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Global seagrass carbon stock variability and emissions from seagrass loss

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Seagrass ecosystems are recognized for their capacity to sequester and store organic carbon, but there is large variability in soil organic carbon stocks associated with plant traits and environmental conditions, making the quantification and scaling of carbon storage and fluxes needed to contribute to climate change mitigation highly challenging. Here, we provide estimates of carbon stocks associated with seagrass systems (biomass and soil) through analyses of a comprehensive global database including 2700+ seagrass soil cores. The median global soil C_{org} stock estimate is 24.2 (12.4 – 44.9) Mg C_{org} ha^{-1} in the top 30 cm of soil, 27% lower than estimates from previous global syntheses, refining the IPCC Tier 1 soil C_{org} stock currently used for carbon accounting in places without local data. We estimate that seagrass carbon stocks at risk of degradation could emit 1,154 Tg (665 – 1699) CO_2 with a social cost of $213 billion (2020 US dollars), if no action is taken to conserve these habitats.

Vegetated coastal ecosystems (VCEs), including seagrasses, are significant greenhouse-gas sinks[1] that store as much as 8.3–23.1 Pg organic carbon (C_{org}) in biomass and underlying soil (known as "blue carbon")[2]. These ecosystems play an outsized role in oceanic carbon burial because they account for nearly half of the annual C_{org} burial in oceanic sediments despite covering only 2% of the ocean[3]. As such, restoration, protection, or enhancement of VCEs relative to the status quo are considered natural climate solutions[4]. However, their important contribution to climate change mitigation is at risk because VCEs are declining globally, and their loss could further exacerbate climate change by reducing carbon sequestration capacity, shrinking an already limited natural buffer against rising greenhouse gas emissions. In addition, seagrass and other VCE loss and degradation also puts at risk the C_{org} stored in underlying soils, some of which may be eroded, resuspended and remineralized, turning C_{org} stocks accumulated over centuries into a new source of greenhouse gas emissions[5–7].

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Although the conservation of VCEs has many benefits beyond blue carbon[4,8], it is primarily their carbon sequestration and storage capacity that is being integrated into national and international policy frameworks and financing mechanisms, including carbon credits[9]. For example, VCE protection and restoration are recognized strategies to achieve the goals set by the Paris Agreement, which include limiting greenhouse gas emissions and keeping long-term global temperature increases to well below 2 °C relative to that before the industrial revolution[10]. Multiple countries are already including VCEs in their commitments (known as Nationally Determined Contributions, NDCs) to achieving the targets of this agreement[11]. Additionally, methodologies exist for generating carbon credits from the restoration and conservation of VCEs that can be purchased by those wishing to offset greenhouse gas emissions[12,13], and the number of associated projects generating "blue carbon credits" to support conservation-related activities is rapidly accelerating[9]. However, seagrasses have large uncertainties in soil C_{org} density and sequestration rate and have also received less policy and related financial attention than other VCEs[9], resulting in fewer conservation and restoration activities targeting seagrass ecosystems. Greater knowledge of the variation in, and drivers of, seagrass C_{org} stocks is essential to guide the development, integrity, and reliability of climate change policy and financing to support seagrass conservation and restoration.

Seagrass ecosystems have long been recognized as globally significant C_{org} stocks with considerable risk of emissions following their degradation[3,5,6]. However, earlier estimates of seagrass C_{org} stocks were subject to large uncertainty due to limited C_{org} stock data that did not capture the full variety of seagrass habitat types across their geographic distribution[5,6]. More than a decade has passed since the seminal synthesis of seagrass C_{org} stock data by Fourqurean et al.[5], and increased interest in seagrass blue carbon has sparked research activity on all continents. As a result, we now have comprehensive data to form a more complete and nuanced understanding of seagrass blue carbon. For example, recent work has shown that seagrass C_{org} sequestration and storage depend on a variety of influences relating to plant traits, climate, geomorphology, and hydrology[14–16]. Seagrass morphology and biomass[16,17], soil properties[18,19], and hydrodynamic regime[20] can all also influence seagrass C_{org} stocks. However, these recent advances in our understanding of seagrass C_{org} storage are mostly regional or species-specific[17,19,21–23] and a global synthesis of these newly available data is needed to enable a comprehensive seagrass C_{org} stock assessment across all species, environments and bioregions[5,6,16,24,25].

Here, we assess C_{org} stock data across the full geographic distribution and taxonomic variety of seagrass habitats and do this by assembling a global database of seagrass C_{org} stocks via a systematic review of published data, supplemented with previously unpublished data. We provide updated estimates of global, regional, and genus-specific mean C_{org} stocks (see Table S1) and determine global correlates of C_{org} stock variability relating to biogeography, plant physiology, and coastal geomorphology. The database is also delineated by records per country to enable readers to assess carbon stocks with reference to practical applications such as National Greenhouse Gas Inventories required under the Paris Agreement. We combine our seagrass C_{org} stock estimates with recent assessments of seagrass loss risks, carbon remineralization factors, and global seagrass area to derive first-order estimates of potential emissions resulting from a failure to protect current seagrass ecosystems.

Results and discussion

Global seagrass carbon stocks

We compiled data from 2771 soil cores (Fig. 1), out of which 1022 soil cores had a depth of at least 30 cm with a mean C_{org} stock of 41.1 ± 1.8 Mg C_{org} ha^{-1} in the top 30 cm of soil (Table 1). These C_{org} stock data were skewed high by very large stock estimates (mostly from Mediterranean *Posidonia oceanica* meadows), thus making estimates of the median of 27.5 (15.8–44.9) Mg C_{org} ha^{-1} (interquartile range) more representative of the central tendency. We used a further

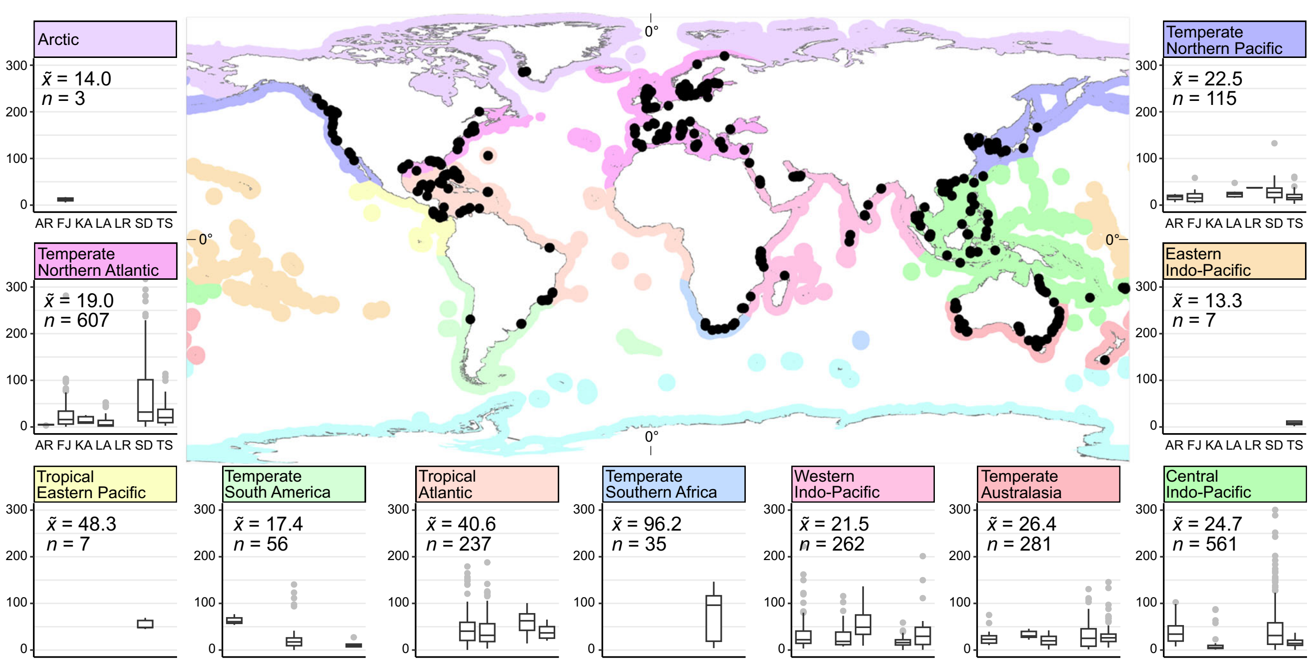

Fig. 1 | Seagrass soil organic carbon (C_{org}) stocks (to 30 cm, Mg C_{org} ha^{-1}) by coastal typology and marine ecoregion. Map shows sampling locations (black circles) with marine ecoregions[55]. Panels show boxplots of 30 cm seagrass C_{org} stocks by coastal typology[37], where AR = Arheic, FJ = Fjords, KA = Karst, LA = Lagoons, LR = Large Rivers, SD = Small deltas, TS = Tidal systems. Median C_{org} stocks ($\tilde{x}$) and sample size (n) are shown in panels for each marine ecoregion, where the center line shows the median, box limits show upper and lower quartiles, whiskers are 1.5x the interquartile range and points are outliers. Basemap from ESRI.

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Table 1 | Database summary and comparison to previous estimates

		Study	Mean ± SE	Median (interquartile range)	*n*
Soil properties	Dry bulk density (g cm^{-3})	This study	1.1 ± 0.0	1.1 (0.8–1.4)	18,436
		Fourqurean et al.[5]	1.0 ± 0.0	0.9	2484
	% C_{org}	This study	1.3 ± 0.0	0.7 (0.3–1.6)	18,658
		Fourqurean et al.[5]	2.0 ± 0.1	1.4	3561
Soil C_{org} stock (Mg C_{org} ha^{-1})	30 cm; Including predicted	This study	37.7 ± 1.1	24.2 (12.4–44.9)	2171
	30 cm; Measured only	This study	41.1 ± 1.8	27.54 (15.8–47.2)	1022
		Kennedy et al.[16]	33.5 ± 1.2	23.1	576
		Fourqurean et al.[5]	36.8 ± 1.7	33.2 (23.1–45.6)	183
	1 m; Including predicted	This study	120.8 ± 3.5	77.6 (41.9–139.7)	1625
		Fourqurean et al.[5]	165.6	139.7	219
		IPCC[26]		108 (84–139)	89
	1 m; Measured only	This study	194.3 ± 13.4	145 (62.2–263.7)	227
		Fourqurean et al.[5]	329.5 ± 55.9	173.3	41

Soil properties were summarized for all available data in the database, where most soil cores contain multiple data points representing individual core increments. Soil C_{org} stocks were calculated per soil core. IPCC[26] reported the geometric mean with a 95% confidence interval, based on both measured and interpolated 1 m C_{org} stocks.

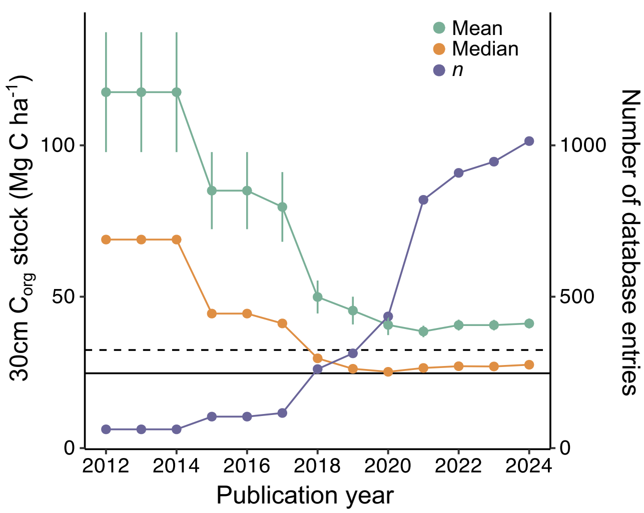

Fig. 2 | Seagrass soil organic carbon (C_{org}) stock database summary statistics by data publication year. Seagrass soil C_{org} stock mean (green), median (orange), and number of cores (purple) cumulatively calculated for each publication year from 2012. Organic carbon stocks include only measured values (minimum core length of 30 cm). Standard error shown for the mean. Horizontal lines indicate the IPCC Tier 1 estimate (dashed; IPCC[26]) and our new database median (solid line, includes predicted stocks).

1,149 soil cores that had a length of 5 to 29 cm to model 30 cm soil C_{org} stocks and report our best estimate of median global seagrass C_{org} stocks in the top 30 cm of soil to be 24.2 (12.4–44.9) Mg C_{org} ha^{-1}, based on 2171 cores. An additional 600 soil surface samples did not reach to 5 cm depth and were not part of 30 cm C_{org} stock estimates.

This predicted median 30 cm soil C_{org} stock is 5% higher than recent estimates by Kennedy et al.[16] based on 576 cores, but 27% lower than the first global estimate by Fourqurean et al.[5], while the median predicted 1 m soil C_{org} stock is 28% lower than the IPCC Tier 1 estimate[26] and 44% lower than Fourqurean et al.[5] (Table 1). Compared to these earlier studies, our database greatly expands the geographic and taxonomic distribution of seagrass C_{org} estimates and includes data from seagrass meadows in minerogenic settings with soils of higher dry bulk density and lower soil C_{org} content, which were underrepresented in earlier syntheses (Table 1). Indeed, each year since the publication of Fourqurean et al.[5], the addition of new seagrass C_{org} stock measurements reduced the global mean and median estimates (Fig. 2), indicating that early available data were biased toward seagrass habitats with high soil C_{org} stocks. Notably, since 2019, the mean and median estimates have stabilized, suggesting that the current number of available measurements is sufficient to derive a more robust and reliable seagrass soil C_{org} stock estimate to inform future blue carbon studies reliant on a global average.

Our synthesis also provides data on seagrass above-ground biomass ($n = 902$), below-ground biomass ($n = 633$), and total biomass ($n = 722$), with a mean (median) of 0.66 ± 0.1 (0.23) Mg C ha^{-1} for above-ground biomass, 1.37 ± 0.1 (0.35) Mg C ha^{-1} for below-ground biomass, and 2.01 ± 0.1 (0.61) Mg C ha^{-1} for total biomass (Supplementary Table S1). Although these estimates are based on at least twice the sample size, they are very similar to previously published values (Supplementary Table S2)[5,27], except for below-ground biomass, which we estimate 50% higher than Duarte and Chiscano[27]. A more recent, much larger compilation of seagrass biomass data by Strydom et al.[28] also suggests higher below-ground than above-ground biomass in seagrasses, albeit with lower overall biomass C_{org} stocks (Supplementary Table S2). However, neither Strydom et al.[28] nor Duarte and Chiscano[27] reported biomass C_{org} content, and we calculated stocks under the simplifying assumption that 1/3 of biomass is C_{org}.

There are pronounced differences in seagrass soil C_{org} stocks depending on taxonomic identity and functional group. The highest soil C_{org} stocks were associated with the seagrass genera *Posidonia*, *Thalassia*, *Syringodium*, as well as mixed species meadows, although these groups also had the largest variability in soil C_{org} stocks (Fig. 3; Supplementary Table S1). Interestingly, these taxa also showed the highest below-ground biomass, while the seagrass genus with the lowest soil C_{org} stocks (*Halophila*) had the lowest average below-ground biomass, suggesting a relationship of genera-specific soil C_{org} stocks and seagrass biomass (Supplementary Fig. S1).

Global correlates of seagrass carbon stocks

Large, persistent seagrass species are associated with larger soil C_{org} stocks than ephemeral species (Fig. 3). This finding is likely related to the increased production of biomass, particularly below-ground roots and rhizomes that directly contribute autochthonous organic matter to the soil carbon pool[29,30], as well as above-ground biomass that may facilitate trapping of particles at higher rates, including allochthonous organic matter[31,32]. These large seagrass species also typically persist in the same location over multiple years, indicating an absence of—or resistance to—disturbance. This stable sedimentary environment may

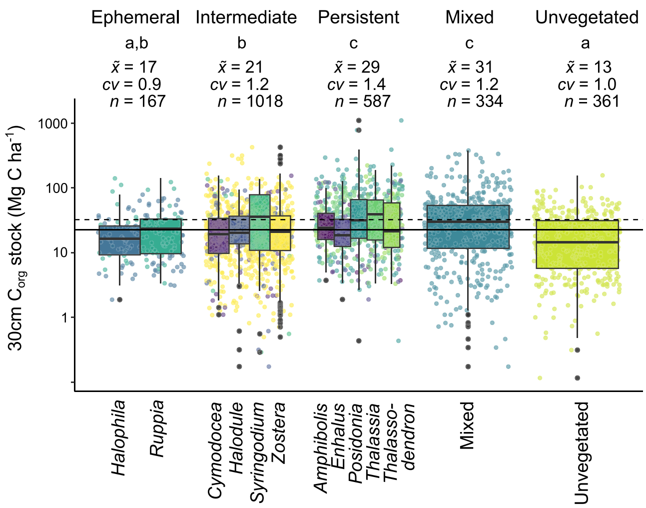

Fig. 3 | Box plots showing soil C_{org} stocks by seagrass genus (colors), nested within functional group. Box plot elements are defined as in Fig. 1. Note the logarithmic *y*-axis. Also shown are letters indicating differences ($\alpha = 0.001$) between functional groups (Kruskal–Wallis, Dunn's post hoc[56]), median carbon stocks ($\tilde{x}$), coefficients of variation (*cv*), and sample size (*n*) for functional groups. Horizontal lines indicate the IPCC Tier 1 estimate[26] (dashed) and our new database median (solid). Note that *Zosteraceae* were recently revised to encompass multiple genera, which is not reflected in this study[57]. Two very low carbon stocks of the "unvegetated" group were excluded for display purposes.

contribute to their underlying soils having higher C_{org} stocks, as sediment resuspension and remineralization rates may be lower[33].

In contrast, small and ephemeral seagrass species may trap fewer allochthonous organic matter particles, contribute less autochthonous organic matter from biomass, and may be more prone to lose C_{org} stocks to remineralization when vegetation cover is low or absent[34]. In fact, many small and ephemeral seagrass species are considered early colonizers and, as such, are associated with unstable or recently disturbed habitats[29], which may have low soil C_{org} stocks upon colonization. However, our data show that both ephemeral species of *Halophila* and *Ruppia* can, in some cases, be associated with carbon stocks of more than 100 Mg C ha^{-1} in the top 30 cm. This may reflect their ability to settle on soil previously occupied by persistent species[35], their potential for high rates of autochthonous production[28], or their settling in depositional environments with allochthonous sources of carbon such as mangroves[36]. Further studies are required to understand the contribution of small and ephemeral seagrasses to soil C_{org} stocks.

These findings show that seagrass carbon stock estimates need to consider seagrass species, or functional group identity, to improve current estimates. Extrapolating soil C_{org} stock estimates derived from persistent species to meadows comprised of ephemeral seagrasses will likely lead to overestimations of blue carbon stocks, and vice versa. This highlights the need to distinguish seagrass meadow types (functional groups or species composition) in both seagrass extent mapping and field collection of C_{org} stock data. Seagrass C_{org} stock estimates that rely solely on presence-absence maps and utilize C_{org} stock data exclusively derived from dense, persistent meadows are likely to overestimate true stocks. However, the considerable variability in C_{org} stocks even within genera emphasizes the need to consider further site characteristics for blue carbon projects (Fig. 4). For example, where ephemeral seagrasses grow on soil with high C_{org} stocks that may have been previously deposited by other species (e.g., persistent seagrasses or mangroves), their conservation might prevent emissions of legacy C_{org} stocks even if recent C_{org} burial is low.

Seagrass soil C_{org} stocks also differ geographically, with higher stocks in the Tropical Atlantic, Tropical Eastern Pacific, and Temperate Southern Africa marine ecoregions, although the latter two regions are still relatively under-sampled (Fig. 1; Supplementary Table S1). Absolute sampling effort was highest in Australia, USA, Denmark, UK, and Singapore (Supplementary Fig. S2), but normalized for seagrass area within territorial waters, Jordan, Malta, Singapore, US Virgin Islands, Malaysia, Kenya, and Colombia had the highest data density (Supplementary Fig. S3). We also tested for differences among coastal typologies[37] because the geomorphic setting has been identified as a good predictor of C_{org} stocks in VCEs[16,38,39]. We found higher soil C_{org} stocks in small deltas, Karst, and arheic settings (Supplementary Table S1; Supplementary Fig. S4), particularly in small deltas of the Temperate North Atlantic and Central Indo-Pacific (Fig. 1). This coastal typology may provide ideal conditions for seagrass C_{org} storage, because small deltas can be sheltered, depositional environments with a potential additional supply of allochthonous C_{org} from terrestrial sources and inorganic material that rapidly buries and preserves deposited C_{org} (Fig. 4). The highest C_{org} stocks associated with these settings harbor *Posidonia* meadows in the Mediterranean, as well as *Enhalus* and *Thalassia* meadows in the Central Indo-Pacific, all persistent species with high biomass.

Overall, global variability in seagrass soil C_{org} stocks was only partially explained by the broad geographical and taxonomic predictors in our database (Random Forest: $R^2 = 0.39$, RMSE = 38.6; Supplementary Fig. S5), suggesting that other regional and local-scale drivers may exert control over seagrass soil C_{org} stocks (e.g., hydrology, sedimentology, disturbance history, etc.). The best models of seagrass soil C_{org} stocks will therefore be local or regional, considering predictors specific to these scales[18,19,21] or including more detailed predictor variables[16]. In addition, biogeographical (coastal typology, marine ecoregion) as well as taxonomic (seagrass species, genus, and functional group) predictors were significant, highlighting that globally, both plant traits and the environmental setting interact to determine seagrass blue carbon stocks[15,16] (Fig. 4). But even our best models still leave a large proportion of the variance in C_{org} stocks unexplained; the study identifier ("Article ID") was the most important predictor of C_{org} stocks (Supplementary Fig. S5), suggesting that study design or other site idiosyncrasies (see Fig. 4) may explain a large portion of the variability. Further work is needed to better constrain the factors responsible for determining seagrass soil C_{org} stocks at a global and local scale.

Potential carbon emissions from seagrass loss

We produced a first-order estimate of potential CO_2 emissions resulting from a failure to protect at-risk seagrass carbon stocks globally. To do this, we combined spatially explicit seagrass soil C_{org} stocks to 30 cm depth with a recently published global map of risk of rapid seagrass decline[40]. If no conservation actions are taken to halt this rapid decline, we estimate that 5.25 ± 0.36 Mg C ha^{-1} might be lost by 2050, assuming 53% of soil C_{org} stocks are being remineralized after conversion of seagrass habitat to an unvegetated state[41]. Adding the loss of seagrass biomass (2.01 ± 0.1 Mg C ha^{-1}, Supplementary Table S1) and assuming that the available risk and carbon stock estimates are representative of the total global seagrass area (433,281 km^2, adapted from McKenzie et al.[42] and UNEP-WCMC[43]), loss of C_{org} stocks from at-risk seagrass conversion to an unvegetated state could result in emissions of 1154 (665–1699) Tg CO_2 by 2050 (Table 2). With a social carbon cost of $185 (2020 US dollars) per Mg of CO_2 emissions through climate change impacts[44], a failure to protect seagrass habitats could have a social cost of $213 (123–314) billion ($2020 US) until 2050, based on the loss of C_{org} stores alone. This estimate is likely conservative because it only includes the loss of existing seagrass C_{org} stocks to a 30 cm depth and does not consider any foregone sequestration, which is associated with much greater uncertainty due to high

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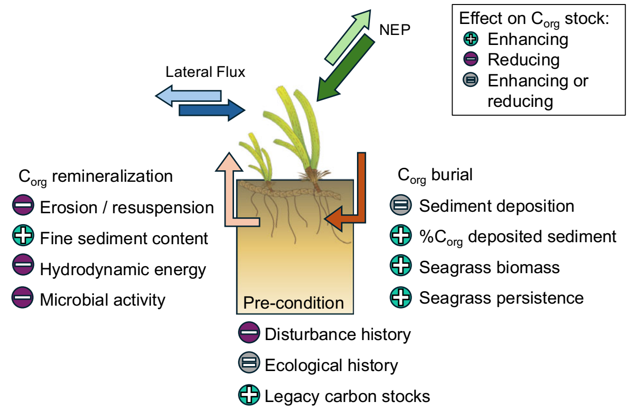

Seagrass soil Corg stock = Precondition + Corg burial − Corg remineralization

Fig. 4 | Conceptual diagram of factors driving soil C_{org} stocks in seagrass systems. Seagrasses produce C_{org} (net ecosystem productivity, NEP) and may exchange C_{org} with adjacent systems (lateral flux). Soil C_{org} stocks are a function of legacy carbon stocks, ecological and disturbance history (Pre-condition), increased by C_{org} burial (affected by sediment deposition, C_{org} content of deposited sediment, seagrass biomass, and persistence), and reduced by C_{org} remineralization (affected by erosion, fine sediment content, hydrodynamic energy, and microbial activity). Factors with green symbols (+) generally increase soil C_{org} stocks, while purple symbols (-) generally decrease soil C_{org} stocks, and factors with gray symbols (=) have no generalizable direction. Seagrass symbol adapted from Catherine Collier, JCU (license: creativecommons.org/licenses/by-sa/4.0/).

variability in C_{org} burial rates and the complexity of their accurate determination[45,46]. Despite this conservative approach, we derive an annualized rate of 0.05 (0.03–0.07) Pg CO_2 yr^{-1}, assuming that emissions are occurring at a constant rate until 2050. Previous estimates included the loss of deeper (1 m) C_{org} stocks and assumed 100% conversion of C_{org} stocks to CO_2, but without spatially explicit C_{org} stock and degradation risk data, derived annualized loss rates of 0.06–0.8 Pg CO_2[47] at a cost of $6.1 billion US yr^{-1} ([6]).

Reference depth for carbon stock accounting

In this work, we report seagrass-associated soil C_{org} stocks to a depth of 30 cm, although previous assessments used a 1 m depth horizon[5,6,25]. Using 30 cm reference depth for seagrass soil C_{org} stock accounting is more conservative and reflects that most available data are from soil cores less than 1 m long (only 227 out of 2171 cores in our database reach 1 m depth, Table 1), likely because obtaining longer subtidal soil cores is logistically more complicated, or impossible where seagrass grows on soils less than 1 m deep, as can be the case in nearshore and backreef environments. We emphasize that for carbon stock accounting, it is important to measure soil depth and caution against assuming a soil depth of 1 m exists at all meadows. Thus, the common practice of linear extrapolation of measurements from shorter cores to 1 m depth can be inappropriate, particularly as analysis of 1 m cores in our database suggests that this practice overestimates 1 m C_{org} stocks, especially in high-C_{org} soils (Supplementary Methods).

Evidently, estimating seagrass C_{org} stocks to a greater reference depth yields larger stocks, but for the purpose of carbon accounting it is appropriate to use the reference depth that is at risk of loss. There is currently insufficient data to ascertain the depth to which seagrass C_{org} stocks are affected when seagrass meadows are degraded or lost, and this depth will likely vary with environmental conditions and disturbance type. Seagrass systems globally are mainly threatened by coastal development, bottom trawling and anchoring, and deterioration of water quality[40,48]. Bottom trawling represents one of the greatest risks[40], and both modeling[49] and field studies[50] suggest that its effect on C_{org} stocks extends to a soil depth of 10–30 cm. Similarly, little is known about the balance of C_{org} in seagrass-associated soils that is labile and at risk of remineralization, as opposed to recalcitrant C_{org} that would not be remineralized upon soil erosion and resuspension following seagrass loss. Typically, the surface layer of marine soils contains more labile C_{org} than deeper layers[45], so that the remineralization rate of C_{org} upon disturbance may decrease with depth. We therefore chose to limit our assumptions of C_{org} losses to the more vulnerable and higher-C_{org} top 30 cm of seagrass soils.

Lastly, it is important to note that seagrass meadows and other VCEs can cycle greenhouse gases not only by organic matter production and burial, but also via carbonate production and dissolution, as well as fluxes of total alkalinity, methane, and nitrous oxide. While the benefit of blue carbon may be outweighed by these processes in individual seagrass meadows[22,46,51], research suggests that globally, alkalinity production and carbonate dissolution increase carbon dioxide removal capacity[52] while methane and nitrous oxide production are low and not sufficient to offset their status as greenhouse gas sinks[1,22].

Outlook

Since the initial global seagrass soil C_{org} stocks summary was published[5] and incorporated into IPCC Tier 1 estimates for carbon storage and potential emissions[26], the global scientific community has made considerable effort to generate data for previously understudied regions, seagrass taxa, and environments. Our new understanding of global biomass and soil C_{org} stocks suggests that the central tendency of global seagrass soil C_{org} stocks is lower than previously thought. Our analyses suggest that this new estimate is robust to the addition of new data and more accurately and reliably represents global seagrass soil C_{org} stocks. Our estimate refines the Tier 1 soil C_{org} stock for places without local data, and our models of the correlates of soil C_{org} stocks allow for the calculation of Tier 2 estimates by considering species traits, bioregion, and geomorphic setting. We also highlight that there are still critical knowledge gaps with regard to drivers of seagrass soil C_{org} stocks, the extent of C_{org} remineralization following seagrass loss, the fate of remineralized C_{org} stocks, and the global seagrass extent.

Despite these unknowns, the benefit of conserving existing C_{org} stocks in seagrass habitats is abundantly clear. Even with a more conservative approach than previous studies[6,47], seagrass C_{org} stocks at risk of loss are still significant at a global scale, with potential emissions of 1.15 Gt CO_2 by 2050. The protection of existing VCEs and their associated carbon stocks, including avoided habitat loss and resealing ancient soil C_{org} stocks with seagrasses, is among the most cost-effective strategies for climate change mitigation via natural climate solutions[4,24]. In addition to protecting seagrass systems as greenhouse gas sinks, the conservation of these habitats yields substantial co-benefits, from supporting biodiversity and livelihoods, to nourishing endangered species, protecting coastlines, and improving water quality[4,8]. The increased reliability of our C_{org} stock estimates and better understanding of the drivers of variability provide climate change policy and financing sectors with increased access to high-integrity resources that can further drive conservation and restoration.

Methods

Literature search

A search was conducted on the 24th of October 2021 of the bibliographic databases Web of Science (WoS) and Scopus. The search string used in the systematic review was generated using a list of keywords arising from the project aims. Keywords were organized under the headings of population, comparator, and outcome, a common approach for systematic reviews. Keywords were formed into search strings using the Boolean operators OR between similar terms, and the Boolean operator AND between each major heading (i.e., population,

Table 2 | Potential global carbon emissions from seagrass at risk of loss and associated social cost

	Soil C_{org} stocks (30 cm) at risk (Mg C_{org} ha^{-1})	Seagrass biomass (Mg C_{org} ha^{-1})	Global seagrass extent (ha)	Global potential emissions (Tg CO_2)	Social cost (Billion 2020 US Dollar)
Lower	4.89	2.00	26,656,200	665	123
Central	5.25	2.01	43,328,100	1,154	213
Upper	5.61	2.02	60,000,000	1,699	314

Central estimate is based on mean of soil and biomass carbon stocks at risk (upper and lower estimates are mean ± SE). For global seagrass extent, the upper estimate is from UNEP-WCMC[43], the lower estimate is from McKenzie et al.[42] (their lower confidence estimate), and the central estimate is their average. Potential emissions are expressed as Tg CO_2 (mass of carbon multiplied by 3.67). The social cost of one ton of CO_2 is $185 ($2020 US)[44].

comparator, and outcome). These terms and search strings were then trialed in WoS and Scopus and selected based on an iterative process of screening search results. After search strings were trialed, search results were compared with a test library to assess search comprehensiveness. The test library contained 20 relevant studies selected by the review team for gauging the accuracy of the search results. Out of the 20 studies from the test library, 18 studies were found in both Scopus and WoS. We therefore concluded that our search string was both sensitive and manageable in returning a relevant number of results.

The final search string, delineated by populations, comparators, and outcomes was Seagrass OR seagrass meadow OR Cymodocea OR eelgrass OR Halodule OR Halophila OR Hydrocharitaceae OR Posidonia OR seagrasses OR submerged aquatic vegetation OR Thalassia OR vegetated coastal ecosystems OR Zosteraceae AND sink OR biomass OR density OR organic soil OR soil OR stock OR stocks OR storage OR accumulation OR balance OR budget OR net ecosystem carbon balance OR net ecosystem exchange OR net ecosystem production OR net primary productivity OR sediment OR sediment OR accretion OR sediment burial OR sequestration OR soil burial OR algae OR alkalinity OR atmospheric exchange OR $CaCO_3$ OR calcification OR calcifying algae OR calcium carbonate OR carbonate cycling OR DIC OR dissolution OR dissolved inorganic carbon OR dissolved organic carbon OR DOC OR emission OR emissions OR epiphytes OR exchange OR flux OR lateral exchange OR particulate organic carbon OR POC OR respiration OR source OR vertical exchange AND Blue carbon OR Greenhouse gas OR GHG OR carbon OR CH_4 OR CO_2 OR methane OR N_2O OR nitrous oxide.

The final search string was last run on December 1st 2024, and resulted in 2071 articles from Scopus and 3764 articles from the WoS database. The review also included the full database developed by Fourqurean et al.[5] to ensure previous carbon stocks studies are included, as well as other databases held by the author group. The resulting library of articles was used to extract data on study site and environmental data, soil properties of soil core intervals, seagrass biology, and carbon stocks in biomass and soils (see database for a complete list of all variables captured). The final version of the database contains information from 415 published articles and 24 unpublished datasets for a total of 19,650 core intervals and 3245 carbon stock estimates (biomass and soil).

Calculating carbon stocks

We calculated carbon stocks from soil core profile data (at minimum $\%C_{org}$, dry bulk density, interval depth, and thickness), where available, and used published values in the absence of downcore data. Carbon stocks were calculated to "standard depths" of 15 cm, 30 cm, 50 cm, and 100 cm, but only up to the maximum sampling depth without extrapolating. If no downcore data were available and the reported carbon stock referred to a sampling depth other than 15 cm, 30 cm, 50 cm, or 100 cm, we scaled the reported value linearly to reference depths not exceeding the sampling depth. If calculated from downcore data, the carbon density for each available core interval was calculated, and all intervals were summed to the reference depths. If core intervals did not represent the entire core depth (e.g., 1–5 cm, 10–15 cm), data for the missing intervals were filled via linear interpolation between the next available intervals above and below the missing interval. In cases where the reference depth for stock calculation was within a downcore interval, that interval was scaled linearly to the next reference depth. If no information on core compaction was provided by the original study, it was assumed that no core compaction occurred.

Our database includes 1022 carbon stock estimates to a depth of at least 30 cm. For the analysis presented in this paper, we added a further 1149 data points by predicting 30 cm C_{org} stocks from shorter cores (5 to 29 cm) (Supplementary Fig. S6). We used a subset of data, including only C_{org} stocks measured to 30 cm, and compared the performance of two predictive models (linear and 2nd order polynomial). We found that both models were equally as accurate and used the following polynomial model to predict 30 cm soil C_{org} stocks (y) from 15 cm C_{org} stocks (x): $y = 1.93233x - 0.00102x^2$.

In addition, we predicted 100 cm C_{org} stocks from shorter cores in a similar fashion and found that a 2nd order polynomial function more accurately predicted 100 cm cores from 30 cm and 50 cm cores than linear extrapolations. We performed a similar analysis to predict 1 m C_{org} stocks from shorter reference depths (15 cm, 30 cm, 50 cm), see Supplementary Methods section "Prediction of C_{org} stocks from short cores" and Supplementary Fig. S7, Supplementary Table S3.

There were 553 carbon stock estimates from the Fourqurean et al.[5] database for which dry bulk density data were not available and instead were set to a constant value of 1.091 g/cm^3. We predicted dry bulk densities for these samples from C_{org} content by fitting exponential decay functions to all database entries with available C_{org} content and dry bulk density data. The most accurate predictions were achieved when separate functions were fit for each coastal typology (e.g., Karst, arheic, lagoons, etc.)[37]. See Supplementary Methods section "Prediction of missing dry bulk density values from C_{org} content", Supplementary Fig. S8, and Supplementary Table S4 for further details of dry bulk density modeling.

Random forest model of carbon stock drivers

We used random forest modeling to predict seagrass C_{org} stocks (30 cm), from metadata categories coastal typology, marine ecoregion, seagrass genus, seagrass species, seagrass functional group, and Article ID. We then assessed variable importance to estimate which metadata category was most predictive of seagrass C_{org} stocks (Supplementary Fig. S5). Random Forest models and variable importance were implemented in R version 4.3.1[53] using the package randomForestSRC[54]. Ideal model parameters mtry (= 3) and nodesize (= 2) were determined using the tune function and the final model run used the parameters ntree (= 3000), sampling with replacement, block.size (= 20), and importance (= permute). Estimated variable importance was extracted using the subsample and extract.subsample functions and plotted using the plot.subsample function.

CO_2 emissions resulting from seagrass loss

To estimate loss of C_{org} stocks from seagrass meadow conversion of seagrass habitat to an unvegetated state (i.e., loss), we used the predicted risk of rapid seagrass decline from Turschwell et al.[40], a geospatial layer consisting of 100 × 100 km grid cells populated with the modeled probability that seagrasses in a given cell experience rapid decline (loss of 25–100% over 10 years) from a set of stressors (demersal fishing, water quality, etc.). We extracted this probability value at the locations of 1323 seagrass stock database entries and multiplied the seagrass loss probability with location-specific 30 cm C_{org} stocks to derive an estimate of C_{org} stocks at risk. Not all database entries fell within risk grid cells, because the risk layer from Turschwell et al.[40] was calculated on the spatial footprint of a smaller seagrass distribution database[48]. We treated locations where only carbon stocks were available as equal to locations with no data, implicitly assuming that stock data not covered by the risk layer were not different from stock data included in this calculation. We then multiplied seagrass soil C_{org} stocks at risk of loss by 53%, the current best estimate of C_{org} stock reduction after 25 years (by 2050) following conversion of seagrass habitat to an unvegetated state, calculated using the empirically derived formula $y = -12.76 * \ln(x) - 11.955$, where x is time in years and y is percent C_{org} loss[41]. We then estimated the loss of carbon bound in biomass upon seagrass loss based on the median total biomass estimated from our database (2.01 ± 0.1 Mg C ha^{-1}, Supplementary Table S1), assuming all biomass is lost. To estimate the total C_{org} stock at risk globally, we multiplied the product of soil C_{org} stock at risk of loss and seagrass biomass by our best estimates of total global seagrass area (433,281 km^2). There is still large uncertainty associated with seagrass area estimates, and we used the average of a minimum of 266,562 km^2 (ref. 42) and a maximum area of 600,000 km^2 (ref. 43). We then converted the mass of carbon lost to CO_2, by multiplication with 3.67, the molecular ratio of CO_2 to C. In addition, we estimated how much carbon would not be sequestered by the seagrasses that were lost, but did not include this term in our final estimate of CO_2 emission, because of the considerable uncertainty associated with carbon sequestration rates of bare sediment where seagrass was lost. Instead, we used the estimate of seagrass carbon stock loss without foregone sequestration to determine the social cost of the associated CO_2 emissions, assuming a social cost of $185 (2020 US dollars) per ton of CO_2[44].

Methodological limitations and future research needs

We acknowledge that our estimates of carbon efflux due to erosion of soil C_{org} stocks and seagrass biomass are unlikely to equal air-sea CO_2 flux, because not all C_{org} entering the water column will be converted to CO_2 and outgas to the atmosphere. There is currently insufficient data on fractions and depth-distribution of non-reactive C_{org} in seagrass soils, as well as potential redistribution and subsequent re-burial of eroded C_{org}. Additionally, considerable uncertainty in our estimations arises from the large range of possible global seagrass extent[42,43], highlighting the need for improved global extent mapping[25,42]. Although we found differences in C_{org} stocks of seagrass functional groups and genera, we could not incorporate specific C_{org} stocks into our emissions calculation, because they are currently not resolved in global seagrass extent estimates. In addition, a methodological limitation in seagrass blue carbon research is the common practice to assess C_{org} in seagrass soils without removing seagrass below-ground material, which could potentially lead to double-counting if such material is included in both below-ground biomass and soil C_{org} estimates.

Data availability

The seagrass carbon stock database is available on Figshare at https://doi.org/10.6084/m9.figshare.27198915.

Code availability

All R code necessary to reproduce the analysis is made available as Supplementary Software 1 to this article.

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Author contributions

All authors conceived of the paper and contributed extensively to the work. J.R.K. wrote the initial draft and performed formal analysis. C.C. performed the initial literature search and designed the initial database. J.R.K., C.C., M.D., K.E.L., M.P.J.O., L.W.W., and J.W.F. performed data extraction. C.C., A.A.O., M.C.J., S.C., M.D., D.F., H.K., C.E.L., N.M., K.J.M., M.P.J.O., E.P., O.S., M.A.V., S.M.Y., and J.W.F. critically reviewed and contributed to several drafts of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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