

Understanding how nutrient limitation and plant traits influence carbon in mangrove-seagrass coastal ecosystems

Sandra Kammann ^{1,*}, Daniel Arturo Saavedra Hortua ², John S. Kominoski ³, Theresa-Marie Fett, ⁴
Lucy Gwen Gillis ⁵

¹Faculty of Applied Ecology and Phycology, University of Rostock, Rostock, Germany

²EcoSecurities, Geneva, Switzerland

³Institute of Environment and Department of Biological Sciences, Florida International University, Miami, Florida

⁴The Leibniz Centre for Tropical Marine Science (ZMT), Bremen, Germany

⁵International Marine and Dredging Consultants Company (IMDC), Antwerpen, Belgium

Abstract

Mangrove forests and seagrass meadows provide critical ecosystem services, including the accumulation of “blue carbon.” Plants’ functional traits could influence this blue carbon accumulation. To test for interactions among functional traits and blue carbon accumulation, we conducted a study in connected mangrove-seagrass coastal ecosystems in southeast Florida (USA). We quantified how plants’ above-ground traits correlated with sediment nutrient content, and how changes in traits along inland-to-coastal gradients influenced inorganic and organic carbon storage potential. Physical traits of *Thalassia testudinum* were higher at sites with higher sediment phosphorus (SP) and nitrogen (SN) concentrations. Sediment organic carbon concentrations were positively correlated to *T. testudinum* physical traits. Root density, pneumatophore abundance, specific leaf area, leaf toughness, leaf nitrogen, and phosphorus content were positively correlated with SN concentrations in the mangrove forest coastal fringe. Mangrove leaf thickness and root complexity index were negatively correlated with SP concentrations in the coastal fringe. Our results also indicate that seagrass above-ground traits and blue carbon were strongly correlated in areas with higher sediment nutrient concentrations. Moreover, mangrove root complexity is coupled with phosphorus limitation, whereby highly complex root systems develop with decreasing phosphorus concentrations. Distinct functional traits of plants drive variation in carbon retention capacity even in interconnected ecosystems.

Coastal ecosystems, like mangrove forests and seagrass meadows, provide various ecosystem services, including carbon sequestration (Duarte et al. 2010; Donato et al. 2011). Coastal wetlands store large amounts of carbon in their above-ground

biomass (AGB) and below-ground biomass (BGB), as well as in sediments (Donato et al. 2011). Carbon stored in coastal and marine ecosystems is summarized as “blue carbon.” Some marine ecosystems (e.g., coral reefs) do not meet the key criteria to become a blue carbon ecosystem. Others (e.g., macroalgae) are under ongoing scientific investigation and might one in the future. Mangrove forests and seagrass beds are already established blue carbon ecosystems (Nellemann et al. 2009; Lovelock and Duarte 2019). Although seagrass meadows and mangrove forests occupy a small proportion of global coastal areas (mangrove forests ~138,000 km²; seagrass meadows ~330,000 km²), their carbon burial rates are estimated in mangrove forests at 24 Tg C yr⁻¹ (Alongi 2014) and 48–112 Tg C yr⁻¹ in seagrass meadows (McLeod et al. 2011). Tides connect mangrove forests with near-shore waters and support exchanges of carbon-rich organic matter and nutrients, such as nitrogen and phosphorus (Feller et al. 2010; Chen et al. 2017). Ecological and hydrological connectivity driven by pulses of fresh and marine water can stimulate both localized and adjacent ecosystem productivity and carbon storage (Odum 1980; Odum et al. 1995; Ward et al. 2017). Thereby, not only tides are of importance.

*Correspondence: sandra.kammann@uni-rostock.de

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

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

Author Contribution Statement: S.K., L.G.G., and D.S.-H. conceived the ideas and designed methodology. S.K. and D.S.-H. collected the data in 2018, and analyzed the field samples in the laboratories of Florida Bay District Interagency Science Centre, Key Largo, Florida, USA, and at the Leibniz Centre for Tropical Marine Research, Bremen, Germany. The data were statistically analyzed by D.S.-H. and T.F. S.K. and L.G.G. led the writing of the manuscript. All authors contributed substantially to drafting the manuscript and gave final approval for publication.

Special Issue: Carbon sequestration in Aquatic Ecosystems. Edited by: Isaac R. Santos, Vanessa Hatje, Oscar Serrano, David Bastviken, Dorte Krause-Jensen and Deputy Editor Julia C. Mullarney

human impacts (de los Santos et al. 2013). The availability of nitrogen and phosphorus in mangrove forests and seagrass meadows could alter development processes in their plant attributes and patterns, which has recently gained great interest in relation to ecosystem functioning (Ravaglioli et al. 2017; Dangremond et al. 2020). Fertilization experiments highlighted an area-dependent nutrient limitation of nitrogen and phosphorus with mangroves (Feller 1995; Lovelock et al. 2004, 2006b). Similar patterns have also been detected within seagrass meadows, revealing phosphorus limitation and retention in Florida Bay (Fourqurean et al. 1992; Armitage et al. 2011; Alexandre et al. 2021).

Seagrasses and mangroves have several key functional traits associated with above-ground and below-ground components. Trapping of sediment organic and inorganic matter is especially supported by above-ground components such as mangrove stilt-roots and seagrass shoots (Fig. 1a). In addition to above-ground traits of coastal vegetation, multiple interacting physical factors like tidal regimes, hydrodynamics, temperature, and sedimentation lead to a network of mechanisms that can promote carbon sequestration. Structural traits like leaf hardness and thickness are strongly related to nutrient conservation and associated with the survival of *Rhizophora mangle* in phosphorus-limited ecosystems (Feller 1995).

Nutrient effects on plant trait expression have been studied closely in field and laboratory settings (Fujita et al. 2013; Armitage and Fourqurean 2016). Reef et al. (2010) concluded that mangroves achieved high growth rates under nonlimited nutrient conditions. These findings support the assumption that high nutrient availability could promote the manifestation of traits such as higher relative AGB (Fig. 1b). Whereas lower soil nutrients would enhance BGB, especially in terms of fine root biomass (Fig. 1b) (Charles et al. 2020). Powell et al. (1989) showed a similar pattern within a seagrass meadow in Florida Bay that nutrient addition increased areal leaf production and standing crop of *T. testudinum* and *Halodule wrightii*. The standing crop of *T. testudinum* was produced primarily through longer, wider and longer blades and increased short shoot density by *H. wrightii*. Changes in trait structure alter how traits manifest themselves and therefore could either enhance or diminish their influence on the environment.

Nitrogen and phosphorus limitations influence different plant traits, especially in seagrass meadows (Fourqurean et al. 1992; Armitage et al. 2011), but how these processes feed back onto carbon storage in coastal ecosystems is uncertain. For example, in seagrass meadows, higher phosphorus and nitrogen sediment contents increase above-ground canopy components (Agawin et al. 1996; Barry et al. 2017), which could have a greater effect on hydrodynamics facilitating carbon deposition (Fig. 1b). In mangrove forests, nitrogen availability has increased above-ground growth (Lovelock et al. 2006b), this could increase potential leaf litter input (Fig. 1b). Limited SP can increase above-ground root components (Hayes et al. 2017). That could lead to an increase in the

trapping capacity of material and consequently to sediment and carbon retention (Fig. 1b).

Our objective was to quantify how variations in sediment nutrient availability is related to changes in traits of connected mangrove forests and seagrass meadows. We measured functional traits (Fig. 1a) associated with surficial carbon trapping. For simplicity we chose among different classifications of traits (i.e., community, morphological, mechanical and chemical), which we categorized as either physical or chemical traits. The mechanisms associated with plant traits across connected ecosystems could increase the quantity of sediment carbon in both mangrove forests and seagrass meadows, but these mechanisms also change with nutrient availability. To understand interactions among nutrients, traits, and carbon, we tested two research questions: (1) How do physical and chemical traits of mangroves and seagrasses vary with sediment nitrogen (SN) and phosphorus (SP) concentrations? and (2) How do these traits function as drivers of inorganic and organic carbon accumulation in connected mangrove-seagrass ecosystems? We hypothesized that functional trait changes of mangrove and seagrass plants alter carbon accumulation. This information can be used to help make predictions about where carbon storage potential is highest or limited for management or conservation.

Material and methods

Study sites

Our study area was located in Biscayne National Park, Homestead, Florida (USA), which has a subtropical climate with distinctive annual wet and dry seasons. Dry season brings a mild climate with an average air temperature of 25°C in January. The climate is hot and humid in the wet season with average air temperatures between 24°C and 29°C. Biscayne Bay is a shallow semi-enclosed lagoon with a tidal range of 60 cm and is characterized by freshwater inputs from canals draining the coast that mix with saltwater from the sea. Freshwater flows transport nutrients from inland into the bay. Data were collected between February and March 2018. Samples were collected along $n = 12$ transects (approx. 1.2 km) (Fig. 2). This gradient represents two connected intertidal ecosystems (mangrove forests and seagrass meadows). Points 1 through 3 of each transect were located within the seagrass meadow. Transect numbering continued with point 4 representing fringing mangroves. Point 6 was the westernmost in the mangrove forests (Fig. 2). Seagrass meadows were dominated by *T. testudinum*. Only a few shoots of *H. wrightii* were identified in shallow water. Mangrove forests were dominated by *R. mangle*, individuals of *Avicennia germinans* and *Laguncularia racemosa* were observed.

Sampling points were separated from each other by ~200 m within each ecosystem. Three points per transect were located in the seagrass meadow and three within the adjacent mangrove forest (except for one transect). From the total sampling points ($n = 70$), $n = 36$ were located within the seagrass meadow, and $n = 34$ inside the mangrove forest (two points were removed due to inaccessible terrain). At each

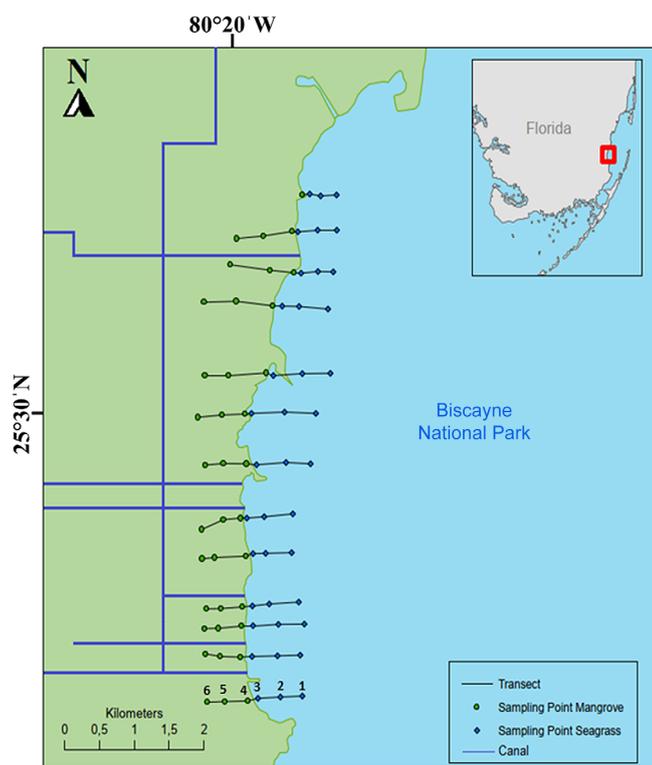


Fig. 2. Map showing the study area of Florida (inset picture) and a section of Biscayne National Park (Florida, USA). See example of the distribution of points in the most southern transect, from left to right: Point 6 is the closest to the terrestrial ecosystem. Point 1 is at the ocean site.

sampling point along all transects, a sediment core was taken and a quadrat (0.25 m^2) was placed five-times randomly in proximity to the core. The quadrats ($n = 5$) were used as biological replicates per point. Within each quadrat, the same set of functional traits was measured (see “Methods” section). Five seagrass shoots of *T. testudinum*, the dominant species in this area, were randomly collected within each single quadrat and stored in labeled, plastic bags filled with seawater to reduce stress during shoot transportation. These shoots were further analyzed for plant chemistry (see “Chemical traits” section). Shoots of *H. wrightii* were not collected due to their rare occurrence (small quantity for statistical tests). In the mangrove forest, five *R. mangle* trees per point were chosen for analyses of functional trait parameters. The sampled trees grew within a distance of 2–3 m in proximity to the sediment core. Mangrove saplings <50 cm were excluded from the analysis. Furthermore, one leaf per branch was picked from the exterior canopy for leaf trait analysis. In total four leaves from each tree were collected ($n = 20$ per sampling point). Monitored branches grew at an approximately height of 2–2.5 m in the fringing forest (point 4 of all transects) and at approximately 0.7–1.5 m in the dwarf forest (points 5 and 6 at all transects). None of these branches were part of the top canopy and therefore for the majority of day light hours were under shade

conditions. Only leaves from the 2nd order (the 2nd leaf pair after the apical bud) were picked to guarantee approximately the same leaf age (Supporting Information Fig. S1). This sampling design took five individuals (mangrove trees and seagrass shoots) per sampling point along each transect, into account for further trait analysis. Each tree and shoot at one point represent a biological replicate, in the statistical analysis the replicates were used for the calculation of the mean and standard deviation of the measured parameters.

Sediment cores

Sediment was sampled using a polyvinyl chloride PVC tube (30 cm length, 5 cm diameter). At each sampling point of all transects ($n = 70$) one core was taken. The surface sediment section (0–5 cm) was used for further analyses. We expected that the high trapping capacity of mangrove forests and seagrass meadows would lead to an accumulation of leaf litter on the sediment surface (Gillis et al. 2014a). De Boer (2000) highlighted the decomposition of this trapped organic material as the dominant nutrient source of the intertidal system. Therefore, we measured carbon and nutrients in surface sediments (0–5 cm). This allowed estimation of the potential connection between the nutrient-induced traits development and blue carbon storage. Samples were stored in labeled, plastic bags, placed on ice, and transported to the Florida Bay District Interagency Science Center, Key Largo, Florida, USA. Root material was removed from cores, and samples were oven-dried at 50°C for ~ 72 h until a constant weight. Dried samples were then transported to the analytical laboratory at the Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany.

These samples were homogenized, and three portions (~ 15 mg) were taken. One portion was wrapped in tin caps to measure total sediment carbon, while the 2nd was wrapped inside silver caps and acidified, to measure sediment organic carbon (SOC) and SN. Both portions were analyzed by combustion in an elemental analyzer (EuroVector EA 3000) using acetanilide 4 (71.6% C) for calibration and low soil standard (OAS4) as standard (precision of 0.06% for carbon and 0.01% for total nitrogen in sediments). Percentages of sediment inorganic carbon (SIC) were calculated by subtracting SOC from total sediment carbon. The 3rd portion was used for phosphorus analyses applying the hydrochloric acid digestion method. Samples were continuously heated at 110°C for 30 min during digestion. After cooling to room temperature, $325 \mu\text{L}$ of this digest was added to $6.5 \mu\text{L}$ of acidic ascorbic acid and $6.5 \mu\text{L}$ of molybdate mix solution into a 96-well plate. The measurement was completed after 10–30 min at 880 or 810 nm according to a calibration curve with PO_4^- standards from 0 to $18 \mu\text{M}$ PO_4^- P with a TECAN Infinite M200 microplate reader. As reference material SRM1515 (apple leaves with $1593 \mu\text{g P g}^{-1}$) was used. All parameters were reported in percentage of dry tissue.

Trait measurements—physical traits—seagrass meadows

At all sampling quadrats per point ($n = 5$), canopy height (cm), shoot density (number of shoots m^{-2}), and coverage per species (%) were recorded. BGB and AGB were measured as follows. A 2nd sediment core (30 cm depth \times 5 cm diameter) was collected close to the 1st core which was only used for elemental analyses of the sediment surface. The total 2nd core was used for BGB calculation. Plant material above the sediment surface of the biomass core was removed and separately stored in a plastic bag. In the lab, the fresh weight of the removed plant material was measured and the shoots were dried later in the oven for 2 d at 50°C and weighed again to calculate the AGB (Ohaus, Voyager, Switzerland). The above-ground area of each core represented 19.6349541 cm^2 . This value was rounded-up to 20 cm^2 for further mathematical analysis. Therefore, the seagrass biomass values were multiplied by 500 to represent a square meter. The sediment within the core was washed within a fine mesh sieve (2 mm mesh size) to remove coarse debris, like shells and undecomposed organic material, in preparation to calculate the BGB. The freshly taken sediment core was weighed and then oven-dried for 2–3 d at 50°C and weighed again to calculate BGB as dry mass. As for AGB, the BGB was standardized per m^2 . Roots of less than 2 mm length were excluded due to the difficulty of distinguishing them from debris and litter.

Within quadrats at each point ($n = 5$), five seagrass shoots were collected. The number of leaves per shoot was counted. The 2nd seagrass leaf counted from the inner shoot to the older leaves on the outside was separated from the shoot. In total $n = 117$ leaves were sampled. Leaf length (l) and width (w) were measured and the values were used to calculate the leaf area index (LAI).

$$LAI = l \times w. \quad (1)$$

In addition, leaf thickness (lt) was measured. Values of leaf thickness and width were used to calculate the cross-sectional area (mm^2).

$$\text{Cross-sectional area} = (lt \times w) \times 100. \quad (2)$$

Leaf toughness was estimated by measuring the force needed to penetrate the leaf tissue with a simplified penetrometer (Graça and Zimmer 2005).

Trait measurements—physical traits—mangrove forests

At each sampling point in the mangrove forest, a picture of each sampling quadrat (5 per point as biological replicates) was taken to determine pneumatophore density (pneumatophore m^{-2}), and root density (roots m^{-2}) via image evaluation. The pneumatophore height (cm) was measured in situ. Mangrove BGB calculation followed the same procedure as for the seagrass meadow. Mangrove canopy height (m) was estimated visually, and the basal area of individual mangroves

was estimated using a meter tape. AGB (m^2) was calculated following established relationships from measured height and basal area (Komiya et al. 2008). Pictures of collected mangrove leaves ($n = 680$ from 34 sampling points) were taken from above a plate. These pictures were later used for LAI (cm^2) calculation with ImageJ[®]. Also, leaf thickness (cm) was measured. For both types of leaf samples (mangroves and seagrasses), leaf dry weight (DWg) was recorded with a digital scale (Ohaus, Voyager, Switzerland). Values for DWg and LA were used to calculate the specific leaf area (SLA, $cm^2 DWg^{-1}$).

$$SLA = LA DWg^{-1}. \quad (3)$$

Five *R. mangle* trees in proximity to sediment cores were randomly chosen for tree height and stem circumference. Due to dwarf mangrove trees at points 5 and 6, a measuring tape was used for allometric measures. In point 4, tree height was visually estimated having length references due to tall trees. The number of aerial roots arising from the trunk (prop roots) was counted (prop roots tree⁻¹). The uppermost aerial root of each tree was used to sample the total number of root columns and arches, length (cm) of each arch, and distance (cm) from the last root tip connected to the sediment to the trunk (Supporting Information Fig. S1). All of the root data were used to evaluate the above-ground aerial root architecture of *R. mangle* per tree. A root complexity index (RCI) was designed to differentiate between root complexities magnitudes per tree. The complexity of a root was defined as numbers of columns per root's distance to the trunk. To express root complexity per tree, the complexity value for the single root complexity was then multiplied by the number of prop roots tree⁻¹.

$$RCI = (\text{number of columns} \times \text{distance to trunk}) \times \text{prop roots tree}^{-1}. \quad (4)$$

Mangrove leaf toughness was measured with the same protocol as seagrass leaves and $n = 680$ mangrove leaves (*R. mangle*) were tested. The amount of seagrass shoot samples is smaller since the research permit limited seagrass tissue collection.

Trait measurements—chemical traits—seagrass meadows and mangrove forests

For chemical analyses, plant tissue samples (mangrove leaves and seagrass shoots) were returned to the laboratory in Key Largo, Florida, oven-dried at 50°C for 72 h until weight was constant, and then milled until homogenized (Retsch ZM 100) at ZMT. Milled samples were prepared for chemical analyses with the Euro EA3000 Element Analyzer, analyzing carbon and nitrogen by flash combustion, with a precision of 0.36% for carbon and 0.05% for total nitrogen for plant materials (apple leaves standard SRM1515 reference material). Total organic carbon (TOC) was determined after removing

carbonate carbon by acidification with hydrochloric acid in situ. TOC is subtracted from the total carbon to calculate the total inorganic carbon (TIC) of a given sample. Total phosphorus was measured using spectrophotometric determination of orthophosphate. For digestion of organic material, the alkaline persulfate digestion was used. All parameters are given in %. Carbon-to-nitrogen ratio (C : N molar ratio) was calculated after chemical analysis.

Statistical analyses

All statistical analyses were conducted in R version 4.0.1 (R Core Team 2020, <https://www.R-project.org>). Data were tested for normality using the Shapiro-Wilks test. To test for significant differences of SOC, inorganic carbon, and phosphorus and nitrogen between mangroves and seagrass meadows, we conducted either a *T*-test (parametric data) or a Mann–Whitney *U*-test (nonparametric data). We used a one-way ANOVA (ANOVA) for normally distributed data and a Kruskal–Wallis test for nonparametric data to test for significant differences between points 1–3 (seagrass meadow with $n = 5$ replicates at each point, 36 points in total) and 4–6 (mangrove forest with $n = 5$ replicates at each point, 34 points in total) and across all points (1–6) with respect to sediment carbon and nutrient (P and N), and plant traits. Models were run separately for each habitat type (mangrove, seagrass). Significant pair-wise differences were compared using Tukey's (parametric data) or Dunn's post hoc test (nonparametric). We used an alpha of 0.05 ($p < 0.05$) to determine statistically significant differences.

We investigated relationships among plant physical and chemical traits for mangroves and seagrasses separately using a principal component (PC) analysis. For performing a PC analysis on the data matrix the R function `prcomp()` was used. Within this function, we used arguments to center and scale the data. Subsequently data were \log_{10} -transformed for approximate normality and homogeneity of residuals. A PC analysis does not admit NA values in the data matrix. Therefore, we used the R package `missMDA` (Josse and Husson 2016) to estimate the number of components for the PC analysis by “K-fold” cross-validation with the function `estim_ncpPCA()`. Then, missing values were imputed using the function `imputePCA()` with the iterative PC analysis algorithm “EM.” BGB of mangroves was not included in the PC analysis, since we did not have allometric equations that allowed us to calculate the BGB for dwarf trees.

Extracted PC axis scores were used as a measure of trait coordination, instead of taking traits individually. PC axis scores were reported if they had a correlation coefficient of at least 0.6 and a significant value below 0.05. Selected PC axis scores were used to analyze the influence (1) of sediment nutrient (N % and P %) on trait development and further (2) the influence of traits on carbon (%) in the sediment. Correlation analyses between extracted PC axes and nutrients and carbon (%) in the sediment were conducted. To determine the

correlation relationship, we used the Pearson (*R*, parametric data) and Spearman rank correlation coefficient (ρ , nonparametric data). With scatter plots significant correlations (correlation coefficient of 0.6 and above, and a *p*-value below 0.05) were visualized.

Results

Sediment nutrients

The sediment nitrogen (SN) (mean: $1.58\% \pm 0.84\%$) in mangrove forests exceeded mean SN values in seagrass meadows ($0.48\% \pm 0.22\%$) and was significantly different between the two ecosystems (Fig. 3a; Supporting Information Table S1). Mean sediment phosphorus (SP) in the mangrove forest ($0.03\% \pm 0.02\%$) was significantly higher than in the seagrass meadow ($0.01\% \pm 0.004\%$) (Fig. 3b; Supporting Information Table S1). Within the seagrass meadow, no significant differences between points 1 and 3 for SN and SP were detected (Supporting Information Table S2). Whereas in the mangrove forest, SP differed significantly between points 4 and 6. Dunn's post hoc test detected significant differences between P4 and P5 and P4 and P6 (Supporting Information Table S2). The SN in the mangrove forest showed no significant differences between points 4 and 6 (Supporting Information Table S2).

Sediment carbon

Mangrove forests SOC ($22.11\% \pm 11.8\%$) exceeded SOC values in seagrass meadows ($4.67\% \pm 2.3\%$) and was significantly different between the two ecosystems (Fig. 3c; Supporting Information Table S1). The mean value of SIC was significantly higher in the seagrass meadow ($8.4\% \pm 1.1\%$) than in the mangrove forest ($5.58\% \pm 3.45\%$) (Fig. 3d; Supporting Information Table S1). Results for sediment carbon parameters (TOC, TIC, C : N) showed significant differences between the two ecosystems when values per ecosystem were pooled. Whereas within each ecosystem no significant differences between points (1–3 seagrass meadow and 4–6 mangrove forest) for SOC and SIC could be ascertained (Supporting Information Table S2).

Variation in traits across ecosystems

Coverage (%) of *H. wrightii*, however, showed higher coverage at point 3 compared to points 1 and 2 (Supporting Information Table S3). *H. wrightii*, also had higher shoot density at point 3 vs. point 2 (Supporting Information Table S3). Significant differences were detected for seagrass (*T. testudinum*) leaves TOC and TIC (%) across points, TOC was higher at point 1 compared to point 3, whereas TIC was greater at point 3 than to points 1 and 2 (Supporting Information Table S3). No differences were detected in any other seagrass meadow or plant traits (Supporting Information Table S3).

As *R. mangle* was the dominant species at all mangrove sites, all further analyses did not consider the sporadic occurrence of other species. Differences in AGB, canopy height (m), SLA ($\text{cm}^2 \text{g}^{-1}$), root complexity index, and number of prop

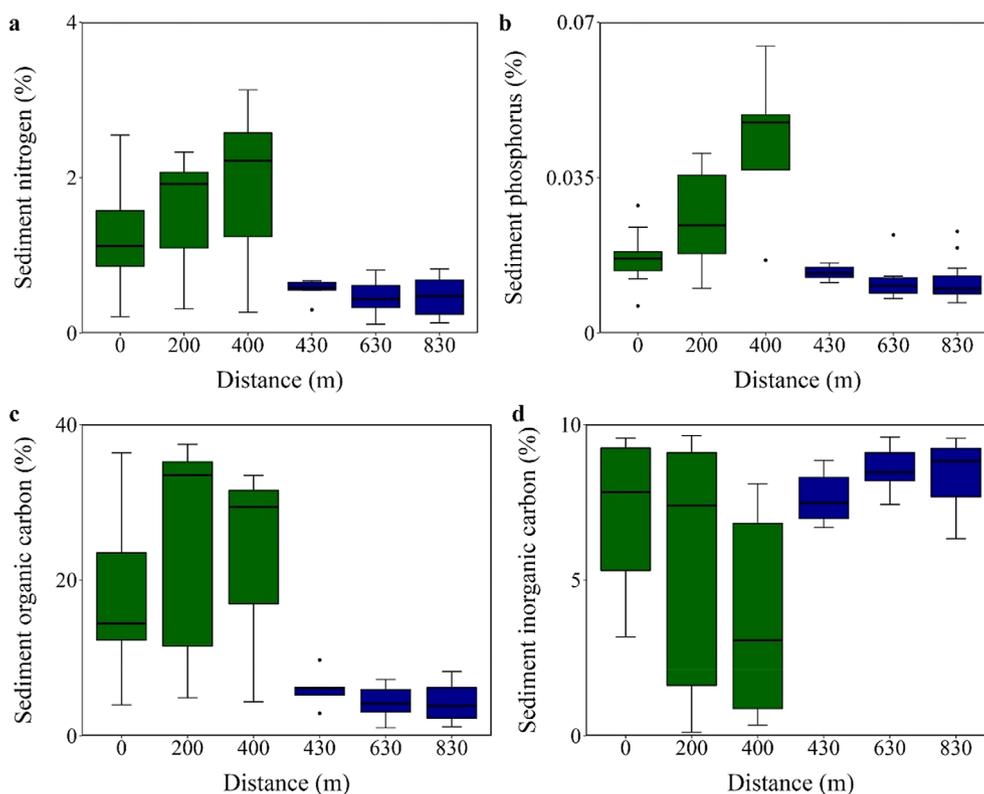


Fig. 3. Boxplots showing changing sediment characteristics across the two ecosystems, mangrove forests (green) and seagrass meadows (blue): (a) and (b) represent SN (%) and SP (%), respectively; (c) and (d) show SOC (%) and SIC (%), respectively. Values expressed in percentage of the sediment dry weight. Lines in the boxes represent the median. Whisker ends represent the minimum and the maximum of the values per point. Outliers are visualized as dots.

roots per tree were detected along transects. For all these traits, values were higher at point 4 compared to points 5 and 6 (Supporting Information Table S4). Mean root density also showed a significant difference across points; root density (roots m^{-2}) was lower for point 4 than for points 5 and 6 (Supporting Information Table S4). Pneumatophores were only found in point 4 they had a mean length of 0.2 ± 0.05 m and a density of 21.9 pneumatophores m^{-2} . Leaf thickness (mm) showed a significant different along transects, being greatest at point 6 compared to points 4 and 5 (Supporting Information Table S4). A significant difference in leaf toughness ($g\ mm^{-2}$) was also found, which was higher at point 6 compared to point 4 (Supporting Information Table S4). The majority of mean values for mangrove leaves TIC (%) per point were under $>1\%$ and therefore negligible for analysis. There were differences in mangrove leaf TOC content (%) along transects, comparing points 4 ($43.5\% \pm 0.9\%$) and 5 ($44.9\% \pm 0.4\%$) and points 4 and 6 ($45.4\% \pm 1.2\%$) (Supporting Information Table S4).

Physical and chemical trait covariation

Based on PC analysis results of six chemical and ten physical traits of seagrass meadows could be summarized by three PCs, together accounting for 91.2% of total variance (Fig. 4;

Supporting Information Table S5). The 1st PC axis explained approximately 62.7% of variance and was heavily loaded on physical traits such as ratio for AGB and BGB, and chemical

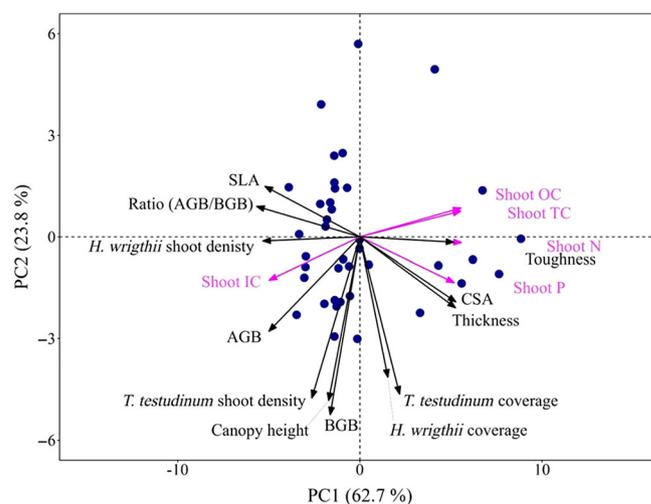


Fig. 4. Results of PC analysis for traits in seagrass meadows (all points) for PC1 and PC2. Loading scores for each trait on all components of PCs are given in the Supporting Information Table S5. Traits with red arrows are chemical traits and black arrows are physical traits. All traits were \log_{10} transformed, centered, and scaled.

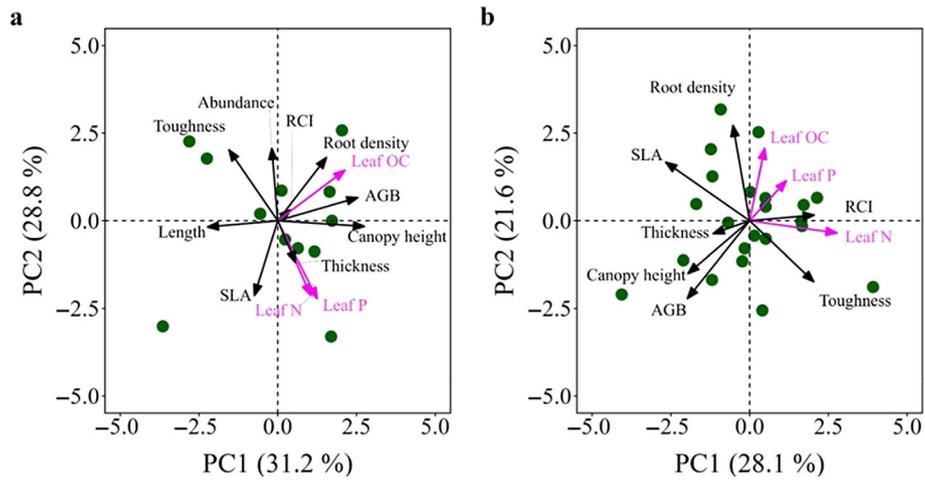


Fig. 5. Results of PC analysis for traits in mangrove forests: (a) point 4 and (b) points 5/6. Loading scores for each trait on each component of PCs are given in the Supporting Information Table S5. Red arrows are chemical traits and black arrows are physical traits. All traits were \log_{10} transformed and centered.

traits such as total nitrogen and carbon in shoots. The 2nd PC axis described an additional 23.8% of variance and was more loaded on *H. wrightii* and *T. testudinum* coverage, *T. testudinum* canopy height, *T. testudinum* shoot density, BGB and leaf cross sectional area and thickness. The 3rd PC described 4.5% and corresponded to leaf toughness. High correlation was seen between these groups of traits (Supporting Information Table S7).

As we found significant differences across the majority of chemical and physical traits between mangrove forest points 4, and points 5/6, separate PC analysis were completed on point 4 and points 5/6. Mangrove PC analysis for point 4, and points 5/6 showed the three chemical traits and nine physical traits (point 4)/seven physical traits (points 5/6) could be

summarized by three PCs, which together accounted for 71.4% of total variance for point 4 (Fig. 5a; Supporting Information Table S5) and 61.3% of the total variance for points 5/6 (Fig. 5b; Supporting Information Table S5). The 1st PC axis for point 4 explained approximately 31.2% of variance and was loaded on organic carbon of leaves (%), AGB (m^2), canopy height (m) and pneumatophore length (cm). PC2 for point 4 described an additional 28.8% of variance and related to physical traits such as root density (m^2), pneumatophore abundance (m^2), SLA ($cm^2 g^{-1}$) and leaf toughness ($g mm^2$) in addition to two chemical traits, phosphorus and nitrogen content of leaves (%). PC3 explained 11.4% of variance and was loaded for leaf thickness (mm) and root complexity. High correlation was seen between these groups of traits (Supporting

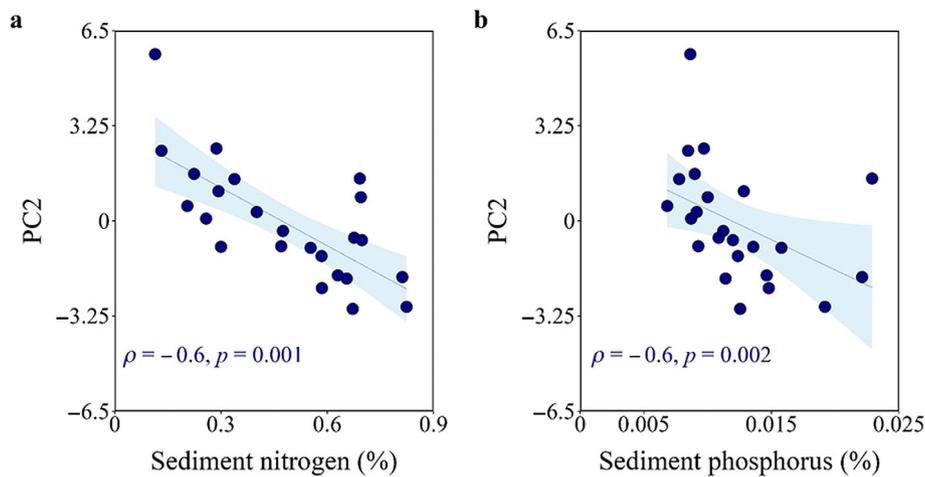


Fig. 6. Scatter plots visualizing the extracted PC2 for seagrass sites (*Halodule wrightii* and *Thalassia testudinum* coverage, *T. testudinum* canopy height, *T. testudinum* shoot density, BGB, leaf cross-sectional area and thickness) vs. sediment nitrogen or phosphorus (%). (a) PC2 vs. sediment nitrogen (%) and (b) PC2 vs. SP (%). ρ symbolizes Spearman's correlation coefficient, p represents the significance level.

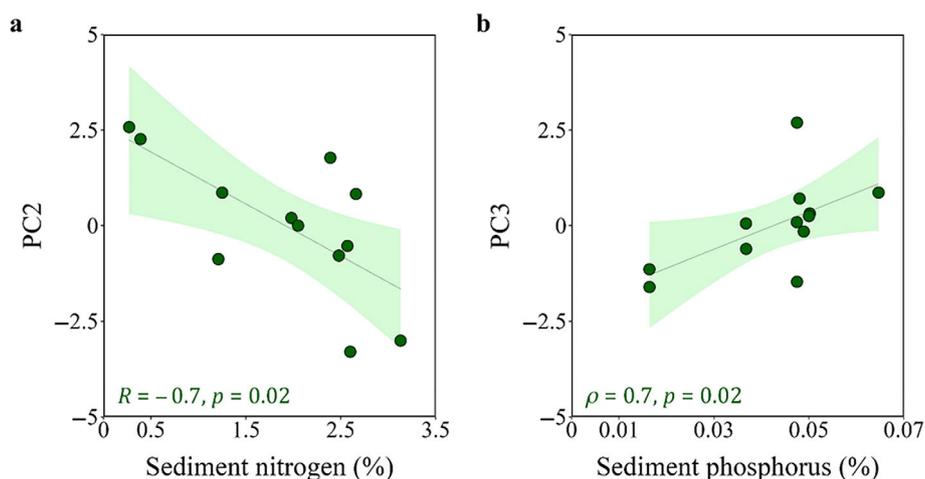


Fig. 7. Scatter plots visualizing the extracted PC2 component axis for mangrove sites (mangroves: root density, pneumatophore abundance, SLA, leaf toughness, phosphorus, and nitrogen content of leaves) vs. SN (%) (**a**) and the extracted PC3 component axis (leaf thickness and root complexity index) vs. SP (%) (**b**). Both panels represent mangrove forest point 4. R represents the Pearson correlation coefficient and ρ symbolizes Spearman's correlation coefficient, p represents the significance level.

Information Table S8). Mangrove points 5/6, PC1 explained 28.1% of variance, mainly related to root complexity, SLA ($\text{cm}^2 \text{g}^{-1}$), leaf toughness (g mm^{-2}) and nitrogen content in leaves (%) and PC2 (points 5/6) described 21.6% of variance and was related to root density (m^2) and AGB (m^2). High correlation was seen between these groups of traits (Supporting Information Table S9). PC3 (points 5/6) described 11.7% of variance and was not significantly loaded toward any traits.

Nutrients and trait development

For seagrass meadows we used extracted PC2 axis scores (Supporting Information Table S5) as a measure of trait coordination because this was the only PC showing a significant

correlation with SN and SP (Supporting Information Table S6). These traits were found to have a significant negative correlation with SN (Fig. 6a) and SP (Fig. 6b). PC2 was negatively correlated with associated physical traits indicating higher nitrogen and phosphorus showed increasing values of these traits.

For mangrove forests at point 4, we used extracted PC axis scores from PC2 for nitrogen sediment and PC3 for phosphorus sediment (Supporting Information Table S5) as a measure of trait coordination. We found a significant negative correlation between nitrogen and PC2 and a positive correlation between PC3 and SP (%) (Fig. 7a,b). PC1 showed no correlation with SN or SP (%) (Supporting Information Table S6).

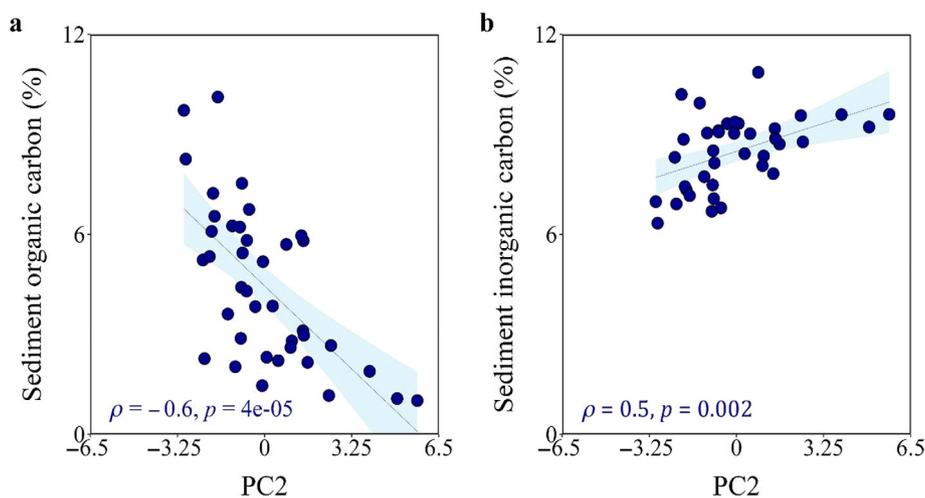


Fig. 8. Scatter plot visualizing the extracted PC2 for seagrass sites (*Halodule wrightii* and *Thalassia testudinum* coverage, *T. testudinum* canopy height, *T. testudinum* shoot density, BGB, leaf cross sectional area and thickness) vs. sediment organic carbon (%). ρ symbolizes Spearman's correlation coefficient, p represents the significance level.

PC2 was negatively correlated with the associated physical and chemical traits, this negative correlation indicates higher nitrogen with decreasing values of these traits. PC3 was positively correlated with the associated physical traits showing increasing phosphorus with increasing values of these traits. No correlation was found between any PCs, nitrogen and phosphorus sediment (%), and mangrove forest points 5 and 6 (Supporting Information Table S6).

Traits and carbon accumulation

For seagrass meadows, we used extracted PC2 axis scores (Supporting Information Table S5) as a measure of trait coordination. For these traits we found a significant negative correlation with SOC and positive correlation with SIC (Fig. 8). PC1 and PC3 showed no correlation with SOC or SIC (Supporting Information Table S6). PC2 was negatively correlated with associated *H. wrightii* and *T. testudinum* traits indicating higher SOC showing increasing values of these traits. PC2 was also positively correlated with associated *H. wrightii* and *T. testudinum* traits indicating higher SIC showing decreasing values of these traits. No correlation was found between any PC's, SOC and SIC, and mangrove

forest points 4 or 5 and 6 (Supporting Information Table S6).

Discussion

Trait responds to nutrient limitation

Our results agreed with previous studies that an increase in nutrient sediment corresponds to an increase in seagrass canopy height and shoot density (Agawin et al. 1996; Barry et al. 2017) (Fig. 9). Seagrass coverage was related to density and canopy height which also showed increasing values with sediment nutrient (Fig. 9).

Higher sediment nutrients corresponded with an increase of AGB, leaf thickness, and cross-sectional area (AGB components). Studies have shown nutrient availability has increased rhizome branching, therefore controlling seagrass plant density (Agawin et al. 1996). Available SN and SP were associated with higher canopy height, that is, leaf length. Longer leaves allow plants to access more lights, which can enhance photosynthesis (Barry et al. 2017). Higher density, canopy height, and coverage could also lead to greater capacity to trap senescent leaves with high nitrogen content either

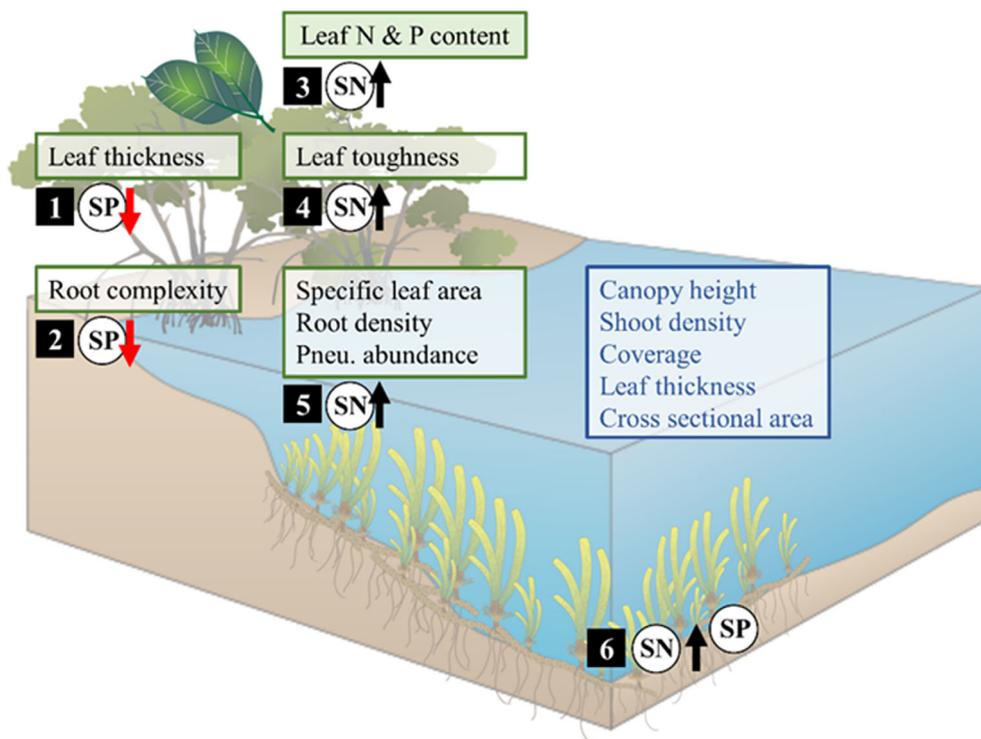


Fig. 9. Showing connected seascape of mangrove forests (left-hand side) and seagrass meadows (right-hand side, submerged). White circles represent sediment nutrient components, SN (%), and SP (%). White boxes are physical traits, the light green box is chemical traits. Numbered mechanisms for correlations (from left to right) are explained as follows: (1) Greater leaf thickness protects inner leaf tissues when phosphorus is limited. (2) Reduced SP equates to trees using their roots to search for phosphorus in the sediment, therefore greater root complexity. (3) Nutrients from mangrove leaves increase nitrogen availability in the sediment. (4) Leaf toughness is an adaptive mechanism against herbivory in nitrogen rich environments. (5) Increased nitrogen available allows for greater AGB and BGB components. (6) Seagrass plant AGB components all increase with higher sediment nutrients as nutrient limitation increases BGB components. Drawings taken from the Integration and Application Network (www.ian.umces.edu/symbols/) and were assembled using biorender.com.

from within the seagrass meadow or outside sources. Fourqurean et al. (1995) also showed higher nutrient impact changes from a *T. testudinum*-dominated seagrass meadow to a *H. wrightii*-dominated meadow. *T. testudinum* requires lower nutrient concentrations than *H. wrightii*. Therefore, it takes advantage in low SN concentration. This agrees with our findings that in areas with higher nutrient loads (close to shore) *H. wrightii* was present while in areas with lower sediment nutrient percentage *T. testudinum* was the dominant species. Nevertheless, epiphytic algae growth tends to cause negative effects on the seagrass shoots they grow on. Less light gets transmitted to the cells by shading the seagrass shoots, reducing photosynthetic efficiency. Asaeda et al. (2004) could show a significant change in morphological attributes and biomass accumulation of leaves of *Potamogeton perfoliatus*, a perennial aquatic plant. The total shoot length and the number of newly recruited shoots were reduced. It has to be considered that such epiphytic algae growth could have influenced the seagrass meadow in this study, having a significant impact on the carbon storage potential.

Overall, the trait gradient within the mangrove forest showed trees with a high AGB, root complexity and number of prop roots per tree fringing the shoreline, and trees with a low root complexity, less prop roots per tree in the interior. Coastal mangroves are often characterized by strong tree height gradients declining from the coastal fringe to interior dwarf mangrove forests (Ross et al. 2001; Lovelock et al. 2005; Charles et al. 2020). The fringing area also showed a significant increase in phosphorus sediment percentage, agreeing with previous work that these mangroves are likely to be nitrogen limited (Feller et al. 2002). Mangrove physical traits responded to both SP and SN; however, all correlations were seen at point 4, which was closest to the ocean zone. Hayes et al. (2017) found nitrogen addition resulting in increased above and below-ground components in mangroves, this agrees with our results as SLA, root density, and pneumatophore abundance all increased with higher SN (Fig. 9).

Leaf toughness increased with SN, previous studies in Belize have also found nitrogen-enriched mangrove trees were sclerophyllous (Feller 1996) (Fig. 9). This may be because these leaves had higher nitrogen content and sclerophylly is an adaptive defense mechanism against herbivory where the leaves become thicker, harder, and resistant to water loss (Feller 1996). Our results showed phosphorus and nitrogen (%) in leaves was related to SN concentration (Fig. 9). Generally, only a small quantity of nutrients in leaves are thought to end up in sediment due to reabsorption of nutrients from leaves just before litter fall (Feller et al. 2002). Smaller quantities of SP force trees to develop mechanisms for nutrient capture and uptake from sediments low in nutrients (McKee 2001). Therefore, a more complex and spacious root system could be a possible strategy. Our findings showed a more complex root system at all points where SP was lowest, indicating trees are developing roots to search for phosphorus in the sediment. Studies have also found fertilization of

sediments with phosphorus or nitrogen has increased BGB (Lovelock et al. 2006a; Hayes et al. 2017) and mangrove seedlings root complexity (Gillis et al. 2019). Leaf thickness decreased with increasing SP, in agreement with a study from Belize (Feller 1996). Variation in hypodermis thickness in mangrove leaves accounts for most differences in leaf thickness, a thick hypodermis may protect photosynthetic tissue in the leaf when mangroves metabolic rate is limited by phosphorus deficiency (Feller 1996) (Fig. 9).

Plant functional traits and blue carbon accumulation

We found increasing nitrogen and phosphorus sediment content, increased canopy height, shoot density, coverage, leaf thickness, leaf cross sectional area in seagrass meadows. These above-ground components were positively correlated with SOC. Within the seagrass meadow, a combination of two separate processes might be a reason for physical traits being correlated with SOC. First, the seagrass canopy can attenuate wave energy and flow turbulence. This leads to indirect trapping of particles. Higher sedimentation of particles reduces resuspension and erosion (Agawin and Duarte 2002). Second, a collision of particles with seagrass leaves leads directly to their loss of momentum and therefore to their capture within the seagrass meadow. We found that higher shoot density (shoots m^{-2}), coverage (%) and canopy height of *T. testudinum* positively correlated with SOC (%). A dense seagrass meadow stabilizes the sediment and reduces carbon resuspension (Dahl 2016). Moreover, Ricart et al. (2015) showed landscape configuration influences exchanges of materials across the coastal seascape. A patchy low-density meadow accumulates less detrital seagrass leaves than a continuous meadow. This study could support these findings since higher carbon was found in areas with higher shoot density and coverage. Breaking force describes the maximum capacity a plant structure has to withstand an extrinsic force. The breaking force is determined by the two components tensile strength and the cross-sectional area. Thicker leaf thickness can cause a larger cross-sectional area, but also influences leaf's flexural stiffness. The stiffer a leaf is, the more constrained is its ability to bend and reconfigure with water movement (de los Santos et al. 2013). These facts lead to the assumption a thick leaf with a big cross-sectional area will have a higher impact on water flow velocity and lead to a higher settling and trapping rate of organic matter, which influences the carbon accumulation in the sediment. Nevertheless, we identified a negative correlation between the above-ground traits and SIC. Gullström et al. (2006) reported calcifying microorganisms living epiphytically on seagrass tissue. Hence a by-product of the calcification process is a reduction in the seawater's pH, and CO_2 from the water body is released into the atmosphere (Frankignoulle and Gattuso 1993).

In less dense seagrass meadows, less calcifying organisms would find seagrass shoots to grow on, less calcification takes place, consequently less CO_2 is released into the atmosphere. The SIC rather stays as a carbon stock than can be considered a potential CO_2 source.

Relative differences in hydrologic connectivity and nutrient limitation create zones of productivity and material exchange along coastal margins (Sheaves 2009). The lack of correlation between mangrove traits and sediment carbon accumulation in our study could be driven by interior, phosphorus-limited dwarf mangrove forests. Dwarf mangroves are lower in productivity and biomass accumulation compared to fringe mangroves (Ross et al. 2001). Furthermore, interior dwarf mangrove forests are less hydrologically connected to marine nutrient subsidies and adjacent ecosystems such as seagrass meadows than fringe mangrove forests, this reduction in hydrological connectivity limits the exchange of nutrient and matter to and from these mangroves and perpetuates the nutrient-limited dwarf growth form driven by localized nutrient-poor conditions. Consequently, carbon burial rates are lower in dwarf forests compared to higher productivity fringe mangrove forests (Ross et al. 2001). In fringe mangrove forests, tidal exchange driven by pulsing marine water can stimulate both localized mangrove and adjacent seagrass productivity (Odum 1980; Odum et al. 1995). The exchange of allochthonous production of organic matter and nutrients in connected mangrove-seagrass ecosystems facilitates in situ plant traits and carbon storage. Coastal ecosystems are connected through lateral subsidies of carbon and nutrients supplied by tidal exchange and facilitated by the high trapping capacity of vegetation. Odum et al. (1995) showed the impact on those water-flow regimes not only leads to an adaptation of the affected organisms, but also causes an enhancement in productivity. The outwelling of carbon-rich plant material due to the tides may exceed its burial into nearshore sediments (Odum 1980). The pulsing of tides leads to a continuous outwelling of dissolved organic and inorganic nutrients, as well as particular organic carbon (Alongi 2020). This shows that plant trait effects on carbon accumulation may be strengthened or mitigated by repeating tidal events. The relation and possible feed backs of plant traits and connectivity across coastal adjacent ecosystems should be considered as an important long-term carbon sequestration mechanism that would increase carbon stocks in mangrove forest and seagrass meadows. Further research using tools such as isotopes (Gillis et al. 2014b) to determine the origin of carbon as well as nutrients would be important in identifying these feedbacks for carbon sequestration.

Organic carbon content in mangrove soils can also be affected by geophysical processes. An increased nutrient input can enhance the microbial respiration which promotes organic matter decomposition, depending on the growth rates and biomass of the organisms (Feller et al. 1999; Suárez-Abelenda et al. 2014). Granulometry also can affect sediment carbon. Finer fractions of sediment are thought to hold more than 60% organic matter due to their higher surface area (Prasad and Ramanathan 2008; Gillis et al. 2017). Lastly, geomorphological setting can interact with both nutrient content and granulometry and ultimately alter organic carbon content

in sediments. For example, as mentioned previously tidal exchange facilitates nutrient exchange and the oxygenation of sediments controlling organic material decomposition in mangroves (Castañeda-Moya et al. 2013; Lovelock et al. 2015). Different geomorphological settings will have different tidal exchanges such as size and frequency. Higher SOC are found in carbonate settings and lower values can be found in deltaic and estuarine coastal settings (Rovai 2018).

Conclusions

The direct and indirect influences of mangrove tree and seagrass plant functional traits may facilitate trapping, settling, and accumulation of organic carbon. Future research into functional traits would provide quantification on mechanisms controlling the long-term amount of sediment carbon. This study showed an insight into how sediment nutrient content altered the expression of seagrass plant traits which were positively correlated with sediment carbon accumulation. We clarified these insights in a phosphorus limited, mangrove-seagrass connected system. Further research is required to understand these relationships in other mangrove environments with different nutrient dynamics. Functional trait development occurs from months to year scales, in this study we did not consider seasonal and yearly fluctuations in precipitation, runoff and subsequent nutrient availability. Differences between the response of traits to nutrients, and potential physical effect of traits on their environment could also be linked to soil composition, water column nutrient, salinity, oxidation status, pH or hydrodynamic differences, degree of connectivity which we did not measure within the site. For example, connective ecosystems could facilitate carbon sequestration compared to isolated ecosystems. Nevertheless, the potential mechanisms we have identified here relating plant functional traits and carbon sediment stocks offer insight into disentangling the influence of climate, water, and sediment characteristics with rapid increases in sea-level rise. In the Southeast Florida, loss of coastal freshwater marsh ecosystems due to sea-level rise, saltwater intrusion, water diversions, and mangrove encroachment have been occurring for nearly a century (Ross et al. 2000; Gaiser et al. 2006). These changes have increased mangrove peat soil accumulation, due to strong near-shore phosphorus gradients present in the region that have contributed to belowground peat soil accumulation (Gaiser et al. 2004; Meeder et al. 2021). In addition, climate and human-induced stressors, such as increasing nutrients and temperatures are increasing and interacting to reduce seagrasses in this and other regions (Burkholder et al. 2007). Multiple stressors can increase mangrove mortality (Radabaugh et al. 2020; Lagomasino et al. 2021) and also impact trait development and carbon sequestration (Senger et al. 2020). How interacting stressors in coastal wetlands affect functional trait development, carbon sequestration, and storage remains a global research goal. Further data on drivers of blue carbon sequestration supports our understanding of mangroves and seagrasses' climate change mitigation potential.

Highlighting the role of blue carbon ecosystems in climate change adaptation could be used to support more protected areas and used to enhance conservation measures.

Data availability statement

Data are publicly available and stored in PANGAEA (Data Publisher for Earth & Environmental Science).

References

- Agawin, N. S. R., C. M. Duarte, and M. D. Fortes. 1996. Nutrient limitation of Philippine seagrasses (Cape Bolinao, NW Philippines): In situ experimental evidence. *Mar. Ecol. Prog. Ser.* **138**: 233–243. doi:[10.3354/meps138233](https://doi.org/10.3354/meps138233)
- Agawin, N. S. R., and C. M. Duarte. 2002. Evidence of direct particle trapping by a tropical seagrass meadow. *Estuaries* **25**: 1205–1209. doi:[10.1007/BF02692217](https://doi.org/10.1007/BF02692217)
- Alexandre, A., L. Collado-Vides, and R. Santos. 2021. The takeover of *Thalassia testudinum* by *Anadyomene* sp. at Biscayne Bay, USA, cannot be simply explained by competition for nitrogen and phosphorous. *Mar. Pollut. Bull.* **167**: 112326. doi:[10.1016/j.marpolbul.2021.112326](https://doi.org/10.1016/j.marpolbul.2021.112326)
- Alongi, D. M. 2014. Carbon cycling and storage in mangrove forests. *Ann. Rev. Mar. Sci.* **6**: 195–219. doi:[10.1146/annurev-marine-010213-135020](https://doi.org/10.1146/annurev-marine-010213-135020)
- Alongi, D. M. 2020. Carbon cycling in the world's mangrove ecosystems revisited: Significance of non-steady state diagenesis and subsurface linkages between the forest floor and the Coastal Ocean. *Forests* **11**: 977. doi:[10.3390/f11090977](https://doi.org/10.3390/f11090977)
- Armitage, A. R., T. A. Frankovich, and J. W. Fourqurean. 2011. Long-term effects of adding nutrients to an oligotrophic coastal environment. *Ecosystems* **14**: 430–444. doi:[10.1007/s10021-011-9421-2](https://doi.org/10.1007/s10021-011-9421-2)
- Armitage, A. R., and J. W. Fourqurean. 2016. Carbon storage in seagrass soils: Long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences* **13**: 313–321. doi:[10.5194/bg-13-313-2016](https://doi.org/10.5194/bg-13-313-2016)
- Asaeda, T., M. Sultana, J. Manatunge, and T. Fujino. 2004. The effect of epiphytic algae on the growth and production of *Potamogeton perfoliatus* L. in two light conditions. *Environ. Exp. Bot.* **52**: 225–238. doi:[10.1016/j.envexpbot.2004.02.001](https://doi.org/10.1016/j.envexpbot.2004.02.001)
- Barry, S. C., C. A. Jacoby, and T. K. Frazer. 2017. Environmental influences on growth and morphology of *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* **570**: 57–70. doi:[10.3354/meps12112](https://doi.org/10.3354/meps12112)
- Burkholder, J. M., D. A. Tomasko, and B. W. Touchette. 2007. Seagrasses and eutrophication. *J. Exp. Mar. Biol. Ecol.* **350**: 46–72. doi:[10.1016/j.jembe.2007.06.024](https://doi.org/10.1016/j.jembe.2007.06.024)
- Castañeda-Moya, E., R. R. Twilley, and V. Rivera-Monroy. 2013. Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. *For. Ecol. Manage.* **307**: 226–241. doi:[10.1016/j.foreco.2013.07.011](https://doi.org/10.1016/j.foreco.2013.07.011)
- Charles, S. P., J. S. Kominoski, A. R. Armitage, H. Guo, C. A. Weaver, and S. C. Pennings. 2020. Quantifying how changing mangrove cover affects ecosystem carbon storage in coastal wetlands. *Ecology* **101**: e02916. doi:[10.1002/ecy.2916](https://doi.org/10.1002/ecy.2916)
- Chen, G., and others. 2017. Mangroves as a major source of soil carbon storage in adjacent seagrass meadows. *Sci. Rep.* **7**: 42406. doi:[10.1038/srep42406](https://doi.org/10.1038/srep42406)
- Dahl, M. D., and others. 2016. Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: A comparison of four European areas. *PLoS One* **11**: e0167493. doi:[10.1371/journal.pone.0167493](https://doi.org/10.1371/journal.pone.0167493)
- Dangremond, E. M., L. T. Simpson, T. Z. Osborne, and I. C. Feller. 2020. Nitrogen enrichment accelerates mangrove range expansion in the temperate–tropical ecotone. *Ecosystems* **23**: 703–714. doi:[10.1007/s10021-019-00441-2](https://doi.org/10.1007/s10021-019-00441-2)
- de Boer, W. F. 2000. Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem. *Aquat. Bot.* **66**: 225–239. doi:[10.1016/S0304-3770\(99\)00072-8](https://doi.org/10.1016/S0304-3770(99)00072-8)
- de los Santos, C. B., F. G. Brun, J. J. Vergara, and J. L. Pérez-Lloréns. 2013. New aspect in seagrass acclimation: Leaf mechanical properties vary spatially and seasonally in the temperate species *Cymodocea nodosa* Ucria (Ascherson). *Mar. Biol.* **160**: 1083–1093. doi:[10.1007/s00227-012-2159-3](https://doi.org/10.1007/s00227-012-2159-3)
- Donato, D. C., J. Boone Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* **4**: 293–297. doi:[10.1038/ngeo1123](https://doi.org/10.1038/ngeo1123)
- Duarte, C. M., N. Marbà, E. Gacia, J. W. Fourqurean, J. Beggins, C. Barrón, and E. T. Apostolaki. 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochem. Cycles* **24**: GB4032. doi:[10.1029/2010GB003793](https://doi.org/10.1029/2010GB003793)
- Feller, I. C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecol. Monogr.* **65**: 477–505. doi:[10.2307/2963499](https://doi.org/10.2307/2963499)
- Feller, I. C. 1996. Effects of nutrient enrichment on leaf anatomy of dwarf *Rhizophora mangle* L. (red mangrove). *Biotropica* **28**: 13–22. doi:[10.2307/2388767](https://doi.org/10.2307/2388767)
- Feller, I. C., D. F. Whigham, J. P. O'Neill, and K. L. McKee. 1999. Effects of nutrient enrichment on within-stand cycling in a mangrove forest. *Ecology* **80**: 2193–2205. doi:[10.1890/0012-9658\(1999\)080\[2193:EONEOW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2193:EONEOW]2.0.CO;2)
- Feller, I. C., K. L. McKee, D. F. Whigham, and J. P. O'Neill. 2002. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry* **62**: 145–175. doi:[10.1023/A:1021166010892](https://doi.org/10.1023/A:1021166010892)
- Feller, I. C., C. E. Lovelock, U. Berger, K. L. McKee, S. B. Joye, and M. C. Ball. 2010. Biocomplexity in mangrove ecosystems. *Ann. Rev. Mar. Sci.* **2**: 395–417. doi:[10.1146/annurev.marine.010908.163809](https://doi.org/10.1146/annurev.marine.010908.163809)

- Fourqurean, J. W., J. C. Zieman, and G. V. N. Powell. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* **37**: 162–171. doi: [10.4319/lo.1992.37.1.0162](https://doi.org/10.4319/lo.1992.37.1.0162)
- Fourqurean, J. W., G. V. N. Powell, W. Judson Kenworthy, and J. C. Zieman. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* **72**: 349–358. doi: [10.2307/3546120](https://doi.org/10.2307/3546120)
- Frankignoulle, M., and J.-P. Gattuso. 1993. Air-sea CO₂ exchange in coastal ecosystems, p. 233–248. *In* R. Wollast, F. T. Mackenzie, and L. Chau [eds.], *Interactions of C, N, P and S biogeochemical cycles and global change*. Springer.
- Fujita, Y., P. M. van Bodegom, and J.-P. M. Witte. 2013. Relationships between nutrient-related plant traits and combinations of soil N and P fertility measures. *PLoS One* **12**: e83735. doi: [10.1371/journal.pone.0083735](https://doi.org/10.1371/journal.pone.0083735)
- Gaiser, E. E., A. Wachnicka, P. Ruiz, F. Tobias, and M. S. Ross. 2004. Diatom indicators of ecosystem change in coastal wetlands, p. 127–144. *In* S. Bortone [ed.], *Estuarine indicators*. CRC Press.
- Gaiser, E. E., A. Zafiris, P. L. Ruiz, F. A. Tobias, and M. S. Ross. 2006. Tracking rates of ecotone migration due to salt-water encroachment using fossil mollusks in coastal South Florida. *Hydrobiologia* **569**: 237–257.
- Gill, A. M., and P. B. Tomlinson. 1977. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 4. The adult root system. *Biotropica* **9**: 145–155.
- Gillis, L. G., T. J. Bouma, W. Kiswara, A. D. Ziegler, and P. M. J. Herman. 2014a. Leaf transport in mimic mangrove forest and seagrass beds. *Mar. Ecol. Prog. Ser.* **498**: 95–102. doi: [10.3354/meps10615](https://doi.org/10.3354/meps10615)
- Gillis, L. G., A. D. Ziegler, D. van Oevelen, C. Cathalot, P. J. M. Herman, J. W. Wolters, and T. J. Bouma. 2014b. Tiny is mighty: Seagrass beds have a large role in the export of organic material in the tropical coastal zone. *PLoS One* **9**: e111847. doi: [10.1371/journal.pone.0111847](https://doi.org/10.1371/journal.pone.0111847)
- Gillis, L. G., F. E. Belshe, A. D. Ziegler, and T. J. Bouma. 2017. Driving forces of organic carbon spatial distribution in the tropical seascape. *J. Sea Res.* **120**: 35–40. doi: [10.1016/j.seares.2016.12.006](https://doi.org/10.1016/j.seares.2016.12.006)
- Gillis, L. G., D. A. S. Hortua, M. Zimmer, T. C. Jennerjahn, and L. S. Herbeck. 2019. Interactive effects of temperature and nutrients on mangrove seedling growth and implications for establishment. *Mar. Environ. Res.* **151**: 104750. doi: [10.1016/j.marenvres.2019.104750](https://doi.org/10.1016/j.marenvres.2019.104750)
- Graça, M. A., and M. Zimmer. 2005. Methods to study litter decomposition, p. 121–125. *In* M. A. Graça, F. Bärlocher, and M. O. Gessner [eds.], *Leaf toughness*. Springer, Dordrecht. doi: [10.1007/1-4020-3466-0_18](https://doi.org/10.1007/1-4020-3466-0_18)
- Gullström, M., B. Lundén, M. Bodin, J. Kangwe, J. M. C. Öhman, M. S. P. Mtolera, and M. Björk. 2006. Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. *Estuar. Coast. Shelf Sci.* **67**: 399–408. doi: [10.1016/j.ecss.2005.11.020](https://doi.org/10.1016/j.ecss.2005.11.020)
- Hayes, M., A. Jesse, B. Tabet, R. Reef, J. A. Keuskamp, and C. E. Lovelock. 2017. The contrasting effects of nutrient enrichment on growth, biomass allocation and decomposition of plant tissue in coastal wetlands. *Plant and Soil* **416**: 193–204. doi: [10.1007/s11104-017-3206-0](https://doi.org/10.1007/s11104-017-3206-0)
- Josse, J., and F. Husson. 2016. missMDA: A package for handling missing values in multivariate data analysis. *J. Stat. Softw.* **70**: 1–31. doi: [10.18637/jss.v070.i01](https://doi.org/10.18637/jss.v070.i01)
- Komiyama, A., J. E. Ong, and S. Pongpan. 2008. Allometry, biomass, and productivity of mangrove forests: A review. *Aquat. Bot.* **89**: 128–137. doi: [10.1016/j.aquabot.2007.12.006](https://doi.org/10.1016/j.aquabot.2007.12.006)
- Lagomasino, D., and others. 2021. Storm surge and ponding explain mangrove dieback in southwest Florida following Hurricane Irma. *Nat. Commun.* **12**: 1–8. doi: [10.1038/s41467-021-24253-y](https://doi.org/10.1038/s41467-021-24253-y)
- Lovelock, C. E., I. C. Feller, K. L. McKee, B. M. J. Engelbrecht, and M. C. Ball. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panamá. *Functional Ecology* **18**: 25–33. doi: [10.1046/j.0269-8463.2004.00805.x](https://doi.org/10.1046/j.0269-8463.2004.00805.x)
- Lovelock, C. E., I. C. Feller, K. L. McKee, and R. Thompson. 2005. Variation in mangrove Forest structure and sediment characteristics in Bocas del Toro, Panama. *Caribb. J. Sci.* **41**: 456–464.
- Lovelock, C. E., R. W. Ruess, and I. C. Feller. 2006a. Fine root respiration in the mangrove *Rhizophora mangle* over variation in forest stature and nutrient availability. *Tree Physiol.* **26**: 1601–1606. doi: [10.1093/treephys/26.12.1601](https://doi.org/10.1093/treephys/26.12.1601)
- Lovelock, C. E., M. C. Ball, B. Choat, B. M. J. Engelbrecht, N. M. Holbrook, and I. C. Feller. 2006b. Linking physiological processes with mangrove forest structure: Phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant Cell Environ.* **29**: 793–802. doi: [10.1111/j.1365-3040.2005.01446.x](https://doi.org/10.1111/j.1365-3040.2005.01446.x)
- Lovelock, C. E., and others. 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**: 559–563. doi: [10.1038/nature15538](https://doi.org/10.1038/nature15538)
- Lovelock, C. E., and C. M. Duarte. 2019. Dimensions of Blue Carbon and emerging perspectives. *Biol. Lett.* **15**: 20180781. doi: [10.1098/rsbl.2018.0781](https://doi.org/10.1098/rsbl.2018.0781)
- McKee, K. L. 2001. Root proliferation in decaying roots and old root channels: A nutrient conservation mechanism in oligotrophic mangrove forests? *J. Ecol.* **89**: 876–887. doi: [10.1046/j.0022-0477.2001.00606.x](https://doi.org/10.1046/j.0022-0477.2001.00606.x), 5
- McLeod, E., and others. 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* **9**: 552–560. doi: [10.1890/110004](https://doi.org/10.1890/110004)

- Meeder, J. F., R. W. Parkinson, D. Ogurcak, M. S. Ross, and J. S. Kominoski. 2021. Changes in sediment organic carbon accumulation under conditions of historical sea-level rise, Southeast Saline Everglades, Florida, USA. *Wetland* **41**: 41. doi:10.1007/s13157-021-01440-7
- Moore, W. S., J. L. Sarmiento, and R. M. Key. 2008. Submarine groundwater discharge revealed by 228Ra distribution in the upper Atlantic Ocean. *Nat. Geosci.* **1**: 309–311. doi:10.1038/ngeo183
- Nellemann, C., E. Corcoran, C. M. Duarte, L. Valdrés, C. D. Young, L. Fonseca, and G. Grimsditch. 2009. Blue carbon: The role of healthy oceans in binding carbon. United Nations Environment Programme. GRID-Arendal.
- Nock, C. A., R. J. Vogt, and B. E. Beisner. 2016. Functional traits. In eLS. John Wiley & Sons, Ltd. doi:10.1002/9780470015902.a0026282
- Odum, E. P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: Tidal subsidy, outwelling, and detritus-based food chains, p. 485–495. In *Estuarine Perspectives*. Academic Press. doi:10.1016/B978-0-12-404060-1.50045-9
- Odum, W. E., E. P. Odum, and H. T. Odum. 1995. Nature's pulsing paradigm. *Estuaries* **18**: 547–555. doi:10.2307/1352375
- Powell, G. V. N., J. W. Kenworthy, and J. W. Fourqurean. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. Mar. Sci.* **44**: 324–340.
- Prasad, M. B. K., and A. L. Ramanathan. 2008. Sedimentary nutrient dynamics in a tropical estuarine mangrove ecosystem. *Estuar. Coast. Shelf Sci.* **80**: 60–66. doi:10.1016/j.ecss.2008.07.004
- Radabaugh, K. R., and others. 2020. Mangrove damage, delayed mortality, and early recovery following Hurricane Irma at two landfall sites in Southwest Florida, USA. *Estuaries and Coasts* **43**: 1104–1118. doi:10.1007/s12237-019-00564-8
- Ravaglioli, C., and others. 2017. Nutrient loading fosters seagrass productivity under ocean acidification. *Sci. Rep.* **7**: 13732. doi:10.1038/s41598-017-14075-8
- Reef, R., I. C. Feller, and C. E. Lovelock. 2010. Nutrition of mangroves. *Tree Physiol.* **30**: 1148–1160. doi:10.1093/treephys/tpq048
- Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**: 505–514. doi:10.1016/j.tree.2009.03.018
- Ricart, A. M., A. Dalmau, M. Pérez, and J. Romero. 2015. Effects of landscape configuration on the exchange of materials in seagrass ecosystems. *Mar. Ecol. Prog. Ser.* **532**: 89–100. doi:10.3354/meps11384
- Ross, M. S., J. F. Meeder, J. P. Sah, P. L. Ruiz, and G. J. Telesnicki. 2000. The southeast saline Everglades revisited: 50 years of coastal vegetation change. *J. Veg. Sci.* **11**: 101–112. doi:10.2307/3236781
- Ross, M. S., P. L. Ruiz, G. J. Telesnicki, and J. F. Meeder. 2001. Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (USA). *Wetlands Ecol. Manage.* **9**: 27–37. doi:10.1023/A:1008411103288
- Rovai, A. S., and others. 2018. Global controls on carbon storage in mangrove soils. *Nat. Clim. Change* **8**: 534–538. doi:10.1038/s41558-018-0162-5
- Senger, D. F., D. A. S. Hortua, S. Engel, M. Schnurawa, N. Moosdorf, and L. G. Gillis. 2020. Impacts of wetland die-back on carbon dynamics: A comparison between intact and degraded mangroves. *Sci. Total Environ.* **753**: 141817. doi:10.1016/j.scitotenv.2020.141817
- Sheaves, M. 2009. Consequences of ecological connectivity: The coastal ecosystem mosaic. *Mar. Ecol. Prog. Ser.* **391**: 107–115. doi:10.3354/meps08121
- Suárez-Abelenda, M., T. O. Ferreira, M. Camps-Arbestain, V. H. Rivera-Monroy, F. Macías, G. Nuto Nóbrega, and X. L. Otero. 2014. The effect of nutrient-rich effluents from shrimp farming on mangrove soil carbon storage and geochemistry under semi-arid climate conditions in northern Brazil. *Geoderma* **213**: 551–559. doi:10.1016/j.geoderma.2013.08.007
- Ward, N. D., T. S. Bianchi, P. M. Medeiros, M. Seidel, J. E. Richey, R. G. Keil, and H. O. Sawakuchi. 2017. Where carbon goes when water flows: Carbon cycling across the aquatic continuum. *Front. Mar. Sci.* **4**: 7. doi:10.3389/fmars.2017.00007

Acknowledgments

The authors would like to thank lab members from Mangrove Ecology Department at ZMT, the Kominoski Lab in the Department of Biological Sciences at Florida International University (Miami, Florida, USA) for advice on experimental design, data analyses, and feedback on earlier manuscript drafts. The authors thank the analytical laboratory at ZMT for conducting chemical analyses of collected samples. This study was funded by the DFG (Deutsche Forschungsgemeinschaft), project number Gl 121011-1. Samples were collected under permit. Open Access funding enabled and organized by Projekt DEAL.

Conflict of Interest

None declared.

Submitted 27 September 2021

Revised 05 March 2022

Accepted 12 August 2022

Associate editor: Vanessa Hatje