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, particle sizes <63 µm), however, empirical tests of this theory are lacking for coastal

31 vegetated ecosystems. Here, we compiled data (n = 1345) on the relationship between C_{org} and

32 mud contents in seagrass ecosystems (79 cores) and adjacent bare sediments (21 cores) to

33 address whether mud can be used to predict soil C_{org} content. We also combined these data with

34 the $\delta^{13}C$ signatures of the soil C_{org} to understand the sources of C_{org} stores. The results showed

35 that mud is positively correlated with soil C_{org} content only when the contribution of seagrass-

36 derived C_{org} to the sedimentary C_{org} pool is relatively low, such as in small and fast-growing

37 meadows of the genera *Zostera*, *Halodule* and *Halophila*, and in bare sediments adjacent to

38 seagrass ecosystems. In large and long-living seagrass meadows of the genera *Posidonia* and

39 *Amphibolis* there was a lack of, or poor relationship between mud and soil C_{org} content, related to

40 a higher contribution of seagrass-derived C_{org} to the sedimentary C_{org} pool in these meadows.

41 The relative high soil C_{org} contents with relatively low mud contents (e.g. mud-C_{org} saturation) in

42 bare sediments and *Zostera*, *Halodule* and *Halophila* meadows was related to significant

43 allochthonous inputs of terrestrial organic matter, while higher contribution of seagrass detritus

44 in *Amphibolis* and *Posidonia* meadows disrupted the correlation expected between soil C_{org} and

45 mud contents. This study shows that mud is not a universal proxy for blue carbon content in

46 seagrass ecosystems, and therefore should not be applied generally across all seagrass habitats.

47 Mud content can only be used as a proxy to estimate soil C_{org} content for scaling up purposes

48 when opportunistic and/or low biomass seagrass species (i.e. *Zostera*, *Halodule* and *Halophila*)

49 are present (explaining 34 to 91% of variability), and in bare sediments (explaining 78% of the

50 variability). The results obtained could enable robust scaling up exercises at a low cost as part of

51 blue carbon stock assessments.

52

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

76 to the C_{org} pool in seagrass soils (Kennedy et al. 2010; Watanabe and Kuwae, 2015). Plant net

77 primary productivity is a key factor controlling the amount of C_{org} potentially available for

78 sequestration in seagrass ecosystems (Serrano et al. 2014), but the depositional environment is an

79 important factor controlling C_{org} storage in coastal habitats (De Falco et al. 2004; Lavery et al.

80 2013).

81 Previous studies have shown a large variation in C_{org} stores among morphologically different

82 seagrass species (Lavery et al. 2013; Rozaimi et al. 2013). Also, that C_{org} accumulates more in

83 estuaries compared to coastal ocean environments (estimated at 81 Tg C_{org} y^{-1} and 45 Tg C_{org} y^{-1},

84 respectively; Nellemann et al. 2009). This is due largely to estuaries being highly depositional

85 environments, receiving fine-grained particles from terrestrial and coastal ecosystems which

86 enhance C_{org} accumulation (i.e. silt and clay sediments retain more C_{org} compared to sands; Keil

87 and Hedges, 1993; Burdige 2007) and preservation (i.e. reducing redox potentials and

88 remineralization rates; Hedges and Keil, 1995; Dauwe et al. 2001; Burdige, 2007; Pedersen et al.

89 2011). The inputs of seagrass-derived C_{org} in the sedimentary pool could break the linear

90 relationship among mud (i.e. silt and clay particles) and C_{org} contents typically found in

91 terrestrial (Nichols, 1984; McGrath and Zhang, 2003) and marine sedimentary environments

92 (Bergamaschi et al. 1997; De Falco et al. 2004). However, the amount of C_{org} that can be

93 associated with mud particles is limited (Hassink, 1997), which could lead to a poor relationship

94 between mud and soil C_{org} contents. Also, other factors found to play a key role in controlling

95 soil C_{org} accumulation in terrestrial and coastal ecosystems, such as chemical stabilization of

96 organic matter (Percival et al. 1999; Burdige, 2007), carbon in microbial biomass (Sparling,

97 1992; Danovaro et al. 1995), and soil temperature (Pedersen et al. 2011), could also influence

98 C_{org} storage in seagrass meadows.

99 A significant relationship between mud and C_{org} contents would allow mud to be used as a

100 proxy for C_{org} content, thereby enabling robust scaling up exercises at a low cost as part of blue

101 carbon stock assessments. Furthermore, since most countries have conducted geological surveys

102 within the coastal zone to determine sediment grain size, a strong, positive relationship between

103 mud and C_{org} contents would allow the development of geomorphology models to predict blue

104 carbon content within seagrass meadows, dramatically improving global estimates of blue carbon

105 storage. The purpose of this study was therefore to test for relationships between C_{org} and mud

106 contents within seagrass ecosystems and adjacent bare sediments.

107

2. MATERIAL AND METHODS

109 Data was compiled from a number of published and unpublished studies from Australia and

110 Spain, in seagrass meadows across diverse habitats (Table 1). The study sites encompass

111 monospecific and/or mixed meadows from a variety of temperate and tropical seagrass species of

112 the genera *Posidonia*, *Amphibolis*, *Zostera*, *Halophila* and *Halodule*, and adjacent bare

113 sediments, while including a variety of depositional environments (from estuarine to exposed

114 coastal areas encompassing different water depths, from intertidal to the deep limit of seagrass

115 distribution; Table 1). Data from 100 cores (79 from seagrass meadows and 21 from bare

116 sediments) on sediment grain size, organic carbon (C_{org}) content and stable carbon isotope

117 signatures of the C_{org} ($\delta^{13}C$) was explored in this study (N = 1345).

118 Sediment cores were sampled by means of percusion and rotation, or vibrocoring (ranging

119 from 10 to 475 cm long). The core barrels consisted of PVC or aluminium pipes (50 to 90 mm

120 inside diamater) with sharpenned ends to cut fibrous material and minimize core shortening

121 (compression) during coring (Serrano et al. 2012, 2014). All cores were sealed at both ends,

122 transported vertically to the laboratory and stored at 5°C before processing.

123 The cores were sliced at regular intervals, each slice/sample was weighed before and after

124 oven drying to constant weight at 70°C (DW), and subsequently sub-divided for analysis. The

125 C_{org} elemental and isotopic composition of the organic matter was measured in milled

126 subsamples from several slices along the cores. The sediment core sub-samples were acidified

127 with 1 M HCl, centrifuged (3500 RPM; 5 minutes) and the supernatant with acid residues was

128 removed using a pipette, then washed in deionized water, centrifuged again and the supernatant

129 removed. The residual samples were re-dried (70°C) before carbon elemental and isotopic

130 analyses. The samples were encapsulated and the organic carbon elemental and isotopic

131 composition was analyzed using an elemental analyzer interfaced with an isotope ratio mass

132 spectrometer. Percentage C_{org} was calculated for the bulk (pre-acidified) samples. Carbon isotope

133 ratios are expressed as δ values in parts per thousand (‰) relative to VPDB (Vienna Pee Dee

134 Belemnite). For sediment grain size analysis, a Coulter LS230 laser-diffraction particle analyzer

135 was used following digestion of the samples with 10% hydrogen peroxide. The mud content in

136 the sediments (<63 μm) was determined, and expressed as a percentage of the bulk sample.

137 Pearson correlation analysis was used to test for significant relationships among C_{org} and

138 mud contents, and C_{org} and $\delta^{13}C$ signatures. Correlations between the variables studied were

139 tested among seagrass species (9 categories) and bare sediments, seagrass genera (4 categories),

140 habitat geomorphology (coastal and estuarine habitats) and soil depth (in 1 to 10 cm-thick and 11

141 to 110 cm-thick deposits).

142

143 **3. RESULTS**

144	The soil organic carbon (C_{org}) and mud contents varied within the seagrass meadows and

145	bare sediments studied in Australia and Spain. The soil C_{org} and mud contents were higher in

146	seagrass meadows (average ± SE, 1.5 ± 0.2% and 18 ± 2.4%, respectively) compared to bare

147	sediments (0.6 ± 0.1% and 10.8 ±1 .2%, respectively; Table 2). On average, seagrass meadows

148	of the genera *Amphibolis* and *Posidonia* contained higher soil C_{org} (1.6 ± 0.1%) and lower mud

149	(7.2 ± 0.4) than meadows of *Halophila*, *Halodule* and *Zostera* (1.2 ± 0.2% and 34.9 ± 5.4%,

150	respectively; Table 2). Overall, carbon isotopic ratios from sedimentary organic matter (δ^{13}C)

151	were similar between seagrass soils and bare sediments (-17.6 ± 0.3‰ and -17.3 ± 0.2‰,

152	respectively). The C_{org} in soils from *Posidonia* and *Amphibolis* meadows were ^{13}C-enriched (-

153	15.5 ± 0.3‰) compared with seagrass soils from *Halophila*, *Halodule* and *Zostera* meadows (-

154	20.7 ± 0.4‰; Table 2). The C_{org} content in soils from estuarine and coastal habitats were similar,

155	while mud content in estuarine sediments was higher and δ^{13}C values depleted when compared

156	to coastal habitats (Table 2).

157	The relationships between the variables studied (i.e. %C_{org}, %mud, and δ^{13}C signatures of

158	sedimentary C_{org}) among different species and habitat geomorphologies, and among different soil

159	depths were explored in Figures 1 to 3, and Table 3. When accounting for the whole dataset (up

160	to 475 cm long cores), the C_{org} content increased with increasing mud content in bare sediments

161	(R^2 = 0.78) and at species level, except for *Posidonia oceanica* (i.e. C_{org} content decreased with

162	increasing mud content; R^2 = 0.15) and *Amphibolis griffithii* (i.e. no relationship was found, R^2 =

163	0.05; Table 3). Although most of the correlations at species level were significant, they only

164	explain 2 to 39% of the variance in trends described, except for *Halophila ovalis* (91%; Table 3).

165	In particular, *Posidonia* meadows (*P. australis*, *P. sinuosa* and *P. oceanica*) had the lower

166	correlation values (R^2 ranged from 0.02 to 0.15). When combining mud and C_{org} contents in

167   seagrass meadows of the colonizing and opportunistic genera *Halophila*, *Halodule* and *Zostera*

168   (Kilminster et al. 2015), a relatively high correlation was found (R^2 = 0.56; Figure 1), while soil

169   C_{org} and mud contents in persistent genera were only slightly positively correlated in combined

170   *Amphibolis* spp and not correlated in *Posidonia* spp meadows (Figure 1).

171   The relationships between soil C_{org} and mud contents within different core depths (from 1 to

172   10 cm-thick deposits, and from 11 to up to 110 cm-thick deposits) for bare sediments and each

173   group of seagrass species were explored in Figure 2. The C_{org} content increased with increasing

174   mud content in bare sediments for both 1 to 10 cm-thick (R^2 = 0.74) and 11 to 110 cm-thick (R^2

175   = 0.81) soils. When combining mud and C_{org} contents in seagrass meadows of the genera

176   *Halophila*, *Halodule* and *Zostera*, a higher correlation was found for deeper core sections (11 to

177   110 cm-thick; R^2 = 0.74) compared to top core sections (1 to 10 cm-thick; R^2 = 0.17). For

178   combined *Amphibolis* and *Posidonia* species, soil C_{org} and mud contents were only slightly

179   positively correlated in deeper *Amphibolis* spp sections (11 to 110 cm-thick; R^2 = 0.23) and not

180   correlated in *Posidonia* spp meadows (Figure 2). The classification of habitats based on

181   geomorphology (i.e. coastal and estuarine) showed a lack of correlation between soil C_{org} and

182   mud contents in coastal ecosystems, and a poor correlation in estuarine ecosystems (R^2 = 0.14;

183   Figure 3 and Table 3).

184   The relationships between soil %C_{org} and $\delta^{13}C$ signatures were poor for all individual

185   *Amphibolis* and *Posidonia* species studied (R^2 ranging from 0.09 to 0.3; Table 3), and for

186   combined *Amphibolis* spp (Figure 1), with a tendency of C_{org}-rich soils being enriched in ^{13}C

187   (Figure 1). In contrast, %C_{org} and $\delta^{13}C$ signatures were not correlated in any of the small and

188   fast-growing *Halodule*, *Zostera*, *Halophila* meadows studied (Table 3), neither individually nor

189   when combined (Figure 1 and Table 3). A lack of correlation between soil %C_{org} and $\delta^{13}C$

190 signatures was also found in bare sediments adjacent to seagrass meadows (Figure 3 and Table

191 3).

192

4. DISCUSSION

194 Overall mud content is a poor predictor of soil C_{org} in seagrass meadows and care should be

195 taken in its use as a cost-effective proxy or indicator of C_{org} for scaling-up purposes in the

196 emerging field of blue carbon science. Although we describe some promise for opportunistic and

197 early colonizing *Halophila*, *Halodule* and *Zostera* meadows (i.e. mud content explained 34 to

198 91% of variability in C_{org} content) and in bare sediments adjacent to seagrass meadows

199 (explaining 78% of the variability), mud is not a universal proxy for blue carbon content and

200 therefore should not be applied generally across all seagrass habitats. In particular, mud content

201 only explained 5 to 32% of soil C_{org} content in *Amphibolis* spp meadows and 2 to 15% of soil

202 C_{org} content in *Posidonia* spp meadows, and therefore, mud content is not a good proxy for blue

203 carbon content in these meadows.

204 A tenet of carbon cycling within the coastal ocean is that fine-grained sediments (i.e. mud)

205 have higher C_{org} contents. The positive relationship found between mud and C_{org} contents in

206 coastal bare sediments (explaining 78% of the variability) is in agreement with previous studies

207 (e.g. Bergamaschi et al. 1997; De Falco et al. 2004), and is related to their larger surface areas

208 compared to coarse-grained sediments, providing more binding sites for C_{org} on the surface of

209 minerals (Keil and Hedges, 1993; Mayer, 1994a, 1994b; Galy et al. 2007; Burdige 2007). In

210 addition, the predominance of fine sediments reduces oxygen exchange and results in low

211 sediment redox potentials and remineralization rates, contributing to the preservation of

212 sedimentary C_{org} after burial (Hedges and Keil, 1995; Bergamaschi et al. 1997; Dauwe et al.

213   2001; Burdige 2007; Pedersen et al. 2011). However, the maximum capacity of a given soil to

214   preserve C_{org} by their association with clay and silt particles is limited (i.e. mud-C_{org} saturation;

215   Hassink, 1997). The results obtained showed that bare sediment samples with relative high C_{org}

216   contents (i.e. >4% C_{org}) and relatively low mud contents were also ^{13}C-depleted (Figure 1),

217   suggesting significant contributions of soil C_{org} from allochthonous sources (e.g. terrestrial and

218   sestonic; Kennedy et al. 2010). This could have disrupted the correlation found between soil C_{org}

219   and mud contents in the bare sediments studied.

220   Mud is not a universal proxy for soil C_{org} content in seagrass meadows, which could be

221   mainly explained by additional inputs of seagrass-derived C_{org} and/or allocthonous C_{org} to the

222   sedimentary C_{org} pool, obviating the linear relationship between mud and C_{org} contents found in

223   the absence of vegetation. The δ^{13}C values indicated that both seagrass-C_{org} and non-seagrass-

224   derived C_{org} (i.e. epiphytes, algae, seston or terrestrial matter) were buried in the soils of all

225   studied meadows, but are consistent with a model of increasing capture of seagrass-derived C_{org}

226   at meadows formed by persistent, high-biomass seagrasses (i.e. genera *Posidonia* and

227   *Amphibolis*) relative to opportunistic, low-biomass seagrasses (i.e. genera *Halophila*, *Halodule*

228   and *Zostera*).

229   On one hand, the soil δ^{13}C signatures measured in these long-living and large seagrass

230   meadows (averaging -15 ± 0.2‰ in both cases) were closer to the δ^{13}C signatures of *Posidonia*

231   and *Amphibolis* tissues (ranging from -8 to -14‰; Hyndes and Lavery 2005; Hindell et al. 2004;

232   Cardona et al. 2007; Fourqurean et al. 2007; Collier et al. 2008; Kennedy et al. 2010; Hanson et

233   al. 2010; Serrano et al. 2015) than to δ^{13}C values of algae or terrestrial organic matter (ranging

234   from -18 to -32‰; e.g. Smit et al. 2006; Cardona et al. 2007; Kennedy et al. 2010; Hanson et al

235   2010; Deudero et al. 2011). The poor relationship between mud and soil C_{org} contents in

236 *Amphibolis* soils could be explained by samples with relative high C_{org} contents (i.e. >2.5% C_{org})

237 and relatively low mud contents, as a result of both the contribution of seagrass-derived C_{org} (i.e.

238 ^{13}C-enriched) and C_{org} from allochthonous sources (i.e. ^{13}C-depleted; Figure 1). In *Posidonia*

239 soils, the poor relationship between mud and soil C_{org} contents could be explained by samples

240 with relative high C_{org} contents (i.e. >10% C_{org}) and relatively low mud contents, as a result of

241 the contribution of seagrass-derived C_{org} (i.e. ^{13}C-enriched; Figure 1). The contribution of

242 seagrass-derived C_{org} (i.e. root, rhizome and sheath detritus) in *Posidonia* soils play a much

243 larger role than the accumulation of fine, organic-rich allochthonous particles.

244   On the other hand, the soil $\delta^{13}C$ signatures measured in *Halodule*, *Halophila* and *Zostera*

245 meadows (averaging -21 ± 0.4‰) were more similar to $\delta^{13}C$ values of algae or terrestrial organic

246 matter than to $\delta^{13}C$ values of their seagrass tissues (ranging from -10 and -14‰; e.g. Hemminga

247 and Mateo, 1996; Kennedy et al. 2010; Hanson et al. 2010). The positive relationship between

248 mud and soil C_{org} contents in *Halodule*, *Halophila* and *Zostera* soils could be explained their

249 relatively high mud content and ^{13}C-depleted C_{org}, indicating that allochthonous C_{org} inputs and

250 mud content play a major role in soil C_{org} accumulation in these opportunistic and early-

251 colonizing seagrasses. However, the relative high C_{org} contents found with relatively low mud

252 contents (i.e. mud-C_{org} saturation) disrupted the correlation found between soil C_{org} and mud

253 contents in these meadows (C_{org} >1% in samples with 0-20% mud; C_{org} >2% in samples with 20-

254 70% mud and C_{org} >3.5 in samples with 70-100% mud; Figure 1).

255   The results obtained showed a tendency for high-biomass and persistent meadows (i.e.

256 *Posidonia* and *Amphibolis*) to accumulate higher C_{org} stores and seagrass-derived C_{org} compared

257 to ephemeral and low-biomass meadows (i.e. *Halophila*, *Halodule* and *Zostera*), suggesting that

258 factors (biotic and abiotic) affecting the production, form and preservation of C_{org} within habitats

259 exert a significant influence on soil C_{org} content (Lavery et al. 2013; Serrano et al. 2014, 2015).

260 The above- and belowground biomass in meadows of the genus *Posidonia* (averaging 535 and

261 910 g DW m^{-2}, respectively) is up to 2-fold higher than in *Amphibolis* meadows (averaging 641

262 and 457 g DW m^{-2}, respectively) and 4 to 18-fold higher than in small and opportunistic

263 seagrasses of the genera *Halophila*, *Halodule* and *Zostera* (125 and 49 g DW m^{-2}, on average;

264 respectively; Duarte and Chiscano, 1999; Paling and McComb 2000). Indeed, larger seagrasses

265 tend to have larger and more persistent rhizomes, constituted by more refractory forms of C_{org},

266 more prone to be preserved in soils than simpler, more labile forms of C_{org} such as seston and

267 algal detritus which are more suitable to experience remineralization during early diagenesis

268 (Henrichs 1992; Burdige, 2007). In addition, the larger size of detritus within *Amphibolis* and

269 *Posidonia* meadows compared to *Halophila*, *Halodule* and *Zostera* meadows could also

270 contribute to the larger accumulation of C_{org} in the former, since decay rates of seagrass detritus

271 increase with decreasing particle size due to larger surfaces available for microbial attack

272 (Harrison, 1989). Differences in above- and belowground biomass and recalcitrance between

273 *Posidonia* and *Amphibolis* spp could explain the larger contribution of seagrass-derived C_{org} (i.e.

274 ^{13}C-enriched) in the former, thereby obviating the linear relationship between mud and C_{org}

275 contents (Figure 1).

276   The soil C_{org} content tend to decrease with soil depth and ageing in seagrass ecosystems (e.g.

277 Serrano et al. 2012), thereby the persistence of discrete organic detritus within upper soil

278 horizons could lead to organic matter concentrations above those levels explained by the

279 association with clay and silt particles, as previously demonstrated for terrestrial soils (Mayer

280 and Xing, 2001; Gami et al. 2009). The organic matter preserved in most marine sediments is

281 intimately associated with mineral surfaces (i.e. selective preservation by sorption of organic

282   matter into minerals; Keil et al 1994) and therefore the correlation between soil C_{org} and mud

283   contents in seagrass meadows could vary as a function of soil depth and ageing. The results

284   obtained show that soil depth is not an important factor when attempting to predict soil C_{org}

285   content based on mud content in bare sediments (i.e. $R^2 > 0.74$ for all core depths explored; 1 to

286   110 cm-thick, 1 to 10 cm-thick, and 11 to 110 cm-thick; Figure 2). However, a clearer pattern

287   appeared when exploring the correlation between soil C_{org} and mud contents in top 10 cm and

288   within 11-110 cm soil depths of combined *Halodule*, *Halophila* and *Zostera* species ($R^2 = 0.17$

289   and $R^2 = 0.74$, respectively). These results suggest that the relatively small belowground biomass

290   of these species (i.e. organic detritus) only has an impact on the expected positive correlation

291   between soil C_{org} and mud content within the top 10 cm, while the correlation for deeper soil

292   depths (11-110 cm) improved ($R^2 = 0.74$) compared to the whole dataset (1 to 110 cm-thick; R^2

293    $= 0.56$). For combined *Amphibolis* and *Posidonia* species, the results obtained show that soil

294   depth is not an important factor when attempting to predict soil C_{org} content based on mud

295   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;

296   Figure 2). These results suggest that the relatively large belowground biomass of these species

297   (i.e. organic detritus) has an impact on the expected positive correlation between soil C_{org} and

298   mud content within all depths studied.

299   Habitat conditions in seagrass meadows not only influence the amount of C_{org} accumulation

300   through detrital plant inputs, but the capacity of the plant canopies to retain particles (Gacia et al.

301   1999). The amount of fine suspended particles available for burial varies among sites, driven by

302   geomorphological features (e.g. run-off, hydrodynamic energy and water depth), while meadow

303   structure (i.e. density, cover and morphology of the canopy) constrains their capacity to

304   accumulate sediment particles (Hendriks et al. 2010; Peralta et al. 2008). Although the number of

305 cores and species studied in coastal and estuarine ecosystems was unbalanced (i.e. *Amphibolis*

306 and *Posidonia* dominate in coastal habitats and *Halophila*, *Halodule*, *Zostera* dominate in

307 estuarine habitats), the lack of, or poor correlations found within estuarine and coastal

308 ecosystems, precludes the general use of mud as a predictor of blue carbon content based on

309 habitat geomorphology (Figure 3). Seagrass meadows and bare sediments in environments

310 conducive for depositional processes (i.e. estuaries) accumulated up to 4-fold higher amounts of

311 mud compared to other coastal ecosystems, but the saturation of mud with C_{org} and the large

312 contribution of seagrass detritus into the sedimentary C_{org} pool (^{13}C-enriched soils) in some study

313 sites disrupted the positive relationship expected between mud and soil-C_{org} contents. In

314 estuarine ecosystems, soil C_{org} originated from both mud inputs linked to allochthonous-C_{org} via

315 deposition from upstream transport (e.g. Aller, 1998) and seagrass inputs (i.e. in samples with

316 C_{org} >5%; Figure 3). The insignificant relationship between mud and soil C_{org} contents in coastal

317 habitats could be explained by their relatively low mud content and the accumulation of

318 seagrass-derived C_{org}, in particular in samples with C_{org} >5% (Figure 3).

319   In sum, mud is not a universal proxy for blue carbon content in seagrass ecosystems and

320 should not be applied generally across all habitat and vegetation types. Overall, the positive

321 relationship between mud and C_{org} contents found in bare sediments and in opportunistic and/or

322 low biomass seagrass meadows (i.e. genera *Zostera*, *Halodule* and *Halophila*) allow mud to be

323 used as a proxy for C_{org} content in these ecosystems, thereby enabling robust scaling up exercises

324 (i.e. benefiting from existing geological surveys and models) at low cost as part of blue carbon

325 stock assessment programs. However, mud content is not a good predictor of C_{org} content in

326 highly productive meadows such as those constituted by *P. oceanica* in the Mediterranean Sea

327 and *P. australis, P. sinuosa* and *Amphibolis* spp in Australia. Analyses of soil grain size (i.e.

328 %mud) could constitute a relatively cheap method to estimate soil organic carbon content in

329 seagrass ecosystems, particularly dry and wet sieving using standard geological sieves

330 (Erftemeijer and Kach, 2001). These could be used to cheaply quantify mud content as a proxy

331 for carbon, particularly in student projects, citizen science and in countries where funding for

332 science is limited and they do not have access to higher technology methods or cannot afford to

333 pay for analysis. In addition, since most countries have conducted geological surveys within the

334 coastal zone to determine sediment grain size (e.g. Passlow et al. 2005), a strong, positive

335 relationship between mud and C_{org} contents could allow the development of geomorphology

336 models to predict blue carbon content within seagrass meadows, dramatically improving global

337 estimates of blue carbon storage. Indeed, maps of soil grain-size could be obtained using remote

338 sensing (Rainey et al. 2003; De Falco et al. 2010), opening new opportunities for scaling

339 exercises.

340   Previous studies suggested that the relationship between organic matter and the sediment

341 matrix is best seen with clay-sized fractions (<0.004 mm; Bergamaschi et al., 1997; De Falco et

342 al. 2004). However, the grain size cut-off selected in this study (mud, <0.063 mm) is more

343 representative of the bulk soil and their C_{org} content (Pedrosa-Pàmies et al. 2013) and therefore a

344 higher correlation is expected when comparing bulk soil C_{org} with a larger and more

345 representative fraction of the sediment (i.e. including the silt fraction, 0.004-0.063 mm, also

346 provides binding sites for C_{org}; Burdige, 2007). Other biological, chemical and geological factors

347 not explored in detail in this study may also play a key role in C_{org} storage, and ultimately in the

348 relationship between soil C_{org} and mud contents. For example, the effects of habitat

349 geomorphology (e.g. hydrodynamic energy, terrestrial mud and C_{org} inputs, export of seagrass

350 biomass) and species identity (e.g. variation in terms of productivity, oxygen exposure and

351　recalcitrance of C_{org} stores, and plant influence on sediment retention) within both coastal and

352　estuarine environments, are among the factors identified in this study which might explain

353　significant variation in the C_{org} stores of meadows in relatively similar exposure conditions

354　(Serrano et al. 2015). Other factors found to play a key role in controlling soil C_{org} accumulation

355　in terrestrial ecosystems, such as chemical stabilization of organic matter (Percival et al. 1999;

356　Galy et al. 2008) and microbial biomass carbon (Danovaro et al. 1994), could also influence C_{org}

357　storage in seagrass ecosystems. Further studies are needed to identify the influences of these

358　other factors on C_{org} storage in seagrass meadows, and in addition to the mud content, other

359　characteristics should be taken into account when attempting to obtain robust estimates of C_{org}

360　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

549 soils were gathered from a variety of seagrass meadows (and also from adjacent bare sediments)

550 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

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556 **Table 2.** Average ± SE organic carbon (C_{org}) content (in %), $\delta^{13}C$ signatures and mud content in

557 all habitats and soil depths studied. a) Descriptive statistics based on species identity. b)

558 Descriptive statistics based on habitat geomorphology (estuarine *vs* coastal environments). N,

559 number of samples.

a)

Habitat (species)	Organic carbon (%)			$\delta^{13}C$ (‰)			Mud (%)		
	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 (geomorphology)	Organic carbon (%)			$\delta^{13}C$ (‰)			Mud (%)		
	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

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563 **Table 3.** Pearson correlation analyses to test for significant relationships among soil C_{org} and

564 mud contents, and soil C_{org} and $\delta^{13}C$ signatures in up to 475 cm long cores; based on (a) species

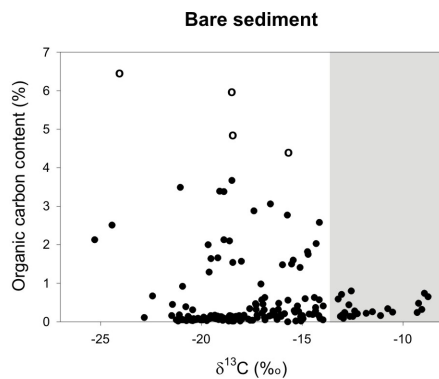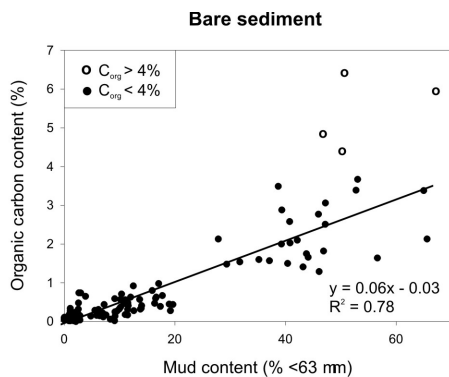565 identity and (b) habitat geomorphology. *ns*, non significant correlation.

a)

Habitat (species)	Organic carbon (%) vs mud (%)			Organic carbon (%) vs $\delta^{13}C$ (‰)		
	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 (geomorphology)	Organic carbon (%) vs mud (%)			Organic carbon (%) vs $\delta^{13}C$ (‰)		
	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	**

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571 **Figure 1.** Relationships among soil C_{org} and mud contents, and soil C_{org} and $\delta^{13}C$ signatures in

572 all habitats and all soil depths studied: bare sediments, combined *Halodule*, *Halophila* and

573 *Zostera* species, and combined *Amphibolis* and *Posidonia* species. Only correlations with R^2

574 >0.5 are shown. The grey shaded areas showed the range of $\delta^{13}C$ signatures of plant detritus

575 (based on literature values; see main text). The white circles indicate the samples obviating the

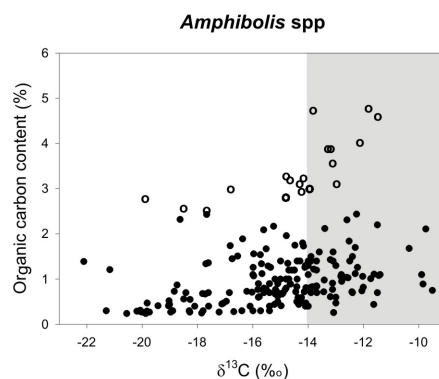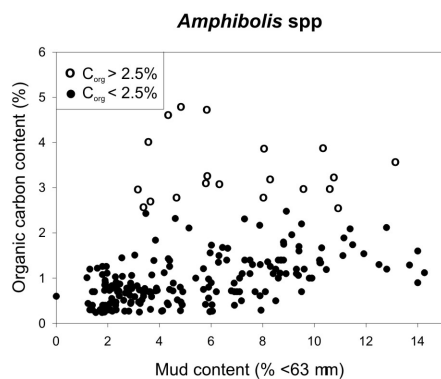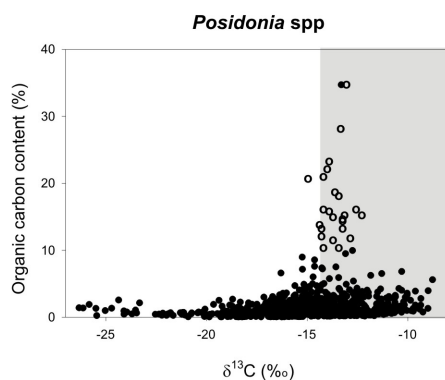576 expected correlation between soil C_{org} and mud contents.

Bare sediment

y = 0.06x - 0.03
R² = 0.78

○ C_org > 4%
● C_org < 4%

Organic carbon content (%)

Mud content (% <63 mm)

YES

Bare sediment

Organic carbon content (%)

δ¹³C (‰)

Halodule & Halophila & Zostera spp

○ 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

YES

Organic carbon content (%)

Mud content (% <63 mm)

Halodule & Halophila & Zostera spp

Organic carbon content (%)

δ¹³C (‰)

Amphibolis spp

○ C_org > 2.5%
● C_org < 2.5%

NO

Organic carbon content (%)

Mud content (% <63 mm)

Amphibolis spp

Organic carbon content (%)

δ¹³C (‰)

Posidonia spp

○ C_org > 10%
● C_org < 10%

NO

Organic carbon content (%)

Mud content (% <63 mm)

Posidonia spp

Organic carbon content (%)

δ¹³C (‰)

577

578

579   **Figure 2.** Relationships among soil C_{org} and mud contents in 1 to 10 cm and 11 to 110 cm thick

580   soils: bare sediments, combined *Halodule*, *Halophila* and *Zostera* species, and combined

581   *Amphibolis* and *Posidonia* species. Only correlations with R^2 >0.5 are shown. The white

582   circles indicate the samples obviating the expected correlation between soil C_{org} and mud
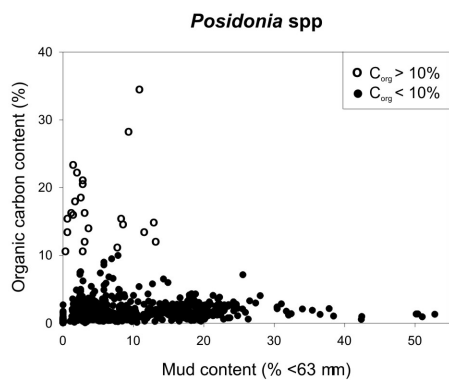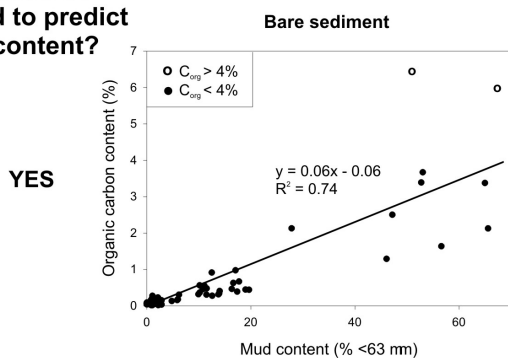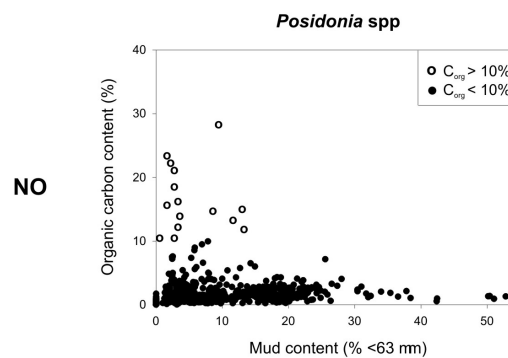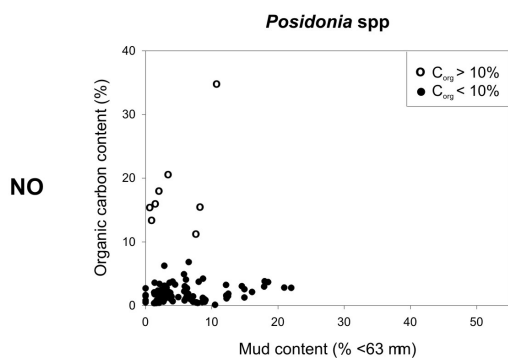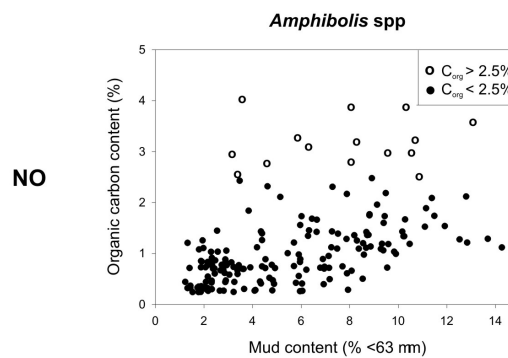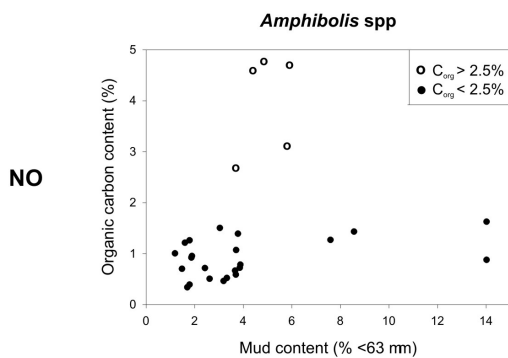
583   contents.

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

Bare sediment

$C_{org} > 4\%$

$C_{org} < 4\%$

YES

$y = 0.06x - 0.06$
$R^2 = 0.74$

Organic carbon content (%)

Mud content (% <63 mm)

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

Bare sediment

$C_{org} > 4\%$

$C_{org} < 4\%$

YES

$y = 0.06x - 0.004$
$R^2 = 0.81$

Organic carbon content (%)

Mud content (% <63 mm)

***Halodule* & *Halophila* & *Zostera* spp**

$C_{org} > 1\%$ (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)

NO

Organic carbon content (%)

Mud content (% <63 mm)

***Halodule* & *Halophila* & *Zostera* spp**

$C_{org} > 1\%$ (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)

YES

$y = 0.03x + 0.10$
$R^2 = 0.74$

Organic carbon content (%)

Mud content (% <63 mm)

***Amphibolis* spp**

NO

$C_{org} > 2.5\%$

$C_{org} < 2.5\%$

Organic carbon content (%)

Mud content (% <63 mm)

***Amphibolis* spp**

NO

$C_{org} > 2.5\%$

$C_{org} < 2.5\%$

Organic carbon content (%)

Mud content (% <63 mm)

***Posidonia* spp**

NO

$C_{org} > 10\%$

$C_{org} < 10\%$

Organic carbon content (%)

Mud content (% <63 mm)

***Posidonia* spp**

NO

$C_{org} > 10\%$

$C_{org} < 10\%$

Organic carbon content (%)

Mud content (% <63 mm)

584

585

586　**Figure 3.** Relationships among soil C_{org} and mud contents, and soil C_{org} and $\delta^{13}C$ signatures in

587　　the coastal and estuarine habitats studied. The grey shaded areas showed the range of $\delta^{13}C$

588　　signatures of plant detritus (based on literature values; see main text). The white circles

589　　indicate the samples obviating the expected correlation between soil C_{org} and mud contents.

590

591

592