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Inés Mazarrasa

Jimena Samper-Villarreal

Oscar Serrano
Edith Cowan University

Paul S. Lavery
Edith Cowan University

Catherine E. Lovelock

See next page for additional authors

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Authors

Inés Mazarrasa, Jimena Samper-Villarreal, Oscar Serrano, Paul S. Lavery, Catherine E. Lovelock, Núria N. Marbà, Carlos M. Duarte, and Jorge A. Cortés

Habitat characteristics provide insights of carbon storage in seagrass meadows

Inés Mazarrasa^{1,2*}, Jimena Samper-Villarreal³, Oscar Serrano⁴, Paul S. Lavery^{4,7}, Catherine E. Lovelock⁵, Núria Marbà¹, Carlos M. Duarte⁶, Jorge Cortés^{3,8}

1. Department of Global Change Research. IMEDEA (CSIC-UIB) Institut Mediterrani d'Estudis Avançats, C/ Miguel Marqués 21, 07190 Esporles (Mallorca), Spain.
2. Environmental Hydraulics Institute "IH Cantabria", Universidad de Cantabria, Parque Científico y Tecnológico de Cantabria, 39011 Santander, Spain.
3. Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica.
4. Centre for Marine Ecosystems Research, School of Science, Edith Cowan University, 270 Joondalup Drive, Joondalup WA 6027, Australia.
5. School of Biological Sciences, The University of Queensland, St Lucia, QLD, 4072, Australia.
6. King Abdullah University of Science and Technology, Red Sea Research Center, Thuwal 23955-6900, Kingdom of Saudi Arabia.
7. Centro de Estudios Avanzados de Blanes (CEAB-CSIC), Calle de Acceso a la Cala Sant Francesc, 14, 17300 Blanes, Girona, Spain.
8. Escuela de Biología y Museo de Zoología, Universidad de Costa Rica, San Pedro, 11501-2060 San José, Costa Rica.

*ines.mazarrasa@unican.es

Abstract:

Seagrass meadows provide multiple ecosystem services, yet they are among the most threatened ecosystems on earth. Because of their role as carbon sinks, protection and restoration of seagrass meadows contribute to climate change mitigation. Blue Carbon strategies aim to enhance CO₂ sequestration and avoid greenhouse gas emissions through the management of coastal vegetated ecosystems, including seagrass meadows. The implementation of Blue Carbon strategies requires a good understanding of the habitat characteristics that influence C_{org} sequestration. Here, we review the existing knowledge on Blue Carbon research in seagrass meadows to identify the key habitat characteristics that influence C_{org} sequestration in seagrass meadows, those factors that threaten this function and those with unclear effects. We demonstrate that not all seagrass habitats have the same potential, identify research priorities and describe the implications of the results found for the implementation and development of efficient Blue Carbon strategies based on seagrass meadows.

1. Introduction

Meeting the commitments made in the CoP21 meeting (Paris Agreement) requires climate change mitigation through a reduction of CO₂ emissions and an increase in carbon sequestration (Rogelj et al., 2016). Among carbon sequestration strategies is the enhancement of ecosystems that act as natural carbon sinks, when CO₂ absorbed through photosynthesis and stored as biomass (organic carbon, C_{org}) is greater than that released through respiration and decomposition (Trumper et al., 2009). Coastal vegetated ecosystems (i.e. tidal marshes, mangroves and seagrasses) are among the most significant natural carbon sinks (Smith, 1981; Duarte et al., 2005). Yet, they have been often neglected in the global carbon cycle models and not considered within the traditional greenhouse gases (GHG) abatement schemes (Macreadie et al., 2014; Duarte, 2017). The publication of two reports (Laffoley and Grimsditch 2009, Nelleman et al., 2009) building on the demonstration of their relevance as carbon sinks at a global scale (Duarte et al. 2005) triggered the development of climate change mitigation strategies based on their protection and restoration, similar to those already existing for terrestrial ecosystems (e.g. REDD+ program). The organic carbon sequestered by coastal vegetated ecosystems has been termed Blue Carbon and the initiatives to mitigate climate change through their protection and restoration are known as Blue Carbon

strategies (Nelleman et al., 2009).

Seagrass meadows are especially relevant due to their global distribution and large aerial extent (Hemminga and Duarte, 2000; Chmura et al., 2003). The largest C_{org} deposits in seagrass meadows are located in the soil compartment, formed by refractory belowground biomass, seagrass detritus and allochthonous C_{org} embedded in the soil matrix (Gacia et al., 2002; Kennedy et al., 2010). Due to the anoxic conditions of the sediment, soil C_{org} deposits may remain for millennia, constituting long-term carbon sinks (Mateo et al. 2006). On the contrary, seagrass above-ground biomass, which is more labile than below-ground biomass due to their exposure to aerobic conditions and herbivory and their more labile chemical composition (Enriquez et al., 1993), is considered a short-term carbon sink and has a low contribution to the total C_{org} deposits found in seagrass meadows (Mateo et al., 2006; Fourqurean et al., 2012). In addition to C_{org} sequestration, seagrass meadows provide multiple other ecosystem services critical for coastal communities, including support of fisheries, the improvement of water quality, coastal protection and cultural services, and they are considered among the most valuable ecosystems on earth (Costanza et al., 1997; Nordlund et al., 2017). Seagrass meadows are, however, experiencing a global decline (Waycott et al., 2009), leading to the loss of all the ecosystem services they provide including C_{org} sequestration, and potentially leading to CO_2 emissions when soil C_{org} deposits are eroded and exposed to aerobic conditions (Marbà et al., 2014; Serrano et al., 2016a; Lovelock et al., 2017).

The significant role that seagrass meadows play as carbon sinks opens new opportunities for coastal managers to promote their conservation and restoration as a strategy to mitigate climate change. For instance, Blue Carbon can be used as a tool to access carbon financing and compensate part of the costs for the protection and restoration of seagrass meadows, contribute to national GHG emission reduction targets and be incorporated as an additional benefit to enhance the creation of marine protected (Adame et al., 2015; Herr and Landis, 2016; Herr et al., 2017; Howard et al., 2017). However, soil C_{org} stocks and sequestration rates are highly variable among seagrass species and sites (Lavery et al., 2013; Miyajima et al., 2015; Mazarrasa et al., 2017a). The use of Blue Carbon as a tool for climate change mitigation or conservation purposes requires considering this variability and to identify areas which may become important CO_2 sources in the future (Herr et al., 2015, 2017). Thus, a robust understanding of the

factors that enhance or inhibit C_{org} sequestration and storage in seagrass soils as well as those that may cause CO_2 emissions following disturbance and subsequent remineralization of soil C_{org} deposits is needed.

Seagrass meadows develop across a wide range of climatic regions (from tropical to high temperate latitudes) and habitat types (from sheltered bays and estuaries to highly exposed areas), and from the intertidal zone to 40 m depth (Duarte, 1991a; Carruthers et al., 2007). These different habitats are characterized by different environmental factors. For example, they vary in terms of temperature, hydrodynamic energy, light availability and turbidity, which determines meadow biotic characteristics, such as species composition, structural and physiological traits (e.g. density, cover, biomass allocation and productivity) (Alcoverro et al., 2001; Carruthers et al., 2007) and abiotic parameters, such as the load of allochthonous C_{org} in the water column, the depositional vs. erosional nature of the meadow and the sedimentation rates (Carruthers et al., 2007). All these habitat characteristics influence the sequestration and storage of C_{org} in seagrass soils as demonstrated in recent studies (Lavery et al., 2013; Serrano et al., 2014; Samper-Villarreal et al., 2016; Serrano et al., 2016b). In addition, seagrass habitats are expected to change in the near future due to consequences of climate change, including increasing temperature, ocean acidification and sea level rise, and also due to the intensification of human pressure in coastal areas. It is unclear what effect this will have on the global carbon sink capacity of seagrass meadows (Duarte, 2002; UNEP, CIFOR, 2014).

Despite the increasing number of studies assessing the role of habitat characteristics on C_{org} stocks and sequestration rates in seagrass soils, information remains sparse and difficult to apply for management purposes due to: a limited number of habitat characteristics assessed in each study; the different spatial scales at which factors influence C_{org} sequestration, from large regions (e.g. climatic region; Lavery et al., 2013; Miyajima et al., 2015) to regional scales across different meadows (i.e. hydrodynamic energy, turbidity, canopy complexity) (Samper-Villarreal et al., 2016; Mazarrasa et al., 2017a) or to small spatial scales within the same meadow (e.g. water depth gradient, Serrano et al., 2014); and the contradictory results found among different studies regarding some habitat characteristics (i.e. water depth; Lavery et al., 2013; Serrano et al., 2014; Mazarrasa et al., 2017a), which points to potential interactions among factors.

Here we aim to identify and synthesize the key habitat characteristics that influence long-term C_{org} sequestration in seagrass meadows. Our analysis is based on the current knowledge of seagrass ecology and on a review of the most recent literature on Blue Carbon research (Table SI 1). Firstly, we review the main mechanisms that lead to C_{org} sequestration in seagrass soils. Then we describe how variation in habitat characteristics, both biotic and abiotic, influences those mechanisms and thus C_{org} sequestration and how climate change and human pressure may affect this process. We provide guidance for the identification of habitats where C_{org} sequestration is enhanced and habitats where this function is reduced or even threatened. Finally, we identify key research priorities and describe the implications of the results found in this study for the implementation and development of Blue Carbon strategies in seagrass meadows.

2. Mechanisms enhancing Blue Carbon storage in seagrass meadows.

Seagrass meadows sequester both autochthonous and allochthonous C_{org} . Autochthonous C_{org} is composed of above-ground (i.e. shoots and leaves) and below-ground (i.e. roots and rhizomes) biomass, and seagrass detritus accumulated in the soil. Allochthonous C_{org} refers to non-seagrass carbon deposited mainly from the water column (e.g. sestonic carbon) (Kennedy et al., 2010) which is enhanced by the presence of the seagrass canopy (Gacia et al., 2002; Hendriks et al., 2008). Allochthonous C_{org} , particularly that derived from macroalgae and phytoplankton, is much more labile than seagrass C_{org} , especially compared to below-ground biomass (Enriquez et al., 1993; Klap et al., 2000; Banta et al., 2004). Yet, once incorporated within the soil compartment, where low oxygen levels inhibit microbial activity (Trevathan-tackett et al., 2017), remineralization of allochthonous C_{org} is reduced, leading to a significant contribution to the long-term C_{org} deposits that develop in seagrass soils (global average of 50%; Kennedy et al., 2010).

In addition, by favoring particle sedimentation, seagrass meadows tend to enhance the formation of muddy soils (Gacia et al., 2002; Hendriks et al., 2008; Dahl et al., 2016a; Serrano et al., 2016b). A high mud content in seagrass soils has been demonstrated to reduce remineralization of organic C_{org} by enhancing soil anoxic conditions (lowering permeability and oxygen penetration) and by protecting organic particles from microbial action following absorption to fine mineral particles (Kell et al., 1994; Mayer, 1994; Burdige, 2007; Serrano et al., 2016b; Miyajima et al., 2017)

Hence, the formation of sedimentary C_{org} deposits in seagrass meadows relies on three main processes: seagrass meadow productivity and biomass accumulation (particularly below-ground tissue); the input of allochthonous C_{org} into the sediment compartment; and the C_{org} burial efficiency in seagrass sediments, which is enhanced by the anoxic conditions of the sediments, the mud content and the proportion of refractory C_{org} being stored (e.g. the relative contribution of autochthonous and allochthonous C_{org}) (Mateo et al., 2006; Serrano et al., 2016b). Thus, seagrass habitats where those three processes concur (seagrass biomass accumulation, allochthonous C_{org} sedimentation and C_{org} burial efficiency) will have the largest potential for C_{org} sequestration and storage. In the following section, we describe the expected effect of different habitat characteristics on seagrass biomass accumulation, allochthonous C_{org} sedimentation and/or C_{org} burial efficiency and, as a consequence, on the capacity of seagrass meadows for C_{org} sequestration and storage.

3. Effect of habitat characteristics on the long-term C_{org} sequestration in seagrass soils

3.1. Biotic factors:

Species composition

Seagrass species are highly variable in terms of size, biomass, biomass distribution and dynamic features such as life span, primary productivity and turnover rates, resulting in different ecological roles (Den Hartog, 1977; Duarte, 1991b; Duarte and Chiscano, 1999). In general, small species (e.g. *Halophila* spp. and *Halodule* spp.) are typical “colonizers”, having high growth and turnover rates, which leads to lower biomass accumulation than larger and long-lived ‘persistent’ species (e.g. *Posidonia* spp. and *Thalassia* spp.) (Duarte and Chiscano, 1999; Kilminster et al., 2015; Serrano et al., 2016c). In addition, larger seagrasses species have higher below-ground : above-ground biomass ratios than smaller species (Duarte and Chiscano, 1999). This variation in biomass allocation enhances the efficiency of preservation of the autochthonous C_{org} due to the proximity of this material to anoxic conditions in seagrass soils and the more refractory nature of below-ground tissues (e.g. enriched in lignin) compared to above-ground tissues (Klap et al., 2000; Fourqurean and Schrlau, 2003). Furthermore, lignin content seems to be higher in long-lived and large seagrass species (Duarte, 1991b; Klap et al., 2000).

At the same time, the capacity of seagrass meadows to reduce hydrodynamic energy from currents, waves and tides, generally increases as leaf size increases and the percentage of the water column occupied by the seagrass canopy increases (Fonseca and Fisher, 1986; Fonseca and Cahalan, 1992). Thus, meadows formed by large seagrass species are expected to be more effective at enhancing particle sedimentation from the water column, favoring the accumulation of allochthonous C_{org} and fine sediment particles, and at reducing erosion and export. Due to their higher resistance to hydrodynamic forces, larger species also tend to form more stable and permanent meadows than small and ephemeral species (Duarte, 1991b; Mellors et al., 2002; Ondiviela et al., 2014).

As a consequence, large and persistent seagrass species generally show larger soil C_{org} deposits (Lavery et al., 2013; Rozaimi et al., 2016; Figure 1a). Meadows formed by relatively small species may contain high C_{org} stocks if they occur in depositional areas (Lavery et al., 2013) although, due to their low below-ground biomass, most of the C_{org} sequestered is of allochthonous origin and thus relatively labile and vulnerable to remineralization compared to the C_{org} stored in meadows formed by large and persistent species (Enriquez et al., 1993; Lavery et al., 2013; Serrano et al., 2016c).

Meadow canopy complexity

Even when formed by a single species, seagrass meadows differ in the complexity of their canopy, with important implications for their C_{org} sequestration capacity. Canopy complexity is defined as shoot density, leaf area and species-specific characteristics such as biomass (Samper-Villarreal et al., 2016) and represents a pool of sequestered C_{org} that will potentially accumulate in the soil compartment. As canopy complexity increases, the efficiency of seagrasses at reducing hydrodynamic energy and sediment resuspension is expected to be enhanced, particularly so in the case of seagrass with blade-like morphologies such as *Zostera* or *Thalassia* spp. (Verduin and Backhaus, 2000), leading to high particle trapping from the water column and to the formation of muddy soils (Koch et al., 2006; Hendriks et al., 2008; Peralta et al., 2008; Peterson et al., 2004).

Canopy complexity may also be enhanced by epiphytic algal assemblages that may account for up to 50% of the above-ground biomass (Borowitzka et al., 2006). As with other canopy features, these epiphytes likely affect hydrodynamics and particle

trapping and often include large amounts of calcified algae which could contribute to both organic and inorganic C_{org} loading and soil accretion rates (Lavery and Vanderklift, 2002; Perry and Beavington-Penney, 2005).

Thus, higher canopy complexity is expected to lead to the formation of higher soil C_{org} deposits in seagrass meadows, as has been reported in recent studies (Samper-Villarreal et al. 2016; Serrano et al. 2016b; Figure 1b), but that effect may be more predictable in species with a blade-like morphology.

Seagrass landscape: patchy vs. continuous meadows

Seagrasses may form extensive and continuous meadows or patchy meadows, with different shapes and sizes of seagrass patches separated by unvegetated patches (Robbins and Bell, 1994). Seagrass landscape parameters include patchiness, patch size, and distance to patch edge. These parameters determine many ecological characteristics in seagrass ecosystems, such as associated biodiversity (Turner et al., 1999; Boström et al., 2006; Jackson et al., 2006), detritus transfer (Ricart et al., 2015a), sedimentation patterns and sediment grain size distribution (Turner et al., 1999; Zong and Nepf, 2011; Ricart et al., 2017).

Recent studies suggest that continuous seagrass meadows are more efficient at soil C_{org} sequestration and storage due to a greater capacity to retain autochthonous C_{org} (i.e. leaf detritus) and to accumulate a higher proportion of finer sediments (i.e. silt and clay) (Miyajima et al., 2017; Oreska et al., 2017; Ricart et al., 2017). The magnitude of the soil C_{org} deposits inside the seagrass patches tend to increase with the distance from the seagrass-sand edge (Ricart et al., 2015b; Oreska et al., 2017), indicating that large continuous meadows are more efficient at C_{org} storage (Figure 1c).

Biotic interactions and the role of trophic webs

Interactions between seagrass plants and other organisms can be determinant of the capacity of seagrass meadows to sequester C_{org} . For example, grazers and burrowers not only benefit from seagrass productivity or protection (Orth et al., 1984; Siebert and Branch, 2007) but are also critical for the maintenance of meadows' health and thus for supporting all the ecosystem services they provide (including C_{org} sequestration). Both groups of organisms prevent the development of high levels of sulfide in seagrass soils (which may cause seagrass mortality) by inhibiting the accumulation of excessive detritus in seagrass soils and by enhancing soil oxygenation (Barber and Carlson, 1993;

Carlson et al., 1994; Bertics and Zierbis, 2010).

However, dramatic increases in the population of grazers or burrowers may threaten C_{org} sequestration and storage in seagrass meadows. Overgrazing and increased burrower density has been described in situations where top-down control is absent, as occurs with the introduction of invasive grazer and burrower species or the demise of predator populations due, for example, to overfishing (Eklöf et al., 2008; Atwood et al., 2015; Lokko et al., 2015). Over-grazing may lead to a significant removal of the C_{org} stored as biomass (both above and below-ground) and thus to a lower accumulation of autochthonous C_{org} (Atwood et al., 2015). With overgrazing, leaves are shortened or removed and the capacity of the canopy to reduce water flow is expected to decrease, leading to a lower accumulation of allochthonous C_{org} from the water column and potentially higher exposure to erosional forces (Dahl et al., 2016b). In addition, it may change meadow species composition favoring the dominance of small colonizer species (e.g. *Halophila* spp.) over larger species (Preen, 1995) which, as discussed above, generally reduces the C_{org} sequestration capacity of the meadows. On the other hand, increased bioturbation could also reduce C_{org} sequestration efficiency, as soil oxygenation will be favored and the remineralization of organic matter enhanced (Banta et al., 1999; Kirstensen, 2000), as suggested for saltmarsh soil C_{org} deposits (Coverdale et al., 2014; Martinetto et al., 2016) and seagrass meadows (Thomson, 2017).

Thus, shifts in predator-prey relationships due to top predator populations' extinction or the settlement of invasive grazer or burrower species in seagrass meadows may alter their capacity to sequester and store C_{org} in the long-term. All other factors being equal, meadows where complex and intact trophic webs are maintained are likely to show higher C_{org} storage capacity than ecosystems where trophic downgrading has occurred (Figure 1d).

3.2. Abiotic factors:

Exposure to hydrodynamic energy

The degree of exposure to hydrodynamic forces such as waves, tides and currents, determines the patterns of sedimentation and erosion in coastal areas. In seagrass meadows, the level of exposure is usually reflected by the proportion of fine sediment particles, which is higher in sheltered areas compared to more exposed sites (van Keulen and Borowitzka, 2003). Thus, hydrodynamic energy is expected to affect C_{org} accumulation and storage in seagrass meadows through: 1) the balance between

C_{org} (both autochthonous and allochthonous) accumulation vs. export; 2) the sediment grain size and the formation of muddy soils; and 3) the erosional patterns and the potential exposure to aerobic conditions of the already buried C_{org} (Burdige, 2007; Serrano et al., 2016b). In meadows located in sheltered bays or estuaries and under calm conditions, sedimentation is typically enhanced compared to meadows located in more exposed sites, resulting in a higher content of fine sediment particles and larger C_{org} sedimentary deposits (Murphey and Fonseca 1995; Fonseca and Bell, 1998; Röhr et al., 2016; Samper-Villarreal et al., 2016) (Figure 2a).

Due to the close relationship between sediment grain size and hydrodynamics in coastal areas, sediment grain size is often used as a proxy of the hydrodynamic conditions in seagrass meadows (Cabaço et al., 2010; Mazarrasa et al., 2017a). Recently, the content of mud has been proposed as a useful indicator of the soil C_{org} stocks in seagrass meadows formed by small, fast growing species (e.g. *Zostera* spp. and *Halophila* spp.) (Dahl et al., 2016a; Röhr et al., 2016; Serrano et al., 2016c). In this type of meadows the contribution of autochthonous C_{org} to the soil deposits is low and the major C_{org} source is allochthonous organic matter that settles from the water column along with other fine mineral particles (Serrano et al., 2016c). On the contrary, in meadows formed by large, long-living species, (e.g. *Posidonia* spp. and *Amphibolis* spp.), where the soil C_{org} deposits develop mainly through the accumulation of the large and recalcitrant below-ground biomass typical of these genera (Duarte and Chiscano, 1999; Klap et al., 2000), the soil's mud content is not a useful proxy of its C_{org} stocks or sequestration rates (Serrano et al., 2016c).

Turbidity

Increased turbidity in coastal waters reduces irradiance, which is a primary factor controlling photosynthetic activity in seagrass meadows while determining seagrass distribution, growth and morphology (Duarte, 1991a; Lee et al., 2007). Several shading experiments demonstrate that the reduction of light availability leads to a decrease in shoot density and growth (Collier et al., 2009; Lavery et al., 2009; Ruiz and Romero, 2001) and field observations have confirmed this trend (Ruiz and Romero, 2003). As meadow biomass and shoot density decreases, the sequestration of autochthonous C_{org} decreases and, simultaneously, the capacity of the canopy to capture and retain allochthonous C_{org} from the water column is also reduced (Bos et al., 2007; Peralta et al., 2008). However, increased turbidity can potentially result in a greater

accumulation of allochthonous C_{org} and fine sediment particles from the water column, leading to higher soil C_{org} accumulation rates and preservation after burial associated to low levels of oxygen concentrations in fine sediments (Samper-Villarreal et al., 2016; Serrano et al., 2016b).

So far, there are only three studies that assess the effect of turbidity and light attenuation on seagrass soil C_{org} deposits (Table S11). Dahl et al., (2016b) found that, after a five-month shading experiment, decreased irradiance led to lower C_{org} stocks in below-ground biomass but did not cause a significant effect in soil C_{org} stocks, likely due to the short duration of their experiment. Samper-Villarreal et al. (2016) found a significant increase in soil C_{org} stocks along a natural gradient of increasing turbidity that was partially explained by the enhanced stocks of allochthonous C_{org} . Yet, total C_{org} sequestration rates decreased as turbidity increased (Samper-Villarreal, 2016).

Thus, over a turbidity gradient, the largest sedimentary C_{org} stocks and sequestration rates (particularly of autochthonous origin) will likely occur in low turbidity environments as submarine irradiance, and presumably seagrass productivity, would be higher (Figure 2b). However, enhanced accumulation of allochthonous C_{org} with increased turbidity may counterbalance the reduction in the input of autochthonous C_{org} and may result in similar, or even higher, C_{org} stocks in sedimentary deposits (Samper-Villarreal et al., 2016).

Water depth

Seagrass meadows are distributed from the intertidal zone to up to 40 m depth, mainly constrained by the availability of irradiance (Duarte, 1991). Similar to the effects caused by turbidity, light attenuation with water depth leads to a decrease in seagrass productivity, shoot density and growth (Alcoverro et al., 2001; Collier et al., 2007). Thus, it is reasonable to expect that C_{org} stocks and sequestration rates in seagrass soils would be higher in shallower meadows compared to deeper ones, as demonstrated in recent studies (Mateo and Romero, 1997; Serrano et al., 2014; Dahl et al., 2016a; Serrano et al., 2016b).

However, highlighting the complex interaction of factors that can drive C_{org} accumulation, increasing depth not only implies a reduction in irradiance but it also leads to changes in hydrodynamic conditions. Shallow meadows are, in general, more susceptible to wave action (Gambi et al., 1989; Koch et al., 2006) and, as a consequence, processes such as the export of seagrass detritus through soil erosion and

subsequent soil aeration are favored whereas sedimentation might be reduced (Mateo and Romero, 1997; van Katwijk and Hermus, 2000; Koch et al., 2006). All these processes may contribute to enhance C_{org} deposits in deep seagrass meadows compared to shallower ones, as found by Lavery et al., (2013) in two meadows of *Posidonia sinuosa* and *Amphibolis antarctica*.

Thus, due to the attenuation of irradiance with depth and the associated reduction in seagrass productivity, density and cover (Weidemann and Bannister, 1986; Gallegos et al., 1990; Alcoverro et al., 2001), shallow subtidal meadows are, generally, expected to have larger soil C_{org} stocks and accumulation rates than deeper meadows, especially in terms of autochthonous C_{org} (Serrano et al., 2014, 2016b) (Figure 2c). Yet, significant differences in hydrodynamic conditions between shallow and deeper areas might disrupt this trend.

Intertidal vs. subtidal meadows

Intertidal meadows are subject to more extreme and variable environmental conditions than subtidal meadows, including intermittent exposure to air, higher irradiance, changes in water levels and generally higher hydrodynamic forces (i.e. wave action and tide currents) that lead to plants in these areas having different physiological and ecological traits (Grady, 1981; Pérez-Lloréns and Niell, 1993; Silva et al., 2005). The response of seagrass primary productivity to aerial exposure during low tide is complex and variable. Whereas some studies found that, during low tides, intertidal seagrass meadows can rapidly assimilate atmospheric CO_2 leading to comparable or even higher photosynthetic rates than in submerged conditions (Leuschner and Rees, 1993; Leuschner et al., 1998; Silva et al., 2005), others showed lower primary productivity and photosynthetic rates in aerial conditions compared to submerged conditions (Pérez-Lloréns and Niell, 1993; Clavier et al., 2011). CO_2 assimilation during periods of exposure to air seem to be constrained by the water content in seagrass tissue, with desiccation reducing carbon gains (Leuschner et al., 1998; Silva et al., 2005). Thus, the duration of emersion is a determinant factor of photosynthetic rates in intertidal seagrass meadows leading, generally, to higher growth rates and biomass in low intertidal meadows compared to high intertidal meadows (van Lent et al., 1991).

On the other hand, intertidal seagrass meadows are generally exposed to stronger hydrodynamic conditions that reduce their capacity to trap particles from the water column and their capacity to reduce erosion. Thus, lower mud and C_{org} contents are

found in the soils of intertidal meadows compared to subtidal meadows (Grady, 1981; Heiss et al., 2000). In addition, intertidal meadows are expected to be affected by higher temperatures during emersion, that may enhance C_{org} remineralization, especially if strong hydrodynamic conditions lead to sediment suspension and oxygen exposure (Harrison, 1989; Burdige, 2007; Pedersen et al., 2011).

As a result, within the same species, intertidal meadows are expected to show lower soil C_{org} deposits and sequestration rates than subtidal meadows (Figure 2d). However, the only available study that has assessed this effect did not find significant differences between the soil C_{org} stocks in intertidal and subtidal habitats (Lavery et al., 2013), providing evidence of the complex interactions in these environments.

Nutrient availability

Seagrass growth, abundance and morphology are strongly linked to nutrient availability (Short, 1987). Fertilization experiments show that seagrass meadows tend to be nutrient limited, with higher nutrient availability enhancing productivity, biomass, shoot length and density (Perez et al., 1991; Fourqurean and Zieman, 1992; Agawin et al., 1996; Lee and Dunton, 2000). Therefore, it is reasonable to expect that seagrass meadows in areas with a high nutrient availability would accumulate more autochthonous C_{org} . These meadows would also be more efficient at reducing water flow, thereby enhancing the accumulation of allochthonous C_{org} and fine sediment particles and reducing sediment erosion compared to meadows in oligotrophic waters. Yet recent studies revealed different effects of nutrient availability on the C_{org} stored in seagrass soils. Armitage and Fourqurean (2016) found an increase in the magnitude of the soil C_{org} stocks along a natural gradient of increasing phosphate availability in Florida Bay. In contrast, Howard et al., (2016) found no significant effect of increased nutrient availability, from natural fertilization, on the C_{org} stored in seagrass soils in a smaller area of Florida Bay, despite marked differences in the seagrass community structure and primary production. On the other hand, short-term experimental increases in nutrient availability have led to lower soil C_{org} stocks (Martínez-Crego et al., 2014; Armitage and Fourqurean, 2016) despite observed increases in the C_{org} content in below-ground biomass (Armitage and Fourqurean, 2016). This finding is likely related to an increase in microbial remineralization activity induced by the higher nutritional value of the seagrass tissues (Martínez-Crego et al., 2014) or to the short temporal and spatial scales of the experiments, that might have been insufficient to detect any positive

effects of the increase in biomass C_{org} sequestration on the soil C_{org} deposits (Armitage and Fourqurean, 2016).

On the other hand, excessive nutrient availability often leads to changes in the species composition of seagrass meadows (Howard et al., 2016) enhancing the spread of fast-growing and “colonizer” species such as *Halophila* spp., which, as described previously, are less efficient at sequestering autochthonous C_{org} than larger and persistent species. Nutrient enrichment can also lead to the proliferation of phytoplankton (i.e. eutrophication), epiphytes or macroalgae (McGlathery et al., 2007) that, when in excess, detrimentally affect seagrass productivity through competition for light and nutrients (Hauxwell et al., 2003), while increasing the amount of labile allochthonous C_{org} available to be trapped and stored in the soil C_{org} pool (Macreadie et al., 2012; Serrano et al., 2016d). Furthermore, increased nutrient availability may enhance above-ground biomass relative to below-ground biomass (Lee and Dunton, 2000; Peralta et al., 2003), which is more vulnerable to export and grazing and is generally more labile than below-ground biomass (Klap et al., 2000; Macreadie et al., 2014).

Due to the potential complex interactions, the effect of nutrient availability on C_{org} accumulation in seagrass soils is still unclear. As suggested by Armitage and Fourqurean (2016), relatively high nutrient availability in oligotrophic coastal waters may lead to higher C_{org} storage in seagrass meadows if it affects sufficiently large areas over the long-term (e.g. decades). However, in excess or as a pulsed supply, nutrient inputs may compromise the long-term C_{org} sequestration capacity of seagrass meadows (Macreadie et al., 2017; Martínez-Crego et al., 2014) (Figure 2e).

Climatic regions

Seagrasses are distributed across a broad range of latitudes encompassing a wide variability in temperature, irradiance and day length (Hemminga and Duarte, 2000; Olesen et al., 2015). Seagrass latitudinal variation has been related to differences in metabolic rates and ecosystem dynamics, with potential implications for C_{org} sequestration in seagrass soils.

Seagrass mean annual biomass and productivity tend to increase from lower to higher latitudes, particularly for above-ground biomass (Duarte, 1989; Duarte and Chiscano, 1999; Clausen et al., 2014), whereas biomass turnover rates tend to decrease from lower to higher latitudes (Duarte, 1989; Olesen et al., 2015). In general, temperate

meadows show higher seasonal variability in biomass compared to tropical meadows (Duarte, 1989), suggesting a seasonal fluctuation in their C_{org} sequestration capacity, that would be higher during the productive, spring/summer season, particularly in the case of annual seagrass meadows (Bos et al., 2007). However, Clausen et al., (2014) found the opposite trend for *Zostera marina*, suggesting that latitudinal effects on seasonal C_{org} sequestration in seagrass biomass might vary among species. Thus, due to the higher biomass and productivity and the lower turnover rates showed by meadows at higher latitudes compared to meadows located at lower latitudes, we would expect higher soil C_{org} stocks in temperate meadows (Figure 2f) although the seasonal variability in biomass observed at higher latitudes may disrupt this trend (Duarte, 1989; Duarte and Chiscano, 1999; Olesen et al., 2015).

On the other hand, high temperatures increase the rates of organic matter remineralization in seagrass soils (Pedersen et al., 2011) which could lead to lower C_{org} burial efficiency in tropical meadows compared to temperate ones. Yet, a recent study conducted in terrestrial soils suggests that across a latitudinal gradient, variation in the composition and total biomass of the microbial community is a more important determinant in the rate of remineralization of sedimentary organic matter than differences in temperature (Bradford et al., 2017).

To date, only two studies have addressed the effect of climatic regions in C_{org} storage in seagrass soils (Table SI1). Lavery et al., (2013) did not find any significant variation of soil C_{org} stocks in 17 tropical vs. temperate Australian seagrass meadows, whereas Miyajima et al., (2015) found higher soil C_{org} stocks in temperate meadows compared to tropical and subtropical meadows from East and Southeast Asia. As both of those studies encompassed a broad range of seagrass meadows, including different species and habitats, it is likely that the effect of temperature may have been confounded by other habitat factors acting at a smaller scale.

Future drivers of seagrass habitat: climate change and human pressure

Seagrass habitats are expected to vary in the near future due to climate change and increasing human pressures in coastal areas (Duarte, 2002). Among climate change consequences, we consider sea level rise, ocean acidification and increasing temperature (including extreme heat events) as the most relevant for C_{org} sequestration in seagrass meadows.

Sea level rise will lead to an increase in water depth and a subsequent reduction

in submarine irradiance, not only due to increasing water depths but also due to potential increase in suspended sediments arising from coastal erosion, at least in the short-term. This will likely lead to the reduction of seagrass net primary production and seagrass C_{org} sequestration in deeper waters, possibly compensated by potential expansion of the meadow upslope on the landward edge (Saunders et al., 2013). Sea level rise might, in contrast, enhance C_{org} sequestration by intertidal seagrass meadows in some regions where the increase in low tide is expected to be higher than in high tide as the emersion and desiccation periods will be shortened (Short and Neckles, 1999).

The global increase in sea temperature is likely to lead to changes in seagrass species distribution and metabolic and dynamic features (e.g. phenology, annual mean biomass, productivity, or turnover rates) (Clausen et al., 2014; Hyndes et al., 2016). Specifically, warming of temperate regions could lead to a reduction of seagrass biomass and productivity and an increase in turnover rates (Duarte, 1989; Duarte and Chiscano, 1999; Clausen et al., 2014; Olesen et al., 2015), with the subsequent reduction in net autochthonous C_{org} sequestration. However, ocean warming could enhance seagrass meadows expansions towards northern latitudes, such as the Arctic region, as has been suggested for eelgrass species, leading to new seagrass-based Blue Carbon ecosystems (Krause-Jensen and Duarte, 2014). Yet, seagrass expansion to the Arctic region may be limited by propagule supply, as dispersal through seeds is constrained by failure to complete the reproductive cycle in northernmost populations under the present low temperatures (Krause-Jensen and Duarte, 2014).

On the other hand, episodic high temperature anomalies have been shown to result in extensive death of temperate/sub-tropical seagrass meadows (Díaz-Almela et al., 2009; Marbà and Duarte, 2010; Fraser et al., 2014). In addition, the success of sexual reproduction in seagrass meadows, that enhances their resilience against environmental changes, shows contradictory responses to heat waves: whereas flowering seems to be enhanced (Díaz-Almela et al., 2007; Ruiz et al., 2017), seed survival has been found to be negatively affected (Thomson et al., 2014). In addition, increasing temperature is expected to enhance the activity of seagrass soil microbial communities that would lead to higher C_{org} remineralization rates in seagrass soils (Pedersen et al., 2011) and to a lower C_{org} sequestration efficiency.

Ocean acidification could potentially increase the sequestration of autochthonous C_{org} , as suggested by recent studies that report an increase in above- and below-ground biomass under acidified conditions (Palacios and Zimmerman, 2007;

Hall-Spencer et al., 2008; Fabricius et al., 2011; Russell et al., 2013). However, the only available study that assessed the effect of acidification on seagrass soil C_{org} deposits reported a significant negative effect (Martínez-Crego et al., 2014).

Finally, the increase in human pressure in coastal areas, particularly during the last century (Duarte, 2014), is leading to an increase of nutrient and terrestrial sediments loading into coastal waters, causing detrimental effects in seagrass meadows and associated C_{org} deposits (Orth et al., 2006; Ralph et al., 2006; Macreadie et al., 2012). Eutrophication and increased turbidity threaten seagrass meadows survival (Nixon, 1995; Short and Wyllie-Echeverria, 1996; Waycott et al., 2009) and favor the accumulation of allochthonous C_{org} (e.g. microalgae-derived C_{org}) into the soil deposits, as reported in recent studies (Macreadie et al., 2012; Serrano et al., 2016c; Mazarrasa et al., 2017b; Samper-Villareal et al., 2018). Although the enhanced accumulation of allochthonous C_{org} may lead to an increase in the total C_{org} sequestration in seagrass meadows under high human pressure (Serrano et al. 2016c; Mazarrasa et al. 2017b; Samper-Villareal et al., 2018), it may also lead to the weakening of the soil deposits due to its higher lability and vulnerability to remineralization compared to seagrass-derived C_{org} (Enriquez et al., 1993; Macreadie et al., 2012). In addition, enhanced nutrient supply may trigger soil microbial activity leading to the acceleration of C_{org} remineralization rates (Macreadie et al., 2017). Finally, the increase in human pressure in coastal areas is also leading to seagrass habitat fragmentation (Montefalcone et al., 2010), that negatively affects C_{org} sequestration and storage in seagrass soils (Oreska et al., 2017; Ricart et al., 2017).

Thus, it is apparent that climate change and increased human pressure in coastal areas generally threaten the role of seagrasses as long-term carbon sinks. The effect of ocean acidification is still to be clarified.

4. Key habitat characteristics enhancing C_{org} sequestration in seagrass meadows and future research.

The analysis conducted in the previous sections demonstrates that not all seagrass meadows have the same potential for long-term C_{org} sequestration and storage and that habitat characteristics strongly influence this function. It is also apparent that the accumulation of autochthonous C_{org} (i.e. derived from seagrass biomass) and the input of allochthonous C_{org} usually show different responses to habitat settings, particularly to abiotic factors. For instance, turbidity leads to lower biomass

productivity and accumulation but enhances allochthonous C_{org} accumulation. The largest C_{org} deposits (particularly of autochthonous C_{org}) usually occur in continuous meadows formed by large and persistent species with complex canopies and when located in sheltered, shallow, low energy and clear environments with low/mid nutrient inputs (Figures 1 and 2). However, large C_{org} deposits formed, mainly, by allochthonous C_{org} , can also be found in meadows formed by small and colonizer species, located in sheltered and depositional bays where the soil mud content will be a good proxy of the soil C_{org} deposits (Serrano et al., 2016c). Habitats where trophic webs have been disturbed and where there is a lack of top-down control may show lower C_{org} deposits and sequestration rates due to overgrazing or an excessive bioturbation (Atwood et al., 2015; Macreadie et al., 2017) (Figure 1d). Finally, meadows under high and increasing human pressure are likely to experience a decline in their capacity to sequester and store C_{org} in the long-term due to habitat fragmentation, eutrophication and the weakening of the soil C_{org} deposits (Montefalcone et al., 2010; Macreadie et al., 2012; Macreadie et al., 2017; Ricart et al., 2017).

The general conclusions presented above are based on a scarce number of studies available, particularly limited in the case of restored meadows (Table SII). In addition, few studies report C_{org} sequestration rates along with, or instead of, C_{org} stocks, which limits our ability to resolve relationships between habitat characteristics and C_{org} sequestration in seagrass meadows. C_{org} stocks provide information on the magnitude of the sedimentary deposits and potentially avoided GHG emissions following meadow disturbances but they do not necessarily indicate the current state of a carbon sink (i.e. if it is being sequestered or released; Macreadie et al., 2014). Thus, further research is needed in order to better understand the effect that the variability in habitat settings have in the capacity of seagrass meadows to act as carbon sinks. Research efforts should be especially addressed to measure C_{org} sequestration rates under different habitat settings, considering both preserved and restored meadows, and to resolve the effect of those factors with unclear effects. We identified the variability on carbon sinks due to intertidal vs. subtidal positions, the implications of climatic region, the potential impact of ocean acidification, and the effects of nutrient enrichment as key gaps in our understanding of the habitat factors determining C_{org} sequestration (Table 1). Importantly, the interactive effects of multiple factors acting on C_{org} sequestration needs to be evaluated, a complex issue that may benefit from modelling approaches.

5. Implications for the implementation of Blue Carbon strategies.

Conservation and restoration of seagrass meadows contributes to climate change mitigation through the sequestration and preservation of Blue Carbon. Conversely, Blue Carbon may be used by managers as a tool to enhance seagrass conservation and restoration. This could be achieved by obtaining financial support (e.g. carbon credits, Emmer et al., 2015), by promoting the consideration of seagrass meadows within national GHG accounting schemes and reduction targets (Herr et al., 2017) or as an additional value to be considered, along with other ecosystem services and biodiversity targets, when planning the creation of marine protected areas or when selecting cost-effective areas for seagrass restoration projects (Adame et al., 2015; Howard et al., 2017).

Through the analysis conducted in the previous sections, we identify certain aspects that should be taken into account when developing and implementing efficient climate change mitigation strategies based on seagrass meadows: the large heterogeneity of C_{org} deposits and sequestration rates across habitats and the need to use site-specific C_{org} storage values; the different responses of autochthonous and allochthonous C_{org} to habitat factors; and how climate change and human pressure potentially affect C_{org} sequestration in seagrass soils.

The use of site specific values of C_{org} storage instead of values from the literature should be encouraged whenever possible (IPCC, 2013; Emmer et al., 2015). Using values derived for specific sites or derived from comparable habitats elsewhere will reduce the likelihood of over- or under-estimations of C_{org} stocks and sequestration rates, as has been recently suggested (Oreska et al., 2017).

The different responses of the autochthonous and allochthonous C_{org} pools to habitat characteristics identified in this study needs to be considered, as it has important implications for the efficiency of climate change mitigation strategies. Due to its higher lability, high levels of allochthonous C_{org} accumulation may compromise the stability of the sedimentary C_{org} deposits in the long-term. Thus, habitat settings that favor the accumulation of autochthonous C_{org} rather than allochthonous C_{org} are expected to lead to stable C_{org} deposits. In contrast, meadows where the accumulation of allochthonous C_{org} is high will lead to the formation of more vulnerable carbon sinks that, in the case of meadow degradation, have a higher potential to be remineralized and released as CO_2 to the atmosphere. In addition, allochthonous enriched C_{org} soil stocks are often found

in meadows under a high level of anthropogenic and urban pressure (Mazarrasa et al. 2017b). These meadows are threatened by different impacts caused by human activities (e.g. dredging, eutrophication), increasing the risk of meadow degradation and CO₂ emissions from the remineralization of the sedimentary C_{org} deposits. The allochthonous C_{org} pool is currently not considered under the available C_{org} accounting scheme for seagrass restoration projects (Verified Carbon Standard, Emmer et al., 2015) due to the risk of double accounting. Yet, due to its significant contribution to some seagrass soils and its vulnerability to remineralization, we consider it critical that the allochthonous C_{org} pool is incorporated in future carbon accounting schemes to avoid the risk of neglecting the protection of large C_{org} soil deposits particularly vulnerable to remineralization.

Finally, the effect that human pressure and climate change may have in the C_{org} sequestration of seagrass meadows should also be taken into account when designing the implementation of Blue Carbon strategies. Managing direct, local human impacts may provide significant opportunities for buffering the effects of those factors that threaten C_{org} sequestration in seagrass meadows and for increasing and preserving their C_{org} sequestration capacity in the future. For instance, reducing nutrient loading to coastal waters (Saunders et al., 2013; Macreadie et al., 2017) or regulating activities that lead to habitat fragmentation (e.g. dredging, boat anchoring) or to the extinction of top-predators (i.e. overfishing; Atwood et al., 2015) will help to maintain C_{org} sequestration and long-term storage by seagrass meadows. Sea-level rise could be buffered by limiting the impacts of coastal urbanization and by restoring natural wetlands, allowing seagrass to expand upslope along the landward edge (Macreadie et al., 2017). However, the effect of other climate change consequences, such as ocean acidification and increasing temperature on the C_{org} sequestration capacity of seagrass meadows are less clear and more difficult to manage locally but should, at least, be recognized when planning the implementation of Blue Carbon strategies (UNEP, CIFOR, 2014).

In this review we have focused on the relative capacity of different seagrass habitats to sequester C_{org} in the long-term. Managers or proponents of Blue Carbon projects should take these differences among habitats into account but they should not be the sole criteria considered as carbon sequestration and storage is only one of the many ecosystems services which managers should seek to conserve. Habitats with lower C_{org} sequestration and storage capacity may be valued for a range of other ecosystem services and although Blue Carbon may be lower compared to other seagrass

habitats, it may strengthen the argument for their conservation and provide a means of partially funding conservation measures (Adame et al., 2015; Howard et al., 2017).

Conclusions.

Through the review of the most recent literature on seagrass Blue Carbon research we have identified the habitat settings that are likely to enhance or reduce the C_{org} sequestration capacity in seagrass meadows, those that may threaten this function and the gaps of knowledge that need to be addressed. The findings of this review may provide guidance to managers aiming to support seagrass conservation and restoration, to policy makers willing to enhance the implementation of efficient Blue Carbon strategies and to the scientific community aiming to resolve uncertainties on the habitat characteristics that govern the carbon sequestration capacity of seagrass meadows.

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References:

- Adame, M.F., Hermoso, V., Perhans, K., Lovelock, C.E., Herrera-Silveira, J.A., 2015. Selecting cost-effective areas for restoration of ecosystem services. *Conserv. Biol.* 29, 493–502. <https://doi.org/10.1111/cobi.12391>
- Agawin, N.S.R., Duarte, C.M., Fortes, M.D., 1996. Nutrient limitation of Philippine seagrasses (Cape Bolinao, NW Philippines): In situ experimental evidence. *Mar. Ecol. Prog. Ser.* 138, 233–243. <https://doi.org/10.3354/meps138233>
- Alcoverro, T., Cerbian, E., Ballesteros, E., 2001. The photosynthetic capacity of the seagrass *Posidonia oceanica*: influence of nitrogen and light. *J. Exp. Mar. Bio. Ecol.* 261, 107–120.
- Armitage, A.R., Fourqurean, J.W., 2016. Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences* 13, 313–321. <https://doi.org/10.5194/bgd-12-16285-2015>
- Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., Fourqurean, J.W., Macreadie, P.I., 2015. Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Chang.* 5, 1038–1045. <https://doi.org/10.1038/NCLIMATE2763>
- Banta, G.T., Holmer, M., Jensen, M.H., Kristensen, E., 1999. Effects of two polychaete worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in a sandy marine sediment. *Aquat. Microb. Ecol.* 19, 189–204. <https://doi.org/10.3354/ame019189>
- Banta, G.T., Pedersen, M.F., Nielsen, S.L., 2004. Decomposition of marine primary producers: consequences for nutrient recycling and retention in coastal ecosystems.

- In: Nielsen, S.L., Banta, G.T., Pedersen, M.F. (Eds.), *Estuarine Nutrient Cycling: The Influence of Primary Producers*. Kluwer Academic Publisher, Dordrecht, Netherlands, pp. 187–216.
- Barber, T.R., Carlson, P.R., 1993. Effects of seagrass die-off on benthic fluxes and porewater concentrations of ΣCO_2 , $\Sigma\text{H}_2\text{S}$, and CH_4 in Florida Bay sediments. In: Oremland, R.S. (Ed.), *Biogeochemistry of Global Change*. Springer, Boston, MA, pp. 530–550. https://doi.org/10.1007/978-1-4615-2812-8_29
- Bertics, V.J., Zierbis, W., 2010. Bioturbation and the role of microniches for sulfate reduction in coastal marine sediments. *Environ. Microbiol.* 12, 3022–3034.
- Borowitzka, M.A., Lavery, P.S., van Keulen, M., 2006. Epiphytes of seagrasses. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Netherlands, pp. 441–461.
- Bos, A.R., Bouma, T.J., de Kort, G.L.J., van Katwijk, M.M., 2007. Ecosystem engineering by annual intertidal seagrass beds: Sediment accretion and modification. *Estuar. Coast. Shelf Sci.* 74, 344–348. <https://doi.org/10.1016/j.ecss.2007.04.006>
- Boström, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. *Estuar. Coast. Shelf Sci.* 68, 383–403. <https://doi.org/10.1016/j.ecss.2006.01.026>
- Bradford, M.A., Veen, G.F.C., Bonis, A., Bradford, E.M., Classen, A.T., Cornelissen, J.H.C., Crowther, T.W., de Long, J.R., Freschet, G.T., Kardol, P., Manrubia-Freixa, M., Maynard, D.S., Newman, G.S., Logtestijn, R.S.P., Viketoft, M., Wardle, D.A., Wieder, W.R., Wood, S.A., van der Putten, W.H., 2017. A test of the hierarchical model of litter decomposition. *Nat. Ecol. Evol.* 1, 1836–1845. <https://doi.org/10.1038/s41559-017-0367-4>
- Burdige, D.J., 2007. Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chem. Rev.* 107, 467–485. <https://doi.org/10.1021/cr050347q>
- Cabaço, S., Ferreira, Ó., Santos, R., 2010. Population dynamics of the seagrass *Cymodocea nodosa* in Ria Formosa lagoon following inlet artificial relocation. *Estuar. Coast. Shelf Sci.* 87, 510–516. <https://doi.org/10.1016/j.ecss.2010.02.002>
- Carlson, P.R.J., Yarbro, L.A., Barber, T.R., 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bull. Mar. Sci.* 54, 733–746.
- Carruthers, T.J.B., Dennison, W.C., Kendrick, G.A., Waycott, M., 2007. Seagrasses of south – west Australia : A conceptual synthesis of the world’s most diverse and extensive seagrass meadows. *J. Exp. Mar. Bio. Ecol.* 350, 21–45. <https://doi.org/10.1016/j.jembe.2007.05.036>
- Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochem. Cycles* 17(4), 1111, doi:10.1029/2002GB001917
- Clausen, K.K., Krause-jensen, D., Olesen, B., Marbà, N., 2014. Seasonality of eelgrass biomass across gradients in temperature and latitude. *Mar. Ecol. Prog. Ser.* 506, 71–85. <https://doi.org/10.3354/meps10800>
- Clavier, J., Chauvaud, L., Carlier, A., Amice, E., Van der Geest, M., Labrosse, P., Diagne, A., Hily, C., 2011. Aerial and underwater carbon metabolism of a *Zostera noltii* seagrass bed in the Banc d’Arguin, Mauritania. *Aquat. Bot.* 95, 24–30. <https://doi.org/10.1016/j.aquabot.2011.03.005>
- Collier, C.J., Lavery, P.S., Masini, R.J., Ralph, P.J., 2007. Morphological , growth and meadow characteristics of the seagrass *Posidonia sinuosa* along a depth- related gradient of light availability. *Mar. Ecol. Prog. Ser.* 337, 103–115.

- Collier, C.J., Lavery, P.S., Ralph, P.J., Masini, R.J., 2009. Shade-induced response and recovery of the seagrass *Posidonia sinuosa*. *J. Exp. Mar. Bio. Ecol.* 370, 89–103. <https://doi.org/10.1016/j.jembe.2008.12.003>
- Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Coverdale, T.C., Brisson, C.P., Young, E.W., Yin, S.F., Donnelly, J.P., Bertness, M.D., 2014. Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. *PLoS ONE* 9(3): e93296. <https://doi.org/10.1371/journal.pone.0093296>
- Dahl, M., Deyanova, D., Gütschow, S., Asplund, M.E., Lyimo, L.D., Karamfilov, V., Santos, R., Björk, M., Gullström, M., 2016a. Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: a comparison of four European areas. *PLoS ONE* 11 (12): e0167493. <https://doi.org/10.1371/journal.pone.0167493>
- Dahl, M., Deyanova, D., Lyimo, L.D., Näslund, J., Samuelsson, G.S., Mtolera, M.S.P., Björk, M., Gullström, M., 2016b. Effects of shading and simulated grazing on carbon sequestration in a tropical seagrass meadow. *J. Ecol.* 104, 654–664. <https://doi.org/10.1111/1365-2745.12564>
- Den Hartog, C., 1977. Structure, function and classification in seagrass communities. In: McRoy, P., Helfferich, C. (Eds.), *Seagrass Ecosystem: A Scientific Perspective*. Marine Science 4. Marcel Dekkar, Inc., New York, pp. 90–121.
- Díaz-Almela, E., Marbà, N., Duarte, C.M., 2007. Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. *Global Change Biol.* 13, 224–235. <https://doi.org/10.1111/j.1365-2486.2006.01260.x>
- Díaz-Almela, E., Marbà, N., Martínez, R., Santiago, R., Duarte, C.M., 2009. Seasonal dynamics of *Posidonia oceanica* in Magalluf Bay (Mallorca, Spain): Temperature effects on seagrass mortality. *Limnol. Oceanogr.* 54, 2170–2182. <https://doi.org/10.4319/lo.2009.54.6.2170>
- Duarte, C.M., 2017. Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences* 14, 301–310. <https://doi.org/10.5194/bg-14-301-2017>
- Duarte, C.M., 2014. Global change and the future ocean: A grand challenge for marine sciences. *Front. Mar. Sci.* 1, 1–16. <https://doi.org/10.3389/fmars.2014.00063>
- Duarte, C.M., 2002. The future of seagrass meadows. *Environ. Conserv.* 29, 192–206.
- Duarte, C.M., 1991a. Seagrass depth limits. *Aquat. Bot.* 40, 363–377.
- Duarte, C.M., 1991b. Allometric scaling of seagrass form and productivity. *Mar. Ecol. Prog. Ser.* 77, 289–300. <https://doi.org/10.3354/meps077289>
- Duarte, C.M., 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. *Mar. Ecol. Prog. Ser.* 51, 269–276. <https://doi.org/10.3354/meps051269>
- Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: A reassessment. *Aquat. Bot.* 65, 159–174.
- Duarte, C.M., Middelburg, J.J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1–8. <https://doi.org/10.5194/bg-2-1-2005>
- Eklöf, J.S.S., de la Torre-Castro, M., Gullström, M., Uku, J., Muthiga, N., Lyimo, T., Bandeira, S. O., 2008. Sea urchin overgrazing of seagrasses: A review of current

- knowledge on causes, consequences, and management. *Estuar. Coast. Shelf Sci.* 79, 569–580. <https://doi.org/10.1016/j.ecss.2008.05.005>
- Emmer, I., Needelman, B., Emmett-Mattox, S., Crooks, S., Megonigal, P., Myers, D., Oreska, M., McGlathery, K., Shoch, D., 2015. VM0033 Methodology for tidal wetland and seagrass restoration. VCS Verified Carbon Standard.
- Enriquez, S., Duarte, C., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* 94, 457–471. <https://doi.org/10.1007/BF00566960>
- Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S., Lough, J.M., 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat. Clim. Chang.* 1, 165–169. <https://doi.org/10.1038/NCLIMATE1122>
- Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar. Ecol. Prog. Ser.* 171, 109–121.
- Fonseca, M.S., Cahalan, J.A., 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuar. Coast. Shelf Sci.* 35, 565–576.
- Fonseca, M.S., Fisher, J.S., 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Mar. Ecol. Prog. Ser.* 29, 15–22. <https://doi.org/10.3354/meps029015>
- Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., Apostolaki, E.T., Kendrick, G.A., Krause-Jensen, D., McGlathery, K.J., Serrano, O., 2012. Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* 5, 505–509. <https://doi.org/10.1038/ngeo1477>
- Fourqurean, J.W., Schrlau, J.E., 2003. Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. *Chem. Ecol.* 19, 373–390. <https://doi.org/10.1080/02757540310001609370>
- Fourqurean, J.W., Zieman, J.C., 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* 37, 162–171. <https://doi.org/10.4319/lo.1992.37.1.0162>
- Fraser, M.W., Kendrick, G.A., Statton, J., Hovey, R.K., Zavala-Perez, A., Walker, D.I., 2014. Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. *J. Ecol.* 102, 1528–1536. <https://doi.org/10.1111/1365-2745.12300>
- Gacia, E., Duarte, C.M., Middelburg, J.J., 2002. Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnol. Oceanogr.* 47, 23–32. <https://doi.org/10.4319/lo.2002.47.1.0023>
- Gallegos, C.L., Correll, D.L., Pierce, J.W., 1990. Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. *Limnol. Oceanogr.* 35, 1486–1502. <https://doi.org/10.4319/lo.1990.35.7.1486>
- Gambi, M.C., Buia, M.C., Casola, E., Scardi, M., 1989. Estimates of water movement in a *Posidonia oceanica* bed: a first approach. In: Boudouresque, C.F., Meinesz, A., Fresi, E., Gravez, V. (Eds.), *Workshop on Posidonia Beds, GIS Posidonie 2*: 101–112.
- Grady, J.R., 1981. Properties of seagrass and sand flat sediments from the intertidal zone of St. Andrew Bay, Florida. *Estuaries* 4, 335–344.
- Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D., Buia, M.-C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454, 96–99.

- <https://doi.org/10.1038/nature07051>
- Harrison, P.G., 1989. Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. *Aquat. Bot.* 23, 263–288.
- Hauxwell, J., Cebrián, J., Valiela, I., 2003. Eelgrass *Zostera marina* loss in temperate estuaries: Relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Mar. Ecol. Prog. Ser.* 247, 59–73.
<https://doi.org/10.3354/meps247059>
- Heiss, W.M., Smith, A.M., Probert, P.K., 2000. Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *New Zeal. J. Mar. Freshw. Res.* 34, 689–694.
<https://doi.org/10.1080/00288330.2000.9516970>
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, UK.
- Hendriks, I.E., Sintes, T., Bouma, T.J., Duarte, C.M., 2008. Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Mar. Ecol. Prog. Ser.* 356, 163–173.
<https://doi.org/10.3354/meps07316>
- Herr, D., Agardy, T., Benzaken, D., Hicks, F., Howard, J., Landis, E., Soles, A., Vegh, T., 2015. Coastal “blue” carbon. A revised guide to supporting coastal wetland programs and projects using climate finance and other financial mechanisms. IUCN, Gland, Switzerland.
- Herr, D., Landis, E., 2016. Coastal blue carbon ecosystems. Opportunities for Nationally Determined Contributions. Policy Brief. IUCN, Gland, Switzerland.
- Herr, D., Unger, M. Von, Laffoley, D., Mcgovern, A., 2017. Pathways for implementation of blue carbon initiatives 27, 116–129.
<https://doi.org/10.1002/aqc.2793>
- Howard, J., Fox, M., Mcleod, E., Thomas, S., Wenzel, L., Pidgeon, E., 2017. The potential to integrate blue carbon into MPA design and management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 27, 100–115. <https://doi.org/10.1002/aqc.2809>
- Howard, J.L., Perez, A., Lopes, C.C., Fourqurean, J.W., 2016. Fertilization changes seagrass community structure but not blue carbon storage: results from a 30-year field experiment. *Estuaries and Coasts*. <https://doi.org/10.1007/s12237-016-0085-1>
- Hyndes, G.A., Heck, K.L., Vergés, A., Harvey, E.S., Kendrick, G.A., Lavery, P.S., McMahan, K., Orth, R.J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S., Wilson, S., 2016. Accelerating tropicalization and the transformation of temperate seagrass meadows. *Bioscience* 66, 938–945. <https://doi.org/10.1093/biosci/biw111>
- IPCC, 2013. 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands methodological guidance on lands with wet and drained soils, and constructed wetlands for wastewater treatment task force on national greenhouse gas inventories, in: Hiraiishi, T., Krug, T., Tanabe, K., Srivastava, N., Jamsranjav, B., Fukuda, M., Troxler, T. (Eds.), . IPCC, Switzerland.
- Jackson, E.L., Attrill, M.J., Rowden, A.A., Jones, M.B., 2006. Seagrass complexity hierarchies: Influence on fish groups around the coast of Jersey (English Channel). *J. Exp. Mar. Bio. Ecol.* 330, 38–54. <https://doi.org/10.1016/j.jembe.2005.12.016>
- Kell, R.G., Montluçon, D.B., Prahl, F.G., Hedges, J.I., 1994. Sorptive preservation of labile organic matter in marine sediments. *Nature* 370, 549–552.
- Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbà, N., Middelburg, J.J., 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochem. Cycles* 24, n/a-n/a.
<https://doi.org/10.1029/2010GB003848>

- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G.A., Scanes, P., McKenzie, L., O'Brien, K.R., Lyons, M., Ferguson, A., Maxwell, P., Glasby, T., Udy, J., 2015. Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Sci. Total Environ.* 534, 97–109. <https://doi.org/10.1016/j.scitotenv.2015.04.061>
- Kirstensen, E., 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426, 1–24.
- Klap, V.A., Hemminga, M.A., Boon, J.J., 2000. Retention of lignin in seagrasses: angiosperms that returned to the sea. *Mar. Ecol. Prog. Ser.* 194, 1–11.
- Koch, E.M., Ackerman, J.D., Verduin, J., van Keulen, M., 2006. Fluid dynamics in seagrass ecology- from molecules to ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Dordrecht, Netherlands, pp. 193–225.
- Koch, E.W., Sanford, L.P., Chen, S.-N., Shafer, D.J., Smith, J.M., 2006. Waves in seagrass systems: review and technical recommendations. System-Wide Water Resources Research Program and Submerged Aquatic Vegetation Restoration Research Program. US Army Corps of Engineers. ERDC TR-06-15.
- Krause-Jensen, D., Duarte, C.M., 2014. Expansion of vegetated coastal ecosystems in the future Arctic. *Front. Mar. Sci.* 1, 1–10. <https://doi.org/10.3389/fmars.2014.00077>
- Laffoley, D., Grimsditch, G., 2009. The management of natural coastal carbon sinks. IUCN, Gland, Switzerland.
- Lavery, P.S., Mateo, M.Á., Serrano, O., Rozaimi, M., 2013. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS ONE* 8(9): e73748. <https://doi.org/10.1371/journal.pone.0073748>
- Lavery, P.S., McMahon, K., Mulligan, M., Tennyson, A., 2009. Interactive effects of timing, intensity and duration of experimental shading on *Amphibolis griffithii*. *Mar. Ecol. Prog. Ser.* 394, 21–33. <https://doi.org/10.3354/meps08242>
- Lavery, P.S., Vanderklift, M.A., 2002. A comparison of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrasses *Amphibolis griffithii* and *Posidonia coriacea*. *Mar. Ecol. Prog. Ser.* 236, 99–112. <https://doi.org/10.3354/meps236099>
- Lee, K., Dunton, K.H., 2000. Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass. *Mar. Ecol. Prog. Ser.* 196, 39–48. <https://doi.org/10.3354/meps196039>
- Lee, K.S., Park, S.R., Kim, Y.K., 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *J. Exp. Mar. Bio. Ecol.* 350, 144–175. <https://doi.org/10.1016/j.jembe.2007.06.016>
- Leuschner, C., Landwehr, S., Mehlig, U., 1998. Limitation of carbon assimilation of intertidal *Zostera noltii* and *Z. marina* by desiccation at low tide. *Aquat. Bot.* 62, 171–176.
- Leuschner, C., Rees, U., 1993. CO₂ gas exchange of two intertidal seagrass species, *Zostera marina* L. and *Zostera noltii* Hornem., during emersion. *Aquat. Bot.* 45, 53–62. [https://doi.org/10.1016/0304-3770\(93\)90052-X](https://doi.org/10.1016/0304-3770(93)90052-X)
- Lokko, K., Kotta, J., Orav-Kotta, H., Nurkse, K., Pärnoja, M., 2015. Introduction of a functionally novel consumer to a low diversity system: Effects of the mud crab *Rhithropanopeus harrisi* on meiobenthos. *Estuar. Coast. Shelf Sci.* 1–8. <https://doi.org/10.1016/j.ecss.2015.11.017>

- Lovelock, C., Atwood, T., Baldock, J., Duarte, C., Hickey, S., Lavery, P., Masque, P., Macreadie, P., Ricart, A., Serrano, O., Steven, A., 2017. Assessing the risk of CO₂ emissions from blue carbon ecosystems. *Front. Mar. Sci.* In Press. <https://doi.org/10.1002/fee.1491>
- Macreadie, P.I., Allen, K., Kelaher, B.P., Ralph, P.J., Skilbeck, C.G., 2012. Paleoreconstruction of estuarine sediments reveal human-induced weakening of coastal carbon sinks. *Global Change Biol.* 18, 891–901. <https://doi.org/10.1111/j.1365-2486.2011.02582.x>
- Macreadie, P.I., Baird, M.E., Trevathan-Tackett, S.M., Larkum, A.W., Ralph, P.J., 2014. Quantifying and modelling the carbon sequestration capacity of seagrass meadows - A critical assessment. *Mar. Pollut. Bull.* 83, 430–9. <https://doi.org/10.1016/j.marpolbul.2013.07.038>
- Macreadie, P.I., Nielsen, D.A., Kelleway, J.J., Atwood, T.B., Seymour, J.R., Petrou, K., Connolly, R.M., Thomson, A.C.G., Trevathan-Tackett, S.M., Ralph, P.J., 2017. Can we manage coastal ecosystems to sequester more blue carbon? *Front. Ecol. Environ.* 15, 206–213. <https://doi.org/10.1002/fee.1484>
- Marbà, N., Díaz-Almela, E., Duarte, C.M., 2014. Mediterranean seagrass (*Posidonia oceanica*) loss between 1842 and 2009. *Biol. Conserv.* 176, 183–190. <https://doi.org/10.1016/j.biocon.2014.05.024>
- Marbà, N., Duarte, C.M., 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global Change Biol.* 16, 2366–2375. <https://doi.org/10.1111/j.1365-2486.2009.02130.x>
- Martinetto, P., Montemayor, D.I., Alberti, J., Costa, C.S.B., Iribarne, O., 2016. Crab bioturbation and herbivory may account for variability in carbon sequestration and stocks in South West Atlantic salt marshes. *Front. Mar. Sci.* 3, 1–12. <https://doi.org/10.3389/fmars.2016.00122>
- Martínez-Crego, B., Olivé, I., Santos, R., 2014. CO₂ and nutrient-driven changes across multiple levels of organization in *Zostera noltii* ecosystems. *Biogeosciences* 11, 7237–7249. <https://doi.org/10.5194/bg-11-7237-2014>
- Mateo, M.A., Cebrián, J., Dunton, K., Mutchler, T., 2006. Carbon flux in seagrass ecosystems. In: Larkum, A., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Netherlands, pp. 159–192. https://doi.org/10.1007/1-4020-2983-7_7
- Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: elements for an ecosystem carbon and nutrient budget. *Mar. Ecol. Prog. Ser.* 151, 43–53.
- Mayer, L.M., 1994. Relationship between mineral surfaces and organic carbon concentrations in soils and sediments. *Chem. Geol.* 114, 347–363.
- Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., Duarte, C.M., 2017a. Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of *Posidonia oceanica* meadows. *Limnol. Oceanogr.* 62, 1436–1450. <https://doi.org/10.1002/lno.10510>
- Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., Duarte, C.M., 2017b. Dynamics of carbon sources supporting burial in seagrass sediments under increasing anthropogenic pressure. *Limnol. Oceanogr.* 62, 1451–1465. <https://doi.org/10.1002/lno.10509>
- McGlathery, K.J., Sundbäck, K., Anderson, I.C., 2007. Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Mar. Ecol. Prog. Ser.* 348, 1–18. <https://doi.org/10.3354/meps07132>
- Mellors, J., Marsh, H., Carruthers, T.J.B., Waycott, M., 2002. Testing the sediment-

- trapping paradigm of seagrass: Do seagrass influence nutrient status and sediment structure in tropical intertidal environments? *Bull. Mar. Sci.* 71, 1215–1226.
- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Adachi, H., Yamano, H., Nakaoka, M., 2015. Geographical variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Global Biogeochem. Cycles* 29, 397–415.
- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Yoshida, G., 2017. Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnol. Oceanogr.* 62, 954–972. <https://doi.org/10.1002/lno.10478>
- Montefalcone, M., Parravicini, V., Vacchi, M., Albertelli, G., Ferrari, M., Morri, C., Bianchi, C.N., 2010. Human influence on seagrass habitat fragmentation in NW Mediterranean Sea. *Estuar. Coast. Shelf Sci.* 86, 292–298. <https://doi.org/10.1016/j.ecss.2009.11.018>
- Murphey, P.L., Fonseca, M.S., 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. *Mar. Ecol. Prog. Ser.* 121, 91–98.
- Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., De Young, C., Fonseca, L., Grimsditch, G., 2009. Blue carbon. The role of healthy oceans in binding carbon. Birkeland Trykkeri AS, Norway.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41, 199–219.
- Nordlund, L.M., Jackson, E.L., Nakaoka, M., Samper-Villarreal, J., Beca-Carretero, P., Creed, J.C., 2017. Seagrass ecosystem services – What’s next? *Mar. Pollut. Bull.* 0–1. <https://doi.org/10.1016/j.marpolbul.2017.09.014>
- Olesen, B., Krause-Jensen, D., Marbà, N., Christensen, P.B., 2015. Eelgrass *Zostera marina* in subarctic Greenland : dense meadows with slow biomass turnover in cold waters. *Mar. Ecol. Prog. Ser.* 518, 107–121. <https://doi.org/10.3354/meps11087>
- Ondiviela, B., Losada, I.J., Lara, J.L., Maza, M., Galván, C., Bouma, T.J., Belzen, J. Van, 2014. The role of seagrass in coastal protection in a changing climate. *Coast. Eng.* 87, 158–168.
- Oreska, M.P.J., McGlathery, K.J., Porter, J.H., 2017. Seagrass blue carbon spatial patterns at the meadow-scale. *PLoS ONE* 12(4): e0176630. <https://doi.org/10.1371/journal.pone.0176630>
- Orth, R., Heck, J.K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationship. *Estuaries* 7, 339–350.
- Orth, R.J., Carruthers, T.I.M.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Jr, K.L.H., Hughes, A.R., Kendrick, A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., Kendrick, G.A., 2006. A global crisis for seagrass ecosystems. *Bioscience* 56, 987–996.
- Palacios, S.L., Zimmerman, R.C., 2007. Response of eelgrass *Zostera marina* to CO₂ enrichment: Possible impacts of climate change and potential for remediation of coastal habitats. *Mar. Ecol. Prog. Ser.* 344, 1–13. <https://doi.org/10.3354/meps07084>
- Pedersen, M.Ø., Serrano, O., Mateo, M.Á., Holmer, M., 2011. Temperature effects on decomposition of a *Posidonia oceanica* mat. *Aquat. Microb. Ecol.* 65, 169–182. <https://doi.org/10.3354/ame01543>
- Peralta, G., Bouma, T.J., van Soelen, J., Perez-Llorens, J.L., Hernandez, I., 2003. On the

- use of sediment fertilisation for seagrass restoration: a mesocosm study on *Zostera marina* L. *Aquat. Bot.* 75, 95–110.
- Peralta, G., Van Duren, L.A., Morris, E.P., Bouma, T.J., 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: A hydrodynamic flume study. *Mar. Ecol. Prog. Ser.* 368, 103–115. <https://doi.org/10.3354/meps07574>
- Pérez-Lloréns, L.J., Niell, X.F., 1993. Temperature and emergence effects on the net photosynthesis of two *Zostera noltii* Hornem. morphotypes. *Hydrobiologia* 254, 53–64.
- Perez, M., Romero, J., Duarte, C.M., Sand-Jensen, K., 1991. Phosphorus limitation of *Cymodocea nodosa* growth. *Mar. Biol.* 109, 129–133. <https://doi.org/10.1007/BF01320239>
- Perry, C.T., Beavington-Penney, S.J., 2005. Epiphytic calcium carbonate production and facies development within sub-tropical seagrass beds, Inhaca Island, Mozambique. *Sediment. Geol.* 174, 161–176. <https://doi.org/10.1016/j.sedgeo.2004.12.003>
- Peterson, C.H., Jr, R.A.L., Micheli, F., Skilleter, G.A., 2004. Attenuation of water flow inside seagrass canopies of differing structure. *Mar. Ecol. Prog. Ser.* 268, 81–92.
- Preen, A., 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Mar. Ecol. Prog. Ser.* 124, 201–213.
- Ralph, P.J., Tomasko, D., Moore, K., Seddon, S., Macinnis-Ng, C.M.O., 2006. Human impacts on seagrasses: Eutrophication, sedimentation and contamination. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht, Netherlands, pp. 567–593.
- Ricart, A.M., Dalmau, A., Pérez, M., Romero, J., 2015a. Effects of landscape configuration on the exchange of materials in seagrass ecosystems. *Mar. Ecol. Prog. Ser.* 532, 89–100.
- Ricart, A.M., Pérez, M., Romero, J., 2017. Landscape configuration modulates carbon storage in seagrass sediments. *Estuar. Coast. Shelf Sci.* 185, 69–76. <https://doi.org/10.1016/j.ecss.2016.12.011>
- Ricart, A.M., York, P.H., Rasheed, M.A., Pérez, M., Romero, J., Bryant, C. V., Macreadie, P.I., 2015b. Variability of sedimentary organic carbon in patchy seagrass landscapes. *Mar. Pollut. Bull.* 100, 476–482. <https://doi.org/10.1016/j.marpolbul.2015.09.032>
- Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: A terrestrial approach to the marine subtidal environment. *Trends Ecol. Evol.* 9, 301–304. [https://doi.org/10.1016/0169-5347\(94\)90041-8](https://doi.org/10.1016/0169-5347(94)90041-8)
- Rogelj, J., Elzen, M. Den, Franssen, T., Fekete, H., Winkler, H., Schaeffer, R., Sha, F., Riahi, K., Meinshausen, M., 2016. Perspective: Paris Agreement climate proposals need boost to keep warming well below 2° C. *Nat. Clim. Chang.* 534, 631–639. <https://doi.org/10.1038/nature18307>
- Röhr, M.E., Boström, C., Canal-Vergés, P., Holmer, M., 2016. Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences* 13, 6139–6153. <https://doi.org/10.5194/bg-13-6139-2016>
- Rozaimi, M., Lavery, P.S., Serrano, O., Kyrwood, D., 2016. Long-term carbon storage and its recent loss in an estuarine *Posidonia australis* meadow (Albany, Western Australia). *Estuar. Coast. Shelf Sci.* 170, 58–65. <https://doi.org/10.1016/j.ecss.2016.01.001>
- Ruiz, J.M., Marín-Guirao, L., García-Muñoz, R., Ramos-Segura, A., Bernardeau-Esteller, J., Pérez, M., Sanmartí, N., Ontoria, Y., Romero, J., Arthur, R.,

- Alcoverro, T., Procaccini, G., 2017. Experimental evidence of warming-induced flowering in the Mediterranean seagrass *Posidonia oceanica*. *Mar. Pollut. Bull.* In press. <https://doi.org/10.1016/j.marpolbul.2017.10.037>
- Ruiz, J.M., Romero, J., 2003. Effects of disturbances caused by coastal constructions on spatial structure, growth dynamics and photosynthesis of the seagrass *Posidonia oceanica*. *Mar. Pollut. Bull.* 46, 1523–1533. <https://doi.org/10.1016/j.marpolbul.2003.08.021>
- Ruiz, J.M., Romero, J., 2001. Effects of *in situ* experimental shading on the Mediterranean seagrass *Posidonia oceanica*. *Mar. Ecol. Prog. Ser.* 215, 107–120. <https://doi.org/10.3354/meps215107>
- Russell, B.D., Connell, S.D., Uthicke, S., Muehlllehner, N., Fabricius, K.E., Hall-Spencer, J.M., 2013. Future seagrass beds: Can increased productivity lead to increased carbon storage? *Mar. Pollut. Bull.* 73, 463–469. <https://doi.org/10.1016/j.marpolbul.2013.01.031>
- Samper-Villarreal, J., 2016. Dynamics of carbon storage in subtropical seagrass meadows. PhD Dissertation. University of Queensland, Brisbane, Australia.
- Samper-Villarreal, J., Lovelock, C.E., Saunders, M.I., Roelfsema, C., Mumby, P.J., 2016. Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnol. Oceanogr.* 61, 938–952. <https://doi.org/10.1002/lno.10262>
- Samper-Villarreal, J., Mumby, P.J., Saunders, M.I., Barry, L.A., Zawadzki, A., Heijnis, H., Morelli, G. and Lovelock, C.E., 2017. Vertical accretion and carbon burial rates in subtropical seagrass meadows increased following anthropogenic pressure from European colonisation. *Estuarine, Coastal and Shelf Science.* 202: 40-53.
- Saunders, M.I., Leon, J., Phinn, S.R., Callaghan, D.P., O'Brien, K.R., Roelfsema, C.M., Lovelock, C.E., Lyons, M.B., Mumby, P.J., 2013. Coastal retreat and improved water quality mitigate losses of seagrass from sea level rise. *Global Change Biol.* 19, 2569–2583.
- Serrano, O., Lavery, P.S., Rozaimi, M., Mateo, M.A., 2014. Influence of water depth on the carbon sequestration capacity of seagrass. *Global Biogeochem. Cycles* 28, 950–961. <https://doi.org/10.1002/2014GB004872>.
- Serrano, O., Ruhon, R., Lavery, P.S., Kendrick, G.A., Hickey, S., Masqué, P., Arias-Ortiz, A., Steven, A., Duarte, C.M., 2016a. Impact of mooring activities on carbon stocks in seagrass meadows. *Scient. Rep.* 6:23193. <https://doi.org/10.1038/srep23193>.
- Serrano, O., Ricart, A.M., Lavery, P.S., Mateo, M.A., Arias-Ortiz, A., Masque, P., Steven, A., Duarte, C.M., 2016b. Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences* 13, 4581-4594. <https://doi.org/10.5194/bg-13-4581-2016>.
- Serrano, O., Lavery, P.S., Duarte, C.M., Kendrick, G.A., Calafat, A., York, P.H., Steven, A., Macreadie, P.I., 2016c. Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences* 13, 4915–4926. <https://doi.org/10.5194/bg-13-4915-2016>.
- Serrano, O., Lavery, P.S., Masqué, P., Inostroza, K., Bongiovanni, J., Duarte, C.M., 2016d. Seagrass sediments reveal the long-term deterioration of an estuarine ecosystem. *Global Change Biol.* 22, 1523–1531.
- Short, F.T., 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. *Aquat. Bot.* 27, 41–57. [https://doi.org/10.1016/0304-3770\(87\)90085-4](https://doi.org/10.1016/0304-3770(87)90085-4)

- Short, F.T., Neckles, H.A., 1999. The effects of global climate change on seagrasses. *Aquat. Bot.* 63, 169–196. [https://doi.org/10.1016/S0304-3770\(98\)00117-X](https://doi.org/10.1016/S0304-3770(98)00117-X)
- Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. *Environ. Conserv.* 23, 17–27.
- Siebert, T., Branch, G.M., 2007. Influences of biological interactions on community structure within seagrass beds and sandprawn-dominated sandflats. *J. Exp. Mar. Bio. Ecol.* 340, 11–24. <https://doi.org/10.1016/j.jembe.2006.08.007>
- Silva, J., Santos, R., Calleja, M.L., Duarte, C.M., 2005. Submerged versus air-exposed intertidal macrophyte productivity: From physiological to community-level assessments. *J. Exp. Mar. Bio. Ecol.* 317, 87–95. <https://doi.org/10.1016/j.jembe.2004.11.010>
- Smith, A.S. V., 1981. Marine macrophytes as a global carbon sink. *Science* 211, 838–840. DOI: [10.1126/science.211.4484.838](https://doi.org/10.1126/science.211.4484.838)
- Thomson, A.C.G., 2017. The role of bioturbators in seagrass blue carbon dynamics. PhD Dissertation. University of Sydney, Sydney, Australia.
- Thomson, J.A., Burkholder, Derek, A., Heithaus, M.R., Fourqurean, J.W., Fraser, M.W., Statton, J., Kendrick, G.A., 2014. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Global Change Biol.* 21, 1463–1474.
- Trevathan-Tackett, S.M., Seymour, J.R., Nielsen, D.A., Macreadie, P.I., Jeffries, T.C., Sanderman, J., Baldock, J., Howes, J.M., Steven, A.D.L., Ralph, P.J., 2017. Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. *FEMS Microbiol. Ecol.* 93(6). doi: 10.1093/femsec/fix033.
- Trumper, K., Bertzky, M., Dickson, B., van Der Heijden, G., Jenkins, M., Manning, P., 2009. The natural fix? The role of ecosystems in climate mitigation. A UNEP rapid response assessment. Birkeland Trykkeri AS, Norway. <https://doi.org/978-82-7701-057-1>
- Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morrisey, D.J., Thrush, S.F., Cummings, V.J., Funnell, G.A., 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22, 1016–1032. <https://doi.org/10.2307/1353080>
- UNEP, CIFOR, 2014. Guiding principles for delivering coastal wetland carbon projects. United Nations Environment Programme (Kenya) and Centre for International Forestry Research (Bogor, Indonesia).
- van Katwijk, M.M., Hermus, D.C.R., 2000. Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* 208, 107–118.
- van Keulen, M., Borowitzka, M.A., 2003. Seasonal variability in sediment distribution along an exposure gradient in a seagrass meadow in Shoalwater Bay, Western Australia. *Estuar. Coast. Shelf Sci.* 57, 587–592. [https://doi.org/10.1016/S0272-7714\(02\)00394-3](https://doi.org/10.1016/S0272-7714(02)00394-3)
- van Lent, F., Nienhuis, P.H., Verschuure, J.M., 1991. Production and biomass of the seagrass *Zostera noltii* Hornern, and *Cymodocea nodosa* (Ucria) Aschers, at the Banc D'Arguin (Mauretania, NW Africa): a preliminary approach. *Aquat. Bot.* 44, 353–367.
- Verduin, J.J., Backhaus, J.O., 2000. Dynamics of plant–flow interactions for the seagrass *Amphibolis antarctica*: Field observations and model simulations. *Estuar. Coast. Shelf Sci.* 50, 185–204. <https://doi.org/10.1006/ecss.1999.0567>
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck Jr, K.L., Hughes, A.R., Kendrick, G.A.,

- Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* 106, 12377–12381.
- Weidemann, A.D., Bannister, T.T., 1986. Absorption and scattering coefficients in Irondequoit Bay. *Limnol. Oceanogr.* 31, 567–583.
<https://doi.org/10.4319/lo.1986.31.3.0567>
- Zong, L., Nepf, H., 2011. Spatial distribution of deposition within a patch of vegetation. *Water Resour. Res.* 47, 1–12. <https://doi.org/10.1029/2010WR009516>

Table 1. Summary of habitat characteristics that have a favorable effect on the long term C_{org} storage in seagrass soils, those that threaten this function and those whose effect is still unresolved, based on the review of Blue Carbon research conducted in this study.

Effect	Habitat parameter	Indicator
Favorable	Species composition Canopy complexity Meadow landscape Biotic interactions Exposure to wave energy Turbidity Water depth Nutrient availability	Dominated by large species High Continuous Complex and stable trophic webs Sheltered Low Shallow except if exposed to high hydrodynamic energy Low but not limited
Threat	Altered trophic webs: lack of predators Human pressure Climate change	Over grazing, excess bioturbation Eutrophication, habitat fragmentation Temperature increase and sea level rise
Unresolved	Intertidal vs. Subtidal Climatic region Acidification	

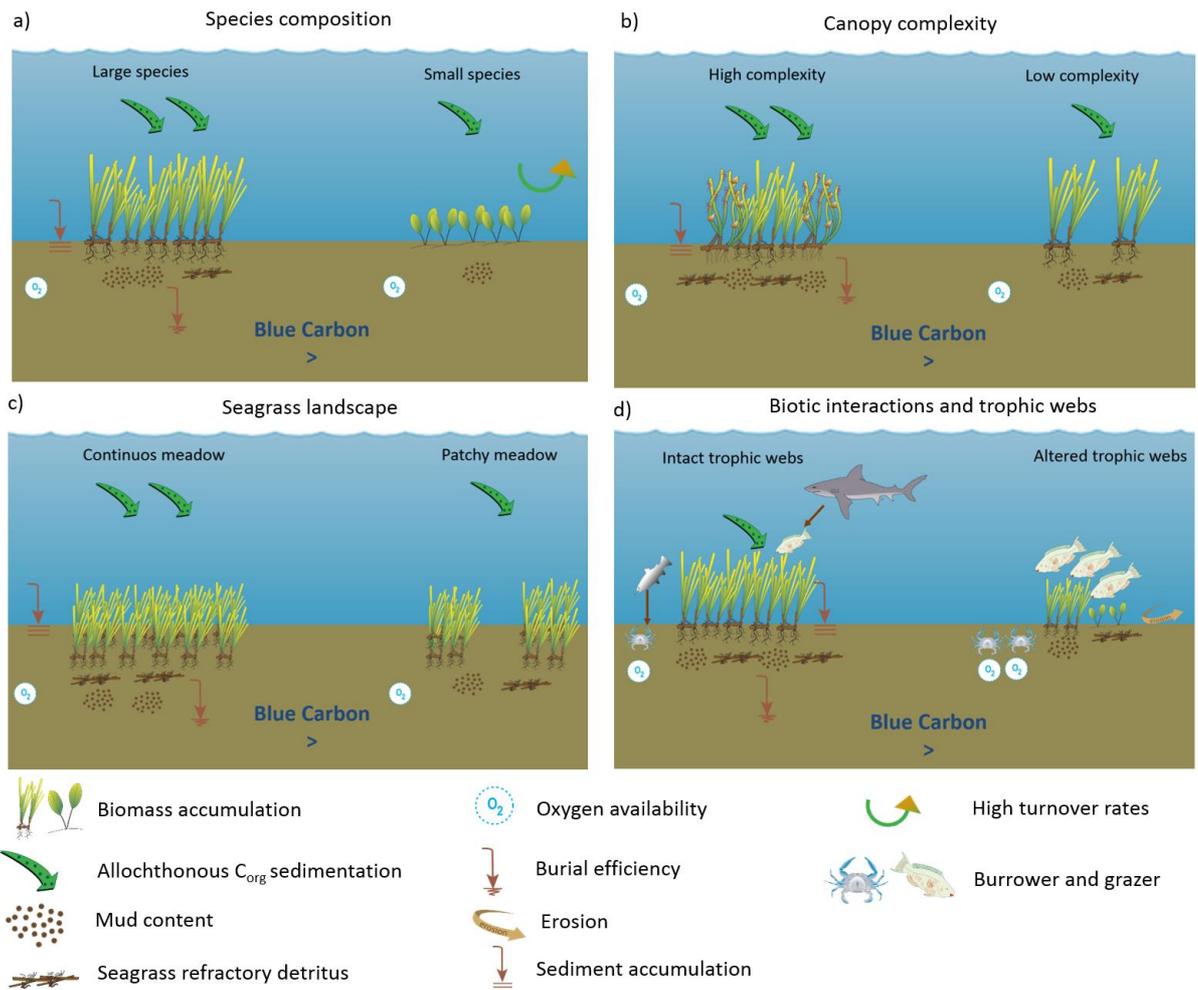


Figure 1: Effect of biotic habitat characteristics on the formation of Blue Carbon deposits in seagrass soils through biomass accumulation, the input of allochthonous C_{org} and C_{org} burial efficiency (i.e. mud content, refractory organic matter and anoxic conditions). The effects of variation in (a) species composition and size, (b) canopy complexity, (c) seagrass landscape and (d) biotic interactions and trophic webs on soil C_{org} stocks and processes are shown. Diagram symbols are from the Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>).

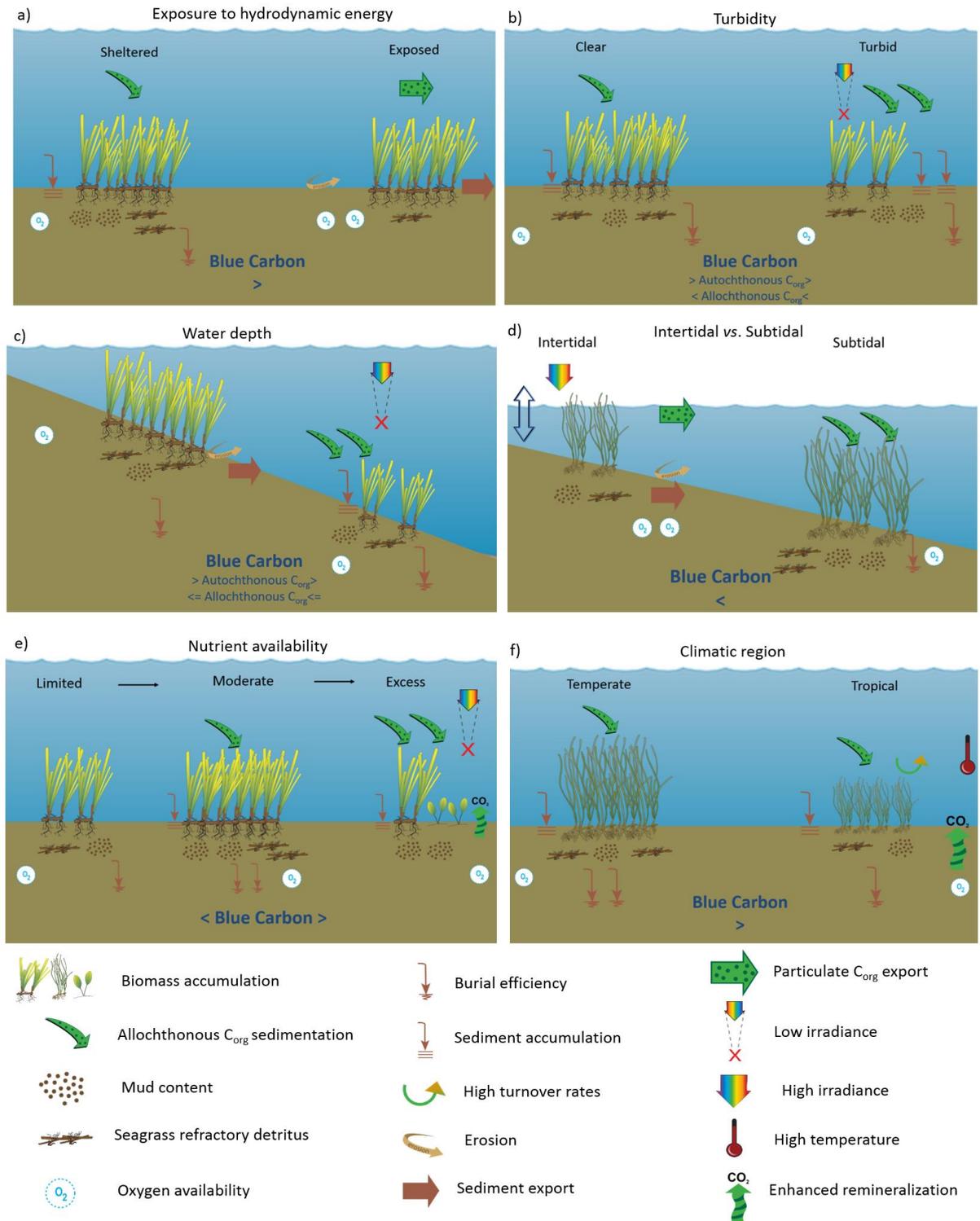


Figure 2: Effect of abiotic habitat characteristics on the formation of Blue Carbon deposits in seagrass soils through seagrass biomass accumulation, the input of allochthonous C_{org} and C_{org} burial efficiency (i.e. mud content, refractory organic matter and anoxic conditions). The effects of variation of (a) exposure to hydrodynamic energy, (b) turbidity, (c) water depth, (d) intertidal vs. subtidal condition, (e) nutrient availability and (f) climatic region of soil C_{org} stocks and processes are shown. Diagram symbols are from the Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/imagelibrary/>)

Table S11: Compilation of experimental and *in situ* studies assessing the effect of habitat settings on seagrass soil C_{org} stocks and sequestration rates in restored and preserved meadows.

Habitat characteristics	Region	Species	Preserved / Restored	Experimental / <i>In situ</i>	Soil C _{org} variable reported	Study		
Biotic	Species composition	Australia	<i>Amphibolis antarctica</i> , <i>Cymodocea rotundata</i> , <i>Halodule uninervis</i> , <i>Syringodium isoetifolium</i> , <i>Cymodocea serrulata</i> , <i>Halophila ovalis</i> , <i>Posidonia australis</i> , <i>Posidonia sinuosa</i> , <i>Thalassia hemprichii</i> , <i>Zostera muelleri</i>	Preserved	<i>In situ</i>	Stocks	Lavery et al., 2013	
		Western Australia	<i>Halophila ovalis</i> , <i>Posidonia australis</i>	Preserved	<i>In situ</i>	Stocks	Rozaimi et al., 2013	
	Canopy complexity	Moreton Bay, Queensland, Australia	<i>Zostera muelleri</i> and <i>Halophila ovalis</i>	Preserved	<i>In situ</i>	Stocks and sequestration rates	Samper-Villarreal et al., 2016, Samper-Villarreal 2016	
		Cockburn Sound, Western Australia	<i>Posidonia sinuosa</i>	Preserved	<i>In situ</i>	Stocks and sequestration rates	Serrano et al., 2014, 2016b	
		Simulation	<i>Cymodocea nodosa</i> , <i>Halodule wrightii</i> , <i>Syringodium filiforme</i> , <i>Zostera marina</i> , <i>Zostera noltii</i>	Restored	Experimental	Sequestration rates	Duarte et al., 2013	
	Landscape configuration	Port Curtis Harbour, Queensland, Australia	<i>Zostera muelleri</i>	Preserved	<i>In situ</i>	Stocks	Ricart et al., 2015b	
		Catalonia and Balearic Is., NW Mediterranean	<i>Posidonia oceanica</i>	Preserved	<i>In situ</i>	Stocks	Ricart et al., 2017	
		Seto Islands Sea, Japan	<i>Zostera marina</i>	Preserved	<i>In situ</i>	Stocks	Miyajima et al., 2017	
		Virginia Coast Reserve, USA	<i>Zostera marina</i>	Restored	<i>In situ</i>	Stocks	Oreska et al., 2017	
		Simulation	<i>Cymodocea nodosa</i> , <i>Halodule wrightii</i> , <i>Syringodium filiforme</i> , <i>Zostera marina</i> , <i>Zostera noltii</i>	Restored	Experimental	Sequestration rates	Duarte et al., 2013	
	Biotic interactions: grazing	Chwaka Bay, Zanzibar	<i>Thalassia hemprichii</i>	Preserved	Experimental	Stocks	Dahl et al., 2016b	
		Shark Bay, Western Australia	<i>Amphibolis antarctica</i> ; <i>Cymodocea angustata</i> , <i>Halodule uninervis</i> , <i>Halophila ovalis</i>	Preserved	<i>In situ</i>	Stocks	Atwood et al., 2015	
	Biotic interactions: burrowing.	Curtis Island, Queensland, Australia	<i>Zostera muelleri</i>	Preserved	<i>In situ</i>	Stocks	Thomson et al., 2017	
	Abiotic	Hydrodynamic energy	Moreton Bay, Queensland, Australia	<i>Zostera muelleri</i> , <i>Halophila ovalis</i> , <i>Halophila uninervis</i> , <i>Syringodium isoetifolium</i> , <i>Cymodocea serrulata</i>	Preserved	<i>In situ</i>	Stocks	Samper-Villarreal et al., 2016a

	Finland and Denmark	<i>Zostera marina</i>	Preserved	<i>In situ</i>	Stocks	Röhr et al., 2016
	Balearic Islands, Western Mediterranean	<i>Posidonia oceanica</i>	Preserved	<i>In situ</i>	Sequestration rates	Mazarrasa et al., 2017a
Turbidity	Moreton Bay, Queensland	<i>Zostera muelleri, Halophila ovalis</i>	Preserved	<i>In situ</i>	Stocks and sequestration rates	Samper-Villarreal et al., 2016a, Samper-Villarreal 2016
	Chwaka Bay, Zanzibar	<i>Thalassia hemprichii</i>	Preserved	Experimental	Stocks	Dahl et al. 2016b
Water depth	Cockburn Sound, Western Australia	<i>Posidonia sinuosa</i>	Preserved	<i>In situ</i>	Stocks and sequestration rates	Serrano et al., 2014
	Balearic Islands, Western Mediterranean	<i>Posidonia oceanica</i>	Preserved	<i>In situ</i>	Stocks	
	Geographe Bay, Australia	<i>Posidonia sinuosa</i>	Preserved	<i>In situ</i>	Stocks	Lavery et al., 2013
	Geographe Bay, Australia	<i>Amphibolis antarctica</i>	Preserved	<i>In situ</i>	Stocks	
	Medes Island, Spain	<i>Posidonia oceanica</i>	Preserved	<i>In situ</i>	Sequestration rates	Mateo and Romero 1997
	Moreton Bay, Queensland, Australia	<i>Zoster muelleri, Halophila ovalis, Halophila uninervis, Syringodium isoetifolium, Cymodocea serrulata</i>	Preserved	<i>In situ</i>	Stocks	Samper-Villarreal et al., 2016a
	Balearic Islands, Western Mediterranean	<i>Posidonia oceanica</i>	Preserved	<i>In situ</i>	Sequestration rates	Mazarrasa et al., 2017a
	Europe	<i>Zostera marina</i>	Preserved	<i>In situ</i>	Stocks	Dahl et al., 2016a
Intertidal vs. subtidal	Australia	<i>Amphibolis antarctica, Halodule uninervis, Posidonia australis, C.rotundata-H.uninervis</i>	Preserved	<i>In situ</i>	Stocks	Lavery et al., 2013
Nutrient availability	Everglades, Florida Bay	<i>Thalassia testudinum</i>	Preserved	<i>In situ</i>	Stocks	Armitage and Fourqurean 2016
	Everglades, Florida Bay	<i>Thalassia testudinum</i>	Preserved	Experimental	Stocks	
	Cross Bank, Florida Bay	<i>Thalassia testudinum, Halophila wrightii</i>	Preserved	<i>In situ</i>	Stocks	Howard et al., 2016
	Ria Formosa, Portugal	<i>Zostera noltii</i>	Preserved	Experimental	Stocks	Martínez-Crego et al., 2014
Temperature and climatic regions	Australia	<i>Amphibolis antarctica, Posidonia australis</i>	Preserved	<i>In situ</i>	Stocks	Lavery et al., 2013
	East and Southeast Asia	<i>Zostera marina, Zostera japonica, Thalassia hemprichii, Cymodocea serrulata, Enhalus acoroides</i>	Preserved	<i>In situ</i>	Stocks	Miyajima et al., 2015