Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania.

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Abstract. The aim of this work was to explore the feasibility of using seagrass functional traits to predict differences in sediment carbon storage. At 19 sites within highly diverse seagrass meadows of Zanzibar, Tanzania, species cover was estimated along with three community traits hypothesized to influence sediment carbon storage (amount of above and belowground biomass, seagrass tissue nitrogen content, and shoot density). We identified five distinct seagrass communities that had notable variations in key plant traits but these differences did not translate into differences is sediment organic carbon (OC) storage. Across all communities, sediment OC was very low (ranging from 0.15% to 0.75%) and there were no differences in OC storage among communities, which was considerably lower (33.9 ± 7.7 Mg C ha^{-1}) than the global average (194.2 ± 20.2 Mg C ha^{-1}) reported for other seagrass ecosystems. In spite of high seagrass diversity and clear zonation among plant communities, sediments in all communities were shallow (ranging from 19 to 78 cm) and composed of medium-coarse grained carbonate sand on top of carbonate rock. We propose that geophysical conditions of the sediment were not conducive to OC stabilization, and outweighed any variation in the quantity or quality of plant litter inputs, ultimately leading to low OC storage within all seagrass communities. This highlights the complexity of OC cycling in seagrass ecosystems and cautions against the use of plant traits as a proxy for OC storage across all seagrass ecosystems.

1 Introduction

Seagrasses influence key ecological functions within coastal ecosystems through their productivity and by trapping sediment, altering hydrodynamics, and modifying biogeochemical processes in the water column and sediment (Duarte and Chiscano, 1999; Marba et al., 2006). Through their effects on ecosystem processes seagrasses provide numerous ecosystem services including sediment stabilization, coastline protection, nutrient cycling, pathogen reduction, support of fisheries, and enhancement of biodiversity (Duffy, 2006; la Torre Castro and Rönnbäck, 2004; Lamb et al., 2017; Orth et al., 2006). In the last decade, seagrasses have been recognized as potentially important 'blue' carbon (organic carbon sequestered by vegetated coastal ecosystems) sinks, adding climate regulation to their list of well-established ecosystem services (Nellemann et al., 2009).

A surge in research efforts has revealed the wide range (up to 18-fold) of sediment organic carbon (OC) storage within seagrass sediments, with OC stocks varying with seagrass species (Lavery et al. 2013, Serrano et al. 2014; Serrano et al. 2016; Gullstrom et al. 2017), plant characteristics (Campbell et al. 2014; Dahl et al. 2016; Jankowska et al. 2016; Samper-Villarreal et al. 2016), meadow attributes (Serrano et al. 2014; 2015; Armitage and Fourquean 2016; Samper-Villarreal et al. 2016), sediment characteristics (Campbell et al. 2014; Röhr et al. 2016; Serrano et al. 2016; Dahl et al. 2016; Miyajima et al. 2017), landscape configurations (Lavery et al. 2013; Phang et al. 2015; Gullstrom et al. 2017) and climatic zones (Lavery et al. 2013; Miyajima et al. 2015; Fourqurean et al. 2012a). This high variation in OC stocks, in conjunction with a wide array of potential mediating factors, presents a formable obstacle for reliably valuing the ecosystem service of OC storage because a site-specific baseline of the OC stock is required before conservation or restoration can be incentivized under a blue-carbon framework (Barbier et al., 2011; Costanza et al., 1997; Herr et al., 2012; Macreadie et al., 2014), which requires time-intensive OC inventories.

A potential solution is to utilize easy-to-measure functional traits that can be linked to ecosystem functions underlying the service of carbon storage (de Bello et al., 2010; de Chazal et al., 2008; Grime, 2001; Kremen, 2005). Plant functional traits have been shown to be valuable tools for assessing and managing ecosystem services (de Bello et al., 2010; Díaz et al., 2007). An important trade-off of plant traits linked to OC cycling, known as the 'fast-slow plant economic spectrum', consists of a suite of coordinated characteristics that either promote fast carbon acquisition and decomposition, or promote the conservation of resources within well-protected tissues with inherently slower decomposition rates (Conti and Díaz, 2012; Díaz et al., 2004; Freschet et al., 2012; Grime, 2001; Reich et al., 1997; Wright et al., 2004). Acquisition traits such as high specific leaf area, high nutrient content, low tissue longevity and density are consistently associated with high carbon inputs via photosynthesis and high carbon losses through decomposition (Cornwell et al., 2008; Díaz et al., 2004; Grime et al., 1997; Herms and Mattson, 1992; Reich, 2014; Wright et al., 2004). Conservative traits include the opposite of the above characteristics and promote slow-growing, long-lived biomass with low carbon losses via decomposition. At the ecosystem level, acquisition traits promote high carbon fluxes, while conservation traits are conducive for high carbon stocks (Conti and Díaz, 2012; De Deyn et al., 2008; Díaz et al., 2009; Wardle et al., 2004).

Several seagrass traits have been proposed to be important determinates of organic carbon sequestration and storage within seagrass sediments (Duarte et al., 2011). Canopy characteristics, such as high leaf density and complexity, have been shown to enhance OC burial within the sediment by filtering and trapping particles from the water column and promoting sediment deposition and retention (Duarte and Chiscano 1999, Gacia et al. 1999, Gacia and Duarte 2001, Hendriks et al. 2008, Duarte et al. 2005, Peterson et al. 2004). Seagrass tissue stoichiometry has been correlated with decomposition rates and carbon preservation within seagrass sediments, with tissues containing relatively higher nitrogen and phosphorus content decomposing faster (Duarte et al., 2010; Enriquez et al., 1993). Seagrass biomass has been correlated to OC storage (Armitage and Fourqurean, 2016; Serrano et al., 2016). Belowground production of seagrass roots and rhizomes places OC directly into sediments, which can be stabilized on mineral surfaces, within aggregates, or if microbial activity is suppressed due to lack of oxygen (Belshe et al., 2017; Duarte et al., 2010). In addition, the binding of the sediment by the root-rhizome

system (Christianen et al., 2013) and the high lignin content of belowground tissues (Klap et al., 2000), promote OC storage. And larger plants disproportionately contribute to OC accumulation by shedding more biomass per unit ground area (Garnier et al., 2004; Lavorel and Grigulis, 2011). Seagrass interspecies variation in these traits place them within the continuum of the 'fast-slow' ecological spectrum, with small-bodied, ephemeral species, such as *Halophila spp.*, *Halodule spp.*, and

5   *Zostera spp.* on the 'fast' acquisition end, and large-bodied, persistent species, such as *Enhalus spp.*, *Thalassia spp.* and *Posidonia spp.*, on the 'slow' conservation end (Orth et al., 2006).

      The objective of this study was to determine whether seagrass community traits can be used to identify where high sediment OC stocks occur within diverse meadows of Zanzibar, Tanzania. We measured three plant community traits (above- and belowground biomass, tissue nitrogen content, and shoot density) within five seagrass communities and

10   hypothesized that communities with either high shoot density, low tissue nitrogen content, or a high proportion of belowground biomass would store more OC within their sediments.

2 Methods

2.1 Description of study sites

This study was conducted within the diverse seagrass meadows of the Western Indian Ocean (WIO), specifically in coastal

15   waters of Unguja Island (-6.15809°S, 39.19181°E) of Zanzibar, Tanzania. This region contains meadows with up to 12 co-occurring seagrass species, with a wide breath of functional traits (Gullstrom et al. 2002). Yet, the seagrass of the WIO are largely understudied (Gullstrom et al. 2002), especially in regards to carbon sequestration (Dahl et al. 2016, Gullstrom et al. 2017). The climate is warm and moist, with temperatures between 27 and 35°C, with an annual rainfall of 1600 mm that is strongly influenced by two opposing monsoon seasons driven by the southeast monsoonal circulation of the central WIO

20   (Mahongo and Shaghude, 2014; McClanahan, 1988). The regional hydrodynamics are complex and primarily influenced by ebb-flood tidal phases but are also influenced by the East African Coastal Current (EACC) and monsoon winds (Mahongo and Shaghude, 2014; Shaghude et al., 2002; Zavala-Garay et al., 2015). The tidal cycles are semi-diurnal ranging from mesotidal during neap tide (~1 meter amplitude) to macrotidal (from 3 to 4 meters in amplitude) during spring tide (Shaghude et al., 2002; Zavala-Garay et al., 2015). Strong tidal currents can reach velocities that range from 0.25 to 2 m/s

25   (Shaghude et al., 2002).

      Sample sites were established within three seagrass meadows (M1, M2, M3) in open coastal waters adjacent to coral cays west of the main city, Zanzibar Town (Figure 1). M1 is located on a coral platform in shallow waters to the southeast of Kibandiko Island and encompasses an area of 15 hectares, which include several, small intermittent patch reefs. M2 is also located on a coral platform 1.5 km to the west if M1, and encompasses an area of 4.8 hectares. M2 resides within

30   a shallow lagoon adjacent to a sand spit and fringing reef on the northeastern side Changu Island. M3 covers 4.6 hectares and is located on a coral platform in shallow waters north of Chumbe Island, adjacent to patch reefs and a sand spit. M3 resides 16 to 17 km south of M1 and M2, respectively.

During October 2013, physical properties (temperature, pH, dissolved oxygen and conductivity) of the water column were measured using a WTW 3430 multi-parameter probe (Weilheim, Germany). Light levels at the surface (I0) and bottom (Id) of the water column were measured with Li-1400 (Li-Cor Biosciences, Lincoln, Nebraska, USA). Light attenuation (k) at a given depth (d) was calculated using the following equation: $k = \ln(Id/I0)/-d$. Landscape sediment

5 characteristics were assessed within four biogeographic zones (reef flat, fore reef, tidal channel and seagrass meadow). The upper 5-10 cm of sediment was collected using a Van Veen sampler (3 mm plate, 250 cm²) at 27 locations following the bathymetric gradient and covering the four biogeographic areas. Sedimentary samples were rinsed with clean freshwater in order to remove soluble components and dried at 40°C for at least 48h. Two subsamples (of each set) were sieved in a stack-shaker sieve for 10 min. We applied the Udden-Wentworth scale (Wentworth, 1922) as following: gravel (>2000 μm),

10 coarse sand (1000-2000 μm), medium sand (500-1000 μm), medium-fine sand (250-500 μm), fine sand (125-250 μm), very fine sand (63-125 μm) and silt (<63 μm). Each individual fraction was calculated as weight percentage of the total bulk sediment. We used the logarithmic Folk and Ward (Folk and Ward, 1957) method to convert the measurements into phi scale, and the physical description of sediments was based on the granulometric output and appearance of the bulk sediment after Folk (Folk, 1954). Summary statistics for each zone were estimated from log-transformed data using the G2Sd R

15 package (Fournier et al., 2014). Surface sediments (top 2-3 cm) were also collected within different seagrass species assemblages to assess differences in local sediment characteristics, compared to landscape sediment properties. A representative sediment sample of each community (see below for information on seagrass communities) was photographed at high-resolution over a 5-mm grid and qualitatively compared based on appearance and texture (Folk, 1954).

2.2 Community data and analysis

20 In October of 2013, 19 sample sites were established across the three meadows (M1, M2, M3) to capture the zonation of species assemblages found across the extent of each meadow. After conducting a snorkeling survey that included five, 50-meter transects distributed throughout each meadow, 6 to 7 visually distinct vegetation zones per meadow were identified. Within each zone, a quadrat was haphazardly tossed to establish a site. Within a meadow, sites ranged from 15 to 370 meters apart, with the average distance of between sites of 261±194 meters for M1, 170±93 meters for M2 and 165±98 meters for

25 M3 (Figure 1).

At each site, seagrass species composition was quantified within six haphazardly tossed 0.25 m² quadrats by visually estimating seagrass cover and assigned values based on a modified Braun-Blanquet scale (Mueller-Dombios and Ellenberg, 2012). In total, eight seagrass species were identified: *Thalassodendron ciliatum, Cymodocea serrulata, Cymodocea rotundata, Thalassia hemprichii, Syringodium isoetifolium, Halodule univervis, Holophila ovalis,* and *Halophila*

30 *stipulacea.* Multivariate analyses were used to describe and categorize the patterns in seagrass species assemblages found at the 19 sample sites. First, Braun-Blanquet cover categories were converted to the midpoint of the cover range (Wilkum and Shanholtzer, 1978), square root transformed to down weight the influence of abundant species, and relativized to the total abundance of each site. A Bray-Curtis similarity index was then calculated based on the similarity of species composition

and cover among sites (Bray and Curtis, 1957). Then, based on this similarity matrix, both nonmetric multidimensional scaling (NMDS) and hierarchical cluster analysis (average linkage) were preformed to group sites by similarity in seagrass species composition and cover (Braak, 1995; Kent and Coker, 1992; Legendre and Legendre, 1998). These categorizations were used to identify the seagrass species assemblages (communities) present in the sampled meadows. The vegan package

5   (version 2.2-0; (Oksanen et al., 2014)) in R (R Core Development Team 2016) was used for all multivariate analysis.

2.3 Trait data and analysis

To quantify traits of each seagrass community, three biomass cores and five seagrass plants of each species present were collected at each of the 19 sites. Core samples were taken with a 13-cm diameter PVC core and used to quantify shoot density and above and below ground biomass. Plant material from the cores was washed free of sediment in the field, stored

10   in plastic bags, and frozen for subsequent analysis. After thawing in the lab, seagrasses were sorted by species and short shoot density (number m^{-2}) was calculated. Green leaves (above-ground biomass) and living root, rhizome, and short-shoots (below-ground biomass) were separated and dried at 60°C until a constant weight was reached, then weighed to obtain above and below ground biomass (g DW m^{-2}) for each species. Species weights were then summed for core-level estimates of above and below ground biomass. Five seagrass plants per species were collected from each site and used to quantify the %

15   nitrogen (N) of leaf and rhizome tissue of each species. A section of rhizome and the second-ranked leaf of each of the five shoots was taken, cleaned of epiphytes, and dried at 60°C for 48 hours. Tissue samples were then homogenized and measured on an elemental analyzer (Euro EX 3000; EuroVector) to determine the % N of each species at each site.

For all analysis of trait differences among communities, the unbalanced sample design created from the unequal grouping of the original 19 sites into communities (based on similarity of species and cover), necessitated special attention in

20   regards to model appropriateness and validation of assumptions. Model residuals were tested for homogeneity of variance and normality with Levene's and Shapiro-Wilks tests, respectively. Selected models were also validated visually with plots of model residuals (fitted values vs absolute residuals (homogeneity of variance), a qqplot comparing the distribution of the standardized residuals to the normal distribution (normality), and a lag plot of the raw residuals vs the previous residual (independence); Zuur et al. 2009). Further, spatial independence was confirmed with variogram plots of model residuals

25   using the gstat package (Zuur et al., 2009).

Differences in above and below ground biomass among communities and meadows were determined using a two-way ANOVA with post-hoc Tukey HSD at $p \leq 0.05$ significance level on log transformed data to meet model assumptions. With the transformation, both assumptions of homogeneity of variance (Levene's test, AG: $F=1.262$, $p=0.274$; BG $F=0.609$, $p=0.833$) and normality (Shapiro-Wilk, AG: $W=0.969$, $p=0.180$; BG: $W=0.961$, $p=0.126$) were met. Because sites were

30   distributed across three meadows, models included both community and meadow as direct effects along with their interaction. All models were fit using the base package in R (R Core Development Team 2016).

Differences in short-shoot density among the seagrass communities and meadows were determined using a generalized linear model, specifically a negative binomial model (link=log) because the data were counts and found to be

over dispersed (Zuur et al., 2009). The negative binomial distribution allows for variances not equal to the mean and does not necessitate equal variances among groups (Zuur et al., 2009). Differences among communities, and across meadows within each community, were determined when there was no overlap in 95% confidence intervals of predicted model estimates. All models were fit using the MASS package (version 7.3-35; Venables and Ripley, 2002) in R.

5   The % N of each community was estimated by calculating the mean and standard deviation of the % N weighted by the abundance of each species present within the community specific to each meadow. Because of our unequal sample sizes and variance heterogeneity, communities and meadows within a community, were simply compared visually and considered different when there was no overlap between 95% confidence intervals, which were calculated as the weighted mean ± with $t_{0.95}$ *weighted SD, with $t_{0.95}$ =2.26 based on a t-distribution to account for the smallest sample size of our groups (n=10).

10   **2.4 Sediment cores and organic carbon analysis**

To determine if carbon storage within sediments varied among different seagrass communities and if this variation could be explained by specific traits, sediment cores were taken within the seagrass communities (determined from the multivariate analysis) at the same sites during October of 2014. Three sediment cores were taken with a hand-driven corer on SCUBA, within each of the identified seagrass communities and outside of seagrass meadows on bare sediment. In the lab, cores were

15 sectioned into 3 cm slices. From each slice, a subset of 15 ml of sediment was taken and oven dried (60°C) for bulk density determination. Dried sediments were homogenized in a ball mill and % organic carbon (OC) was determined, after acidification to remove carbonates, on an elemental analyzer (Euro EX 3000; EuroVector). The OC content (CC) of each 3-cm slice was calculated from measured % OC and the dry bulk density (DBD) of the slice following Eq. (1):

$$CC_{slice} = z_{slice} \text{ x } DBD_{slice} \text{ x } OC_{slice} / 100 \tag{1}$$

20 where z_{slice} is the slice thickness (cm), and the % OC content of the slice is multiplied by 100 to convert % to grams OC per dry weight. The amount of carbon stored in each core was calculated by summing the OC content in each depth increment (slice). Because the total core length varied among sites (from 19 to 78 cm) total core carbon storage was estimated in two ways. First, estimates of storage in the top 25 cm of sediment were calculated because at this depth there were nearly full data sets in all cores. Second, to make estimates comparable to other studies, storage in the top meter of sediment was

25 estimated by gap filling missing data down to one meter using a negative exponential model with the drc package (version 3.0-1; (Ritz et al., 2015)).

       To explore how OC varied among communities and across our sites, models that included both community and meadow as direct effects were evaluated. Because of our relatively small sample size (n=18) and the general rule of thumb of needing ~10 data points for each parameter estimated, we did not include the interaction among community and meadow.

30 Models were fit for each response variable (percent OC in the top 25 cm, OC storage to 25 cm, and OC storage to 1 meter) using an ANOVA with post-hoc Tukey HSD at $p \leq 0.05$ significance level. Model assumptions were assessed with Shapiro-wilks test, and plots of residuals as described above, and spatial independence was confirmed with variogram plots of model

residuals. All graphics were produced with the ggplot package (version 1.0.0; (Wickham, 2009)) in R (R Core Development Team 2016).

3 Results

3.1 Seagrass meadow environment

5   Physical properties of the water column were similar among meadows, with pH ranging from 8.19 to 8.31 ($F_{2,35}$=9.01, p=0.06), dissolved oxygen ranging from 6.5 to 8.8 mg/L ($F_{2,35}$=2.53, p=0.09), conductivity ranging from 53.7 to 54.1 S/m ($F_{2,35}$=0.18, p=0.84). Water temperature ranged from a mean of 26.4°C in M1, to 26.3°C in M2 and 27.1°C in M3. In general water clarity was high and light attenuation (Kd) through the water column was similar among meadows (mean Kd= 0.35, $F_{2,29}$=1.45, p=0.25). Sediments across the landscape were composed of coarse to medium sized carbonate sands, that

10 were poorly sorted but actively reworked, suggesting energetic hydrodynamic conditions. The texture was consistently classified as gravelly sand; however, the mean grain size was slightly smaller within seagrass meadows (1953 μm) when compared to the reef flat (2818 μm), fore reef (2352 μm) or sediments found on deeper areas of the channel (2546 μm; Supplementary Table S1). There were no major (compositional or granumetrical) differences among the four bioregions, with all classified as poorly-sorted, gravelly sand. At the local scale, there were no large qualitative visual differences among

15 surface sediments beneath the different seagrass communities, and all were consistent with the sediment characterization of the region (Supplementary Figure S1).

3.2 Seagrass community composition

Five distinct seagrass species assemblages were identified using a combination of nMDS and hierarchical clustering (Figure 2a & 2b). Because both methods produced similar results, we felt confident that these five groupings represented an inherent

20 structure in the similarity of seagrass species composition and cover found at the 19 sites within the three meadows. For simplicity, we refer to the five distinct assemblages as communities A, B, C, D and E. The first two communities, A and B are monospecific, composed 100% of *Cymodocea serrulata* (CS) and *Thalassodendron ciliatum* (TC), respectively (Figure 2c). Although a single species does not fit the strict definition of a community, we use the terminology for congruity throughout the manuscript. Community C was comprised mostly of small-bodied, fast-growing species 67% *Halodule*

25 *uninervis* (HU), 19% *Cymodocea rotundata* (CR), 8% *Halophila ovalis* (HO), 1% *Halophila stipulacea* (HS), but also contained a small percentage (5%) of *Thalassia hemprichii* (TH). Community D was dominated by TH (91%) with a lesser occurrence of CR (8%) and TC (1%). Community E had the highest evenness of all communities with 46% TH, 26% CS, 22% *Syringodium isoetifolium* (SI), 5% HU, and 1% TC.

3.3 Community traits

There was a significant effect of both community ($F_{4,41}$=46.45, p<0.0001) and meadow ($F_{2,41}$=13.15, p<0.0001) on above ground (AG) biomass but no interaction effect ($F_{7,41}$=1.73, p=0.128). Community differences were driven by the significantly higher AG biomass in community B (972±74 g DWm^{-2}), which contained at least seven-fold higher AG

5   biomass than the other communities and was dominated by the large-bodied species *Thalassodendron ciliatum* (TC; Figure 3; Supplementary Table S2). There were also significant differences among the other four communities, with community A (127±33 g DWm^{-2}) containing greater AG biomass than communities C, D and E; community C (38±18 g DWm^{-2}) composed of small-bodied species having the lowest AG biomass, and communities' D (69±50 g DWm^{-2}) and E (67±33 g DWm^{-2}) with similar intermediate AG biomass (Figure 3). Differences among meadows were driven by M3 (96±52 g DWm^{-2}) having significantly less AG biomass than meadows 1 and 2 (M1: 350±72 g DWm^{-2}; M2: 123±40 g DWm^{-2}), which was

10   due to the absence of the high-biomass community B within M3. Within communities, there were no significant among-meadow differences in AG biomass (Supplementary Table S2).

     Below ground (BG) biomass followed a similar pattern with significant effects of community ($F_{4,41}$=11.01, p<0.0001) and meadow ($F_{2,41}$=4.140, p=0.023) but no interaction effect ($F_{7,41}$=1.81, p=0.111). Community differences were

15   again mainly driven by a significantly higher BG biomass in the TC-dominated community B (682±392 g DWm^{-2}), which contained on average twice as much BG biomass than the other four communities (Figure 3). However, BG biomass within community B was not significantly different from community E (392±144 g DWm^{-2}), which had the highest species evenness. BG biomass within community E was not significantly different than community D (303±103 g DWm^{-2}), but Communities A (256±66 g DWm^{-2}) and C (233±82 g DWm^{-2}) contained similarly low BG biomass (Figure 3;

20   Supplementary Table S3). Differences among meadows were due to M2 (325±170 g DWm^{-2}) containing on average significantly less BG biomass than meadows 1 and 3 (M1:390±132 g DWm^{-2}; M3:335±109 g DWm^{-2}). Within communities, there were no significant among-meadow differences in BG biomass (Supplementary Table S3).

     There was a significant effect of community on seagrass short shoot density (χ^2=45.1, df=4, p<0.001), and a marginally significant effect of meadow (χ^2=5.49, df=2, p=0.064). Community C, dominated by small-bodied fast-growing

25   seagrass species, had the highest shoot density with an estimated mean shoot density of 4178 shoots m^{-2} (based on the negative binomial model); however, only meadows 1 (M1:5285 shoots m^{-2}) and 3 (M3: 5696 shoots m^{-2}) were found to contain densities different from other communities (determined by no overlap in 95% confidence intervals of model predictions, Figure 4). Meadow 2 of community C (M2: 2105 shoots m^{-2}) and the meadow-specific estimated means of the remaining communities were all similar and ranged from 775 to 1781 shoots m^{-2}. Within communities A, B, D and E, there

30   were no consistent trends or significant differences among meadows in predicted short shoot densities (Figure 4).

     The nitrogen content within seagrass leaves varied among seagrass communities (determined by no overlap in 95% CI), with community D having the highest % nitrogen (M1:2.58±0.11%, M2: 2.77±0.10%, M3: 2.45±0.28%), which was significantly higher than communities A (M1:1.34±0.08%, M3:1.46±0.06%) and B (M1:1.56±0.05%, M2:1.52±0.04%)

regardless of within community variation due to among meadow-specific differences (Figure 5). The higher level of leaf nitrogen in community D was driven by the high relative abundance of *Thalassia hemprichii*, which contained the highest leaf nitrogen (on average 2.46%) of any seagrass species. The entire range of leaf nitrogen content of communities A and B fell below the global threshold (1.82%) indicating nutrient limitation in seagrasses (Duarte, 1990). Communities C

5 (M1:1.45±0.48%, M2:1.19±0.23%, M3:2.20±0.23%) and E (M1:1.61±0.11%, M2:1.48±0.12%, M3:1.70±0.21%) had intermediate leaf nitrogen concentrations. However, within community C one meadow (M3) contained leaf N content on par with community D due to the presence of *Cymodocea rotundata* (2.2%N) at this site. Leaf stoichiometry (C:N ratio) was on average within the range of 20-25, for all communities except community D (mean C:N = 16.9, M1:19.3, M2:13.8, M3:17.6). C:N ratios for communities A (mean= 24.3, M1:25.6, M3:22.9) and B (mean=24.5, M1:23.6, M2:25.4) were at the

10 upper limit of the threshold (20-25) indicating the potential for nitrogen limitation and low microbial carbon-use efficiency during litter decomposition, both of which can lead to higher sediment OC sequestration (Berg and McClaugherty, 2003; Hessen et al., 2004).

   The nitrogen content within seagrass rhizomes did not significantly vary among communities or meadows, with the weighted mean % nitrogen in all communities across all meadows ranging from 0.42% to 0.67% (Figure 5) and rhizome C:N

15 ratios ranging from 78 to 97. However, within community D there was notably higher variability in rhizome nitrogen content within M2, which had the highest tissue % N (0.92%) due to the high relative abundance (74%) of *Thalasia hemprichii*.

3.4 Sediment carbon

The depth that cores penetrated into the sediment varied from 19 to 78 cm and was dictated by the limited sediment accumulation on top of carbonate rock. The percentage of OC within the sediment was low within all communities (A-E),

20 varying from a maximum of 0.75% in surface sediments to a minimum of 0.15% down core (Figure 6). There were no differences in % OC in the top 25 cm (where all cores had data) among seagrass communities (A-E; $F_{4,9}$=1.34, p=0.34) or among meadows ($F_{2,9}$=3.16, p=0.09) but there was significantly higher % OC in communities with seagrass (A-E) compared to bare sediment (F, $F_{5,11}$=6.97, p=0.004; Supplementary Table S4). Generally, all cores exhibited the typical trend of decreasing % OC with depth into the sediment, except two cores taken outside of seagrass meadows (F: bare sediment;

25 Figure 6). This indicates that the bare areas may have been colonized by seagrass in the past, contributing to an increase in carbon storage within deeper layers of the sediment. Thus, it must be noted that in order to associate present seagrass communities with long term carbon storage in sediments, we assumed there were no historic differences in communities during past carbon deposition.

   OC storage within the top 25 cm of sediment did not differ among seagrass communities (A-E, $F_{4,9}$=1.43, p=0.30)

30 or among meadows ($F_{2,9}$=3.35, p=0.08), and was low, on average 14.1±2.2 Mg C ha^{-1}, but was significantly higher than adjacent bare sediment (7.5±2.1 Mg C ha^{-1}, $F_{5,11}$=7.96, p=0.002; Figure 7; Supplementary Table S4). Similarly, OC storage down to 1 meter did not differ among seagrass communities (A-E, $F_{4,9}$=0.20, p=0.93) or meadows ($F_{2,9}$=0.04, p=0.99) and was on average 33.9±7.7 Mg C ha^{-1}, but with the gap filled data there was no longer a significant difference in OC storage

between seagrass communities and bare sediment (19.3±8.2 Mg C ha^{-1}, $F_{5,11}$=1.448, p=0.28). Model validation of normality (Shapiro Wilks test) were met for all OC models (Supplementary Table S2), and variogram plots of model residuals showed no clear patterns indicating that the assumption of independence was met (Supplementary Figure S4).

4 Discussion

5   In three seagrass meadows off the coast of Zanzibar Town, Tanzania, we identified five distinct seagrass communities, and even with the natural variation across meadows there were still notable differences among communities in key plant traits shown in other ecosystems to influence ecological processes linked to OC sequestration and storage (Aerts and Chapin, 2000; Chapin, 2003; Díaz et al., 2004). We hypothesized that communities with either high shoot density, low tissue nitrogen content, or a high proportion of belowground biomass would store more OC within their sediments. From this, it

10   would be expected that community B (dominated by *Thalassodendron ciliatum*), with combined traits of high AG and BG biomass and low tissue nutrient content, or community C with high shoot density in two of the three meadows sampled would store more sediment OC. However, these trait differences did not translate into differences in sediment OC storage among seagrass communities. The OC storage in the top 25 cm (14.1±2.2 Mg C ha^{-1}) or the top 1 m (33.9±7.7 Mg C ha^{-1}) of sediment at our sites was comparatively lower than the global average (194.2±20.2 Mg C ha^{-1} in the top meter) for seagrass

15   ecosystems (Fourqurean et al., 2012a), and considerably lower to what has been reported for *Posidonia oceanica* (105 to 829 Mg C ha^{-1}), *Thalassia testudinum* (124 to 210 Mg C ha^{-1}) and *Amphibolis antarctica* (115 to 335 Mg C ha^{-1}) meadows (Fourqurean et al., 2012b; Mateo et al., 1997; Serrano et al., 2014; 2012). All four of these seagrass species (*P. oceanica*, *T. testudinum, A. antarctica* and *T. ciliatum*) are late-successional, slow-growing species with traits that place them on the 'slow' conservation-side of the plant economic spectrum associated with higher ecosystem OC storage (Díaz et al., 2004;

20   Orth et al., 2006; Reich, 2014; Wright et al., 2004). The breakdown of the relationship among plant traits and OC storage in our study indicates that other factors must be interacting to control OC deposition and/or stabilization within the sediment.

       Our sample sites are located in the Tropical Indo-pacific seagrass bioregion on an uplifted Pleistocene carbonate platform (Kent et al., 1971; Short et al., 2007). Water flow in the area is energetic and tidal-dominated with moderate to high current velocities, ranging from 0.25 to 2 ms^{-1} (Shaghude et al., 2002). The sediments are biogenic, with the major

25   constituents being benthic foraminifera, molluscs (pelecypods and gastropods) and coral, with negligible terrigenous inputs (G.R. Narayan unplub.; Shaghude et al., 2002). The seagrasses are growing within a shallow sediment layer (ranging from 19 to 78 cm) on top of solid carbonate rock, which determined the maximum depth of our sediment cores (Figure 6). The limited sediment available under the seagrass meadows and the small amount of fine sediments (~1% <63 size fraction) suggest an overall low-depositional environment (Supplementary Table S1, G.R. Narayan unplub.) or that the sediment

30   source is a limiting factor. Some of the shallowest sediments were found under *T. ciliatum* stands, which uncommon to other seagrasses are known to survive on rocky substrate in highly energetic hydrodynamic environments (Bandeira, 2002; Gullström et al., 2002), and still maintain dense meadows with high biomass. The combined attributes of the energetic flow

regime, carbonate parent material, and the large species pool of the tropical Indo-pacific, lead to diverse meadows with species containing a wide-spectrum of plant traits residing within a relatively coarse, sediment-limited environment. This combination of biological and physical properties did not support a high accumulation and retention of OC within the sediment at our study sites.

5   The geophysical constraint of sediment limitation has been attributed to low OC storage in seagrass meadows of the Arabian Gulf, where similar to this study, OC storage was low (0.7 to 13.2 Mg C ha^{-1}), and not correlated with seagrass biomass (Campbell et al., 2014). Likewise, seagrass meadows in Florida Bay are located on a carbonate platform with a gradient of sediment accumulation from northeast (low) to southwest (high) within the Bay (Fourqurean and Robblee, 1999), which mirrors the pattern of OC storage and seagrass biomass (Armitage and Fourqurean, 2016; Hackney and Durako, 2004;

10   Hall et al., 1999). The potential effect of geophysical conditions on OC storage at our sites on the western coast of Unguja Island, Zanzibar, is revealed when compared to meadows located in the south and east coast of the island. Within meadows at these locations, sediment OC storage is two to three times higher than what was measured in our sites, and is positively correlated to seagrass biomass at the landscape scale, with the largest stocks located in sediments beneath large, persistent species (Gullström et al., 2017). Because most seagrass species occur at all locations, the contrast in OC storage among sites

15   is likely influenced by differences in the depositional environment and/or sediment. The biogenic carbonate sediments that occur on the western side (where our sites occur) differ greatly from the eastern and southern coasts of the Island (Shaghude et al., 2001). The western carbonate sediments are composed of reefal foraminifera, mollusk, echinoderm and coral components, whereas the eastern and southern sediments are composed primarily of the calcareous green algae *Halimeda* (Shaghude et al., 2001), which form algal mounds, allowing for greater deposition of fine particles (carbonate mud) and

20   deeper sediment accumulation (Kangwe et al., 2012; Muzuka et al., 2005).

In other seagrass ecosystems, the relative importance of plant characteristics versus geophysical attributes as indicators for OC storage has been shown to be location or species specific (Alongi et al., 2016; Armitage and Fourqurean, 2016; Dahl et al., 2016; Röhr et al., 2016; Samper-Villarreal et al., 2016; Serrano et al., 2016). As a general trend, in high-depositional environments with relatively high allochthonous OC inputs (where small-bodied, ephemeral species often

25   occur), the abundance of fine grain sediments has been correlated with high OC stocks (Dahl et al., 2016; Röhr et al., 2016; Serrano et al., 2016; van Katwijk et al., 2011). This correlation holds for small-bodied seagrass species at 20 sites across three bioregions (Temperate Southern Ocean, Tropical Indo-Pacific, and Mediterranean; (Serrano et al., 2016)). At adjacent estuarine sites in Thailand with a high contribution of terrestrial inputs and fine sediment, a relatively smaller-bodied seagrass (*Cymodocea serrulata*: 120 Mg C ha^{-1}) had higher OC storage than the large-bodied, persistent seagrass (*Enhalus*

30   *acoroides*: 86 Mg C ha^{-1}), indicating a modulation of plant trait effects by geophysical properties of the site (Miyajima et al., 2015). A similar association between high OC storage and fine sediment was demonstrated across a range of conditions in the Temperate North Atlantic for the small-bodied species, *Zostera marina* (Dahl et al., 2016). However, at sites with relatively coarser sediment, characteristics of *Z. marina* (biomass, density, and cover) became better predictors for OC storage (Dahl et al., 2016). This shift in explanatory power from fine sediments to plant traits was also seen for large-bodied,

persistent species (*Posidonia spp.* and *Amphibolis spp.*) inhabiting coarser sediments in more exposed sites (Serrano et al., 2016). Sites with the largest stores of OC recorded for seagrass are not correlated with fine sediment content and occur within dense meadows of the long-lived species *P. oceanica*, which form and persist in stable environments without high sediment loading (Peirano and Bianchi, 1995; Serrano et al., 2016). This again indicates that the relative importance of plant

5   traits for determining OC storage is in part dependent on the geophysical environment.

Based on the results presented here, in combination with the findings outlined above, we hypothesize the interaction between plant traits and sediment properties is non-linear, with the effect of sediment properties dominating at the extremes of the sedimentation spectrum. In high-depositional areas with an abundance of fine sediment, OC storage can be high even in meadows composed of species with "fast" traits. In moderate depositional areas, the importance of plant traits increase

10   and meadows with "slow" traits will store more OC. Once the flow-regime becomes energetic enough to create sediment limitation, properties of the sediment can again outweigh plant traits to limit OC storage even under meadows with traits conducive to OC storage. Of course, this hypothesis needs to be rigorously tested but the modulation of trait effects by geophysical properties provides hints that different OC stabilization mechanisms are potentially operating within the different environments (Belshe et al., 2017; Burdige, 2007; Lutzow et al., 2006; Miyajima et al., 2017), and the persistence

15   of seagrass sediment OC is a whole-ecosystem property (Lehmann and Kleber, 2015; Schmidt et al., 2011).

This study, placed into the context of the growing body of evidence of the large variation in OC storage in seagrass ecosystems (Dahl et al., 2016; Lavery et al., 2013; Miyajima et al., 2015; Röhr et al., 2016; Samper-Villarreal et al., 2016; Serrano et al., 2014; 2016; 2015), illustrates the complexity of controls and mechanisms that govern OC storage in seagrass sediments. Care must be taken to not narrow our understanding of OC dynamics when searching for broad unifying

20   predictors of OC storage across all seagrass ecosystems. Misidentifying why OC is stabilized within seagrass sediments will hinder our ability to correctly predict the magnitude and rate of OC emissions with the degradation and loss of seagrass ecosystems (Waycott et al., 2009).

5 Conclusion

In this study, we were unable to link variations in plant traits to differences in sediment OC stocks within diverse

25   seagrass meadows off the coast of Zanzibar Town, Tanzania. The geophysical constraints of the environment outweighed any effects of trait differences on OC stabilization and resulted in low OC storage across all seagrass communities. In spite of being constrained within the particular environment, seagrasses still managed to store twice as much OC as bare sediment (Figure 7). In addition, seagrass density and biomass was high in most communities; therefore, the production not stored within sediment beneath the meadows was either exported to support secondary production (la Torre Castro et al., 2014) or

30   sequestered within marine sediments elsewhere (Duarte and Krause-Jensen, 2017). This highlights the importance of seagrass habitats for OC cycling in coastal marine ecosystems; however, further research is needed to identify under which geophysical conditions seagrass traits can be linked to the ecosystem function of OC storage.

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Competing Interest

The authors declare that they have no conflict of interest.

15 **Author Contribution**

All authors contributed to this manuscript; specifically, EF Belshe contributed to the design, data acquisition, analysis, interpretation and wrote the first draft of the manuscript; D Hoeijmakers contributed to the design, data acquisition and analysis, and provided critical review of the manuscript; N Herran contributed to the design, data acquisition, analysis and provided critical review of the manuscript, M Mtolera contributed to the design and data acquisition, and critically revised
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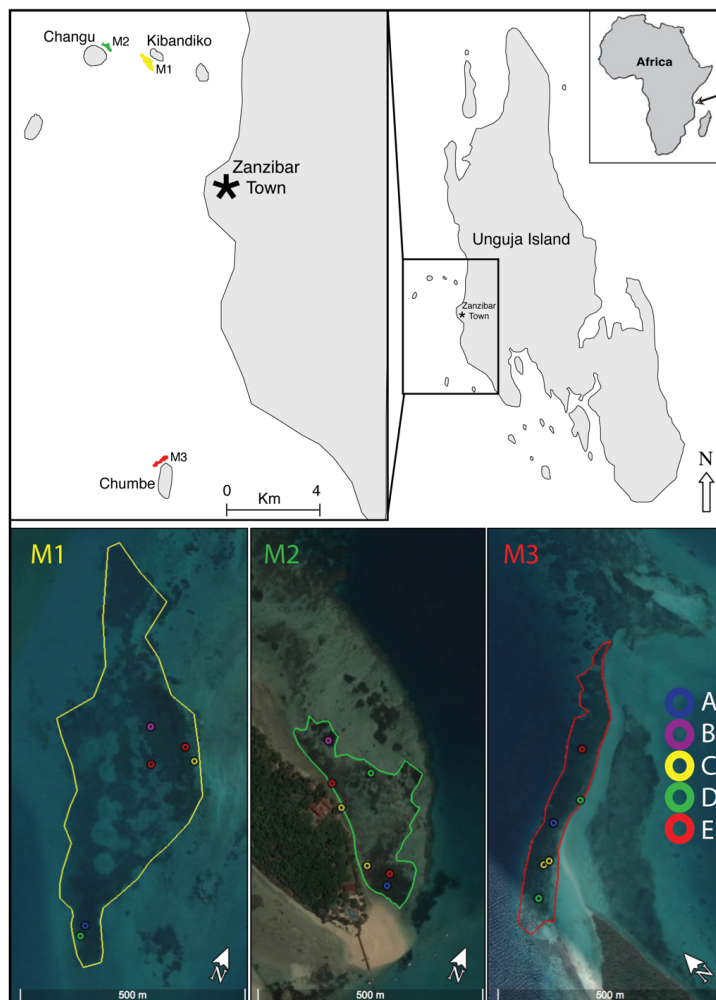
Figure 1: Study sites were located within three meadows (M1, M2, M3) in open coastal waters adjacent to coral cays west of the main city, Zanzibar Town, Unguja Island (-6.15809°S, 39.19181°E) of Zanzibar, Tanzania. Locations of the 19 sample sites within the three meadows (M1, M2, M3) shown in the bottom panels. Sites are colored to correspond to the communities (A, B, C, D, E), which they were classified using multivariate analysis based on similarities of species composition and cover. Images were produced in Google earth Pro V 7.3.0.3832 (August 18, 2017), Data SIO, NOAA, US Navy, IGA and GEBCO. Images © 2017 DigitalGlobe. http://www.earth.google.com
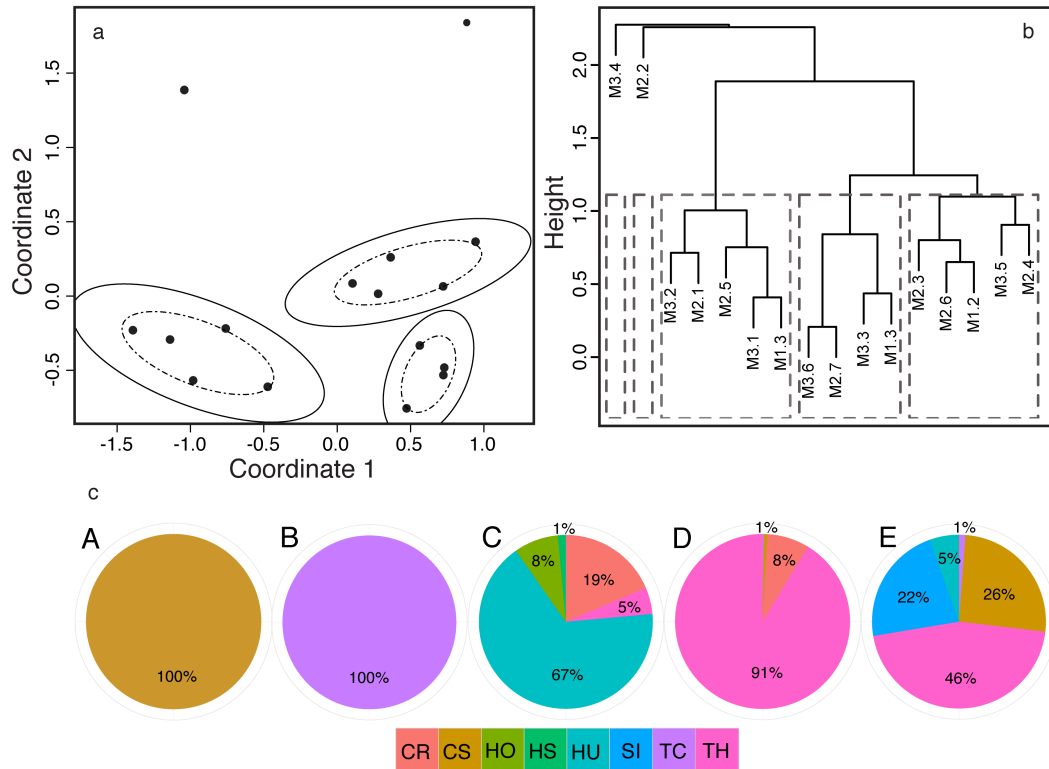
Figure 2: Seagrass communities were determined by grouping the 19 sites based their similarity in seagrass species composition and cover. Two different methods were utilized. First, a) NMDS ordination plot was used to group sites (●) into a community if
5 **they fell within the dashed and solid ellipses representing the 66% and 95% confidence intervals of groupings. Note that within two communities there was 100% overlap in site similarities, so multiple sites are overlain and confidence ellipses were not plotted. Second, b) hierarchical cluster analysis (average linkage) grouped the same 19 sites from the three meadows (M1, M2, M3) and converged on the same five communities. Again, because of the high similarity (100%) of sites within the first two grouping, only one site name is plotted even though multiple sites were grouped into these communities. c) Pie charts of each community (A-E)**
10 **show the mean percent cover and species composition, with colors representing the different species: CR: *Cymodocea rotundata*, CS: *Cymodocea serrulata*, HO: *Holophila ovalis*, HS: *Halophila stipulacea*, HU: *Halodule univervis*, SI: *Syringodium isoetifolium*, TC: *Thalassodendron ciliatum*, TH: *Thalassia hemprichii*.**
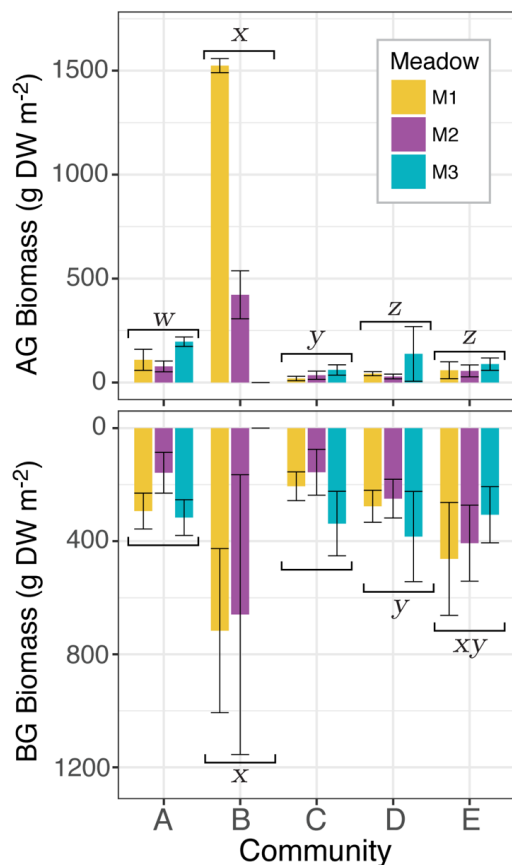
Figure 3: Mean seagrass above- (AG) and belowground (BG) biomass (g DW m-2) of sites from the three meadows (M1, M2, M3) for each seagrass community (A-E). Whiskers represent the standard deviation and statistical differences among communities at the significance level p ≤ 0.05 indicated by letters (w,x,y,z). Differences among meadows within each community were tested for with Tukey's post hoc test but no significant differences were found (Supplementary Tables S3 and S4).
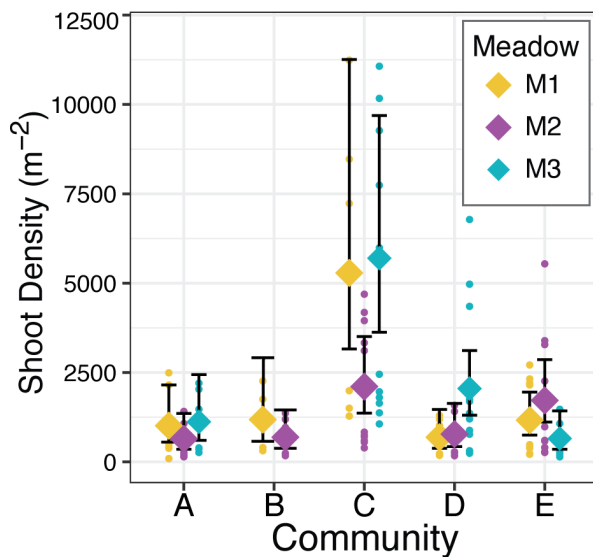
Figure 4: Meadow-specific estimated mean (◆) and 95% confidence intervals of seagrass shoot density (shoots/m-2) for each seagrass community (A-E).
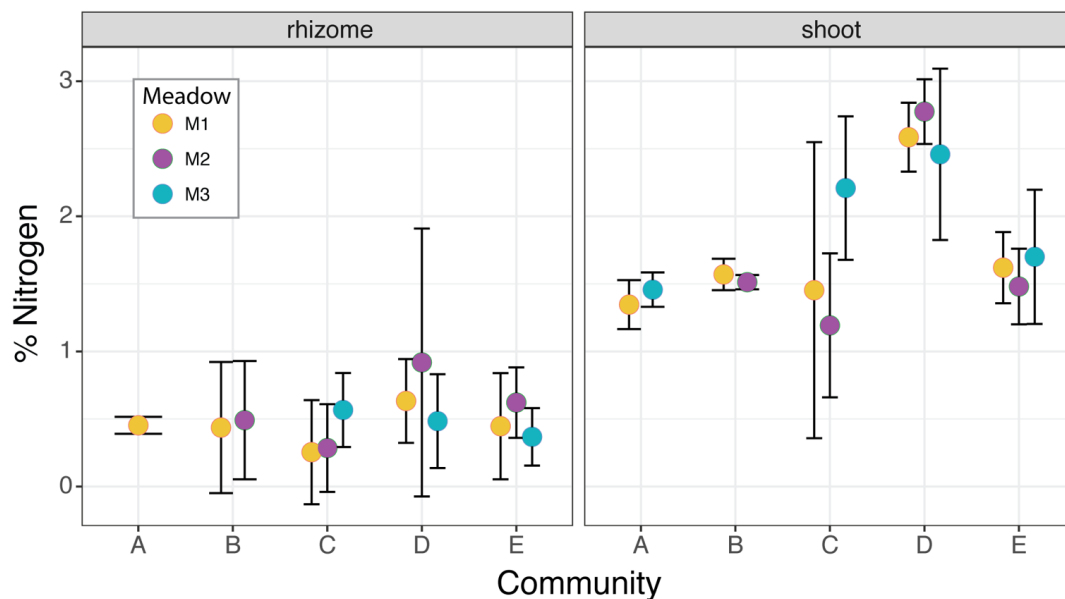
Figure 5: Percent nitrogen (N) in rhizome (left) and leaf (right) tissues from seagrass species assemblages of each community specific to each meadow (M1, M2, M3). Circles (●) denote the mean and whiskers the 95% confidence intervals of the % N weighted by the meadow-specific abundance of each species present within the community (weighted mean ± $t_{0.95}$*weighted standard deviation).
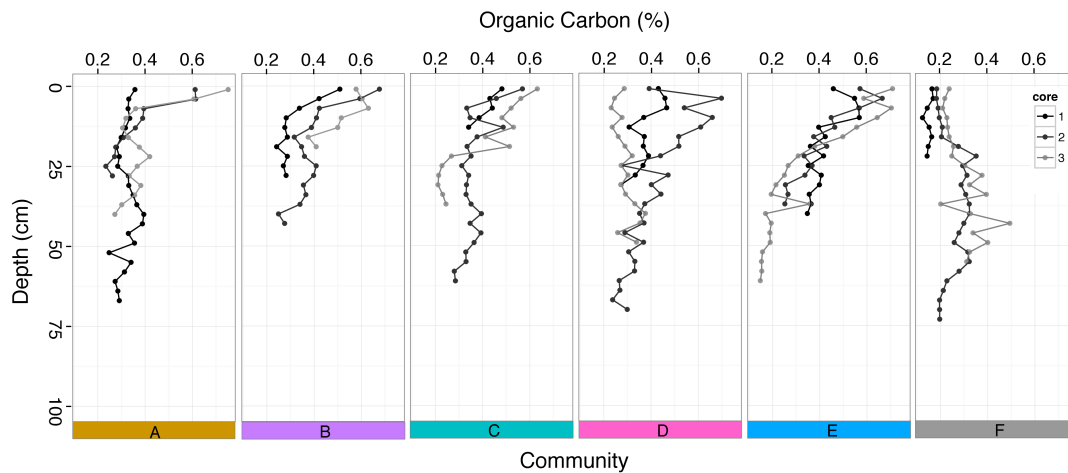
Figure 6: Percent organic carbon at different depths (cm) down each sediment core taken within the five seagrass communities (A–E) and bare sediment (F).
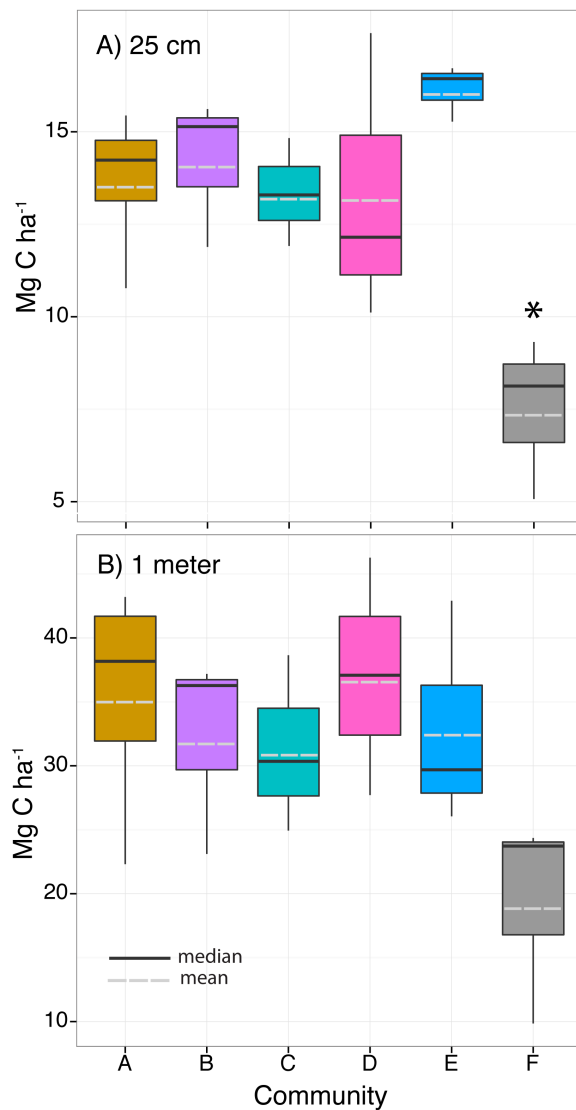
Figure 7: Organic carbon storage of A) the top 25 cm of the sediment and B) the top meter of sediment within the five seagrass communities (A-E) and bare sediment (F). Box and whiskers denote the 25th and 75th, and the 5th and 95th quartiles, respectively, with the solid line denoting the median and dashed line denoting the mean. Statistical difference at the significance level $p \leq 0.05$ indicated by the asterisk (*).