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Organic–inorganic carbon coupling shapes carbon dioxide fluxes in seagrass ecosystems

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Seagrass meadows can remove atmospheric carbon dioxide through organic carbon production and storage, but they also alter seawater chemistry through calcium carbonate formation and dissolution. Most blue carbon assessments focus on organic carbon burial and overlook how inorganic carbon cycling regulates carbon dioxide exchange. This Perspective presents a framework linking organic carbon metabolism, carbonate cycling, and sedimentary processes to explain when seagrass ecosystems function as net carbon dioxide sinks or sources. We introduce a compensation ratio that defines the balance between organic carbon uptake and calcification-driven carbon dioxide release and show how this balance changes with environmental conditions and sediment carbon sources. Using the Dongsha Island lagoon as a case study, we show how seagrass metabolism coupled to dissolution of geologically derived carbonate sediments can sustain alkalinity generation and long-term carbon dioxide uptake. Together, this framework provides a more complete basis for evaluating blue carbon and the climate mitigation potential of carbonate-rich coastal ecosystems.

Challenges in understanding coupled carbon dynamics

Seagrass meadows are among the most productive ecosystems in the coastal ocean and play a disproportionate role in climate mitigation through carbon sequestration[1,2]. Despite occupying <0.1% of the global ocean, they account for ~10–25% of coastal organic carbon (OC) burial (27–44 Tg C yr^{-1}) and accumulate sedimentary OC at rates comparable to, and in some high-biomass systems exceeding, those of terrestrial forests[3,4]. These estimates have driven global efforts to quantify seagrass carbon sequestration, with most studies focusing on net community production (NCP) and sedimentary OC burial.

While NCP is widely used as a proxy for ecosystem carbon balance, its relationship to long-term sedimentary OC burial is neither direct nor fixed, as much organic production is not retained locally. At the global scale, seagrass net primary production (NPP ≈ 490 Tg C yr^{-1}) is largely remineralized (~ 50%), with substantial export (~ 24%) and only ~16% buried within the meadows, highlighting that most production is not preserved as long-term carbon storage[5,6]. In the open ocean, this decoupling is more pronounced, as most organic matter is remineralized during export through the water column[7,8]. By contrast, shallow depths and strong benthic–pelagic coupling in seagrass meadows enhance the sediment transfer of organic matter, yet substantial losses still occur through remineralization and lateral export[6,9]. Thus, NCP constrains the potential for carbon sequestration but does not determine its long-term magnitude or direction.

Beyond its contribution to sedimentary carbon storage, OC metabolism directly regulates local seawater carbonate chemistry. Mechanistically, photosynthesis consumes CO_2 (or HCO_3^-), reducing dissolved inorganic carbon (DIC) and partial pressure of carbon dioxide (pCO_2), with minimal effect on total alkalinity (TA). The same effect on TA also occurs during aerobic respiration, which releases CO_2 and increases both DIC and pCO_2[10,11]. In contrast, anaerobic pathways in the seafloor can exert additional control on TA. Meadows function as carbon sinks when photosynthesis exceeds respiration (NCP > 0) and as carbon sources when respiration dominates (NCP < 0), with neutral metabolic balance when NCP ≈ 0 (Fig. 1)[12,13]. However, this interpretation assumes a local

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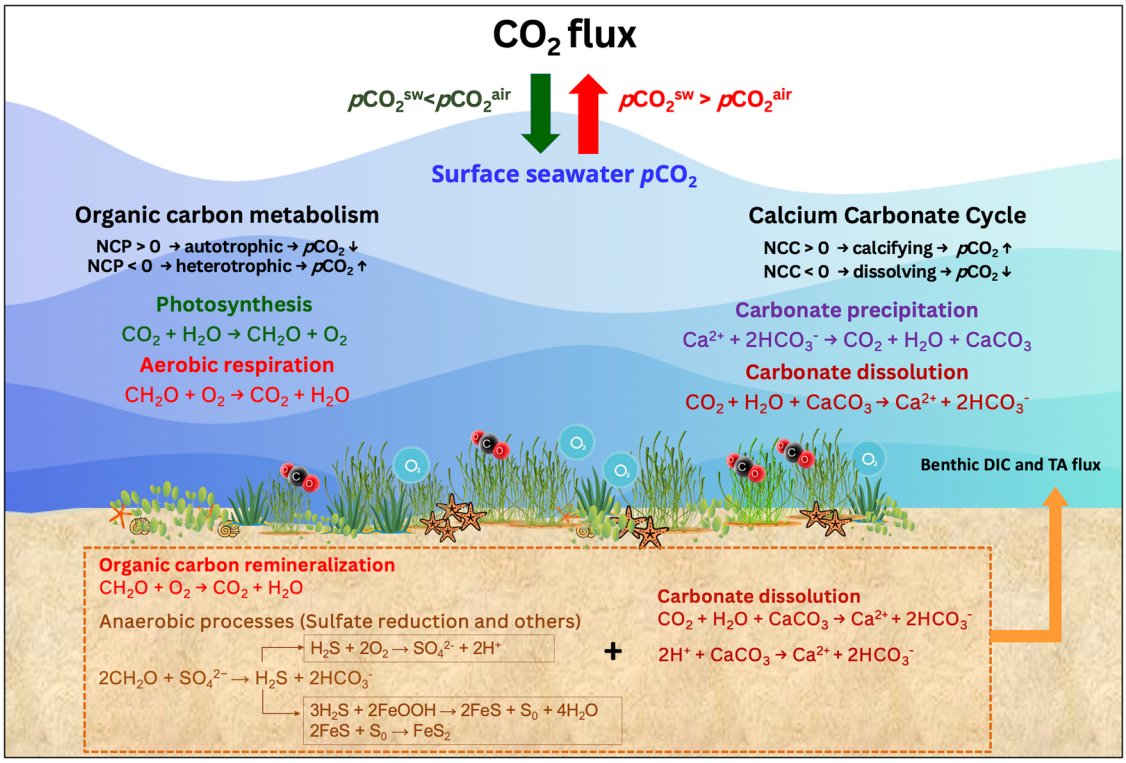

Fig. 1 | Organic carbon metabolism (photosynthesis and respiration) controls net community production (NCP), while $CaCO_3$ precipitation and dissolution govern net community calcification (NCC) in both the water column and sediments. Autotrophic conditions (NCP > 0) reduce surface seawater partial pressure of carbon dioxide (pCO_2), whereas heterotrophy (NCP < 0) elevates pCO_2. In contrast, net calcification (NCC > 0) increases pCO_2 through total alkalinity (TA) consumption, while net dissolution (NCC < 0) enhances CO_2 uptake via TA generation. Benthic fluxes of dissolved inorganic carbon (DIC) and TA, driven by organic matter remineralization and carbonate reactions, further modulate seawater carbonate chemistry. The net effect of dissolution depends on whether it reflects internal carbonate recycling or net TA generation. The balance between NCP and NCC ultimately determines surface seawater pCO_2 and the direction of air–sea CO_2 exchange in seagrass meadows.

meadow–sediment system boundary and does not explicitly account for lateral OC transport. Because a fraction of exported OC may be remineralized elsewhere in the ocean rather than being permanently stored, the framework should be regarded as an upper-bound estimate of the net CO_2 sequestration potential of seagrass ecosystems. As such, organic-centric framing underpins most blue-carbon assessments–yet it implicitly assumes that carbonate chemistry responds passively to metabolism, despite evidence that it is regulated by multiple interacting processes[1,14].

Seagrass ecosystems also host large reservoirs of inorganic carbon (IC) in the form of calcium carbonate ($CaCO_3$) stored within sediments, particularly in tropical carbonate-rich environments, and these pools can exert a first-order control on air–sea CO_2 exchange[15]. These sediments contain an estimated 11–39 Pg of particulate inorganic carbon in the upper meter, with burial rates comparable to or exceeding OC burial in some systems (22–75 Tg C yr^{-1})[16].

IC cycling encompasses processes that directly modify DIC, TA, and seawater pCO_2, thereby fundamentally controlling whether a system behaves as a net CO_2 source or sink (Fig. 1). Through calcification and dissolution, seagrass meadows alter these parameters in opposing ways. Net calcification removes TA twice as much as DIC, thereby raising seawater pCO_2 and promoting CO_2 outgassing. Metabolically mediated carbonate dissolution occurs through two pathways. In shallow carbonate sediments, oxygen supplied by seagrass roots and rhizomes, together with high organic matter availability, enhances aerobic respiration, releasing CO_2 and lowering pH, thereby promoting sedimentary carbonate dissolution[17–19]. In the deeper sediments, anaerobic respiration, dominated by sulfate reduction and, to a lesser extent, denitrification and iron reduction, produces HCO_3^-, increasing both TA and DIC in porewaters; however, net TA is only preserved when reduced species are buried or escape re-oxidation (e.g., via pyrite formation)[20,21,22,23].

The net outcome of these inorganic processes, expressed as net community calcification (NCC), often shifts ecosystems between net CO_2 sources (NCC > 0) and sinks (NCC < 0). Field studies show contrasting outcomes: calcification offset OC gains in Florida Bay[24], whereas at Dongsha Atoll, organic inputs and carbonate dissolution sustained CO_2 uptake despite active calcification[25]. At broader scales, sedimentary $CaCO_3$ dissolution enhances TA and buffering capacity, thereby promoting CO_2 uptake and contributing non-negligibly to the ocean carbon sink, with coastal and shelf dissolution estimated at ~11 ± 9 Tmol yr^{-1} (ref 26). This process can also be anthropogenically accelerated on continental shelves, operating as a fast climate feedback on annual to decadal timescales[27]. Together, these findings highlight a fundamental limitation of organic-only blue carbon accounting in carbonate-rich sediments, which cannot fully explain observed CO_2 fluxes.

This divergence arises from the distinct yet overlapping timescales governing NCP, NCC, air–sea CO_2 exchange, and sedimentary carbon burial. In shallow seagrass meadows, strong benthic–pelagic coupling efficiently transmits metabolic signals through the water column, linking short-term metabolism to near-surface carbonate chemistry[6,28], with metabolic variability further modulated across environmental gradients[13]. NCP and NCC vary over diel to seasonal cycles[29,30], air–sea CO_2 equilibration occurs over hours (in extremely shallow systems) to weeks[31–33], and sedimentary burial integrates over annual to centennial timescales[2,12]. Thus, these spatially coupled systems are temporally decoupled, such that short-term metabolic CO_2 fluxes may diverge from long-term sequestration. The influence of sedimentary metabolism on seawater carbonate chemistry also depends on its connectivity to overlying waters. Sediment-derived DIC and

TA affect surface-water pCO_2 only when sediment–water exchange and water-residence times are sufficient to transmit benthic signals, whereas rapid hydrodynamic flushing dilutes these benthic inputs before they can significantly alter surface-water chemistry. Accordingly, NCP and NCC serve as diagnostics of short-term water-column CO_2 regulation, whereas climate mitigation depends on the fraction of carbon retained beyond remineralization.

Beyond the context-dependent balance between NCP and NCC, CO_2 dynamics are further modulated by the origin and timescale of carbon inputs (autochthonous versus allochthonous; modern versus geogenic–recently formed vs. geologically derived $CaCO_3$). Source attribution remains a critical yet often overlooked uncertainty. For OC, only autochthonous production reflects true seagrass-mediated carbon uptake[2], whereas allochthonous inputs (e.g., mangrove litter, phytoplankton) may enhance burial while stimulating respiration and CO_2 release[16]. A similar challenge exists for IC: biogenic calcification consumes TA and releases CO_2, whereas dissolution of geogenic carbonates increases TA, lowers pCO_2, and promotes uptake[14]. Importantly, burial of geogenic carbonate is biogeochemically distinct because its eventual dissolution releases TA derived from long-term geological reservoirs, altering seawater chemistry and TA fluxes[34]. Including such carbonate in carbon stock assessments can therefore bias CO_2 flux estimates by conflating geologically sourced TA inputs with biologically mediated carbon emissions[20].

Recent evidence shows that much of the OC in coastal wetlands originates from external sources rather than from habitat-forming plants[35,36]. Similarly, IC burial often exceeds in situ production and limited enrichment relative to bare sediments[16,20,37]. Thus, carbon accounting frameworks that ignore carbon sources risk systematically misrepresenting carbon sequestration potential, consistent with emerging 'forensic carbon accounting' approaches that distinguish between autochthonous and allochthonous carbon inputs[38]. Ultimately, whether seagrass ecosystems act as net CO_2 sinks or sources cannot be inferred from NCP or OC burial alone, but from the coupled balance between OC metabolism and carbonate cycling.

Against this backdrop, there is a clear need for an integrated framework that captures the coupled roles of OC and IC in seagrass ecosystems. Here, we propose two complementary perspectives to fill this gap. First, the NCP/NCC compensation ratio—a diagnostic metric that quantifies the threshold balance between organic production and calcification, more completely linking biogeochemical processes to seawater carbonate chemistry and pCO_2 balance. Second, a sedimentary source–dependent conceptual model that expands this framework by incorporating the benthic processes that modulate water-column carbonate dynamics.

Together, these perspectives provide a unified framework for resolving whether seagrass ecosystems function as net atmospheric CO_2 sources or sinks, advance our understanding of their biogeochemical functions, and offer stronger guidance for restoration, conservation, and the inclusion of seagrass in climate policy and nature-based solutions.

Threshold dynamics of the NCP/NCC compensation ratio

We propose the NCP/NCC compensation ratio as a diagnostic metric linking OC metabolism and $CaCO_3$ cycling in regulating seawater pCO_2 and potential air–sea CO_2 exchange. This ratio defines the threshold at which the opposing effects of NCP and NCC balance along iso-pCO_2 trajectories in a TA–DIC space (Fig. 2a), with the corresponding compensation threshold varying systematically with ambient pCO_2 (Fig. 2b). The theoretical basis and derivation are provided in Box 1.

Within this framework, distinct metabolic regimes emerge relative to the compensation threshold (Fig. 2c, d). A net pCO_2 decrease occurs when DIC uptake and/or TA generation dominate (sub-regions I–III in Fig. 2d), including:

I. autotrophy with net $CaCO_3$ dissolution (NCP > 0; NCC < 0), typical of rapidly growing seagrass meadows over carbonate sediments[25,39];
II. systems where both NCP and NCC are positive (NCP > 0; NCC > 0) but the NCP/NCC ratio exceeds the compensation threshold (NCP/NCC > 0.63), characteristics of highly productive water columns[40,41];
III. heterotrophic systems (NCP < 0) that remain weak CO_2 sinks when TA generation offsets respiratory CO_2 release (NCC < 0; NCP/NCC < 0.63), as observed in organic-rich carbonate sediments[42].

In contrast, a net pCO_2 increase arises when respiration and/or calcification dominate (sub-regions IV–VI in Fig. 2d), including:

IV. heterotrophy with net calcification (NCP < 0; NCC > 0), producing strong CO_2 sources such as in patchy seagrass in seagrass-coral reefs mosaics[43];
V. systems where TA generation cannot offset respiratory CO_2 inputs (NCP < 0; NCC < 0; NCP/NCC > 0.63), as observed in some subtropical seagrass meadows[44]; and
VI. autotrophic systems where calcification overwhelms photosynthetic CO_2 uptake (NCP > 0; NCC > 0; NCP/NCC < 0.63), leading to elevated pCO_2 during calcification-dominated conditions in carbonate seagrass meadows[24].

Thus, potential air–sea CO_2 exchange emerges from the stoichiometric balance between NCP and NCC relative to the compensation threshold, rather than from either process alone.

The compensation ratio should be viewed as a state-dependent diagnostic metric that varies with temperature, salinity, and ambient carbonate chemistry. Variability in TA and DIC—driven by physical and biogeochemical processes—alters the TA–DIC slope and the corresponding threshold. Accordingly, locally derived NCP/NCC ratios provide a more accurate and context-specific assessment than fixed global values.

Although the framework assumes fully autochthonous, water-column processes, natural seagrass ecosystems are influenced by allochthonous inputs and sedimentary transformations that modify DIC and TA, shifting states relative to the compensation threshold. These effects are pronounced in sediments, where external OC and IC drive coupled biogeochemical feedbacks regulating TA and DIC. For example, dissolution of allochthonous geogenic $CaCO_3$ increases TA and promotes CO_2 uptake, whereas remineralization of allochthonous OC elevates DIC and enhances CO_2 release. Sedimentary redox processes further regulate TA dynamics[45]. Sulfate reduction generates TA, but its net effect depends on sulfur cycling pathways. Sulfide may be buried as pyrite[20,23], preserving TA for export, or re-oxidized under oxygen supply (e.g., radial oxygen loss, bioturbation, tidal flushing)[46–48]. Re-oxidation generates protons that lower porewater TA and pH and can promote $CaCO_3$ dissolution[49]. While this dissolution enhances benthic TA fluxes[19], it may largely reflect internal carbonate recycling rather than a net TA source if the carbonates are modern biogenic.

Together, these externally driven modifications decouple carbonate chemistry from purely metabolic fluxes, so that the observed signal reflects an apparent NCP/NCC balance that integrates metabolic, sedimentary, and source-dependent processes. Consequently, deviations from the compensation threshold capture these superimposed influences, with seawater pCO_2 reflecting their integrated effects. This underscores the need to extend the NCP/NCC framework to explicitly incorporate sedimentary dynamics and carbon-source dependencies, as developed in the following section.

Source-dependent controls on seawater carbonate chemistry

Sedimentary sources exert a critical yet underappreciated control on carbon dynamics in seagrass ecosystems. While the NCP–NCC balance governs CO_2 exchange in the seawater column, carbonate chemistry is also strongly shaped by the origin (autochthonous versus allochthonous) and temporal nature (modern biogenic versus geogenic) of sedimentary carbon pools, which determine their coupling to contemporary carbon cycling and their influence on DIC and TA.

This control is expressed through carbonate mineral composition. Carbonate may derive from modern biogenic production[16,22] or from geogenic sources formed over the geological past[34,50], a distinction central to pCO_2 regulation. Dissolution of recently precipitated $CaCO_3$ largely reflects internal recycling, yielding limited net CO_2 uptake under most conditions[30,50]. In contrast, dissolution of geogenic carbonates mobilizes TA

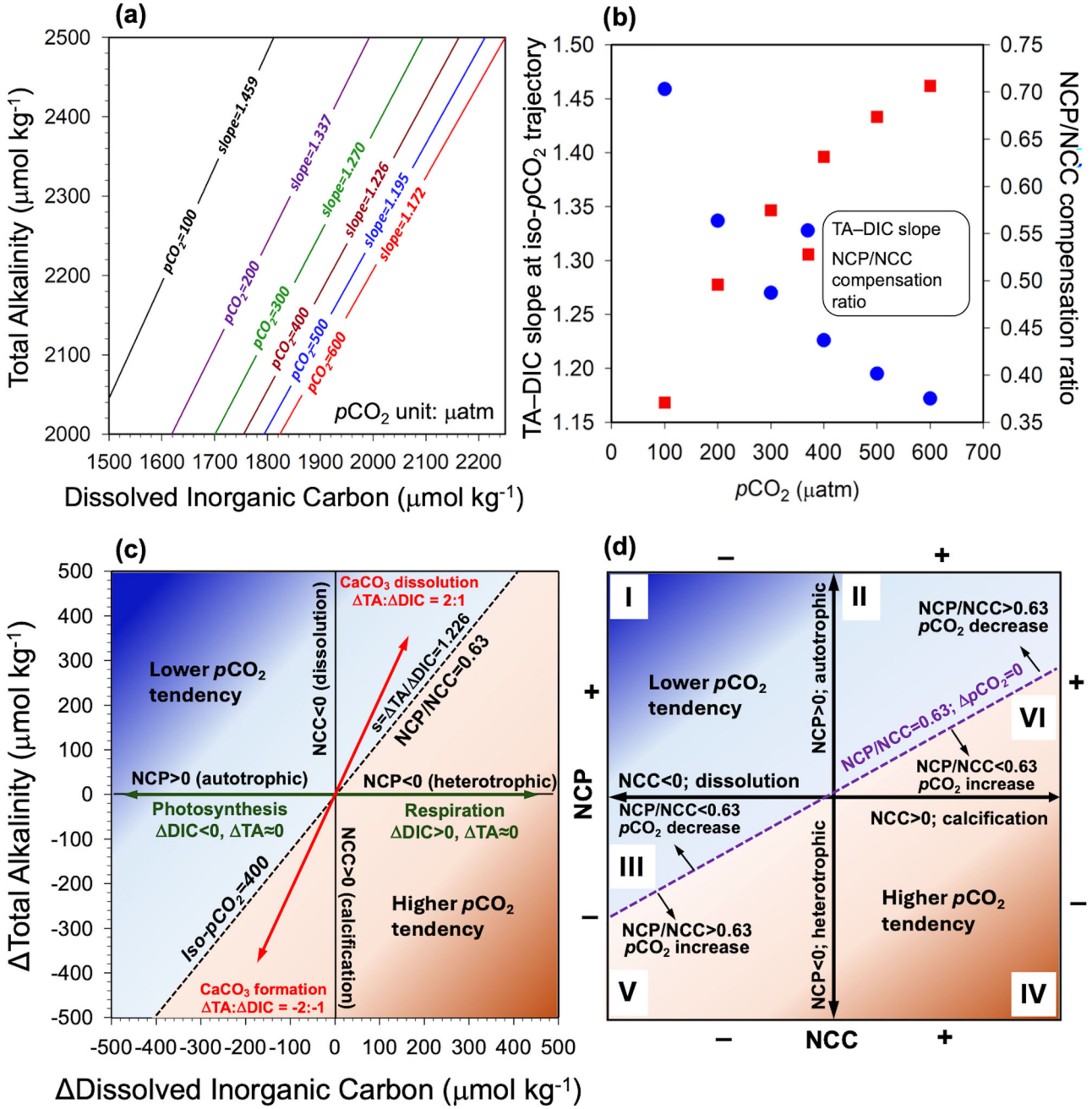

Fig. 2 | Diagnostic role of the ΔTA: ΔDIC and NCP: NCC ratios in regulating seawater pCO_2 balance. Here, ΔTA and ΔDIC denote changes in total alkalinity and dissolved inorganic carbon, respectively, while NCP and NCC denote net community production and net community calcification, respectively. **a** Modeled TA–DIC slopes along iso-pCO_2 trajectories (100–600 μatm) at 25 °C and salinity 35, with TA ranging from 2000 to 2500 μmol kg^{-1} and corresponding DIC values. **b** Variation in TA–DIC slopes (blue circles) and NCP/NCC compensation ratios (red squares) along iso-pCO_2 trajectories. **c** Conceptual framework linking ΔTA and ΔDIC to the combined effects of organic metabolism (NCP) and carbonate cycling (NCC), and their control on seawater pCO_2. The dashed line represents the ΔTA:ΔDIC ratio of 1.226 required to maintain a constant pCO_2 (~400 μatm). The green and red solid arrows in (**c**) represent net shifts in the carbonate-system state (TA and DIC) driven by organic carbon metabolism (i.e., photosynthesis and respiration) and inorganic carbonate cycling (i.e., $CaCO_3$ formation and dissolution), respectively. Background color gradients indicate pCO_2 tendencies: stronger CO_2 uptake (blue) and CO_2 release (orange). **d** Regime diagram illustrating how the NCP (vertical axis) and NCC (horizontal axis) govern seawater pCO_2. The dashed line represents the compensation threshold (NCP/NCC ≈ 0.63 at ~400 μatm), regions I–III indicate CO_2 sinks and IV–VI sources. pCO_2 denotes the partial pressure of carbon dioxide.

from long-term reservoirs, enhancing buffering capacity and promoting CO_2 uptake[25,26,51], consistent with natural ocean alkalinization driven by mineral weathering[52]. Recent evidence shows that carbonate dissolution can be dynamically stimulated under rising atmospheric CO_2, particularly in shallow shelf environments where strong sediment–water coupling enables rapid TA feedbacks[27]. Thus, resolving both carbon origin and carbonate age is essential for evaluating seagrass climate mitigation potential.

To capture the importance of these source-dependent pathways, we define four conceptual scenarios based on sedimentary OC and IC sources (Box 2), which are further illustrated in Fig. 3.

Scenario A: autochthonous OC and $CaCO_3$ production;

Scenario B: autochthonous OC production with allochthonous $CaCO_3$ input;

Box 1: | NCP/NCC compensation ratio and its control on seawater pCO_2

The NCP/NCC compensation ratio defines the threshold at which organic carbon-driven CO_2 uptake (NCP) balances calcification-driven CO_2 release (NCC), resulting in no net change in seawater pCO_2. This balance emerges along iso-pCO_2 trajectories in the TA–DIC space, where the slope (s = ΔTA/ΔDIC) reflects carbonate system buffering. The corresponding slopes vary from ~1.172 to 1.459 across pCO_2 levels of 100–600 µatm (S = 35; T = 25 °C).

Given the stoichiometry of carbonate precipitation (ΔTA:ΔDIC = 2:1) and organic metabolism (ΔDIC = 1; negligible ΔTA):

$$s = \frac{2 \cdot \mathrm{NCC}}{\mathrm{NCC} + \mathrm{NCP}} = \frac{2}{1 + \frac{\mathrm{NCP}}{\mathrm{NCC}}} \quad (1)$$

Thus,

$$\frac{\mathrm{NCP}}{\mathrm{NCC}} = \frac{2 - s}{s} \quad (2)$$

At present-day conditions (~ 400 µatm, representative of recent surface ocean pCO_2), this yields a threshold of NCP/NCC ≈ 0.63, indicating that organic production must exceed ~63% of calcification to maintain constant pCO_2. Cooling from 25 °C to 20 °C under temperate ocean conditions (S = 35; pCO_2 = 400 µatm) increases the threshold to ≈ 0.66, corresponding to s ≈ 1.21.

Across 100–600 µatm, the compensation ratio ranges from ~0.37 to 0.71 (Fig. 2b), demonstrating sensitivity to ambient carbonate chemistry. Consequently, greater organic production is required to offset calcification-driven CO_2 release under elevated pCO_2 conditions, consistent with decreased buffer sensitivity (i.e., increased CO_2 sensitivity; Revelle factor)[70,71], although reduced calcification rates under ocean acidification may partially moderate this effect[72].

Scenario C: allochthonous OC input with autochthonous $CaCO_3$ production; and

Scenario D: both OC and $CaCO_3$ are allochthonous.

These scenarios represent idealized end-members designed to isolate dominant pathways rather than to serve as deterministic predictors of CO_2 source–sink status, although natural systems are more likely to span a continuum in which multiple processes co-occur. Accordingly, each scenario may still include contributions from both autochthonous and allochthonous OC and IC, but is defined by the predominance of a particular combination of inputs.

Across these scenarios, carbon-source configuration controls the pathways of carbonate-system modification, but not necessarily the climate-relevant outcome. Sustained ocean–atmosphere CO_2 removal arises only from processes that generate net TA and/or enhance long-term OC storage beyond baseline conditions (i.e., the corresponding unvegetated or pre-restoration state). Distinguishing internal recycling from TA production driven by geogenic IC sources is therefore critical for resolving the true mitigation potential of seagrass ecosystems.

In Scenario A (Fig. 3A, see Table S1), autochthonous OC production (i.e., photosynthesis) decreases DIC with minimal effect on TA, thereby lowering pCO_2 (reaction ①). By contrast, autochthonous $CaCO_3$ production (i.e., calcification) removes both DIC and TA in a 1:2 ratio, thereby increasing pCO_2 (reaction ②). The net pCO_2 response thus depends on the relative balance between NCP and NCC, defined by the NCP/NCC compensation ratio introduced earlier.

In the sediments, aerobic respiration of autochthonous OC restores water-column carbonate chemistry (reactions ① + ③) if all OC is respired and the resulting DIC returns to the overlying water. Autochthonous OC metabolism coupled with autochthonous $CaCO_3$ dissolution similarly produces no net change (reactions ① + ② + ④), since both CH_2O and $CaCO_3$ are internally produced and recycled within the same system.

This apparent balance (ΔDIC ≈ 0 and ΔTA ≈ 0) in Scenario A applies only to the fraction of internally produced CH_2O and $CaCO_3$ that is fully recycled (reaction ④). In practice, remineralization and dissolution are often incomplete and condition-dependent, governed by porewater saturation state and redox conditions, allowing unreacted OC and $CaCO_3$ to persist as sedimentary reservoirs rather than being returned to the water column[53,54]. The removal of this buried fraction from active cycling exerts a corresponding net influence on seawater pCO_2, with the magnitude of the effect depending on the proportion retained in the sediment. Thus, canonical stoichiometries represent theoretical endmembers, whereas in situ carbonate-system responses depend on the balance between recycling and burial.

Under oxygen-depleted conditions, sulfate reduction—a dominant form of anaerobic respiration–becomes the primary pathway of OC remineralization in marine sediments[51,55], although other processes (e.g., denitrification and metal reduction) may also contribute[56]. When fueled by autochthonous OC (reaction ①), sulfate reduction initially increases both DIC and TA. Crucially, this TA gain is only preserved if reduced sulfur is buried (e.g., as FeS or FeS_2). If H_2S is instead re-oxidized in near-surface sediments or overlying water, this consumes the produced TA and promotes carbonate dissolution, with the net effect depending on carbonate source[45,46,48,49]. In contrast, the stable burial of reduced sulfur (e.g., via reaction with Fe^{2+}) locks in the TA increase, thereby enhancing the system's CO_2 uptake potential[22,23] (reaction ⑤). Consequently, Scenario A results in a nearly balanced state where ΔDIC ≈ 0 and ΔTA ≈ 0 for the fully recycled fraction, whereas a net TA surplus arises only when reduced-sulfur burial is sustained and effectively coupled to the overlying water column, potentially leading to a weak CO_2 sink.

In Scenario B (Fig. 3B), autochthonous OC metabolism promotes the dissolution of imported geogenic $CaCO_3$, producing simultaneous increases in DIC and TA at a 1:2 ratio (reactions ① + ④). The disproportionately larger rise in TA offsets the DIC addition, resulting in a pCO_2 drawdown and a net TA surplus. Sulfate reduction proceeds similarly to Scenario A, with net TA generation contingent on reduced-sulfur burial (reaction ⑤). This configuration maximizes local CO_2 uptake potential, although its net climate benefit depends on whether $CaCO_3$ dissolution reflects modern internal recycling or net TA generation from geogenic sources[34,52].

In Scenario C (Fig. 3C), allochthonous OC is respired aerobically (reaction ③), increasing DIC and pCO_2, with negligible impact on TA. When this process is coupled with dissolution of autochthonous $CaCO_3$ (reactions ② + ④), DIC rises, whereas TA remains unchanged, leading to additional CO_2 release. Because OC is not produced within the system, reaction ④ adds DIC without any compensating local organic uptake, resulting in a net DIC enrichment and elevated pCO_2. Again, in practice, the actual net change in pCO_2 may vary, as the relative amounts of OC and $CaCO_3$ that participate in recycling versus those remain unreacted or buried are seldom well constrained. Sulfate reduction of external OC further enriches DIC and TA in a 1:1 ratio (reaction ⑤); but yields net TA only when reduced sulfur is buried; otherwise, re-oxidation consumes TA, limiting CO_2 uptake and potentially reinforcing a net CO_2-releasing regime.

In Scenario D (Fig. 3D), similar to sulfate reduction (reaction ⑤), the respiration of external OC combined with dissolution of imported $CaCO_3$

Box 2: | source-dependent controls on OC–IC coupling

We define four end-member sedimentary configurations that determine how OC and IC pathways regulate seawater pCO_2:

(A) Autochthonous OC + autochthonous $CaCO_3$→ Internal cycling dominates; limited net change unless OC or $CaCO_3$ is buried
(B) Autochthonous OC + allochthonous $CaCO_3$→ Enhanced alkalinity production via $CaCO_3$ dissolution; promotes CO_2 uptake
(C) Allochthonous OC + autochthonous $CaCO_3$→ DIC enrichment without compensating uptake; promotes CO_2 release
(D) Allochthonous OC + allochthonous $CaCO_3$→ Coupled increases in DIC and TA; typically CO_2-releasing systems

Scenario B (autochthonous OC coupled with allochthonous geogenic $CaCO_3$) represents the optimal configuration with the greatest potential for pCO_2 reduction, as it enhances alkalinity generation and thereby promotes sustained CO_2 uptake.

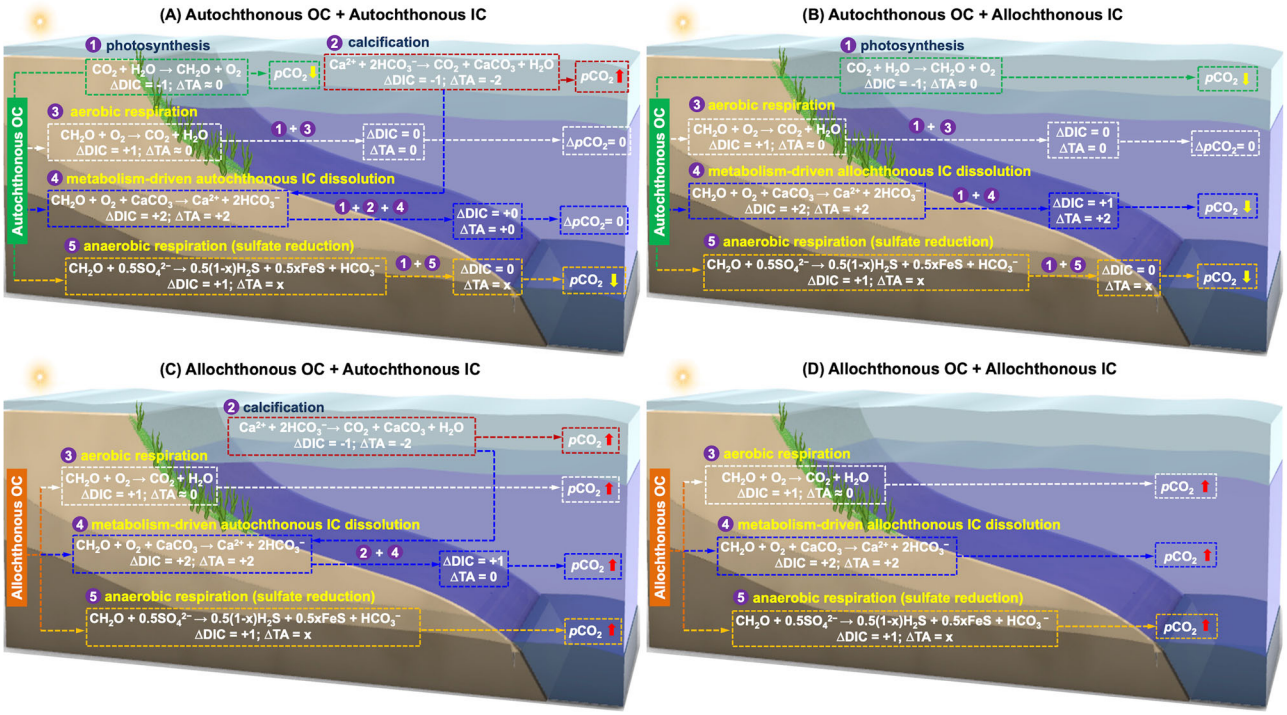

Fig. 3 | Conceptual framework of organic carbon (OC) and inorganic carbon (IC) cycling in seagrass ecosystems under different source configurations. **A** Autochthonous OC + autochthonous IC. **B** Autochthonous OC + allochthonous IC. **C** Allochthonous OC + autochthonous IC. **D** Allochthonous OC + allochthonous IC. Scenarios highlight how OC and IC sources regulate dissolved inorganic carbon (DIC), total alkalinity (TA), and potential air–sea carbon dioxide (CO_2) exchange. pCO_2 denotes the partial pressure of carbon dioxide.

raises both DIC and TA in roughly a 1:1 ratio (reaction ④). Although TA increases, the concurrent rise in DIC exerts a stronger control on the carbonate system, leading to higher pCO_2. This configuration reinforces a CO_2-releasing regime typical of heterotrophy with external carbonate-dominated environments.

Within this framework, Scenario B emerges as the configuration most conducive to CO_2 uptake, where autotrophic meadows supply autochthonous OC to sediments while promoting the dissolution of allochthonous geogenic $CaCO_3$ and anaerobic remineralization (e.g., sulfate reduction). Under these conditions, enhanced TA generation counterbalances DIC accumulation, lowers pCO_2, and maximizes the capacity of seagrass ecosystems to act as effective CO_2 sinks. Such process coupling is supported by studies showing that seagrass meadows on reef-derived sediments (i.e., allochthonous geogenic $CaCO_3$) can act as natural biogeochemical factories for TA production, lowering seawater pCO_2, and enhancing atmospheric CO_2 uptake[19,25,34].

In summary, the mitigation potential of seagrass ecosystems is governed not only by the balance between NCP and NCC in the overlying water column, but also by sedimentary carbon-source dynamics. Crucially, the net effect depends on whether seagrass presence enhances TA generation or carbon retention relative to baseline conditions. Recent work shows that restored seagrass meadows can shift benthic systems toward net autotrophy relative to adjacent unvegetated sediments, enhancing carbon uptake despite concurrent calcification, as OC production exceeds CO_2 release[41]. Consistently, NCP in developing meadows can increase by an order of magnitude relative to bare sediments, indicating a pronounced metabolic shift following restoration[57]. Restoration also promotes the accumulation of sediment OC as meadow structure develops, reinforcing long-term carbon storage[58,59]. However, such responses are not universal; restored temperate meadows may remain net heterotrophic, underscoring the role of local biogeochemical conditions and baseline states in determining carbon balance[60]. Climate relevance thus depends on net system-scale modification of carbon fluxes relative to baseline conditions.

Sedimentary alkalinity production drives persistent pCO_2 suppression: a natural case from the Dongsha inner lagoon

Within the NCP–NCC compensation and source–dependent control frameworks, a CO_2 sink is expected to be most pronounced in autotrophic

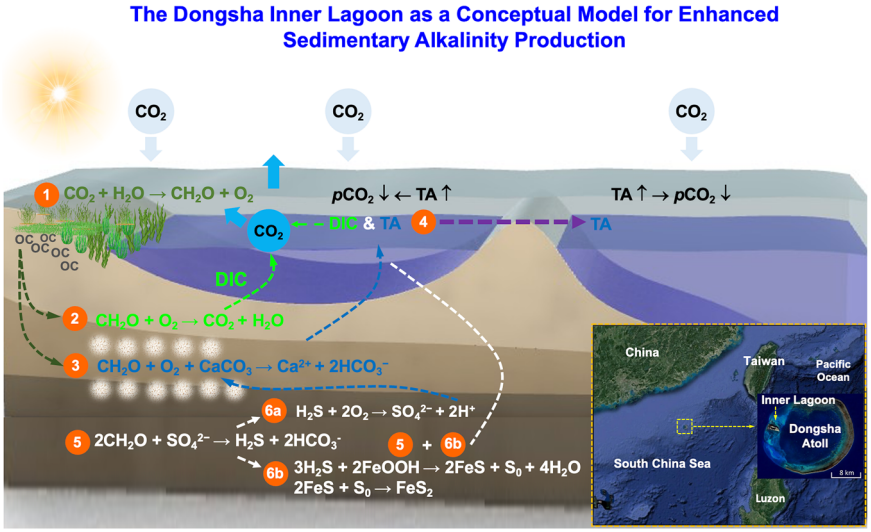

Fig. 4 | Conceptual model of enhanced sedimentary alkalinity production and sustained low pCO_2 in the Dongsha inner lagoon. The Dongsha Inner Lagoon, located in the northern South China Sea (see the insert map), illustrates how strong sediment–water biogeochemical coupling in seagrass-dominated, carbonate-rich reef systems regulates water-column carbonate chemistry under conditions of elevated autochthonous organic carbon (OC) supply and abundant allochthonous geogenic calcium carbonate ($CaCO_3$) sediments. (1) Seagrass photosynthesis removes carbon dioxide (CO_2) from the water column and produces autochthonous OC; a substantial fraction of this OC is buried and transported into underlying reef sediments. (2) Aerobic remineralization of autochthonous OC near the sediment surface generates CO_2, while (3) this metabolically produced CO_2 promotes dissolution of allochthonous geogenic $CaCO_3$, releasing total alkalinity (TA) and dissolved inorganic carbon (DIC) to porewaters and the overlying water. (4) Sediment-derived TA accumulates in the water column, whereas DIC is largely taken up by seagrass photosynthesis, enhancing buffering capacity and suppressing partial pressure of carbon dioxide (pCO_2). At depth, (5) anaerobic remineralization of autochthonous OC–mainly sulfate reduction–further increases TA production and generates hydrogen sulfide (H_2S). (6a) Subsequent sulfide re-oxidation and (6b) iron–sulfur reactions (e.g., pyrite formation) promote additional carbonate dissolution and TA generation. Map data: Google Earth Pro V 7.3.1.4507.

systems with net $CaCO_3$ dissolution (NCP > 0; NCC < 0; Metabolic Regime I), particularly where high autochthonous OC supply coincides with abundant allochthonous geogenic $CaCO_3$ in sediments (Scenario B in Fig. 3).

The inner lagoon (IL) of Dongsha Island in the northern South China Sea (Fig. 4) provides a natural example of this coupled biogeochemical condition. Open-water O_2 mass-balance approaches and benthic chamber measurements consistently show that seagrass meadows in the IL exhibit autotrophy with net $CaCO_3$ dissolution (NCP > 0; NCC < 0), supporting sustained pCO_2 suppression. This semi-enclosed reef lagoon is further characterized by abundant allochthonous geogenic $CaCO_3$ sediments, high autochthonous OC accumulation, and long water-residence times, which enhance sediment–water coupling and allow benthic processes to exert strong control on water-column carbonate chemistry[14,37,39]. The Dongsha IL thus serves as a natural model for enhanced sedimentary TA production. Detailed analyses of carbonate chemistry dynamics and benthic TA fluxes are presented elsewhere[19,25,61].

A defining feature of the Dongsha IL, driven by strong sediment–water coupling, is its persistently low pCO_2 and weak diel variability[12]. Unlike typical seagrass meadows, where nighttime respiration elevates pCO_2 above and daytime photosynthesis suppresses it below the atmospheric value, pCO_2 remains consistently low throughout the diel cycle. This reflects dominant sedimentary control, whereby benthic processes act as a time-integrated regulator, dampening short-term metabolic oscillations in the overlying water column.

As conceptualized in Fig. 4, this regulation arises from intense processing of seagrass-derived autochthonous OC within allochthonous geogenic carbonate reef sediments[12]. Aerobic remineralization near the sediment surface generates CO_2 that promotes carbonate dissolution, while anaerobic pathways–primarily sulfate reduction, with contributions from denitrification and other redox processes–likely dominate at depth. These processes enhance TA production and shift carbonate equilibria toward lower pCO_2[21,34,51]. Additional carbonate dissolution associated with sulfide re-oxidation further reinforces TA generation, establishing reef sediments as a sustained benthic control on pCO_2 despite ongoing OC degradation[25,42].

Several environmental characteristics further amplify this sediment-driven TA production and pCO_2 suppression. Hydrodynamic confinement promotes autochthonous OC accumulation and prolongs porewater residence times, while fine-grained, low-permeability sediments restrict oxygen penetration and favor anaerobic remineralization[51,62]. Extended water residence times allow sediment-derived TA signals to accumulate in the water column rather than being rapidly diluted or flushed, unlike more open seagrass systems[63].

Critically, the biogeochemical fates of sediment-released constituents diverge, leading to a decoupling of TA and DIC. Sediment-derived DIC is largely taken up by seagrass photosynthesis, resulting in a near-balanced DIC budget consistent with autotrophic conditions[4,64]. Conversely, TA–largely unaffected by photosynthetic uptake–accumulates in the water column and may be advected beyond the lagoon, enhancing buffering capacity and suppressing pCO_2 across diel to seasonal timescales[19,25,61]. This TA–DIC decoupling provides a mechanistic explanation for the persistently low pCO_2 observed in the Dongsha IL.

Benthic TA flux at Dongsha IL is exceptionally high relative to model predictions and global synthesis. A recent model predicted that benthic TA fluxes in $CaCO_3$-rich seagrass sediments reach ~5.5 ± 2.2 mmol m^{-2} d^{-1} [65], while global syntheses report ~18.3 ± 9.1 mmol m^{-2} d^{-1} [26]. Conversely, measured TA fluxes in the Dongsha IL were substantially higher (72.8 ± 64 mmol m^{-2} d^{-1}). This disparity indicates that abundant sedimentary $CaCO_3$ and high OC loading—amplified by hydrodynamic confinement and limited detrital export–strongly enhance TA production. Enhanced anaerobic remineralization, particularly sulfate reduction, together with metabolically driven carbonate dissolution owing to CO_2 production from aerobic respiration and H^+ production from H_2S oxidation, likely drives these exceptionally high TA fluxes.

Together, the Dongsha IL demonstrates that autotrophic seagrass meadows with net $CaCO_3$ dissolution on OC-rich reef sediments can function as sediment-driven regulators of pCO_2. By coupling autochthonous OC remineralization, allochthonous geogenic carbonate dissolution, and hydrodynamic confinement, these ecosystems promote sustained atmospheric CO_2 uptake, revealing a previously underrecognized pathway for regulating marine pCO_2.

Future outlook

Seagrass ecosystems are increasingly recognized as climate-mitigation assets, yet their net CO_2 effect is strongly context dependent. This study demonstrates that blue-carbon assessments based solely on OC burial can misrepresent blue carbon and, by extension, climate benefits in carbonate-rich systems. Whether seagrass meadows function as net CO_2 sinks or sources is governed by the coupled balance between NCP and NCC, as modulated by local carbonate chemistry and the origin and age of sedimentary carbon pools. The NCP/NCC compensation ratio provides a quantitative, site-specific diagnostic for distinguishing effective CO_2 sinks from systems in which calcification or heterotrophic respiration offsets OC uptake. This framework enables the classification of restoration sites relative to the compensation threshold, rather than relying on uniform assumptions, and identifies environments in which sedimentary TA production and organic metabolism act synergistically to sustain CO_2 uptake.

From a policy perspective, these findings call for a shift from uniform blue-carbon accounting toward site-specific, process-based evaluation, consistent with broader syntheses showing that restoration outcomes depend strongly on system-level responses to management and environmental context[66,67]. Our analysis further shows that prioritizing environments with abundant non-modern allochthonous $CaCO_3$, such as reef sediments or other geogenic sources (e.g., karst systems), can substantially enhance TA production and maximize CO_2 uptake and long-term carbon sequestration. However, the persistence of these alkalinity-driven sinks is tied to their geochemical and physical stability. Anthropogenic disturbances, such as trawling, dredging, or mining, of carbonate-rich sediments can trigger rapid re-oxidation of buried reduced species, resulting in TA loss and CO_2 release that may offset prior sequestration[68]. Thus, the climate efficacy of these systems is contingent on maintaining low-disturbance regimes rather than being inherently permanent.

Consequently, restoration strategies should prioritize settings where sedimentary processes sustain TA generation and/or enhance long-term carbon storage beyond baseline conditions, while minimizing physical disturbance that compromises sink integrity (e.g., dredging, trawling). By identifying sedimentary TA production as a key mechanism that sustains CO_2 uptake, this framework also provides a bridge to emerging ocean-based carbon dioxide removal (CDR) strategies. In contrast, systems dominated by allochthonous organic inputs or strong autochthonous calcification may yield limited or even negative climate benefits.

Without these diagnostics, blue carbon-crediting schemes risk systematically over- or under-valuing seagrass restoration outcomes. We therefore recommend that climate policies, carbon-crediting schemes, and restoration programs explicitly incorporate carbonate-system diagnostics, sedimentary context, and alkalinity-generation potential into project design and evaluation. Targeted mapping of regions with high geogenic carbonate availability, coupled with improved monitoring of TA fluxes, will reduce uncertainty and improve the durability and verifiability of blue-carbon credits.

System-scale considerations and applications

Although this framework is developed in the context of seagrass ecosystems, the coupling between organic metabolism, carbonate dynamics, and sedimentary redox processes is broadly applicable across coastal systems, including mangroves, salt marshes, and reef-associated systems. However, the relative importance of these processes varies with sediment composition, hydrodynamic setting, and carbon-source configuration, requiring system-specific evaluation. Future work on seagrass should explicitly address lateral carbon transport, an increasingly recognized yet currently poorly constrained component of the blue carbon cycle. Emerging evidence suggests that TA outwelling can rival OC burial, revealing a substantial yet overlooked sequestration pathway[69].

Ultimately, advancing blue-carbon science requires a shift from single-process metrics (e.g., OC burial) toward multi-process, system-scale frameworks that resolve the full carbonate system. Integrating hydrodynamic connectivity into carbon accounting is essential for quantifying the distal fate of exported TA and DIC, constraining the true atmospheric CO_2 uptake signal, and evaluating whether local sinks translate into regional or global climate benefits. This integration enables a more complete representation of coastal carbon cycling by capturing both organic and inorganic pathways and their interactions across spatial and temporal scales, providing a more mechanistic and scalable basis for evaluating coastal ecosystems in climate mitigation strategies.

Data availability

No new data were generated in this study.

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Author contributions

W.-C.C. and M.B.N. conceptualized the study and wrote the original draft. W.-C.C., M.B.N., W.-J.C., and N.B. contributed substantially to manuscript revision and intellectual development. J.-J.C. contributed to the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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