



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

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## 26 **ABSTRACT**

27 The emerging field of blue carbon science is seeking cost-effective ways to estimate the organic  
 28 carbon content of soils that are bound by coastal vegetated ecosystems. Organic carbon ( $C_{org}$ )  
 29 content in terrestrial soils and marine sediments has been correlated with mud content (i.e. silt  
 30 and clay), however, empirical tests of this theory are lacking for coastal vegetated ecosystems.  
 31 Here, we compiled data ( $n = 1345$ ) on the relationship between  $C_{org}$  and mud (i.e. silt and clay,  
 32 particle sizes  $<63 \mu m$ ) contents in seagrass ecosystems (79 cores) and adjacent bare sediments  
 33 (21 cores) to address whether mud can be used to predict soil  $C_{org}$  content. We also combined  
 34 these data with the  $\delta^{13}C$  signatures of the soil  $C_{org}$  to understand the sources of  $C_{org}$  stores. The  
 35 results showed that mud is positively correlated with soil  $C_{org}$  content only when the contribution  
 36 of seagrass-derived  $C_{org}$  to the sedimentary  $C_{org}$  pool is relatively low, such as in small and fast-  
 37 growing meadows of the genera *Zostera*, *Halodule* and *Halophila*, and in bare sediments  
 38 adjacent to seagrass ecosystems. In large and long-living seagrass meadows of the genera  
 39 *Posidonia* and *Amphibolis* there was a lack of, or poor relationship between mud and soil  $C_{org}$   
 40 content, related to a higher contribution of seagrass-derived  $C_{org}$  to the sedimentary  $C_{org}$  pool in  
 41 these meadows. The relative high soil  $C_{org}$  contents with relatively low mud contents (i.e. mud-  
 42  $C_{org}$  saturation) together with significant allochthonous inputs of terrestrial organic matter could  
 43 overall disrupt the correlation expected between soil  $C_{org}$  and mud contents. This study shows  
 44 that mud (i.e. silt and clay content) is not a universal proxy for blue carbon content in seagrass  
 45 ecosystems, and therefore should not be applied generally across all seagrass habitats. Mud  
 46 content can only be used as a proxy to estimate soil  $C_{org}$  content for scaling up purposes when



47 opportunistic and/or low biomass seagrass species (i.e. *Zostera*, *Halodule* and *Halophila*) are  
48 present (explaining 34 to 91% of variability), and in bare sediments (explaining 78% of the  
49 variability).

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51



## 52 1. INTRODUCTION

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

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

70 The accumulation of  $C_{org}$  in seagrass meadows results from several processes: accretion  
71 (autochthonous plant and epiphyte production, and trapping of allochthonous  $C_{org}$ ; Kennedy et al.  
72 2010), erosion (e.g. export; Romero and Pergent, 1992; Hyndes et al. 2014) and decomposition  
73 (Mateo et al. 1997). Previous studies demonstrate that both autochthonous (e.g. plant detritus and  
74 epiphytes) and allochthonous (e.g. macroalgae, seston and terrestrial matter) sources contribute



75 to the  $C_{org}$  pool in seagrass soils (Kennedy et al. 2010; Watanabe and Kuwae, 2015). Plant net  
76 primary productivity is a key factor controlling the amount of  $C_{org}$  potentially available for  
77 sequestration in seagrass ecosystems (Serrano et al. 2014), but the depositional environment is an  
78 important factor controlling  $C_{org}$  storage in coastal habitats (De Falco et al. 2004; Lavery et al.  
79 2013).

80 Previous studies have shown a large variation in  $C_{org}$  stores among morphologically different  
81 seagrass species (Lavery et al. 2013; Rozaimi et al. 2013). Also, that  $C_{org}$  accumulates more in  
82 estuaries compared to coastal ocean environments (estimated at  $81 \text{ Tg } C_{org} \text{ y}^{-1}$  and  $45 \text{ Tg } C_{org} \text{ y}^{-1}$ ,  
83 respectively; Nellemann et al. 2009). This is due largely to estuaries being highly depositional  
84 environments, receiving fine-grained particles from terrestrial and coastal ecosystems which  
85 enhance  $C_{org}$  accumulation (i.e. silt and clay sediments retain more  $C_{org}$  compared to sands; Keil  
86 and Hedges, 1993; Burdige 2007) and preservation (i.e. reducing redox potentials and  
87 remineralization rates; Hedges and Keil, 1995; Dauwe et al. 2001; Burdige, 2007; Pedersen et al.  
88 2011). The inputs of seagrass-derived  $C_{org}$  in the sedimentary pool could break the linear  
89 relationship among mud (i.e. silt and clay particles) and  $C_{org}$  contents typically found in  
90 terrestrial (Nichols, 1984; McGrath and Zhang, 2003) and marine sedimentary environments  
91 (Bergamaschi et al. 1997; De Falco et al. 2004). However, the amount of  $C_{org}$  that can be  
92 associated with silt and clay particles is limited (Hassink, 1997), which could lead to a poor  
93 relationship between mud and soil  $C_{org}$  contents. Also, other factors found to play a key role in  
94 controlling soil  $C_{org}$  accumulation in terrestrial and coastal ecosystems, such as chemical  
95 stabilization of organic matter (Percival et al. 1999; Burdige, 2007), carbon in microbial biomass  
96 (Sparling, 1992; Danovaro et al. 1995), and soil temperature (Pedersen et al. 2011), could also  
97 influence  $C_{org}$  storage in seagrass meadows.



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

106

## 107 2. MATERIAL AND METHODS

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

117 Sediment cores were sampled by means of percussion and rotation, or vibrocoreing (ranging  
118 from 10 to 475 cm long). The core barrels consisted of PVC or aluminium pipes (50 to 90 mm  
119 inside diameter) with sharpened 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<sub>org</sub> 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<sub>org</sub> was calculated for the bulk (pre-acidified) samples. Carbon isotope ratios are expressed as  $\delta$  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  $\mu$ m) was determined, and expressed as a percentage of the bulk sample.

Pearson correlation analysis was used to test for significant relationships among C<sub>org</sub> and mud contents, and C<sub>org</sub> and  $\delta^{13}\text{C}$  signatures. Correlations between the variables studied were tested among seagrass species (9 categories) and bare sediments, seagrass genera (4 categories) and habitat geomorphology (coastal and estuarine habitats).

### 3. RESULTS



143 The soil organic carbon ( $C_{org}$ ) and mud contents varied within the seagrass meadows and  
144 bare sediments studied in Australia and Spain. The soil  $C_{org}$  and mud contents were higher in  
145 seagrass meadows (average  $\pm$  SE,  $1.5 \pm 0.2\%$  and  $18 \pm 2.4\%$ , respectively) compared to bare  
146 sediments ( $0.6 \pm 0.1\%$  and  $10.8 \pm 1.2\%$ , respectively; Table 2). On average, seagrass meadows  
147 of the genera *Amphibolis* and *Posidonia* contained higher soil  $C_{org}$  ( $1.6 \pm 0.1\%$ ) and lower mud  
148 ( $7.2 \pm 0.4$ ) than meadows of *Halophila*, *Halodule* and *Zostera* ( $1.2 \pm 0.2\%$  and  $34.9 \pm 5.4\%$ ,  
149 respectively; Table 2). Overall, carbon isotopic ratios from sedimentary organic matter ( $\delta^{13}C$ )  
150 were similar between seagrass soils and bare sediments ( $-17.6 \pm 0.3\text{‰}$  and  $-17.3 \pm 0.2\text{‰}$ ,  
151 respectively). The  $C_{org}$  in soils from *Posidonia* and *Amphibolis* meadows were  $^{13}C$ -enriched ( $-$   
152  $15.5 \pm 0.3\text{‰}$ ) compared with seagrass soils from *Halophila*, *Halodule* and *Zostera* meadows ( $-$   
153  $20.7 \pm 0.4\text{‰}$ ; Table 2). The  $C_{org}$  content in soils from estuarine and coastal habitats were similar,  
154 while mud content in estuarine sediments was higher and  $\delta^{13}C$  values depleted when compared  
155 to coastal habitats (Table 2).

156 The relationships between the variables studied (i.e.  $\%C_{org}$ ,  $\%$  mud, and  $\delta^{13}C$  signatures of  
157 sedimentary  $C_{org}$ ) in all cores were explored in Figure 1 and 2, and Table 3. The  $C_{org}$  content  
158 increased with increasing mud content in bare sediments ( $R^2 = 0.78$ ) and at species level (9  
159 species in total), except for *Amphibolis griffithii* (Table 3). Although most of the correlations at  
160 species level were significant, they only explain 2 to 39% of the trends described, except for  
161 *Halophila ovalis* (91%; Table 3). In particular, *Posidonia* meadows (*P. australis*, *P. sinuosa* and  
162 *P. oceanica*) had the lower correlation values ( $R^2$  ranged from 0.02 to 0.15). When combining  
163 mud and  $C_{org}$  contents in seagrass meadows of the colonizing and opportunistic genera  
164 *Halophila*, *Halodule* and *Zostera* (Kilminster et al. 2015), a relatively high correlation was found  
165 ( $R^2 = 0.56$ ; Figure 1), while soil  $C_{org}$  and mud contents in persistent genera were only slightly





166 positively correlated in combined *Amphibolis* spp and not correlated in *Posidonia* spp meadows  
167 (Figure 1). The classification of habitats based on geomorphology (i.e. coastal and estuarine)  
168 showed a lack of correlation between soil  $C_{org}$  and mud contents in coastal ecosystems, and a  
169 poor but slightly significant correlation in estuarine ecosystems ( $R^2 = 0.14$ ; Figure 2 and Table  
170 3).

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

179

#### 180 4. DISCUSSION

181 Overall mud content is a poor predictor of soil  $C_{org}$  in seagrass meadows and care should be  
182 taken in its use as a cost-effective proxy or indicator of  $C_{org}$  for scaling-up purposes in the  
183 emerging field of blue carbon science. Although we describe some promise for opportunistic and  
184 early colonizing *Halophila*, *Halodule* and *Zostera* meadows (i.e. mud content explained 34 to  
185 91% of variability in  $C_{org}$  content) and in bare sediments adjacent to seagrass meadows  
186 (explaining 78% of the variability), mud is not a universal proxy for blue carbon content and  
187 therefore should not be applied generally across all seagrass habitats. In particular, mud content  
188 only explained 5 to 32% of soil  $C_{org}$  content in *Amphibolis* spp meadows and 2 to 15% of soil



189  $C_{org}$  content in *Posidonia* spp meadows, and therefore, mud content is not a good proxy for blue  
190 carbon content in these meadows.

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

208 Mud is not a universal proxy for soil  $C_{org}$  content in seagrass meadows, which could be  
209 mainly explained by additional inputs of seagrass-derived  $C_{org}$  to the sedimentary  $C_{org}$  pool,  
210 ending the linear relationship between mud and  $C_{org}$  contents found in the absence of vegetation.  
211 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  $-15 \pm 0.2\%$  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 *Posidonia* and *Amphibolis* soils could be explained by their relatively low mud content and  $^{13}C$ -enriched soil  $C_{org}$ , indicating that the contribution of seagrass-derived  $C_{org}$  (i.e. root, rhizome and sheath detritus) in their soils play a much larger role than the accumulation of fine, organic-rich allochthonous particles.

On the other hand, the soil  $\delta^{13}C$  signatures measured in *Halodule*, *Halophila* and *Zostera* meadows (averaging  $-21 \pm 0.4\%$ ) were more similar to  $\delta^{13}C$  values of algae or terrestrial organic matter than to  $\delta^{13}C$  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



235 contents (i.e. mud- $C_{org}$  saturation) disrupted the correlation found between soil  $C_{org}$  and mud  
236 contents in these meadows (Figure 1).

237 The results obtained showed a tendency for high-biomass and persistent meadows (i.e.  
238 *Posidonia* and *Amphibolis*) to accumulate higher  $C_{org}$  stores and seagrass-derived  $C_{org}$  compared  
239 to ephemeral and low-biomass meadows (i.e. *Halophila*, *Halodule* and *Zostera*), suggesting that  
240 factors (biotic and abiotic) affecting the production, form and preservation of  $C_{org}$  within habitats  
241 exert a significant influence on soil  $C_{org}$  content (Lavery et al. 2013; Serrano et al. 2014, 2015).  
242 The above- and belowground biomass in meadows of the genus *Posidonia* (averaging 535 and  
243 910 g DW m<sup>-2</sup>, respectively) is up to 2-fold higher than in *Amphibolis* meadows (averaging 641  
244 and 457 g DW m<sup>-2</sup>, respectively) and 4 to 18-fold higher than in small and opportunistic  
245 seagrasses of the genera *Halophila*, *Halodule* and *Zostera* (125 and 49 g DW m<sup>-2</sup>, on average;  
246 respectively; Duarte and Chiscano, 1999; Paling and McComb 2000). Indeed, larger seagrasses  
247 tend to have larger and more persistent rhizomes, constituted by more refractory forms of  $C_{org}$ ,  
248 more prone to be preserved in soils than simpler, more labile forms of  $C_{org}$  such as seston and  
249 algal detritus which are more suitable to experience remineralization during early diagenesis  
250 (Henrichs 1992; Burdige, 2007).

251 Habitat conditions in seagrass meadows not only influence the amount of  $C_{org}$  accumulation  
252 through detrital plant inputs, but the capacity of the plant canopies to retain particles (Gacia et al.  
253 1999). The amount of fine suspended particles available for burial varies among sites, driven by  
254 geomorphological features (e.g. run-off, hydrodynamic energy and water depth), while meadow  
255 structure (i.e. density, cover and morphology of the canopy) constrains their capacity to  
256 accumulate sediment particles (Hendriks et al. 2010; Peralta et al. 2008). Although the number of  
257 cores and species studied in coastal and estuarine ecosystems was unbalanced (i.e. *Amphibolis*



258 and *Posidonia* dominate in coastal habitats and *Halophila*, *Halodule*, *Zostera* dominate in  
259 estuarine habitats), the lack of, or poor correlations found within estuarine and coastal  
260 ecosystems, precludes the general use of mud as a predictor of blue carbon content based on  
261 habitat geomorphology (Figure 2). Seagrass meadows and bare sediments in environments  
262 conducive for depositional processes (i.e. estuaries) accumulated up to 4-fold higher amounts of  
263 mud compared to other coastal ecosystems, but the saturation of mud with  $C_{org}$  and the large  
264 contribution of seagrass detritus into the sedimentary  $C_{org}$  pool ( $^{13}C$ -enriched soils) in some study  
265 sites disrupted the positive relationship expected between mud and soil- $C_{org}$  contents. In  
266 estuarine ecosystems, soil  $C_{org}$  originated from both mud inputs linked to allochthonous- $C_{org}$  via  
267 deposition from upstream transport (e.g. Aller, 1998) and seagrass inputs. The insignificant  
268 relationship between mud and soil  $C_{org}$  contents in coastal habitats could be explained by their  
269 relatively low mud content and the accumulation of seagrass-derived  $C_{org}$ .

270 In sum, mud is not a universal proxy for blue carbon content in seagrass ecosystems and  
271 should not be applied generally across all habitat and vegetation types. Overall, the positive  
272 relationship between mud and  $C_{org}$  contents found in bare sediments and in opportunistic and/or  
273 low biomass seagrass meadows (i.e. genera *Zostera*, *Halodule* and *Halophila*) allow mud to be  
274 used as a proxy for  $C_{org}$  content in these ecosystems, thereby enabling robust scaling up exercises  
275 (i.e. benefiting from existing geological surveys and models) at low cost as part of blue carbon  
276 stock assessment programs. However, mud content is not a good predictor of  $C_{org}$  content in  
277 highly productive meadows such as those constituted by *P. oceanica* in the Mediterranean Sea  
278 and *P. australis*, *P. sinuosa* and *Amphibolis* spp in Australia. Other biological, chemical and  
279 geological factors not explored in detail in this study may also play a key role in  $C_{org}$  storage, and  
280 ultimately in the relationship between soil  $C_{org}$  and mud contents. For example, the effects of



281 habitat geomorphology (e.g. hydrodynamic energy, terrestrial mud and  $C_{org}$  inputs, export of  
282 seagrass biomass) and species identity (e.g. variation in terms of productivity, oxygen exposure  
283 and recalcitrance of  $C_{org}$  stores, and plant influence on sediment retention) within both coastal  
284 and estuarine environments, are among the factors identified in this study which might explain  
285 significant variation in the  $C_{org}$  stores of meadows in relatively similar exposure conditions.  
286 Other factors found to play a key role in controlling soil  $C_{org}$  accumulation in terrestrial  
287 ecosystems, such as chemical stabilization of organic matter (Percival et al. 1999; Galy et al.  
288 2008) and microbial biomass carbon (Danovaro et al. 1994), could also influence  $C_{org}$  storage in  
289 seagrass ecosystems. Further studies are needed to identify the influences of these other factors  
290 on  $C_{org}$  storage in seagrass meadows, and in addition to the mud content, other characteristics  
291 should be taken into account when attempting to obtain robust estimates of  $C_{org}$  stores within  
292 coastal areas.

293

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## 458 Tables and Figures

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

462

Species	Study site	Geomorphology	Number of cores	Number of samples	Core depth (cm)	Water depth (m)
<i>Amphibolis</i> (mixed spp)	Rottneest Island, WA, Australia	Coastal	2	68	0-120	2
	Shark Bay, WA, Australia	Coastal	1	38	0-170	2
<i>Amphibolis antarctica</i>	Shark Bay, WA, Australia	Coastal	2	63	0-200	2-3
<i>Amphibolis griffithiae</i>	Jurien Bay, WA, Australia	Coastal	2	41	0-70	4
<i>Posidonia australis</i>	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
<i>Posidonia sinuosa</i>	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
<i>Posidonia oceanica</i>	Portlligat, Spain	Coastal	1	192	475	3
	Balearic Islands, Spain	Coastal	6	25	0-270	3
<i>Halodule uninervis</i>	Carnarvon, WA, Australia	Estuarine	1	39	0-210	2
	Gladstone, QLD, Australia	Estuarine	6	6	0-10	intertidal
<i>Halophila decipiens</i>	Gladstone, QLD, Australia	Estuarine	2	2	0-10	intertidal
<i>Halophila ovalis</i>	Rottneest 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
<i>Zostera muelleri</i>	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

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

a)

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

b)

Habitat (geomorphology)	Organic carbon (%)			$\delta^{13}C$ (‰)			Mud (%)		
	N	Mean	SE	N	Mean	SE	N	Mean	SE
<i>Coastal</i>	1026	1.59	0.09	1014	-15.70	0.10	1026	6.85	0.24
<i>Estuarine</i>	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; based on (a) species identity and (b) habitat geomorphology.

a)

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

b)

Habitat (geomorphology)	Organic carbon (%) vs mud (%)			Organic carbon (%) vs $\delta^{13}C$ (‰)		
	Formula	$R^2$	P value	Formula	$R^2$	P value
Coastal	na	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	**

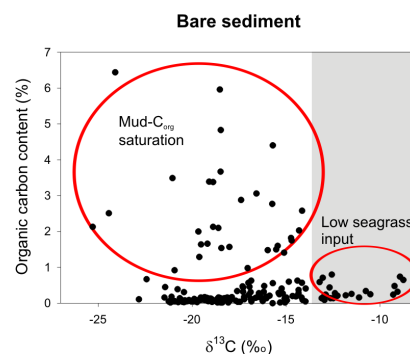
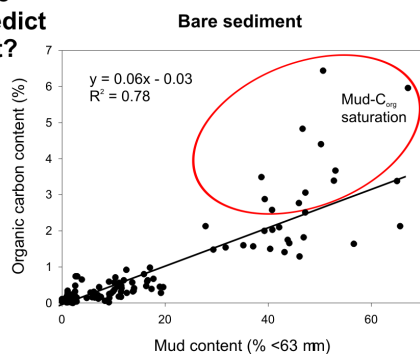


484 **Figure 1.** Relationships among soil C<sub>org</sub> and mud contents, and soil C<sub>org</sub> and  $\delta^{13}\text{C}$  signatures in  
485 the habitats studied: bare sediments, combined *Halodule*, *Halophila* and *Zostera* species, and  
486 combined *Amphibolis* and *Posidonia* species. Only correlations with  $R^2 > 0.5$  are showed. The  
487 grey shaded areas showed the range of  $\delta^{13}\text{C}$  signatures of plant detritus (based on literature  
488 values; see main text). The red circles indicate the samples showing mud-C<sub>org</sub> saturation, while  
489 the red intermittent circles showed samples with high contribution of seagrass-derived C<sub>org</sub>.

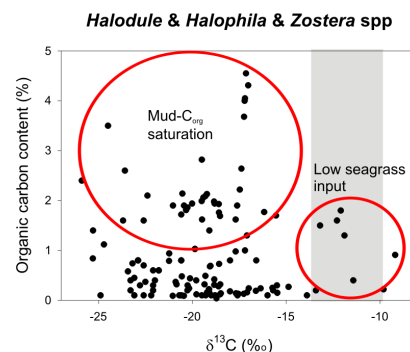
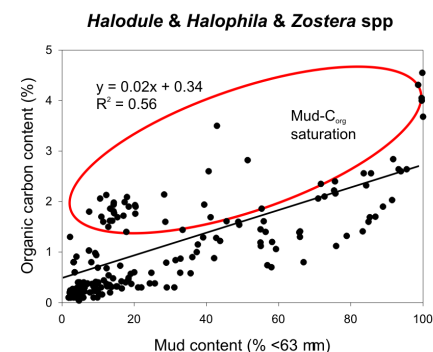


Can mud be  
 used to predict  
 $C_{org}$  content?

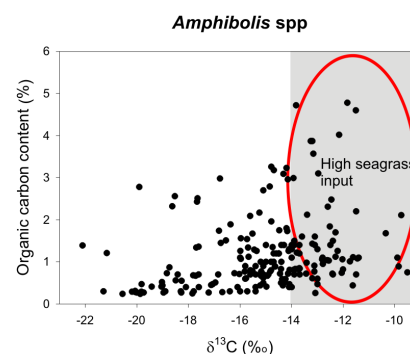
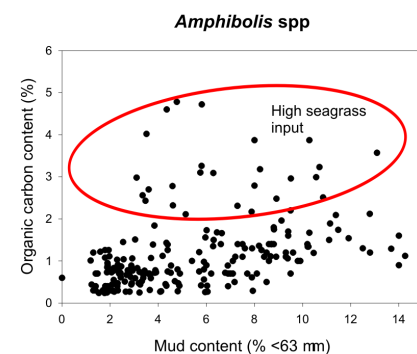
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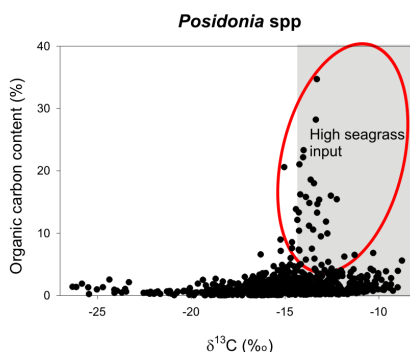
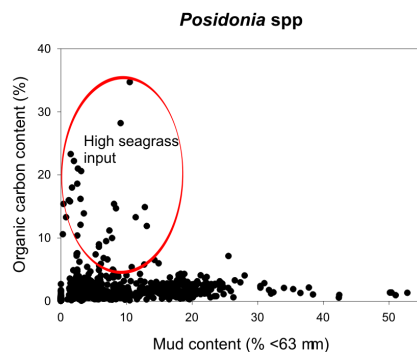
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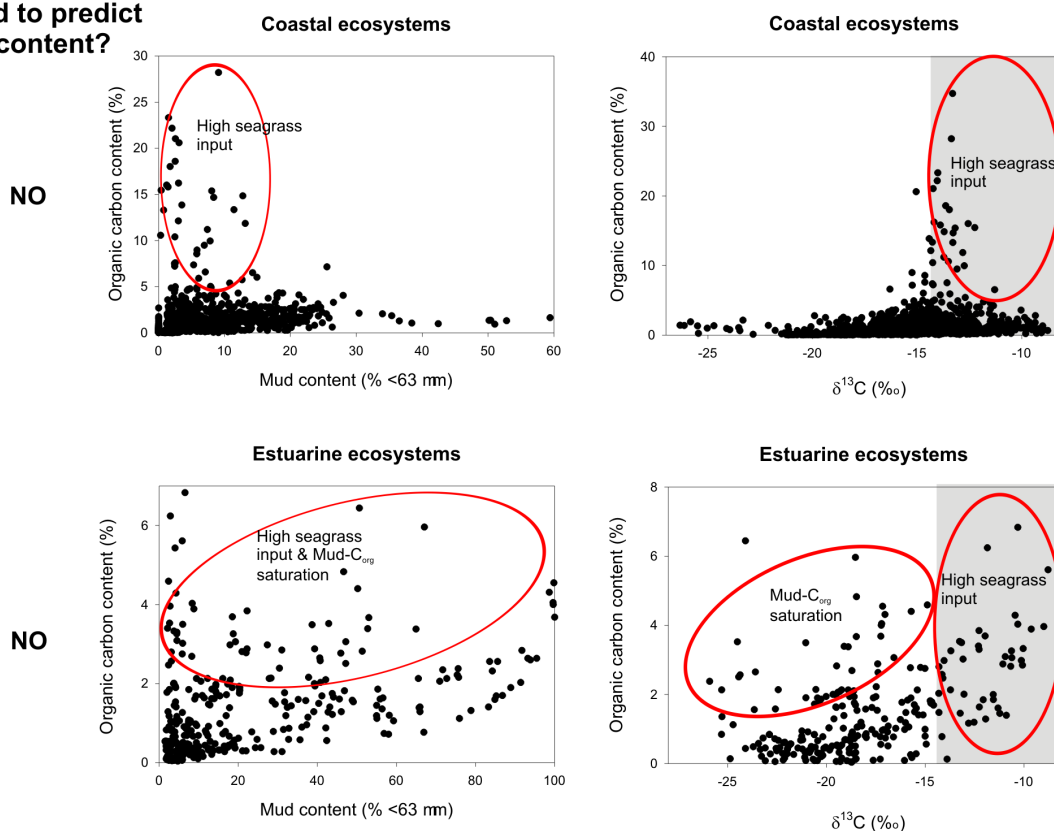
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491 **Figure 2.** Relationships among soil  $C_{org}$  and mud contents, and soil  $C_{org}$  and  $\delta^{13}C$  signatures in  
 492 the coastal and estuarine habitats studied. The grey shaded areas showed the range of  $\delta^{13}C$   
 493 signatures of plant detritus (based on literature values; see main text). The red circles indicate  
 494 the samples showing mud- $C_{org}$  saturation, while the red intermittent circles showed samples  
 495 with high contribution of seagrass-derived  $C_{org}$ .

**Can mud be  
 used to predict  
 $C_{org}$  content?**



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