



## Review Article

## Stabilisation and destabilisation of coastal blue carbon: The key factors

Peter I. Macreadie<sup>a,b,\*</sup>, Anirban Akhand<sup>b,a,1</sup>, Stacey M. Trevathan-Tackett<sup>a,b</sup>,  
 Carlos M. Duarte<sup>c</sup>, Jeff Baldock<sup>d</sup>, Jennifer L. Bowen<sup>e</sup>, Rod M. Connolly<sup>f</sup>

<sup>a</sup> Centre for Nature Positive Solutions, Biology Discipline, School of Science, RMIT University, Melbourne, VIC 3000, Australia

<sup>b</sup> Deakin Marine Research and Innovation Centre, Deakin University, Burwood campus, 221 Burwood Hwy, VIC 3125, Australia

<sup>c</sup> Marine Science Program, Bioscience and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

<sup>d</sup> Research Consultant, Highland Valley, SA 5255, Australia

<sup>e</sup> Department of Marine and Environmental Science, Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, MA, United States

<sup>f</sup> Coastal and Marine Research Centre, Australian Rivers Institute, School of Environment and Science, Griffith University, Gold Coast, Qld, Australia

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## ABSTRACT

Blue carbon ecosystems (BCEs), which include seagrass meadows, tidal marshes and mangrove and supratidal forests, hold large reservoirs of organic carbon. Despite the impact of BCEs as natural climate solutions, the mechanisms responsible for carbon retention have not been clearly summarised, limiting our chance to manage BCEs for maximum carbon storage. Here, we explore a great mystery of the blue carbon cycle by reviewing existing published literature: Why is some coastal carbon remineralised into CO<sub>2</sub> and CH<sub>4</sub> by microbes within seconds/min while other carbon escapes microbial attack and becomes sequestered for millennia? The answer to this question will help predict and manage the global blue carbon cycle. We find that microbial communities are fundamental drivers of carbon mineralisation in BCE sediments, with their metabolic pathways dictating the fate of sequestered organic matter. Contrary to earlier notions, microbial diversity and composition are shown to significantly impact carbon stabilisation, with distinct microbial taxa targeting different organic compounds. Furthermore, anthropogenic disturbances such as habitat alteration and eutrophication can disrupt microbial communities, leading to increased carbon mineralisation and CO<sub>2</sub> and CH<sub>4</sub> emissions. Environmental parameters such as temperature, salinity, and nutrient availability also exert considerable influence on carbon stability in BCEs. Changes in these factors can alter microbial activity and the degradation rate of organic matter, highlighting the importance of understanding their additive and synergistic effects. For instance, warming combined with oxygen exposure due to habitat disturbance can amplify microbial carbon mineralisation, particularly in submerged BCEs like seagrass beds. Future research directions include characterising carbon at molecular levels, understanding region-specific drivers of carbon stability, and prioritising conservation efforts based on physiographic and geomorphologic settings. This review underscores the need for a holistic approach to BCE management, considering both microbial processes and environmental factors. By elucidating the factors governing carbon stability, this study aims to enhance our understanding of the role of BCEs in climate change mitigation and inform conservation strategies.

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\* Corresponding author.

E-mail address: [peter.macreadie@rmit.edu.au](mailto:peter.macreadie@rmit.edu.au) (P.I. Macreadie).

<sup>1</sup> Dual first author.

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### 1. Blue carbon ecosystems and their organic carbon storage and stabilisation potential

It has been more than a decade since the concept of blue carbon was introduced, recognising the tremendous potential of the mangroves, seagrasses, and salt marshes to act as a nature-based solution to mitigate climate change (Nellemann et al., 2009). These coastal marine ecosystems sequester disproportionately higher quantities of organic carbon per unit area than terrestrial and open oceanic systems (Mcleod et al., 2011; Macreadie et al., 2019a). These blue carbon ecosystems (BCEs) have a remarkable capacity for storing and locking away both the autochthonous (produced within the system) and allochthonous (produced outside the system) carbon for millennia in their sediment column (Saintilan et al., 2013; Macreadie et al., 2021; Komada et al., 2022).

Continued urbanisation and industrialisation, coastal tourism, unsustainable fishing activities and other forms of human/climate disturbances pose ongoing threats to BCEs to the point of imminent extinction in some places (Karani and Failler, 2020; Chanda, 2022; Sahavacharin et al., 2022). One fundamental reason behind calls for conservation,

management, and restoration of BCEs is the knowledge that they provide carbon sinks, lowering concentrations of greenhouse gases in the atmosphere and thereby helping to mitigate climate change (Macreadie et al., 2017; Serrano et al., 2018; Hori et al., 2019). Anthropogenic and climate change-induced challenges, like sea level rise and global to local warming, may affect blue carbon stock in both beneficial and detrimental ways, individually and through their synergistic effects (Dahl et al., 2023; Hao et al., 2024; Wang et al., 2021). Climate change can, for example, positively impact carbon sequestration and storage in coastal ecosystems through landward migration of blue carbon habitats, maintenance of sediment supply, and improved water quality, but in the worst-case scenario, could cause losses of as much as 3.4 Pg of sequestered carbon by 2100 (Lovelock and Reef, 2020). Restoration practices, like tidal reinstatement, are an example of anthropogenic activities having net beneficial impacts on the storage and stability of blue carbon (Cadier et al., 2023; Gulliver et al., 2020). However, attention has focussed primarily on the quantity of carbon they sequester, not the quality (especially the recalcitrance of carbon) that they maintain and retain in their habitats.

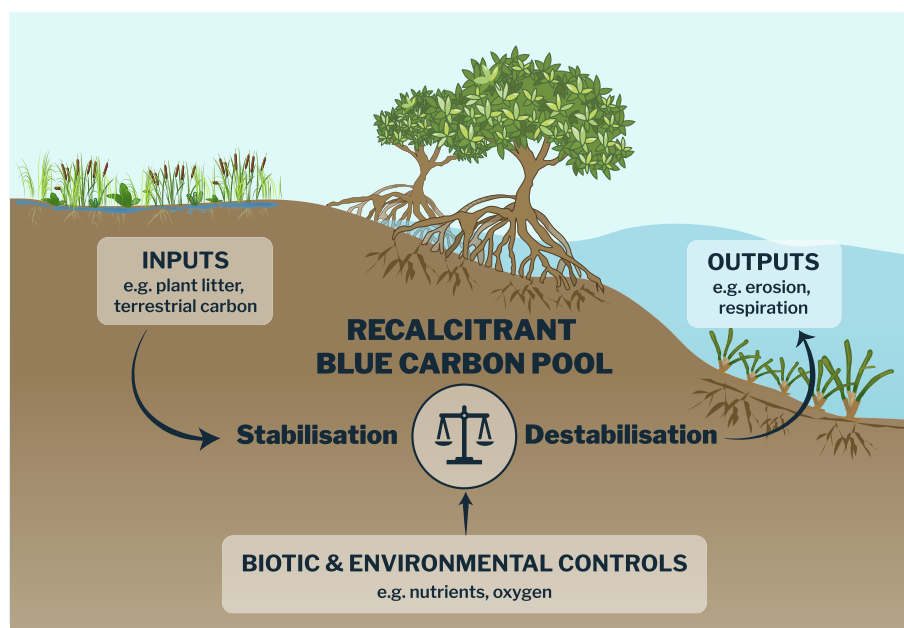


Fig. 1. Blue carbon ecosystems accumulate soil organic carbon when inputs and stabilisation processes outweigh destabilisation processes that lead to outputs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Some studies indicate that molecular structure plays a crucial role in ascertaining the degree of recalcitrance to the carbon locked in BCE sediments (Kaal et al., 2019; Spivak et al., 2019). Burial of minerals also provides a protective shield to the sequestered organic carbon that enhances its stability (Sun et al., 2019). Environmental parameters like oxygen, redox potential, salinity, pH, and temperature and their interplay between each other and organic carbon across varying depths are often critical in regulating the stability of blue carbon (Gao et al., 2019; Kida and Fujitake, 2020; Sasmito et al., 2020). Microbial diversity, their metabolic pathways, their interaction with BCE vegetation, and their response to anthropogenic disturbances are key attributes governing the stability of organic carbon in BCEs (Kristensen et al., 2008; Trevathan-Tackett et al., 2020; Mohapatra et al., 2022). These observations point to the quantity as well as the quality of sediment being important determinants of storage capacity while multifarious environmental and anthropogenic factors are at play (Fig. 1) (Stockmann et al., 2013).

Prioritising the conservation measures to safeguard these crucial shallow coastal marine ecosystems requires answering the following questions. Are some specific forms of blue carbon, irrespective of their molecular degree of lability, mostly inaccessible to microbial attack? To what degree will coastal development trigger the release of CO<sub>2</sub> and CH<sub>4</sub> via microbial remineralisation? How will warming affect the stability of existing blue carbon stocks? Is the carbon in all blue carbon systems equally susceptible to loss, or do some systems retain greater proportions of their carbon? Answers to such questions are critical for predicting future carbon budgets, constructing defensible processes within national inventories, and developing viable carbon sequestration and avoided-emission projects internationally.

Based on the research questions above, we aimed to explore and ideally quantify the relative contributions of potential pathways to blue carbon recalcitrance. An understanding of the contributions that these pathways make to recalcitrance will help guide decisions about managing blue carbon systems and potential management outcomes. These pathways were identified based on a long legacy of terrestrial research (reviewed in Lützwow et al., 2006; Sollins et al., 1996), yet they remain untested and largely ignored within marine and estuarine ecosystems (Burdige, 2007). Because terrestrial and marine/coastal sediments have very different biogeochemical conditions (Fenchel et al., 1998), we take a fundamental approach to discovering which carbon cycling pathways are key for blue carbon sediments.

## 2. Formation and stability of blue carbon

Why is it that some coastal organic carbon becomes remineralised into CO<sub>2</sub> and CH<sub>4</sub> by microbes within seconds/min while other carbon escapes the microbial attack and becomes sequestered for millennia? In this section, we review pathways to the formation and stability of blue carbon (Fig. 1).

### 2.1. Formation of autochthonous carbon pool in BCEs

The very high net photosynthetic carbon uptake potential, high primary productivity (higher than many terrestrial vegetated ecosystems), and a high rate of carbon burial in the sediments lay the foundation of the global autochthonous carbon pool in BCEs (Alongi, 2012; Duarte, 2017). Despite being geographically limited to less than 0.5 % of the total oceanic area, these shallow coastal ecosystems account for more than 50 % of the carbon stored in the oceans (Hori et al., 2019). This results from the very high net primary productivity of BCEs, which can be attributed to the nutrient-rich environment (Duarte et al., 2013; Huxham et al., 2018), stable growing conditions (McLeod et al., 2011), efficient carbon sequestration mechanisms (Chmura et al., 2003), and resilient, productive plant species adapted to coastal environments (Duarte et al., 2013). These ecosystems support both high biomass productivity and carbon storage in both plant tissues and sediments, which help form the BCE habitats in the first place and, in turn, allow

other allochthonous carbon to remain trapped in these ecosystems.

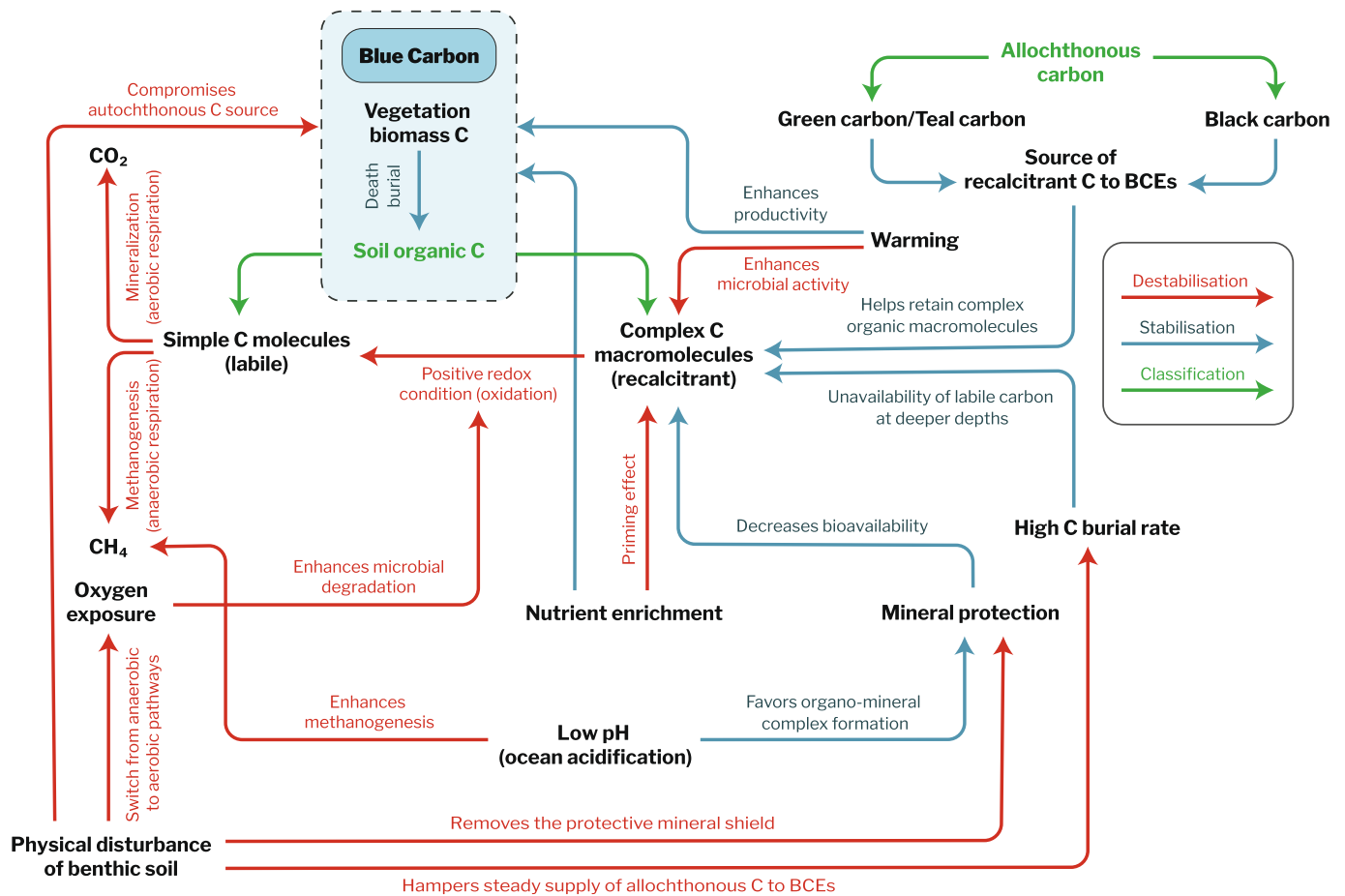
The combination of adequate solar insolation, salt tolerance, efficient carbon allocation to roots, and low decomposition rates of sediment carbon due to anoxia and anaerobic conditions make BCEs particularly effective at storing autochthonous carbon. Abundant sunshine in the latitudinal range where BCEs are mostly available (between 24°N and 38°S) has been postulated as underlying their enhanced primary productivity (Giri et al., 2011; Meng et al., 2021). The adaptive salt tolerance mechanisms of these plants enable them to store carbon, thus leading to very high autochthonous carbon production in their biomass (Ball, 1988; Parida and Jha, 2010). BCEs like mangroves and seagrasses are capable of storing substantial quantities of carbon in their roots, and the roots also consolidate the soil and thus help maintain the autochthonous carbon pool (Lovelock, 2008; Adame et al., 2017). The BCE sediment environment is discussed in more detail below, but in summary, it is the intrinsic anaerobic conditions and anoxia that are principally responsible for high burial efficiency as they help prevent the widespread oxidation and, thus, remineralisation of autochthonous organic carbon (Kristensen et al., 2008; Trevathan-Tackett et al., 2017b). These environmental and plant physiological factors are central to the building of the autochthonous carbon repository in BCEs and governing storage per unit area.

### 2.2. Role of molecular structure

Several studies directly state that molecular structure largely governs the stability of organic carbon in BCEs (Fig. 2) (Spivak et al., 2019). Complex polycyclic particulate organic macromolecules like lignin and polysaccharides (including tannin) usually exhibit environmental recalcitrance under submerged and anoxic conditions, especially in seagrass sedimentary beds (Kaal et al., 2019). Pyrogenic macromolecules, mainly comprising polycyclic aromatic hydrocarbons, are essentially allochthonous black carbon and ancient kerogens also show a significant degree of recalcitrance, as shown in mangrove and salt marsh sediments (Burdige, 2007; Chew and Gallagher, 2018).

Despite debate about whether allochthonous (mainly terrestrial) carbon should be accounted for within the realm of blue carbon (Adame et al., 2024), several studies indicate that BCEs provide viable biogeochemical conditions that help some forms of allochthonous carbon remain undecomposed better than autochthonous blue carbon. This could be due to an intrinsic greater degree of recalcitrance in the organic matter from the allochthonous source, as well as the possible decomposition of more labile organic matter during transport to BCEs. Thermogravimetric analysis on sediments indicates that the lignocellulose matrix or other polysaccharides inherent in the cell walls of both seagrasses and macroalgae renders them recalcitrant in nature (Trevathan-Tackett et al., 2015). Thus, macroalgae, which is typically considered allochthonous in BCEs, has the potential to donate significant quantities of carbon that show greater stability than many labile autochthonous counterparts within the BCEs.

The recalcitrance of carbon varies among Blue Carbon species (Cragg et al., 2020). For example, there is a significant latitudinal gradient in seagrass recalcitrance, with tropical seagrasses having a higher proportion of recalcitrant carbon than temperate ones (Trevathan-Tackett et al., 2017a). The quantity of recalcitrant macromolecules depends on the morphology of the species. It also varies across different plant parts like root, sheath, rhizome, etc. However, the intrinsic complexity of the organic macromolecules cannot solely determine their recalcitrance; it also depends on the environmental conditions (Kaal et al., 2020). Many studies indicated that even the most complex forms of organic macromolecules can be decomposed under favourable conditions (Arndt et al., 2013; Lehmann and Kleber, 2015), which often arise when BCEs are disturbed.



**Fig. 2.** How environmental factors in and around blue carbon ecosystems (BCEs) affect the stability of organic carbon in the sediment profile. Green arrows denote the classes of a particular attribute. Red arrows denote processes that destabilise organic carbon (labels in red). Blue arrows denote processes that stabilise organic carbon (labels in blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3. Shielding by minerals

The complexity of carbon deposited in BCEs, and hence its stability, is also governed by mineral deposition, as it is for terrestrial carbon sequestration (Hemingway et al., 2019). The presence of minerals introduces multivalent cations and changes the sediment matrix along with the architecture of sediment-mineral complex formation, which enhances the protection of organic carbon above sediments devoid of minerals (Baldock and Skjemstad, 2000). Minerals deposited concomitantly with carbon in BCEs encapsulate organic carbon macromolecules and occupy narrow pore spaces within organic matter, shielding it from contact with the decomposers (Blair and Aller, 2012; Kida and Fujitake, 2020). The minerals amidst the sequestered carbon act as a catalyst, facilitating the condensation reactions, altering the molecular structure to enhance its recalcitrance (by increasing the degree of structural and chemical complexity), and impeding access to the enzymes responsible for decomposition (Greathouse et al., 2014; Morrison et al., 2020; Kleber et al., 2021). However, the efficacy of the organo-mineral bonding depends on the ambient environmental conditions where the carbon is stored in BCEs. The degree of physical protection is high in submerged and anoxic conditions but less in drier conditions because the organo-mineral bonds weaken and allow hydrophobic molecules to adsorb to decomposers (Liu and Lee, 2006; Kaiser et al., 2015). Exposure to oxygen and light due to erosion and resuspension of surficial sediments, for example, through sea-level rise and storm surges in shallow regions, can be critical in compromising the stability of otherwise recalcitrant and even labile carbon as they remove the shield provided by the minerals (Li et al., 2023a). Iron, one of the most abundant elements in the Earth's

crust, plays a crucial role in the preservation and long-term burial of organic carbon in marine sediments through ligand exchange (Hassler et al., 2020; Hu et al., 2023). At the same time, some studies have cautioned against over-simplification, as dissimilatory microbial Fe(III) reduction can lead to significant anaerobic oxidation of organic carbon (Yu et al., 2021). Additionally, the production of reactive oxygen species through the oxygenation of Fe(II) in minerals has the potential to elevate microbial activity, thereby facilitating the degradation of organic carbon (Dong et al., 2023). Several organophosphates of phytic acid remain bound to aluminium, which also enhances their stability in the sediments under water (Guan et al., 2006). Thus, mineral protection offers a pathway that enhances the recalcitrance of organic matter in BCE sediments; however, its effectiveness is greater in deeper layers than in surficial layers more exposed to disturbances (Spivak et al., 2019; Sun et al., 2019).

### 2.4. Organic carbon burial rate

The amount of organic matter being deposited or buried into the sediments and its rate of deposition or burial also play a critical role in governing their stability in the oxic environments of BCEs (Cuellar-Martinez et al., 2019; Chuan et al., 2020). Under a steady supply of organic matter within BCEs, despite the presence of sufficient oxygen, the microbes primarily target the simpler compounds in the fresh organic matter deposits and do not undergo the energy-intensive depolymerisation of complex molecules (Jiao et al., 2014). This preference of the microbial population for the easier pathway to draw energy allows the complex, hydrolysis-resistant macromolecules of

polymers to settle and remain submerged under freshly deposited organic matter. Where oxygen is low or severely depleted, these complex organic molecules are robbed of the essential enzymatic cofactor, i. e., oxygen, which is required for their degradation (Arndt et al., 2013; Bianchi et al., 2016). However, contrary schools of thought also indicate that fresh deposition of unstable organic matter, even in a low-oxygen environment, leads to the priming effect (Trevathan-Tackett et al., 2018), thereby jeopardising the stability of the recalcitrant organic carbon (Kuzyakov et al., 2000; Kristensen et al., 2012). The microbial priming effect is a phenomenon in which the addition of fresh organic carbon or inorganic nutrients stimulates microbial communities to decompose existing, previously stable organic carbon that would otherwise remain undecomposed or degrade only very slowly (Kuzyakov et al., 2000). These assertions are mostly generated from terrestrial observations (Guenet et al., 2010; Liu et al., 2020a, 2020b; Mo et al., 2022) and require further studies on dynamic blue carbon environments. The decomposition mechanism beneath the sediment surface is governed by mixed redox conditions, which include the anaerobic processes that produce another greenhouse gas, CH<sub>4</sub>, and lead to the loss of carbon (Jørgensen et al., 2022). The global warming potential of CH<sub>4</sub>, being 25 times higher than CO<sub>2</sub>, compels us to reconsider whether enhancing the recalcitrance by eliminating oxygen results in a more detrimental consequence of anaerobic degradation of carbon (Wallmann et al., 2006; Beulig et al., 2018; McTigue et al., 2021; Schuster et al., 2024). Some studies indicate that the anaerobic oxidation of CH<sub>4</sub> in the depths of wetland sediments is accentuated by the electron-accepting functional groups like quinones, which help suppress around 114 Tg of CH<sub>4</sub> efflux to the atmosphere per year (Valenzuela et al., 2017).

## 2.5. Environmental factors

Environmental parameters like oxygen, redox potential, salinity, pH, and temperature play a significant role in allowing less stable carbon to stabilise and recalcitrant carbon to destabilise (Fig. 2).

### 2.5.1. Oxygen and redox state

Microbes make use of oxygen as an electron acceptor and thereby utilise it as a fuel to decompose carbon from the detritus and sediments of BCEs (Palit et al., 2022). However, the presence or absence of oxygen can regulate the bioavailability of minerals like iron, aluminium, and manganese and nutrients like nitrogen, phosphorus, and sulphur, depending on the redox state of the sediments, which indirectly governs carbon breakdown (Fig. 2) (Burdige, 2011). Oxygen principally leads to the breakdown of organic matter in two steps; the first involves the breakdown of complex polymers (like lignin) into simple monomers (like amino acids, phenols, and sugars) (Graves et al., 2022). This step is redox potential-dependent, meaning that the higher the oxygen levels, the greater the propensity for this first step to be completed (Bianchi et al., 2016). The second step is the mineralisation of these simple compounds to CO<sub>2</sub>, which is relatively less redox potential dependent (Yamuz-Magdalenó et al., 2024). Hence, the absence of oxygen (or a low-oxygen environment) can positively influence the stabilisation of organic carbon, as it limits the potential for aerobic oxidation. Furthermore, oxygen deficiency enhances the residence time of the remaining sequestered organic carbon in the long term, making the less energetically efficient anaerobic metabolism the only option to decompose this part as it prevents the first step (Chapman et al., 2019).

### 2.5.2. pH dependence

The decline in pH levels in coastal nearshore waters due to acidification has been shown to exert both positive (Garrard and Beaumont, 2014; Russell et al., 2013) and negative (Vizzini et al., 2019; Chuan et al., 2020) effects on carbon stocks in BCEs. Positive effects are linked to increased availability of bicarbonate and CO<sub>2</sub>, which can enhance primary productivity, leaf growth, and above- and below-ground

biomass in seagrass beds (Garrard and Beaumont, 2014). Experimentally lowered pH levels in seagrass sediments, combined with thermal stress, necessitate a shift in membrane composition to maintain fluidity. This induces a shift in fatty acid synthesis toward the extra-plastidial pathway to counteract excessive membrane fluidity. As a result, alterations to chloroplastidial monogalactosyldiacylglycerol and digalactosyldiacylglycerol lipids, along with reduced  $\alpha$ -linolenic acid levels, can compromise the physical integrity of seagrasses—reflected in reduced meadow growth and density—and thereby diminish the input of autochthonous carbon to sediments (Franzitta et al., 2021). Contrary to the previously mentioned positive effects on organic carbon stability in BCEs, the carbon concentrating mechanisms of macroalgae are not expected to change in a low pH environment, and, hence, they cannot render any effective enhancement in terms of primary productivity, owing to increased CO<sub>2</sub> concentrations in the coastal water (Hill et al., 2015). Lowering of pH in blue carbon sediments has been hypothesised in some studies to be the primary driver of methanogenesis that facilitates stable carbon to escape to the adjacent water column and, hence, to the atmosphere in the absence of adequate methanotrophs (Chuan et al., 2020). However, some findings indicated that alkaline conditions (pH > 8) in marsh sediments on the seaward edge allow the dissolution of organic matter locked in the sediments (Grey et al., 2023b). High pH has been found to increase the electron-exchange capacity of organic matter, stimulate microbial Fe(III) reduction (Bai et al., 2020), and promote organic matter solubilisation by facilitating shifts in microbial community structure and partitioning behaviour (You et al., 1999; Anderson et al., 2018). However, such direct linkages have yet to be explored in BCEs. Lower pH levels, by contrast, result in the formation of metal complexes (Magdziak et al., 2017), which, in turn, can shield organic carbon locked in sediments. Depth-wise pH variability (lowering of pH with increasing depths) gives rise to an aerobic (near surface) to anaerobic (deeper layers) gradient of microbial communities that governs the metabolic pathways and, hence, the stability of carbon in BCEs (Qian et al., 2023).

### 2.5.3. Role of salinity

Salinity, an indicator of freshwater-seawater mixing, plays an indirect but crucial role in governing the stability of carbon stocks as this parameter regulates microbial community composition and metabolism (i.e. remineralisation) by altering oxygen diffusion, mineral ion mobility, and osmotic stress of the microbial communities (Röthig et al., 2023; Wang et al., 2019; Yu et al., 2020). Some studies found no relationship between salinity and sedimentary carbon stock (Kelleway et al., 2016). However, others reported a significant positive relationship between dissolved organic carbon and salinity, indicating the higher chances of dissolution of organic matter in the presence of saline and alkaline seawater dominance (Yu et al., 2020). The relationship between salinity and sedimentary carbon content in BCEs is site and water content dependent. Higher salinity often disrupts the cellular balance of freshwater-loving microbes, hence providing negative feedback to remineralisation; however, the abundance of freshwater alleviates the salinity stress and enables the microbes to use the organic substrate even under brackish conditions (Mavi et al., 2012a, 2012b; Yang et al., 2018). By contrast, salinity stress has also been shown to indirectly enhance subsidence through the destruction of coastal vegetation, followed by compaction of sediments, which ultimately reduces the input of autochthonous carbon to the system (Röthig et al., 2023).

### 2.5.4. Temperature dependence

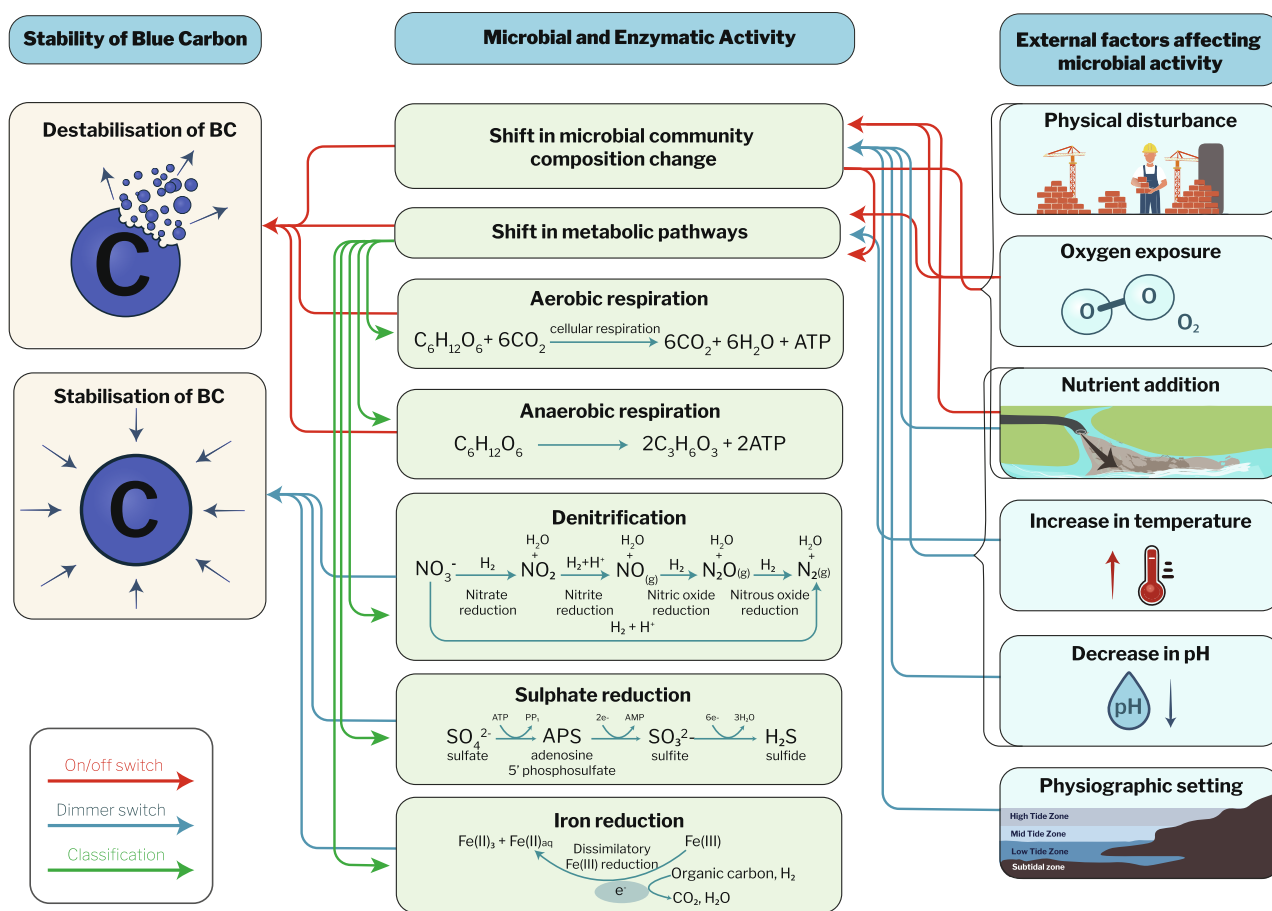
As global warming has accelerated, temporal variability of temperature has become a significant driver of several biogeochemical processes (Gruber, 2011), and the stability of carbon in BCEs is no exception. Several studies unequivocally point out that increasing temperature can actually increase the productivity of any green ecosystem (Li et al., 2021). Mangrove root production and, thus, an increase in mangrove root biomass is expected under elevated air

temperature, which inevitably would contribute to higher organic carbon in the pedosphere of BCEs (Arnaud et al., 2023). However, seagrass ecosystems, owing to their high sensitivity to warming, might exhibit a reduction in live biomass under elevated temperatures (Greiner et al., 2013; Cuellar-Martinez et al., 2019). Supply of allochthonous carbon sources into BCEs in the form of macroalgae is also likely to be jeopardised as increasing temperature reduces productivity (Oliver et al., 2018; Gao et al., 2022). Thus, the elevation of temperature can have both positive and negative effects on the source of autochthonous carbon, i.e., live biomass and decomposition in BCEs (Deb and Mandal, 2021; Ouyang et al., 2023). Elevated temperature in future is expected to increase decay in BCEs, but this is expected to be offset by organic carbon production on a global scale (Ouyang et al., 2023). Studies in terrestrial ecosystems have reported that elevated temperatures can accelerate carbon mineralisation in sediments, likely by stimulating the activity of ligninase and cellulase enzymes that play a key role in organic matter degradation (Chen et al., 2020). Temperature effects need further studies in BCE sediments (Hidayah et al., 2022), but one study clearly indicated that a sustained increase in water temperature did not affect organic carbon reserves in seagrass beds (Macreadie and Hardy, 2018). Yet, seagrass mortality under simulated heatwaves was shown to lead to large CO<sub>2</sub> and CH<sub>4</sub> emissions in experimental Red Sea seagrass meadows (Burkholz et al., 2020). The overall increase in temperature in air, water and soil has been reported to increase the efflux of CO<sub>2</sub> to the atmosphere from mangrove ecosystems, thus offsetting carbon storage (Akhand et al., 2024). Global shifts in temperature have, however, enabled mangrove encroachment in saltmarshes of higher latitudes and

poleward range extensions of kelps (allochthonous to BCEs), saltmarshes, and seagrasses (Lovelock and Reef, 2020).

### 2.6. Preferential role of enzymes

Regardless of the environmental conditions that influence the rate of organic carbon decomposition, it is the enzymes secreted by microbial communities that ultimately drive the breakdown of complex macromolecules into simpler forms and, eventually, into CO<sub>2</sub> or CH<sub>4</sub>. A wide variety of hydrolytic enzymes, mainly belonging to the subcategories of glycosyl hydrolases and peptidases, govern the initiation of the entire remineralisation process of both aerobic and anaerobic pathways (Arnosti, 2011). Studies have shown that aerobic mineralisation of organic carbon to CO<sub>2</sub> takes place at a ten times higher rate than the anaerobic counterpart (Kristensen et al., 1995). One of the fundamental reasons could be that aerobic decomposition involves innumerable enzymes. Many of these enzymes can act upon specific classes of compounds. Each such compound is usually rapidly and completely metabolised by a single microorganism (Canfield, 1994). Enzymes partaking in anaerobic pathways (like methanogenic and sulphate-reducing) are usually unable to degrade most polymeric organic compounds as they rely on relatively slow hydrolytic and fermentative bacteria for the supply of metabolisable low-molecular substrates. However, contrary observations indicated that extracellular hydrolysis of complex organic molecules (usually considered to be the slowest step of anaerobic remineralisation) progressed rapidly under the treatment of mixed cultures of anaerobic bacteria, mostly facilitated by the



**Fig. 3.** Interlinkages of the microbial activities and the factors that govern the stability of OC in BCE sediments. The green arrows denote the classes of a particular attribute. The red arrows denote the processes that act as an on/off switch to trigger the destabilisation of OC. The blue arrows denote the processes that act as a dimmer switch or introduce a gradient in stabilisation to destabilisation. The black-coloured second brackets show the synergistic effects of the components the brackets comprise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pullulanase enzyme (Arnosti et al., 1994). Sulphate-reducing anaerobic enzymes have been found to mineralise two to three times faster than nitrate-reducing ones; however, the rates of both these reduction processes rely on the release rate of low-molecular organic substrates by hydrolysis and fermentation (Kristensen and Holmer, 2001). Though the secretion of certain types of enzymes matters in triggering the extracellular hydrolysis and regulating the remineralisation rate, the optimal activity of the enzymes, like pullulanase, protease, and amylase, depends on environmental factors like temperature of the medium and oxygen availability (Arnosti et al., 1998).

### 3. Does microbial control of carbon burial efficiency prevail over environmental control?

Microbial organisms within BCE sediments are the fundamental drivers of the mineralisation of already sequestered carbon (Fig. 3) (Ren et al., 2022; Williamson and Gattuso, 2022). Contrary notions also exist that microbes help mediate long-term carbon sequestration potential in BCE sediments. For example, microbes alter kelp detritus, leaving behind a considerable amount of stable aromatic compounds (comprising lignins, tannins, and phenolics, which require special enzymes to break them down) that contribute to the allochthonous carbon reservoir of BCEs (Cragg et al., 2020; Feng et al., 2022). Therefore, microbial phylogeny and functional diversity play a crucial role in stabilising/destabilising carbon in the BCE sediment profile; for e.g., *Desulfococcus* microbes abundantly available in seagrass beds target labile and bioavailable simple organic compounds (Sun et al., 2015). In contrast, Flavobacteria prefer to act upon complex macromolecules (Kirchman, 2002). Microbial diversity can vary among blue carbon habitats. For example, microbial diversity can change across a mangrove-salt marsh continuum (Sun et al., 2019). This is attributed to the higher occurrence of recalcitrant carbon in mangroves than in salt marsh sediments (Sun et al., 2019). Archaeal communities in coastal microbiomes are also significant in the metabolism of methane (leading to less CH<sub>4</sub> emission), transformation of detritus into biopolymers (thereby increasing its stability), and fixation of atmospheric and aquatic CO<sub>2</sub> (Zhang et al., 2023). More importantly, the presence (or absence) of BCE can lead to marked differences in the microbial community composition, which, in turn, plays a crucial role in stabilising (or destabilising) carbon sequestered in the coastal sediment profile across the depths (Sun et al., 2020).

Microbial metabolic pathways determine the stability of carbon in BCE environments to a large extent. Microautoradiographic studies show that sulphur-oxidising prokaryotes (Gammaproteobacteria) in sulphide-rich BCE sediments are the chief drivers of incorporating CO<sub>2</sub> in surficial sediments of BCEs through chemolithoautotrophic metabolic pathways (Fig. 3) (Lenk et al., 2011). Chemoautotrophic sulphur oxidisers are reported to boost mineral-associated microbial necromass that consists of stable carbon, which can persist for millennia (Yu et al., 2023). However, anthropogenic stress on microbial communities has been found to alter the biomass lipids, primarily by the accumulation of polyhydroxyalkanoates and the alteration of membrane phospholipid fatty acids, which compromises the bacterial fitness to survive in a changing environment and, hence, become susceptible to species composition change that favours degradation of complex carbon (Grey et al., 2023a). Semi-arid mangrove sediments in the Middle East exhibited luxurious growth of microbial mats (mainly cyanobacteria) that store significant quantities of carbon; however, due to the absence of a reducing environment, these mats often act as labile sources of carbon to other microbiomes and as a consequence do not enhance the stability of carbon in the mangrove sediments (Schile et al., 2017). Mycorrhizal fungi have been found to play a crucial role in the formation of soil aggregates and the stabilisation of organic carbon in terrestrial forest soils (Li et al., 2023b). These fungi can produce glomalin-related soil proteins and amino sugars that are recalcitrant, sticky, and hydrophobic in nature (Wright et al., 1998), which can make them resistant to

decomposition. However, these observations from terrestrial soils are yet to be validated in BCE sediments. Microbes can also have a purely physical influence, especially phototrophic microorganisms that help compact and consolidate sediments through exudation of extracellular polymeric substances, which bind and glue the non-carbon and carbon-rich fractions of the sediment and enhance recalcitrance of carbon in BCEs (Stal, 2010).

While microbes are widely considered to be responsible for the degradation of organic matter, it is their abiotic environment that determines whether the stability of organic matter is compromised and the subsequent rate of degradation. It is noteworthy that microbes themselves encompass around 30 % of the sedimentary carbon in BCEs (Alongi, 2005; Booth et al., 2023). Intertidal microphytobenthos that remain attached to sediments host a consortium of diatoms, algae, bacteria, fungi, and protozoa, and their primary productivity varies from 27 to 234 g C m<sup>-2</sup> y<sup>-1</sup> (Mandal et al., 2021). Recalcitrant organic carbon and microbial biomass carbon often show similar composition and source; thus, microbial biomass can itself be a chief carbon pool, especially in the upper layer of the sediments (Lian et al., 2018). In this regard, Noman et al. (2024) argued that microplastics in BCE sediments (Ouyang et al., 2022) can promote microbial biomass carbon growth by facilitating a substrate and by also preserving recalcitrant carbon present in the plastic itself.

#### 3.1. On/off or dimmer switch?

##### 3.1.1. Bioturbation, oxygen exposure, and warming

Among the many activities that act as an on/off switch that triggers/suppresses the microbial activities in BCEs favouring mineralisation is the bioturbation of sediments (Johannessen, 2022). It has been hypothesised in a previous study that excessive increase in bioturbators (like crabs, and fish) in BCEs due to the loss of predator species that feed upon them and maintain a top-down ecosystem control has become a severe threat to the stability of carbon in the sedimentary column, especially the top layers (Atwood et al., 2015). It can be considered a trigger switch that leads to the onset or at least enhances the rate of decay of both stable and unstable carbon. Habitat disturbances owing to anthropogenic factors like unsustainable fishing and aquaculture, changes in tidal regime, eutrophication, and oil spills also have the same effect on BCEs by enabling the microbes that sequestered carbon to react differently, leading to considerable CO<sub>2</sub> emission (Macreadie et al., 2013, 2015, 2019b). Disturbance of coastal sediments releases reactive organic substances like algae-derived DOM, which leads to an upheaval in the microbial community composition that stimulates CO<sub>2</sub> emission by using complex organic compounds that remain unreactive in the absence of such disturbance (Macreadie et al., 2019b; Ward et al., 2019).

Controlled experiments showed that oxygenation of otherwise anoxic coastal sediments leads to the proliferation of facultative anaerobic bacteria, which facilitate the oxidation of long-sequestered carbon in the sediments (Broman et al., 2017), hence making oxygen exposure an on/off switch. The effect of warming can also enhance microbial activities that are responsible for the mineralisation of stable carbon and CO<sub>2</sub> emissions from mangrove sediments (Chanda et al., 2014; Jacotot et al., 2019). However, as the change in temperature and its effects are often gradual, it can be considered as a dimmer switch. For submerged BCEs like seagrass, the prevalent anoxic conditions in the sediment further protect recalcitrant carbon (Trevathan-Tackett et al., 2017b). However, warming concurrent with habitat disturbance leading to exposure to oxygen propels the degradation of organic carbon, leading to CO<sub>2</sub> emission from depths that, under an undisturbed and anoxic state, mostly remain occupied by anaerobic methanogens (Macreadie et al., 2019b). Studies on sediment cores collected from eroding marsh sites indicated the prevalence of higher amounts of recalcitrant carbon at depths and suppressed anaerobic microbial activity across all depth ranges, in contrast to more vulnerable organic pools in upper sediments, due to erosion and exposure to aerobic carbon remineralisation (Sapkota

and White, 2021).

### 3.1.2. Nutrient enhancement

The addition of nutrients can augment the primary productivity and enhance the autochthonous carbon burials in BCEs, or it can act as a thermodynamically favourable electron acceptor, encouraging heterotrophic degradation of organic matter (Fig. 3) (Friesen et al., 2018). Anthropogenic activities like agricultural runoffs and aquacultural effluents can introduce nutrients suddenly and, thus, can act as a trigger switch. However, a slow increase in nutrient concentrations in BCEs might act as a dimmer switch. Nitrate addition altered microbial diversity by enhancing nitrate reducers that decompose complex carbon compounds in salt marsh sediments into simple bioavailable forms. This compromises the recalcitrance of existing carbon (Bulsecò et al., 2019) while rendering the residual carbon less vulnerable to additional decomposition via nitrate reducers (Bulsecò et al., 2024). Eutrophication, through the addition of dissolved inorganic nitrogen and phosphorus, enables the microbial community to mineralise recalcitrant lignin and chitin components in BCE sediments by enriching the genes encoding manganese peroxidase, glyoxal oxidase, and extracellular chitinase (Li et al., 2024). Even a brief spike in nutrient levels can lead to a 23 % reduction of surficial carbon stock and a 33 % reduction in microbial species richness, all leading to the degradation of stable carbon in mangroves and salt marsh sediments (Palacios et al., 2021). One study found that eutrophication can lead to irreversible organic carbon accumulation in estuarine sediments, which promotes the stability of a substantial fraction of the carbon introduced through eutrophication under anoxic conditions (Valdemarsen et al., 2014). They observed that initial disturbance led to significant CO<sub>2</sub> emission; however, over two years, 43 to 95 % of the organic carbon remained undegraded even after microbial richness and diversity shifted. It seems that the synergistic effect of temperature and oxygen exposure might destabilise carbon in sediments more than the synergistic effect of temperature and nutrients.

Studies on the enrichment of carbon rather than nutrients show that the addition of biochar can eliminate opportunistic bacteria (Cellvibrionaceae and Bacillus) and augment low carbon turnover bacteria (Actinobacteria and Acidobacteria) and, thereby, enhance the stability of carbon in the sediments of degraded salt marshes (Yu et al., 2022). Introducing carbon-enriched biochar can increase soil microbial biomass carbon and lead to a lower metabolic quotient, suggesting that biochar-amended soils can sequester carbon for a long time by preventing mineralisation and enhancing bacterial taxa that stabilise soil aggregates (Acidobacteria and Actinobacteria) and negate priming effects (Zheng et al., 2018).

### 3.1.3. Vegetation types

The interaction between BCE vegetation and the intrinsic microbiome can also govern the stability of carbon in BCEs. Studies have shown that variations in plant inputs (e.g., tannins, lignin) from different mangrove species can alter the composition and quantity of organic carbon and nutrients available to microbial communities, thereby influencing microbial activity (Muwawa et al., 2020; Lang et al., 2024). Differences in root structure among mangrove species can also lead to varying redox conditions (Gleason et al., 2003), which in turn may shape species-specific microbial diversity (Sui et al., 2023). A study pointed out that a higher density of live roots in the sedimentary substratum releases nitrogen but helps enhance the stability of carbon (Ridgeway et al., 2024). Depending upon the mangrove floral species, the resilience of the microbial community varies, as a study observed that the sediments adjacent to *Rhizophora mucronata* showed a greater propensity to retain the native microbial composition when persistently fed with domestic wastewater discharges compared to other species (Capdeville et al., 2019). The same holds true for seagrasses, where comparative analyses showed that *Thalassia hemprichii*-derived plant materials contribute twice the amount of bacterial organic carbon and have a greater influence on organic matter-decomposing enzymes in

their sediments than *Enhalus acoroides* under a similar nutrient loading scenario (Liu et al., 2017a). Microbial communities also govern the ratio of seagrass-derived to macroalgae-derived carbon in the sedimentary beds, where though macroalgal biomass increases with increasing nutrients, sediments show higher signatures of seagrass-derived carbon by altering the polyphenol cellulase, invertase, and oxidase-based extracellular enzymatic activities (Liu et al., 2017b). However, the synergistic effects of co-metabolism and priming exhibited by the microbes in seagrass sediment beds led to compromising the stability of recalcitrant carbon (Liu et al., 2020a, 2020b). Thus, the role of vegetation types can be considered a dimmer switch with respect to the emission of carbon from BCE sediments.

### 3.1.4. Physiographic settings

Physiographic settings plays a crucial role in governing the total blue carbon content of a coastal ecosystem by regulating its microbial activities in the sediment. In some coastal regions, open mangroves having less blue carbon density stretch over large areas, whereas, in some regions, dense mangroves grow with high blue carbon density and flourish over a comparatively small area, making the total blue carbon stocks of open and dense mangroves comparable (Datta et al., 2024). Thus, physiography and geomorphology often dictate the vegetative structure and, hence, the microbial activities as well in BCEs depending upon species diversity and vegetation density. However, the conversion of the physiographic setting for anthropic purposes often proves to be detrimental to blue carbon stocks, as it impairs the BCEs and alters their microbial activity. Region-specific drivers of carbon content in salt marshes suggest that physiography coupled with geomorphology within BCEs regulates the sediment texture, bulk density, and permeability, which, in turn, governs the oxygen content and redox potential, and, hence, the microbial community composition, which is accountable for the stability of the sequestered carbon (Leiva-Dueñas et al., 2024). Like physiography, the hydrographic regime controls the grain size of sediments in BCEs (Kelleway et al., 2016; Kim et al., 2022). Seagrasses in similar geomorphic settings have variable BC stock across temperate, sub-tropical, and tropical seagrasses (Lavery et al., 2013). However, this does not lead to such variability in blue carbon stock; rather, they stressed the changes in the recalcitrant nature of blue carbon owing to the differences in microbial composition that were a coupled output of both geomorphic setting and climate. Muddy substratum has often been found to safeguard the locked carbon from microbial activities that can lead to remineralisation by diminishing the penetrability of oxygen into deeper layers (Mazarrasa et al., 2018). Thus, the presence or absence of blue carbon vegetation, their physiographic setting, and the conditions that the presence of vegetation together with their capability to alter the physiographic setting plays a crucial role in regulating the microbiome and enhancing the storage capacity vis-à-vis the stability of carbon (Schaeffer-Novelli et al., 2016; Potouroglou et al., 2017; Röhr et al., 2018; Taillardat et al., 2018). As physiographic changes do not take place overnight unless impacted anthropogenically, this aspect can be treated as a dimmer switch.

## 4. Future directions

We have highlighted why the stability, not just the presence of carbon in BCE sediments, should be put under the lens to develop a deeper understanding of the events, processes, and ideal conditions where BCEs are likely going to store carbon for longer. Future research should strive to characterise the carbon stored in BCEs at the molecular level to understand the ratio of labile to recalcitrant carbon content. The augmentation of the complexity of carbon through bonding with minerals should be considered. The role of environmental parameters like oxygen, redox potential, salinity, pH, and temperature in stabilising/destabilising the carbon locked in BCEs and especially their synergistic effects remain poorly constrained. Climate and anthropogenic changes are assumed to alter these parameters in the marine sectors. Therefore,



more studies modelling how these changes alter the stability of carbon in BCEs are needed in future in order to shape up all types of BCEs. Region-specific identification of the drivers that govern the stability of sequestered carbon needs to be prioritised for effective management and conservation of these globally significant but declining ecosystems.

More than ever, empirical knowledge about the interaction between sediment- and plant-associated microbes (including metabolic and enzymatic pathways) and the environment is needed to inform how we can safeguard stored carbon from destabilisation and remineralisation. We show that anthropogenic disturbances lead to physical vulnerability of the carbon stored in BCEs even when the systems are not directly damaged or converted to other land use classes. Any form of disturbance, through temperature alteration, pH fluctuation, salinity amendment, nutrient addition, and oxygen exposure, can shift microbial community composition, structure, and metabolic pathways that can trigger the mineralisation of otherwise stable carbon that had remained in those habitats for thousands of years. It is important to note that not all anthropogenic interventions have negative impacts on blue carbon storage and stability; in some cases, such as tidal reinstatement, restoration can enhance carbon retention. Thus, a holistic approach should be taken to accommodate all these factors under one frame and predict the ideal conditions for the stability of locked carbon. Keeping in view the varied hydrodynamic, geomorphologic, and physiographic settings of the BCEs globally, the characterisation of recalcitrant carbon and the role of microbes in carbon recalcitrance needs finer resolution.

Conserving and not disturbing BCEs has long become imperative with our impending climate change future. Knowing the potential of BCEs in sequestering atmospheric CO<sub>2</sub>, endeavours should be undertaken in the near future to expand the area of BCEs and to maximise their potential fruitfully. In order to conserve the BCEs and restore the degraded BCEs, generating a clear perception of the factors governing the stability of carbon in sediments should be prioritised. Microbial assay of conventionally stable carbon at depths in all BCEs needs further study. The processes and conditions that act as an on/off switch and those that act as a dimmer switch to the microbial-driven stabilisation and destabilisation of carbon are complex and likely interacting and require mechanistic-drive research to resolve this critical Blue Carbon black box.

The following are the key takeaways from this study:

1. Future research is necessary to attempt to characterise the carbon stored in BCEs at the molecular level and understand the ratio of labile to recalcitrant carbon content.
2. Microbial and enzymatic activities are fundamental to organic carbon mineralisation. However, environmental parameters like oxygen, redox potential, salinity, pH, and temperature are also crucial in stabilising/destabilising the carbon locked in BCEs.
3. Climate and anthropogenic changes may alter these parameters in the marine sectors, and hence, more studies on modelling the alterations of the stability of carbon in BCEs are needed in future.
4. Regional and local-specific identification of the drivers of stability of the sequestered carbon needs to be prioritised for efficient management and conservation.
5. To conserve the BCEs and restore the degraded BCEs, a clear perception of the factors governing the stability as an on/off switch and those that act as a dimmer switch of carbon in sediments should be prioritised.

#### CRediT authorship contribution statement

**Peter I. Macreadie:** Conceptualization, Data curation, Visualization, Supervision, Writing – original draft. **Anirban Akhand:** Conceptualization, Data curation, Visualization, Writing – original draft. **Stacey M. Trevathan-Tackett:** Writing – review & editing. **Carlos M. Duarte:** Writing – review & editing. **Jeff Baldock:** Writing – review & editing. **Jennifer L. Bowen:** Writing – review & editing. **Rod M. Connolly:**

Writing – review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial or any kind of interests.

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#### Data availability

No data was used for the research described in the article.

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