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Seascape connectivity with mangroves positively influences tropical saltmarsh blue carbon stocks

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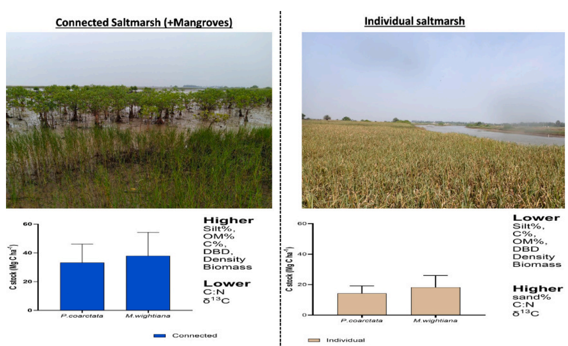
HIGHLIGHTS

- Connected saltmarsh meadows store 2–3-fold higher C stocks than individual meadows
- Influence of connectivity on saltmarsh meadows is species and zonation specific
- Connectivity increased saltmarsh below ground biomass contribution to sediment C pool
- Regional factors influence species-specific saltmarsh sediment C_{org} stocks
- Tropical saltmarsh ecosystems of India have climate change mitigation relevant C stocks

GRAPHICAL ABSTRACT



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ABSTRACT

Despite exponential increase in global blue carbon studies over the last decade, critical knowledge gaps remain regarding the role of drivers such as seascape connectivity that mediate the carbon storage in tropical saltmarsh ecosystems. The present study addresses this knowledge gap by investigating how seascape-level drivers, specifically connectivity between ecosystems, sediment traits and plant biomass, influence carbon stocks, in connected versus individual tropical saltmarsh (*Porteresia coarctata* and *Myrostachia wightiana*) meadows. This study compared the influence of connected saltmarsh meadows (adjacent to mangroves) with individual saltmarsh meadows across four tropical locations and assessed their carbon (C) and nitrogen (N) content in sediment, biomass, various plant traits and C stocks. Stable isotopes tracers (^{13}C and ^{15}N) were used to determine the C contribution from autochthonous and allochthonous carbon sources. Connectivity resulted in increased of plant shoot density, and biomass by 1.7-fold and 1.5-fold respectively than individual saltmarsh meadows. Connectivity resulted in 2.3-fold higher C_{org} stocks (sediment + biomass) than individual meadows. Connectivity increased the below -ground biomass contribution to sediment C pool by 2 to 10 %, whereas the combined contribution of mangrove leaf biomass was between 7.8 and 26.8 % in both saltmarsh species probably depending on the mangrove density, leaf litterfall and organic matter trapping efficiency of these saltmarsh

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species. The study underscores the positive role of seascape connectivity with mangroves in enhancing the carbon stocks in tropical saltmarsh ecosystems.

1. Introduction

Saltmarshes are highly valuable coastal halophytic plants that inhabit the dynamic interface between land and sea (Levin and Talley, 2002). These ecosystems are generally found associated with mangrove ecosystems in tropical (Banda et al., 2021b; Huxham et al., 2018; Raw et al., 2019) and with seagrasses in temperate regions (de los Santos et al., 2023). Their global distribution covers an area of 54,951 km^2 (Mcowen et al., 2017) and provide an array of ecosystem services such as natural storm defense, soil stabilization and erosion prevention, food and habitat provisioning, coastal water quality enhancement by filtering run-off and efficient nitrogen sequestration (Ermgassen et al., 2021; Jinks et al., 2020; Rendón et al., 2019). Other important ecosystem services include climate change mitigation through carbon sequestration. Globally these ecosystems store an estimated 1.44Pg of organic carbon (C_{org}) in their sediment (Campbell et al., 2022; Ermgassen et al., 2021; Gilby et al., 2021; Maxwell et al., 2024; Rendón et al., 2019). Additionally, they also capture 0.0048–0.0873 Pg of carbon (C) annually from allochthonous sources contributing significantly to long-term C storage (Mcleod et al., 2011). The high burial and C storage activities of saltmarshes are a result of multiple factors, such as i) high primary productivity providing autochthonous C_{org}, ii) reduction in tidal flow by saltmarsh plants for burial and retaining of allochthonous C_{org} and iii) the anaerobic environment of saltmarsh soils (Mcleod et al., 2011). However, various human-induced habitat disturbances and saltmarsh ecosystem loss can result in substantial carbon emissions amounting to 16.3 Tg carbon dioxide (CO_2) equivalent annually (Campbell et al., 2022; Cunha et al., 2024; Mason et al., 2023; Saintilan et al., 2022).

In tropical regions, saltmarshes are often found alongside mangroves, and this ecological connectivity plays a significant role in the functioning (e.g., biodiversity assemblages) of both ecosystems. The enhancement of C accumulation in saltmarshes due to transfer of materials, including C, between connected mangroves and saltmarsh ecosystem has been recently documented (Fu et al., 2021; Raw et al., 2019). Recent studies suggest that these connected saltmarsh ecosystems are highly efficient in burial and sequestrate up to twice as much C as previously estimated due to efficient trapping of allochthonous C (Miller et al., 2023; Reithmaier et al., 2023). Despite these insights, there remains a significant knowledge gap regarding the impact of various drivers (e.g., hydrology, plant morphometrics, sediment traits etc.,) that mediate the C transfer and storage in these connected systems, especially at regional scales (Saavedra-Hortua et al., 2023).

Specifically, there is a significant lack of studies on assessing the saltmarsh C storage potential in the tropical saltmarshes (e.g., global south), as depicted from global saltmarsh studies (Maxwell et al., 2024; Perera et al., 2022; Stankovic et al., 2023; Strydom et al., 2023). These tropical saltmarsh meadows are found inhabiting semi-sheltered low-energy coastlines associated with fringing mangrove ecosystems or as individual systems (Cuellar-Martinez et al., 2019; Mishra and Farooq, 2022b; Perera et al., 2022). These tropical saltmarshes are generally ignored for their climate change mitigation role, as more emphasis has been provided towards tropical mangrove ecosystems followed by seagrasses (Cusack et al., 2018; Rabaoui et al., 2020; Saderne et al., 2020). Recent literature reviews suggest, tropical countries with saltmarsh ecosystems have significant coverage (e.g., 27,520 ha in Sri Lanka, >100,000 ha in Bangladesh, >25,000 ha in India) which needs to be studied for the evaluation of their C stocks and other ecosystem services (Mishra and Farooq, 2022a; Perera et al., 2022; Shafiqul Islam et al., 2021; Veettil et al., 2024). Assessments of these existing knowledge gaps can help in driving policy frameworks for inclusion of tropical saltmarsh ecosystems (along with mangroves and seagrass) within the Nationally Determined Contributions (NDCs) of these tropical countries and improve their climate change mitigation potential (Akhand et al., 2022; Stankovic et al., 2023). Furthermore, these assessments can help in blue carbon crediting frameworks and in mobilizing focused conservation efforts (Dencer-Brown et al., 2022; Pétillon et al., 2023; Wang et al., 2022).

Given these gaps, this study aims to improve the understanding on the effects of two important drivers, (a) connectivity between ecosystems (saltmarshes connected with mangroves vs isolated systems) and (b) standing vegetation biomass and their effect on C stocks in tropical saltmarsh ecosystems. Specifically, we will quantify the C_{org} stocks of two understudied tropical saltmarsh species, *Porteresia coarctata* (Roxb.) and *Myrostachia wightiana* (Nees ex Steud), in both connected and isolated settings. We will also investigate the contributions of various C_{org} sources to saltmarsh C dynamics by using stable isotopes of carbon ($\delta^{13}C$, $\delta^{15}N$ and C:N ratios). By achieving these objectives, the study will highlight the role of connected coastal ecosystems in influencing saltmarsh C storage at local scale. We hypothesize that seascape connectivity can positively influence saltmarsh C stocks, and that standing biomass will be a significant factor in influencing C storage between species. Our findings will contribute to filling the existing critical knowledge gaps on tropical saltmarsh meadows and help advocate for the inclusion of tropical saltmarshes in climate mitigation policies (in NDC's) alongside mangroves and seagrasses.

2. Materials and methods

2.1. Study area

This study covers four major estuarine areas in the state of Odisha, India. These regions have tropical conditions with high humidity and temperature which promotes luxuriant growth of saltmarshes in these areas (Fig. 1). The study locations have the presence of mono-specific meadows of *P. coarctata (*at Chandipur, Dhamra and Astaranga) and *M. wightiana* (at Dhamra, Astaranga and Rushikulya) (Fig. 1). At each location, two distinct types of saltmarsh habitats were found; (i) individual saltmarsh meadows (hereafter referred to as "individual") and (ii) saltmarsh meadows connected to mangroves (hereafter referred to as "connected"). Both these habitats were selected at least 1500 m apart (Fig. 2). These study locations cover the north to the south latitudinal gradient of estuaries along the coast of Odisha that drains into the Bay of Bengal. The study sites include areas chosen as Important Coastal and Marine Biodiversity Areas (ICMBA, 2021).

A hand-held GPS (Garmin GPS, Etrex 10) was used to map the total area of individual and connected *P. coarctata* and *M. wightiana* meadows during the post-monsoon season. Both individual and connected *P. coarctata* meadows are located in the lower intertidal zone that received daily tidal flooding. The connected *M. wightiana*, meadows are located in the middle intertidal zones, whereas the individual meadows are present at high intertidal zones that experience less frequent tidal inundation and after the mangroves towards the high tidal zones. The connected *P. coarctata* meadows were associated with mangrove species such as *Kandelia candel* and *Avicennia marina,* while *M. wightiana* meadows were associated with mixed mangrove species of *A. marina* and *Rhizophora apiculata*. Sampling of sediment and saltmarsh plants (for biomass) was conducted during the post-monsoon (November–January 2021).

2.2. Sediment sampling and analysis

Replicate sediment cores ($n = 9$), spaced 10 m apart, were collected from individual and connected meadows of *P. coarctata* and *M. wightiana* at each study location randomly in the intertidal zone using a stainless-steel C-section core (100 cm long and 5 cm diameter). At each sampling site, surface debris or leaves were removed first and the corer was inserted steadily into the sediment until the top of the corer was in level with the soil surface. The descent rate of the corer was kept low to minimize core compaction. Once the maximum depth was reached the core was twisted few times to cut through any remaining fine roots and was gently pulled out while continuing to twist to ensure the retrieval of the intact and complete sediment core. Each core was sectioned at 5 cm intervals in the field, and stored in zip-locked plastic bags, labelled and transported to the laboratory in dark boxes to prevent degradation.

In the laboratory, each sediment section before drying was removed of any roots and debris and was oven-dried at 60 °C for 48 h to determine the dry bulk density (DBD: g cm^{-3}; Eq. (1)) following the protocols mentioned in 'Blue Carbon Manual' (Howard et al., 2014). From these dried sediment sections ($n = 3$ cores per habitat type), five grams of sediment samples was acidified with 10 ml of 10 % HCl and heated for 2 h in an oven at 45 °C to remove carbonates and treated again with 10 ml of 30 % H_2O_2 for removal of any organic matter (Prajith et al., 2016). The resulting residue was oven-dried and used to determine the sediment grain size distribution using a Laser Particle Size Analyzer (LPSA, Horiba, LA-950V2). Homogenized sediment samples of five grams from each core section were combusted in a muffle furnace at 550 °C for 4.5 h to determine the sediment organic matter (OM%) through loss on ignition (LOI; Eq. (2)) method.

$$DBD = (weight\ of\ dry\ sediment)/(core\ volume) \quad (1)$$

$$LOI\ (\%) = \left[\frac{initial - final}{initial}\right]*100 \quad (2)$$

$$SCD = DBD \times \%Corg \quad (3)$$

2.3. Stable isotope analysis and source determination

From the remaining fraction of homogenized sediment, 0.30 mg of each replicate was prepared using tin capsules for total carbon (C%) and nitrogen (N%) content, and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) analysis. An additional fraction of 0.30 mg was acidified with 1 M HCl to remove carbonates. After the addition of HCl, the sediment samples were left in a fume hood until no further bubble formation was detected. Then the sediment samples were oven dried in a hot air oven at 60 °C for 24 h till completely dried. Both acidified and non-acidified sediment samples were analyzed in duplicate for total C, N and $\delta^{13}C$ and $\delta^{15}N$ analysis using a Flash Elemental Analyzer coupled to a Delta V Isotope Ratio Mass Spectrometer (IRMS, Euro Vector, EA3028 EA-Nu). Calibrations and precision (0.2 ‰) were verified using in-house acetanilide standards (Iacet#1, $\delta^{15}N = 1.18$ ‰ $\delta^{13}C = -29.53$ ‰). Vienna Pee Dee Belemnite (VPDB) and atmospheric air were used as isotope references for C and N, respectively. The sediment carbon density (SCD) was calculated following the Eq. (3) as mentioned above.

Stable Isotope Mixing Models in R (SIMMR), based on the Bayesian isotopic mixing frameworks, were utilized to estimate the contribution of various autochthonous and allochthonous sources of C_{org} to the sediment C pool of individual and connected saltmarsh meadows (Phillips et al., 2005; Phillips and Gregg, 2001). The analysis employed 'simmr' and 'rjags' packages, which use $\delta^{13}C$, $\delta^{15}N$, and C:N ratios as inputs, running 10,000 iterations via a Markov Chain Monte Carlo (MCMC) algorithm to maintain mass balance across isotopes (Parnell et al., 2013) and the results are presented as boxplots which depict the 50 % credible intervals. The MCMC technique is used to evaluate the probability of source proportions in the recorded samples while accounting for uncertainties such as diagenetic fractionation changes, isotopic, residual error, etc. The 'simmr' package allows for the incorporation of $\delta^{13}C$ uncertainty into mixing models, while producing a Bayesian quantification of the most likely source contributors where there is a greater than $n + 1$ sources when matching against an isotope (Tanaya et al., 2018; Parnell et al., 2013; Watanabe and Kuwae, 2015).

For this study, $\delta^{13}C$, $\delta^{15}N$ and C:N ratios were measured for *P. coarctata*, *M. wightiana*, associated mangrove species (*Kandelia candel*, *Avicennia marina*, *Rhizophora apiculata*), and sediment samples (see Supplementary Fig. S1) to avoid overlap of $\delta^{13}C$ sources between C4 plants of marine and terrestrial origin (Fry, 2006; Kusumaningtyas et al., 2019; Bouillon et al., 2002). The isotopic and C:N values for the end

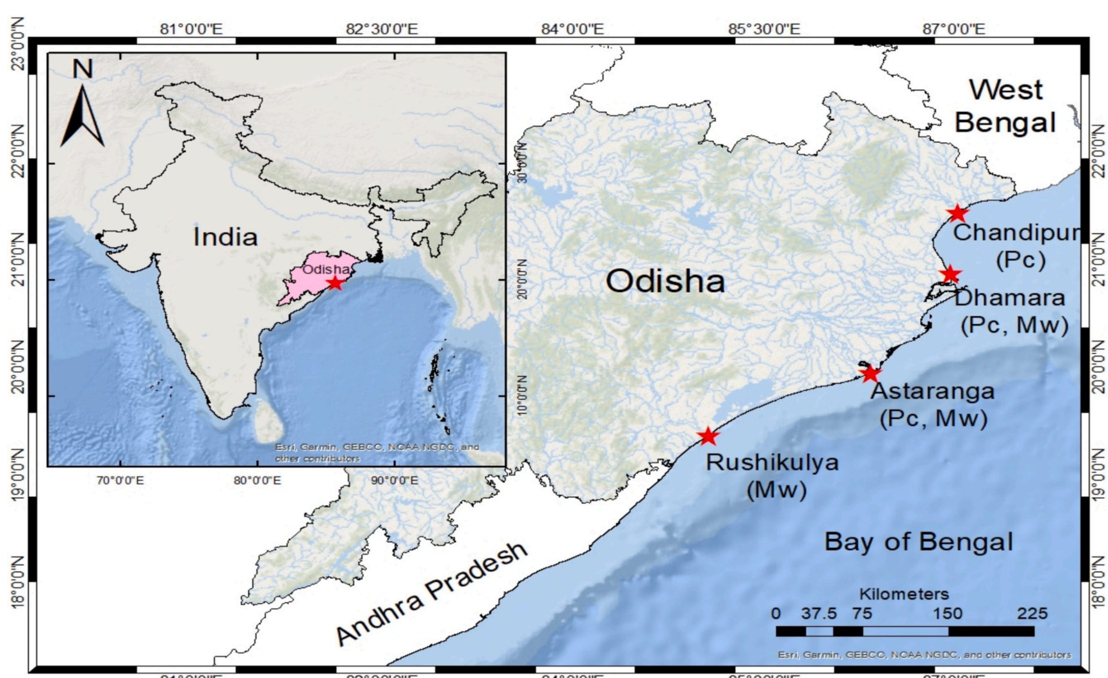

Fig. 1. Map showing the study sites in the state of Odisha on the east coast of India with *P. coarctata* (Pc) and *M. wightiana* (Mw) meadows. West Bengal and Andhra Pradesh are the neighboring coastal states of Odisha on the east coast of India.

members; particulate organic matter (POM) of both marine (δ^{13}C;-21.34 ± 1.21 ‰, δ^{15}N; 5.64 ± 0.32 ‰, C:N; 10.2 ± 1.6 %) and terrestrial (δ^{13}C;-29.17 ± 2.31 ‰, δ^{15}N; 3.99 ± 1.68 ‰, C:N; 9.5 ± 0.9 %) origin for our study locations were derived from literature of local studies (Amir et al., 2019; Bala Krishna Prasad and Ramanathan, 2009; Krishna et al., 2024; Mukherjee et al., 2019; Saha et al., 2022).

2.4. Plant sampling and analysis

At each location, five random quadrats (20 cm × 20 cm) spaced at least 5 m apart, were sampled for saltmarsh biomass across individual and connected meadows. From each quadrat, the saltmarsh plants were dug up using a hand spade to a depth of 10 cm. These plant samples along with their roots were washed off any debris with saltwater in the field, stored in zip-locked plastic bags and brought to the laboratory (Mishra et al., 2025). In the laboratory, plant samples were washed again with deionized water and any epiphytes on the leaf or shoot surface were cleaned off with a glass slide. Shoot density (individual shoots m^{-2}) was quantified by counting the total number of individual shoots per quadrat (Mishra et al., 2021). Plants were then separated into above-ground (AG: leaves) and below-ground (BG: roots+ rhizomes) biomass and oven-dried at 60 °C for 72 h. These dried biomass samples were weighed for dry biomass values (g DW m^{-2}) and then homogenized in the vibratory disc mill (see *Section 2.2*). Similarly, the leaves from various mangrove species were hand-picked during sampling, dried and grinded for isotope analysis (see *Section 2.3*). Duplicate homogenized samples of 0.5 mg were used to derive the elemental and isotopic C and N composition following the methods described for the sediment samples (see *Section 2.3*). The total sediment C_{org} stock (Mg C ha^{-1}) was calculated by summing the C_{org} content of each sediment section per core following the methods described in the 'Blue Carbon Manual' (Howard et al., 2014). The total C_{org} stock was upscaled towards the total meadow area for individual and connected meadows of each saltmarsh species (i.e., Tier II assessment; IPCC, 2014).

2.5. Statistics

A two-way ANOVA was used to assess the statistical significance between, physical parameters of surface water, sediment OM%, total C% and N% content, C_{org} stocks, and plant shoot density, biomass, and biomass C_{org} stocks using the connectivity (individual vs connected) and saltmarsh species (*P. coarctata* and *M. wightiana*) as fixed factors. All data was pre-checked for normality and homogeneity of variance using Shapiro-Wilk and Levine's tests, respectively. Linear regression was used to derive relationship between sediment OM and sediment C content. Principal Component Analysis (PCA) was used to derive the effects of various sediment and plant traits. Statistical tests were conducted at a significant level of $p < 0.05$. Data is presented as mean ± standard deviation (SD) and was analyzed using Graph pad Prism software (Ver. 10.4.0).

3. Results

3.1. Influence of connectivity on sediment abiotic variables

Saltmarsh connectivity with mangroves significantly influenced the

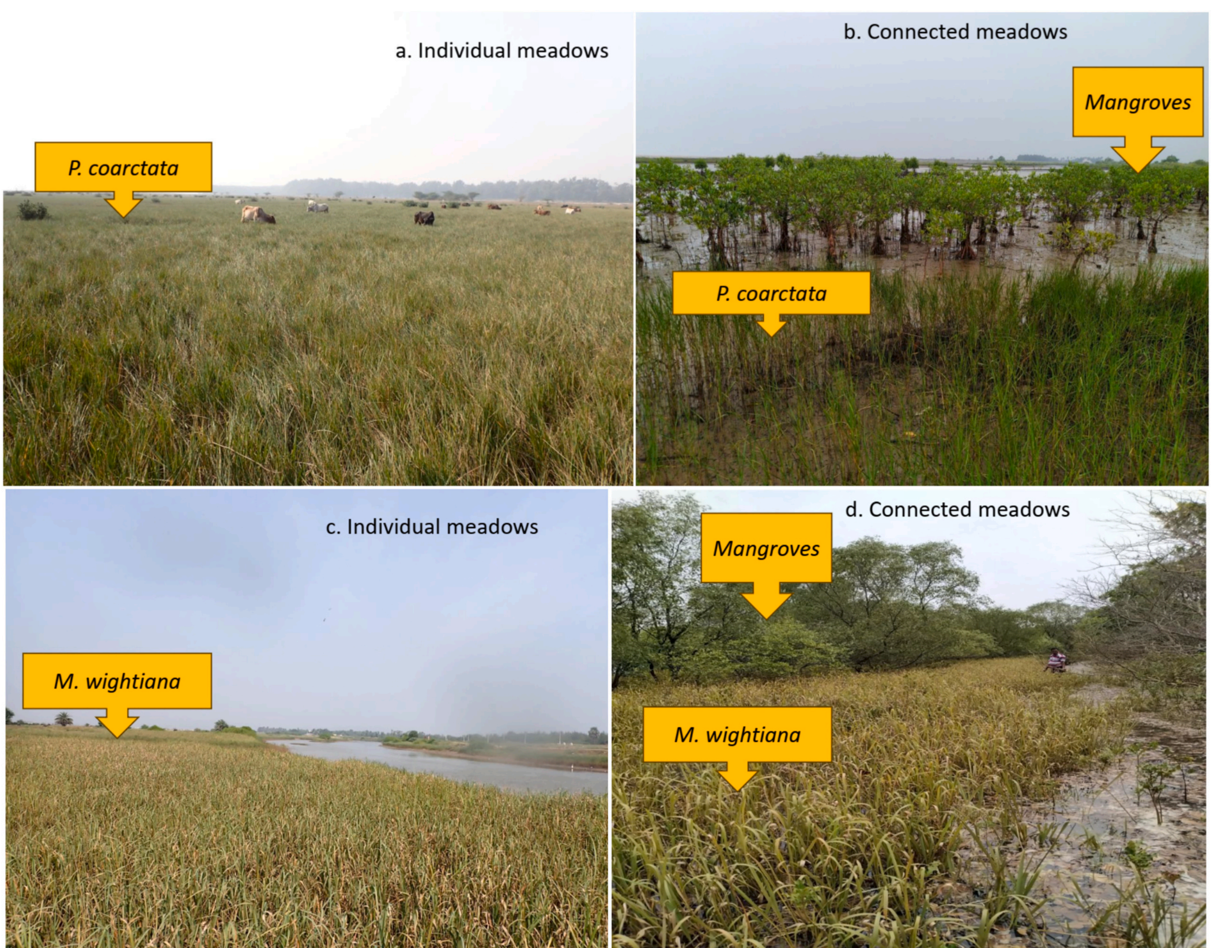

Fig. 2. Presence of individual and connected saltmarsh meadows of *P. coarctata* (a, b) and *M. wightiana* (c, d) from the coast of Odisha, India.

sediment abiotic variables such as sand, silt, clay, OM and N (Table 1 and Supplementary Table, S3). In the connected saltmarsh meadows, the sediment sand content of *P. coarctata* (31.11 ± 9.03 %) and *M. wightiana* (34.67 ± 7.53 %) decreased by 1-fold compared to the individual meadows (Table 1). Contrastingly, the sediment silt content of the connected *P. coarctata* (68.03 ± 8.34 %) and *M. wightiana* (65.15 ± 7.58 %) meadows increased 1-fold than their respective individual meadows (Table 1). However, connectivity with mangroves increased the sediment clay content of *P. coarctata* meadows (0.98 ± 0.10 %) by 2.8-fold, whereas for *M. wightiana* the sediment clay content (0.20 ± 0.10 %) decreased by 1.2-fold than individual meadows. Similarly in connected meadows, the sediment OM content of *P. coarctata* (7.97 ± 0.43 %) and *M. wightiana* (7.87 ± 1.53 %) increased by 1.3-fold and 1.7-fold respectively than individual meadows. Connectivity increased the sediment N content of *P. coarctata* (0.75 ± 0.50 %) and *M. wightiana* (0.58 ± 0.40 %) by 2.6-fold and 4.5-fold respectively than individual meadows (Table 1).

In general, connectivity with mangroves resulted in significant differences in the sediment DBD, C%, and SCD and across depth, whereas $\delta^{13}C$ varied significantly only across connectivity (Supplementary Fig. S4). The mean DBD across depth in *P. coarctata* (0.11 ± 0.03 g cm^{-3}) and *M. wightiana* (0.13 ± 0.02 g cm^{-3}) increased 1-fold and 1.2-fold across the connected saltmarshes than individual meadows. Similarly, the mean sediment C across depth for *P. coarctata* (6.45 ± 3.53 %) and *M. wightiana* (6.86 ± 2.57 %) increased 3.2-fold and 2.9-fold than individual meadows. The increase in DBD and sediment C content across depth resulted in similar increased pattern of SCD across depth for both saltmarsh species. In connected meadows, the mean SCD of *P. coarctata* (0.10 ± 0.01 g cm^{-3}) and *M. wightiana* (0.11 ± 0.09 g cm^{-3}) increased 1.7-fold and 1-fold than their individual meadows (Fig. S3c). The relationship between sediment OM and C content for both *P. coarctata* and *M. wightiana* across individual and connected meadows are presented in Fig. 3. Interestingly, the mean sediment $\delta^{13}C$ of *P. coarctata* (−22.90 ± 1.81 ‰) and *M. wightiana* (−22.01 ± 1.69 ‰) in connected meadows were 1-fold lighter compared to individual meadows (Supplementary Fig. S4). In general, connectivity with mangroves, resulted in negative relationship between sediment OM and sediment C_{org} stocks only for *P. coarctata* meadows (Fig. 4). Sediment clay content showed a significant positive correlation in connected meadows of *P. coarctata* compared to the individual meadows (Fig. 4).

3.2. *Influence of connectivity on saltmarsh plant traits*

In general, connectivity influenced positively the plant traits; shoot density and biomass and significant differences were also observed across species level (Table 1 and Supplementary Table, S3). Across the

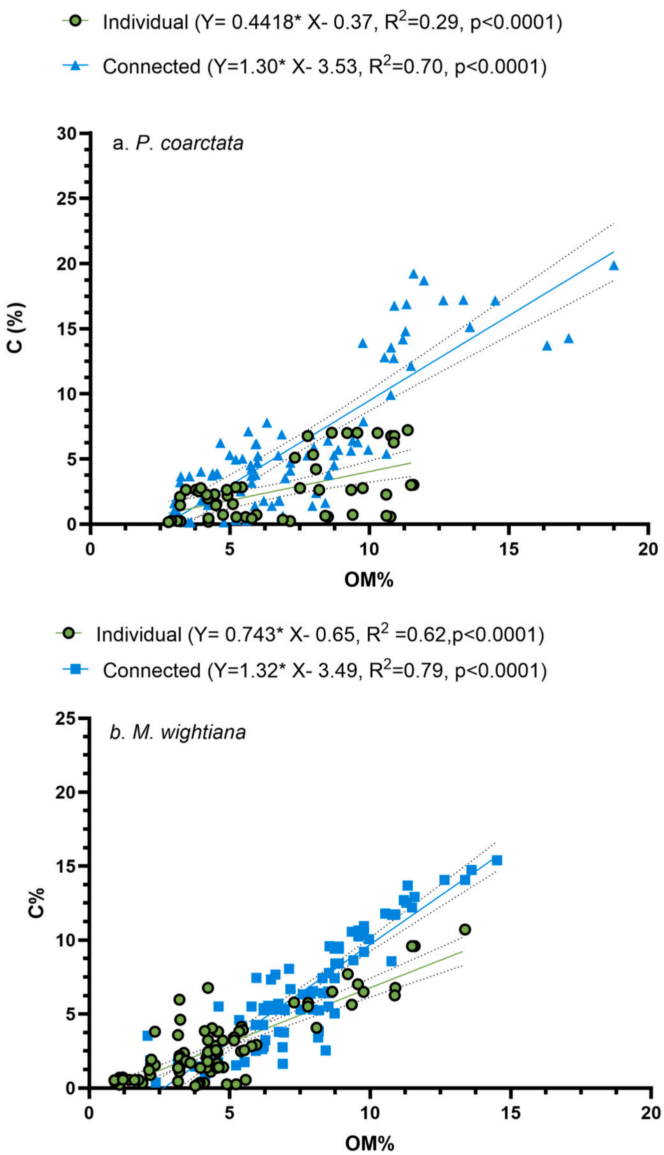

Fig. 3. Linear relationship between sediment organic matter (OM%) and carbon (C %) between individual and connected saltmarsh meadows of *P. coarctata* and *M. wightiana* meadows from the coast of Odisha, India.

Table 1
Mean ± SD values of a) sediment variables and b) saltmarsh density and biomass of the individual and connected saltmarsh meadows from the coast of Odisha, India. *P* value derived from two-way ANOVA analysis for connectivity is presented here. All other statistical variables are presented in details in Supplementary Table S3. Not significant (Ns).

Variables	*P. coarctata*		*M. wightiana*		P value
	Individual	Connected	Individual	Connected	
a. Sediment					
Sand%	39.43 ± 7.06	31.11 ± 9.03	39.26 ± 10.03	34.67 ± 7.53	0.001
Silt%	60.23 ± 7.28	68.03 ± 8.34	60.50 ± 10.14	65.15 ± 7.58	0.001
Clay%	0.34 ± 0.01	0.98 ± 0.35	0.24 ± 0.10	0.20 ± 0.10	0.04
OM%	6.27 ± 0.45	7.97 ± 0.43	4.61 ± 2.61	7.87 ± 1.53	<0.001
N%	0.28 ± 0.34	0.75 ± 0.50	0.13 ± 0.20	0.58 ± 0.40	<0.0001
b. Saltmarsh					
Density (individuals m^{-2})	1082 ± 41.36	1884.22 ± 102.08	182.08 ± 10.76	298 ± 43.61	<0.0001
Biomass (AG: g DW m^{-2})	719.78 ± 10.23	978.53 ± 89.09	1582.27 ± 90.23	2320 ± 100.51	<0.001
Biomass (BG: g DW m^{-2})	1195. 45 ± 19.34	1680.16 ± 43.05	962.90 ± 48.55	1220.73 ± 43.71	<0.0001
Biomass (AG:C%)	42.07 ± 5.12	42.07 ± 3.23	35.36 ± 2.20	36.05 ± 2.63	Ns
Biomass (BG:C%)	34.18 ± 1.05	34.18 ± 0.89	29.12 ± 2.14	29.45 ± 1.97	Ns

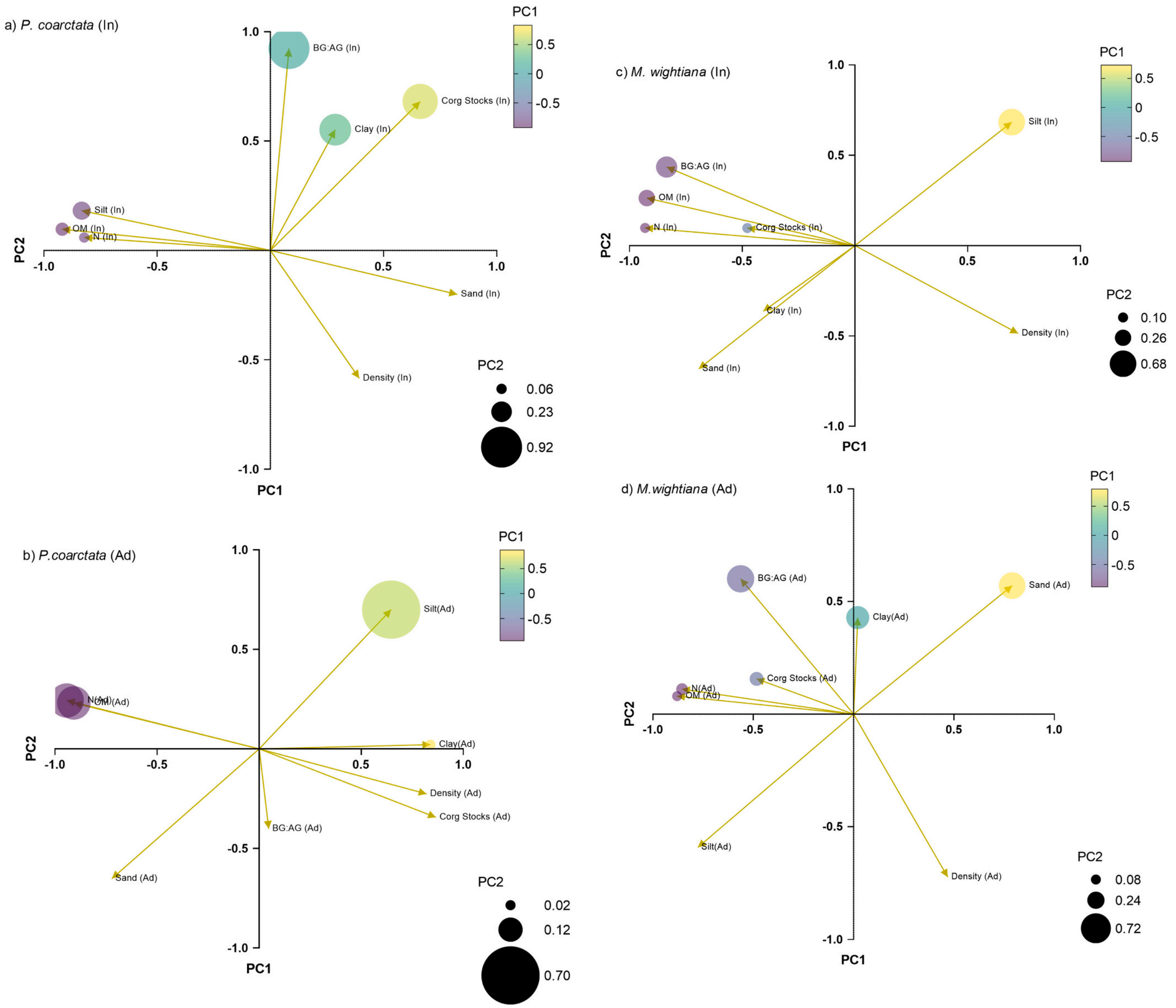

Fig. 4. PCA results of sediment and plant variables in individual and connected meadows of *P. coarctata* (a and b) and *M. wightiana* (c and d) from the coast of Odisha, India.

connected habitats, the shoot density of *P. coarctata* (1884.22 ± 102.08 ind. m^{-2}) and *M. wightiana* (298 ± 43.61 ind. m^{-2}) increased 1.7-fold and 1.6-fold than individual meadows (Table 1). In connected meadows, the AG-biomass of *P. coarctata* (978.53 ± 89.09 g DW m^{-2}) and *M. wightiana* (2320 ± 100.51 g DW m^{-2}) increased 1.4-fold and 1.5-fold higher than respective individual meadows. Similarly, the BG-biomass of *P. coarctata* (1680.16 ± 43.05 g DW m^{-2}) and *M. wightiana* (1220.73 ± 43.71 g DW m^{-2}) increased 1.4-fold and 1.3-fold than individual meadows (Table 1). However, connectivity did not influence the biomass C content of both saltmarsh species, but significant differences across species were observed (Table 1 and Supplementary Table, S3).

3.3. Influence of connectivity on carbon stocks, and source contribution

In general, connectivity with mangroves resulted in significant differences in the sediment total C_{org} stocks and total biomass C_{org} stocks (Fig. 5). In connected meadows, the mean sediment C_{org} stocks of *P. coarctata* (23.45 ± 12.54 Mg C ha^{-1}) and *M. wightiana* (25.81 ± 13.28 Mg C ha^{-1}) increased 3.2-fold and 2.6-fold than individual meadows (Fig. 5a). Similarly, in connected saltmarsh meadows the biomass C_{org} stocks of *P. coarctata* (9.77 ± 1.6 Mg C ha^{-1}) and *M. wightiana* (12.13 ± 4.98 Mg C ha^{-1}) increased 1.3-fold and 1.4-fold than individual meadows (Fig. 5c & d). The increase in total sediment and biomass C_{org} stocks across connected meadows, resulted in higher total ecosystem C_{org} stocks (sediment + biomass) in connected meadows. The total ecosystem C_{org} stocks of *P. coarctata* (33.22 ± 12.86 Mg C ha^{-1}) and *M. wightiana* (37.96 ± 16.33 Mg C ha^{-1}) increased 2.3-fold and 2-fold respectively compared to individual meadows (Fig. 5e). The BG:AG biomass ratios was positively corelated with sediment C stocks only in connected *M. wightiana* meadows (Fig. 4).

The contribution of various sources of carbon to the sediment C_{org} pool derived from stable isotope mixed modelling are presented in Fig. 6. Connectivity increased the BG-biomass contribution to sediment C pool by 2 % in *M. wightiana* and by 10 % in *P. coarctata* meadows. The combined contribution of mangrove leaf biomass was between 7.8 % in *P. coarctata* and 26.8 % for *M. wightiana* meadows. Connectivity resulted in increased of marine and terrestrial particulate organic matter (POM) contribution to sediment C pool only for *P. coarctata* by 1.5 % and 1.2 % respectively. Contrastingly, connectivity resulted in decrease of marine

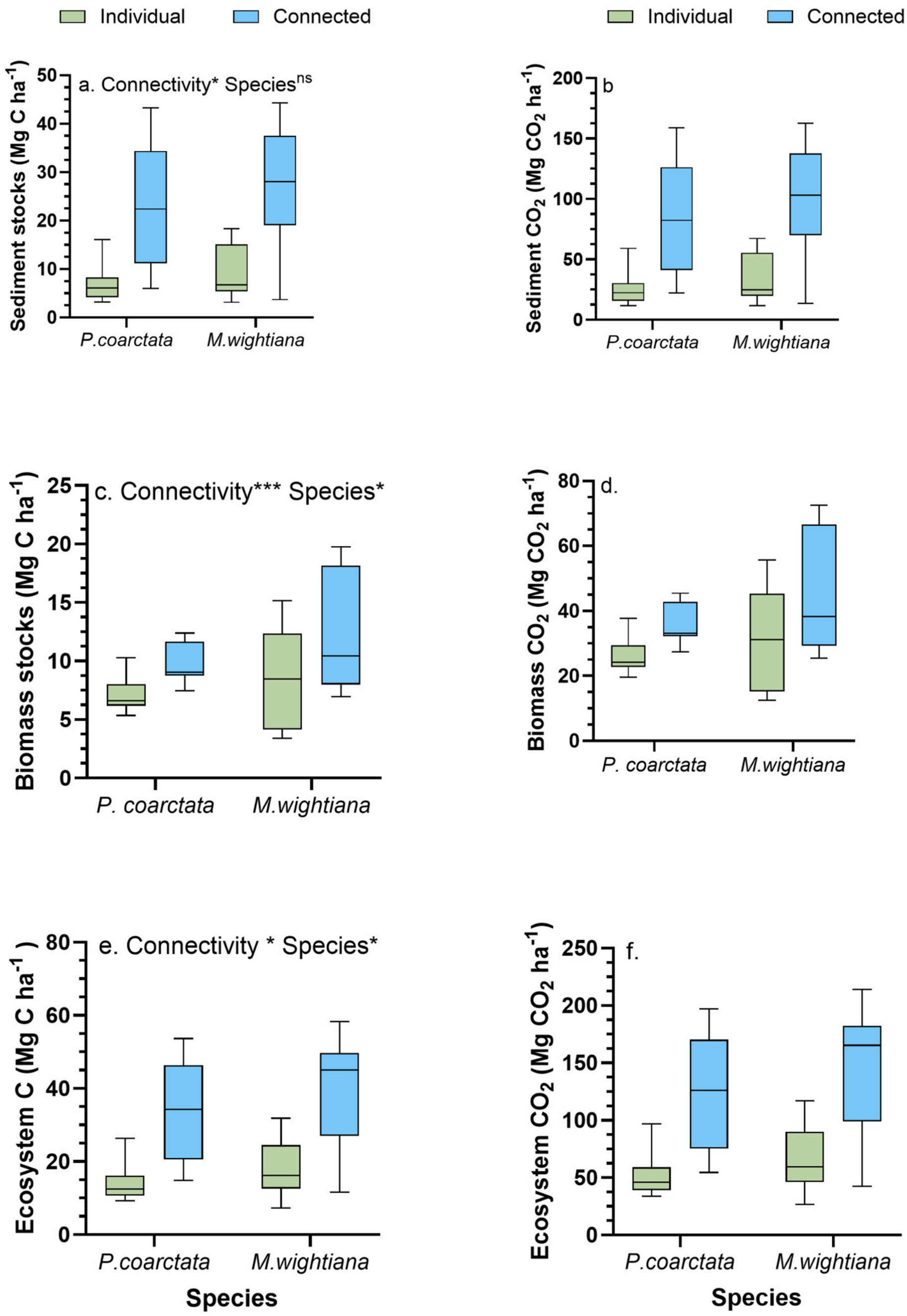

Fig. 5. Mean ± SD of carbon stocks and CO_2 equivalent in sediment (a & b), biomass (c & d) and ecosystem (e & f) across individual and connected meadows of *P. coarctata* and *M. wightiana* from coast of Odisha, India. Statistical significance ($p < 0.05$) was derived from two-way ANOVA analysis using connectivity and species as fixed factors. ($p < 0.0001$****, $p < 0.001$***). No statistical analysis was carried out for CO_2 equivalent data.

and terrestrial POM by 1.2 % and 2.8 % for *M. wightiana* respectively due to their presence at difference tidal zones (Fig. 6).

4. Discussion

4.1. Influence of connectivity on saltmarsh sediment abiotic variables and Corg stocks

Connected blue carbon habitats are more efficient in creating complex ecological networks, with cross boundary flows of materials, energy and organisms, thus, enhancing the ecosystem services (e.g., blue carbon stocks) and functioning compared to isolated ecosystems (Doughty et al., 2016; Jones and Russell, 2021; Raw et al., 2019). In this study, we observed that connected saltmarsh ecosystems are positively influenced by input of organic matter (OM), silt and clay, cross habitat subsidies of C_{org} and N from adjacent mangrove ecosystems. This influx enhanced plant traits (increase in density and biomass), and boosted ecosystem C_{org} stocks compared to individual saltmarshes as observed for other connected ecosystems of India (Mishra et al., 2023).

The influence of localized abiotic factors, such as hydrodynamics, play a key role in positively influencing the sediment fluxes and deposition of finer sediment fractions (e.g. silt and clay) in connected saltmarsh meadows compared to individual meadows (Gorham et al., 2021; Serrano et al., 2016). Enhanced hydrodynamic conditions result in an increased influx of silt and clay into the connected saltmarsh meadows. These finer particles are effectively retained by the dense rhizome network of saltmarsh meadows during daily tidal inundation. This retention of silt and clay not only supports sediment stabilization buts

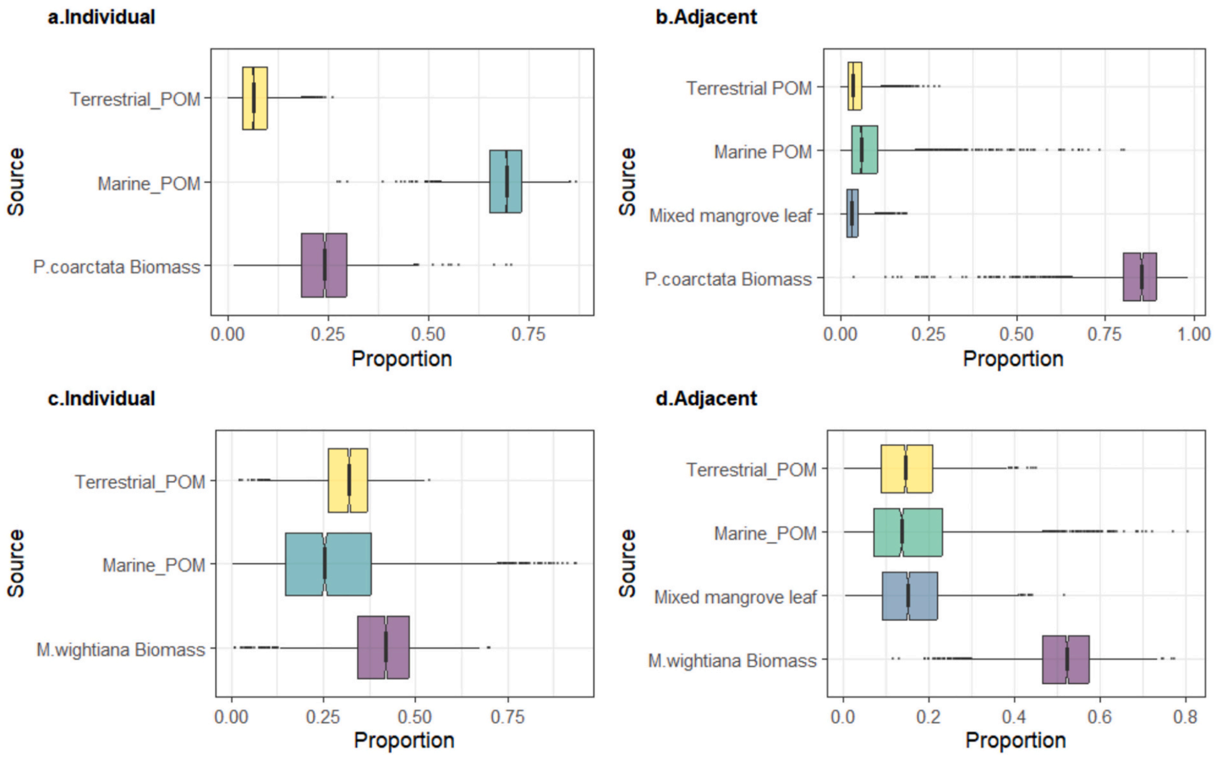

Fig. 6. SIMMR mixing model results displaying the average source contributions to saltmarsh sediment carbon pool in individual and connected meadows of *P. coarctata* in a) individual and b) connected, and in *M. wightiana* c) individual and d) connected meadows from the coast of Odisha, India. POM (Particulate organic matter), Mixed mangrove leaf; *P. coarctata* adjacent meadows (*Rhizophora apiculata* + *Kandela kandel*), and Mixed mangrove leaf; *M wightiana* adjacent meadows (*Rhizophora apiculata* + *Avicennia marina*). 50 % credible intervals are presented in Supplementary Table S2.

also enhances the sequestration of various autochthonous and allochthonous C sources, thus contributing to the larger sedimentary C pool. This higher rate of sediment deposition observed in the connected meadows positively influenced the sediment DBD for both saltmarsh species, thus, resulting in higher sediment C_{org} stocks in connected meadows. However, the effect of connectivity and increased sediment C_{org} stocks was predominately confined to the top 20 cm of the sediment profile (Fig. 5), showcasing the highly dynamic nature of these estuarine environment at our study sites. Our results coincide with the recent estimation of global saltmarsh soil C data, where majority of the soil C variations globally was recorded in the top 30 cm, indicating the effects of local environmental drivers (Maxwell et al., 2024; Saavedra-Hortua et al., 2023). Additionally, the input of increased OM into the connected habitats also resulted in positively increasing the sediment N content (Fig. 4). This also highlights the role of connected meadows as sediment N sink and contributing towards increase in plant productivity and biomass compared to individual saltmarsh meadows.

4.2. Contribution of connected habitats to sediment C pool

The isotopic signatures of all samples across connected saltmarsh habitats were within a similar range of various primary producers ($\delta^{13}C$: −25.5 to −7.8 ‰), (Supplementary Table S1). This indicates most of the saltmarsh C are generated within the saltmarsh meadows with majority of C contribution from the saltmarsh plants (biomass). However, with the presence of mangroves adjacent to saltmarsh this sediment C pool is enriched with various marine and riverine inputs. However, as observed in this study for the connected saltmarsh meadows, the contribution of marine and terrestrial input is more location and saltmarsh zonation specific (Fig. 6). The saltmarsh *M. wightiana* was generally observed behind the mangroves (towards the high tide zone), efficiently trapped increased amount of terrestrial POM as observed through stable isotope source's, compared to *P. coarctata* which inhabits the low intertidal zones with more frequent tidal inundations and loss of terrestrial POM and increased contribution of marine POM (Fig. 6). Similar, trends of increased marine POM contribution have been observed for one of our study sites (e.g., Chandipur) for *P. coarctata* from the coast of Odisha (Saha et al., 2022). This highlights the importance of saltmarsh species zonation and cross-habitat interactions in influencing sediment C_{org} stocks and variation in sediment C pool (Chen et al., 2016; Yuan et al., 2017). This influence of zonation on sediment C stocks has also been observed for *P. coarctata* from other regions of India (Banerjee et al., 2022; Chowdhury et al., 2023) and other saltmarsh species globally (Banda et al., 2021a; Doughty et al., 2016; Fu et al., 2021; Owers et al., 2022).

Additionally, our finding confirms that saltmarsh meadows connected to mangroves can efficiently trap a high percentage of C derived from mangrove leaf biomass, in their sediment C pool, leading to enhanced saltmarsh sediment C_{org} stocks (Gillis et al., 2014; Reithmaier et al., 2023; Raw et al., 2019). Additionally, the sediment traits (such as sand, silt and clay and N content) also positively affected the sediment C_{org} stocks (as observed by various correlations in Fig. 4) by playing a more important role in trapping OM and various C sources in the sediment of connected meadows (Fig. 3). These correlations between sediment traits and sediment C_{org} stocks were low in individual meadows, probably showcasing the role of lack of N input and its associated effects on saltmarsh plant growth and density resulting in lower sediment C_{org} stocks. This highlights the increased influence of connectivity for tropical saltmarsh meadows, where tropical saltmarshes contribute towards sediment accretion by trapping finer particles and contribute towards increased sediment C stocks(Bulmer et al., 2020).

4.3. Influence of connectivity on saltmarsh plant traits

In connected saltmarsh meadows, the additional input of OM and nutrients (especially N), from mangroves out-welling enhances saltmarsh productivity and biomass (Alongi, 2020; Huxham et al., 2018). This was evident in this study with the presence of strong positive relationship between OM input and sediment N content for both saltmarsh species across the connected meadows (Fig. 4). These findings further highlight that the individual saltmarsh meadows are N–limited, and the enhanced inflow of N from mangroves in connected meadows significantly increase N availability. This, in-turn, supports the plant growth and productivity, resulting in increased plant density and biomass for both saltmarsh species (Table 1, Supplementary Fig. 5). In addition to mangrove-derived N inputs, connected saltmarsh meadows also retain nutrients, particularly N, from seasonal monsoonal riverine inputs, as documented in previous studies from this region (Naik et al., 2020; Begam et al., 2017; Saha et al., 2022). These dual sources of nutrient enrichment - mangrove outwelling and monsoonal riverine contributions - further emphasize the ecological advantage of habitat connectivity in enhancing saltmarsh plant traits and overall productivity.

Additionally, in the connected meadows the increase in saltmarsh shoot density and AG-biomass may have helped in trapping more allochthonous biomass (e.g., mangrove leaves or other materials) inflows and POM that sequesters (as evident from stable isotope modelling, see Section 4.2) and settles in the saltmarsh sediments due to root-reducing hydrodynamics (Alongi, 2020; Gillis et al., 2014; Saavedra-Hortua et al., 2023). High shoot density also resulted in increased BG-biomass production, and enhanced sediment retention, leading to higher sediment C_{org} stocks in connected saltmarsh meadows (Guest et al., 2006). However, species-specific increase in plant traits and their sediment retention functions resulted in the marked differences between sediment C_{org} stocks in connected *P. coarctata* and *M. wightiana* meadows (Fig. 5), which needs further exploration in combination with other local factors such as seasonality.

The positive influence of connectivity on increased N inflow and subsequent increase in biomass C_{org} stocks has been observed for other saltmarsh species in China and South Africa (Raw et al., 2019; Yando et al., 2016). An increase in sediment C_{org} stocks due to cross-habitat subsides of carbon and nutrients across connected habitats with mangroves has been observed for various saltmarsh species globally (Banda et al., 2021a; Doughty et al., 2016; Owers et al., 2022; Raw et al., 2019; Simpson et al., 2017). However, there are no such connectivity studies from tropical saltmarshes (Table 2) and this study serves as a baseline in that direction. The sediment C_{org} stocks in both individual and connected saltmarsh species in this study (7.21 to 25.81 Mg C ha^{-1}) were lower than surface sediment (top 10 cm) C stocks observed in *P. coarctata* meadows from the Bhitarkanika National Park (BNK), Odisha but higher than those reported from the Sundarbans National Park, West Bengal, India (Table 2). These marked differences are attributed to varying shoreline stability: Sundarbans experience significant sediment erosion, whereas the BNK has relatively stable shorelines (Banerjee et al., 2022; Chowdhury et al., 2023). Interestingly, no prior studies provide sediment or biomass C stocks data on *M. wightiana* meadows from India, highlighting the novelty of this study. Notably, the C stocks in connected saltmarsh meadows of this study has higher sediment C stocks than BNK degraded mangrove ecosystems (Table 2), showcasing the importance of these connected saltmarsh habitats in carbon sequestration.

Similarly, the saltmarsh sediment C stocks of this study were compared with other tropical saltmarsh ecosystems globally (Table 2). The sediment C stocks observed for both species in this study were found to be within the sediment C_{org} stocks range for saltmarsh meadows along the U.S. coast (12.88 to 49 Mg C ha $^{-1}$) but were lower than those in tropical saltmarshes from South Africa, Australia and China (Banda et al., 2021a; Raw et al., 2019; Fu et al., 2021; Owers et al., 2022). These variations in saltmarsh C_{org} stocks reflects the difference in local environmental conditions, hydrodynamics and species-specific C_{org} accumulation mechanisms which has been highlighted recently in European and Australian saltmarshes (de los Santos et al., 2023; Kelleway et al., 2017; Leiva-Dueñas et al., 2024). Furthermore, the differences in C_{org} stocks in our studies with global saltmarsh meadows may be attributed to high riverine inputs during Indian monsoon and tidal flows, and the low water residence time in our study locations. Such a hydrodynamics could result in flushing out of sedimentary OM, as observed in *P. coarctata* meadows from one of the study locations (Saha et al., 2022). However, the *P. coarctata* plants have adapted to inhabiting these highly dynamic zones by increasing their BG-biomass, which is evident in this study in both individual and connected *P. coarctata* meadows (Table 1). Furthermore, the observed species-specific utilization of available sediment N, can lead to either positive or negative relationship (Supplementary Figure, S5) and subsequent growth and productivity of plants (Alldred et al., 2017). These relationships explain the higher effect of AG:BG ratios towards sediment C_{org} stocks saltmarsh (Fig. 4). This study also highlights that both individual and connected saltmarsh

Table 2
Comparison of saltmarsh sediment carbon stocks (mean ± SD) or as range in this study to various other saltmarsh and mangroves (only from Odisha coast) studies across India and other tropical saltmarsh regions of the world from literature review. Individual (In), Connected (Ad). # (saltmarsh meadows in presence of mangroves).

Ecosystem (species)	Location	Soil core depth (cm)	Mean sediment Corg stocks (Mg C ha^{-1})	Reference
Saltmarsh (*P. coarctata*)	Odisha, India	50	7.21 ± 3.78 (In) 23.45 ± 12.54 (Ad)	**This study**
Saltmarsh (*M. wightiana*)			9.79 ± 5.34 (In) 25.81 ± 13.28 (Ad)	
#Saltmarsh + Mangroves *(P. coarctata)*	Odisha, India	10	42.08 ± 1.15	Banerjee et al., 2022
#Saltmarsh +Mangroves *(P. coarctata)*	Sundarbans, West Bengal, India	10	7.0	Chowdhury et al., 2023
Mix saltmarsh species	Tamil Naidu, India	30	10–60	Kaviarasan et al., 2019
Saltmarsh (*Salicornia brachiata*)	Gujarat, India	30	4.5–8.2	Rathore et al., 2016
Saltmarsh (*Suaeda maritima*)	Sundarbans, West Bengal, India	30	9.4–13.4	Das et al., 2015
Mangroves	Mahanadi Mangroves, Odisha, India	30	54.3 ± 7.4	Sahu et al., 2016
	Bhitarkanika Mangroves, Odisha, India	30	102.5 ± 12.3	Bhomia et al., 2016
	Bhitarkanika mangroves, Odisha, India	30	54.3 ± 3.0	Pattnayak et al., 2019
	Bhitarkanika mangroves, Odisha, India	10	16.49 ± 6.59	Rasquinha and Mishra, 2021
Mix Tropical Saltmarsh	USA	50	49 ± 16.99 (In) 41 ± 12.88 (Ad)	Doughty et al., 2016; Simpson et al., 2017
	South Africa	50	109.62 ± 2.61 (In) 110.14 ± 228 (Ad)	Raw et al., 2019; Banda et al., 2021a
	Australia	50	29.16 ± 202 (In) 65.88 ± 28.20 (Ad)	Jones and Russell, 2021; Owers et al., 2022
	China	50	81 (In) 190 (Ad)	Fu et al., 2021

ecosystems of the coast of Odisha has relevant ecosystem C stocks that can help in mitigation of climate change through C sequestration and needs to be incorporated into India's Nationally Determined Contributions (INDCs).

5. Conclusions

To our knowledge, this is for the first time the influence of seascape connectivity with mangroves on data deficient tropical saltmarsh meadows and the cross-habitat subsidies towards increase in sediment and biomass C_{org} stocks has been quantified. The outcomes of this study highlight that seascape connectivity with mangroves, significantly affects the cross-habitat subsidies of sediment grain size fractions, OM and N that directly contributes towards increasing saltmarsh plant traits and sediment C_{org} stocks. Additionally, in connected meadows, saltmarsh sources dominated C contributed to the sediment C pool followed by mangroves sources and POM of marine or terrestrial origin. Future studies need to highlight the, i) seasonal influence of C_{org} out welling from connected habitats, ii) C_{org} data from species-specific adjacent mangroves to generate a better picture of the ecological networks that influence sedimentary C_{org} stocks in tropical conditions and iii) include the adjacent mangrove ecosystem C stocks and assess the cross-habitat subsidy of saltmarsh generated materials in the adjacent mangroves. Most importantly, this study serves as a baseline for saltmarsh C stocks from the Indian sub-continent and suggests more efforts are needed to generate species-specific C stocks of other saltmarsh species. This study highlights saltmarsh ecosystems of the India have C stocks relevant for climate change mitigation and needs to be included in India's NDCs. Better management and conservation of these ecosystems along with mangroves and seagrasses needs to be prioritized to avail their climate change mitigation services.

CRediT authorship contribution statement

Amrit Kumar Mishra: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Arindam Dey:** Writing – original draft, Methodology, Formal analysis, Data curation. **Anjalis Mishra:** Writing – original draft, Methodology, Formal analysis, Data curation. **Sandip Kumar Mohakud:** Writing – original draft, Methodology, Formal analysis, Data curation. **Syed Hilal Farooq:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.178929.

Data availability

Data will be made available on request.

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