass meadows.

Here, we explore the spatial variability in carbon stocks and fluxes across seagrass meadows of different geomorphic settings in Singapore. We hypothesised that geomorphic settings such as reef-associated settings, estuaries and lagoonal settings would shape soil organic carbon and GHG emissions in tropical seagrass meadows, and a higher soil C_{org} would be associated with higher GHG fluxes under these geomorphic gradients. We ask 1) what is the magnitude of soil organic carbon stocks and GHG emissions (CO_2 and CH_4) of tropical seagrass meadows, 2) How do organic carbon and GHG fluxes vary across spatial scales

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encompassing local (within-site, across sites) and landscape (geomorphic settings) levels, and 3) are patterns in organic carbon storage associated with GHG fluxes, and which environmental parameters define these associations?

2 Methodology

2.1 Site description

The study was conducted on six intertidal seagrass meadows across the tropical island state of Singapore (Fig. 1). The climate of the area is humid tropical; therefore, temperature does not vary much throughout the year, with the highest average monthly temperature of 28.8°C during May and the lowest average monthly temperature of 26.8°C during December and January (Meteorological Service Singapore, 2024). Mean annual rainfall is 2,113 mm (1991–2024), with two monsoon periods during June–September and December–early March separated by inter-monsoon seasons in late March–May and October–November. These meadows experience a diurnal tidal cycle such that they are only briefly exposed during low tide (<0.7m, tidal range >2.5 m) and remain fully submerged during high tide. We selected six intertidal meadows representing three geomorphic classes (Mckenzie et al., 2016): reef-associated (Cyrene Reef, Labrador Nature Reserve), lagoonal (Tanah Merah, Eagle Bay), and estuarine (Chek Jawa, Changi Beach Park, both located in Johor Estuary) (Fig. 1).

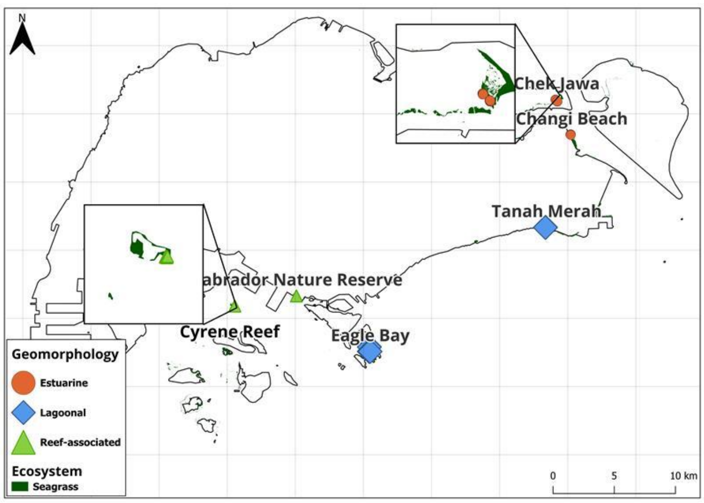

Figure 1: Singapore seagrass extent map (Tan et al., 2022) and study sites locations of intertidal seagrass meadows across estuarine, lagoonal and reef-associated geomorphic settings. Two sites with the largest seagrass extent among the studied sites are zoomed in.

2.2 Field sampling design

We collected field data during low tide from October 2022 to May 2024 and targeted the same time of the day and season for consistency and to avoid seasonal variations affecting GHG fluxes. We selected the sampling months when Singapore's climate

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is generally consistent with an average monthly temperature of 27.5-28.8°C and average monthly rainfall of 150-160 mm (Meteorological Service Singapore, 2024). At each site, 3–5 transects (30 m length) were laid parallel to shore, >5 m apart, positioned to encompass the meadow extent following visual assessment. Three 1 m × 1 m plots were established along each transect at 5, 15, and 25 m. Where transects could not capture site heterogeneity, additional random plots were sampled within the meadow to improve coverage.

2.3 Carbon stocks

To quantify sediment carbon stocks, we collected 9–15 replicate sediment cores per site using a gouge auger (5.08 cm internal diameter) to 1 m depth or refusal. Because the upper 20–50 cm typically exhibits the strongest gradients in carbon content (ref), the top 50 cm was sectioned at 5 cm increments. Each core was divided into 11 sections: 0–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–35, 35–40, 40–45, 45–50, and 50–100 cm. Core compaction during extraction was minimal (<10%). Sediment was transported to the laboratory and dried at 60 °C to a constant mass. Dry bulk density (g dry weight cm−3) was calculated as dry mass divided by the in-situ sample volume (Howard et al., 2014). A subsample was ground and homogenised, then fumigated overnight with 0.1 M HCl to remove inorganic carbon, dried, weighed, encapsulated in tin, and analysed for total organic carbon (C_{org}, %) using an organic carbon analyser. Carbon stocks (Mg C_{org} ha^{-1}) were calculated following Howard et al. (2014), integrating section-specific C_{org}, dry bulk density, and layer thickness to 1 m (or core maximum) and upscaling to a hectare. Shorter cores were extrapolated linearly up to 1 m, and carbon stocks were reported at 15cm, 30 cm and 1 m depth for comparison (Table 1). For grain size, dried subsamples were disaggregated, sieved at 2 mm to remove coarse fragments (shells, pebbles), dispersed in deionised water, and analysed with a laser diffraction particle size analyser (Horiba LA, 350), reporting median grain size (µm).

2.4 Sediment-air greenhouse gas fluxes

Sediment–air CO_2 and CH_4 fluxes were measured during low tide using static, manual dark chambers. Chambers consisted of round PVC collars (internal diameter 15 cm) inserted 5 cm into the sediment, fitted with airtight lids; total enclosed headspace height was 30 cm. Within each plot, three chambers were deployed at random positions and sealed (with rubber bands/gaskets). Headspace gas was sampled by syringe at 0, 20, 40, and 60 min and transferred to 15mL pre-evacuated glass vials (Labco, High Wycombe, UK). Concentrations were measured in the laboratory using a cavity ring-down spectrometer (Picarro G220-i). Fluxes (surface-area-normalised) were calculated from the linear rate of change in headspace concentration over time, corrected for chamber volume, surface area, ambient temperature and pressure via the ideal gas law. Flux estimates were retained when linear fits met $r^2 \geq 0.8$ and non-linear and leaky time series were excluded.

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2.5 Data Analysis

Data were tested for normality through the Kolmogorov–Smirnov and Shapiro–Wilk tests. When data did not comply with the requirements of normality and homoscedasticity, we performed log, inverse, or square root transformations to meet the assumptions of normality. For data that was not normal after transformations, we performed a Kruskal-Wallis test followed by Dunn's test with Bonferroni correction to assess the significance of differences among plots, sites and geomorphic settings. We quantified monotonic associations among environmental variables, soil carbon metrics, and fluxes using pairwise Spearman rank correlations. With 15 variables, there were 105 unique pairs. To control for multiple testing across all pairs, p-values were adjusted using the Benjamini–Hochberg FDR procedure (reporting q-values). We identified near-duplicate (redundant) predictors as those with $|\rho| \geq 0.95$ (e.g., pH vs redox; salinity vs conductivity; water vs soil temperature) and included a single representative from each redundant pair for interpretation and modelling. To examine the hierarchical variance in greenhouse gas fluxes and their relationship with environmental parameters, we used mixed-effect models with random intercepts for plots nested within transects nested within sites and included geomorphic setting as a fixed effect. Model performance was assessed using marginal and conditional R2, AIC, and leave-one-site-out cross-validation. Model families and link functions were chosen based on response distributions: Gaussian for approximately normal responses (on transformed scales if needed), or Gamma with a log link for positive, right-skewed fluxes. Predictors were centred and scaled to aid interpretation and convergence. Analyses were run in R using the following packages: dunn.test or FSA for Dunn's tests, car for VIF, multcomp or emmeans for post-hoc contrasts, ggplot2 for figures. Spearman correlations and FDR adjustments used stats::cor.test and p.adjust(method = "BH").

2.6 Methodological limitations

We acknowledge the methodological limitations of our study due to logistical constraints. For this study, we targeted high-resolution spatial variation within the sites, including intensive replication of ≤ 15 soil cores and 27 chambers per site; however, for gas flux measurements, our study is limited to temporal replication of daily and seasonal changes.

3 Results

3.1 Soil carbon stocks and fluxes in tropical seagrass meadows

Total organic carbon across seagrass ecosystems averaged 1.1 ± 0.8% (Range: 0.1 to 3.6%) for all study locations. Soil carbon stocks recorded in the top 100 cm of seagrass meadows were 131.6 ± 77.6 Mg ha^{-1} (Range: 18.8 to 302.6 Mg ha^{-1}). Seagrasses had CO_2 fluxes of 30.5 ± 27.8 mg m^{-2} h^{-1} (Range: -73.9 to 95 mg m^{-2} h^{-1}) and CH_4 fluxes of 0.8 ± 20.4 µg m^{-2} h^{-1} (Range: -76.5 to 81.8 µg m^{-2} h^{-1}) for all measured sites.

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3.2 Spatial variability in seagrass soil carbon stocks and fluxes

Intra-site heterogeneity in soil C_{org} % was observed, with significant plot-to-plot variation detected at 50% of the surveyed sites. Among sites, significant spatial differences in soil C_{org} % were recorded (KW test; n = 62, df = 5, $\chi 2 = 45.67$, $p < 0.001$). Tanah Merah had the highest C_{org}% at 2.5 ± 0.5% (Range: 1.8 to 3.6%), while Eagle Bay had the lowest concentrations at 0.2 ± 0.1% (Range: 0.1 to 0.4%, Figure 2a). Across geomorphic settings, soil C_{org} % differed significantly ($\chi 2 = 28.9$, $p < 0.001$), with values of 0.7 ± 0.4%, 1.3 ± 1.2% and 1.3 ± 0.4% recorded for estuarine, lagoonal and reef-associated seagrass systems, respectively (Figure 2b). Vertical distribution showed consistent decreases in C_{org} % across all geomorphic settings, with estuarine systems showing the smallest reduction (25% from 0.8% at the surface to 0.6% in the subsurface). Lagoonal systems had the strongest depth gradient, with surface C_{org}% of 1.5% declining by 40% to 0.9% in subsurface sediments, reaching particularly low values (0.2%) below 40 cm. Reef-associated systems showed intermediate patterns, with surface concentrations of 1.5% decreasing by 30% to 1% in deeper layers, indicating moderate C_{org} % preservation with depth.

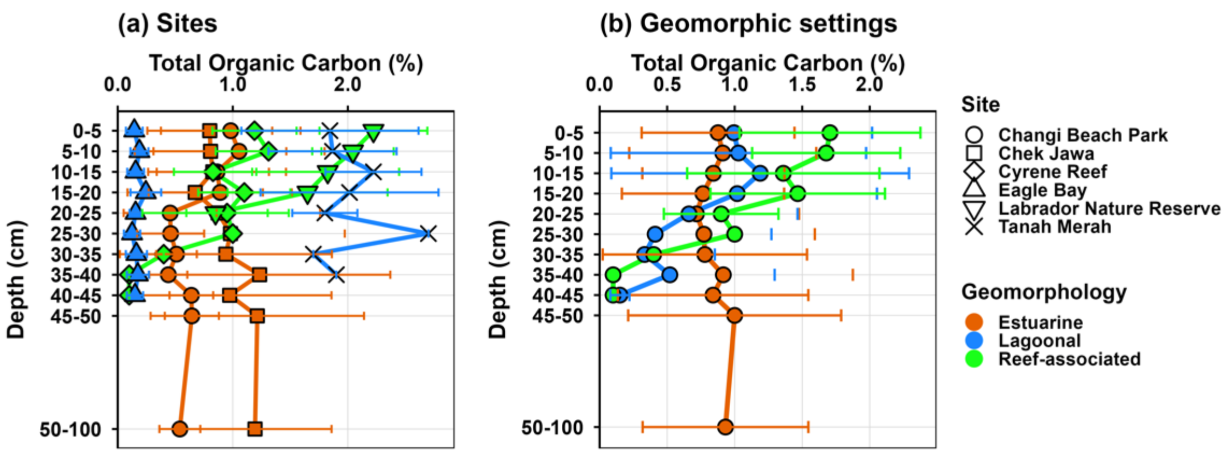

Figure 2: Seagrass soil total organic carbon % (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings.

Overall, the carbon stocks recorded in the top 100 cm of seagrass meadows were 131.6 ± 77.6 Mg $ha^{-1,}$ with Reef-associated meadows having the highest C_{org} stock of 180.8 ± 110.6 Mg ha^{-1}, followed by lagoonal sites at 131.9 ± 49.3 Mg ha^{-1} and estuarine meadows at 31.1 ± 17.3 Mg ha^{-1} (Figure 3a, b).

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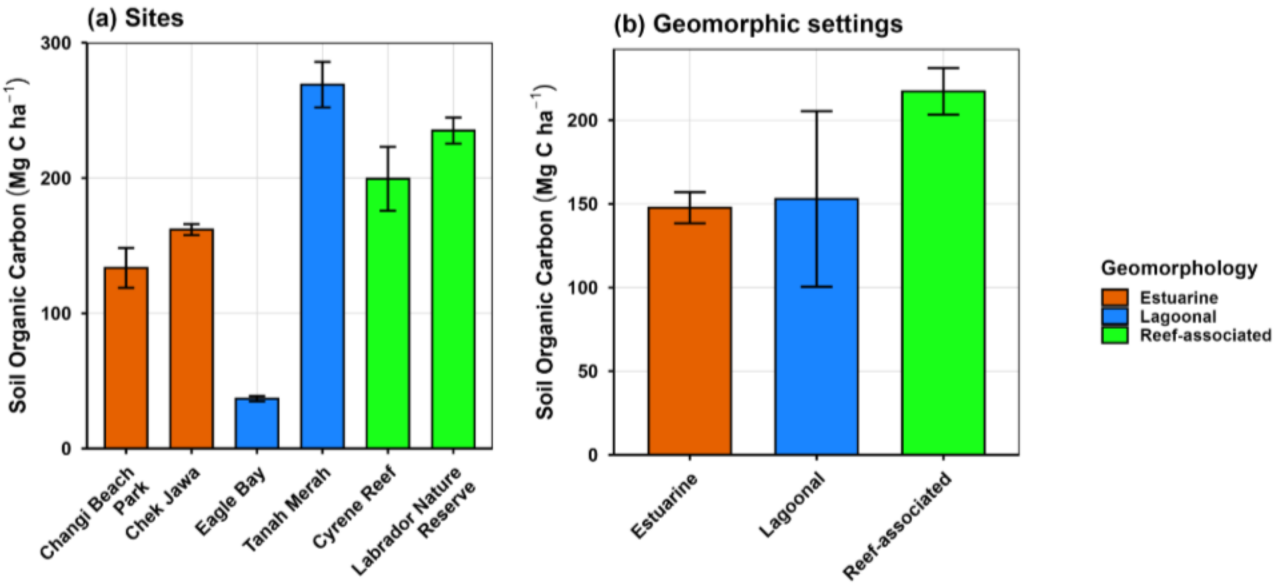

Figure 3: Seagrass soil organic carbon stocks (Mg ha-1, mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings.

At the intra-site level, soil CO_2 fluxes did not show significant intra-site variability in 67% of the surveyed sites. Soil CO_2 fluxes varied significantly among sites (KW test; n = 162, df = 5, $\chi 2$ = 35.7, p < 0.001, Figure 4a). The highest CO_2 fluxes were recorded at Chek Jawa at 42.5 ± 40.8 mg m^{-2} h^{-1} (Range: -24.8 to 104.8 mg m^{-2} h^{-1}) and the lowest at Changi Beach at 15.0 ± 15.3 mg m^{-2} h^{-1} (Range: -31.1 to 37.1 mg m^{-2} h^{-1}, Figure 4a). Among geomorphic settings, mean soil CO_2 fluxes did not vary significantly ($\chi 2$ = 2.33, p = 0.313) at 28.8 ± 33.6 mg m^{-2} h^{-1}, 30.0 ± 16.4 mg m^{-2} h^{-1} and 32.8 ± 30.6 mg m^{-2} h^{-1} for estuarine, lagoonal and reef-associated seagrasses, respectively (Figure 4b).

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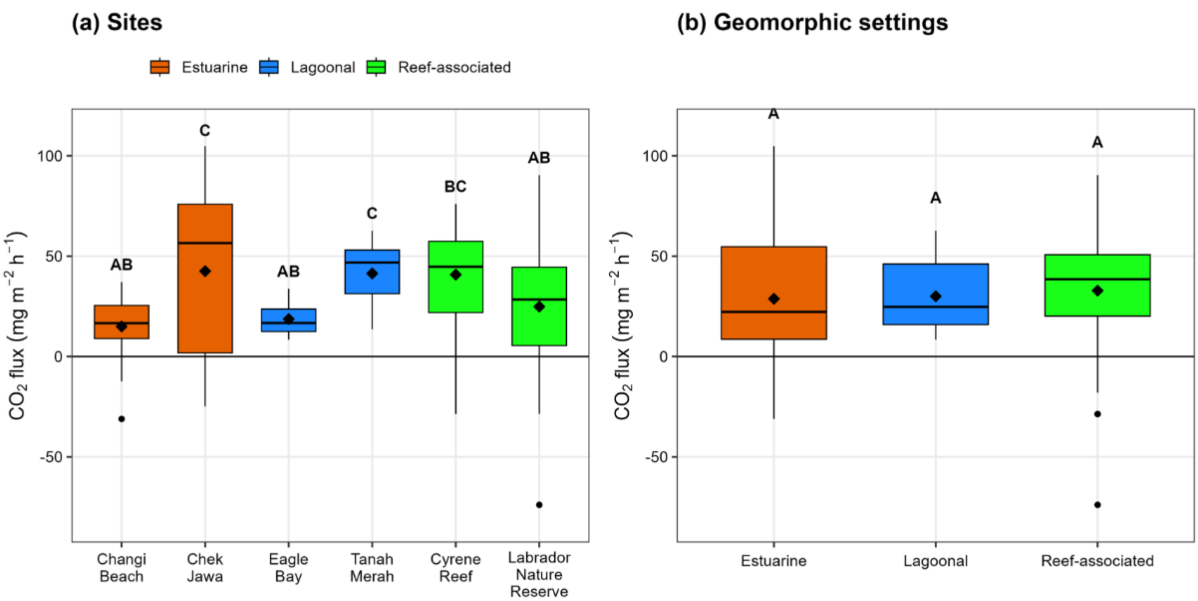

Figure 4: Seagrass soil carbon dioxide fluxes (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings. Positive fluxes indicate emission into the air, while negative fluxes indicate uptake by the sediment. Different upper-case letters indicate significant differences ($p \leq 0.05$) across the sites and geomorphic settings following Dunn's test with Bonferroni correction.

At the intra-site level, soil CH_4 fluxes did not vary significantly for 83% of the measured sites. Soil CH_4 emissions varied significantly among sites (KW test; df = 5, $\chi2$ = 15.62, p = 0.008, Fig. 5a). The highest CH_4 fluxes were recorded at Tanah Merah at 8.0 ± 21.2 µg m^{-2} h^{-1} (Range: -29.2 to 32.7 µg m^{-2} h^{-1}). Changi Beach and Cyrene Reef had the lowest CH_4 fluxes with an uptake of -6.7 ± 38.3 µg m^{-2} h^{-1} (Range: -76.5 to 81.8 µg m^{-2} h^{-1}, Fig. 5a) and -4.5 ± 8.7 µg m^{-2} h^{-1} (Range: -18.7 to 15.4 µg m^{-2} h^{-1}, Fig. 5a), respectively. Soil CH_4 emissions did not vary significantly among geomorphic settings (KW test; df = 2, $\chi2$ = 3.69, p = 0.158; Fig. 5b). Mean CH_4 fluxes were -1.0 ± 30.2 µg m^{-2} h^{-1}, 4.7 ± 15.6 µg m^{-2} h^{-1} and -1.1 ± 9.5 µg m^{-2} h^{-1} for estuarine, lagoonal and reef-associated seagrasses, respectively.

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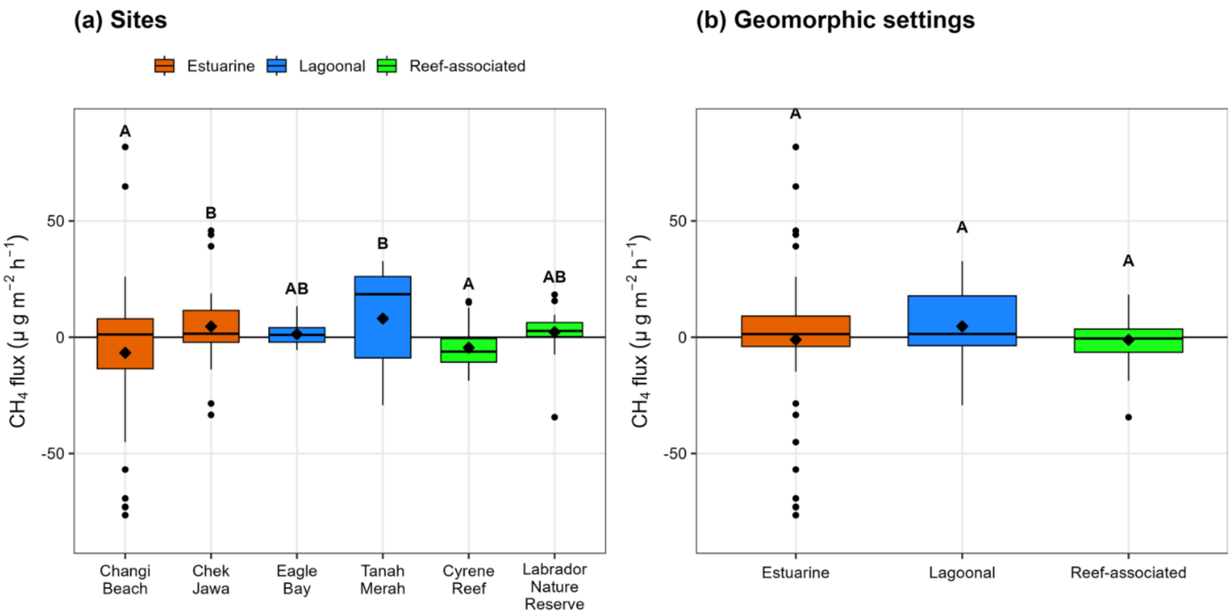

Figure 5: Seagrass soil methane fluxes (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings. Positive fluxes indicate emission into the air, while negative fluxes indicate uptake by the sediment. Different uppercase letters indicate significant differences ($p \leq 0.05$) across sites and geomorphic settings, as determined by Dunn's test with a Bonferroni correction.

3.3 Relationship between carbon stocks and fluxes and environmental parameters

Seagrass soil cores from all sites contained, on average (± SD), 585.8 ± 293.8 µm grain size, 1.4 ± 0.3 g cm^{-3} dry bulk density, 0.9 ± 0.8 C_{org} % and 0.01 ± 0.01 g cm^{-3} soil C_{org} density in the top 100 cm. Grain size varied significantly across depth intervals (KW; df = 423, χ^2 = 41.4, p < 0.0001), (KW; df = 5, χ^2 = 184.7, p < 0.0001), sites (KW; df = 5, χ^2 = 184.7, p < 0.0001) and geomorphic settings (KW; df = 2, χ2 = 161.8, p < 0.0001). Grain size was larger >200 µm in the upper 30cm soil profile and decreased to <125 µm in the lower 40-100 cm soil profile (Fig. 6a). Across sites, Eagle Bay had a high grain size of 604.3 ± 254.7 µm, while Changi Beach Park had the lowest grain size of 99.1 ± 117.1 µm (Fig. 6a). Across geomorphic settings, estuarine sites had a significantly lower grain size of ~119.1 ± 137.7 µm followed by reef- associated at and lagoonal sites, which contained a grain size of 393.7 ± 283.9 µm and 517.1 ± 137.7 µm respectively (Fig. 6b).

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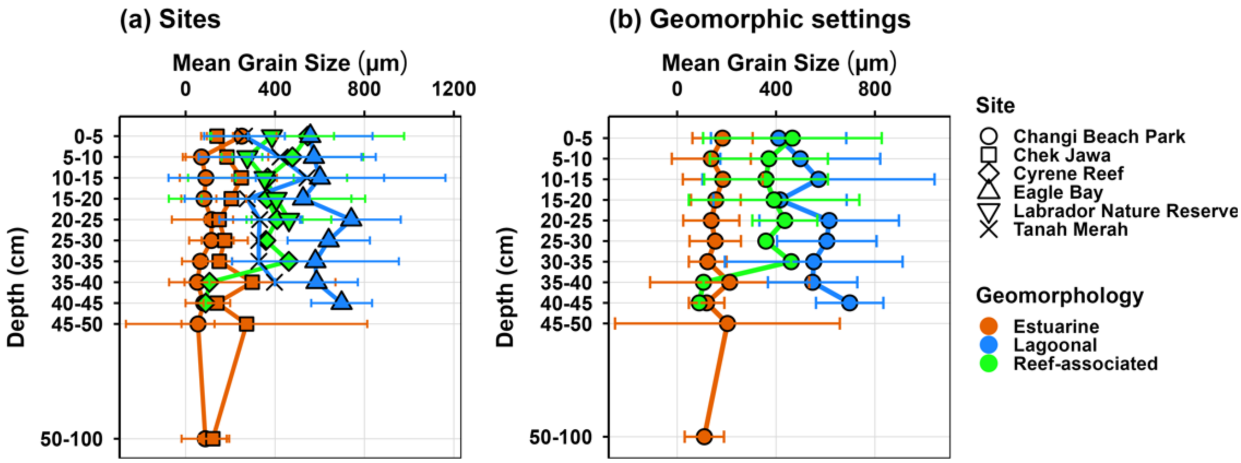

Figure 6: Seagrass soil grain size (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings.

Dry bulk density did not show significant intra-site variability in 83% of the surveyed sites. However, significant spatial differences in soil DBD were observed among study sites (KW test; n = 62, df = 5, $\chi2$ = 38.9, p < 0.001, Fig. 7a). Eagle Bay exhibited the highest DBD at 1.7 ± 0.1 g cm^{-3} (Range: 1.5 to 1.9 g cm^{-3}), while Tanah Merah had the lowest values at 0.9 ± 0.2 g cm^{-3} (Range: 0.7 to 1.3 g cm^{-3}, Fig. 7a). Across geomorphic settings, soil DBD differed significantly (df = 2, $\chi2$ = 24.2, p < 0.001), with values of 1.5 ± 0.3 g cm^{-3}, 1.3 ± 0.4 g cm^{-3} and 1.4 ± 0.2 g cm^{-3} recorded for estuarine, lagoonal and reef-associated seagrass systems, respectively (Fig. 7b). Across depth profiles within geomorphic settings, estuarine and reef-associated seagrass meadows showed negligible to minimal change, while lagoonal meadows showed more variable depth profiles, with surface DBD of 1.3 g cm^{-3} increasing by 12% to 1.4 g cm^{-3} below 15 cm, though this pattern varied considerably between the two measured sites (Fig 6b).

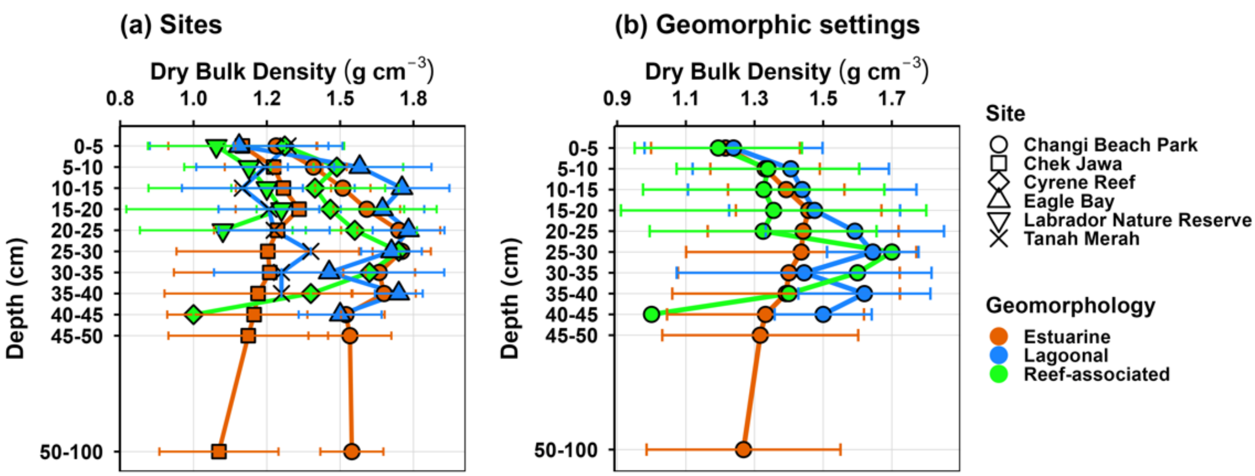

Figure 7: Seagrass soil dry bulk density (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings.

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Soil organic carbon density across seagrass ecosystems averaged 0.013 ± 0.008 g cm^{-3} (Range: 0.002 to 0.030 g cm^{-3}) for all study locations. Intra-site heterogeneity in soil SOC density was not significant for 67% of the surveyed sites. Significant spatial differences in soil SOC density were recorded among study sites (KW test; n = 62, df = 5, $\chi2 = 42.3$, $p < 0.001$). Tanah Merah exhibited the greatest SOC density at 0.024 ± 0.003 g cm^{-3} (Range: 0.019 to 0.030 g cm^{-3}), while Eagle Bay displayed the lowest SOC density at 0.003 ± 0.001 g cm^{-3} (Range: 0.002 to 0.004 g cm^{-3}, Fig. 8a). Across geomorphic environments, soil SOC density differed significantly ($\chi2 = 26.7$, $p < 0.001$), with values of 0.010 ± 0.005 g cm^{-3}, 0.013 ± 0.011 g cm^{-3} and 0.018 ± 0.005 g cm^{-3} recorded for estuarine, lagoonal and reef-associated seagrass systems, respectively (Fig. 8b). Vertical distribution patterns varied markedly among geomorphic settings, with estuarine systems maintaining uniform SOC throughout the profile at 0.011 g cm^{-3} for 0-15 cm top and 0.010 g cm^{-3} for >15 cm, representing only an 11% decrease. In contrast, lagoonal systems showed pronounced stratification with 37% SOC reduction from surface (0.013 g cm^{-3}) to subsurface (0.008 g cm^{-3}), reaching minimum values of 0.002 g cm^{-3} at 40-45 cm depth. Reef-associated systems exhibited the highest surface SOC at 0.019-0.022 g cm^{-3} in the top 0-10 cm but showed a 29% reduction in subsurface layers, with minimal SOC density at 0.001 g cm^{-3} below 35 cm depth.

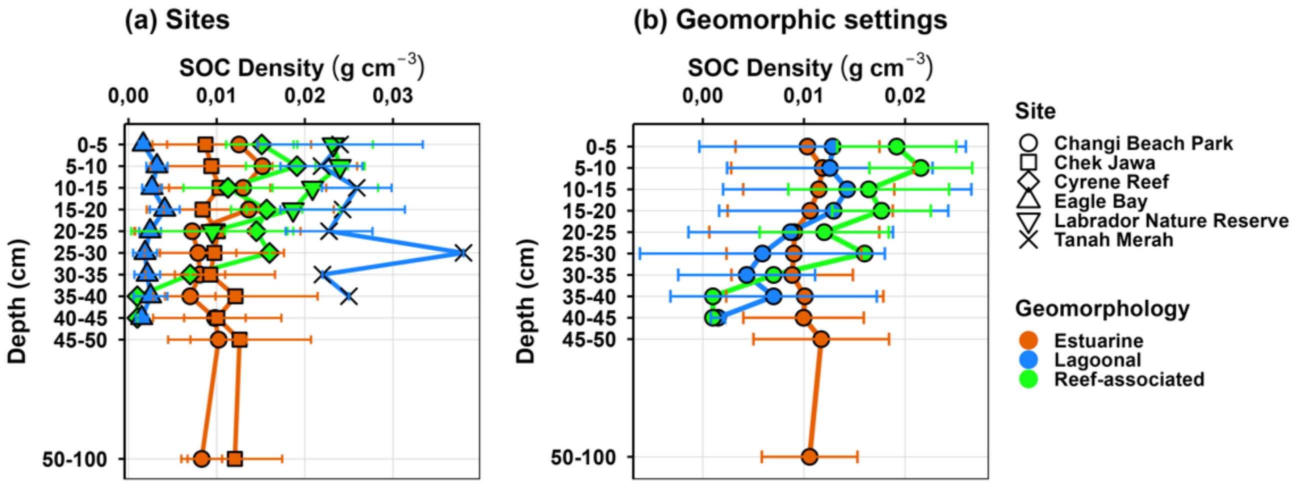

Figure 8: Seagrass soil organic carbon density (mean ± SE) across spatial scales, including (a) sites and (b) geomorphic settings.

We found carbon stocks were significantly and positively associated with soil temperature ($\rho=0.59$, $q\approx1.6e{-}05$) and salinity ($\rho=0.85$, $q\approx2.9e{-}14$, Fig. S1, S2). Soil temperature and salinity significantly co-varied ($\rho=0.841$, $q\approx3.9e{-}14$), reflecting a shared gradient. Corg% decreased with bulk density ($\rho=-0.35$, $q\approx0.029$) and increased with salinity ($\rho=0.60$, $q\approx1.0e{-}05$). Redox was inversely associated with bulk density ($\rho=-0.48$, $q\approx1.0e{-}03$). CO_2 flux was moderately negatively associated with C stocks ($\rho=-0.33$, $q=0.0398$) and significantly negatively correlated with median grain size ($\rho=-0.68$, $q\approx1.0e{-}07$). Other CO_2 associations were marginal after FDR. CH_4 flux was moderately positively associated with carbon stocks ($\rho=0.42$, $q=0.00499$)

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but strongly correlated with C_{org}% (ρ=0.75, q≈1.1e−09). CH_4 flux decreased with bulk density (ρ=−0.58, q≈2.6e−05) and increased significantly with median grain size (ρ=0.54, q≈1.2e−04) and redox (ρ=0.74, q≈2.2e−09).

Multivariate model explained ~60% of variance in CO_2 fluxes (marginal R^2 = 0.60), with total variance explained ~79% (conditional R2 = 0.79; cross-validated mean R^2=~0.31). CO_2 flux increased with redox (β = +4.02 ± 1.18, p = 0.001) and decreased with dry bulk density (β = −4.44 ± 1.06, p < 0.001). Reef-associated (Δ = −16.85 ± 3.86, p < 0.001) and lagoonal (Δ = −6.95 ± 1.86, p < 0.001) meadows had lower CO_2 fluxes than estuarine. Despite strong bivariate correlations, C_{org}% and grain size were not significantly associated with CO_2 flux in the multivariate model, indicating confounding with structure/chemistry gradients. About ~80% of the variance (marginal R^2 = 0.80) in CH_4 flux was explained by the multivariate model, and cross-validation highlighted modest predictive skill across sites (mean R2 = 0.25). As expected, CH_4 flux increased with C_{org}% (standardised β = 0.36 ± 0.15, p = 0.021), with a higher increase rate in reef-associated (Δ = +1.63 ± 0.45, p < 0.001) and lagoonal (Δ = +0.66 ± 0.23, p = 0.007) meadows relative to estuarine. After accounting for the hierarchy and geomorphic settings, redox was a borderline predictor (p = 0.054), while dry bulk density, salinity, grain size, and soil temperature were not significant predictors of CH_4 flux.

4 Discussion

4.1 Soil carbon stocks and fluxes of tropical seagrass meadows in Singapore

Our soil organic carbon stocks for the top 15 and 30 cm fall within the ranges reported for local and regional seagrass meadows (Table 1). Although our measured 100 cm soil organic carbon stocks are almost half of those reported for global seagrass meadows, they are consistent with those reported for the Halophila genus globally (Krause et al., 2025). These findings situate intertidal seagrass meadows of Singapore as low to moderate carbon stores. The fluxes of CO_2 measured in this study are within the range of 5 to 920 mg/m²/h, reported for seagrasses in South and Southeast Asia (Stankovic et al., 2023; Zheng et al., 2023). An important observation from this study was the presence of negative fluxes from dark chambers, which had not been reported previously for seagrasses. However, this has been observed in other coastal ecosystems and linked to the presence of novel microbiota that can respire in the absence of light. This microbiota included acetogens, chemosynthetic microbes able to sequester CO_2 in dark conditions ((Rodriguez et al., 2025). The potential presence of similar chemosynthetic microbes in the seagrass ecosystem suggests a yet unconstrained mechanism of CO_2 sequestration. CH_4 emissions were within the lower range of reported values of sediment-water and sediment-air CH_4 fluxes for tropical and temperate seagrasses in the region and globally (Asplund et al., 2022; Henriksson et al., 2024; Zheng et al., 2023). The relatively low CH_4 emissions in our study may be due to the presence of CH_4 consumption processes in the sediments of tropical seagrass meadows. Marine sediments are inhabited by sulfate-reducing bacteria and methane-oxidising archaea that are known to efficiently oxidise CH_4 produced in sediments before it is released into the atmosphere (Orphan et al., 2001). These bacterial communities may

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260 consume up to 90% of the CH_4 produced in marine sediments (Reeburgh, 2007). Our findings show that tropical seagrasses are sinks or negligible sources of CH_4.

Table 1. Comparison of seagrass soil carbon stocks with previous estimates.

Top 15 cm comparison					
References	Number of cores	Scale	Location	Mean ± SD Mg C_{org} ha^{-1} (median)	Min-Max Mg C_{org} ha^{-1}
This study, Estuarine	26	Landscape	Singapore	16.7 ± 10.2 (12.7)	6.1-43.4
This study, Lagoonal	18	Landscape	Singapore	19.9 ± 17 (17.2)	2.2-48.4
This study, Reef-associated	14	Landscape	Singapore	26.7 ± 10.8 (28.3)	2.2-43.7
Alemu et al. (2022), Estuarine	9	Landscape	Singapore	14.6 ± 12.6 (11.3)	4-28.6
Alemu et al. (2022), Lagoonal	9	Landscape	Singapore	25.2 ± 18.7 (19.6)	9.9-46.1
Alemu et al. (2022), Reef-associated	9	Landscape	Singapore	30.9 ± 37.3 (17.9)	4.1-83.6
Top 30 cm comparison					
This study measured only	43	Landscape	Singapore	39.7 ± 24.8	6.2-97.8
Mazarrasa et al. (2021)	43	Bioregion (Tropical)		20.3 ± 1.5	-
Kennedy et al. (2022)	576	Global	Global	33.5 ± 1.2	-
Krause et al. (2025)	1022	Global	Global	41.1 ± 1.8	-
Top 100 cm comparison					
This study including predicted	62	Landscape	Singapore	131.6 ± 77.6 (128.6)	18.8-302.6
This study measured only	8	Landscape	Singapore	95.6 ± 43.6 (84.7)	29.1-160.3
Phang et al. (2015)	20	Site (Local)	Singapore	138 ± 8.6	-
Stankovic et al. (2021)	-	Regional	Southeast Asia		0.10-205
Krause et al. (2025)	227	Global	Global	194.3± 13.4 (145)	-

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4.2 Scale-dependent variability in seagrass soil carbon stocks and fluxes

Our findings highlight strong spatial variability in soil C_{org} stocks, with geomorphic setting emerging as a primary control at the landscape scale. Reef-associated and lagoonal meadows stored substantially more carbon than estuarine sites in the upper 30 cm soil profile (Table 1), consistent with the limited hydrodynamic energy environments of reef-associated and lagoonal meadows creating depositional conditions which favour carbon storage and retention (Kennedy et al., 2022; York et al., 2018). In contrast, estuarine meadows showed lower storage, similar to patterns reported in other estuarine meadows (Carruthers et al., 2007; Alemu et al., 2022). Despite large amounts of terrestrial runoff, site-specific exposure to strong hydrodynamic energy and sediment dynamics, such as resuspension of fine sediment, may reduce net C_{org} stocks in estuarine sites (Mazarrasa et al., 2023). At the site scale, differences in salinity and bulk density contributed to variability in carbon stocks. Sites with higher salinity and lower bulk density had higher C_{org}, aligning with global evidence that salinity and sediment characteristics influence carbon retention (Miyajima et al., 2015; Kauffman et al., 2020; Serrano et al., 2019). High intra-site variability was likely due to patchiness in seagrass cover, species composition, and microtopography. This heterogeneity underscores the importance of adequate replication in sampling design to avoid misrepresentation of local stocks (Dahl et al., 2025).

Unlike soil C_{org} storage, CO_2 and CH_4 fluxes showed limited variation across geomorphic settings at the landscape scale of Singapore, which represents an intermediate level due to its seagrass extent. Emissions were relatively consistent, suggesting that at intermediate landscape scales, either GHG dynamics may be regulated by biogeochemical processes that are not influenced by geomorphology, geomorphic gradients may not be distinct enough at this scale, or the influence of geomorphology may be overwhelmed by other factors. Kirwan et al. (2023) proposed that geomorphic processes constrain carbon stocks, whereas fluxes are largely controlled by small-scale and short-term ecological and biogeochemical dynamics. Geomorphic settings, including estuaries, deltas, lagoons, etc., establish unique sedimentary processes that influence environmental parameters such as sediment supply, organic matter decomposition and persistent anoxia; all of which ultimately control long-term carbon storage in blue carbon ecosystems (Twilley et al., 2018). By contrast, ecological processes such as species composition, plant productivity, electron acceptor availability and oxygen transport between soil and atmosphere can govern GHG fluxes in blue carbon ecosystems (Rosentreter et al., 2021). Our findings highlight that carbon stock variability can be explained by geomorphic settings (estuarine vs barrier-lagoon systems, sediment supply, tidal range) even in an intermediate landscape context, while fluxes can appear similar across sites because they track production and deposition rather than long-term preservation dynamics.

4.3 Patterns and environmental controls on soil carbon stocks and fluxes

The bivariate patterns suggest that sites along a shared salinity–temperature gradient accumulate more carbon, with carbon stocks rising alongside both salinity and soil temperature, and salinity–temperature themselves strongly co-vary. This is consistent with the previous findings reporting higher soil C_{org}% in marine seagrass meadows (comparatively saltier) than

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estuarine meadows (Juma et al., 2020) and increasing salinisation increased soil carbon storage in seagrass meadows (Ruiz-Fernández et al., 2020). Mechanistically, saltier, warmer, and typically more marine-influenced meadows may favour higher organic matter retention and slower mineralisation, especially where lower bulk density indicates looser, potentially finer, and more organic-rich sediments. These background gradients help explain the flux patterns in our study: CO_2 flux is higher when redox is higher (more oxidising) and lower when bulk density is higher, indicating aerobic respiration is a dominant pathway for CO_2 production where oxygen availability is greater, and sediments are less compact. Our data did not show a direct correlation between soil C_{org} stocks and CO_2 fluxes, suggesting that high carbon storage does not necessarily imply elevated CO_2 emissions. Methane emissions appear more tightly linked to the quantity and perhaps nature of organic substrate than to the broader physical gradients once hierarchical structure is considered. The multivariate model confirms C_{org}% as a significant predictor (standardised $\beta \approx 0.36$) of CH_4 flux. Though not significant, reef-associated and lagoonal meadows showed slightly higher CH_4 flux relative to estuarine, aligning with their relatively higher organic content and perhaps microbially favourable conditions for methanogenesis. This indicates CH_4 production as a function of organic matter quantity, which is regulated by localized redox conditions and microbial processes (Al-Haj and Fulweiler, 2020). Overall, these findings reflect the nuanced interplay between environmental parameters and biogeochemical processes at multiple spatial scales, highlighting the importance of habitat-specific factors in controlling GHG emissions and organic carbon dynamics in tropical seagrass meadows and their implications for blue carbon budgets.

5 Conclusions

This study advances understanding of tropical seagrass carbon dynamics by quantifying soil organic carbon stocks and greenhouse gas fluxes across multiple spatial scales in Singapore. We show that soil C_{org} storage is highly variable, with geomorphic setting acting as a dominant control at the landscape scale; intra-site heterogeneity in soil C_{org} highlights the importance of adequate sampling to capture spatial variability; and greenhouse gas emissions (CO_2 and CH_4) are relatively uniform across settings, and CH_4 fluxes directly correspond to carbon storage levels.

Our results underscore two important implications for blue carbon accounting. First, soil C_{org} storage in tropical seagrasses is highly variable and strongly influenced by geomorphic settings, highlighting the need for spatially explicit approaches to stock estimation. Applying global averages to local contexts risks substantial under- or overestimation, with consequences for policy and carbon market applications (Dahl et al., 2025). Second, since GHG fluxes complicate and can reduce the climate benefits of blue carbon ecosystems (Malerba et al., 2022), accounting for GHG fluxes, particularly CH_4 emissions, is important for understanding the climate change mitigation potential of seagrass ecosystems.

Our findings contribute critical baseline data from Southeast Asia—a region of high seagrass biodiversity but limited empirical data. They also provide a methodological framework for other small island states with comparable seascapes. Importantly, our study demonstrates that while tropical seagrasses can store substantial carbon, this ecosystem function is context-dependent, shaped by geomorphology and site-specific factors. Accounting for such variability is essential for robust integration of seagrasses into national and global climate strategies.

Data availability

Author contributions

Lian Pin Koh and Daniel A. Friess, funding acquisition; Naima Iram, Daniel A. Friess, Lian Pin Koh, and Kiah Eng Lim, conceptualising; Naima Iram, Kiah Eng Lim, Muhammad Ariq Khalingga, Sheryl Chan Si Ern and Pierre Taillardat, sampling and laboratory analysis, Naima Iram Muhammad, Ariq Khalingga data analysis, Naima Iram and Daniel A. Friess writing the first draft, and all authors contributed to the final draft.

Competing interests

The contact author has declared that neither of the authors has any competing interests.

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