

Global Biogeochemical Cycles^{*}



RESEARCH ARTICLE

10.1029/2024GB008239

Blue Carbon Stocks Along the Pacific Coast of North America Are Mainly Driven by Local Rather Than Regional Factors

Key Points:

- Sediment organic carbon stocks were greatest in woody tidal wetlands, followed by marshes, mudflats, and seagrass habitats
- Unvegetated tideflats store much greater sediment carbon stocks than previously recognized
- Most stocks variability was explained by local-scale drivers rather than large-scale climate gradients

Supporting Information:

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

Correspondence to:














































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Citation:

Janousek, C. N., Krause, J. R., Drexler, J. Z., Buffington, K. J., Poppe, K. L., Peck, E., et al. (2025). Blue carbon stocks along the Pacific coast of North America are mainly driven by local rather than regional factors. *Global Biogeochemical Cycles*, 39, e2024GB008239. <https://doi.org/10.1029/2024GB008239>

Received 28 MAY 2024

Accepted 31 JAN 2025

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Abstract Coastal wetlands, including seagrass meadows, emergent marshes, mangroves, and temperate tidal swamps, can efficiently sequester and store large quantities of sediment organic carbon (SOC). However, SOC stocks may vary by ecosystem type and along environmental or climate gradients at different scales. Quantifying such variability is needed to improve blue carbon accounting, conservation effectiveness, and restoration planning. We analyzed SOC stocks in 1,284 sediment cores along >6,500 km of the Pacific coast of North America that included large environmental gradients and multiple ecosystem types. Tidal wetlands with woody vegetation (mangroves and swamps) had the highest mean stocks to 1 m depth (357 and 355 Mg ha⁻¹, respectively), 45% higher than marshes (245 Mg ha⁻¹), and more than 500% higher than seagrass (68 Mg ha⁻¹). Unvegetated tideflats, though not often considered a blue carbon ecosystem, had noteworthy stocks (148 Mg ha⁻¹). Stocks increased with tidal elevation and with fine (<63 μm) sediment content in several ecosystems. Stocks also varied by dominant plant species within individual ecosystem types. At larger scales, marsh stocks were lowest in the Sonoran Desert region of Mexico, and swamp stocks differed among climate zones; otherwise stocks showed little correlation with ecoregion or latitude. More variability in SOC occurred among ecosystem types, and at smaller spatial scales (such as individual estuaries), than across regional climate gradients. These patterns can inform coastal conservation and restoration priorities across scales where preserving stored carbon and enhancing sequestration helps avert greenhouse gas emissions and maintains other vital ecosystem services.

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Plain Language Summary Coastal blue carbon ecosystems such as seagrass meadows, marshes, mangroves, and other tidal wetlands, efficiently accumulate and store organic carbon in their sediments. For the west coast of North America, we investigated whether the amount of carbon stored in the sediment (“carbon stock”) differed by ecosystem type and whether differences were linked to local-scale factors such as elevation and plant type or to regional-scale factors such as latitude and climate conditions. We found the highest sediment carbon stocks in mangroves in Mexico and tidal swamps in the Pacific Northwest, ecosystems both dominated by woody plants. Tidelands had stocks at least as large as seagrass meadows, while marshes were intermediate among all ecosystems. Overall, differences in stocks were more related to factors like site elevation or the specific wetland sampled than broad geographic-scale differences in climate conditions. Knowing how soil carbon stocks differ across various coastal conditions will help incorporate blue carbon information into planning and decision-making in coastal conservation and restoration efforts.

1. Introduction

Intertidal and shallow-subtidal wetlands provide many important functions and services in nearshore environments, including high rates of primary productivity, provision of habitat for diverse flora and fauna, production of commercially important fish and crustacean species, coastal protection from flooding, and biogeochemical processing including organic carbon storage and sequestration (Barbier et al., 2011; Shepard et al., 2011). Despite their global economic, ecological, and cultural importance, many of these ecosystems have been degraded or converted to other land uses globally, including in western North America (Brophy et al., 2019; Campbell et al., 2022; Crooks et al., 2018; Maurice-Hammond et al., 2023). Recently, a greater appreciation of the important functions and services provided by these wetlands has elevated restoration and conservation priorities for blue carbon ecosystems (Bertolini & da Mosto, 2021; Valderrábano et al., 2021).

Sediment organic carbon (SOC) accumulation (sequestration) and long-term storage (stocks) in intertidal and shallow subtidal wetlands (hereafter also termed “blue carbon ecosystems”) are high per unit area relative to terrestrial ecosystems such as tropical, temperate, and boreal forests (Chastain et al., 2022; Kauffman, Giovanonni, et al., 2020; Mcleod et al., 2011). Wang et al. (2019) estimated that 4.2 to 5.0 Tg C accumulate per year in United States tidal wetlands. Saline tidal wetlands worldwide have a substantial overall climate mitigation effect, even after accounting for their methane and nitrous oxide emissions (Rosentreter et al., 2023). The majority of organic carbon in blue carbon ecosystems is stored in sediments/soils (hereafter, sediments), but additional storage in above- and below-ground plant biomass can be substantial, especially in wetlands with woody species such as tropical mangroves and temperate tidal swamps (Hu et al., 2021; Kauffman, Giovanonni, et al., 2020). High sediment deposition rates and frequent anoxic conditions with reduced decomposition favor the long-term preservation of organic carbon in blue carbon ecosystems, especially from vascular plant roots (Cragg et al., 2020). These wetland sediments vary considerably in age from years to millennia, with some of the oldest sites having organic carbon-rich layers several meters thick that represent thousands of years of SOC accumulation since the last period of glacial retreat in the northern hemisphere initiated rising sea-level (e.g., Costa, Ezcurra, Aburto-Oropeza, et al., 2022; Drexler et al., 2009; Mateo et al., 1997). Degradation of blue carbon ecosystems or their conversion to other land uses can potentially lead to large emissions if SOC is mineralized, in addition to the loss of future sequestration capacity (Jacquemont et al., 2022; Kauffman et al., 2017; Tan et al., 2020).

SOC may vary across spatial scales because multiple drivers affect carbon dynamics in these ecosystems. At smaller scales (within individual estuaries or watersheds), factors correlated with SOC in mangrove ecosystems included sediment particle size, species composition, salinity, proximity to channels, and intertidal position (Hu et al., 2021; Ouyang et al., 2017). Stocks increased along an elevation gradient from intertidal seagrass to low marsh to high marsh and tidal swamps in the US Pacific Northwest (Kauffman, Giovanonni, et al., 2020). At intermediate spatial scales, carbon stocks and accumulation rates may vary with hydrogeomorphic differences among estuaries (Saintilan et al., 2013; Santos et al., 2019) or salinity (Hansen et al., 2017). At larger spatial scales (across broader climate, geographic, and latitudinal gradients), other factors have been found to correlate with tidal marsh sediment carbon density or stocks, including temperature and latitude (Chmura et al., 2003; Maxwell

et al., 2024). In sum, factors that affect in situ organic matter (OM) production, sediment particle trapping, or long-term OM decomposition may thus affect SOC storage.

Although studies quantifying blue carbon stocks have become increasingly common, those conducted across a broad gradient of climate conditions to better understand biogeographic patterns and drivers of variation have mostly been conducted in mangroves (Atwood et al., 2017; Costa, Ezcurra, Ezcurra, et al., 2022; Kauffman, Adame, et al., 2020; but see Miyajima et al. (2015), Mazarrasa et al. (2021) for seagrass and Macreadie et al. (2017) for marshes). Greater insight into spatial variability and environmental drivers of carbon stocks is required in all blue carbon ecosystems to inform conservation priorities and restoration planning, including determining the optimal spatial granularity at which stock estimates should be applied to blue carbon quantification in geographic analysis (Holmquist et al., 2018). Spatial patterns in the eastern North Pacific may inform global analyses in other geographic regions, particularly those with a similar range of climate conditions (Beck et al., 2018) and a similar diversity of ecosystem types.

To quantify variability in stocks and potential drivers across spatial scales, we compiled SOC data from nearly 1,300 sediment cores from five blue carbon ecosystem types across several ecoregions along the west coast of North America and tested three groups of hypotheses. First, we tested for differences in stocks among ecosystems, hypothesizing that stocks in higher-elevation wetlands supporting relatively high perennial above-ground plant biomass (marshes, mangroves, and tidal swamps) would be greater than stocks in lower-elevation ecosystems with typically more ephemeral above-ground vegetation (seagrass and tideflats). Second, we examined stocks relationships with several local-scale environmental drivers, hypothesizing that stocks are correlated with wetland elevation, differences in vegetation composition within ecosystem types, and fine grain content of sediments. Finally, we tested whether variation in stocks was greater at regional (ecoregion, climate zone, and latitude) than local spatial scales (ecosystem type, estuary/watershed, and elevation).

2. Materials and Methods

2.1. Data Compilation

We compiled sediment bulk density and SOC data for the Pacific coast of North America from southern Mexico to the Gulf of Alaska (Figure 1) from 69 published and unpublished sources comprising 1,284 individual cores (Table S1 and Figure S1 in Supporting Information S1). We identified data sets through collaborative networking with the Pacific Northwest Blue Carbon Working Group and California Blue Carbon Collaborative; searches of the Coastal Blue Carbon Atlas, hosted by the Smithsonian Environmental Research Center (<https://ccrcn.shinyapps.io/CoastalCarbonAtlas/>); and review of literature in the Web of Science database (searches were a combination of terms including *blue carbon*, *wetland carbon*, *marsh carbon*, and geographic names such as *Alaska*). In many cases, authors provided carbon and/or associated environmental data directly to the first author.

Our analysis focused on stocks data from estuarine and near-shore shallow-water ecosystems where the majority of blue carbon data have been collected. Therefore data included in this study were cores meeting the following criteria: (a) collected from an intertidal or shallow-subtidal sedimentary environment between the estuarine head of tide and shallow subtidal habitat; (b) included carbon data from near the wetland surface to at least 20 cm depth; and (c) collected from a least-disturbed wetland in one of five classes (described below). We did not use cores from sites that were diked former tidal wetlands, restored wetlands, or sites known to be heavily disturbed by human activities since land-use impacts could affect sediment stocks. Moreover, we did not use shorter cores since extrapolation could result in higher uncertainty.

We grouped cores into one of five ecosystem types: unvegetated tideflats (FL); shallow subtidal and intertidal seagrass meadows (SG); emergent marsh (EM); tropical and sub-tropical mangroves (MG); and temperate tidal swamps (TS) including both shrub and forested tidal wetlands (Table 1; Figure 1). Tideflats consisted of mudflats and sandflats without significant vascular plant cover (although benthic algae and plant wrack may have been present). Seagrass meadows were typically native eelgrass beds (*Zostera marina* and *Z. pacifica*) but also included non-native *Nanozostera japonica* (Sullivan & Short, 2023). Marshes consisted of annual and perennial herbaceous vegetation generally <3 m tall, including grasses, rushes, sedges, forbs, and the subshrub *Salicornia pacifica*. Mangrove forests (limited to Mexico) ranged from tall trees to shrubs (Adame et al., 2018). Tidal swamps from central California to the Pacific Northwest were mostly forested tidal wetlands dominated by taller

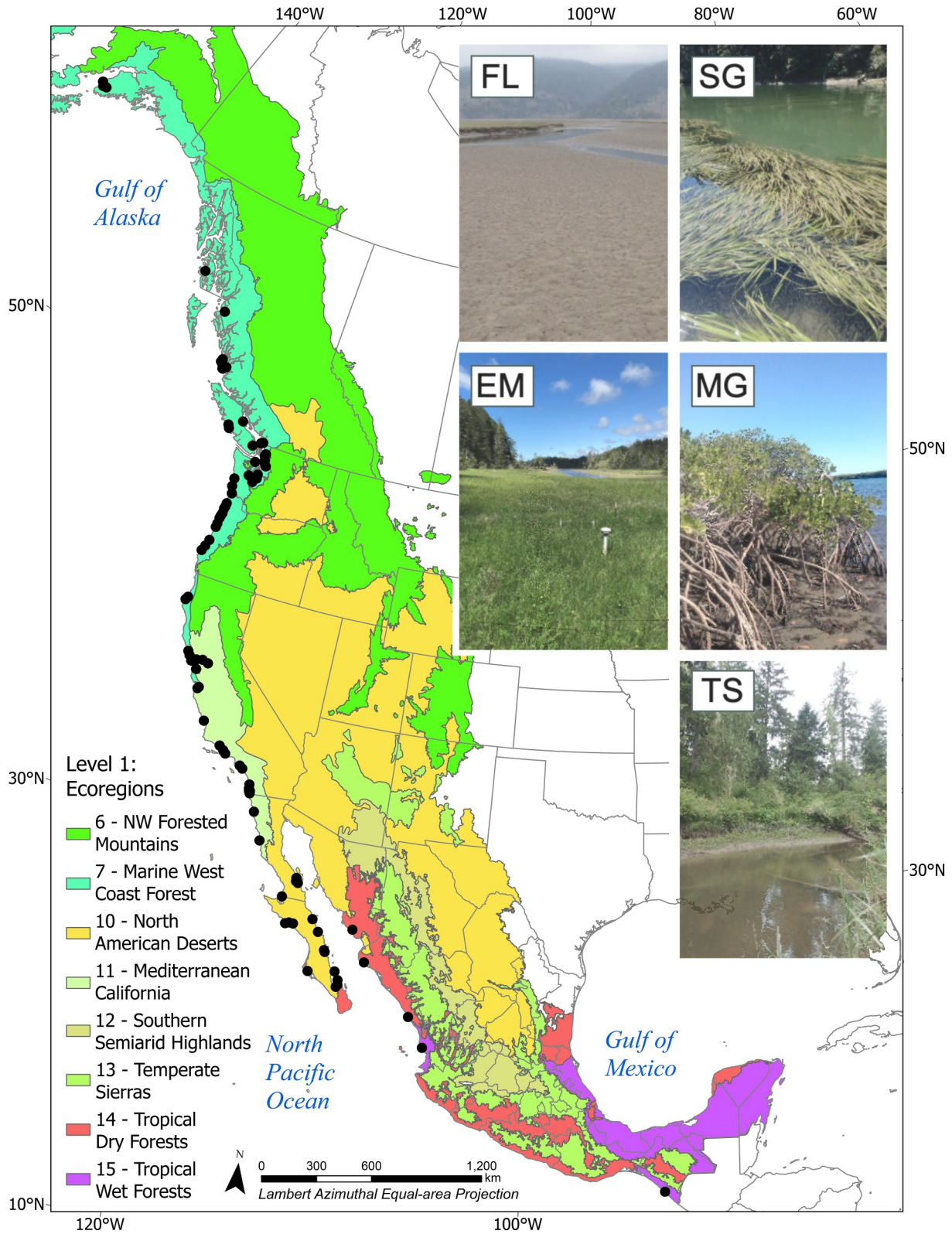


Figure 1. Estuaries sampled along the west coast of North America for blue carbon stocks (black points). Colors represent level 1 ecoregions (Commission for Environmental Cooperation, 1997; EPA, 2022). Inset photos show the five blue carbon ecosystem types sampled. EM, emergent marsh; FL, tideflat; MG, mangrove; SG, seagrass; TS, tidal swamp. Photos by C. Janousek and J. Ochoa Gómez.

Table 1

Summary of the North American Pacific Coastal Blue Carbon Ecosystem Types Included in This Study

Ecosystem type	Regional distribution	Example vegetation	Data sets	Cores
Unvegetated tideflats (FL)	Throughout Pacific North America	Generally, there are no vascular plants, but benthic algae are often present	15	84
Seagrass meadows (SG)	Throughout Pacific North America	<i>Nanozostera japonica</i> , <i>Zostera marina</i> , <i>Zostera pacifica</i>	19	256
Emergent marsh (EM)	Throughout Pacific North America	<i>Carex lyngbyei</i> , <i>Distichlis spicata</i> , <i>Deschampsia cespitosa</i> , <i>Potentilla anserina</i> , <i>Salicornia pacifica</i> , <i>Spartina foliosa</i>	46	696
Mangrove (MG)	Pacific Baja California, Gulf of California, Pacific Mexico	<i>Avicennia germinans</i> , <i>Laguncularia racemosa</i> , <i>Rhizophora mangle</i>	8	181
Tidal swamps (TS)	San Francisco Estuary (CA) to Pacific Northwest	<i>Alnus rubra</i> , <i>Cornus sericea</i> , <i>Lonicera involucrata</i> , <i>Picea sitchensis</i> , <i>Salix lasiolepis</i>	11	67

stands of Sitka spruce (*Picea sitchensis*) or other conifer and hardwood trees but also included 10 cores from shrub wetlands characterized by shorter woody plants such as willows (*Salix* spp.).

2.2. Sediment Carbon Profiles and Stocks

For each core, we compiled down-core data on dry bulk density (g cm^{-3}) and percent organic carbon (C_{org} , %) or percent OM (%). In 49.5% of the cores, C_{org} was determined with an elemental analyzer. In the remaining cores, OM content was determined by loss-on-ignition (35.4%; Heiri et al., 2001), chemical oxidation (1.2%; e.g., Ochoa-Gómez et al., 2019), or a combination of elemental analysis and loss-on-ignition (13.8%). In some studies, inorganic carbon was subtracted from total carbon via acidification or combustion of the sample at higher temperatures (e.g., Adame et al., 2015; Krause et al., 2022), although exact methods for treatment of inorganic carbon were not available for all data sets. Inorganic carbon is not a major contributor to total measured carbon in temperate marshes and swamps (Crooks et al., 2014; Drexler et al., 2009; Kauffman, Giovanonni, et al., 2020; Postlethwaite et al., 2018), although tropical blue carbon ecosystem sediments may have a higher prevalence of carbonates (Mazarrasa et al., 2015).

Studies that measured both OM and percent C_{org} from elemental analysis allowed us to estimate C_{org} content when only OM content was available for other samples. We examined individual data sets and used those that had a linear relationship between OM and C_{org} with $R^2 \geq 0.88$. From this set of 22 studies, we combined data to develop separate relationships for (a) tideflats and seagrass, (b) emergent marsh in ecoregion 7 (marine west coast forest; Figure 1), (c) emergent marsh in ecoregions 10 (North American deserts) and 11 (Mediterranean), (d) temperate tidal swamps, and (e) mangroves. We determined linear fits for each data set with the function “lm” in R (R Core Team, 2020). Because regressions using the full range of OM values gave non-zero model intercepts that could impact C_{org} estimates in samples where OM was low, we also generated equations by forcing the regression through a y-intercept of zero and used these latter equations to estimate C_{org} whenever OM was <5%.

To derive core-level total carbon stocks, we calculated vertical profiles of SOC density (g cm^{-3}) by multiplying bulk density by the fraction of C_{org} for each depth interval. Vertical profiles in the raw data comprised two cases. In the first case (57.6% cores), profiles comprised contiguous subsamples from the wetland surface to the core bottom (e.g., subsamples at 0–2, 2–4 cm depth, etc.; e.g., Callaway, Borgnis, et al., 2012). In the remaining profiles, cores consisted of non-contiguous subsamples from discrete but regular sediment depths (e.g., Kauffman, Giovanonni, et al., 2020) or from sediment horizons of unequal length (e.g., Ezcurra et al., 2016) that represented a broader depth interval (e.g., a 5–10 cm deep sample was analyzed to represent carbon density for the larger 0–15 cm depth interval). In such cases, we assumed the carbon density of subsamples was uniform across those broader depth intervals. One or more missing values for bulk density, OM, or C_{org} also occurred in about 14% of core profiles. In these cases, we used linear interpolation between adjacent values in the core profile or extrapolation up to the sediment surface. Additionally, a few core profiles (<1%) had a few suspect values, such as negative carbon content values, which we omitted and replaced with interpolated values. Information on the

amount of core compaction caused by sampling was not available for most cores, but was compensated for in some vertical profiles. Cores in which compaction was not compensated for may slightly overestimate bulk density and thus carbon density and stocks estimates.

To compile SOC stocks per unit area (Mg ha^{-1}) and standardize by depth, we multiplied carbon density values by the length of the subsample and then summed SOC through each core profile to 30, 50, and 100 cm depths. To avoid excessive extrapolation of SOC below the depth actually sampled, we only calculated stocks to 30 cm depth for cores that were at least 20 cm long, to 50 cm depth for cores that were at least 35 cm long, and to 100 cm for cores that were at least 75 cm long. We extrapolated the deepest bulk density, OM, and %C values as needed to each 30, 50, or 100 cm depth.

2.3. Core Locations, Ecoregions, and Other Attributes

For each core, we compiled geographic location, elevation, proportion of fine sediment, and dominant plant species. If precise coordinates for the collection site of the core were unknown, we used a value for the approximate center of the named site. Cores were from 86 estuaries or coastal areas. For the large San Francisco Estuary, which was well sampled, we divided cores into four areas that differ in tide range and salinity: South San Francisco Bay, San Pablo Bay, Suisun Bay, and the Sacramento-San Joaquin Delta. Salinity and tide range decrease from San Francisco and San Pablo bays (saline to brackish) to Suisun Bay (brackish) and the Delta (tidal freshwater). Similarly, for the Salish Sea in northern Washington and southern British Columbia (a large fjord-type estuary), we assigned cores to individual embayments (e.g., Padilla Bay), river deltas, or (for a few seagrass cores) sections of coastline near an island. For many cores in the Gulf of California and central British Columbia, we grouped cores into geographic clusters, each consisting of multiple small embayments along a coastline or around one or more islands because each location typically had low replication (e.g., one core). One data set of seagrass cores scattered widely throughout inlets in southeast Alaska was treated as one system. We classified all estuaries and coastal areas into one of four settings based on simplified hydrogeomorphic characteristics, using a combination of site-specific knowledge and satellite imagery (Boyd et al., 1992; Yando et al., 2023): wave-dominated estuary, tide-dominated estuary, river delta, and embayment/bay. These broad classes were chosen as representative types of coastal geomorphologies, which can influence sediment carbon storage (e.g., Gorham et al., 2021).

Based on geographic location, we assigned each core to one of five level 1 ecoregions within North America following the Commission for Environmental Cooperation (1997): marine west coast forest (ecoregion 7, “PNW-For”), the Mediterranean region of the California Floristic Province (ecoregion 11, “Med”), North American deserts (ecoregion 10, “Son-Des”), tropical dry forest (ecoregion 14, “Trop-Dry”), and tropical wet forest (ecoregion 15, “Trop-Wet”) (Table S2 in Supporting Information S1). We also classified each core into climate zones using the Köppen-Geiger climate maps developed by Beck et al. (2018) at 0.0083° spatial resolution (circa 1 km at the equator) (Table S3 in Supporting Information S1). For the small percentage of cores that were not classified because they occurred in areas mapped as open water, we used coarser scale (0.083°) maps or the classification for a nearby embayment. For cores in the conterminous US, we compiled climate normal data from 1991 to 2020, including air temperature, precipitation, and maximum vapor pressure deficit (VPD max) from the PRISM climate model at 800 m horizontal resolution (PRISM Climate Group, 2022).

Elevation data (at the wetland surface at or near the point of core collection) were available for many cores in California, Oregon, and Washington, and some in Alaska. Typically, elevation data were relative to the North American Vertical Datum of 1988 (NAVD88) measured with real-time kinematic GPS (a geodetic datum) or local mean lower low water (MLLW). We used the geographic position of cores to estimate ground surface elevation for some additional cores missing elevation data, particularly in emergent marshes, by applying the Lidar Elevation Adjustment with NDVI (LEAN) model with LIDAR raster data (Buffington et al., 2016). The LEAN model uses NDVI data from remotely sensed imagery to statistically correct for overestimates of elevation in LIDAR data due to vegetation presence (average RMSE of the model rasters was 0.087 m). Since elevation within the intertidal zone is strongly correlated with the frequency and duration of inundation (Janousek et al., 2016), and tidal amplitude varies considerably across the northeastern Pacific coast (tidesandcurrents.noaa.gov), we converted elevation values for each core to relative tidal elevations using local tidal datums. For marshes and tidal swamps, which typically occur high in the tidal frame from about mean tide level (MTL) to above mean higher high water (MHHW), we used $z^*_{\text{high}} = (z - \text{MTL}) / (\text{MHHW} - \text{MTL})$, where z is the measured elevation

(Swanson et al., 2014). For interpretation, $z^*_{\text{high}} = 0$ is defined as local MTL and would be inundated about 50% of the time, while $z^*_{\text{high}} = 1$ is local MHHW and would be inundated infrequently. For seagrass and tideflats, which typically occur from the shallow subtidal zone up to about MTL, we developed a similar metric to scale elevation to tide range: $z^*_{\text{low}} = (z - \text{MLLW}) / (\text{MTL} - \text{MLLW})$. For interpretation, z^*_{low} values >0 are above MLLW (frequently but not constantly inundated), and negative values are below MLLW (nearly constantly inundated to subtidal).

To obtain local values of MLLW, MTL, and MHHW relative to NAVD88, we used the best available sources of tidal data. This usually consisted of current or historical NOAA tide gauge data from the same estuary or, in some cases, recent water-level time-series data collected and analyzed for local projects (e.g., Janousek & Cornu, 2025; Janousek, Cornu, et al., 2025; Janousek et al., Unpublished, <https://cdmo.baruch.sc.edu/>). If neither of those sources was available within several km of the core location, we used NOAA's VDATUM model (<https://vdatum.noaa.gov/>). We only calculated z^* metrics for cores along the US coastline where most elevation data were available and where we could apply consistent tidal definitions and approaches.

Where available, we compiled data on sediment particle size, averaging values in the top 30 cm of the sediment column to compare with 30 cm stocks. We combined silt and clay fractions (size $<63 \mu\text{m}$) to determine how stocks varied with percent fines.

We used available vegetation data (usually only a list of dominant species at the core collection location), supplemented with salinity data when available (or the inferred general salinity regime based on location within each estuary) to subdivide cores from each ecosystem type (except tideflats) into two or more general major vegetation types. For seagrass meadows, we divided cores into those dominated by *Z. marina* or *Z. pacifica* versus *N. japonica*. For mangroves, we divided cores into those dominated by *A. germinans*, *L. racemosa*, *R. mangle*, or mixtures of two or three species. For tidal swamps, we divided cores into those with Sitka spruce present (*Picea sitchensis*; freshwater to brackish conditions), western red cedar present (*Thuja plicata*; freshwater conditions), or those where hardwood tree species were present but conifers were absent (*Cornus sericea*, *Salix* spp., *Alnus rubra*, *Lonicera involucrata*; freshwater conditions).

For marshes, we assigned cores to one of six vegetation categories based on major plant form and supplemental salinity information (detailed in Table S4 in Supporting Information S1 with example taxa): (a) saline succulent-dominated marshes; (b) saline graminoid-dominated marshes; (c) brackish graminoid marshes tending to be dominated by single species; (d) brackish marshes with mixtures of forbs and graminoids; (e) freshwater to oligohaline graminoid-dominated marshes; and (f) freshwater mixed graminoid and forb marshes. We did not classify a few marsh cores that lacked sufficiently detailed plant data or did not fit one of the six categories above.

2.4. Analyses

For common blue carbon ecosystems along the Pacific coast, we used down-core sample data to generate relationships between sediment OM content (determined by LOI) and percent organic carbon (determined by elemental analyzer) (Figure S2 and Tables S5–S7 in Supporting Information S1). Among the linear relationships generated, slopes were highest for emergent marshes and temperate forested tidal wetlands.

We calculated C_{org} stocks in 1,284 cores to 30 cm depth, 1,037 cores to 50 cm depth, and 592 cores to 1 m depth. Of the 1,284 cores, 54% ($n = 696$) were from marsh, 20% ($n = 256$) were from seagrass meadows, 14% ($n = 181$) were from mangroves, 7% ($n = 84$) were from tideflats, and 5% ($n = 67$) were from tidal swamps. We used Welch's one-factor ANOVA, a test robust to unequal variances, to test for differences in SOC stocks among the five types of blue carbon ecosystems, regarding each core as an independent sample. We tested for differences in stocks to 30, 50, and 100 cm depth separately and conducted pairwise comparisons of ecosystem types with Games Howell tests. Because cores were spatially aggregated to varying degrees, we confirmed results by also using a nested ANOVA, grouping cores by estuary or coastal region (mixed model with the package “lme4” in R; Bates et al., 2015).

We compared stock estimates to 30 cm depth with estimates made to 50 and 100 cm from deeper core profiles to determine if shallower cores over- or underestimated sediment stock estimates due to systematic changes in carbon density with depth by comparing data sets with expected relationships based on the scaled depths. We compared slopes of linear relationships with expected slopes for the null hypothesis of consistent carbon density with depth.

We used data on wetland elevation, sediment grain size, and plant composition/salinity regime to test for relationships between local ecological drivers and carbon stocks to 30 cm depth. We examined relationships between stocks, tidal elevation, and grain size with linear regression and checked diagnostic plots for linear regression models. For the tideflat grain size model we determined relationships each with and without a single outlier (Cook's $D > 1$); for the marsh model, we discarded one outlier in a high marsh in Netarts Bay very unlikely to be in a sandy environment. For vegetation groups within wetland classes, we tested for stock differences with Welch's ANOVA and Games Howell tests.

We used several approaches to examine differences in carbon stocks spatially along the Pacific coast. First, we tested for differences in stocks among ecoregions and climate zones for each ecosystem type with Welch's ANOVA (only for stocks to 30 cm depth, which had the largest sample sizes) and tested for linear trends in stocks with latitude using linear regression. Second, we examined variability in SOC stocks at four nested spatial scales (within estuary, within KG climate zone, within ecoregion, and among ecoregions) with variance decomposition using a Bayesian random effects model (Hobbs & Hooten, 2015) as outlined in Equation 1:

$$\begin{aligned}
 C_i &\sim N(\mu_j + \beta_{\text{estuary},j,k} + \beta_{\text{kg},\text{zone},j,l} + \beta_{\text{ecoregion},j,m}, \sigma_{\text{subestuary},j}^2) [0, \infty] \\
 \beta_{\text{estuary},j,k} &\sim N(0, \sigma_{\text{estuary},j}^2) \\
 \beta_{\text{site},j,l} &\sim N(0, \sigma_{\text{kg},\text{zone},j}^2) \\
 \beta_{\text{ecoregion},j,m} &\sim N(0, \sigma_{\text{ecoregion},j}^2)
 \end{aligned} \tag{1}$$

where C_i is the i 'th observation of carbon stock in the data set, μ_j is the global mean carbon stock for each combination of ecosystem type and depth, and β is a random effect representing k sites, l Köppen–Geiger climate zones, and m level-1 ecoregions. C_i was normally distributed, but we truncated the distribution so that carbon stock values are strictly positive (Holmquist et al., 2018). Each random effect was distributed as normal with a mean of zero and a variance attributed to that spatial scale. Priors were lightly informed with the prior for each μ_j uniformly distributed between 0 and 500 (Hobbs & Hooten, 2015). We assigned each variance parameter an inverse gamma prior, with both alpha and beta parameters set to 0.001.

We fit the model with the R package “rjags” using four chains and 5,000 iterations (Plummer et al., 2021) and examined trace plots to ensure model convergence on a single solution. Data were summarized as the variance partitioned at each spatial scale (Corstanje, Kirk, & Lark, 2008; Corstanje, Kirk, Pawlett, et al., 2008) for each ecosystem type and depth as a percentage of summed variance. We present median estimates and standard deviations from the posterior distributions of the parameters.

We compared the relative effects of local- versus regional-scale factors on stocks to 30 cm depth with boosted regression tree (BRT) models using the “gbm” package in R, and tuning completed with the “caret” package (Kuhn, 2022; Ridgeway et al., 2022). These non-linear models are a machine learning method that iteratively fits classification and regression trees to the residuals of the previous tree and can include both continuous and categorical data (Elith et al., 2008). For the full data set of 1,284 cores, the model included two local or watershed-scale factors (estuary and ecosystem) and four regional-scale factors linked to climate and regional setting (latitude, ecoregion, climate zone, and estuary type). We ran a second BRT model using only cores from California, Oregon, and Washington, where more factors could be included ($n = 649$). In the second model, an additional local scale factor was elevation (z^*_{high}), and additional regional scale factors were climate normals (precipitation, air temperature, VPD max).

Finally, we determined a first-order estimate of total SOC stocks in blue carbon ecosystems along the west coast of North America (to 1 m depth) by compiling estimates of ecosystem area from Mexico to Alaska and then multiplying by the mean (\pm SD) stocks value computed from core data in this study. We regard these total stocks estimates as closer to minimum values because many blue carbon ecosystems in the region likely have sedimentary layers exceeding 1 m depth (Drexler et al., 2009; Kauffman, Giovanonni, et al., 2020) and because mapping efforts to date may underestimate the extent of coastal wetland habitat (CEC, 2021; Endris et al., 2024). In the discussion we compare our results from the northeastern Pacific with per hectare SOC (to 1 m depth) stocks estimates from other blue carbon studies conducted at large spatial scales (e.g., national or global estimates) and with data from other major terrestrial ecosystems present in North America.

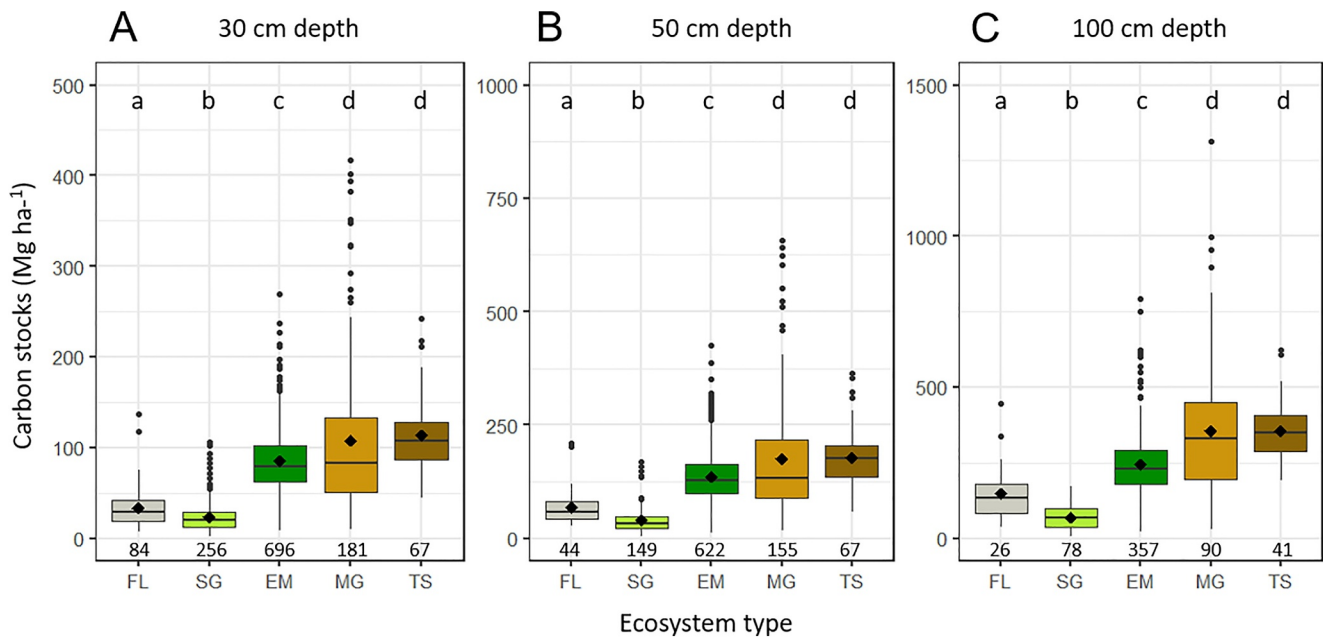


Figure 2. Sediment carbon stocks to (a) 30, (b) 50, and (c) 100 cm depth for five blue carbon ecosystems along the Pacific coast of North America. FL = tideflat; SG = seagrass; EM = marsh; MG = mangrove; TS = tidal swamp. Boxplots in this and subsequent figures show the median (horizontal line), mean (filled diamond), 25% and 75% of the data distribution (top and bottom of boxes), 1.5 times the interquartile range (whiskers), and outliers (dots). Ecosystem types sharing the same letters were not significantly different. Numbers below boxplots indicate sample sizes. Note different y-axis scales across panels.

3. Results

3.1. Stocks by Ecosystem Type

There were significant differences in stocks to 30 cm depth among ecosystem types ($F_{4,260.2} = 384.7, P < 0.0001$), with tideflats and seagrass meadows having the lowest mean stocks, and marshes, mangroves, and tidal swamps having about 3–4.5 times higher mean SOC than seagrass meadows (Figure 2; Table S8 in Supporting Information S1). For stocks to 50 and 100 cm depth, we found the same general patterns of increasing stocks from tideflats and seagrass meadows to marshes, mangroves, and tidal swamps (50 cm: $F_{4,183.9} = 275.4, P < 0.0001$; 100 cm: $F_{4,106.3} = 202.7, P < 0.0001$). For all depths, mixed models with stocks nested by estuary gave similar overall results, although tideflat and seagrass stocks were only significantly different from each other in the 50 cm model.

3.2. Relationships Between Shallow and Deeper Stock Estimates

There were strong linear correlations between stocks computed to 30 cm depth relative to 50 and 100 cm depths (Pearson's $r = 0.97$ and 0.88 , respectively) (Figure 3). However, when stocks for the top 30 cm were extrapolated to 50 or 100 cm depth, they overestimated deeper stocks in 66% of cases (e.g., 66% of the values were below the dashed lines in each panel in Figure 3) since carbon density tended to decrease with depth. Average overestimates were 5% and 13% to 50 and 100 cm depths, respectively. Overestimates tended to be highest for marshes (7% and 18%) and tidal swamps (7% and 2%), followed by mangroves (4% and 5%), and then seagrass (1% and 9%) and tideflats (1% and 5%).

3.3. Stocks and Local Ecological Drivers

Tideflat and seagrass cores spanned a range of coastal elevations from the shallow subtidal to somewhat above MTL, with seagrass cores tending to be lower (most below MLLW) in the tidal frame than tideflats (Figure 4). Emergent marsh cores were distributed from wetlands below MTL (overlapping to some degree with tideflats) to well above MHHW. Tidal swamp cores were generally collected from wetlands with surface elevation above MHHW. There was a significant positive relationship between standardized wetland elevation (z^*_{low}) and SOC stocks to 30 cm depth for seagrass ($R^2_{adj} = 0.11, P = 0.0006, n = 94$), but not for tideflats ($R^2_{adj} = -0.01$,

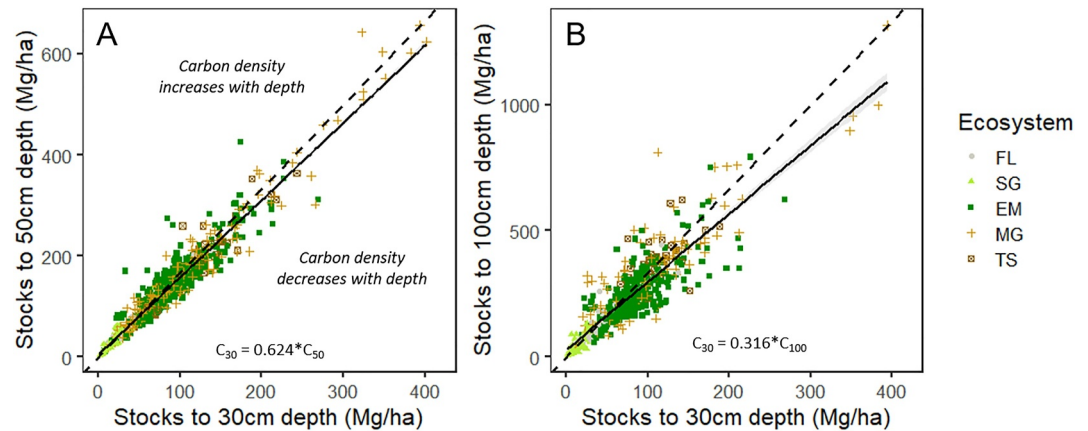


Figure 3. Correlation between sediment carbon stocks estimated to 30 cm depth versus (a) 50 cm depth and (b) 100 cm depth for all blue carbon ecosystems. Dashed lines show the null relationship expected between shallower and deeper stock estimates if carbon density were exactly uniform with depth. Solid lines and equations show actual relationships. Points below the dashed lines are cores in which carbon density decreased with depth (e.g., 30 cm stocks overestimate deeper stocks estimates), while points above the dashed lines are cores where carbon density increased with depth.

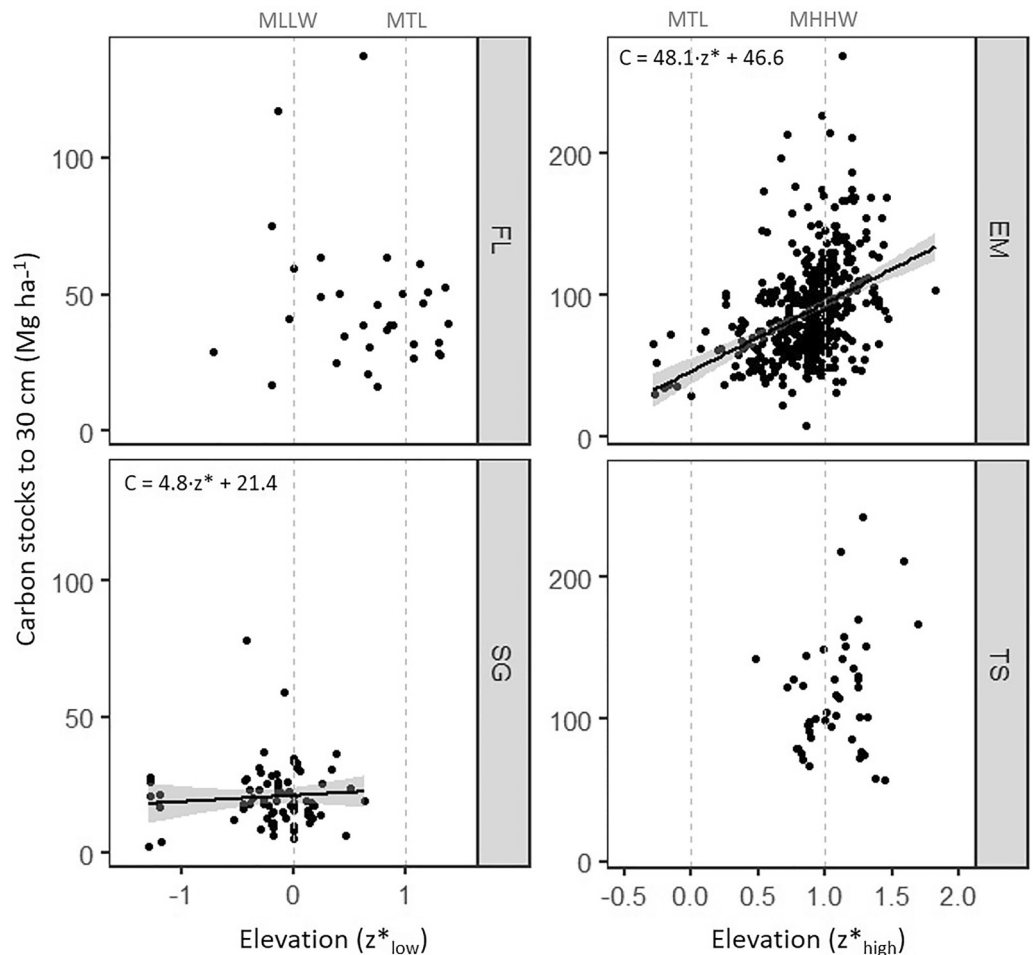


Figure 4. Relationships between carbon stocks and wetland elevation in tideflats (FL), seagrass meadows (SG), marshes (EM), and tidal swamps (TS). Gray bands show the standard error around significant regression lines. In the equations, C refers to sediment carbon stocks. The positions of local mean lower low water (MLLW), mean tide level (MTL), and mean higher high water (MHHW) are shown by vertical dashed lines for reference.

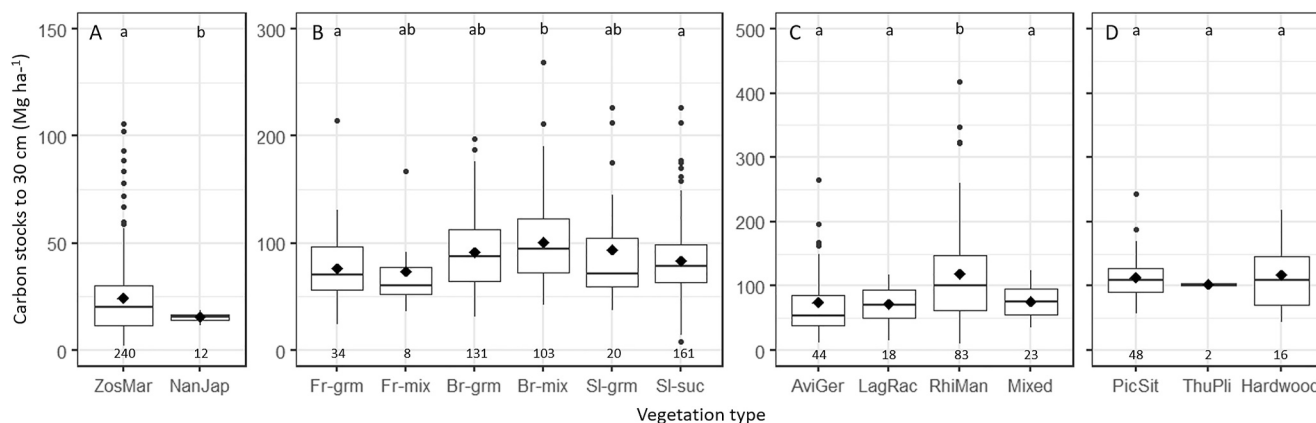


Figure 5. Carbon stocks to 30 cm depth by vegetation type for (a) seagrass meadows, (b) emergent marshes, (c) mangroves, and (d) tidal swamps. ZosMar = *Zostera marina* and *Z. pacifica*; NanJap = *Nanozostera japonica*. Fr-grm = freshwater graminoid; Fr-mix = freshwater mixed graminoid and forb; Br = brackish; SI = saline; suc = succulent; AviGer = *A. germinans*; LagRac = *L. racemosa*; RhiMan = *R. mangle*, mixed = 2 or 3 mangrove species; PicSit = *P. sitchensis*; ThuPli = *T. plicata*. Numbers below each box are sample sizes.

$P = 0.41$, $n = 34$). Stocks were also positively correlated with elevation (z^*_{high}) in marshes ($R^2_{\text{adj}} = 0.15$, $P < 0.0001$, $n = 484$), though not for tidal swamps ($R^2_{\text{adj}} = 0.05$, $P = 0.08$, $n = 45$). Insufficient elevation data were available to examine this relationship in mangroves.

Carbon stocks to 30 cm depth increased with higher content of fine sediments (silt + clay fractions) in lower elevation tideflats ($R^2_{\text{adj}} = 0.33$, $P = 0.04$, $n = 11$) and seagrass meadows ($R^2_{\text{adj}} = 0.33$, $P < 0.0001$, $n = 41$; Figure S3 in Supporting Information S1). (The tideflat model was only marginally significant when an outlier was removed ($R^2_{\text{adj}} = 0.28$, $P = 0.07$, $n = 10$)). There was a similar significant positive linear relationship for marshes ($R^2_{\text{adj}} = 0.18$, $P = 0.0001$, $n = 73$). In mangroves percent fines and SOC were not related ($R^2_{\text{adj}} < 0.00$, $P = 0.74$, $n = 34$), while limited grain size data precluded analysis for tidal swamps.

We used available data on plant species composition to assess whether stocks within ecosystem types varied among plant assemblages. In seagrass meadows, mean (\pm SD) SOC in native *Zostera* meadows was 57% greater (24.3 ± 18.9 vs. 15.5 ± 2.1 Mg ha⁻¹) than in non-native *Nanozostera* beds ($F_{1,157.9} = 41.9$, $P < 0.0001$; Figure 5a). In emergent marshes, there were significant differences among specific assemblages ($F_{5,51.1} = 3.8$, $P = 0.005$; Figure 5b), with brackish mixed plant assemblages (101.2 ± 39.2 Mg ha⁻¹) having 21%–32% higher mean stocks than saline succulent-dominated and freshwater graminoid marshes respectively. In mangroves, *R. mangle* forests (119.2 ± 81.5 Mg ha⁻¹) had 57%–67% greater mean stocks than other assemblage types, including mixed species forests ($F_{5,68.7} = 7.1$, $P = 0.0003$; Figure 5c). In tidal swamps, stocks were similar among the three assemblage types ($F_{2,26.4} = 2.3$, $P = 0.12$; Figure 5d).

3.4. Spatial Scales of Variation in Stocks

At the estuary scale, mean stocks to 30 cm depth varied several-fold among estuaries for most ecosystem types, based on means and other summary statistics for all estuaries with at least four cores for a given ecosystem type (Tables S9–S13 in Supporting Information S1). For stocks to 30 cm, coefficients of variation at the estuary scale were highest for mangroves (0.58), intermediate for seagrass meadows (0.43), tideflats (0.44), and marshes (0.27), and lowest for tidal swamps (0.13).

We examined differences in stocks to 30 cm depth by ecoregion, climate zone, and latitude for each ecosystem type. Tideflat samples spanned from 32.8° to 52.1° latitude. Mean tideflat stocks were 77% higher in the Mediterranean ecoregion (occurring from northern Baja California to northern California; 47.3 ± 28.2 Mg ha⁻¹) than in the marine west coast forest ecoregion (northern California to Alaska; 26.7 ± 13.9 Mg ha⁻¹) ($F_{1,30.6} = 12.5$, $P = 0.001$; Figure 6). Similarly, mean tideflat stocks were 92% higher in BSk (mid-latitude steppe; 42.6 ± 12.3 Mg ha⁻¹) and 68% higher in Csb (Mediterranean, cool summers; 37.2 ± 22.8 Mg ha⁻¹) climate zones than in Cfb (marine west coast, warm summer; 22.1 ± 14.8 Mg ha⁻¹) (Figure S4 in Supporting Information S1). Tideflat stocks decreased linearly with increasing latitude ($R^2_{\text{adj}} = 0.29$, $P < 0.0001$, $n = 84$; Figure S5 in Supporting Information S1).

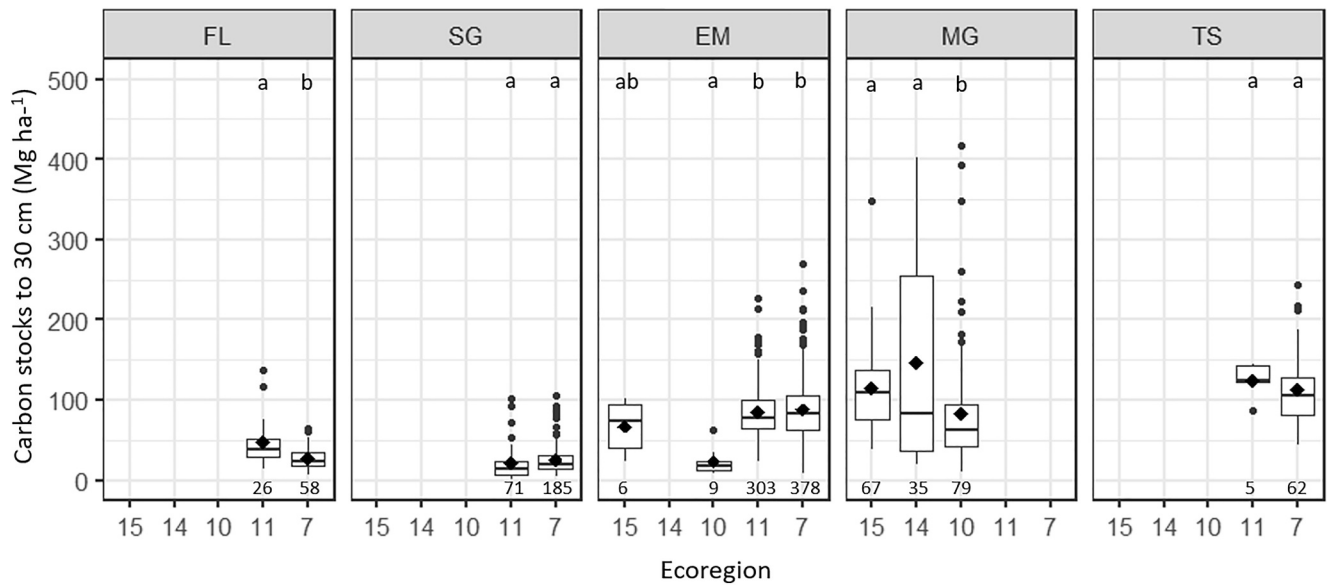


Figure 6. Sediment carbon stocks to 30 cm depth by ecoregion for five blue carbon ecosystem types along the west coast of North America. Box plots sharing the same letters within an ecosystem are not statistically different. Numbers below each box are sample sizes. FL = tideflats; SG = seagrass meadows; EM = marshes; MG = mangroves; TS = tidal swamps. Ecoregion 15 = tropical wet forest; 14 = tropical dry forest; 10 = desert; 11 = Mediterranean; 7 = marine west coast forest.

For seagrass (samples ranged from 30.4° to 55.9° latitude) there was no significant difference in stocks between the Mediterranean and marine west coast forest ecoregions (20.9 ± 22.7 and 25.0 ± 16.4 Mg ha⁻¹ respectively; $F_{1,99.3} = 1.9$, $P = 0.18$; Figure 6). Yet for the four climate zones for which data were available, zone BSk had the lowest stocks (13.6 ± 11.7 Mg ha⁻¹) while other zones had 22.0–25.5 Mg ha⁻¹ ($F_{3,46.6} = 7.8$, $P = 0.0003$; Figure S4 in Supporting Information S1). Seagrass stocks had a weak positive correlation with latitude ($R^2_{adj} = 0.01$, $P = 0.04$, $n = 256$; Figure S5 in Supporting Information S1), a pattern opposite of tideflats.

Emergent marsh data were available for four ecoregions from southern Mexico to Alaska and for nine climate zones, from 15.0° to 59.8° latitude. Marsh stocks varied by ecoregion ($F_{3,16.1} = 36.6$, $P < 0.0001$; Figure 6), with the lowest mean stocks in the Sonoran Desert ecoregion (22.7 ± 17.2 Mg ha⁻¹) and several fold higher stocks (67.3 – 87.9 Mg ha⁻¹) in the other three ecoregions. Marsh stocks also differed by climate zone ($F_{8,44.4} = 8.4$, $P < 0.0001$; Figure S6 in Supporting Information S1), with the mean tending to be higher in the Csa zone (Mediterranean, hot summers; 109.5 ± 29.5 Mg ha⁻¹) than in other climate zones (65.8 – 104.0 Mg ha⁻¹). Stocks were not correlated with latitude ($R^2_{adj} = 0.004$, $P = 0.058$, $n = 696$; Figure S5 in Supporting Information S1).

Mangrove stocks differed significantly by ecoregion in Mexico ($F_{2,77.5} = 6.1$, $P = 0.003$; Figure 6), with 37%–74% higher mean stocks in tropical wet and tropical dry forests (115.1 ± 50.3 and 146.2 ± 125.2 Mg ha⁻¹ respectively) than in mangroves farther north in the Sonoran Desert ecoregion (83.8 ± 76.7 Mg ha⁻¹). However, there were no differences between climate zones ($F_{2,38.1} = 1.8$, $P = 0.18$; Figure S7 in Supporting Information S1). Mangrove stocks were also very weakly negatively correlated with latitude ($R^2_{adj} = 0.02$, $P = 0.052$, $n = 181$; sample range 15.1°–29.0° latitude; Figure S5 in Supporting Information S1).

Finally, stocks were similar in tidal swamps located in the west coast's Mediterranean (San Francisco Bay-Delta; 124.2 ± 23.0 Mg ha⁻¹) and PNW forest ecoregions (Oregon and Washington; 112.5 ± 39.3 Mg ha⁻¹) ($F_{1,6.1} = 1.0$, $P = 0.35$; Figure 6). Tidal swamp stocks differed significantly overall by climate zone overall ($F_{2,4.1} = 9.1$, $P = 0.03$; Figure S7 in Supporting Information S1), but no pairwise comparisons were significant due to low sample sizes. Tidal swamp stocks were not correlated with latitude ($R^2_{adj} = 0.04$, $P = 0.06$, $n = 67$; samples ranged from 38.0° to 48.3° latitude; Figure S5 in Supporting Information S1).

For each ecosystem type, we examined stock variability across a hierarchy of spatial scales from local variation (within estuaries) to the continental scale (among ecoregions). In most ecosystem types and for most depths, smaller spatial scales tended to explain more variance than larger spatial scales (Figure 7). Exceptions included the relatively high variability in emergent marsh stocks among ecoregions (Sonoran Desert stocks were

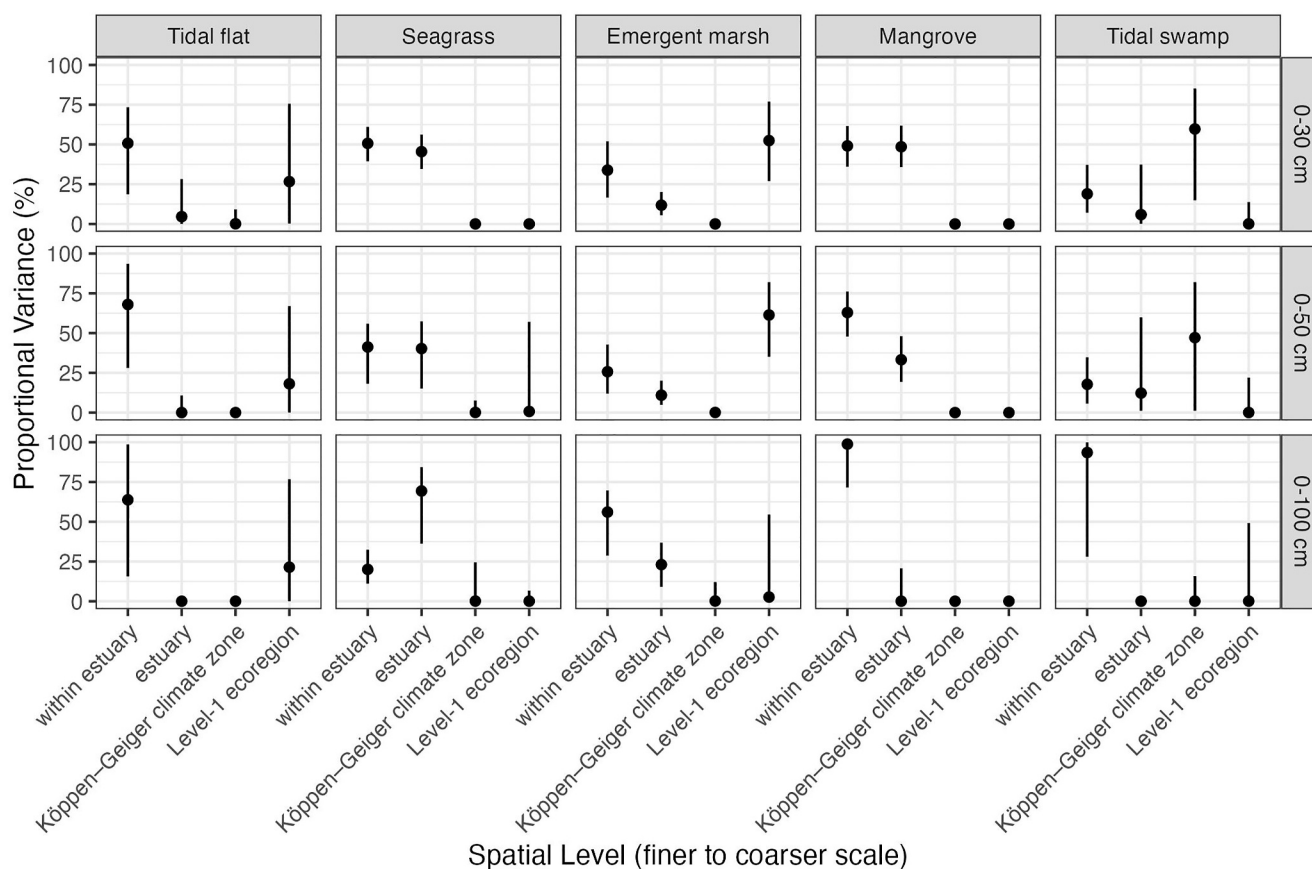


Figure 7. Variability in carbon stocks at three depths along a nested spatial scale from within individual estuaries to between ecoregions along the west coast of North America. Error bars are one standard deviation.

considerably lower than other ecoregions; see also Figure 6) and large variability in tidal swamp stocks among climate zones (Cfb > Csb and Csa, though not significantly so; see also Figure S7 in Supporting Information S1).

For cores from all ecosystem types, we tested the relative influence of a suite of local and regional scale factors on variation in stocks to 30 cm depth using BRT models. For the full model using all 1,284 cores for the west coast of North America, model cross-fold validation was $R^2 = 0.60$ and RMSE was 33.2; for the reduced model for California, Oregon, and Washington, $R^2 = 0.59$ and RMSE = 33.5. For both models, local-scale factors such as estuary, elevation, and ecosystem type explained considerably more variability in stocks than regional-scale factors linked to climate, such as ecoregion, latitude, and climate normals (Figure 8).

3.5. Total Stock Estimates for the West Coast of North America

Using area estimates of blue carbon ecosystems for the west coast of North America, we estimate that mangroves hold at least 97.4 ± 62.8 to 116.8 ± 75.2 million metric tons (Tg) of SOC (to 1 m depth) while marshes hold at least 83.5 ± 34.3 Tg (Table 2). Seagrasses hold five times less carbon than marshes at 16.0 ± 9.9 Tg. Tidal swamps, which are presently rare, but not completely mapped, are estimated to have 2.7 ± 0.8 million tons of organic carbon in the top meter of sediments.

4. Discussion

4.1. Ecosystem-Level Differences in Stocks

We found large differences in SOC stocks among five major blue carbon ecosystem types along the west coast of North America. There were 3–5 times lower carbon stocks per hectare in shallow subtidal to mid-intertidal

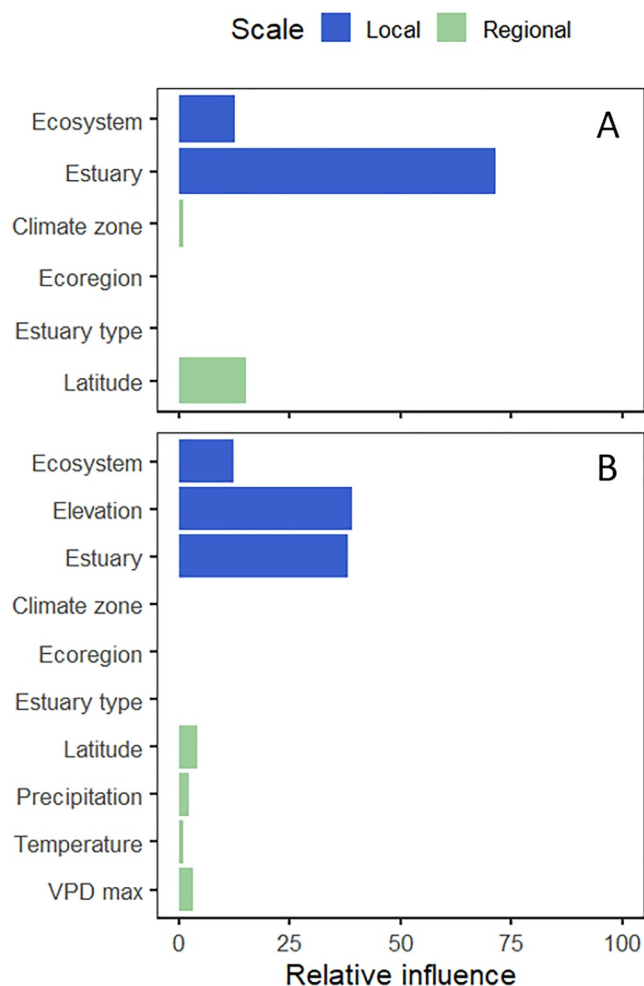


Figure 8. Relative influence of regional-scale factors such as climate zone and latitude (green bars) and local-scale factors such as estuary identity (blue bars) on stocks to 30 cm depth in two boosted regression tree models. The model in A includes all 1,284 cores in North America; the model in B includes 649 cores from California, Oregon, and Washington. VPD Max = maximum vapor pressure deficit.

ecosystems, where tideflats and seagrass occur, than upper-intertidal ecosystems where marshes, mangroves, and tidal swamps occur. At a similar regional scale, Ewers Lewis et al. (2018) also found about 3- to 4-fold higher stocks in marshes and mangroves than in seagrass meadows in southeast Australia. The global marsh median of 231 Mg ha⁻¹ determined by Maxwell et al. (2023) is almost identical to our median estimate of 230 Mg ha⁻¹ for emergent marsh stocks to 1-m depth, the best-sampled ecosystem on the Pacific coast of North America (for median data, see Tables S8–S13 in Supporting Information S1).

Expanding on the tidal swamp data set in Kauffman, Giovanonni, et al. (2020), we also found that tidal swamps from the San Francisco Bay-Delta region to the temperate PNW region of North America have very high SOC stocks (mean 354.7 Mg ha⁻¹ to 1 m), 45% greater than those of the region's emergent marshes (244.5 Mg ha⁻¹) and very similar to mangrove values (356.5 Mg ha⁻¹) for the Pacific coast of Mexico (Figure 2). Stocks in northeast Pacific tidal swamps are also well within the range of 1-m deep stocks modeled for tropical mangrove ecosystems globally. For example, tidal swamp values exceed mangroves from some regions of South Asia and are similar to those from Central America, Southeast Asia, and northern Australia, but usually are less than those from mangroves in Indonesia, equatorial west Africa, and a few other regions (Sanderman et al., 2018). These temperate forested tidal wetlands (with canopy species including Sitka spruce, dogwood, and Pacific crab apple) and shrub-dominated wetlands (with species including twinberry and willows) are currently rare in northern California and the PNW because of very high rates of tidal wetland conversion to other land uses (Brophy, 2019; Marcoe & Pilson, 2017; Simenstad et al., 2011; Table 2). Our data set included only 10 samples from shrub-dominated tidal wetlands, indicating a need to better quantify SOC in this particular type of tidal swamp, particularly because these samples had stocks comparable to the more prevalent tidal Sitka spruce forests with large trees. When including living and dead plant biomass in Sitka spruce dominated swamps, total ecosystem carbon stocks can exceed 1,000 Mg C ha⁻¹ (Kauffman, Giovanonni, et al., 2020). Our results highlight the critical importance of tidal swamps from a blue carbon perspective, in addition to their other functions and services, and emphasize the need for more restoration and conservation efforts directed toward these highly impacted ecosystems.

Table 2

Estimated Total Sediment Carbon Stocks (to 1 m Depth) for Four Types of Vegetated Blue Carbon Ecosystems Along the West Coast of North America

Ecosystem	Region	Estimated area (ha)	Estimated total carbon stocks to 1 m depth (Mg) (±SD)	Sources (area)
SG	Pacific Canada, US, and Baja California ^a	233,970	16.0 ± 9.9 × 10 ⁶	Lopez-Calderon et al. (2016), CEC (2021), Krause et al. (2021), and Ward et al. (2022)
EM	Pacific Canada, US, and Mexico	341,482	83.5 ± 34.3 × 10 ⁶	CEC (2021)
MG	Pacific Mexico	273,295	97.4 ± 62.8 × 10 ⁶	CEC (2021)
MG	Pacific Mexico	327,510	116.8 ± 75.2 × 10 ⁶	globalmangrovetwatch.org
TS	Oregon coast, Lower Columbia River, and Puget Sound, WA ^b	7,558	2.7 ± 0.8 × 10 ⁶	Simenstad et al. (2011), Marcoe and Pilson (2017), and Brophy (2019)

Note. For each ecosystem, the mean (±SD) stocks to 1 m depth from this study (Table S8 in Supporting Information S1) were multiplied by the estimated area of the ecosystem in the region. SG, seagrass; EM, emergent marsh; MG, mangroves; TS, temperate tidal swamp. ^aSG area estimates are from CEC for Canada and the US and from other sources for Baja California; no reliable estimate from mainland Mexico was identified. ^bAdditional tidal swamps occur in northern California, the outer coast of Washington, British Columbia, and possibly Alaska, but area estimates are not available.

Table 3
Sediment Organic Carbon Stocks per Hectare in Northeast Pacific Blue Carbon Ecosystems (This Study) Compared With Other Global Blue Carbon Ecosystems and Other North American Ecosystems

Ecosystem	Region	Stocks (Mg ha ⁻¹)	Data type	Source
Blue carbon ecosystems				
FL	Northeast Pacific	148 ± 93	Mean ± SD (26 cores)	This study
SG	Northeast Pacific	68 ± 43	Mean ± SD (78 cores)	This study
SG	Indonesia	130 ± 10	Mean ± SE (60 cores)	Alongi et al. (2016)
SG	Global	330 ± 56	Mean ± 95%CI (41 cores)	Fourqurean et al. (2012)
EM	Northeast Pacific	245 ± 100	Mean ± SD (357 cores)	This study
EM	Australia	165 ± 7	Mean ± SE (323 cores)	Macreadie et al. (2017)
EM	UK	269 ± 163	Mean ± SD (26 marshes)	Smeaton et al. (2023)
EM	Global	268	Modeled global mean	Maxwell et al. (2024)
MG	Pacific Mexico	357 ± 230	Mean ± SD (90 cores)	This study
MG	China	270 ± 76	Mean ± 95%CI (49 sites)	Liu et al. (2014)
MG	Global	334 ± 11	Mean ± SE (190 cores)	Kauffman, Adame, et al. (2020)
MG	Global	250 ± 5 to 282 ± 8 ^a	Mean ± SE (2,356 cores)	Zhang et al. (2024)
TS	US Pacific Northwest	355 ± 230	Mean ± SD (41 cores)	This study
TS	SE United States	448 ± 258	Mean ± SD (5 sites)	Krauss et al. (2018)
Other ecosystems in North America				
Coniferous forest	Pacific Northwest (WA)	185 ± 20	Mean ± SE (<i>n</i> = 28)	Stewart et al. (2024)
Coniferous forest wetlands	Pacific Northwest (WA)	346 ± 89	Mean ± SE (<i>n</i> = 8)	Stewart et al. (2024)
Great Plains grasslands and northern US forests	North Central United States	117	Regional mean	Franzmeier et al. (1985)
Freshwater peatlands	Canada	810 ± 670	Mean ± SD (modeled)	Sothe et al. (2022)

Note. All stocks values are means to 1 m depth. FL, tideflats; SG, seagrass; EM, emergent marsh; MG, mangroves; TS, temperate tidal swamp. For datatype, SD, standard deviation; SE, standard error; CI, confidence interval. ^aMarine and estuarine mangroves respectively.

Mangroves and tidal swamps along the Pacific coast are comparable in soil carbon storage capacity to other carbon-rich terrestrial ecosystems in North America. For instance, Pacific coast mangroves and tidal swamps have about twice as much SOC as coniferous forests and similar values to freshwater wetlands within coniferous forests in the Pacific Northwest (Table 3; Stewart et al., 2024). They also have about three times as much carbon as forests and grasslands of the upper Midwest region of the United States (Franzmeier et al., 1985). However, they may hold only about half the carbon than modeled estimates from Canadian peatlands (Sothe et al., 2022). Anthropogenic pressures on these carbon-rich ecosystems vary; while estuarine wetlands are vulnerable to drainage, fill, and sea-level rise (Lovelock & Reef, 2020), global warming threatens the stability of peatland soils (Sothe et al., 2022).

Our synthesis also highlighted that unvegetated tideflats in Pacific coast estuaries of North America are an important pool of stored carbon. In fact, tideflat stocks across the region were about twice that of regional seagrass meadows, a major focus of blue carbon studies worldwide. Seagrass beds in the Northeast Pacific, however, which are almost all dominated by *Z. marina*, have lower stocks than meadows in Indonesia and globally (Table 3). Comparison of mudflat and seagrass in individual studies has shown that locally they can have similar SOC densities (Bulmer et al., 2020; Krause et al., 2022; Mazarrasa et al., 2023; Prentice et al., 2019, 2020). Some tideflat SOC could represent legacy carbon stocks from formerly vegetated areas. For instance, our results may be partly influenced by a large number of tideflat samples from Elkhorn Slough in central California (18% of stocks estimates to 30 cm depth were from this estuary), which is noted for its drowning tidal marshes. However, other estuaries also had high tideflat stocks, including Padilla and Skagit Bays in Washington, and Tomales Bay in northern California where tideflat stocks were roughly equal to or higher than those of seagrass meadows from those same estuaries (Tables S9 and S10 in Supporting Information S1). In other estuaries, tideflat stocks were lower than seagrass meadows; for example, higher carbon stocks and accumulation rates were found in some

seagrass meadows compared to nearby tideflats in British Columbia (Postlethwaite et al., 2018; Prentice et al., 2019). Interestingly these two ecosystems showed opposite trends with latitude with seagrass having higher SOC farther north.

For the west coast of North America, tideflat stocks represent an important but under-recognized SOC pool in the coastal zone. The nutrient cycling role of unvegetated flats has long been under-recognized (Schlacher et al., 2014). Because tideflats often cover a substantial area in Pacific coast estuaries (Emmett et al., 2000), they could comprise a large fraction of total blue carbon stocks for many estuaries. Similar conclusions were reached in a New Zealand estuary where extensive tideflats were estimated to harbor 57% of carbon stocks (Bulmer et al., 2020), and in China, where tideflats are rapidly accreting sediment and expanding, thus potentially forming a large and important pool of coastal blue carbon (J. Chen et al., 2020).

In blue carbon ecosystems the origin of SOC is important to understanding the role of tidal wetlands in coastal carbon cycles, as both a direct and indirect sink for carbon removal from the atmosphere. Tideflat sediments specifically have been previously viewed as sites where carbon import outweighs local production (Kuipers et al., 1981). Carbon accumulation rates in tideflats are comparable to those of seagrass meadows (Z. L. Chen & Lee, 2022), but few studies have identified the origin and permanence of tideflat carbon, which may be imported from adjacent coastal vegetated ecosystems (Krause et al., 2022), may be derived partly from in-situ production by benthic microalgae (Lin et al., 2020), or may be transported from terrestrial sources (Hatten et al., 2012). The question of autochthonous versus allochthonous carbon sources in all blue carbon ecosystems needs further study, but we hypothesize that the proportion of autochthonous inputs is probably greater in higher elevation vegetated tidal wetlands like marshes and swamps that are less frequently inundated and have higher plant biomass than in lower elevation estuarine wetlands like seagrass meadows and tideflats.

4.2. Effects of Local Environmental Drivers

We found evidence that several local ecological drivers, including elevation (a proxy for inundation in tidal ecosystems), sediment particle composition, and plant species composition, were correlated with carbon stocks. Elevation was a common environmental driver of SOC in this study, with stocks increasing at higher elevations within three of the four ecosystems we investigated. Similarly, a nearly three-fold increase in mean sediment carbon stocks from the low to the high intertidal zone was observed in an Australian mangrove forest (Hu et al., 2021). In Oregon tidal marshes and shrub-dominated tidal swamp, Peck et al. (2020) also showed a positive relationship between elevation and carbon content. However, sediment OM was only weakly, or even negatively associated with elevation along coastal gradients in southwestern Europe covering several ecosystem types (de los Santos et al., 2022, 2023). The SOC relationship we observed with elevation could reflect a greater contribution of root biomass and particulate OM to sediment volume at higher elevations, whereas higher rates of mineral sediment deposition may dilute carbon density lower in the intertidal (Costa, Ezcurra, Ezcurra, et al., 2022). Additionally, higher elevation wetlands may have more productive plant communities (Janousek et al., 2016) because they are subject to less salt stress or because they may have lower decomposition rates in some cases (Kirwan et al., 2013).

The relationship between carbon storage and sediment grain size has been widely reported for seagrass (Dahl et al., 2016; Röhr et al., 2018) and tideflat (Z. L. Chen & Lee, 2022) habitats, including for the Pacific coast of North America (Krause et al., 2022; Prentice et al., 2020; Röhr et al., 2018). Generally, marine sediments with a higher proportion of fine mineral content are associated with higher OM (Mayer, 1994) because they offer a larger particle surface area available for sorption and preservation (Keil et al., 1994). In addition, remineralization of SOC may be lower in fine-grained sediment, because low permeability promotes anoxic conditions and microbial enzymatic access is reduced in nanopores of fine sediment grains (Mayer, 1994). We found linear increases in 30 cm carbon stocks with fine sediment content for seagrass and marshes in this study (Figure S3 in Supporting Information S1), and likely for tideflats, but not for mangroves. This might be explained in part by the formation of peats by mangrove vegetation, where particulate OM may make up a larger portion of the sediment matrix, decreasing the importance of OM sorption to mineral particle surfaces. In contrast, ecosystems that receive much or all of their SOC from allochthonous sources, such as seagrass meadows and tideflats (Prentice et al., 2020), and potentially many marshes in which OM particles are redeposited and buried among sediment grains (Thom et al., 2018), may have carbon delivery dynamics and storage capacity that is more sensitive to particle size than

those where most carbon storage is autochthonous and derived from the in-situ production of root biomass (Serrano et al., 2016).

Finally, at local scales, plant community composition may play a role in SOC storage. For seagrass meadows, mangroves, and to some extent marshes in the northeastern Pacific, plant assemblage type was correlated with sediment stock differences. These relationships may be due to differences in productivity among species or their ability to trap sediments from the water column (Alongi et al., 1993), the composition of OM (Simpson et al., 2023), the correlation of plant composition with the same drivers that affect sediment processes, or some combination of factors. Plant community was the strongest predictor of 30 cm deep carbon stocks across 96 sites in southeastern Australia (Ewers Lewis et al., 2020). They noted that although plant community can be correlated with elevation and inundation regime, plant community was a stronger predictor than these other variables by themselves.

4.3. Spatial Scales of Variability

The scale(s) at which SOC varies is relevant to developing local and regional blue carbon inventories, prioritizing conservation areas, and planning future restoration of blue carbon ecosystems. Our results suggest that much of the variability in SOC occurs at relatively local spatial scales including gradients in elevation and sediment grain size, and differences among plant communities and individual estuaries. For example, with plant composition often varying within sites (e.g., along elevation and salinity gradients; Janousek & Folger, 2014), between sites, and between estuaries with differing hydrology (Borde et al., 2020), vegetation could be one potential indicator of SOC stocks. Additionally, the prominence of estuary identity as a factor explaining variation in our BRT models may reflect the importance of local watersheds in determining stocks. For example, watershed processes influence freshwater and nutrient delivery to estuarine plants, affecting their productivity (autochthonous carbon inputs). Moreover, temporal variability in river flow may affect quantities of allochthonous carbon delivered to estuaries, and land-use change in watersheds affecting sediment supplies to the coast can cause intertidal habitats either to accrete or erode out of the tidal frame, reducing overall wetland area and thus carbon burial (Ezcurra et al., 2019; Ma et al., 2019).

At spatial scales greater than individual estuaries, we generally did not find evidence of any consistently strong drivers of SOC variability. In emergent marshes for example, there was only a modest increase in variability from estuary and watershed to the Pacific coast ecoregion scale, whereas in other ecosystem types larger spatial scales tended to explain even less variance. The predictive power in the emergent marsh data set for 30 cm stocks may be attributable to the fact that this was the largest data set in the study and included samples from a very widespread geographic region. At a global scale, Maxwell et al. (2024) noted that temperate emergent marshes tended to have higher stocks than tropical regions. In contrast, climate and ecoregion explained essentially no variance in stocks for mangroves which ranged from arid coastal environments in northwestern Mexico to wet tropical conditions in southern Mexico. We found modest changes in seagrass and tideflat stocks with latitude but not in other ecosystem types.

Notably, spatial scale shaped the variability of carbon stocks more prominently in cores to 100 cm depth than in shallower cores (Figure 7). The SOC data from deeper cores characterizes a longer history of varying sedimentation, productivity, and decomposition than shallower cores and may include periods when estuaries had substantially different conditions than in the recent past (e.g., salinity or productivity changes due to drought). While this study removes the effect of total sediment depth on carbon stock by extrapolating stocks to fixed depth intervals, depth-explicit estimates of stocks are strongly influenced by the climatic and geological factors that have controlled sediment deposit formation over recent millennia (Costa, Ezcurra, Ezcurra, et al., 2022). The relatively greater importance of local factors and reduced importance of larger scale variability is consistent with results in Mazarrasa et al. (2021) who found that variation in seagrass stocks around Australia was driven more by species identity than bioregion.

Characterizing regional-scale patterns in SOC in terms of simple trends remains elusive. At best, stocks varied only modestly with latitude along the Northeast Pacific coast. Widely varying climate conditions across coastal North America often were characterized by similar stocks within each particular blue carbon ecosystem type. One notable exception to this general pattern is the relatively lower stocks in marshes and mangroves in the Sonoran Desert ecoregion, which is the northern limit for the distribution of mangroves on the North American Pacific coast. Sonoran Desert ecoregion mangroves may have relatively low carbon stocks today, but are nonetheless

important for conservation because existing communities are relatively undisturbed, and mangroves may become more abundant in that region with future climate change (e.g., due to the tropicalization of the Gulf of California; Ochoa-Gómez et al., 2021).

The poor explanatory power of climate variables in our analyses is surprising because temperature and precipitation can be important drivers of plant production and OM decomposition (Feher et al., 2017). Decomposition, for instance, tends to increase with temperature in tidal marshes (Kirwan & Blum, 2011). One potential explanation for this pattern is that warmer regions of the northeastern Pacific (e.g., Mexico and California) may have greater plant production that is offset by increased decomposition, leaving SOC density relatively unchanged across temperature gradients (Chmura et al., 2003; Feher et al., 2017; Kirwan & Blum, 2011). Sediments in the warmer, drier climates of the Mediterranean and desert ecoregions are subject to periodic drying and subsequent rewetting in places, likely increasing SOC decomposition rates (Feller et al., 2002; Lockaby & Walbridge, 1998). An alternative explanation is that greater salinity stress in estuaries in more southerly ecoregions may depress both production (Janousek et al., 2020) and decomposition (Luo et al., 2019).

These findings may aid in sampling design and stock estimation for estuaries where little to no blue carbon data are available. For example, median regional stocks values may be a starting point for assembling stock inventories in estuaries where no data are otherwise available, with recognition that within-site or within-estuary gradients such as elevation or plant community composition could drive spatial differences. While stocks varied considerably by ecosystem, for any given ecosystem type, our data generally do not support the notion that any particular biogeographic or climatic region has consistently higher stocks than other regions (with the exception of the Sonoran Desert ecoregion). Rather, factors within an estuary or a watershed may play larger roles and this is thus one area of important future research on stock variability. Hu et al. (2021) found considerable variability in sediment carbon stocks at a <0.2 ha spatial scale within a single mangrove site and suggested that much more intensive sampling would be needed to obtain estimates of SOC stocks that meet the standards of carbon accounting. As new blue carbon studies are planned for the northeast Pacific, we suggest that data be collected at finer spatial scales (e.g., increased sampling within sites).

4.4. Implications for Best Practices and Data Syntheses

The collation of many data sets in this study highlights the need for better sampling of under-represented blue carbon ecosystem types or geographic regions, and improved standardization of sampling methodology to facilitate syntheses such as this one and to support additional applications of data by the blue carbon community for policy development, restoration planning, and carbon accounting. As additional SOC data are collected and reported, we suggest the following best practices where possible: (a) careful attention to analytical methods and reporting, particularly loss-on-ignition methods (Heiri et al., 2001), methods for handling of root matter and inorganic carbon (Sanderman et al., 2018), and bulk density measurements (Sternberg-Rodríguez et al., 2022); (b) preferential analysis of sediment carbon by elemental analysis, or, if LOI is used, generation of site-specific OM-C_{org} relationships with large (>100) sample sizes; (c) concurrent collection of key environmental variables at blue carbon coring locations including salinity, elevation, sediment pH, plant composition, and grain size data, each of which could help explain observed variability; and (d) sampling carbon stocks as deeply as possible, but to at least 0.5 m depth or coring refusal.

Our regional synthesis suggests that stock estimates to only 30 cm depth can predict stocks to 50 and 100 cm depth moderately well, but tend to overestimate deeper stocks more often than not (Figure 3). This disparity is likely caused at least in part by the lower biomass of roots below 30 cm (many studies did not remove roots before analysis or only removed large roots and overestimates tended to be highest on average for marshes, tidal swamps, and mangroves). Additionally, sediments below 30 cm are older and therefore have likely undergone greater decomposition of SOC. We suggest that when possible, blue carbon cores should be taken to 50 or 100 cm depths so that uncertainties associated with extrapolating shallow cores are reduced. Moreover, one of the most valuable types of data that is very seldom collected (but see Drexler et al. (2009), Drexler (2011), Chastain et al. (2022), Costa, Ezcurra, Ezcurra, et al. (2022) for the northeastern Pacific) is the depth of the entire blue carbon sedimentary layer itself. The vertical extent of the organic-rich sediment layer is key to determining the overall storage capacity of blue carbon ecosystems (Smeaton et al., 2023) since even stock measurements to 1 m may underestimate total sediment carbon reservoirs.

This synthesis also identifies regional blue carbon data gaps that include: (a) relatively sparse data from tidal swamps, particularly those that are shrub-dominated, (b) lack of data from many smaller Pacific coast estuaries, especially intermittently closed estuaries in the Mediterranean ecoregion, and (c) relative undersampling of blue carbon ecosystems in certain geographic regions (e.g., all ecosystem types from northern British Columbia to Alaska, and tideflats south of central California). The lack of data from smaller estuaries from Alaska to northern California has been recognized as a research gap previously, in particular because of the relatively high ratio of smaller to larger estuaries in the region, and the collective importance of small estuaries for delivery of high-precipitation flows and associated materials from coastal watersheds to the nearshore Pacific Ocean (Bidlack et al., 2021; Callaway, Borde, et al., 2012; Hunt et al., 2024).

4.5. Management Implications

Our synthesis of blue carbon data for the Pacific coast of North America highlights regional ecological patterns informative for wetland conservation and restoration planning, and helps identify specific data gaps to advance regional blue carbon science. Among blue carbon ecosystems on the Pacific coast of North America, stocks were highest in woody-dominated tidal wetlands (43%–52% higher than emergent marshes), suggesting a need to increase conservation efforts on existing mangrove forests in Mexico and temperate tidal swamps in the Pacific Northwest for their carbon storage benefits (in addition to other important co-benefits). For decades, tidal wetland restoration along the Pacific coast of the United States and Canada has primarily focused on emergent marshes, even resulting in the conversion of tidal swamps to marshes (Miller & Simenstad, 1997). Today, increasing recognition of the importance of tidal swamps to estuarine ecosystem services in the PNW, including their very high blue carbon storage capacity, suggests that these ecosystems should be a high conservation priority and should receive more attention in estuarine restoration planning (Brophy, 2019).

The finding that local factors tend to be more important drivers of stocks than regional-scale climate drivers also has implications for blue carbon ecosystem management. For example, along estuarine elevation gradients in the northeastern Pacific, higher elevation marshes tend to have greater carbon stocks than low-elevation marshes, patterns that can help inform spatial conservation planning, restoration priorities, and climate change modeling outcomes. Higher elevation tidal wetlands also tend to have lower methane emissions in the Pacific Northwest, which is a potent greenhouse gas (Williams et al., 2025). Management plans that incorporate anticipated estuarine habitat change due to sea-level rise (e.g., Thorne et al. (2018) for the Pacific coast of the US) should consider that longer-term shifts among ecosystem types could alter carbon stocks and sequestration rates, potentially increasing or decreasing the risk that these wetlands become sources of additional GHG emissions. Additionally, local stock data can help inform the expected blue carbon benefits of specific wetland restoration projects - such as when a proposed seagrass restoration project is compared against the carbon storage capacity of nearby mudflat which may or may not have stocks as high as the planned seagrass meadow.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data on which this study is based are available at Janousek, Krause, et al. (2025). This work is an original work of the authors without use of generative AI.

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Acknowledgments

We thank the many researchers who conducted the field and laboratory work to generate the data used in this study or compile data sets including but not limited to Kristin Byrd, John Callaway, Darwyn Coxson, Brandon Drucker, Exequiel Ezcurra, Leila Giovanoni, Tessa Hill, J. Boone Kauffman, T Chris Mochon Collura, Heather Perillat, Victoria Postlethwaite, Paul Sanborn, Tiffany Stephens, Ron Thom, Rob Wheatcroft, Jude Apple, and Libia Pérez-Bernal. Major funding for development of the Northeast Pacific Blue Carbon Database and this paper was provided by the NERRS Science Collaborative (Grants NA14NOS4190145 and NA19NOS4190058), the National Oceanic and Atmospheric Administration (Grant NA19NOS4780176), and the Pew Charitable Trusts. A. Gray was supported in part by USDA NIFA Hatch Project CA-R-ENS-5120-H and USDA Multi-State Project W4188. M. Hessing-Lewis and C. Prentice were supported by the Tula Foundation and the Hakai Institute. The views expressed in this article are those of the authors and do not necessarily represent the views or policies of the U.S. Environmental Protection Agency or the U.S. Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government or the U.S. Environmental Protection Agency. This paper is a contribution of the Pacific Northwest Blue Carbon Working Group and contribution #1809 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University.

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