Reviews and syntheses: Bioturbation impacts on sediment accretion and erosion in tidal marshes, with implications for carbon burial and sequestration

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1.1) Abstract

Tidal marshes offer multiple ecosystem services, but are some of the most threatened coastal ecosystems worldwide. One of these valued services is their ability to sequester and store large amounts of carbon. Bioturbating macrofauna are ecosystem engineers that can influence the geomorphology and biogeochemistry of tidal marshes. Bioturbators can influence accretion and erosion processes in tidal marshes by either stabilizing or destabilizing sediment. Through this reworking of sediment, they can also influence the amount of carbon that can be stored. The impact of bioturbation on tidal marshes depends on a number of factors, such as~~,~~ species composition, burrow morphology, diet, behaviour and habitat type. This review assesses the current knowledge on the role benthic bioturbators play in shaping sediment processes in tidal marshes and identifies key knowledge gaps for future research. For example, the impact of individual benthic species on sediment dynamics is mostly unknown. Bioturbation effects cannot be generalised, and predicting ~~when and where these effects will be most prominent~~ impacts is challenging. Future studies should investigate family and species-specific effects on sediment properties, such as erodibility or texture, under controlled laboratory conditions and in the field. This should be compared across different habitat types such as ecotones, mudflats, salt marshes and mangroves. Furthermore, the role of consumers, as bioturbators, remains an understudied driver of the carbon cycle because it is complex. In order to better predict how tidal marshes may persist in the face of future climate change, such as sea level rise, it is important to understand the role of bioturbators on sediment and carbon dynamics to enable better mitigation of global change effects through conservation and restoration of tidal habitats.

Keywords: blue carbon, benthic organisms, coastal ecosystems, ecosystem engineers, sediment processes

1.2) Introduction: Tidal marsh sediment and carbon processes

Tidal marshes, such as salt marshes and mangroves, are vegetated coastal ecosystems that are highly important in terms of their ecological value, because they exist between terrestrial, estuarine and near–shore marine environments (Barbier, 2015). These coastal habitats offer natural protection against storm surges and erosion (Perkins et al., 2015), in addition to other essential services such as sediment retention, flood attenuation and nutrient processing (Bos et al., 2007; Hatje et al., 2021). They provide important nursery areas for estuarine and marine fishes and invertebrates (Sogard and Able, 1991; Barbier et al., 2011), and are also valuable for tourism and food production (Hawkins et al., 2020; Lynch et al., 2023). Another important ecosystem service provided by salt marshes and mangrove forests, is their ability to sequester and store carbon (Macreadie et al., 2021). The carbon sequestered by these coastal habitats is referred to as blue carbon (Nellemann and Corcoran, 2009; Mcleod et al., 2011). Although seagrass beds are also classified as blue carbon habitats, they are primarily a subtidal habitat and therefore not strictly part of tidal marshes in the context of this review. The term 'blue carbon' was coined more than a decade ago (Duarte De Paula Costa and Macreadie, 2022), with blue carbon research having increased over the last decade. This growing interest allows for a better understanding of the global distribution of tidal marshes and the factors that determine their persistence.

Salt marshes cover at least 41,700-54,900 km^2 of the globe (McOwen et al., 2017), mangrove forests 150,000 km^2 (Spalding, 2010), and unvegetated mudflats approximately 127,921 km^2 of the globe (Murray et al., 2019). The Northern Hemisphere has roughly double the ~~amount~~ area of tidal marshes as the Southern Hemisphere, due to their longer coastline (He et al., 2025). The long–term persistence of tidal marshes is driven by the interactions between surface elevation, sea level, sediment accretion and primary production (Morris et al., 2002). Surface elevation and sediment accretion is regulated by abiotic and biotic factors, which includes suspended sediment supply, climate, geography and bioturbation (Ouyang et al., 2022).

Coastal ecosystems are some of the most threatened systems worldwide with approximately 35 % of mangroves and 50 % of salt marshes being lost or degraded by anthropogenic activities (Van Katwijk et al., 2016; Li et al., 2018). By means of satellite observations, looking at changes in water presence, land loses, and gains can be estimated. It is estimated that 28

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Commented [A2]: The introduction could be strengthened with some reworking. Currently, description of wetlands is long and needs to be tied t bioturbators. Additionally, some broad grouping of wetlands (macrotidal/microtidal, minerogenic/organogenic, marsh platform/creekbank would help to later summarize impacts.

This section could be split into 1) sediment/geomorphology and 2) carbon processes fo more organization

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000 km^2 of land has been eroded in tidal marshes, which is double that of land gained (Mentaschi et al., 2018). Some studies have revealed that accretion rates are insufficient for tidal marshes to keep pace with sea level rise (e.g. Van Wijnen and Bakker, 2001), while others have found that accretion rates are high enough to keep pace with moderate rises in sea level (e.g. Morris et al., 2002). A dominant driver of coastal erosion is anthropogenic influence, such as the clearing of mangrove forests, as well as natural disasters, such as extreme storms (Mentaschi et al., 2018). Sea level rise and a changing climate is likely to enhance coastal erosion. While these ecosystems are increasingly threatened, the vegetation within them is a key contributor to the ecosystem services they provide.

Plants capture carbon dioxide from the atmosphere which they store as organic carbon, but through respiration, some of this carbon also gets released. The carbon budget of a vegetated habitat is used to provide an indication as to whether it is a carbon 'sink' or a carbon 'source', which is related to the accumulation and discharge of carbon (Sitch et al., 2015). Salt marshes and mangroves are important carbon sinks, even though these habitats cover less than 2 % of the area of the global ocean (Duarte, 2017). These blue carbon habitats store up to 70 % of carbon, relative to the ocean carbon cycle (Macreadie et al., 2014). It is estimated that they store up to 276 to 822 Tg of atmospheric carbon dioxide per year, worldwide (Spivak et al., 2019). However, a loss or degradation of blue carbon habitats not only reduces the capacity of these ecosystems to act as natural carbon sinks but if degraded and disturbed these habitats directly release high amounts of carbon into the atmosphere as CO_2 emissions (Pendleton et al., 2012; Hatje et al., 2021). A loss of one hectare of any blue carbon ecosystem is equal to losing 10-40 hectares of native forest, in terms of carbon emissions (Macreadie et al., 2017). Blue carbon includes carbon that is stored in living biomass (branches, leaves, stems), non–living biomass (dead wood, leaf litter), roots and soil (Mcleod et al., 2011; Lovelock and Duarte, 2019a). When carbon is stored in this manner it is an important ecosystem service as it is an essential component of the carbon cycle (Keller et al., 2018). Blue carbon habitats, if conserved, are able to act as net carbon sinks (Spivak et al., 2019).

There are three factors that determines the capture and storage of carbon in these habitats: the ability to maintain particulate organic carbon, high productivity and the conversion of carbon dioxide into plant biomass (Alongi, 2002). The sediment biogeochemistry then leads to a slow decay of organic material (Kelleway et al., 2017c).

The storage of carbon in tidal marshes is influenced by environmental factors such as differences in moisture, nutrients, sediment supply, salinity and acidity as this is important for decomposition and primary productivity (Lovelock et al., 2007). Sediment depth, type and

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Commented [A9]: This and the following paragraph could be combined for a more cohesive flow deposition is also linked to carbon storage ability (Kelleway et al., 2016b). Sediment grain size has a strong influence on carbon storage because it influences the amount of organic particles that can accumulate. The storage of carbon is greater in fine grained sediment because of the lower oxygen exchange and porosity. Furthermore, these conditions decrease sediment redox potential and the rates of remineralisation, thus enhancing carbon storage (Kelleway et al., 2016b). Fine grained sediment also allows for the preservation of more organic matter because of their higher surface area, which reduces the oxygen in the sediment as it is consumed by detritivores which in turn decreases the decomposition of organic matter (Dahl et al., 2016). Coarse grained sediment (sandy sediment) is more permeable and has more aeration, increasing remineralisation of carbon (Van Ardenne et al., 2018). Carbon stored in salt marsh sediment is also influenced by the community composition of vegetation due to the differences in leaf and root morphology of different plant species. In general, shrubby salt marsh vegetation has low carbon stock (Saintilan et al., 2013). The input of organic material and the rate at which it decays is what ultimately determines the long term storage of carbon. Carbon storage has been shown to be higher in mature salt marshes compared to restored or new salt marshes (Alongi, 2018). Marshes that experienced rapid relative sea level rise during the late Holocene have higher concentrations of soil carbon compared to those that were subject to long periods of sea level stability (Rogers et al., 2019). Carbon storage is also higher in salt marshes which experience limited erosion and where mangrove encroachment is limited (Alongi, 2018).

For mangroves forests, latitude, productivity rates, the age of the forest, and elevation are factors that have been linked to carbon stocks (Radabaugh et al., 2018). Mangroves are more productive than salt marshes which results in salt marshes storing less carbon (Saintilan et al., 2013). This has been attributed to lower redox potential, less anaerobic conditions and higher tidal elevations of salt marshes which are not conducive to carbon storage (Schile et al., 2017). Mangroves accumulate and store carbon over longer time periods (Lovelock and Duarte, 2019). They also have a higher above and belowground biomass which enables them to store more carbon (Donato et al., 2011). ~~Mangroves are trees and therefore have a greater biomass than salt marsh which are dominated by succulent herbs and grasses.~~ Moreover, water velocity is decreased by their aerial roots and more carbon rich sediment is able to be deposited, as well as plant matter which further promotes the formation of carbon rich sediment (Horstman et al., 2015).

A significant proportion of the global tidal marsh carbon is found in the temperate Northern

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Atlantic, which has 45 % of the world's tidal marsh extent (Worthington et al., 2024). The U.S, Canada and Russia are the top three countries with the highest predicted total sediment organic carbon in their tidal marshes, because they have extensive marsh cover and high carbon per unit area (Worthington et al., 2024). The global estimate of carbon in the top metre of marsh sediment is 1.44 Pg C (Maxwell et al., 2024; Table 1). The average sediment organic carbon per hectare is predicted to be about 83.1 Mg C ha^{-1} in the 0-30 cm layer and 185.3 Mg C ha^{-1} in the 30-100 cm layer (Maxwell et al., 2024). Globally, it is estimated that mangroves store around 11.7 Pg C, with most of the carbon stocks being in the sediment (Kauffman et al., 2020). The global sediment stock of tidal flats is estimated to be 0.9 Pg C (Chen and Lee, 2022).

Table 1: Continent–level summary for tidal marsh area and sediment organic carbon (SOC).

Habitat	Region	Area (km^2)	SOC (Mg ha^{-1}) [a]	SOC (Pg C)
Salt marsh		41,700-54,900 [a]		1.44[a]
	Africa	2 241.37	1046.05	
	South America	4 537.76	710.53	
	North America	30 259.07	1045.54	
	Europe	11 054.68	1377.9	
	Asia	2 301.71	400.02	
	Oceania	2 378.58	172.86	
Mangrove		150,000[b]		11.7[b]
Tidal flats		127,921[c]		0.9[c]

[a] (Maxwell et al., 2024)
[b] (Kauffman et al., 2020) [c] (Chen and Lee, 2022)

Tidal marshes have gained interest for their recently recognised value of carbon storage, leading to extensive research on carbon stocks and factors influencing carbon sequestration and storage. Similarly, accretion and erosion dynamics of tidal marshes and the processes driving these changes is well understood. However, the influence of animal interactions on these processes is poorly understood, even though soil animals are key components of aquatic environments (Adams et al., 2025). This review provides an overview of the current knowledge on the influence of bioturbation on sediment accretion and erosion in tidal marshes, including the impact of bioturbation on carbon sequestration. Table S1 in the Supplementary material provides a summary of key bioturbation studies relating to accretion, erosion, and carbon sequestration, emphasising their methodologies and main findings that are discussed in the following pages, while Figure 2 shows where these studies were conducted.

To quantify the extent of research conducted on sediment processes and carbon in tidal marshes, a systematic literature search was performed in the web of science database using key words related to tidal marshes, carbon storage/sequestration and sediment dynamics. This search yielded 544 publications between the years 1993 and 2025. While a fair amount of research has been conducted on carbon stocks and sediment dynamics in tidal marshes, there remains a gap in our understanding of the role of bioturbators and their interaction processes on sediment dynamics. When key words relating to bioturbation were included, only 64 publications were yielded. Thus, the influence of these interactions on carbon sequestration and storage, and how this might be impacted in the face of climate change, which is a pressing future concern, is poorly understood compared to the overall science of tidal marsh carbon and sediment processes. This review therefore aims to improve our understanding of how bioturbators shape sediment dynamics and carbon cycling.

1.3) Bioturbation in coastal tidal marshes

Bioturbation in tidal marshes is associated with a number of organisms, found above and below the surface sediment (Macreadie et al., 2017). Benthic invertebrates under the classes Oligochaeta (worms), Gastropoda (snails), Polychaeta (polychaetes), Crustacea (crabs, shrimp and malacostracans) and Bivalvia (cockles and mussels) are common bioturbators found in tidal marshes (Van Der Wal and Herman, 2012). Some of the best studied groups include crustaceans and molluscs (Booth et al., 2023). Bioturbators are significant components of both terrestrial and aquatic ecosystems as they modify habitats, decompose litter, and ~~are also~~ consume~~rs~~ organic material (Wang et al., 2010). Bioturbation involves any transport process performed by animals that affects sediment matrices, either directly or indirectly (Kristensen et al., 2012), which includes burrow ventilation and particle reworking. Darwin (1881) was the first to recognize the significance of animal bioturbation and its role in influencing soil ecosystem processes. A dominant form of bioturbation in coastal wetlands includes that of burrowing, with burrow architecture being species specific (Min et al., 2023; Fig. 1). One of the most diverse groups, with special adaptations for burrow construction is Decapoda (Giraldes et al., 2017; Hajializadeh et al., 2022). Burrow construction and maintenance, in addition to ingestion and defecation results in particle reworking and biomixing. As a result, microorganisms and organic matter are displaced within the sediment matrix, both laterally and vertically (Kristensen et al., 2012). Benthic organisms can

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Commented [A23]: Later in the text, burrow architecture becomes key context in differentiating impacts. Different architectures should be defined he significantly affect the composition of sediment, with destabilizing organisms generally decreasing mud content, while stabilizing organisms can increase mud content (Arlinghaus et al., 2021). Animals that rework sediment particles can be categorized as upward conveyors, downward conveyors, biodiffusors and regenerators depending on their feeding type, behaviour and life style (François et al., 2002). Collapsed burrows that are abandoned and become filled in, can be considered as indirect bioturbation (Kristensen et al., 2012). Ventilation happens when animals flush their burrows with water for feeding and respiration, and can be open with two or more openings, or blind ended with one opening. This results in the rapid transport of solutes from in the burrow to the overlying water (Kristensen, 2001). The activities associated with bioturbation can therefore influence the physical, chemical and biological characteristics of tidal marshes (Min et al., 2023).

Burrowing activities decreases sediment hardness, breaks up and transports sediment (Botto and Iribarne, 2000), and increases the coarse particle density on the surface layers of the sediment (Warren and Underwood, 1986). In addition, burrowing influences the chemistry of the sediment, increases the oxygenation of the sediment and changes the pore water salinity (Fanjul et al., 2007; Booth et al., 2023). Fine grained sediment, as well as sediment containing high concentrations of organic matter can be trapped by crab burrows, which assists with organic matter decomposition and increases the availability of nutrients (Fanjul et al., 2007). The rate of nutrient and sediment turnover is further accelerated by means of excavation by crabs, which transports nutrients and sediment from deep layers to the surface layers of the salt marsh (Fanjul et al., 2007). Belowground processes are therefore impacted by burrowing crabs which in turn influences marsh plants and trees by promoting growth (Botto et al., 2006; Ngo-Massou et al., 2018). The interaction between the environment, the biology and the density of a bioturbator determines the extent of the bioturbation effect (Wang et al., 2010; Xie et al., 2020; Pan et al., 2023), which varies over space and time. For example, the presence or absence of vegetation plays a key role in shaping this impact. When vegetation was present, the quantity and quality of excavated and deposited soils (in burrow mimics) was influenced, and thus, so was the burrowing effect (Wang et al., 2010). Vegetation can improve nutrient concentrations, but its roots can obstruct the vertical movement of sediment.

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Figure 1: Examples of burrow openings of different crab species: *Scylla serrata* (A), *Neosarmaticum africanum* (B), *Cyclograpsus punctatus/Parasesarma catenatum* (C and D). The scale bar represents 10 cm in the foreground.

1.4) Impacts of bioturbation on sediment processes

Bioturbation influences a number of sediment processes such as accretion, erosion, sediment transport and deposition, which are outlined below and summarised in Table 2 and Table S1.
These processes are visually represented in Figure 3 and further explained in Table 3.

1.4.1) Accretion

Sedimentation is a key process~~es~~ shaping tidal marshes, improving water clarity and quality which helps submerged plants access sunlight (Nahlik and Mitsch, 2008). The sequestration of carbon is also enhanced by sedimentation (Bernal and Mitsch, 2013) because the active burial of carbon limits its exposure to oxygen thus, limiting oxidation (McCarty et al., 2009). Salt marshes and mangroves persist when sediment carried by tides is deposited in vegetation (Saintilan et al., 2022). This builds elevation and promotes the growth of plants which increases belowground organic matter, resulting in elevation gain, slower water movement and allows for more suspended sediment to settle (Kirwan and Guntenspergen, 2012). Plant shoots promote the deposition of sediment while plant roots bind and stabilize the sediment and can help prevent erosion (Buffington et al., 2020). Accretion therefore involves sedimentation, root growth, and development of peat (Krauss et al., 2014; MacKenzie et al., 2024)

Benthic organisms are able to facilitate sediment transport and sedimentation patterns over extended periods and across surrounding areas (Arlinghaus et al., 2021). Their biological activity impacts sediment structure in terrestrial, marine, and intertidal zones, either stabilizing or destabilizing these environments. Some organisms enhance sediment cohesion by

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Stronger text support: Currently, the text is organized using impacts of bioturbation, while Figure 3 is organized by types of bioturbation and mechanisms that drive the impacts. This makes the figure difficult follow along with through the text. Organizing the figu in the same structure as the text would improve legibility.

Figure reorganization: the lower diagram doesn't line up with visual representations in the upper diagram, and this makes the figure difficult to follow. There are also some elements that are small/difficult to read in print. Also, the box for bioturbation impact #5 is blue, while the rest are grey – I don't see an explanation fo this in the caption.

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producing an organic coating in the burrow walls from extracellular polymeric substances (EPS), mainly mucus (Watling, 1991). *Sesarma reticulatum* (a crab occurring in northern hemisphere temperate salt marshes) for example does this (Kristensen, 2008). These biostabilization processes can therefore influence the strength of sediment in intertidal zones. In a similar fashion microphytobenthic organisms form biofilms which can also improve the stabilization of sediment (Decho, 2000).

Burrowing animals affect important ecosystem functions, while influencing the structure and function of plant communities, with these effects varying in direction and magnitude regionally (Vanni, 2002). Changes in the burrowing activities could have important consequences for the functioning of salt marshes and mangroves. Low to moderate levels of bioturbation can be beneficial to primary productivity (Kristensen et al., 2008). For example, burrowing by fiddler crabs has been seen to benefit the growth of *Spartina alterniflora* by increasing soil drainage, enhancing decomposition of plant debris and improving soil redox potential (Bertness, 1985). Burrows can increase the surface area of the marsh allowing for the exchange of oxygen from tidal water and the atmosphere which can increase the uptake of nitrogen increasing plant productivity (Bradley and Morris, 1990; Sharbaugh et al., 2025)

Recent studies have highlighted the importance of bioturbation in determining changes in surface elevation (Bennion et al., 2024). The accretion or erosion of sediment is partially related to the burrowing and feeding activities of the species (Morelle et al., 2024). For example, it was found that crab species, which differ in diet and burrow morphology, had a larger influence on sediment than crab density ~~superfamily, whether it was an Ocypodoidea or Grapsoidea, had the biggest influence on sediment, as opposed to crab density~~ (Rinehart et al., 2024), ~~which is related to their burrow morphology and diet~~ (Table S1, Fig. 3). The composition of crabs has the potential to influence ecosystems differently (Agusto et al., 2021). In mangroves, changes in surface elevation ~~is~~ are strongly influenced by species composition of the vegetation and was positively influenced by the frequency of bioturbation. In salt marshes, however, bioturbation had no significant effect on changes in surface elevation because they had lower levels of bioturbation compared to the mangroves (Bennion et al., 2024) (Table S1, Fig. 3).

Excavated sediment through bioturbation activities, along with sediment from eroding areas of the marsh, can contribute material for accretion on the surrounding marsh platform, helping to increase marsh elevation (Wilson and Allison, 2008). Mussels, for example *Geukensia demissa,* can also contribute to vertical accretion in salt marshes, as they harvest sediment through their filtration activities, thus contributing to the sediment budget (Crotty et al. 2023)

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(Table S1, Fig. 3). They also deposit faeces which is nutrient rich, indirectly increasing vegetation biomass, improving soil shear strength (resistance to erosion) and stability. These interactions therefore play an important role in promoting elevation gain and improving marsh resilience.

1.4.2) Erosion

Due to coastal wetlands being situated at low elevation at the land sea interface, they are susceptible to submergence and lateral erosion driven by wave activity, storm surges and increased sea levels (Leonardi et al., 2018). The morphology and long-~~-~~term persistence of tidal marshes is influenced by erosion. Erosion rates are ~~determined~~ influenced by vegetation, which affects sediment deposition rates and biological activity (Mudd et al., 2010; Cahoon, 2024). Benthic organisms, specifically bioturbators, play a crucial role in influencing erosion processes through their activities. Bioturbators can affect sediment roughness and alter its characteristics, thereby influencing the erodibility of sediment (Dairain et al., 2020). ~~Bioturbators can have both direct and indirect effects on the erosion of tidal marshes. These positive and negative impacts are expected to vary over time, as macrofaunal bioturbation is temperature- dependent and tends to be more pronounced during warmer months (Cozzoli et al., 2018).~~ By reworking the sediment, bioturbators repack the sediment that was once compact, which changes the texture and granulometry, causing larger aggregates of grains to form (Grabowski et al., 2011). For example, *Scrobicularia plana* (a clam commonly found in temperate European salt marshes) caused the sediment to become coarser and changed the bed topography~~, which showed a loss by~~resulting in erosion (Morelle et al., 2024) (Table S1, Fig. 3). Fine grained sediment such as clay and silt are more susceptible to the effects of benthos (Arlinghaus et al., 2021). There are however still uncertainties with regards to the role that benthic organisms play in sediment dynamics (Dairain et al. 2020; Farron et al. 2020). For example, the influence of *S. reticulatum* bioturbation on the erodibility of sediment has not yet been quantified as it is difficult to measure the processes in the field (Farron et al., 2020). Thus, few studies have explored the connection between sediment stability and burrow building bioturbators (Needham et al., 2013).

Burrowing activities weaken mud and clay banks in tidal marshes, making them more susceptible to erosion through wave action. Dairain et al. (2020) observed that *Cerastoderma edule* (common cockle, native to salt marshes in Europe and northwestern Africa) promotes erosion of the surface sediment by increasing the roughness of the sediment, and this is due to their sediment reworking activities (Table S1, Fig. 3). The same was true for the lugworm, *Arenicola marina* (common in mudflats and salt marshes in Europe), which increased the

Commented [A35]: Is this always true? Earlier it was written that burrowers can enhance sediment cohesi permeability and roughness of the sediment (Montserrat et al., 2011) (Table S1, Fig. 3). *Sesarma reticulatum* contributes to changing erosion patterns by facilitating greater erosion (Farron et al., 2020), which is likely driving the headward expansion of straight, low–order tidal creeks in salt marshes within the Georgia Bight (Vu et al., 2017).

In addition to sediment disturbance, bioturbators can impact sediment cohesion and erodibility. When the density of infauna were experimentally reduced in the Humber estuary (UK), there was a 300 % increase in sediment stability on the intertidal mudflats (De Deckere et al., 2001) (Table S1, Fig. 3). Invertebrates, such as crabs, can influence sediment stability by consuming microphytobenthic organisms (Booth et al., 2023) which can indirectly promote the destabilization of sediment (Daborn et al., 1993). Crabs can also contribute to sediment destabilization by causing vegetation loss (Smit et al., 2024). Burrowing by *Sesarma reticulatum* caused the upper 10-15 cm of the marsh to become oxidized which caused enhanced degradation of belowground biomass of *S. alterniflora* (Wilson et al., 2012) (Table S1, Fig. 3). This process reduces the shear strength of the sediment, increasing the erosion potential which facilitates creek extension. Compared to the surrounding marsh platform, the heads of newly formed creeks have lower topography, lack vegetation, and are densely populated with both burrowing and herbivorous crabs. Over time these creek heads extend further into the marsh platform as the creek migrates, which causes dieback of vegetated areas and a loss of elevation of up to 50 cm (Day et al., 2011; Wilson et al., 2012). Similarly, *Chasmagnathus granulatus* (a crab inhabiting the salt marshes of South America), through their burrowing activities, have also been shown to increase the growth rate of tidal creeks, causing larger creeks to form, which can promote salt marsh erosion (Escapa et al., 2008) (Table S1, Fig. 3). In addition to their large scale effects on creek formation and vegetation loss, crabs can also affect sediment structure at finer scales, through the formation of burrows.

Crab burrows, particularly those of species that do not plug their burrows during inundation, may function as passive sediment traps (Grabowski et al., 2011; Escapa et al., 2008). However, water filled burrows often lead to a reduced bulk shear strength and density, and reduced erosion thresholds, which in areas that are heavily burrowed would increase the mass of sediment eroded (Grabowski et al., 2011). Sediment trapping rate is dependent on burrow architecture, density and possibly bed roughness (Escapa et al., 2008), therefore, different species of burrowing crabs have different effects on the erosion and transport of sediment (Min et al., 2023, Fig. 1).

1.4.3) Sediment transport and deposition

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Sediment transport is often considered to be only a physical process, as a result of sediment beds responding to hydrodynamic forces in coastal habitats (Le Hir et al., 2007). However, biological components are also able to influence sediment transport processes. The interaction between organisms and the sediment is complex and generally context specific, due to factors such as hydrodynamics, sediment composition or species-specific behaviours (Needham et al., 2013). The influence of individual species on sediment dynamics are therefore poorly understood. This makes it difficult to predict the overall impact of organisms on sediment transport. While erosion and deposition are primarily driven by hydrodynamics, benthic organisms influence the extent of these processes on a spatial and seasonal scale. Studies have shown that benthos can cause change of the same order of magnitude as hydrodynamic processes (Arlinghaus et al., 2021).

Crab burrow morphology is related to biological (e.g. sex or size; Sen and Homechaudhuri, 2016) and environmental (e.g. vegetation or sediment composition; Penha-Lopes et al., 2009) factors, with morphology influencing their effectiveness in trapping sediment and organic matter. Intertidal decapods construct funnel shaped burrows which aids in the trapping of organic matter and sediment (Botto et al., 2006). Funnel shaped burrows with low aspect ratios trapped a greater percentage of organic matter while tubular shaped burrows with a higher aspect ratio trapped a greater amount of sediment (Botto et al., 2006) (Table S1, Fig. 3). Gutiérrez et al. (2006) and Wang et al. (2010) deployed burrow mimics and found that less material by weight was collected in the mimics than was excavated by crabs, indicating a net export of sediment material (Table S1, Fig. 3). Excavation allows for buried material to be brought to the surface, increasing the amount of sediment available for export by tidal flushing. The quantity of sediment and organic matter available for transport is therefore a balance between material deposited into crab burrows and material excavated from them.

Crabs create sediment mounds when they move sediment from their burrow to the surface. During flooding and ebbing tide, this fresh mound sediment is transported. It remains a challenge to predict when burrowing engineers will have a significant effect on their environment (Coggan et al., 2018). However, the engineering effect is anticipated to intensify as crab population densities increase (Rinehart et al., 2024). For example, burrowing crabs are often found to have site specific effects on ecosystems (Beheshti et al., 2021), such as promoting sediment trapping in one area of the marsh, but enhancing sediment removal in other areas (Escapa et al., 2008). Crabs were found to promote the trapping of sediment in open mudflats and intertidal salt marsh where current speeds are low, whereas in the salt marsh edge, they were increasing sediment removal (Escapa et al., 2008) (Table S1, Fig. 3). This was due to funnel shaped burrows being more frequent in the low intertidal zones as well as the assistance of plants in trapping sediment. In habitats with weak flow, burrowing animals are expected to promote sediment trapping, whereas in high flow energy habitats, burrowing activity is anticipated to increase sediment removal rates, determined by the strength of the current. In addition to crabs, Thalassinidea which are shrimp–like organisms, commonly referred to as mud or sandprawns in South Africa, also influence sediment transport and deposition. These burrowing species similarly create mounds by expelling sediment from their burrows (Pillay and Branch, 2011). The transport of sediment by thalassinideans is greater than that achieved by diffusion processes or abiotic burial (Grigg, 2003). The sediment expelled from callianassid burrows is easily eroded at low current speeds because it is unconsolidated, making it more prone to resuspension and redeposition in adjacent areas (Pillay et al., 2007). *Kraussillichirus kraussi* (sandprawn characteristic of temporarily closed estuaries in South Africa) consumes organic matter around its burrow, thus is an effective mover of sediment (Pillay and Branch, 2011). Burrowing organisms are therefore key drivers of sediment transport and redistribution in tidal marshes.

1.5) Impact of bioturbation on carbon burial and sequestration

Consumers can influence the carbon cycle directly and indirectly. For instance, small bioturbating grazers change sediment properties and remove plant biomass. While they are known to have an effect, they remain an understudied driver of carbon cycling (Guimond et al., 2020; Ren et al., 2022). It was estimated by Montague (1982) that *Uca pugnax* (a species of fiddler crab native to salt marshes along the coast of North America) excavated an amount of carbon that is equal to 20 % of what *S. alterniflora* produces belowground annually, in Sapelo Island, Georgia, U.S. (Table S1, Fig. 3). The amount of carbon collected in burrows was lower than that made available for tidal flushing by excavation (Montague, 1982). The concentration of labile and total carbon at the marsh surface is expected to decrease with crab activities because of the lower carbon content in the sediment that is excavated in relation to that deposited into the burrow (Gutiérrez et al., 2006). Burrowing organisms, such as crabs, can influence the carbon balance of tidal marshes by releasing carbon that would otherwise remain stored deeply in the sediment. Wittyngham et al. (2024) showed that small grazers cause a decrease in carbon stocks with *S. reticulatum* accounting for a loss in carbon stocks of 40-70 % (Table S1, Fig. 3). In Cape Cod where marsh die off and erosion occurred due to overgrazing by *S. reticulatum*, an estimate of 248.6 ± 4.8 gigagrams of belowground

Commented [A37]: Paragraph should have a more descriptive topic sentence carbon was released (Coverdale et al., 2014) (Table S1, Fig. 3). A correlation exists between crab burrows and carbon content, with higher densities of crab burrows associated with decreased carbon in the topsoil (Carpenter et al., 2023). The highest carbon content was found in salt marsh with minimal burrowing by crabs.

Complex burrow networks can have an effect on soil carbon stocks. A study conducted in Kenya found that mangrove forests that had a greater abundance of sesarmid crabs, had higher soil carbon stocks (Andreetta et al., 2014) (Table S1, Fig. 3). Crabs can also directly transfer carbon to sediments through the transportation of faeces, algae, leaf litter, and exuviae into their burrows (Alongi, 2002). This vertical transport of carbon was demonstrated through radiocarbon dating of sediment cores. Modern carbon was found to depths of 115 cm (Andreetta et al., 2014), which means that crabs are supplying new organic matter to deep~~er~~ sediments. It is possible that the diversity of macrofauna in these ecosystems could be an important driver of carbon dynamics (MacKenzie et al., 2021). Macrofaunal diversity means a variety of sediment reworking activities, through bioturbation and bio-irrigation, which in turn can exert control on sedimentary biogeochemical cycling, such as carbon cycling (Meysman et al., 2006). On the other hand, crabs can also decrease carbon stocks because their burrows increase sediment surface area, aiding organic matter decay as more sediment becomes oxic, which leads to carbon loss via tidal flushing (Klaassen et al., 2025).

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The effects of bioturbation on carbon cycling ~~is~~ are context specific. For instance, *Macrophthalmus japonicas*, a salt marsh crab species from East Asia, increased the mineralization of sediment organic matter (SOM), stimulating the release of organic carbon, thus slowing the accumulation of organic carbon within sediment surface layers (Nie et al., 2021) (Table S1, Fig. 3). Similarly, bioturbation by *S. reticulatum* led to the remineralization of belowground organic matter by increasing the permeability and aeration of the sediment, leading to the degradation of organic material (Wilson et al., 2012). Crabs decreased SOM and carbon content in vegetated habitats and increased SOM and carbon in unvegetated habitats (Rinehart et al., 2024). Crab bioturbation has been shown to improve benthic metabolism and exchange of dissolved organic matter from the sediment to the water column (Fanjul et al., 2015) (Table S1, Fig. 3). It was also found that the distribution, quality and bioavailability of sedimentary organic matter is influenced by bioturbation. Furthermore, efficient remineralisation of detritus occurs at bioturbated sediment and is exported as CO_2 and DOC to the water column. Bioturbation, by crabs, therefore improves the amount of labile organic carbon of bioturbated sediments and alters the pathway of carbon export to coastal waters (Fanjul et al., 2015).

While bioturbation can contribute to carbon loss, some bioturbating organsims can promote carbon storage. Burrows of *Upogebia major* (mudshrimp found in salt marshes in East Asia) and other thalassinideans have been found to trap organic matter (Kinoshita et al., 2008), which can increase the storage of carbon. Moreover, it was found that grazing by livestock had a neutral to positive effect on carbon sequestration (Graversen et al., 2022) (Table S1, Fig. 3). Crab burrowing was found to increase the turnover of nitrogen and carbon, with excavated soil having higher inorganic carbon concentration compared to soil deposited into burrows (Wang et al., 2010). This indicates that excavation activities accelerates the mineralization of organic matter from organic to inorganic carbon (Wang et al., 2010). Such changes to organic matter availability and benthic metabolism by bioturbation have the potential to decrease the storage capacity of carbon (Gutiérrez et al., 2006). Under accelerated sea level rise, consumers' impact on the carbon cycle, through carbon consumption and marsh stability, is expected to intensify as a result of the accelerated migration rates of consumer fronts, which are clusters of consumers bordering a specific resource (Wittyngham et al., 2024).

1.6) Global change impacts on tidal marsh bioturbation

Blue carbon ecosystems are threatened by climate change, particularly sea level rise (Borchert et al., 2018; MacKenzie et al., 2024), as well as increasing temperatures and alterations in precipitation regimes (Arias-Ortiz et al., 2018; Adams et al., 2025). Coastal geomorphology, sedimentation patterns, geographic locality and regional oceanographic properties cause tidal marshes to become susceptible to these threats (Mcleod et al., 2010). The resilience of salt marshes and mangroves to sea level rise is determined by physical drivers, such as unrestricted landward migration or increase in surface elevation (Schuerch et al., 2018; Lovelock and Reef, 2020) as well as biological drivers such as ~~diversity~~ productivity (Branoff, 2020; He et al., 2025). The extent of development along the coast and the local topography controls the area available for these ecosystems to migrate landward, however, the rate of sedimentation controls the ability of salt marshes and mangroves to resist the rise in sea levels via the gain in relative surface elevation. The ability for sediment to be retained in the intertidal region is dependent on local coastal dynamics and drainage basin geology (Adams et al. 2019). Furthermore, the structure of a wetland ecosystem affects its resistance to a disturbance as well as recovery from a disturbance, therefore, local geomorphology contributes substantially towards the resilience of these systems (Phillips, 2018). Mangrove and salt marsh responses to sea level rise is thus not uniform across

Commented [A39]: This can also be from biological drivers

Commented [A40]: Repetitive with above different regions and even between sites within the same mangrove or salt marsh habitat (Passeri et al., 2015; Adams et al., 2025).

Mangroves are specifically vulnerable to changes in temperature and precipitation regimes, because the distribution range globally is linked to sea surface temperature. Mangrove occurrence is limited to regions that are tropical or subtropical, and this by the winter 20 °C sea surface isotherm (Tomlinson 1999; Hamilton and Casey, 2016). With rising temperatures comes an expansion of mangroves polewards, to higher latitudes. Expansion of mangroves leads to a loss of salt marsh habitats which results in ecological shifts as well as changes in the provisioning of ecosystem services, for example carbon storage (Kelleway et al., 2017a). Furthermore, mangroves that are found at range limits are also commonly smaller and shrub–like (Morrisey et al., 2010), which influences their capacity to store and sequester carbon (Raw et al., 2021). With rising sea levels, salt marshes are expected to migrate landwards (Enwright et al., 2016). If the rate of sea level rise surpasses that of surface elevation gain it will cause a shift in habitat with lower intertidal regions becoming subtidal and upper intertidal species will encroach the terrestrial boundary (Fagherazzi et al., 2019). In salt marshes, as sea level and consequently tidal prism begins to increase, it is expected that tidal creeks will develop, which has been observed in Bahamas (Kirwan and Guntenspergen, 2012).

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Regions that are more flooded (e.g. seaward areas) generally have smaller, shallower burrow networks compared to those in drier regions (Egawa et al., 2021). Crab activity is highest in summer and lowest in winter (Egawa et al., 2021), because of this seasonal change in behaviour, it could further complicate the influence of crabs on carbon budgets (Guimond et al., 2020) as regional historical temperatures change lined to behavioural phenology. Changes in water levels and temperature, major components of climate change, can influence the distribution of crabs and the extent of bioturbation (Wilson et al., 2022). Increased flooding can suppress these activities, thus leading to redox conditions becoming more anoxic in tidal marshes (Pan et al., 2023). On the other hand, faunal activities can interact with climate stressors. For example, cordgrass (*Spartina ~~A~~alterniflora*) loss and erosion have been caused by combined effects of sea level rise and *S. reticulatum* density increases in US Atlantic salt marshes (Crotty et al., 2020; Morrison et al., 2024).

Crabs create burrow structures in the form of tunnels and chimneys which can potentially provide material available for erosion. Flow velocities of 60 cm/s or higher are required to erode these structures, which can be reached at tidal creek heads under typical conditions (Farron et al., 2020) (Table S1, Fig. 3). These velocities are also likely during high flow events such as storms, which are expected to increase in frequency and intensity due to climate change (Zhang and Colle, 2018; Raw et al., 2023). Rainfall events, in contrast, do not erode marsh substrate that is consolidated but rather mobilize recently deposited, unconsolidated sediment (Voulgaris and Meyers, 2004). In areas that are heavily burrowed, this would include sediment deposited in the past few tidal cycles, in addition to burrow structures and pellets. This means that storms associated with climate change will have major effects on erosion patterns, especially in regions that are heavily burrowed, which can lead to morphological changes (Farron et al., 2020). Increases in drainage density is necessary to manage the expanding tidal prism and effectively drain the marsh surface to prevent waterlogging. Crab activity at tidal creeks may help alleviate the effects of accelerating sea level rise on the marsh platform (Farron et al., 2020). In a regime of increasing sea level rise, the presence of burrowing organisms, such as crabs, may possibly increase marsh sustainability, by forming creeks or extending existing creeks, and enhancing erosion. Overpopulation of crabs, through changes in predation pressure, however can cause loss of marsh area and increase vulnerability to erosion, negatively impacting the marsh.

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1.7) Synthesis and way forward

A positive sediment budget is important for the accretion and resilience of tidal marshes, as it promotes marsh elevation and enhances carbon storage by actively burying carbon. Bioturbation activities on the other hand can either stabilize or destabilise sediment, influence sediment transport and ultimately influence marsh elevation. These two processes can therefore be viewed as being interconnected rather than being independent of one another. The reworking of sediment by some organisms increases surface roughness and decreases sediment cohesion, leading to erosion and in some cases creek formation. While the stabilization of sediment is possible through burrows of other species, functioning as passive sediment traps, which in turn can promote accretion. Apart from sediment properties being affected by bioturbation activities, carbon cycling is also influenced by these activities. Activities such as burrowing and feeding can lead to a loss of carbon through increased mineralization of organic matter, or through erosion. However, bioturbators can also promote the burial of carbon by trapping sediment, and transporting organic matter such as faeces and leaf litter into their burrows.

This review has highlighted a number of knowledge gaps, specifically the lack of understanding of the influence that bioturbators and their interactions have on sediment processes and their role in carbon cycling. This is despite increasing recognition that biological components have an influence on the functioning of tidal marshes. Sediment–organism interactions are often context specific and complex, and our understanding of species specific impacts are limited. It is challenging to predict how bioturbators might influence their environment as the impact of individual species on sediment dynamics varies, therefore, bioturbation effects cannot be generalized. For example, the effects of crabs from the family Ocypodidae versus crabs from the family Sesarmidae will have different effects on sediment because of burrow morphology, diet and behaviour, all of which influence bioturbation effects. Moreover, these families are often found co-occurring in the same habitat making it important to understand their individual as well as combined impacts on sediment processes. Such studies could be done under experimental conditions and in situ, and should be extended across different habitat types as sediment characteristics and vegetation also have an influence on bioturbation impacts.

Sediment–species interactions also have an influence on carbon cycling in tidal marshes, yet consumers are an understudied driver of these processes. There is a need to quantify carbon stocks, sequestration and greenhouse gas fluxes and to investigate how these processes respond to bioturbation activities. Studies comparing regions with varying intensities of bioturbation are important for a better understanding of the contribution of bioturbators to carbon dynamics in tidal marshes. It is clear that there is no real consensus as to whether bioturbation has a positive or negative influence on sediment dynamics and carbon cycling (Table 2 and S1). By advancing our understanding, management and restoration efforts could be improved, and better predict the resilience of tidal marshes under future climate change pressures.

1.8) Author contributions

Conceptualization: GMR, JBA; writing original draft preparation: LS; writing review and editing:
GMR, JBA, LS; supervision: GMR, JBA; funding acquisition: GMR, JBA.

1.9) Conflict of interest

The authors declare that they have no conflict of interest.

1.10) Acknowledgements

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Figure 2: Global distribution of studies conducted in tidal marshes investigating the influence of bioturbation on sediment dynamics and carbon cycling. The size of each dot indicates the number of studies conducted in each country. Yellow dots represent studies focused on sediment dynamics, while blue dots represent studies focused on carbon cycling. Argentina and United States of America are the leading countries in terms of the number of studies conducted. Details on each study can be found in Table 2 and Table S1. Diagram is not to scale. Graphics were sourced from and created using the software Canva Pro.

Table 2: Overview of the influence and directiona l effects of bioturbation on sediment and carbon dynamics across tidal habitats and continents. Adapted from Table S1.

Continent	Habitat type	Sediment/Carbon focused	Directional effect	Effect	Reference
Europe	Laboratory	Sediment	Negative	Erosion	Dairain et al., 2020
	Mudflat	Sediment	Negative	Decrease sediment stability	De Deckere et al., 2001
	Mudflat	Sediment	Negative	Decrease sediment stability	Montserrat et al., 2011
	Mudflat	Sediment	Both negative & positive (species dependent)	One species caused erosion, one species caused accretion	Morelle et al., 2024
	Salt marsh	Carbon	Neutral to Positive	Neutral to positive effect on carbon sequestration	Graversen et al., 2022
North America	Salt marsh	Sediment	Negative	Change biogeochemistry of sediment	Wilson et al., 2012
	Laboratory	Sediment	Negative	Increase sediment roughness, decrease shear strength=erosion	Farron et al., 2020
	Salt marsh	Sediment	Positive	Accretion	Crotty et al., 2023
	Salt marsh	Carbon	Negative	Hinders accretion, loss of carbon sequestration	Coverdale et al., 2014
	Salt marsh	Carbon	Negative	Decrease carbon stocks	Wittyngham et al., 2024
	Salt marsh	Carbon	Negative	Decrease carbon stocks	Montague, 1982
South America	Salt marsh & Mudflat	Sediment	Both negative & positive (species dependent)	One species caused sediment trapping=accretion, one species caused erosion	Escapa et al., 2008
	Mudflat	Carbon	Positive	Increase carbon sequestration	Botto et al., 2006
	Salt marsh	Carbon	Negative	Decrease carbon stocks	Gutiérrez et al., 2006
	Salt marsh	Carbon	Negative	Decrease carbon stocks	Fanjul et al., 2015
Oceania	Mangrove & Salt marsh	Sediment	Neutral to positive	Increase surface elevation in mangroves, no influence in salt marsh	Bennion et al., 2024
Asia	Salt marsh	Carbon	Negative	Promote movement of carbon, can decrease long term storage of carbon	Wang et al., 2010
	Estuary	Carbon	Negative	Decrease carbon stocks	Nie et al., 2021
Africa	Mangrove	Carbon	Positive	Increase carbon storage	Andreetta et al., 2014

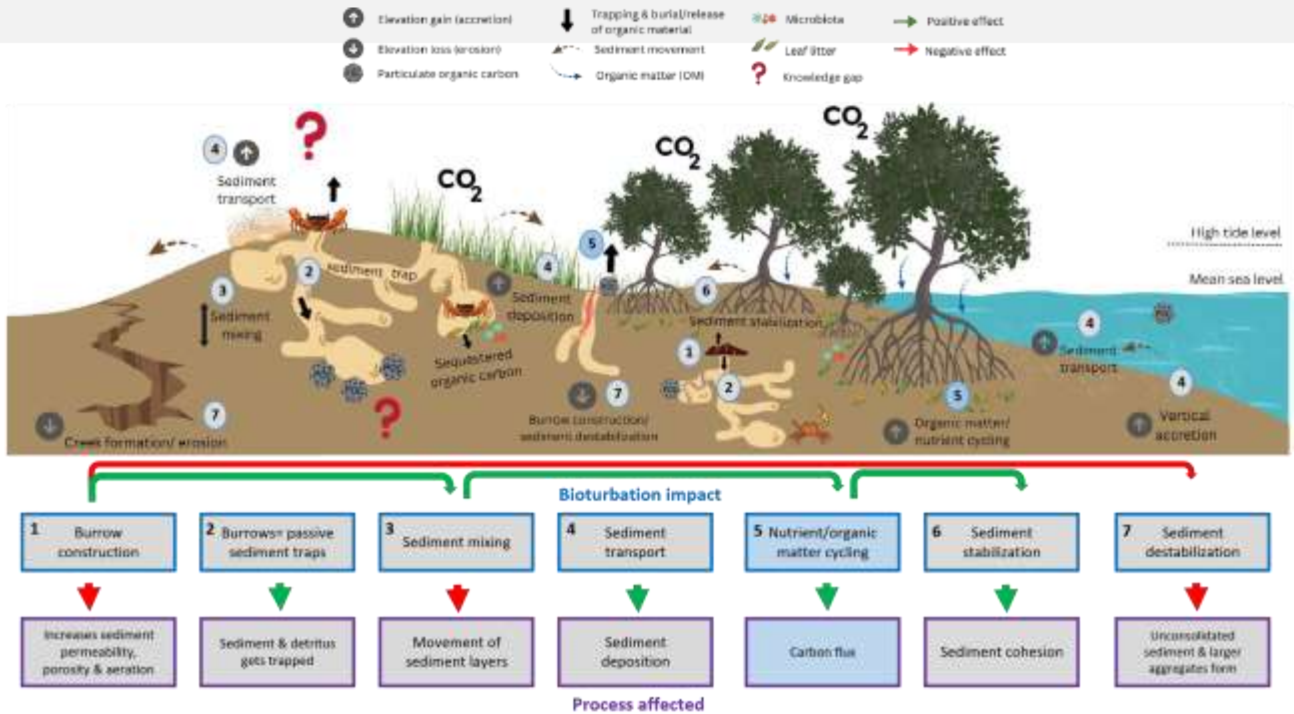

Figure 3: Conceptual diagram illustrating the processes influenced by bioturbators, specifically their impact on sediment dynamics and carbon cycling, and how they are linked. The knowledge gaps, indicated by question marks, relate to the role of benthic organisms in sediment dynamics, species specific effects, as well as the influence of bioturbators on the carbon cycle. The flow diagram indicates the graphics in terms of the bioturbation impacts and which processes are affected within the marsh, with green arrows indicating a positive effect and red indicating a negative effect. Diagram is not to scale. Graphics were sourced from and created using the software Canva Pro.

Table 3 Bioturbation impacts on sedimentation and carbon sequestration. Negative effects are italicised, while positive effects are indicated in bold. This table corresponds to the network diagram in Figure 3.

Bioturbation impact	Process	Effect on sedimentation	Effect on carbon sequestration
Sediment mixing	Movement of sediment layers	*Effects sediment structure- can lead to erosion*[a]	*Excavate stored carbon*[b]
Burrow construction	Increase sediment permeability, porosity & aeration	*Reduces sediment stability- can lead to erosion*[c]	*Increases organic matter decomposition- decreases carbon sequestration*[d]
Passive sediment trap (burrows)	Sediment and detritus gets trapped in and around burrow	**Increases sediment deposition and overall concentration of sediment organic matter**[e]	**Increases burial of organic rich sediment enhancing carbon storage**[f]
Sediment destabilization	Sediment becomes unconsolidated & larger aggregates are formed	*Increases sediment erosion*[g]	*Decreases organic matter burial- decreases carbon sequestration*[g]
Sediment transport	Sediment deposition	**Causes particles to be resuspended and transported**[h] **- can contribute to accretion**	**If resuspended particles are trapped, it can increase carbon burial**[j]
Sediment stabilization	Some bioturbators promote sediment cohesion	**Increases sediment strength and retention**[i] **- can contribute to accretion**	**Sediment retention enhances carbon burial because active burial limits oxidation**[j]
Nutrient/ organic matter cycling	Organic matter transported to deeper layers	**Influences plant growth**[k] **which increases sediment trapping and stability- can contribute to accretion**	**Enhanced carbon storage**[e,f] **– decomposition is slowed down**

[a] Dairain et al., 2020
[b] Gutierrez et al. 2006
[c] Grabowski et al. 2011
[d] Nie et al., 2021
[e] Botto and Iribarne 2000
[f] Andreetta et al., 2014
[g] Coverdale et al., 2014
[h] Pillay et al., 2007
[i] Kristensen 2008
[j] McCarty et al., 2009
[k] Botto et al., 2006

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