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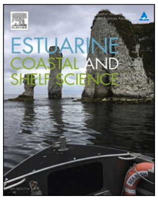

Geomorphic gradients in shallow seagrass carbon stocks

Jahson Berhane Alemu I[a,b,1,*], Siti Maryam Yaakub[c], Erik S. Yando[a,b,d], Rachel Yu San Lau[a], Cheng Chang Lim[a], Jun Yu Puah[a], Daniel A. Friess[a,e,**]

[a] *Department of Geography, National University of Singapore, 1 Arts Link, 117570, Singapore*
[b] *Campus for Research Excellence and Technological Enterprise, 138602, Singapore*
[c] *Sustainability & Climate Solutions, DHI Water & Environment, 2 Venture Drive, #18-18, 608526, Singapore*
[d] *Department of Biological Sciences, Old Dominion University, Norfolk, VA, 23529, USA*
[e] *Centre for Nature-based Climate Solutions, National University of Singapore, 16 Science Drive 4, 117558, Singapore*

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ABSTRACT

Seagrass meadows are important sinks of organic carbon (C_{org}), in particular the near-surface C_{org} pool (≤ 15 cm) compared to deeper sediments. Near-surface carbon is highly susceptible to disturbance and loss to the atmosphere, however, inadequate accounting for variability in this pool of carbon limits their uptake into carbon accounting frameworks. We therefore investigated the spatial variability in seagrass near-surface C_{org} and biomass C_{org} across different geomorphic (estuary, lagoonal and reef-associated) and community typologies (pioneer and persistent). Near-surface C_{org} stock in vegetated areas (25.78 Mg C_{org} ha^{-1} ± 26.64) was twice that from unvegetated areas (14.27 Mg C_{org} ha^{-1} ± 15.86), reinforcing the paradigm that the presence of seagrass enhances carbon stocks. Lagoonal and reef-associated meadows showed similar C_{org} stocks ($p > 0.05$), which were substantially higher ($p < 0.05$) than estuary meadows. Likewise, persistent seagrass communities (*Cymodocea* dominance) stored higher ($p < 0.05$) stocks of C_{org} than pioneer communities (*Halophila* and *Halodule* dominance). Linear regression models showed significant but weak relationships between seagrass cover, shoot density and standing biomass with near-surface C_{org} stocks, whereas significant and strong relationships were observed for organic matter, dry bulk density and median grain size. The results highlight the need for higher resolution carbon assessments to better understand local and regional variability, in order to better inform carbon accounting and conservation policy.

1. Introduction

Wetland conservation is attracting substantial attention from a wide range of governmental, commercial and private stakeholders, who have obligations to mitigate greenhouse gas emissions. Coastal vegetated wetlands or "*blue carbon*" ecosystems (i.e. mangroves, seagrass meadows and tidal marshes) in particular, have been identified as important sinks of carbon due to their ability to sequester and store carbon at rates that greatly exceed many terrestrial forests. Seagrass ecosystems for instance, sequester at least twice as much carbon per unit area compared to tropical (40 g C m^{-2} yr^{-1}) and temperate (22.5 g C m^{-2} yr^{-1}) forests (Grace et al., 2006; Taillardat et al., 2018), and have an estimated global storage of 3.76–21 Pg C (Macreadie et al., 2021), that can potentially be trapped over timescales relevant to climate change. However, high rates of seagrass loss and degradation at local, regional and global scales (Dunic et al., 2021) are driving the release of previously sequestered and stored carbon into the water column and atmosphere (Duarte et al., 2005; Githaiga et al., 2019; Howard et al., 2018), adding to global carbon emissions.

Seagrasses meadows are found along the coasts of most continents, with local species distributions that reflect physiological, phenotypic and morphological adaptations to tidal flooding, disturbance, sediment supply, wave action and geomorphology (Hemminga and Duarte, 2000; Serrano et al., 2016; Gullström et al., 2018). The ability of seagrasses to trap and store suspended material from the water column in the soil, is driven by the interaction between abiotic (e.g. edaphic conditions and indundation) and biotic (e.g. growth and productivity) parameters at the site scale (Chmura et al., 2001; Mateo et al., 2006; Kennedy et al., 2010).

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[*] Corresponding author. Department of Geography, National University of Singapore, 1 Arts Link, 117570, Singapore.
[**] Corresponding author. Department of Geography, National University of Singapore, 1 Arts Link, 117570, Singapore.
E-mail addresses: jahsonb@gmail.com (J.B. Alemu I), dan.friess@nus.edu.sg (D.A. Friess).
[1] Present address. Department of Marine and Environmental Sciences, Northeastern University, Boston, MA, 02115, USA.

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Likewise, carbon storage at the landscape scale varies along hydro-geomorphic gradients between tidally-influenced and river-influenced settings (Sasmito et al., 2020; Hayes et al., 2017; Marchio et al., 2016).

National, regional and global seagrass carbon estimates often extrapolate from a limited set of field samples (Lavery et al., 2013), which reduces confidence in their utility to policy and decision-making (Macreadie et al., 2014). However, blue carbon assessments that incorporate spatial variation at a higher resolution may boost confidence in blue carbon accounting at multiple scales. By linking sediment supply to geomorphology, we hypothesize that the geomorphic setting may be an important control on seagrass species dominance, edaphic conditions and carbon stocks. This study therefore aims to examine the variation in seagrass C_{org} through the lenses of geomorphology and community persistence, and uses the island of Singapore to test this hypothesis. Further, this study also investigates the relationships between meadow and edaphic characteristics with the near-surface carbon stocks. Near-surface carbon (<15 cm) represents a significant sink of carbon that is highly susceptible to disturbance and loss to the atmosphere compared to deeper sediments, but remains largely unaccounted for in carbon accounting schemes. This study builds on a limited body of literature from an underrepresented area in Southeast Asia, with outputs are particularly important for understanding the local and regional variability of seagrass carbon, informing carbon accounting, and guiding conservation policy.

2. Materials and methods

2.1. Study area

This study was conducted on ten intertidal seagrass meadows the surround the tropical island-state of Singapore (Fig. 1). These meadows are exposed to diurnal tides, such that they are fully submerged during the high-tide and exposed during the low-tide (tidal range: exceeds 2.5m). These meadows are also exposed to chronic sedimentation and turbidity owing to rapid urbanisation over recent decades (Yaakub et al., 2014; Lai et al., 2015). There is no distinct wet or dry season, but rainfall is highest during the two monsoonal seasons (December to March and June to September, respectively) and lowest from May to July (Meteorological Service Singapore, 2016).

The seagrass meadows were selected for continuity, similar size, accessibility and have existed for the last 5 years. All sites supported mixed-species meadows except for the Labrador Nature Reserve site which supported a mono-specific stand of *Thalassia hemprichii*. Mixed-species meadows were dominated by species from the genera *Halophila* and *Halodule* or *Cymodocea.* Based on the physiological, phenotypic and morphological traits of the dominant species (contributed > 75% to cover), seagrass meadows were broadly classified as either pioneer or persistent (Table 1). The pioneer community typology refers to communities of small stature seagrasses, dominated by ephemeral, fast colonizing and fast growth species with high turnover rates such as *Halodule uninervis*, *Halophila ovalis* and *Halophila spinulosa.* The pioneer community typology was observed at Changi Beach, Chek Jawa-outer meadow, Bendera Bay, SJI Jetty and Cyrene Reef. In contrast, the persistent community typology refers to communities of large stature seagrasses, dominated by long-lasting and slow colonizing species with slow turnover rates following disturbance such as *Cymodocea rotundata/ serrulata, Thalassia hemprichii* and *Enhalus acoroides.* The persistent community typology was observed at Eagle Bay, Tanah Merah, Chek Jawa-inner meadow, Pulau Semakau and Labrador Nature Reserve.

Additionally, broad geomorohic, biological and hydrodynamic site characteristics were used to classify the seagrass meadows into distinct geomorphic settings (McKenzie et al., 2016): Estuary, reef-associated and lagoonal . The estuary typology is sheltered and located in deltaic conditions, receiving riverine sediments characterised by fine silts and muds (in this case from the Johor River). The estuary meadows are Chek Jawa-inner meadow, Chek Jawa-outer meadow and Changi Beach. In contrast, sediment supply in meadows along carbonate coastlines (i.e. reef-associated meadows) is tidally-influenced. The limited input of sediment means that seagrass meadows develop on comparatively thin sediment layers overlaying carbonate rock. The reef-associated meadows are Pulau Semakau, Cyrene Reef, SJI Jetty and Labrador Nature Reserve. The lagoonal typology displays characteristics between estuary and reef-associated typologies. They are man-made in origin, where sandy lagoons were constructed behind the shelter of coastal revetments (groynes and breakwaters) for recreational activities (e.g.

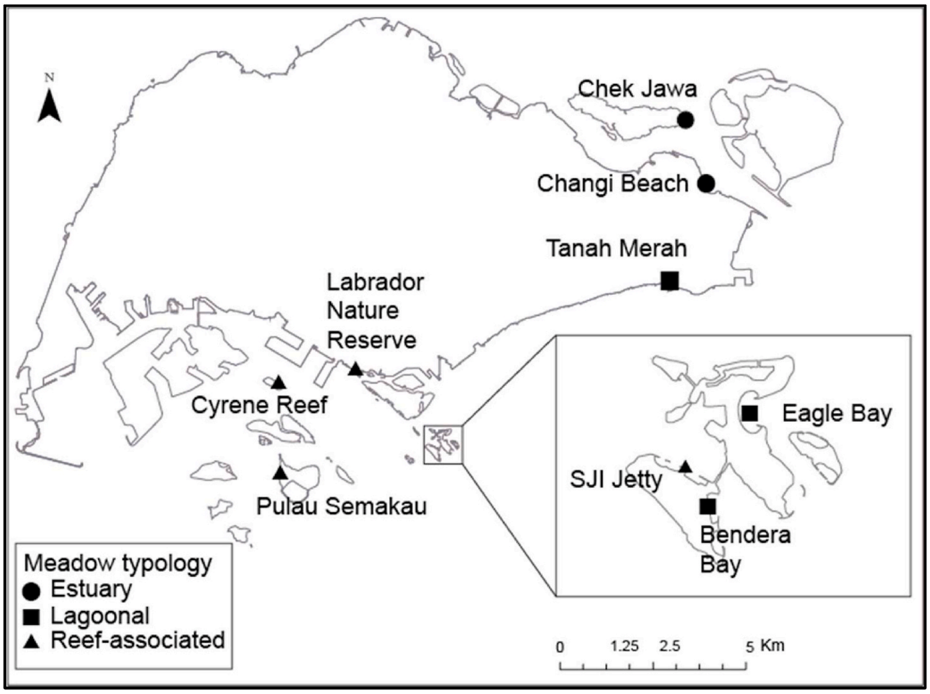

Fig. 1. Map of Singapore indicating sampling sites across seagrass meadow typologies.

Table 1

Summary of site typologies, species richness and species dominance.

Site	Meadow typology	Community typology	Species observed (dominant species)	Latitude Longitude
Changi Beach	Estuary	Pioneer	(Ho/Hu), Hs	1.3751 104.0061
Chek Jawa - outer meadow	Estuary	Pioneer	(Ho/Hu), Hs	1.4106 103.9915
Chek Jawa - inner meadow	Estuary	Pioneer	(Cr/Cs), Ho, Hs, Hu	1.4095 103.9919
Bendera Bay	Lagoonal	Pioneer	(Ho/Hu), Si, Ea	1.2198 103.8509
Eagle Bay	Lagoonal	Persistent	(Th), Cr/Cs, Ho, Hu, Hs	1.2256 103.8543
Tanah Merah	Lagoonal	Persistent	(Cr/Cs), Ea, Si, Ho, Hu, Hs	1.3166 103.9834
Cyrene Reef	Reef-associated	Pioneer	(Cr/Cs), Ho, Hu, Si, Ea, Th	1.2588 103.7562
Labrador Nature Reserve	Reef-associated	Persistent	(Th), Ea, Ho	1.2664 103.8009
Pulau Semakau	Reef-associated	Persistent	(Cr/Cs), Ho, Hu, Ea, Th	1.2061 103.7571
SJI Jetty	Reef-associated	Pioneer	(Ho/Hu)	1.2222 103.8472

Cr *Cymodocea rotundata*; Cs *Cymodocea serrulata*; Hu *Halodule uninervis*; Si *Syringodium isoetifolium*; Ea *Enhalus acoroides*; Ho *Halophila ovalis*; Hs *Halophila spinulosa*; Th *Thalassia hemprichii.*

Eagle Bay), commercial needs (e.g. Bendera Bay) or industrial developments (e.g. Tanah Merah). Sediment supply in lagoonal meadows is largely tidally-influenced, although terrestrial sediment inputs may also occur in some instances (e.g. Tanah Merah).

2.2. Data collection

Field data were collected at low-tides from August to November 2020. Data were separated into three groups – meadow-related data, edaphic data and carbon-related data. Meadow-related data included seagrass cover (%), standing biomass (g DW cm^{-2}) and shoot density (shoots m^{-2}). Edaphic data related to soil dry bulk density (g DW cm^{-3}), organic matter (%) and median grain size (Φ, phi units).

2.2.1. Measurement of meadow-related parameters

Seagrass cover and shoot density were estimated along three parallel 30 m transects, laid parallel to shore with each transect at least 5 m apart from another. The transects were laid through the center of the seagrass meadow to minimize edge effects. Cover was estimated within 1 m x 1 m (1 m^2) quadrats placed at 3 m intervals along each transect, leading to 30 measurements per site. Each quadrat was photographed, 100 random points overlaid onto each photo with the substrate beneath each point was determined, and the percent cover was averaged across the transects. Shoot density was counted *in situ* within a 0.25 m × 0.25 m (0.0625 m^2) quadrat placed in the top right corner of each seagrass cover quadrat. Six replicate biomass cores were collected per site (two cores per transect at pre-determined 15 m intervals along each transect, i.e. $n = 2$ per transect, $n = 6$ per site) using an 8.8 cm diameter PVC corer, pushed into the soil through the rooting zone to 20 cm depth. Biomass cores were wet sieved and the remaining seagrass material retained for lab analysis. In the lab, seagrass materials were separated into aboveground (shoots and leaves) and belowground (roots and rhizomes) components. Leaves were scraped of epiphytes, but because of the high amount of epiphytic growth, they were also washed in a weak acid to remove any calcareous material (Short et al., 2015), rinsed in distilled water, then dried in an oven at 60 °C to a constant weight (g DW m^{-2}). Standing biomass was calculated as the sum of the aboveground and belowground components.

2.2.2. Measurement of edaphic conditions

Nine replicate 5.8 cm diameter x 15 cm long soil cores were collected from each seagrass meadow and 5-7 soil cores from adjacent unvegetated areas to serve as controls. Soil cores within the seagrass meadows were taken at 10 m intervals along each transect ($n = 3$ per transect, $n = 9$ per site). In adjacent unvegetated areas, the same transect sampling design was used, unless unvegetated areas were not large enough, in which case random sampling was conducted instead. It should be noted, that no suitable unvegetated area was available at Labrador Nature Reserve. Compaction during coring was minimal (<10%). The coring depth of 15 cm was used based on rooting depth of the seagrass species present and for consistency across sites, as at some locations (Labrador Nature Reserve and SJI Jetty) the carbonate substrate prevented deeper cores using the gouge corer. Soil cores were taken to the lab, dried in an oven at 60 °C to a constant weight. Dry bulk density and organic matter were determined using the methods described in Howard et al. (2014). Dry bulk density (g DW cm^{-3}) was calculated as the ratio between the soil dry weight and wet sample volume. Organic matter (%) was calculated as the percent loss in weight following combustion of a 2.0 g ± 0.5 subsample of each soil sample at 550 °C for 5 h in a muffle furnace. Grain size was measured using the dry-sieve method on a 100–150 g subsample of each soil core, to separate soil fractions along the Udden-Wentworth scale (Wentworth, 1922): gravel/shell (>2000 μm), coarse sand (<2000-1000 μm), medium sand (<1000-500 μm), sand (<500-250 μm), fine sand (<250-125 μm), very fine sand (<125-63 μm) and mud (<63 μm). The cumulative weights of grain size distribution data were used to calculate median grain size (D_{50}) expressed in phi units, where $phi = -\log_2 D$, where D is particle diameter in millimeters.

2.2.3. Measurements of carbon-related data

The entirety of each 15 cm soil core was homogenized into a fine powder using a Vertical Planetary ball mill, and ~15 mg ± 0.5 subsample was used for carbon analysis. In order to determine total organic carbon content in each subsample was exposed to an acidified atmosphere for 24 h to remove any carbonate that may be present, rinsed with ultra-pure water, again dried in an oven at 60 °C until constant weight and wrapped in tin foil, and compacted into airtight pellets. Similarly, the aboveground and belowground biomass samples were also homogenized, compacted within tin into airtight pellets before carbon analysis. All carbon analyses for soil and plant materials were conducted using the elemental analyzer method, which returned percent carbon (% C_{org}) content per sample. Carbon stock per hectare (Mg C_{org} ha^{-1}) was calculated as described in Howard et al. (2014), by applying the following formulae and conversions:

$$Biomass\ carbon\ \left(g\ C_{org}\ cm^{-2}\right) = \frac{\left(C_{org}\ (\%) \times\ dry\ weight\ (g)\right)}{area\ (cm^2)}$$

$$Soil\ carbon\ density\ C_{org}\ \left(g\ C_{org}\ cm^{-2}\right) = DBD\ \left(g\ cm^{-3}\right) \times C_{org}(\%) \times core\ length(cm)$$

g C cm^{-2} was converted to the standard Mg C ha^{-1} using the following: 1 Mg = 10^6 g; 1 ha = 10^9 cm^2.

2.3. Data analysis

All data are reported as the mean ± standard deviation (SD). As the data did not meet the requirements of normality and homoscedasticity, the non-parametric Mann-Whitney (MW) test was used to assess the significance of differences in near-surface carbon between vegetated and unvegetated areas. Kruskal-Wallis (KW) tests with MW post-hoc tests were used to assess the significance of differences in the pools of carbon (aboveground, belowground and soil) among meadow typologies.

Generalized Linear Model were used to explore the relationship between meadow related characteristics (seagrass cover, standing biomass, shoot density, organic matter, dry bulk density, median grain size, aboveground biomass C_{org} and belowground biomass C_{org}) as explanatory variables, and soil C_{org} (response variable). All analyses were conducted in R v4.1.0 (R Core Team, 2018).

3. Results

3.1. Variation in C_{org} stocks

The near-surface C_{org} (i.e. C_{org} stock in the top 15 cm of soil) varied widely across meadows (KW test; df = 8, $\chi^2 = 50.22$, $p < 0.001$) and was as much as two times higher under seagrass vegetation than in unvegetated soil (Fig. 2a). Seagrass covered soils exhibited a mean ± SD dry bulk density of 1.21 g DW cm^{-3} ± 0.27, medium (0.25–0.5 mm) and fine (125–250 μm) sands, which contained 3.36% ± 1.95 organic matter and 1.40% ± 1.60 total organic carbon (C_{org}), resulting in an estimated carbon stock of 25.78 Mg C_{org} ha^{-1} ± 26.64 (Tables S1 and S2). Among seagrass meadows near-surface C_{org} was highest at Pulau Semakau (83.64 Mg C_{org} ha^{-1} ± 10.35) and lowest at Chek Jawa-inner meadow (4.00 Mg C_{org} ha^{-1} ± 2.51) (Fig. 2a; Table S1). Overall, vegetated areas stored significantly higher amounts of near-surface C_{org} (MW: U = 899, $p = 0.01$) than unvegetated areas (mean: 14.27 Mg C_{org} ha^{-1} ± 15.86).

Near-surface C_{org} did not significantly differ between meadow typologies (KW: $\chi^2 = 5.06$, $p = 0.08$; Fig. 2b) or between community typologies (MW: U = 847, $p = 0.11$; Fig. 2c), likely owing to the extremely large within group variation. Nevertheless, at the landscape scale, the highest near-surface C_{org} was recorded for reef-associated (36.97 Mg C_{org} ha^{-1} ± 34.13) and persistent (35.57 Mg C_{org} ha^{-1} ± 31.66) typologies, and the lowest near-surface C_{org} stock was recorded for the estuary (11.19 Mg C_{org} ha^{-1} ± 9.23) and pioneer (13.97 Mg C_{org} ha^{-1} ± 10.68) typologies.

Standing biomass C_{org} (KW: df = 8, $\chi^2 = 43.00$, $p < 0.001$), aboveground biomass C_{org} (KW: df = 8, $\chi^2 = 33.69$, $p < 0.001$) and belowground biomass C_{org} (KW: df = 8, $\chi^2 = 42.75$, $p < 0.001$) significantly differed ($p < 0.001$) between sites (Fig. 3a, Table S2). Labrador Nature Reserve displayed the highest mean standing biomass C_{org} (1.00 Mg C_{org} ha^{-1} ± 0.61) and belowground biomass C_{org} (0.81 Mg C_{org} ha^{-1} ± 0.58), whereas the meadow at Tanah Merah showed the highest mean aboveground biomass C_{org} (0.76 Mg C_{org} ha^{-1} ± 0.26). Across meadow typologies (Fig. 3b), mean standing biomass C_{org} (KW: df = 2, $\chi^2 = 2.54$, $p = 0.28$) and belowground biomass C_{org} (KW: df = 2, $\chi^2 = 4.13$, $p = 0.13$) trended higher but were statistically insignificant ($p > 0.05$) for reef associated meadows, and the highest mean aboveground biomass C_{org} (KW: df = 2, $\chi^2 = 0.65$, $p = 0.72$) was recorded for lagoonal (0.19 Mg C_{org} ha^{-1} ± 0.18). Lastly, higher ($p < 0.001$) standing biomass C_{org}, aboveground biomass C_{org} and belowground biomass C_{org} were reported for the persistent typology compared to the pioneer typology (Fig. 3c).

Overall, total mean C_{org} stocks (near-surface C_{org} and standing C_{org}) in seagrass habitats was 26.19 Mg C_{org} ha^{-1} 26.69, which ranged from 4.48 to 83.89 Mg C_{org} ha^{-1} (Table S2).

3.2. Relationships between seagrass meadow-related and edaphic parameters with near-surface C_{org}

Seagrass cover, shoot density, dry bulk density and grain size varied significantly ($p < 0.05$) across meadow typologies (Fig. 4). Seagrass cover in the estuary and lagoonal typologies were as much as 75% higher ($p < 0.001$) than in reef-associated meadows (Fig. 4a). Mean standing biomass was similar ($p > 0.05$) across meadow typologies (Fig. 4b). Shoot density was as much as two-fold higher ($p < 0.05$) in estuary and lagoonal meadows than in reef-associated meadows (Fig. 4c). Mean soil organic matter was similar ($p > 0.05$) across meadow typologies (Fig. 4d). Dry bulk density in the lagoonal typology was significantly higher ($p < 0.001$) than the other meadow typologies (Fig. 4e). Median grain size was significantly larger ($p < 0.001$) at reef-associated meadows than other typologies (Fig. 4f).

In terms of pairwise relationships, near-surface C_{org} among estuary meadows poorly correlated ($-0.12 < R < 0.25$, $p > 0.05$) with most meadow-related and edaphic parameters, except for seagrass cover ($R = -0.49$, $r^2 = 0.21$; $p < 0.05$), which increased with decreasing near-surface C_{org} and explained 21% of the variation in near-surface C_{org} among estuary meadows (Table 2). The variation in near-surface C_{org}

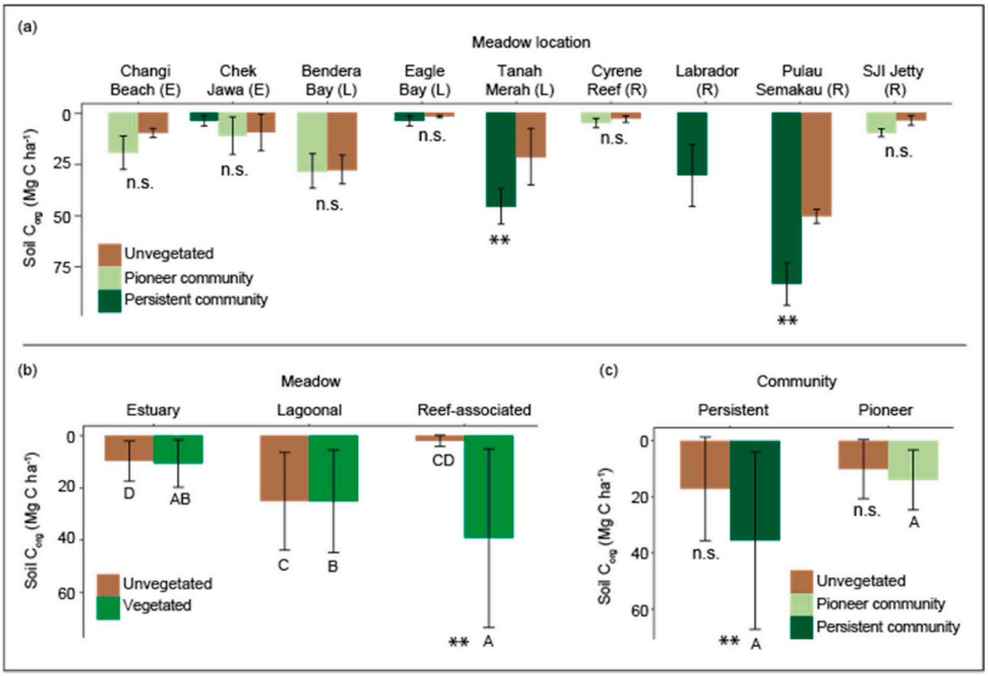

Fig. 2. Variation in near-surface C_{org} stocks across (a) meadow locations, (b) Estuary (E), Lagoonal (L) and Reef-associated (R) meadow typologies and (c) community typologies. Bars indicate mean ± SD. Asterisks indicate significant difference ($p < 0.05$) between vegetated and unvegetated areas within groups; same letters indicate significant difference in soil C_{org} within typology sub-groups. n.s. no significant difference.

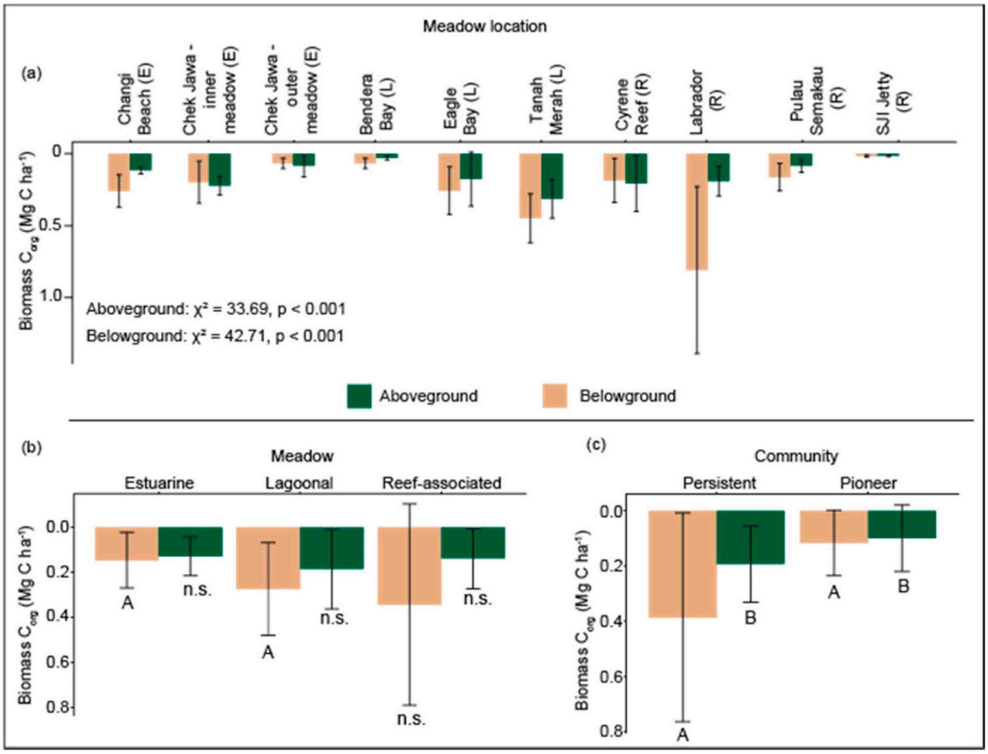

Fig. 3. Variation in aboveground and belowground C_{org} across (a) meadow locations, (b) Estuary (E), Lagoonal (L) and Reef-associated (R) meadow typologies and (c) community typologies. Bars indicate mean ± SD; same letters indicate where significant difference occurs in biomass C_{org} within typology sub-groups, n.s. no significant difference within typology sub-groups.

among the lagoonal meadows was best explained by standing biomass ($R = 0.43$. $r^2 = 0.18$; $p < 0.05$), dry bulk density ($R = 0.69$, $r^2 = 0.47$; $p < 0.01$) and median grain size ($R = -0.52$, $r^2 = 0.27$; $p < 0.01$). That is, near-surface C_{org} increased with standing biomass and dry bulk density, but decreased with median grain size. The inverse pattern was observed for the reef-associated typology, where near-surface C_{org} increased with organic matter ($R = 0.84$, $r^2 = 0.70$; $p < 0.01$) and median grain size ($R = 0.69$, $r^2 = 0.48$; $p < 0.01$), but decreased with shoot density ($R = -0.40$, $r^2 = 0.16$; $p < 0.05$) and dry bulk density ($R = -0.72$, $r^2 = 0.52$; $p < 0.01$).

4. Discussion

4.1. *Variation in C_{org} stocks*

This study highlights the variation in different pools of blue carbon across the seagrass landscape of Singapore, with geomorphoc gradients playing a key role. At the site level, the wide variation in carbon stocks reflects site-specific differences in species domiannce, habitat configuration and edaphic characteristics. At the landscape scale, these differences reflect are largely driven by variations in sediment supply where tidally-influenced settings store greater amounts of carbon than river-influenced settings. More broadly, this study reinforces the paradigm that the presence of seagrass enhances carbon storage, although this may not always be the case, such as for pioneer communities dominated by small stature species. Lastly, this study points to the complexity of carbon stocks in estuary, lagoonal and reef-associated settings using classical seagrass habitat monitoring parameters. This is particularly important when considering scaling up carbon estimates.

It was expected that the deltaic sites (Chek Jawa-inner meadow, Chek Jawa-outer meadow and Changi Beach) would have higher carbon stocks in near-surface soils owing to regular inputs of riverine sediments and higher sedimentation rates compared to tidally-influenced sites (e.g. Pulau Semakau, Labrador Nature Reserve, SJI Jetty and Cyrene Reef). This expectation is reasonable, as it commonly occurs in other blue carbon ecosystems such as tidal marshes and mangroves (Cacho et al., 2021; Gorham et al., 2021; Hayes et al., 2017). However, the results in our study show the opposite, where tidally-influenced sites maintain greater carbon stocks compared to river-influenced meadows. We hypothesize that although the deltaic sites received greater inputs of allochthonous sediment, these sediments may be of lower organic amounts compared to authochthonous systems in reef-associated sites with little outside inputs.

Despite chronic physiological stress, the mean near-surface C_{org} stock (25.78 Mg C_{org} ha^{-1} ± 26.64) was well within the range of C_{org} stock for Southeast Asia (14.51–37.65 Mg C_{org} ha^{-1} downscaled from syntheses by Alongi et al., 2016; Thorhaug et al., 2020; Stankovic et al., 2021) and the global mean (17.25–124.35 Mg C_{org} ha^{-1}; Fourqurean et al., 2012), but lower than estimates from other tropical seagrasses at a similar latitude (Kenya: 48.21–70.14 Mg C_{org} ha^{-1} downscaled from 50 cm cores; Githaiga et al., 2017). At Chek Jawa, the near-surface C_{org} estimate reported for pioneer communities this study (11.44 Mg C_{org} ha^{-1}) was almost half that reported for the same community in an earlier assessment (20.7 Mg C_{org} ha^{-1} downscaled from 1 m depth; Phang et al., 2015). This disparity may be due to spatial variability in carbon supply from adjacent blue carbon ecosystems (Saavedra-Hortua et al., 2020).

Across geomorphic settings, reef-associated meadows (specifically, Pulau Semakau and Labrador Nature Reserve) maintained greater carbon stocks than lagoonal and estuary meadows, and in both reef-associated and lagoonal meadows, persistent communities showed higher near-surface C_{org} stocks than meadows formed by pioneer communities, except at estuary meadow where the opposite was observed. The seagrass meadow at Pulau Semakau is tidally connected to both mangroves and macroalgae-dominated corals reefs in the landscape. Isotope analysis shows that tidally-connected mangroves and macroalgae can act as donors to seagrasses in Singapore, accounting for up to 60% of the soil C_{org} stock in seagrass meadows (Saavedra-Hortua et al., 2020). Other studies have also shown how strong cross-habitat carbon

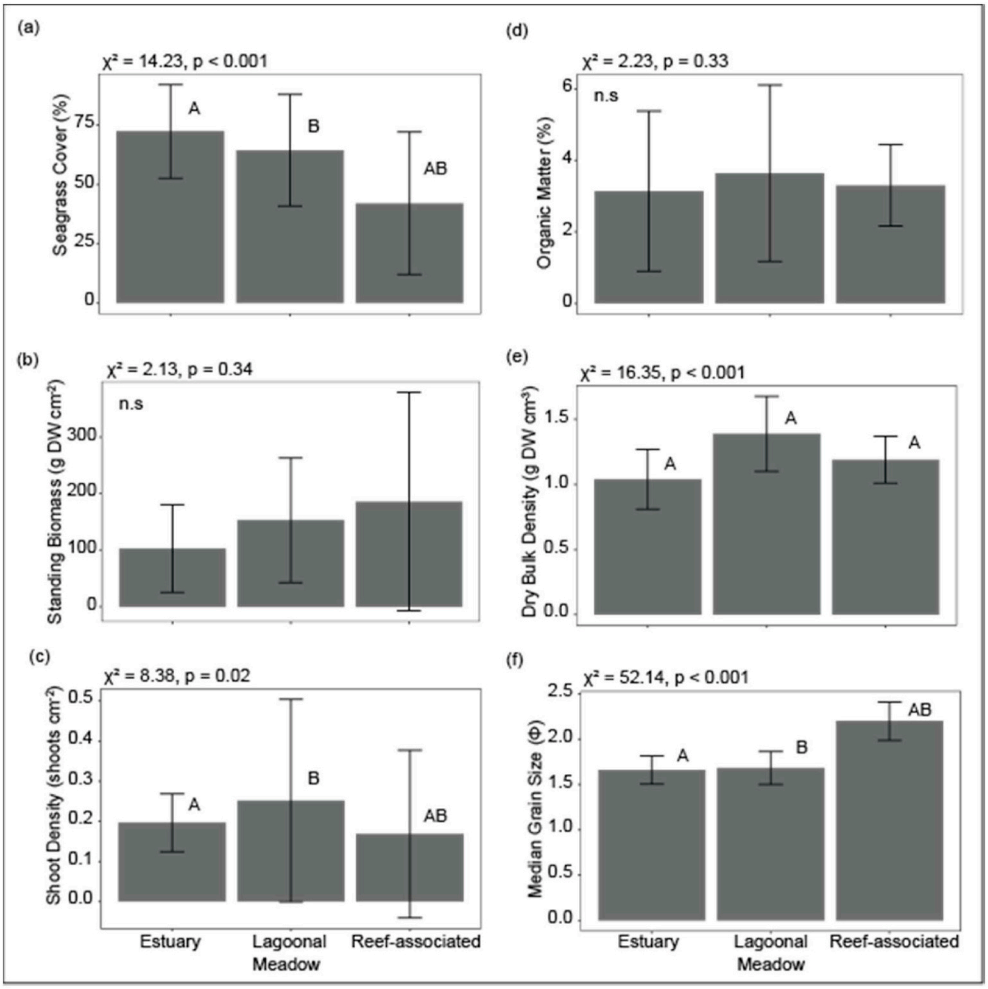

Fig. 4. Variation in meadow-related (a–c) and edaphic (d–f) characteristics across meadow typologies. Bars indicate mean ± SD; same letters indicate where significant difference occurs withn panels; n.s. indicates no significant difference within panels.

exchange may enhance blue carbon in downstream ecosystem (Watanabe and Kuwae, 2015; Bouillon and Connolly, 2009; Bouillon et al., 2007). For instance, in Southeast Asia mangroves have been identified as a significant source of carbon to seagrasses, accounting for as much as 50% of the soil carbon (Kennedy et al., 2004). Carbon storage is also influence by hydrodynamic and edaphic conditions (Dahl et al., 2016). In other landscape configurations, fringing coral reefs surrounding seagrass meadows decrease erosion of stored sediments by buffering wave energy, which creates conditions favouring sediment deposition and carbon burial in seagrass soils (Guerra-Vargas et al., 2020). The slowing of wave energy, decreases the potential for erosion which coupled with the high belowground biomass and high shoot density at Labrador Nature Reserve may have also led to conditions favouring a high efficiency of carbon retention. Likewise, high dry bulk density and fine grain size, reduces soil porosity and conditions for microbial decomposition, favouring carbon burial at Tanah Merah and Bendera Bay.

The efficiency of carbon storage is also affected by species-specific physiological, phenotypic and/or morphological adaptations on water movement and sediment trapping (Koch et al., 2009), which may vary with geomorphology (Carmen et al., 2016). On one hand, the flexibility and length of *Cymodocea* spp. leaves in the water column, coupled with its dense rooting systems is more efficient at increasing sediment deposition from the water column and sediment retention and stabilization in the soil compared to smaller stature species, with small leaves and shallow roots such as *Halophila* and *Halodule* seagrasses. However, the low near-surface C_{org} observed in the top 15 cm of soil the *Cymodocea* meadow at Eagle Bay may be due to its relatively recent formation compared to older *Cymodocea* meadows at Chek Jawa and Pulau Semakau; or due to large inputs of sediments of low organic matter content due to nearby coastal development works, such as at Cyrene Reef. On the other hand, despite the small stature of *Halodule* and *Halophila* species, the pioneer communities can also further reduce water movement, promote sedimentation and bury carbon in the same manner as comparatively larger stature seagrasses (Fonseca, 1989). Although, some have argued that the presence of pioneer seagrass communities is coincident with carbon-rich soils, given their physiological predisposition to thrive in naturally depositional environments (Lavery et al., 2013).

The biomass C_{org} reported in this study (0.4 Mg C_{org} ha^{-1} ± 0.40) was within the range of previous estimates for Singapore (0.02–1.4; Phang et al., 2015; Saavedra-Hortua et al., 2020) and lower than the global mean (2.51 Mg C_{org} ha^{-1} ± 0.49; Fourqurean et al., 2012). The low biomass C_{org} is as a result of the dominance of smaller-stature seagrass communities around Singapore compared to larger stature species such as *Zostera marina* and *Posidonia oceanica*, upon which the global estimates are largely based. Expectedly, large-stature species such as *Cymodocea rotundata/serrulata* and *Thalassia hemprichii* showed greater above- and belowground C_{org}.

Table 2

Summary of univariate regression models between the near-surface C_{org} stocks and meadow-related and edaphic characteristics across meadow typologies. Significant models are highlighted in bold.

Meadow Characteristic	Estuary (df = 1,20)	Lagoonal (df = 1,21)	Reef-associated (df = 1,29)
Seagrass Cover[a]	**F = 5.14, p = 0.03** **R = -0.49, r^2 = 0.21**	F = 2.06, p = 0.17 R = −0.30, r^2 = 0.09	F = 1.77, p = 0.19 R = −0.24, r^2 = 0.06
Standing Biomass	F = 0.19, p = 0.67 R = 0.10, r^2 = 0.01	**F = 4.73, p = 0.04** **R = 0.43, r^2 = 0.18**	F = 0.18, p = 0.67 R = −0.08, r^2 = 0.06
Shoot Density	F = 0.32, p = 0.58 R = −0.12, r^2 = 0.02	F = 0.05, p = 0.83 R = −0.05, r^2 < 0.01	**F = 5.37, p = 0.03** **R = -0.40, r^2 = 0.16**
Organic Matter[a]	F = 2.98, p = 0.10 R = 0.36, r^2 = 0.13	F = 0.26, p = 0.62 R = 0.11, r^2 = 0.01	**F = 65.61, p < 0.01** **R = 0.84, r^2 = 0.70**
Dry Bulk Density	F = 1.51, p = 0.23 R = 0.26, r^2 = 0.07	**F = 18.64, p < 0.01** **R = 0.69, r^2 = 0.47**	**F = 30.44, p < 0.01** **R = -0.72, r^2 = 0.52**
Median Grain Size	F = 0.02, p = 0.88 R = 0.03, r^2 < 0.01	**F = 7.81, p < 0.01** **R = -0.52, r^2 = 0.27**	**F = 25.74, p < 0.01** **R = 0.69, r^2 = 0.48**
Aboveground C_{org}	F = 0.05, p = 0.83 R = −0.05, r^2 < 0.01	F = 3.27, p = 0.09 R = 0.37, r^2 = 0.14	F = 1.60, p = 0.22 R = −0.23, r^2 = 0.05
Belowground C_{org}	F = 1.31, p = 0.27 R = 0.25, r^2 = 0.06	F = 3.90, p = 0.06 R = 0.40, r^2 = 0.16	F = 0.05, p = 0.82 R = −0.04, r^2 < 0.01

[a] Square-root transformed; df = degrees of freedom.

4.2. *Relationship between seagrass meadow biotic and abiotic characteristics with soil C_{org}*

Near-surface C_{org} stocks varied strongly with edaphic parameters but weakly with meadow-related parameters. Under estuary settings, seagrass cover, which is dominated by pioneer species, weakly predicted near-surface C_{org}, supporting the hypothesis that pioneer seagrass communities may be coincident with carbon rich soil. For lagoonal meadows, dry bulk density was a strong predictor of near-surface C_{org}, where increasing soil density suggests decrease in soil porosity, permeability and ventilation, favouring carbon burial, which as also seen in other blue carbon ecosystems (e.g. Cacho et al., 2021). In contrast, under reef-associated settings, increasing density soil suggested decreasing near-surface C_{org}. However, the strong positive effect of soil organic matter on near-surface C_{org} in reef-assoicated settings may be masking the effect of soil density, ultimately favouring a high carbon stocks.

Taken together, our analysis highlights the importance of landscape configuration in affecting blue carbon processes and showcases the potential of dry bulk density and organic matter content as good predictors of near-surface C_{org}, as well as complexity of estimating C_{org} across a range of geomorphic. This is particularly important when considering scaling up carbon estimates.

5. Conclusions

This study assessed near-surface C_{org} along geomorphic gradients across the Singapore seagrass landscape. The results highlight the importance of reef-associated meadows as important sinks of blue carbon, the potential for lagoonal meadows to store significant amounts of carbon, as well as the importance in considering landscape configuration in blue carbon assessments. Near-surface C_{org} in estuary and unvegetated may represent background levels of carbon against which comparisons can be made. The variability in near-surface C_{org} is likely influenced by the interactions between species, edaphic conditions and geomorphic setting. More broadly, this study fits into the emerging framework of higher resolution blue carbon assessment to better understand local and regional variability, informing carbon accounting efforts, and guiding conservation policy. Additionally, management strategies for greenhouse gas mitigation should incorporate this variability into models which estimate carbon based on key predictor values such as organic matter.

CRediT authorship contribution statement

JA: Conceptualisation, methodology, formal analysis, investigation, data curation, writing – original draft, writing – reviewing and editing, visualisation, project administration; SY: Conceptualisation, methodology, writing: original draft, writing: reviewing and editing; visualisation; EY: data curation, writing: original draft, writing: reviewing and editing; RL: formal analysis, data curation, writing: original draft, writing: reviewing and editing; JYP and CCL: Data curation, writing: reviewing and editing; DF: Conceptualisation, formal analysis, writing: original draft, writing – review and editing, funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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