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Seagrass ecosystems as a globally significant carbon stock

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The protection of organic carbon stored in forests is considered as an important method for mitigating climate change. Like terrestrial ecosystems, coastal ecosystems store large amounts of carbon, and there are initiatives to protect these 'blue carbon' stores. Organic carbon stocks in tidal salt marshes and mangroves have been estimated, but uncertainties in the stores of seagrass meadows—some of the most productive ecosystems on Earth—hinder the application of marine carbon conservation schemes. Here, we compile published and unpublished measurements of the organic carbon content of living seagrass biomass and underlying soils in 946 distinct seagrass meadows across the globe. Using only data from sites for which full inventories exist, we estimate that, globally, seagrass ecosystems could store as much as 19.9 Pg organic carbon; according to a more conservative approach, in which we incorporate more data from surface soils and depth-dependent declines in soil carbon stocks, we estimate that the seagrass carbon pool lies between 4.2 and 8.4 Pg carbon. We estimate that present rates of seagrass loss could result in the release of up to 299 Tg carbon per year, assuming that all of the organic carbon in seagrass biomass and the top metre of soils is remineralized.

The remineralization of organic carbon (C_{org}) stored in terrestrial ecosystems because of deforestation and land-use change now accounts for 8–20% of anthropogenic greenhouse-gas emissions[1]. The importance of reducing these fluxes to mitigate climate change has led to efforts to protect terrestrial C_{org} stores through forest conservation, such as the United Nations collaborative initiative on Reduced Emissions from Deforestation and Degradation (REDD+) in developing countries[2]. REDD+ maintains terrestrial C_{org} stores through financial incentives for forest conservation, which requires rigorous monitoring of C_{org} stores and emissions[3,4]. Unlike terrestrial forests, where the C_{org} stores are dominated by the living trees[5], the C_{org} stores of coastal vegetated habitats are dominated by the C stored in their organic-rich soils[6–9]. Whereas the C stores of mangroves have been estimated at 1,023 $Mg\,C\,ha^{-1}$ (ref. 7), the global C_{org} stores in seagrass ecosystems have not yet been assessed, despite the recognition of seagrass meadows as some of the most productive of the Earth's ecosystems[10,11].

Seagrass meadows occupy less than 0.2% of the area of the world's oceans but are estimated to bury 27.4 $Tg\,C\,yr^{-1}$, roughly 10% of the yearly estimated C_{org} burial in the oceans[8] (Fig. 1). Although some components of C_{org} storage have been reported, most notably living biomass[10], seagrasses may develop organic-rich soils composed of both autochthonous and allochthonous C_{org} (ref. 12). These soils are largely anaerobic, and as a result, the C_{org} in the soils can be preserved for millennia[13–16]. Below-ground C_{org} storage in seagrass soils has rarely been quantified, because concurrent measurements of C_{org} and bulk density have rarely been reported, and no studies so far have integrated the necessary measurements for estimating C_{org} storage in seagrass ecosystems on a global scale. Given the importance of seagrasses to the C budget of the oceans[8,17], estimating the magnitude of the pools of C_{org} provides the first step to our understanding of the potential impact of the release of stored CO_2 from degrading seagrass meadows to atmospheric CO_2 budgets. Widespread and accelerating losses of seagrass meadows[18] underscore the importance of understanding the significance of these C-rich ecosystems to global C_{org} pools.

Here we compiled published and unpublished data on the C_{org} content of seagrass living biomass and C_{org} content and dry bulk density (DBD) of soils underlying seagrass meadows to deliver conservative, first-order estimates of the amount of C_{org} stored in these ecosystems.

The database on C_{org} in seagrass meadows contained 3,640 observations from 946 distinct sampling locations across the world (Supplementary Information). The distribution of the data was geographically biased (Fig. 2) owing to an imbalance in research effort across regions[19], with most of the data from North America, Western Europe and Australia. Data were notably scarce from South America and Africa. Furthermore, given the spatial extent of seagrasses in the tropical Indo-Pacific, relatively few data points represented this region.

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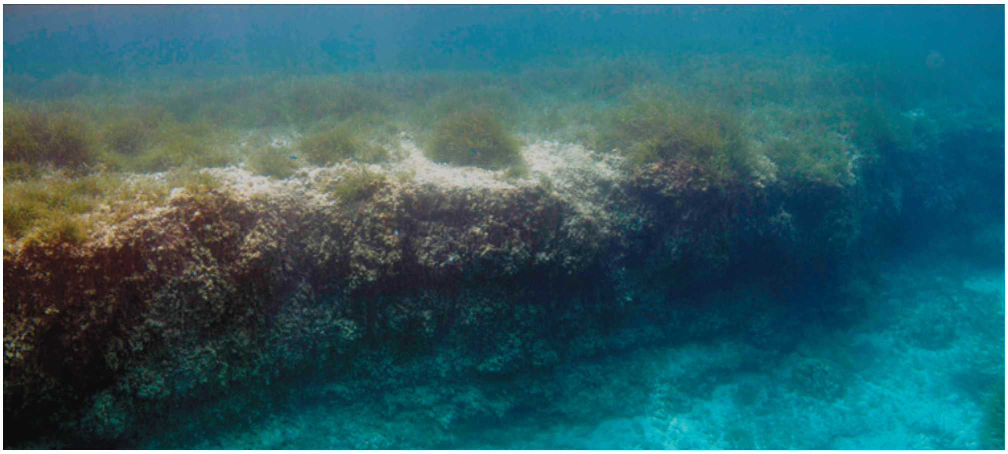

Figure 1 | Mediterranean seagrass meadows of *P. oceanica* have the largest documented C_{org} stores, which can form 'mattes' of high C_{org} content not reported for other seagrass species. An erosional escarpment in a *P. oceanica* meadow in Es Pujols Cove, Formentera, Balearic Islands, Spain, in the Mediterranean Sea illustrating the organic-rich soils.The water depth at the top of the formation is 3 m, the exposed face of the matte has a thickness of 2.7 m. The age of the base of the exposure is 1,200 years BP. Photo credit: Miguel Angel Mateo.

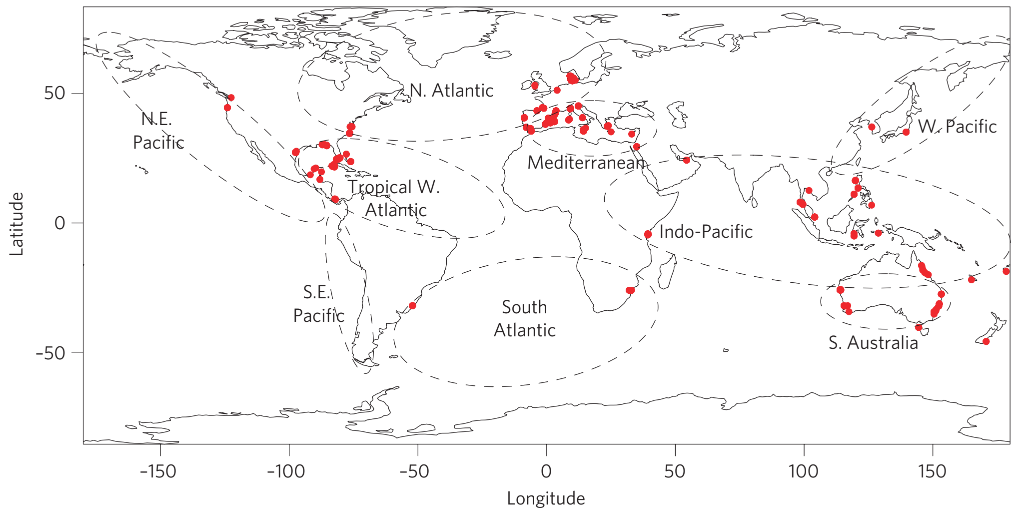

Figure 2 | Locations of data on the C_{org} content of seagrass meadows, showing seagrass bioregions.

C_{org} in living seagrass biomass

The amount of C_{org} stored in living seagrass biomass globally averaged 2.52 ± 0.48 Mg C ha^{-1}(±95% CI), two-thirds of which was buried in the soil as rhizomes and roots (Table 1; for seagrass dry weight biomass and other soil properties, see Supplementary Table S1). However, total C_{org} in living seagrasses varied over four orders of magnitude across meadows, largely reflecting seagrass species composition. The largest pools of C_{org} stored in living seagrasses (with mean living biomass of 7.29 ± 1.52 Mg C ha^{-1}) were found in Mediterranean meadows dominated by *Posidonia oceanica*, a large seagrass with extensive, long-lived rhizomes (Supplementary Table S2). Given the general lack of data from many geographic regions and for many seagrass species, especially the northeast Pacific, southeast Pacific, western Pacific and the South Atlantic, comparing relative stores among other geographic regions and seagrass species may be premature.

C_{org} content of seagrass meadow soils

DBD of seagrass soils had a wide range (Supplementary Fig. S1, Table 1). The median DBD of the entire data set was 0.92 g ml^{-1}, slightly lighter than the mean of 1.03 ± 0.02 g ml^{-1}. C_{org} of seagrass soils varied widely, with a median measured C_{org} of 1.8% of dry weight, and relatively infrequent high values (Fig. 3 and Table 1), resulting in a global average of 2.5%. Assuming that the median DBD and median C_{org} content of soils in our database represent the central tendency of the top metre of all seagrass soils worldwide, we estimate that the top metre of seagrass soils contains 165.6 Mg C_{org} ha^{-1}. However, C_{org} and DBD were not constant with depth. Averaged across all soil profiles, C_{org} decreased with depth in the core at the rate of $-0.005 \pm 0.003 \log_{10}(C_{org}+1)$ cm^{-1} ($n = 269$ cores, ±95% confidence interval of the mean) and DBD increased at a rate of 8.6 ± 4.0 (mg (dry weight) ml^{-1}) cm^{-1} ($n = 133$), suggesting that the estimate of the global C_{org} of seagrass meadows based on median DBD and C_{org} could be inaccurate.

We accounted for the depth variability of DBD and C_{org} to further refine our estimates. Of the 219 core sites in our database that contained data on C_{org} and/or DBD at multiple depths, only 41 cores contained data as deep as one metre to allow for accurate accounting of C storage in the soils. These 41 deep-core sites were concentrated in three geographic regions: Florida Bay, Florida, USA; the Spanish coast of the Western Mediterranean; and Shark Bay, Western Australia. Soil C_{org} stocks over the top metre cores ranged from 115.3 to 829.2 Mg C_{org} ha^{-1}, with a mean value of 329.5 ± 55.9 Mg C_{org} ha^{-1} (Fig. 4). Extrapolating data on both DBD and C_{org} reported to at least 20 cm deep at a further 48 sites down to 1 m using the rates derived above, we

Table 1 | Summary of collected data on seagrass biomass and soil properties from the global data set.

	n	Range	Median	Mean ± 95% CI
Above-ground biomass (Mg (C_{org}) ha^{-1})	251	0.001–5.548	0.264	0.755 ± 0.128
Below-ground biomass (Mg (C_{org}) ha^{-1})	251	0.001–17.835	0.540	1.756 ± 0.375
Total seagrass biomass (Mg (C_{org}) ha^{-1})	251	0.001–23.382	1.000	2.514 ± 0.489
Soil C_{org} (percentage of dry weight)	2,535	0–48.2	1.8	2.5 ± 0.1
	3,561	**0–48.2**	**1.4**	**2.0 ± 0.1**
DBD (g (dry weight) ml^{-1})	2,484	0.06–2.35	0.92	1.03 ± 0.02

Values in bold include estimates based on statistical relationships with other variables.

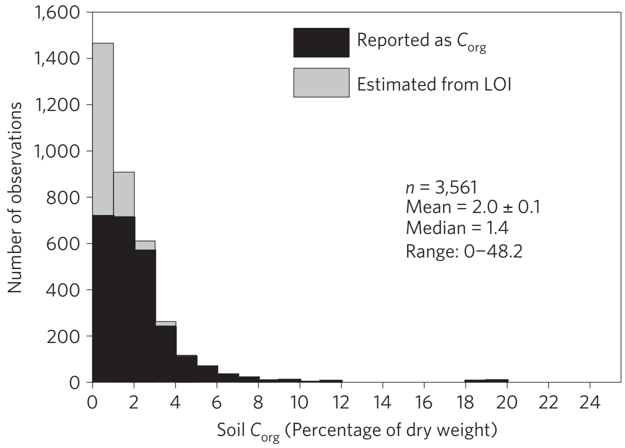

Figure 3 | Frequency distribution of reported and calculated observations of soil C_{org} from seagrass meadows. Mean values are given ±95% confidence interval. LOI, loss on ignition (see Methods).

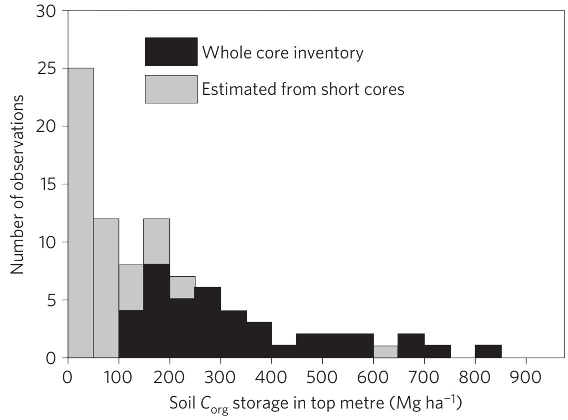

Figure 4 | Frequency histogram of estimates of soil C_{org} stored in the world's seagrass meadows. Light grey shading indicates estimates made from surficial sediments, as well as general patterns in increases in DBD (see Methods) and decreases in C_{org} with depth, and should be considered as preliminary until more detailed, site-specific studies of C_{org} in deeper soils are done at these sites.

estimated C storage at those sites to range between 9.1 and 628.1 Mg C_{org} ha^{-1}, generally lower than at sites for which full inventories of the top metre were available. These data were not normally distributed, with many low values and fewer high values (Fig. 4); the median estimate was 47.2 Mg C_{org} ha^{-1}. Combining the estimates extrapolated from shallow cores with full core inventories, the resulting median soil C_{org} storage was 139.7 Mg C_{org} ha^{-1}, probably a conservative estimate of global C_{org} storage in seagrass meadow soils. For our estimates of global stocks, we used the median areal estimates so that the high values found in Mediterranean *P. oceanica* meadows did not unduly influence the global estimates. In a pattern that mirrored the geographic differences in C_{org} stored in living biomass of seagrasses, the studied seagrass meadows in the Mediterranean had the highest average soil C_{org} storage (372.4 ± 74.5 Mg C_{org} ha^{-1}, Supplementary Table S2), but regional or species-specific differences in soil C_{org} storage should be viewed as preliminary owing to the scarcity of data from many locations.

These estimates make seagrass meadows global hotspots for C_{org} storage in soils, with about twice the average C_{org} storage per hectare as terrestrial soils (Fig. 5). Whereas seagrass biomass, which averaged 7.29 ± 1.52 Mg C ha^{-1}, is small when compared with that in forests, which range from 30 Mg C ha^{-1} for boreal tundra woodlands to 300 Mg C ha^{-1} for tropical rainforests[20], soil C_{org} stores in seagrass meadows are large when compared with terrestrial ecosystems and rival with the C_{org} stores of mangroves underlined by extensive peat deposits (Fig. 5).

Estimates of global seagrass C_{org} stocks

The total area of the Earth covered by seagrass meadows is poorly known, but recent estimates are between 300,000 and 600,000 km^2 (refs 8,21). Multiplying our median estimates of C stored in seagrass biomass and in the top metre of seagrass soils by these estimates of global seagrass extent, global seagrass biomass is between 75.5 and 151 Tg C, an order of magnitude less than that in the top metre of seagrass soils, estimated at 4.2 to 8.4 Pg C. If we assume that the data from soil cores at least a metre deep is a better estimate of the global average soil C_{org} content, our estimates of the global stocks are higher, at 9.8 to 19.8 Pg C. These estimates make the amount of C_{org} stored in seagrass soils roughly equal to the combined amount of C_{org} stored in the world's marine tidal marshes and mangrove forests, estimated to be ≈10 Pg C (ref. 6). In comparison, the top metre of terrestrial soils contain 1,500–2,000 PgC (ref. 22) over the roughly 150 × 10^6 km^2 of land surface.

The high capacity of seagrass meadows to store C has been explained to result from the high primary production of seagrass meadows and their capacity to filter out particles from the water column and store them in soils[12,23,24], combined with low decomposition rates in the oxygen-poor seagrass soils and the lack of fires underwater[23]. The resulting stability of seagrass C_{org} storage allows C_{org} to accumulate over millennia into deposits much deeper than 1 m in seagrass soils[14–16], with 11-m-thick C_{org} millenary deposits documented in Mediterranean seagrass meadows[25]. Hence, the estimates of seagrass C_{org} stores to 1 m depth presented here underestimate the total C_{org} stores, because deposits can be several metres thick, but we consider the top 1 m to be that most vulnerable to being remineralized when seagrass meadows are lost. The results presented also indicate that the earlier finding that roughly 10% of the yearly estimated C_{org} burial in the oceans occurs in seagrass meadows[8] underestimates the magnitude of seagrass C_{org} burial, because this estimate was based on an estimated C_{org} content of seagrass soils of 0.7%, whereas we found the median C_{org} of seagrass soils to be, conservatively, 1.4%, twice as high as

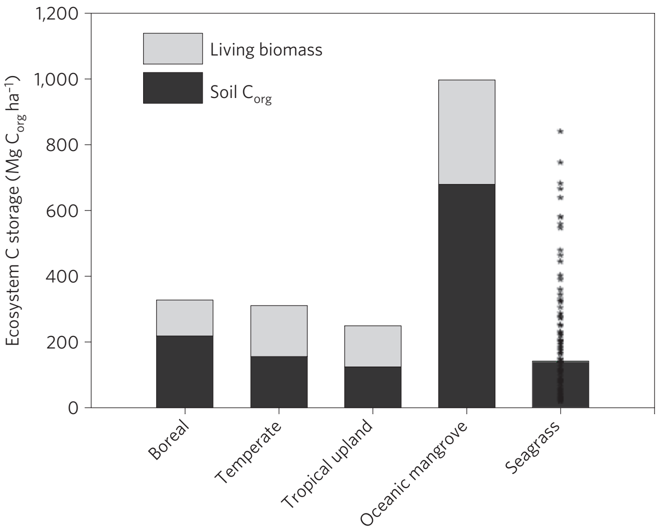

Figure 5 | A comparison of seagrass soil C_{org} storage in the top metre of the soil with total ecosystem C_{org} storage for major forest types. Terrestrial forest C storage data from ref. 3; mangrove storage data from ref. 7. Note that individual forests can have C_{org} storage above or below these mean values. The individual points represent the individual values for seagrass meadows in the database. Living seagrass biomass C storage is minor when compared with that found in forests and when compared with the soil C_{org} storage in seagrass meadows, so it has been omitted for clarity.

this previous estimate. Therefore, seagrass meadows may be even more important to the oceanic C cycle than previously thought, contributing twice as much C burial as hitherto believed.

Anthropogenic perturbation of C_{org} stores through deforestation, commonly recognized as a problem in terrestrial environments, also occurs in seagrass meadows. Seagrasses can be physically removed by dredging and filling activities, but degradation of water quality because of poor land-use practices (including deforestation) is the most common cause of seagrass meadow destruction[26]. Seagrasses are among the world's most threatened ecosystems, with annual global loss rates of seagrass extent averaging 1.5% since the beginning of the twentieth century and accelerating in recent decades[18]. An estimated 29% of the seagrasses known to exist at the beginning of the twentieth century have disappeared, generally replaced with unvegetated, unconsolidated mud and sand soils. This rapid loss of seagrasses resulted in a substantial decrease in C sequestration by seagrass ecosystems of 6 to 24 Tg C yr^{-1} (ref. 27). In addition to this loss in annual sequestration, it is likely that much of the C_{org} stored in soils under lost seagrass meadows was released back into the ocean–atmosphere CO_2 pool over the past 100 years, and the accelerating loss of seagrass meadows[18] suggests that this flux will also accelerate. At a minimum, the seagrass biomass from degraded or destroyed seagrass meadows is likely to be rapidly remineralized; assuming a conservative estimate of 1.5% yr^{-1} of seagrass loss, between 11.3 and 22.7 Tg C yr^{-1} is returning to the ocean–atmosphere system from the decomposition of seagrass biomass. C_{org} stored in seagrass soils should also be oxidized, at least in part, when seagrass meadows are lost. Assuming all of the C_{org} in the top metre of soils to be eventually oxidized following seagrass loss and not redeposited in unvegetated sediments, between 63 and 297 Tg C yr^{-1} previously stored in seagrass sediments is re-entering the ocean–atmosphere CO_2 pool at the present estimate of loss of seagrasses[19], which are accelerating. Of course, there would be C_{org} stored in the unvegetated bottoms left behind after seagrasses disappear[12], which would reduce the net change in C_{org} stocks of coastal ecosystems following seagrass loss, but our calculations identify seagrass loss as a large potential source of CO_2 emissions contributing as much as 10% of the 0.5–2.7 Gt C yr^{-1} released from changes in land use[1].

Afforestation of terrestrial ecosystems can increase C_{org} stocks in biomass, and, under certain circumstances, in the soil[28,29], helping to sequester C_{org}. Although seagrasses can also be planted, restoring seagrass meadows has a mixed history of success[30], largely because the mechanism that led to the loss of much of the world's seagrass meadows—water quality degradation and reduced light penetration to the seagrasses[31]—has left many of the areas that used to support seagrasses in a degraded state that prevents the success of replanting efforts. In some cases, however, seagrass 'afforestation' is possible[32]. For example, areas of seagrasses lost owing to disease and storm disturbances in the 1930s along the mid-Atlantic coast of Virginia, USA, did not recover because of seed limitation[33,34]. In the early 1990s a small patch of naturally recruited seagrass was found in the area, indicating that the habitat was suitable for supporting seagrasses and prompting a large-scale seagrass restoration effort that has resulted in the creation of 1821 hectares of new seagrass habitat[35]. In the first 10 years following the seagrass meadow creation, organic content of the sediments increased from 1.4% to 2.4%, with a doubling of the total storage of C in the upper 5 cm of sediments[36]. Similarly, colonization of a Mediterranean bay by the seagrass *Cymodocea nodosa* following a perturbation led to an increase in the C_{org} store at a rate of about 40 g C m^{-2} yr^{-1} (refs 37,38). Hence, conserving and restoring seagrass meadows has the potential to effectively and rapidly restore lost C sinks and stores, while providing a range of other valuable ecosystem services, including high rates of primary production, water quality protection, sediment stabilization, enhanced biodiversity, habitat for ecologically and commercially important species, and fisheries production[19].

Our results show that seagrass meadows are key sites for C storage in the biosphere and probably are far more important as CO_2 sinks than previously realized. The organic C stored per unit area of seagrass meadows is similar to that of forests. Whereas most forest C stores are eventually returned to the atmosphere during forest fires, the submarine stores of seagrass can accumulate over millennia, to reach phenomenal thickness[25]. However, the stability of these C stores is compromised, with present losses of seagrass stores possibly accounting for 10% of all emissions attributed to changes in land use. Conserving and restoring seagrass meadows has the capacity, as proposed in 'Blue Carbon' initiatives[9,39], to reduce greenhouse-gas emissions and increase C_{org} stores while delivering key ecosystem services to coastal communities.

Methods

We used ISI Web of Knowledge (search terms SEAGRASS* and ((SEDIMENT and ORGANIC) or DIAGENESIS)) and our personal literature collections to search for data on sediment bulk properties and C content from cores collected in or near seagrass meadows. The published data were augmented with unpublished data generated by our laboratories, students and colleagues (Supplementary Information). At a minimum, we had to have a location, a measure of organic matter or C_{org} content and a definition of the depth in the soil from which the samples were collected, for inclusion in our database. Different sources used various methods for determining soil properties; we treated all values reported by each source equally. When necessary, we digitized figures from published works to extract the data.

We standardized nomenclature across studies. DBD was defined as the mass of dry matter divided by the volume of the undisturbed soil sample (g ml^{-1}). Organic matter content was determined by loss on ignition (LOI), the fractional weight loss of dry sediment samples after combustion at 500–550 °C. C_{org} was determined by measuring the organic C content of a known mass of soil using an elemental analyser, expressed as a percentage of the dry weight. Inorganic C content was also expressed as a percentage of the dry weight of the soil.

We used regression equations to estimate C_{org} for samples in our data set that reported LOI but not C_{org} (Supplementary Information); this resulted in 3,561 total estimates of C_{org} for seagrass soils. C_{org} data reported as C_{org} tended to have higher values than the C_{org} estimated from LOI (Fig. 3, Table 1), so that the median estimate of the C_{org} content of seagrass soils was reduced to 1.4% from the 1.8% based on direct estimates of C_{org}.

For those meadows where only seagrass above-ground biomass was provided, we used the species-specific ratio of above: below-ground biomass[10] to estimate below-ground and total biomass. When C content of seagrass biomass was not indicated, we assumed C content = 35% of dry weight[40–43].

Soils underlying seagrass meadows are of varying thickness, and the total depth of soil is rarely reported. Accordingly, we standardized our accounting of C_{org} in seagrass soils to a 1 m depth. Given that the C_{org} in top layers is more labile and more likely to be eroded if seagrass beds are lost, we hold that the C_{org} in the top 1 m is the most important in the discussion of the importance of seagrass C_{org} to global anthropogenic alterations of CO_2 budgets. Where necessary, we extrapolated below the limits of the reported data to 1 m using general trends in DBD and C_{org} (Supplementary Information). We calculated the total C_{org} in the top metre of soil per area for each location.

We used seagrass biogeographic regions[44] (Fig. 2) to summarize available data. Owing to the few available data for many seagrass species, we did not attempt an analysis of the influence of species composition on C_{org} storage.

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Additional information

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