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Carbon storage of seagrass ecosystems may experience tipping points in response to anthropogenic stress - a modeling perspective

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Coastal Blue Carbon ecosystems like seagrass meadows are foundation habitats with a capacity to sequester and store organic carbon in their sediments, and their protection and restoration may thereby support climate change mitigation while also supporting biodiversity and many other ecosystem functions. However, seagrass ecosystems are being lost due to human activities, disease and, in some regions, climate change, which may trigger the release of stored carbon into the atmosphere. Yet, we do not fully understand how global change-induced seagrass loss influences sedimentary carbon dynamics. What is even less clear is whether seagrass loss may also result in tipping points, *i.e.*, abrupt and difficult-to-reverse shifts, in carbon flux dynamics turning seagrass ecosystems from net carbon sinks to net carbon sources. Here, we propose that conceptual mechanistic models of coupled ecological and biogeochemical dynamics can help to study the effects of major stressors on seagrass meadows and associated carbon fluxes. We then illustrate one case of such a conceptual model that focuses on anthropogenic induced mortality by physical stress as an example. Our perspective highlights how a modeling approach for understanding the response of carbon fluxes in seagrass ecosystems to global change stressors may be useful in informing coastal seagrass management towards climate change mitigation actions.

KEYWORDS

blue carbon, tipping cascade, coastal ecosystem, ecosystem function, regime shift, climate change, biogeochemical model

1 Introduction

Coastal Blue Carbon (BC) ecosystems, which include seagrass meadows, mangrove forests, and tidal marshes, can store carbon in their underlying sediments over centennial to millennial scales, and their protection and restoration could contribute to offsetting greenhouse gas emissions (Nellemann et al., 2009; Duarte et al., 2013; Macreadie et al., 2021). Concurrently, seagrass meadows are biodiversity hotspots, support fisheries, provide natural protection by attenuating wave energy and accreting sediments, so they offer several ecosystem services beyond carbon sequestration,. Therefore, the sustainable management of seagrass meadows and the assurance of their integrity has been recognized as a low-regret Nature-based Solution (NbS) towards mitigation and adaptation to climate change safeguarding coastal resilience (Hoegh-Guldberg et al., 2019; Hoegh-Guldberg et al., 2020; Gattuso et al., 2021).

However, seagrass sensitivity to stressors is acute, and global change impacts have resulted in extensive loss of meadows worldwide (Orth et al., 2006; Unsworth et al., 2022). The loss of at least 20% of the global seagrass area since 1880 (Dunic et al., 2021), with accelerating loss rates from 0.9% yr^{-1} in the 1940s to 7% y^{-1} in the 1990s and 2000s (Waycott et al., 2009), highlights a need for further conservation (Unsworth et al., 2022). The loss is attributed to multiple direct pressures and climate change acting synergistically, including coastal eutrophication, mechanical damage, warming and extreme events (de los Santos et al., 2019). Seagrass loss could compromise the climate change mitigation and adaptation potential of seagrass meadows. Yet, there is a significant lack of understanding of the extent to which global change stressors could affect carbon storage in these critical ecosystems. Seagrass loss usually decreases their carbon sequestration capacity (Marbà et al., 2015; Dahl et al., 2016; Thorhaug et al., 2017; Trevathan-Tackett et al., 2017; Githaiga et al., 2019; Salinas et al., 2020; Moksnes et al., 2021), and increases the risk of erosion and subsequent mineralization of historical carbon accumulated in sediments (Marbà et al., 2015; Arias-Ortiz et al., 2018; Roca et al., 2022; Egea et al., 2023), potentially transforming the meadows from sinks to sources of greenhouse gasses (Lovelock et al., 2017). However, the relationship between seagrass ecosystem integrity and carbon storage is not straightforward, and ecological transformations (even dramatic ones such as complete cover loss) may not necessarily threaten the carbon that is already stored in the sediments (Piñeiro-Juncal et al., 2021; Apostolaki et al., 2022). Despite the progress in blue carbon science over the past decade, we still lack an in-depth understanding of how seagrass deterioration and loss affect the functioning of seagrass ecosystems as carbon sinks, and it is not well-understood if there are thresholds to changes in carbon fluxes linked to ecological and/or biogeochemical processes.

Recent studies in seagrass ecosystems have suggested that biogeochemical and biophysical feedbacks (*i.e.*, direct or indirect reciprocal interactions between system parts) can cause seagrass meadows to abruptly and irreversibly shift from a healthy growing state to a deteriorated barren state (Maxwell et al., 2017). Similar shifts due to competition by invasive species have also been modeled (Llabrés et al., 2023; Beca-Carretero et al., 2024). Abrupt shifts can occur at the crossing of thresholds with irreversible changes in ecological functions and services. Such regime shifts might be associated with the presence of tipping points that cause a radical shift to a usually contrasting state propelled by a strong positive feedback (van Nes et al., 2016). Regime shifts have been described for a range of ecosystems like clear lakes turning turbid (Scheffer et al., 1993), coral reefs getting overgrown by macroalgae (Knowlton, 1992), or drylands shifting to desertification (Kéfi et al., 2007), seaweed forests collapsing into urchin barrens (Ling et al., 2015) and seagrasses turning to bare or algae dominated meadows (Unsworth et al., 2015), or degraded dead matte (Rindi et al., 2024). But how likely it is that such nonlinear seagrass responses can also induce tipping responses in the dynamics of carbon storage in seagrass meadows remains unknown.

Although mechanisms and models for describing tipping responses in seagrass ecosystems have been proposed (van der Heide et al., 2007a; Carr et al., 2010; Christianen et al., 2014; Maxwell et al., 2017; Ruiz-Reynés et al., 2017; Adams et al., 2018; Mayol et al., 2022; Minguito-Frutos et al., 2023; Ruiz-Reynés et al., 2023), those have not been directly linked to the loss of carbon storage. This aspect is critical because these abrupt changes can directly influence carbon dynamics by modifying the biogeochemical processes and their potential feedbacks that ultimately will determine the fate of stored carbon. Perhaps the closest modeling approach is based on patch growth models simulating growth and colonization processes under different restoration scenarios and timeframes, by relating cover maps with carbon sequestration rates at local scales (Duarte et al., 2013). Another study modeled CO_2 emissions following the degradation of seagrass using decay rates of C_{org} in above- and below-ground tissues and underlying sediments (Lovelock et al., 2017). For both restoration projects and seagrass degradation scenarios, the most common model used is the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model (Moritsch et al., 2021; González-García et al., 2022). The InVEST model estimates the carbon sequestration potential of seagrass ecosystems by calculating the amount of carbon that is stored in seagrass biomass, as well as the carbon that is stored in the underlying sediment. Yet, to the best of our knowledge, no mechanistic model has so far been developed to evaluate the potential cascading effects of tipping points in seagrass and associated carbon dynamics (see Supplementary Material S1). If abrupt seagrass shifts could also lead to cascading responses in carbon source-sink dynamics, it is important to understand under which conditions and at what scale such an effect takes place.

Here, we propose a minimal modelling perspective for studying the likelihood of tipping point responses in the carbon storage (i.e., from carbon sink to source of CO2) of seagrass ecosystems under global change stressors. We show how conceptual mechanistic models could be built based on expert knowledge by coupling a minimal set of biogeochemical interactions and ecological feedbacks. We then develop one such model to showcase that seagrass meadows can abruptly shift from sink to carbon source in response to anthropogenic induced physical damage. We use this type of anthropogenic induced mortality only as an example, as the mechanistic modelling framework we present could be used to study any other pressure by itself or in combination. We outline limitations and opportunities presented by such minimal modeling approaches towards improving the management of seagrasses to enhance their functioning as carbon storage systems.

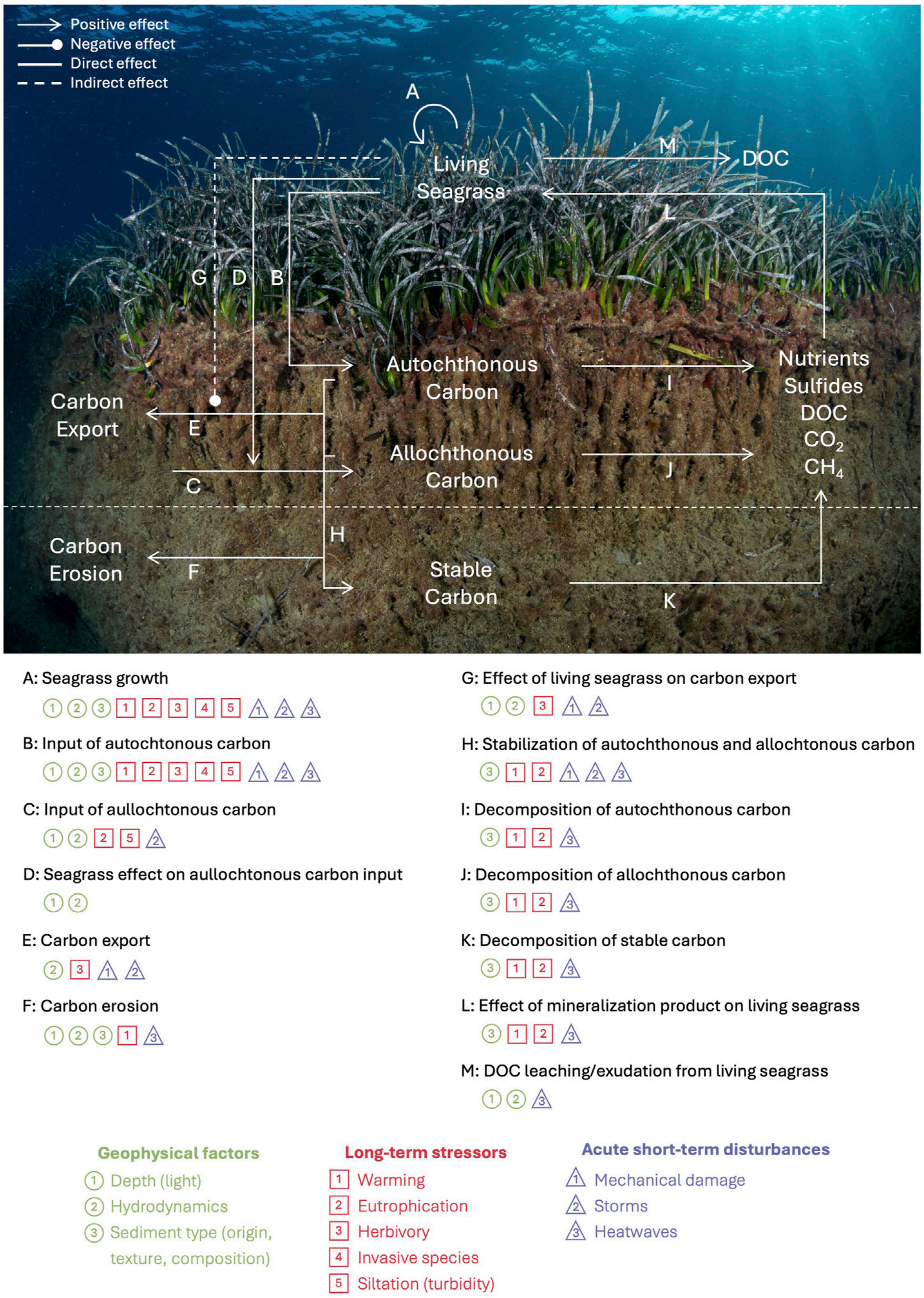

FIGURE 1
Interactions and feedbacks between living seagrass and sedimentary carbon as well as the major factors and stressors affecting their dynamics. Factors affecting seagrass and carbon compartments, numbered and colored according to whether they represent environmental settings, long-term stressors, or acute short-term disturbances. Geophysical factors (green): depth (light availability) (1), hydrodynamics (2), and sediment type (origin, texture and composition) (3). Long-term stressors (red): warming (1), eutrophication (2), herbivory (3), invasive species (4) and siltation (turbidity) (5). Acute short-term disturbances (blue): mechanical damage (1), storms (2), and heatwaves (3).

2 Processes governing carbon storage in seagrass meadows and their main stressors

We drew a simplified overview of the main processes that govern interactions in the carbon storage of seagrass ecosystems (Figure 1). We distinguished the three pools that make up the carbon stores in seagrass ecosystem: a) the seagrass, b) the upper sediment layer (*i.e.*, the newly deposited organic matter (OM) within the rhizosphere that undergoes faster mineralization), and c) the lower sediment layer (*i.e.*, the more stable OM pool). The origin of organic carbon in the sediment can be autochthonous (*i.e.*, deriving from above- and below-ground tissues) or allochthonous (*i.e.*, deriving from the suspended material trapped by seagrasses), often with similar contributions by the two sources (Kennedy et al., 2022). During the mineralization of OM in the sediment, nutrients are released to pore water and the water column (Figure 1). The factors affecting the different compartments were grouped according to whether they represent environmental settings (*i.e.*, hydrodynamics, nutrient and light availability, and sediment origin, texture and composition), long-term stressors (*e.g.*, warming, eutrophication, siltation, invasive species, herbivory), or acute short-term disturbances (*e.g.*, mechanical damage, storms, heatwaves). Figure 1 summarizes how each of these factors potentially affects the processes that govern carbon dynamics across the three carbon pools in seagrass ecosystems.

3 A conceptual mechanistic model of carbon dynamics in seagrass meadows

To build our mechanistic model that couples ecological and biogeochemical dynamics in seagrass meadows we used the processes described above (Figure 1) that were derived through expert knowledge and previous theoretical work. Thus, we did not build nor parameterize a model based on collected ecological data but only developed a conceptual model based on processes. Furthermore, we did not include all described processes (Figure 1), but we focused on the impact of anthropogenic stress – related to physical damage like dredging and anchoring – that could lead to seagrass meadow degradation. There are two dynamical parts in the model: the ecological dynamics that describe seagrass growth (*i.e.*, metabolic capture of carbon) and the biogeochemical dynamics that describe carbon storage in the sediment. Our aim is to show how such a mechanistic model can help understand the qualitative responses of seagrass carbon storage to stressors, even if we cannot fully describe and parameterize the model (Scheffer and Beets, 1994).

3.1 Ecological dynamics: seagrass growth

We followed the model structure proposed by Maxwell et al. (2017) to describe changes in seagrass biomass (Equation 1). There are three main terms in the model: a logistic growth term of seagrass biomass, and two loss terms which result from the physical (hydrodynamics) and natural mortality. The model includes a positive hydrodynamic feedback where the seagrass canopy can decrease the negative physical stress of water currents on the meadow:

$$\frac{dS}{dt} = \underbrace{r_{max}S\left(1-\frac{S}{K}\right)}_{\text{logistic growth}} - \underbrace{m_H H_{max}\frac{S_{hh}}{S_{hh}+S}}_{\text{loss due to hydrodynamics}} S - \overbrace{ms}^{\text{loss due to natural mortality}} - \underbrace{m_A S}_{\text{loss due to anthropogenic stress}} \tag{1}$$

where S is the seagrass biomass, r_{max} the maximum growth rate, K the carrying capacity, m_H the mortality rate due to hydrodynamic intensity, H_{max} the maximum hydrodynamic intensity, and S_{hh} the half-saturation constant for the seagrass biomass effect on hydrodynamic intensity (we used a Monod function to describe the effect of seagrass biomass on the hydrodynamic intensity). S_{hh} determines the strength of the hydrodynamic feedback and depends on local conditions (*e.g.*, depth, exposure) and seagrass traits (Figure 1). m is natural seagrass mortality and m_A is mortality attributed to anthropogenic stress due to physical damage like dredging and anchoring.

3.2 Biogeochemical dynamics: sedimentary carbon

We consider two different origins of carbon stored in seagrass sediments: autochthonous carbon, C_{Au} (Equation 3), which depends on the proportion of seagrass debris deposited in the sediment, β, and allochthonous carbon, C_{Al} (Equation 2), which depends on the maximum input of suspended carbon-bearing particles, α. Once deposited, both autochthonous and allochthonous carbon can either be exported, mineralised, or stored at a given rate (ϕ_{EX}, ϕ_{DX}, ϕ_{BX} respectively, where X defines the different carbon pools *Au:* autochthonous, *Al:* allochthonous, *St*: stable). Given the highly recalcitrant nature of seagrass debris (Kaal et al., 2018), the mineralization of C_{Au} is slower than that of the C_{Al} (Spivak et al., 2019). Lastly, stable carbon C_{St} (Equation 4) which sits below the rhizosphere, is decomposed at a slower rate than the two newly deposited carbon pools (C_{Au}, C_{Al}, Figure 1). Assuming linear relationships for export, decomposition and storage (de Mazancourt et al., 1999; Boudsocq et al., 2009), our three-compartment biogeochemical dynamic model reads:

$$\frac{dC_{Al}}{dt} = \alpha \underbrace{\frac{H_{CAl}}{H_{CAl}+H_{max}\frac{S_{hh}}{S_{hh}+S}}}_{\text{deposition by trapping}} - \underbrace{C_{Al}\left(\Phi_{DAl}+\Phi_{EAl}+\Phi_{BAl}\right)}_{\text{loss by erosion,decomposition,storage}} \tag{2}$$

$$\frac{dC_{Au}}{dt} = \underbrace{\beta S}_{\text{dead seagrass}} - \underbrace{C_{Au}\left(\Phi_{DAu}+\Phi_{EAu}+\Phi_{BAu}\right)}_{\text{loss by erosion,decomposition,storage}} \tag{3}$$

$$\frac{dC_{St}}{dt} = \underbrace{\Phi_{BAl}C_{Al}+\Phi_{BAu}C_{Au}}_{\text{storage}} - \underbrace{\Phi_{DSt}C_{St}}_{\text{loss by decomposition}} \tag{4}$$

Details on model analysis and parameter values can be found in the Supplementary Material.

4 Tipping point cascades from seagrass to sedimentary carbon dynamics

The bifurcation diagrams of Figure 2 show the asymptotic equilibria of seagrass and the three carbon pools within the sediment for a given level of anthropogenic induced mortality m_A. The greater the anthropogenic mortality (Figure 2A), the more likely it is that the meadow shifts from a seagrass-vegetated state to a bare state. At a certain threshold of anthropogenic induced mortality m_A, the seagrass meadow crosses a tipping point and shifts to a bare state with no standing seagrass biomass, thereby leaving the sediment exposed to faster mineralization and erosion. Looking at the carbon stored in each compartment in relation to the same anthropogenic mortality gradient (Figure 2B), we find that the carbon mass in each compartment responds in a similar way to the seagrass dynamics under different hydrodynamic regimes. Both allochthonous and autochthonous carbon mass decreases with

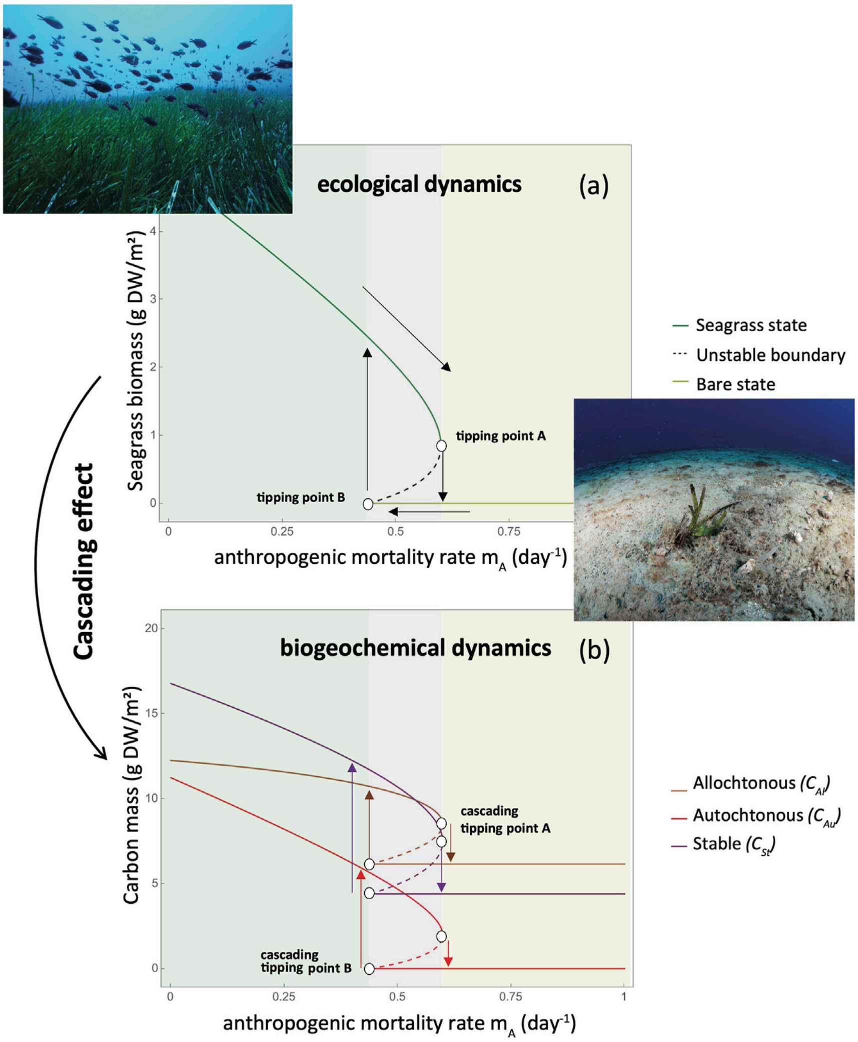

FIGURE 2
Asymptotic equilibria and tipping points in a coupled seagrass and sedimentary carbon conceptual mechanistic model. Bifurcation diagram of seagrass and sedimentary carbon dynamics along a hypothetical gradient of anthropogenic induced mortality (m_A). A seagrass state means that there is one stable equilibrium with the presence of seagrasses. A bare state means that there is only one stable equilibrium with no seagrass. A bistable state means that there are two alternative equilibria, the seagrass and bare state equilibria. (a) Equilibrium states of seagrass biomass (S). Once anthropogenic stress increases, seagrass biomass decreases, until a tipping point A where the seagrass shifts abruptly to a bare state. Seagrass biomass recovers at tipping point B at a lower level of anthropogenic induced mortality compared to tipping point A due to the hysteresis effect. (b) Allochthonous (C_{Al}), autochthonous (C_{Au}) and stable (C_S) carbon mass equilibria states along the same anthropogenic stress gradient. The carbon equilibria reflect the equilibrium state changes of living seagrass biomass. Once seagrass crosses the tipping points A or B, it collapses and effect cascades to the carbon compartment, leading to sudden loss of carbon and a low carbon equilibrium state as the sole carbon contribution originates from the allochthonous sources in the water column. [Model parameters used are not specific to a given seagrass species or meadow but constrained by realistic assumptions to showcase the qualitative behavior of the system; see detailed model and parameter description in the Supplementary Material. Photo insets depict a healthy (upper left) and a degraded (lower right) *Posidonia oceanica* meadow (Photo credits: Julius Glambedakis and Thanos Dailianis).

increasing anthropogenic stress. In fact, the absence of standing seagrass biomass results in the loss of C_{Au} inputs and their erosion from the sediment, and in a greater hydrodynamic intensity that causes fewer particles to be trapped and less C_{Al} input. Consequently, the C_{St} follows the same decreasing pattern. Eventually, all carbon pools experience a tipping point to a low carbon storage state (that can be interpreted as carbon loss) as the tipping event in the seagrass ecological dynamics cascades on the carbon dynamics.

5 Discussion

In this perspective paper, we suggest that there are thresholds beyond which seagrass meadows turn from net carbon sinks to net sources of CO_2 due to the crossing of tipping points in seagrass meadows. We described a set of positive and negative interactions at the level of seagrass meadows, as well as between the sediment and the seagrass that altogether affect carbon dynamics in seagrass meadows (Figure 1). We proposed that incorporating this knowledge into a coupled ecological-biogeochemical conceptual model can improve our understanding of the potential response of carbon storage to seagrass meadow degradation. We then built a simplified version of such model to showcase how tipping events in seagrass meadows driven by anthropogenic stress could cascade into the sedimentary carbon dynamics, leading to the eventual loss of stable carbon that implies a transition of the meadow from a net sink to a source of CO_2 (Figure 2).

5.1 Model limitations/extensions

Clearly, our model focusing on a single positive feedback is only a starting point. Seagrass clonal integration, for instance, can be considered among the main reinforcing feedbacks (Nielsen and Pedersen, 2000), as well as increasing light quality through sediment trapping by the canopy, or belowground biomass allocation in response to hydrodynamic and nutrient conditions (Burkholder et al., 2007; Maxwell et al., 2017). Although the choice of the modelled feedback may affect features of the tipping behavior of seagrasses, we do not expect that it will change the overall cascading effect on sedimentary carbon dynamics qualitatively. Instead, it is the approximations and parameters of the feedback functions that are key in predicting carbon storage responses. For instance, in the presented model (Figure 2), the most important parameter that determines the occurrence of tipping points in the system is the half-saturation constant *Shh* that modulates the feedback effect of seagrass on reducing hydrodynamic intensity. The question is to identify how other feedback functions would be as crucial in modulating tipping responses.

We have assumed the most parsimonious relationships (*i.e.*, linear) in the fluxes between the different compartments, neglecting, for example, priming effects that have been shown to enhance carbon decomposition in seagrass meadows (Trevathan-Tackett et al., 2018). At the same time, we have not considered that decomposition contributes to the pore water nutrient pools (Figure 1) that could create either positive or negative feedbacks in nutrient fluxes from the sediment to the seagrass or other primary producers (de Boer, 2007). A more complete model could integrate light and nutrient limitation as well as temperature dependence of growth and decomposition in order to study the effects of multiple stressors both in isolation and in combination. Future work should also investigate the effect of different time scales, ranging from hours to centuries, involved in the metabolic capture of carbon, and carbon decomposition and preservation dynamics. Processes occurring at different time scales could lead to significant time lags and long transients which may be more relevant than the asymptotic dynamics we focused on here (Hastings et al., 2018). Yet, to achieve all these, robust data on seagrass ecology and carbon biogeochemistry are needed.

5.2 Empirical needs to match modeling needs

Current knowledge gaps in BC science limit our ability to develop and parameterize accurate mechanistic models of carbon fluxes following seagrass deterioration. In our model, we used arbitrary parameter values to explore in general the possibility of tipping responses. The next step is to have species-specific parameter values to estimate the likelihood of tipping responses to occur given the model we use. For example, field experiments could help us to obtain estimates of hydrodynamic shear stress under different depths and canopy densities (e.g., (van der Heide et al., 2007b; Infantes et al., 2009), whereas mortality rates due to anthropogenic disturbances (like anchoring) could be derived from existing surveys (Pergent-Martini et al., 2022).

We also need further empirical evidence of the dynamics between the capture of carbon, its burial and erosion, and its post-depositional transformation to be able to predict the possible change in the carbon sequestration capacity of seagrass ecosystems following disturbance. Long-term laboratory experiments are necessary to quantify the decomposition rates and diagenesis of organic carbon and how these change with the type, intensity and frequency of stressors (Spivak et al., 2019). Spatially larger assessments will allow accounting for the variability in carbon storage caused by large-scale factors (*e.g.*, geomorphic setting, temperature), whereas localized assessments will allow accounting for local variability in carbon budgets, considering the effect of small-scale factors (*e.g.*, sediment typology, hydrodynamics) on carbon fluxes (Mazarrasa et al., 2021; Kennedy et al., 2022).

5.3 Conclusion

Conserving the BC capacity of seagrass meadows requires a mechanistic understanding of the most important processes affecting the response of seagrass and associated carbon pools to different environmental, ecological and climate change conditions. Our proposed modeling framework can contribute to such understanding and inspire further model development. For example, by accounting for a combination of stressors, like warming, turbidity or eutrophication, it will be possible to outline potential projections of BC storage while embracing the uncertainty in the model structure and parameter estimates. Or, we can explore possible responses of seagrass meadows and their C-pools under high and low hydrodynamic regimes along a gradient of temperature in the presence of stochastic mechanical damage in hypothetical meadows. Such numerical experiments though require gathering robust ecological data that will eventually allow us to calibrate and validate mechanistic models like the conceptual one we developed here that could be implemented in BC accounting frameworks.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

Author contributions

VD: Conceptualization, Funding acquisition, Methodology, Software, Writing–original draft, Writing–review and editing. AL:

Conceptualization, Formal Analysis, Writing–review and editing. ET: Conceptualization, Methodology, Writing–review and editing. TA: Conceptualization, Writing–review and editing. JB: Conceptualization, Writing–review and editing. EI: Conceptualization, Writing–review and editing. DK-J: Conceptualization, Writing–review and editing. NM: Conceptualization, Writing–review and editing. OS: Conceptualization, Writing–review and editing. SV: Conceptualization, Writing–review and editing. EA: Conceptualization, Funding acquisition, Writing–original draft, Writing–review and editing.

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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcpxs.2025.1534330/full#supplementary-material

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