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# Species Traits and Geomorphic Setting as Drivers of Global Soil Carbon Stocks in Seagrass Meadows

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**Abstract** Our knowledge of the factors that can influence the stock of organic carbon (OC) that is stored in the soil of seagrass meadows is evolving, and several causal effects have been used to explain the variation of stocks observed at local to national scales. To gain a global-scale appreciation of the drivers that cause variation in soil OC stocks, we compiled data on published species-specific traits and OC stocks from monospecific and mixed meadows at multiple geomorphological settings. Species identity was recognized as an influential driver of soil OC stocks, despite their large intraspecific variation. The most important seagrass species traits associated with OC stocks were the number of leaves per seagrass shoot, belowground biomass, leaf lifespan, aboveground biomass, leaf lignin, leaf breaking force and leaf OC plus the coastal geomorphology of the area, particularly for lagoon environments. A revised estimate of the global average soil OC stock to 20 cm depth of 15.4 Mg C ha$^{-1}$ is lower than previously reported. The largest stocks were still recorded in Mediterranean seagrass meadows. Our results specifically identify *Posidonia oceanica* from the Mediterranean and, more generally, large and persistent species as key in providing climate regulation services, and as priority species for conservation for this specific ecosystem service.

## 1. Introduction

Seagrass meadows represent the most geographically widespread of the vegetated coastal ecosystems and are found along the coastal fringes of most continents (UNEP-WCMC & Short, 2021), where they provide a range of ecosystem services including direct benefits to local communities and helping adapt to climate change (Cullen-Unsworth et al., 2014; Duarte et al., 2013; Ruiz-Frau et al., 2017). Local services include food provision, nursery habitat, nutrient cycling, and coastal protection; whereas global services accrue through the ability of seagrass meadows to sequester and store C and thus contribute to climate change mitigation through conservation and restoration (Jänes et al., 2020; UNEP, 2020).

Seagrass meadows are highly productive ecosystems and generally tend to be net autotrophic (Duarte & Cebrián, 1996; Duarte & Chiscano, 1999; Duarte et al., 2010), resulting in a net gain of organic carbon (OC), the majority of which is stored in the underlying soil for decades to millennia (Fourqurean et al., 2012). The OC that

**Key Points:**

- To understand global drivers of seagrass carbon stocks, we compiled data on species traits and stocks at multiple geomorphological settings
- Globally, we identify large and long-lived seagrass species in lagoon environments as key in providing climate regulation services
- The Mediterranean is a hotspot of seagrass carbon sequestration, given the distinct capacity of *Posidonia oceanica* to support large stocks

**Supporting Information:**

Supporting Information may be found in the online version of this article.

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is stored in the soil is generally associated with two sources that can be present in varying proportions. Firstly, OC of autochthonous origin, derived from the aboveground (seagrass sheaths and leaves, and production from seagrass-associated algae within the meadows) and belowground (roots and rhizomes) production. Secondly, allochthonous, being derived from outside the meadow with a marine or terrestrial origin (Kennedy et al., 2010). Once the OC is incorporated in the soil, the waterlogged, anoxic conditions slow down decomposition, while the canopies and root systems contribute to prevent erosion and resuspension, aiding OC burial and the preservation of OC stocks (Duarte et al., 2013).

The stock of OC in 1 m depth of seagrass soils worldwide has been estimated at 19.9 Pg with a median OC stock per unit area of 138 Mg C ha$^{-1}$ but including distinct regional differences (Fourqurean et al., 2012). The OC stock ranged from 23.6 ± 8.3 Mg C ha$^{-1}$ in the Indo-Pacific to 372 ± 74.5 Mg C ha$^{-1}$ in the Mediterranean (Fourqurean et al., 2012). Similar variability has also been observed on a smaller regional scale, such as around the coast of Australia, where an 18-fold difference in OC stocks was documented among meadows (Lavery et al., 2013). Such spatial variability across different scales observed in seagrass soil stocks has been attributed to several factors, which can vary locally and regionally due to differences in environmental settings, but also to species-specific controls on the OC input to the soils.

Among the environmental factors controlling OC stocks, landscape configuration, wave exposure, current speed, water depth, temperature, and sediment type have all been implicated (Howard et al., 2021; Mazarrasa et al., 2018; Miyajima et al., 2017; Ricart et al., 2017; Röhr et al., 2016; Samper-Villarreal et al., 2016; Serrano et al., 2014), as has the distance from additional OC sources such as rivers and mangroves or quiescent depositional environments. The allochthonous contribution of organic matter sources to the soils in different environmental settings can contribute between 33% and 62% (25th and 75th percentiles) of the OC in the soil, adding another contributor to the observed variability in soil stocks (Asplund et al., 2021; Chen et al., 2017; Dahl et al., 2016; Kennedy et al., 2010; Serrano, Ricart, et al., 2016).

Species-specific seagrass traits can affect the delivery and storage of autochthonous as well as allochthonous OC. Species-specific differences have been reported to arise from differences in their productivity, cover, canopy height, shoot density, above and belowground biomass (BGB) and rates of biomass turnover and meadow species richness (De los Santos et al., 2016; Duarte & Chiscano, 1999; Lavery et al., 2013; Mazarrasa et al., 2021; Miyajima et al., 2015; Serrano et al., 2014). Seagrass biomass may have a direct influence on soil stocks, while seagrass canopies with their different levels of height, density and habitat structural complexity will affect water velocities, enhance particle sedimentation, reduce resuspension, all of which will aid both allochthonous input and sediment retention capacity (Fonseca et al., 2019; Gacia & Duarte, 2001; Samper-Villarreal et al., 2016). The preservation of the OC that is incorporated into the soil can subsequently depend on the relative allocation of plant production to above and belowground tissues, water depth, and the chemical composition of the biomass in terms of structural components and nutrient content (Duarte, 1990; Howard et al., 2021; Torbatinejad et al., 2007; Trevathan-Tackett, Macreadie, et al., 2017).

Even within a single species there can be considerable variation in the underlying OC soil stock. In *Zostera marina* meadows, OC stocks were found to have a 15-fold difference in magnitude across the northern hemisphere (Röhr et al., 2018), and a ~9-fold over the smaller ranges of the NW Pacific (Prentice et al., 2020) and along the UK south coast (Lima et al., 2020). Around Australia, 4-fold intra-specific differences were found for *Posidonia australis* and *Amphibolis antarctica* (Lavery et al., 2013) and a ~10-fold difference between *Posidonia oceanica* meadows around the Balearic Islands (Mazarrasa et al., 2017). Thus, differences in plant traits as well as the geomorphic or local environmental setting of the meadows can be implicated in driving the variability in seagrass soil OC stocks.

While local or country specific studies have been used to examine the differences in soil OC stock between different environmental settings and seagrass species, and regional studies have been made of stocks supported by a single species, the relative importance of plant traits versus geomorphic controls to explain the variation in seagrass soil OC stocks on a global scale has not been explored. Here, we investigate whether there are consistent differences in soil OC stocks between monospecific and mixed seagrass meadows and monospecific meadows supporting different seagrass species to determine the relative influence of plant traits and geomorphic setting on the global variation in the OC stocks and provide, based on the large data set compiled, a revised estimate of global mean seagrass OC stock. Given the ability of seagrass meadows to store large amounts of OC in their soils, it is important to understand any potential drivers of these stocks and their variability and whether this could allow us to define the species and/or regions globally where seagrass conservation and restoration is most beneficial and loss most critical in terms of climate change mitigation potential.

## 2. Materials and Methods

### 2.1. Data Collection

Soil data was collated from mixed and monospecific seagrass meadows using information from published articles, personal and gray literature. Data were not derived from a systematic review of the literature, but from the previous compilations conducted by or associated with this paper's authors (e.g., Fourqurean et al. (2012); Lavery et al. (2013); Serrano et al. (2019); Mazarrasa et al. (2015)). The data sets used were all published prior to May 2019 and represented cores over 20 or 50 cm length (data set deposited in Kennedy, Pagès, et al., 2022). To remove any differences in approach used to estimate OC stocks, papers where full downcore data were available were used and stocks estimated in a standard manner. At a minimum, studies needed to include the seagrass species present, latitude and longitude of sample location, soil dry bulk density (DBD; g DW $cm^{-3}$), thickness of each core section, and OC content (%OC), organic matter (OM) content and/or loss on ignition (LOI) downcore. The inclusion of OM and LOI allowed addition of information from regions where generally less data is available. Where possible OM and LOI were converted to %OC using locally provided equations. If no locally derived equation was available those presented in Fourqurean et al. (2012) were used. If authors had not explicitly corrected for core compression, it was assumed that core compaction was equal to zero. Soil carbon density ($C_{density}$), that is, the grams of OC per unit volume of soil (g C $cm^{-3}$), was calculated from 0.01*%OC*DBD. In those cores with low sampling resolution along their depth, an equation representing the best fit trend of $C_{density}$ with depth (0–20 or 0–50 cm) was used to estimate intermediate values. Where replicate cores were collected at any location, all individual cores were included in our data set to reflect spatial variability in soil OC stocks. Stocks from all monospecific and mixed meadows were used both separately, and combined, to provide a global estimate of mean/median values of monospecific, mixed and overall OC stocks, respectively.

For some cores in the monospecific seagrass meadows, the soil carbon stable isotope values ($\delta^{13}C_{soil}$) were also available. The mean $\delta^{13}C_{soil}$ was used, in conjunction with literature values of the mean $\delta^{13}C$ of the leaf ($\delta^{13}C_{seagrass}$) of the relevant seagrass species reported in the literature (Hemminga & Mateo, 1996), to assess the presence of allochthonous OC. The $\delta^{13}C$ of OM from major allochthonous sources to seagrass soils, derived from the adjacent land mass, mangroves, tidal marshes or phytoplankton are all more negative than the $\delta^{13}C_{seagrass}$. As many of the data sources did not specify the location of the seagrass meadow sampled in relation to these potential allochthonous sources, the magnitude difference between $\delta^{13}C_{soil}$ and $\delta^{13}C_{seagrass}$, termed $\Delta^{13}C$ ($\Delta^{13}C = \delta^{13}C_{seagrass} - \delta^{13}C_{soil}$), was taken to represent the presence, and in a limited way the proportional contribution, of allochthonous and autochthonous source material to the soils.

The latitude and longitude of each of the sampled cores allowed categorization using an independent, modeled global classification scheme of nearshore coastal geomorphological features (Dürr et al., 2011). Each core was assigned one of the following geomorphological categories: glaciated (type 0), small deltas (type I), tidal systems (II), lagoons (III), fjords (IV), large rivers (type V), karstic (type VI), and arheic (dry) coasts (type VII). The cores from monospecific and mixed meadows had been collected from all but one of the geomorphological settings. As no cores were assigned to large rivers (type V), this category is not included in any further discussion of the data.

Data on seagrass traits was also collated, mostly from compilations in published literature, and included data for mechanical attributes, form, nutrient, and chemical content, stable isotopic composition, biomass and productivity (De los Santos et al., 2016; Duarte, 1990, 1991; Duarte & Chiscano, 1999; Hemminga & Duarte, 2000; Marbà et al., 2002; Trevathan-Tackett, Macreadie, et al., 2017).

### 2.2. Limitations of the Data Set

There was a large intra-specific variation in OC stocks (Table S1 in Supporting Information S2) in monospecific meadows. To avoid an extremely unbalanced design and hence to improve model behavior, only those species with ≥10 stock estimates (*n* = 17) were included in statistical analysis of monospecific meadows (*n* = 25). The global reach of the data set was also limited by the coring effort per country, with nearly half (43%) of the cores coming from Australian meadows, although this may be considered appropriate as they comprise between ~15–43% of the estimated global seagrass extent as well (Serrano et al., 2019). Like other studies, data from Central and South American and African countries were poorly represented or absent. The lack of sites from the geomorphic setting "large rivers" may be due to the innate characteristics of these sites making them unsuitable for seagrass colonization or may be simply due to a lack of data from these settings in our compilation. The Dürr classification may not always assign an accurate setting and a proportion of the cores came from locations that were adjacent, rather than falling inside, the setting to which they were assigned while in some areas of the world, such as the Mediterranean coast, very heterogeneous coastlines make exact boundaries difficult to establish (Dürr et al., 2011). At each site it was assumed that the seagrass species recorded at the time of coring, had been present during the period of soil accumulation inferred from soil thickness. To examine the presence of allochthonous OC, the use of mixing models would have entailed many more assumptions beyond those already taken here, for example, no isotope fractionation during OM decay, not fully accounting intraspecific and site specific differences in $\delta^{13}C_{seagrass}$. Only 13 of the 17 seagrass species with ≥10 OC stock estimates had sufficient soil stable isotope data for estimates of $\Delta^{13}C$ to be made.

While some account was taken of the potential limitations of the core data, the same approach was not possible for the plant traits as it was much more difficult to obtain compilations of large volumes of traits data. Not all the traits that could potentially predict OC stocks were included in the analysis due to a lack of available data across species. The traits that were included in the data set, were not from the same location as the cores in this study. Some traits were represented by a single data point, or by a small number of observations, meaning that trait values or averages may not be representative of the global range or global mean value.

### 2.3. Statistical Assessment of Downcore Trends

The standard practice for determining OC stocks involves taking 1-m deep cores, in order to assess the soil's vulnerability to management and disturbance associated with excavation. Here, in contrast, the study focusses on the drivers that influence OC stocks, which facilitated data over shorter cores to be used. Every core provided data to 20 cm depth, which can be taken to represent recent soils and the site of most intense remineralization (Macreadie et al., 2019). In a review of OC accumulation rates in seagrass meadows Arias-Ortiz (2019) reported a mean sedimentation rate of 2 mm $yr^{-1}$ (95%CI 1.6–2.1 mm $yr^{-1}$) indicating that the 0–20 cm section represent, on average, around 100 years deposition. A smaller number of cores additionally provided data from 20 to 50 cm depth, more representative of the long-term buried OC. Under constant sedimentation and OC source, differences in OC stock over these two depth horizons can be due to diagenesis and compaction, leading to downcore trends in both OC content and DBD. Fourqurean et al. (2012) in a global analysis of seagrass stocks, reported downcore trends in seagrass soils with, on average, OC content decreasing by $0.005\log_{10}(OC+1)$ and DBD increasing by 0.0086 g $cm^{-3}$, each centimetre downcore, leading to a net increase in $C_{density}$ with depth. In other location-or species-specific studies (Kindeberg et al., 2018; Potouroglou et al., 2021) no distinct pattern with depth has been observed. If there is no evidence for differences between surficial (recent) and deeper (buried) carbon stocks, further analysis of the drivers that influence OC stocks could be made using data derived from either surficial or deeper sections of a core. To test for downcore trends in OC content, DBD and $C_{density}$, a meta-analytic framework was used (see Supporting Information S1 html R notebook for more details). For all cores sampled at least at three depth-levels downcore ($n = 254$), the slopes and variance of the linear regressions of the response variable of interest (i.e., OC content, DBD and $C_{density}$) against the predictor 'depth' were estimated. The slopes of linear regressions can directly be used as effect sizes in meta-analysis (Koricheva et al., 2013). For each response variable, a random effects linear model was used to combine individual effect sizes to estimate an overall mean effect with 95% confidence interval. Models were fitted with restricted maximum likelihood using the rma.mv() function within the package "metafor" (Viechtbauer, 2010) in R (R Development Core Team, 2021). Article (i.e., publication) was included as a random factor to account for non-independence of multiple cores extracted from the same study. In addition, funnel plots were examined to assess publication bias (see html R notebook). There was only moderate evidence for a decrease of OC content ($p$-value = 0.047) with depth, very strong evidence for increasing DBD ($p$-value < 0.001) with depth, but no evidence for changes in $C_{density}$ downcore ($p$-value = 0.712) (Figure S1 in Supporting Information S2). As a result, subsequent analysis of OC stocks was undertaken on stocks of 20 cm, which either represented the 0–20 cm cores, or the 0–20 cm or 20–50 cm sections of the longer cores, with the provisor that a core identifier, termed "Core ID" was always used as a random effect in the models, to identify 0–20 cm and 20–50 cm sections of the same core to avoid pseudoreplication (see next subsection). The OC stocks for the 20–50 cm sections were calculated as $\text{OC stock} = \left(\frac{\text{OC}_{(20-50\,\text{cm})}}{30}\right)20$.

### 2.4. Analysis of Carbon Stocks and $\Delta^{13}$C in Relation to Potential Drivers Using Stepwise Linear Models

To investigate the drivers of OC stocks, three different linear mixed effects models were used, where the response variable "OC stocks" (log-transformed) was modeled with different combinations of fixed explanatory variables. First, the relationship of "seagrass species identity" (17 levels) and "coastal geomorphology" (7 levels) with the "OC stocks" of monospecific seagrass meadows was tested.

Second, the relationship between the response variable "OC stocks" and "meadow type" was tested. "Meadow type" was a fixed explanatory variable with three levels: monospecific meadows, multispecific (mixed) meadows, and *P. oceanica* meadows (given that the OC stocks for this seagrass species stood out from the rest of monospecific meadows, see results). Ideally, it would have been desirable to test the relationship of 'meadow type', 'species identity', and 'geomorphology' within the same model. In this way, we would have been able to decipher the relative influence of each variable holistically. However, this was not possible since preliminary analyses already showed a strong relationship between 'species identity' and 'OC stocks"; and in order to assign a core to a seagrass species, the sampled meadow (or at least the patch) must be monospecific. In addition, the explanatory variables "meadow type" and "species identity" were fully collinear, which is incompatible with their simultaneous inclusion in linear models.

Third, $\Delta^{13}$C, the difference in $\delta^{13}$C between soil and seagrass leaves, was used to assess the presence of allochthonous OC. We used linear mixed effects models to identify the relationship between "$\Delta^{13}$C" (response variable) and "seagrass species identity" (13 levels) and "coastal geomorphology" (7 levels) (both variables as fixed predictors).

All the linear mixed effects models specified above, additionally included the random effects "Article", to account for the shared variability between those OC stocks obtained from the same publication; and "Core ID" nested in "Article", to account for the shared variability of OC stocks coming from the same core identifier (i.e., the two different sections from the 50 cm long cores). The inclusion of both random effects was supported by the Akaike Information Criterion (AIC) and log-likelihood ratio tests after comparing different options for the random structure (Zuur et al., 2009). In the case of the second linear mixed effects model (see above), "coastal geomorphology" was included as an additional random effect, since for this model we were only interested in the effect of "meadow type" on "OC stocks", but we still needed to control for the variability resulting from cores coming from the same geomorphologies (see html R notebook for more details). Once the random structure of the model was defined, model selection started from a full model including all explanatory variables and relevant interactions. Then, each fixed effect (i.e., each explanatory variable or interaction) was dropped one by one, and the best model was selected using the Akaike Information Criterion and the likelihood ratio test statistic (Zuur et al., 2009). Furthermore, marginal *F*-tests with univariate analysis of deviance (Zuur et al., 2009) were performed to investigate the effects of the remaining explanatory variables on "OC stocks" for each best-selected model. Tukey Honestly Significant Difference (HSD) post hoc tests were undertaken using the package multcomp (Hothorn et al., 2008) to determine level-specific differences within model variables. Model validation was assessed by inspecting model residuals and fitted values. Whenever model residuals were clearly heteroscedastic, variance structure was specified with weights using the package nlme (Pinheiro et al., 2011) in R (R Development Core Team, 2021). See Supporting Information S1 html R notebook for a summary of the main analyses, or the raw R code (Kennedy et al., 2022) for the full details.

### 2.5. Principal Component Analysis (PCA) of Plant Traits

A Principal Component Analysis (PCA) was run on species traits to better understand whether particular traits define a single or group of seagrass species. The outcome of this analysis complements the subsequent assessment of which combination of traits potentially drive bigger or smaller OC stocks (see Partial Least Squares (PLS) regression in next subsection). Some of the species in the data set only had information for a small subset of traits, thus, given that PCAs do not accept matrices with missing data points, 3 out of the 17 species that had

$\geq$10 soil stock estimates and used in the stepwise linear models were dropped from traits analysis (i.e., *Thalassodendron ciliatum*, *A. antarctica* and *Zostera muelleri*). As a result, the PCA was run on 14 species, for which 25 traits were available. The PCA was implemented on scaled data (given the variety of trait units) and the main components were retained after inspecting scree plots. See Supporting Information S1 html R notebook or the raw R code (Kennedy et al., 2022) for more details on this analysis.

### 2.6. Analysis of Carbon Stocks Using Partial Least Squares Regression (PLSR)

PLS regression was used to explore the effects of plant traits and coastal geomorphology on the response variable "OC stocks." PLS regression is a multivariate technique that produces latent variables (linear combinations of several predictors, i.e., PLS components) that maximize the explained variance of the response variable. PLS regression is especially useful when the number of predictor variables is high (25 predictors were used in this study) and particularly when these variables are highly correlated (Carrascal et al., 2009). The PLS regression models were evaluated based on the level of variance explained ($R^2$), the loadings of the predictor variables on PLS components, and the Variable Importance in Projection (VIP). The loadings describe the relative strength and direction of the relationship between the predictors and the response variable (OC stocks in this case). The VIP value summarizes the importance of each predictor variable on the multivariate relationship. The limit for a variable to be considered important was a VIP value of 1 (Chong & Jun 2005; Farrés et al., 2015). Since PLS performance metrics (such as $R^2$, e.g.,) require a training data set (to train the model) and a test data set (to test the performance of the model), a subsampling technique was used where the training data set was composed of a random sample of 80% of the original data set, with the remaining 20% of samples used as test data. Then PLS regression was carried out on the training data set, and the resulting model was applied to the test data set for validation. To make this analysis even more robust, the above-mentioned procedure was iterated 100 times. This resulted in a distribution of VIP values and loadings for each variable, allowing VIP values and loadings to be represented as boxplots and barplots with error bars. PLS regression analyses were performed using the packages pls (Mevik et al., 2020) and caret (Kuhn, 2021) in R (R Development Core Team, 2021). See Supporting Information S1 html R notebook or the raw R code (Kennedy et al., 2022) for details on this analysis. Once the PLS regression output had identified the important predictors of OC stocks (VIP>1), the relationship between each of the selected predictors and OC stocks were plotted, as a guide for interpreting Partial Least Squares Regression (PLSR) results, given that picturing latent variables (combined variables) can be challenging without this context.

## 3. Results

All results have been written translating *p*-values into the language of evidence, following recommendations in Muff et al. (2021).

### 3.1. Overview of the Data Set

Data from a total of 576 cores was collated from seagrass meadows covering 22 countries between 64°N and 40°S, with cores from the sub-arctic, both hemispheres of the temperate and tropical zones, and with the Arabian Peninsula and Australia particularly well represented (Figure 1, and inset). Out of the total 576 cores, 350 cores were surficial (only one section 0–20 cm), while the remaining 226 cores were longer and were divided into two depth categories (0–20 cm and 20–50 cm). Thus, the total number of sections analyzed in this study was 802. The data set comprised cores taken from meadows representing 25 different seagrass species (Table S1 in Supporting Information S2) out of the 72 seagrass species present globally (Short et al., 2011) and 17 of these species were included in our analysis (those with $\geq$10 stock estimates, $n_{\text{sections}}$). The most frequently sampled meadows were dominated by species from the genus *Posidonia* ($n_{\text{sections}} = 217$), from either Australian or Mediterranean coastal waters; and meadows with species from the genus *Zostera* ($n_{\text{sections}} = 205$), covering temperate regions and the sub-arctic.

The cores from monospecific and mixed meadows had been collected from seven geomorphological settings, but at different frequencies. The largest data set was from small deltas (41%), followed by dry coasts (arheic) (21%) and tidal systems (18%).

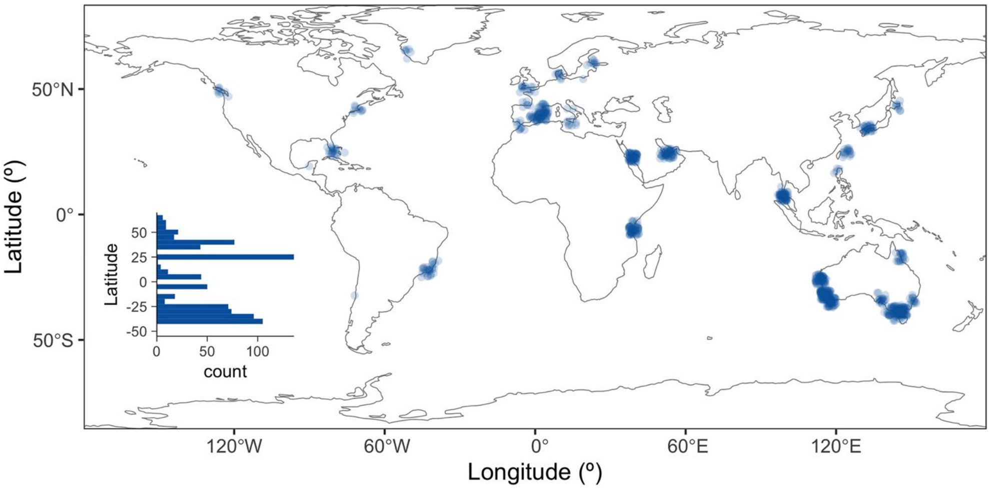

**Figure 1.** Geographical distribution of the 802 seagrass soil sections compiled in this study. Note that points have some transparency, thus, the darker blue the point, the greater the density of samples (e.g., around Australia, Arabian Peninsula, east of Iberian Peninsula). Note that points have been jittered for improved visualization.

### 3.2. OC Stocks and Their Relation to Explanatory Variables

The global mean ± SE and median OC stocks (representing a 20 cm stock) were 22.3 ± 0.8 and 15.4 Mg C $ha^{-1}$ respectively and *P. oceanica* meadows supported the largest stocks ($n = 79$; 71.2 ± 6.2 and 55.1 Mg C $ha^{-1}$ respectively) compared to other monospecific meadows ($n = 611$; 16.4 ± 0.4 and 14.2 Mg C $ha^{-1}$ respectively), or mixed meadows ($n = 112$; 19.8 ± 1.3 and 17.0 Mg C $ha^{-1}$ respectively). The differences in OC stocks were between *P. oceanica* meadows and the rest of monospecific and mixed meadows (Figure 2a), while no evidence for differences between mixed and the rest of monospecific meadows was observed (Figure 2a).

According to the linear mixed effects model, the variables showing closest relationships with OC stocks from monospecific seagrass meadows were the seagrass species identity ($p$-value < 0.001, Table 1) and the coastal geomorphology of the area where the core had been collected ($p$-value < 0.001, Table 1). With these two fixed effects together, the model explained a 32% of the variance in OC stocks ($R^2_{\text{marginal}} = 0.32$), while the inclusion of the random effects "Article" and "Core ID" increased the overall amount of variance explained by the model to 93% ($R^2_{\text{conditional}} = 0.93$), highlighting the intrinsic small-scale variability of OC stocks.

There was strong evidence for the Mediterranean endemic seagrass *P. oceanica* having higher mean OC stocks 71.2 ± 6.2 Mg C $ha^{-1}$ than *Zostera noltii* (19.3 ± 1.8 Mg C $ha^{-1}$), *Halophila ovalis* (9.5 ± 1.2 Mg C $ha^{-1}$), *T. ciliatum* (7.5 ± 1.6 Mg C $ha^{-1}$) and *Halophila stipulacea* (7.3 ± 0.8 Mg C $ha^{-1}$). In contrast, despite *P. oceanica* OC stocks being roughly double those of the second ranked seagrass (*Thalassia testudinum,* 30.8 ± 2.2 Mg C $ha^{-1}$), there was little to no evidence for differences between *P. oceanica* OC stocks and those of species with mean stocks ranging from 10 to 30 Mg C $ha^{-1}$, according to Tukey HSD multiple comparisons (Figure 3a), likely due to the high variance of *P. oceanica* OC stock values. When cores taken from *P. oceanica* meadows were removed from the analysis, the evidence for an influence of seagrass species identity on OC stocks was still moderate ($p\text{-value}_{\text{without } P.\ oceanica} = 0.013$), although Tukey HSD no longer found evidence for differences between pairs of the remaining species (Figure 3c). In terms of coastal geomorphology, there was strong evidence that cores from fjords showed the lowest OC stocks (mean ± SE 9.8 ± 1.9 Mg C $ha^{-1}$), lower than dry coasts (arheic) (13.3 ± 0.7 Mg C $ha^{-1}$), tidal systems (20.8 ± 1.1 Mg C $ha^{-1}$), small deltas (26.5 ± 1.9 Mg C $ha^{-1}$), and lagoons (43.1 ± 7.3 Mg C $ha^{-1}$) (Figure 3b). The evidence for an influence of coastal geomorphology on seagrass OC stocks remained when cores from *P. oceanica* were removed from the analysis ($p$-value < 0.001, Figure 3d).

There was very strong evidence for an effect of seagrass species identity and geomorphology on OC provenance/source ($\Delta^{13}$C), with an obvious trend for large persistent species, such as those from the genus *Posidonia*, to have lower $\Delta^{13}$C, suggesting a smaller allochthonous contribution of OC (Figure 4a). There was also a clear trend for a higher $\Delta^{13}$C in cores collected from meadows in lagoonal and glaciated coastal settings, suggestive of a substantial allochthonous OC contribution at these settings (Figure 4b).

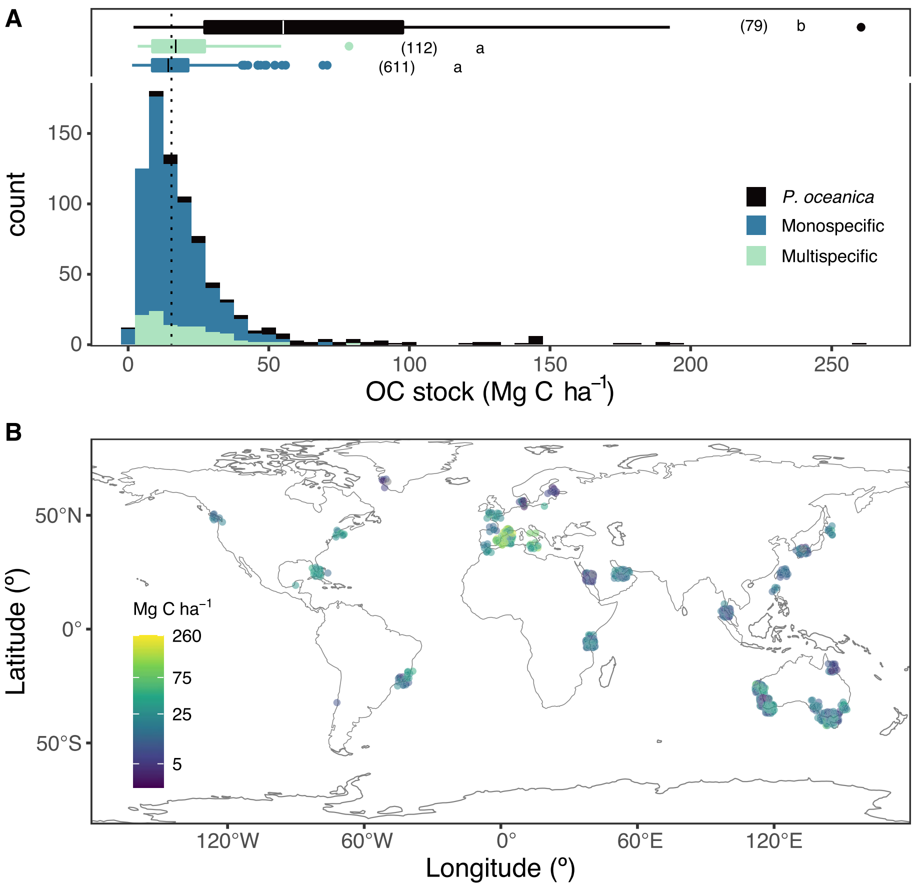

**Figure 2.** Influence of meadow type on organic carbon (OC) stocks and global map of OC stocks "hotspots." (a) Histogram showing the distribution of OC stocks for each type of meadow considered by our model (*Posidonia oceanica*, monospecific, and multispecific). Note that the distribution of *P. oceanica* OC stocks is extremely skewed to the right, compared to the rest of monospecific and mixed meadows. Overlaid on the histogram, boxplots for each meadow type support model results, with *P. oceanica* meadows having higher OC stocks than the rest of monospecific and mixed meadows. Dotted vertical line illustrates the global median considering all samples together. Different lower-case letters next to each box correspond to Tukey Honestly Significant Difference post-hoc tests with $p$-value $< 0.05$. Number of cores for each group are given in brackets. (b) Geographical distribution of seagrass soil sections compiled in this study colored according to their OC stocks. The Mediterranean appears as the clearest hotspot of OC stocks, coherent with *P. oceanica* (endemic to the Mediterranean) being the seagrass with highest OC stocks. Note that points have some transparency, thus, the more solid the point looks, the greater the density of samples. Note that points have been jittered for improved visualization, as well.

The first three components of the PCA of seagrass species traits explained 67% of the variance in OC stocks, with the first component (PC1) already explaining 41% of the variance. PC1 was positively loaded with traits such as rhizome diameter, leaf lifespan and BGB, among others; and negatively loaded with leaf turnover (Figure 5, arrows). As a result, species from the genera *Posidonia* and *Enhalus* were found on the positive side of the axis, and *Halophila*, *Halodule*, *Zostera* and *Cymodocea* species on the negative side (Figure 5, points). PC2 and PC3 defined gradients of plant nutrient contents, with PC2 linked to nitrogen and productivity, and PC3 related to phosphorus.

**Table 1**
*Analysis of Deviance Table for the Two Main Linear Mixed Effects Models*

| Response | Fixed effects | Df | $\chi^2$ | $p$-value |
|---|---|---|---|---|
| log(OC stock) | Species | 16 | 105.6 | <0.001*** |
| | Coastal geomorphology | 6 | 36.4 | <0.001*** |
| log(OC stock) | Meadow type | 2 | 92.3 | <0.001*** |

*Note.* Df.: degrees of freedom.
***, *p*-value 〈 0.001, that is very strong evidence for the effect influencing the response variable.

PLSR showed that the most important seagrass species traits related to OC stocks (those with VIP > 1) were the number of leaves per seagrass shoot, BGB, leaf lifespan, aboveground biomass (AGB), leaf lignin, leaf breaking force and leaf OC, plus a level of the categorical variable coastal geomorphology (lagoons) (Figure 6a). All predictors (except leaf carbon) positively loaded the first PLS component (PLS1) (Figure 6c), which already explained 39% of the variance of predictors and 27% of the variance in OC stocks.

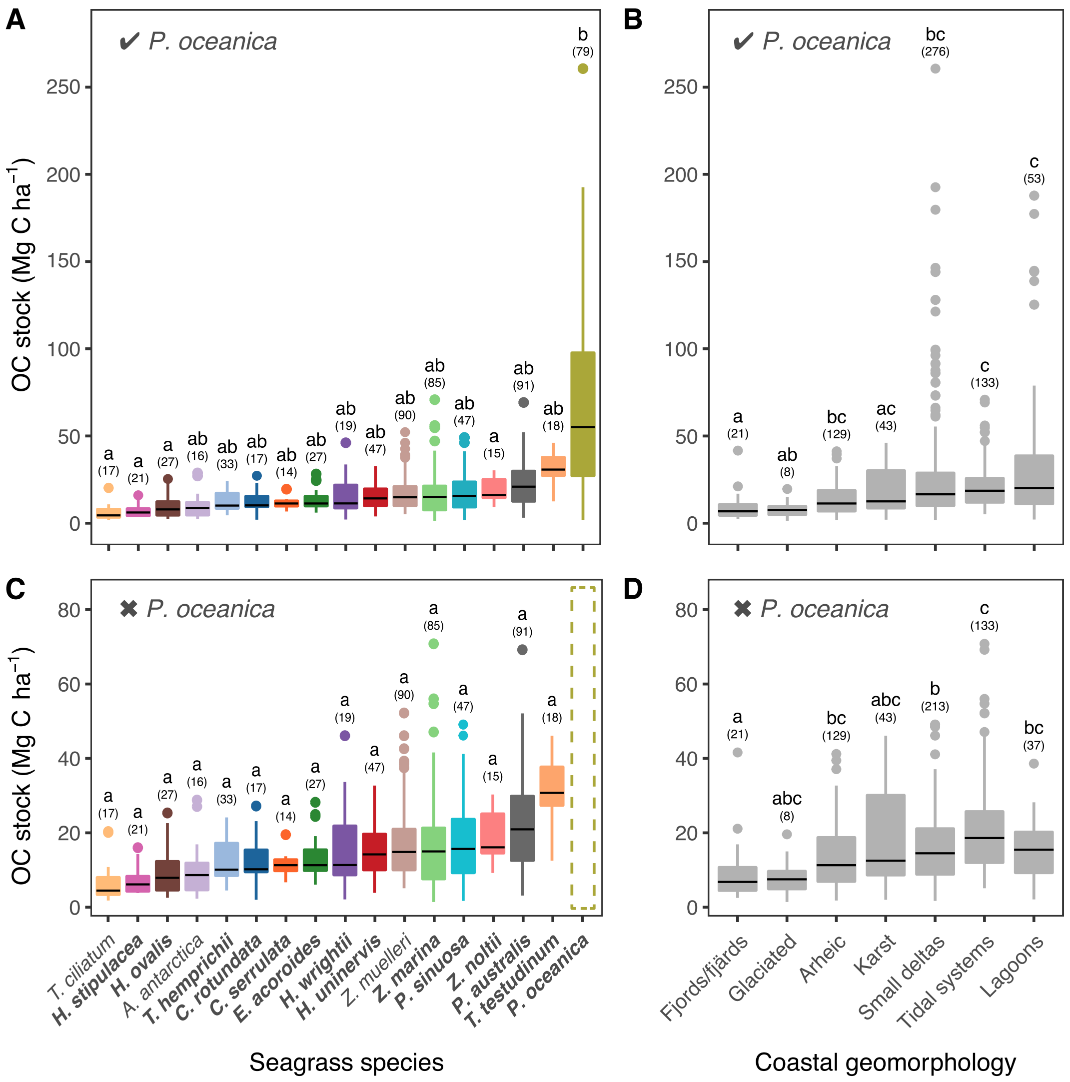

**Figure 3.** Drivers of seagrass organic carbon (OC) soil stocks for monospecific seagrass meadows. According to stepwise linear mixed effects models, (a) there was very strong evidence for an influence of species identity, (b) and coastal geomorphology on OC stocks when cores extracted from *Posidonia oceanica* meadows were included. In contrast, (c) without *P. oceanica* cores, the influence of species identity on OC stocks was reduced, (d) while the effect of coastal geomorphology was maintained. Different lower-case letters above each box correspond to Tukey Honestly Significant Difference post-hoc tests with $p$-value < 0.05. Number of core sections for each group are given in brackets. Species in bold in panel (c) correspond to those included in trait-analyses (see Figures 5 and 6). The dashed square in panel (c) emphasizes the lack of *P. oceanica* data for the model results presented in panels (c and d). Note that the $y$ axes in panels (c and d) cover a narrower range than those in (a and b).

PLS1, was therefore very similar to PC1 from Figure 5, with a dominance of the variables leaf lifespan and AGB and BGB on the positive side and leaf carbon on the negative side. The final PLS regression model, with just 2 PLS components explained 44% of the variation in OC stocks and 49% of the predictor variance; and PLS2 was dominated by number of leaves per shoot on the positive side and leaf breaking force on the negative side (again similar to PC2, from Figure 5). When the relationship between each of the selected predictors and OC stocks were plotted, BGB was the only plant trait, from those identified as important by the PLSR, for which we had evidence for a direct influence on soil OC stocks, on its own (Figure S2A in Supporting Information S2, $p$-value < 0.001).

As with linear mixed effects models, the PLS regressions appeared to be highly influenced by *P. oceanica* data (see Figures 2a and 6d). When *P. oceanica* data was omitted from the PLS analysis, the results were very different, with none of the predictors considered important anymore (all variables with VIP < 1, Figure 6b), and the

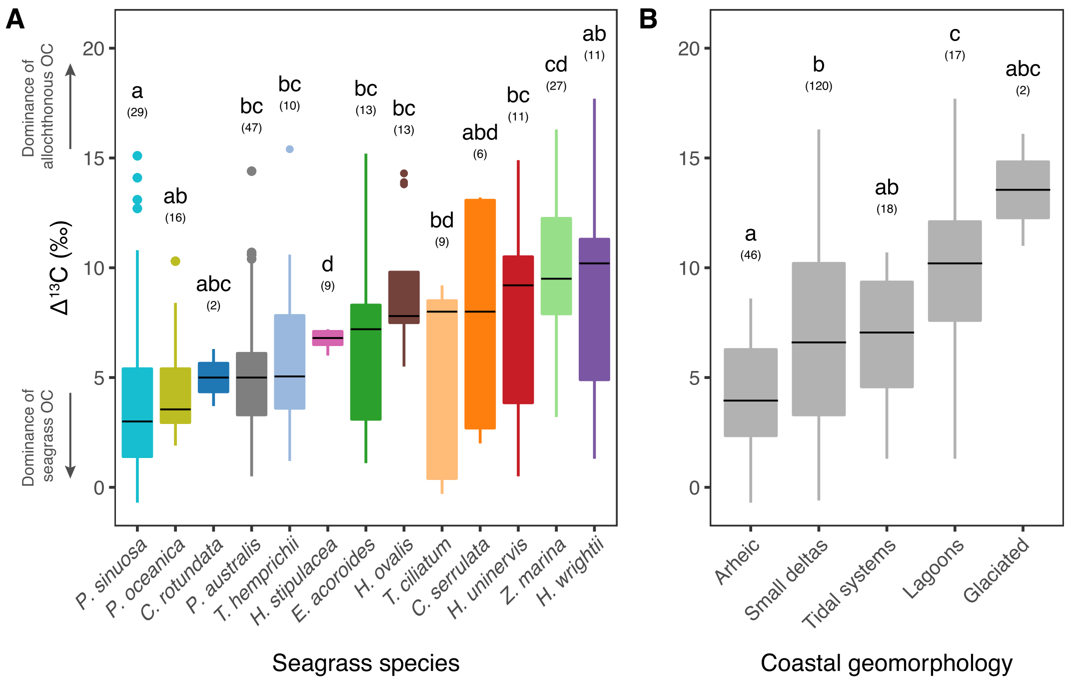

**Figure 4.** Drivers of seagrass C provenance/source ($\Delta^{13}$C) for monospecific meadows. According to stepwise linear mixed effects models, (a) there was very strong evidence for an effect of seagrass species identity and (b) geomorphology on $\Delta^{13}$C. Different lower-case letters above each box correspond to Tukey Honestly Significant Difference post-hoc tests with *p*-value < 0.05. Number of core sections for each group are given in brackets.

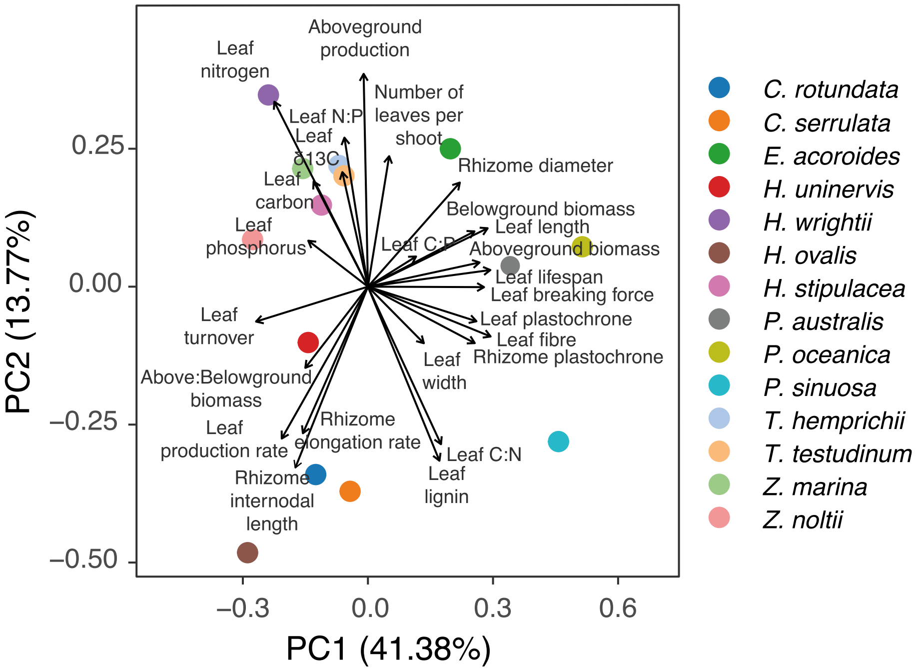

**Figure 5.** Principal Component Analysis (PCA) of seagrass traits. In this biplot we show the scores of each seagrass species (points) and the loadings of each seagrass trait (arrows) on the first and second principal components. The angles between arrows approximate to their correlations (smaller angles imply high correlations between variables, and perpendicular arrows imply zero correlation). Points that are close together correspond to seagrass species that have similar scores on the PCA components (i.e., trait space). Note that species from the same genus tend to cluster together (e.g., *Posidonia spp*., *Thalassia spp*., *Cymodocea spp*.).

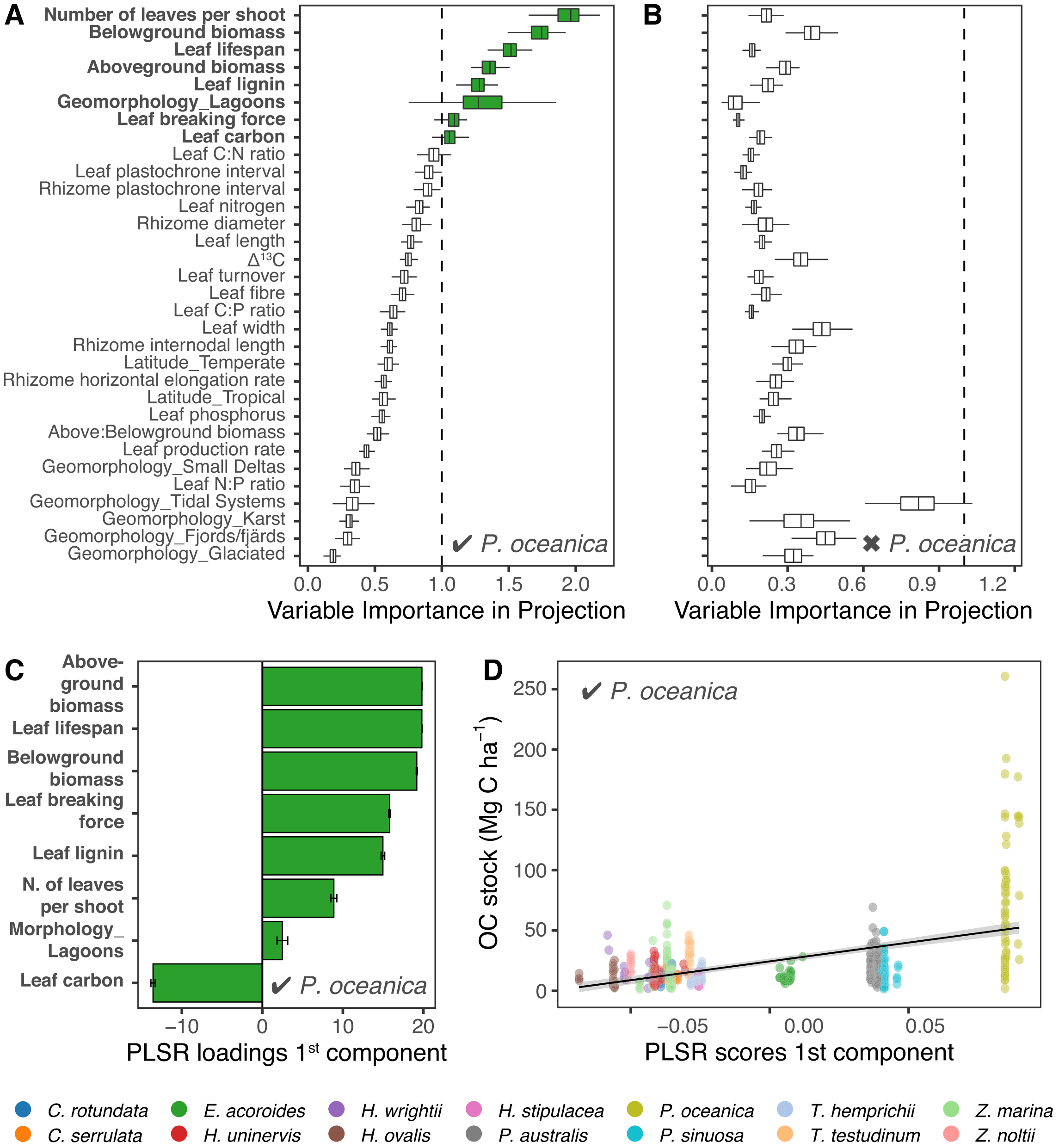

**Figure 6.** Relationship between organic carbon (OC) stocks and seagrass species traits and geomorphology, as shown by Partial Least Squares Regression. (a and b) List of the most important variables influencing OC stocks, according to the Variable Importance in Projection (VIP; variables with VIP > 1 appear in green). Note that this analysis found eight variables with VIP > 1, when the data set included *Posidonia oceanica* samples (a), while no variables were selected when *P. oceanica* was removed from the analysis (b). (c) Loadings of the most important variables according to VIP on PLS1 (model with *P. oceanica* samples). Variables with positive loadings on PLS1 are positively related with OC stocks. (d) OC stocks and Partial Least Squares Regression (PLSR) scores on PLS1 were positively correlated. The *x* axis of this plot can be interpreted as a latent variable, that is, a combination of the most important variables according to VIP (see panel a). Thus, linking the information from panels (a and c) together, the points more to the right in panel (d), represent samples of species characterised by high biomass, long leaf lifespan, high number of leaves per shoot, high leaf lignin, high breaking force, low leaf carbon, and concomitantly high OC stocks (*y* axis).

final variance in OC stocks explained by the model with 3 PLS components fell to 22%, compared to 47% in the model with *P. oceanica*.

## 4. Discussion

### 4.1. Drivers of Global Seagrass Soil C Stocks

While variation in seagrass soil OC content and stocks is known to occur across the globe (Fourqurean et al., 2012), investigating drivers of this variation has mainly been undertaken over local, regional or country-wide scales that have considered differences between a few species and over a limited range of environmental settings (Belshe et al., 2018; Dahl et al., 2016; Githaiga et al., 2017; Howard et al., 2016; Kindeberg et al., 2018; Lavery et al., 2013; Lima et al., 2020; Mazarrasa et al., 2021; Röhr et al., 2016). The majority, though not all (e.g., Belshe et al., 2018; Howard et al., 2016) of the above-cited studies observed differences in soil OC stocks associated with one or more species within the same or at different locations. Our results confirm, on a global scale, that species identity is an influential driver of seagrass soil OC stocks (Figure 3a and Table 1), despite high levels of within-species variation. This study, therefore, highlights the importance of biological factors in defining global seagrass OC stocks, and shows that on a global scale, species identity and specifically, the variation in plant traits between species are key factors of OC stocks. Species identity, characterized by a particular combination of plant traits such as size, biomass, productivity, life span, turnover, morphology, production, and OM quality, had been previously inferred as potentially driving the observed differences in seagrass soil OC stocks (Mazarrasa et al., 2018, 2021). However, the influence of the combination of plant traits that characterize each seagrass species on OC stocks had not been explicitly tested, until now. In this study, the larger stocks were found to be associated with seagrass species with large biomass, high mechanical strength, recalcitrant tissues, and long lifespan.

Geomorphology has been identified as a good predictor of tidal marsh soil stocks in Australia (Macreadie et al., 2017) and as a driver of variation in global mangrove soil stocks (Rovai et al., 2018; Twilley et al., 2018). The Dürr global classification scheme of coastal geomorphology has been employed to understand the distribution of OC stocks in mangroves, while for seagrass meadows only simpler categorizations have been used. For example, adding the categories "estuaries" and "coasts" did not improve the prediction of soil stocks (Mazarrasa et al., 2021; Serrano, Ricart, et al., 2016). In our study, using the Dürr model, we only found lagoons were identified as an important geomorphological category in predicting soil OC stocks on a global scale. Interestingly, coastal geomorphology appeared to be more closely related to soil OC stocks when *P. oceanica* was removed from the analysis (both for the stepwise and PLS regressions), confirming this species is partly responsible for the dominance of species identity and plant traits over geomorphology for predicting OC stocks. In fact, soil grain size, which is strongly controlled by geomorphology, is the best predictor of surficial OC stocks across the landscape of south Florida (Howard et al., 2021), suggesting more research into how landscape-scale variations in geomorphology affect OC stock are needed to truly understand the role that sedimentation regime plays in determining soil OC stocks.

### 4.2. The Influence of Species Identity and Plant Traits on Variation in Soil OC Stocks

Each of the traits identified as influencing soil OC stocks in our analysis has previously been implicated as drivers, but generally based on studies of a single trait or seagrass species, whereas our analysis indicates that it is a suite of traits that are most influential in predicting soil OC stocks. From the combination of plant traits identified as drivers of soil OC stocks in our study, AGB and BGB were both identified by the PLSR analysis (Figure 6). AGB has been implicated as a potential driver of OC stocks in other studies, although often from meadows characterized by large species with a long lifespan (e.g., *T. hemprichii, E. acoroides, and P. oceanica*), and where biomass and OC stocks have also varied in relation to water depth, nutrient availability, different positions in a meadow or between meadows (Serrano et al., 2014; Serrano, Ricart, et al., 2016; Stankovic, Tantipisanuh, & Prathep, 2018). From the listed influential traits, BGB uniquely provided a significant relationship when plotted selectively with soil OC stocks (Figure S2A in Supporting Information S2, $p$-value $< 0.001$). It might not be surprising to find seagrass BGB as a strong predictor of soil OC stocks, as these tissues grow directly into the soil pool, in predominantly anoxic conditions, thereby representing a direct input of carbon to the soil stock (Trevathan-Tackett, Macreadie, et al., 2017). In Florida Bay, the east African coast, Japan, Thailand

and Taiwan a relationship between BGB and soil OC stocks and/or soil OC content have also been observed (Armitage & Fourqurean, 2016; Gullström et al., 2018; Stankovic, Tantipisanuh, & Prathep, 2018). Moreover, Trevathan-Tackett, Macreadie, et al. (2017) found that root tissues contained the highest proportion of refractory material, and suggested that BGB could be the most consistent contributor of recalcitrant material to the soil.

The link between BGB and global seagrass soil OC stocks (Figure S2A in Supporting Information S2) suggests that measurement of BGB could constitute a good proxy for soil OC stocks. However, BGB is not often measured, compared to AGB, as it is not visually quantifiable and cannot be estimated using remote sensing techniques, requiring destructive sampling for quantification. A lack of current BGB data is apparent, as the most recent compilation is that of maximum BGB by Duarte and Chiscano (1999), who were only able to compile BGB values from 15 out of 29 species and with only three species having more than five estimates to define a mean value. As our investigation used the limited values available from Duarte and Chiscano (1999), any further investigation of BGB, or inclusion of BGB production and turnover as drivers of soil OC stocks would benefit from a wider range of measurement across species. Alternatively, other plant traits, if they had more representative global mean values, could be used to predict BGB and/or soil OC stocks. For example, relationships between seagrass cover and BGB have been observed in individual species such as *E. acoroides* in Thailand and Gazi Bay (Githaiga et al., 2017; Stankovic, Tantipisanuh, & Prathep, 2018) and *T. testudinum* and *Syringodium filiforme* in the Gulf of Mexico (Congdon et al., 2017). Furthermore Stankovic, Tantipisanuh, Rattanachot, and Prathep (2018) used a connected chain of predictive models to estimate soil OC stocks from simple observations of *E. acoroides* cover. However, these relationships have generally been observed for large, persistent species and the same kind of trend may not be universal. For example, only one out of three species had any relationship between AGB and BGB in Gazi Bay (Githaiga et al., 2017). A more comprehensive suite of variables including those related to the type of environmental conditions at the meadow location widened the predictive capacity for BGB estimates and was extended to include more opportunistic species such as *H. ovalis, Halophila uninervis,* and *Z. muelleri*, as well as the persistent long-lived species (Collier et al., 2021). In any case, a potential drawback of using variables such as seagrass cover, and AGB is their reliance on measurement at time of collection, which may not be representative of the whole period of soil accumulation. Nevertheless, given the observed links between these parameters and soil OC stocks, further investigation of the opportunity presented by the use of these simple measures may produce a cost-effective means of evaluating global scale OC stocks.

Our PLSR results identified leaf lignin content as an important trait driving high soil stocks, as exemplified by *P. oceanica* (Figure 5, Figure S2E in Supporting Information S2). Two other traits that were influential in defining the variation in OC stocks, as shown by the PLSR, were leaf life span and breaking force, both of which have been associated with seagrass species having large biomass and high lignin concentration (De los Santos et al., 2016). However, in our PCA, leaf lignin was not particularly linked to leaf-lifespan, leaf breaking force or biomass, possibly a result of the relatively low leaf-breaking force of *P. oceanica* (Figure 5, Figure S2F in Supporting Information S2). Lignin content has been implicated in driving high soil OM stocks as it resists decomposition and aids preservation of the OM in the soils. Refractory OM, and the tissues of *Posidonia spp.* in particular, contain high concentrations of lignin compounds (Kaal et al., 2018; Klap et al., 2000; Serrano et al., 2020; Torbatinejad et al., 2007; Trevathan-Tackett, Macreadie, et al., 2017). Similarly, low nutrient content has also been connected to OM recalcitrance (Enríquez et al., 1993; Nakakuni et al., 2021; Trevathan-Tackett, Macreadie, et al., 2017) but not always substantiated by field studies, as nutrient additions to decomposition experiments with *Z. muelleri* had no significant effect on remineralisation rates (Trevathan-Tackett, Seymour, et al., 2017). Moreover, Belshe et al. (2018) found that meadows dominated by *T. ciliatum* with low nutrient content did not have a higher soil OC stock compared to other species with higher nutrient content at different locations. Consistent with these field studies, nutrient content was not an important variable in influencing OC stocks, according to our results (Figure 6).

The evidence that large, long-lived species, with high BGB containing refractory OM, drive high soil OC stocks, might be expected to be reflected in the carbon stable isotopic composition of the soil (Kennedy et al., 2010). However, the $\Delta^{13}$C value (the difference in $\delta^{13}$C between seagrass leaves and soil), which indicates the potential contribution of seagrass derived OM to the soil, was not found as an important driver of OC stocks, according to our PLSR model (Figure 6). Nevertheless, stepwise linear mixed effect models found very strong evidence for $\Delta^{13}$C being different across species, and specifically being more positive (lower contribution of seagrass OC) for the smaller species with shorter life span, and closer to zero (higher contribution of seagrass OC) for larger, long-lived species such as those from the genus *Posidonia* (Figure 4a). This observation was consistent with results from Spain and Australia that showed that soil colonised by genera such as *Posidonia* and *Amphibolis*, displayed less positive $\Delta^{13}C$ values, indicating a higher autochthonous contribution than soils colonised by *Halodule*, *Halophila,* and *Zostera* meadows (Mazarrasa et al., 2021; Serrano, Ricart, et al., 2016).

Overall, we found that the combination of traits related to high soil OC stocks characterise persistent, large seagrass species (found to the right-hand side of the PLSR plot, Figure 6d). In contrast, traits characterising ephemeral species were associated with lower stocks. Generally, the results of our global study are consistent with those inferred from other studies and conceptualised as soil stocks increasing along the classification of seagrass into pioneer, opportunistic and climax species (Kilminster et al., 2015; Mazarrasa et al., 2018, 2021; Walker et al., 1999).

### 4.3. Geomorphological Influence on Variation in Soil C Stocks

Our linear mixed effects models found very strong evidence for an overall effect of coastal geomorphology on seagrass soil stocks, despite a modest differentiation between geomorphological categories (see Figure 2b). These findings were not a result of the species found in these settings, as multiple regression models allow for the assessment of the relationship between a response variable (OC stocks) and a predictor variable (geomorphology) in isolation, while the other variables (species identity) are held constant (e.g., Breheny & Burchett, 2017). Lagoons and tidal systems had the highest overall OC soil stocks (Figure 2b), according to linear mixed effects models, while only meadows designated as being associated with lagoons were picked as important in influencing stocks by our PLSR analysis (Figure 6a). The association of lagoons and tidal systems with riverine inputs can lead to a dominant contribution of allochthonous carbon to these systems (Signa et al., 2017; Watanabe & Kuwae, 2015), which may partly explain the higher OC stocks found in these environments (Figure 2b), and is coherent with the trend of more positive $\Delta^{13}C$ values (more dominated by allochthonous C) found, particularly, in lagoons (Figure 4b). The largest allochthonous input was observed for glacial settings, which had one of the lowest OC stocks.

Large (3–137-fold), differences were apparent in soil OC stocks of a particular species, with coefficients of variation >40% for most species and >70%, for some seagrass species (Table S1 in Supporting Information S2, Figure 3a). This within-species variability in soil stocks has been a common feature of studies of small-scale variability within meadows, between continuous and patchy meadows, along estuarine gradients and between different environmental (i.e., landscape) settings (Githaiga et al., 2017; Ricart et al., 2020). Mapping at the global scale using the Dürr typology, does not aim to distinguish differences at a local scale, but additional parameterization of models to take some account of this variability may be possible. With a limited number of cores representing some species there is the possibility that these localized influences may detract from any potential larger scale influence of plant species or geomorphic setting. In some localities, high inputs of allochthonous organic matter, with a high refractory OC content, may over-ride the influence of other drivers or post-depositional sediment re-working could become dominant controlling factors on the OC stocks (Belshe et al., 2018; Githaiga et al., 2017; Thomson et al., 2019). Processes such as hydrodynamic forcing and bioturbation, or other types of disturbance, can stimulate erosion or carbon decomposition through exposure to oxygen (Macreadie et al., 2019; Trevathan-Tackett, Seymour, et al., 2017), and could potentially be assessed using Pb-210 if carbon accumulation rate data was more available in the literature.

For colonizing and/or ephemeral species, which according to our results tend to have lower OC stocks, Serrano, Lavery et al. (2016) found that mud content accounted for a major part of the variance in soil OC content in meadows of *H. uninervis*, *Z. muelleri,* and *H. ovalis*. While BGB is small and production fast in these species, BGB is also likely to be decomposed quickly, leading to little net accumulation of seagrass OM, resulting in allochthonous carbon dominating the stored soil carbon (consistent with Figure 4a) and therefore sediment properties being more influential in defining OC content and stocks (Dahl et al., 2016; Lima et al., 2020; Mazarrasa et al., 2021; Serrano, Lavery, et al., 2016). This contrasts with larger species, having longer lifespans and a more persistent presence, where their recalcitrant tissues and high BGB is a major factor in defining carbon content and stocks (again consistent with Figure 4a).

Given that many seagrass species are adapted to live across strong environmental gradients, which are of smaller scale than any modeled geomorphic setting category, it may be necessary to further categorize core location by its environmental setting before we can gain a better understanding of how drivers of seagrass soil stocks vary across the globe. Soil grain size, which is strongly controlled by local environmental gradients, was the best predictor of surficial OC stocks across the landscape of south Florida rather than differences in the species traits (Howard et al., 2021), suggesting a better understanding of how landscape-scale variations affect OC stock is needed.

### 4.4. Global Seagrass Soil C Stocks

In this global study, additional publications than were available to Fourqurean et al. (2012) allowed a revised estimate of the soil OC stocks over 20 cm (mean 22.3 ± 0.8 and median 15.4 Mg C $ha^{-1}$), which is lower than previously reported (calculated as 20% of 1 m stock, median 28 Mg C $ha^{-1}$; Fourqurean et al., 2012). The mean value for Mediterranean soils (Fourqurean et al., 2012) is the same as ours for *P. oceanica* (74 Mg C $ha^{-1}$), indicating that it might be the more extensive data set outside the Mediterranean available to our study, which has contributed most to the revised values. Viewing soil stocks across the globe (Figure 2b), the results from the Mediterranean emphasize the distinct capacity of *P. oceanica* to support large OC stocks. Therefore, management policies to ensure the conservation of this species will guard against potential emission consequent with their loss. Another aspect of this global overview is that regional studies of *P. oceanica* meadows should not be extrapolated to represent global stocks or seagrass species in general.

## 5. Conclusions

Based on the plant traits, geomorphological setting and OC stock data available, our analysis indicates that, globally, species with a specific combination of traits (mainly related to large and long-lived seagrass species) and particularly in lagoon environments give the best indication of areas where OC stocks are larger and would benefit most from conservation, based on a consideration of this ecosystem service alone. This is a significant finding in view of the environmental heterogeneity of the geomorphological settings in which seagrass meadows are found across the globe, and the morphological plasticity seagrass species can display in response to their growth environment.

*P. oceanica*, which has the most extreme values for most of the traits compiled here, had a strong effect on our analysis and the major difference in stocks was observed between *P. oceanica* and some of the smallest ephemeral species. Even though plant traits influence global soil OC stocks, there is still some uncertainty about how this influence is diluted by the input of allochthonous OC in sites where more ephemeral species are found. Further studies are needed to identify whether the influence of allochthonous inputs on sediment properties in conjunction with species specific traits can provide even more robust estimates of OC stocks. At the same time, a focus should be maintained on investigating whether relationships between easy and affordable-to-measure parameters, such as seagrass cover and mud content, can be used as proxies for the suite of environmental, geomorphic and plant traits that are most influential in explaining global variation in OC stocks.

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## Data Availability Statement

The data that support the findings of this study can be found on Kennedy et al. (2022) and R scripts are available from https://github.com/jordipages-repo/seagrass_Cstocks_pub.

## References

Arias-Ortiz, A. (2019). *Carbon sequestration rates in coastal blue carbon ecosystems: A perspective on climate change mitigation*. Universitat Autònoma de Barcelona.

Armitage, A. R., & Fourqurean, J. W. (2016). Carbon storage in seagrass soils: Long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, *13*(1), 313–321. https://doi.org/10.5194/bg-13-313-2016

Asplund, M. E., Dahl, M., Ismail, R. O., Arias-Ortiz, A., Deyanova, D., Franco, J. N., et al. (2021). Dynamics and fate of blue carbon in a mangrove–seagrass seascape: Influence of landscape configuration and land-use change. *Landscape Ecology*, *36*(5), 1489–1509. https://doi.org/10.1007/s10980-021-01216-8

Belshe, E. F., Hoeijmakers, D., Herran, N., Mtolera, M., & Teichberg, M. (2018). Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania. *Biogeosciences*, *15*(14), 4609–4626. https://doi.org/10.5194/bg-15-4609-2018

Breheny, P., & Burchett, W. (2017). Package 'visreg': Visualization of regression models. *The R Journal*, *9*(2), 56–71. https://doi.org/10.32614/rj-2017-046

Carrascal, L. M., Galván, I., & Gordo, O. (2009). Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos*, *118*(5), 681–690. https://doi.org/10.1111/j.1600-0706.2008.16881.x

Chen, G., Azkab, M. H., Chmura, G. L., Chen, S., Sastrosuwondo, P., Ma, Z., et al. (2017). Mangroves as a major source of soil carbon storage in adjacent seagrass meadows. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep42406

Chong, I. G., & Jun, C. H. (2005). Performance of some variable selection methods when multicollinearity is present. *Chemometrics and Intelligent Laboratory Systems*, *78*(1), 103–112. https://doi.org/10.1016/j.chemolab.2004.12.011

Collier, C. J., Langlois, L. M., McMahon, K. M., Udy, J., Rasheed, M., Lawrence, E., et al. (2021). What lies beneath: Predicting seagrass below-ground biomass from above-ground biomass, environmental conditions, and seagrass community composition. *Ecological Indicators*, *121*, 107156. https://doi.org/10.1016/j.ecolind.2020.107156

Congdon, V. M., Wilson, S. S., & Dunton, K. H. (2017). Evaluation of relationships between cover estimates and biomass in subtropical seagrass meadows and application to landscape estimates of carbon storage. *Southeastern Geographer*, *57*(3), 231–245. https://doi.org/10.1353/sgo.2017.0023

Cullen-Unsworth, L. C., Nordlund, L. M., Paddock, J., Baker, S., McKenzie, L. J., & Unsworth, R. K. F. (2014). Seagrass meadows globally as a coupled social-ecological system: Implications for human wellbeing. *Marine Pollution Bulletin*, *83*(2), 387–397. https://doi.org/10.1016/j.marpolbul.2013.06.001

Dahl, M., Deyanova, D., Gütschow, S., Asplund, M. E., Lyimo, L. D., Karamfilov, V., et al. (2016). Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: A comparison of four European areas. *PLoS One*, *11*(12), 1–21. https://doi.org/10.1371/journal.pone.0167493

De los Santos, C. B., Onoda, Y., Vergara, J. J., Pérez-Lloréns, J. L., Bouma, T. J., La Nafie, Y. A., et al. (2016). A comprehensive analysis of mechanical and morphological traits in temperate and tropical seagrass species. *Marine Ecology Progress Series*, *551*, 81–94. https://doi.org/10.3354/meps11717

Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, *67*, 201–207. https://doi.org/10.3354/meps067201

Duarte, C. M. (1991). Allometric scaling of seagrass form and productivity. *Marine Ecology Progress Series*, *77*, 289–300. https://doi.org/10.3354/meps077289

Duarte, C. M., & Cebrián, J. (1996). The fate of marine autotrophic production. *Limnology & Oceanography*, *41*(8), 1758–1766. https://doi.org/10.4319/lo.1996.41.8.1758

Duarte, C. M., & Chiscano, C. L. (1999). Seagrass biomass and production: A reassessment. *Aquatic Botany*, *65*(1–4), 159–174. https://doi.org/10.1016/S0304-3770(99)00038-8

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*(11), 961–968. https://doi.org/10.1038/nclimate1970

Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., & Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, *24*(4), 1–8. https://doi.org/10.1029/2010GB003793

Dürr, H. H., Laruelle, G. G., van Kempen, C. M., Slomp, C. P., Meybeck, M., & Middelkoop, H. (2011). Worldwide typology of nearshore coastal systems: Defining the estuarine filter of river inputs to the oceans. *Estuaries and Coasts*, *34*(3), 441–458. https://doi.org/10.1007/s12237-011-9381-y

Enríquez, S., Duarte, C. M., & Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content. *Oecologia*, *94*(4), 457–471. https://doi.org/10.1007/BF00566960

Farrés, M., Platikanov, S., Tsakovski, S., & Tauler, R. (2015). Comparison of the variable importance in projection (VIP) and of the selectivity ratio (SR) methods for variable selection and interpretation. *Journal of Chemometrics*, *29*(10), 528–536. https://doi.org/10.1002/cem.2736

Fonseca, M. S., Fourqurean, J. W., & Koehl, M. A. R. (2019). Effect of seagrass on current speed: Importance of flexibility vs. shoot density. *Frontiers in Marine Science*, *6*(JUL), 1–13. https://doi.org/10.3389/fmars.2019.00376

Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. Á., et al. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, *5*(7), 505–509. https://doi.org/10.1038/ngeo1477

Gacia, E., & Duarte, C. M. (2001). Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuarine, Coastal and Shelf Science*, *52*(4), 505–514. https://doi.org/10.1006/ecss.2000.0753

Githaiga, M. N., Kairo, J. G., Gilpin, L., & Huxham, M. (2017). Carbon storage in the seagrass meadows of Gazi Bay, Kenya. *PLoS One*, *12*(5), e0177001. https://doi.org/10.1371/journal.pone.0177001

Gullström, M., Lyimo, L. D., Dahl, M., Samuelsson, G. S., Eggertsen, M., Anderberg, E., et al. (2018). Blue carbon storage in tropical seagrass meadows relates to carbonate stock dynamics, plant–sediment processes, and landscape context: Insights from the Western Indian Ocean. *Ecosystems*, *21*(3), 551–566. https://doi.org/10.1007/s10021-017-0170-8

Hemminga, M. A., & Duarte, C. M. (2000). *Seagrass ecology*. Cambridge University Press. https://doi.org/10.1017/CBO9780511525551

Hemminga, M. A., & Mateo, M. Á. (1996). Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. *Marine Ecology Progress Series*, *140*(1–3), 285–298. https://doi.org/10.3354/meps140285

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Howard, J. L., Lopes, C. C., Wilson, S. S., McGee-Absten, V., Carrión, C. I., & Fourqurean, J. W. (2021). Decomposition rates of surficial and buried organic matter and the lability of soil carbon stocks across a large tropical seagrass landscape. *Estuaries and Coasts*, *44*(3), 846–866. https://doi.org/10.1007/s12237-020-00817-x

Howard, J. L., Perez, A., Lopes, C. C., & Fourqurean, J. W. (2016). Fertilization changes seagrass community structure but not blue carbon storage: Results from a 30-year field experiment. *Estuaries and Coasts*, *39*(5), 1422–1434. https://doi.org/10.1007/s12237-016-0085-1

Jänes, H., Macreadie, P. I., Zu Ermgassen, P. S. E., Gair, J. R., Treby, S., Reeves, S., et al. (2020). Quantifying fisheries enhancement from coastal vegetated ecosystems. *Ecosystem Services*, *43*, 101105. https://doi.org/10.1016/j.ecoser.2020.101105

Kaal, J., Serrano, Ó., del Río, J. C., & Rencoret, J. (2018). Radically different lignin composition in *Posidonia* species may link to differences in organic carbon sequestration capacity. *Organic Geochemistry*, *124*, 247–256. https://doi.org/10.1016/j.orggeochem.2018.07.017

Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., & Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, *24*(4), 1–8. https://doi.org/10.1029/2010GB003848

Kennedy, H., Pagès, J. F., Lagomasimo, D., Arias-Ortiz, A., Colarusso, P., Fourqurean, J. W., et al. (2022). Code and data sets used in the manuscript "Species traits and geomorphic setting as drivers of global soil carbon stocks in seagrass meadows. https://doi.org/10.5281/zenodo.5834006

Kilminster, K., McMahon, K., Waycott, M., Kendrick, G. A., Scanes, P., McKenzie, L., et al. (2015). Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, *534*, 97–109. https://doi.org/10.1016/j.scitotenv.2015.04.061

Kindeberg, T., Ørberg, S. B., Röhr, M. E., Holmer, M., & Krause-Jensen, D. (2018). Sediment stocks of carbon, nitrogen, and phosphorus in Danish eelgrass meadows. *Frontiers in Marine Science*, *5*, 1–14. https://doi.org/10.3389/fmars.2018.00474

Klap, V., Hemminga, M. A., & Boon, J. (2000). Retention of lignin in seagrasses: Angiosperms that returned to the sea. *Marine Ecology Progress Series*, *194*, 1–11. https://doi.org/10.3354/meps194001

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). Handbook of meta-analysis in ecology and evolution.

Kuhn, M. (2021). caret: Classification and Regression Training. R package version 6.0-86.

Lavery, P. S., Mateo, M. Á., Serrano, Ó., & Rozaimi, M. (2013). Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One*, *8*(9), e73748. https://doi.org/10.1371/journal.pone.0073748

Lima, M. D. A. C., Ward, R. D., & Joyce, C. B. (2020). Environmental drivers of sediment carbon storage in temperate seagrass meadows. *Hydrobiologia*, *847*(7), 1773–1792. https://doi.org/10.1007/s10750-019-04153-5

Macreadie, P. I., Atwood, T. B., Seymour, J. R., Fontes, M. L. S., Sanderman, J., Nielsen, D. A., & Connolly, R. M. (2019). Vulnerability of seagrass blue carbon to microbial attack following exposure to warming and oxygen. *Science of the Total Environment*, *686*, 264–275. https://doi.org/10.1016/j.scitotenv.2019.05.462

Macreadie, P. I., Ollivier, Q. R., Kelleway, J. J., Serrano, Ó., Carnell, P. E., Ewers Lewis, C. J., et al. (2017). Carbon sequestration by Australian tidal marshes. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep44071

Marbà, N., Hemminga, M. A., Mateo, M. A., Duarte, C. M., Mass, Y. E. M., Terrados, J., & Gacia, E. (2002). Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series*, *226*, 287–300. https://doi.org/10.3354/meps226287

Mazarrasa, I., Lavery, P. S., Duarte, C. M., Lafratta, A., Lovelock, C. E., Macreadie, P. I., et al. (2021). Factors determining seagrass blue carbon across bioregions and geomorphologies. *Global Biogeochemical Cycles*, *35*(6), 1–17. https://doi.org/10.1029/2021gb006935

Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., & Duarte, C. M. (2017). Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of *Posidonia oceanica* meadows. *Limnology & Oceanography*, *62*(4), 1436–1450. https://doi.org/10.1002/lno.10510

Mazarrasa, I., Marbà, N., Lovelock, C. E., Serrano, Ó., Lavery, P. S., Fourqurean, J. W., et al. (2015). Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, *12*(16), 4993–5003. https://doi.org/10.5194/bg-12-4993-2015

Mazarrasa, I., Samper-Villarreal, J., Serrano, Ó., Lavery, P. S., Lovelock, C. E., Marbà, N., et al. (2018). Habitat characteristics provide insights of carbon storage in seagrass meadows. *Marine Pollution Bulletin*, *134*, 106–117. https://doi.org/10.1016/j.marpolbul.2018.01.059

Mevik, B.-H., Wehrens, R., & Liland, K. H. (2020). pls: Partial least squares and principal component regression. R package version 2.7.0.

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Adachi, H., Yamano, H., & Nakaoka, M. (2015). Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Global Biogeochemical Cycles*, *29*(4), 397–415. https://doi.org/10.1002/2014GB004979

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., & Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnology & Oceanography*, *62*(3), 954–972. https://doi.org/10.1002/lno.10478

Muff, S., Nilsen, E. B., O'Hara, R. B., & Nater, C. R. (2021). Rewriting results sections in the language of evidence. *Trends in Ecology & Evolution*, *37*(3), 1–8. https://doi.org/10.1016/j.tree.2021.10.009

Nakakuni, M., Watanabe, K., Kaminaka, K., Mizuno, Y., Takehara, K., Kuwae, T., & Yamamoto, S. (2021). Seagrass contributes substantially to the sedimentary lignin pool in an estuarine seagrass meadow. *Science of the Total Environment*, *793*, 148488. https://doi.org/10.1016/j.scitotenv.2021.148488

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R DevelopmentCoreTeam (2011). nlme: Linear and nonlinear mixed effects models. *R Package Version*, *3*, 1–98.

Potouroglou, M., Whitlock, D., Milatovic, L., MacKinnon, G., Kennedy, H., Diele, K., & Huxham, M. (2021). The sediment carbon stocks of intertidal seagrass meadows in Scotland. *Estuarine, Coastal and Shelf Science*, *258*, 107442. https://doi.org/10.1016/j.ecss.2021.107442

Prentice, C., Poppe, K. L., Lutz, M., Murray, E., Stephens, T. A., Spooner, A., et al. (2020). A synthesis of blue carbon stocks, sources, and accumulation rates in Eelgrass (*Zostera marina*) meadows in the Northeast Pacific. *Global Biogeochemical Cycles*, *34*(2), 1–16. https://doi.org/10.1029/2019GB006345

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Ricart, A. M., Pérez, M., & Romero, J. (2017). Landscape configuration modulates carbon storage in seagrass sediments. *Estuarine, Coastal and Shelf Science*, *185*, 69–76. https://doi.org/10.1016/j.ecss.2016.12.011

Ricart, A. M., York, P. H., Bryant, C. V., Rasheed, M. A., Ierodiaconou, D., & Macreadie, P. I. (2020). High variability of Blue Carbon storage in seagrass meadows at the estuary scale. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-62639-y

Röhr, M. E., Boström, C., Canal-Vergés, P., & Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*, *13*(22), 6139–6153. https://doi.org/10.5194/bg-13-6139-2016

Röhr, M. E., Holmer, M., Baum, J. K., Björk, M., Chin, D., Chalifour, L., et al. (2018). Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) Meadows. *Global Biogeochemical Cycles*, *32*(10), 1457–1475. https://doi.org/10.1029/2018GB005941

Rovai, A. S., Twilley, R. R., Castañeda-Moya, E., Riul, P., Cifuentes-Jara, M., Manrow-Villalobos, M., et al. (2018). Global controls on carbon storage in mangrove soils. *Nature Climate Change*, *8*(6), 534–538. https://doi.org/10.1038/s41558-018-0162-5

Ruiz-Frau, A., Gelcich, S., Hendriks, I. E., Duarte, C. M., & Marbà, N. (2017). Current state of seagrass ecosystem services: Research and policy integration. *Ocean & Coastal Management*, *149*, 107–115. https://doi.org/10.1016/j.ocecoaman.2017.10.004

Samper-Villarreal, J., Lovelock, C. E., Saunders, M. I., Roelfsema, C., & Mumby, P. J. (2016). Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnology & Oceanography*, *61*(3), 938–952. https://doi.org/10.1002/lno.10262

Serrano, Ó., Lavery, P. S., Duarte, C. M., Kendrick, G. A., Calafat, A., York, P. H., et al. (2016). Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? *Biogeosciences*, *13*(17), 4915–4926. https://doi.org/10.5194/bg-13-4915-2016

Serrano, Ó., Lavery, P. S., Rozaimi, M., & Mateo, M. Á. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, *28*(9), 950–961. https://doi.org/10.1002/2014GB004872

Serrano, Ó., Lovelock, C. E., Atwood, B. T., Macreadie, P. I., Canto, R., Phinn, S., et al. (2019). Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-12176-8

Serrano, Ó., Ricart, A. M., Lavery, P. S., Mateo, M. A., Arias-Ortiz, A., Masque, P., et al. (2016). Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences*, *13*(15), 4581–4594. https://doi.org/10.5194/bg-13-4581-2016

Serrano, Ó., Rozaimi, M., Lavery, P. S., & Smernik, R. J. (2020). Organic chemistry insights for the exceptional soil carbon storage of the seagrass *Posidonia australis*. *Estuarine, Coastal and Shelf Science*, *237*, 106662. https://doi.org/10.1016/j.ecss.2020.106662

Short, F. T., Polidoro, B., Livingstone, S. R., Carpenter, K. E., Bandeira, S., Bujang, J. S., et al. (2011). Extinction risk assessment of the world's seagrass species. *Biological Conservation*, *144*(7), 1961–1971. https://doi.org/10.1016/j.biocon.2011.04.010

Signa, G., Mazzola, A., Kairo, J., & Vizzini, S. (2017). Small-scale variability in geomorphological settings influences mangrove-derived organic matter export in a tropical bay. *Biogeosciences*, *14*(3), 617–629. https://doi.org/10.5194/bg-14-617-2017

Stankovic, M., Tantipisanuh, N., & Prathep, A. (2018). Carbon storage in seagrass ecosystems along the Andaman coast of Thailand. *Botanica Marina*, *61*(5), 429–440. https://doi.org/10.1515/bot-2017-0101

Stankovic, M., Tantipisanuh, N., Rattanachot, E., & Prathep, A. (2018). Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems. *Marine Ecology Progress Series*, *596*, 61–70. https://doi.org/10.3354/meps12597

Thomson, A. C. G., Trevathan-Tackett, S. M., Maher, D. T., Ralph, P. J., & Macreadie, P. I. (2019). Bioturbator-stimulated loss of seagrass sediment carbon stocks. *Limnology & Oceanography*, *64*(1), 342–356. https://doi.org/10.1002/lno.11044

Torbatinejad, N. M., Annison, G., Rutherfurd-Markwick, K., & Sabine, J. R. (2007). Structural constituents of the seagrass *Posidonia australis*. *Journal of Agricultural and Food Chemistry*, *55*(10), 4021–4026. https://doi.org/10.1021/jf063061a

Trevathan-Tackett, S. M., Macreadie, P. I., Sanderman, J., Baldock, J., Howes, J. M., & Ralph, P. J. (2017). A global assessment of the chemical recalcitrance of seagrass tissues: Implications for long-term carbon sequestration. *Frontiers of Plant Science*, *8*, 1–18. https://doi.org/10.3389/fpls.2017.00925

Trevathan-Tackett, S. M., Seymour, J. R., Nielsen, D. A., Macreadie, P. I., Jeffries, T. C., Sanderman, J., et al. (2017). Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. *FEMS Microbiology Ecology*, *93*(6), 1–15. https://doi.org/10.1093/femsec/fix033

Twilley, R. R., Rovai, A. S., & Riul, P. (2018). Coastal morphology explains global blue carbon distributions. *Frontiers in Ecology and the Environment*, *16*(9), 503–508. https://doi.org/10.1002/fee.1937

UNEP. (2020). *Out of Blue: The value of seagrasses to the environment and to people*. UNEP.

UNEP-WCMC, & Short, F. T. (2021). *Global distribution of seagrasses (version 7.1). Seventh update to the data layer used in Green and Short (2003)*. UN Environment World Conservation Monitoring Centre. https://doi.org/10.34892/x6r3-d211

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Walker, B. H., Kinzig, A., & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems*, *2*(2), 95–113. https://doi.org/10.1007/s100219900062

Watanabe, K., & Kuwae, T. (2015). How organic carbon derived from multiple sources contributes to carbon sequestration processes in a shallow coastal system? *Global Change Biology*, *21*(7), 2612–2623. https://doi.org/10.1111/gcb.12924

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. H. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science+Business Media.