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Review

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Current status and emerging perspectives of coastal blue carbon ecosystems

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Abstract

Blue carbon ecosystems require conservation and restoration to maximize organic carbon (C_{ORG}) sequestration to ameliorate greenhouse gas emissions. Salt marshes, mangrove forests and seagrass meadows are all autotrophic and are considered blue carbon ecosystems. Macroalgae and tidal flats are currently not considered blue carbon habitats. Blue carbon ecosystems contribute globally to climate change mitigation and at local and national scales, especially in the provision of other ecosystem goods and services. Financial investment is constrained by large uncertainties in C_{ORG} dynamics and best practices in restoration, rehabilitation and conservation. Several key emerging perspectives include (1) the fact that groundwater discharge of dissolved carbon is a major pathway of blue carbon loss; (2) allochthonous C_{ORG} inputs are required to achieve ecosystem carbon mass balance; (3) blue carbon dynamics are enhanced by habitat connectivity and biotic activities; (4) CH_4 and N_2O emissions reduce blue carbon potential; (5) habitat destruction causes blue carbon stock losses, but variable gas emissions; (6) sediment blue carbon stocks are increasing at the poles; and (7) land-use and land-cover changes (LULCC) drive changes in blue carbon stocks and emissions. Further research is needed to clarify the applicability of these emerging perspectives.

Keywords: Blue carbon, carbon sequestration, coastal, ecosystem, mangrove, mangrove forest, organic carbon, salt marsh, seagrass, seagrass meadow

INTRODUCTION

The term "blue carbon" is defined as the sequestration or burial of C_{ORG} by coastal ecosystems[1,2]. The term was first coined in a report[3] highlighting the role of ocean ecosystems in the earth's climate. Blue carbon science and management focus on adaptation and mitigation by these ecosystems to help ameliorate greenhouse gas emissions to reduce the effects of a changing climate.

Blue carbon ecosystems, namely tidal salt marshes, mangrove forests, and seagrass meadows, and possibly tidal flat and macroalgal habitats, are important sources of food and wood for fuel and housing, shoreline protection and other ecosystem services for coastal residents. These habitats can be restored or rehabilitated and sustainably managed, and are important because they provide a wide variety of ecological and economic services and goods in addition to the ability to sequester carbon[4].

The United Nations, in collaboration with Conservation International (CI) and the International Union for the Conservation of Nature (IUCN), has established initiatives aimed at mitigating climate change by restoring, rehabilitating, and sustainably using marine ecosystems. One policy has dealt with policy matters to integrate blue carbon activities into both global policy and financing of the United Nations Framework on Climate Change (UNFCCC) to (1) facilitate climate change mitigation and other carbon finance processes, including carbon markets; (2) develop pilot projects to test their viability; (3) meld blue carbon into other frameworks and policies; and (4) include the carbon value of coastal ecosystems into the financial accounting of ecosystem services[3,5]. Empirical data was therefore urgently needed to fill in knowledge gaps in coastal blue carbon cycling. It has been well known that coastal habitats store large amounts of C_{ORG} in their sediment and biomass, confirming that they must play a major role in blue carbon science and management[1,4]. Salt marshes, mangroves and seagrass meadows must therefore be considered in the provision of ecosystem services, particularly in fostering C_{ORG} sequestration and in minimizing conversion of these habitats which results in their stored C_{ORG} being emitted as greenhouse gases, negating REDD+ (Reducing Emissions from Deforestation and Forest Degradation; +refers to conservation and sustainable management to enhance C stocks) efforts and other rehabilitation projects[3,5].

By 2010, it was necessary to know how coastal habitats acquire and store C_{ORG}, how burial can be maximized while minimizing C_{ORG} losses and determining under what conditions sequestration occurs. It was also necessary to understand how quickly these habitats were being destroyed or altered to other habitats (e.g., human dwellings, factories, agriculture establishments) and the likelihood that C_{ORG} will be lost, including CO_2 and CH_4 emissions that follow destruction and conversion of coastal habitats. Three components of carbon biogeochemistry need to be better understood to improve the knowledge base of blue carbon: (1) the annual burial rate (i.e., yearly flux of organic carbon incorporated into reducing sediments where oxidation and subsequent loss of CO_2 to the atmosphere does not occur); (2) the magnitude of C_{ORG} stored in above- and belowground biomass; and (3) the total sediment C_{ORG} stock due to earlier sequestration (i.e., geological burial over a given habitat's lifetime).

This paper offers a critical overview and some key perspectives that have emerged from what is now over a decade of empirical research and management attempts to foster blue carbon sequestration in coastal ecosystems. The purpose of presenting these perspectives is to provide clarity of progress and direction to future blue carbon science and management.

BLUE CARBON PROCESSES IN COASTAL ECOSYSTEMS: CURRENT STATUS

A schematic [Figure 1] illustrates the main carbon fluxes between coastal habitat, sea, and atmosphere, showing that most C_{ORG} captured and stored (buried) in seagrass meadows, tidal salt marshes and

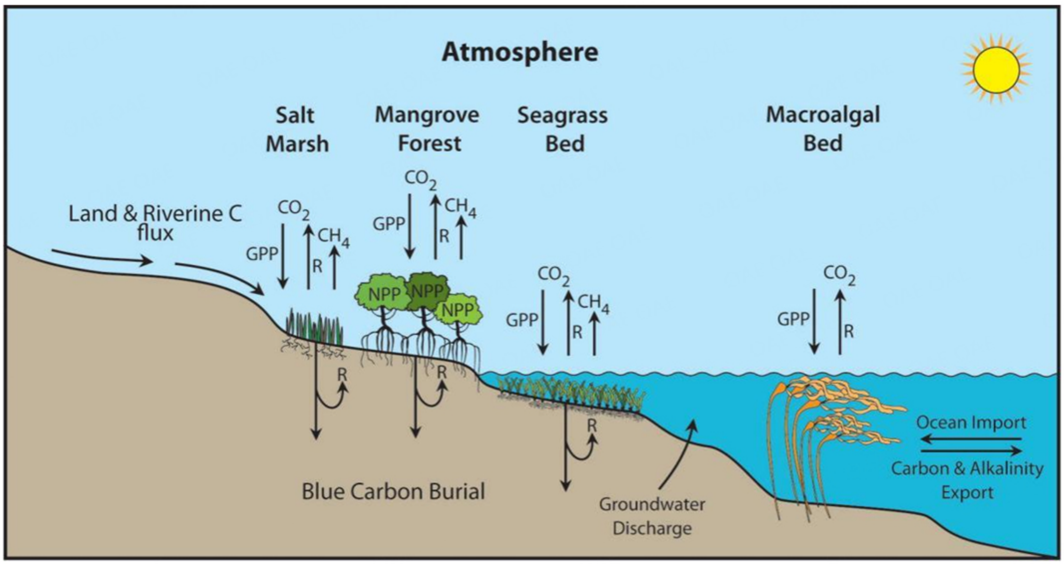

Figure 1. Diagram of major blue carbon pathways in coastal marine ecosystems. Note that nearly all macroalgal DOC and POC is exported to adjacent coastal ocean sediments. "Ocean Import" refers to allochthonous C_{ORG} inputs to blue carbon ecosystems. GPP: Gross primary production; NPP: net primary production; R: respiration; CO_2: carbon dioxide; CH_4: methane.

mangroves (and possibly macroalgal beds and tidal flats) is blue carbon. The remaining C_{ORG} is respired to the atmosphere by plants, sediment microbes and animals, or lost to the coastal ocean as dissolved inorganic carbon (DIC), dissolved organic (DOC) carbon, particulate organic carbon (POC) and alkalinity. Only in mangrove forests are large amounts of C_{ORG} stored in aboveground tree and root biomass. Rates of gross (P_{GPP} or GPP) and net forest production (P_{NPP} or NPP) are important aspects of blue carbon because tree growth leads to an increase in biomass as forests mature. It is important to understand spatial and temporal variations in rates of C_{ORG} sequestration in order to accurately scale up local estimates to larger scales. It is further necessary to better understand land-cover and land-use changes and to identify priority areas for rehabilitation, restoration, conservation, and management.

Productivity and carbon balance in blue carbon ecosystems

Ecosystem respiration (R_E = sum of all respiration within an ecosystem) is greatest in mangroves, followed by seagrasses and tidal marshes [Table 1]. Global R_E (= total R_E × global area of each ecosystem) is greatest for seagrasses [Table 1] whereas mangroves account for most gross primary production (GPP or P_{GPP}), but seagrass meadows contribute the most to global GPP. All three ecosystems are net autotrophic (ratio of $P_{GPP}/R_E > 1$), producing more plant C_{ORG} than is lost via respiration (R_E). In contrast, the coastal ocean is in overall carbon balance with a mean P_{GPP}/R_E ratio of 0.98 [Table 1].

Net ecosystem production (NEP = ecosystem GPP - R_E) differs among the three ecosystems, with salt marshes having the lowest NEP and mangrove and seagrasses the highest NEP. However, all three ecosystems contribute disproportionately to oceanic C_{ORG} storage.

Blue carbon stocks, sequestration rates and CO_2 emissions

Unsurprisingly, such highly autotrophic ecosystems are carbon-rich habitats. Estimates of area-specific and global C_{ORG} stocks, C_{ORG} burial rates and CO_2 emissions due to habitat conversion [Table 2] show large differences between habitats, with seagrasses encompassing the most global area, C_{ORG} sequestration, the highest loss rates and subsequent CO_2 emissions. Mangroves have the greatest mean C_{ORG} stocks and lowest mean C_{ORG} sequestration rates, whereas salt marshes occupy the least global area, and have the lowest global

Table 1. Contribution of coastal ecosystems to the carbon balance of the global coastal ocean. Percent values indicate percentage contribution of each ecosystem to gross primary production and ecosystem respiration in the global coastal ocean. Global areas are in Table 2. Table is cited with permission from Alongi[6]

Ecosystem	R_E	Global R_E	GPP	Global GPP	Mean P_{GPP}/R_E	NEP	Global NEP
Mangrove forest	35	306 1.1%	4,186	360 1.3%	1.18	628	54
Salt marsh	17	95 0.33%	2,109	116 0.41%	1.22	382	21
Seagrass meadow	21	342 1.2%	2,752	441 1.56%	1.29	619	99
Global Coastal Ocean	10	28,435	1,028	28,270	0.98	-6	-165

$R_{E:}$ Ecosystem respiration (g C m^{-2} year^{1}); GPP: gross primary production (g C m^{-2} year^{-1}); NEP: net ecosystem production (g C m^{-2} year^{-1}); global R_E, global GPP, and global NEP were calculated by multiplying global habitat area by R_E, GPP, and NEP, respectively.

Table 2. Area-specific and global C_{ORG} stocks, C_{ORG} burial rates and CO_2 emission losses from habitat conversion. Data sources: Alongi[6]; Hill *et al.*[7]; Gao *et al.*[8]; Duarte *et al.*[9]

	Mangrove	Salt marsh	Seagrass
Global area (10^6 ha)	8.34	5.50	16.0
Mean C Stock (Mg C_{ORG} ha^{-1})	738.9	317.2	163.3
Global Mean C Stock (Pg C_{ORG})	6.17	1.74	2.61
Mean C Sequestration (g C_{ORG} m^{-2} year^{-1})	179.6	212.0	220.7
Global C Sequestration (Tg C_{ORG} year^{-1})	14.98	11.66	35.31
Current Conversion Rate (% year^{-1})	0.16	1.32	1.5
C Emissions (Pg $CO_{2\text{-eq}}$ year^{-1})	0.088	0.084	0.144

ha: Hectare; C_{ORG}: organic carbon; Mg: megagram; Pg: petagram; g: gram; Tg: teragram.

mean C_{ORG} stocks and lowest global sequestration rates. Mangrove habitat losses are lowest among the coastal habitats, but all three have similar rates of CO_2 emissions [Table 2]. Most of these habitat differences reflect their global areas, but some differences do reflect inherent differences in rates of various biogeochemical processes[1,4,5].

There is considerable uncertainty in these mean and global carbon values, given the inherent differences in various methods used and the masking of large and certain spatial and temporal trends in the data. Therefore, caution must be applied in assessing comparisons within and between ecosystems. For instance, wet tropical mangroves on average have larger C_{ORG} stocks and greater rates of greenhouse gas emissions than those measured in arid-zone mangroves[1].

RESTORATION, REHABILITATION AND CONSERVATION

Fostering blue carbon storage requires augmenting conservation efforts by restoring and rehabilitating coastal habitats that have been lost. This is urgent as losses of blue carbon, particularly when sediment carbon is oxidized during disturbance and/or removal, result in erosional losses as well as subsequent oxidation upon exposure of sediment C_{ORG} and CO_2 efflux to the atmosphere, negating the impacts of burial.

Trajectories for blue carbon

Nations can directly offset their carbon emissions, restore and preserve sequestered C_{ORG} and facilitate other ecosystem services (e.g., coastal protection, wood, fisheries) by protecting, planting, and rehabilitating blue carbon ecosystems. Having information on sediment sequestration rates and increases in plant C_{ORG}

biomass with the growth and maturity of restored ecosystems is important to more accurately measure C_{ORG} increases via restoration and rehabilitation. These management tools assist in climate change mitigation via removal and burial of C_{ORG} in sediments.

Re-establishment of mangroves, seagrasses, and salt marshes results in a progressive increase in biomass C_{ORG} from early pioneering phases to maturity. A detailed example of such increases in a restored mangrove stand was found in *Avicennia marina* forests in southern Australia[10]. Using dating techniques and gas measurements to estimate carbon increases in restored 13-35 year old forests had a positive impact on C_{ORG} additionality and C_{ORG} sequestration rate. The older forests (17- and 35-year old) had twice the total C_{ORG} standing amounts and sediment sequestration rates than the youngest stand [Figure 2]. Although sediment C_{ORG} stocks increased with forest age, aboveground stocks were greatest in the 17-year old forest. Older mangroves released 25% of CH_4 emissions and twice the CO_2 flux compared to young stands, reflecting the fact that forest age had a significant impact on sediment C_{ORG} dynamics. This study and others[11-13] show that restored mangroves store increased amounts of C_{ORG} as they age, but this sink stabilizes once forests reach maturity. Blue carbon dynamics appears to be more complex in naturally regenerated (NR) mangroves[14].

In naturally expanding mangroves in Malaysia, standing amounts of ecosystem C_{ORG} in intact and different aged, naturally regenerated forests were similar despite a wide age difference (3-, 6-, 12-, 18-, 25- year). Sediment C_{ORG} stocks were unchanged, driving the constancy of total ecosystem C_{ORG} stocks over many years. Younger stands had greater C_{ORG} sequestration rates than the more mature stands. As the mangroves expand seaward, high suspended sediment loads upstream support higher bulk sediment density and C_{ORG} accumulation rates, suggesting that naturally regenerated mangroves composed mainly of young forests are significant C_{ORG} sequestrators, suggesting that nature-based solutions can be sought through avoidance of replanting[14].

Like mangroves, standing stocks of blue carbon and burial rates in restored salt marshes often show positive trajectories of establishment and growth, but no clear linear increase in sediment C_{ORG} storage and accumulation[15-18]. In restored salt marshes in England[15], C_{ORG} accumulation rates over a 150-year restoration period were initially rapid during the first 20-year, then slowly declined at a steady rate thereafter. In the century following restoration, a total accumulation of 74 t C_{ORG} ha^{-1} was estimated, with comparisons to natural marsh C_{ORG} content, inferring that about 100 year is needed for restored marsh C_{ORG} to approximate that in natural marshes. A comparison of C_{ORG} accumulation rates in restored versus old salt marshes in the United States[16] found that restored salt marshes can rapidly accumulate sediment C_{ORG}, although both old and restored habitats can have nearly identical C_{ORG} accumulation rates. In a naturally restored chronosequence of Chinese marshes[17], sediment C_{ORG} storage increased rapidly for the first 8-year after which it slowed down to the point that storage at the oldest restoration marsh (27-year) was 45% lower than in an adjacent natural marsh. Blue carbon may accumulate early in the chronosequence, but the patterns are complex and restoration of sediment C_{ORG} to the level of natural marshes may take decades. Across a 32-year chronosequence in Louisiana marshes[18], there was no significant difference in C_{ORG} accumulation rates among marshes with increasing age; all marshes were influenced by site-specific environmental conditions such as plant stem density and sediment type, with sites with high stem densities facilitated high long-term C_{ORG} accumulation[18].

Plant invasion

Warming temperatures and subsequent habitat contraction and expansion are impacting C_{ORG} sequestration and standing stocks in mangroves and marshes. A pattern has emerged of increased concentrations of

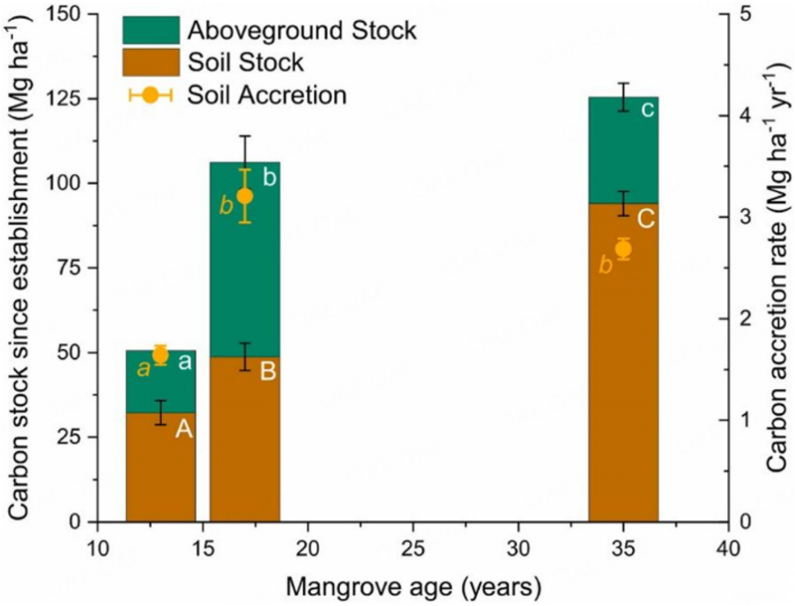

Figure 2. Increases in C_{ORG} stocks since establishment of mangrove forests aged 13-, 17- and 35-year old. Sediment C_{ORG} stocks (sediment C_{ORG} + belowground C_{ORG} stock) are brown bars. Values indicate mean ± 1 SE with different letters indicating significant differences in aboveground C_{ORG} stock (lowercase), sediment C_{ORG} stock (uppercase), and C_{ORG} accretion rate (italics). Reproduced with permission from Carnell *et al.*[10].

mangrove sediment and tree carbon as mangrove trees invade salt marsh habitats in warm temperate regions. In created *Spartina* marshes in Florida, most marshes have transitioned to mangrove habitat[19]. Mature habitats had greater C_{ORG} stocks than middle-aged transitional sites or young salt marshes; belowground C_{ORG} stocks were similar along the ecotone, indicating that aboveground C_{ORG} stocks (mangrove and marsh) were responsible for the difference in total ecosystem stocks. Over the salt marsh-mangrove ecotone, C_{ORG} storage correlated with ecosystem age, indicating that these transitional habitats can potentially become significant sites of C_{ORG} storage.

Restoration is an important climate mitigation strategy for seagrass meadows[20-24]. Across the Gulf of Mexico[20], seagrass restoration sites increased in sediment C_{ORG} stocks with an increase in restoration age from 13 (young meadow) to 22 (15-16-year-old meadows) Mg C_{ORG} ha^{-1} with a significant increase to 64 Mg C_{ORG} ha^{-1} (30-35-year-old meadows). C_{ORG} content between natural and restored sediments was similar, suggesting the potential for seagrass restoration to offset anthropogenic losses. In Virginia, USA[21], restored *Zostera marina* meadows of different ages (0-, 4-, and 10-year) showed higher sediment C_{ORG} content and accumulation rates in the 10-year meadow relative to the younger beds with restored seagrasses accumulating C_{ORG} at a similar rate to those in natural seagrass beds. Revegetated *Posidonia australis* meadows in Western Australia[22] restored seagrass C_{ORG} standing stocks [Figure 3A] and sequestration capacity [Figure 3B] 18-year after planting, like that in natural seagrass meadows (26 g C_{ORG} m^{-2} year^{-1}). Although seagrass restoration facilitated autochthonous and allochthonous C_{ORG} sedimentation and burial, sediment profiles indicated that seagrass losses triggered the erosion of historic C_{ORG} deposits. In carbonate seagrass meadows, CO_2 emissions driven by calcification can surpass C_{ORG} burial[23]. Eddy covariance measurements in Floridan seagrass meadows indicated that net consumption of alkalinity by calcification explained most of the measured CO_2 emissions, exceeding anaerobic alkalinity production and C_{ORG} burial. In seagrass meadows containing carbonate-rich sediments, C_{ORG} sequestration may, therefore, be overestimated if CO_2 emissions from calcification are not considered.

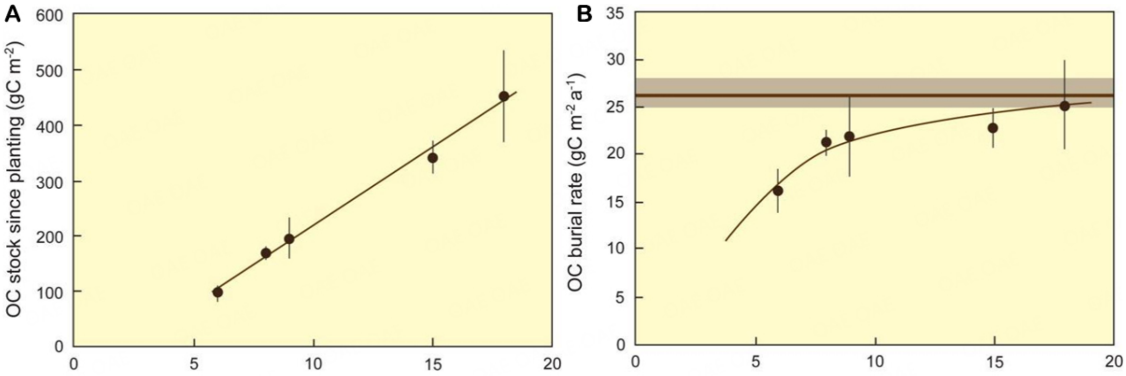

Figure 3. Blue carbon stock (A) and burial rate (B) changes across revegetated plots of the seagrass *Posidonia australis* at Oyster Harbour, Western Australia. The fitted linear regression line in (A) is significant ($P < 0.01$). The horizontal and darkened lines in (B) are the mean and 95% confidence limits, respectively, of the carbon burial rate. Reproduced with permission from Marbá *et al.*[22].

Macroalgal beds, such as kelp forests, may produce large standing stocks of blue carbon[24], but such habitats do not sequester C_{ORG} but export C_{ORG} to adjacent coastal sediments[1,25,26]. Measurements of carbon flux within a Japanese *Sargassum* bed[26] found that 6%-35% of net community production was transported offshore as DOC.

BLUE CARBON PROJECTS: FACTORS DETERMINING SUCCESS OR FAILURE

Restored mangroves and seagrasses usually show a positive blue carbon trajectory, but commercial restoration or rehabilitation projects designed to provide an income for local community participants and to utilize carbon offset methodology to participate in voluntary carbon markets have mostly been unsuccessful[1-5]. Many lessons still need to be learned to establish a successful project. A typical experience has been a blue carbon wetland pilot project located in Louisiana[27], where carbon offset methodology published by the American Carbon Registry was applied. Although modeling indicated a strong potential for C_{ORG} sequestration, the project was withdrawn due to very large uncertainty estimates mostly associated with greenhouse gas emissions and limitations of *in situ* sampling. Several steps were identified to increase the commercial viability of carbon offsets:

- Develop a strategy to minimize monitoring, reporting, and verification costs.

- Accounting fully for losses and preventing losses.

- Develop biogeochemical models and remote sensing methods to predict, monitor and verify greenhouse gas emissions and C_{ORG} sequestration and stock changes.

These problems have been universal in early and currently operating projects[1]. Most projects have had problems from poor management issues, such as improper success or failure criteria and poor or uncertain methodology. Many factors have constrained restoration, including habitat settings and types, hydrology, sediment characteristics, disturbance history, adequate seed banks and biodiversity issues.

Several restoration principles[28,29], if properly applied, can result in some successful blue carbon projects:

- Proper site selection.

- Utilizing local community participation and knowledge is highly recommended.

- Restoring natural hydrological processes.

- Adhering to clear and measurable ecological objectives, including success and failure criteria.

- Recognition that these habitats are immature ecosystems that require a long period of time to mature.

- Monitoring changes in blue carbon stocks, sequestration rates and greenhouse gas fluxes.

- Permit sufficient manipulation of physical processes to allow for habitat development.

- Understand the disturbance history of the site.

- Identify factors preventing natural recolonization

- Select a reference site for comparing plantation with natural forest processes, including topography.

- Construct, where deemed necessary, tidal channels.

- Assess costs early in the project design to ensure its cost-effectiveness.

Principles specifically for seagrass restoration include:

- Cover transplanted rhizomes for protection against storms and sediment movement.

- Application of a shell layer works to stabilize sediments.

From a policy viewpoint[30], most blue carbon conservation and restoration require not only community engagement, but several additional considerations, including:

- Need for genuine community participation.

- Need to maintain indigenous livelihoods and income.

- Need to integrate local work into government practices and policies.

- Need to include project governance.

- Need to simplify accounting and verification procedures.

Three potential management strategies[31] may help optimize the acquisition of blue carbon:

1. Reducing human disturbances, including flow of excess nutrients.

2. Restoring and maximizing proper tidal and hydrological flows.

3. Restoring top-down control of populations of bioturbating organisms.

Excessive nutrient additions, increasing stocks of sediment C_{ORG}, high densities of bioturbators and restrictions in water flow all result in disruption of sequestration and a decrease in C_{ORG} storage and net losses. Avoiding these disturbances serves to increase primary production and minimize blue carbon losses, either via greenhouse gas fluxes or surface and/or groundwater discharges.

Key international policy and carbon market frameworks

Restoration, management and conservation of blue carbon habitats have led to the development of climate mitigation, finance and policy frameworks that can be complex[1,30,32,33]. For instance, sufficient financing remains a problem for starting and sustaining blue carbon projects.

Climate finance and carbon markets

Loans, grants, or investments can all be mechanisms to finance projects[32]. Other forms may include bonds that are meant to generate profits for investors. Other finance mechanisms require strict processes for measurement of net abatement, such as payments within a REDD+ scheme. Carbon markets are a widely used means for generating finance. Such markets have standards because grants and donations are insufficient to generate significant funds to properly finance a project; the private sector has been seen as possibly resolving such monetary problems.

Ecosystems such as mangroves and salt marshes are covered by standards of voluntary carbon markets[32]. Some schemes link net emissions reductions to a greenhouse gas inventory and are therefore limited by blue carbon activities in IPCC guidance. Three main principles for blue carbon viability from a marketing perspective are: additionality, permanence, and leakage[33]. Additionality ensures that reduced emissions occur not only to project activities, but also when restoration gains are greater than ecosystem losses. Coral reefs do not meet the additionality principle because they produce a net release of CO_2. Mangroves, salt marshes and seagrasses, in contrast, produce a net uptake of CO_2 and thus meet the additionality principle[33]. Permanence means sustainable net greenhouse gas reductions. This is a requirement in carbon markets. Leakage refers to any activity likely to cause an unforeseen enhanced rate of emissions. For instance, increased emissions of CH_4 and/or N_2O, both of which have higher global warming potentials than CO_2, can create leakage[33].

Blue carbon accounting and return-on-investment

Few credit- or revenue-generating projects have been successful due to (1) low incentives for credit buyers; (2) high uncertainty of credible reductions in emissions; (3) high project costs; (4) limited guidance to measure return-on-investment (ROI); and (5) unknown viability of new projects, are all factors that reduce and/or limit investment. For example, in the Philippines, mapping and modeling of mangrove natural regeneration (NR) versus manual replanting (ANR) in abandoned shrimp ponds[34] indicated that return-on-investment was greater under manual replanting, but neither mode of restoration strategy was profitable at the current carbon market prices.

EMERGING PERSPECTIVES

Blue carbon research has now been ongoing for more than twelve years, and therefore, some perspectives have emerged regarding blue carbon science and management. The perspectives offered below are not comprehensive but do provide some guidance as a way forward on this issue. These perspectives are not necessarily listed in order of importance.

Only net autotrophic ecosystems that sequester carbon meet the carbon market criteria of additionality and permanence

A genuine blue carbon ecosystem produces more net ecosystem C_{ORG} than it loses as ecosystem respiration (P:R ratio > 1). That is, it must be a net producer of blue carbon to allow sufficient C_{ORG} sequestration and storage. Coral reefs are not blue carbon systems because they are in overall metabolic balance (P:R ratio ≈ 1). Tidal flats, which store large amounts of C_{ORG}, are most often net heterotrophic (P:R ratio < 1). Tidal salt marshes mangroves and seagrass beds qualify, being net autotrophic and C_{ORG} storage habitats [Table 1]. Arguments have been raised suggesting that tidal flats, seaweeds and macroalgal beds constitute blue carbon ecosystems. Negative arguments have been raised[34,35], including critical data gaps such as rates of CO_2 emissions and, in the case of macroalgae, the proportion of algal C_{ORG} exported to adjacent ecosystems, such as adjacent beaches and the deep ocean. Other workers, however, have concluded that macroalgae constitute a blue carbon ecosystem[36-40]. For example, macroalgae contributed more C_{ORG} to seagrass sediments in Malaysia[40] than seagrasses themselves , with mangrove C_{ORG} contributing the bulk of the material. Off Singapore[41], *Ulva* and *Sargassum* assemblages accounted for 650 Mg C_{ORG} in biomass, greater than aboveground seagrass C_{ORG} but lower than mangrove C_{ORG} with a potential sequestration rate comparable to tropical grasslands and temperate forests. Similarly, arguments have been raised that although tidal flats are not necessarily net autotrophic, they often sequester large amounts of $C_{ORG.}$ A global meta-analysis[42] calculated that tidal flats accumulate C_{ORG} at a mean rate of 129.8 g C m^{-2} $year^{-1}$, slightly less than rates in acknowledged blue carbon habitats [Table 2]. However, as measured in Chinese tidal flats[43], C_{ORG} sequestration rates vary widely from 35 to 361 g C m^{-2} $year^{-1}$. Tidal flat sediments to a depth of 1 meter contain an average of 86.3 Mg C ha^{-1} which is less than in blue carbon environments[40]. At this stage, insufficient evidence exists to support the notion that macroalgal and tidal flat habitats are blue carbon ecosystems, especially since in the former case most macroalgal C_{ORG} tends to be sequestered in other habitats[1,34,35]. In the latter case, tidal flats are declining globally due to extensive coastal degradation due to human developments, reduced riverine sediment export, sinking of river deltas, increased erosion and sea-level rise[44].

Constraints on carbon accounting and investment are the large ecological and economic uncertainties; investor interest indicates a huge demand, but supply of blue carbon credits remains small

All ecosystems have large natural uncertainties that limit carbon accounting and investment that rely on knowing precise details to attract investors[1]. Risk must be reduced to maximize the probability of return-on- investment; the likelihood of attractive returns needs to be demonstrated[45]. Constraints include: (1) measurement uncertainty and significant variability in blue carbon storage, burial and greenhouse gas emissions; (2) logistical problems; (3) technical infrastructure and capacity; (4) governance issues; (5) existence (or not) of proper regulatory frameworks; (6) habitat permanence; (7) viability of property tenure; (8) long timeframe of blue carbon ecosystem maturity; and (9) possible need for different policy mechanisms for a specified finance type (e.g., public or private funding).

The potential need for carbon credits from investors and companies may be as much as $10 billion, but market-related challenges currently limit project implementation and the sale of resulting credits. Problems include blue carbon verification and costs, the small scale of blue carbon projects, and dual credit counting between national and commercial institutions[46]. Other financial instruments such as ecosystem service insurance and bonds may be viable alternatives to more conventional forms of funding. A detailed analysis of the role of economics in blue carbon ecosystem marketing[47] concluded that several actions are needed to view coastal blue carbon habitats as a natural climate solution: (1) improving legal and policy arrangements to ensure equitable sharing of benefits; (2) improving stewardship by incorporating local community knowledge and values; (3) clarifying property rights; (4) improving financial approaches and accounting tools to incorporate co-benefits; (5) developing technological solutions for low-cost measurement of blue carbon sequestration; and (6) clarifying information gaps of blue carbon cycling. Additional improvements to current practices include better stakeholder engagement, targeted use of public and philanthropic funding to subsidize pilot projects, reduce financial risks through collaterals, and promote low-risk but high-profit projects[46,47].

Salt marshes, seagrasses and mangroves contribute to climate change mitigation at national, regional and global scales

Early studies[3,31] justified their interest in blue carbon by asserting, without any empirical data, that blue carbon ecosystems must sequester significant amounts of C_{ORG} to the extent that they play a globally significant role in mitigating greenhouse gas emissions. Global areas of salt marshes and mangroves are small[48] and their contributions are disproportionate, but recent calculations show that they mitigate only 0.4% (including seagrasses) of global CO_2 emissions related to fossil fuel use[49]. Another estimate for mangroves indicates that they mitigate only 0.2% of total fossil fuel emissions. However, mangroves contribute significantly (18%) to emissions from the tropical ocean[6] and both mangroves and salt marshes account for ≈70% of air-sea CO_2 exchange from global wetlands, and ≈30% of DIC export and ≈15% of DOC and POC export to the global coastal ocean[6]. Nevertheless, revised estimates of global areas and C_{ORG} standing stocks of seagrasses [Tables 1 and 2] suggest that they are likely to be the main contributors to climate change mitigation. Global sequestration rates of seagrasses are ≈3 and 15 times, respectively, greater than salt marshes and mangroves [Table 2]. However, due to high habitat losses, seagrasses currently emit nearly double the amounts of CO_2 from salt marshes and mangroves [Table 2]. Salt marshes, mangroves and seagrasses account for 1.0%, 2.4% and 4.5% of global NEP of the global ocean, respectively[42].

Climate change impacts on blue carbon dynamics are complex and highly variable over space and time

Climate change-related disturbances usually result in highly variable and significant changes in blue carbon stocks, sequestration rates, and greenhouse gas fluxes. Increasing sea temperatures, increasing frequency and intensity of heat waves, and extreme weather events lead to positive, negative or complex changes in blue carbon dynamics. A long-term record of sediment C_{ORG} stocks in a restored *Zostera marina* meadow[50], depending on the position in the meadow, showed that a single heat wave led to significant losses of sediment C_{ORG}, with patterns of C_{ORG} losses and re-accumulation lagging seagrass recovery times within the central meadow. However, in the outer meadow, there was a net increase of 60% of sediment C_{ORG} throughout the following 3-year. Overall, areas of higher seagrass recovery maintained nearly twice as much C_{ORG} compared to areas of lower recovery. Under conditions of extreme weather events that result in mangrove dieback, degraded mangroves lose significant amounts of blue carbon, often as DIC outwelled to the adjacent coastal ocean[51]. Degraded mangroves in the Dutch Caribbean, for example, lost 1.5 Mg CO_2 ha^{-1} $year^{-1}$ from a 10% loss of sediment C_{ORG} compared with intact mangroves. Modeling exercises[52,53] suggest complex effects of climate change on blue carbon dynamics will depend on future rates of sea-level rise and rates of temperature and precipitation increases and patterns. One model[52] found a rise in global C_{ORG} storage by coastal tidal wetlands by 2100 based on projected emissions scenarios and current climate factors, with a rapid change driven by sea-level rise in salt marshes and higher temperature changes and changes in precipitation patterns in mangrove forests. Modeling the effects of two IPCC climate change scenarios ("business-as-usual" and "high-emissions") and using model estimates of past, present, and future deforestation rates of mangroves[53], another model found that global C_{ORG} stocks will increase by ~7% regardless of scenario; this gain will be greater than losses from mangrove deforestation by 2100. However, results will vary regionally, with some areas seeing a drop in sediment sequestration rates. Thus, both empirical data and models indicate the complex effects of climate change on these ecosystems.

Export of porewater dissolved carbon and alkalinity via subsurface groundwater discharge is a major pathway of blue carbon loss, but alkalinity and DIC discharge can result in localized buffering of coastal acidification

Two preliminary mangrove carbon budgets[54,55] show that ≈50% of mangrove carbon fixation was unaccounted for (known as "the missing carbon"), representing a large global carbon flux. This gap prompted extensive research, which ultimately revealed that large amounts of porewater DIC and DOC are exported from mangroves via subsurface discharge. This finding has resulted in a revision of the blue carbon budget[56], in which the missing carbon is a large export of dissolved carbon. Tidal pumping[57] is a major driver of mangrove porewater exchange and associated dissolved CO_2 export; global porewater-derived CO_2 export from mangroves (83 Tg C year^{-1}) was considerably greater than earlier estimates of flow via water-air exchange (34.1 Tg C year^{-1}) and C burial (18.4-34.4 Tg C a^{-1}), suggesting that the escape of porewater CO_2 is an important pathway of CO_2 flux to adjacent coastal waters[57]. Work in Chinese mangroves[58] indicates that about half of DIC produced in mangrove sediments is derived from both sulfate reduction and terrestrial groundwater discharge. Salt marshes are also an important reservoir of dissolved carbon in the coastal waters[59-62], with most DIC generated in summer when higher temperatures stimulate anaerobic respiration[59-62]. In some salt marshes, groundwater export of dissolved carbon exceeds sediment C_{ORG} burial rates[62], reflecting the large amounts of dissolved carbon released to adjacent waters. Seagrass meadows laterally transport DOC with their rapid metabolism causing overlying waters to contain low CO_2 concentrations and enhancing atmospheric CO_2 uptake[63,64]. Carbon fluxes are more complex in seagrasses inhabiting carbonate environments[64], with variable rates of CO_2 flux in relation to seagrass composition. Downward fluxes were found only over seagrasses, whereas the presence of calcifying algae resulted in CO_2 release.. DIC export from a *Posidonia* meadow[65] exceeded above-meadow CO_2 outgassing, with DIC uncoupled from alkalinity fluxes. The slight release of alkalinity suggested that ≈90% of exported DIC was eventually lost offshore as CO_2 was released to the atmosphere; combined flows indicated a carbon loss exceeding C_{ORG} sequestration.

Microbial decomposition of benthic organic matter via fermentation, sulfate, iron and manganese reduction, and methanogenesis results in several metabolic by-products (e.g., DIC and alkalinity) that are then transported via subsurface groundwater to adjacent coastal waters[56,66]. In mangroves inhabiting carbonate deposits in the Red Sea[66], total alkalinity emission from carbonate dissolution supported a CO_2 uptake of 345 g C m^{-2} year^{-1}, 23-fold the C_{ORG} sequestration rate; total alkalinity emission was large (403 mmol m^{-2} d^{-1}). In the Everglades[67], most DIC was exported as total alkalinity (97 mmol m^{-2} d^{-1} of a total dissolved carbon export of 142 mol m^{-2} d^{-1}), with both values several times greater than C_{ORG} burial rates. Large alkalinity export was also measured across an inshore to offshore mangrove continuum on the Amazon coast[68], with export rates of DIC (20 mmol m^{-2} d^{-1}) and alkalinity (15.2 mmol m^{-2} d^{-1}) equating to nearly 80% of C burial rates. Globally, mangroves export 17 T_{MOL} year^{-1} of alkalinity[56]. Seagrass meadows and salt marshes produce and export alkalinity but at lower rates than mangroves[68,69]. Alkalinity is produced via sulfate reduction coupled with pyrite formation, with greater pyrite stocks in mangroves than in salt marshes and seagrasses[69]. Global alkalinity release from mangroves, apparently linked to the formation of pyrite, equals ~24% of the global mangrove C_{ORG} sequestration rate. Macrotidal salt marshes such as those in China[70] export large amounts of DIC (202 mmol m^{-2} d^{-1}) and alkalinity (78 mmol m^{-2} d^{-1}) with a ratio which implies alkalinity production from anaerobic mineralization in sediment. Further, lateral exports were equivalent to C_{ORG} burial rates.

DIC and alkalinity export results in an observable, localized increase in pH in adjacent coastal waters, partially counteracting coastal acidification. The magnitude and impact of this effect will be site-specific, depending on residence times of tidal waters and on other sources or sinks of DIC and alkalinity. For mangroves[71,72], a pH change is likely to be greater in greater areas of mangrove and likely to be more significant where coral reefs also occur. For seagrasses[73], several factors influence their ability to buffer ocean pH, including photosynthetic activity[73], mode of DIC uptake[74], extent of seagrass loss[75] and seasonality[76]. For instance, in 7 *Zostera marina* meadows spanning the US west coast[76], amelioration by seagrasses showed an improvement compared to non-vegetated areas, with an overall increase of 65% over 6 years, accompanied by a mean pH increase of 0.07. Sustained elevations of pH > 0.1 occurred for up to 21 days, even at night, with maximum pH increases in warmer months during maximum growth season. The buffering influence of seagrasses on ocean pH can also positively impact their epibionts and neighboring calcifying algae[77,78]. Salt marshes similarly exhibit variations in pH, reflecting oscillations in DIC and alkalinity export[79], complex mixing of estuarine water[80], and climate[81]. Macroalgae in the form of kelp beds[82] and seaweed farms[83] have the capacity to locally ameliorate ocean acidification via photosynthetic drawdown of CO_2 and may serve as refugia for carbonate-rich organisms, such as sea urchins and foraminifera[84]. Furthermore, coastal acidification stimulates macroalgal germination[85], growth[86] and photosynthetic[87] rates.

Mineralization of ancient wetland deposits contributes to DIC and DOC groundwater discharge to adjacent coastal waters

The large rates of dissolved carbon and alkalinity export from blue carbon ecosystems imply correspondingly rapid rates of microbial C_{ORG} mineralization in sediments, the source of these solutes. It was once assumed that the bulk of bacterial activity in wetland sediments occurs mostly in surface sediments (< 1-20 cm), mainly in association with recent deposition and subsequent decomposition of fresh organic material or surface microalgae and in proximity to roots and rhizomes, animal tubes and burrows[55,56]. However, large C_{ORG} stocks exist several meters into the sediment and, in at least one location, to a mangrove sediment depth of 6 meters[88]. Such deep deposits have been dated to 1,000-5,000 ^{14}C BP (before present)[56] and are thus derived from extinct habitats that are not directly linked to contemporary wetland habitats. Studies have also found that old porewater can be exported and that bioturbation can stimulate the decomposition of ancient, buried carbon[89,90]. ^{226}Ra measurements in mangrove sediments indicate that construction of new crab burrows exposes old deposits, enhancing mineralization of old carbon via deep sediment oxygenation by crab bioturbation[89]. Measurements of $\Delta^{14}C$ in exported DIC from subtropical Australian mangroves indicate the release of old DIC that is isotopically depleted, derived from at least a century-old sediment deposit[90]. Century-old C_{ORG} buried in deep deposits is still in the process of being decomposed and transported via porewater and/or submarine groundwater discharge. This scenario is reminiscent of results in a coastal marsh[91] where sediment $\Delta^{14}C$ profiles indicated that sequestration rates at the decadal scale were much higher than rates at the millennial scale. This finding indicates either that old buried carbon was still being mineralized or that there was a recent increase in plant productivity. Bacterial metabolism in mangrove sediments has been measured to a depth of 1 meter[56], showing no clear trends in bacterial metabolism with increasing depth, suggesting that mineralization of old buried carbon may persist to even greater depths. More research is needed to clarify the role of ancient wetland deposits on blue carbon cycling and wetland biogeochemistry.

Blue carbon ecosystems require allochthonous organic carbon inputs to achieve carbon mass balance

A recent carbon mass balance for mangrove ecosystems[56] found that rates of autochthonous C_{ORG} incorporation (root, wood, leaf litter production) into forest sediments were not sufficient to balance microbial decomposition rates. One possibility to redress this imbalance is to include mineralization from deep ancient deposits (Perspective 6) as an ecosystem carbon input. Another possibility is that mangroves are reliant on allochthonous inputs to balance ecosystem carbon flow. In fact, about 58% of $\delta^{13}C$ data of mangrove sediment[92] is low (< -25‰), suggesting mangrove litter, but relatively high values indicate large inputs of ^{13}C-enriched carbon sources, such as various algae and river-derived POC rather than mangrove-derived plant matter. About 60% of known mangrove study sites[56] show that sediment C_{ORG} is derived mostly from allochthonous sources, including seaweed and algal-derived detritus from seagrasses and coral reefs, higher terrestrial land plants, dead bacterial biomass, and phytoplankton and POC derived from adjacent rivers, estuaries, coastal and open ocean sources. However, the proportion of mangrove litter, roots and wood detritus to the sediment C_{ORG} pool increases with stand age. In many seagrass meadows, non-seagrass detritus accounts for ~50% of sediment C_{ORG}, likely originating from allochthonous organic material that is transported and trapped by seagrass sediments. The percentage of allochthonous inputs to seagrasses is partly a function of distance from the source[93]. For example, salt marshes at San Quintin (an arid Eastern Pacific lagoon) receive 40% of their C_{ORG} from external inputs, whereas in seagrass meadows open to lagoonal currents, the C_{ORG} source is largely allochthonous[94].

Restored ecosystems often reveal temporal differences in blue carbon sources. In restored and pristine salt marshes in Washington, USA[95], autochthonous marsh C3 plants contributed 73%-89% to unaltered marshes, whereas restored marshes received a wide array of mostly allochthonous C_{ORG}, which varied in relative contribution by distance from the source and abundance. All three coastal ecosystems thus receive and are greatly reliant on allochthonous sources of C_{ORG} to maintain their metabolic requirements and to balance their carbon inputs and outputs.

Habitat connectivity enhances blue carbon uptake and release

The export of allochthonous matter from one ecosystem to another illustrates the importance of connectivity between habitats, enhancing the flow of blue carbon. Mangrove-derived seston exported to adjacent seagrasses in Gazi Bay, Kenya[96] resulted in increased CO_2 concentrations and increased C_{ORG} content in the water column; flow reverses via tides transport high-quality seagrass carbon to the mangrove forest. The extent of input from one habitat to another partly depends on distance. On the north Sulawesi coast, Indonesia[97], seagrasses adjacent to mangroves have significantly higher sediment C_{ORG} concentrations than in non-adjacent meadows; in the adjacent meadows, mangrove C_{ORG} contributes 34%-83% to sediment C. Several mechanisms exist through which one blue carbon habitat may influence C_{ORG} concentration and sequestration in adjacent habitats, such as outwelling, sediment trapping, nutrient fluxes, wave dampening, trophic cascades, and tidal regimes[98]. The co-metabolism effect may also result in enhanced carbon flow[99]. In experiments where macroalgal detritus was mixed with seagrass detritus, high density macroalgal addition stimulated the decomposition of 20% more seagrass compared to other treatments. Coral reefs and seagrass meadows often co-occur and are connected by various ways, including enhancement of water column and sediment carbon. For instance, seagrasses benefited by close association with Colombian coral reefs[100], with seagrasses within reef barriers having greater sediment C_{ORG} concentrations than seagrasses without a reef barrier. Seagrasses also benefit from close physical proximity to mangroves as found on the Andaman and Nicobar Islands, India[101], and along a mangrove-seagrass-reef continuum fringing Iriomote Island, Japan[102], where carbon transport from adjacent mangroves and rivers offsets uptake of CO_2 by seagrasses; the coral reefs take up DIC, DOC and alkalinity, fostered by suppression of high sedimentation by the ability of mangroves to trap sediment particles.

Bioturbation, grazing, and predation affect blue carbon dynamics

Biota can affect several aspects of blue carbon via a network of trophic interactions among plants, animals and microbes, exerting strong effects on biogeochemical dynamics in blue carbon habitats[103]. For instance, a variety of predators influence blue carbon stocks and sequestration rates[104], including the effects of reduced predation on C_{ORG} sequestration in salt marshes and mangroves and C_{ORG} concentrations in seagrasses. Declines in various predators (e.g., New England blue crabs, predatory mangrove fish in Australia) result in an increase in bioturbator numbers but a decline in the capacity for C_{ORG} sequestration[104]; in Shark Bay, Western Australia, the presence of tiger sharks results in sea turtles and dugongs foraging in seagrass communities that are low in terms of risk from predation, but leads to these seagrasses having lower C_{ORG} stocks than areas associated with high predation risk. Arguably the greatest and most direct impacts by biota on blue carbon are produced by bioturbators[105,106]. For example, salt marsh crabs produce burrows that enhance CO_2 release across the sediment-water interface due to tidally-driven hydraulic gradients[105,106]. Grazing has a similar effect on seagrass meadows, resulting in a several-fold increase in CH_4 emissions; this increase can be attributed to the decline in loss of downward oxygen transport caused by the grazing decline in living seagrass biomass[107]. An assessment of risks[108] indicates that indirect, large-scale threats from ocean warming, heatwaves, and sea-level rise and direct small-scale threats from activities such as dredging and the building of jetties or a marina have a higher risk of increasing CO_2 emissions from seagrass than to recover their ability to sequester C_{ORG}.

Calcium carbonate chemistry affects blue carbon budgets

The presence of calcium carbonate ($CaCO_3$), especially in tropical seagrass meadows, plays a crucial role in inorganic carbon cycling (Perspective 5) and cycling of blue carbon. $CaCO_3$ production emits CO_2, partially offsetting the role of carbonate-rich ecosystems as CO_2 sinks through C_{ORG} sequestration[109]. A global analysis[109] of inorganic carbon (C_{INORG}) burial rates indicates rates of 0.8 Tg C_{INORG} year^{-1} and 15 to 62 Tg C_{INORG} year^{-1} in mangroves and seagrasses, respectively. Burial of $CaCO_3$ may correspond to an offset of as much as ≈30% of seagrass CO_2 sequestration. Seagrasses living in $CaCO_3$-rich sediments may have CO_2 sequestration neutralized by CO_2 released via calcification[110]. Thus, CO_2 emissions driven by calcification processes may exceed rates of C_{ORG} sequestration in carbonate seagrass habitats[111]. In Florida seagrass meadows, net consumption of alkalinity by calcification accounts for nearly all CO_2 emissions[111]. Therefore, net carbon sequestration in carbonate-rich environments may be overestimated if calcification is not included in chemical budgets. Some tropical seagrass meadows with calcareous algae may have higher seagrass productivity and C_{ORG} storage[112]. Off Zanzibar, Tanzania, biomass production was higher in meadows containing both seagrass and calcareous algae than in meadows without algae; sediment C_{ORG} levels were also highest in seagrass meadows with calcareous algae.

Methane and nitrous oxide emissions reduce blue carbon potential

As both CH_4 and N_2O are significantly more potent greenhouse gases than CO_2, their emissions reduce the value of a given habitat as a carbon sink, and in salt marshes, may negate the value of stored C_{ORG} towards mitigating climate change[113]. In coastal marshes in Georgia, USA[114], CH_4 fluxes via groundwater average ≈3 g CH_4 m^{-2} year^{-1} as a greenhouse gas over a century timeframe, which is equal to rates from other salt marshes. Submarine groundwater discharge results in a large increase in CH_4 export that offsets about 30% of the cooling potential from C_{ORG} sequestration. In mangroves, CH_4 efflux rates similarly have the potential to partly offset C_{ORG} burial rates, possibly by as much as 20%[115]. Both dead and living mangrove tree stems release CH_4 to the atmosphere, with rates 8-fold higher from standing dead stems than from living stems; upscaling to mangrove dieback in the Gulf of Carpentaria, Australia, dead tree emissions may account for as much as 26% of net ecosystem CH_4 flux[116]. Processes regulating CH_4 and N_2O fluxes in mangroves, marshes, and seagrasses are complex, complicating efforts to derive blue carbon benefits[117].

Black carbon reduces estimates of labile carbon in blue carbon budgets

"Black carbon", defined as carbon formed by incomplete combustion of fossil fuels, burning biomass, and other pollution, is highly recalcitrant and found in increasing abundance and proportion in soils and sediments, entering coastal waters via rivers and atmospheric deposition. Black carbon can account for as much as 9% to 25% of organic carbon content in subtropical-temperate deltas of the major rivers in China[118], with an accumulation rate of 33 g m^{-2} $year^{-1}$ in China's coastal wetlands, suggesting they act as a hotspot for black carbon and a substantial contributor to blue carbon storage. Similar results have been measured in a temperate salt marsh in Tasmania, Australia, and in a tropical Malaysian seagrass meadow[119]. Black carbon accounted for 38% and 22% of the sediment TOC fraction in the seagrass and marsh ecosystems, respectively, demonstrating the need to account for black carbon in future blue carbon assessments. The contribution of black carbon to total C_{ORG} standing stocks depends partly on environmental history of the ecosystem[120]. For example, in a fire-affected region of Malaysia[121], the black carbon to total C_{ORG} ratio was 43% in an adjacent seagrass meadow but 18% in a sandy, low organic content meadow; in moderately polluted mangroves, the ratio was 2% but higher (6%) in highly polluted mangroves. The black carbon to total C_{ORG} ratio for seagrasses also varies between urban and rural meadows and is twice as predicted, at 28% and 36%, respectively. The high fractions are likely the result of variability of black carbon atmospheric supply, an increase in seagrass litter loss close to exposed meadow edges, and sediment resuspension within the dispersed patchy meadow. Black carbon thus has an overall negative impact on the storage of labile blue carbon.

Habitat destruction results in blue carbon stock losses, but variable gas emissions

Rates of sediment C_{ORG} changes and greenhouse gas emissions vary partially depending on the type of disturbance to which an ecosystem is subjected. Clear-felling of mangroves, for instance, reduces sediment C_{ORG} stocks via erosion and subsequent transport[1], but short-term increases in CO_2 release may occur[122]. In Mexican mangroves[123] subjected to hydrological perturbations, CH_4 emissions were highest in the wet season in a dead mangrove area, whereas CO_2 emissions were highest during the dry season with no significant differences among disturbance levels; N_2O release did not vary among seasons and degradation levels. In a mangrove area in Vietnam[124] that was cleared 2-year prior to sampling, sediment losses amounted to ~10 Mg C_{ORG} ha^{-1} $year^{-1}$ with mean sediment CO_2 fluxes of 24 mmol m^{-2} d^{-1}, nearly 3 times lower than rates in planted 16-year old forests. Reforested and rehabilitated forests reveal different rates of greenhouse gas release depending on the state of the forest and the type of gas. In managed forests in the Ranong Biosphere Reserve, Thailand[125], the highest CO_2 effluxes were measured in an undisturbed primary forest compared to reforested and naturally rehabilitated forests. However, CH_4 emissions were significantly higher from the natural rehabilitation forest, especially in low-intertidal areas with longer tidal flooding; N_2 O emissions did not vary among mangrove forest types. In cyclone areas, mangroves can lose blue carbon mostly as enhanced export of litter and DIC[126]. For salt marshes, various disturbances can affect blue carbon fluxes such as sediment metabolism. In high salt marshes in Virginia, USA[127], impacted by sea-level rise, modeling indicates that increased inundation would reduce respiration rates to a greater extent than primary production, resulting in a moderate loss of blue carbon. Impoundment can also have significant impacts on blue carbon gas emissions in salt marshes. In *Phragmites*- invaded marshes in Massachusetts, USA, freshening to lower salinity led to a 50-fold increase in CH_4 emissions but with only moderate increases in CO_2 efflux[128]. Although freshened, impounded marshes can be strong carbon sinks with CH_4 release partially offsetting C sink capacity.

Benthic blue carbon stocks are increasing in polar and subpolar regions

Blue carbon stocks are increasing in polar seas partly due to prolonged phytoplankton blooms driven by losses of sea ice and collapsing ice shelf as a result of climate change; these blooms, in turn, fuel productivity of benthic infauna and, to a much lesser extent, epibenthos[129]. Sea ice losses also make the West Antarctica continental shelf a central location for iceberg disturbance as ice scour limits C_{ORG} storage and resets succession of benthic biota, fertilizing the ocean with nutrients and generating phytoplankton blooms in which excess organic carbon eventually deposits onto the seabed where it is partly consumed and buried[130]. Along Antarctic fjords, glacial retreat also results in blue carbon gains, leading to an increase in zoobenthic blue carbon of up to 4,536 t C_{ORG} $year^{-1}$[131]. At three fjords along the West Antarctic Peninsula, further pathways of C_{ORG} storage were measured along a temporal gradient since the last glacier cover to test the idea that seabed carbon standing stocks would be a function of glacial ice cover[132]. The results were complex, with highly variable infauna numbers and carbon concentrations over time, like the epifauna. However, sediment C_{ORG} concentrations were much greater than total benthic faunal carbon. In shallower waters around the Antarctic Peninsula, infauna contained 60% less blue carbon (391 t C_{ORG} km^{-2}) than epibenthic communities (648 t C_{ORG} km^{-2})[133]. This carbon sink may double as climate-mediated ice loss continues. Increasing melt from glaciers not only results in blue carbon storage but shifts benthic communities from net autotrophs to heterotrophs[134]. Clear waters during cold El Niño in spring 2015 facilitated high benthic microalgal productivity, shifting the benthic community to net autotrophy. However, increased glacial melt during the La Niña spring of 2016 resulted in water column turbidity, limiting benthic algal productivity, and turning the benthic faunal community from net autotrophic to net heterotrophic.

Data from the Arctic is extensive for carbon accumulation in infauna and sediments, whereas most Antarctic blue carbon data was confined until recently to epifauna. In Arctic fjords, pelagic and benthic carbon is abundant, with high rates of C_{ORG} deposition, sediment burial and faunal consumption[135-137]. Both terrestrial and macroalgal C_{ORG} were important sources of sedimentary C_{ORG} in most fjords, many of which are hotspots of C_{ORG} sequestration. However, there are strong spatial gradients in sedimentation rate and primary productivity that in turn impact benthic C_{ORG} uptake and burial[136,137]. Driven by warmer temperatures, glaciated fjords may become less efficient at burying C_{ORG} in deep sediments[137]. One cause for the long-term persistence and high C_{ORG} sequestration rates in Arctic sediments may lie in the tight binding of C_{ORG} to reactive iron and manganese, resulting in preservation for thousands of years[138]. In Arctic coastal wetlands in Norway[139], carbon sequestration rates were highly variable over space and time (9-603 g C_{ORG} m^{-2} $year^{-1}$), correlating with an increased growing season. Blue carbon storage is low mostly due to new marsh formation with a thin organic sediment layer. Stocks of C_{ORG} and the increasing frequency of shallow polar habitats may be greater than previously assumed, equating to negative feedback on the rapidly changing polar climate.

Historical ecological shifts occur among blue carbon ecosystems

Historical ecological shifts occur in coastal blue carbon ecosystems. Tidal mudflats can be colonized by mangrove propagules until successive changes result in a mangrove forest beneath which lies the remnants of the original tidal flat. These historical deposits can continue to participate in contemporary carbon cycles (Perspective 6). In four Australian wetlands, environmental histories were reconstructed with respect to blue carbon conditions to assess the impact of historical factors on modern C_{ORG} stocks and burial rates[140]. High C_{ORG} stocks were linked to thick mangrove peat layers below the modern salt marsh deposits in both marine and fluvial sites where historic mangrove roots were found to be chemically stable, considering their advanced age. Cores from marine-influenced and fluvial-influenced salt marshes did not contain mangrove root C_{ORG}, but there was significant preservation of charcoal at the fluvial-influenced marsh. These results suggest that both classification of modern vegetation structure and geomorphic setting are insufficient to account for carbon stock variability and accumulation rates. Ecosystem changes are not uncommon and can still result in the preservation of old C_{ORG}. Stratigraphic evidence of extensive mangrove root networks beneath modern grasslands and salt flats in northern Australia suggests the existence of extensive, pre-historic mangroves approximately 5,500-7,000 years BP[141]. Other studies such as in the Mekong River delta have similarly revealed the presence of ancient mangroves, salt marshes, and tidal flats below modern deltaic sediments[142]. The significance of this ancient preserved carbon remains unknown, but may be of great biogeochemical and geological significance considering the sizes of many deltaic systems. Evidence of successional patterns in mangrove vegetation in locations such as the Mekong Delta[143] may also be of great importance with regard to blue carbon, but similarly are undetermined. Molecular fingerprinting can now identify sources and preservation state of organic matter in blue carbon habitats[144,145]. Moreover, habitat shifts affecting blue carbon stocks have occurred, and continue to occur, among coastal communities in Spencer Gulf, South Australia. The main source of sediment organic matter in these habitats is vascular plant material that is well-preserved due to enhanced lignocellulose preservation under anoxic conditions[144]. There was a clear molecular change discovered at a salt marsh where encroachment of young mangroves is occurring, but with a sediment core from the marsh-mangrove location reflecting a complex history. However, most C_{ORG} sequestered in the upper sediment layers may have originated from invading mangroves. Further, a sediment core from a mangrove habitat shows a dramatic shift in C_{ORG} content between surficial and deeper sediment layers, coinciding with a major shift in $\delta^{13}C$. This change indicates that about a millennia ago, seagrasses inhabited this area, delimiting a change from a subtidal to a more intertidal environment, coinciding with a known sea-level decrease in this region[145].

Land-use and land-cover changes (LULCC) drive changes in emissions and blue carbon stocks

Blue carbon ecosystems are impacted by various types of natural and anthropogenic changes due to LULCC, the most common being unsustainable extraction of wood and other products, clearing and conversion for agriculture (pastures, plantations) and aquaculture (shrimp ponds, salt farms), impoundment and drainage for pest control, urban development (construction for housing and industry), constructed and restored wetlands, pollution, climate change, and natural and coastal erosion induced by land-use change. The level of impact depends on factors such as spatial and temporal change, and the frequency and magnitude of the disturbance. A meta-analysis determining the blue carbon response of coastal wetlands to LULCC[146] concluded that conversion to various land-use changes resulted in decreased sediment C_{ORG} concentrations and stocks by an average of 18%, with the loss of sediment C_{ORG} causing likely CO_2 emissions in the range of 2 to 23 Mg CO_{2eq} ha^{-1} $year^{-1}$; in contrast, conversion to artificial wetlands may result in a net uptake of about -3 Mg CO_{2eq} ha^{-1} $year^{-1}$.

A model forecast of CO_2 emissions from blue carbon ecosystems post-disturbance[147] indicates that more than 40-year post-disturbance, the total CO_2 emitted from blue carbon habitats was about 70%-80% of the initial C_{ORG} standing stock. Empirical evidence from blue carbon ecosystems along the Mexican coasts[148-150] indicates historical changes in blue carbon stocks in sediments. Increasing salinization in the Gulf of Mexico[148], as a result of sea-level rise, resulted in higher C_{ORG} stocks and sequestration in *Halodule wrightii* beds than in *Thalassia testudinium* meadows where only sequestration rates increased due to erosion caused by land-use change and sea-level rise. In Mexican mangroves, seagrasses, and salt marshes[149], most stored sediment C_{ORG} (60%-86%) during the Anthropocene (circa 1950) and contemporary mangrove C_{ORG} stocks were up to 6 times higher than pre-1950, probably because of land-use changes. Increased C_{ORG} sequestration rates in seagrasses were primarily due to increases in sediment accumulation as a result of land erosion and changes in sea level. Changes in C_{ORG} concentrations in mangroves and salt marshes were likely due to productivity increases in the runoff of fertilizer and sewage. Salt marshes in the northeast Pacific coast of Mexico have low input rates of terrestrial matter and sediment accumulation rates than in adjacent seagrass meadows. However, throughout the past century, accumulation rates have steadily increased due to soil erosion from land-use change (agriculture, aquaculture)[150]. In tropical seagrass meadow sediments off Zanzibar, Tanzania, mass accumulation rates similarly increased due to land-use change from 1998 until 2018, linked to shifts in C_{ORG} sources[151]. However, different land-based activities resulted in different $\delta^{13}C$ signatures of sediment C_{ORG} between two meadows, with one meadow indicating increased $\delta^{13}C$ signatures after a sewage outlet was moved and the other meadow showing a decrease in $\delta^{13}C$ signatures because of increased sediment runoff post-deforestation. Long-term data from salt marshes in the Yellow River delta, China, show that continuous LULCC transformation driven by natural and anthropogenic processes decreased carbon storage by 10.2% during 1970-2010[152].

Globally, mangrove conversion to shrimp ponds remains the most common type of land-use change, with significant loss of sediment and vegetation carbon from land clearing. In the Dominican Republic[153], where such conversion and subsequent abandonment of ponds is common, C_{ORG} stocks were lowest in abandoned shrimp ponds (11% of that of mangroves) and highest in intact mangroves. Estimated emissions from such conversions range from 2,244-3,799 Mg CO_{2eq} ha^{-1}. The conversion of mangroves to aquaculture ponds in the Dominican Republic resulted in total emissions of ≈4 million Mg CO_{2eq} or ~21% of pre-converted blue carbon. Shrimp ponds similarly led to massive losses of mangrove carbon in Brazil[154] with 58%-82% loss of C_{ORG} stocks and estimated emissions of 1,390 Mg CO_{2eq} ha^{-1} $year^{-1}$. In Thailand, where mangrove losses to aquaculture and agriculture have been historically severe[155], high-resolution data sets were used to quantify mangrove C_{ORG} stock changes over the past 60-year. Net loss of mangrove carbon over the period was about 32.3 million Mg C_{ORG}, but during the same period, 2.6 million Mg C_{ORG} accumulated due to recovery gains in mangrove extent, mostly in areas of pristine forests; substantial increases in C_{ORG} stock (1.3 million Mg C) were measured as a result of the establishment of new mangrove on accreting tidal flats. Conversion to other land uses similarly resulted in large losses of mangrove C_{ORG} and CO_2 as such pasture conversion[156] resulted in emissions of ~ 1,460 Mg CO_{2eq} ha^{-1}.

Several estimates[157,158] have documented the net loss of mangrove carbon stocks globally from LULCC. These estimates reveal a net reduction in mangrove C_{ORG} biomass by 82%, while sediment C_{ORG} experienced a reduction of 54%, with relative losses depending on LULCC type, the time since LULCC occurred, and the geographical and climatic conditions of the respective locations. Losses of sediment C_{ORG} stocks are linked to decreased sediment C_{ORG} content and increased sediment bulk density over the upper 1 m depth, but there are no significant effects of LULCC on greenhouse gas emissions from mangrove sediments. The global mangrove C_{ORG} stock declined by 158.4 million t C_{ORG} between 1996 and 2016[158], representing a 1.8% reduction compared to the stock present in 1996. The relatively small to moderate losses of C_{ORG} stocks over the last two decades can be partly attributed to efforts to conserve and restore mangroves.

CONCLUSION

Much progress has been made in blue carbon science, management and economics since the term "blue carbon" was coined 14 years ago. Unsurprisingly, the dynamics of blue carbon in mangroves, salt marshes and seagrasses is perceived as being more complex than first thought. Blue carbon investment remains constrained by large uncertainties inherent in natural ecosystem carbon dynamics and in the uncertainties of applying economic concepts to ecosystem science. All blue carbon ecosystems sequester carbon and are net autotrophic with P_{GPP}/R_E ratios > 1. Mangrove forest chronosequences show net increases in blue carbon stocks with ecosystem maturity, indicating that habitat restoration leads to increased carbon sequestration and standing stocks. Salt marshes, seagrasses and mangroves contribute to climate change mitigation at local and national levels as well as on the global scale. Submarine groundwater discharge of dissolved carbon and alkalinity is a major pathway of blue carbon loss, resulting in localized buffering of acidified coastal waters. Mineralization of ancient, deep subsurface deposits contributes to groundwater discharge of dissolved microbial by-products due to deep, metabolically active, and highly diverse bacterial assemblages in deep deposits which originate from historical changes and habitat shifts and from LULCC over time. Further, allochthonous C_{ORG} inputs are necessary to achieve carbon mass balance. Other complexities of management and science that must be addressed in future are the enhancement of blue carbon fluxes by habitat connectivity, biotic activities, and climate-induced changes in polar regions. Other factors often result in negative feedback, such as $CaCO_3$ dynamics in carbonate environments, methane and nitrous oxide emissions, inputs and dilution of blue carbon by black carbon, fisheries extraction, and various types, aerial extent, intensity, and frequency of habitat disturbance. It is also necessary to determine if macroalgal and tidal flat ecosystems qualify as blue carbon ecosystems, as further research and empirical data are urgently needed.

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Author contribution

The author contributed solely to the article.

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The author declares that there are no conflicts of interest.

Ethical approval and consent to participate

Not applicable.

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Not applicable.

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