OPEN

High variability of Blue Carbon storage in seagrass meadows at the estuary scale

Aurora M. Ricart[1,2*], Paul H. York[3], Catherine V. Bryant[3], Michael A. Rasheed[3], Daniel Ierodiaconou[4] & Peter I. Macreadie[4]

Seagrass meadows are considered important natural carbon sinks due to their capacity to store organic carbon (C_{org}) in sediments. However, the spatial heterogeneity of carbon storage in seagrass sediments needs to be better understood to improve accuracy of Blue Carbon assessments, particularly when strong gradients are present. We performed an intensive coring study within a sub-tropical estuary to assess the spatial variability in sedimentary C_{org} associated with seagrasses, and to identify the key factors promoting this variability. We found a strong spatial pattern within the estuary, from 52.16 mg C_{org} cm^{-3} in seagrass meadows in the upper parts, declining to 1.06 mg C_{org} cm^{-3} in seagrass meadows at the estuary mouth, despite a general gradient of increasing seagrass cover and seagrass habitat extent in the opposite direction. The sedimentary C_{org} underneath seagrass meadows came principally from allochthonous (non-seagrass) sources (~70–90 %), while the contribution of seagrasses was low (~10–30 %) throughout the entire estuary. Our results showed that C_{org} stored in sediments of seagrass meadows can be highly variable within an estuary, attributed largely to accumulation of fine sediments and inputs of allochthonous sources. Local features and the existence of spatial gradients must be considered in Blue Carbon estimates in coastal ecosystems.

Seagrass ecosystems are among the most significant natural carbon sinks worldwide, since they can sequester significant amounts of carbon, store it as organic carbon (C_{org}) in the sediments for long periods of time, and have a worldwide distribution[1–3]. It is estimated that seagrass ecosystems store globally up to 19.9 petagrams (Pg) of C_{org} in sediments[2], or between 4.2 and 8.4 Pg of C_{org} from a more conservative approach[2], where C_{org} could be stored in sediments for hundreds of years and even millennia[4].

Due to the high mitigation potential for seagrass ecosystems to help offset carbon dioxide (CO_2) emissions, there has been a major effort in recent years to improve the accuracy of estimates of carbon stored in seagrass sediments, and so, include seagrass ecosystems within greenhouse gases (GHG) abatement schemes[5,6]. Consequently, an increasing number of studies have attempted to quantify sedimentary C_{org} stocks associated with seagrass meadows from direct measurements[7–9], demonstrating an enormous variability in the seagrass sedimentary C_{org} stocks reported worldwide.

Variability of sedimentary C_{org} stocks has been associated with multiple interrelated biological and environmental factors: type of seagrass species[7], depth and light availability[10,11], landscape configuration[12], physical disturbances[13], wave height and turbidity[14], and even faunal presence such as bioturbators and top predators[15,16]. Most of these studies highlighted the type of carbon sources and the sediment grain size as the main factors influencing carbon storage in seagrass sediments, suggesting that the processes affecting these factors explain the high variability found in seagrass sedimentary C_{org} stocks[17].

Variability in seagrass sedimentary C_{org} stocks has been described at a range of spatial scales: from cm and meters, at the seagrass patch and meadow scale[18–20] to bioregions and latitudinal scales[7,9]. Studies at small scales (up to ~1's km) have shown how sedimentary C_{org} can be spatially distributed inside seagrass meadows[18,20,21]. However, in studies at higher spatial scales (~100's to ~1000's km), comparisons and estimates are usually made based on a relatively low number of sediment cores from each site[22–24], therefore, not accounting for the potential

[1]Bodega Marine Laboratory- Department of Earth and Planetary Sciences, University of California Davis, Davis, USA. [2]Departament de Biologia Evolutiva, Ecologia i Ciències ambientals, Universitat de Barcelona, Barcelona, Spain. [3]Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, Australia. [4]School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Burwood, Australia. *email: amricart@ucdavis.edu

spatial variability in seagrass sedimentary C_{org} stocks among meadows in the same area. Just a few studies focus on the variability at intermediate spatial scales (~10′s km), comparing among seagrass meadows within a local system[14,25,26], such as estuaries, where seagrasses can make up a large proportion of available habitat[27].

Estuaries are dynamic transition zones acting as pathways for the transfer of sediments and organic materials from land to the sea. Estuaries are characterized by a high variability in geo-morphology, and the presence of spatial gradients, influenced by large tidal cycles, longer water residence times and poorer mixing compared to the open ocean. Carbon fluxes to estuarine sediments can be conceptualized in two main axes[28]. The horizontal axis is determined by a hydrodynamic control, exerted between the river and the ocean and/or following estuary geo-morphology, where terrestrial carbon is directly delivered and rapidly deposited in the sediments[29], thus creating a strong spatial gradient of C_{org} in sediments from the upper parts of the estuary to the ocean. The vertical axis is determined by a biological control, where C_{org} in sediments is the result of direct deposition and burial of *in situ* photosynthetic production between the surface (i.e. phytoplankton) and the benthos (i.e. seagrasses and/ or algae if present). The prevalence of one control or the other will largely determine the magnitude and origin of C_{org} stocks in the sediments within estuaries, and also its spatial distribution, thus, expecting a more homogeneous spatial distribution of C_{org} in sediments of seagrass meadows with a prevalence of biological control, and a more heterogeneous distribution where hydrodynamic control dominates.

Variation also exists among and within estuaries, in terms of turbidity and water flow, which may determine seagrass meadows' habitat extent or landscape configuration[30,31] and also species composition and structural traits, such as shoot density and cover[32]. Other coastal vegetated habitats, such as mangroves and saltmarshes can be present in estuaries also contributing to C_{org} stocks[33,34] and to seagrass sedimentary C_{org} stocks[35]. Variation is also reflected in sedimentation rates, which can be influenced by seagrass canopies trapping particulate organic materials, thus decreasing turbidity and increasing sedimentary C_{org} stocks[36]. Some of these factors may determine spatial patterns of C_{org} storage in sediments of seagrass meadows. However, despite the large number of studies that have appeared recently providing empirical evidence of processes explaining C_{org} storage in seagrass sediments, there are a lack of studies providing the spatial component needed to improve accuracy of Blue Carbon assessments, particularly at the within estuary scale. The current work aimed to contribute to understanding the spatial variability of C_{org} storage in seagrass sediments by providing a comprehensive assessment of the spatial distribution of sedimentary C_{org} stocks and carbon sources in seagrass meadows within a coastal plain estuary and exploring the site-specific factors driving the patterns found.

We expected that sedimentary C_{org} storage in seagrass meadows within the estuary will present a high spatial heterogeneity due to the presence of spatial gradients of environmental and biological factors. Therefore, we investigated how sediment C_{org} content (%), C_{org} stocks (mg C_{org} cm^{-3}) and carbon sources (δ^{13}C) vary as a function of seagrass cover, meadow extent or landscape configuration (hereinafter "meadow type"), sediment particle size, water turbidity and the proximity to mangroves, as the main environmental and biological factors present within the estuary studied that have been already described to be affecting C_{org} storage in seagrass sediments[12,14,26]. Specifically, we hypothesized that (1) seagrass sedimentary C_{org} storage will increase with seagrass cover and will be higher in continuous meadows due to a greater accumulation of seagrass carbon sources and fine sediments; (2) proximity to mangroves and a higher water turbidity will increase sedimentary C_{org} storage due to higher contribution of allochthonous carbon sources.

Results

All sediment parameters and environmental and biological drivers are summarized in Table 1. The sediment C_{org} content in seagrass meadows within the estuary ranged from 0.08% to 6.01%, and C_{org} stocks ranged from 1.06 mg C_{org} cm^{-3} to 52.16 mg C_{org} cm^{-3}, where in both cases the lowest values were found in seagrass meadows at the mouth of the estuary and the highest values in seagrass meadows at the upper estuary reaches. Values of δ^{13}C were in general highly depleted along the estuary, from −18.32‰ to −26.20‰, with enriched (more positive) values in sediments of seagrass meadows at the mouth of the estuary and more depleted values in sediments in the upper estuary. Similar patterns were found at all depths analysed. All three sediment carbon variables assessed presented spatial autocorrelation on the original data (Moran I test p < 0.01; Supplementary Table S1). Sediment dry bulk density ranged from 0.38 g cm^{-3} to 3.08 g cm^{-3}, with the lowest values in seagrass meadows at the upper parts of the estuary and the highest in seagrass meadows at the mouth. The proportion of fine sediments (<63 μm) ranged from 3.16% to 93.92%, with the lowest values in seagrass meadows at the mouth of the estuary and the highest in seagrass meadows at the upper estuary.

The non-spatial GLS models (except those with meadow type as explanatory variable and those assessing C_{org} (%) with proportion of fine sediments) presented spatial autocorrelation on the residuals (Moran I p < 0.01, Supplementary Table S2), showing that the explanatory variables were not removing the effect of spatial dependence among samples, and that error correlation structures were then necessary. All the spatial GLS models, except some cases assessing δ^{13}C in core section 1–3 cm, did not present spatial autocorrelation in the residuals (Moran I p > 0.01, Supplementary Table S2). We will therefore describe just the results from spatial GLS models when spatial autocorrelation was removed by the correlation structure (Table 2).

The C_{org} (%) content in the sediment for all core sections was positively related with the proportion of fine fraction of sediments (Fig. 1a, p ≤ 0.02, Table 2). The C_{org} stocks (mg C_{org} cm^{-3}) in the sediment for all core sections were significantly related to meadow type (p ≤ 0.02, Table 2). The highest C_{org} stocks were associated with continuous meadow types and patchy meadows, although there was a high variability present in patchy meadows as shown by the model estimates' standard errors and confidence intervals (Supplementary Table S3, Fig. 1b). The δ^{13}C values in the sediments for all core sections were significantly related to meadow type, turbidity and seagrass cover (p ≤ 0.01, Table 2). The most depleted values were associated with patchy meadows (Fig. 2a) and to high water turbidity (Fig. 2b); and these were positively related with seagrass cover (Fig. 2c).

Site	Environmental and Biological drivers					Sediment parameters									
	Seagrass species and number of cores sampled in brackets	Seagrass cover (%)	Meadow type	Turbidity level	Distance to mangroves (m)	<63 µm (%)		DBD (g cm⁻³)		C_{org} (%)		$\delta^{13}C$ (‰)		C_{org} stocks (mg C_{org} cm⁻³)	
Redcliffe	*Z. muelleri* (1); *H. ovalis* (1); *H. decipiens* (1)	0–1	patchy	high	140–140	80.17	85.19	0.38	0.87	2.81	6.01	−26.00	−24.46	12.91	52.16
Black Swan	*Z. muelleri* (3)	0–10	patchy	high	200–300	27.82	75.92	0.86	1.48	0.87	2.92	−25.67	−24.72	11.26	35.58
Fishermans Landing	*Z. muelleri* (2); *H. ovalis* (1)	0–1	patchy	medium	515–565	47.16	85.47	0.82	1.47	0.44	2.51	−25.37	−23.32	4.60	25.11
Channel Islands	*Z. muelleri* (3)	5–20	patchy	medium	100–200	8.29	35.60	1.25	2.97	0.28	2.03	−25.09	−22.51	4.55	31.81
Wiggins Island	*Z. muelleri* (3)	0–10	patchy	high	610–680	50.62	73.73	0.90	1.45	0.19	0.99	−24.10	−22.99	2.08	10.79
Grahams Creek	*H. decipiens* (3)	0–5	patchy	high	35–35	56.37	93.92	0.71	1.04	1.50	4.55	−26.20	−25.29	11.61	33.84
Pelican Banks South 1	*Z. muelleri* (3)	0–15	continuous	medium	3500–3500	9.49	12.47	1.38	2.12	0.39	1.45	−22.07	−20.90	7.07	21.62
Pelican Banks South 2	*Z. muelleri* (2); *H. ovalis* (1)	10–20	continuous	medium	3400–3400	7.73	11.56	1.37	1.93	0.37	2.08	−21.83	−19.11	5.21	34.57
Pelican Banks North 1	*Z. muelleri* (3)	30–65	continuous	low	1230–1230	13.69	16.55	1.13	1.83	0.44	1.03	−19.99	−18.51	5.96	17.15
Pelican Banks North 2	*Z. muelleri* (3)	45–70	continuous	low	1120–1120	15.02	18.43	1.06	1.63	0.39	1.17	−19.44	−18.61	5.65	12.41
Facing Island	*Z. muelleri* (2); *H. ovalis* (1)	0–5	patchy	medium	3255–3280	7.45	28.87	1.25	1.91	0.24	1.42	−23.35	−19.87	4.47	19.67
Pelican Banks North 3	*Z. muelleri* (3)	57–60	continuous	low	1950–1950	9.91	16.11	1.33	1.75	0.3	1.72	−19.17	−18.32	4.70	24.86
South Trees	*Z. muelleri* (3)	0–1	variable	medium	150–250	5.96	17.71	1.12	1.95	0.18	1.57	−24.11	−20.44	3.49	17.52
Boyne Island	*H. uninervis* (3)	2–10	variable	medium	1000–1025	3.16	3.45	1.07	3.08	0.08	0.25	−22.89	−20.43	1.06	3.68
South Facing Island	*Z. muelleri* (3)	0–10	variable	medium	250–250	12.50	17.35	1.45	2.54	0.09	1.41	−21.99	−20.40	1.30	22.18

From land to the ocean →

Table 1. Environmental and biological drivers, and sediment parameters. A total of 45 cores were collected in 15 sites along the estuary. For summary purposes data is shown per site but cores are treated independently on the spatial GLS models applied. Data show ranges of minimum and maximum values or category of each variable.

The mixing models applied indicated that allochthonous, non-seagrass, sources were the most important source of sediment C_{org} (contribution range from 58% to 92%; Table 3), followed by seagrass (contribution range from 8% to 42%; Table 3). In general, seagrass presented a minor contribution to sedimentary C_{org} stocks along the estuary (~8 mg C_{org} cm⁻³) (Fig. 3), although this contribution increased in the lower regions of the estuary (up to ~20 mg C_{org} cm⁻³), coincident with the presence of the largest seagrass meadows in the estuary (Table 1). The contribution from adjacent habitat sources and marine algae was higher (~35 mg C_{org} cm⁻³ on average) and also decreasing along a gradient from the upper (with up to ~92 mg C_{org} cm⁻³) to the lower parts of the estuary (Fig. 3).

Predicted seagrass C_{org} stocks within the estuary were five times higher in the upper regions than in the lower regions, with C_{org} stocks ranging from 25 Mg C_{org} ha⁻¹ to 5 Mg C_{org} ha⁻¹ in the first 10 cm of sediment (Fig. 4).

Discussion

The distribution of sedimentary C_{org} storage in seagrass meadows within the Port Curtis estuary, Queensland, Australia, was spatially heterogeneous, following a general pattern of higher C_{org} accumulation in sediments of seagrass meadows in the upper reaches of the estuary than in seagrass meadows at the estuary mouth. Contrary to our expectations, seagrass sedimentary C_{org} content (%) or C_{org} stocks (mg C_{org} cm⁻³) did not increase with seagrass cover. Although, C_{org} content (%) was significantly related with a higher proportion of fine sediments and sedimentary C_{org} stocks (mg C_{org} cm⁻³) were related with the meadow type. Water turbidity was related with carbon sources, as well as seagrass cover and meadow type. Thus, a higher seagrass contribution was found in sedimentary C_{org} in continuous meadows, which also presented higher seagrass cover and low water turbidity. Despite this, the contribution from seagrasses (as a source) to C_{org} stored in sediments was still very low through all seagrass meadows in the estuary. Overall, sedimentary C_{org} storage in seagrass meadows within the estuary studied seems to be governed by the accumulation of fine sediments and allochthonous carbon sources along a gradient from land to the ocean, suggesting that these patterns should be considered when quantifying C_{org} stocks at similar scales.

Sedimentary C_{org} beneath seagrass meadows in the upper parts of the estuary, were more than ten times higher than in the lower estuary. The highest values in the upper estuary are comparable to those from long-lived seagrass species of the *Posidonia* genus, while values for the same seagrass species (*Zostera muelleri*) in the lower estuary are comparable to other fast-growing seagrass species[7] including those from estuaries within the same region[14,37]. The strong spatial gradient on sedimentary C_{org} stocks in seagrass meadows exerted from the upper to the lower estuary suggests that the estuary studied is governed by a strong hydrodynamic control of carbon

Depth	Dependent variable / Driver	C_{org} (%) ΔAIC	Estimate	SE	C stocks (mg C_{org} cm^{-3}) ΔAIC	Estimate	SE	δ^{13}C (‰) ΔAIC	Estimate	SE
	Driver	ΔAIC	Estimate	SE	ΔAIC	Estimate	SE	ΔAIC	Estimate	SE
0–1 cm	Seagrass cover*	38.75	0.00	0.00	30.61	0.00	0.00	**63.93**	**0.03**	**0.01**
	<63 μm*	**12.28**	**0.01**	**0.00**	18.44	0.00	0.00	47.21	−0.01	0.01
	Distance from mangroves*	36.74	0.00	0.00	33.64	0.00	0.00	71.45	0.00	0.00
	Turbidity (low)	22.78	0.55	0.34	19.26	2.23	0.64	**36.68**	**−20.14**	**0.83**
	Turbidity (medium)	22.78	−0.20	0.27	19.26	−0.12	0.29	**36.68**	**−2.09**	**0.42**
	Turbidity (high)	22.78	0.42	0.39	19.26	0.16	0.40	**36.68**	**−4.05**	**0.57**
	Meadow type (continuous)	24.38	0.51	0.47	**5.34**	**2.52**	**0.17**	24.64	−19.94	0.96
	Meadow type (patchy)	24.38	0.42	0.55	**5.34**	**0.20**	**0.24**	24.64	−4.55	1.11
	Meadow type (variable)	24.38	−0.19	0.56	**5.34**	**−0.90**	**0.27**	24.64	−1.12	1.24
1–3 cm	Seagrass cover*	28.51	0.00	0.00	7.64	0.00	0.01	**61.09**	**0.04**	**0.01**
	<63 μm*	**8.06**	**0.01**	**0.00**	3.21	0.01	0.00	48.06	0.00	0.01
	Distance from mangroves*	30.54	0.00	0.00	8.57	0.00	0.00	60.62	0.00	0.00
	Turbidity (low)	17.52	0.34	0.32	9.27	1.61	1.29	**29.26**	**−19.11**	**0.76**
	Turbidity (medium)	17.52	0.12	0.27	9.27	0.44	0.40	**29.26**	**−2.95**	**0.87**
	Turbidity (high)	17.52	0.67	0.38	9.27	0.50	0.51	**29.26**	**−5.93**	**0.95**
	Meadow type (continuous)	19.21	0.46	0.43	**2.87**	**2.47**	**0.20**	21.41	−19.95	0.46
	Meadow type (patchy)	19.21	0.50	0.50	**2.87**	**0.21**	**0.27**	21.41	−4.71	0.62
	Meadow type (variable)	19.21	−0.19	0.52	**2.87**	**−0.65**	**0.31**	21.41	−1.67	0.74
3–10 cm	Seagrass cover*	26.84	−0.01	0.00	13.19	−0.01	0.01	**48.87**	**0.04**	**0.01**
	<63 μm*	**8.94**	**0.01**	**0.00**	9.92	0.00	0.00	55.64	0.00	0.01
	Distance from mangroves*	27.19	0.00	0.00	11.85	0.00	0.00	69.80	0.00	0.00
	Turbidity (low)	16.28	0.38	0.31	13.04	1.62	1.53	**31.19**	**−18.97**	**1.10**
	Turbidity (medium)	16.28	0.19	0.27	13.04	0.63	0.48	**31.19**	**−3.74**	**1.15**
	Turbidity (high)	16.28	0.56	0.37	13.04	0.38	0.61	**31.19**	**−5.95**	**1.29**
	Meadow type (continuous)	16.56	0.45	0.42	**6.94**	**2.60**	**0.24**	36.75	−20.34	0.80
	Meadow type (patchy)	16.56	0.49	0.49	**6.94**	**0.12**	**0.33**	36.75	−4.47	0.95
	Meadow type (variable)	16.56	−0.19	0.47	**6.94**	**−0.89**	**0.37**	36.75	−1.69	1.08

Table 2. Coefficient estimates for carbon sediment variables in the GLS spatial models. Significant terms (p-value < 0.05) are shown in bold. ΔAIC represents the AIC difference between the non-spatial GLS and the spatial GLS accounting for spatial autocorrelation on the response variable; positive value means lower AIC on the spatial GLS model. SE, standard error. (*) shows continuous explanatory variables.

deposition processes[28]. Therefore, it is likely that a higher deposition of fine sediments, carrying particulate organic materials through freshwater inputs (e.g. land runoff), is occurring in the upper parts of the estuary. This explains the higher carbon levels in these seagrass meadows and is corroborated also by the more depleted values of δ^{13}C in these areas[38]. These results highlight the necessity to account for spatial gradients when assessing C_{org} stocks within estuaries to adequately account for the variability present. Our results also support that spatial autocorrelation is an important consideration when assessing drivers of C_{org} stocks where strong spatial gradients are present[20].

Among the main environmental and biological factors explaining the variability found within the estuary, the proportion of fine sediments appeared as the only significant explanatory variable for C_{org} content (%) in sediments. Seagrass sediment carbon storage has been widely related with a high proportion of fine sediments[12,39] as fine sediments will slow down decomposition processes by avoiding oxygenation[40]. In agreement with our results, recent studies suggest that in fast growing seagrass species, such as the ones in this study, this relationship is even stronger when the contribution of seagrass-derived carbon to the sedimentary C_{org} pool is relatively low[41].

Seagrass meadow type (i.e. landscape configuration) was among the main factors associated with sedimentary C_{org} stocks (mg C_{org} cm^{-3}) and carbon sources within the estuary. As shown by the spatial models applied C_{org} stocks were positively related with continuous seagrass meadows and negatively related with variable non-permanent meadows, while results on patchy meadows were uncertain due to the high variability present. In fact, in the different patchy meadows sampled in this study, sedimentary C_{org} storage varied by one order of magnitude depending on the location within the estuary. In addition, the cores with the highest records of C_{org} stocks on this study were from patchy meadows in the upper extreme of the estuary, demonstrating that the spatial
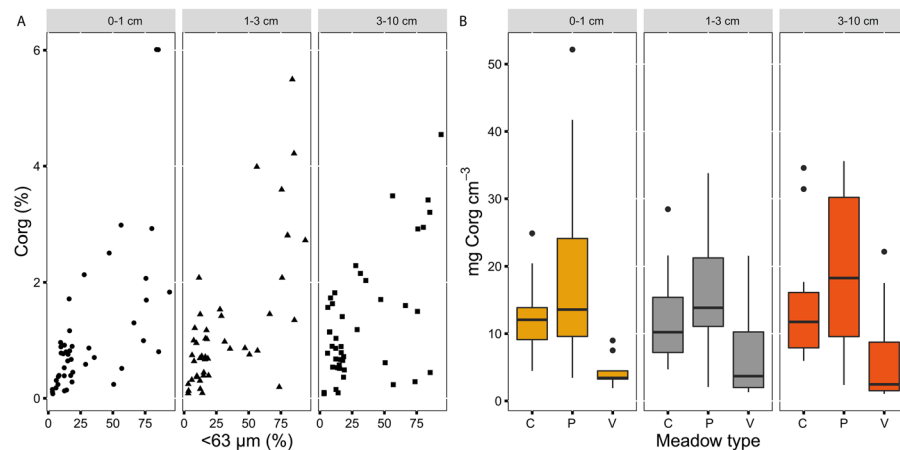
Figure 1. Relationships among sediment carbon variables and drivers per each depth core section. (**a**) Biplot of C_{org} content (%) and sediment grain size <63 µm (%); (**b**) Boxplot of C_{org} stocks (mg C_{org} cm^{-3}) and meadow type. Symbols for grain size: circle, depth section 0–1 cm; triangle, depth section 1–3 cm; quadrat, depth section 3–10 cm. Legend for meadow type: C, permanent continuous meadows; P, permanent patchy meadows; V, variable meadows.
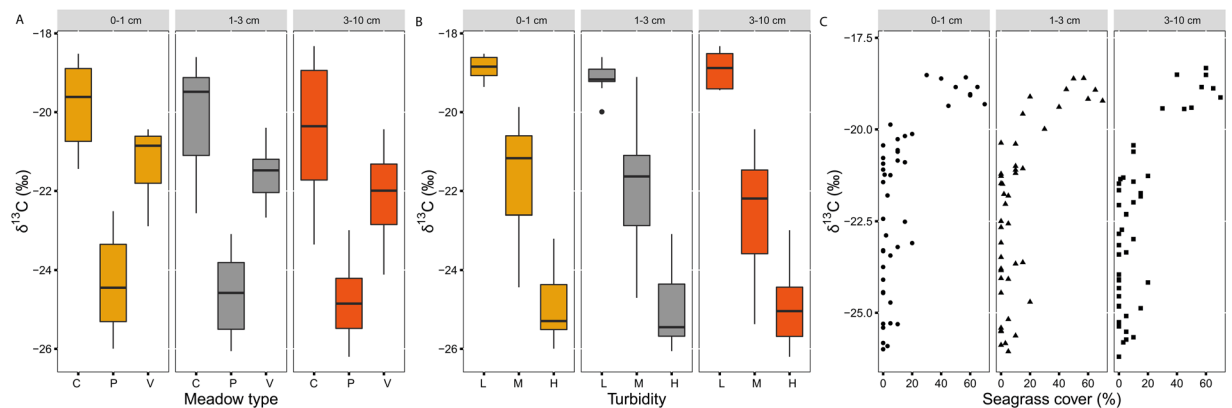

Figure 2. Relationships among sediment carbon sources and drivers per each depth core section. (**a**) Boxplot of δ^{13}C (‰) and meadow type; (**b**) Boxplot of δ^{13}C (‰) and turbidity; (**c**) δ^{13}C (‰) and seagrass cover. Legend for meadow type: C, permanent continuous meadows; P, permanent patchy meadows; V, variable meadows. Legend for water turbidity: H, high; M, medium; L, low. Symbols for seagrass cover: circle, depth section 0–1 cm; triangle, depth section 1–3 cm; quadrat, depth section 3–10 cm.

location of seagrass meadows within the estuary matters in Blue Carbon assessments. On the other hand, continuous meadows showed a low variability in sedimentary C_{org} stocks, and a higher contribution from seagrass sources. This could be related to higher, and probably more constant, burial of seagrass-derived carbon in continuous meadows, compared to patchy and non-permanent variable meadows, promoting more accumulation and burial of seagrass-derived material[18], that are generally less labile and will decompose at lower rates promoting long lasting C_{org} stocks[42]. This relationship could also be related with the capacity of seagrass meadows to avoid resuspension and mixing of sediments[36,43–45], which is presumably higher in continuous meadows[18]. This fact is also corroborated by the positive relationship found here among seagrass cover and carbon isotopic signature, and the low isotopic signature of C_{org} in patchy and non-permanent variable seagrass meadows suggesting less seagrass contribution in these meadows.

Although we found a significant relationship between carbon sources and water turbidity, but not water turbidity and C_{org} stocks (mg C_{org} cm^{-3}), our results support the hypothesis[14] that high sediment carbon storage occurs in areas of high turbidity due to high levels of allochthonous carbon. High water turbidity was related with depleted values of δ^{13}C, suggesting a high contribution of allochthonous sources, while low water turbidity was related with δ^{13}C values close to seagrass sources. The latter suggests two potential mechanisms: (1) in low turbidity conditions, higher levels of light promote seagrass growth, and so, more seagrass contribution to sediment C_{org}; and (2) that the seagrass canopies filtering capacity decreases water turbidity, thus relating seagrass contribution and low turbidity (see also results for seagrass cover and meadow type). In fact, low water turbidity occurred only in areas with presence of continuous seagrass meadows. However, in this study we did not assess
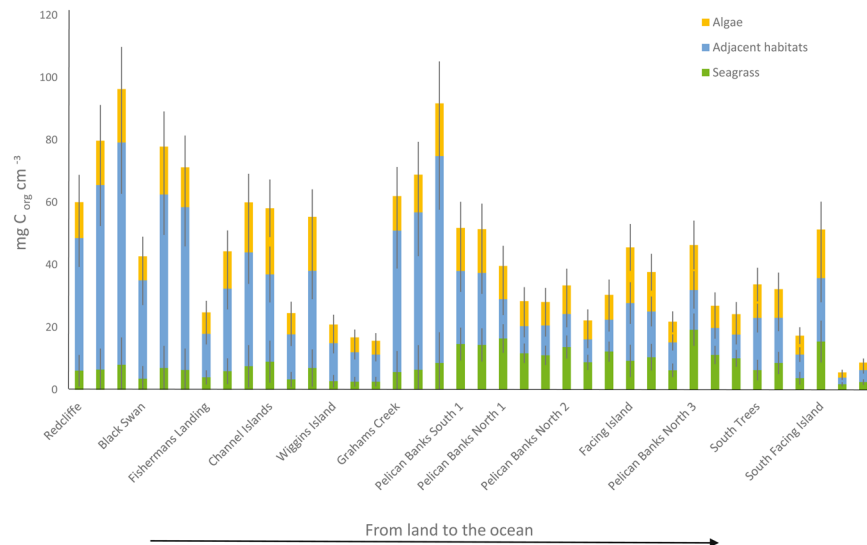
Figure 3. Contribution of the different carbon sources to total sediment C_{org} stocks (mg C_{org} cm^{-3}) of seagrass meadows on each core within the estuary. Sources: adjacent habitats sources (including mangroves and saltmarshes); marine algae (including benthic algae and seston); seagrass sources. This figure is based on the mean results and standard deviation of each source fraction from mixing models (see Table 3). Total sediment C_{org} stocks (mg C_{org} cm^{-3}) represent the cumulative amount of C_{org} on each 10 cm depth core.

	Adjacent habitats (mangroves & saltmarshes)	Algae (benthic algae & seston)	Seagrass	Allochthonous sources	Autochthonous sources
Mean	50.57	26.65	22.79	77.21	22.79
SD	15.50	5.50	12.37	12.37	12.37
Min	27.45	17.59	8.12	58.39	8.12
Max	74.07	39.04	41.61	91.88	41.61

Table 3. Results from the mixing models. Values represent summary statistics of the proportion (%) of each source (mean, standard deviation and range by minimum and maximum values). Autochthonous sources represent the seagrass contribution, while allochthonous sources represent the sum of non-seagrass sources.

the relative importance of each driver compared to the others, making it difficult to make conclusions about the particular processes involved, which should be further studied. In addition, if measured during the rainy season, water turbidity could have led to different results in the surface sediments, by affecting seagrass physiology (e.g. photosynthetic processes), sedimentation and eventually C_{org} storage. Finally, despite the presence of mangroves being highlighted as an important factor promoting seagrass carbon storage in other studies[35], our results showed no relationship between proximity to mangroves and seagrass sedimentary C_{org} for any variable assessed, probably due to the low carbon exchange between those habitats within the estuary.

These results suggest that, within this estuary, the seagrass plant itself is not governing the amount of C_{org} stored in the sediment, and that multiple other interacting factors are involved (e.g. sediment deposition). Light availability is known to be a major control of seagrass growth[46] and seems to be dominating seagrass meadows distribution within the estuary. The upper parts of the estuary presented higher water turbidity, a low seagrass cover, and a higher presence of patchy meadows when compared with the lower parts of the estuary, usually with less turbid water, more seagrass cover and where continuous meadows are found. Although seagrass cover is usually associated with higher C_{org} storage[12], in this estuary, seagrass cover values found were small, and seagrass sedimentary C_{org} seems overwhelmingly driven by the proximity to the upper estuary. This leads to an inverse correlation between C_{org} and seagrass cover that we suggest is coincidental and driven by the light environment rather than a causal link between seagrass cover and low C_{org} storage.

In this study plant traits other than seagrass cover were not measured. However, annual seagrass monitoring in Port Curtis estuary since 2009 show that aboveground biomass follows the same spatial pattern as seagrass cover in the same study sites used here, ranging from 0.88 g DW m^{-2} in the upper estuary to 18.02 g DW m^{-2} in continuous meadows at the estuary mouth[47–49]. All seagrass species found in the estuary are considered fast growing, characterized by a small size and a small above- and below-ground fraction, with roots and rhizomes that do not penetrate deeper than the first few centimetres. This could be related with the small seagrass contribution to carbon storage found in this estuary. Small intra-specific or inter-specific variation in plant traits could potentially influence spatial patterns of carbon storage[14,20] and should be included in further studies.

Although seagrass cover was a determinant of the type of carbon sources entering into the sediments, the contribution of seagrasses as carbon sources along the estuary was low. The increase of seagrass contribution to
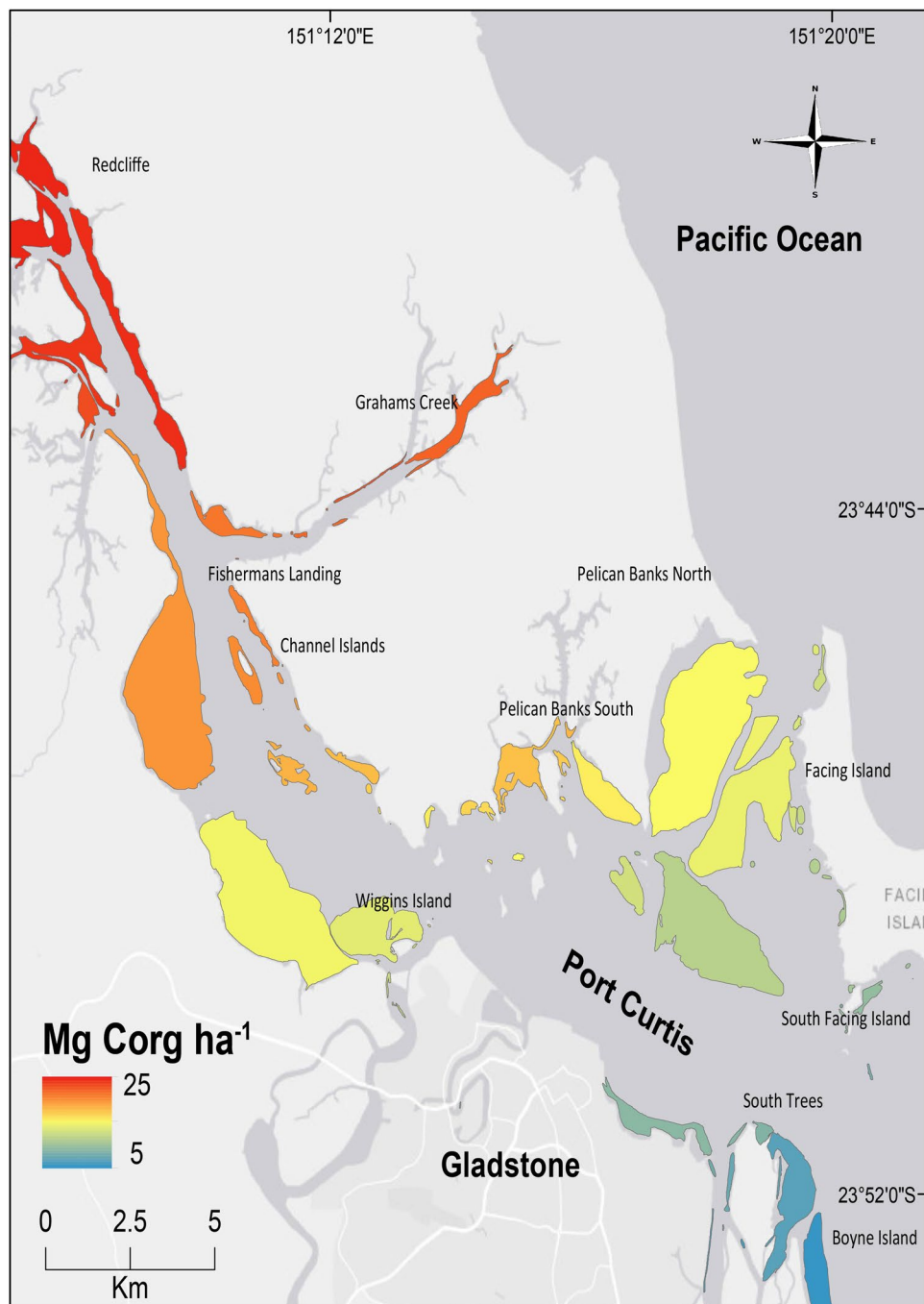
Figure 4. Predictive map of C_{org} stocks (Mg C_{org} ha^{-1}) in the first 10 cm of sediment of seagrass meadows within the Port Curtis estuary, Queensland, Australia, based on data from this study. The map was built using Esri ArcGIS 10.4 (www.esri.com/software/arcgis).

sedimentary C_{org} in the lower parts of the estuary could be related to a lower deposition of allochthonous carbon (compared to the upper parts), and also a major presence of continuous meadows that could facilitate the trapping and burial of seagrass materials into the sediments and a higher local production contributing autochthonous carbon[50]. Despite this, allochthonous sources were the most important contributors, and followed the same spatial pattern as C_{org} stocks within the estuary.

Overall, fine sediments and allochthonous carbon sources accumulating more in the upper parts of the estuary seem to be driving spatial heterogeneity found in sedimentary C_{org} storage in seagrass meadows within the estuary studied. This highlights the necessity to account for the river-ocean continuum gradients on Blue Carbon assessments within-estuaries. We therefore recommend, when assessing carbon stocks in seagrass meadows within estuaries, to identify the main sources of variation, and, in order to adequately capture the highest variability, sample sediments in different seagrass meadows following the main spatial gradients. Comprehensive and

accurate assessments of sediment C_{org} stocks are required to understand the role of estuaries as carbon sinks, and ultimately disentangle their total carbon budget and climate change mitigation potential.

Materials and methods

Study site and sampling design. The study was conducted in Port Curtis (23°46′57″S; 151°18′0″E), a macro-tidal estuary on the central Queensland coast of north-eastern Australia. Port Curtis is a large natural harbour that has been industrialized and urbanized over the last half century. Despite this, much of it remains in a relatively natural state with a forested catchment dominating, and mangrove vegetation followed by saltmarshes landward of the mangroves in the upper estuary. The estuary contains large intertidal and subtidal sand and mud flats, which support seagrass meadows dominated mainly by the species *Zostera muelleri*, with *Halodule uninervis, Halophila decipiens, Halophila ovalis* and *Halophila spinulosa* also present. Seagrass appears sparsely distributed in the upper reaches of the estuary while meadows become larger (and more continuous) on the lower parts[47–49]. These relatively low cover seagrass meadows are typical of much of the tropical and sub-tropical Queensland coast where they play key roles in supporting megagrazers, such as dugong and green turtles, and as a fish habitat for juvenile commercial and recreationally important species[51].

To study the C_{org} storage variability of seagrass sediments within the estuary, and to identify the main factors promoting it, we sampled across all areas of seagrass distribution within the estuary (Fig. 5)[47,48]. We sampled a total of 45 sediment cores in order to cover the main environmental and biological gradients within the estuary. Thus, sediment cores were taken in 15 sites along the estuary in groups of three. In each site, cores were sampled with a minimum distance of 50 m among them and sampling all the seagrass species present inside each site in order to embrace all potential variability present (Table 1). Cores of sediments were sampled at low tide by manually inserting open-barrel PVC pipes (20 cm length, 5 cm internal diameter) into soils to a depth of 10 cm and using a piston to provide suction as cores were withdrawn. Compaction during coring was low (<10%). Once extracted, cores were capped at both ends and transported to the laboratory. Cores were kept upright during transport to prevent mixing of sediment layers within the core. GPS coordinates and a 50 × 50 cm photo quadrat were taken at each core location. Seagrass cover (%) and species composition in each quadrat were estimated visually following Seagrass-Watch percent cover standards[52].

Laboratory procedures. In the laboratory, the sediments were sliced into three sections at 0–1, 1–3, 3–10 cm intervals. Coarse inorganic particles (i.e. large carbonate materials) and living plant material were manually removed[7,9]. Depth sediment sections were dried at 60°C and weighed in order to calculate bulk density. Each depth section was then homogenized by mixing the sediments with a clean stainless-steel spoon thoroughly or until visually homogeneous, and split into two sub-samples, with grain size particle distribution analysed from the first subsample using a Malvern Mastersizer 2000 laser microgranulometer. Prior to grain size analysis, organic matter in this sub-sample was removed by addition of hydrogen peroxide 10%. Particle size distribution was expressed as percentage (%) of volume for particle diameters from 0 to 2000 μm. The second sub-sample was ground to a fine powder with a laboratory ball grinding mill and split again into two sub-samples for C_{org} and N elemental and isotopic analysis. Half were washed with acid for C_{org} analysis, and the other half remained untreated, as this chemical procedure has been reported to alter $\delta^{15}N$ values[53]. Sub-samples were acidified drop by drop with HCl 1M, until there was no visual evidence of effervescence to remove any carbonates and re-dried without rinsing[54,55]. After drying, samples were re-ground, placed in tin capsules and analysed for C_{org} and N elemental and isotopic composition. Measurements of C_{org} and N elemental composition and stable isotope ratios were performed using a continuous-flow isotope-ratio mass spectrometer MAT253 (Thermo Finnigan) coupled to an elemental analyser EA1108 (Carlo Erba Instruments) through a Conflo III interface (ThermoFinnigan). The C and N isotope ratios are expressed as δ values in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and the atmospheric air standard, respectively, according to standard notation ($\delta X = [(Rsample/Rstandard) − 1] \times 1000$, where R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$). International Atomic Energy Agency standards were inserted every 12 samples for calibration. Replicate assays of standards indicated measurement errors of ± 0.1 and ± 0.2 ‰ for C and N, respectively. Standing C_{org} stocks per volume unit were calculated using dry bulk density data and C_{org} content and expressed as mg C_{org} cm^{-3}.

Environmental and biological drivers of seagrass carbon storage. Environmental and biological drivers of seagrass carbon storage were characterized using categorical and numerical variables as a function of the seagrass cover, meadow type, sediment particle size, water turbidity and their proximity to other vegetated habitats such as mangroves (Table 1). We did not compare among the different seagrass species due to the low number of cores for some of them (Table 1) and cores from different species were integrated in data analysis (see below). Meadow type was classified based on definitions by[47,49] using three categories, permanent continuous meadows, permanent patchy meadows and variable meadows, the last defining non-permanent meadows that have been reported to appear intermittently as continuous or as isolated or aggregated patches. The proportion (%) of the smallest sediment fraction (silt and clay < 63 μm) was used for further statistical analysis. Water turbidity was classified using three categories, based on monthly averaged data from Gladstone Ports Corporation[56] in Nephelometric Turbidity Units (NTU) measured in the bottom of the water column during the dry season (May to October) where: low was <6 NTU, medium <7–15>, high 15 NTU>. Finally, we calculated the shortest distance from each core to mangroves using aerial photographs (Google Earth, 2013) and Euclidean distance measures representing shortest travel paths (ArcGIS 10.4; ESRI Software Inc).

Data analysis. Due to the potential presence of spatial gradients within the estuary and the grouped sampling of the sediment cores, we initially estimated the spatial autocorrelation in carbon sediment variables C_{org} (%), $\delta^{13}C$ (‰) and C_{org} stocks (mg C_{org} cm^{-3}) for each core depth section by calculating Moran I statistics. We
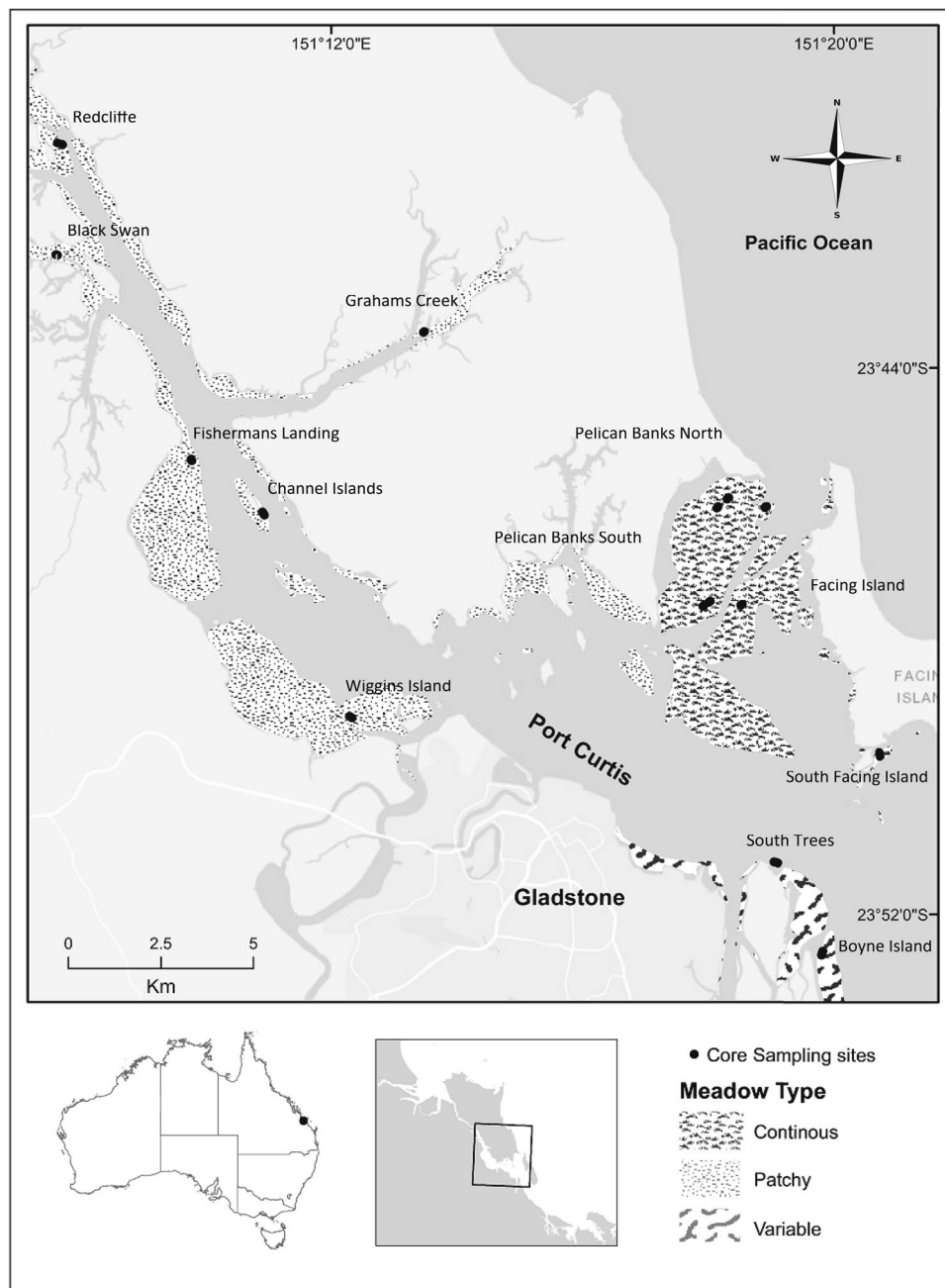
Figure 5. Map of the Port Curtis estuary, Queensland, Australia, and areas of seagrass distribution. Sediment core locations are indicated with black dots. The map was built using Esri ArcGIS 10.4 (www.esri.com/software/arcgis).

then used generalized least squares (GLS) to model carbon sediment variables for each core depth in relation to the environmental and biological explanatory variables (i.e. *seagrass cover (%), meadow type, <63 μm (%), distance to mangroves (m)* and *turbidity)*. Each explanatory variable was assessed individually in separate models given the high correlation among them. All GLS models were developed with and without spatial correlation structure in the error term of the regression model (GLS spatial models and GLS non-spatial models, respectively) to model spatially autocorrelated residuals when present[57]. Exponential, rational quadratic, gaussian, linear and spherical correlation structures were assessed for each spatial GLS model. The best fitting model and correlation structure were defined by the minimum Akaike's Information Criterion (AIC)[58–61]. The non-spatial GLS model is equivalent to Ordinary Least Squares (OLS), and the spatial GLS extends OLS by providing for possibly unequal residual variances and covariance of residuals between locations[62]. Finally, we tested for spatially autocorrelated residuals visualizing semivariograms of normalized residuals and calculating Moran's I statistic for the GLS non-spatial and GLS spatial models. Normality and homoscedasticity were explored in final models via visual estimation of trends of model residuals (errors associated with homogeneity of variance, independence,

and normality). We also checked if the 95% confidence intervals for parameter estimates of numerical explanatory variables were reasonable or included zero, which indicates fitting problems[63]. We fit all the models using restricted maximum likelihood with the nlme package[64], and Moran tests and semivariograms were done with package ape[65] and spdep[66] in the R Statistical Computing Environment. Non-transformed values (means ± SE) are shown in the figures and tables. For all analyses, core section values of C_{org} (%) and C_{org} stocks (mg C_{org} cm^{-3}) were log transformed.

The Bayesian mixing model SIAR 4.2[67] in the R Statistical Computing Environment was used to estimate the contribution of potential sources to the sedimentary C_{org} pool. The model was run with two isotopes (δ^{13}C and δ^{15}N) and three sources (see Supplementary Fig. S1): seagrasses (δ^{13}C −12.94 ‰ ± 3.08 SD; δ^{15}N 4.06 ‰ ± 1.31 SD), adjacent habitat sources (including mangroves and saltmarshes) (δ^{13}C −26.23 ‰ ± 1.03 SD; δ^{15}N 3.4 ‰ ± 1.1 SD), and marine algae (including benthic algae and seston) (δ^{13}C −21.34 ‰ ± 3.29 SD; δ^{15}N 4.69 ‰ ± 1.47 SD). Isotopic signatures of sources were collected and averaged from previous studies in the same area (see Supplementary Table S4). Separate mixing models were computed for each core. The isotopic values for all sources were assumed to be constant for each model. We did not consider any fractionation with aging (0 ‰) in the model because previous studies suggest small diagenetic shifts for δ^{13}C and δ^{15}N during decomposition[68,69]. The proportion of each source on the mixing model outputs was used to calculate the total contribution of each source to the C_{org} stocks accumulated per core (the sum of mg C_{org} cm^{-3} in 10 cm of core depth).

Finally, to elaborate a predictive map of C_{org} stocks, and their variability, at the estuary scale the total C_{org} stock in the first 10 cm soil depth in tonnes per hectare (Mg C_{org}ha^{-1}) was interpolated across known areas of seagrass distribution[47–49] in the estuary extent using ArcGIS and the Empirical Bayesian kriging tool Geostatistical Analyst extension (ArcGIS 10.4; ESRI Software Inc). Areas of seagrass distribution integrated information of all seagrass species within the estuary because of the non-monospecific nature of most seagrass meadows. Empirical Bayesian kriging is an interpolation method that accounts for the error in estimating the underlying semivariogram through repeated simulations[70]. The standard deviation from each site (see Table 1) was interpolated to provide a measure of variability in the values and used as error terms. For each seagrass defined area or seagrass patch we calculated the mean and error term per hectare.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

1. Nellemann, C. *et al.* Blue carbon. A rapid response assessment. *United Nations Environ. Program. GRID-Arendal*, www.grida.no (2009).
2. Fourqurean, J. *et al.* Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **5**, 1–7 (2012).
3. Duarte, C. M., Kennedy, H., Marbà, N. & Hendriks, I. Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. *Ocean Coast. Manag.* **83**, 32–38 (2013).
4. Mateo, M. A., Romero, J., Pérez, M., Littler, M. M. & Littler, D. S. Dynamics of millenary organic deposits resulting from the growth of the mediterranean seagrass *Posidonia oceanica*. *Estuar. Coast. Shelf Sci.* **44**, 103–110 (1997).
5. Macreadie, P. I., Baird, M. E., Trevathan-Tackett, S. M., Larkum, A. W. D. & Ralph, P. J. Quantifying and modelling the carbon sequestration capacity of seagrass meadows - A critical assessment. *Mar. Pollut. Bull.* **83**, 430–439 (2014).
6. Duarte, C. M. Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences* **14**, 301–310 (2017).
7. Lavery, P. S., Mateo, M. A., Serrano, O. & Rozaimi, M. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One* **8**, e73748 (2013).
8. Röhr, M. E., Boström, C., Canal-Vergés, P. & Holmer, M. Blue Carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences* **13**, 6139–6153 (2016).
9. Miyajima, T. *et al.* Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Global Biogeochem. Cycles* **29**, 397–415 (2015).
10. Serrano, O., Lavery, P., Rozaimi, M. & Mateo, M. Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochem. Cycles* **28**, 1–12 (2014).
11. Serra no, O. *et al.* Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences* **13**, 4581–4594 (2016).
12. Ricart, A. M., Pérez, M. & Romero, J. Landscape configuration modulates carbon storage in seagrass sediments. *Estuar. Coast. Shelf Sci.* **185**, 69–76 (2017).
13. Macreadie, P. I. *et al.* Losses and recovery of organic carbon from a seagrass ecosystem following disturbance. *Procedings R. Soc. Biol. Sci.* **282**, 20151537 (2015).
14. Samper-Villarreal, J., Lovelock, C. E., Saunders, M. I., Roelfsema, C. & Mumby, P. J. Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnol. Oceanogr.* **61**, 938–952 (2016).
15. Atwood, T. B. *et al.* Predators help protect carbon stocks in Blue Carbon ecosystems. *Nat. Clim. Chang.* 1–8 (2015).
16. Thomson, A. C. G., Trevathan-Tackett, S. M., Maher, D. T., Ralph, P. J. & Macreadie, P. I. Bioturbator-stimulated loss of seagrass sediment carbon stocks. *Limnol. Oceanogr.* 1–15 (2018).
17. Mazarrasa, I. *et al.* Habitat characteristics provide insights of carbon storage in seagrass meadows. *Mar. Pollut. Bull.* 0–1 (2018).
18. Ricart, A. M. *et al.* Variability of sedimentary organic carbon in patchy seagrass landscapes. *Mar. Pollut. Bull.* **100**, 476–482 (2015).
19. Liu, S. *et al.* Effects of nutrient load on microbial activities within a seagrass-dominated ecosystem: Implications of changes in seagrass blue carbon. *Mar. Pollut. Bull.* **117**, 214–221 (2017).
20. Oreska, M. P. J., McGlathery, K. J., Porter, J. H., Bost, M. & McKee, B. A. Seagrass blue carbon accumulation at the meadow-scale. *PLoS One* **12**, 1–18 (2017).
21. Santos, R. *et al.* Superficial sedimentary stocks and sources of carbon and nitrogen in coastal vegetated assemblages along a flow gradient. *Sci. Rep.* **9**, 1–11 (2019).

22. Howard, J., Hoyt, S., Isensee, K., Pidgeon, E. & Telszewski, M. *Coastal blue carbon methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows*. (Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, 2015).

23. Kindeberg, T., Ørberg, S. B., Röhr, M. E., Holmer, M. & Krause-Jensen, D. Sediment stocks of carbon. *nitrogen, and phosphorus in Danish eelgrass meadows. Front. Mar. Sci.* **5**, 1–14 (2018).

24. Young, M. A. *et al.* Optimal soil carbon sampling designs to achieve cost-effectiveness: a case study in blue carbon ecosystems. *Biol. Lett.* **14**, 20180416 (2018).

25. Githaiga, M. N., Kairo, J. G., Gilpin, L. & Huxham, M. Carbon storage in the seagrass meadows of. *PLoS One* **12**, 1–13 (2017).

26. Gullström, M. *et al.* Blue Carbon storage in tropical seagrass meadows relates to carbonate stock dynamics, plant–sediment processes, and landscape context: Insights from the Western Indian Ocean. *Ecosystems* 1–16 (2017).

27. Ierodiaconou, D. A. & Laurenson, L. J. B. Estimates of *Heterozostera tasmanica*, *Zostera muelleri* and *Ruppia megacarpa* distribution and biomass in the Hopkins Estuary, western Victoria, by GIS. *Aust. J. Bot.* **50**, 215–228 (2002).

28. Matson, E. A. & Brinson, M. M. Stable carbon isotopes and the C-N Ratio in the estuaries of the Pamlico and Neuse Rivers, North-Carolina. *Limnol. Oceanogr.* **35**, 1290–1300 (1990).

29. Cai, W. J. Estuarine and coastal ocean carbon paradox: CO_2 sinks or sites of terrestrial carbon incineration? *Ann. Rev. Mar. Sci.* **3**, 123–145 (2011).

30. Fonseca, M. & Bell, S. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar. Ecol. Prog. Ser.* **171**, 109–121 (1998).

31. Bell, S., Fonseca, S. & Stafford, N. B. Seagrass ecology: new contributions from a landscape perspective. *Seagrasses Biol. Ecol. Conserv.* 625–645 (2006).

32. Alcoverro, T., Cebrian, E. & Ballesteros, E. The photosynthetic capacity of the seagrass *Posidonia oceanica*: influence of nitrogen and light. *J. Exp. Mar. Bio. Ecol.* **261**, 107–120 (2001).

33. Kelleway, J. J. *et al.* Seventy years of continuous encroachment substantially increases 'Blue Carbon' capacity as mangroves replace intertidal salt marshes. *Glob. Chang. Biol.* **22**, 1097–1109 (2016).

34. Sousa, A. I. *et al.* 'Blue Carbon' and nutrient stocks of salt marshes at a temperate coastal lagoon (Ria de Aveiro, Portugal). *Sci. Rep.* **7**, 1–11 (2017).

35. Chen, G. *et al.* Mangroves as a major source of soil carbon storage in adjacent seagrass meadows. *Sci. Rep.* **7**, 1–10 (2017).

36. Gacia, E. & Duarte, C. M. Sediment retention by a mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuar. Coast. Shelf Sci.* **52**, 505–514 (2001).

37. Samper-Villarreal, J., Mumby, P. J., Saunders, M. I., Roelfsema, C. & Lovelock, C. E. Seagrass organic carbon stocks show minimal variation over short time scales in a heterogeneous subtropical seascape. *Estuaries and Coasts* **41**, 1732–1743 (2018).

38. Kennedy, H. *et al.* Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochem. Cycles* **24**, GB4026–GB4026 (2010).

39. Dahl, M. *et al.* Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: A comparison of four european areas. *PLoS One* (2016).

40. Burdige, D. J. Preservation of organic matter in marine sediments: controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chem. Rev.* **107**, 467–485 (2007).

41. Serrano, O. *et al.* Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences* **13**, 4915–4926 (2016).

42. Trevathan-Tackett, S. M. *et al.* Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology* 150511125256001 (2015).

43. Ward, L. G., Michael Kemp, W. & Boynton, W. R. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar. Geol.* **59**, 85–103 (1984).

44. Gacia, E. *et al.* Sediment deposition and production in SE-Asia seagrass meadows. *Estuar. Coast. Shelf Sci.* **56**, 909–919 (2003).

45. Dahl, M. *et al.* Increased current flow enhances the risk of organic carbon loss from *Zostera marina* sediments: Insights from a flume experiment. *Limnol. Oceanogr.* 1–13 (2018).

46. Green, E P., Short, F. T. *World atlas of seagrasses*. (University of California Press, 2003).

47. Rasheed, M. A., Thomas, R., Roelofs, A. J., Neil, K. M. & Kerville, S. P. *Port Curtis and Rodds Bay seagrass and benthic macro-invertebrate community baseline survey November / December 2002*, (2002).

48. Bryant, C., Davies, J., Sankey, T., Jarvis, J. & Rasheed, M. *Long term seagrass monitoring in Port Curtis: Quarterly seagrass assessments & permanent transect monitoring progress report 2009 to 2013*, https://doi.org/10.13140/RG.2.1.3689.5204 (2014).

49. Carter, A. *et al.* Seagrasses in Port Curtis & Rodds Bay Seagrasses in Port Curtis & Rodds Bay Annual long-term monitoring, biannual Western Basin, and updated baseline survey, (2015).

50. Ricart, A. M., Dalmau, A., Pérez, M. & Romero, J. Effects of landscape configuration on the exchange of materials in seagrass ecosystems. *Mar. Ecol. Prog. Ser.* **532**, 89–100 (2015).

51. Coles, R. G. *et al.* The Great Barrier Reef World Heritage Area seagrasses: Managing this iconic Australian ecosystem resource for the future. *Estuarine, Coast. Shelf Sci.* **153**, A1–A12 (2015).

52. Mckenzie, L. J., Campbell, S. J. & Roder, C. A. *Seagrass-Watch: Manual for Mapping & Monitoring Seagrass Resources by Community (citizen) Volunteers. INFORMATION SERIES QI01094*.

53. Bunn, S. E., Loneragan, N. R. & Kempster, M. A. Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: Implications for food-web studies using multiple stable isotopes. *Limnol. Oceanogr.* **40**, 622–625 (1995).

54. Jacob, U., Mintenbeck, K., Brey, T., Knust, R. & Beyer, K. Stable isotope food web studies: a case for standardized sample treatment. *Mar. Ecol. Prog. Ser.* **287**, 251–253 (2005).

55. Carabel, S., Godínez-Domínguez, E., Verísimo, P., Fernández, L. & Freire, J. An assessment of sample processing methods for stable isotope analyses of marine food webs. *J. Exp. Mar. Bio. Ecol.* **336**, 254–261 (2006).

56. Aurecon Australia Pty, L. *Western basin dredging and disposal (onshore and offshore) project water quality management plan Gladstone Ports Corporation*, (2011).

57. Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. *Mixed effects models and extensions in ecology with R.* (Springer, 2009).

58. Littel, R., MIlliken, G., Stroup, W. & Wolfinger, R. *SAS Systems for Mixed Models.* (SAS Institute Inc, 1996).

59. Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S.* (Springer, 2002).

60. Crawley, M. J. *The R Book.* (John Wiley & Sons, 2007).

61. Selmi, S. & Boulinier, T. Ecological biogeography of Southern Ocean islands: The importance of considering spatial issues. *Am. Nat.* **158**, 426–437 (2001).

62. Fox, J. & Weisberg, S. *Time-series regression and generalized least squares: an appendix to an R companion to applied regression. An R Companion to Applied Regression* (SAGE, 2018).

63. Bolker, B. M. *et al.* Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).

64. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Core Team, R. nlme: Linear and nonlinear mixed effects models. *R package version* **3**, 1–140 (2019).

65. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2018).

66. Bivand, R. S. & Wong, D. W. S. Comparing implementations of global and local indicators of spatial association. *TEST* **27**, 716–748.
67. Parnell, A. C., Inger, R., Bearhop, S. & Jackson, A. L. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* **5**, e9672 (2010).
68. Zieman, J., Macko, S. & Mills, A. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bull. Mar. Sci.* **35**, 380–392 (1984).
69. Mateo, M. A., Renom, P. & Michener, R. H. Long-term stability in the production of a NW Mediterranean *Posidonia oceanica* (L.) Delile meadow. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **291**, 286–296 (2010).
70. Gribov, A. & Krivoruchko, K. New flexible non-parametric data transformation for trans-gaussian kriging in Geostatistics Oslo, vol 17 (eds. Abrahamsen P., Hauge R., Kolbjørnsen (Springer, 2012).

Acknowledgements

Author contributions

A.M.R., P.H.Y., C.V.B., M.A.R. and P.I.M. conceived and designed the study. A.M.R., P.H.Y., M.A.R., P.I.M. and C.V.B. performed field research and laboratory analyses. A.M.R. and D.I. analysed the data. A.M.R. led the paper with substantial input from all the authors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41598-020-62639-y.

Correspondence and requests for materials should be addressed to A.M.R.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.