Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems?

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ABSTRACT

The emerging field of blue carbon science is seeking cost-effective ways to estimate the organic carbon content of soils that are bound by coastal vegetated ecosystems. Organic carbon (C_{org}) content in terrestrial soils and marine sediments has been correlated with mud content (i.e. silt and clay), however, empirical tests of this theory are lacking for coastal vegetated ecosystems. Here, we compiled data (n = 1345) on the relationship between C_{org} and mud (i.e. silt and clay, particle sizes <63 μm) contents in seagrass ecosystems (79 cores) and adjacent bare sediments (21 cores) to address whether mud can be used to predict soil C_{org} content. We also combined these data with the $\delta^{13}C$ signatures of the soil C_{org} to understand the sources of C_{org} stores. The results showed that mud is positively correlated with soil C_{org} content only when the contribution of seagrass-derived C_{org} to the sedimentary C_{org} pool is relatively low, such as in small and fast-growing meadows of the genera *Zostera*, *Halodule* and *Halophila*, and in bare sediments adjacent to seagrass ecosystems. In large and long-living seagrass meadows of the genera *Posidonia* and *Amphibolis* there was a lack of, or poor relationship between mud and soil C_{org} content, related to a higher contribution of seagrass-derived C_{org} to the sedimentary C_{org} pool in these meadows. The relative high soil C_{org} contents with relatively low mud contents (e.g. mud-C_{org} saturation) in bare sediments and *Zostera*, *Halodule* and *Halophila* meadows was related to significant allochthonous inputs of terrestrial organic matter, while higher contribution of seagrass detritus in *Amphibolis* and *Posidonia* meadows disrupted the correlation expected between soil C_{org} and mud contents. This study shows that mud (i.e. silt and clay content) is not a universal proxy for blue carbon content in seagrass ecosystems, and therefore should not be

applied generally across all seagrass habitats. Mud content can only be used as a proxy to estimate soil C_{org} content for scaling up purposes when opportunistic and/or low biomass seagrass species (i.e. *Zostera*, *Halodule* and *Halophila*) are present (explaining 34 to 91% of variability), and in bare sediments (explaining 78% of the variability).

1. INTRODUCTION

The sedimentary organic carbon (C_{org}) stores of seagrass meadows – often referred to as 'blue carbon' – can vary among seagrass species and habitats, with reports of up to 18-fold differences (Lavery et al. 2013). Ambiguity remains in the relative importance of the depositional environment and species characteristics contributing to this variability. Seagrasses occur in a variety of coastal habitats, ranging from highly depositional environments to highly exposed and erosional habitats (Carruthers et al. 2007). Since seagrass species differ in their biomass and canopy structure, and occur in a variety of habitat types, this raises the question of whether mud content can be used to predict C_{org} content within coastal sediments, or whether the species composition will significantly influence the soil C_{org} stores independently of the geomorphological nature of the habitat.

Geomorphological settings (i.e. topography and hydrology), soil characteristics (e.g. mineralogy and texture) and biological features (e.g. primary production and remineralization rates) control soil C_{org} storage in terrestrial ecosystems (Amundson, 2001, De Deyn et al. 2008; Jonsson and Wardle, 2009) and in mangrove and tidal salt marshes (Donato et al. 2011; Adame et al. 2013; Ouyang and Lee, 2014). While it is clear that habitat interactions have a large influence on stores of soil C_{org}, our understanding of the factors regulating this influence in seagrass meadows is limited (Nellemann et al. 2009; Duarte et al. 2010; Serrano et al. 2014).

The accumulation of C_{org} in seagrass meadows results from several processes: accretion (autochthonous plant and epiphyte production, and trapping of allochthonous C_{org}; Kennedy et al. 2010), erosion (e.g. export; Romero and Pergent, 1992; Hyndes et al. 2014) and decomposition (Mateo et al. 1997). Previous studies demonstrate that both autochthonous (e.g. plant detritus and epiphytes) and allochthonous (e.g. macroalgae, seston and terrestrial matter) sources contribute to the C_{org} pool in seagrass soils (Kennedy et al. 2010; Watanabe and Kuwae, 2015). Plant net primary productivity is a key factor controlling the amount of C_{org} potentially available for sequestration in seagrass ecosystems (Serrano et al. 2014), but the depositional environment is an important factor controlling C_{org} storage in coastal habitats (De Falco et al. 2004; Lavery et al. 2013).

Previous studies have shown a large variation in C_{org} stores among morphologically different seagrass species (Lavery et al. 2013; Rozaimi et al. 2013). Also, that C_{org} accumulates more in estuaries compared to coastal ocean environments (estimated at 81 Tg C_{org} y^{-1} and 45 Tg C_{org} y^{-1}, respectively; Nellemann et al. 2009). This is due largely to estuaries being highly depositional environments, receiving fine-grained particles from terrestrial and coastal ecosystems which enhance C_{org} accumulation (i.e. silt and clay sediments retain more C_{org} compared to sands; Keil and Hedges, 1993; Burdige 2007) and preservation (i.e. reducing redox potentials and remineralization rates; Hedges and Keil, 1995; Dauwe et al. 2001; Burdige, 2007; Pedersen et al. 2011). The inputs of seagrass-derived C_{org} in the sedimentary pool could break the linear relationship among mud (i.e. silt and clay particles) and C_{org} contents typically found in terrestrial (Nichols, 1984; McGrath and Zhang, 2003) and marine sedimentary environments (Bergamaschi et al. 1997; De Falco et al. 2004). However, the amount of C_{org} that can be associated with silt and clay particles is limited (Hassink, 1997), which could lead to a poor relationship between mud and soil C_{org} contents. Also, other factors found to play a key role in controlling soil C_{org} accumulation in terrestrial and coastal ecosystems, such as chemical stabilization of organic matter (Percival et al. 1999; Burdige, 2007), carbon in microbial biomass (Sparling, 1992; Danovaro et al. 1995), and soil temperature (Pedersen et al. 2011), could also influence C_{org} storage in seagrass meadows.

A significant relationship between mud (i.e. silt and clay) and C_{org} contents would allow mud to be used as a proxy for C_{org} content, thereby enabling robust scaling up exercises at a low cost as part of blue carbon stock assessments. Furthermore, since most countries have conducted geological surveys within the coastal zone to determine sediment grain size, a strong, positive relationship between mud and C_{org} contents would allow the development of geomorphology models to predict blue carbon content within seagrass meadows, dramatically improving global estimates of blue carbon storage. The purpose of this study was therefore to test for relationships between C_{org} and mud contents within seagrass ecosystems and adjacent bare sediments.

2. MATERIAL AND METHODS

Data was compiled from a number of published and unpublished studies from Australia and Spain, in seagrass meadows across diverse habitats (Table 1). The study sites encompass monospecific and/or mixed meadows from a variety of temperate and tropical seagrass species of the genera *Posidonia*, *Amphibolis*, *Zostera*, *Halophila* and *Halodule*, and adjacent bare sediments, while including a variety of depositional environments (from estuarine to exposed coastal areas encompassing different water depths, from intertidal to the deep limit of seagrass distribution; Table 1). Data from 100 cores (79 from seagrass meadows and 21 from bare sediments) on sediment grain size, organic carbon (C_{org}) content and stable carbon isotope signatures of the C_{org} ($\delta^{13}C$) was explored in this study (N = 1345).

Sediment cores were sampled by means of percusion and rotation, or vibrocoring (ranging from 10 to 475 cm long). The core barrels consisted of PVC or aluminium pipes (50 to 90 mm inside diamater) with sharpenned ends to cut fibrous material and minimize core shortening (compression) during coring (Serrano et al. 2012, 2014). All cores were sealed at both ends, transported vertically to the laboratory and stored at 5°C before processing.

The cores were sliced at regular intervals, each slice/sample was weighed before and after oven drying to constant weight at 70°C (DW), and subsequently sub-divided for analysis. The C_{org} elemental and isotopic composition of the organic matter was measured in milled subsamples from several slices along the cores. The sediment core sub-samples were acidified with 1 M HCl, centrifuged (3500 RPM; 5 minutes) and the supernatant with acid residues was removed using a pipette, then washed in deionized water, centrifuged again and the supernatant removed. The residual samples were re-dried (70°C) before carbon elemental and isotopic analyses. The samples were encapsulated and the organic carbon elemental and isotopic composition was analyzed using an elemental analyzer interfaced with an isotope ratio mass spectrometer. Percentage C_{org} was calculated for the bulk (pre-acidified) samples. Carbon isotope ratios are expressed as δ values in parts per thousand (‰) relative to VPDB (Vienna Pee Dee Belemnite). For sediment grain size analysis, a Coulter LS230 laser-diffraction particle analyzer was used following digestion of the samples with 10% hydrogen peroxide. The mud content in the sediments (silt and clay, <63 µm) was determined, and expressed as a percentage of the bulk sample.

Pearson correlation analysis was used to test for significant relationships among C_{org} and mud contents, and C_{org} and $\delta^{13}C$ signatures. Correlations between the variables studied were tested among seagrass species (9 categories) and bare sediments, seagrass genera (4 categories), habitat geomorphology (coastal and estuarine habitats) and soil depth (in 1 to 10 cm-thick and 11 to 110 cm-thick deposits).

3. RESULTS

The soil organic carbon (C_{org}) and mud contents varied within the seagrass meadows and bare sediments studied in Australia and Spain. The soil C_{org} and mud contents were higher in seagrass meadows (average ± SE, 1.5 ± 0.2% and 18 ± 2.4%, respectively) compared to bare sediments (0.6 ± 0.1% and 10.8 ±1 .2%, respectively; Table 2). On average, seagrass meadows of the genera *Amphibolis* and *Posidonia* contained higher soil C_{org} (1.6 ± 0.1%) and lower mud (7.2 ± 0.4) than meadows of *Halophila*, *Halodule* and *Zostera* (1.2 ± 0.2% and 34.9 ± 5.4%, respectively; Table 2). Overall, carbon isotopic ratios from sedimentary organic matter ($\delta^{13}C$) were similar between seagrass soils and bare sediments (-17.6 ± 0.3‰ and -17.3 ± 0.2‰, respectively). The C_{org} in soils from *Posidonia* and *Amphibolis* meadows were ^{13}C-enriched (-15.5 ± 0.3‰) compared with seagrass soils from *Halophila*, *Halodule* and *Zostera* meadows (-20.7 ± 0.4‰; Table 2). The C_{org} content in soils from estuarine and coastal habitats were similar, while mud content in estuarine sediments was higher and $\delta^{13}C$ values depleted when compared to coastal habitats (Table 2).

The relationships between the variables studied (i.e. %C_{org}, %mud, and $\delta^{13}C$ signatures of sedimentary C_{org}) among different species and habitat geomorphologies, and among different soil depths were explored in Figures 1 to 3, and Table 3. When accounting for the whole dataset (up to 475 cm long cores), the C_{org} content increased with increasing mud content in bare sediments ($R^2 = 0.78$) and at species level, except for *Posidonia oceanica* (i.e. C_{org} content decreased with increasing mud content; $R^2 = 0.15$) and *Amphibolis griffithii* (i.e. no relationship was found, $R^2 = 0.05$; Table 3). Although most of the correlations at species level were significant, they only explain 2 to 39% of the variance in trends described, except for *Halophila ovalis* (91%; Table 3). In particular, *Posidonia* meadows (*P. australis*, *P. sinuosa* and *P. oceanica*) had the lower correlation values (R^2 ranged from 0.02 to 0.15). When combining mud and C_{org} contents in seagrass meadows of the colonizing and opportunistic genera *Halophila*, *Halodule* and *Zostera* (Kilminster et al. 2015), a relatively high correlation was found (R^2 = 0.56; Figure 1), while soil C_{org} and mud contents in persistent genera were only slightly positively correlated in combined *Amphibolis* spp and not correlated in *Posidonia* spp meadows (Figure 1).

The relationships between soil C_{org} and mud contents within different core depths (from 1 to 10 cm-thick deposits, and from 11 to up to 110 cm-thick deposits) for bare sediments and each group of seagrass species were explored in Figure 2. The C_{org} content increased with increasing mud content in bare sediments for both 1 to 10 cm-thick (R^2 = 0.74) and 11 to 110 cm-thick (R^2 = 0.81) soils. When combining mud and C_{org} contents in seagrass meadows of the genera *Halophila*, *Halodule* and *Zostera*, a higher correlation was found for deeper core sections (11 to 110 cm-thick; R^2 = 0.74) compared to top core sections (1 to 10 cm-thick; R^2 = 0.17). For combined *Amphibolis* and *Posidonia* species, soil C_{org} and mud contents were only slightly positively correlated in deeper *Amphibolis* spp sections (11 to 110 cm-thick; R^2 = 0.23) and not correlated in *Posidonia* spp meadows (Figure 2). The classification of habitats based on geomorphology (i.e. coastal and estuarine) showed a lack of correlation between soil C_{org} and mud contents in coastal ecosystems, and a poor correlation in estuarine ecosystems (R^2 = 0.14; Figure 3 and Table 3).

The relationships between soil $\%C_{org}$ and $\delta^{13}C$ signatures were poor for all individual *Amphibolis* and *Posidonia* species studied (R^2 ranging from 0.09 to 0.3; Table 3), and for combined *Amphibolis* spp (Figure 1), with a tendency of C_{org}-rich soils being enriched in ^{13}C (Figure 1). In contrast, $\%C_{org}$ and $\delta^{13}C$ signatures were not correlated in any of the small and fast-growing *Halodule*, *Zostera*, *Halophila* meadows studied (Table 3), neither individually nor when combined (Figure 1 and Table 3). A lack of correlation between soil %C_{org} and $\delta^{13}C$ signatures was also found in bare sediments adjacent to seagrass meadows (Figure 3 and Table 3).

4. DISCUSSION

Overall mud content is a poor predictor of soil C_{org} in seagrass meadows and care should be taken in its use as a cost-effective proxy or indicator of C_{org} for scaling-up purposes in the emerging field of blue carbon science. Although we describe some promise for opportunistic and early colonizing *Halophila*, *Halodule* and *Zostera* meadows (i.e. mud content explained 34 to 91% of variability in C_{org} content) and in bare sediments adjacent to seagrass meadows (explaining 78% of the variability), mud is not a universal proxy for blue carbon content and therefore should not be applied generally across all seagrass habitats. In particular, mud content only explained 5 to 32% of soil C_{org} content in *Amphibolis* spp meadows and 2 to 15% of soil C_{org} content in *Posidonia* spp meadows, and therefore, mud content is not a good proxy for blue carbon content in these meadows.

A tenet of carbon cycling within the coastal ocean is that fine-grained sediments (i.e. mud) have higher C_{org} contents. The positive relationship found between mud and C_{org} contents in coastal bare sediments (explaining 78% of the variability) is in agreement with previous studies (e.g. Bergamaschi et al. 1997; De Falco et al. 2004), and is related to their larger surface areas compared to coarse-grained sediments, providing more binding sites for C_{org} on the surface of minerals (Keil and Hedges, 1993; Mayer, 1994a, 1994b; Galy et al. 2007; Burdige 2007). In addition, the predominance of fine sediments reduces oxygen exchange and results in low sediment redox potentials and remineralization rates, contributing to the preservation of sedimentary C_{org} after burial (Hedges and Keil, 1995; Bergamaschi et al. 1997; Dauwe et al. 2001; Burdige 2007; Pedersen et al. 2011). However, the maximum capacity of a given soil to preserve C_{org} by their association with clay and silt particles is limited (i.e. mud-C_{org} saturation; Hassink, 1997). The results obtained showed that bare sediment samples with relative high C_{org} contents (i.e. >4% C_{org}) and relatively low mud contents were also ^{13}C-depleted (Figure 1), suggesting significant contributions of soil C_{org} from allochthonous sources (e.g. terrestrial and sestonic; Kennedy et al. 2010). This could have disrupted the correlation found between soil C_{org} and mud contents in the bare sediments studied.

Mud is not a universal proxy for soil C_{org} content in seagrass meadows, which could be mainly explained by additional inputs of seagrass-derived C_{org} and/or allocthonous C_{org} to the sedimentary C_{org} pool, obviating the linear relationship between mud and C_{org} contents found in the absence of vegetation. The $\delta^{13}C$ values indicated that both seagrass-C_{org} and non-seagrass-derived C_{org} (i.e. epiphytes, algae, seston or terrestrial matter) were buried in the soils of all studied meadows, but are consistent with a model of increasing capture of seagrass-derived C_{org} at meadows formed by persistent, high-biomass seagrasses (i.e. genera *Posidonia* and *Amphibolis*) relative to opportunistic, low-biomass seagrasses (i.e. genera *Halophila*, *Halodule* and *Zostera*).

On one hand, the soil $\delta^{13}C$ signatures measured in these long-living and large seagrass meadows (averaging -15 ± 0.2‰ in both cases) were closer to the $\delta^{13}C$ signatures of *Posidonia* and *Amphibolis* tissues (ranging from -8 to -14‰; Hyndes and Lavery 2005; Hindell et al. 2004; Cardona et al. 2007; Fourqurean et al. 2007; Collier et al. 2008; Kennedy et al. 2010; Hanson et al. 2010; Serrano et al. 2015) than to $\delta^{13}C$ values of algae or terrestrial organic matter (ranging from -18 to -32‰; e.g. Smit et al. 2006; Cardona et al. 2007; Kennedy et al. 2010; Hanson et al

2010; Deudero et al. 2011). The poor relationship between mud and soil C_{org} contents in *Amphibolis* soils could be explained by samples with relative high C_{org} contents (i.e. >2.5% C_{org}) and relatively low mud contents, as a result of both the contribution of seagrass-derived C_{org} (i.e. ^{13}C-enriched) and C_{org} from allochthonous sources (i.e. ^{13}C-depleted; Figure 1). In *Posidonia* soils, the poor relationship between mud and soil C_{org} contents could be explained by samples with relative high C_{org} contents (i.e. >10% C_{org}) and relatively low mud contents, as a result of the contribution of seagrass-derived C_{org} (i.e. ^{13}C-enriched; Figure 1). The contribution of seagrass-derived C_{org} (i.e. root, rhizome and sheath detritus) in *Posidonia* soils play a much larger role than the accumulation of fine, organic-rich allochthonous particles.

On the other hand, the soil δ^{13}C signatures measured in *Halodule*, *Halophila* and *Zostera* meadows (averaging -21 ± 0.4‰) were more similar to δ^{13}C values of algae or terrestrial organic matter than to δ^{13}C values of their seagrass tissues (ranging from -10 and -14‰; e.g. Hemminga and Mateo, 1996; Kennedy et al. 2010; Hanson et al. 2010). The positive relationship between mud and soil C_{org} contents in *Halodule*, *Halophila* and *Zostera* soils could be explained their relatively high mud content and ^{13}C-depleted C_{org}, indicating that allochthonous C_{org} inputs and mud content play a major role in soil C_{org} accumulation in these opportunistic and early-colonizing seagrasses. However, the relative high C_{org} contents found with relatively low mud contents (i.e. mud-C_{org} saturation) disrupted the correlation found between soil C_{org} and mud contents in these meadows (C_{org} >1% in samples with 0-20% mud; C_{org} >2% in samples with 20-70% mud and C_{org} >3.5 in samples with 70-100% mud; Figure 1).

The results obtained showed a tendency for high-biomass and persistent meadows (i.e. *Posidonia* and *Amphibolis*) to accumulate higher C_{org} stores and seagrass-derived C_{org} compared to ephemeral and low-biomass meadows (i.e. *Halophila*, *Halodule* and *Zostera*), suggesting that factors (biotic and abiotic) affecting the production, form and preservation of C_{org} within habitats exert a significant influence on soil C_{org} content (Lavery et al. 2013; Serrano et al. 2014, 2015). The above- and belowground biomass in meadows of the genus *Posidonia* (averaging 535 and 910 g DW m^{-2}, respectively) is up to 2-fold higher than in *Amphibolis* meadows (averaging 641 and 457 g DW m^{-2}, respectively) and 4 to 18-fold higher than in small and opportunistic seagrasses of the genera *Halophila*, *Halodule* and *Zostera* (125 and 49 g DW m^{-2}, on average; respectively; Duarte and Chiscano, 1999; Paling and McComb 2000). Indeed, larger seagrasses tend to have larger and more persistent rhizomes, constituted by more refractory forms of C_{org}, more prone to be preserved in soils than simpler, more labile forms of C_{org} such as seston and algal detritus which are more suitable to experience remineralization during early diagenesis (Henrichs 1992; Burdige, 2007). In addition, the larger size of detritus within *Amphibolis* and *Posidonia* meadows compared to *Halophila*, *Halodule* and *Zostera* meadows could also contribute to the larger accumulation of C_{org} in the former, since decay rates of seagrass detritus increase with decreasing particle size due to larger surfaces available for microbial attack (Harrison, 1989). Differences in above- and belowground biomass and recalcitrance between *Posidonia* and *Amphibolis* spp could explain the larger contribution of seagrass-derived C_{org} (i.e. ^{13}C-enriched) in the former, thereby obviating the linear relationship between mud and C_{org} contents (Figure 1).

The soil C_{org} content tend to decrease with soil depth and ageing in seagrass ecosystems (e.g. Serrano et al. 2012), thereby the persistence of discrete organic detritus within upper soil horizons could lead to organic matter concentrations above those levels explained by the association with clay and silt particles, as previously demonstrated for terrestrial soils (Mayer and Xing, 2001; Gami et al. 2009). The organic matter preserved in most marine sediments is intimately associated with mineral surfaces (i.e. selective preservation by sorption of organic matter into minerals; Keil et al 1994) and therefore the correlation between soil C_{org} and mud contents in seagrass meadows could vary as a function of soil depth and ageing. The results obtained show that soil depth is not an important factor when attempting to predict soil C_{org} content based on mud content in bare sediments (i.e. $R^2 > 0.74$ for all core depths explored; 1 to 110 cm-thick, 1 to 10 cm-thick, and 11 to 110 cm-thick; Figure 2). However, a clearer pattern appeared when exploring the correlation between soil C_{org} and mud contents in top 10 cm and within 11-110 cm soil depths of combined *Halodule*, *Halophila* and *Zostera* species ($R^2 = 0.17$ and $R^2 = 0.74$, respectively). These results suggest that the relatively small belowground biomass of these species (i.e. organic detritus) only has an impact on the expected positive correlation between soil C_{org} and mud content within the top 10 cm, while the correlation for deeper soil depths (11-110 cm) improved ($R^2 = 0.74$) compared to the whole dataset (1 to 110 cm-thick; $R^2 = 0.56$). For combined *Amphibolis* and *Posidonia* species, the results obtained show that soil depth is not an important factor when attempting to predict soil C_{org} content based on mud content (i.e. $R^2 < 0.2$ in all cases; 1 to 110 cm-thick, 1 to 10 cm-thick, and 11 to 110 cm thick; Figure 2). These results suggest that the relatively large belowground biomass of these species (i.e. organic detritus) has an impact on the expected positive correlation between soil C_{org} and mud content within all depths studied.

Habitat conditions in seagrass meadows not only influence the amount of C_{org} accumulation through detrital plant inputs, but the capacity of the plant canopies to retain particles (Gacia et al. 1999). The amount of fine suspended particles available for burial varies among sites, driven by geomorphological features (e.g. run-off, hydrodynamic energy and water depth), while meadow structure (i.e. density, cover and morphology of the canopy) constrains their capacity to accumulate sediment particles (Hendriks et al. 2010; Peralta et al. 2008). Although the number of cores and species studied in coastal and estuarine ecosystems was unbalanced (i.e. *Amphibolis* and *Posidonia* dominate in coastal habitats and *Halophila*, *Halodule*, *Zostera* dominate in estuarine habitats), the lack of, or poor correlations found within estuarine and coastal ecosystems, precludes the general use of mud as a predictor of blue carbon content based on habitat geomorphology (Figure 3). Seagrass meadows and bare sediments in environments conducive for depositional processes (i.e. estuaries) accumulated up to 4-fold higher amounts of mud compared to other coastal ecosystems, but the saturation of mud with C_{org} and the large contribution of seagrass detritus into the sedimentary C_{org} pool (^{13}C-enriched soils) in some study sites disrupted the positive relationship expected between mud and soil-C_{org} contents. In estuarine ecosystems, soil C_{org} originated from both mud inputs linked to allochthonous-C_{org} via deposition from upstream transport (e.g. Aller, 1998) and seagrass inputs (i.e. in samples with C_{org} >5%; Figure 3). The insignificant relationship between mud and soil C_{org} contents in coastal habitats could be explained by their relatively low mud content and the accumulation of seagrass-derived C_{org}, in particular in samples with C_{org} >5% (Figure 3).

In sum, mud is not a universal proxy for blue carbon content in seagrass ecosystems and should not be applied generally across all habitat and vegetation types. Overall, the positive relationship between mud and C_{org} contents found in bare sediments and in opportunistic and/or low biomass seagrass meadows (i.e. genera *Zostera*, *Halodule* and *Halophila*) allow mud to be used as a proxy for C_{org} content in these ecosystems, thereby enabling robust scaling up exercises (i.e. benefiting from existing geological surveys and models) at low cost as part of blue carbon stock assessment programs. However, mud content is not a good predictor of C_{org} content in highly productive meadows such as those constituted by *P. oceanica* in the Mediterranean Sea and *P. australis, P. sinuosa* and *Amphibolis* spp in Australia. Previous studies suggested that the relationship between organic matter and the sediment matrix is best seen with clay-sized fractions (<0.004 mm; Bergamaschi et al., 1997; De Falco et al. 2004). However, the grain size cut-off selected in this study (mud, <0.063 mm) is more representative of the bulk soil and their C_{org} content (Pedrosa-Pàmies et al. 2013) and therefore a higher correlation is expected when comparing bulk soil C_{org} with a larger and more representative fraction of the sediment (i.e. including the silt fraction, 0.004-0.063 mm, also provides binding sites for C_{org}; Burdige, 2007). Other biological, chemical and geological factors not explored in detail in this study may also play a key role in C_{org} storage, and ultimately in the relationship between soil C_{org} and mud contents. For example, the effects of habitat geomorphology (e.g. hydrodynamic energy, terrestrial mud and C_{org} inputs, export of seagrass biomass) and species identity (e.g. variation in terms of productivity, oxygen exposure and recalcitrance of C_{org} stores, and plant influence on sediment retention) within both coastal and estuarine environments, are among the factors identified in this study which might explain significant variation in the C_{org} stores of meadows in relatively similar exposure conditions (Serrano et al. 2015). Other factors found to play a key role in controlling soil C_{org} accumulation in terrestrial ecosystems, such as chemical stabilization of organic matter (Percival et al. 1999; Galy et al. 2008) and microbial biomass carbon (Danovaro et al. 1994), could also influence C_{org} storage in seagrass ecosystems. Further studies are needed to identify the influences of these other factors on C_{org} storage in seagrass meadows, and in addition to the mud content, other characteristics should be taken into account when attempting to obtain robust estimates of C_{org} stores within coastal areas.

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Tables and Figures

Table 1. Data on soil organic carbon and mud contents, and stable carbon isotope from coastal soils were gathered from a variety of seagrass meadows (and also from adjacent bare sediments) and habitat types.

Species	**Study site**	**Geomorphology**	**Number of cores**	**Number of samples**	**Core depth (cm)**	**Water depth (m)**
Amphibolis (mixed spp)	Rottnest Island, WA, Australia	Coastal	2	68	0-120	2
	Shark Bay, WA, Australia	Coastal	1	38	0-170	2
Amphibolis antarctica	Shark Bay, WA, Australia	Coastal	2	63	0-200	2-3
Amphibolis griffithii	Jurien Bay, WA, Australia	Coastal	2	41	0-70	4
Posidonia australis	Oyster Harbour, WA, Australia	Estuarine	3	31	0-120	2
	Waychinicup Inlet, WA, Australia	Estuarine	2	79	0-150	2
	Robbins Island, TAS, Australia	Coastal	6	138	0-180	3
Posidonia sinuosa	Frenchman's Bay, WA, Australia	Coastal	4	100	0-80	2-8
	Cockburn Sound, WA, Australia	Coastal	3	50	0-30	6
	Garden Island, WA, Australia	Coastal	5	147	0-120	2-8
Posidonia oceanica	Portlligat, Spain	Coastal	1	192	475	3
	Balearic Islands, Spain	Coastal	6	25	0-270	3
Halodule uninvervis	Carnarvon, WA, Australia	Estuarine	1	39	0-210	2
	Gladstone, QLD, Australia	Estuarine	6	6	0-10	intertidal
Halophila decipiens	Gladstone, QLD, Australia	Estuarine	2	2	0-10	intertidal
Halophila ovalis	Rottnest Island, WA, Australia	Coastal	1	17	0-30	3
	Swan River, WA, Australia	Estuarine	1	5	0-70	2
	Leschenault Inlet, WA, Australia	Estuarine	1	8	0-120	1
	Harvey Inlet, WA, Australia	Estuarine	1	5	0-20	2
	Gladstone, QLD, Australia	Estuarine	2	2	0-10	intertidal
Zostera muelleri	Fagans Bay, NSW, Australia	Estuarine	2	20	0-10	intertidal
	Gladstone, QLD, Australia	Estuarine	23	23	0-10	intertidal
	Tuggerah Lakes, NSW, Australia	Estuarine	2	64	0-400	3
Bare	Cockburn Sound, WA, Australia	Coastal	10	131	0-30	2-9
	Garden Island, WA, Australia	Coastal	1	16	0-30	4
	Oyster Harbour, WA, Australia	Estuarine	1	26	0-110	3
	Gladstone, QLD, Australia	Estuarine	9	9	0-10	intertidal

Table 2. Average ± SE organic carbon (C_{org}) content (in %), $\delta^{13}C$ signatures and mud content in all habitats and soil depths studied. a) Descriptive statistics based on species identity. b) Descriptive statistics based on habitat geomorphology (estuarine *vs* coastal environments). N, number of samples.

a)

Habitat	Organic carbon (%)			$\delta^{13}C$ (‰)			Mud (%)		
(species)	N	Mean	SE	N	Mean	SE	N	Mean	SE
Posidonia oceanica	217	3.91	0.35	217	-14.92	0.08	217	11.73	0.53
Posidonia australis	248	1.87	0.08	244	-15.79	0.24	248	11.79	0.68
Posidonia sinuosa	297	0.80	0.04	291	-14.08	0.16	297	2.59	0.18
Amphibolis (mixed spp)	106	1.41	0.11	106	-15.20	0.23	106	4.75	0.33
Amphibolis antarctica	63	0.99	0.06	62	-14.62	0.24	63	6.64	0.44
Amphibolis griffithii	41	0.85	0.07	36	-15.83	0.56	41	5.44	0.29
Halodule uninervis	45	0.78	0.12	45	-19.86	0.53	45	17.68	3.04
Zostera muelleri	107	1.10	0.07	43	-20.02	0.30	107	31.68	2.59
Halophila decipiens	2	1.87	0.51	2	-25.60	0.31	2	65.99	9.62
Halophila ovalis	37	0.97	0.23	37	-17.22	0.44	37	24.09	6.23
Bare	182	0.59	0.08	182	-17.25	0.24	182	10.83	1.20
Grand Total	1345	1.56	0.07	1265	-16.18	0.10	1345	10.83	0.43

b)

Habitat	Organic carbon (%)			$\delta^{13}C$ (‰)			Mud (%)		
(geomorphology)	N	Mean	SE	N	Mean	SE	N	Mean	SE
Coastal	1026	1.59	0.09	1014	-15.70	0.10	1026	6.85	0.24
Estuarine	319	1.44	0.07	251	-18.10	0.24	319	23.62	1.41

Table 3. Pearson correlation analyses to test for significant relationships among soil C_{org} and mud contents, and soil C_{org} and $\delta^{13}C$ signatures in up to 475 cm long cores; based on (a) species identity and (b) habitat geomorphology. *ns*, non significant correlation.

a)

Habitat	Organic carbon (%) vs mud (%)			Organic carbon (%) vs $\delta^{13}C$ (‰)		
(species)	Formula	R^2	P value	Formula	R^2	P value
Posidonia oceanica	$C_{org} = -0.26*mud + 6.95$	0.15	***	$C_{org} = 1.59*\delta^{13}C + 27.61$	0.13	***
Posidonia australis	$C_{org} = 0.02*mud + 1.69$	0.02	*	$C_{org} = 0.18*\delta^{13}C + 4.73$	0.30	***
Posidonia sinuosa	$C_{org} = 0.07*mud + 0.61$	0.09	***	$C_{org} = 0.12*\delta^{13}C + 2.44$	0.23	***
Amphibolis (mixed spp)	$C_{org} = 0.17*mud + 0.61$	0.26	***	$C_{org} = 0.14*\delta^{13}C + 3.53$	0.09	**
Amphibolis antarctica	$C_{org} = 0.08*mud + 0.47$	0.32	***	$C_{org} = 0.14*\delta^{13}C + 3.10$	0.29	***
Amphibolis griffithii	*ns*	0.05	0.18	$C_{org} = 0.06*\delta^{13}C + 1.79$	0.21	**
Halodule uninervis	$C_{org} = 0.02*mud + 0.37$	0.34	***	*ns*	0.00	0.89
Zostera muelleri	$C_{org} = 0.02*mud + 0.54$	0.39	***	*ns*	0.08	0.07
Halophila ovalis	$C_{org} = 0.04*mud + 0.12$	0.91	***	*ns*	0.00	0.89
Bare	$C_{org} = 0.06*mud - 0.03$	0.78	***	*ns*	0.01	0.24

b)

Habitat	Organic carbon (%) vs mud (%)			Organic carbon (%) vs $\delta^{13}C$ (‰)		
(geomorphology)	Formula	R^2	P value	Formula	R^2	P value
Coastal	*ns*	0.01	0.85	$C_{org} = 0.17*\delta^{13}C + 4.14$	0.03	***
Estuarine	$C_{org} = 0.02*mud +1.01$	0.14	*	$C_{org} = 0.17*\delta^{13}C + 4.52$	0.22	**

Figure 1. Relationships among soil C_{org} and mud contents, and soil C_{org} and $\delta^{13}C$ signatures in all habitats and all soil depths studied: bare sediments, combined *Halodule*, *Halophila* and *Zostera* species, and combined *Amphibolis* and *Posidonia* species. Only correlations with R^2 >0.5 are showed. The grey shaded areas showed the range of $\delta^{13}C$ signatures of plant detritus (based on literature values; see main text). The white circles indicate the samples obviating the expected correlation between soil C_{org} and mud contents.

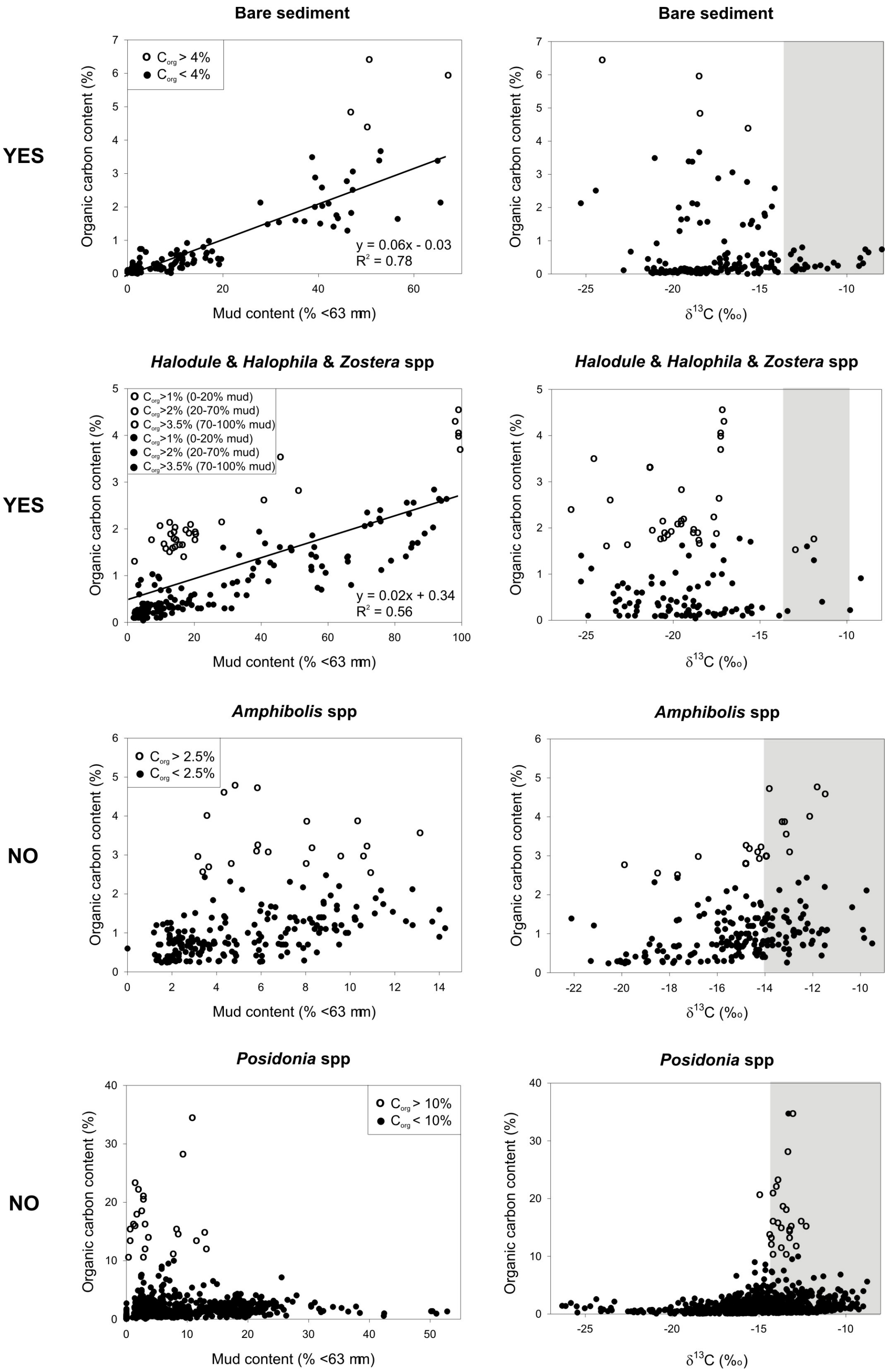
Bare sediment
YES
Organic carbon content (%)
C_org > 4%
C_org < 4%
y = 0.06x - 0.03
R² = 0.78
Mud content (% <63 mm)
Bare sediment
δ13C (‰)
Halodule & Halophila & Zostera spp
YES
C_org>1% (0-20% mud)
C_org>2% (20-70% mud)
C_org>3.5% (70-100% mud)
C_org>1% (0-20% mud)
C_org>2% (20-70% mud)
C_org>3.5% (70-100% mud)
y = 0.02x + 0.34
R² = 0.56
Mud content (% <63 mm)
Halodule & Halophila & Zostera spp
δ13C (‰)
Amphibolis spp
NO
C_org > 2.5%
C_org < 2.5%
Mud content (% <63 mm)
Amphibolis spp
δ13C (‰)
Posidonia spp
NO
C_org > 10%
C_org < 10%
Mud content (% <63 mm)
Posidonia spp
δ13C (‰)

Figure 2. Relationships among soil C_{org} and mud contents in 1 to 10 cm and 11 to 110 cm thick soils: bare sediments, combined *Halodule*, *Halophila* and *Zostera* species, and combined *Amphibolis* and *Posidonia* species. Only correlations with $R^2 > 0.5$ are showed. The white circles indicate the samples obviating the expected correlation between soil C_{org} and mud contents.

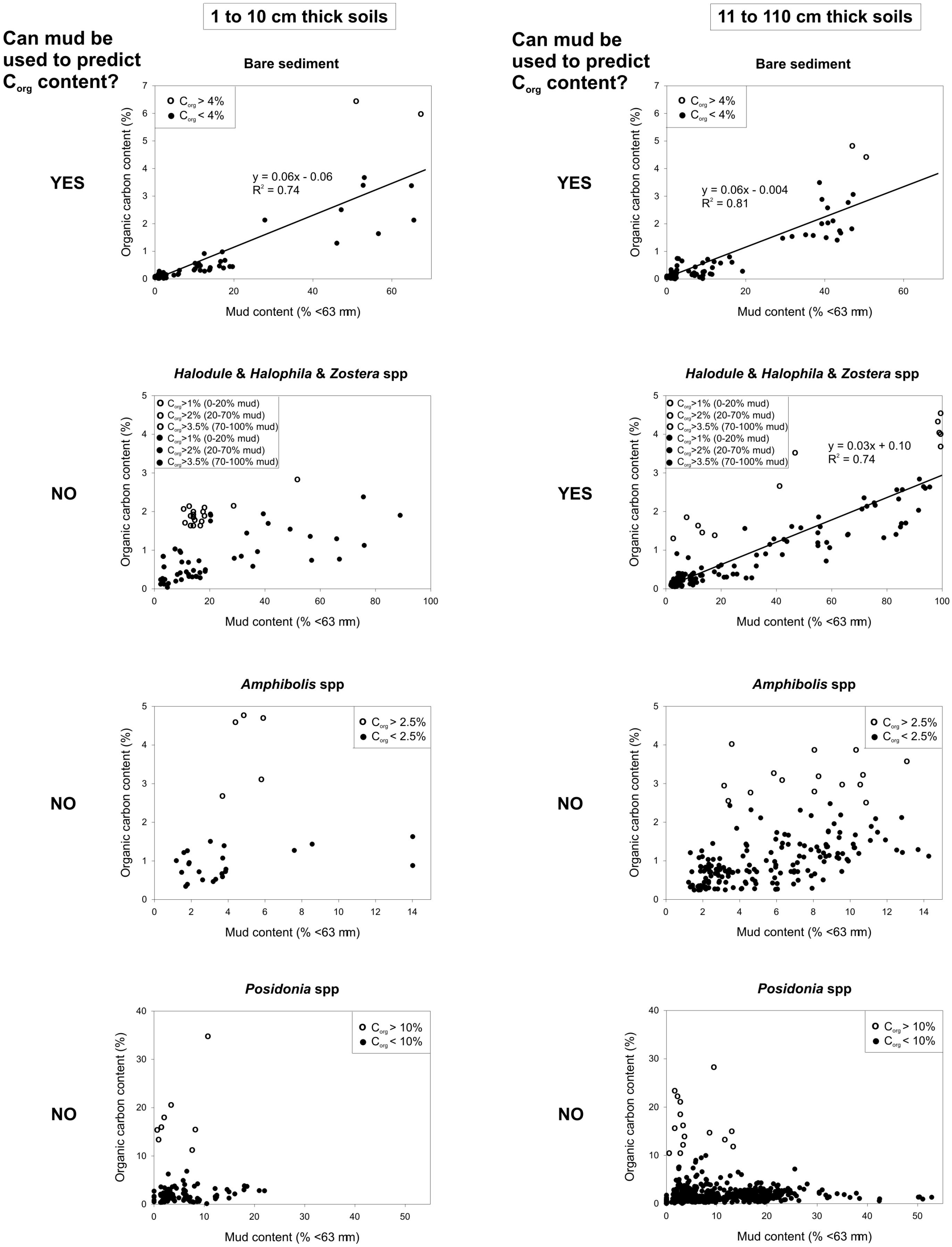
1 to 10 cm thick soils
11 to 110 cm thick soils
Can mud be used to predict C_{org} content?
Can mud be used to predict C_{org} content?
Bare sediment
YES
C_{org} > 4%
C_{org} < 4%
y = 0.06x - 0.06
R^2 = 0.74
Bare sediment
YES
y = 0.06x - 0.004
R^2 = 0.81
Halodule & Halophila & Zostera spp
NO
C_{org}>1% (0-20% mud)
C_{org}>2% (20-70% mud)
C_{org}>3.5% (70-100% mud)
Halodule & Halophila & Zostera spp
YES
y = 0.03x + 0.10
R^2 = 0.74
Amphibolis spp
NO
C_{org} > 2.5%
C_{org} < 2.5%
Amphibolis spp
NO
Posidonia spp
NO
C_{org} > 10%
C_{org} < 10%
Posidonia spp
NO
Organic carbon content (%)
Mud content (% <63 μm)

Figure 3. Relationships among soil C_{org} and mud contents, and soil C_{org} and $\delta^{13}C$ signatures in the coastal and estuarine habitats studied. The grey shaded areas showed the range of $\delta^{13}C$ signatures of plant detritus (based on literature values; see main text). The white circles indicate the samples obviating the expected correlation between soil C_{org} and mud contents.