Exploring carbon dynamics in connected mangrove forests and seagrass beds: How important is it?

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Abstract

Carbon sequestration is one of the most important ecosystem services provided by mangrove forests and seagrass beds that helps with climate change adaptation. Mangrove forests and seagrass beds are important ecosystems in tropical and subtropical locations that sequester significant greater amounts of carbon within their living biomass as well as in their sediments compared to terrestrial ecosystems. Ecosystems that exchange energy, organisms and materials are considered connected. This dissertation, however, will focus on connectivity as the specific exchange of particulate organic matter (POM). Connectivity across coastal vegetated ecosystems could have an important impact for ecosystem services across the seascape. Although mangrove forests and seagrass beds usually occur adjacent to each other they are frequently evaluated independently without taking into account how connectivity between these coastal vegetated ecosystems can influence carbon accumulation. Therefore, a comparison of connected with isolated mangrove forests and seagrass beds will help to understand the effect of connectivity on carbon accumulation at the seascape scale. Five field studies in Singapore (Asia), Adelaide (Oceania), Zanzibar (Africa), Florida and Bonaire (Americas), were chosen to evaluate the influence of connectivity. Sampling for sediment carbon content analysis was conducted across all places in different locations with connected mangrove forests and seagrass beds and/or isolated ecosystems. The general hypothesis was that mangrove forests and seagrass beds that are connected with each other would have greater quantities of carbon in the sediment, compared to those that are isolated from each other. Furthermore, other aspects such as connectivity with other ecosystems (i.e. salt marsh, macroalgal beds), community characteristics, sediment nutrient concentration and geomorphic settings were tested and compared separately in each place.

Results of this dissertation in Singapore and Zanzibar showed that no significant differences were observed between mangrove forests connected with seagrasses beds and mangrove forests isolated from seagrass beds. Connectivity between mangrove forests and seagrass beds for carbon accumulation only increased sediment carbon accumulation in South Australia´s mangrove forests, where the sediment carbon content was higher in connected forests compared with an isolated mangrove patch. In general, sediment in seagrass beds have higher inorganic carbon indicating that mangrove forests are not the main allochthonous carbon source. Contrary to the general hypothesis, isolated seagrass beds had up to double sediment carbon content compared with connected beds. This was mainly driven by higher amounts of inorganic carbon in isolated beds since sediment organic carbon quantity was similar across the sampled beds. Thus, autochthonous production of inorganic carbon and connectivity with carbonate rich ecosystems (i.e. coral reefs) could be important for seagrass beds carbon accumulation.

Although connected seagrass beds did not have higher sediment carbon content compared with isolated beds, results of this dissertation showed that mangrove forests are crucial donors of organic carbon to adjacent ecosystems such as seagrass beds and mud flats. The contributions to POM in the coastal

water body of the main primary producers across all coastal vegetated ecosystems were measured in Singapore and South Australia. In both places, mangrove trees contributed between 10 to 70% and significantly more compared with other ecosystems with respect to the area occupied in the seascape by mangrove forests. Additionally, in Singapore and Bonaire it was observed that the export of dissolved organic carbon is an important pathway of exchanging carbon from mangroves forests to adjacent ecosystems. Besides mangrove trees, macroalgae thalli were with 10-50% the main contributors to the POM stocks in Singapore and South Australia. These results highlight the importance of mangrove forests as well as other coastal vegetated ecosystems, such as macroalgal beds, for carbon exchange and potential carbon accumulation across the seascape.

Interactions between community composition and environmental parameters (i.e. water particle transportation or sediment nutrient concentration) could enhance the sediment carbon content. In Zanzibar, although functional diversity indices were not associated with higher sediment organic or inorganic carbon content, community species composition associated with prop roots in mangrove forests and large-leaved seagrass plants were correlated with higher sediment carbon content. In both ecosystems the area of tidal channels was also an important predictor of sediment carbon content although there were differences in the influence on sediment organic and inorganic carbon content. Additionally, in Florida the gradient of physical traits of mangrove roots and seagrass plants were compared against different carbon content type (organic and carbonate). A negative correlation was found between the sediment organic carbon content and the root complexity index, whilst higher sediment organic carbon levels were found in areas with higher shoot density and coverage.

Besides connectivity other factors at the seascape level such us geomorphic settings or anthropogenic induced changes in the seascape settings could influence the connectivity and the sediment carbon content. In Zanzibar the area of tidal channels as well as the area covered by mangrove forest were positively correlated with sediment organic carbon content in mangrove forests. Anthropogenic induced changes such as changing freshwater fluxes and reduction of mangrove forest area in Singapore as well as reduction of area of healthy mangrove trees in Bonaire could affected carbon accumulation dynamics not only in mangrove forests but also in adjacent coastal ecosystems such as seagrass beds. In both places the same underlying mechanism was discussed, the reduction of mangrove forest area could reduce the exported amount of POM and decrease the amount of carbon accumulated in the adjacent ecosystems.

I conclude that connectivity between mangrove forests and seagrass beds is affected by different localized factors and that degrees of connectedness between those two ecosystems and other adjacent ecosystems should be further study. Factors such as mangrove forests cover area, community composition and health state of mangrove communities influence both the sediment carbon accumulation in mangrove forests and their exportation of carbon to adjacent ecosystems. Additionally, including sediment inorganic carbon content in blue carbon studies concerning seagrass beds is critical, since sediment inorganic carbon content was an important component of their sediment carbon content. Geomorphic settings such as presence of low energy streams or rivers as well as presence of macroalgal beds can also enhance sediment carbon accumulation in mangrove forests and seagrass beds. Results of this dissertation in connectivity between different coastal vegetated ecosystems as well as terrestrial ecosystems highlight the importance of the conservation of all interconnected ecosystems (i.e. mangrove forests, seagrass beds, salt marches, macroalgae beds, coral reefs as well as connected terrestrial ecosystems) for carbon accumulation ecosystem service.

Kurzfassung

Die Bindung von Kohlenstoff ist eine der wichtigsten Ökosystemdienstleistungen von Mangrovenwäldern und Seegraswiesen, die bei der Anpassung an den Klimawandel hilft. Mangrovenwälder und Seegraswiesen sind wichtige Ökosysteme an tropischen und subtropischen Standorten, die im Vergleich zu terrestrischen Ökosystemen erheblich größere Mengen Kohlenstoff in ihrer lebenden Biomasse, sowie ihren Sedimenten, binden. Ökosysteme, die Energie, Organismen und Materialien austauschen, gelten als miteinander vernetzt. Diese Dissertation wird sich jedoch auf die Konnektivität als den spezifischen Austausch von partikulärem organischem Material (POM) konzentrieren. Die Konnektivität über Küstenökosysteme mit Pflanzenwuchs hinweg könnte einen wichtigen Einfluss auf die Ökosystemdienstleistungen in der gesamten Meereslandschaft haben. Obwohl Mangrovenwälder und Seegraswiesen in der Regel nebeneinander vorkommen, werden sie häufig unabhängig voneinander betrachtet, ohne zu berücksichtigen, wie die Konnektivität zwischen diesen Küstenökosystemen mit Pflanzenwuchs die Kohlenstoffakkumulation beeinflussen kann. Daher wird ein Vergleich von miteinander verbundenen mit isolierten Mangrovenwäldern und Seegraswiesen helfen, den Einfluss der Konnektivität auf die Kohlenstoffakkumulation auf der Skala der Meereslandschaft zu verstehen. Fünf Feldstudien in Singapur (Asien), Adelaide (Ozeanien), Sansibar (Afrika), Florida und Bonaire (Nord- und Südamerika) wurden ausgewählt, um den Einfluss der Konnektivität zu bewerten. Proben für die Analyse des Kohlenstoffgehalts der Sedimente wurden in allen Gebieten an verschiedenen Standorten mit zusammenhängenden Mangrovenwäldern und Seegraswiesen und, oder isolierten Ökosystemen entnommen. Die allgemeine Hypothese war, dass mit einander verbundene Mangrovenwälder und Seegraswiesen größere Mengen an Kohlenstoff im Sediment aufweisen würden, als solche, die voneinander isoliert sind. Darüber hinaus wurden weitere Aspekte wie die Konnektivität mit anderen Ökosystemen (z.B. Salzmarschen, Makroalgenbeständen), Eigenschaften der Lebensgemeinschaften, Nährstoffkonzentration im Sediment und geomorphologischen Gegebenheiten in jedem Gebiet separat getestet und verglichen.

Die Ergebnisse dieser Dissertation in Singapur und Sansibar zeigten, keine signifikanten Unterschiede zwischen Mangrovenwäldern mit Verbindung zu Seegraswiesen und Mangrovenwäldern isoliert von Seegraswiesen. Konnektivität zwischen Mangrovenwäldern und Seegrasbeeten in Bezug auf Kohlenstoffakkumulation erhöhte nur die Akkumulation von Kohlenstoff im Sediment in den Mangrovenwäldern Südaustraliens, wo der Sedimentkohlenstoffgehalt in verbundenen Wäldern höher war als in isolierten Mangrovenbereichen. Im Allgemeinen weisen die Sedimente in Seegraswiesen einen höheren anorganischen Kohlenstoffgehalt auf, was darauf hinweist, dass Mangrovenwälder nicht die wichtigste allochthone Kohlenstoffquelle sind. Entgegen der allgemeinen Hypothese hatten isolierte Seegraswiesen einen bis zu doppelt so hohen Sedimentkohlenstoffgehalt im Vergleich zu zusammenhängenden Wiesen. Dies war hauptsächlich auf höhere Mengen an anorganischem Kohlenstoff in isolierten Wiesen zurückzuführen, da die Menge an organischem Kohlenstoff in den Sedimenten der untersuchten Gebiete ähnlich war. Daher könnte die autochthone Produktion von anorganischem

Kohlenstoff und die Konnektivität mit karbonatreichen Ökosystemen (d.h. Korallenriffen) wichtig für die Kohlenstoffakkumulation in Seegraswiesen sein.

Obwohl verbundene Seegraswiesen im Vergleich zu isolierten Wiesen keinen höheren Sedimentkohlenstoffgehalt aufwiesen, zeigten die Ergebnisse dieser Dissertation dennoch, dass Mangrovenwälder entscheidende Quellen von organischem Kohlenstoff für angrenzende Ökosysteme wie Seegraswiesen und Wattflächen sind. In Singapur und Südaustralien wurden die Beiträge zu POM im Küstengewässer der wichtigsten Primärproduzenten in allen Küstenökosystemen mit Pflanzenbewuchs gemessen. An beiden Orten trugen Mangrovenbäume zwischen 10 bis 70% und im Vergleich zu anderen Ökosystemen deutlich mehr dazu bei, als die von Mangrovenwäldern eingenommene Fläche in der Meereslandschaft vermuten lässt. Zusätzlich wurde in Singapur und Bonaire beobachtet, dass der Export von gelöstem organischem Kohlenstoff einen wichtigen Weg des Austausches von Kohlenstoff zwischen Mangrovenwäldern und angrenzenden Ökosystemen darstellt. Neben den Mangrovenbäumen trugen vor allem Makroalgen mit deren Thalli mit 10-50 % zum POM-Beständen in Singapur und Südaustralien bei. Diese Ergebnisse unterstreichen die Bedeutung der Mangrovenwälder sowie anderer Küstenökosysteme mit Pflanzenbewuchs, wie Makroalgenbestände, für den Kohlenstoffaustausch und die potenzielle Kohlenstoffakkumulation in der gesamten Meereslandschaft.

Wechselwirkungen zwischen der Zusammensetzung der Gemeinschaft und Umweltparametern (z.B. Wasserpartikeltransport oder Nährstoffkonzentration im Sediment) könnten den Kohlenstoffgehalt im Sediment erhöhen. In Sansibar waren die Indizes der funktionellen Diversität zwar nicht mit einem höheren Gehalt von organischem oder anorganischem Kohlenstoff im Sediment assoziiert, aber die Zusammensetzung der Artengemeinschaften, die mit Stelzwurzeln in Mangrovenwäldern und großblättrigen Seegraspflanzen assoziiert ist, korrelierte mit einem höheren Kohlenstoffgehalt im Sediment. In beiden Ökosystemen war auch die Fläche von Gezeitenkanälen ein wichtiger Prädiktor für den Sedimentkohlenstoffgehalt, obwohl es Unterschiede im Einfluss auf den organischen und anorganischen Anteil am Kohlenstoffgehalt der Sedimente gab. Zusätzlich wurde in Florida der Gradient der physikalischen Merkmale von Mangrovenwurzeln und Seegraspflanzen mit unterschiedlichen Arten von Kohlenstoffgehalten (organischem und anorganischem) verglichen. Es wurde eine negative Korrelation zwischen dem Gehalt an organischem Kohlenstoff im Sediment und dem Wurzelkomplexitätsindex festgestellt, während in Gebieten mit höherer Sprossdichte und flächenbezogene Bedeckung ein höherer Gehalt von organischem Kohlenstoff im Sediment gefunden wurde.

Neben der Konnektivität könnten auch andere Faktoren auf der Ebene der Seelandschaft, wie geomorphologische Gegebenheiten oder anthropogen bedingte Veränderungen der Seelandschaft, die Konnektivität und den Sedimentkohlenstoffgehalt beeinflussen. In Sansibar waren die Fläche von Tidenkanälen sowie die von Mangrovenwald bedeckte Fläche positiv mit dem Gehalt von organischem Kohlenstoff in den Sedimenten der Mangrovenwälder korreliert. Anthropogen bedingte Veränderungen, wie veränderte Süßwasserflüsse und die Verringerung der Mangrovenwaldfläche in Singapur sowie die Verringerung der Fläche gesunder Mangrovenbäume in Bonaire könnten die Dynamik der

Kohlenstoffakkumulation nicht nur in Mangrovenwäldern, sondern auch in angrenzenden Küstenökosystemen wie Seegraswiesen beeinflussen. An beiden Orten wurde derselbe zugrundeliegende Mechanismus diskutiert: Die Verringerung der Mangrovenwaldfläche könnte die exportierte Menge an POM reduzieren und die Menge des in den angrenzenden Ökosystemen akkumulierten Kohlenstoffs verringern.

Ich komme zu dem Schluss, dass die Konnektivität zwischen Mangrovenwäldern und Seegraswiesen durch verschiedene lokalisierte Faktoren beeinflusst wird und dass der Grad der Konnektivität zwischen diesen beiden Ökosystemen und anderen angrenzenden Ökosystemen weiter untersucht werden sollte. Faktoren wie die Fläche der Mangrovenwälder, die Zusammensetzung der Gemeinschaft und der Gesundheitszustand der Mangrovengemeinschaften beeinflussen sowohl die Akkumulation von Kohlenstoff im Sediment der Mangrovenwälder, als auch deren Export von Kohlenstoff in benachbarte Ökosysteme. Darüber hinaus ist die Einbeziehung des anorganischen Kohlenstoffgehalts der Sedimente in Blue-Carbon-Studien über Seegraswiesen von entscheidender Bedeutung, da der anorganische Kohlenstoffgehalt der Sedimente ein wichtiger Bestandteil des Gesamtkohlenstoffgehalts dieser Sedimente war. Geomorphologische Gegebenheiten wie das Vorhandensein von kleinen Flüssen mit geringer Strömungsenergie sowie das Vorhandensein von Makroalgenbeständen können ebenfalls die Akkumulation von Sedimentkohlenstoff in Mangrovenwäldern und Seegraswiesen fördern. Die Ergebnisse dieser Dissertation über die Konnektivität zwischen verschiedenen Küstenökosystemen mit Pflanzenbewuchs sowie terrestrischen Ökosystemen unterstreichen die Bedeutung der Erhaltung aller miteinander verbundenen Ökosysteme (d.h. Mangrovenwälder, Seegraswiesen, Salzmarschen, Makroalgenbestände, Korallenriffe sowie verbundene terrestrische Ökosysteme) für die Kohlenstoffakkumulation als Ökosystemdienstleistung.

Glossary *

Blue carbon: “The carbon stored in mangroves, tidal salt marshes, and seagrass meadows within the soil, the living biomass above-ground (leaves, branches, stems), the living biomass below-ground (roots), and the non-living biomass (litter and dead wood)” (Howard et al. 2014).

Carbon accumulation: Process in which the carbon is retained in long term inside the ecosystems, in sediments as well as long term within the biomass.

Carbon pool: “Carbon pools refer to carbon reservoirs such as soil, vegetation, water, and the atmosphere that absorb and release carbon. Together carbon pools make up a carbon stock” (Howard et al. 2014).

Carbon sequestration: Processes in which the CO_2 in the atmosphere and oceans is taken in by primary producers during photosynthesis and stored in the ecosystem (Howard et al. 2014).

Carbon stock: “A carbon stock is the total amount of organic carbon stored in a blue carbon ecosystem of a known size. A carbon stock is the sum of one or more carbon pools” (Howard et al. 2014).

Carbon store: Refers to the carbon that is kept in reservoirs such as plants or sediments but not necessarily accumulating in long term, since it can be converted into CO_2 or exported to adjacent ecosystems.

Connectivity: The fact of being connected (i.e. exchange of material and organisms).

Connectedness: Refers to the quality or quantity of the connectivity a higher exchange of materials will imply a high connectedness between 2 ecosystems.

Levels: Refers to a determined spatial scale i.e. sediment level, community level, and seascape level.

Seascape structure: includes the spatial arrangement and composition of seascape elements (i.e. patches of different ecosystems) and ecological fluxes (i.e. movements of water, nutrients, organisms and other materials). Adapted from Wu (2012).

Sediment inorganic carbon (SIC): In this dissertation the inorganic carbon refers only to carbonate particles concentration. Does not include other fomrs of inorganic carbon.

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* The terms of this glossary are to be considered in the introduction and in the discussion of this dissertation. Punctual discrepancies are due to the rich contribution of and slight interpretation divergencies between co-authors of the different chapters. In those cases, the correspondent definition or point-of-view is indicated in the chapter proper.

List of abbreviations

POM = Particulate organic matter

SPM = Suspended particulate matter

POC = Particulate organic carbon

PIC = Particulate inorganic carbon

DOC = Dissolved organic carbon

DIC = Dissolved inorganic carbon

SOC = Sediment organic carbon

SIC = Sediment inorganic carbon

CVE = Coastal vegetated ecosystem

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Chapter 1 Introduction

1.1. Coastal vegetated ecosystems and carbon sequestration

The tropical and subtropical coastal estuary zones frequently include a mosaic of coastal vegetated ecosystems (CVE) such as mangrove forests, seagrass beds and salt marshes. That zone is one of the most bio-geochemical active areas of the biosphere (Jennerjahn and Ittekkot 2002; Borges et al. 2005). Mangrove forests and seagrass beds as well as other CVE (i.e. salt marshes) are important providers of ecosystem services that are essential for economic development (Agardy et al. 2005; Berkström et al. 2012; Cullen-Unsworth et al 2014). Those services include carbon sequestration of “blue carbon”, which is one of the most potential economically valuable ecosystem services provided by mangroves forests and seagrass beds (Barbier et al. 2011).

Mangrove forests and seagrass beds bury annually around ten times more organic carbon (OC) when compared with terrestrial forests (Figure 1.1), despite the extent of coastal marine vegetation being less than 3% of terrestrial systems (Duarte et al. 2013; Alongi 2014). Different CVE have different sequestration capacity due to differences in primary production, respiration and sediment burial rates. Primary production is one of the main carbon fixation processes within the CVE, systems (Duarte and Cebrián 1996; Duarte et al. 2013). Carbon fixed from the atmosphere by primary production is usually sequestered in the biomass of CVE; therefore, primary production is an important factor for carbon accumulation. The gross primary production and the sediments accumulation of mangrove forests is the greatest compared with other CVE, however the respiration rate in those forests is also the highest. When calculating the net ecosystem production, the order is Mangrove > Seagrass > Saltmarshes > Macroalgae (Table 1.1).

Across the seascape, carbon dynamics in the sediments and biomass in each CVE are influenced by environmental, mechanical and physicochemical parameters at different levels; such as seascape level (i.e. geomorphology; hydrodynamics, cover area of the different CVE ecosystem patch, sediment interchange) and vegetation community composition level (such as species composition and community state).

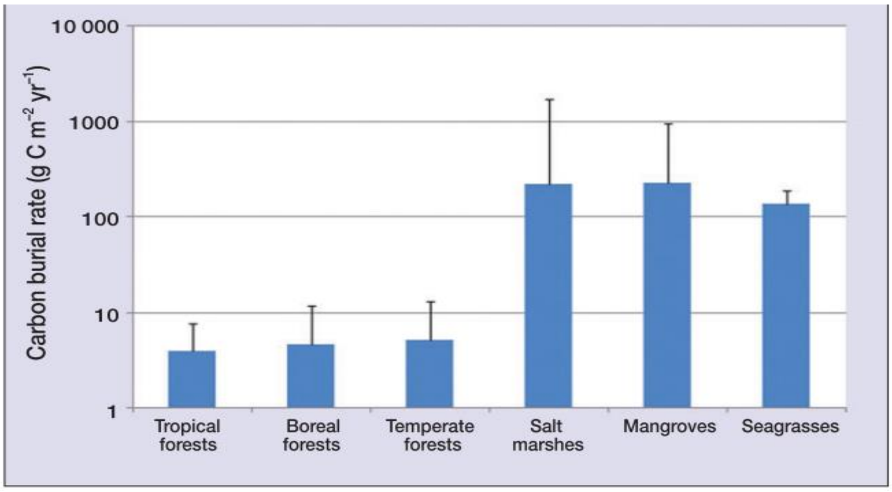

Figure 1.1. Mean long-term rates of carbon burial (g C m^{-2} yr^{-1}) in sediments of terrestrial forests (tropical, boreal and temperate) and CVE (salt marshes, mangroves and seagrasses). Error bars indicate maximum rates of accumulation. Note the logarithm scale of the y axis. Source: McLeod et al. (2011).

Table 1.1. Values of local net ecosystem production (NEP), gross primary production (GPP), respiration difference in NPP (R). Based in databases for coastal ecosystems including mangrove forests, seagrass beds, salt marshes and macroalgae (§ = Duarte et al. (2005) and references therein; * = Alongi (2014) and references therein).

Ecosystem	NEP (g C m^{-2} y $^{-1}$)	R (g C m^{-2} y $^{-1}$)	GPP (g C m^{-2} y $^{-1}$)	Local burial rate (g C^{-2} y^{-1})
Mangrove forests	652* 221§	4413* 1866§	5065* 2087§	174 +/- 23*
Seagrass beds	1211§	692§	1903§	138 +/- 38*
Salt marshes	1585§	2010§	3595§	218 +/- 24*
Macroalgae beds	1587§	2116§	3702§	

1.2. Connectivity at seascape level

1.2.1. Connectivity between mangrove forests and seagrass beds and its potential importance for blue carbon at the seascape level

Coastal vegetated ecosystems are open systems that exchange energy, materials and organisms (Gillis et al. 2014; Huxham et al. 2018). Interchange of material can play an important role for primary and secondary productions, allochthonous carbon is also an important source for blue carbon in the sediments of both mangrove forests (Alongi 2014; Lovelock et al. 2014) and seagrass beds (Fourqurean et al. 2012). The transfer of matter and therefore vectors of carbon (i.e. organisms, particulate or dissolved material) may be grouped into two main categories: passive, i.e., detrital material, POC, particulate inorganic carbon (PIC), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), passively transported organism (i.e. propagules); and active, i.e., mobile consumers that transport carbon. The relative importance of those vectors differs among systems and primary producers present in the ecosystems (Hyndes et al. 2014) (Figure 1.2). Carbon sediment pools in CVE are in general a big part of the OC stocks. In general, OC comes from both autochthonous and allochthonous sources, mainly derived by primary producers at the seascape as well as inland upstream by some mangrove forests (Kennedy et al. 2010; Alongi 2014). Hence, the exchange of material across the seascape is an important driver for carbon accumulation in sediments (Figure 1.2) more localized data on how exchange of material occurs across the seascape is necessary to understand the role of connectivity between mangrove forest and seagrass beds for carbon accumulation.

There is evidence that the variability of mangrove forest settings influences the exchange of carbon between these ecosystems and adjacent ones. In times, mangrove forests mainly export carbon, in others they may mainly receive it. There are also settings that benefit the mutual exchange of carbon. Approximately 60% of the net primary production of mangroves is exported in the form of POC and DOC, although variations may occur locally across the globe (Alongi 2014). The 'outwelling hypothesis' states that secondary production in waters adjacent to salt marshes can only be sustained if the marsh exports materials and chemical energy (Odum 1968); this hypothesis was applied for mangrove forests in the tropics (Lee 1995; Adame and Lovelock 2011). Recent studies and literature reviews understand that mangroves may serve both as exporters and importers of organic material and nutrients (Lee 1995; Bouillon et al. 2007; Adame and Lovelock 2011; Walton et al. 2014; Gillis et al. 2014a, 2014b, 2015). For example, it has been reported by Walton et al. (2014) that arid mangroves in the Arabian Gulf cannot be susteined without considering the connectivity of adjacent systems such as seagrasses due to mangrove productivity being sustained by inwelling of seagrass material.

Seagrasses beds have been reported to accumulate up to 50% of sediment organic carbon (SOC) derived for terrestrial and/or mangroves sources derived organic carbon (Kennedy et al. 2010) with a variations across the sampled locations. However, they are also important donors, for example around 24% of the net primary production of seagrass beds are exported (Duarte et al. 2005), The exporting of net primary production depends mainly on hydrodynamic conditions in which materials can be exported to adjacent ecosystems or to the deep sea (Kennedy et al. 2010; Duarte et al. 2013).

Mangrove forests and seagrass beds exchange material between them (Gillis et al. 2014; Walton et al. 2014; Huxham et al. 2018), however localized characteristics such as tidal amplitude can influenced the quantity and type of material that they exchange impacting on the SC accumulation. Indirect and direct feedbacks of seagrass beds on mangroves forest and vice versa that benefit carbon accumulation across the seascape have been reported. A direct feedback would be for example the exchange of detritus material that will be further accumulated in the sediments by the donation of carbon from mangrove to seagrass beds sediments. An indirect positive feedback is the diminishing of the wave dumping done by seagrass beds and coral reefs which helps to decrease sediment erosion in mangrove forests, benefiting carbon accumulation in the forest sediment (Gillis et al. 2014; Huxham et al. 2018) (Figure 1.2). Both the directs and indirect positive feedbacks will be impacted by localized seascape structure, therefore comparing different connected mangrove forest and seagrass beds will help to elucidate the importance of this connectivity for SC accumulation at the seascape level as well as individually in each ecosystem.

1.2.2. Carbon accumulation: seascape structure and connectivity with other ecosystems

Coastal vegetated ecosystems exchange a large amount of materials due to hydrodynamics (Hyndes et al. 2014; Krauss et al. 2014; Huxham et al. 2018). At the seascape level, local climate seasonality (i.e. rainfall amount and intensity), geomorphology and hydrology (i.e. topography, riverine flows, currents and tidal amplitudes) can be determining factors for carbon accumulation in mangrove forests sediments (Bouillon et al. 2008; Kristensen et al. 2008). Same factors can also modify the connectivity of mangrove forest and therefore influence on SC accumulation in adjacent ecosystems. For example, riverine mangroves mainly export material to the coastal zone, while tidal mangroves are more likely to import materials; this argument is based on the principle that tidal mangroves are dominated by bidirectional flows, while riverine mangroves are dominated by unidirectional flows that increase outwelling (Adame and Lovelock 2011; Woodroffe et al. 2016). Differences in that interaction among connected ecosystems remain poorly quantified and more data is necessary in order to understand the dynamics of carbon exchange between mangrove forests, seagrass beds and other CVE (Adame and Lovelock 2011; Gillis et al. 2014; Hyndes et al. 2014).

Recently sediment inorganic carbon (SIC) content has been reported to be an important component of the total sediment carbon in seagrass beds. In many seagrass beds carbonate particles accumulation increases sediment accretion rate, which is an important process for the capacity of CVE to preserve OC derived from burial of biomass within the sediments (Mazarrasa et al. 2015; Macreadie et al. 2017; Saderne et al. 2019). The SIC content in seagrass beds differs across the globe; SIC stocks tend to decrease with increasing latitude being higher in the tropics when compared to temperate regions. Globally, the SOC:SIC content ratio ranges from 0 to 108 (0.74 average, 0.20 median) (Mazarrasa et al. 2015). Even, the carbonates can be produced by inhabitantns of seagrass beds (i.e. molluscs, epyphytes etc.) a broad range of extreanl organisms including corals and calcareous algae are involved in the production and subsequent accumulation of carbonates in the seagrasses sediments, (Westphal et al. 2010; Mazarrasa et al. 2015; Belshe et al. 2018). Therefore, connectivity os seagrass beds with ecosystems that produced carbonates can be critical for SC store.

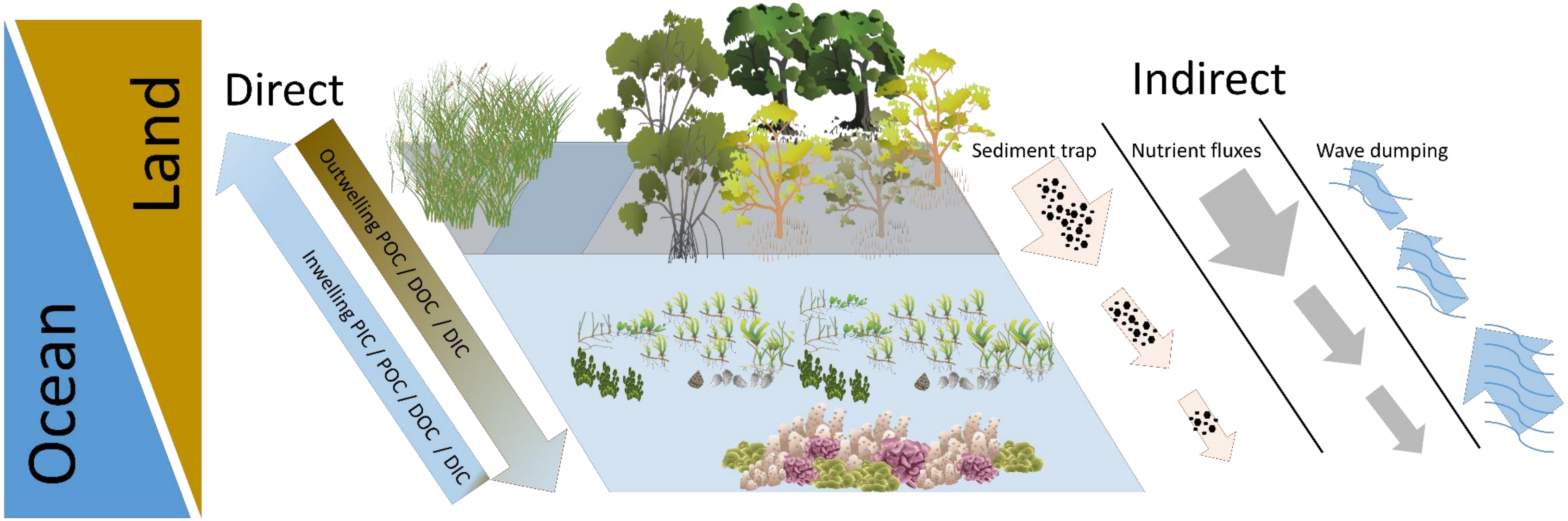

Figure 1.2. Conceptualization of connection between land and seascape matrix (salt marsh, mangrove forest, seagrass bed and coral reef), depicting direct and indirect mechanisms by which a CVE may influence the carbon sequestration and retention in adjacent CVEs. Left part shows direct transfers (outwelling and inwelling), the arrows indicate the direction, brown tip indicates where carbon is exported to. Right part shows indirect protection of adjacent habitats from excess sediments, nutrients and wave energy. The arrows indicate the direction and approximate magnitude (arrow width), hydrodynamic energy (blue), nutrient (brown), and sediment (orange). Adapted from Gillis et al. (2014), Huxham et al. (2018), and Hyndes et al. (2014)).

1.3. Community level

The interaction between biological (i.e. primary production, species composition) and physical factors (i.e. hydrodynamics) will determine the carbon content inside the CVE (Duarte et al. 2010; Kennedy et al. 2010; Samper-Villarreal et al. 2016). Both mangrove forests and seagrass beds storage carbon in two ways: directly as biomass of living tissues of inhabitant organisms, and indirectly by the trapping of materials and sediment of high carbon content (Alongi 2014, Fourqurean et al. 2012). Even, mangrove trees (Feller et al, 2010) and seagrass plants (Mcdonald et al. 2016) have a high plasticity in terms phenotypic expression depending on environmental characteristics such as nutrients content, how this functional diversity may influenced SC accumulation needs further investigation.

1.3.1. Carbon storage in mangrove forests

Across all CVE, mangroves are the ecosystems that store the most carbon in the living biomass, with approximately 25% of the overall stock (Alongi 2014). Models based on climate and latitude relationships have been developed to estimate above ground biomass (AGB) via satellite images (Hutchison et al. 2014; Rovai et al. 2016), showing the high influence that climatic factors have on AGB and therefore carbon sequestration. Globally, the biggest AGB has been reported in the equatorial regions, decreasing northwards and southwards (Hutchison et al. 2014; Simard et al. 2019). Wood density and carbon content vary across species (Komiyama et al. 2008 and references therein), showing that species composition within the forest may influence the ecosystem carbon biomass pool.

Sedimentation in mangrove ecosystems can determine productivity and surface accretion, processes which in turn influence the ecosystem's interactions with nearshore habitats as well as its responses towards environmental changes (Krauss et al. 2003; Feller et al. 2010). Mangrove trees influence sedimentation rate, for example; mangrove roots facilitate the accretion and gradual elevation of the sediment surface in relation to sea level. A variation in the level of sediment retention has been observed to vary spatially and temporally (Bouillon et al. 2008; Krauss et al. 2014; Woodroffe et al. 2016). Functionally distinctive, aerial roots are produced by different mangrove genera, including prop roots (*Rhizophora*), large and small pneumatophores (*Avicennia* and *Sonneratia*), knee roots (*Bruguiera* and *Ceriops*) and plank roots (*Xylocarpus* and *Heritiera*). Shape traits of the different mangrove species play an important role for sediment retention, furthermore, morphological and biochemical traits of mangrove species could define the species distribution and thus the carbon retention capacity within a mangrove ecosystem (Feller et al. 2010; Alongi 2014; Woodroffe et al. 2016).

1.3.2. Carbon storage in seagrass beds

The biomass pool of seagrass beds is not relevant for the ecosystem's carbon stock and contributes on average 130 times less to it in comparison to the sediment pool (Fourqurean et al. 2012). A number of factors influence the amount of carbon along the plants' structures, such as nutrient availability, underwater irradiance, inter-specific competition for light, type of sediment and grazing rate (Touchette and Burkholder 2000). The leaves and rhizomes of seagrasses are often colonized by epiphytic autotrophic and heterotrophic organisms, however, the production of seagrasses accounts for most of the primary production of seagrass beds communities (Hemminga et al. 1999). In seagrasses there are differences in above and below-ground biomass allocation among species; nevertheless, above-ground exceeds below-ground biomass for most of them. The species of the genera *Zostera*, *Halophila* and *Halodule* are characterized by a particularly high above-ground biomass allocation, while *Enhalus* spp. and *Posidonia* spp. have the largest below-ground biomass per unit area (Duarte and Chiscano 1999). Difference across the globe in seagrass beds' metabolic rates revealed significant differences in gross primary production (Table 1.1). In general, tropical seagrass beds in the Indian Ocean and Australia presented higher production than other community types (Duarte et al. 2010).

Sediment trapping and stabilization are important processes for the retention capacity of carbon in the sediments. Different studies have shown the importance of seagrass leaves in reducing sediment erodibility by attenuation of waves and retention of carbon-rich particles (Bos et al. 2007; Christianen et al. 2013). Biological factors that determine carbon and sediment retention are related also with seagrass traits' structural complexity (leaf area index, biomass production, shoot density, and architecture of the species) (De Boer 2000; Samper-Villarreal et al. 2016). For instance, in Australian seagrass beds, Lavery et al. (2013) reported that there was two to three times more SOC in *H. ovalis* beds when compared to beds of larger species (i.e. *Amphibolis antratica* and *Cymodocea. rotundata*). Larger seagrasses species (i.e. genera *Posidonia*, *Enhalus*, *Zostera*, *Thalasodendrum*) tend to have deeper, larger, more persistent rhizomes, often characterized by more refractory forms of structural carbon. These traits make them more likely to be preserved in marine sediments than simpler, more labile forms of carbon of smaller species (De Boer 2007; Lavery et al. 2013). Surprisingly, species of the genus *Halophila*, which has small leaves, short canopy and a small root system compared with other species, have been reported to have similar retention rates of carbon and sedimentation rates as species with bigger leaves (Fonseca 1989; Fonseca and Bell 1998).

1.4. Dissertation objectives and outline

Even though the connectivity between mangrove forests and seagrass beds has been discussed in the literature, there is still a need for more detailed data sets comparing isolated and connected CVEs, additionally research on coastal carbon stocks is usually carried out separately in mangrove forest and seagrass beds. An approach at the coastal seascape level comparing processes in mangrove forests and seagrass beds at the same time will help to elucidate carbon storage-related process. The overall aim of this doctoral dissertation is to approach carbon store at the biomass and sediment with focus on connectivity between mangrove forests and seagrass beds (as adjacency as an approach for being connected) and evaluate the importance of this connectivity for carbon store.

Connected mangrove forest and seagrass beds will exchange and accumulate more organic carbon in the sediments when they occur adjacent due to higher chages of exchange POM between then. But if one ecosystem (either mangrove forest or seagrass beds) is not present less carbon will be accumulated inside the mangrove forests or the seagrass beds due to the lack of the carbon donor ecosystem. The general hypothesis is that mangrove forests and seagrass beds that are connected with each other will have more carbon in the sediments, whilst CVEs that are isolated from each other will have less carbon. In order to evaluate the importance of this connectivity in a global perspective for carbon stored, I selected five different places where isolated and connected mangrove forests and seagrass beds could be studied and compared (Figure 1.3). At each place, one to six different location of similar climatic conditions were selected. I explore factors that could influence carbon stocks at a local scale (Chapters 2 to 6), followed by a general discussion (Chapter 7) in which I compare the data obtained throughout this doctoral dissertation with public data available in databases.

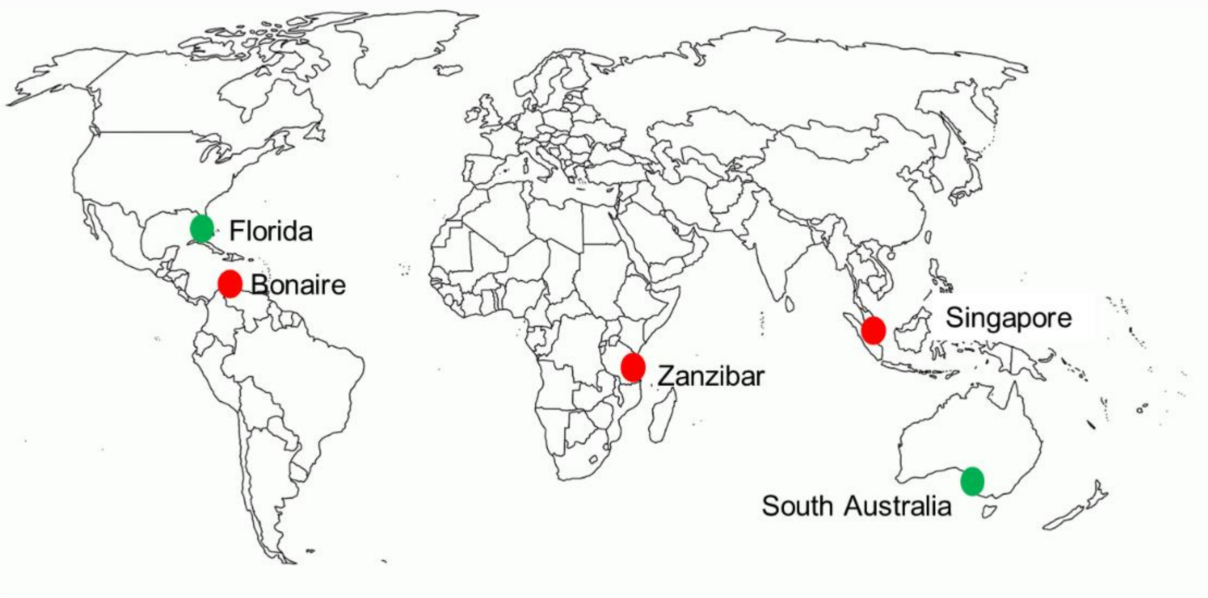

Figure 1.3. Five different tropical and subtropical places where sampling measurements were taken. Red circles indicate tropical places whilst green circles indicate subtropical places.

1.5. Chapter overview

Chapter 2 Focus on evaluating different geomorphic settings of mangrove forest and its influence on POM transfer.

The role of mangrove forests and adjacent ecosystems as donors and recipients of POM across different geomorphic settings was explored in Singapore in mangrove forests that had similar climatic conditions but different geomorphic settings (riverine vs. fringing, according to (Ewel et al 1998). The relative contribution of mangrove trees, seagrass plants, macroalgae, terrestrial plants and oceanic sources (plankton and SPM), to the POM pool in the coastal water body was determined in three different locations. Additionally, the carbon pools in the mangrove tree biomass, seagrass plants and the upper 15 cm of sediment, and CO_2 fluxes from the sediment to the atmosphere of the mangrove forests were measured to evaluate the different influence that those factors could have on the export of POM or DOC. We hypothesized that biomass, CO_2 fluxes and connectivity (through POM exchange) with adjacent ecosystems is influenced by landscape structure (i.e. mangrove forest or catchment area spatial arrangement).

Chapter 3 Focus on evaluating connectivity and the influence of different predictors in the sediment carbon content of mangrove forests and seagrass beds.

A comparison of the sediment carbon content of isolated (separated by approximately 3 km) and connected mangrove forest with seagrass beds under similar climatic conditions at Unguja Island, Zanzibar was explored. The influence of around 19-21 predictors were analyzed separately on SOC and SIC content across mangrove forests and seagrass beds in six different locations. In order to have a holistic approach we divided our variables in levels such as: (1) seascape (i.e. mangrove forest area, channel presence etc.) (2) community structure (i.e. biomass, species abundance) and (3) sediment characteristics (i.e. sand and mud percentage). We hypothesized that variables at the seascape level will influence SIC content, compared to SOC, due to the high carbonate presence in Unguja Island. Whilst SOC content will be more affected by variables at community and sediment level because of species composition and trait related features of the dominant species.

Chapter 4 Focus on comparing the cover area and living biomass of the main CVE on the contribution of POM.

A seascape structure approach using the cover area of the main CVE (mangrove forest, seagrass beds, salt marshes and macroalgae beds) was used to calculate the living biomass and the carbon and nitrogen stocks in South Australia. Across three types of seascapes in South Australia: i) connected mangrove patches and seagrass beds (adjacent to each other within 3 km), ii) isolated seagrass beds, iii) and isolated mangroves patches (apart from each other within 3 km) the exchange of POM was tested. By studying the differences in exchange of POM together with surface area and living biomass of the CVE, it was aimed to identitfy the possible role and impact of each CVE on carbon and nitrogen store, inside the ecosystem and on the seascape. We hypothesized that connected mangrove forests and seagrass beds will have higher carbon and nitrogen stored because of connected ecosystems have more exchange carbon and nitrogen with each other, and connectivity between ecosystems is modulated by habitat surface areas and standing living biomass.

Chapter 5 Focus on the exploration of how the functional traits of coastal ecosystem engineers will variate with changing sediment nutrient availability and how this gradient of trait expression could potentially affect SC accumulation.

To explore the influce on SC accumulation we aimed to answer two main research questions: 1) Do physical and chemical traits of mangrove and seagrass plants alter with a natural gradient of phosphorus and nitrogen content in the sediment? and 2) Is the accumulation of organic and inorganic carbon in a connected mangrove-seagrass gradient correlated with physical and chemical functional traits? We hypothesized the functional traits of coastal ecosystem engineers will variate with changing sediment nutrient availability. High nutrients in mangrove forests and seagrass meadows could promote higher relative AGB and associated traits, whilst lower nutrients could promote higher BGB specially in terms of fine root biomass.

Chapter 6 focus on the comparison of carbon dynamics in degraded vs intact part of a mangrove forest connected with a seagrass bed

This chapter compares the effect of degradation of a connected mangrove forest in Bonaire. A mapping and comparison of the forest structure explores how the degradation of the forests has changed in recent years, additionally the carbon stocks, CO_2 emissions, DOC and DIC outwelling were compared across intact and degraded mangrove sites. We hypothesized that gradually degradation of mangroves will equate to reduced trapping of material, which will influence the carbon dynamics, such as increased loss of CO_2 to the atmosphere and reduced DOC and DIC concentrations to adjacent coastal waters or seagrass beds.

1.6. Author's contribution

The author's contribution varied across chapters, according to the study's conceptualization and design, participation in data acquisition, analysis and interpretation of data, the making of figures and tables, and drafting of the manuscript (Table 1.2).

Table 1.2. Contribution of the doctoral candidate to the different chapter contained in the dissertation (in percentage).

Chapters	Concept and design	Data acquisition	Data analysis and interpretation	Figures and tables	Drafting of manuscript	State of publication
2	80	95	90	90	85	Published in Wetlands https://doi.org/10.1007/s13157-019-01261-9
3	90	90	95	85	90	In preparation
4	90	90	40	75	90	In preparation
5	10	10	40	20	20	In preparation
6	40	40	40	40	20	Published in Science of the Total Environment https://doi.org/10.1016/j.scitotenv.2020.141817

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Chapter 2 Sources of particulate organic matter across mangrove forests and adjacent ecosystems in different geomorphic settings

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2.1. Abstract

Mangrove forests are among the world's most productive ecosystems and provide essential ecosystem services such as global climate regulation through the sequestration of carbon. A detailed understanding of the influence of drivers of ecosystem connectivity (in terms of exchange of suspended particulate organic matter), such as geomorphic setting and carbon stocks, among coastal ecosystems is important for being able to depict carbon dynamics. Here, we compared carbon stocks, CO_2 fluxes at the sediment-air interface, concentrations of dissolved organic carbon and suspended particulate organic carbon across a mangrove-seagrass-tidal flat seascape. Using stable isotope signatures of carbon and nitrogen in combination with MixSIAR models, we evaluated the contribution of organic matter from different sources among the different seascape components. Generally, carbon concentration was higher as dissolved organic carbon than as suspended particulate matter. Geomorphic settings of the different locations reflected the contributions to particulate organic matter of the primary producers. For example, the biggest contributors in the riverine location were mangrove trees and terrestrial plants, while in fringing locations oceanic and macroalgal sources dominated. Anthropogenic induced changes at the coastal level (i.e. reduction of mangrove forests area) may affect carbon accumulation dynamics in adjacent coastal ecosystems.

Keywords: Connectivity; Blue Carbon; Carbon flux; Seagrass beds; Tidal flats; Suspended particulate matter.

2.2. Introduction

Mangrove forests play an important role of the tropical seascape, as well as for blue carbon accumulation, as they are sites of storage and exchange of carbon (Kristensen et al. 2008; Dittmar et al. 2012; Duarte et al. 2013). Mangrove forests store carbon within their aboveground (AGB) and belowground living biomass (BGB), non-living biomass (e.g. dead wood) and sediments (Alongi 2014). Together with saltmarshes and seagrasses, mangrove forests are known as a "blue carbon" ecosystem, referring to the high rates at which these coastal ecosystems sequester and store carbon (Lovelock and Duarte 2019).

Multiple studies have quantified mangrove carbon stocks (Kauffman et al. 2011; Murdiyarso et al. 2015; Bhomia et al. 2016), suggesting an important role in climate regulation. Moving beyond stock assessments, studies have now started to show how carbon stocks may differ with climate (Simard et al. 2019) or geomorphic setting (Rovai et al. 2018) at regional to global scales. On a local scale, physical and bio-geographic factors (i.e. climate regime, tidal regime, geomorphology, hydrodynamics, and nutrient dynamics) influence the carbon dynamics in mangrove forests (Alongi 2014). Understanding the factors that influence carbon storage and estimating carbon emissions and exchange at the seascape level across physical and ecological gradients is important to understand blue carbon dynamics.

Landscape structure includes the spatial arrangement and composition of landscape elements (corridors, patches and matrix) and ecological fluxes (e.g., movements of water, nutrients, organisms and other materials), and is an important landscape ecology research topic (Wu 2012). The fluxes and exchange of organic carbon among ecosystems are particularly important in networks of coastal ecosystems that release and trap carbon and nutrient subsidies from adjacent ecosystems (Gillis et al. 2017, 2014a). Carbon stored in coastal tropical vegetated ecosystems can either be produced autochthonously, or imported from adjacent ecosystems (Adame and Lovelock 2011; Duarte et al. 2013; Hyndes et al. 2014). Carbon flow among ecosystems can occur actively by motile consumers (Bouillon and Connolly 2009) or passively by tides, coastal currents and/or river discharge transporting suspended detrital particulate carbon and dissolved organic and inorganic carbon (Bouillon et al. 2008; Gillis et al. 2014b; Hyndes et al. 2014). Several studies suggest that connectivity is important to the understanding of the ecosystem processes that underlie blue carbon sequestration (Twilley et al. 1992; Gillis et al. 2014A; Walton et al. 2014; Olds et al. 2016). However, only few studies have directly measured carbon stocks (Phang et al. 2015) or nutrient fluxes (Huxham et al. 2018) across adjacent ecosystems such as tidal flats and seagrass beds.

The aim of this study was to evaluate the relative contribution of mangrove trees, seagrass plants, macroalgae, terrestrial plants and oceanic sources (plankton and suspended particulate matter (SPM)), to the particulate organic matter (POM) pool in the coastal water body. We define SPM as all suspended matter including inorganic and organic matter, while POM only includes the organic pool of the suspended matter. In order to explore carbon stocks, CO_2 and carbon exchange and the contributions of the main primary producers to POM, we chose three mangrove-seagrass/tidal flat ecotones along the coast of Singapore. Our research questions were: (1) what are the carbon stocks in the mangrove tree biomass, seagrass plants and the upper 15 cm of sediment, and CO_2 fluxes from the sediment to the atmosphere of three mangrove forests under similar climatic conditions but different geomorphic settings (riverine vs. fringing, according to (Ewel, et al. 1998)) and (2) what is the role of mangrove forests and adjacent ecosystems as donors and recipients of POM across different geomorphic settings? We hypothesized that biomass, CO_2 fluxes and connectivity (through POM exchange) with adjacent ecosystems is influenced by landscape structure (i.e. mangrove forest or catchment area spatial arrangement).

2.3. Material and methods

2.3.1. Sampling design

Three intertidal continuums in northern Singapore were selected: Sungei Buloh (1°26’47”N, 103°43’25”E), Seletar Island (1°26’36”N, 103°51’43”E) and Chek Jawa (1°24’39”N, 103°59’26”E). Those sites included two mangrove forests-tidal flat (Sungei Buloh and Seletar Island) and one mangrove forests-seagrass bed ecotones (Chek Jawa). In each location, mangrove forests were present alongside other intertidal ecosystems such as tidal flats or seagrass beds (Figure 2.1). Sampling was conducted during the late Northeast Monsoon (Dry Phase) from February to March 2017. Daily averages of temperature were between 23 and 32° C and total daily rainfall between 0 and 31 mm (Meteorological service Singapore, http://www.weather.gov.sg).

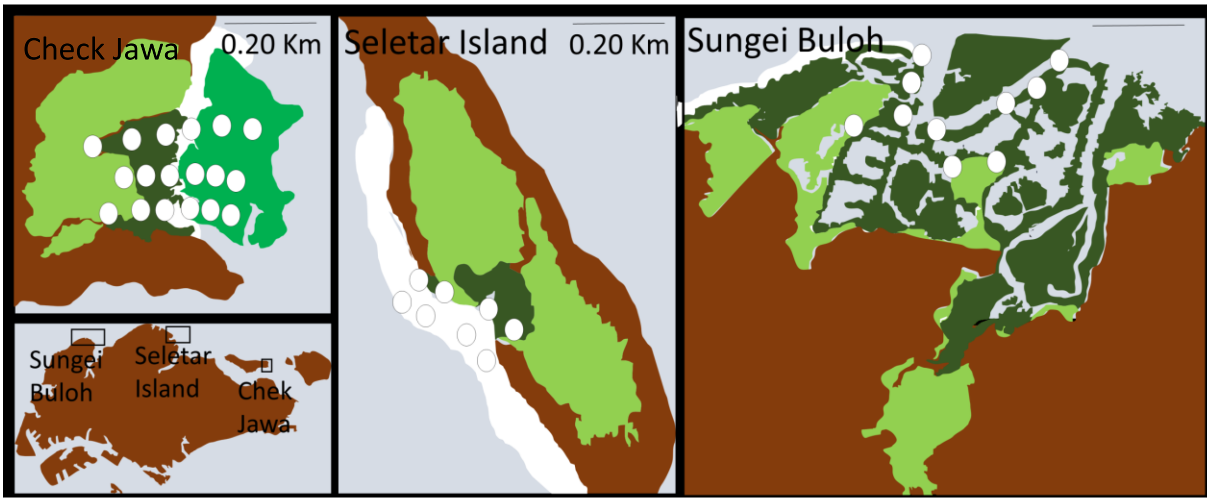

Figure 2.1. Sampling locations in Singapore along the North coast (white dots) and the distribution of mangrove forest (dark green), seagrass meadows (medium green), catchment areas (light green) and tidal flats (white).

Transects were set across the intertidal zone, starting at the tidal flat or seagrass bed and ending at the mangrove forest-terrestrial ecotone, extending landward. Within each location we established three transects separated by a distance of 50 to 500 m, depending on alongshore mangrove forest extent. The distance between points along each transect was determined by the total cross-shore length along the intertidal gradient of the mangrove forest, but sampling points were generally separated by 20 to 120 m, to gain a representation of the entire forest width.

Sungei Buloh and Chek Jawa had between three to five points on each transect, whilst Seletar Island had two points on each transect; terrestrial sampling points were not possible here due to impenetrable forest cover. Terrestrial points at Sungei Buloh did not follow a line but were taken at the closest point possible to the last mangrove-terrestrial forest ecotone. Terrestrial sampling was not possible at Seletar due to impenetrable forest cover. Transect points inside the mangrove that were closest to the ocean are defined as mangrove forest 1 (MF1), and the three points furthest from the ocean as mangrove forest 3 (MF3). For seagrass beds, the three transect points furthest from the mangrove forest are defined as seagrass bed 1 (SB1), and the three closest to the mangrove forest as seagrass bed 3 (SB3). The tidal flat transect point was classified with (TF), and the terrestrial area with (TE).

2.3.2. Biomass carbon estimation

At each transect point inside the mangrove forest, a plot of 100 m^2 was established, all mangrove species were identified, and the total number of trees of each species present was recorded. The diameter at breast height (DBH) at 1.3 m from the forest floor, was measured for each tree, except for species of the genus *Rhizophora* sp. where the diameter at 30 cm above the highest root of the main stem was taken (Kauffman and Donato 2012). From this, we estimated aboveground and belowground biomass (AGB and BGB respectively), using species-and region-specific allometric equations (Table 2.1). If no allometric equation had been developed for the species, a genus-level or general equation was used, as commonly conducted in other studies (e.g., Mizanur-Rahman et al. 2015). Species-specific wood densities were used, which is recommended if stand-specific measurements are not available (Chave et al. 2005). Carbon pools were derived from the living biomass measurements using a standard and conservative biomass-to-carbon ratio of 0.464 (Kauffman and Donato 2012).

Table 2.1. Allometric equations used for estimation of biomass of mangrove trees using measured diameter at breast height (DBH) and wood density (ρ) of trees. Wood density values ρ were obtained at (worldagroforestry.org).

No	Species	Aboveground	Belowground	Reference
1	*Avicennia alba*	0.251ρDBH2.46	0.199ρ0.899DBH2.22	Komiyama et al. 2005
2	*Avicennia officinalis*	0.251ρDBH2.46	0.199ρ0.899DBH2.22	Komiyama et al. 2005
3	*Avicennia rumphiana*	0.251ρDBH2.46	0.199ρ0.899DBH2.22	Komiyama et al. 2005
4	*Bruguiera cylindrica*	0.251ρDBH2.46	0.199ρ0.899DBH2.22	Komiyama et al. 2005
5	*Rhizophora apiculata*	0.1709ρDBH2.516	0.199ρ0.899DBH2.22	Putz and Chan 1986; Komiyama et al. 2005
6	*Rhizophora stylosa*	0.1709ρDBH2.516	0.199ρ0.899DBH2.22	Putz and Chan 1986; Komiyama et al. 2005
7	*Sonneratia alba*	0.251ρDBH2.46	0.199ρ0.899DBH2.22	Komiyama et al. 2005

At each transect point inside the seagrass bed a core of 15 cm diameter, total area of 176 cm^2 and 20 cm depth was used to harvest seagrass ABG and BGB. Seagrass parts were cleaned and rinsed in the field with seawater, and again in the laboratory with distilled water. The amount of organic carbon in seagrass structures was calculated by multiplying % carbon content of each species by the biomass present at each point (Howard et al. 2014). Carbon content in the plant biomass and carbon stocks in the ecosystems were calculated as explained below. Carbon stocks were reported in Mg (megagrams) of carbon per hectare, however other units were reported in mg (milligrams) due to the quantities differing by at least ten orders of magnitude.

2.3.3. Sediment sampling

At each point along the transects, two types of suspended sediment samples were evaluated, one from sediment traps on the sediment surface, and a second one from the water column (suspended particulate matter (SPM)).

Sediment traps were installed during low tide at a height of 0.05 m above the sediment. The traps were plastic cylinders of 24 cm length and 6 cm diameter, with twenty-four 0.5 cm-diameter holes evenly distributed in the upper 10 cm, with a lid at the bottom that collected the suspended particulate matter that entered the trap. Sediment traps were attached to steel rods that were anchored in the sediment. The traps were emptied after 24 h. To avoid salt contamination, samples were exposed in the oven at 60 °C for 24 h, supernatant water was carefully removed, and an additional 150 mL of distilled water was added to dissolve remaining salt. This process was repeated until salt particles were not detected visually.

For SPM, water samples of 1 L from the upper 40 cm of the water column were taken at each point during ebb tide. Admittedly, we acknowledge that SPM being sampled at ebb tide may be biased towards mangroves and terrestrial sources, whereas sediment traps captured POM over two ebb and two flood tides. Samples were kept in freezer bags with freezer blocks and transported within 4 h to the laboratory, where they were filtered onto pre-combusted (450 ° C, 24 h) glass fiber filters (GF/C, 696 grade, 1.2 µm pore diameter). Suspended particulate material, dry filters and sediment trap samples were analyzed for isotopic composition and used later in the mixing model to determine the origin of the POM.

At all transect points, a sediment core of 15 cm depth and 7 cm diameter was taken during low tide. The core was divided into three subsamples of 0-5, 5-10 and 10-15 cm sediment layers. The amount of organic carbon in each layer was calculated by measuring the % OC in the sample and multiplying by sediment density (Howard et al. 2014).

2.3.4. Water and gas flux sampling

Fluxes of CO_2 were measured using a portable sampling CO_2 data logger (K33-BLG CO2Meter), with an internal CO_2 sensor using NDIR (non-dispersive infrared), with an accuracy of ± 0.2% volume CO_2. The loggers were calibrated using outdoor air as a reference, having 400 ppm as reference value, and the software DAS gas lab®. The sensor was configured with a 15 cm diameter light and dark (covered with aluminum foil) 9 L survey chamber. Light and dark chambers were used to evaluate the influence that photosynthetic microorganism could have on CO_2 fluxes. CO_2 flux density (mg CO_2 -C m^{-2} h^{-1}) (FCO_2) was calculated following the methods and equation described by Chojnicki et al. (2009) using light and dark chambers.

$$FCO_2 = kCO_2 \cdot (273 \cdot Tair\text{-}1) \cdot (V \cdot A\text{-}1) \cdot (dc \cdot dt\text{-}1) \qquad (1)$$

Where kCO_2 is the gas-constant at 273.15 K = 0.536 (μg C $μl^{-1}$), Tair represents the air temperature inside the chamber (K), V is the chamber volume (L), A is the collar area (m^2) and dc·dt-1 is the rate of CO_2 concentration change in chamber (ml l^{-1} h^{-1}).

At each plot, 20 mL of water was taken from the water column during the ebb tide and filtered (45 μm pore size) into pre-combusted glass vials. Samples were kept in a cooler bag with external freezer blocks and transported to the laboratory. For DOC samples, approximately 200 μL of HCl was added to decrease pH below 2, and preserved samples were transported to ZMT. Dissolved organic carbon was analyzed using an infra-red gas analyzer with a Skalar SAN System.

Samples for Chlorophyll a (Chl-a) were obtained by filtering 500 mL through GF/F filters (1.2 μm). After filtering, samples were stored frozen until measurements were done. All samples were transported in cooler bags with freezer blocks, before being analyzed at ZMT chemical analytical laboratories. For Chl-a, each filter was cut in pieces and left in constant agitation overnight in 8 mL of 96 % ethanol in the dark at 20° C. Later, samples were centrifuged for 20 min at 5000 rpm at 4° C. Absorbance was measured at 665 nm and 470 nm using a photometer (Shimadzu UV-1700). Calculations of Chl-a were done following the procedure described by Ritchie (2008).

2.3.5. Carbon source analysis

Five sources of POM were considered in this study: oceanic (plankton and SPM), mangrove tree leaves, seagrass leaves, terrestrial plants' leaves and macroalgal tissues. Stable isotope signatures, $\delta^{13}C$ and $\delta^{15}N$, of the five different POM sources, analyzed through the Bayesian mixing model MixSIAR (Stock, 2018), were used for estimating the contribution of the different sources to the POM sampled in each plot. Isotopic signal values for oceanic sources used in this study were taken from studies done in Johor strait (Zhang et al. 2017), in this instance oceanic samples were mostly comprised of plankton and suspended sediment matter. The most abundant species at each mangrove location (*Rhizophora apiculata, Avicennia alba, Bruguiera cylindrica, Avicennia rumphiana, Nypa fruticans* (dominant only in Chek Jawa)), seagrass (*Cymodocea rotundata, Halodule uninervis, Halophila ovalis*), terrestrial plants (*Caryota mitis, Canavalia cathartica, Barringtonia* sp., *Thespesia populnea, Pinus* sp. (dominant only in Seletar Island)) and macroalgae (*Ulva* sp. and *Dictyota* sp.) were sampled. Fresh plant leaves (4-5) and algal thalli were taken, placed in separate sample bags and transported to the laboratory. The leaves and thalli were rinsed with distilled water and dried at 60 °C for 48-72 h to constant weight.

All samples were analyzed for POC, and δ13C and δ15N. Sediment traps, SPM, plant, and macroalgal samples were homogenized, then acidified to remove carbonates and analyzed for OC by combustion in an elemental analyzer (EuroVector EA 3000) with a precision of 0.06 % for OC and 0.01 % for total nitrogen for sediments (organic soil standard), and a precision of 0.36 % for OC and 0.05 % for total nitrogen for plant materials (Apple leaves standard SRM1515 reference material). Carbon and nitrogen stable isotope ratios were determined using a gas isotope ratio mass spectrometer (Thermo Finnigan Delta Plus) after high temperature combustion in an elemental analyzer (Flash 1112 EA). Isotope ratios were expressed in the delta notation (δ13C, δ15N) relative to Vienna PDB and atmospheric nitrogen. Analytical precision was ±0.10 ‰ for nitrogen and 0.13 ‰ for carbon, as estimated from an international standard (Peptone) analyzed together with the samples.

2.3.6. Data analysis

We compared the water parameters (DOC; Chl-a, and POC), SPM concentration, CO_2 fluxes and sediment OC stocks across the three locations and the different ecosystems present in the intertidal zone (i.e. mangrove forest, seagrass bed or tidal flat). A Generalized Linear Mixed-Effects Model was constructed for each variable using location and ecosystem as a fixed effect, and the transect point within the ecosystem (MF1, MF2, SB1 etc.) as a nested random effect within each location. For carbon in AGB and BGB of mangrove trees, only location was used as the fixed effect, and the transect point within the ecosystem (MF1, MF2, etc.) was a random effect, nested within the location.

To test significant differences across the locations, transects points and the different ecosystems in each location, an Analysis of Variance (ANOVA), followed by Tukey's HSD post hoc comparisons were used. T-tests were used to test for differences between light and dark CO_2 incubations. A type 1-linear regression was used to evaluate the relationship between Chl-a and SPM, POC, and DOC, to evaluate the influence of phytoplankton on DOC, POC and PN.

Diagnostic plots and visual assessments of normality and homogeneity of variation were used to confirm the data conformed to major statistical assumptions (residual homogeneity, independence and normality). Statistical significance was assessed using α=0.05. Statistical analyses were completed using R version 3.0.2 (R Core Team, 2013), using the packages ˋ1m4ˊ for GLMM (Bates et al. 2015), ˋCARˋ for ANOVA (Fox and Weisberg, 2011) and ˋeemeansˋ for Tukey's HSD post hoc comparisons (Lenth et al. 2018).

For the MixSIAR, both SPM and sediment traps isotopic samples were in the range of the 5 potential sources (Figure 2.6). Markov Chain Monte Carlo MCM runs with a Chain Length of 1000000 were selected, in order to obtain Gelman diagnostics < 1.05. Discrimination coefficient was set at 0 (Stock et al. 2018). The relative contribution dimensionless index was calculated by dividing the contribution of each source given by the mixing model (% Contribution) by the percent of surface area (% Area) occupied by the respective ecosystem (terrestrial, mangrove forest, seagrass bed).

$$\textit{Relative Contribution} = \frac{\%\,Contribution}{\%\,Area} \tag{2}$$

Percent of surface (% Area) was calculated by dividing the surface area of the ecosystem (i.e. mangrove forest) by the area of the adjacent catchment terrestrial system plus the intertidal systems (mangrove forest, plus tidal flats or seagrass beds).

2.4. Results

2.4.1. *Carbon stocks in biomass and sediments*

Mangrove biomass carbon stocks were significantly different across locations for above ground (GLMM; p<0.01, df=2, X^2=10.7) and below ground (GLMM; p<0.01, df=2, X^2=9.7) and ranged from 9.5 to 214.8 Mg C ha^{-1} being lowest at Seletar Island (Figure 2.2). Carbon stocks in seagrass plants ranged from 0.02 to 1.4 Mg C ha^{-1} at Chek Jawa.

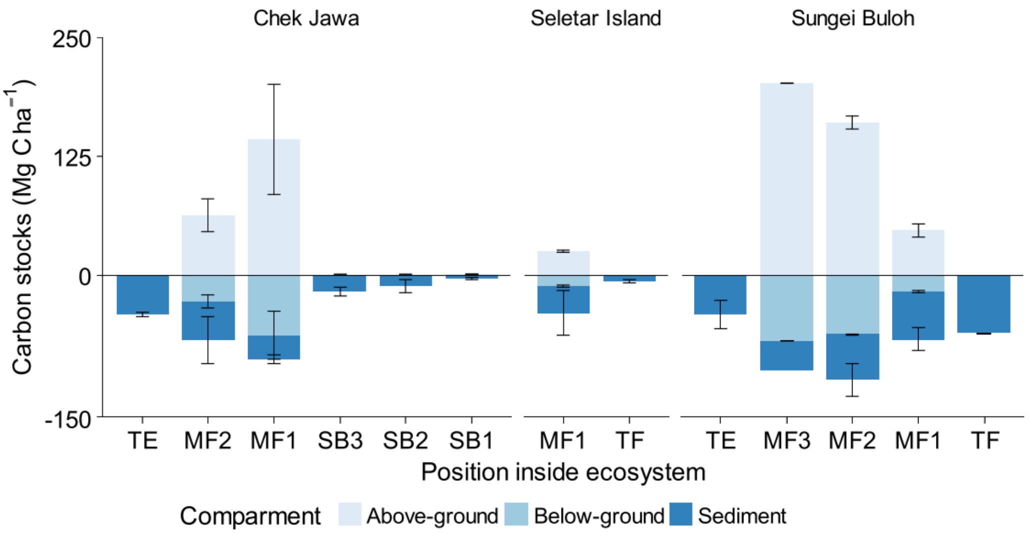

Figure 2.2. Carbon stocks in the sediment and the biomass in coastal ecosystems of northern Singapore, portioned in aboveground, belowground biomass and sediment (0-15 cm). The x-axis shows the transect point, where measurements were taken; the lowest the number is closer to the oceanic fringe of the ecosystem. Mangrove forest (MF), seagrass beds (SB); terrestrial (TE) and tidal flat (TF).

Carbon content in the top 15 cm of the sediment ranged from 0.2 to 0.9 Mg C ha^{-1}. Sediment carbon stocks in the 0-15 cm did not differ significantly among mangrove locations (GLMM; p=0.06, df=2, X^2=5.5), nor were significant nested random effects detected for sediment carbon stocks for locations or transect points within the ecosystem (GLMM; p=0.08, df=1, X^2=2.9) (Figure 2.2). No significant differences were found among seagrass beds, mangrove forests and terrestrial soils at Chek Jawa (GLMM; p=0.05, df=2, X^2=5.9) or at Sungei Buloh among tidal flats, mangrove forests and terrestrial soils (GLMM; p=0.5, df=2, X^2=1.4).

2.4.2. *Carbon content in the water column*

Mangrove forest organic carbon (OC) was transported towards the sea with the ebb tide as dissolved organic carbon (DOC) and suspended particulate organic carbon (sPOC), the ratio of sPOC/DOC ranging on average across sampling points from 0.3 to 0.8 (Figure 2.3B). There was a significant difference among locations for both DOC (GLMM; p<0.01, df=2, X^2=45.3) and sPOC (GLMM; p-value=0.03, df=2, X^2=6.9); POC was lowest at Sungei Buloh (Figure 2.3A). No random effects of the transect point within the ecosystem, were detected in any of the water parameters measured, DOC (GLMM; p=0.8, df=2, X^2=0.5) and POC (GLMM; p=0.05, df=2, X^2=5.9), indicating that neither DOC nor POC concentrations were significantly different inside the mangrove forest and the seagrass bed in Check Jawa. Further, DOC and POC concentrations did not differ significantly among mangrove forests, seagrass beds or tidal flats (Figure 2.3).

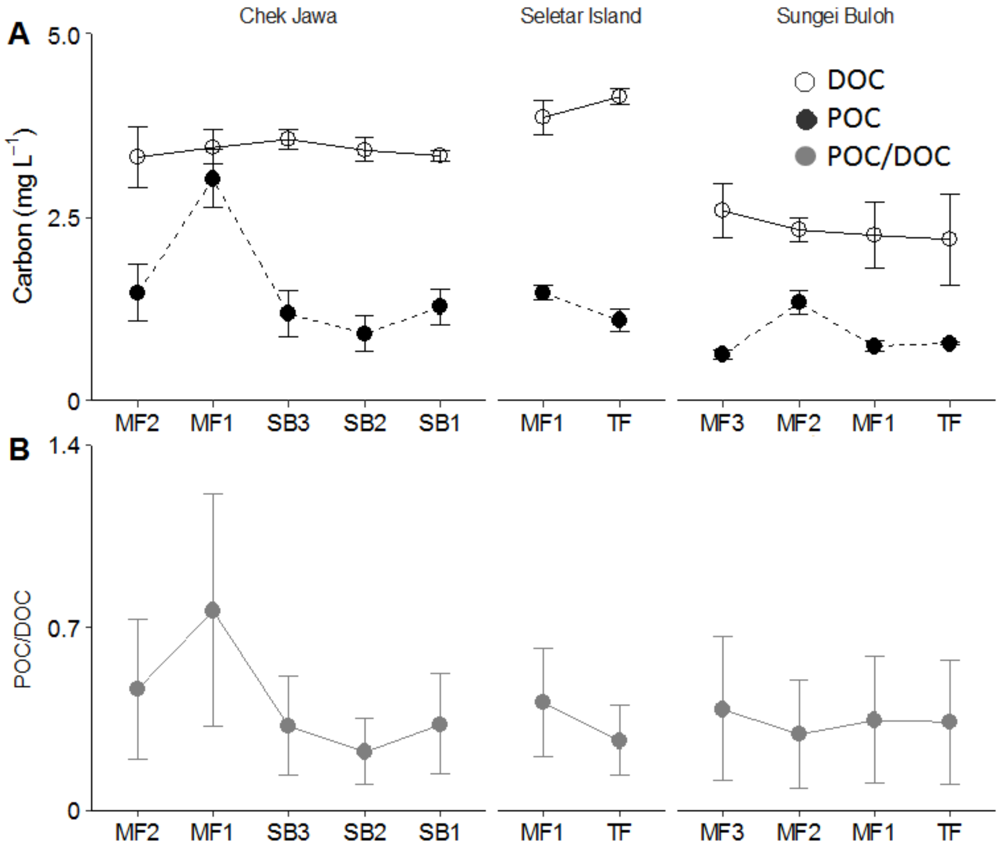

Figure 2.3. Organic carbon concentration in ebb tide across the mangrove forest, seagrass beds or tidal flats, DOC (solid line) and POC (dashed line) in the 3 different locations; the values are means ± SE (n=3) in panel A. A ratio POC/DOC gray line values are means ± SE is shown in panel B. The x-axis shows the transect points inside the ecosystem where samples were taken; the lowest the number is closer to the oceanic fringe of the ecosystem. Mangrove forests (MF), seagrass bed (SB), tidal flat (TF).

No significant differences in the quantity of SPM among locations (GLMM; p=0.2, df=2, X^2=3.6) or ecosystems (GLMM; p=0.9, df=2, X^2=0.1) were observed (Figure 2.4A). Chlorophyll-a and DOC showed a significant correlation (p<0.01, R^2=0.3) (Figure 4B). Location had a significant effect on Chl-a (GLMM; p<0.01, df=2, X^2=31.6), with Chl-a concentrations being higher at Seletar Island than the other locations (Figure 2.4).

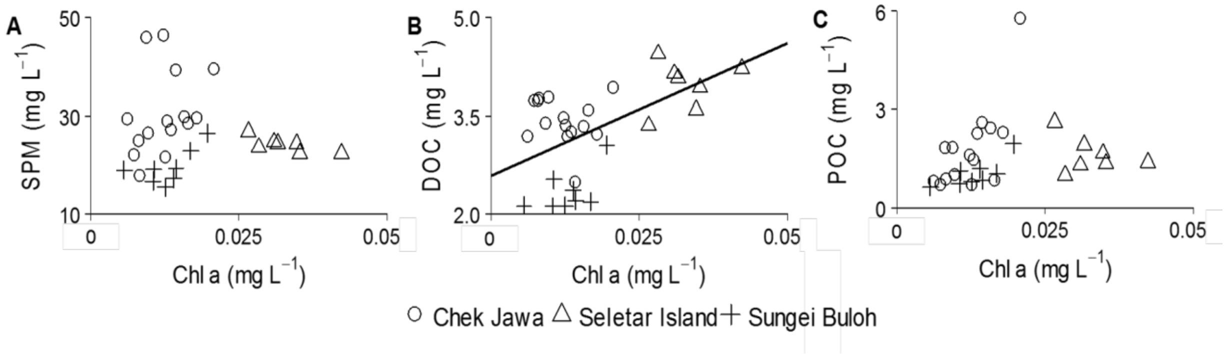

Figure 2.4. Chlorophyll a (Chl-a) vs. SPM (mg L^{-1}) panel A, DOC (mg L^{-1}) panel B, POC (mg L^{-1}) panel C and PN (mg L^{-1}) panel D. Different shapes indicate different locations indicated in the legend. A linear correlation (solid line) was found in Chl-a vs. DOC in panel B. No significant correlation was observed between Chl-a vs. SPM panel A, Chl-a vs. POC, panel C.

2.4.3. Sediment CO_2 fluxes

Fluxes of CO_2 from sediment to the atmosphere were variable among transect points. Dark incubations varied between 4 and 79 mmol CO_2 m^{-2} * d^{-1}, and light incubations fluxes between 5 and 61 mmol CO_2 m^{-2} * d^{-1} (Figure 2.5). No significant differences were observed between Seletar Island and Sungei Buloh in dark (GLMM; p=0.6, df=1, X^2=0.3) or light incubations (GLMM; p=1, df=1, X^2=<0.01). Among mangrove forests and tidal flats, only Sungei Buloh presented significantly different values for light incubation (GLMM; p=<0.01, df=1, X^2=8.5), being higher in tidal flats.

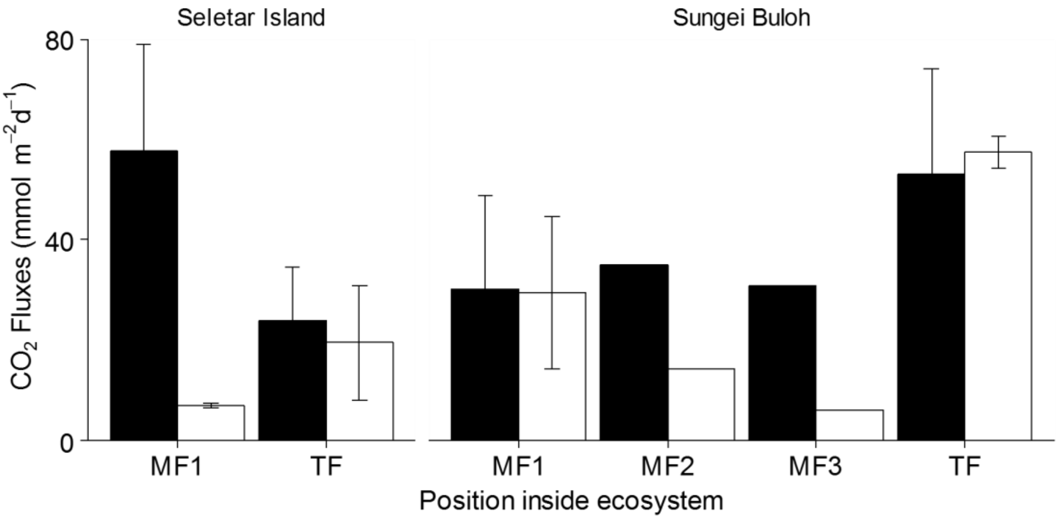

Figure 2.5. Dark and light chambers incubation CO_2 fluxes in coastal mangrove forest (MF) and tidal flat (TF) in Seletar Island and Sungei Buloh. The x-axis shows the transect point inside the ecosystem where measurements were taken; the lowest the number is closer to the oceanic fringe of the ecosystem. Mangrove forests (MF) and tidal flat (TF). The values are means ± SE (n=3 for all except for MF1 and MF3 in Sungei Buloh where only one measurement was taken).

Overall no significant difference was observed between dark and light incubation chambers at each transect point (T-test; p=0.4, df=12, t=1) with the exception of transect point MF1 at Seletar Island (Figure 2.5), where CO2 fluxes out of the sediment were significantly higher in dark chamber than in light chamber incubations (T-test; p=0.01, df=1, t=63.7). We did not complete a statistical test for the transect points at Sungei Buloh due to insufficient replication.

2.4.4. Carbon sources in SPM and trap samples

The isotopic signatures of SPM grouped close to oceanic and macroalgae in Seletar Island and Chek Jawa (Fig 2.6A and C), whereas Sungei Buloh samples grouped closer to the terrestrial and mangrove sources (Figure 2.6A). Whilst most of the isotopic signatures of sediment trap samples grouped closer to mangrove and terrestrial sources in Sungei Buloh and Seletar Island, in Chek Jawa the signatures were spread mainly among mangrove plants, terrestrial plants, macroalgae and oceanic sources (Fig 2.6B and D).

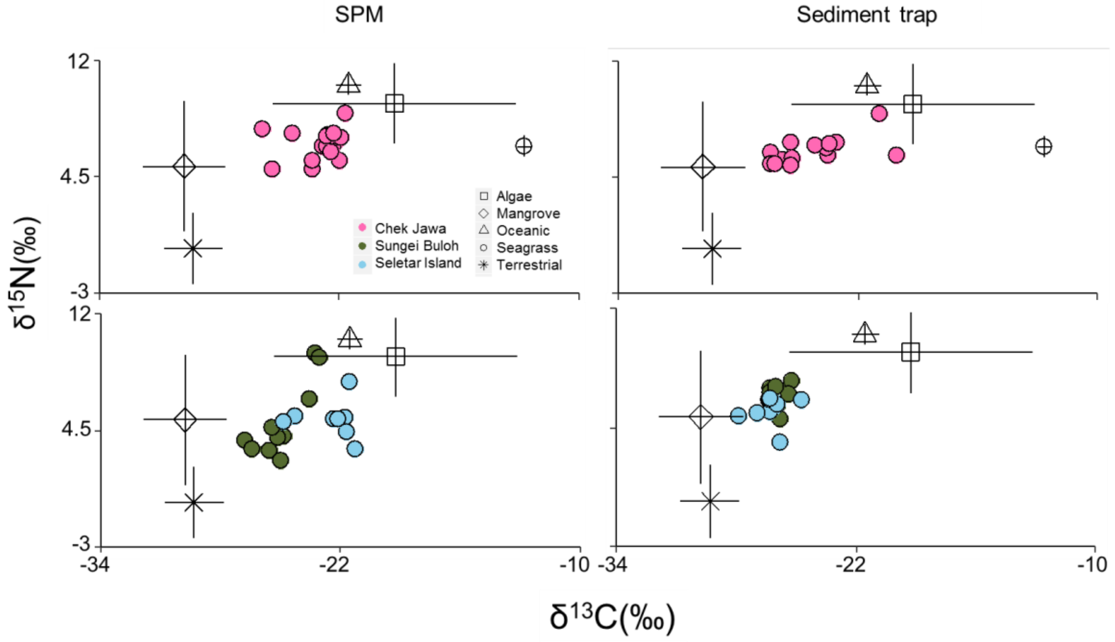

Figure 2.6. Scatter plots with isotopic of carbon (δ13C o/oo) and nitrogen (δ15N o/oo) composition of suspended particulate matter (SPM) (Panels A and C) and sediment trap samples (Panels B and D). Sources are expressed as mean +/- SE in different shapes without fill, in Isolated locations only 4 sources (Panel C and D), see legend for details. Check Jawa was the only connected location therefore the only location where seagrass was used as a source (Panels A and B).

Contributions of the different sources to the POM analysed at the different points varied among locations and between type of sample (SPM or trap). Oceanic sources were the highest contributor of POM for

SPM at all locations, while sediment trap samples were dominated by mangrove POM (Figure 2.7A and B). Seagrass beds were only present at Chek Jawa and covered a smaller area than the terrestrial zone (Figure 2.1), their relative contribution was similar in both SPM and trap samples (Figure 2.7C and D). The relative contributions showed that mangrove forests were the greatest contributor of the three ecosystems with fixed area (mangrove, seagrass, terrestrial) at all locations and for all samples except for the SPM samples in Sungei Buloh.

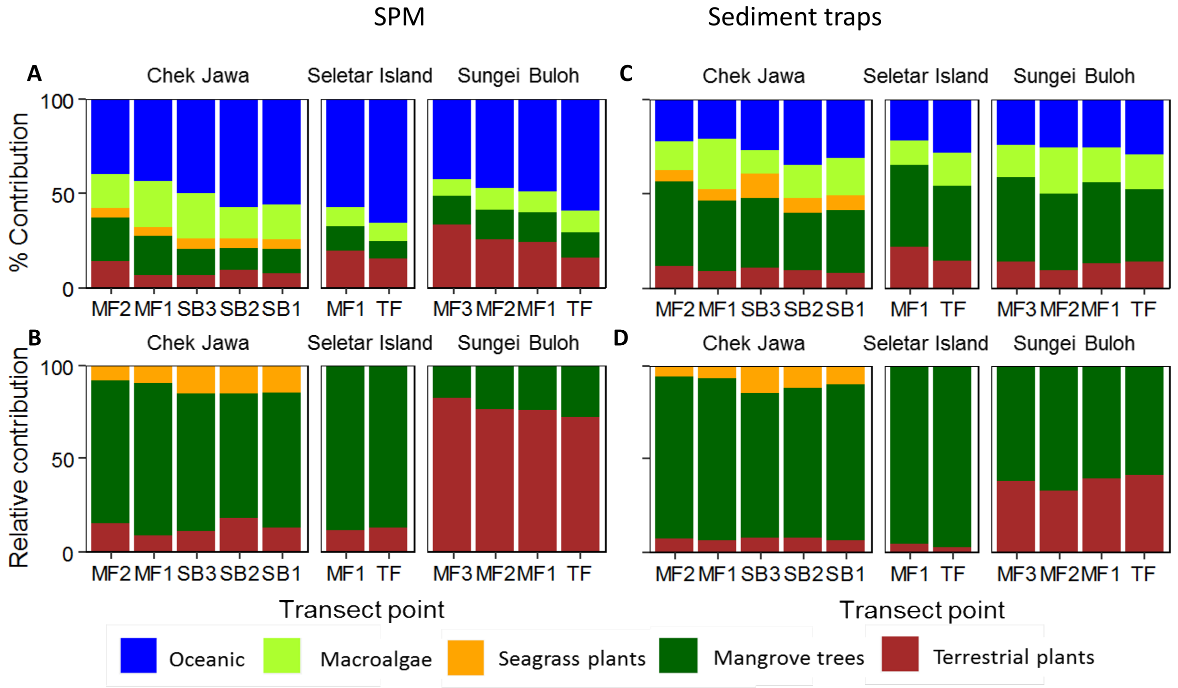

Figure 2.7. Stacked columns with percentage contributions of each source determined from the mixing model (A and B) and relative contribution calculated from equation 2 (C and D). A-B show total percentage contribution of each source for suspended particulate matter (SPM) and sediment trap samples. C-D represents a dimensionless index indicating the relative contribution of terrestrial zone, mangrove forest and seagrass bed sources for SPM and sediment trap samples. X-axis shows the transect points inside the ecosystem where samples were taken; mangrove forests (MF), seagrass bed (SB), tidal flat (TF). The lowest the number is closer to the oceanic fringe of the ecosystem. Different colors indicate different sources indicated in the legend.

Suspended particulate matter samples exhibited greater contribution of terrestrial sources than sediment trap samples at all locations. Seagrass beds were not a strong contributor of POM in SPM or sediment traps samples (Figure 2.7A and B). However, at Chek Jawa the contribution of macroalgae was higher than that of seagrass in both SPM and sediment traps samples (Figure 2.7).

2.5. Discussion

2.5.1. Carbon stocks, carbon in the ebb tide and CO_2 fluxes

Despite similar climatic conditions, mangrove forests in Northern Singapore exhibited differing standing biomass stocks, but carbon stocks in, and CO_2 fluxes from, the upper sediment layers 0-15 cm showed no difference. Mangrove forests at Sungei Buloh presented the highest carbon stocks (Figure 2.2), and Sungei Buloh also had the largest mangrove forest cover with a higher riverine/fresh water influence and terrestrial contribution than Chek Jawa and Seletar Island (Figs. 2.1 and 2.2). Carbon stocks in the upper sediment layer (0-15 cm) did not significantly differ among mangrove forests, terrestrial forests, tidal flats and seagrass beds at each location. This could mainly be due to high variability of organic carbon content in the sediment across the sampled transect points especially at the mangrove forests. Mangroves at Seletar Island were smaller, patchier, and without riverine influence (Figure 2.1), and as such showed lower aboveground carbon stocks (Figure 2.2). Results of this study, compared to a previous study of mangrove above- and belowground biomass measurements in northern Singapore, were lower at Chek Jawa (Phang et al. 2015) but similar or higher at Sungei Buloh (Friess et al. 2016). However, variation may be due to differences in specific sampling sites, temporal variation, or calculations of carbon biomass methods between the studies. Mangrove forests in Singapore, as well as other mangrove forests, show spatial variation in biomass density, and therefore in carbon stocks observed between the locations, corroborating a common pattern in mangrove forests, due to variation in natural factors such as geomorphic setting and previous disturbances (e.g., Ewel et al. 1998; Ward et al. 2017; Rovai et al. 2018).

Mangrove forest organic carbon (OC) was transported towards the sea on the ebb tide as dissolved organic carbon (DOC) and suspended particulate organic carbon (sPOC), the ratio of sPOC and DOC ranging in average from 0.3 to 0.8 (Figure 2.3); this is consistent with other reports where DOC was higher than sPOC in mangrove systems (Dittmar and Lara, 2001; Bouillon et al. 2007; Taillardat et al. 2018). Dissolved organic carbon and sPOC was lower in Sungei Buloh than at other locations. We found a positive correlation between DOC and Chl-a concentrations (Figure 2.4B), suggesting that DOC could be derived mostly from phytoplankton. Phytoplankton has been shown to influence the DOC concentration by passive leakage and active exudation (Thornton 2014) and by cell lysis (Agustí and Duarte 2013). Nonetheless, further research elucidating the origin of DOC is necessary in order to measure the contribution of different ecosystem sources to transported organic carbon, since in this study DOC had higher concentration than sPOC (Figure 2.3).

In general, CO_2 fluxes were highly variable, with no significant differences between Sungei Buloh and Seletar Island. Different studies have shown that densely vegetated and conserved mangrove forest sediments appear to have lower fluxes of CO_2, compared with clear-cut forests (Kristensen et al. 2008; Lovelock et al. 2011; Gillis et al. 2017) or strongly eutrophic forests (Chen et al. 2010). Physical and biological factors such as tidal regime, nutrient content in the sediment, and presence of biofilms have been shown to influence the CO_2 fluxes from the sediment (Kristensen et al. 2008; Alongi 2014). Fluxes of CO_2 in Shenzhen and Hong Kong, South China, were positively correlated with soil organic carbon, total nitrogen, total phosphate, total iron, ammonium and soil porosity (Chen et al. 2010). Light chamber fluxes of CO_2 tend to be lower than dark fluxes, indicating the importance of biofilms in terms of CO2-uptake upon photosynthesis. The activity of photosynthetic microbial communities is also important in retaining carbon from respiration within the ecosystem (Lovelock 2008) and the formation of biofilms may create a physical barrier by clogging the pore space (Leopold et al. 2013). We found differences in the mangrove forest and tidal flat in Sungei Buloh (Figure 2.5), with light chamber CO_2 fluxes being higher on tidal flats, where sediments were mainly muddy with no visual presence of benthic microalgae biofilms. In mangrove forests, CO_2 light chamber fluxes were lower indicating either more oxygen production or less respiration under light conditions. Data of this study is limited to conclude which process is occurring since we did not remove the biofilms of the sediments to measure CO_2 fluxes and we could not measure CO_2 fluxes in Chek Jawa. Additional studies including different tidal regimes and removal of biofilms will help to determine what controls CO_2 fluxes in Singapore mangrove forest. As we found no differences across locations and only in one location light chambers show between mangrove forest and seagrass beds.

2.5.2. Mangrove forests and adjacent ecosystems: donors and recipients

While climatically similar, the mangrove forests in this study had different local geomorphic settings and landscape structures, such as higher riverine influence in Sungei Buloh, fringing patches of mangrove forests in Seletar Island, and fringing mangrove forests with an adjacent seagrass bed in Chek Jawa (Fig 2.1). Sampling was completed during late Northeast Monsoon, which is a season of low rainfall and high wind speeds, suggesting that POM from runoff within the catchment area contributed little during this time of the year. We hypothesize that the influence of terrestrial plants will be higher during highly rainy seasons due to the higher input of terrestrially derived POM. However, further studies are needed to test this hypothesis.

The transport of POC from mangroves to adjacent ecosystems depends on different factors, such as river discharge, surface area of ecosystems, estuarine geomorphology and hydrodynamics (Hyndens et al. 2014). Geomorphic settings corresponded to the isotopic signal of SPM samples. For example, Sungei Buloh (riverine location) had isotopic signals closer to mangrove trees and terrestrial plants, while fringing locations had signals closer to oceanic and macroalgal sources (Figs. 2.6 and 2.1). The geomorphic setting of Sungei Buloh facilitates the transport of detrital material from terrestrial plants and mangrove trees into coastal water bodies due to channel-associated water movement. Samples of SPM at Sungei Buloh showed a higher terrestrial contribution than the other locations (Figure 2.7A), as Sungei Buloh is influenced by upstream freshwater sources containing terrestrial plant detritus (Figure 2.1). In general, the biggest contribution of all sediment trap samples was mangrove vegetation (Fig 2.7B and D), as indicated by the closer grouping of all samples to the isotopic signatures of mangrove tress (Fig 2.6B and D). While fringing mangrove forests, such as Chek jawa and Seletar island, are less likely to have terrestrial inputs to the POM, due to the lack of water inflow from the catchment area. Therefore, we hypothesize that exchange of POM between terrestrial and coastal waters would be mainly driven by wind action or runoff. At Seletar Island, the terrestrial plant sources are located closer to the oceanic fringe, hence, leaves move easily (i.e. via wind action) and therefore are transported out with the wave currents faster. In Chek Java, the terrestrial plant area is isolated from the ocean by the mangrove forest (Figure 2.1) showing a higher contribution of mangrove trees to the POM than Sungei Buloh (Figure 2.7).

According to the relative contribution dimensionless index (equation 2), catchment areas contributed relatively (as per unit area) more to POM than seagrass in Chek Jawa, whereas the mangrove forest contributed relatively more to POM than the catchment area in Seletar Island. In contrast, the relative POM contribution of the catchment area was higher than that of the mangrove forest in Sungei Buloh (Figure 2.7C). The relative contribution was not calculated for oceanic and macroalgal sources, because no representative surface area for the 'ocean' could be calculated. Additionally, we suspect that the macroalgae found in the mangrove forest were mainly allochthonous and transported by local currents, since collected algae were not attached to any hard substrate. Local geomorphological setting together with local differences in hydrodynamics will influence the relative contribution of vegetated coastal ecosystems and catchment area. However, more studies with more with different landscape structure mangrove forests are necessary to understand those processes, since patch size and seascape configuration are rarely included in connectivity studies, and if so, mainly focus on fish (Boström et al. 2011). In addition to landscape structure, information on litter production and decay will be necessary for understanding the contributions of each primary producer, since it has been shown that decay rates are slower for mangrove trees and terrestrial plants, intermediate for seagrass plants and fast for macroalgae (Kristensen 1994; reviewed in Zimmer 2019).

High oceanic contribution was found in SPM samples (Figure 2.7A), corroborating former studies (Gao et al. 2012; Gillis et al. 2014b; Almahasheer et al. 2017) and stressing the importance of ocean-derived input for coastal ecosystems (Orr et al. 2005). Inputs of detritus from adjacent ecosystems (i.e. seagrass and macroalgal beds) can enhance sediment respiration (Lovelock 2008). Even though the catchment area was smaller than the seagrass bed in Chek Jawa, terrestrial plants had a greater contribution to the POM. Isotopic signatures of SPM grouped closer to oceanic and macroalgae, while sediment trap samples grouped closer to terrestrial and mangrove sources (Figure 2.6). According to these findings, as well as the results of the MixSIAR models (Figure 2.7), seagrass did not contribute markedly. Seagrass beds have been reported significant donors of POM in other studies (Gillis et al. 2014b; Almahasheer et al. 2017). However, these studies reported larger seagrass beds dominated by larger species, such as *Enhalus acoroides*. Seagrass beds in the study area, by contrast, are relatively small and dominated by smaller species like *Cymodocea rotundata, Halodule uninervis,* and *Halophila* spp. (Phang et al. 2015).

The contribution of seagrass beds could be more important than macroalgal contributions in long-term sediment carbon stocks at the coastal and seascape level, as they are formed by recalcitrant compounds, which could be buried for a longer period within sediments (Trevathan-Tackett et al. 2017).

While we did not measure the standing biomass of all primary producers, we assumed that macroalgal biomass was less than mangrove trees, seagrass and terrestrial plants biomass. However, macroalgal contributions were larger than, or almost equal to, those of mangrove trees or terrestrial plants in fringing landscape structure (i.e. Chek Jawa) (Figure 2.7). Particulate organic matter had a higher percentage of material derived from macroalgae than from seagrass plants in Chek Jawa. (Figure 2.7 A and B). Contrary, in Sungei Buloh (riverine geomorphic setting), even macroalgae contributed more than terrestrial plants to sediment trap samples, they contributed equal to, or less than, mangrove trees and oceanic sources, and they were the smallest contributors of SPM samples. Those results highlight that despite their low biomass, macroalgae are an important source of POM for fringing mangroves along the northern coast of Singapore. The role of macroalgae has been discussed as a potential carbon donor to adjacent ecosystems, due to algal material being exported and stored into adjacent habitats (Hill et al. 2015; Krause-Jensen et al. 2018). Macroalgal carbon compounds degrade faster, being released in form of DOC or CO_2 (Mews et al. 2006; Hill et al. 2015; Krause-Jensen et al. 2018). The presence of refractory macroalgal compounds (carbonates, long-chain lipids, alginates, xylans, and sulfated polysaccharides), combined with factors such as retention time in the coastal habitat, fast burial, and anaerobic decay, could render macroalgae a significant contributor to long-term carbon storage (Trevathan-tackett, et al. 2015). However, further research is needed to quantify these contributions (Hill et al. 2015). To our knowledge, no research has focused on the exchange of POM derived from macroalgae in the tropics; our results suggest that the contribution of macroalgae could be significant in understanding carbon dynamics in tropical coastal areas.

Other studies have shown that mangrove forests that extend inland may retain much of their POM and nutrients of allochthonous origin (Adame and Lovelock 2011; Alongi et al. 2016). Interactions between productivity, geomorphology and hydrology influence the connectivity of ecosystems, changes in connectivity could alter the exchange and storage of organic matter provided by mangrove forests (Feller et al. 2010; Alongi 2014). Recently, a global study showed the influence of coastal morphology on carbon budgets (Twilley et al. 2018). They found that mangrove stocks in the sediment varied markedly across different types of coastal environmental settings, increasing from river-dominated to tide/wave-dominated to carbonate coastlines, but independently of forest architecture. Our results also showed that local landscape structure was important for carbon stocks and for connectivity in the sense of the exchange of organic matter. In our study location, mangrove forests with riverine influence (Sungei Buloh) and with seagrass beds (Chek Jawa) tend to have higher carbon stocks i.e. and compared to Seletar Island. Nevertheless, further studies evaluating these and additionally landscape structure interactions will help to further understand carbon dynamics.

2.6. Conclusions

In order to sustain carbon storage provided by coastal ecosystems, geomorphological settings and ecosystem connectivity should be taken into account in conservation and restoration plans. Mangrove forests clearly contributed the most to POM across the intertidal landscape, with differences in contributions from different primary producers across different landscape spatial arrangements. Therefore, anthropogenic induced modifications of local geomorphic settings at the coastal level (i.e. reduction of mangrove forests area or changing freshwater fluxes) may affect carbon accumulation in mangrove forests and adjacent coastal ecosystems. Conversely, active human modifications of local geomorphic settings may also increase carbon sequestration in mangrove forests and adjacent coastal ecosystems, such as seagrass and tidal flats. Further studies determining the origin of DOC together with tidal fluxes will help to elucidate the role of hydrodynamics, driven by the geomorphic setting, in the interchange and sequestration of dissolved and particulate organic carbon at the coastal landscape level.

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Chapter 3 Blue carbon in connected tropical coastal ecosystems: What are drivers of organic and inorganic carbon stocks?

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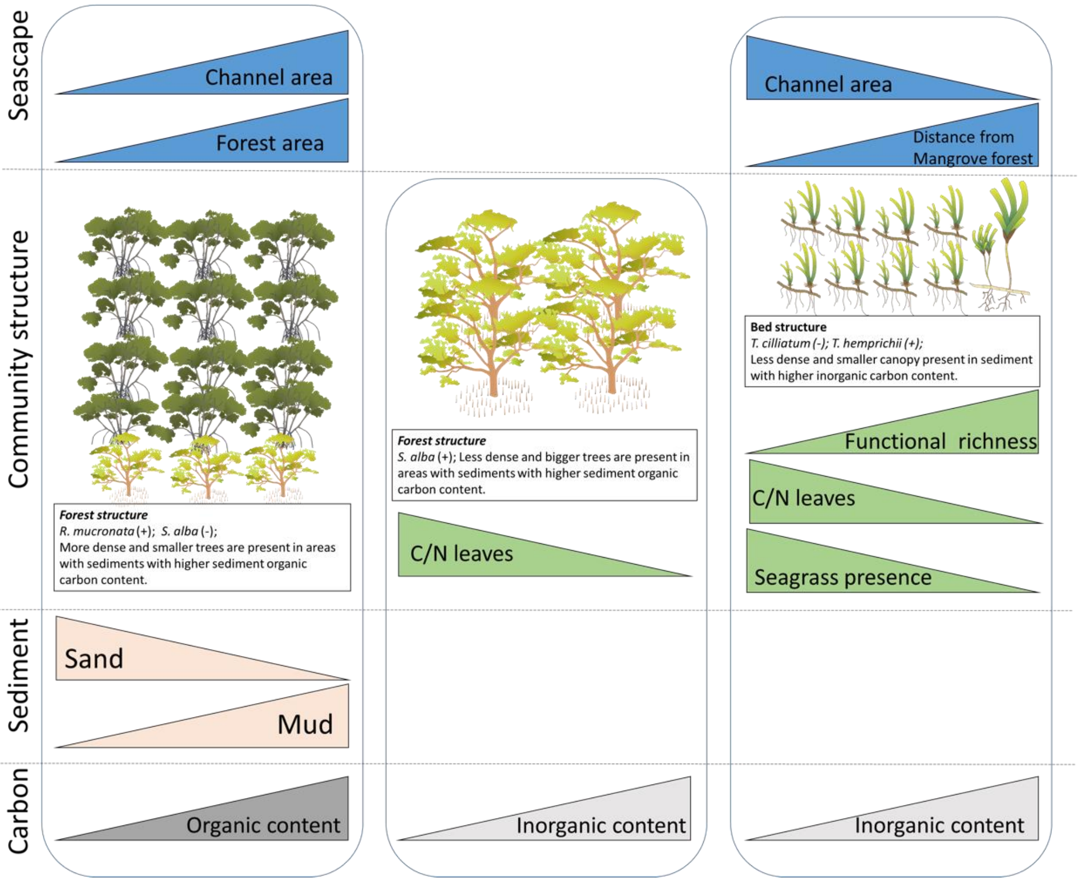
3.1. Abstract

Coastal vegetated ecosystems are areas of importance for carbon sequestration, especially within their sediments, which help to mitigate climate change. Besides their importance most research has focused on organic carbon accumulation without taking into account the multiple factors that can affect accumulation of both organic and inorganic carbon including the connected seascape. We measured the organic and inorganic carbon content in sediments of mangrove forests and seagrass beds adjacent to each other (connected) as well as in mangrove forests and seagrass beds that are not adjacent (isolated) in Unguja Island Zanzibar, across six different locations. Using a partial least square regression analyses and predictors classified within 3 levels, seascape, community structure and sediment, we determined the significance of different predictors on sediment carbon content. In connected ecosystems similar sediment carbon contents were found with high percentage of either organic or inorganic carbon. Whilst sediments with higher contents of inorganic carbon were found commonly in isolated seagrass beds. At the seascape level mangrove forest area and channel area were positively correlated with sediment organic carbon content in mangrove forest. At the community structure level species composition was a significant predictor for carbon content in both mangroves forest and seagrass beds. Interactions between seascape and community level factors can enhance the sediment carbon content for example by transportation of carbon particles within the channel and later the particle retention within the ecosystems by mangrove roots. Connectivity with high rich carbonate ecosystems (i.e. coral reefs) can be important for seagrass beds since rich carbonate particles coming from allochthonous sources were found in seagrass bed sediments. A holistic view across the coastal seascape including factors of adjacent ecosystems at different levels is recommended as a useful approach to improve knowledge about ecosystems services such as carbon sequestration.

Keywords: Mangrove forests; seagrass beds; seascape characteristics; community structure; biodiversity; sediment carbon.



Forest structure
R. mucronata (+); *S. alba* (-);
More dense and smaller trees are present in areas with sediments with higher sediment organic carbon content.

Forest structure
S. alba (+); Less dense and bigger trees are present in areas with sediments with higher sediment organic carbon content.

Bed structure
T. cilliatum (-); T. hemprichii (+);
Less dense and smaller canopy present in sediment with higher inorganic carbon content.

Graphical abstract. Showing the variables that correlated with the sediment organic and inorganic carbon content. The triangles pointed in the same direction indicate a positive correlation, whilst those in the opposite direction indicate a negative correlation. The symbol (+) indicates a positive or negative (-) correlation with the number of individuals of the species named.

3.2. Introduction

Coastal vegetated ecosystems (CVE) have a significantly higher carbon burial rate than most terrestrial ecosystems and, therefore, are important in terms of carbon sequestration irrespective of their small global area extent (McLeod et al. 2011; Duarte 2017). Blue carbon is defined as carbon stored in CVE, such as mangrove forests and seagrass beds(McLeod et al. 2011; Howard et al. 2014), although some other researchers define blue carbon as only organic carbon (Macreadie et al. 2019). Carbon in coastal ecosystems accumulates in living biomass, but the biggest fraction of the carbon is stored in sediments (Fourqurean et al. 2012; Alongi 2014). The majority of studies measuring carbon stocks in mangrove forests and seagrass beds have focused mainly on sediment organic carbon (SOC), showing that carbon stocks have a high variability at spatial and regional scales (Kennedy et al. 2010a; Rovai et al. 2018). However, carbonate production can be up to 30 % of the net CO_2 sequestration, and studies have shown that sediment inorganic carbon (SIC), especially carbonates, are an important component of carbon dynamics and burial in tropical coastal ecosystems (Macreadie et al. 2017; Saderne et al. 2019).

In adjacent connected mangrove forest and seagrass bed systems, the organic carbon inside seagrass bed sediments can be derived from mangrove tissues up to 50-83 % (Kennedy et al. 2010b; Chen et al. 2017), and organic carbon derived from seagrass plants is also transported and buried inside mangrove forest sediments, but the extent remains unknown (Huxham et al. 2018). We refer to seascape level variables as those related to cover area of different CVE as well as environmental settings (i.e. mangrove forest or tidal flat area, channel presence etc.). The balance of organic and inorganic carbon burial in blue carbon ecosystems is highly influenced by seascape level factors, and SOC and SIC contents are determined by inputs (both autochthonous and allochthonous) and outputs (i.e. respiration, dissolution and export) across coastal ecosystems (Macreadie et al. 2017; Saderne et al. 2019). Inorganic carbon burial in coastal vegetated ecosystems is mainly supported by allochthonous sources coming from adjacent ecosystems rather than autochthonous calcification processes (Saderne et al. 2019). When mangrove forests and seagrass beds are located as adjacent ecosystems with high rates of calcium carbonate cycling (i.e. coral reefs), organic and inorganic carbon cycle interactions among these three ecosystems can occur (Macreadie et al. 2017; Macreadie et al. 2019). Initial estimates of global carbon burial rates in mangroves forests show that SIC accounts for only 3 % of carbon burial rates, whereas in seagrass beds SIC burial rates are approximately 31-55 % of sediment carbon burial rates (Saderne et al. 2019). Mangrove trees and seagrass plants, with the exception of *Thalassia testudinum* (Enríquez and Schubert 2014), do not produce carbonates, but a broad range of organisms are involved in the production and subsequent accumulation of carbonates in marine sediments, including corals, calcareous algae and plankton (Westphal et al. 2010; Mazarrasa et al. 2015). Therefore, connectivity and seascape characteristics of CVE are important factors that could determine SOC and SIC content.

In addition to evaluating seascape level characteristics, community and sediment levels have been shown to affect SIC and SOC. It is challenging to untangle the interaction and influence of biotic factors (e.g. root traits of mangrove trees or seagrass leaves) from abiotic factors (sediment retention and sediment characteristics) from accretion and elevation of carbon rich sediments (Gacia et al. 2003; Krauss et al. 2014). Community structure level refers to variables that are related with the structure and diversity of the forest (mangrove) or bed (seagrass). Sediment level includes variables that are related with sediment structure characteristics for example, sediment grain size and fine root biomass. Mangrove forests are systems that show complex interrelationships among all ecosystem components (Feller et al. 2010; Alongi 2014). Competition and facilitation studies among mangrove tree species are rare, the range in plasticity that mangrove species present in response to biotic and abiotic factors may influence community composition and zonation of the forest, therefore affecting carbon cycling processes (Feller et al. 2010). Environmental factors inside the root zone may influence root traits, such as root volume and density, therefore affecting the carbon trapping capacity within the sediment (Alongi 2014; Krauss et al. 2014). In seagrass beds, species composition, canopy height, shoot density and patchiness can influence the reduction of water flow speed, and thus, SOC (Samper-Villarreal et al. 2016; Güllstrom et al. 2017) and SIC (Mazarrasa et al. 2015; Güllstrom et al. 2017) retention. Simultaneously, leaves with larger area could also provide a greater area, than seagrass species with smaller leaf area for settlement by calcareous epiphytes which contribute to the SIC concentration (Gacia et al. 2003; Mazarrasa et al. 2015).

We define connected ecosystems as mangrove forests or seagrass beds that are adjacent to each other whilst isolated ecosystems are defined as locations where either mangrove forest or seagrass beds only were present. To our knowledge there are few studies evaluating the drivers of SOC and SIC dynamics in mangrove forest and seagrass beds simultaneously (see (Gullström et al. 2017; Rozaimi et al. 2017). Studies of the different drivers that influence SOC and SIC dynamics in mangrove forests and seagrass beds have been done separately without taking into account environmental settings and adjacent ecosystems. Additionally, no studies have included factors at different levels (Seascape, community structure and sediment levels) with a seascape-connectivity perspective. Having a holistic view that explores the importance of different predictors on SOC and SIC content in mangrove forests and seagrass beds at different levels will contribute to our knowledge of the drivers of carbon stocks in the tropical coastal seascape.

We evaluated the influence of different predictors on SOC and SIC content across connected and isolated (more than 3km away from each other) mangrove forests and seagrass beds at Unguja Island Zanzibar, Tanzania. In order to have a holistic approach we divided our variables into the following levels: (1) seascape (2) community structure and (3) sediment characteristics. Our research questions included: (1) Is the sediment carbon content similar in connected and isolated coastal vegetated ecosystems under equal climatic conditions?; (2) What variables affect sediment carbon content in mangrove forests and seagrass beds? We hypothesized that variables at the seascape level will influence SIC content, compared to SOC, due to the high carbonate presence in Unguja Island. Sediment organic carbon content will likely be more affected by variables at the community and sediment levels due to stronger influence of species composition and trait related features of the dominant species.

3.3. Material and methods

3.3.1. Study areas

During the dry season in September-October 2017, 6 locations were selected in Unguja Island, Zanzibar (Figure 3.1). Three locations had adjacent seagrass beds and mangrove forests, Pete (6°17'19.94"S, 39°25'44.66"E), Weni (6°12'13.78"S, 39°12'15.07"E), and Nyamanzi (6°16'6.23"S, 39°14'48.33"E), one location had isolated mangrove forests, Kama (6° 3'52.02"S, 39°12'28.97"E), and two locations had only seagrass beds present, Bweleo (6°17'32.03"S, 39°17'37.51"E) and Matenwe (6°18'31.49"S, 39°33'2.09"E) (Figure 3.1). At each location, three transects were set up. In order to gain a broad representation of each ecosystem, each transect had 5 to 6 transect points separated by 70 to 200 m, depending on the area of the mangrove forest or seagrass bed. In connected and isolated mangrove forest locations, transect points began at the terrestrial area through the mangrove forest and continued through the seagrass bed or tidal flat (Figure 3.1.). In isolated seagrass bed locations transect points started at the beach or terrestrial zone. In this study we consider the tidal flat as the space separating mangrove forests from seagrass beds (in connected ecosystems), seagrass beds from the beach (in isolated seagrass beds) and inundated flat area in front of the mangrove forests (in isolated mangrove forests) (Figure 3.1).

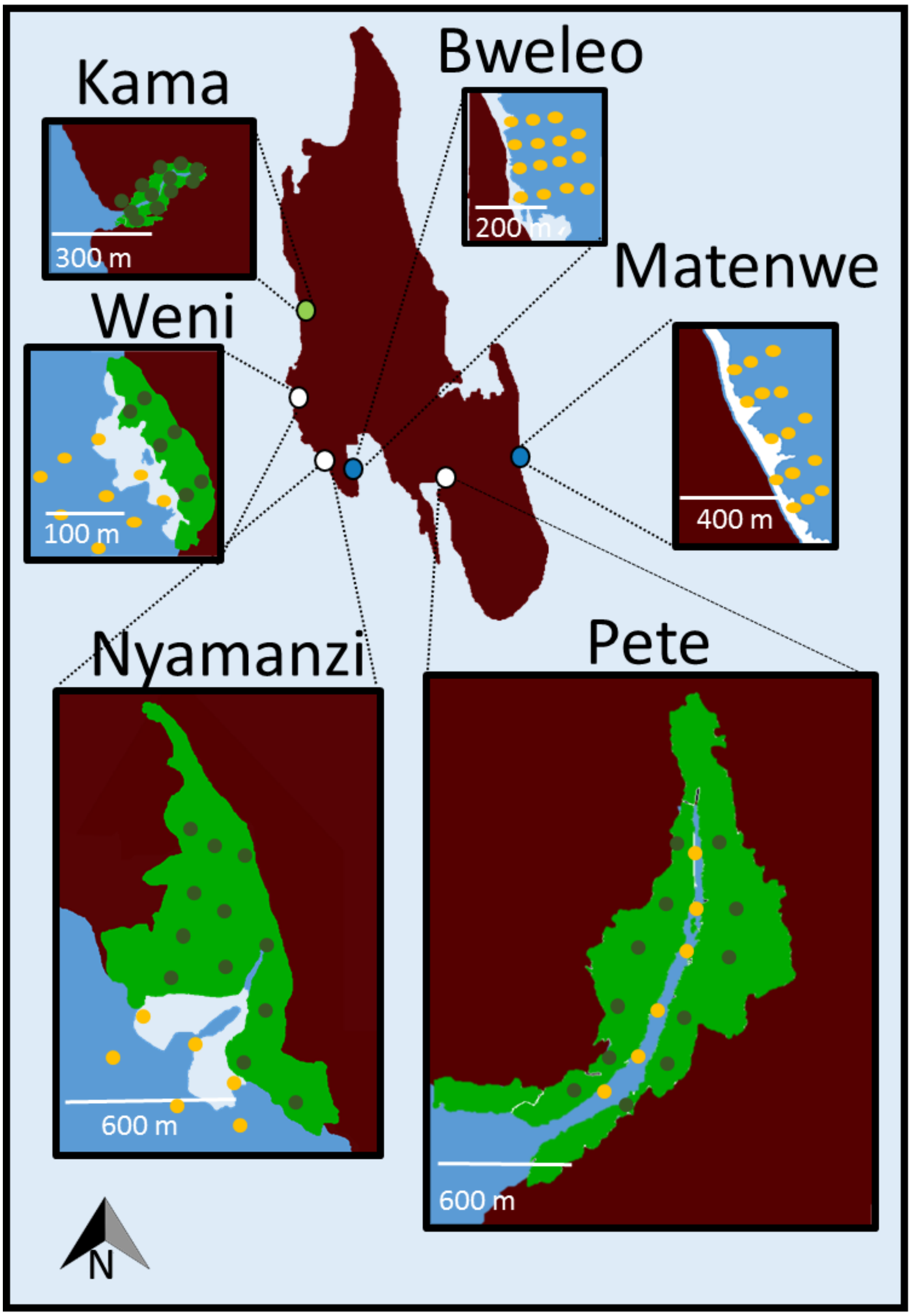


Figure 3.1. Map of study sites with the position of the six locations at Unguja Island, Zanzibar, Tanzania. Three connected locations (white circles): Pete, Weni, Nyamanzi; one mangrove forest (green circle on Unguja Island map): Kama; two isolated seagrass beds (blue circles on Unguja Island map): Bweleo and Matenwe. The green area denotes mangrove forests, brown area denotes terrestrial area, and white area denotes tidal flats. Seagrass beds are not

depicted in the map, as they could not be mapped. Dark green points indicate transect-points inside the mangrove forest, whilst orange points indicate transect points inside the seagrass beds within the locations' maps.

3.3.2. Carbon in the sediment

At each transect point, a core of 15 cm depth and 7 cm diameter was taken during low tide. The core was divided into three subsamples of 0-5, 5-10 and 10-15 cm sediment layers. Each sample of sediment was dried at 60 °C for 3 to 5 days, and the density of the sediment core was calculated by dividing the dry weight of each subsample by the volume of the subsample (192.5 cm^3). In case sediment was compressed during the sediment sampling process, the compression factor was taken into account for calculation (Howard et al. 2014).

Total carbon and organic carbon content in each sediment layer sample was calculated by measuring the content of total carbon and organic carbon and multiplying by the sediment density (g cm^{-3}) (Howard et al. 2014). All sediment samples were transported to the laboratory of the Leibniz Centre for Tropical Marine Research (ZMT), Germany. There, samples were homogenized, and 2 aliquots of approximately 15 mg were taken. One portion was wrapped in tin caps to measure percent total carbon, whilst the other was wrapped in silver caps and then acidified to measure percent organic carbon. Both portions were analyzed by combustion in an elemental analyzer (EuroVector EA 3000) using acetanilid 4 (71.6 % C) for calibration and low soil standard (OAS4) as standard with a precision of 0.06 %. Percentage of inorganic carbon in the sediment was calculated by subtracting organic carbon percentage from total organic carbon.

3.3.3. Sediment grain size

Approximately 20-25 g of sediment from each subsample (0-5, 5-10 and 10-15 cm depth) of the sediment cores were sieved in an analytical sieve shaker (RETSCH® AS-200) for 4 minutes, with amplitude of 1.18 mm g^{-1}. Seven different grain size classes of the Udden–Wentworth scale were selected (Wentworth 1922): gravel (> 2000 µm), coarse sand (1000–2000 µm), medium sand (500–1000 µm), medium-fine sand (250–500 µm), fine sand (125–250 µm), very fine sand (63–125 µm), and silt (< 63 µm). The fraction of each class of sediment was calculated as the weight percentage of the total bulk sediment.

3.3.4. Mangrove fresh root biomass

To determine mangrove fresh root biomass in the upper sediment at each transect point in the mangrove forests, a core of 30 cm depth and 7 cm diameter was taken within the mangrove sediment, placed in a mesh bag of 0.5 mm and prewashed in the field with seawater to separate fresh root biomass from the attached sediments. At the laboratory, the fresh root biomass was further cleaned and separated following Robertson and Dixon (1993). In a first step, the prewashed material from the core was placed into a glass measuring cylinder of 2 liters with an 11 % solution of colloidal silicate LUDOX® (TM, Sigma-Aldrich Inc.), which separated large particulate dead material and sediments from fresh live roots. Most of the dead material sank to the bottom of the cylinder. The supernatant, classified as fresh live roots, was further separated (dead apart from live fine roots) using a 6 % LUDOX® solution, again collecting the supernatant. After separation, the supernatant which contained the fresh live roots was washed with tap water and dried at 60 °C until constant weight.

3.3.5. Mangrove species composition and carbon tree biomass

To determine the mangrove species composition in the mangrove forests a plot of 100 m^2 was established at each transect point. The species of all trees were determined and at 1.3 m height diameter breast height (DBH) was measured, except for the species *Rhizophora mucronata* where the diameter was measured at 30 cm above the highest prop root of the main stem (Howard et al. 2014). Additionally, the number of saplings (young trees with a slender trunk with less than 4 cm DBH and not greater than 1.7 m height) and seedlings (germinated and established young propagules of maximum 70 cm) were also counted and separated by species where possible. From the DBH, aboveground and belowground biomass (AGB and BGB respectively) were estimated, using species- and region-specific allometric equations (Table 3.1). When no species-specific equation was available, we used a general equation reported for mangrove in the same region (Njana et al. 2016). Carbon pools from the living biomass were derived using the conservative biomass to carbon conversion value of 0.464 (Kauffman and Donato 2012).

Table 3.1. Allometric equations of the mangrove species found in the four locations. AGB, aboveground biomass; BGB, belowground biomass. § indicates species with no reported allometric equation, and therefore, a general equation was used. Equations used were developed by (Njana et al. 2016).

Species	AGB	BGB
Avicennia marina	$0.25\ dbh^{2.243}$	$1.420\ dbh^{1.442}$
§ *Ceriops tagal*	$0.25\ dbh^{2.240}$	$1.420\ dbh^{1.596}$
Rhizophora mucronata	$0.25\ dbh^{2.260}$	$1.420\ dbh^{1.689}$
Sonneratia alba	$0.25\ dbh^{2.217}$	$1.420\ dbh^{1.657}$
§ *Bruguiera gymnorrhiza*	$0.25\ dbh^{2.240}$	$1.420\ dbh^{1.596}$

3.3.6. Seagrass bed characteristics and seagrass plant carbon biomass

In seagrass beds, a quadrat of 1 m^2 was placed at each transect point during low tide. The cover of each seagrass species was measured in the quadrat using a grid (with 400 squares of 25 cm^2) within the quadrat. Shoot density was calculated counting all shoots within a smaller quadrat of 100 cm^2. Additionally, a core of 15 cm diameter and 20 cm depth was used to harvest all AGB and BGB within the transect point. Seagrass parts were separated in AGB (shoots) and BGB (rhizomes and roots) cleaned and rinsed in the field with seawater, and again in the laboratory with distilled water. Carbon content of seagrass structures was calculated by multiplying the average % carbon content of species present in the location with the biomass at each point (Howard et al. 2014).

3.3.7. Statistical analysis

Due to the unbalanced sample size of isolated mangrove forest and seagrass beds compared with connected ecosystems, all statistical comparisons were implemented using generalized linear mixed models (GLMER) with gamma distribution link function. The function glmer and analysis of variance ANOVA from the R software (R Studio team 2015) and the package lme4 (Bates et al. 2015) was used. Comparison of sediment total carbon, SOC and SIC content between connected and Isolated ecosystems were completed using the formula glmer (x ~ ecosystem * connected status + (1 | Location)) with gamma distribution family, where x was the variable response i.e. STC; ecosystem was a factor with two levels (mangrove forest and seagrass bed) (Zuur et al. 2009). Connected status was a factor with 2 levels (connected ecosystems and isolated ecosystems) and location was a random factor with 6 levels (Pete, Weni, Nymanzi, Kama, Bweleo and Matenwe). For all tests, a p-value less than 0.05 was considered significant. Akaike information criterion (AIC) stepwise selection was applied to determine if removing one varible improved the quality of the model. Grain Size summary statistics, as well as mud and sand percentages were estimated for each zone using the G2Sd R package (Fournier et al. 2014). Comparison of grain size summary statistics between mangrove forests and seagrass beds at each connected location were performed with the formula lm (x ~ ecosystem) as described above.

For all linear models, assumptions of normality, homogeneity and independence were tested using the R package gvlma (Peña and Slate 2006). If assumptions were not validated, a generalized linear model with gamma distribution and link function log were used (i.e. Sand ~ ecosystem, family=gamma link=log). When significant differences across ecosystems or locations where detected, a Tukey post-hoc test was run to evaluate differences between the level(s) of the factor evaluated. Tukey post-hoc tests were completed using the R package emmeans. For all tests a p-value less than 0.05 was considered significant.

Leaf traits included in the FD analysis of both seagrass plants and mangrove trees were measured as follows: 5 leaves per species was taken randomly from different shoots for at a least 3 specimens from the most abundant species at each point. Leaf perimeter (mm) and Leaf surface area (mm^2) were calculated using digital photographs and the software ImageJ. Specific leaf area was calculated dividing the weight of each leaf by its own area ($g\ cm^{-2}$). Leaf thickness (mm) was measured using a digital caliper.

Samples of the roots from the most abundant mangrove species were taken at each plot. A cylindrical root piece of approximately 200 cm^3 to 300 cm^3 were cleaned and transported to the laboratory. The volume was calculated using a cylinder shape formula (cm^3) and then dried until constant mass. Root wood density of each root was calculated dividing the weight of the root piece by the volume ($g\ cm^{-3}$).

For seagrasses, rhizome and root diameter were measured using a digital caliper. The ratio of ABG to BGB was calculated by dividing the biomass above ground biomass by the below ground biomass.

Diversity indices were estimated using a Functional Diversity approach. The FD of a community was approached through the measurements of traits, number and abundance of species. We used the functional richness (FRic) index which is positively correlated with the number of species present in the community (Schleuter et al. 2010). Analyses were run using the R package 'FD' (Laliberté et al. 2014).

Different predictor variables were selected for evaluating their influence on the SOC and SIC content using partial least square regression analyses (PLS) separately for mangrove forests and seagrass beds. Predictors were classified within 3 levels: sediment, community structure and seascape, in order to determine the significant influence of each predicator within level on SIC or SOC content. Details of the number of predictors in each level are further explained (Table 3.2).

Table 3.2. Predictors used in partial least square (PLS) regression models for organic and inorganic carbon content (g cm^{-3}) in mangrove forests and seagrass beds. Predictors were classified within 3 levels: sediment, community structure and seascape, in order to determine the significant influence of each predicator within level on SIC or SOC content. Abbreviation is the abbreviated name of each predictor used in the results section. In the mangrove forest and seagrass bed columns, yes and no indicate predictors were included or not included respectively in the model. Type of predictor indicates which type of variable the predictor was, i.e. continuous-percentage or discrete. NA means not applicable.

Variable	Mangrove forest	Seagrass bed	Type of variable
Sediment			
Mud (%)	Yes	Yes	Continuous percentage
Sand (%)	No	Yes	Continuous percentage
Fine root biomass (g)	Yes	NA	Continuous
Community structure			
Wildlings (#)	Yes	NA	Discrete
Seedlings (#)	Yes	NA	Discrete
Number of tree species	Yes	NA	Discrete
% cover of species	NA	Yes	Continuous percentage
Number of trees	Yes	NA	Discrete
Mean DBH	Yes	NA	Continuous
Density (shoots cm^{-2}) of the dominant species	NA	Yes	Continuous
Total seagrass cover (%)	NA	Yes	Continuous
Canopy height (cm)	NA	Yes	Continuous
AG Biomass (kg)	Yes	Yes	Continuous
BG Biomass (kg)	Yes	Yes	Continuous
C/N ratio leaf of dominant species	Yes	Yes	Continuous
Presence/absence of seagrass	Yes	Yes	Presence/Absence
Seascape			
Mangrove forest area (m^2)	Yes	Yes	Continuous
Tidal flat area (m^2)	Yes	Yes	Continuous

Functional richness (Index)	Yes	Yes	Continuous
Channel area (km^2)	Yes	Yes	Continuous
Distance to seagrass bed limit (m)	Yes	NA	Continuous
Distance to mangrove forest (m)	NA	Yes	Continuous

*In the abbreviation is the scientific name of the number of trees or percentage of cover of a given species.

Means of partial least square regression (PLS) were selected for analyzing the relative importance of each environmental predictor on the variable response (i.e. SOC or SIC content) separately for mangrove forests and seagrass beds. Partial least square regression is applicable when the number of predictors is larger than the number of samples and when predictors that show high collinearity need to be used in the same model (Carrascal and Galva 2009). Partial least square was run using the R package pls (Mevik and Wehrens 2007). Number of components were selected using the Root Mean Squared Error of Prediction (RSMP) choosing the number of components that explained the most variance with the lowest RSMP.

3.4. Results

3.4.1. Sediment carbon in coastal locations

Connected and isolated ecosystems were significantly different in their total sediment carbon density and no differences were observed across the depths (Figure 3.2). Connected ecosystems and the isolated mangrove forest (Kama) also had significantly different SIC content, but no significant differences were observed for SOC across connected and isolated systems. Sediment total carbon and inorganic carbon content was also significantly different between mangrove forest and seagrass beds (Table 3.3). The GLMER models indicated that location affected sediment total carbon density, SIC and SOC content (Figure 3.2; Table 3.3). Results of Sediment grain size composition are showed in supplementary figure 3.1.

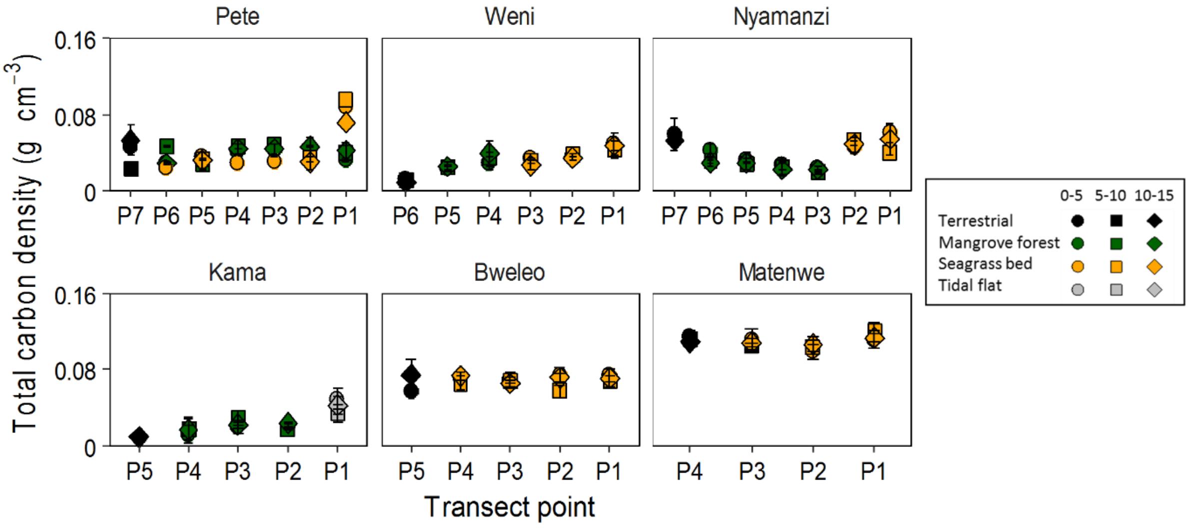


Figure 3.2. Total carbon densities at transect points in the sediment for each coastal ecosystem (mangrove forest, seagrass bed and tidal flat) and the terrestrial zone, from 0-5, 5-10 and 10-15 cm depth see legend across six locations (Pete, Weni, Nyamanzi, Kama, Bweleo and Matenwe). Points are means and error bars are standard error (SE). Mangrove forests and seagrass bed points at Pete were at the same distance from the terrestrial part. P represents distance within the ecosystems, the lower the number is closer to the oceanic zone along the transect. For example, P1 is the closest point to the oceanic fringe while P6 is the closest to the terrestrial ecosystem. Pete, Weni and Nyamanzi are connected locations, while Kama is an isolated mangrove forest and Bweleo and Matenwe are isolated seagrass beds.

Table 3.3. Results of the GLMER model comparing fixed effects connectivity status (connected and Isolated) and ecosystem (mangrove forests and seagrass beds); as well as, random effect location. SE is standard error; t is t value. P-values in bold are significant. SD is standard deviation. P-values of isolated mangrove forests and seagrass bed show differences between those isolated locations with connected ecosystems.

		Fixed effects				Random effects		
Response variable	Model component	Estimate	Standard error	*t*	*P*		Variance	Standard deviation
Sediment total carbon content model	Intercept	32.20	2.66	12.11	<0.01	Location	1.83	1.35
	Connected status Isolated	25.57	8.75	2.92	<0.01	Residuals	0.12	0.35
	Ecosystem seagrass	-9.10	3.09	-2.94	<0.01			
	Connected status: Ecosystem	-36.90	9.13	-4.04	<0.01			
Sediment organic carbon content model	Intercept	80.51	28.33	2.84	<0.01	Location	956.41	30.92
	Connected status Isolated	-15.90	52.12	-0.31	0.76	Residuals	0.41	0.64
	Ecosystem seagrass	15.89	10.03	1.59	0.11			
	Connected status: Ecosystem	98.41	55.99	1.76	0.08			
Sediment inorganic carbon content model	Intercept	99.67	14.41	6.92	<0.01	Location	65.09	8.06
	Connected status Isolated	148.76	77.69	1.92	0.06	Residuals	0.24	0.49
	Ecosystem seagrass	-58.13	12.51	-4.65	<0.01			
	Connected status: Ecosystem	-177.06	78.04	-2.27	0.02			

By plotting organic vs inorganic carbon in a 1:1 plot, it is possible to see the relative differences in SOC and SIC across connected and isolated habitats, where points that lie along the gray line indicate that equal percentage of SOC and SIC and those on left or right side of the line indicate higher SIC or SOC percentage, respectively (Figure 3.3).

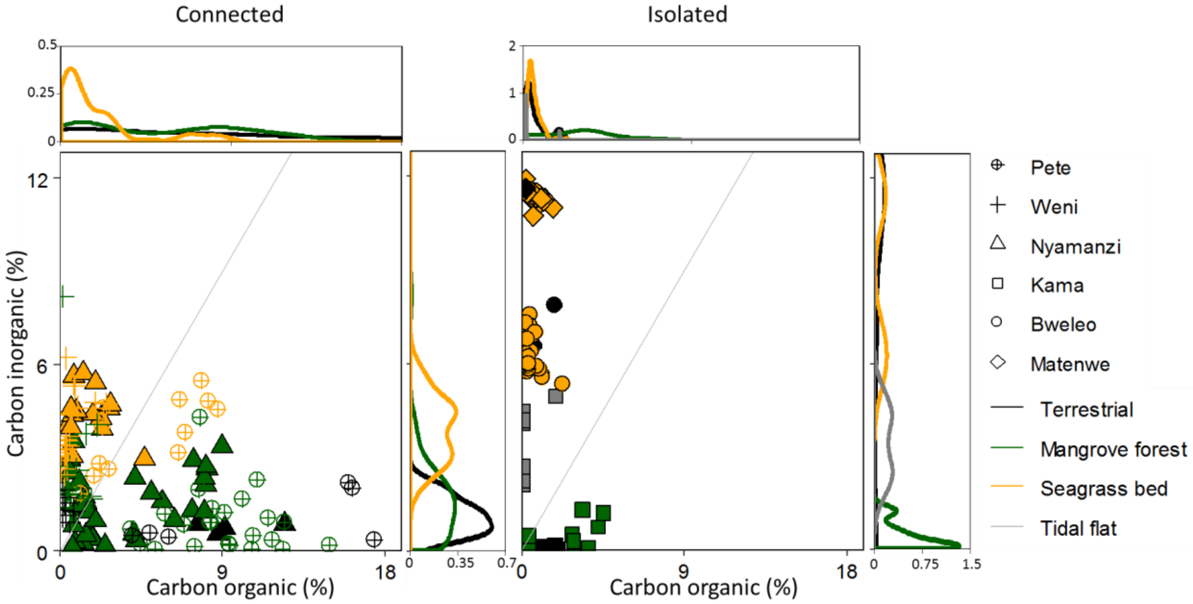


Figure 3.3. Scatter plot of organic (%) vs. inorganic carbon (%) in the sediment at coastal ecosystems (mangrove forest, seagrass bed and tidal flat) and the terrestrial zone, from 0-15cm depth across the six locations (Pete, Weni, Nyamanzi, Kama, Bweleo and Matenwe) see legend. The gray line indicates a 1:1 relation between organic (%) vs. inorganic carbon (%). Pete, Weni and Nyamanzi are connected locations, while Kama is an isolated mangrove forest and Bweleo and Matenwe are isolated seagrass beds. Marginal plots on x and y axis show density histogram of data distribution, please note that scales of distribution plots are different.

Marginal plots and GLMER show that seagrass beds had a higher percentage of SIC (%) and therefore carbon content, with some exceptions across locations (Figure 3.3, and Table 3.3; Supplementary table 3.1). Generally, seagrass beds also had significantly higher inorganic carbon contents in isolated seagrass beds than in connected locations. Connected mangrove forests had significantly lower SIC contents than the isolated mangrove (Figure 3.3 and Table 3.3).

3.4.2. Successful predictors of the partial least squared (PLS) models

All predictors selected for the PLS models in the mangrove forests and seagrass beds indicated a relationship with the response variables SOC and SIC using the root mean squared error of prediction (RSMP). The selected number of components for all PLS models was two. In general, models displayed a high degree of determination and fit, except for the models of seagrass beds for SOC, which were not included in the results due to R^2 values of 0.05 predictability of only 26.7 to 46.1 % of the variance.

For the rest of the models, R^2 ranged from 0.32 to 0.45, and the models explained between 53.7 and 70.1 % of the variance (Figure 3.4).

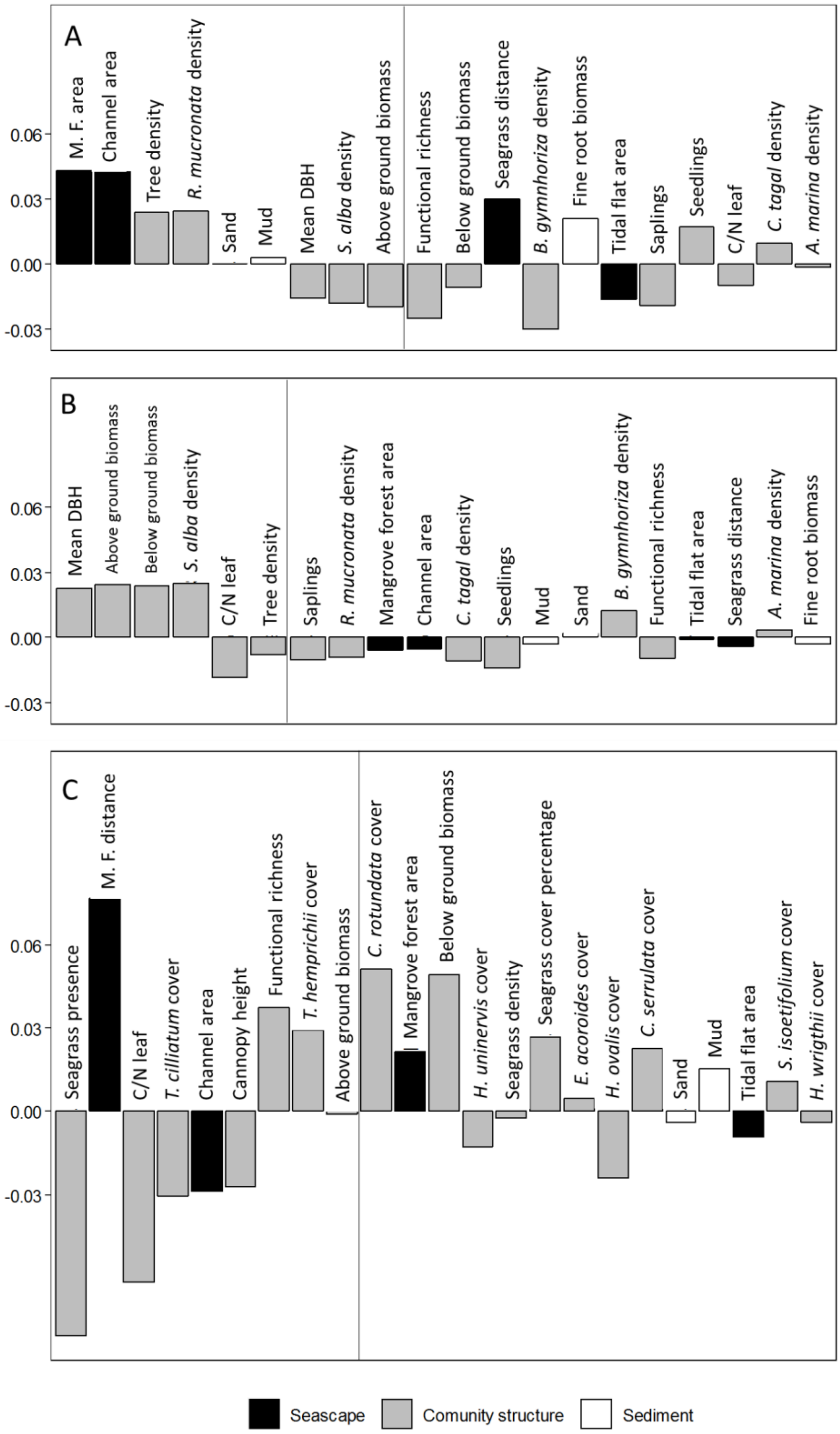


Figure 3.4. Model coefficients of partial least squared (PLS) regression models for sediment organic carbon (SOC) (A); sediment inorganic carbon (SIC) content in mangrove forest (B); and SIC in seagrass beds (C). The color of the bar represents the level of the predictor (see legend for details) Predictors on the x-axis are arranged from the most to

the least influential predictor (left to right), using VIP (Variable influence on the projection). Predictors on the left side of the black vertical line represent predictors with VIP higher than one with an above average influence on the response variable. Whereas those predictors which have less influence are located on the right side of the black vertical line. R^2 expresses the fitting of predicted values versus real values. Explained variation is the percentage of variation explained by the respective model. See Table 3.2 for abbreviations.

Mangrove forest sediment organic and inorganic carbon predictors

Sediment organic carbon content had different predictors at the 3 different levels, seascape, mangrove community structure and sediment (Figure 3.4A and B, Table 3.2). By contrast, SIC content only had significant predictors at the seascape and mangrove community structure level (Figure 3.4C, Table 3.2). Sediment organic carbon content was positively correlated with mangrove forest area and channel area at the seascape level. Whilst at the sediment level SOC had two significant predictors; mud and sand percentage, being positively and negatively correlated, respectively. At the community structure level, SOC content was positively correlated with species dominance, a high density of trees, AGB, BGB and mean DBH. This indicates a negative correlation with lower density and bigger trees. Species dominance was negatively correlated with dominance of *S. alba*, and positively correlated with dominance of *R. mucronata* (Figure 3.4A and B) Species composition is reported in Supplementary table 3.2. Inversely to SOC content, SIC content at the community structure level was negatively correlated with dominance of *R. mucronata* and positively correlated with presence of bigger trees (Figure 3.4A and B). Sediment inorganic carbon was also negatively correlated with the C/N ratio of the leaves of the most dominant species.

Sediment beds sediment inorganic carbon predictors

At the seascape level in seagrass beds, mangrove forest distance was positively correlated, whilst channel area was negatively correlated to SIC content (Figure 3.4C). At the community structure level, the C/N ratio of leaves of the dominant species, *Thalassodendron ciliatum*, AGB and seagrass presence were predictors with negative correlations to SIC content. Functional richness and cover of *Thalassia hemrpichii* were significant predictors only at community structure scale, both being positively correlated to SIC content (Figure 3.4C).

3.5. Discussion

The present study clearly indicates sediment inorganic carbon (SIC) is a significant component for the carbon storage in Zanzibar. All sampled CVE had different coastal environmental settings (i.e. tidal flat area in front, channel area) that could influence the type of carbon stored in the sediment within the CVE. This was reflected in the high variance explained by the random factor of location (Table 3.3). Notwithstanding, a clear pattern emerged beyond these location-specific characteristics and ecosystem type: sediments with higher contents of SIC were found more commonly in isolated CVE. Conversely, higher contents of SOC were found more commonly in connected CVE although no significant difference were detected by GLMMs models for SOC (Table 3.3 and Figure 3.3). Isolated and connected mangrove forests in general had higher SOC content, while seagrass beds had a higher SIC content. Across all locations, predictors at different levels significantly predicted SOC and SIC content for mangrove forests, whilst for seagrass beds only SIC could be significantly predicted (Figure 3.4), mainly because SOC content was very low in seagrass beds (Figure 3.3). Mangrove community structure level variables interacted differently for SIC and SOC showing that species composition is an important factor for the carbon accumulation process. Seagrass community structure, specifically different species composition and ratio of AGB:BGB, showed a significant influence on SIC. Sediment level variables were only significantly correlated for SOC in mangrove forest.

3.5.1. Predictors of carbon at seascape level

Two predictors at the seascape level related with mangrove forest characteristics were significantly important for carbon content: extent of mangrove forest area was positively correlated with SOC content within mangrove forest and distance from the mangrove forest to the seagrass beds was positively correlated with SIC content within seagrass beds (Figure 3.3A and C). Area and patch characteristics of mangrove forests have not been widely studied in the context of carbon accumulation. However, Suyadi et al. (2018) showed sediment accretion to increase with mangrove forest patch size. Mangrove trees are well known to be important agents that enhance the vertical sediment accretion by direct organic contributions and/or increase the sedimentation (Lee et al. 2014). Mangrove tissue carbon concentration varied between 46–50% carbon (Bulmer et al. 2016), therefore retention of mangrove litter and fast burial inside the sediment will increase SOC content. In a previous study comparing west and east side mangrove forest litter production, there were no significant differences observed per unit area (Shunula and Whittick 1999); therefore mangrove forests with bigger areas could produce a greater quantity of litter material in total in comparison with a forest that only have a small patch (Figure 3.5). Thus, mangrove forest area, together with species composition, could increase the accumulation of either SIC or SOC (Figure 3.5). In contrast to our finding a study in the Indian Ocean showed that mangrove distance did not significantly predict SIC content, but rather mangrove forest area in 1 km and 5 km distances were negatively correlated (Gullström et al. 2017).

Channel area was positively correlated to SOC content within mangrove forests and negatively correlated to SIC content within seagrass beds (Figure 3.4). The channel inside the mangrove forest has been reported to play an important role in the transport of particulate organic carbon POC (Bouillon et al. 2007; 2008). Recently, McLachlan et al. (2020) showed that tidal-channel movement impacted the sediment flux pathways inside mangrove forests, therefore potentially influencing the spatial dispersal of carbon rich sediment inside the forest. To our knowledge, there are no studies that report the influence of mangrove forest channels on seagrass beds. The mangrove derived POC could be exported to the open ocean or be trapped within the seagrass plant leaves, and later become part of the organic carbon pool of the seagrass bed. Unguja Island is an Island that geologically is formed by carbonate coralline limestone (Hardy et al. 2015); therefore it is likely that the mangrove creek may also transport particulate inorganic carbon derived by the erosion of the bed coral rocky formation (Figure 3.5). Factors such as the discharge rate of particulate organic matter and the type of material that is being carried by the channel should be taken into account in order to understand the influence of channels in mangrove forests on seagrass beds and vice-versa. Additionally, distance from mangrove forest could be inversely proportional to the distance of an inorganic carbon source (i.e. coral reefs), therefore coral reef distance should also be taken in account (Figure 3.5).

3.5.2. Sediment carbon in mangrove forest: community and sediment level

Our results clearly show that mangrove tree presence at the community structure level is important for total carbon sediment accumulation, but affecting differently SOC and SIC content, especially with variables such as the community composition, tree number or size. Mangrove trees contribute to the sediment carbon accumulation with high production of organic carbon detritus. The trees also capture inorganic and organic particles within their external root structure (Alongi 2014; Guan et al. 2018). Interactions of mangrove trees and sediment are complex and dynamic (Krauss et al. 2008; Krauss et al. 2014); i.e. different tree species have varied influences on sediment carbon, therefore carbon accumulation rates. For example, *R. mucronata* and *S. alba* have different root architectures (prop roots and pneumatophores respectively) which can influence the amount and type of particles trapped within the root system. In a flume experiment, Gillis et al. (2016) found mimicked prop roots and pneumatophores accumulated the same quantity of decaying leaves, however only prop roots trapped significant amounts of fresh leaves on the water surface. Leaves retained by mangrove tree roots will eventually decompose, adding organic carbon to the sediment (Bosire et al. 2005).

Interactions between seascape and community level factors can enhance the SOC content. The presence of channels with a high density of *R. mucronata* with extensive prop roots could enhance the trapping and retention of leaves and organic particles that are transported by water flows in the channel. Those leaves and particles will contribute later to the SOC content (Figure 3.5). In order to clarify SIC and SOC dynamics in mangrove forests and the influence of community structure predictors, it will be necessary to evaluate the capacity of different mangrove root types to retain organic and inorganic carbon particles *in-situ,* as well as, the origin of those particles.

We expected that tree biomass would affect SOC accumulation, with greater biomasses resulting in higher SOC content, as other studies have found a positive relationship with AGB and SOC content (Sanderman et al. 2018). Usually, mangroves trees are highly productive and a significant fraction of SOC is derived from leaves or roots (Alongi 2012; 2014), which could indicate that the presence of more trees could benefit SOC content due to more fine root and litter production. Our results, however, did not show that fine roots were significantly correlated with SOC content. Nevertheless, we acknowledge that the greatest percentage of fine root biomass are deeper in the sediment, as have been reported in mangrove forest with similar species composition (Xiong et al. 2017).

Bigger trees with less density and a higher quantity of *S. alba* were positively correlated with SIC content and negatively correlated with SOC content (Figure 3.4A and B). Mangrove forests are an unfavorable habitat for calcification, because of the low pH (Camp et al. 2016; Guan et al. 2018); hence, an on-site production of abundant carbonates by mangrove trees epiphytes is unlikely. We hypothesize that higher SIC contents at those plots were derived from allochthonous sources at the oceanic fringe, and those inorganic carbon particles are not transported to the inner forest due to the *S. alba* pneumatophores trapping capacity (Spenceley 1977). Difference across species have been observed in litter production in Unguja island, in which *S. alba* was reported to have the highest litter production followed by *B. gymnorrhiza, R. mucronata, A. marina* and *C. tagal* (Shunula and Whittick 1999). The previous observations that *S. alba* produce could indicate that organic carbon rich litter produced could be mainly exported by tides and not being buried in the mangrove forest sediments and adjacent seagrass beds. Further studies comparing export rates of the different species in terms of POC, dissolved organic carbon and export of macro litter (leaves, propagules and fruits) will help to understand the effect of community structure on sediment carbon accumulation dynamics.

Our findings on SOC content at the sediment level are in accordance with studies in other mangrove forests. Finer sediments (i.e. mud) positively correlated with SOC content in China (Yang et al. 2014) and in Vietnam (Tue et al. 2012), whilst in India, SOC content exhibited a negative relation with sand (Badarudeen et al. 1996). The binding of organic carbon to mineral particles that have a much larger surface in mud than in sand can explain the positive relation between SOC and mud content (Burdige 2007; Serrano et al. 2016). Mud (silt and clay particles) is deposited only when there is low flow; once deposited, mud is cohesive and requires much more rapid water flow for re-suspension (Woodroffe et al. 2016). Therefore, SOC is likely to be stored in stable and low energy environments with additional contribution of high organic carbon mangrove litter (Qiang et al. 2015).

3.5.3. Sediment carbon in seagrass beds at the community structure level

Presence of seagrass was a significant predictor that was negatively correlated with SIC content (Figure 3.3). This could be due to rhizomes and roots of seagrass plants contributing to higher SOC, and leaves and other seagrass-plant detritus remaining inside the seagrass beds, reducing the percentage of IC in relation with OC. Seagrass plants are well known ecosystem engineers that sequester particles via diminishing bed shear stress and sediment resuspension, therefore contributing to sediment accretion (Hendriks et al. 2008; Donatelli et al. 2018). Previous studies showed in *Zostera* sp. that seagrass bed structure has an influence on sediment retention, in which edges have a higher turbulence and wave energy preventing sediment and carbon accumulation, whilst inner zones attenuate waves and currents, thereby increasing sediment deposition (Oreska et al. 2017). Rich carbonate particles coming from either autochthonous (i.e. carbonate epiphytes or calcifying algae) or allochthonous adjacent sources (i.e. coral reefs or the high carbonate rocky formation of Unguja Island) could be retained in the seagrass beds differently due to varied community structure (Figure 3.5).

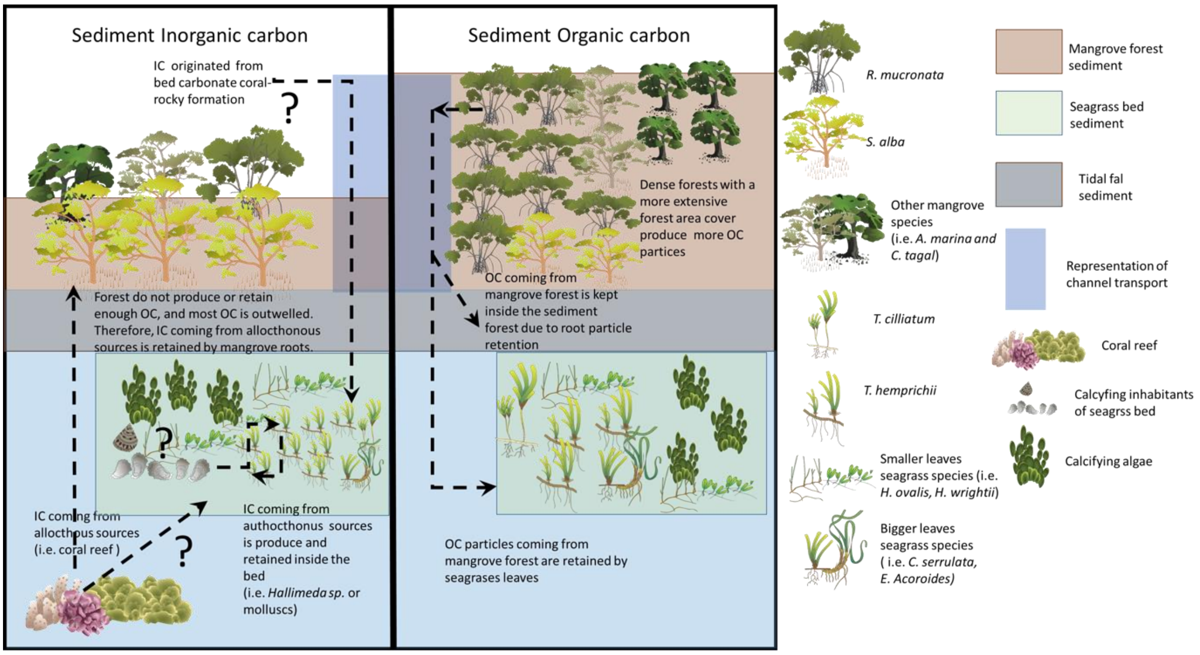


Figure 3.5. Possible origin and the movement of sediment organic carbon (SOC) and sediment inorganic carbon (SIC) across the seascape and the influence and possible interaction of significant predictors of the carbon content at the seascape of vegetated ecosystems. Dashed lines indicate movement and final location place of carbon particles. Mangrove tree and seagrass plant species are represented in the different colors (see legend for details). The black question marks mean possible sources of inorganic carbon (IC) or organic carbon (OC).

In general, the seagrass beds sampled were patchy and formed by multiple species, rather than a continuous or monospecific bed (Supplementary table 3.3). We found that seagrass beds with less dense and smaller canopies with higher diversity and a higher cover of *Thalassia hemprichii* had higher SIC content than seagrass beds with more dense and higher cover of the climax specie *Thalassodendron ciliatum*. Dense seagrass shoots can increase the percentage of organic carbon per unit area and potentially diminish the percentage of inorganic carbon in the sediment. Almost all seagrass bed locations were dominated by medium- to small-size species, such as *Cymodocea serrulata, C. rotundata, Halodule uninervis,* and *T. hemprichii,* with a lower AGB:BGB ratio (Supplementary table 3.3 and supplementary figure 3.2). In high carbonate sediments, due to carbonate tendency to capture bioavailable phosphorous, seagrass plants have to grow larger belowground structures to improve nutrient-absorptive root surface areas, therefore increasing nutrient uptake (Short et al. 1985). Along this line, seagrass locations across Tanzania (including Unguja island) have generally higher quantities of $CaCO_3$ in the sediment than adjacent non-vegetated areas (Gullström et al. 2017; Belshe et al. 2018). Seagrass beds also have mollusks and calcifying algae that are sources of carbonate, and interactions between those calcifying organisms and seagrass species could influence both SOC and SIC content at the same time. For example, seagrass can increase SOC by producing leaves and roots that will be decomposed in the sediment, but by providing growth area and good conditions for calcifying epiphytes could also increase inorganic carbon. Therefore, further studies should take into account not only the plant community structure but also fauna and associated epiphytes (Figure 3.5).

3.6. Conclusions and perspective

Our results show that a holistic view across the coastal seascape for both SOC and SIC in tropical blue carbon stock studies is crucial to improve the understanding of carbon dynamics across tropical coastal ecosystems. Potential changes at seascape level may influence SOC content in mangrove forests and SIC content affecting blue carbon accumulation. Additionally, factors that drive species changes in mangrove forest and seagrass beds could affect the type of carbon that is accumulated in the sediment (either organic or inorganic carbon). This also could help managers and stakeholders to preserve the ecosystem services of carbon sequestration, for example increasing efforts in conservation of adjacent carbon donor ecosystems of both SOC (i.e. mangrove forest) and SIC (i.e. coral reefs).

Further research determining sources, fluxes between ecosystems and long-term storage of both inorganic and organic carbon in the sediment is important to understand the carbon cycles in the tropical coastal zone. Additionally, measuring the contribution of primary producers of OC, such as mangrove trees, seagrass plants and algae, and producers of IC, such as corals, other invertebrates, calcifying epiphytes (both for mangrove and seagrass), and calcifying algae to the sediment will provide critical information for strategic seascape ecosystem conservation, especially with respect to carbon accumulation (Blue carbon) as an ecosystem service.

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3.9. Supplementary material

Supplementary table 3.1. Coefficients of intercept GLMER for sediment total carbon content model, sediment organic carbon content model, and sediment inorganic carbon content model for each location. STCCM = Sediment total carbon content model; SOCCM = Sediment organic carbon content model; SICCM = Sediment inorganic carbon content model.

		Coefficient intercept		
Connectivity status	Location	STCCM	SOCCM	SICCM
Isolated mangrove	Kama	32.19	76.37	99.66
Isolated seagrass	Bweleo	33.37	90.89	101.28
	Metenwe	30.48	65.25	96.45
Connected	Pete	31.92	31.61	113.19
	Nyamanzi	31.6	47.05	90.86
	Weni	32.98	130.15	87.66

Supplementary table 3.2. Showing species composition at each transect point for mangrove forests, number of trees (per 10 m^{-2}), mean (cm), standard error (SE), maximum (max.) and minimum (min.) (cm) of DBH (diameter at breast height). Transect is the 3 transects (T1, T2 and T3) in each location and point (P2, P4, P5 etc.) refers to the position of the transect point with reference and proximity to the ocean (see *Figure 1* for details). Pete, Weni and Nyamanzi are connected locations, while Kama is an isolated mangrove forest.

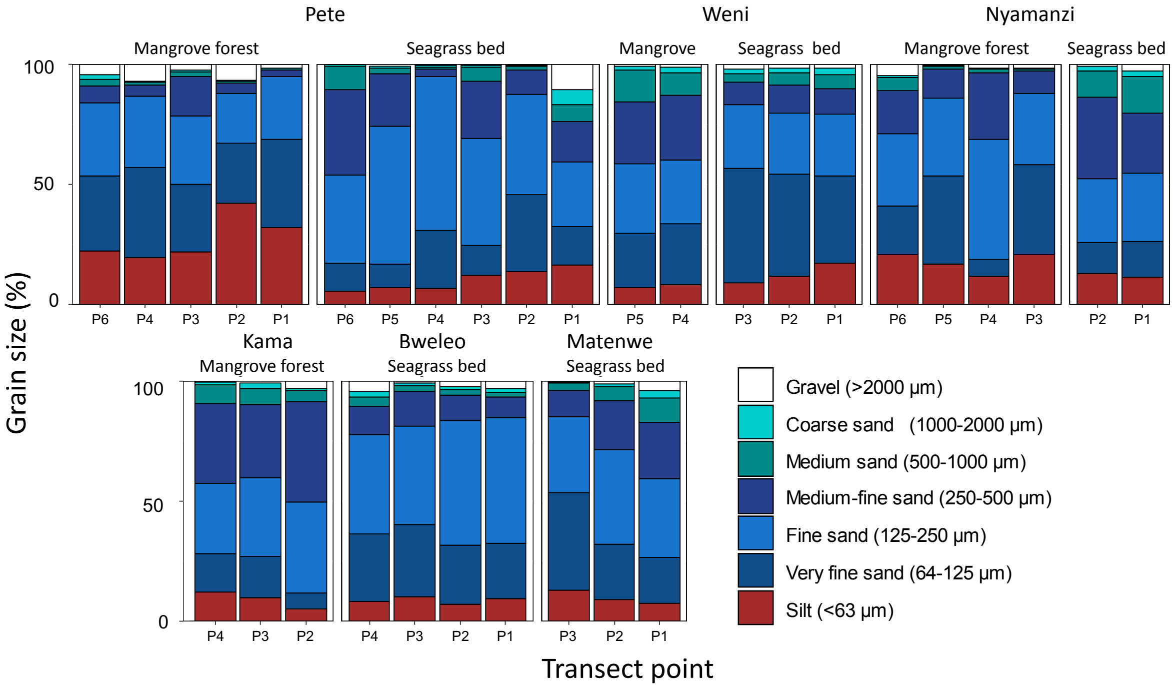
Location	Transect	Point	Species	Number of trees (10 m^2)	DBH mean (cm)	DBH SE (cm)	DBH Max. (cm)	DBH Min. (cm)
Kama	T1	P2	*C. tagal*	7	3.8	0.5	6.4	2.6
		P4	*C. tagal, B. gymnorrhiza, R mucronata*	6	4.2	0.6	5.9	2.1
		P5	*C. tagal,R mucronata*	20	3.4	0.2	5.3	2.4
	T2	P2	*C. tagal*	6	5.0	0.3	6.4	4.1
		P4	*C. tagal, R. mucronata*	9	4.9	0.3	6.4	4.0
		P5	*R. mucronata*	20	3.4	0.1	4.6	2.6
	T3	P2	*C. tagal*	7	3.7	0.4	5.9	2.6
		P4	*C. tagal, R. mucronata*	11	3.4	0.2	4.5	2.7
		P5	*C. tagal, B. gymnorrhiza, S. alba*	9	4.2	0.7	8.8	2.4
Nyamanzi	T1	P3	*C. tagal, B. gymnorrhiza*	10	8.6	2.3	23.9	1.9
		P4	*C. tagal, R mucronata*	11	7.5	0.9	11.1	3.0
		P5	*C. tagal, B. gymnorrhiza, R. mucronata*	11	8.9	0.9	12.6	3.2
		P6	*C. tagal, R mucronata*	11	8.1	1.0	16.4	4.8
	T2	P3	*C. tagal, B. gymnorrhiza, R. mucronata*	20	9.9	2.0	41.5	2.2

		P4	*A. marina B. gymnorrhiza, R. mucronata*	12	14.9	2.1	31.5	5.1
		P5	*C. tagal, R. mucronata*	18	7.1	1.3	19.1	2.9
		P6	*C. tagal, R. mucronata*	12	12.3	1.6	22.9	7.6
	T3	P3	*C. tagal, B. gymnorrhiza*	11	4.8	0.6	9.9	2.9
		P4	*C. tagal, B. gymnorrhiza, R. mucronata*	13	12.2	2.2	34.7	4.5
		P5	*C. tagal, B. gymnorrhiza, R. mucronata*	9	8.7	2.1	24.8	3.5
		P6	*A. marina, C. tagal, R. mucronata*	13	9.3	1.6	20.7	3.8
Pete	T1	P1	*R. mucronata*	11	3.5	0.4	6.4	1.6
		P2	*R. mucronata*	13	5.9	0.8	11.1	1.6
		P3	*R. mucronata*	17	5.6	0.6	11.1	1.6
		P4	*R. mucronata*	14	6.6	0.9	12.7	1.6
		P5	*R. mucronata*	13	5.0	0.7	8.6	1.0
		P6	*C. tagal, B. gymnorrhiza, R. mucronata*	17	5.6	1.7	27.7	1.0
	T3	P1	*R. mucronata*	22	3.0	0.3	6.1	1.6
		P2	*C. tagal, R. mucronata*	21	2.9	0.2	4.5	1.6
		P3	*B. gymnorrhiza, R. mucronata*	21	5.8	0.5	11.8	1.6
		P4	*B. gymnorrhiza, R. mucronata*	19	5.9	0.5	11.1	3.2
		P5	*B. gymnorrhiza, R. mucronata*	8	6.9	1.2	10.8	3.2
		P6	*C. tagal, B. gymnorrhiza, R. mucronata*	12	5.4	0.4	8.0	2.6
Weni	T1	P4	*S. alba*	3	32.8	5.4	42.7	23.9
		P5	*S. alba*	5	19.6	4.2	29.0	8.0
	T2	P4	*S. alba*	3	30.9	11.7	43.5	7.6
		P5	*S. alba*	5	14.8	4.4	31.8	8.0
	T3	P4	*S. alba*	6	24.7	4.0	36.0	8.0
		P5	*A. marina, R. mucronata, S. alba*	6	11.6	1.8	19.1	6.7

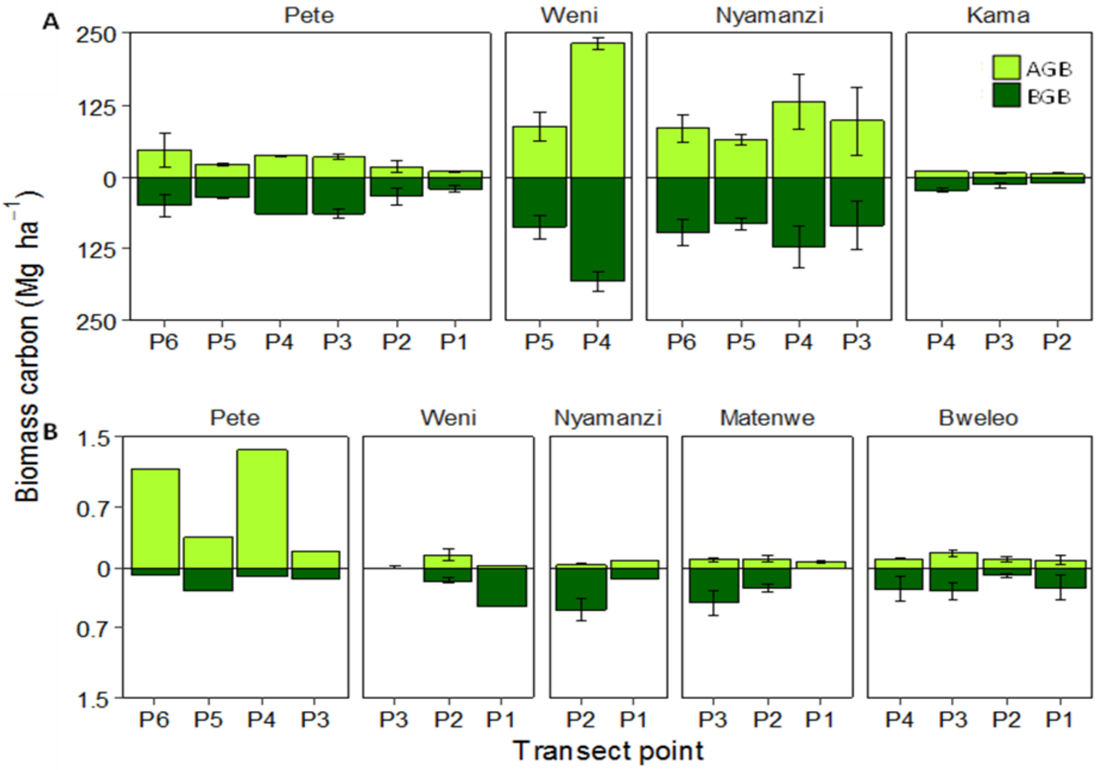
Supplementary table 3.3. Showing species composition at each transect point for seagrass beds and cover (%). NA means no seagrass covered was found during the field survey, SE is the standard error of the cover. Transect is the 3 transects (T1, T2 and T3) in each location and point (P1, P2, P3 etc.) refers to the position of the transect point with reference and proximity to the ocean (see *Figure 1* for details). Pete, Weni and Nyamanzi are connected locations and Bweleo and Matenwe are isolated seagrass bed.

Location	Transect	Point	Species	Cover (%)	SE (%)
Pete	T2	P1	*NA*		
		P2	*NA*		
		P3	*C. serrulata, T. ciliatum*	83	14
		P4	*T. cilliatum*	96	3
		P5	*E. acoroides, T. cilliatum*	66	14
		P6	*T. cilliatum*	100	0.0
Nyamanzi	T1	P1	*T. hemprichii*	63	6
		P2	*T. Hemprichii, H. uninervis*	23	10
	T2	P1	*NA*		
		P2	*NA*		
	T3	P1	*H. wrightii, T. hemprichii*	56	20
		P2	*C. rotundata, H. uninervis, T. hemprichii*	35	7

Weni	T1	P1	*NA*		
		P2	*H. uninervis*	40	4
		P3	*NA*		
	T2	P1	*E. acoroides*	42	8
		P2	*H. ovalis, H. wrightii, T. hemprichii*	35	4
		P3	*H. ovalis, H. wrightii*	8	3
	T3	P1	*NA*		
		P2	*NA*		
		P3	*H. wrightii*	33	12
Bweleo	T1	P1	*C. serrulata, S. isoetifolium*	60	17
		P2	*H. uninervis, T. hemprichii*	43	4
		P3	*H. uninervis, T. hemprichii*	47	1
		P4	*C. serrulata, H. uninervis*	13	1
	T2	P1	*C. serrulata, T. hemprichii*	69	9
		P2	*H. uninervis, T. hemprichii*	41	7
		P3	*C. rotundata, H. uninervis, T. hemprichii*	37	4
		P4	*C. rotundata, C. serrulata, H. uninervis, T. hemprichii*	21	4
	T3	P1	*T. hemprichii*	93	4
		P2	*T. hemprichii*	90	5
		P3	*C. serrulata, H. uninervis, H. wrighttii,*	26	4
		P4	*T. hemprichii*	78	4
	T4	P1	*H. wrightii*	33	9
		P2	*C. rotundata, T. hemprichii*	65	15
		P3	*H. wrightii, T. hemprichii*	66	14
Matemwe	T1	P1	*NA*		
		P2	*T. hemprichii*	83	3
		P3	*C. rotundata, H. wrightii*	43	10
	T2	P1	*NA*		
		P2	*T. hemprichii*	30	15
		P3	*T. hemprichii*	81	4
	T3	P1	*NA*		
		P2	*NA*		
		P3	*T. hemprichii*	60	7
	T4	P1	*T. hemprichii*	16	1
		P2	*T. hemprichii*	40	3
		P3	*T. hemprichii*	80	5
	T5	P1	*T. hemprichii*	33	6
		P2	*C. rotundata, H. wrightii*	44	2
		P3	*C. rotundata, H. wrightii*	11	2



Supplementary figure 3.1. Average sediment grain size (%) based on the Udden–Wentworth grade scale (see legend) at the six locations. Number of samples is different in each ecosystem and location (Figure 3.1). Blue tones are sand categories. Silt category includes all particle size lower than 63 µm which includes silt and clay and are referred to in total mud percentage. Each transect point has a replication of three except for all transect points in Pete's seagrass bed (n=1) and Pete's mangrove forest (n=2), and in Bweleo, seagrass bed P4 where only two samples were measured. P represents distance within the ecosystems, the lower the number is the closer to the oceanic zone the transect point is located. For example, P1 is the closest to the oceanic fringe while P6 is the closest to the terrestrial ecosystems. Pete, Weni and Nyamanzi are connected locations, while Kama is an isolated mangrove forest and Bweleo and Matenwe are isolated seagrass bed.



Supplementary figure 3.2. Carbon stocks (Mg C ha^{-1}) in biomass of mangrove trees (A top section of figure) and seagrass plants (B bottom section of figure) at the different locations. Light green represents above ground biomass (AGB) carbon stocks and dark green represents below ground biomass (BGB). Biomass was calculated for mangrove trees using allometric equations and DBH measurements, while values of seagrass beds were measured directly from sampled cores. Note the difference in scale on y-axis between the A and B panels. The x-axis shows the transect points. Values are means ± SE. Each transect point has a replication of three were used except for all transect points in Pete's seagrass beds (n=1) and mangrove forests (n=2). P represents distance within the ecosystems, the lower the transect point number the closer it is to the oceanic zone. For example, P1 is the closest to the oceanic fringe while P6 is the closest to the terrestrial zone. Pete, Weni and Nyamanzi are connected locations, while Kama is an isolated mangrove forest and Bweleo and Matenwe are isolated seagrass beds.

Chapter 4 Contribution of connected coastal vegetated ecosystems to the particulate organic matter and its potential influence on sediment carbon and nitrogen storage

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4.1. Abstract

Coastal vegetated ecosystems have a disproportionately high capacity for carbon and nitrogen storage compared to terrestrial ecosystems per unit area. However, there is still debate about the drivers of carbon and nitrogen storage, especially at seascape scales. Seascape connectivity in terms of the interchange of particulate organic matter among adjacent ecosystems could enhance processes that facilitate carbon and nitrogen trapping. We still lack quantitative information about the relation between contributions of particulate organic matter from connected and isolated ecosystems, their living biomass and their areal extent. To fill this gap, we studied locations of salt marshes, mangrove patches, seagrass and macroalgal beds with different patch arrangements. Within these locations we determined total area, and carbon and nitrogen store in the biomass and in the sediments per area. To understand the particulate organic matter contributions of ecosystem to the seascape, we used isotopic tracers and estimated the relative contributions relative to ecosystem area and standing biomass. Mangrove patches in connected locations occupied only 3% of the total area, but as the standing mangrove biomass carbon store was 7 times higher than that of seagrass beds and almost twice as high as that of macroalgal beds. The largest contributors to seascape POM in connected locations were mangrove patches (10-50%) and macroalgae (20-50%). Macroalgae were also the main contributors to suspended particulate matter in two thirds of our locations. Exchange of particulate organic matter between coastal vegetated ecosystems could enhance carbon and nitrogen store especially within the sediments of connected mangrove patches. Our results show that the integrity of one coastal vegetated ecosystem will have consequences for carbon and nitrogen store at the seascape level.

Keywords: Seascape ecology; nutrient exchange; blue carbon dynamics; nitrogen retention; connectivity.

4.2. Introduction

Coastal vegetated ecosystems (CVE), such as mangrove patches, seagrass beds, salt marshes and macroalgal beds, are key ecosystems for carbon mitigation services (Duarte et al. 2017; Sanderman et al. 2019). High primary productivity and enhanced sediment trapping allow coastal vegetation to disproportionately sequester carbon compared to terrestrial ecosystems (McLeod et al 2011). For example, carbon accumulation rates range between 20-949 g C m^{-2} yr^{-1} in mangroves and 45-190 g C m^{-2} yr^{-1} in seagrass bed, compared to only 0.7-13.1 g m^{-2} yr^{-1} in terrestrial forests (McLeod et al. 2011). Macroalgal beds have often been excluded from marine carbon sink or stock accounts, because they grow on hard, rocky substrate and do not develop significant carbon deposits (Duarte et al 2013a). However, they have one of the highest primary production rates in the coastal zone (420 NPP g C m^{-2} y^{-1}), which make them an important ecosystem for carbon sequestration (Krause-Jensen and Duarte 2016). Even those CVE usually occurs adjacent to each other, studies of carbon store capacity are usually done separately without having a seascape approach and the differences across the ecosystems.

Recently the role of CVE has been recognized in terms of their capacity to sink nitrogen inside the ecosystem (Reis et al. 2017; Kindeberg et al. 2018; Santos et al. 2019), which ensure to maintain plant primary production (Alongi et al .2003; Walton et al. 2014). From the limited information available, mangrove forests appear to have sediment nitrogen store (12.2-15.4 Mg N h^{-1}; Reis et al. 2017) compared to terrestrial ecosystems (0.5-2.5 Mg N h^{-1}; Xu et al. 2019) and seagrass beds (0.2-4.5 Mg N h^{-1}; (McGlathery et al. 2007; Kindeberg et al. 2018). However, the underlying mechanisms of how carbon and nitrogen stocks relate with have received little attention, therefore, quantification of carbon and nitrogen stored in adjacent ecosystems is critical to understand the role of CVE for carbon accumulation and nitrogen retention.

Seascape connectivity in terms of the interchange of energy (i.e. waves) and materials (e.g. sediments, particulate/dissolved nutrients) influences processes such as ecosystem productivity, carbon and nutrient trapping and storage inside CVE (Gillis et al. 2014a; Huxham et al. 2018). CVE mainly inhabit sedimentary landscapes, which receive and accumulate sediments with a high amount of minerals, carbon and nutrients (Woodroffe et al. 2016; Rogers et al. 2019), except for macroalgal beds (Duarte et al. 2013b). Organic sediments in CVE can be of autochthonous origin – from within the ecosystem due to retention of detrital material – or allochthonous origin – as input of particulate organic matter (POM) from adjacent ecosystems (Hyndes et al. 2014). Through reducing wave action, CVE are efficient in sediment accumulation, allowing for carbon and nitrogen accumulation (Gillis et al. 2014b, Gillis 2017; Saderne et al. 2019). Mangrove forests and salt marshes often outwell nutrients to seagrass beds (Kennedy et al. 2010; Hyndes et al. 2014), but some mangrove forests experience inwelling (Walton et al. 2014). Hence, coastal vegetated ecosystems are part of an interconnected seascape of matter exchange, but we still lack insight into how this seascape connectivity alters the magnitude and direction of carbon and nitrogen export, deposition, and storage compared to ecosystems that exist in isolation (Huxham et al. 2018; Santos et al. 2019).

Particulate organic matter has been shown to be an important vector of carbon (Hyndes et al. 2014) and nitrogen (Inamdar et al. 2015; Huang et al. 2018) exchange among coastal ecosystems. Factors such as habitat surface area and living biomass of CVE strongly influence the quantity of POM that an ecosystem produces and potentially interchanges with another CVE across the coastal seascape, but this has rarely been investigated. This information is essential to understand the full capacity of coastal ecosystem to store carbon and nitrogen, and the ecosystems services they provide on a coastal seascape scale.

Here we test whether connected mangrove and seagrass ecosystems contain larger carbon and nitrogen stores than isolated systems. To test the role of seascape connectivity we measured the contribution of allochthonous vs autochthonous sources of particulate organic matter across CVEs and related this to surface area and living biomass of CVE. We tested this across three types of seascapes in South Australia: i) connected mangrove patches and seagrass beds (adjacent to each other within 3 km), ii) isolated seagrass beds, iii) and isolated mangroves patches (apart from each other within 3 km). By studying the differences in exchange of POM together with surface area and living biomass of the CVE, we can define the possible role and impact of each CVE on carbon and nitrogen store, inside the ecosystem and on the seascape. We hypothesized that connected mangrove forests and seagrass beds will have higher carbon and nitrogen stored because of connected ecosystems have more exchange carbon and nitrogen with each other, and connectivity between ecosystems is modulated by habitat surface areas and standing living biomass.

4.3. Material and methods

4.3.1. Study site

Sampling and measurements were performed during the dry season (April-May 2017) at six locations (four inside Gulf St Vincent and two outside the Gulf) across the South Australian coast (Figure 4.1).

At each location three parallel transects were established during low tide, covering a representative area of the ecosystem. Transects were separated between 50 to 400 meters. Transects had a length between 400 to 1200 m covering as much area of the CVE, starting at the ocean side of the tidal flat or subtidal seagrass bed zones, stretching landwards through the intertidal seagrass bed and/or mangrove patch and continuing up to the salt marsh or terrestrial zone, depending on the location. Each transect had between five and six transect-points separated by 70 to 200 m. We considered the tidal flat as the area that is not occupied by any form of vegetation but is affected by the tidal range. Connected seagrass beds were sampled at low tides close to spring tides to extend the sampling area ocean-wards, whilst mangrove patches were sampled during low neap tides. Field sampling at each location was completed within two to four days. All samples were taken during low tide, except for SPM samples that were taken during low tide.

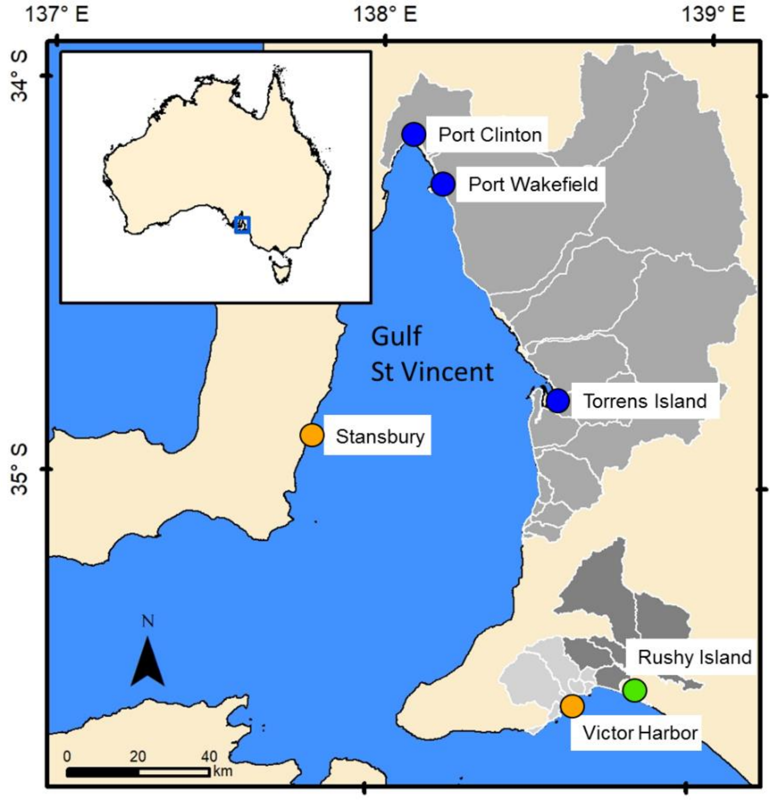

Figure 4.1. Sampled locations of the different coastal vegetated ecosystems. Blue circles indicate connected coastal vegetated ecosystems (Port Clinton, Port Wakefield and Torrens Island), the yellow circles indicate seagrass beds with no adjacent mangrove patches (Victor Harbor and Stansbury), and the light green circle indicates a mangrove patch with no adjacent seagrass bed (Rushy Island). Middle grey tones indicate the catchment zone of the connected locations. Light grey area shows the catchment area of Victor Harbor, the dark grey depicts the catchment area of Rushy Island.

4.3.2. Mapping of coastal vegetated ecosystems

Available geographical layers from the Government of South Australia were used to calculate the surface area of ecosystems. Land cover maps and watersheds (catchment area) were acquired from the Nature maps web server of the Department for Environment and Water of South Australia (DEW) (http://spatialwebapps.environment.sa.gov.au/naturemaps/), Dec. 2019). The South Australian Marine Benthic Habitats map was provided under license number 2696 by the same agency. Coordinates of Gulf St Vincent study area were latitude 34°3 to 35°24' S, and longitude 137°40' to 138°40', whilst Victor Harbor and Rushy Island coordinates were latitude 35°24' to 35°40' and longitude 138°31' to 139°5'. Mangroves and saltmarshes were selected from the DEW land cover map (Willoughby et al. 2018) coast to assess exclusively vegetation that influences the coastal measurements within a 3 km limit landwards from the coastline. The land cover map was based on a predictive model of native vegetation using Landsat imagery, local calibration data, and other supplemented datasets, with a minimum scale of 1:50.000 (Willoughby et al. 2018).

Cover area of seagrass and macroalgal beds were obtained from the Marine Benthic Habitats map (DEW 2017). Data obtained from DEW 2017 were digitized from discernible underwater features of ortho-rectified aerial photographs (2005-2007), field observations and underwater video footage incorporated. Data was updated in 2014, and its scale ranges from 1:5.000 to 1:10.000.

From the seagrasses and macroalgal habitats, we selected the following four vegetation cover classes: continuous dense, continuous medium, patchy dense and patchy medium. Watershed selection was based on the sampling point locations to account for the area of terrestrial influence. Data layers were projected to GDA94 / SA Lambert - EPSG:3107 and converted from raster to shapefiles when necessary. The area of all vegetation classes specified above was calculated in km². The geographical analysis was run in ArcGIS version 10.5.

4.3.3. Calculation of living biomass

In the mangrove patches, at each transect point a plot of 100 m^2 was established and the diameter at breast height (DBH) approximately 1.3 m of each mangrove tree was measured. This was used to estimate the living biomass (Howard et al. 2014), hereafter referred to as 'biomass'. The only species found in the patches was *Avicennia marina*. Aboveground and belowground biomass (AGB and BGB, respectively) was estimated from the DBH, using region-specific allometric equations reported in Bulmer (2016a) which was the allometric equation developed for the same mangrove species in New Zealand. In Port Wakefield some trees closer to the terrestrial zone had heights lower than 1.3 m; therefore, allometric equations reported by Bulmer (2016b) were used to calculate biomass at this location.

In seagrass beds, at each transect point a core (15 cm diameter, total area of 176 cm^2 and 20 cm depth) was taken to sample seagrass biomass. Seagrass plants sampled in the core were separated into AGB (shoots) and BGB (roots and rhizomes), cleaned from attached sediment and epiphytes with seawater and further rinsed with distilled water in the laboratory. Samples were dried for approximately 72 h at 60 °C until constant weight, this weight was used to calculate the seagrass AGB and BGB for each transect point.

4.3.4. Sampling of suspended organic matter

At each point along the transects, two types of suspended sediment samples were collected, one from the suspended particulate matter in the water column (SPM), and one from sediment traps. To measure SPM, 1 L of water was sampled from the upper 40 cm of the water column at each transect-point during ebb tide. Samples were kept in freezer bags with freezer blocks and transported to the laboratory within 4 h, where they were filtered onto pre-combusted (450 °C, 24 h) glass fibre filters (GF/C, 696 grade, 1.2 μm pore diameter). The filters were dried for approximately 72 h at 60° C until a constant weight.

Sediment traps were made of plastic cylinders of 24 cm length and 6 cm diameter, with twenty-four 0.5 cm-diameter holes evenly distributed in the upper 10 cm of the cylinder, and a lid at the bottom collecting the suspended particulate matter that entered the trap. Sediment traps were attached to steel rods anchored in the sediment at a height of 5 cm above the substratum. Sediment traps were deployed during low tide and emptied after 24 h at the following low tide. Samples were kept in freezer bags with freezer blocks and transported to the laboratory within 4 h. To separate the water from the sediments and avoid salt contamination, samples were deposited into 200 mL beakers, dried in the oven at 60° C for 72 h, supernatant water was carefully removed, and an additional 150 mL of distilled water was added to dissolve remaining salt. This process was repeated until salt particles were not detected visually in the dry sediment sample. It should be noted that a higher contribution of mangrove trees, salt marshes and terrestrial plant sources in SPM could have resulted from sampling during ebb tide, whereas sediment traps captured particulate sediments over two ebb and two flood tides.

Dried SPM filters and sediment from the sediment traps were transported to the analytical laboratory of the Leibniz Centre for Tropical Marine Research (ZMT), Germany. Dried SPM filters and sediment from the sediment traps samples were then analysed for isotopic composition (see section below).

4.3.5. Sampling of sediment organic matter

A core of 15 cm depth and 7 cm diameter was taken during low tide at each transect point. Each core was divided into three subsamples of 0-5, 5-10 and 10-15 cm sediment depth, respectively. Samples were kept in freezer bags with freezer blocks and transported to the laboratory within 4 h. Each sediment sample was dried at 60 °C for 72 h or until constant weight.

Dried samples were transported to the analytical laboratory of the Leibniz Centre for Tropical Marine Research (ZMT), Germany, to measure the percentage of total carbon in the sediment. All sub-samples were homogenized, and divided into two parts of approximately 15 mg. One part was wrapped in tin caps to measure total carbon, whilst the other was wrapped in silver caps and then acidified, to measure organic carbon. Both parts were analysed by combustion in an elemental analyser (EuroVector EA 3000), using acetanilide 4 (71.6% carbon) for calibration and a low soil standard (OAS4) as standard with a precision of 0.06% of carbon.

4.3.6. Carbon and nitrogen percentage and stable isotope signatures

For isotopic signatures of C and N, six vegetation sources of particulate organic matter (POM) were considered in this study: oceanic (plankton and oceanic SPM), mangrove trees, seagrass plants, terrestrial plants, macroalgae and salt marsh plants. At each location, fresh plant leaves (4-5) and algal thalli of the most abundant species were taken and placed in separate sample bags to transport to the laboratory. The most abundant species are as follows: mangrove trees (*Avicennia marina*), seagrass plants (*Posidonia* *sinousa, Zostera mucronata, Heterozostera tasmanica*), terrestrial plants (*Maleluca* sp., *Danthonia* sp., *Olearia axillaris*), macroalgae (*Hormosira banksii*, *Ulva sp.*) and salt marshes (*Juncus kraussi, and Juncus* sp.). The leaves and thalli were rinsed with distilled water and dried at 60 °C for 72 h to constant weight. Stable isotope signatures for oceanic sources used in this study were taken from studies done in Victoria and South Australia (Davenport and Bax 2002).

The different plant tissues (sources) at each location, and the two types of particulate organic matter samples (SPM and sediment trap) were analysed separately for isotope ratios of carbon and nitrogen. Isotope ratios were expressed in the delta notation ($\delta^{13}C$, $\delta^{15}N$) relative to Vienna PDB and atmospheric nitrogen. Samples were homogenized, then acidified to remove carbonates and analysed for organic carbon (OC) and total nitrogen by combustion in an elemental analyzer (EuroVector EA 3000). Measurements had a precision of 0.06% for OC and 0.01% for TN for sediment samples, and a precision of 0.36% for OC and 0.05% for TN for plant material samples. Organic soil standard and apple leaf standard SRM1515 were used as reference material.

Ratios of δ13C and δ15N were determined using a gas isotope ratio mass spectrometer (Thermo Finnigan Delta Plus) after high temperature combustion in an elemental analyser (Flash 1112 EA). Analytical precision was ± 0.10‰ for $\delta^{15}N$ and 0.13‰ for $\delta^{13}C$, as estimated from an international standard (Peptone) analysed together with the samples. Carbon store calculation of mangrove was calculated by multiplying the average of % carbon percentage of species with the biomass at each point (Howard et al. 2014). For seagrass plants carbon store was calculated multiplying the biomass value of the seagrass core with the average of % carbon percentage of species.

Some sources were missing $\delta^{13}C$ and $\delta^{15}N$ data, and these were taken from the literature. For example oceanic sources (Davenport and Bax 2002) and salt marshes isotopic signal of pooled samples of *Sporobolus virginicus* and *Sarcocornia quinqueflora* in Gulf St Vincent (Connolly et al. 2005). Additionally, in Torrens Island seagrass beds, due to weather conditions only one sample of macroalgae could be collected, and therefore $\delta^{15}N$ signatures were used from Connolly et al. (2013a), and mean $\delta^{13}C$ values from Gulf St Vincent (Port Wakefield and Port Clinton) were used. We suspect that the macroalgal thalli found in the mangrove patches were mainly an allochthonous source, transported by local currents, since collected algae were not attached to any substrate.

4.3.7. Data analysis

Using stable $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of the six vegetation sources, a Bayesian mixing model MixSIAR (Stock et al. 2018) was used for estimating the percent contribution of these sources to the POM (SPM and sediment traps) sampled at each transect point for each location. Two relative dimensionless contribution indices the area and biomass were calculated. We assumed that when ebb currents flush the tide out of the gulf, the POM for seagrass beds, mangrove patches, etc, is taken to the gulf centre, and when the flood currents inundated the gulf again, they extract POM coming from each ecosystem from the whole gulf. Therefore, for the calculation of the two relative dimensionless contribution indices we used the whole area or biomass inside the gulf or in a space of 15 Km^2 for isolated systems of a certain CVE. For instance, in Gulf St Vincent the area of all mangrove patches was included to calculate the total area of mangrove patches for our study locations in the Gulf. In the isolated locations also the total area and biomass of all patches were used to calculate the indices.

Indices were calculated for total area and biomass, by dividing the contribution of each source as provided by the mixing model (% Contribution) by the relative percentage surface area (% Area) or the percent of biomass (% Biomass) of the respective CVE (mangrove patch, salt marsh, seagrass bed, or macroalgal bed, respectively) as a function of the total seascape surface area at Gulf St Vincent for the locations placed there, and in an area of approximately of 200 km^2 for the isolated CVE in Rushy Island and Victor Harbor.

Percent of surface (% Area) was calculated by dividing the surface area of the ecosystem (i.e. mangrove patch) by the area of the adjacent catchment terrestrial system plus all the intertidal systems (mangrove patch, seagrass and macroalgal beds and salt marshes). Catchment areas were obtained from nature web maps as watershed of the main current water bodies (i.e. rivers or creeks) that lead into the respective study area (available at http://spatialwebapps.environment.sa.gov.au/naturemaps/?locale=en-us&viewer=naturemaps). At the west side of Gulf St. Vincent, there is no watershed that could result in a significant input from terrestrial plants to the Gulf St. Vincent (Figure 4.1). Percent of biomass (% Biomass) was calculated dividing the biomass of a particular CVE by the total estimated biomass of all intertidal systems. Biomass of terrestrial plants of catchment area was not included, as data was not available. The area- and biomass-based contribution was not calculated for oceanic sources, because no representative surface area or biomass for the ‘ocean’ could be calculated.

$$\textit{Area Relative Contribution} = \%\ \textit{Contribution} \ / \ \%\ \textit{Area} \tag{1}$$

$$\textit{Biomass Relative Contribution} = \%\ \textit{Contribution} \ / \ \%\ \textit{Biomass} \tag{2}$$

To compare sediment carbon and nitrogen percentages and store between mangrove patches and seagrass beds in Gulf St Vincent, generalized linear models (GLMs) were used with the formula (x ~ Connectivity type + Ecosystem + 1 | Location) in R version 3.0.2 (R Core Team, 2013), using the lme4 package (Bates et al 2015), where x was the response variable (e.g., carbon percentage), connectivity type was a factor with 2 levels (connected and isolated), ecosystem was a factor with 2 levels (mangrove patch, seagrass bed) and location was a random factor with 6 levels. Percentage data was log-transformed using link= log inside the *glmer* function, continuous data was not transformed using link = identity, percentage and continuous data were analysed using distribution family = gamma (Zuur 2010).

4.4. Results

4.4.1. Carbon and nitrogen store in biomass and sediment

Connected mangrove patches had the highest biomass per area which influence that connected patches presented the highest carbon and nitrogen stores across all CVEs in terms of biomass (Supplementary Table 4.1 and Figure 4.2). Mangrove patches and seagrass beds showed different carbon and nitrogen store in the biomass depending on the connectivity type. Connected mangrove patches had 7 times more carbon than the isolated ones, whilst isolated seagrass also had 4 times higher biomass. In general, seagrass beds had the highest carbon and nitrogen pools in the biomass than other CVE, mainly due to the larger area (Supplementary Table 4.1). The isolated mangrove patch was dominated by salt marshes 99.6%, whilst in the isolated seagrass bed, macroalgal beds had the biggest area (90.8% of the total area). The catchment areas of our locations were 4723 Km^2 in the coast of Gulf St Vincent, 871.6 Km^2 in Rushy Island and 365.7 in Victor Harbor 365.7 Km^2 (Supplementary Table 4.1).

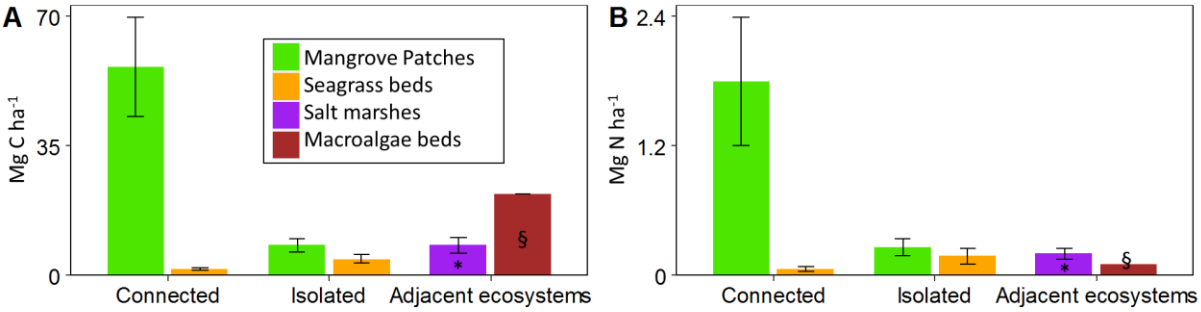

Figure 4.2. Carbon (Panel A) and nitrogen (Panel B) stored in the biomass of connected and isolated mangrove patches and seagrass beds as well as adjacent ecosystems macroalgal beds and salt marshes coastal. Since biomass of salt marsh plants and macroalgal thalli were not directly measured, values were taken from studies in a close location with similar characteristics. *Data taken from Serrano et al. (2019) and references therein in supplementary material (Clarke et al. 1994; Kelleway et al. 2016; Santini et al. 2019, cited in Serrano et al. 2019). §Source: Copertino et al. (2005) and Hill (2015).

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Percentage and store of both carbon and nitrogen in the sediment was different in mangrove patches and seagrass beds, connected mangrove patches and isolated seagrass beds had higher carbon percentage compared with other ecosystems. Even sediment carbon percentages of isolated seagrass beds were the same as connected mangroves, isolated beds carbon store was higher due to those beds had in average 1.3 times denser sediments (data not shown). Therefore, connected mangrove patches had highest percentage of carbon, however the carbon store was higher in seagrass beds. Connected mangrove patches had 2-3 times higher carbon percentage compared with the isolated mangrove patch and connected seagrass. Carbon store was 3 times higher in isolated seagrass compared with isolated mangroves (Figure 4.3). Nitrogen percentage and store was higher in mangrove patches compared with seagrass beds. On average, nitrogen percentage and store were 3-12 times higher in mangroves compared with seagrass beds but not significant differences across connected vs. isolated mangrove patch or connected vs. isolated seagrass beds were detected (Figure 4.2 and Supplementary Table 4.1 and 4.2) (Figure 4.3).

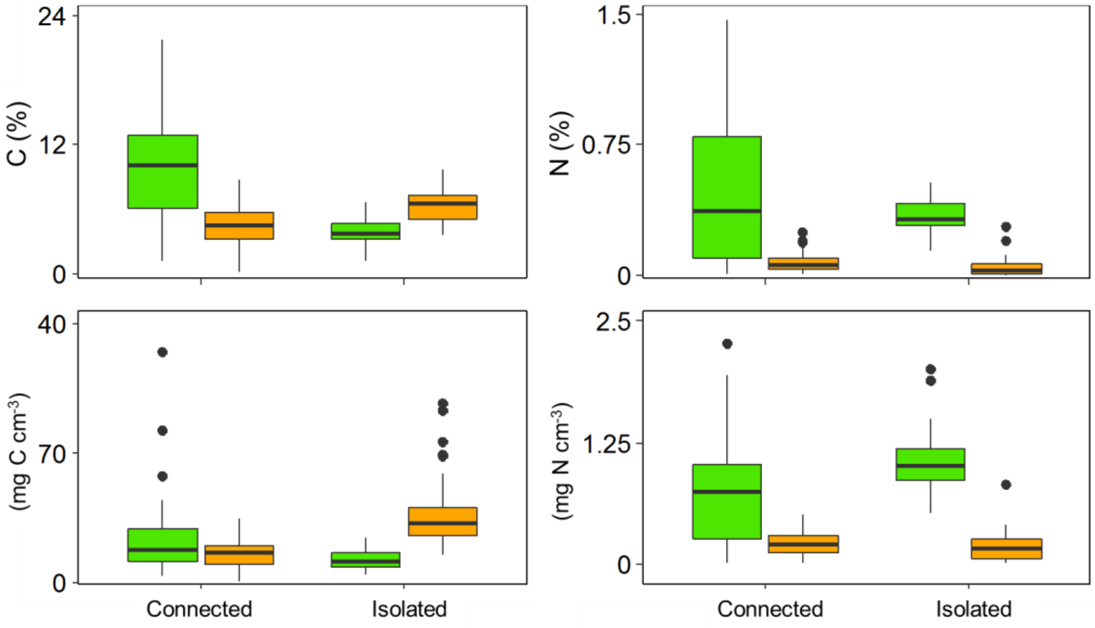

Figure 4.3. Boxplot of sediment carbon and nitrogen percentages (Panels A and B) and carbon and nitrogen store (Panels C and D) show separately on mangrove patches (green) and seagrass beds (orange). Thick line inside the boxplot indicate the median.

4.4.2. Contributions of the main primary producers to the POM: area and biomass indices

Isotopic signatures of all samples were within the range of primary producers δ^{13}C and δ^{15}N, except for samples of SPM in Port Wakefield and sediment traps in Stansbury (Supplementary Figure 4.1). The δ^{15}N signal of primary producers of Torrens Island signal were higher than those of the other locations and were, thus, separated from other locations inside Gulf St. Vincent (Supplementary Figure 4.1), and MIXSiar models were run separately.

In general, the main primary producers that contributed in connected CVE were macroalgal thalli, mangrove trees and seagrass plants in both SPM and sediment traps, with some differences across the sampled locations (Figure 4.4). In all connected locations macroalgal thalli (26.6 to 48.9 %) were the greatest contributor and depending on the location the second or third biggest contributor were mangrove trees (20.3 to 38.4 %) or seagrass plants (11.8 to 25.4 %). Oceanic sources were the second biggest contributor only in Port Clinton (10.3 to 22.4 %) (Figure 4.4 and Supplementary Table 4.4). In connected CVE, salt marshes, macroalgal beds and mangrove trees contributed relatively high in relation to both area and biomass, even though they had smaller areas and AGB across a CVE. Across all connected locations the biomass relative contribution index showed that saltmarsh plants contributed relatively high on realtion to biomass irrespectively of having smaller biomass compare with seagrass beds, with indices between 0.06 and 0.3 (Supplementary Table 4.5 and Figure 4.5 Panels A and B).

In the isolated seagrass beds seagrass plants, macroalgae thalli and oceanic sources contribute the most with differences across the locations. In Stansbury the greatest contributors were seagrass plants (47 to 85.2 %), followed by macroalgal thalli (11.2 to 27.9 %), accounting for more than 70% of SPM and 90% of sediment trap samples. In Victor Harbor, seagrass plants were the main contributor (37.2 to 65%), followed by oceanic sources (32.9 to 35 %), representing more than 70% in both SPM and sediment trap samples (Figure 4.4 and Supplementary Table 4.4). Area and Biomass indices indicate differences of the biggest contributor between seagrass plants and macroalgae thalli depending on the location. In Victor Harbor seagrass bed, seagrass plants were the greatest contributors with area indices ranging between 0.6 and 0.7 and biomass indexes between 0.4 and 0.5. Whilst in Stansbury macroalgae thalli contribute the most respect to the area and biomass with indices ranging between 0.1 and 0.4 in both SPM and sediment traps (Supplementary Table 4.5 and Figure 4.5 Panels A and B).

In the Isolated mangrove patch, salt marshes were the largest contributor (40.3 to 47 %), followed by mangrove trees (24.7 to 26.8 %), accounting for more than 65% in SPM samples (Figure 4.4 and Supplementary Table 4.4). In respect to the area and biomass mangrove trees were greatest contributors to both area and biomass with indices ranging between 120 and 268 accounting for more than the 95% in both SPM and sediment traps. (Supplementary Table 4.1 and Figure 4.5 Panels A and B).

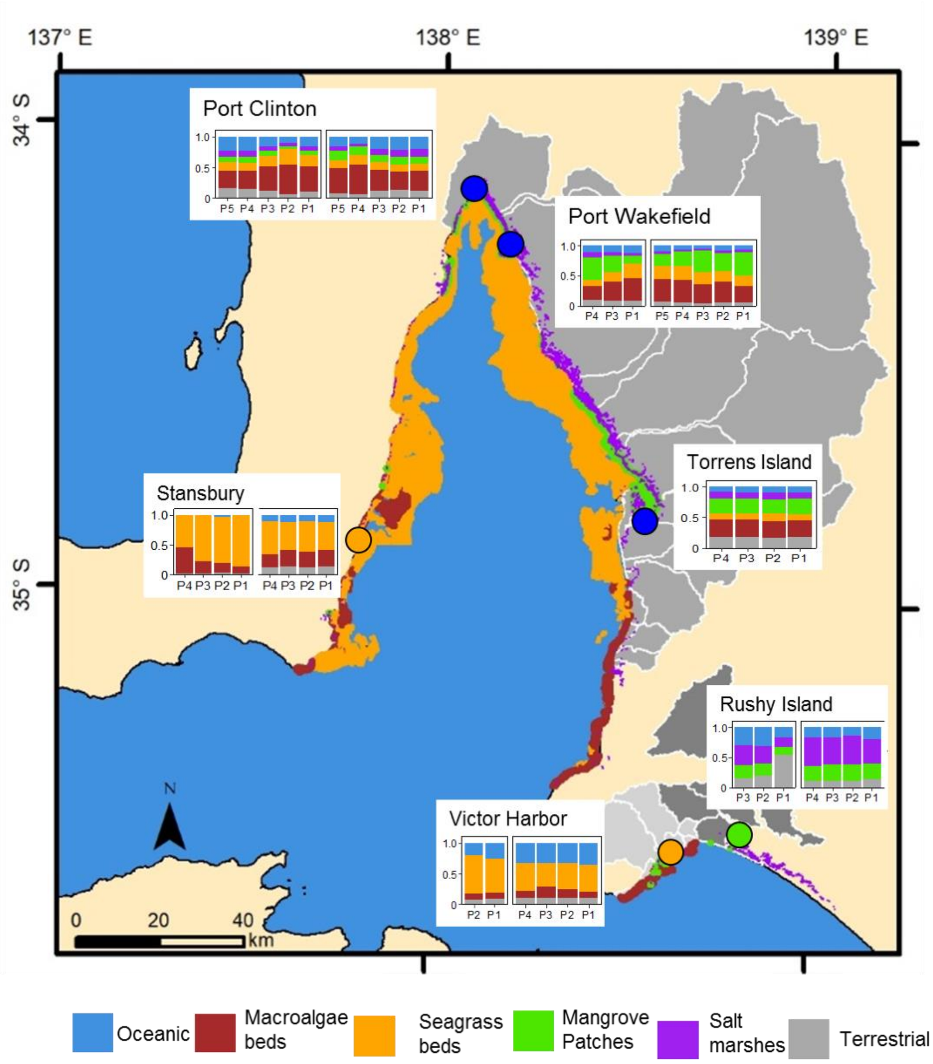

Figure 4.4. MixSIAR model results for connected mangrove patches (blue circles, Port Clinton, Port Wakefield, Torrens Island), as well as the isolated seagrass bed (yellow circle, Stansbury and Victor Harbor) and mangroves patches (Rushy Island, green circle). Each small figure represents contributions of the different sources. Sediment traps are depicted on the left side, suspended particulate matter on the right side. At Torrens Islands, the figure corresponds only to suspended particulate matter samples, because trap samples were lost. Contributions are expressed on the y-axis in proportion to 1, where 1 is 100% of the contribution. See legend for details of the colours representing the sources. The x-axis shows the transect points across each seascape, with the higher the numbers being the closer to the terrestrial zone. Areas occupied by different coastal vegetated ecosystems, catchment area and oceanic are shown in different colours (see legend for details).

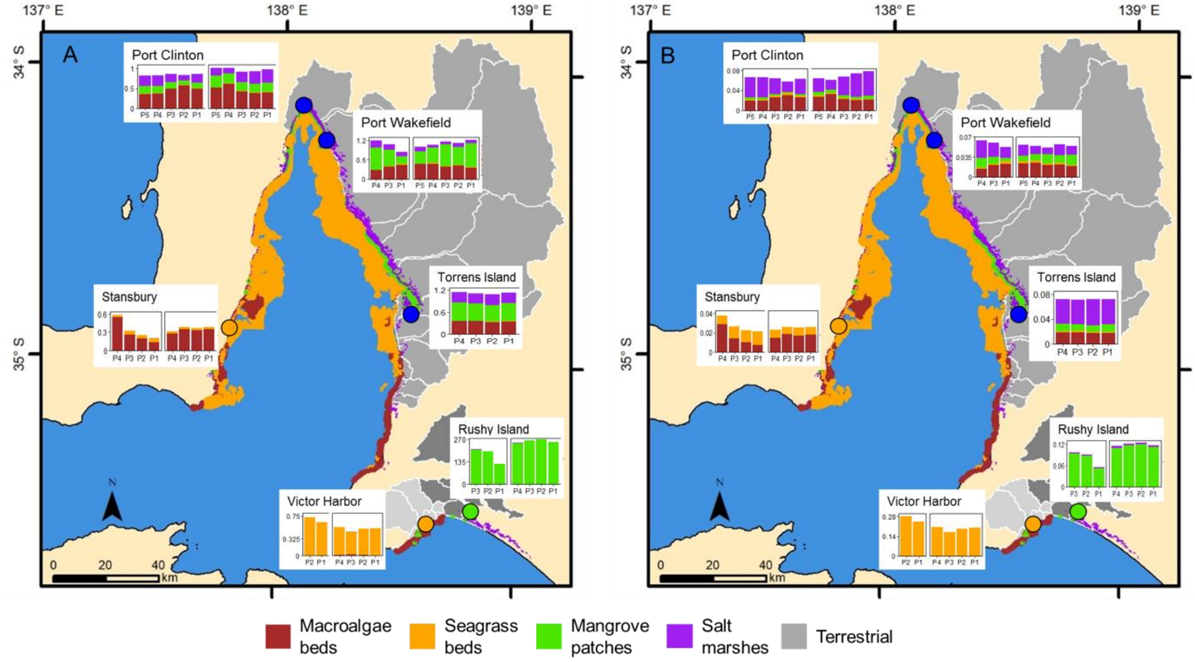

Figure 4.5. Area relative contribution (panel A) and biomass relative contribution (panel B) of the main coastal vegetated ecosystems mangrove patches, seagrass beds, macroalgae, salt marshes and terrestrial ecosystems within the coastal catchment area (see legend for details). Each small figure represents contributions of the different sources, sediment traps are depicted on the left side, suspended particulate matter on the right side. In Torrens Islands, the figure corresponds only to suspended particulate matter samples. Area relative contribution index in the panel A and biomass relative contribution in the panel B are expressed on the y-axis, see legend for details of the colours representing the sources. The x-axis shows the transect points across each seascape, higher numbers being closer to the terrestrial zone of the transect.

4.5. Discussion

4.5.1. Connected versus isolated CVE carbon and nitrogen store

Connectivity between mangrove patches and seagrass beds was beneficial in terms of carbon accumulation biomass and sediments for mangrove patches, carbon in seagrass beds was not increased by connectivity with mangrove patches. Connected mangrove patches had more carbon than the isolated patch in terms of biomass and sediment carbon store, whilst isolated seagrass beds had more carbon store in the biomass and sediments than connected beds (Figs. 4.2 and 4.3). Connectivity has been reported to increase carbon store in mangrove patches by increasing primary production (Huxham et al. 2018) and by adding more particulate material that would be sequestered in the sediments via root particle settings (Alongi 2014). The fact that isolated seagrass beds had higher biomass compared with connected beds suggests that more carbon is produced and kept in the sediment due to higher belowground biomass production and particle setting as reported in other studies (Tanaya et al. 2018). Isolated seagrass beds had denser sediments compared with other ecosystems which can explain that besides having low sediment carbon percentages, the carbon store was higher. In accordance with this, carbon percentages in sediment seagrass beds have been negatively linked to sediment density in other studies (Dahl et al. 2016; Güllstrom et al. 2017). In our study zone, it was shown that mangrove patches increase carbon store when connected with other ecosystems, whilst for seagrass beds other variables such as sediment density are more important to determined carbon store.

Mangrove patches characteristics such as tree structure and higher nitrogen percentage in the sediment determined that nitrogen store was higher regardless of whether they were connected or isolated from seagrass beds. Mangrove patches had greater nitrogen store in both biomass and sediments. The structure of mangroves trees compared with salt marsh or seagrass plants can determine that they have more nitrogen store in the biomass compared with other ecosystems (Figure 4.2). Different to our findings Garcias-Bonet et al. (2019) did not found significance difference between mangrove patches and seagrass beds in sediment nitrogen percentage or store in the Red Sea. Studies in the same location comparing nitrogen in the sediments between mangrove patches and seagrass beds are scarce and more information is needed to compare findings in the present study regarding connectivity and nitrogen accumulation. The only difference between connected and isolated seagrass beds in terms of nitrogen store was mainly driven by isolated seagrass beds having a higher biomass (Figs. 4.2 and 4.3). Whilst mangrove patches are important CVE for nitrogen store across the seascape since they can store high amounts of nitrogen per area compared with other CVEs.

4.5.2. Contribution of area and living biomass of coastal vegetated ecosystems to particulate organic matter

The highest percentage of POM contribution did not come from seagrass that was the CVE with the largest area or living biomass in connected CVE. Seagrass beds are important donors of POM in some locations, but this ecosystem also had the highest cover area and biomass across all CVEs seagrass beds, therefore they did not contribute significantly to the POM compared with other ecosystems. However, in Stansbury (Isolated seagrass beds) highest contribution did came for the CVE with biggest area that was seagrass beds (Figures 4.4 and 4.5). Seagrass beds have been reported to contribute significantly to POM even though they have a small area (Gillis et al. 2014b), as well as contributing nitrogen to mangrove patches (Walton et al. 2014). However, in the present study their relative contribution to POM was lower than that macroalgal beds and mangrove patches in some connected locations such as Port Wakefield or Port Clinton (Figure 4.5). Previous studies using isotopes chemical tracers have also shown that contributions of macroalgae to POM in mangrove patches were higher than those of seagrass plants (Saavedra-Hortua et al. 2019). Nevertheless, they should be also considered as donors to mangrove patches since *Posidonia sp.* leaves were observed in mangrove patches that did not have adjacent seagrass beds such as Port Wakefield (Supplementary Figure 4.2).

Even though mangrove patches and salt marshes had the smallest areas they contribute allot compared with POM from other ecosystems (Figure 4.5), corroborating the out welling hypothesis (Odum 1968; Lee 1995). Isolated mangrove patch in terms of area and living biomass were smaller by two orders of magnitude compared with adjacent salt marshes, and in connected locations mangrove patches were smaller than seagrass and macroalgal beds (Supplementary Table 4.1). This provides additional evidence of the importance of mangrove patches and salt marshes as a carbon and nitrogen source in the coastal seascape, regardless the occupied area.

Macroalgal beds were in general was one of highest contributors to POM across all CVE's, characteristics such as high productivity and drifting of the exported materials are important to determine the contribution to the POM shown by macroalgae thalli. Macroalgal beds contributed to POM across all locations sampled, regardless of the distance of the sampling locations to the macroalgal beds (i.e. short distance in Victor harbor or long-distance Gulf St Vincent) (Figure 4.4). In mangrove patches and seagrass beds in Gulf St Vincent at the oceanic fringe, we observed a considerable amount of *Hormosira banksii* thalli (Supplementary Figure 4.2) that were not attached to the sediment macroalgal beds were located mainly at the south of the gulf (Figure 4.4), with all three major algae groups present (Chlorophyta, Phaeophyceae and Rhodophyta) (Phillips 2001), potentially indicating that thalli drifting up to 100 km. Our results confirm recent findings that due to high productivity and abundant living biomass, macroalgal beds are an important source of blue carbon, partly through exporting considerable amounts of carbon to connected ecosystems (Duarte et al. 2013b; Hill et al. 2015). Differences across the main algal taxonomic groups Chlorophyta, Phaeophyceae and Rhodophyta should be considered in terms of drifting and therefore exporting material (Trevathan-Tackett et al. 2015; Ortega et al. 2019). Macroalgal beds were important donors of POM for mangrove patches and seagrass beds, this exchange of material contributes to the carbon and nitrogen storage in the sediments.

4.6. Conclusion

Ecosystem processes directly or indirectly related to organic matter turnover may be supported by exchange of organic matter among connected ecosystems. Thus, ecosystem connectivity may drive some ecosystems services of global relevance, such as carbon sequestration or nitrogen retention differently in mangrove patches and seagrass beds. Our results show that CVE contributes to POM-exchange across locations, irrespective of their area and living biomass. Hence, the degradation of one of these CVE will have severe consequences for adjacent ecosystems at the seascape level. Considering all the CVE as a continuing system with interchanges across the seascape, rather than each CVE as a separate system will help to manage and improve knowledge of carbon and nitrogen stocks at the seascape.

4.7. Acknowledgements

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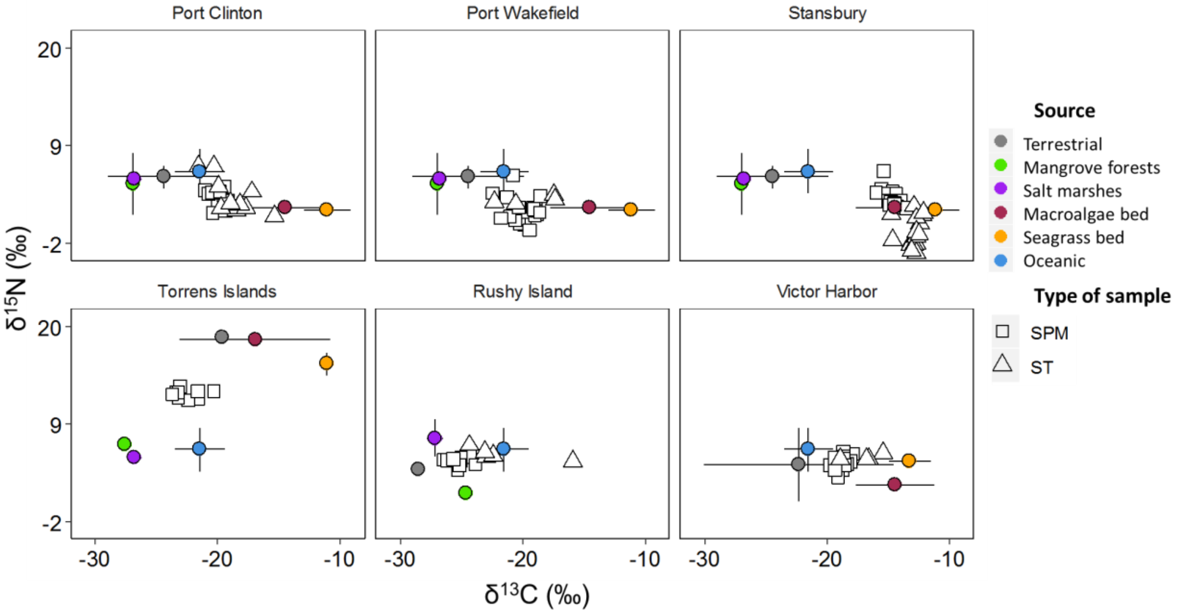
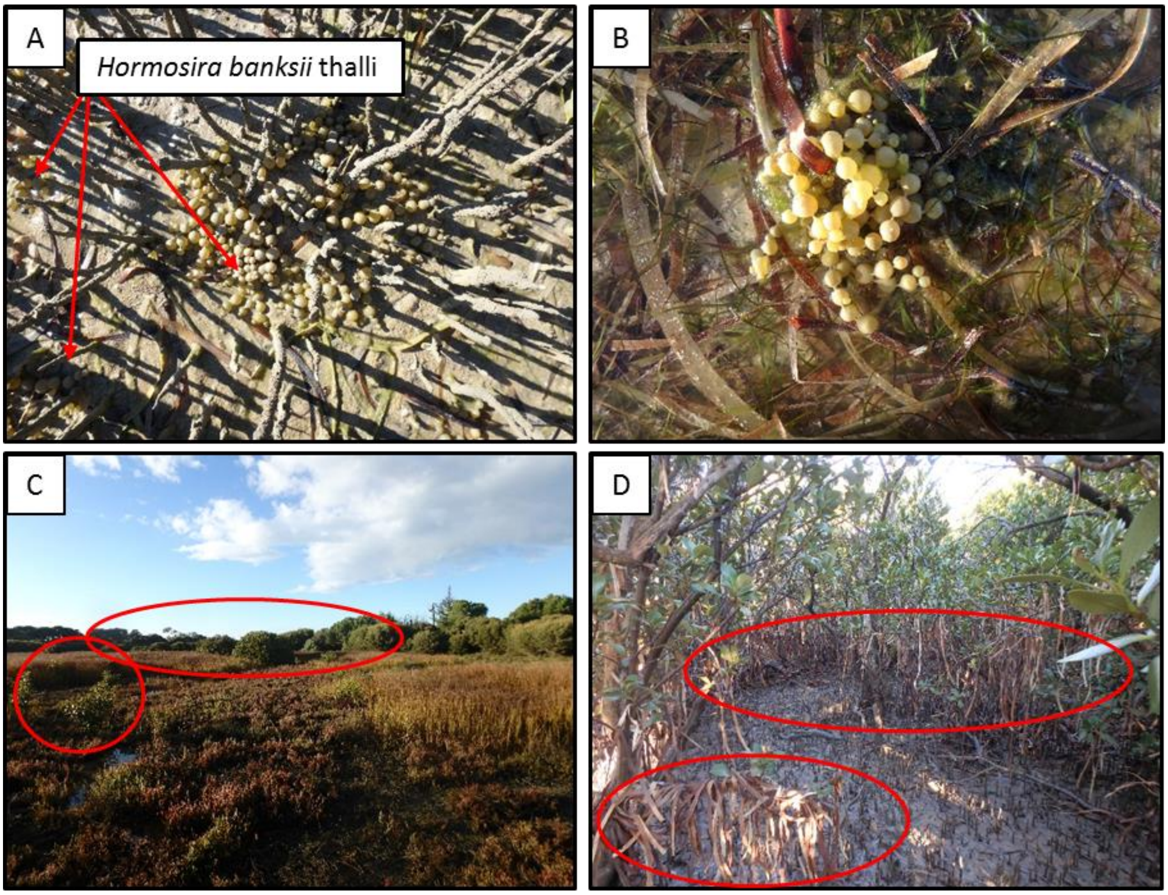
4.9. Supplementary material



Supplementary figure 4.1. Isotopic of carbon δ13C (‰) and nitrogen δ15N (‰) composition of suspended particulate matter (SPM) and sediment trap samples (ST) across the six locations (see legend for details). Sources are expressed as mean +/- Standard error. Sources at Port Clinton, Port Wakefield and Stansbury, were pooled. Whilst sources and samples at Torrens Island had a higher signal δ15N (‰). Port Clinton, Port Wakefield, Stansbury and Torrens Island are locations in Gulf St Vincent. Isolated mangrove patch is at Rushy Island and isolated seagrass bed is at Victor harbour.



Supplementary figure 4.2. *Hormosira banksii* thalli on pneumathophores of *A. marina* in mangrove patches at Port Wakefield (red arrows) (Panel A) and in the seagrass beds of Stansbury (Panel B). Intermixed mangrove trees and salt marsh plants in Rushy Island (see red circles) (Panel C). *Posidonia* sp. blades on the branches of *A. marina* in Port Wakefield (see red circles) (Panel D).

Supplementary table 4.1. Area, biomass carbon and nitrogen store and pools for mangrove patches, seagrass beds, macroalgal beds and salt marshes in Gulf St Vincent and isolated coastal vegetated ecosystems. Since biomass of salt marsh plants and macroalgal thalli were not directly measured, values were taken from studies in a close location with similar characteristics (Hill et al. 2015 and references therein; Serrano et al. 2019, and references therein). Carbon and nitrogen store in sediments was taken from the upper 15 cm. (SD: standard deviation; ND: no data; NA: not applicable; Mg:Megagrams; Tg:Teragrams, ha:hectare, C:carbon, N:nitrogen).

		Coastal vegetated ecosystems (Gulf St Vincent)				Isolated mangrove patch (Rushy Island)		Isolated seagrass bed (Victor Harbor)	
		Mangrove patches	*Seagrass beds*	**Salt marshes*	*§Macroalgae beds*	*Mangrove patch*	**Salt marsh*	*Seagrass bed*	*§Macroalgae bed*
Total area (km^2)		46.6	1288.9	32.9	71.5	0.01	2.7	3.5	34.6
Percentage of area across all CVE (%)		3.2	89.5	2.3	5.0	0.37	99.6	9.2	90.8
Store-aboveground biomass per unit area (Mg C ha^{-1})	*Mean*	56.1	2.1	8.1	22.0	8.1	8.1	7.9	22.0
	SD	55.5	1.5	6.4	ND	6.9	6.4	5.5	ND
Store-belowground biomass per unit area (Mg C ha^{-1})	*Mean*	2.3	1.2	ND	NA	1.2	ND	3.1	NA
	SD	1.6	1.0	ND	NA	0.5	ND	2.8	NA
Carbon pool biomass (Tg C)		2721.4	4266.3	265.6	1573.0	0.1	21.8	38.6	761.2
Store-aboveground biomass per unit area (Mg N ha^{-1})	*Mean*	1.8	0.1	0.2	1.0	0.3	0.2	0.4	1.0
	SD	1.8	0.1	0.2	NA	0.2	0.2	0.2	NA
Store-belowground biomass per unit area (Mg N ha^{-1})	*Mean*	0.1	0.04	ND	NA	0.04	ND	0.1	NA
	SD	0.1	0.04	ND	NA	0.01	ND	0.1	NA
Nitrogen pool biomass (Tg N)		87.6	154.7	7.6	71.5	0.03	5.0	18.5	784.0

* Data taken from Serrano et al. (2019) and references therein in supplementary material (Clarke et al. 1994; Kelleway et al. 2016; Santini et al. 2019, cited in Serrano et al. 2019).
§ Copertino et al. (2005) and Hill (2015).

Supplementary table 4.2. Results of GLMMs (generalized mixed linear model) comparing different response variables to the coastal vegetated ecosystems (mangrove patches vs. seagrass bed) and the connectivity type (connected vs isolated).

Response variable	Model component	Estimate	SE	*t*	*P*		Variance	Standard deviation
Carbon (%)	Intercept	2.26	0.11	19.03	**<0.01**	Location	0.01	0.09
	Ecosystem seagrass	-0.77	0.08	-9.72	**<0.01**	Residuals	0.13	0.35
	Connectivity type Isolated	-0.94	0.22	-4.13	**<0.01**			
	Connectivity type: Ecosystem	1.27	0.25	5.04	**<0.01**			
Nitrogen (%)	Intercept	-0.76	0.41	-1.85	0.06	Location	0.27	0.52
	Ecosystem seagrass	-2.21	0.17	-12.72	**<0.01**	Residuals	0.56	0.74
	Connectivity type Isolated	-0.31	0.82	-0.38	0.70			
	Connectivity type: Ecosystem	-0.46	0.88	-0.52	0.60			
Carbon store (mg cm^{-3})	Intercept	22.52	6.86	3.29	**<0.01**	Location	31.81	5.64
	Ecosystem seagrass	4.74	1.23	3.86	**<0.01**	Residuals	0.17	0.42
	Connectivity type Isolated	-9.18	14.38	-0.64	0.52			
	Connectivity type: Ecosystem	20.96	14.70	1.43	0.15			
Nitrogen store (mg cm^{-3})	Intercept	0.70	0.07	9.51	**<0.01**	Location	0.002	0.05
	Ecosystem seagrass	-0.47	0.07	-6.37	**<0.01**	Residuals	0.38	0.62
	Connectivity type Isolated	0.37	0.17	2.16	**0.03**			
	Connectivity type: Ecosystem	-0.44	0.18	-2.43	**0.01**			

Supplementary table 4.3. Results of Post-hoc Tukey test of the GLMMs (generalized mixed linear model) comparing different response variables to the coastal vegetated ecosystems (mangrove patches vs. seagrass bed) and the connectivity type (connected vs isolated).

Response variable	Comparison	Estimate	SE	z. Ratio	p-value
Carbon (%)	Connected mangrove patches - Connected seagrass beds	0.78	0.08	9.17	**<0.01**
	Connected mangrove patches - Isolated mangrove patch	0.94	0.23	4.14	**<0.01**
	Connected mangrove patches - Isolated seagrass beds	0.44	0.18	2.40	0.08
	Connected seagrass beds - Isolated mangrove patch	0.17	0.23	0.72	0.89
	Connected seagrass beds - Isolated seagrass beds	-0.34	0.19	-1.79	0.28
	Isolated mangrove patch - Isolated seagrass beds	-0.50	0.24	-2.10	0.15
Nitrogen (%)	Connected mangrove patches - Connected seagrass beds	2.21	0.17	12.72	**<0.01**
	Connected mangrove patches - Isolated mangrove patch	0.31	0.82	0.38	0.98
	Connected mangrove patches - Isolated seagrass beds	2.98	0.65	4.60	**<0.01**
	Connected seagrass beds - Isolated mangrove patch	-1.90	0.82	-2.30	0.10
	Connected seagrass beds - Isolated seagrass beds	0.77	0.65	1.18	0.64
	Isolated mangrove patch - Isolated seagrass beds	2.67	0.87	3.08	0.01
Carbon store (mg cm^{-3})	Connected mangrove patches - Connected seagrass beds	-2.44	2.37	-1.03	0.73
	Connected mangrove patches - Isolated mangrove patch	-7.75	2.54	-3.05	**0.01**
	Connected mangrove patches - Isolated seagrass beds	-10.19	2.93	-3.48	**<0.01**
	Connected seagrass beds - Isolated mangrove patch	-5.32	3.95	-1.35	0.53
	Connected seagrass beds - Isolated seagrass beds	-7.75	2.54	-3.05	**0.01**
	Isolated mangrove patch - Isolated seagrass beds	-2.44	2.37	-1.03	0.73
Nitrogen store (mg cm^{-3})	Connected mangrove patches - Connected seagrass beds	0.47	0.07	6.37	**<.01**
	Connected mangrove patches - Isolated mangrove patch	-0.37	0.17	-2.16	0.14
	Connected mangrove patches - Isolated seagrass beds	0.54	0.09	5.77	**<.01**
	Connected seagrass beds - Isolated mangrove patch	-0.84	0.16	-5.12	**<.01**
	Connected seagrass beds - Isolated seagrass beds	0.07	0.08	0.87	0.82
	Isolated mangrove patch - Isolated seagrass beds	0.91	0.16	5.52	**<.01**

Supplementary table 4.4. Results of MixSIAR models for the two different type of organic particulate matter samples (suspended particulate matter and sediment traps); showing the percentage of contribution of each source at each point across all the six different locations. The higher the number of the point is the closer to the terrestrial zone the transect point is located. For example, P5 is the closest to the terrestrial ecosystems while P1 is the closest to the oceanic fringe. N means number of samples.

			Suspended particulate matter			Sediment traps		
Location	Point	Source	Percentage Contribution%	Standard deviation	N	Percentage Contribution%	Standard deviation	N
Port Clinton	P1	Macroalgae thalli	32.1	5.0	3	39.7	1.0	3
		Mangrove trees	12.0	1.5	3	7.3	1.1	3
		Oceanic	19.5	2.3	3	15.5	0.5	3
		Saltmarsh plants	12.4	2.0	3	7.6	1.0	3
		Seagrass plants	11.8	1.9	3	18.5	2.2	3
		Terrestrial plants	12.1	1.3	3	11.5	1.1	3
	P2	Macroalgae thalli	30.6	0.8	3	46.4		1
		Mangrove trees	11.5	1.3	3	5.1		1
		Oceanic	21.5	2.5	3	10.3		1
		Saltmarsh plants	11.7	2.2	3	5.2		1
		Seagrass plants	12.0	0.9	3	25.4		1
		Terrestrial plants	12.7	0.5	3	7.6		1
	P3	Macroalgae thalli	34.6	6.1	3	39.2	0.4	2
		Mangrove trees	11.2	1.3	3	7.8	0.4	2
		Oceanic	20.4	4.8	3	16.0	0.3	2
		Saltmarsh plants	9.5	1.2	3	8.1	0.4	2
		Seagrass plants	12.7	0.2	3	16.7	0.2	2
		Terrestrial plants	11.8	2.3	3	12.4	0.1	2
	P4	Macroalgae thalli	48.9	2.6	3	29.5	5.7	2
		Mangrove trees	13.3	2.2	3	9.4	1.1	2
		Oceanic	12.3	1.3	3	22.4	6.4	2

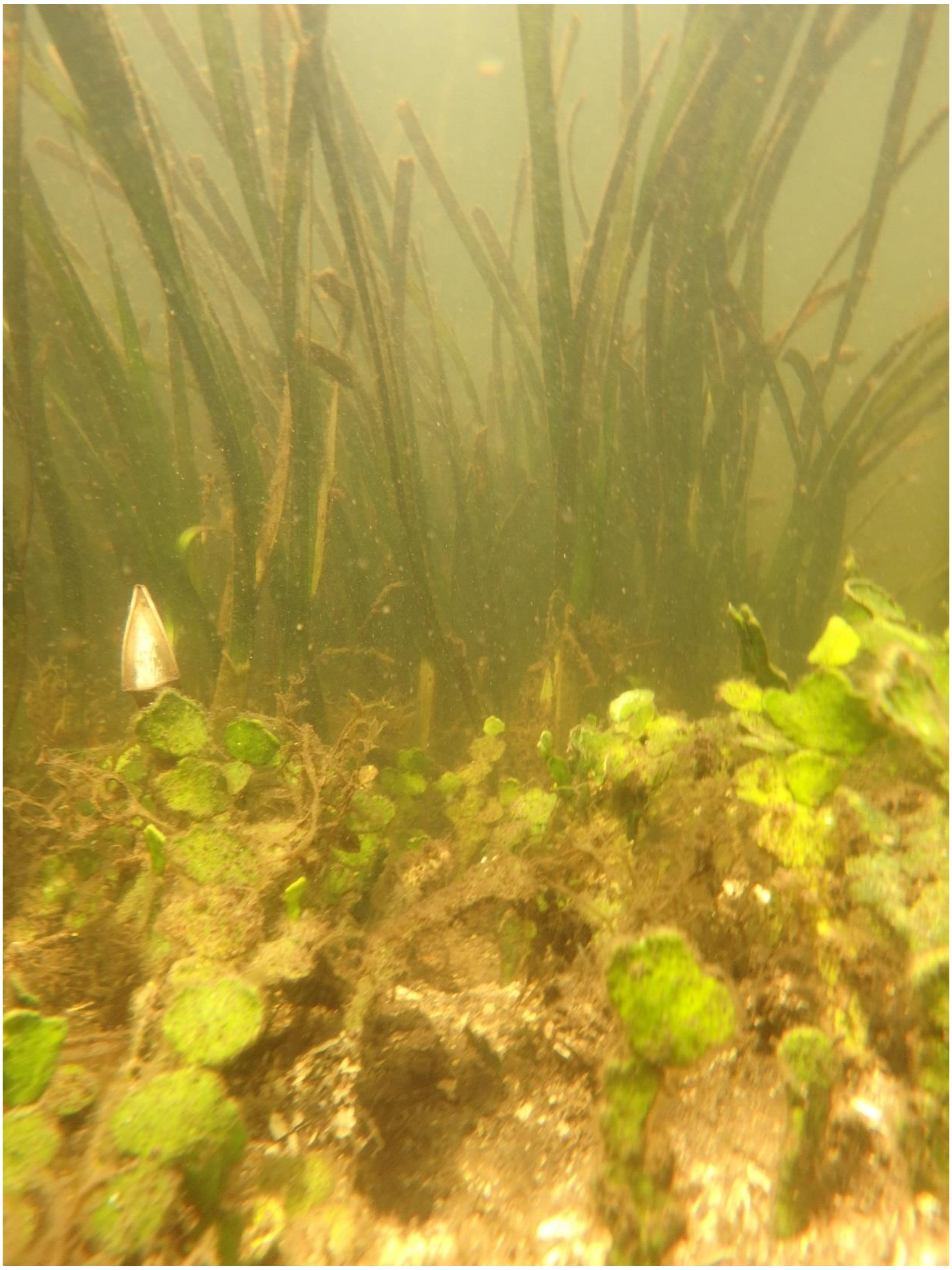
		Saltmarsh plants	5.0	0.2	3	10.1	0.7	2
		Seagrass plants	14.4	1.1	3	13.6	0.1	2
		Terrestrial plants	6.1	0.2	3	15.1	1.2	2
	P5	Macroalgae thalli	41.8	4.2	2	29.3	7.0	3
		Mangrove trees	15.6	7.0	2	9.2	0.8	3
		Oceanic	15.5	1.9	2	22.2	5.3	3
		Saltmarsh plants	6.8	1.6	2	10.1	1.1	3
		Seagrass plants	12.8	1.9	2	13.6	2.4	3
		Terrestrial plants	7.8	1.3	2	15.6	2.3	3
Port Wakefield	P1	Macroalgae thalli	28.4	3.9	3	35.4	2.6	2
		Mangrove trees	38.4	5.9	3	12.8	0.3	2
		Oceanic	7.3	0.5	3	12.9	2.5	2
		Saltmarsh plants	3.9	0.4	3	5.0	0.4	2
		Seagrass plants	16.4	2.7	3	24.4	1.0	2
		Terrestrial plants	5.5	0.4	3	9.6	1.3	2
	P2	Macroalgae thalli	34.0	5.7	3			
		Mangrove trees	29.1	8.5	3			
		Oceanic	8.7	0.9	3			
		Saltmarsh plants	4.7	0.6	3			
		Seagrass plants	17.0	2.0	3			
		Terrestrial plants	6.6	0.9	3			
	P3	Macroalgae thalli	30.9	4.3	3	31.6		1
		Mangrove trees	35.5	6.4	3	26.4		1
		Oceanic	5.6	0.9	3	11.3		1
		Saltmarsh plants	2.9	0.5	3	6.3		1
		Seagrass plants	20.7	1.9	3	15.7		1

		Terrestrial plants	4.2	0.5	3	8.6	1
	P4	Macroalgae thalli	38.3	1.5	3	22.2	1
		Mangrove trees	24.5	1.7	3	36.4	1
		Oceanic	6.8	0.3	3	12.3	1
		Saltmarsh plants	3.5	0.2	3	7.8	1
		Seagrass plants	21.8	0.8	3	11.3	1
		Terrestrial plants	5.1	0.3	3	10.0	1
	P5	Macroalgae thalli	37.3	4.0	3		
		Mangrove trees	20.3	3.5	3		
		Oceanic	9.8	3.6	3		
		Saltmarsh plants	4.7	1.0	3		
		Seagrass plants	20.7	0.4	3		
		Terrestrial plants	7.3	2.7	3		
Torrens Island	P1	Macroalgae thalli	27.6	0.4	2		
		Mangrove trees	25.3	1.8	2		
		Oceanic	9.1	0.4	2		
		Saltmarsh plants	10.2	0.3	2		
		Seagrass plants	10.2	1.9	2		
		Terrestrial plants	17.7	1.1	2		
	P2	Macroalgae thalli	26.6	2.6	3		
		Mangrove trees	23.3	4.4	3		
		Oceanic	9.9	0.6	3		
		Saltmarsh plants	10.6	1.2	3		
		Seagrass plants	12.4	4.0	3		
		Terrestrial plants	17.2	0.9	3		
	P3	Macroalgae thalli	29.2	0.9	3		

		Mangrove trees	24.0	2.2	3			
		Oceanic	8.9	0.7	3			
		Saltmarsh plants	9.9	0.4	3			
		Seagrass plants	10.5	2.0	3			
		Terrestrial plants	17.5	0.6	3			
	P4	Macroalgae thalli	29.0	3.3	2			
		Mangrove trees	26.1	2.8	2			
		Oceanic	8.4	0.3	2			
		Saltmarsh plants	9.9	0.6	2			
		Seagrass plants	8.6	0.8	2			
		Terrestrial plants	18.1	0.4	2			
Stansbury	P1	Macroalgae thalli	27.7	8.0	4	11.2	1.3	3
		Oceanic	12.0	2.8	4	1.6	0.3	3
		Seagrass plants	47.0	4.2	4	85.2	1.0	3
		Terrestrial plants	13.3	3.0	4	2.0	0.3	3
	P2	Macroalgae thalli	26.4	1.3	4	15.3	5.1	4
		Oceanic	10.6	2.0	4	3.0	3.5	4
		Seagrass plants	50.8	5.8	4	77.7	6.6	4
		Terrestrial plants	12.4	2.7	4	4.0	4.9	4
	P3	Macroalgae thalli	27.9	1.4	3	21.2	7.1	4
		Oceanic	12.1	7.4	3	1.4	0.7	4
		Seagrass plants	47.1	12.4	3	75.7	8.4	4
		Terrestrial plants	12.9	6.3	3	1.7	0.8	4
	P4	Macroalgae thalli	21.9	8.0	4	43.5	14.6	4
		Oceanic	11.0	2.1	4	1.0	0.4	4
		Seagrass plants	54.7	4.4	4	54.2	13.9	4

		Terrestrial plants	12.4	1.6	4	1.3	0.5	4
Rushy Island	P1	Mangrove trees	25.3	1.2	3	12.0		1
		Oceanic	20.2	4.5	3	17.1		1
		Saltmarsh plants	40.3	6.0	3	16.8		1
		Terrestrial plants	14.3	2.1	3	54.2		1
	P2	Mangrove trees	26.8	2.9	3	19.8	1.0	2
		Oceanic	15.1	3.9	3	31.2	1.6	2
		Saltmarsh plants	46.4	7.0	3	28.8	1.6	2
		Terrestrial plants	11.7	1.2	3	20.2	1.1	2
	P3	Mangrove trees	26.4	1.5	2	20.9	1.4	2
		Oceanic	17.7	1.3	2	29.5	3.0	2
		Saltmarsh plants	43.6	0.3	2	33.2	4.5	2
		Terrestrial plants	12.4	0.1	2	16.5	2.9	2
	P4	Mangrove trees	24.7	0.7	3			
		Oceanic	16.5	5.8	3			
		Saltmarsh plants	47.0	7.5	3			
		Terrestrial plants	11.7	2.3	3			
Victor Harbor	P1	Macroalgae thalli	11.4	1.1	4	11.1	0.5	2
		Oceanic	35.0	3.6	4	26.8	10.3	2
		Seagrass plants	43.7	3.1	4	53.4	12.6	2
		Terrestrial plants	10.0	0.6	4	8.8	1.8	2
	P2	Macroalgae thalli	14.4	2.5	4	9.3	1.5	2
		Oceanic	33.0	2.2	4	20.5	1.1	2
		Seagrass plants	42.2	4.1	4	62.1	1.6	2
		Terrestrial plants	10.4	1.0	4	8.3	0.9	2
	P3	Macroalgae thalli	18.7	4.3	4			

		Oceanic	32.9	4.2	4
		Seagrass plants	37.2	9.8	4
		Terrestrial plants	11.2	1.6	4
	P4	Macroalgae thalli	11.7	2.3	3
		Oceanic	33.2	4.2	3
		Seagrass plants	45.3	4.2	3
		Terrestrial plants	9.8	0.7	3



Chapter 5 Functional traits of ecosystem engineers increase the potential blue carbon storage in connected mangrove-seagrass coastal ecosystems

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5.1. Abstract

Mangrove forests and seagrass meadows provide an array of ecosystem services to coastal communities, including the accumulation and storage of significant amounts of submerged carbon, known as “blue carbon”. Both are dominated by ecosystem engineers (mangroves and seagrasses), which form several functional traits, defined as measurable properties of organisms. These traits can influence organismal performance and potentially impact mechanically and physiologically based mechanisms, which facilitate the sequestration and storage of blue carbon by trapping and burying particulate carbon. The expression of mangrove and seagrass plant functional traits depends strongly on abiotic and anthropogenic factors, as well as sediment characteristics. Nutrient-rich sediments support fast plant growth rates and trait development, therefore enabling faster nutrient acquisition supported by the traits themselves. Whereas nutrient-poor sediments are associated with slower plant growth. How development of mangrove and seagrass functional traits (physical and chemical) respond to sediment nutrient pools and based on this interactively influence physical processes which facilitate blue carbon storage in coastal ecosystems is unclear. To clarify the role of functional traits, we quantified how development of plant traits respond to sediment nutrients, and how changes in traits of *Rhizophora mangle* (mangrove), *Thalassia testudinum* (seagrass) and *Haladoule wrightii* (seagrass) influence physical processes which then effect blue carbon sink potential. Nitrogen, phosphorus, and organic carbon were higher in mangrove forests compared to seagrass meadows, whereas the inverse relationship was seen for inorganic carbon. The majority of physical traits of *T. testudinum* showed no differences within the seagrass meadow, some differences were seen for *H. wrightii*. In contrast, chemical traits of seagrass leaves did. In mangrove forests, differences between the oceanic fringe and the part of the forest closer to the terrestrial zonewere detected for all physical and chemical traits. A positive correlation was seen between *T. testudinum* traits i.e. seagrass coverage, canopy height, shoot density, below ground biomass, leaf cross-sectional area and thickness and sediment nitrogen and phosphorus content. We identified a positive correlation between *R. mangle* traits (root density, pneumatophore abundance, specific leaf area, leaf toughness, nitrogen and phosphorus content of leaves) sediment nitrogen concentrations in coastal fringe relative to interior mangroves. Whereas leaf thickness and the root complexity index were negatively correlated sediment phosphorus concentrations. A significant positive correlation was found between sediment organic carbon concentrations and *T. testudinum* physical traits (seagrass coverage, canopy height, shoot density, belowground biomass, leaf cross-sectional area and thickness), the opposite relationship was seen for inorganic carbon concentrations. The seaward mangrove showed a negative relationship for sediment organic carbon and *R. mangle* associated traits (leaf thickness and root complexity). As a consequence of the higher nutrient availability in sediments, aboveground biomass components increased in seagrass meadows. Available sediment nutrients in seagrass meadows are known to potentially increase above ground biomass components, our findings support this assumption. The mangrove forest showed attributed of nutrient limitation where trees growing along the coastal fringe appeared to respond to higher sediment phosphorous with increasing above ground biomass and root complexity. Our findings indicated that a higher sediment nutrient content positively influenced physical traits like the specific leaf area, root density, and pneumatophore abundance. Moreover, the nutrient content of the leaves had a positive influence on the nutrient content within the mangrove forest sediment. With lower sediment phosphorus content root complexity increased, confirming previous research that mangroves use their roots to search for phosphorus in the sediment. Greater seagrass above ground biomass components supported the accumulation of blue carbon within the seagrass meadow. The higher root complexity decreased organic carbon sediment content. Tropical marine ecosystems provide a potential important carbon sink; these findings give insights into the unknown mechanisms of functional traits supporting the accumulation of carbon. Importantly this study identified functional trait response to nutrient availability and the potential effects of these traits on physical processes which could facilitate blue carbon accumulation. Enhanced understanding of mangrove trees and seagrass meadows as ecosystem engineers will help us to underline the importance for ecosystem services especially sediment carbon accumulation for climate chance mitigation.

Keywords: Sediment organic carbon; tropical seascape; wetlands; sediment inorganic carbon; nitrogen; phosphorus; chemical traits; physical traits.

5.2. Introduction

Tropical coastal ecosystems, like mangrove forests and seagrass meadows, provide various ecosystem services to humans and maintain biodiversity (Fourqurean et al. 2014; Giri et al. 2011). A critical ecosystem service is carbon accumulation which can help to mitigate climate change, by the plants and trees reducing atmospheric CO_2 levels through sequestration and storage of significant amounts of CO_2 in their above- and belowground biomass, as well as in the sediment (Donato et al. 2011; Duarte et al. 2005). Sediment carbon also referred to as belowground carbon pools are dominated by living and decomposing roots, rhizomes, and leaf litter (Fourqurean et al. 2014). The total amount of carbon stored in aquatic ecosystems, especially in coastal habitats such as seagrass meadows and mangrove forests, is called “blue carbon” (Alongi 2014b; Nellemann et al. 2009).

Even though seagrass meadows and mangrove forests occupy only a small proportion of the global coastal area (mangrove forests≈138.000 km^2; seagrass meadows≈330.000 km^2), they are highly productive ecosystems (Duarte and Chiscano 1999; Feller et al. 2010; Srikanth et al. 2015). Carbon accumulation rate in mangrove forests is estimated at 174 g C m^{-2} y^{-1} (Alongi 2014a) and 160–186 g C m^{-2} yr^{-1} in seagrass meadows (Duarte et al. 2013). Dead plant material accumulates within the ecosystems, decomposes, and is stored in the mangrove or seagrass sediment. Additionally, tidal currents connect mangrove forests with nearshore waters and support the exchange of carbon-rich organic material, essential dissolved nutrients, such as nitrogen and phosphorus, and suspended matter from each ecosystem (mangrove forests and seagrass meadows) (Chen et al. 2017; Feller et al. 2010).

Seagrass plants and mangrove trees are known as ecosystem engineers because they can change chemical and physical attributes to buffer environmental stresses (Peralta et al. 2008; Sippo et al. 2016). These attributes are known as functional traits, there are different classifications of traits (i.e. community, morphological, mechanical and chemical) which can be broadly split into two groups, physical and chemical traits. Plant functional traits are plastic and change their physical or chemical structure with different environmental influences for example nutrient (nitrogen or phosphorous) availability. Functional traits may affect physical processes which have a positive influence on the carbon-rich organic material accumulation. Physical traits such as root length (mangrove trees) and leave height (seagrass plants) reduce the water current, allowing for greater deposition of leaf litter. Whilst, chemical traits (i.e. leaf carbon or phosphorous content) are connected to potential carbon input into the sediment (Enríquez, Duarte and Sand-Jensen 1993; Fourqurean and Schrlau 2003). Due to these mechanisms, the quantity of carbon in the sediments of mangrove forests or seagrass meadows increases.

Previous research has examined the accumulation of carbon in these wetlands (e.g. plant biomass and sediment) (Duarte et al. 2005; Jennerjahn and Ittekkot 2002; Nellemann et al. 2009). But there is a gap in our knowledge on the potential direct and indirect influence of functional traits of plants and trees on the trapping, accumulation and storage of carbon in connected coastal seascape sediments. Especially the development of traits responding to sediment nutrient availability. Given that these ecosystems, mangrove forests, and seagrass meadows are dominated by ecosystem engineers with specific functional traits that could control their physical environment (i.e. changing hydrodynamics, increasing particle retention and sediment accretion), research within this area could give new insights on mechanisms controlling the carbon storage in the sediment. Plant traits are unique and show a high habitat-depending phenotypical plasticity in both mangrove forests (Reef, Feller and Lovelock 2010) and seagrass meadows (de los Santos et al. 2013). To explore this, we aimed to answer two main research questions: 1) Do physical and chemical traits of mangrove and seagrass plants alter with a natural gradient of phosphorus and nitrogen content in the sediment? and 2) Is the accumulation of organic and inorganic carbon in a connected mangrove-seagrass gradient correlated with physical and chemical functional traits? For simplicity in this study we have classified traits as either physical or chemical and not into a more complex classification such as community, morphological, mechanical and chemical. We hypothesized the functional traits of coastal ecosystem engineers will variate with changing sediment nutrient availability. High nutrients in mangrove forests and seagrass meadows could promote higher relative above ground biomass (AGB) and associated traits, whilst lower nutrients could promote higher below ground biomass (BGB) specially in terms of fine root biomass. Higher AGB compared to BGB is expected to promote inorganic carbon capture. Lower nutrients would enhance BGB compared to AGB, which should increase organic carbon accumulation. Future sediment carbon models need to include the carbon storage potential of ecosystem engineers and their functional traits promoting carbon accumulation.

5.3. Material and methods

5.3.1. Study site

The study area was located in the Biscayne National Park in Biscayne Bay, South Florida (USA). This area is dominated by a subtropical climate. It shows a distinctive annual seasonality of wet and dry seasons. The average daily temperature shows little seasonal changes (Davis and Ogden 1994). Dry season brings a mild climate with an average high temperature in January of 25 °C. In the wet season temperatures average between 24 and 29 degrees Celsius, and the climate is hot and humid. The wet season roughly coincides with hurricane season, with frequent thunderstorms from June through

November. Biscayne Bay is a shallow semi-enclosed lagoon (National Park Service, Biscayne) with presence of coral reefs in the east part with a tidal range of 60 cm. Data were collected between February and March 2018. In order to have a representation along a possible gradient in the mangrove forest and seagrass meadow samples were taken along 12 transects (ca. 1.2 km long) running from the terrestrial site of the mangrove forest close to shore into the shallow seagrass meadows (Figure 5.1). The seagrass meadow was dominated by *Thalassia testudinum.* Only a few shoots of *Halodule wrightii* were identified in shallow water. The mangrove forest was dominated by *Rhizophora mangle*. Some individual trees of *Avicennia germinans* and *Laguncularia racemosa* were found.

Figure 5.1. Map showing the study area of Florida (inset picture) and the area of Biscayne National Park (Florida, USA). Point 1 is the closest point to the oceanic fringe while P6 is the closest to the terrestrial ecosystem. Transects were named for better orientation during fieldwork.

Sampling point were separated from each other approximately 200 meters within each ecosystem. Three points per transect were located in the seagrass meadow and the other three within the adjacent mangrove forest (except for one transect). From the total sampling points (N = 70), n = 36 of these were located within the seagrass meadow, and *n* = 34 were located inside the mangrove forest (two points missing due to inaccessible terrain). At each sampling point along the seagrass meadow and mangrove forest transects, a sediment core was taken and a quadrat of 0.25 m^2 was placed randomly (*n* = 5) in proximity to the core. Within these quadrats, a suite of functional traits was measured (see methods below). Along the seagrass meadow transect, five seagrass shoots of *Thalassia testudinum* were randomly collected within each quadrat and stored in labeled plastic bags filled with seawater, to reduce the stress during the transport of the shoots. These shoots were analyzed for chemical analysis. Shoots of *Halodule wrightii* (second present species in the sampled meadow) were not collected due to their rare appearance in the sampling points (small quantity for statistical tests). In the mangrove forest, five *Rhizophora mangle* trees were chosen for analyses of functional trait parameters. The sampled trees grew within a distance of 2-3 meters in proximity to the sediment core. Furthermore, one leaf per branch was picked from the exterior canopy for leaf trait analysis. In total four leaves from each tree were collected. To guarantee the leaves had approximately the same age, only leaves from the second order (the second leaf pair after the apical bud) were picked (Figure 5.2).

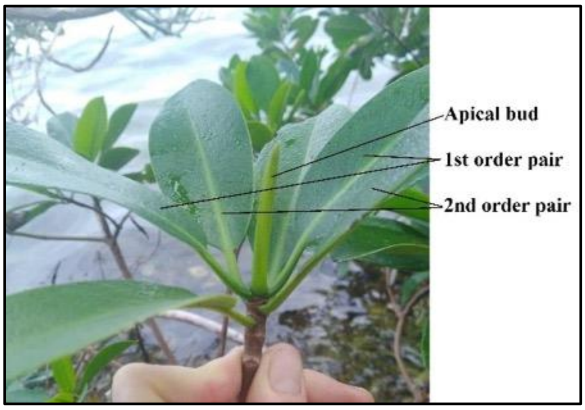

Figure 5.2. *Rhizophora mangle* shoot with indications of the first two orders of leaves (S. Kammann 15.03.2018, Florida, USA).

5.3.2. Sediment cores

Sediment was sampled using a 30 cm long PVC tube with a diameter of 5 cm. At each sampling point in the seagrass meadow and the mangrove forest, one core was taken and divided into five depth sections. The first section (0-5 cm) was used for further analyses. The samples were stored in labeled plastic bags, placed on ice, and transported to the Florida Bay District Interagency Science Centre, Key Largo, FL, USA. At this facility, samples were placed in a drying oven at 50°C until their weight was constant for approximately 72 h. Dried samples were then transported to the analytical laboratory at the Leibniz Centre for Tropical Marine Research (ZMT).

These samples were homogenized, and 3 portions of approximately 15 mg were taken. One portion was wrapped in tin caps to measure total sediment carbon, whilst the second was wrapped inside silver caps and then acidified, to measure sediment organic carbon (SOC) and sediment nitrogen. Both portions were analysed by combustion in an elemental analyser (EuroVector EA 3000) using acetanilid 4 (71.6 % C) for calibration and low soil standard (OAS4) as standard with a precision of 0.06% for the carbon and 0.01 % for total nitrogen in sediments. Percentages of sediment inorganic carbon (SIC) were calculated by subtracting sediment organic carbon content from total sediment carbon content. The third proportion was used for phosphorus analyses. The hydrochloric acid (HCl) digestion method was used. The samples were continuously heated at 110°C for 30 minutes during digestion and afterward cooled to room temperature, 325 µL of this digest was added to 6.5 µL of the acidic ascorbic acid and 6.5 µL of molybdate mix solution into a 96er well plate. The measurement was completed after 10 - 30 minutes at 880 nm or 810 nm according to a calibration curve with PO_4^- Standards from 0 – 18 µM PO_4^- P with a TECAN Infinite M200 plate reader. Phosphate ions react in acidic solution with molybdate to form yellow phosphomolybdic acid, which can be reduced to molybdenum blue with ascorbic acid. Antimony tartrate stabilizes the dye. Molybdenum blue was quantified photometrically. As reference material SRM1515 (apple leaves with 1590 ugg^{-1} P content) was used. All parameters are given in %.

5.3.3. Trait measurements

Seagrass physical traits

In seagrass meadows, two species of seagrasses (*Thalassia testudinum* and *Halodule wrightii*) were found. At all sampling quadrats per point (n = 5), canopy height (cm), shoot density (number of shoots m^{-2}), and coverage per species (%) were recorded. In seagrass meadows, belowground biomass (BGB) and aboveground biomass (AGB) were measured as follows. A second sediment core (30 cm depth x 5 cm diameter, volume = 0.06 cm^3) was collected close to the core used for the elemental analyses. Plant matter above the sediment surface of the core was removed, stored in a plastic bag, and dried later in the oven for 2 days at 50°C and weighed to measure AGB (Ohaus, Voyager, Switzerland). The aboveground area of each core represented 20 cm^2. Therefore, the dry weight of the seagrass shoots was multiplied with 5 to represent a square meter. The sediment core was washed within a fine mesh to remove coarse debris, like shells and undecomposed organic material. The core was then oven-dried for 2-3 days at 50°C and weighed to measure BGB as dry mass. The seagrass AGB and 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.

The number of leaves per shoot was counted and the second seagrass leaf counted from the inner shoot to the older leaves on the outside (order two) was separated from the shoot. In total 117 leaves of order two were sampled. The leaf length (l, cm) and width (w, cm) were measured and the values were used to calculate the leaf area index (LAI, cm^2).

$$LAI = 1 * w \quad (1)$$

Besides this, the leaf thickness (lt) (cm) was measured. The values of leaf thickness and width were used to calculate the cross-sectional area (mm^2).

$$cross\text{-}sectional\ area = (lt * w) * 100 \quad (2)$$

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

Mangrove forests

At the sampling point in the mangrove forest, a picture of each sampling quadrat was taken to determine the pneumatophore height (cm) and density (pneumatophore m^{-2}), and root density (roots m^{-2}) via image evaluation. Mangrove BGB was measured using a second sediment core (30 cm depth x 5 cm diameter, volume = 0.06 cm^3). We processed mangrove sediment cores using the same methods as for seagrass sediment cores, and we estimated mangrove BGB as dry mass per m^2. Mangrove canopy height (m) was estimated visually, and the basal area of individual mangroves was estimated using a meter tape. Aboveground biomass (m^2) was calculated following established relationships from measured height and basal area (Komiyama et al. 2008).

Pictures of the collected mangrove leaves (n = 680) were taken from above a plate. These pictures were later used for LAI (cm^2) calculation with ImageJ®. Besides this, the thickness (cm) of the leaf was measured. For both types of leaf samples (mangroves and seagrasses), the dry weight (DWg) of the leaves was recorded with a digital scale (Ohaus, Voyager, Switzerland). The values for DWg and LA were used to calculate the specific leaf area (SLA, cm^2 DWg^{-1}).

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

The five *Rhizophora mangle* trees in proximity to the sediment cores were chosen for tree height and stem circumference. In the case of trees taller than 2 m, tree height was visually estimated. The number of aerial roots arising from the trunk (prop roots = pr.r.) was counted (pr.r tree ^{1}). The uppermost aerial root of each tree was used to sample the total number of columns and arches of the root, the length (cm) of each arch, and the distance (cm) from the last root tip connected to the sediment to the trunk (Figure 5.3).

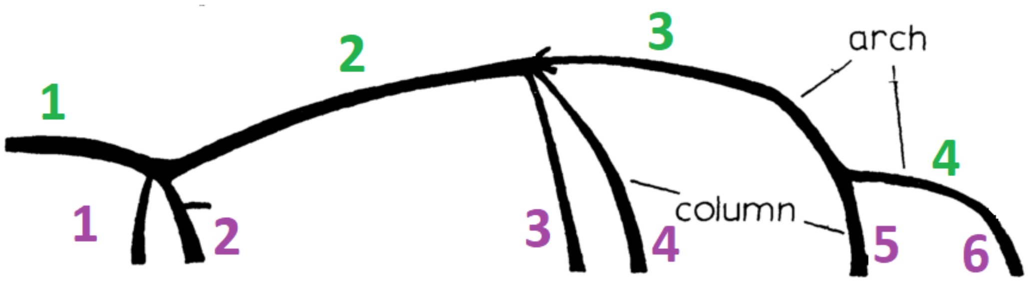

Figure 5.3. Example for the measurement of root trait parameters. Number of arches (green), number of columns (purple) (adapted from Gill and Tomlinson 1977).

All of the root data were used to evaluate the aboveground aerial root architecture of *R. mangle* per tree. A root complexity index (RCI) was designed to differentiate between root complexity magnitude per tree. The complexity of a root was defined as numbers of columns per root's distance to the trunk. To express the root complexity per tree, the complexity value for the single root complexity was then multiplied by the number of prop roots per tree [1]).

$$RCI = (\text{number of columns} * \text{distance to trunk}) * \text{pr.r. tree}^{-1} \qquad (4)$$

Mangrove leaf toughness was measured with the same protocol as seagrass leaves and 680 mangrove leaves (*R. mangle*) were tested. Due to the research permit, seagrass tissue collection was limited and therefore the amount of seagrass shoot samples is smaller.

Chemical traits

For chemical analyses, tissue samples (mangrove leaves and seagrass shoots) were dried in an oven at 50 °C (Laboratory at Key Largo) until the weight was constant and then milled until homogenized (Retsch ZM 100) at the Leibniz Centre for Tropical Marine Science (ZMT). The milled samples were prepared for the chemical analyses with the Euro EA3000 Element Analyzer, which analyses carbon and nitrogen by flash combustion, with a precision of 0.36 % for OC 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*. The total organic carbon content is subtracted from the total carbon content to calculate the total inorganic carbon (TIC) content of a given sample. Total phosphorous content was determined using photometric o-phosphate determination. For the digestion of organic material, the alkaline persulfate digestion was used. All parameters are given in %. The carbon-to-nitrogen ratio (CN molar ratio) was calculated after the chemical analysis.

5.3.4. Statistical analyses

All statistical analyses were conducted in R version 4.0.1 (R Core Team 2020). Data were tested for normality using the Shapiro-Wilks test. To test for significant differences of organic carbon, inorganic carbon, phosphorous and nitrogen sediment content between the two habitats, a T-test (parametric data) or a Mann-Whitney U-test (non-parametric data) was conducted. We used a one-way analysis of variance (ANOVA) for normally distributed data and a Kruskal-Wallis test for non-parametric data to test for significant differences in-between the points 1-3 (seagrass meadow) and 4-6 (mangrove forest)] and across all points (1-6) with respect to sediment carbon and nutrient (P and N) content, and plant traits. Models were run separately for each habitat type (mangrove, seagrass). Significant pair-wise differences were compared using Tukeýs (parametric data) or Dunn ́s post-hoc test (non-parametric). We use an alpha of 0.05 ($P < 0.05$) to determine statistically significant differences.

We investigated the relationships among plant physical and chemical traits for mangroves and seagrasses separately using a Principal Component (PC) analysis. Data were $\log_{10}$- transformed to obtain 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 first 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”. When performing the PC analysis data were centered and scaled. Belowground biomass 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.

Selection of the number and which PC were selected using the K-fold method. The extracted PC axis scores were used as a measure of trait coordination, instead of taking the traits individually by themselves. PC axis scores were reported if they had a correlation coefficient of at least 0.6 and a significant value below 0.05. The selected PC axis scores were used to analyze the influence 1) of sediment nutrient content (N and P) (%) on trait development and further 2) the influence of traits on the carbon content (%) in the sediment, correlation analyses between the extracted PC axes and the nutrients and carbon contents (%) in the sediment were conducted. To determine the correlation relationship, we used the Pearson correlation coefficient (R) for parametric data, Spearman rank correlation coefficient (ρ) for non-parametric data. Scatter plots were used for visualizing the significant correlations with a correlation coefficient of 0.6 and above and a p-value below 0.05. Two exceptions were made when either the correlation coefficients or p-value were very close to our threshold. These were in the case of seagrass meadow traits vs. inorganic carbon which had a correlation coefficient of 0.5 and mangrove forest traits vs. organic carbon where the p value was 0.058.

5.4. Results

5.4.1. Sediment nutrient content

The mangrove forests mean sediment nitrogen (SN) content (1.58 %) exceeded mean sediment nitrogen values in the seagrass meadows (0.48 %) and was found to be not significantly different between the two ecosystems (T-Test, T=1,648, p=0,116) (Figure 5.4 (c)). In common with these findings, the mean sediment phosphorous (SP) content in the mangrove forest (0.03 %) was higher than in the seagrass meadow (0.001 %). For the mean SP content, a significant difference between the two ecosystems (Mann-Whitney U-Test, U=25, $p<0.05$) was found (Figure 5.4 (d)).

Within the seagrass meadow no significant differences between the points (1-3 seagrass meadow) for SN (one-way-ANOVA, F=0,317, p=0,732) and SP (Kruskal-Wallis-Test, χ2=0,152, p=0,927) content could be detected. Whereas in the mangrove forest the SP content differed significantly between points (4-6 mangrove forest) (Kruskal-Wallis-Test, χ2=16,701, $p<0,05$). Dunn´s post hoc test could detect significant differences between P4 and P5 (p=0,003) and P4 and P6 ($p<0,001$). The SN content in the mangrove forest showed no significant differences in-between the points (4-6 mangrove forest).

5.4.2. Sediment carbon content

Mangrove forests SOC content (22.1 %) exceeded SOC values in the seagrass meadows (4.5 %) and was found to be significantly different between the two ecosystems (Mann-Whitney U-Test, U=105, $p < 0.01$) (Figure 5.4 (a)).

The mean value of the SIC content in the seagrass meadow was significantly higher (8.4 %) than the value in the mangrove forest (3.8 %) (Mann-Whitney U-Test, U=223, $p<0.01$) (Figure 4(b)). The results for all analysed 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 the points (points 1-3 seagrass meadow and 4-6 mangrove forest) for SOC and SIC could be ascertained.

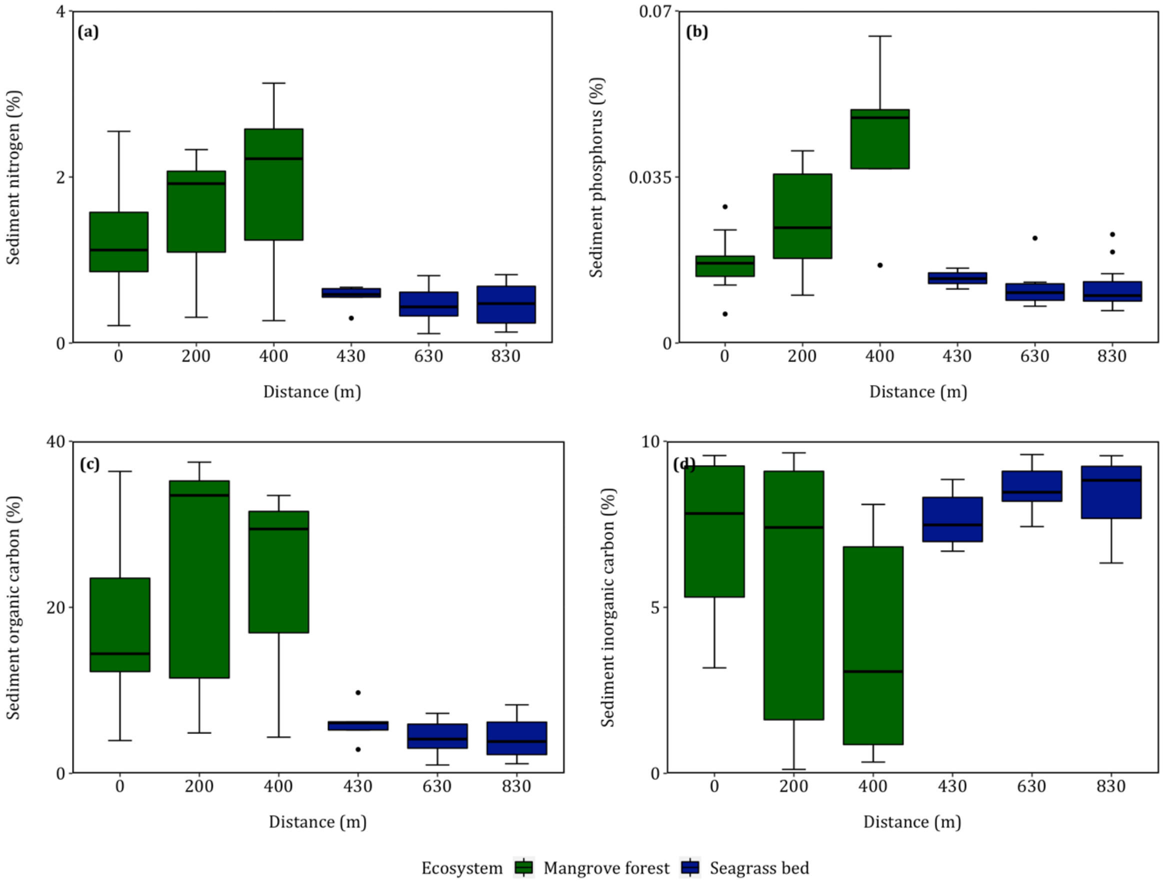

Figure 5.4. Box plots showing changing sediment characteristics across the two ecosystems, mangrove forests (green) and seagrass meadows (blue). Panels (a) and (b) represent sediment organic carbon content (%) and sediment inorganic carbon content (%) respectively. Whilst panels (c) and (d) show sediment nitrogen content and sediment phosphorous content (%). Please note the different y-axis on each panel. Mangrove forests points are located at 0, 200 and 400 m distances and seagrass meadows are 430, 630, and 830 m distances (x-axis). Values expressed in percentage of the sediment dry weight. The lines in the boxes represent the median. The ends of the whisker represent the minimum and the maximum of the values per point. Outliers are visualized as dots.

5.4.3. Variation in traits across ecosystems

No significant differences were seen in canopy height of the seagrass meadow (taking into account both present species *T. testudinum* and *H. wrightii*, *T. testudinum* coverage (%), density (shoots m $^{-2}$), specific leaf area (SLA cm^2 g^{-1}), the cross-sectional area of shoots (shoots mm^2), leaf thickness (mm), and leaf toughness (g mm^{-2}) across all three points (appendix Table 5.1). The coverage (%)of *H. wrightii* however showed higher coverage at point 3 compared to points 1 and 2 (appendix Table 5.1). *H. wrightii,* also had higher shoot density at point 3 versus point 2 (appendix Table 5.1). Significant differences were detected for seagrass leaves TOC and TIC content (%) across points, TOC was higher at point 1 compared to point 3, whilst TIC was greater at point 3 than to points 1 and 2 (appendix Table 5.1).

As *Rhizophora mangle* was the dominant species at all mangrove sites, all further analyses did not take into account the sporadic occurrence of other species. A significant difference was found across points for above ground biomass, canopy height (m), specific leaf area (SLA cm^2 g^{-1}), root complexity index, and the number of prop roots per tree, for all these traits values were higher at point 4 compared to points 5 and 6 (appendix Table 5.2). 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 (appendix Table 5.2). 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 difference, where it was greatest at point 6 compared to points 4 and 5 (appendix Table 5.2). A significant difference in leaf toughness (g mm^{-2}) was also found, which was higher at point 6 compared to point 4 (appendix Table 5.2). The majority of mean values for mangrove leaves TIC content (%) per point were under >1 % and therefore negligible for analysis. There were significant differences across points for mangrove leaves TOC content (%) between point 4 (43.5 %) and 5 (44.9 %) and point 4 and 6 (45.4 %) (appendix Table 5.2).

5.4.4. Physical and chemical trait covariation

Based on the results of PC analysis, the six chemical and ten physical traits of seagrass meadows could be summarized by three principal components, which together accounted for 91.2% of the total variance (Figure 5.5, appendix Table 5.3).

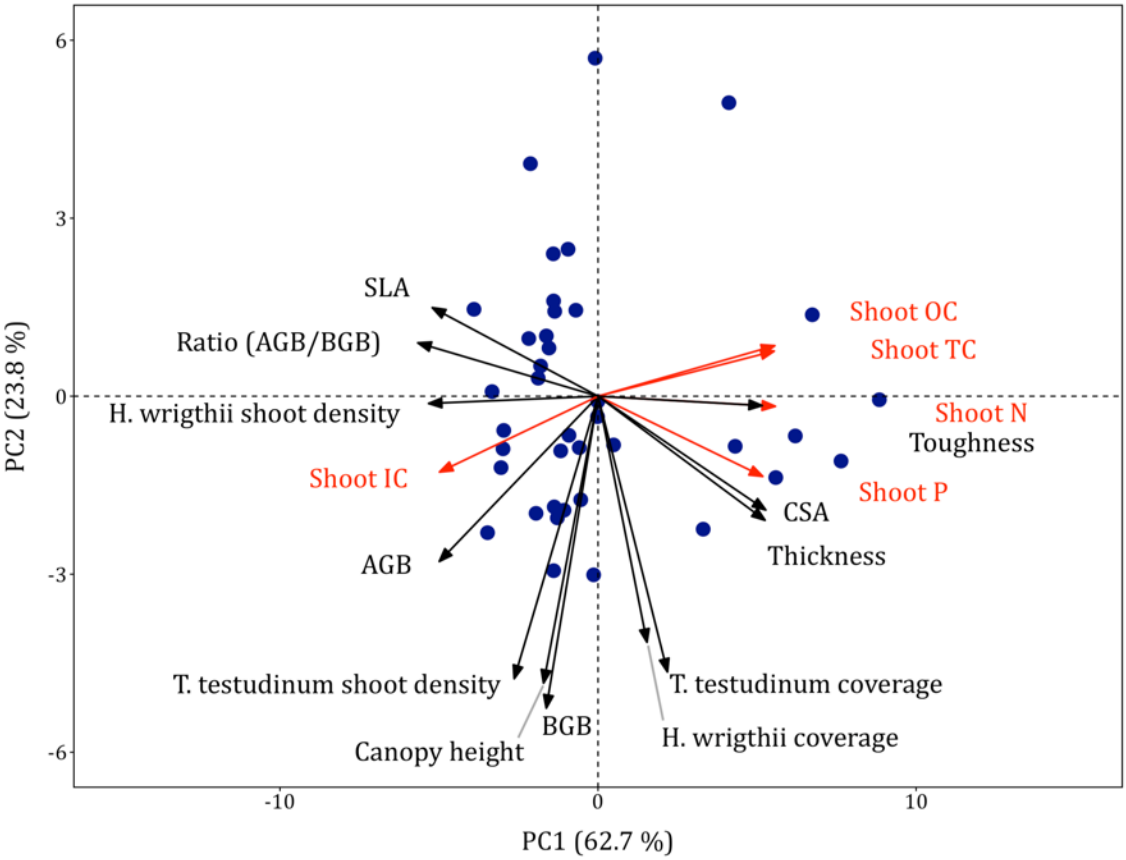

Figure 5.5. Results of principal components (PC) analysis for traits in seagrass meadows (all points) for PC1 and PC2. Loading scores for each trait on all components of PCs are given in appendix Table 5.3. Traits with red arrows are

chemical traits and black arrows are physical traits. Chemical traits are as follows TC represents total carbon, OC and IC are organic and inorganic carbon respectively, N is nitrogen and P is phosphorous. For physical traits, AGB and BGB are above and belowground biomass respectively, CSA is cross-sectional area and SPA represents specific leaf area. All traits were log10 transformed, cantered, and scaled.

The first PC axis explained approximately 62.7% of the variance and was heavily loaded on physical traits such as the ratio for above and below ground biomass, and chemical traits such as total nitrogen and carbon in shoots. The second PC axis described an additional 23.8% of the variance and was more loaded on *Halodule wrightii* and *Thalassia testudinum* coverage, *T. testudinum* canopy height, *Thalassia testudinum* shoot density, BGB and leaf cross sectional area and thickness. The third PC described 4.5% and corresponded to leaf toughness. High correlation was seen between these groups of traits (appendix Table 5.4).

As we found significant differences across almost all of the chemical and physical traits between mangrove forest points 4 and points 5/6, it was decided to complete separate PC analysis on point 4 and points 5/6. Mangrove PC analysis for point 4 and points 5/6 showed that the three chemical traits and nine physical traits (point 4) / seven physical traits (points 5/6) could be summarized by three principal components, which together accounted for 71.4% of the total variance for point 4 (Figure 6 panel (a), appendix Table 5.3) and 61.3% of the total variance for points 5 and 6 (Figure 5.6 panel (b), appendix Table 5.3)

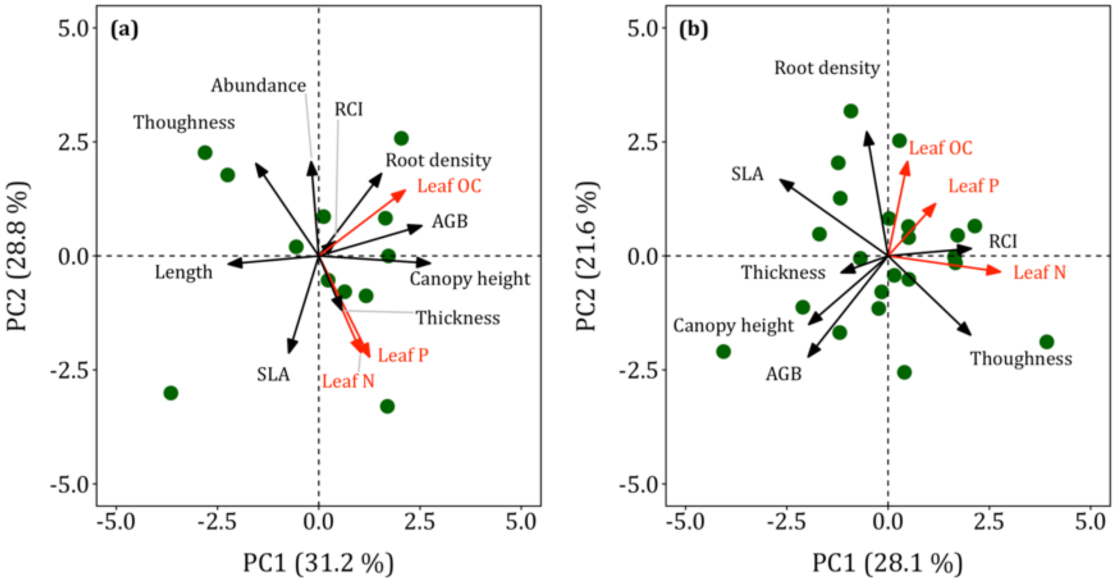

Figure 5.6. Results of principal components (PC) analysis for traits in mangrove forests, panel (a) represents point 4 and panel (b) shows points 5 and 6. Loading scores for each trait on each component of PCs are given in appendix Table 5.3. Red arrows are chemical traits and black arrows are physical traits. Chemical traits are as follows OC represents organic carbon, N is nitrogen and P is phosphorus. For physical traits, AGB is above biomass, SLA is specific leaf area, abundance represents pneumatophore number whilst length denotes pneumatophore length finally RCI represents root complexity index. All traits were log10 transformed, centred and scaled.

The first PC axis for point 4 explained approximately 31.2% of the variance and was loaded on organic carbon of leaves (%), aboveground biomass (m^{2}), canopy height (m) and pneumatophore length (cm). The second PC axis for point 4 described an additional 28.8% of the variance and related to physical traits such as root density (m^{2}), pneumatophore abundance (m^{2}), specific leaf area (cm^{2} g^{-1}) and leaf toughness (g mm ^{2}) in addition to two chemical traits, phosphorus and nitrogen content of leaves (%). The third PC axis explained 11.4% of the variance and was loaded for leaf thickness (mm) and root complexity. High correlation was seen between these groups of traits (appendix Table 5.5). Mangrove points 5 and 6, PC1 explained 28.1% of the variance, mainly related to root complexity, specific leaf area (cm^{2} g^{-1}), leaf toughness (g mm ^{2}) and nitrogen content in leaves (%) and PC2 (points 5 and 6) described 21.6% of the variance and was related to root density (m^{2}) and aboveground biomass (m^{2}). PC3 (points 5 and 6) described 11.7% of the variance and was not significantly loaded towards any traits. High correlation was seen between these groups of traits (appendix Table 5.6).

5.4.5. Nutrients and trait development

For seagrass meadows we used the extracted PC2 axis scores (appendix Table 5.3) as a measure of trait coordination because this was the only PC which showed a significant correlation with sediment nitrogen and phosphorous content. PC2 was associated with *Halodule wrightii* and *Thalassia testudinum* coverage (% m^{2}), *T. testudinum* canopy height (cm), *T. testudinum* shoot density (shoots m^{2}), BGB, leaf cross sectional area (mm^{2}) and thickness (mm). These traits were found to have a significant negative correlation with nitrogen sediment content (Figure 5.7, panel (a)) and phosphorous content (Figure 5.7, panel (b)).

PC2 was negatively correlated with the associated physical traits indicating that higher nitrogen and phosphorus content showed increasing values of these traits. For mangrove forests at point 4, we used the extracted PC axis scores from PC2 for nitrogen sediment content and PC3 for phosphorus sediment content (appendix Table 5.3) as a measure of trait coordination. PC2 was associated with physical traits such as root density (m^{2}), pneumatophore abundance (m^{2}), specific leaf area (cm^{2} g^{-1}), and leaf toughness (g mm ^{2}) in addition to two chemical traits, phosphorous and nitrogen content of leaves (%). PC3 was associated with leaf thickness (mm) and root complexity. We found a significant negative correlation between nitrogen content and PC2 and a positive correlation between PC3 and phosphorus sediment content (%) (Figure 8, panel (a) and (b) respectively). PC1 showed no correlation with sediment nitrogen or phosphorous content (%) (Appendix Table 5.3).

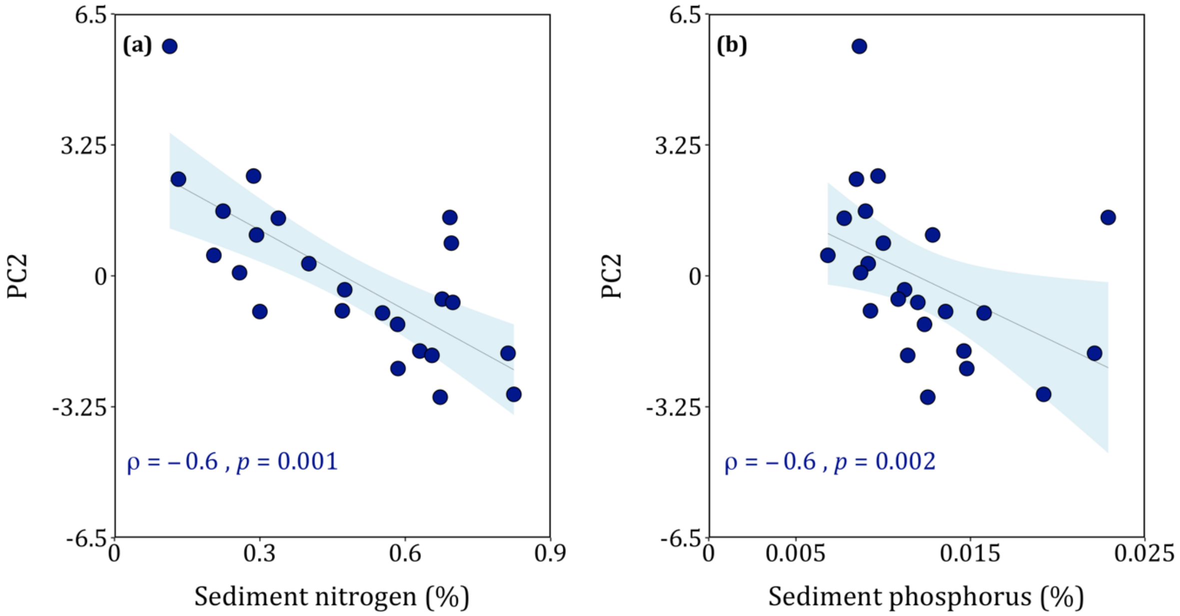

Figure 5.7. Scatter plots visualizing the extracted PC2 (*Halodule wrightii* and *Thalassia testudinum* coverage, *T. testudinum* canopy height, *T. testudinum* shoot density, BGB, leaf cross sectional area and thickness) versus sediment nitrogen or phosphorus content (%). Panel (a) PC2 versus sediment nitrogen content (%), whilst (b) PC2 versus sediment phosphorous content (%). ρ symbolizes Spearman's correlation coefficient, p is the p-value representing the significance level.

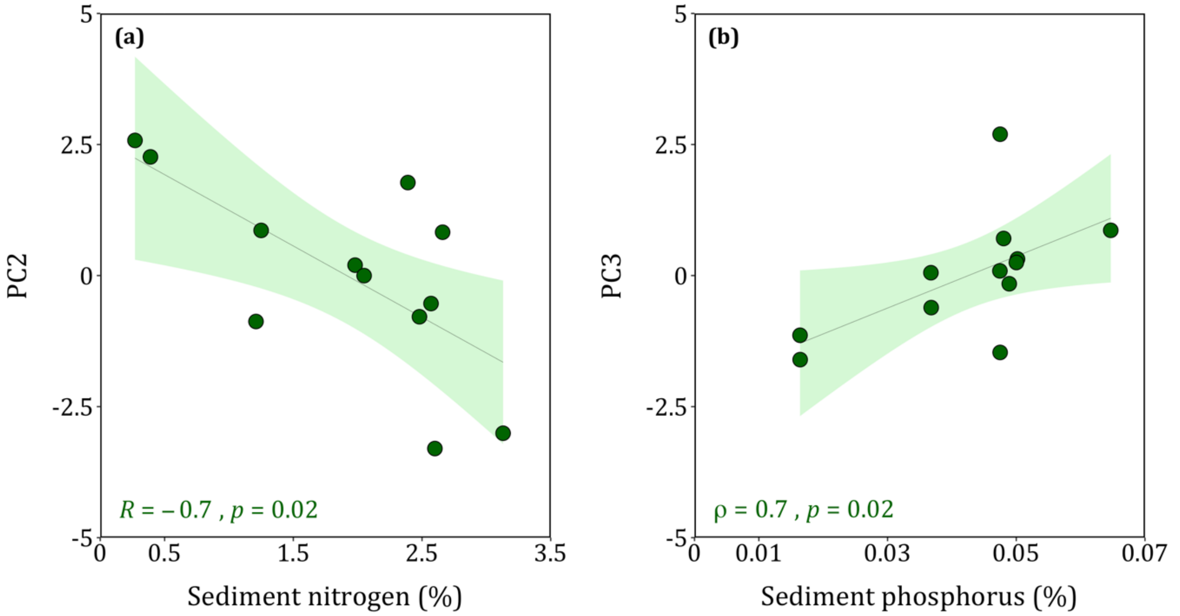

Figure 5.8. Scatter plots visualizing the extracted PC2 component axis (root density, pneumatophore abundance, specific leaf area, leaf toughness, phosphorous, and nitrogen content of leaves) versus sediment nitrogen (%) panel (a) and the the extracted PC3 component axis (leaf thickness and root complexity index) versus sediment phosphorus (%) panel (b). Both panels represent mangrove forest point 4. R represents the Pearson correlation coefficient whilst ρ symbolizes Spearman's correlation coefficient, p is the p-value representing the significance level.

5.4.6. Traits and carbon accumulation

For seagrass meadows, we used the extracted PC2 axis scores, (appendix Table 5.3) as a measure of trait coordination, PC2 was associated with *Halodule wrightii* and *Thalassia testudinum* coverage (% m^2), *T. testudinum* canopy height (cm), *T. testudinum* shoot density (shoots m^2), BGB, leaf cross sectional area (mm^2) and thickness (mm). For these *Halodule wrightii* and *Thalassia testudinum* traits we found a significant negative correlation with sediment organic carbon (Figure 5.9, panel (a)) and a significant positive correlation with sediment inorganic carbon content (Figure 5.9, panel (b)). PC1 and PC3 showed no correlation with sediment organic or inorganic carbon.

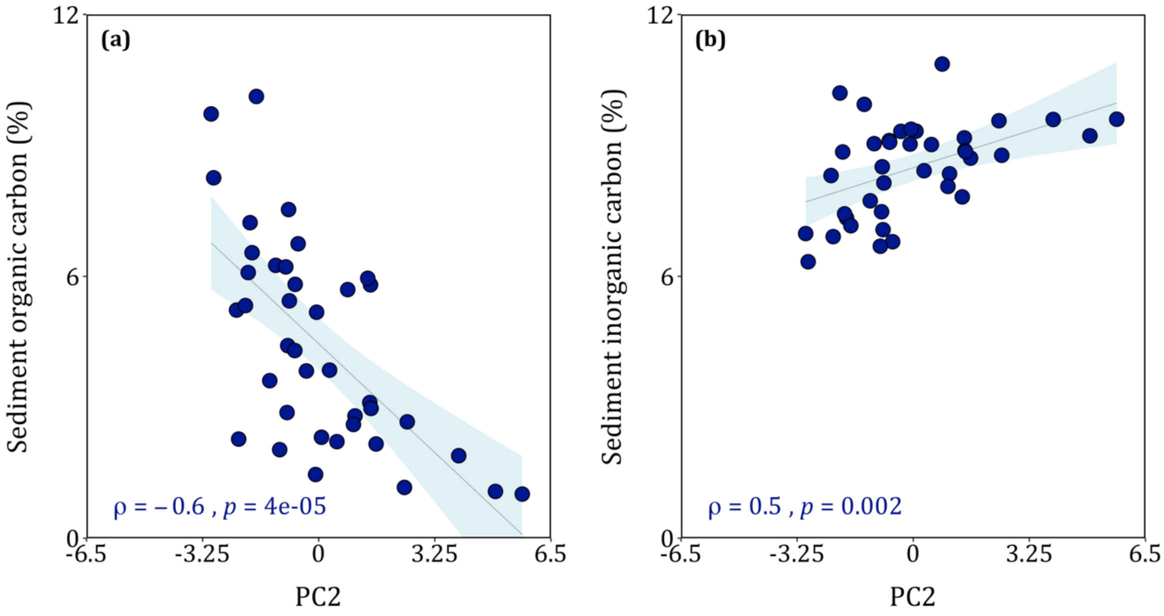

Figure 5.9. Scatter plots visualizing the extracted PC2 (*Halodule wrightii* and *Thalassia testudinum* coverage, *T. testudinum* canopy height, *T. testudinum* shoot density, BGB, leaf cross sectional area and thickness) versus sediment organic carbon content (panel (a)) and inorganic carbon content (panel (b)) (%). ρ symbolizes Spearman's correlation coefficient, p is the p-value representing the significance level.

PC2 was negatively correlated with the associated *Halodule wrightii* and *Thalassia testudinum* traits indicating that higher sediment organic carbon content showed increasing values of these traits. Whilst inorganic carbon content had the opposite relationship.

At mangrove point 4, only sediment organic carbon was correlated significantly to any PC in this case PC3 (Figure 5.10). PC3 was associated with leaf thickness (mm) and root complexity.

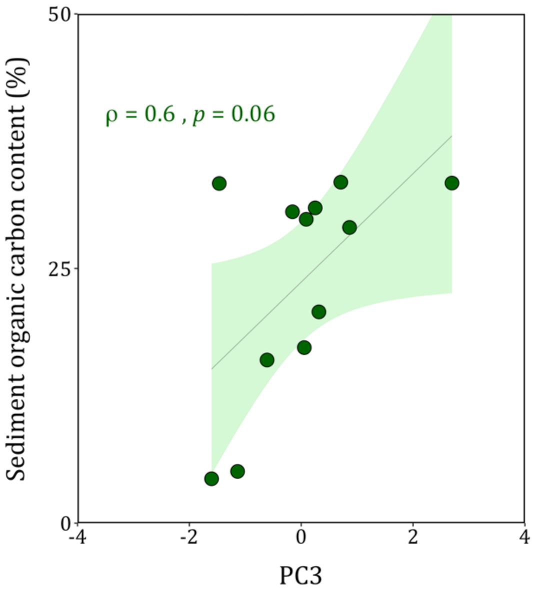

Figure 5.10. Scatter plot visualizing the extracted PC3 versus sediment organic carbon content (%). PC3 was associated with leaf thickness (mm) and root complexity (appendix Table 5.3). ρ symbolizes Spearman's correlation coefficient, p is the p-value representing the significance level.

We found a significant positive correlation with sediment organic carbon content (%) indicating that increasing sediment organic carbon content (%) showed decreasing values of leaf thickness (mm) and root complexity. No correlation was found between any of the PC's, sediment organic and inorganic carbon sediment content, and mangrove forest points 5 and 6.

5.5. Discussion

This study explored the influence of two growth limiting sediment nutrients nitrogen and phosphorous on the structure and development of functional traits in seagrass meadows and mangrove forests. We expected functional traits to respond to nutrient availability. We found that above ground biomass components of seagrass meadows increased with nutrient availability. The same relationship was seen for mangrove root density, pneumatophore abundance and leaf characteristics with nitrogen availability. These relationships supported our hypothesis. However, sediment phosphorous content showed a negative relationship with root complexity and leaf thickness indicating that phosphorous is likely a limiting nutrient. Nutrient-rich sediments were expected to support the development of traits leading to a positive effect on the accumulation of inorganic and organic carbon as mechanistic pathways of long-term storage of blue carbon. The second focus of this project lay on the importance of carbon stocks in tropical marine sediments and the rarely investigated potential of functional plant traits, whose expression may facilitate the input of carbon into these sediments. Seagrass meadow results supported our hypotheses that functional plant traits affect hydrodynamic energy, and thus, change particular matter trapping and facilitate the accumulation of particulate material and litter. An unexpected correlation was seen were increasing root complexity showed decrease organic carbon storage, in divergence with our assumptions.

5.5.1. Trait development responds to nutrient limitation

Our results were in agreement with previous studies that an increase in nutrient sediment content corresponds to an increase in seagrass canopy height (Agawin et al. 1996; Ferdie and Fourqurean 2004; Barry et al. 2017) and shoot density (Agawin et al. 1996; Barry et al. 2007) (Figure 5.11). Seagrass coverage is related to density and canopy height which also showed increasing values with sediment nutrient content (Figure 5.11). Higher sediment nutrients correspond to higher aboveground biomass components, leaf thickness and cross-sectional area could also be considered above ground biomass components. Studies have shown nutrient availability has increased rhizome branching, therefore controlling the density of the seagrass plants, higher quantities of nutrients can equate to a higher density (Agawin et al. 1996). Available sediment nitrogen and phosphorus increases the canopy height i.e. the leaf length. Longer leaves will allow the plants to have more favorable light conditions by extending them (Barry et al. 2017). A decline in shoot density could also occur due to self-thinning which reduces within canopy standing among wider leaves (Ruiz and Romero 2001; Enríquez et al. 2005) although we did not see this relationship. Higher density, canopy height and coverage could also lead to greater capacity to trap senescent leaves with high nitrogen content (Kenworthy et al. 1982) either from within the seagrass meadow or outside sources. Nitrogen and phosphorous limitation have been shown to equate to higher belowground biomass allocation, which increases the absorbing surface (and therefore nutrient acquisition rate) this is generally at the expense of leaf growth or aboveground biomass components (Perez et al. 1991; Agawin et al. 1996). However, the results from this study did not replicate this.

Overall the trait gradient within the mangrove forest showed trees with a high above ground biomass, root complexity and number of prop roots per tree^{-1} fringing the shoreline, and trees with a low root complexity, less prop roots per tree^{-1} in the interior (Figure 5.11).

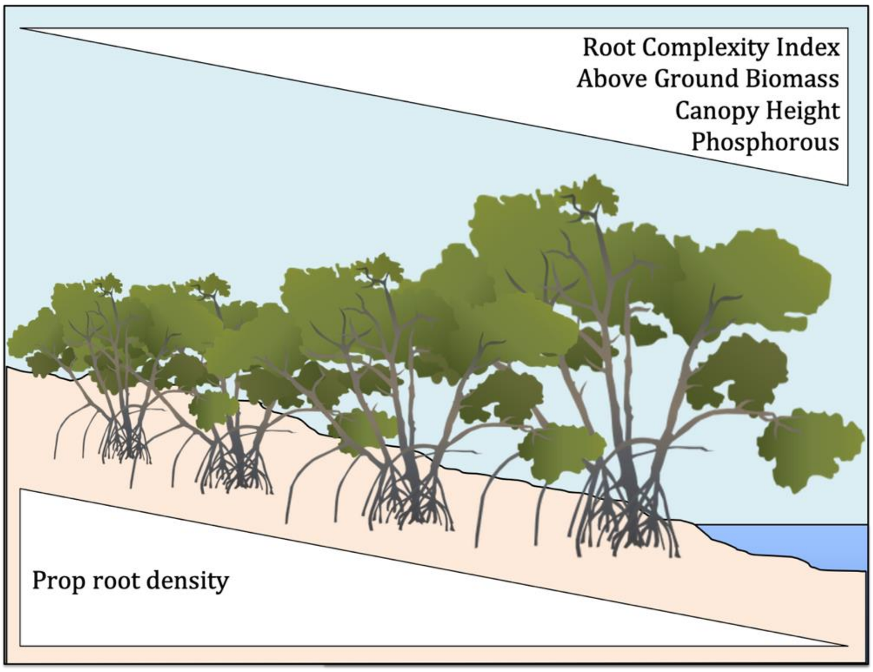

Figure 5.11. Illustration of the mangrove forest at the study site, characterized by a gradient of above ground biomass, tree-height, root density, and root complexity, as well as number of prop roots per tree^{-1} with tall trees and higher phosphorous content. Here we show a high root complexity and number of prop roots per tree^{-1}, but low root density fringing the shoreline, and scrub trees with a low root complexity, less prop roots per tree^{-1}, but a higher root density in the interior. Drawings taken from the Integration and Application Network (www.ian.umces.edu/symbols/).

Mangrove physical traits responded to both sediment phosphorus and nitrogen content; however, all of the correlations were seen at point 4, which was closest to the ocean zone. Hayes et al. (2017) found that nitrogen addition resulting increased above and belowground components in mangroves, this is in agreement with our results as specific leaf area, root density, and pneumatophore abundance all increased with higher sediment nitrogen (Figure 5.12).

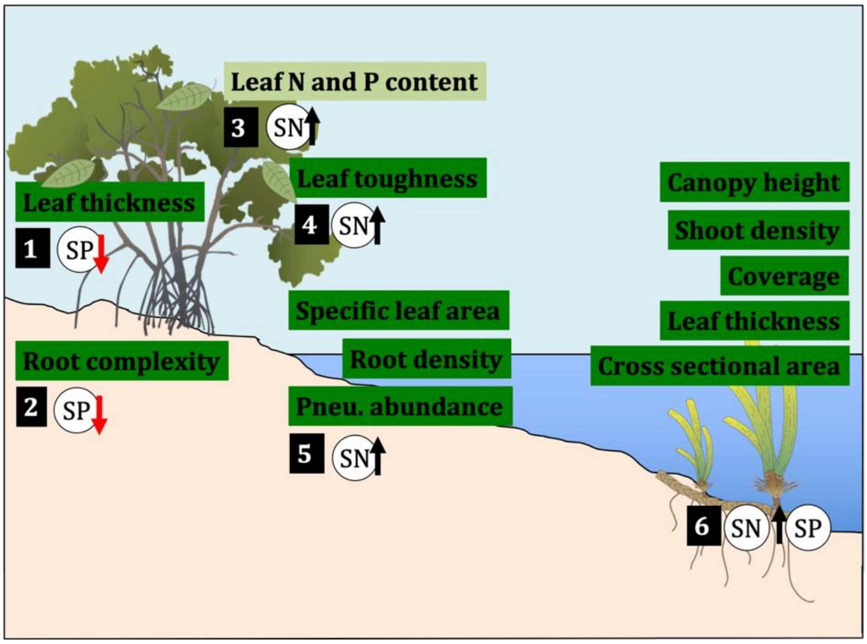

Figure 5.12. Showing connected seascape of mangrove forests (left hand side) and seagrass meadows (right hand side). White circles represent sediment nutrient components, SN is sediment nitrogen and SP is sediment phosphorous (%). Dark green boxes are physical traits (root complexity, pneumatophore length, *H. wrightii* and *T. testudinum* coverage, canopy height, shoot density, leaf thickness and cross-sectional area). The light green box is chemical traits (nitrogen and phosphorus of leaves). 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 sediment phosphorous content equates to the trees using their roots to search for phosphorous 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 above and below ground biomass components 6. Seagrass plant above ground biomass components all increase with higher sediment nutrients as nutrient limitation increases below ground biomass components.

Leaf toughness increased with nitrogen content in the sediment, previous studies have also found that nitrogen-enriched mangrove trees were sclerophyllous (Feller 1996) (Figure 5.12). This may be because these leaves have higher nitrogen content and sclerophylly is an adaptive defence mechanism against herbivory (Feller 1996). Our results showed the phosphorous and nitrogen sediment content (%) in leaves is related to nitrogen concentrations in the sediments. Generally, only a small quantity of nutrients in leaves are thought to end up in the sediment (35 %) due to reabsorption of nutrients from the leaf just before litterfall (Feller et al. 1999, 2003, 2007; Lovelock et al. 2007). Nevertheless, the nutrient content of the leaves especially nitrogen enhanced the nitrogen content in the sediment (Figure 5.11). Smaller quantities of sediment phosphorous content equated to prop root complexity, indicating the trees are using their fine roots to search for phosphorous in the sediment (Figure 5.12). Previous research has shown that root complexity is affected by nutrient availability in early mangrove development stages (Gillis et al. 2019). Other studies have found fertilization of sediments with phosphorous or nitrogen has increased belowground biomass (Lovelock et al. 2006; Hayes et al. 2017), but this is a different dynamic than complexity. Enhanced nutrient addition can enhance aboveground biomass, compared to belowground biomass, due to the development of more shoots and greater leaf area (McKee 1995; Lovelock et al. 2004; Reef et al. 2010). Overall, high root biomass in mangroves, especially the abundance of fine roots biomass (Komiyama et al. 2000) which can be associated with nutrient limitation, is conductive to nutrient capture and uptake from sediments low in nutrients (McKee 2001). Leaf thickness decreased with increasing sediment phosphorous, this is in agreement with Feller 1996. Variation in thickness of the hypodermis in mangrove leaves accounts for most differences in leaf thickness (Tomlinson 1986), a thick hypodermis may protect photosynthetic tissue in the lead when mangroves metabolic rate is limited by phosphorous deficiency (Feller 1996) (Figure 5.12).

5.5.2. Trait effects' blue carbon accumulation

Within the seagrass meadow, a combination of two separate processes might be a reason for physical traits being correlated with sediment organic carbon content. First, the seagrass canopy can attenuate wave energy and flow turbulence. This leads to indirect trapping of particles (Hendriks et al. 2008), higher sedimentation of particles and reduced resuspension and erosion (Agawin and Duarte 2002) (Figure 5.13).

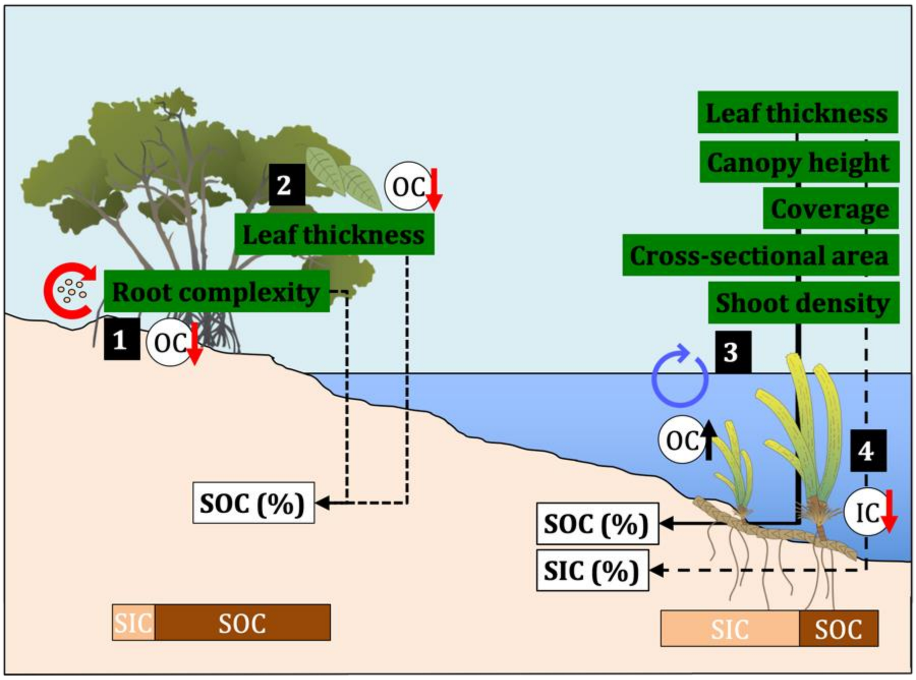

Figure 5.13. Showing connected seascape of mangrove forests (left hand side) and seagrass meadows (right hand side). White boxes represent sediment carbon components, SOC is sediment organic carbon and SIC is sediment inorganic carbon (%). Green boxes are physical traits (Leaf toughness, root complexity, pneumatophore length, *T. testudinum* coverage, canopy height, shoot density). Black arrows and black lines represent positive correlations and black arrows and dotted lines are negative correlations between functional traits (green boxes) and sediment carbon components (white boxes). Numbered mechanisms for strong correlations (from left to right) are explained as follows 1. High complexity of roots increases turbulence which keeps OC in suspension and increases sediment erosion 2. Thinner leaves will degrade faster which has been linked to reduced SOC 3. Canopy height, shoot density, thick leaves (with larger cross-sectional area) and coverage all decrease hydrodynamic energy (blue arrow) to allow for the increase (black arrow) of organic carbon (OC) into the sediment. 4. Canopy height, shoot density, coverage decrease SIC for the increase of organic carbon (OC) into the sediment, decreasing space for SIC accumulation (red arrow). Below the ecosystems (mangrove forests and seagrass meadows) light and dark brown bars represented the percentage of sediment organic and inorganic carbon (SOC and SIC respectively). For the mangrove forest SOC

equates to 85% of the total carbon (22.1 % ±2.03) and SIC is 15 % (3.9 % ±0.7). Whilst for seagrass meadows SOC equates to 35 % (4.5 % ±0.4) and SIC is 35 % (8.4 % ±0.2). Letters are as follows IC is inorganic carbon and OC is organic carbon.

Secondly, a collision of particles with seagrass leaves leads directly to their loss of momentum and therefore to their capture within the seagrass meadow (Ackermann 2002) (Figure 5.13). The findings of this study show a higher shoot density (shoots m^{-2}), coverage (%) and canopy height of *T. testudinum* positively contribute to the SOC (%). A dense seagrass meadow stabilizes the sediment and reduces carbon resuspension (Dahl et al. 2016). Moreover, Ricart et al. (2015) showed landscape configuration influences the exchange 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. Strong water flows and turbulence cause drag forces, which can lead to damage or uprooting of seagrass plants. To tolerate the drag forces, a seagrass plant, which is located in areas with high hydrodynamic forces could have a high breaking force. Breaking force describes the maximum capacity a plant structure has to withstand an extrinsic force. The breaking force is determined by two components: tensile strength and the cross-sectional area (Niklas 1992). Thicker leaf thickness can cause a larger cross-sectional area, but also influences the leafs flexural stiffness. The stiffer a leaf is the more constrained is its ability to bend and reconfigure with water movement. These facts lead to the assumption that a thick leaf with a big cross-sectional area will have a higher impact on the water flow velocity and lead to a higher settling and trapping rate of organic matter, which influences, in the end, the carbon accumulation in the sediment. The slight negative correlation between community traits such as canopy height, coverage and shoot density with SIC (%) could be because, seagrass with greater AGB and BGB components have more effect on the physical dynamics which enhance organic carbon accumulation reducing the space for inorganic carbon (Figure 5.13). However, the interaction of these seagrass physical traits together with the epiphytic organism composition (i.e. higher organic carbon versus carbonate) should be further investigated, as seagrass epiphytic community can contribute to sediment carbon accumulation (Gacia et al. 2003; Mazarrasa et al. 2015).

One hypothesis of this study was that the expression of mangrove trees physical traits such as root complexity index and density have a significant impact decreasing hydrodynamic energy and facilitating the trapping of organic matter, and therefore might lead to a higher accumulation of organic carbon in the sediment. Former studies (Wolanski et al. 1992; Gillis et al. 2015) underlined the ability of aerial roots and stems to influence flow rates, particle settlement, and sediment retention in mangrove forests. The findings in this study did not support this hypothesis since negative correlations were found between the SOC content and certain physical traits. In this particular mangrove forest, potentially the higher complexity index increases hydrodynamic turbulence which keeps sediment in suspension as well as increasing sediment bed erosion around the root structures (Furukawa and Wolanski 1996; Krauss et al. 2003) (Figure 5.13). High mangrove root complexity has been shown to create greater erosion due to higher water turbulence around the root surface (Krauss et al. 2003; Mazda and Wolanski 2009; Samosorn et al. 2018). Such factors could explain the relationship between low sediment carbon and the high complexity of roots this study found. Physical traits such as leaf thickness could be related to the speed of the decomposition process (Gallardo and Merino 1993), where thicker leaves may be slower to degrade (Middleton and McKee 2001). A faster decomposition process of mangrove biomass has been related to reduced organic carbon in the sediment (Hayes et al. 2017). The negative relationship found in this study site between leaf thickness and sediment organic carbon provides further confirmation to this process (Figure 5.13).

5.6. Perspective

The potential of direct and indirect influences of ecosystem engineering functional traits of physical processes which may facilitate the trapping, settling and accumulation of organic are promising mechanisms, which could impact the long-term amount of carbon stored in the sediment. This study showed a first insight into how the expression of connected tropical ecosystem engineering plant traits are linked to the influence the carbon accumulation in the sediment. However, functional trait development can occur over many years, in this study we did not take into account seasonal and yearly fluctuations in precipitation, runoff and subsequent nutrient availability. Differences between the response of traits to nutrients, and the 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. Which we did not measure within the site. Nevertheless, the potential mechanisms that have identified here in turns of the relationship between traits and carbon sediment stocks should be investigated further. Especially with respond to disentangling the influence of climate, water and sediment characteristics.

Functional traits have been described as phenotypically plastic features expressed by plants. The surrounding ecosystem shapes the traits, especially biotic and abiotic stress (i.e. low availability of nutrients, water and oxygen, and extremes in temperature, salinity and pH) (De Deyn et al. 2008). Climate change induced global rising temperature will cause heat stress, Purnama et al. (2018) determined high water temperatures could have an impact on plantś physical and chemical traits. However, stress from temperature could be amplified with other impacts such as eutrophication in the form of agricultural run-off and uncontrolled sewage input in catchment areas and coastal seas (Burkholderc et al. 2007; Lovelock et al. 2009). A change in trait development due to stress can lead consequently to a loss of important ecosystem functions provided by this ecosystem, like carbon sequestration (Fourqurean et al. 2012; Senger et al. 2020). Further research is required to understand how multi-stresses such as eutrophication and rising temperatures may affect functional trait development and what are the predictable consequences for carbon sequestration.

5.7. Acknowledgements

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5.9. Appendix

Appendix table 5.1. Statistical analyses of physical and chemical traits of seagrass meadows across transect points. Coverage of *Thalassia testudinum* and *Halodule wrightii* and leaf thickness of *T. testudinum* were analyzed using Kruskal-Wallis all other analysis was completed using one-way ANOVA. Significant tests are in bold. Tt represents *Thalassia testudinum* and Hw *Halodule wrightii*. TOC represents total organic carbon and TIC is total inorganic carbon.

	Significant	Post-hoc
Physical traits		
Canopy height (m) (n=36)	F=1.8, p>0.05	-
Coverage Tt. (%) (n=36)	χ^2=2.01, p>0.05	-
Coverage Hw. (%) (n=36)	**χ^2=13.7, p<0.05**	P1<P3; P2<P3
Aboveground biomass (gDW) (n=12)	F=0.95, p>0.05	-
Belowground biomass (gDW) (n=12)	F=0.2, p>0.05	-
Shoot density Tt. (shoots m^{-2}) (n=12)	F=2.4, p>0.05	-
Shoot density Hw. (shoots m^{-2}) (n=12)	**F=7.8, p<0.05**	P2<P3*
Specific leaf area Tt. (cm^2 DWg^{-1}) (n=24)	F=0.2, p>0.05	-
Cross-sectional area (mm^2) (n=24)	F=2.7, p>0.05	-
Thickness (cm) (n=24)	χ^2=2.8, p>0.05	-
Leaves per shoot (n=24)	F=0.02, p>0.05	-
Toughness (n=117)	F=0.02, p>0.05	-
Chemical traits		
TOC leaves (%) (n=117)	**F=4.6, p<0.05**	P1>P2*
TIC leaves (%) (n=117)	**F=10.2, p<0.05**	P1<P2; P2<3

* Tukey's, where significance was evaluated as p<0.05.

Appendix table 5.2. Statistical analyses of physical and chemical traits of mangrove forests across transect points. Root complexity index was defined as numbers of columns per root's distance to the trunk. It was calculated the following: [root c.i.= (number of columns x distance to trunk) x pr.r. tree [1]]. A higher value indicates a higher complexity of the root system and therefore provides a potentially better mechanism for the trapping of organic material. Canopy height, root complexity index, prop root density, aboveground biomass and mangrove leaf TOC content were analysed using Kruskal-Wallis and all other analysis was completed using one-way ANOVA. TOC represents total organic carbon and TIC is total inorganic carbon. Significant tests are in bold.

	Significant	Post-hoc
Physical traits		
Canopy height (m) (n=34)	**χ^2=23.8, p<0.05**	P4>P5$^+$ P4>P6$^+$
Coverage Tt. (%) (n=34)	**F=19.1, p<0.05**	P4<P5* P4<P6*
Pneumatophores length (cm) (n=12)	-	-
Pneumatophores density (pneu. m^{-2}) (n=12)	-	-
Aboveground biomass (m^2) (n=12)	**χ^2=19.0, p<0.05**	P4>P5$^+$ P4>P6$^+$
Belowground biomass (m^2) (n=12)	-	-

Specific leaf area Tt. (cm^2 DWg^{-1}) (n=680)	**F=23.3, p<0.05**	P4>P5* P4>P6*
Thickness (cm) (n=680)	**F=8.6, p<0.05**	P4<P5* P4<P6*
Roots complexity index (n=34)	**χ^2=23.3, p<0.05**	P4>P5$^+$ P4>P6$^+$
Prop roots tree^{-1} (n=34)	**χ^2=23.4, p<0.05**	P4>P5$^+$ P4>P6$^+$
Toughness (n=117)	F=4.02, p<0.05	P4<P6*
Chemical traits		
TOC leaves (%) (n=680)	**χ^2=18.6, p<0.05**	P4<P5$^+$ P4<P6$^+$
TIC leaves (%) (n=680)	-	-

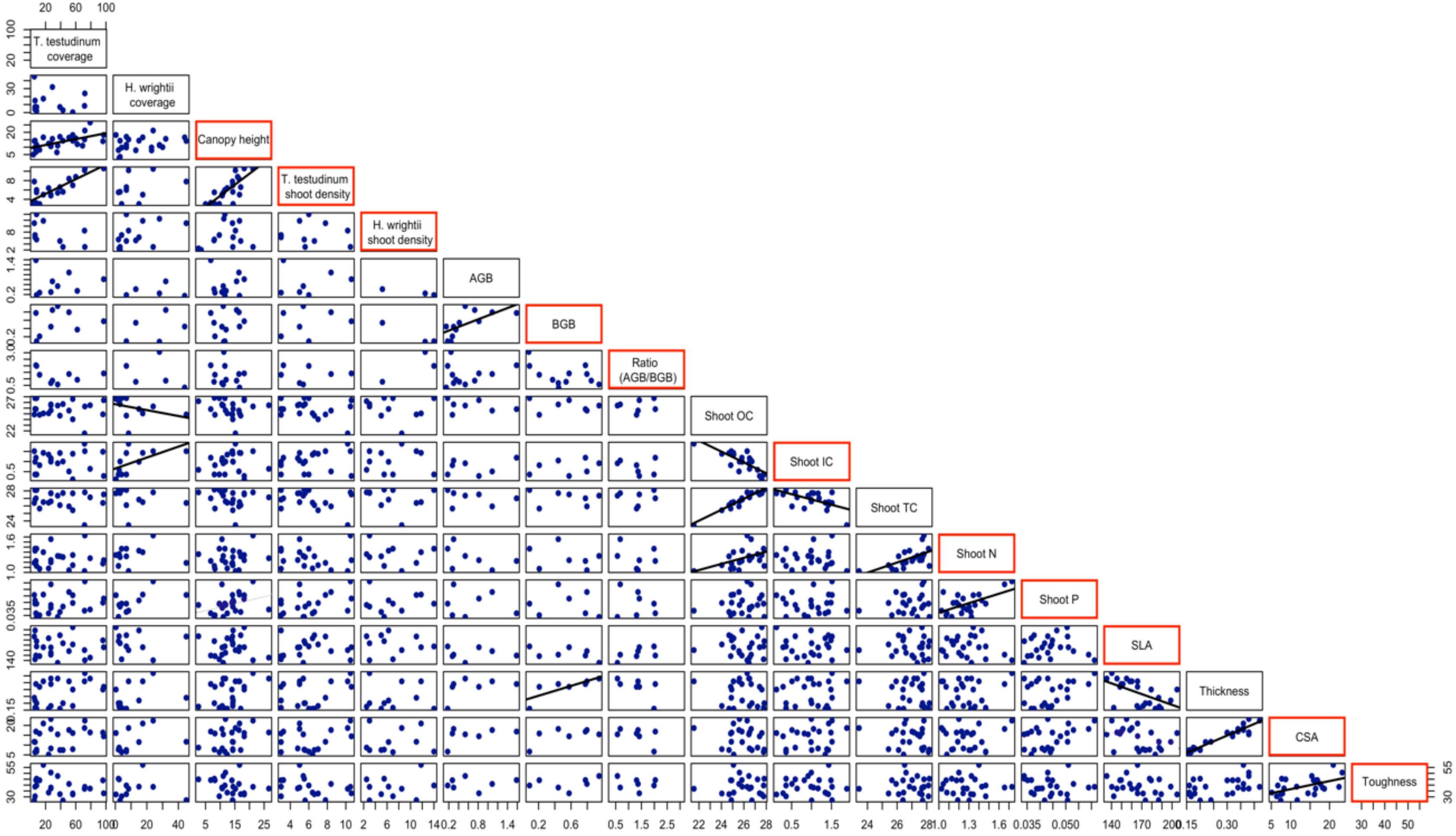
* Tukey's, where significance was evaluated as p<0.05.
$^+$ Dunn's post-hoc, p<0.05.

Appendix table 5.3. Results of the principle components analysis (PC) 1, 2 and 3 for trait loading in the seagrass meadow and mangrove forest.

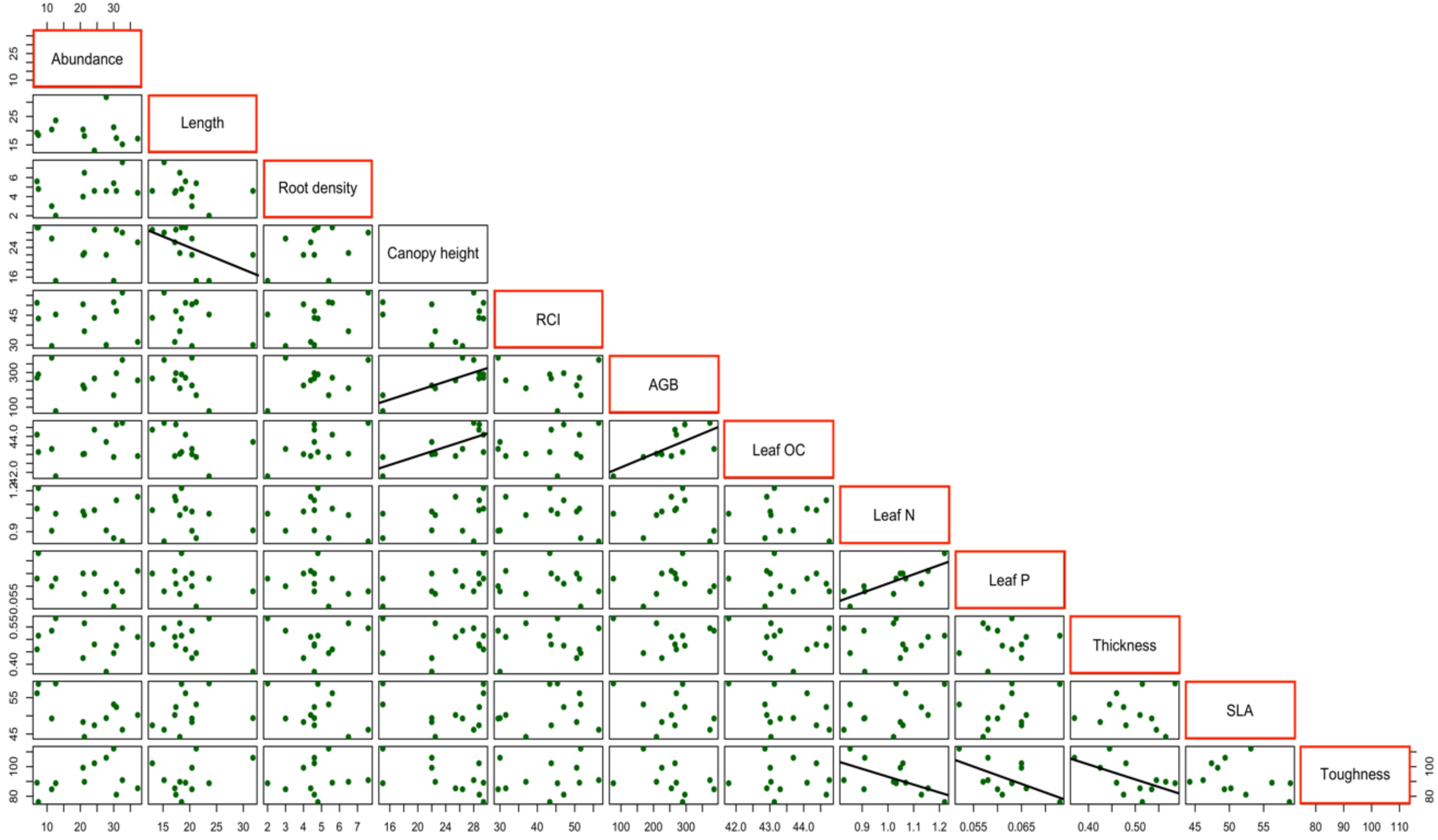
Ecosystem/Trait	PC1	PC2	PC3
Seagrass Meadow			
Eigenvalues	10.7	4.2	0.8
Variance Explained	62.7%	23.8%	4.5%
Thalassia testudinum coverage (% m^2)	0.12	-0.40	0.39
Halodule wrightii coverage (% m^2)	0.08	-0.36	-0.60
Thalassia testudinum Canopy height (cm)	-0.09	-0.41	0.36
Thalassia testudinum shoot density (shoots m^{-2})	-0.14	-0.41	0.16
Halodule wrightii shoot density ((shoots m^{-2})	-0.28	-0.01	-0.11
Aboveground biomass (AGB; m^2)	-0.26	-0.24	-0.04
Belowground biomass (BGB; m^2)	-0.09	-0.45	-0.08
AGB/BGB ratio	-0.30	0.08	0.02
Organic carbon of shoots (OC; %)	0.29	0.07	0.14
Inorganic carbon of shoots (IC; %)	-0.26	-0.11	-0.39
Total carbon of shoots (TC; %)	0.29	0.07	0.10
Nitrogen of shoots (%)	0.29	-0.01	0.02
Phosphorus of shoots (P; %)	0.27	-0.12	0.05
Specific leaf area (cm^2 g^{-1})	-0.28	0.13	0.17
Leaf thickness (cm)	0.28	-0.18	-0.08
Leaf cross sectional area (mm^2)	0.28	-0.16	-0.10
Leaf toughness (g mm ^{2})	0.27	-0.01	-0.29
Mangrove (point 4)			
Eigenvalues	3.7	3.5	1.4
Variance Explained	31.2%	28.8%	11.4%
Pneumatophores abundance (m^2)	-0.03	0.38	-0.01
Pneumatophores length (cm)	-0.39	-0.03	0.41
Root density (m^2)	0.27	0.33	-0.08

Canopy height (m)	0.49	-0.03	0.25
Root complexity index	0.07	0.06	-0.61
Aboveground biomass (AGB; m^2)	0.45	0.12	0.13
Organic carbon of leaves (OC; %)	0.38	0.26	0.10
Nitrogen of leaves (N; %)	0.18	-0.39	0.14
Phosphorus of leaves (P; %)	0.22	-0.41	0.17
Leaf thickness (mm)	0.10	-0.22	-0.55
Specific leaf area (cm^2 g^{-1})	-0.13	-0.39	-0.07
Leaf toughness (g mm ^{2})	-0.27	0.37	0.04
Mangrove (point 5 and 6)			
Eigenvalues	2.8	2.2	1.2
Variance Explained	28.1%	21.6%	11.7%
Root density (m^2)	-0.09	0.53	-0.12
Canopy height (m)	-0.34	-0.29	0.36
Root complexity index	0.35	0.03	0.25
Aboveground biomass (AGB; m^2)	-0.34	-0.43	-0.14
Organic carbon of leaves (OC; %)	0.08	0.40	-0.49
Nitrogen of leaves (N; %)	0.47	-0.07	0.20
Phosphorous of leaves (P; %)	0.20	0.22	0.39
Leaf thickness (mm)	-0.20	-0.07	-0.34
Specific leaf area (cm^2 g^{-1})	-0.46	0.33	0.15
Leaf toughness (g mm ^{2})	0.35	-0.34	-0.45

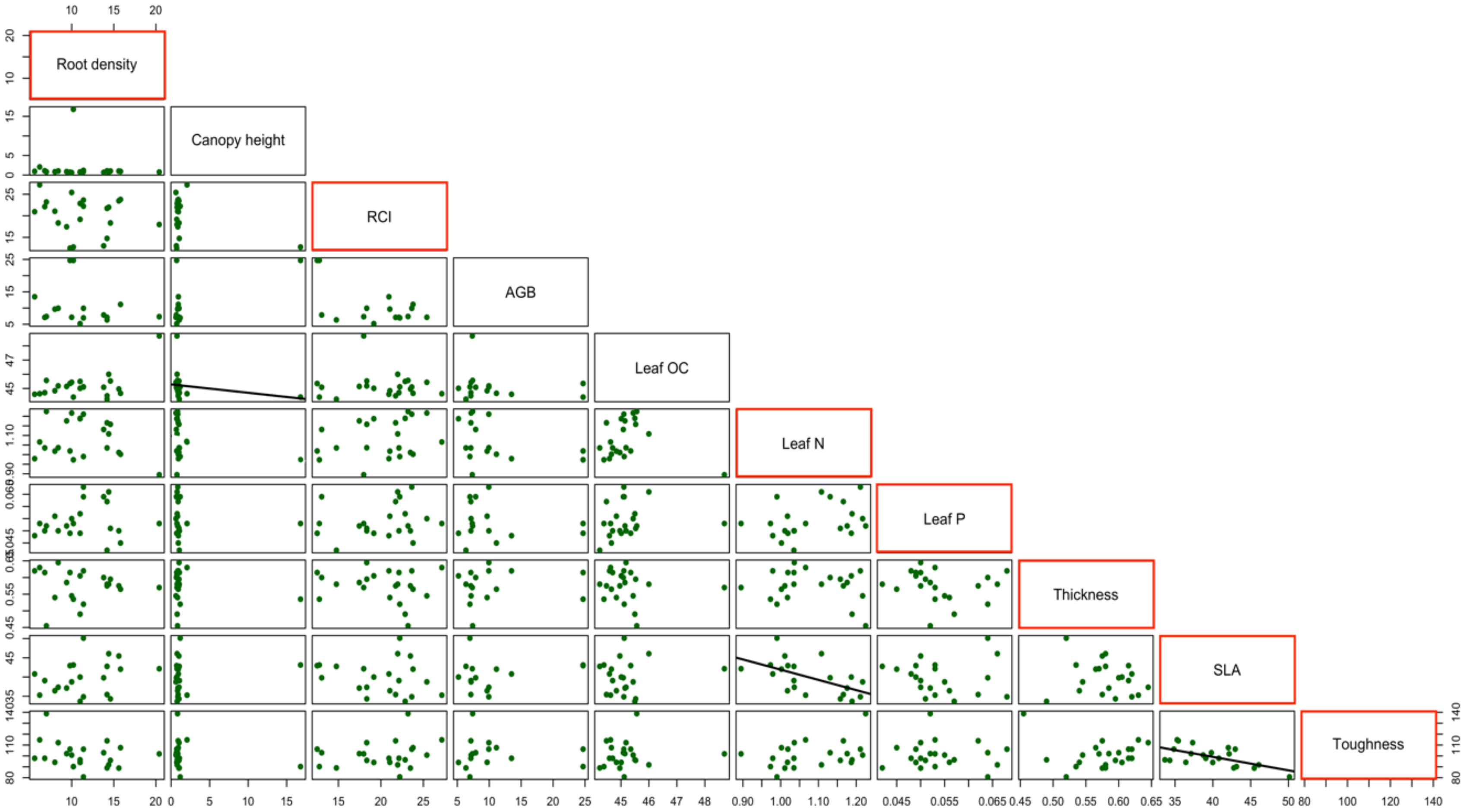
Appendix table 5.4. Variation of the degree of association between the seagrass meadow trait pairs. Significant linear trends are illustrated by a black plain line (correlation coefficient is equal to 0.5 and above). Chemical traits are as follows TC represents total carbon, OC and IC are organic and inorganic carbon respectively, N is nitrogen and P is phosphorous. For physical traits, AGB and BGB are above and belowground biomass respectively, CSA is cross-sectional area and SPA represents specific leaf area. Red boxes represent normal distribution.



Appendix table 5.5. Variation of the degree of association between the mangrove trait pairs (point 4). Significant linear trends are illustrated by a black plain line (correlation coefficient is equal to 0.5 and above). Chemical traits are as follows OC represents organic carbon, N is nitrogen and P is phosphorous. For physical traits, AGB is above and belowground biomass, SLA is specific leaf area, abundance represents pneumatophore number whilst length denotes pneumatophore length finally RCI represents root complexity index. Red boxes represent normal distribution.



Appendix table 5.6. Variation of the degree of association between the mangrove trait pairs (point 5 and 6). Significant linear trends are illustrated by a black plain line (correlation coefficient is equal to 0.5 and above). Chemical traits are as follows OC represents organic carbon, N is nitrogen and P is phosphorous. For physical traits, AGB is above and belowground biomass, SLA is specific leaf area, finally RCI represents root complexity index. Red boxes represent normal distribution.



Chapter 6 Impacts of wetland dieback on carbon dynamics: A comparison between intact and degraded mangroves

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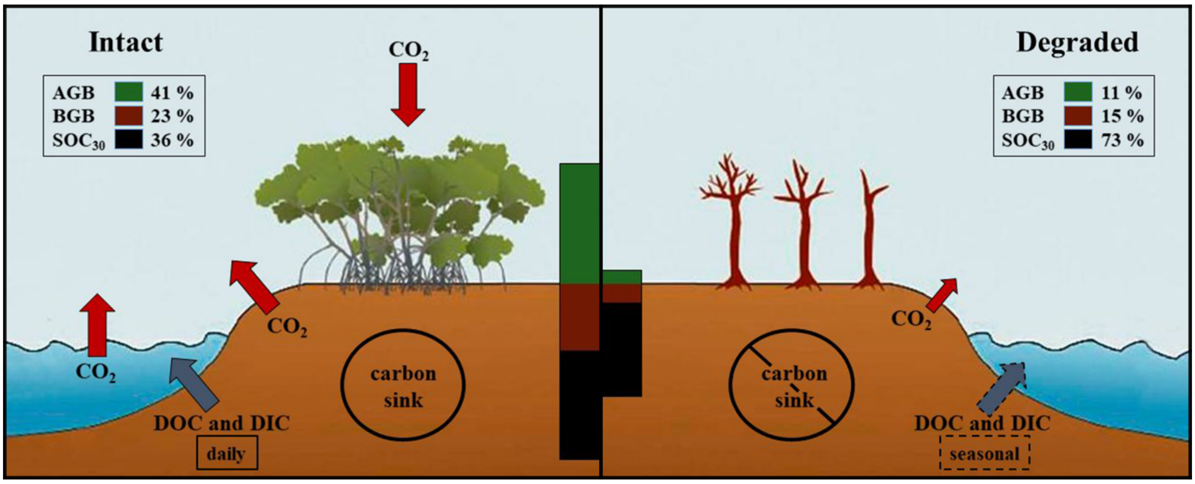
6.1. Abstract

Mangroves are effective blue carbon sinks and are the most carbon rich ecosystems on earth. However, their areal extent has declined by over one-third in recent decades. Degraded mangrove forests result in reduced carbon captured and lead to release of stored carbon into the atmosphere by CO_2 emission. The aim of this study was to assess changes in carbon dynamics in a gradually degrading mangrove forest on Bonaire, Dutch Caribbean. Remote sensing techniques were applied to estimate the distribution of intact and degraded mangroves. Forest structure, sediment carbon storage, sediment CO_2 effluxes and dissolved organic and inorganic carbon in pore and surface waters across intact and degraded parts were assessed. On average intact mangroves showed 31% sediment organic carbon in the upper 30 cm compared to 20% in degraded mangrove areas. A loss of 1.51 $MgCO_2\ ha^{-1}yr^{-1}$ for degraded sites was calculated. Water samples showed a hypersaline environment in the degraded mangrove area averaging 93 which may have caused mangrove dieback. Sediment CO_2 efflux within degraded sites was lower than values from other studies where degradation was caused by clearing or cutting, giving new insights into carbon dynamics in slowly degrading mangrove systems. Results of water samples agreed with previous studies where inorganic carbon outwelled from mangroves might enhance ecosystem connectivity by potentially buffering ocean acidification locally. Wetlands will be impacted by a variety of stressors resulting from a changing climate. Results from this study could inform scientists and stakeholders on how combined stresses, such as climate change with salinity intrusion may impact mangrove´s blue carbon sink potential and highlight the need of future comparative studies of intact versus degraded mangrove stands.

Keywords: Blue carbon; carbon stocks; greenhouse gases; dissolved organic and inorganic carbon; Bonaire; remote sensing.



6.2. Introduction

Saltwater coastal wetlands are generally found in sheltered waters and include mangrove forests, seagrass meadows and tidal salt marshes. These wetlands host highly productive plant communities, which take up substantial amounts of carbon via photosynthesis (Mcleod et al. 2011). The carbon stored in these coastal ecosystems has been coined “blue carbon” (Laffoley and Grimsditch 2009) and mangroves, being a blue carbon sink, are among the most carbon-rich ecosystems on earth (Mcleod 2011). It has been estimated that mangrove forests sequester and store carbon at rate 50 times higher than tropical rainforests (Laffoley and Grimsditch 2009). They not only photosynthesize to acquire carbon from the atmosphere but are also very efficient in trapping suspended matter and associated organic carbon during tidal inundation due to their complex root systems (Furukawa et al., 1996). Carbon can be stored within the aboveground living biomass (leaves, branches, trunks), the belowground living biomass (roots) and the non-living biomass (litter and dead wood) over the short term (decennial) (Howard et al. 2014) or can be stored for longer time scales within the sediments (Brevik et al. 2004). Compared to terrestrial ecosystems, mangrove sediments are saturated with water keeping them in an anaerobic state and thus preventing aerobic microbial carbon oxidation and carbon release into the atmosphere through respiration. Carbon located within mangrove sediment represents the majority of the ecosystem carbon stock within mangrove forests (Donato et al. 2011; Adame et al. 2013) but significant amounts of the captured carbon are exported as organic and inorganic carbon to the coastal zone (Odum 1968; Lee 1995). The coastal zone reflects another important carbon sink. The tidally induced export of dissolved inorganic carbon (DIC) may account for more than 50% of the total net primary production in mangroves (Maher et al. 2013; Sippo et al. 2016; Ray et al. 2018). Due to their high carbon sink potential they can effectively contribute to climate change mitigation strategies on a national scale for tropical and subtropical countries with extensive coastlines (Murdiyarso et al. 2015).

However, total area of mangrove forests has been reduced by over one-third globally over the last decades, mostly due to forest and land conversion for agriculture, aquaculture or urbanization (Valiela et al. 2001). The Caribbean region has the second highest mangrove area loss relative to other global regions, with approximately 24% of mangrove area lost between 1980 and 2005 (FAO 2007). Despite conservation measures, this decline continues today, and the global annual mangrove deforestation trend is estimated to be between 0.2% and 0.4% from 2000 to 2012 (Hamilton and Casey 2016). The loss of mangroves leads to the acceleration of remineralization and erosion processes of organic carbon in mangrove sediments, resulting in the emission of significant amounts of greenhouse gases (GHG) into the atmosphere (CO_2 and CH_4) and turning mangrove ecosystems from a carbon sink into a carbon source (Gillis et al. 2017; Grellier et al. 2017).

Several environmental factors have been shown to influence the emissions of GHGs to the atmosphere from disturbed and undisturbed mangrove sediments, such as sediment water content, the percentage of fine-grained sediment, surface sediment chlorophyll and light condition (Quyang et al. 2017). Seasonal changes in temperature are also an important parameter involved in the variability of GHG emissions, affecting the rates of sediment organic matter decay, and thus GHG production and emissions (Davidson and Jannsen 2006). In addition, the development of biofilm at the sediment surface has been shown to be another major driving factor of GHG emissions from mangroves sediments (Leopold et al. 2015; Jacotot et al. 2019).

Quantifying carbon emissions from mangroves degradation and understanding the factors influencing carbon storage and exchange has become increasingly important due to the rapid rise in atmospheric CO_2 concentrations and associated impact on global climate (IPCC 2014). Globally mangroves account for only 0.7% of tropical forest area, but their destruction currently adds an extra 10% to global CO_2 release from tropical deforestation (Alongi et al. 2015). To reduce this impact, economic mechanisms are emerging to incentivize the conservation of forests at local and national scales especially in developing countries. Policies like the Reducing Emissions from Deforestation and Degradation (REDD+) calculate net carbon savings by 'avoided deforestation'. To apply these strategies, it is important to quantify the total blue carbon stocks, CO_2 emissions and carbon outwelling potential within intact and degraded mangroves. To do this, studies have assessed changes in carbon dynamics after mangroves have been cut or cleared (Lovelock et al. 2011; Bulmer et al. 2015; Grellier et al. 2017) but none have investigated carbon dynamics in a gradually degrading environment. Gradual degradation of mangroves is likely to occur more often in the future as these ecosystems will be impacted by a variety of stressors resulting from a changing climate. A changed climate will alter hydrology and salinity intrusion, and functionality may be impaired by increased temperatures, drought or flooding events (Junk et al. 2013). Additionally, data on the size and variation of mangrove carbon stocks remains scarce in many areas (Atwood et al., 2017) and in the Caribbean only a few studies have quantified the total ecosystem stocks of mangroves (Adame et al. 2013; Kauffman et al. 2014; Bhomia et al. 2016).

In order to understand carbon dynamics in a gradually degrading mangrove environment carbon stocks, CO_2 emissions and carbon outwelling within the mangroves of Bonaire were assessed. The mangroves of Bonaire are of special interest as land use changes within the surrounding areas have led to overall environmental changes over the last decades. Currently the mangroves have high sediment runoff from the hinterland, where no terrestrial forest or undergrowth occurs due to overgrazing by feral cattle. This has caused reduced water circulation and hyper-salinity in the northern mangrove areas, leading to a dieback of mangrove trees and overall ecosystem degradation (Kats et al. 2007; Debrot et al. 2012). Between 1961 and 1996 mangrove losses of 82 ha were reported, most of which occurred in the northernmost part of the mangrove area (Erdmann and Scheffers 2006). In the same period mangrove growth was observed in the direction of the lagoon and an area of 81 ha was added to the mangrove forest (Erdmann and Scheffers 2006). The presence of intact and degraded mangrove sites within the same forest makes Bonaire an ideal place to compare changes in carbon dynamics. This study compared and mapped how the degradation of the mangroves affects the carbon stocks, CO_2 emissions, dissolved carbon outwelling and forest structure inside the forest. The research hypothesis of this study is that gradual degradation of mangroves will equate to reduced trapping of organic material, which will influence the carbon dynamics, such as increased loss of CO_2 to the atmosphere and reduced export of DOC and DIC to adjacent coastal waters.

6.3. Material and methods

6.3.1. Area of study

Bonaire (part of the Dutch Caribbean) is a small island located in the Caribbean Sea 87 km north of Venezuela (Figure 6A). Bonaire has an arid to semi-arid climate (DeFreitas et al. 2005). This study was completed from January to March 2019, rainfall was approximately 12.2 mm, and the average temperature was 26.7 °C (Maximum temperature 30.6 °C and minimum temperature 24.5 °C) (Meteorological Department Curaçao 2019). This research was conducted in Lac Bay (Figure 6B) located on Bonaire's southeast coast. Lac Bay has an area of approximately 700 ha including a coral reef, a small lagoon and a mangrove forest. The forest is tide-dominated and includes three mangrove species; *Rhizopora mangle*, *Avicennia germinans* and *Laguncularia racemosa*. While *A. germinans* grows in mixture with *L. racemosa* in high saline and muddy sediments (DeFreitas et al. 2005; Davaasuren et al. 2012) in the northern area of the forest, *R. mangle* grows towards the lagoon.

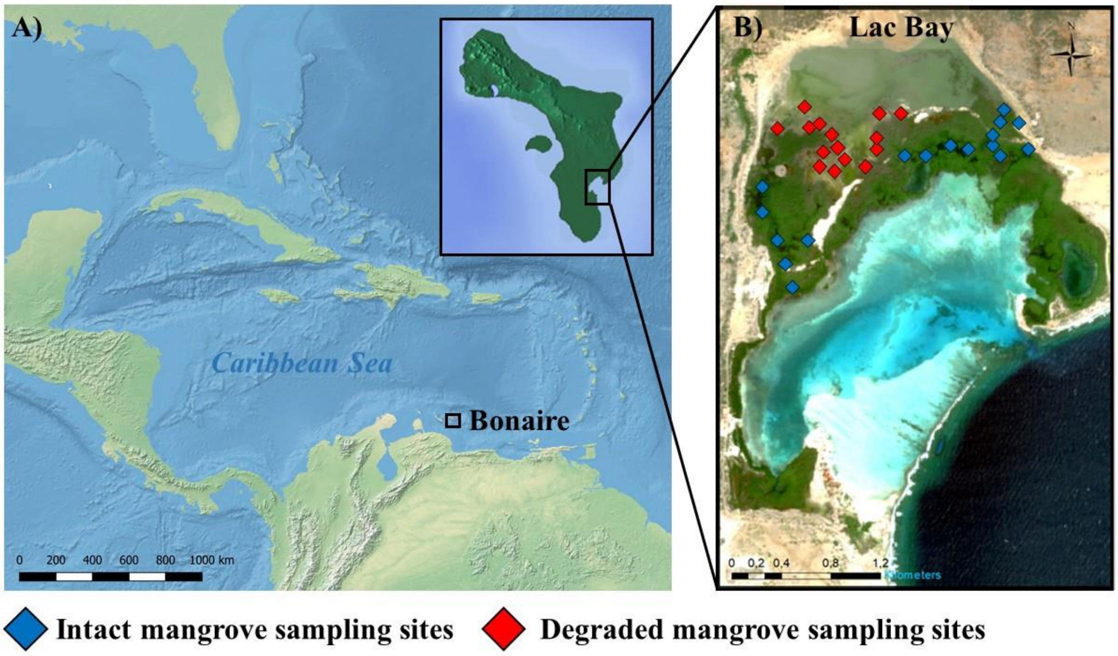


Figure 6.1. A) Location of the island Bonaire in the Caribbean Sea and B) The lagoon Lac Bay located at 12.11734/-68.23997 (Latitude/Longitude). Lac Bay is represented by a Sentinel-2 imagery where the intact and degraded sampling sites were added.

Measurements of forest structure, sediment carbon, surface and pore water samples and sediment CO_2 efflux at 17 intact mangrove plots and at 15 degraded mangrove plots were taken from January to March 2019 during dry season. 10 m x 10 m plots were set up along the channels. Sediment cores and sediment CO_2 efflux measurements were taken during low tide while water samples were taken within one hour after low tide.

6.3.2. Estimating intact and degraded mangrove distribution

In this study two satellite images from the Sentinel-2 program (https://scihub.copernicus.eu) which date from 30.10.2018 (wet season) and 08.01.2019 (dry season) were used. Using two images from different seasons provides increased feature space for classification and a better average reflectance value which is valid throughout the year. The images were already atmospherically corrected and had no cloud cover. Optical sensors can record reflectance of natural features in different wavelengths, which were used to distinguish between intact and degraded mangroves and to identify areas of deep and shallow waters and sandy sediment. To distinguish between the different land cover classes the non-parametric machine-learning method *Random Forest* for a supervised classification (Breiman 2001) was applied, which combines independent decision trees into an ensemble learning algorithm. Only spectral bands with a spatial resolution of 10 and 20 meter were used to describe differences in reflection from the surface inside the mangrove area (In total 9 spectral bands). Twenty-meter spectral bands were down-sampled to 10-meter resolutions making four 10 m x 10 m pixel out of one 20 m x 20 m pixel. Information retrieved from processing the satellite images was combined with ground-truth data which served as reference points for the machine-learning method. Intact mangrove sites were defined as intact if they contained >60% intact trees of the total tree number.

6.3.3. Forest structure

A 10 m by 10 m plot was established and within each plot tree species were identified and the diameter at breast height (DBH) (cm) of each tree inside the plot was noted. Except for the DBH of *R. mangle* species, where measurements were taken at the height of the highest prop root. All dead trees were recorded within the plot and classified according to Howard et al. (2014) into decay status 1, 2 and 3.

To calculate the above ground biomass (AGB) (kg) of each tree the allometric equations from the closest location (French Guiana) to our sampling site (Fromard et al. 1998) was used:

Avicennia germinans: $AGB = 0.14 \text{ x } DBH^{2.4}$ $(r^2 + 0.97)$ (1)

Laguncularia racemosa: $AGB = 0.1023 \text{ x } DBH^{2.5}$ $(r^2 + 0.97)$ (2)

Rhizophora mangle: $AGB = 0.1282 \text{ x } DBH^{2.6}$ $(r^2 + 0.92)$ (3)

No site-specific equations were applied, however, due to the lack of individual allometric equations, this approach (i.e. using closest regional equations) is common practice in mangrove ecology (Adame et al. 2013; Kauffman et al. 2014; Bhomia et al. 2016). Aboveground biomass for the degraded trees was also calculated according to Fromard et al. (1998) and then modified according to Howard et al. (2014). For example, for decay status 1 leaves were subtracted from the biomass estimate by subtracting a constant of 2.5% of the live tree biomass estimate. Trees with decay status 2 had lost some branches in addition to leaves, therefore both leaf biomass and an estimate of branch loss were considered. In total 20% of the biomass was subtracted. Decay status 3 trees have often lost a significant portion of their volume due to advanced breakage. Therefore, the remaining tree´s volume was calculated using an equation for a frustum (truncated cone). To do this the diameter at the base of the tree (d_{base}) (cm) and the tree height (ht) (cm) were additionally recorded in the field to estimate the top diameter (d_{top}) using a taper equation.

$$d_{top} = d_{base} - [ht * ((d_{base} - DBH)/130)] \tag{4}$$

The constant 130 represents the height (cm) at which the DBH was measured. Then the volume (V) of the dead tree was determined by representing the tree as a truncated cone:

$$V(cm^3) = (\pi * (ht)/12) * (d^2_{base} + d^2_{top} + (d_{base} * d_{top})) \tag{5}$$

Dead tree biomass (kg) was determined by multiplying the frustrum volume (cm^3) by its wood density (kg cm^{-3}). Wood densities of 900, 762 and 1000 were used for *Avicennia germinans, Laguncularia racemosa* and *Rhizophora mangle* respectively based on findings of Guerra-Santos et al. (2013).

Belowground biomass (BGB) (kg) was calculated following Komiyama et al. (2008):

$$BGB = 0.199 * ((wood\ density\ (g\ cm^{-3})^{0.899}) * (DBH\ (cm))^{2.22} \tag{6}$$

6.3.4. Sediment carbon sampling

Sediment cores were retrieved at low tide using an open-face stainless steel tube corer. Within each 10 m x 10 m sampling plot three sediment cores were taken. Core samples were obtained to a depth of 30 cm and each core was divided into depth intervals of 0-5 cm, 5-10 cm and 10-30 cm. A 2 cm subsample was cut out of the middle of each layer, stored in a labelled plastic bag and dried at 40 °C until they reached dry weight. The samples were transported to the analytical laboratory at Leibniz Center for Marine Tropical Research (ZMT) for further processing and analysis.

Any large items, such as twigs, roots and stones were removed from the dried sample and large clumps were separated with a spatula. The samples were homogenized using a *Fritsch Pulverisette 7* milling device. For each dried and homogenized sample, a *Mettler Toledo* microscale model MX5 was used to weigh two sub-samples between 10 and 20 mg. One sample for sediment total carbon was put into a tin cup (IVA Analysetechnik®) and one sample for sediment organic carbon was placed into a silver cup (IVA Analysetechnik®). Organic carbon samples were acidified with 0.2 ml HCl to remove all inorganic carbon compounds and then again dried for 48 hours at 40 °C. To measure total and organic carbon content of the samples a *Euro EA Elemental Analyzer* (HEKAtechGmbH®) was applied measuring OAS 5 (Apple Leaves®) standards between each five samples. To determine sediment inorganic carbon (SIC) the sediment organic carbon was subtracted from sediment total carbon.

6.3.5. Measuring CO_2 fluxes

To measure CO_2, a CO_2 gas detector handheld from the company CO2Meter, Inc. (https://www.co2meter.com/) was used, which has a measurement range of 0 – 10.000 ppm (0-1%) CO_2 with an accuracy of 30 ppm ± 3%. This device uses a non-dispersive infrared (NDIR) method to determine CO_2 concentrations. Before each measurement the CO_2 instruments were calibrated to outdoor air which was assumed to have a CO_2 concentration of 400 ppm.

At each sampling plot at low tide three CO_2 gas detectors were positioned adjacent to each other but not covering pneumatophores or crab holes to avoid extra respiration not from the sediment-air interface. A chamber with 305 ml of volume was installed on the sediment surface and shaded to maintain steady temperature inside the chamber and to avoid photosynthesis of microorganisms. Inside the chamber, a HOBO® onset UA 002-08 temperature logger was positioned, with a logging interval of one minute. After setting up the instruments, measurements chambers were left for 10 minutes for gas steady stabilization until logging was started. Each measurement took between 17 and 25 minutes. Data was considered to be obtained under steady state conditions if the temperature did not change more than 1.5 °C (Chojnicki et al. 2009). Carbon dioxide flux density (mg CO_2-C m^2 h^{-1}) (FCO_2) was calculated using the following equation from Chojnicki et al. (2009):

$$FCO_2 = k_{CO2} *(273 * Tair^{-1}) * (V * A^{-1}) * (dc * dt^{-1}) \tag{7}$$

Where k_{CO2} is the gas-constant at 273.15K = 0.536 (µg C µl^{-1}), Tair represents the air temperature in the chamber (K), V is the chamber volume (l), A denotes the collar area (m^2) and dc * dt^{-1} is the concentration change (ml l^{-1}) over time (h) inside the chamber. Calculated FCO_2 values were converted into (mmol m^{-2} d^{-1}) units.

6.3.6. Estimating carbon stocks

Carbon stocks were estimated by adding all relevant carbon pools within the investigated area. The three different carbon pools from aboveground biomass, belowground biomass and sediment were determined. To convert aboveground biomass into carbon values a carbon conversion factor between 0.46 and 0.5

is common (Howard et al. 2014). Within this range we chose a conservative carbon conversion factor of 0.46 in order to not overestimate the carbon pool for the biomass of aboveground live mangroves. Assuming a carbon concentration of 50% in dead wood (Kauffman et al. 1995) the biomass of aboveground degraded mangroves was multiplied by 0.5 to obtain the carbon stock value. Belowground carbon pool within intact sites was determined by multiplying BGB of each tree by the carbon conversion factor 0.39 (Kauffman and Donato, 2011). Values for individual tree carbon content were added together to determine the total carbon content from the trees (kg C) for the given plot size (m^2).

To estimate the sediment carbon pool three parameters had to be quantified for each field plot: dry bulk density (BD), sediment organic carbon content (OC) (%) and sediment depth. To predict sediment dry bulk density a pedotransfer function (PTF) developed by Abdelbaki (2018) was used:

$$BD = 1.449^{0.030C} \qquad (r^2 = 0.6802) \tag{8}$$

Then for each interval of the sampled core the sediment organic carbon density was calculated according Howard et al. (2014):

$$\text{Sediment organic carbon density } (g\ cm^{-3}) = BD\ (g\ cm^{-3}) * (OC/100) \tag{9}$$

The amount of carbon in the various sections of core sampled was calculated by multiplying each sediment carbon density value obtained by the thickness of the sample interval (cm) according Howard et al. (2014):

$$\text{Sediment organic carbon in core section } (g\ cm^{-2}) = \text{Sediment organic carbon density } (g\ cm^{-3}) * \text{thickness interval } (cm) \tag{10}$$

The amount of carbon in the core sections was summed over the complete sampling depth (30 cm) and then extrapolated to the total sediment depth. Total sediment depth was retrieved at each plot by inserting a reinforcement bar of three-meter length into the sediment until reaching the underlying limestone layer. Multiplied by the area of intact and degraded mangroves, which was derived from the generated map (estimating intact and degraded mangrove distribution) the carbon stored in Lac Bay in aboveground biomass, belowground biomass and sediment was calculated. Final carbon stock estimates were converted into Megagrams of organic carbon per hectare (MgC ha^{-1}).

6.3.7. Surface and pore water sampling

Dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) in the water column and pore water was sampled one hour after high tide when the water started to drain from the mangrove forest. Surface water was retrieved from the upper 30 cm with a bucket and filtered through 0.7 µm GF/F filters

(Whatman®) into glass vials with rubber tabs – 24 ml vials for DOC and 12 ml vials for DIC. Porewater samples were retrieved with a push point sampler. The push point sampler was inserted into the sediment along the channels to a depth of 50 cm. Samples were then collected using a syringe. For each sample two replicates were taken. Samples were taken during the field campaign, placed into a cooler and transported to the marine field laboratory on Bonaire within 2 hours for further processing.

Dissolved organic carbon samples were then preserved with 0.2 ml HCl-solution. The HCl-solution was prepared with 2N HCl-solution which was diluted 1:5 with bottled water until the pH was lower than 2. The acidified samples were carefully closed, shaken and stored upright in the fridge until further analysis. Dissolved organic carbon was measured using a *Shimadzu Total Organic Carbon Analyzer* (TOC-VCPH).

Dissolved inorganic carbon samples were preserved with 0.2 ml of saturated mercury chloride ($HgCl_2$) solution. The preserved samples were stored upright in the fridge until further analyzed. Dissolved inorganic carbon was measured using a *QuAAtro* device (Seal Analytical 2012). Dickson standards with a concentration of 2.085 mmol L^{-1} were used as reference material.

Salinity, pH, oxygen and temperature were measured in the surface water at each site using a handheld meter Multi 340i with three different micro sensors (*TetraCon925* for salinity, *Sentix980* for pH and *FDO 925* for oxygen and temperature).

Total alkalinity (TA) and pCO_2 of the surface waters were calculated from DIC, pH, salinity and temperature measurements using carbonic acid dissociation constants of Millero (2006) (based on those of Harned and Scholes (1941) and Harned and Davis (1943)) and the CO_2 solubility from Weiss (1974) as implemented in the CO2SYS program, version 01.05 (Pierrot and Wallace 2006).

6.3.8. Statistical analysis

Normality in the data distribution (Shapiro-Wilk test) was evaluated. For parameters with a non-normal distribution a Kruskal-Wallis test was applied to test if there were significant differences between intact and degraded mangroves. For parameters that showed a normal distribution the variance within intact and degraded mangroves was evaluated for homogeneity (Levene test). If no heteroscedasticity was detected in the data by the Levene test (p-value > 0.05) a one-way analysis of variance (ANOVA) was performed to test for significant differences between intact and degraded sites. If the Levene test produced a p-value < 0.05 the variance within the intact and degraded groups was considered to be not homogeneous and a generalized linear model (GLM) was applied (family = gamma, link function = log). If the model produced Pr(>|t) < 0.05 and p-value < 0.05 differences were considered to be significant. Pearson correlation coefficient (for normally distributed parameters) and Spearman correlation coefficient (for non-normally distributed parameters) were applied in order to measure linear correlation between two parameters and significant correlations (p-value < 0.05) were reported by correlation coefficient (r = Pearson coefficient and r_s = Spearman coefficient) close to -1 or 1. Welch's *t*-test was applied in order to detect significant differences (p-value < 0.05) between DOC and DIC pore water and DOC and DIC surface water between intact and degraded sites. All statistical tests were conducted using R software (R Core Team 2019).

6.4. Results

6.4.1. Estimating distribution of intact and degraded mangroves

The map which combined remote sensing techniques with ground-truth data showed an overall accuracy (OA) of 96% ± 0.01 (Figure A.1 - Appendix). Intact mangroves showed an OA of 100% ± 0.0 with a typical vegetation pattern in their reflectance and a high peak (865 nm) in the near infrared wavelength. Degraded mangroves shared the same pattern but in a much lower reflectance range caused by lower chlorophyll content and a lower OA with 83% ± 0.07. Intact vegetation absorbs blue- and red-light energy to fuel photosynthesis and create chlorophyll. A plant with more chlorophyll reflects more near-infrared energy than a degraded plant. The generated map matched well with field observations and by using GIS techniques the areal extent of the derived sites was calculated from the new map (Table 6.1).

Table 6.1. Area of intact and degraded mangroves in hectare (ha) and carbon stock estimates including the upper 30 cm of the sediment (C-STK$_{30}$) as well as for total measured depth (C-STK$_{Total}$) which varied between 30 and 300 cm. Multiplied by the area a complete carbon stock estimate for Lac Bay was retrieved considering only the upper 30 cm (C-STK$_{30}$ x Area) or including the total depth (C-STK$_{Total}$ x Area).

	Area (ha)	C-STK$_{30}$ (MgC ha^{-1})	C-STK$_{Total}$ (MgC ha^{-1})	C-STK$_{30}$ x Area (MgC)	C-STK$_{Total}$ x Area (MgC)
Intact	199	140	387	27,860	77,017
Degraded	48	60	261	2,867	12,541

6.4.2. Forest structure

Results showed a significant difference between intact and degraded sampling plots in aboveground biomass (AGB), belowground biomass (BGB) and diameter at breast height (DBH) (Table 6.2) with higher values at intact sites (Figure 6.2 and 6.3).

Table 6.2. Average values (Mean values for normal distributed data, and median values for non-normal distributed data) and the standard error (±) of all measured parameters for intact and degraded sites including degrees of freedom (df). For ANOVA test the degrees of freedom of the residuals were equal to 30. Statistical results showed significant differences (p-value < 0.05) between intact and degraded sites of aboveground biomass (AGB), belowground biomass (BGB), diameter at Breast Height (DBH), sediment organic carbon (SOC_{30}) 0-30 cm, sediment CO_2 efflux, DIC surface water, DOC pore and DOC surface water, pH, Salinity, partial pressure of CO_2 (pCO_2) and total alkalinity.

Parameter	Intact	Degraded	Statistical test	df	Chi^2	F-value*	p-value
AGB (kg)	984 ± 197	149 ± 37	Kruskal-Wallis	1	17		0.04
BGB (kg)	556 ± 93	177 ± 54	Kruskal-Wallis	1	11		0.001
DBH (cm)	11 ± 1.3	7 ± 0.7	GLM			<0.001	0.004
SOC_{30} (%)	31 ± 1.4	20 ± 1.6	Kruskal-Wallis	1		18	<0.001
CO_2 (mmol m^{-2} d^{-1})	55 ± 8.3	32 ± 4.1	Kruskal-Wallis	1	4		0.047
DIC pore water (µM)	5182 ± 1196	5103 ± 402	Kruskal-Wallis	1	0.003		0.955
DIC surface water (µM)	2397 ± 51	2686 ± 106	ANOVA	1(30)		6	0.02
DOC pore water (µM)	791 ± 149	2582 ± 173	ANOVA	1(30)		58	<0.001
DOC surface water (µM)	327 ± 26	1820 ± 158	Kruskal-Wallis	1	23		<0.001
pH	7.34 ± 0.05	8.02 ± 0.04	ANOVA	1(30)		112	<0.001
Salinity	39 ± 0.3	93 ± 3.0	Kruskal-Wallis	1	23		0.001
pCO_2 (µatm)	1127 ± 233	82 ± 14	Kruskal-Wallis	1	23		0.001
Total Alkalinity (µM)	2375 ± 43	4778 ± 87	Kruskal-Wallis	1	23		0.001

*Please note that for the GLM analysis $Pr(>|t|)$ value was stated.

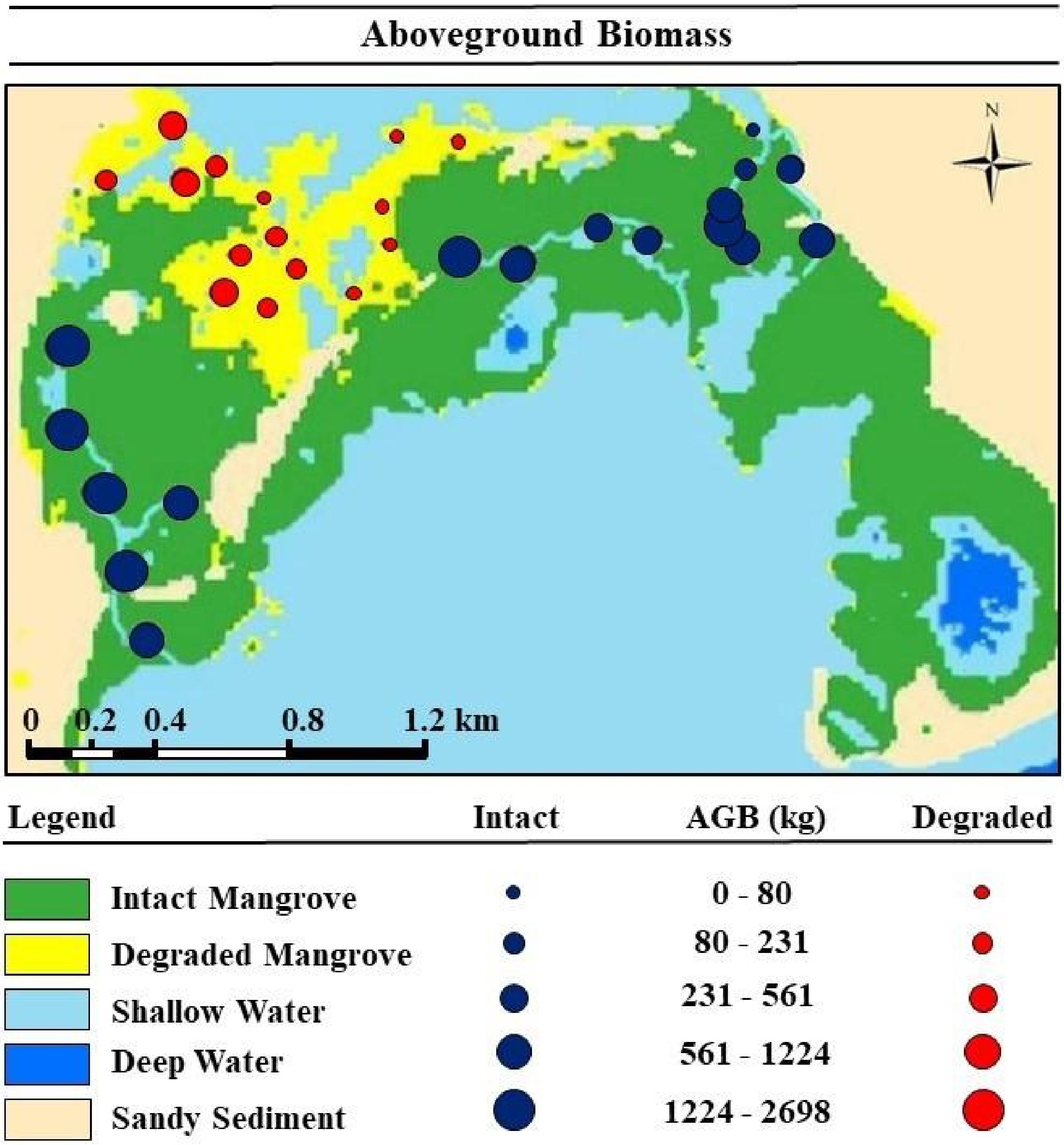


Figure 6.2. Aboveground biomass (AGB) per plot (10 m x 10 m) with the gradient of quantity changes (kg plot^{-1}) below the panel. Small circles are the lowest quantity and larger circles show the biggest quantities. Red filled circles indicate degraded mangroves and blue filled circles are intact mangroves. Channels were geo-tracked and added to the watershed of Lac Bay.

The AGB at the degraded plots ranged from 0 to 512 kg with a median value of 149 ± 37 kg plot^{-1}. One degraded plot was recorded with no standing trees and therefore an AGB of 0. Intact plots showed a great variability with a range from 66 to 2698 kg with a median value of 984 ± 197 kg plot^{-1}. Plots with highest AGB were dominated by *R. mangle.* Plots which were dominated by *A. germinans* or degraded trees showed less AGB. Belowground biomass followed a similar pattern to AGB with lower average value at degraded plots than intact plots. At the degraded plots the median value BGB (177 kg plot^{-1} ± 53) was higher than median value AGB whilst conversely intact plots showed greater AGB than BGB (BGB median: 556 ± 93 kg plot^{-1}).

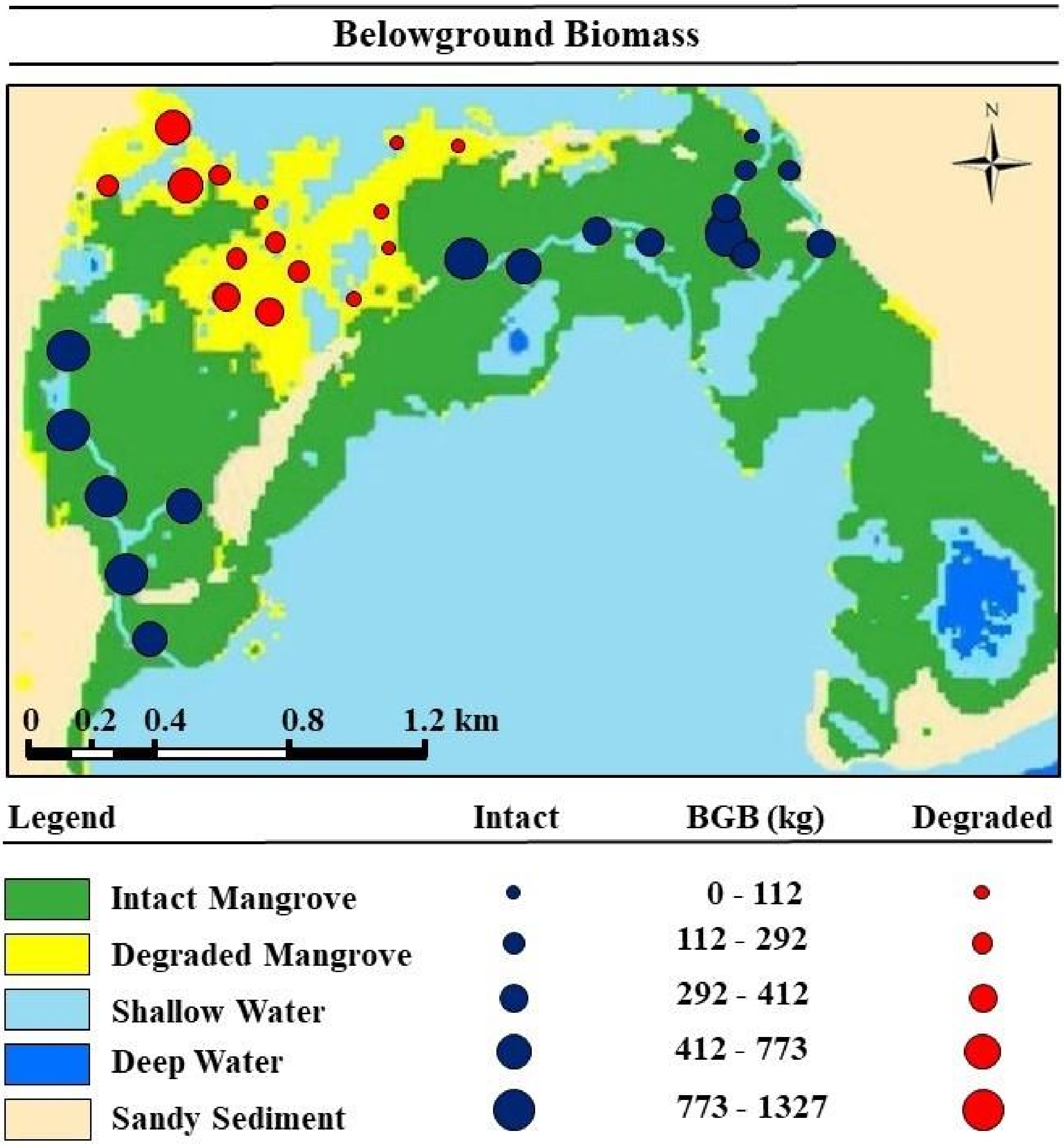


Figure 6.3. Belowground biomass (BGB) per plot (10 m x 10 m) with the gradient of quantity changes (kg plot^{-1}) below the panel. Small circles are the lowest quantity and larger circles show the biggest quantities. Red filled circles indicate degraded mangroves and blue filled circles are intact mangroves. Channels were geo-tracked and added to the watershed of Lac Bay.

6.4.3. Sediment carbon

The retrieved sediment cores showed a sediment total carbon (STC) content between 5 and 36% with no significant change in depth. All samples consisted out of 96-100% sediment organic carbon (SOC). For this reason, sediment inorganic carbon was not included in further analysis. The SOC at the intact plots ranged from 24 to 36% with an overall median value of 31% SOC (Figure 6.4). The average values at the degraded plots ranged from 5% SOC to 25% with a SOC median of 20% (Figure 6.4) and showed a significant difference (p-value < 0.05) compared to intact sites.

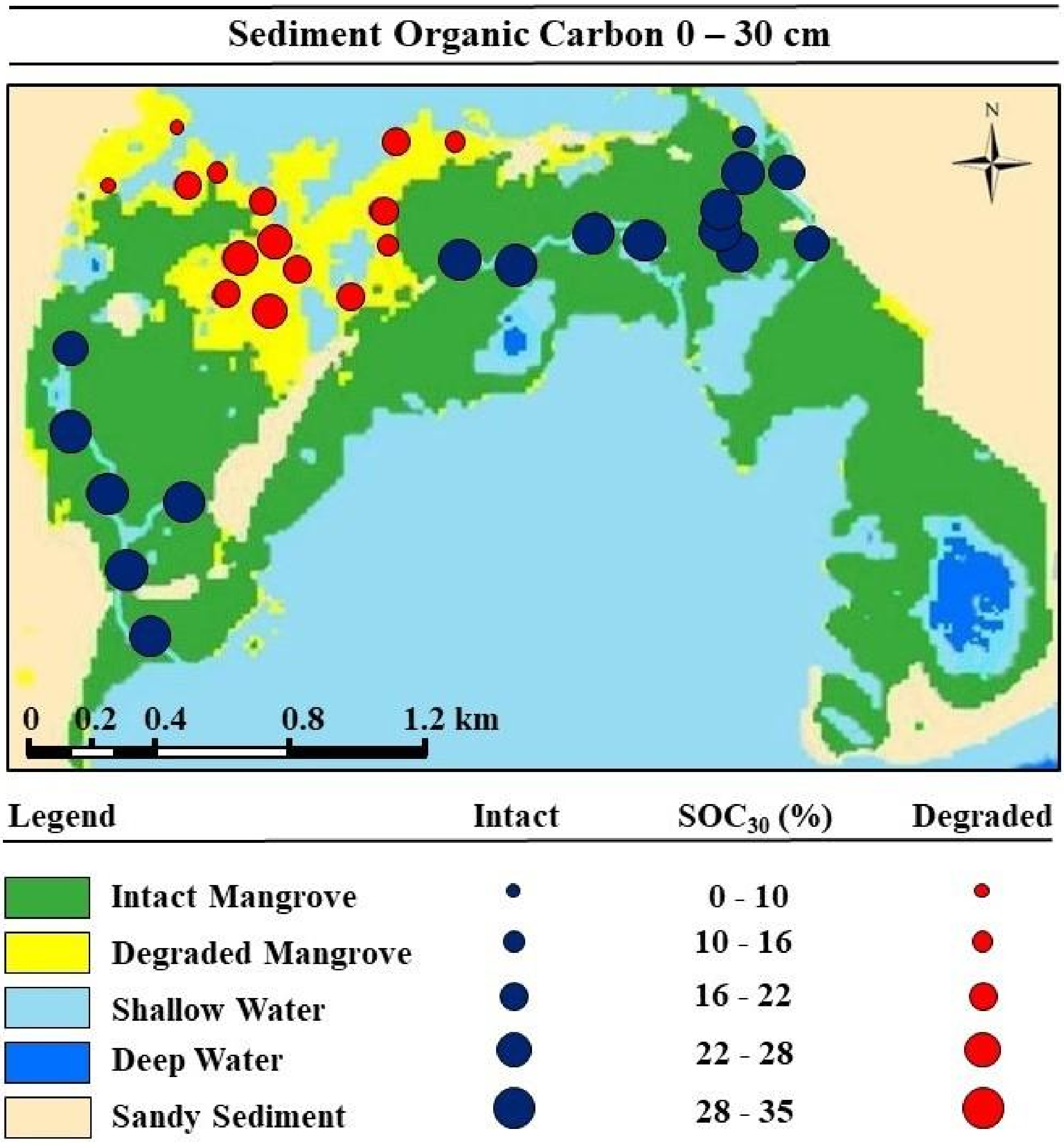


Figure 6.4. Average sediment organic carbon in the upper 30 cm with the gradient of quantity changes (% plot^{-1}) below the panel. Small circles are the lowest quantity and larger circles show the biggest quantities. Red filled circles indicate degraded mangroves and blue filled circles are intact mangroves. Channels were geo-tracked and added to the watershed of Lac Bay.

6.4.4. CO_2 fluxes

Carbon dioxide fluxes showed a large variability ranging from -8 mmol $m^{-2}d^{-1}$ to 107 mmol $m^{-2}d^{-1}$ (Figure 5). At degraded sites CO_2 fluxes ranged from 9 mmol $m^{-2}d^{-1}$ to 66 mmol $m^{-2}d^{-1}$, while the range at intact sites was much larger ranging from -8 mmol $m^{-2}d^{-1}$ to 107 mmol $m^{-2}d^{-1}$. Median values of CO_2 fluxes differed significantly (p-value = 0.047) between degraded (27 mmol $m^{-2}d^{-1}$, n=15) and intact (55 mmol $m^{-2}d^{-1}$, n=17) plots. Although the differences between intact and degraded sites have to be taken with caution regarding the relatively high p-value.

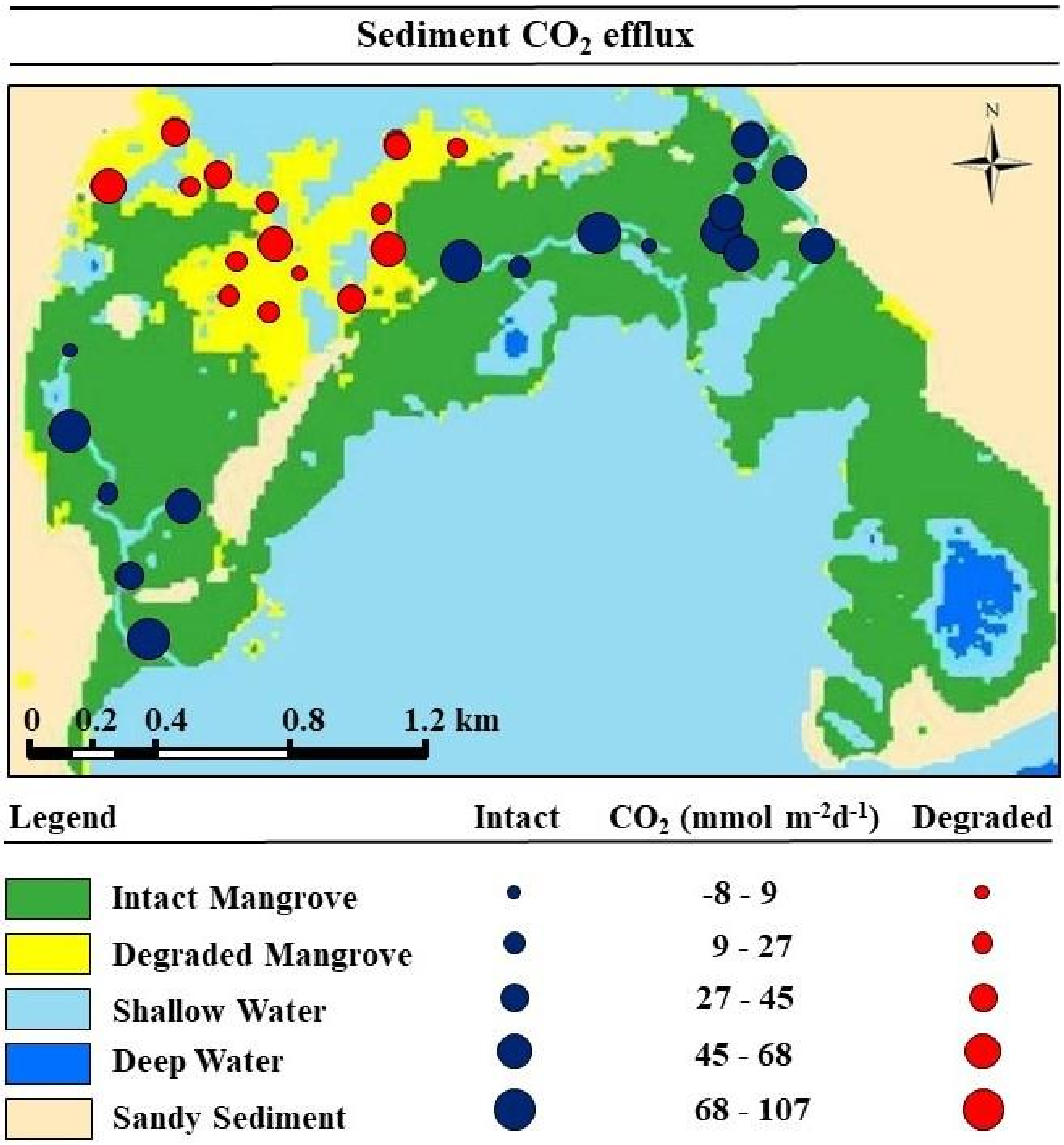


Figure 6.5. Sediment CO_2 efflux with the gradient of flux changes (mmol m^{-2} d^{-1}) below the panel. Small circles are the lowest flux and larger circles show the biggest flux. Red filled circles indicate degraded mangroves and blue filled circles are intact mangroves. Channels were geo-tracked and added to the watershed of Lac Bay.

6.4.5. Estimating carbon stocks

Results from regional equations showed less carbon at degraded sites compared to intact plots in aboveground biomass carbon (intact: 56.67 ± 4.54 MgC ha^{-1}, degraded = 6.53 ± 2.02 MgC ha^{-1}), belowground biomass carbon (intact: 31.59 ± 9.19 MgC ha^{-1}, degraded = 8.95 ± 1.38 MgC ha^{-1}) and sediment organic carbon in the upper 30 cm (intact: 51.44 ± 0.90 MgC ha^{-1}, degraded: 44.25 ± 2.34 MgC ha^{-1}). By adding all carbon pools an average of 387 MgC ha^{-1} for intact sites and 261 MgC ha^{-1} for degraded sites was calculated. When considering only the upper 30 cm, 140 MgC ha^{-1} for intact sites and 60 MgC ha^{-1} for the degraded sites were obtained.

6.4.6. Dissolved organic and inorganic carbon in surface and pore water and physical parameters of surface water

Dissolved organic carbon concentrations showed significant difference between intact and degraded sites with higher concentrations occurring at the degraded sites (Table 6.2). Dissolved inorganic carbon surface water concentrations showed the same tendency (Table 6.2). Dissolved inorganic carbon in pore water was the only parameter which was not significantly different at intact and degraded plots. Dissolved inorganic carbon pore water concentrations were on average higher at intact sites than at degraded sites.

Pore water dissolved carbon concentrations exceeded surface water concentrations for intact and degraded sites (Table 6.2) though DIC pore water concentrations were on average significant higher than the surface water concentrations for intact (Welch's *t*-test, p-value = 0.002, t = 3.6) and degraded (Welch's *t*-test, p-value = <0.001, t = 7.0) sites. Similarly, this pattern occurred for DOC pore water concentrations which were on average significantly higher than the surface water concentrations for intact (Welch's *t*-test, p-value = 0.01, t = 2.8) and degraded (Welch's *t*-test, p-value = 0.01, t = -2.6) sites. Dissolved inorganic carbon concentrations in the surface water exceeded DOC concentrations (Table 6.2). The greatest significant differences (Welch's *t*-test, p-value = <0.001, t = -34.5) were found at the intact sites where DIC often exceeds DOC concentrations by one order of magnitude.

Salinity values at intact sites were on average 39 and showed less variability than at degraded sites. Salinity at degraded sites ranged from 77 to 118 indicating a hypersaline environment. Salinity showed a significant correlation with DOC surface water at intact and degraded sites (intact: $r_s = 0.72$, p-value = 0.001; degraded: $r_s = 0.99$, p-value = $1.7e^{-12}$).

Values for pH and total alkalinity at degraded sites were higher on average than pH values at intact sites (Table 6.2) and pH values showed a strong correlation with DIC surface water at degraded sites (r = 0.89, p-value = $8.1e^{-6}$) and a correlation with DIC surface water at intact sites (r = 0.61; p-value = 0.009). Partial pressure of CO_2 in the surface water of the creeks was significantly higher at intact sites than at degraded sites (Table 6.2). Partial pressure was always higher at intact sites compared to degraded, except at one site.

6.5. Discussion

6.5.1. Remote sensing of intact and degraded mangroves

Although the machine-learning algorithm *Random Forest* showed good overall accuracy and was consistent with field observations in distinguishing intact and degraded mangroves, this result should be taken with caution. An assumption of the statistical approach was that the collected GPS points for validation have a minimum spacing of 2 pixels of its lowest resolution (40 m). Some of the ground-truth

GPS points were closer to each other thus the overall accuracy value might be smaller. Additionally, the Garmin GPS receivers have an uncertainty between 5 and 10 meters, which would further decrease the overall accuracy. The differentiation between degraded mangroves and shallow waters, especially in the northern part of the bay, was more difficult. In many areas of the northern part numerous dead trunks located in the shallow waters were found. This was particularly challenging due to the spatial resolution of 10 and 20 meters, which resulted in mixed pixels (pixel average values from degraded mangroves and shallow water). The results showed mangrove growth and degradation indicated by Erdmann and Scheffers (2006) continued over the last decades and with degrading mangroves located near the front of the forest. This matches with field observations and indicated that the dieback close to the lagoon has been a recent event.

6.5.2. Carbon storage across intact and degraded mangroves

Results showed that degraded mangroves stored significantly less carbon in aboveground biomass (AGB), belowground biomass (BGB) and in their sediments when compared to intact mangroves (Table 6.2). Due to the absence of roots and leaves it was no longer possible to identify the species at degraded sites. Thus, differences in AGB and BGB could be partly caused by different tree species composition at intact and degraded sites. However, degradation of trees and the related loss of leaves, twigs, roots and parts of the stems also has contributed to the observed differences. The differences in sediment carbon storage were probably a result of the current degraded state and unrelated to differences in the tree species composition. Barreto et al. (2016) showed that in the Venezuelan Caribbean no significant differences in carbon storage between *R. mangle* and *A. germinans* existed. There are further limitations to our carbon stock estimates such as the lack of a carbon conversion factor for degrading BGB and site-specific allometric equations for AGB and BGB on Bonaire which could have improved carbon storage estimates for this study.

Degraded mangroves showed greater carbon storage in BGB compared to AGB which can be observed by their ratio (AGB/BGB = 0.73) while intact mangroves showed greater carbon storage in AGB than in BGB (AGB/BGB = 1.87). This difference could be explained by the slow decomposition of wood which does not remain as standing biomass and falls to the forest sediment (Robertson et al. 1989). Mangrove roots can be even more resistant to decomposition because they contain larger quantities of lignin and suberin which degrades slowly (Rasse et al. 2005). Middleton and McKee (2001) showed that degradation of roots did not vary between space and species comparing *R. mangle*, *A. germinans* and *L. racemosa* in a mangrove forest on a Belizean island. The low AGB at degraded sites probably also reduced the sediment organic carbon storage. Less AGB means less photosynthesis and lower intensity of sedimentation, which potentially caused a reduction in OC sequestration (Furukawa et al. 1996) and therefore lower accumulation rates of organic matter (Lovelock et al. 2011). Intact mangroves are known for producing organic carbon well in excess of ecosystem respiration (Bouillon et al. 2008). Degraded sites showed no leaf biomass or root structures which indicates a lack of carbon capture due to their inability to photosynthesize and trap allochthonous material. Therefore, degraded sites should be no longer considered as a carbon sink.

This study identified that sediment carbon was the largest carbon pool in Lac Bay. This is consistent with other studies where sediment carbon is increasingly recognized as the principal carbon pool in mangrove carbon stocks, even when tree biomass is large (Donato et al. 2012; Adame et al. 2013; Murdiyarso et al. 2015; Kusumaningtyas et al. 2019). The extrapolation of all carbon values to the whole depth further highlights the importance of the sediment as a blue carbon sink compared to the AGB and BGB carbon pools. Although this estimate has a high error as the carbon content can vary with depth (Adame et al. 2013; Barreto et al. 2016) and the depth measurements at our sampling sites cannot cover the whole area of Lac Bay, it is possible to give an initial approximation of carbon stock for the area. Carbon stocks from Lac Bay for intact mangroves were within the lower range of carbon stocks reported from this region, such as from Yucatan, Mexico (381–987 MgC ha^{-1}; Adame et al. 2013) and from Honduras (306-1632 MgC ha^{-1}; Bhomia et al. 2016). Sediment organic carbon represents the biggest carbon pool in mangrove forests but still organic carbon burial only accounts for approximately 10-15% of the total net primary production (NPP) (litter fall, wood and root production) in mangrove ecosystems (Breithaupt et al. 2012).

The sediment carbon stored in Lac Bay is mainly organic, thus sediment inorganic carbon (SIC) only played a minor role with an average of 0.5%. With values ranging from 11 to 35% and with an average of 29% (± 1.3) intact sites showed relatively high sediment organic carbon (SOC) content compared to other studies (Kauffman et al. 2014; Adame et al. 2015; Barreto et al. 2016) in the Dominican Republic, Mexican Pacific and the Venezuelan coast. These values might be surprising as Bonaire has a very arid climate and mangroves residing in the dry tropics are supposed to be less productive than those living in the wet tropics where they can likely benefit from an environment with lower salinity and more available fresh water (Alongi et al. 2015). Mangrove accumulation of carbon is also influenced by external particulate organic matter supplied from seagrass meadows, phytoplankton and tidal dynamics (Bouillon et al. 2003; Mcleod et al. 2011). The low tidal amplitude in Lac Bay (Kats et al. 2007) could lead to low outwelling of mangrove derived organic matter with large amounts retained rather than outwelled, leading to higher accumulation in the underlying sediments.

Degraded sites showed significantly lower SOC in the upper 30 cm of the sediment. When the mangroves are degraded, the top layer of the sediment is exposed to physical forces resulting in greater erosion, chemical weathering, and increased rates of decomposition (Lovelock et al. 2011), thus leading to lower carbon storage at the degraded sites. Although prevailing stagnant environmental conditions at the degraded sites probably prevented the sediment from eroding faster and being flushed quicker into the lagoon (Debrot et al. 2012). Less erosion also maintained the anoxic conditions in the sediment which contributed to less loss of SOC by inhibiting the oxidation or alteration by aerobic organism's conditions (Lehmann and Kleber 2015).

6.5.3. Sediment CO_2 efflux and mangrove degradation

Results showed mangroves in Lac Bay have high carbon storage especially in their sediments and therefore can be considered a carbon sink. Degradation of this ecosystem may lead to different emission patterns of CO_2 as the sediment is oxidized thus turning mangroves from a carbon sink into a carbon source (Lovelock et al. 2011; Alongi et al. 2015). This is the first study comparing sediment CO_2 efflux in intact and gradually degrading mangroves within the same forest. While other studies have compared sediment CO_2 efflux from intact mangroves to areas where mangroves have been cleared or cut, Lac Bay reflected a different environment with degradation occurring gradually over decades.

The intact plots showed sediment CO_2 efflux of 55 ± 8 mmol $m^{-2}d^{-1}$ on average which is close to global sediment CO_2 efflux estimates of 61 ± 46 mmol $m^{-2}d^{-1}$ (Bouillon et al. 2008) and 69 ± 8 mmol $m^{-2}d^{-1}$ (Alongi et al., 2014). The data showed a high variability ranging from -8 mmol $m^{-2}d^{-1}$ until 107 mmol $m^{-2}d^{-1}$, which is consistent with overall global CO_2 efflux measurements (Leopold et al. 2013; 2015; Bulmer et al. 2015). Sediment CO_2 efflux in the intact mangroves are likely to be an underestimation because no measurements over pneumatophores or crab burrows were taken, both of which are thought to be major contributors to CO_2 efflux (Kristensen et al. 2008). The flux of CO_2 from sediment and the water column represents approximately 20% of the NPP in mangrove ecosystems and is respired back to the atmosphere (Maher et al. 2018).

Degraded plots differed significantly, even if differences were marginal, and had lower efflux rates on average, which was at least partly due to the loss of trees and thus leading to less or no autotrophic respiration. In Lac Bay site-specific physical processes might play an additional role in explaining the slow carbon loss. As the water circulation is low in the northern part of Lac Bay, these stagnant environmental settings reduced sediment erosion and circulation and thus facilitated anoxic conditions in the sediment leading to minor CO_2 fluxes at degraded plots.

Furthermore, the amount and composition of organic carbon stored in mangrove ecosystems could have influenced the efflux (Leopold et al. 2013). The study by Quyang et al. (2017) identified sediment water content, the percentage of fine-grained sediment, surface sediment chlorophyll and light condition as main drivers for variations in sediment CO_2 flux. Our data showed no significant correlation between SOC and sediment CO_2 efflux, but intact plots showed higher SOC contents associated with higher CO_2 fluxes on average while degraded plots had lower SOC and lower CO_2 fluxes on average. When mangroves are initially cleared, the CO_2 efflux primarily reflects the oxidation of labile fractions of organic matter newly exposed to oxic conditions (Lovelock et al. 2011; Bulmer et al. 2015). However, this fraction is rapidly depleted resulting in slower decomposition of refractory pools, which then dominate the CO_2 efflux (Lovelock et al. 2011; Langát et al. 2014; Gillis et al. 2017). Lallier-Vergés et al. (2008) suggested a two-step decomposition where first carbohydrates from mangrove tissues decompose fast and then lignin phenols decompose slowly depending on redox conditions. The remaining heterotrophic respiration from the sediment at degraded plots could be dominated by this slower pool. At the current rate of sediment CO_2 efflux and assuming no more CO_2 uptake at the degraded sites due to the lack of leaf biomass compared to intact sites, the carbon loss at degraded sites was 1.51 $MgCO_2$ $ha^{-1}yr^{-1}$. This estimated rate is slow if compared to carbon loss to the atmosphere from other cut (Langát et al. 2014) and cleared mangroves (Lovelock et al. 2011; Bulmer et al. 2015; Grellier et al. 2017). Langát et al. (2014) measured sediment CO_2 fluxes between 25.3 and 35.6 $MgCO_2$ $ha^{-1}yr^{-1}$ at cut mangrove sites and Grellier et al. (2017) calculated a carbon loss of 36.7 $MgCO_2$ $ha^{-1}yr^{-1}$ in a cleared mangrove forest. Lovelock et al. (2011) showed that the carbon loss in cleared mangrove forest was 106 $MgCO_2$ $ha^{-1}yr^{-1}$ after one year of clearing and decreased to 30 $MgCO_2$ $ha^{-1}yr^{-1}$ after two years.

The most recent global coverage estimates for mangrove forests in 2014 was 163,925 km^2 which is down from 173,067 km^2 in 2000, representing an annual area during that period of 0.4% (Hamilton and Casey 2016). Harvesting of wood products, infrastructure development and agriculture and aquaculture were the major causes for mangrove degradation worldwide during the last decades (Rivera-Monroy et al., 2017). In addition, mangroves will continue to face changed climate related stressors such as altered hydrology and salinity intrusion, increases in drought and flooding events and increased temperatures (Junk et al. 2013). Especially in parts of the Caribbean, Central and South America, and South Asia where aridity will increase mangrove forests will decline (Alongi 2015). Changes in rainfall and evaporation could potentially lead to the formation of seasonal hypersaline waters that are stressful to mangroves (Andutta et al. 2011) similar to Bonaire. The ongoing wetland loss has triggered an increased interest in implementing better management practices for existing intact mangroves and restoring degraded areas (Ong and Gong 2013). Emerging protocols like the Ecological Mangrove Rehabilitation (EMR) (Stevenson et al. 1999) or "community based ecological mangrove rehabilitation" (CBMER) (Brown et al. 2014; Lewis and Brown 2014) provide useful tools for mangrove restoration programs.

6.5.4. Outwelling of dissolved organic and inorganic carbon

The northern part of Lac Bay is considered to have a very poor water circulation and minimal tidal influence, as tide varies on average 1 cm during dry season (Moorsel and Meijer 1993). This was supported by salinity data showing hypersaline values at the degraded sites averaging 93. Salinity values can be an indicator for the amount of time water stays in a given location (water resident time) and is not flushed by the tide. Dissolved organic carbon concentrations showed high correlation with salinity values. This indicates that DOC is also dependent on tidal influence similar to salinity, which explains the 3-fold higher DOC pore water concentrations at the degraded sites, and more than 5-fold higher DOC surface water concentrations compared to intact sites. Kats et al. (2007) showed that salinity concentrations in the northern area drop dramatically in May when water level inside the lagoon is rising and the tides can flush the degraded sites again. Lac Bay has a rather seasonal tidal fluctuation at the degraded sites while intact sites were flushed by the tide two times a day, therefore it was not possible to compare the outwelling of dissolved organic and inorganic carbon at intact areas of the mangroves with degraded areas. The different environmental conditions at intact and degraded sites might rise doubts about the independence of the replicates especially if they are comparable. However hypersaline conditions only exist during a short period of the year (Kats et al. 2007) whilst sediment carbon storage has been shown not to be dependent on species composition. Therefore, we considered the replicates as independent across the well mixed forest. Furthermore, some of our defined intact sites lie as far north as defined degraded sites and in close proximity to each other (e.g. Figure 6.2). Still they show great differences in carbon which only can be explained by degradation.

Higher DOC concentrations in pore water compared to surface waters (Table 6.2) indicate a flow of tides which is known as "tidal pumping" (Gleeson et al. 2013). Tidally induced pore water flowed from the upper sediment horizon into the creek and subsequently into the lagoon. Surface water DOC averaged 355 µM at intact sites and 1960 µM at degraded sites which leads to the possibility that Lac Bay is a DOC source to adjacent waters where DOC concentrations usually are approximately 40-102 µM (Kumari and Mohan 2018). The export of DOC represents approximately 13% of the NPP in mangrove ecosystems (Maher et al. 2018). The exported DOC can be considered a carbon sink as it is accumulating in marine sediments (Dittmar et al. 2006).

Dissolved inorganic carbon concentrations are much higher than DOC concentrations for surface and pore waters, DIC values exceed DOC by an order of magnitude with highest differences at intact sites (Table 6.2). This is consistent with previous studies comparing DOC and DIC concentrations (Bouillon et al., 2008). The high DIC values may be related to the degradation of SOC. Fixed carbon is processed by benthic invertebrates and microorganisms and mineralized into CO_2 (aerobic respiration) and CO_2 plus bicarbonate (HCO_3^- - produced via denitrification and sulfate reduction) (Alongi et al. 2001). Once the sediment organic carbon is mineralized it can be released as CO_2 to the atmosphere (see previous section) or be transported as DIC with the tidal-induced pore water flow from the upper sediment horizon into the creek, which can then outgas as CO_2 if waters are saturated with DIC (Borges et al. 2003; Kone et al. 2007) or exported into the lagoon. Originally hypothesized (Bouillon et al. 2008), and later quantified (Maher et al. 2013; Sippo et al 2016; Ray et al. 2018; Taillardat et al. 2018), DIC exports to the coastal ocean can be a significant component of mangrove ecosystem carbon budgets representing more than 50% of the total net primary production in mangroves. The fate of DIC once it leaves the sediment is still under discussion. Nevertheless, calculated pCO_2 values showed the creek surface waters at intact sites were supersaturated with CO_2 (Table 6.2) and a large part of this must be outgassed into the atmosphere.

Respiration in mangrove creeks and waterways has only recently emerged as an important pathway of carbon efflux (Borges et al. 2003; Call et al. 2015). An observation in our data showed DIC values correlated strongly with the pH measurements and indicated that DIC rich waters which were supersaturated with CO_2 led to lower pH values (Table 6.2). When the creek waters have outgassed the majority of their CO_2, pH will increase in creek waters and release alkalinity to nearby waters which was observed at degraded sites. Sippo et al. (2016) demonstrated that much of the CO_2 produced in mangroves is outgassed within the mangrove creeks themselves and in contrast to CO_2, the HCO_3^- produced by anaerobic respiration is not released to the atmosphere and is eventually exported by tides from the mangroves. Outflowing waters rich in DIC and total alkalinity could mitigate ocean acidification in nearby coastal waters (Sippo et al. 2016). It is also possible that creek waters rich in CO_2 could enhance the respiration and productivity of coastal primary producers such as seagrasses on their way through the lagoon into the coastal waters (Hemminga et al. 1994; Tussenbroek et al. 1995; Macklin et al. 2019). Additional carbon and isotope measurements in connected ecosystems, such as adjacent waterways, seagrass meadows or coral reefs are required to learn more about the ultimate fate of the mangrove derived dissolved carbon.

6.6. Conclusion

In this multidisciplinary approach, the results showed that intact mangroves on Bonaire are a blue carbon sink as they can store carbon in their biomass and sediment and can export carbon as DOC and especially DIC to adjacent waters. Degraded mangroves were no longer considered a carbon sink due to their inability to photosynthesize and showed significant lower carbon storage than intact mangroves. Mangrove degradation resulted in different CO_2 emission patterns and gave new insights into carbon dynamics in gradually degraded mangrove systems as opposed to those that have been cleared or cut. This is important as the gradually degrading scenario we see on Bonaire, could occur more widely and future comparative studies of degraded versus intact mangrove stands at different locations will be needed to test the resulting hypothesis about carbon dynamics in gradual degrading mangroves. Mangrove forests will decline as climate change increases aridity in parts of the Caribbean, Central and South America, and South Asia altering hydrology and causing seasonal hypersalinity which could lead to gradual diebacks. It is essential that scientists and stakeholders consider how these stresses impact mangrove ecosystems and the blue carbon sink potential. Dissolved inorganic carbon data supports the hypothesis that mangroves could have a strong influence on ecosystem processes in connected habitats, such as coral reefs and seagrass meadows. The water in mangrove creeks near intact sites were supersaturated with CO_2 and need further investigation. More research is needed on how fast these waters outgas CO_2 and the effects mangroves and DIC rich water have on the pH of adjacent waterways and ecosystems.

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Chapter 7 General discussion

In order to better understand the different processes taking place, I will refer to each chapter according to the geographic location: chapter two as Singapore, chapter three as Zanzibar, chapter four as South Australia, chapter five as Florida, chapter six as Bonaire.

In general, geomorphic settings and community structure are important drivers for SC accumulation, connectivtty between mangrove forests and seagrass beds was only significant fo carbon accumulation in South Australia mangrove forests. Results from Singapore, Zanzibar and South Australia demonstrate how mangrove forests' geomorphic settings and seascape structure (i.e. forest area, channels, tide-related water movement etc.) are important in terms of exchange of particulate organic carbon (OC). In Singapore and South Australia, contributions of mangrove forests and macroalgae to the particulate organic matter (POM) indicate that these CVE are important donors of POM across the seascape, even though macroalgae beds did not have the biggest biomass or cover area. Species diversity of the in both seagrass beds and mangrove forests influenced SC content in Zanzibar, the presence of bigger seagrass species correlated with higher carbon content, especially with higher sediment inorganic carbon (SIC) content. Singapore and Bonaire sites indicated how anthropogenic induced modifications of local geomorphic settings at the seascape level, (i.e. reduction of mangrove forests area, degradation of mangrove living biomass, changing water fluxes) affect carbon accumulation in mangrove forests and adjacent coastal ecosystems. In Florida the expression of seagrass plant physical traits (i.e. shoot density and percentage coverage) have a significant positively impact on sediment organic carbon (SOC) content, whilst unexpectedly more complex mangrove root did not show a positive impact on SOC content. Together, seascape structure, main plant ecosystem engineer characteristics and exchange of POM indicated that carbon accumulation within CVEs is an level interdependent process in the mangrove forests and seagrass beds.

To compare connected and isolated mangrove forests and seagrasses beds with a non-localized perspective all SC content data across all chapters in this dissertation were pooled together. A comparison between connected vs. isolated mangrove forests as well as connected vs isolates seagrass beds was done using statistical tests (further explained in the apendix). Additionally, data obtained from different studies across the globe was pooled together separating locations by connected mangrove forest, connected seagrass beds, isolated mangrove forests, and isolated seagrass beds (the methodology is further explained in the apendix). Thus, mainly to compare if the pattern observed in this dissertation is similar with other connected and isolated ecosystems; henceforth, this data set will be called global data set. Additionally, a separation between SOC or SIC contents was done to observed if mangrove forests and seagrass beds that were connected or isolated from each other presented different concentrations for either type of carbon.

In the global datasets SC content was not obtained since some of the studies did not report SC, in addition SIC and SOC content within the same location was not always reported, so differently to this dissertation SOC and SIC content does not correspond to exactly the same locations. Additionally, a potential bias could be observed in the lower number of isolated ecosystems, especially in isolated mangrove forests which also had a high riverine influence compared with connected forests in the global data set (i.e. Amazonas and Sundarbans) (Figure 7.1A). Therefore, general interpretation should be taken with caution but still valid for comparison.

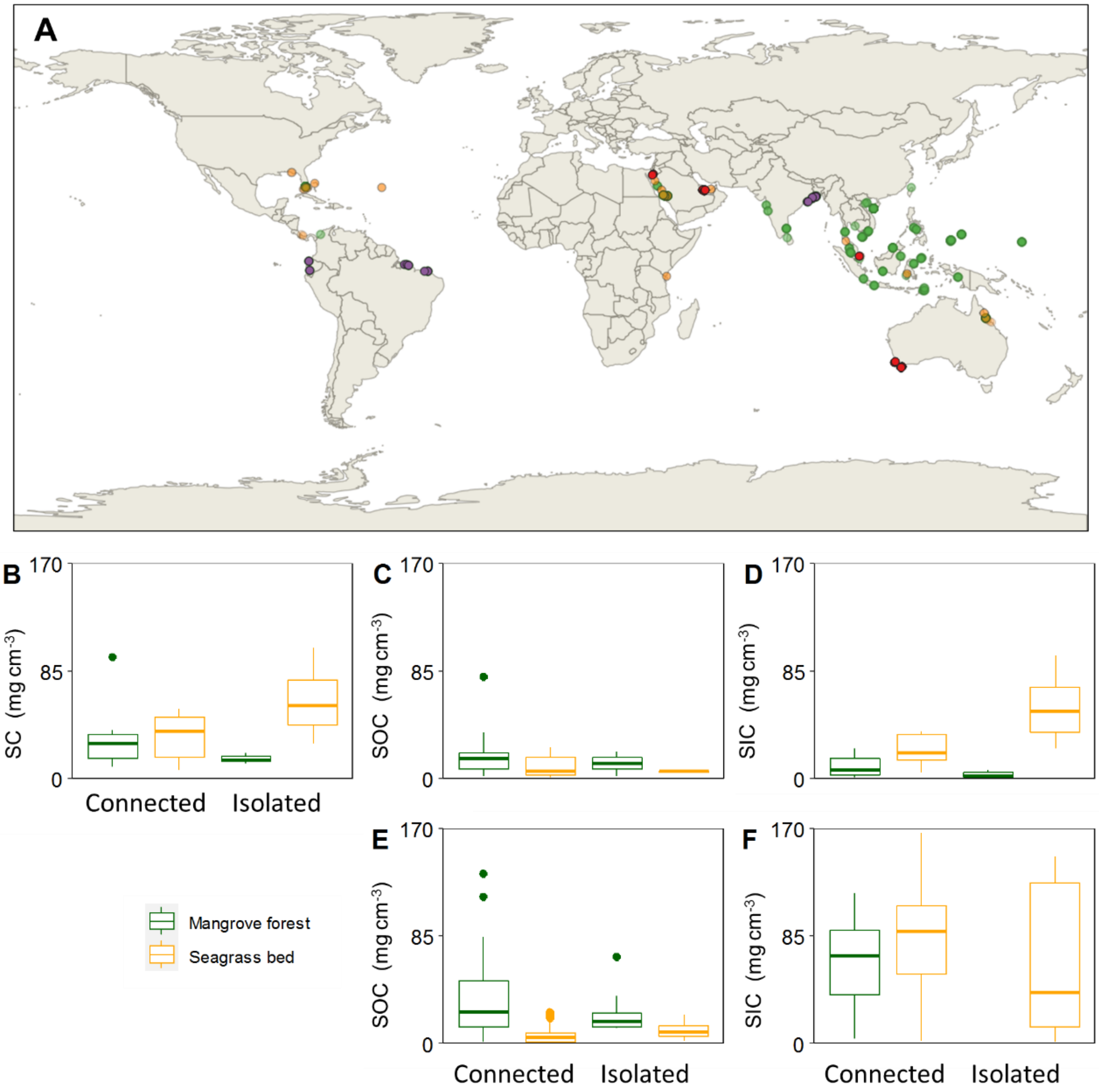

Figure 7.1. Location and sediment carbon content of connected and isolated mangrove forests and seagrass beds reported in this dissertation and selected studies across the globe. Panel A shows distribution of studies selected for comparison across the globe of connected mangrove forests (green dots), isolated mangrove forests (purple dots), and connected seagrass beds (orange dots), isolated seagrass (red dots). Panels A, B and C show data obtained in this dissertation separated by sediment carbon content (SC), sediment organic carbon (SOC) content, sediment inorganic carbon (SIC) content respectively. Panel D, E, shows data obtained in other studies separated by SOC content, and SIC content respectively. Thick line inside the boxplot indicate the median.

Table 7.1. Results of statistical tests of sediment carbon (SC), sediment organic carbon (SOC), and sediment inorganic carbon (SIC) of connected vs isolated mangrove forests and connected vs isolated seagrass beds, where A = type of analysis, *p* = *p* value, W/F = W or F value.

		STC			SOC			SIC		
	Comparison	A	*p*	W/F	A	*p*	W/F	A	*p*	W/F
This dissertation	Connected vs isolated mangrove forests	Wilcoxon-test	0.2	W 21	Wilcoxon-test	0.72	W 16	Anova	0.27	F 1.34
	Connected vs isolated seagrass beds	Anova	0.09	F 3.58	Anova	0.35	F 0.96	Anova	**0.03**	F 6.58
Global dataset	Connected vs isolated mangrove forests				Wilcoxon-test	0.11	W 1102			
	Connected vs isolated seagrass beds				Wilcoxon-test	**<0.01**	W 400	Anova	0.19	F 1.7

7.1. Carbon accumulation at seascape level: geomorphic settings and connectivity with other ecosystems

Contrary to the original hypothesis mangrove forest were connected or isolated for seagrases presented similar SC content, whilst isolated seagrass had higher SC content compred with beds connected with mangrove forests. Localized differences in geomorphic settings influenced differently SC accumulation in both mangrove forest and seagrass beds. For example, in Zanzibar channel area was positively correlated with SOC content mangrove forest and negatively correlated with SIC in seagrass beds, however SOC content was not significantly correlated by area channel in seagrass beds. In Singapore, although no significant difference was observed in SOC across mangrove forests, low energy riverine discharge forests exhibited a higher carbon store biomass pool compared to forests that did not have riverine discharge. Water coming from upstream systems brings carbon particles that will be set and retained in mangrove forest sediments due to particle retention features of mangrove roots (Alongi 2014). Water movement coming for channels and connecting terrestrial systems with mangrove forest and seagrass beds are important driver for carbon accumulation in mangrove forest, but further research is need it for influence on seagrass beds.

Results of this dissertation clearly indicate that mangrove forest are important donors of carbon to other CVE due to mangrove ecosystems contribute to the POM relatively higher per unit area and living biomass compared with another CVE. Across all ecosystems evaluated in this dissertation mangrove trees have the bulkiest structure compared with seagrass or salt mars plants and therefore the highest biomass per unit area. In Zanzibar chapter and in other studies i.e. Gulstrom et al. (2018) it was shown that higher cover area of mangrove forest and less distance of the seagrass beds to the forest influence higher SOC store in seagrass beds. Singapore and South Australia, MixSIAR model results demonstrated that mangrove forest contributed relatively high with respect to the area occupied by this ecosystem. Additionally, in South Australia mangrove forests and salt marshes contributed greatly to POM to adjacent water bodies, despite their comparatively smaller total living biomass. This is in accordance with the outwelling hypothesis (Odum 1968; Lee 1995) that state the mangrove forest outwelling of nutrients and detritus increase productivity in adjacent ecosystems. Since mangrove forests are important donors of carbon, conservation of mangroves is important to keep the carbon accumulation ecosystem service not only inside mangrove forests but also in adjacent ecosystems (i.e. seagrass beds, tidal flats, salt marshes).

Connectivity with other ecosystems such as macroalgae beds and coral reefs are important for mangrove forests and seagrass beds SC accumulation. In Singapore and South Australia, macroalgae were found to be one of the biggest contributors to POM, supporting recent findings that show macroalgae can be one of the biggest ecosystems donors of carbon (Ortega et al. 2019; Santos et al. 2019). In addition, studies of macroalgae thallus exchange, degradation and fluxes of carbon to the atmosphere should be also taken in account for better understing of long term SC acuulation (Trevathan-Tackett et al. 2015). Connectivity with coral reef was not evaluated in this dissertation but based on Zanzibar chapters results one can hypothesize that coral reefs are a potentially important donor of carbonates for mangrove forests and seagrass beds.

Seagrass beds SC accumulation seems to be affected by connectivity with ecosystems that donate OC as well as IC. As showed in the global data set and reported in other studies i.e. Mazarrasa et al. 2015 ratio of SIC and SOC can vary across seagrass beds globally. Mangrove forest and terrestrial ecosystems can contribute up to 50% of the SC content in seagrass beds (Kennedy et al. 2010). Sediment carbon content in seagrass beds can be increased with autochthons carbonates production or connectivity with other CVE that export carbonate particles to dajcent ecosystems (i.e. coral reefs or calcifying macroalgae beds) (Macreadie et al. 2017; Saderne et al. 2019). Isolated seagrasses beds exhibited twice higher SC contents than connected beds in this dissertation, which can indicate that inner production of carbonate and/or connectivity with coral reef was a more important driver for SC in the sampled seagrass beds that connectivity with mangrove forests.

Mangrove forest, seagrass beds, salt marshes, and coral reefs are inter-connected between them mainly due to those ecosystems usually occur at the tropical and sub-tropical seascape, however they can be connected even if they are not adjacent. The definition of connectivity and connectedness was tackled in the glossary, here connectivity was approached as the fact of being adjacent and exchange POM, whilst connectedness is more related as the degree and quality of exchange of materials and energy. The degree of connectedness between all CVE can vary due to localized factors such as hydrodynamics and tidal amplitude, which were not evaluated in this dissertation but are suggested to be included in future studies to elucidate the impact of connectivity of adjacent and/or not adjacent ecosystems for carbon accumulationIn order to keep the ecosystem service of carbon accumulation whithihn the ecosystem, conservation efforts should focus on the individual ecosystem that provide the service, as well as adjacent connected and not adjacent connected ecosystems (i.e. seagrass or macroalgae beds that rea not adajacnet ot mangrove forests). Results of this dissertation showed that connectivity impact SC accumulation goes beyond the exchange of POM between mangrove forest and seagrass beds, therefore conservation efforts should have a seascape level perspective..

7.2. Interaction of seascape level and community composition and their effect on carbon accumulation

Data on species diversity and composition in Zanzibar where *Rhizophora mucronata* and large-leaved seagrass species were associated with higher SOC in mangrove forest and higher SOC seagrass beds (see Chapter 4, annex table 4.4). The presence of the genus *Rhizophora* in mangrove forests has been associated with higher SOC compared to other species composition (Barreto et al. 2016; Atwood et al. 2017). Similarly, seagrass beds with big-leaved species, such as *Enhalus acoroides*, and *Thalassodendron ciliatum*, in seagrass beds tend to have higher SOC content compared to seagrass beds with different species (Gullström et al. 2017). This demonstrates the association between SC content and community composition, while not necessarily implying a causality between community composition and SC stocks, as reported in global mangrove comparisons (Atwood et al. 2017) or seagrass ecoregions and global comparisons (Lavery et al. 2013; Mazarrasa et al. 2015). As shown in this dissertation, evaluating the community structure may aid in recognizing potential localized drivers in carbon accumulation. However, community structure needs to be further analysed together with factors larger scales (i.e. geomorphic settings) and at smaller levels (i.e. difference of traits across species and state of conservation of the ecosystem).

Geomorphic settings (tides, river discharge), climatic conditions (temperature, precipitation) determine not only the species-specific mangrove spatial distribution at the coastal seascape, but also the spatial distribution of above-and belowground biomass allocation patterns and SC content (Rovai et al. 2018; Simard et al. 2019). Many studies have found SC content in seagrasses are determined by a mixed localized influence of seagrass species composition and specific location environmental setting interactions (Kennedy et al 2010; Mazarrasa et al. 2015; Güllstrom et al. 2017).

7.2.1. Florida study case: The influence of variations in the morphology of mangrove roots and seagrass leaves on carbon sequestration

In the Florida chapter, it was identified that values of different functional traits of mangrove trees and seagrass plants changed depending on sediment nitrogen and phosphorus availability. Mangrove trees and seagrass plants promote carbon accumulation due to both type of plants diminish water velocity and increase particle trapping (Furukawa et al. 1997; Miyajima and Hamaguchi 2019). The variation on the different trait expressions in mangrove roots and seagrasses influenced SOC or SIC differently. An unexpected correlation was seen in mangrove forest where increasing mangrove root complexity index (based on diameter, distance to the trunk and number of prop roots per tree) was negatively correlated with SOC content. Thus, the higher the root system complexity, the higher the turbulence, which keeps OC in suspension and increases sediment erosion (Krauss et al. 2003). In seagrass beds, plant traits such as canopy height, shoot density, and leaves with larger cross-sectional area were positively associated with SOC percentage, mainly due to they retaining more detritus and organic matter whithin the beds. This study gave insights on how the diversity in terms of variation of trait expression in the same species could impact SC accumulation.

7.2.2. Bonaire study case: State of the mangrove forest community and impact on carbon accumulation

As discussed before, the degradation of one of the CVEs may impact carbon accumulation not only in the ecosystems itself but also in adjacent ecosystems. In Bonaire, the intact mangrove forest area was considered a carbon sink whilst the degraded part was showing to be exporting carbon to the atmosphere and adjacent ecosytems. The degraded mangrove forest area held 10% lower SOC content and 6.5 times less biomass when compared to the intact area. In addition to that, degraded forests show higher DOC outwelling (up to six times in adjacent waters). These results agree with other studies which demonstrated a greater erosion and chemical weathering in the top layer of the sediment in areas where degraded mangrove trees had lost their root structure (Lovelock et al. 2011). Direct and indirect effects of sediment erosion and chemical weathering should be further investigated in terms of the impact in SC accumulation in adjacent seagrass beds.

7.3. Conclusion and outlook

Connectivity between mangrove forests and seagrass beds affects SC acumulation in each location and in each ecosystem differently, however inter-connectivity with other ecosystems are important drivers of SC accumulation in both mangrove forest and seagrass beds. For example, the mangrove forests connected to seagrass beds in South Australia had higher carbon than isolated forests, whilst connected forests in Zanzibar and Singapore did not show significant value differences from the isolated forests. Divergently to our original hypothesis, seagrass bed connected to mangroves forests in South Australia and Zanzibar had less SC content compared with isolated seagrass beds, mainly because of higher SIC content in the isolated beds. Thus, SC content in mangrove forest could be highly influenced by inner forest processes related with production and accumulation of OC as well as connectivity with other ecosystems that donate OC besides seagrass beds.

Furthermore, SC content in seagrass beds connected to mangrove forests is driven by autochthonous and allochthonous production of both OC and IC particles. It is critical to include SIC content in blue carbon studies concerning seagrass beds, since SIC content was an important component of the SC store. Connectivity of seagrasses with ecosystems that donate carbonate highly influence SC store in seagrass beds, therefore, autochthonous production of IC as well as connectivity with coral reefs should be further explored.

Adjacency to another ecosystem was not a good indicator to measure the quality of connectivity between two or even more connected ecosystems. The MixSIAR results of South Australia showed that ecosystems that were not adjacent can have a higher degree of connectedness. For example, mangrove forest and macroalgae beds in showed a higher connectedness despite the fact that they were more than 10 km apart. There are different factors, such as riverine and tidal transport, that have been reported to be the main pathway of cross-ecosystem carbon flow (Hyndes et al. 2014), therefore factors affecting those transport pathways should be further investigated as an better approach for connectivity.

One of the reasons of the wide distribution of SOC content across connected mangrove forests and seagrass beds is the fact that not all adjacent ecosystems have the same degree of connectedness. Tidal amplitude can influence the degree of connectedness between mangrove forests and seagrass beds; it can be assumed when exposed to a higher tidal amplitude there would be higher POM exchange between them, therefore having a higher connectedness than connected ecosystems in setting of lower tidal amplitude. As an example, South Australia mangrove forests seem to have higher connectedness to seagrass beds due to a high tidal amplitude (maximum 3 m) despite the fact that they were more than 500 m apart (i.e. Port Wakefield). In contrast, mangrove forests adjacent to seagrass beds in Bonaire and Florida would show a lower degree of connectedness due to the smaller tidal amplitude (maximum 0.6 meters). In addition to connectivity across CVEs, other factors that influence connectedness across different CVEs (i.e. tidal amplitude) and terrestrial systems (i.e. riverine discharge) should be included in carbon accumulation studies.

Macroalgae beds and salt marshes were in general important contiburos of POM for both mangrove forests and seagrass beds, and terrestrial ecosystems were important donours depending on geomorphic settings (i.e. Singapore and South Australia). Furthermore, seascape structure differences, such as presence of tidal channels (that connect mangrove forests with terrestrial systems) and presence of macroalgae beds and salt marshes, can enhance SC accumulation especially in mangrove forest. Results of this dissertation highlight the importance of preserving mangrove forests and seagrass beds as well as upstream and marine submerged ecosystems for carbon accumulation at the seascape level. However, further research on localised interactions between the seascape structure and communitty characteristics should be further explored.

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7.5 Appendix

Appendix table 5.1 Mean values of sediment carbon (SC), sediment organic carbon (SOC), and sediment inorganic carbon (SIC) at each sampled mangrove forest and seagrass bed, separated by location and connectivity status. SD= Standard deviation.

Connectivity status and ecosystem	Location	Country/State	SC (mg cm^{-3}) mean	STC (mg cm^{-3}) SD	SOC (mg cm^{-3}) mean	SOC (mg cm^{-3}) SD	SIC (mg cm^{-3}) mean	SIC (mg cm^{-3}) SD
Connected Mangrove forest	Bonarie	Bonaire	15.46	4.04	15.46	4.04	0.37	0.61
	CJ	Singapore	16.11	12.06	1.57	1.16	5.71	5.36
	Florida	Florida	95.45	23.83	79.86	38.29	15.59	16.45
	Nyamanzi	Zanzibar	27.27	9.53	19.44	9.43	8.44	7.54
	Pete	Zanzibar	38.15	9.53	36.57	9.67	2.42	3.84
	Port Clinton	South Australia	9.05	3.59	6.50	3.51	2.55	3.52
	Port Wakefield	South Australia	34.70	21.67	10.79	5.18	23.70	19.56
	Torres Island	South Australia	14.34	3.57	15.18	9.69	1.47	2.21
	Weni	Zanzibar	28.92	12.37	6.84	3.94	22.09	12.56
Connected Seagrass bed	CJ	Singapore	6.32	5.27	0.59	0.50	4.59	3.79
	Florida	Florida	54.10	10.14	18.46	10.07	35.52	7.29
	Nyamanzi	Zanzibar	51.37	13.77	14.18	11.61	37.19	8.70
	Pete	Zanzibar	44.45	24.87	24.77	17.73	19.68	8.44
	Port Clinton	South Australia	14.55	8.34	2.01	1.07	12.54	8.30
	Torres Island	South Australia	17.92	5.73	2.59	0.98	15.32	5.77
	Weni	Zanzibar	37.53	11.29	4.99	4.95	32.54	7.95
Isolated Mangrove forest	Kama	Zanzibar	19.69	12.44	20.53	13.85	1.24	2.21
	Rushy Island	South Australia	11.95	4.87	11.87	5.08	0.58	0.62
	Seletar Island	Singapore	14.13	31.14	1.43	3.32	6.51	10.15
Isolated Seagrass bed	Bweleo	Zanzibar	68.62	11.17	4.52	3.32	64.10	11.23
	Matenwe	Zanzibar	102.78	28.87	5.80	2.67	96.98	27.71
	Stansbury	South Australia	27.52	7.18	3.87	2.29	23.65	6.80
	Victor Harbor	South Australia	46.10	18.08	5.38	6.85	40.72	13.16

7.5.1. Methodology for global data setting and criteria for connectivity

Global data was taken from published studies of Breithaupt et al. (2018), Guan et al. (2018) and Rovai et al. (2018) for mangrove forests that have quite a comprehensive data set of SOC content in mangrove sediments. For seagrass beds, the global data set of SOC and SIC collected by Mazarrasa et al. 2015 were used. Also included are the studies conducted by Garcias-Bonet et al. 2019 that has the reported SIC and SOC in seagrass beds and mangrove forests. Coordinates reported in the studies were mapped using QGIS 3.8 Zanzibar version.

Not all mangrove forest or seagrass beds reported in the studies have information regarding other adjacent CVE, therefore a global map of mangrove forests and seagrass beds covering was produced with data obtained for mangrove forest Link 1. The data evaluates forest cover and height of mangrove trees. For seagrasses the database was reported by Link 2. The global mapping of mangrove forests showed the cover area of the forest. In contrast, presence was mainly reported for seagrass beds across the globe but not cover area. Data and metadata reported in those links were downloaded and graphed using QGIS 3.8 Zanzibar version in order to classify globally if mangrove forests and seagrass beds were connected or isolated from each other this criterion of classification was used.

Connected locations

If coordinates reported in the studies for mangrove forest and seagrass occur adjacent to each other (i.e. less than 500m) it was assumed that those CVE were connected.

Seagrass

If coordinates reported in the studies for seagrass were adjacent to a forest reported in the mangrove global map (less than 500m) it was assumed it was a connected seagrass bed. While if seagrass beds coordinate data was not adjacent to any mangrove cover, it was assumed it was an isolated seagrass bed. Seagrasses reported in the Mediterranean bioregion were not taken into account for this study, since the focus of the thesis was mainly tropical and subtropical.

Mangrove

If the coordinates reported in the studies for mangrove forests were adjacent to the reported in the seagrass global map (less than 500m) it was assumed it was a connected mangrove forest. While if a mangrove forest coordinate data was not adjacent to any seagrass, a visual check was done using available google earth satellite images close to the year when the study was done. If visually seagrass presence was suspected, the location was not included in the comparison since seagrass and algae blooms could be easily confused.

7.5.2. Data analysis

In each location the mean value of SC, SOC and/or SIC store at mangrove forest and seagrass beds connected or isolated from each was calculated. Values of this dissertation and for the global data set were analysed separately for comparative proposes. Comparison of connected vs. isolated mangrove forest were tested separately for connected vs. isolated seagrass beds regardless they were present at the same location. All statistical tests were done using R Core Team, 2019. Normality assumptions were tested using *gvlma()* function. If data was normally distributed one-way analysis of variance ANOVA was used to detect significant differences, whilst if data was not normally distributed Wilcoxon-test was used to detect significant differences. In both cases a *p-value* lower than 0.05 was considered to be significantly different.

7.5.3. References

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