







Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients

J. BOONE KAUFFMAN,^{1,14} MARIA FERNANDA ADAME,² VIRNI BUDI ARIFANTI ,³ LISA M. SCHILE-BEERS ,^{4,5}
ANGELO F. BERNARDINO ,⁶ RUPESH K. BHOMIA ,⁷ DANIEL C. DONATO,⁸ ILKA C. FELLER,⁴ TIAGO O. FERREIRA,⁹
MARIA DEL CARMEN JESUS GARCIA,¹⁰ RICHARD A. MACKENZIE,¹¹ J. PATRICK MEGONIGAL,⁴ DANIEL MURDIYARSO,^{7,12}
LORAE SIMPSON,¹³ AND HUMBERTO HERNÁNDEZ TREJO¹⁰

¹Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

²Australian Rivers Institute, Griffith University, Nathan, Queensland 4111 Australia

³Center for Research and Development of Social, Economy, Policy and Climate Change (P3SEKPI), Ministry of Environment and Forestry of the Republic of Indonesia, Jl. Gunung Batu No. 5, Bogor 16118 Indonesia

⁴Smithsonian Environmental Research Center, Edgewater, Maryland 21037 USA

⁵Silvestrum Climate Associates, San Francisco, California 94103 USA

⁶Departamento de Oceanografia, Universidade Federal do Espírito Santo, Vitória, Espírito Santo 29075-910 Brazil

⁷Center for International Forestry Research (CIFOR), Jalan CIFOR, Situgede, Bogor 16115 Indonesia

⁸School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195 USA

⁹Soil Science Department, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil

¹⁰Universidad Juarez Autónoma de Tabasco, Villhermosa, Tabasco, Mexico

¹¹Institute of Pacific Islands Forestry, Pacific Southwest Research Center, U.S. Forest Service, Hilo, Hawaii 96720 USA

¹²Department of Geophysics and Meteorology, Bogor Agricultural University, Bogor 16680 Indonesia

¹³Department of Biology, University of Alabama, Tuscaloosa, Alabama 35487 USA

Citation: Kauffman, J. B., M. F. Adame, V. B. Arifanti, L. M. Schile-Beers, A. F. Bernardino, R. K. Bhomia, D. C. Donato, I. C. Feller, T. O. Ferreira, M. C. Jesus Garcia, R. A. MacKenzie, J. P. Magonigal, D. Murdiyarsa, L. Simpson, and H. Hernández Trejo. 2020. Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients. *Ecological Monographs* 90(2): e01405. 10.1002/ecm.1405

Abstract. Mangroves sequester large quantities of carbon (C) that become significant sources of greenhouse gases when disturbed through land-use change. Thus, they are of great value to incorporate into climate change adaptation and mitigation strategies. In response, a global network of mangrove plots was established to provide policy-relevant ecological data relating to interactions of mangrove C stocks with climatic, tidal, plant community, and geomorphic factors. Mangroves from 190 sites were sampled across five continents encompassing large biological, physical, and climatic gradients using consistent methodologies for the quantification of total ecosystem C stocks (TECS). Carbon stock data were collected along with vegetation, physical, and climatic data to explore potential predictive relationships. There was a 28-fold range in TECS (79–2,208 Mg C/ha) with a mean of 856 ± 32 Mg C/ha. Belowground C comprised an average 85% of the TECS. Mean soil depth was 216 cm, ranging from 22 to >300 cm, with 68 sites (35%) exceeding a depth of 300 cm. TECS were weakly correlated with metrics of forest structure, suggesting that aboveground forest structure alone cannot accurately predict TECS. Similarly, precipitation was not a strong predictor of TECS. Reasonable estimates of TECS were derived via multiple regression analysis using precipitation, soil depth, tree mass, and latitude ($R^2 = 0.54$) as variables. Soil carbon to a 1 m depth averaged 44% of the TECS. Limiting analyses of soil C stocks to the top 1 m of soils result in large underestimates of TECS as well as in the greenhouse gas emissions that would arise from their conversion to other land uses. The current IPCC Tier 1 default TECS value for mangroves is 511 Mg C/ha, which is only 60% of our calculated global mean. This study improves current assessments of mangrove C stocks providing a foundation necessary for C valuation related to climate change mitigation. We estimate mangroves globally store about 11.7 Pg C: an aboveground carbon stock of 1.6 Pg C and a belowground carbon stock of 10.2 Pg C). The differences in the estimates of total ecosystem carbon stocks based on climate, salinity, forest structure, geomorphology, or geopolitical boundaries are not as much of an influence as the choice of soil depth included in the estimate. Choosing to limit soils to a 1 m depth resulted in estimates of <5 Pg whereas those that included the soil profile >1 m depth resulted in global carbon stock estimates that exceeded 11.2 Pg C.

Manuscript received 29 April 2019; revised 12 November 2019; accepted 20 December 2019. Corresponding Editor: Samantha K. Chapman.

¹⁴E-mail: Boone.kauffman@oregonstate.edu

Key words: blue carbon; carbon dynamics; climate change mitigation; coastal wetlands; forest inventory; soil carbon pools; tropical forests; wetlands.

INTRODUCTION

Mangrove ecosystems are coastal wetlands consisting of woody vegetation that occur in intertidal marine and brackish environments (Lugo and Snedaker 1974, Giesen et al. 2007, Friess 2016). They line the coasts of the oceans in at least 124 tropical and subtropical countries between approximately 30° N and 30° S latitude (Spalding et al. 2010, Giri et al. 2011). Mangrove forests are keystone coastal ecosystems that provide numerous ecosystem services and perform critical ecological functions (Barbier et al. 2011, UNEP 2014).

Renowned for an array of ecosystem services including fish habitat, sediment regulation, and storm surge, tsunami and sea-level rise protection (Barbier et al. 2011), mangroves also are carbon-rich ecosystems that warrant preservation and restoration because they capture and preserve significant amounts of carbon (C), thus counterbalancing anthropogenic greenhouse gas (GHG) emissions (McLeod et al. 2011, Pendleton et al. 2012, Siikamäki et al. 2012, Murdiyarso et al. 2015, Howard et al. 2017). As such, mangroves and other coastal wetlands (“blue carbon”) can play an important crucial role in climate change mitigation (Price and Warren 2016).

Human land uses have resulted in declines of the extent, structure, and function of coastal ecosystems (Alongi 2002, Polidoro et al. 2010, Giri et al. 2011, Murdiyarso et al. 2015, Kauffman et al. 2018a). Globally, between 20% and 35% of mangroves were lost from 1980 to 2000 (Millennium Ecosystem Assessment 2005, Polidoro et al. 2010). Between 2000 and 2012, mean rates of mangrove deforestation in Southeast Asia were 0.18% per year (Richards and Friess 2016). Globally, Sanderman et al. (2018) estimated that 1.67% of all mangroves were deforested between 2000 and 2015 (i.e., a loss of 278,049 ha). Among all anthropogenic factors, conversion to fish and shrimp ponds is regarded as the greatest single cause of mangrove degradation and decline in Southeast Asia (FAO 2007, Giri et al. 2008, Murdiyarso et al. 2015) as well as in many countries in the Americas (Kauffman et al. 2018a). Other causes of loss include conversion to agriculture, development of industrial and urban areas, logging for wood and charcoal, pollution, and conversion to open water due to climate change (Duke et al. 2007, Servino et al. 2018, Sippo et al. 2018).

The losses of C stocks as a result of land-use change in mangroves tend to be higher than losses associated with land-use change in upland forests (Kauffman et al. 2016, 2018b, Arifanti et al. 2019). Kauffman et al. (2017a) reported that the mean decline in total ecosystem C stocks (TECS) from mangrove conversion to aquaculture or cattle pastures was 554 Mg C/ha, and the

associated mean potential GHG emissions were 1,894 Mg CO₂e/ha and 2,599 Mg CO₂e/ha, respectively. By comparison, the mean emissions arising from tropical forest to pasture conversion in the Brazilian Amazon were 583 Mg CO₂e/ha (Kauffman et al. 2018b). While losses of aboveground C stocks due to deforestation are similar between mangrove and upland tropical forests, the loss of large quantities of soil C is the causal factor of such large GHG emissions in mangroves (Kauffman et al. 2017a).

To date, a globally synthetic understanding of mangrove C stocks has been hampered, in part, by the wide variation in environmental settings and drivers that influence their productivity and C dynamics. For example, hydrologic and salinity environments in mangroves range from hypersaline (>96 PSU) and hyperarid (~22 mm annual precipitation), to essentially freshwater environments in the highest rainfall areas of tropical coastlines (Kauffman and Bhomia 2017, Schile et al. 2017). Drivers such as temperature, salinity, geomorphology, and tidal regime impose structural and functional constraints and foster adaptations (e.g., aerial roots, viviparous embryos, and efficient nutrient-retention mechanisms) as well as physiological mechanisms to facilitate mangrove establishment and growth in hydromorphic saline soils (Wolanski et al. 1992, Alongi 2014). Potential influences of these variables have been suggested to also affect, and have been used, to model carbon storage (Sanders et al. 2016, Hamilton and Friess 2018 and Rovai et al. 2018). Uniform collection of mangrove C stocks encompassing broad ranges of biotic, physical, and environmental gradients from throughout the world are needed to test hypotheses of which variables best predict carbon stocks.

The International Panel on Climate Change (IPCC) publication of guidelines to quantify and report stocks and emissions includes those arising from mangroves and other blue carbon ecosystems (Intergovernmental Panel on Climate Change (IPCC) 2014). This reflects the recognition of the roles that mangrove ecosystem conservation and restoration could play in strategies to reduce GHG emissions. Yet, data on the full extent of ecosystem C stocks that are vulnerable to loss are lacking. Especially limited is information on C stocks below the 100 cm soil depth. This is an important omission as significant losses of these deep soil C pools have been measured following land use (Kauffman et al. 2017a, Arifanti et al. 2019). To contribute to the ecological data and knowledge necessary for countries to include mangroves in climate change mitigation and adaptation strategies, a long-term study was established, the Sustainable Wetland Adaptation and Mitigation Program (SWAMP). SWAMP established plots in mangroves around the world and has ultimately resulted in an

enormous global data set collected using a standardized, robust protocol. This data set provides an unprecedented opportunity to quantitatively examine differences in C stocks of mangrove forests across different continents and regions of the world. Our objectives were to describe differences in mangrove C stocks across regions and continents, as well as among mangroves of varying species composition and structure. We investigated the relationships of physicochemical parameters (e.g., salinity, pH), geographic position (latitude), geomorphic setting (estuarine, fringe, interior), aboveground tree biomass, and climate (precipitation) on TECS to determine if development of reliable predictive models was possible for mangrove forests. Further, we examined relationships between aboveground C stocks and total belowground C stocks. We hypothesized that (1) TECS would decrease with increases in porewater salinity and latitude, and increase positively with precipitation, (2) estuarine/riverine mangroves would have the greatest TECS compared to fringe and interior stands due to greater freshwater and sediment inputs, and (3) taller mangroves would have larger TECS, thus facilitating predictions based on both forest structure and climatic or physical attributes. The novelty of this study is the broad area encompassed with five continents and 16 countries across broad environmental and physicochemical gradients, and the inclusion of the entire belowground stocks vulnerable to loss with land cover change (i.e., up to 3 m in depth).

METHODS

Global comparisons

An early objective of the SWAMP project was to establish a global network of mangrove sites where composition, structure, and C stocks would be quantified in a statistically comparable manner. We collected TECS data from mangroves in Central/North America (Costa Rica, Mexico, Honduras, Panama, Belize, Dominican Republic, and the USA); Western South America (Brazil); Central and West Africa (Gabon, Senegal, Liberia); Oceania (Papua Indonesia, Kosrae and Yap, Federated States of Micronesia, and the Republic of Palau); Southeast Asia (Indonesia); and the Middle East (United Arab Emirates) (Fig. 1). This global data set includes permanent plots in mangrove forests located on the shores of the Northern Indian Ocean, the Arabian/Oman Gulf, the Eastern and Western Atlantic Ocean, and the Eastern and Western Pacific Ocean (Fig. 1). In addition, the studied mangrove sites occurred in a wide range of human-influenced environments such as rural protected areas, sites adjacent to indigenous fishing villages, and within protected areas of urban environments (e.g., Dubai United Arab Emirates [UAE], Libreville, Gabon). A total of 190 mangrove sites were included in this analysis (Appendix S1: Tables S1, S2). All sampled mangroves were relatively intact (minimally disturbed) except in some cases where selective tree harvest by local

people had occurred. Clearly, offsite influences such as pollution, sediment regimes and hydrological alterations are now unavoidable in the estuaries and deltas of the world. Notable regions that were not sampled include Australia, the Pacific Coast of South America, East Africa, and South Asia.

Field sampling

Fieldwork was conducted from 2007 through 2017. All sampling was non-destructive and no trees were felled during sampling. The composition, structure, and TECS of the mangrove sites were measured following methods outlined by Kauffman and Donato (2012). At each site, we collected data necessary to determine species composition, tree density, basal area, and total carbon stocks. Total ecosystem C stocks included both above- and belowground C stocks. Aboveground stocks consisted of standing live and dead trees and downed wood (dead wood on forest floor). Belowground stocks consisted of belowground tree biomass and soil organic C to the depths of indurated horizons of marine sands or bedrock. When soils exceeded 3 m in depth, we limited the scope of inference to a depth of 3 m. Therefore, our C storage estimates are conservative in cases where soil depth exceeded 3 m. Carbon-rich soils exceeding this depth are not uncommon in deltas and estuaries (Arifanti et al. 2019).

Biomass of trees and shrubs

At each sampled mangrove stand, five to six plots were established 20–25 m apart along randomly established 100–125 m transects. All components necessary to determine ecosystem C stocks were collected in each plot (Appendix S1: Fig. S1). Composition, tree density and basal area were quantified through identification of the species and measurement of the mainstem diameters of all trees rooted within each plot. The plot size for trees >5 cm in diameter was 154 m² (7 m radius). Trees <5 cm in diameter were measured in a nested plot of 12.6 m² (2 m radius). The diameter of *Rhizophora* spp. trees was measured above the highest prop root. Other mangrove species were typically measured at 1.3 m above the soil surface (see Kauffman and Donato [2012] for exceptions).

Allometric equations were used to calculate tree biomass for each site. Genus or species-specific formulas were utilized for determination of aboveground biomass. Belowground root biomass was calculated using a general mangrove equation (Komiya et al. 2008). Tree C was calculated by multiplying biomass by a factor of 0.48 for aboveground and 0.39 for belowground biomass (Kauffman and Donato 2012).

Standing dead trees were included when present in the aboveground biomass calculations. Dead trees were separated into three classes depending on the existing branches and twigs attached to the tree at the time of

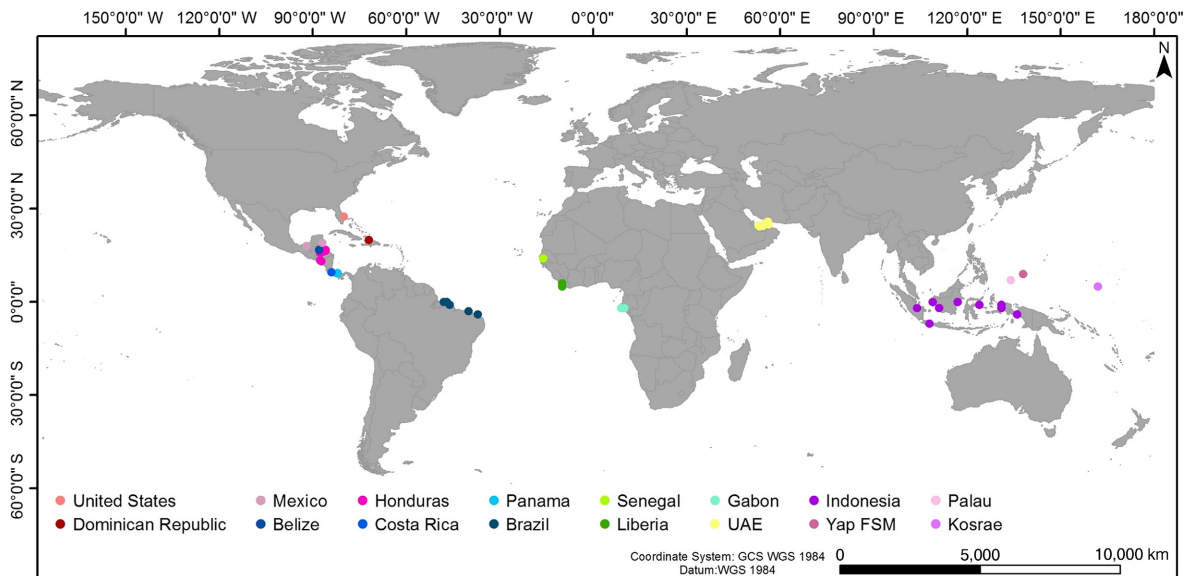


FIG. 1. Locations of the sample plots for the carbon stocks analyses used in this study. Some locations are overlapped at this scale.

sampling (reflecting decay status). Class I represented a recently dead tree with the majority of primary and secondary branches still attached to the tree. Class II dead trees had primary branches but had lost their finer secondary branches. Class III dead trees only had the main trunk (all branches lost). Biomass of class I dead trees was estimated to be 97.5% of a live tree (i.e., loss of foliage); class II, 80% of a live tree (i.e., loss of foliage and fine stems). Class III dead tree biomass (and stumps) was determined through measurement of diameter and height to determine volume, then multiplied by wood density. Dead aboveground vegetation biomass was converted to C mass using the conversion ratio of 0.47 (Kauffman and Donato 2012).

Downed wood

We used the planar intersect technique, adapted for mangroves, to calculate biomass of dead and downed wood (Van Wagner 1968, Kauffman and Donato 2012). At the center of each plot, four 14-m transects were established. The first was established in a direction that was offset 45° from the azimuth of the main transect. The other three were established 90° clockwise from the first transect. At each transect, the diameter of any downed, dead, woody material (branches, prop roots, or mainstems) intersecting the transect was measured. Downed wood ≥ 2.5 cm but < 7.5 cm in diameter at the point of intersection was measured along the last 5 m of each transect. Downed wood ≥ 7.5 cm in diameter at the point of intersection was counted from the second meter to the end of the transect (12 m in total). Large downed wood was separated in two decay categories: sound and rotten. Wood was considered rotten when it visually

appeared decomposed and easily broke apart. To determine mass, we used specific gravity of downed wood determined for mangroves of the same genera. Downed wood was converted to C using a factor of 0.50 (Kauffman and Donato 2012). The understory or litter mass in mangroves is generally negligible (Snedaker and Lahmann 1988, Kauffman et al. 2011) and was not quantified for this study.

Soil carbon

At each of the sampled mangrove plots, soil samples were collected to determine bulk density and C content. This was accomplished by extracting five or six soil cores in each sampled mangrove with an open-faced auger consisting of a semi-cylindrical chamber with an 18–23 cm² cross-sectional area. This auger was efficient for collecting relatively undisturbed soil cores with minimal compaction (Donato et al. 2011, Kauffman and Donato 2012). The soil core was systematically divided into depth intervals of 0–15 cm, 15–30 cm, 30–50 cm, 50–100 cm, and > 100 cm (if indurated soil horizons or layers were not encountered before 100 cm in depth). A 5 cm long sample of a known volume was then collected from the central portion of each depth interval. At each sampling plot, soil depth was determined by inserting a graduated aluminum probe until refusal (indurated soil horizons or layers such as bedrock or/marine sands) at three locations near the center of the plot. The probe length was ~ 3 m, which is the inference limit of study when mangrove soil depth exceeded 3 m. We determined soil carbon stocks of the entire profile depth as well as the mass of soil carbon limited to 1 m in depth. This facilitated what proportion the top meter of soils

comprised of both the total belowground carbon stock and the total ecosystem carbon stock. When soil carbonates were high, both organic and inorganic C was determined following methods outlined in Fourqurean et al. (2014), which are designed to account for soils containing carbonates.

Following soil sampling, samples were transported to laboratories, dried to constant mass at $\leq 65^{\circ}\text{C}$ and then weighed to determine bulk density. In the laboratory, organic C concentrations for all soil samples were determined using the dry combustion method (induction furnace). Prior to carbon analysis, we separated identifiable roots from the soils to be sampled. Soil C pools were obtained as the product of soil C concentration, bulk density, and plot specific soil depth measurements.

Interstitial salinity and pH were measured from porewater samples collected in the core holes using portable handheld refractometers and pH meters following methods described in Kauffman and Bhomia (2017). Care was taken to ensure that no surface water mixed with the porewater. Porewater was sampled at each soil sampling plot ($n = 6$ in each sampled stand). Precipitation and tidal range data were collected from the closest meteorological and tidal gauges to the sampled stands.

Geomorphic and structural classifications

Mangroves were separated into structural and geomorphic classes similar to those defined by Murray et al. (2003) and Adame et al. (2013). The height classes included (1) tall mangroves with a mean height >10 m and usually occurring on the margins of rivers and estuaries; (2) medium mangroves that form dense stands of trees of 3–10 m in height, usually as interior forest environments in areas of higher precipitation but also on estuarine margins in semiarid environments; and (3) low mangroves, composed of dense stands of trees whose heights are <3 m and usually occur inland of riverine/estuarine margins and ecotonal to upland ecosystems.

We partitioned all of the sites based on geomorphic position in a manner modified to that first described by Lugo and Snedaker (1974) and further defined in Adame et al. (2014) and Kauffman et al. (2014). The geomorphic positions were (1) fringing, mangroves occurring along the fringes of protected shorelines and islands and often ecotonal to coastal strand communities; (2) estuarine or riverine, mangroves occurring in estuaries and usually ecotonal to open water; (3) interior, mangroves occurring further inland and ecotonal to the interior of fringing or estuarine mangroves.

Analysis

Differences in C stocks between different regions, geomorphological positions (e.g., fringe, estuarine, interior), mangrove species and height classes (low, medium, tall) were tested with one-way analysis of variance (ANOVA). Differences between the size classes within regions and the

same size classes among regions were also tested using an ANOVA. If significant, a least significant difference (LSD) multiple comparison test was utilized to determine where differences existed. Dependent variables for all of these analyses included the TECS, the total aboveground carbon stock, the total belowground carbon stock and the soil carbon stock limited to the 0–100 cm depth. We also tested for differences in TECS on the basis of precipitation by testing for differences between four precipitation classes ($>1,000$ mm, 1,000–2,000 mm, 2,000–3,000 mm, $>3,000$ mm of annual precipitation). How salinity may influence TECS was first examined by testing for differences in mangroves separated into four porewater salinity classes (<15 PSU, 15–30 PSU, 30–40 PSU, >40 PSU). Effects of latitude were first tested by examining differences in TECS of mangroves in four zones of latitude (equatorial $0-2^{\circ}$, $2-10^{\circ}$, $10-20^{\circ}$, $>20^{\circ}$).

To assess the degrees of influence of physical and climatic variables on C stocks, we developed regression models using precipitation, salinity, tidal range, latitude, tree mass, and soil depth as predictive variables and aboveground, belowground, and total ecosystem C stocks as response variables. Linear, exponential, and power curves were examined to determine the most suitable relationships.

We used multiple regression approaches to develop predictive models for estimating ecosystem C stocks based on climatic, physical, and aboveground biomass parameters. Our primary objective was to determine the strength of possible relationships between ecosystem C stocks and variables that can be obtained via remote sensing (tree mass, longitude), climatic stations (precipitation, tidal range) or easily measured in the field (soil depth, soil porewater salinity, soil pH, tree mass). We used ordinary least-squares regression to determine the results from all possible regression combinations. To address multicollinearity, we developed a correlation matrix for all coefficient estimates. We eliminated any combinations of variables that were strongly correlated (Pearson rank correlation > 0.50). We ran these analyses for all mangrove sites combined and separately for those dominated by the most abundant genera encountered in mangroves throughout the world: *Rhizophora* spp. and *Avicennia* spp.

We also evaluated a posteriori the performance of the predictive regression models by measuring the deviation of the predicted vs. measured means of TECS at regional/continental scales. To eliminate circular bias, the equations utilized to predict TECS for a given region were generated using data only from other regions. For example, in predicting the TECS of Asian mangroves, we developed the predictive equation from data coming from all sites except Asia.

RESULTS

Mangrove forests exist in a very broad range of environmental conditions, and the sampled mangrove sites

reflected the broad precipitation, salinity, tidal, and longitudinal gradients in which they exist (Appendix S1: Table S1). For example, the mean annual precipitation of sites ranged over 50-fold from 75 to >3,500 mm/yr and porewater salinity ranged from 0 to 96 PSU. The latitudinal range of our sampling was from 7° S (Java, Indonesia) to 27° N (USA and the UAE) and the longitudinal range varied from 92° W in Mexico to 162° E in Kosrae (FSM) (Fig. 1). Soil depths ranged from 22 cm (UAE) to >300 cm in many estuarine mangroves (>80 sites).

Across the sites, there was a 28-fold difference in TECS (Fig. 2). The TECS of the individual mangrove sites ranged from 79 to 2,208 Mg C/ha. There were also very large differences in aboveground C stocks ranging from 1 to 501 Mg C/ha while belowground C stocks ranged from 46 to 2,076 Mg C/ha. The global TECS mean \pm SE of the sampled mangroves was 856 ± 32 Mg C/ha. The global mean aboveground C stock was 115 ± 7 Mg C/ha and the mean belowground C stock was 741 ± 30 Mg C/ha. There was large variability in patterns of C sequestration within mangroves; belowground : aboveground ratios ranged from 1.2 to 331.0 with a mean of 21.0.

While most of the carbon in mangrove is partitioned into belowground pools, there is a tremendous variation among individual sites (46–2,076 Mg C/ha; Appendix S1: Table S2). There were profound and significant differences in the belowground carbon stocks comparing

different regions; those of Southeast Asia, Oceania, and Central America exceeded 870 Mg C/ha, while those of the Middle East were about 180 Mg C/ha (Table 1).

Soil carbon pools at depths of 0–100 cm ranged over 23-fold among individual sites from 33 to 789 Mg/ha. Similar to the total belowground C pools, the mean pools of the top 1 m of soils in Oceania and Southeast Asia were significantly greater (>400 Mg C/ha) than those of the Middle East or Central America. The top 1 m of the soil horizon accounted for a mean of 43% of the total ecosystem carbon stock with a range of 11%–98% of the TECS of the individual sites. In the relatively shallow soils of the Middle East containing lower total plant pools, this soil component comprised 55% of the TECS compared to <40% in mangroves of Oceania, Southeast Asia, and West Africa (Table 1).

Carbon stocks separated by continents and regions

There was a significant difference in TECS ($P = 0.002$), aboveground C stocks ($P < 0.0001$) and belowground C stocks ($P = 0.04$) at continental scales (Table 1). The largest TECS were found in Oceania (1,156 Mg C/ha) and were significantly greater ($P < 0.05$) than all other continents (Table 1). Similarly, the lowest ecosystem C stocks were found in the hyperarid, hypersaline, Middle East mangroves (217 Mg

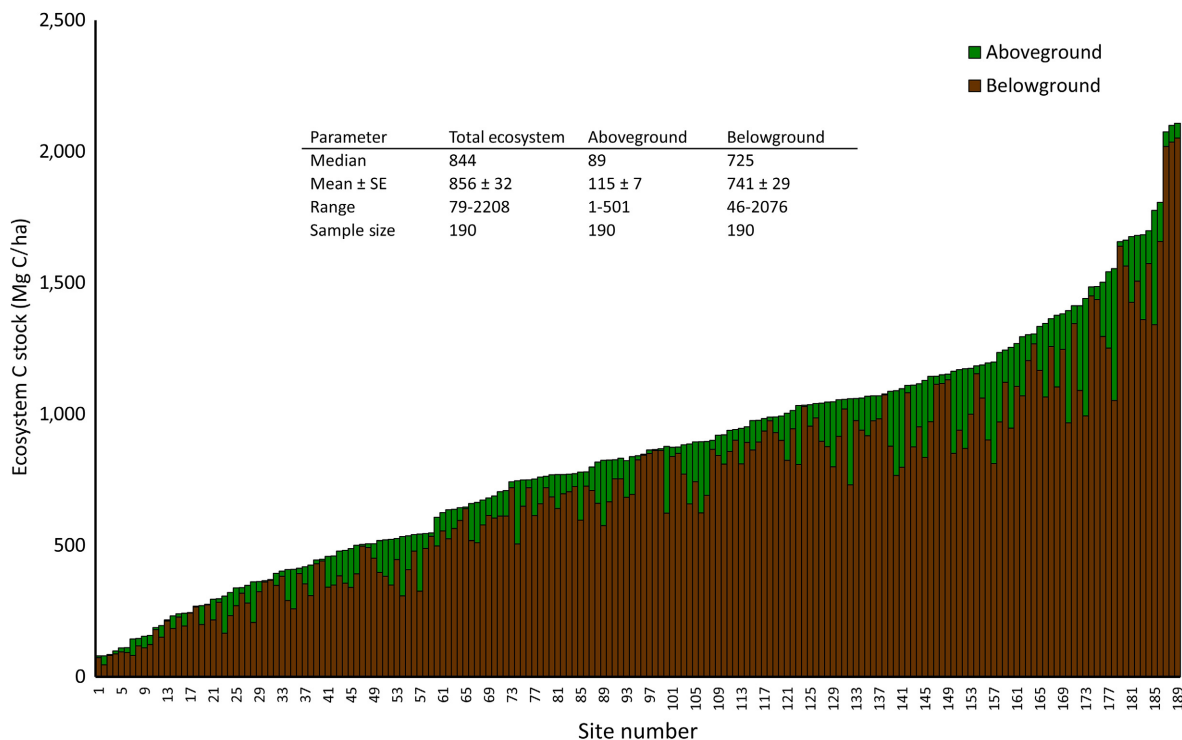


FIG. 2. The range in total ecosystem carbon stocks (Mg C/ha) of 190 mangroves from the Americas, Asia, Africa, and Oceania.

TABLE 1. Total ecosystem carbon stocks, total aboveground carbon stocks, total belowground stocks, and carbon mass of soils at depths of 0–100 cm for mangroves partitioned by continent and geographic region.

Geographic region/Continent	Carbon stocks (Mg C/ha)								
	Total ecosystem		Total above-ground		Total below-ground		Soils (0–100 cm)		N
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
West Africa	800.7 ^{a,3}	57.2	84.4 ^{a,2,3}	14.1	716.3 ^{a,b,2}	54.6	278.4 ^{a,2}	16.5	33
Asia	772.6 ^a	61.6	112.5 ^a	12.1	660.3 ^a	54.4	294.8 ^a	20.4	59
Middle East	217.0 ¹	30.1	37.3 ¹	7.8	179.7 ¹	24.0	110.8 ¹	11.6	18
Southeast Asia	1016.5 ^{4,5}	53.6	145.5 ⁴	14.4	871.3 ^{2,3}	49.7	375.6 ³	17.5	41
Oceania	1141.2 ⁵	69.8	254.8 ^{b,5}	22.2	886.2 ^{b,2,3}	55.9	447.9 ^{c,4}	19.0	25
Americas	850.9 ^a	53.7	82.7 ^a	7.6	768.2 ^{a,b}	53.8	350.9 ^b	19.9	73
Central America	948.7 ^{3,4}	60.4	71.7 ^{1,2}	8.2	877.1 ³	59.2	401.9 ⁴	20.0	58
South America	472.9 ²	42.7	125.2 ^{3,4}	14.6	346.7 ¹	37.6	154.9 ¹	11.7	15
Grand Total	856.1	32.1	114.9	7.2	741.2	29.5	333.7	11.2	190

Notes: There was a significant difference in total ecosystem carbon stocks ($P = 0.002$), aboveground carbon stocks ($P = 0.0000$), belowground carbon stocks ($P = 0.04$), and soils 0–100 cm depth ($P < 0.0001$) at continental scales (i.e., West Africa, Asia, Oceania, and the Americas). Different superscripted letters denote significant differences among these continents ($P \leq 0.05$). Similar significant differences were found at the geographic regional scale (e.g., Middle East, Southeast Asia, Central America, South America, etc.) where specific differences ($P \leq 0.05$) are denoted by different superscripted numbers.

C/ha; $P < 0.05$). Mangroves of South America had a relatively low mean C stock of 473 Mg C/ha, but sampling was limited to Brazil on highly weathered coarse-textured soils with high tidal ranges (Kauffman et al. 2017b, 2018b). The mean C stock of mangroves of Central/West Africa mangroves was 801 Mg C/ha, and those of the Central/North America and Southeast Asia were 949 and 1,017 Mg C/ha, respectively.

Species dominance and carbon stocks

Rhizophora-dominated mangroves (*R. mangle*, *R. racemosa*, or *R. apiculata*) constituted 66% ($n = 126$) of the sampled sites (Table 2). *Avicennia* (e.g., *A. germinans*, *A. marina*, etc.) was the next most widespread genus, dominant in 15% ($n = 29$) of the sampled stands, and was frequently co-dominant with *Rhizophora* spp. (Appendix S1: Table S2). Mangrove forests dominated by *Rhizophora* spp. and *Avicennia* spp. ranged in height from <1 m to >25 m and were found on all geomorphic settings (fringe, interior, and estuarine). Stands dominated or co-dominated by *Laguncularia racemosa* were common in the Americas and were predominately tall or medium in stature. Stands dominated by *Bruguiera* spp. and *Sonneratia* spp. were abundant in Oceania and Asia, and the palm *Nypa fruticans* was also a common mangrove species in Oceania and Asia.

A differentiating feature between the stands dominated by *Avicennia* spp. and that of other species was porewater salinity (Appendix S1: Table S2). The mean porewater salinity in stands dominated by *Avicennia* spp. was 44 ± 4 PSU. In contrast, mean porewater salinity of *Rhizophora*-dominated stands was 28 ± 1 PSU ($P \geq 0.05$), and that of all other stands was <21 PSU.

Total ecosystem C stocks of the sampled stands dominated by *Avicennia* spp. were significantly lower

($P < 0.05$) than stands dominated by other genera (418 Mg C/ha compared to >900 Mg C/ha; Table 2). Nevertheless, *A. germinans* or *A. marina* were a common co-dominant in many sites with large TECS (Appendix S1: Table S1). There was no significant difference in belowground C stocks among genera with the exception of significantly lower C stocks in *Avicennia* spp. In addition, TECS varied widely within stands dominated by the same species, including those dominated by *Avicennia* spp., which ranged from 79 to 1,305 Mg C/ha (Fig. 3). Similarly, TECS of *Rhizophora*-dominated stands ranged from 154 Mg C/ha to the largest C stock sampled: 2,207 Mg C/ha.

The lower ecosystem C stocks of *Avicennia* spp. are reflective of *A. marina* dominance in the most hypersaline and hyperarid environments where mangroves occur. For example, it was the sole species in the UAE. *Avicennia nitida* dominated the most saline habitats in arid Senegal (Appendix S1: Table S2).

Geomorphic position

We hypothesized that geomorphic position would result in different C stocks, predicting that estuarine mangroves would have higher C stocks due to lower salinities, greater inputs of sediment, and usually greater aboveground stature (Krauss et al. 2010). While aboveground C stocks in estuarine mangroves were significantly greater than those of interior mangroves ($P \geq 0.05$), there were no significant differences ($P = 0.36$) in TECS among estuarine, fringing, and interior mangroves. Total aboveground C stocks were 78 Mg C/ha in the interior mangroves, and 114 and 131 Mg C/ha in the fringing and estuarine mangroves, respectively. Mean TECS were 872 Mg C/ha for estuarine

TABLE 2. Total ecosystem carbon stocks (mean \pm SE) of mangroves based on the species dominance of the overstory.

Genus Dominance	Sample size	Carbon stocks (Mg/ha)			
		Total ecosystem ($P \leq 0.00$)	Aboveground ($P \leq 0.00$)	Belowground ($P \leq 0.00$)	Soil carbon limited to 0–100 cm ($P \leq 0.00$)
<i>Avicennia</i>	29	418.3 ^a \pm 62.0	56.7 ^a \pm 9.5	361.6 ^a \pm 57.2	166.7 ^a \pm 24.4
<i>Rhizophora</i>	126	900.8 ^b \pm 35.9	113.3 ^b \pm 8.3	782.8 ^b \pm 34.6	360.5 ^b \pm 12.3
<i>Laguncularia</i>	7	942.8 ^{bc} \pm 254.2	75.2 ^{ab} \pm 10.6	862.1 ^b \pm 250.2	341.0 ^b \pm 92.8
<i>Sonneratia</i>	8	982.9 ^{bc} \pm 159.5	206.4 ^c \pm 52.4	779.1 ^b \pm 112.7	370.6 ^b \pm 35.3
<i>Bruguiera</i>	13	1226.6 ^c \pm 98.5	250.4 ^c \pm 30.7	976.2 ^b \pm 92.0	437.2 ^b \pm 34.1
<i>Nypa</i>	5	992.8 ^{bc} \pm 51.0	60.0 ^{ab} \pm 12.0	932.8 ^b \pm 52.2	309.4 ^b \pm 19.6

Note: Different superscripted letters denote a significant difference ($P \leq 0.05$) in carbon stocks between the different mangrove types.

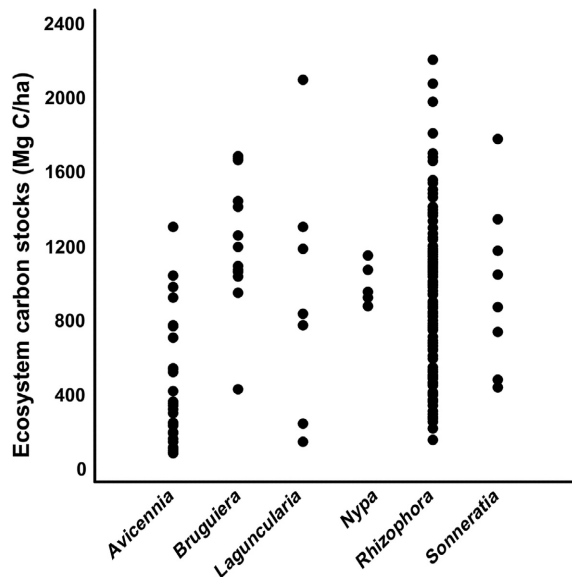


FIG. 3. A scattergram of the ecosystem carbon stocks of sampled mangroves separated by the dominant genera in each sampled stand.

mangroves and \sim 780 Mg C/ha for fringing and interior mangroves (Fig. 3B).

Forest structure

We predicted that ecosystem C stocks of tall mangroves (>10 m height) would exceed that of medium (3–10 m) and low-stature mangroves (<3 m). As would be expected, aboveground C stocks of tall mangroves (154 ± 9 Mg C/ha) were significantly greater than that of medium (87 ± 12 Mg C/ha) and low mangroves (21 ± 9 Mg C/ha; Fig. 4B). However, there were no significant differences in belowground C stocks based on forest stature ($P = 0.21$). In terms of TECS, tall mangroves (930 ± 40 Mg C/ha) were significantly greater than those of low mangroves (652 ± 93 Mg C/ha), but not medium mangroves (815 ± 60 Mg C/ha; Fig. 4B).

Among the forest stature classes, porewater salinity ($P < 0.001$) and precipitation ($P < 0.001$) differed

significantly. Mean precipitation was greater in tall mangroves (2,534 mm) compared to the others. Mean precipitation was also greater in medium mangroves (1,993 mm) compared to low mangroves (1,439 mm). However, it is common to find low, medium, and tall mangroves ecotonal to one another within the same estuary. Mean porewater salinity in tall mangroves (22 PSU) was less than half of that in low mangroves (46 PSU); mean porewater salinity in medium mangroves was 32 PSU (Appendix S1: Table S2).

Relationships between aboveground and belowground carbon stocks

Because tall mangroves were significantly greater in total aboveground C stocks, we hypothesized that aboveground C stocks could predict belowground C stocks and TECS. We found a very poor relationship between aboveground C and either TECS ($r^2 = 0.24$) or belowground C stocks ($r^2 = 0.11$; Figs. 5A,B). Given the wide variation (scatter) in relating aboveground and TECS, the hypothesis that aboveground forest C stocks can reliably predict TECS is not practically tenable. For example, mangroves with aboveground C stocks that were <100 Mg C/ha had total ecosystem C stocks ranging 40-fold from <50 to $>2,000$ Mg C/ha (Fig. 5A,B).

Relationship between carbon stocks and physicochemical ecosystem features

We found significant differences ($P \leq 0.0001$) in TECS among the four precipitation classes. The mean TECS of mangroves in landscapes receiving $\leq 1,000$ mm precipitation was 465 Mg C/ha and was 795 Mg C/ha for mangroves in landscapes receiving 1,000–2,000 mm annual precipitation. The mean TECS of mangroves within the annual precipitation classes exceeding 2,000 mm was significantly greater (≥ 999 Mg C/ha) than those within precipitation classes $<2,000$ mm.

Mangroves from hyperarid zones had lower ecosystem C stocks than those from landscapes with precipitation $>2,000$ mm ($P = 0.05$). For example, the mean TECS of mangroves from the UAE (≤ 135 mm annual

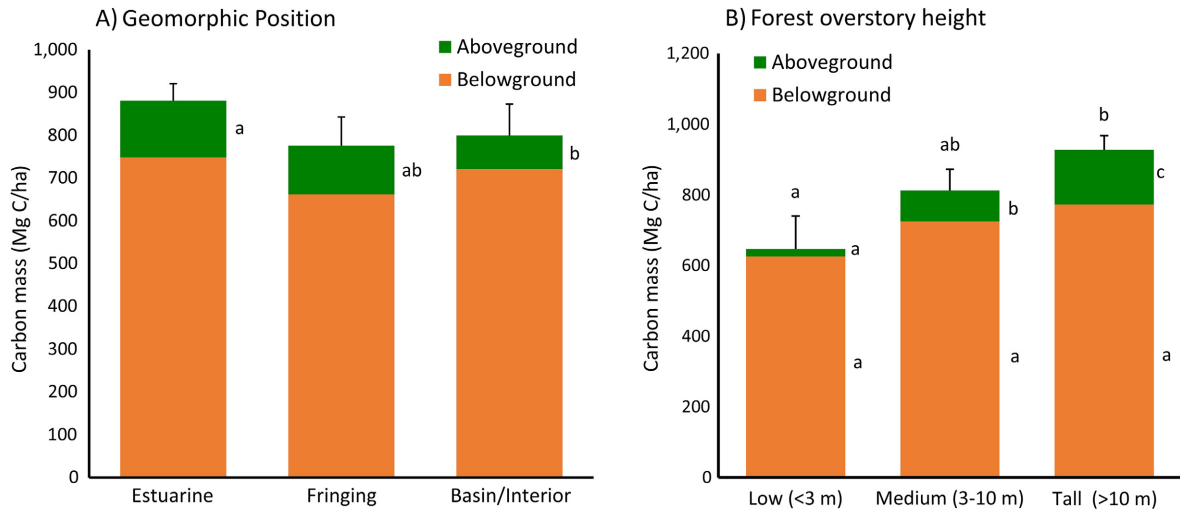


FIG. 4. Ecosystem carbon stocks of mangroves based on (A) geomorphic position (estuarine $N = 98$, fringe $N = 62$, and basin/interior $N = 21$) and (B) forest overstory height (low $N = 24$, medium $N = 66$, and tall $N = 103$). Different letters above the bars denote a significant difference ($P \leq 0.05$) in total ecosystem carbon stocks. Different letters next to the bars denote a significant difference ($P \leq 0.05$) when testing for differences in the aboveground and belowground carbon stocks.

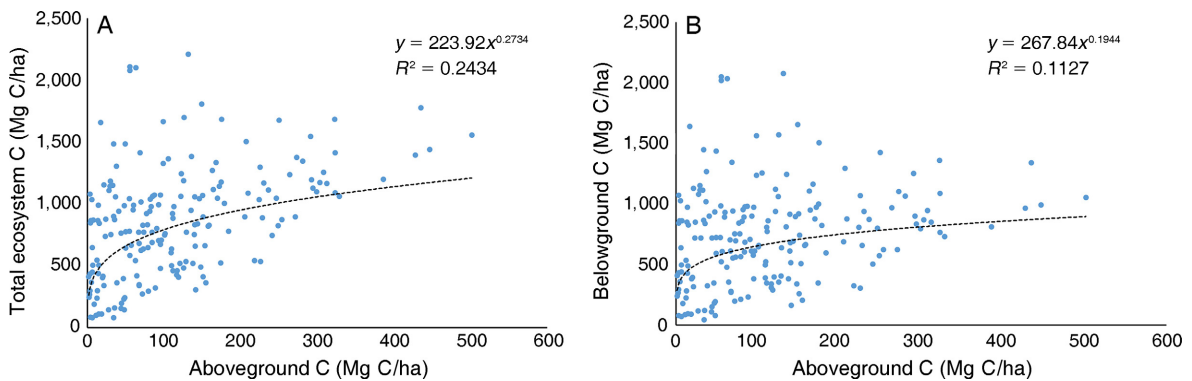


FIG. 5. (A) The relationship of total aboveground carbon with total ecosystem carbon stock (Mg C/ha) and (B) the relationship of total aboveground carbon belowground ecosystem carbon stock (Mg C/ha).

precipitation) was 217 Mg C/ha. In contrast, those from Liberia (3,346 mm precipitation) were 950 Mg C/ha (Appendix S1: Table S1; see also Schile et al. 2017 and Kauffman and Bhomia 2017). However, there is commonly a wide range in TECS of individual stands within estuaries where climatic conditions would not vary. For example, within a single estuary in Liberia, the TECS varied by over fourfold, ranging from 366 to 1,485 Mg C/ha (Appendix S1: Table S2). In the arid Saloum Delta, Senegal (650 mm precipitation), TECS ranged from 296 to 941 Mg C/ha, also demonstrating that even some arid mangrove stands can store significant quantities of C that often exceed the global mean TECS. This wide range in variation of TECS is common within many watersheds explaining why there was only a moderately strong relationship, best explained by a power model, between TECS and precipitation ($r^2 = 0.45$; Fig. 6A). Averaging C stocks sampled at all

sites within the same precipitation zones improved the model moderately ($r^2 = 0.61$; Fig. 6B). As predicted, we observed lower ecosystem C stocks in locations with lower precipitation and higher C stocks in locations of higher precipitation; however, a linear model only explains about 21% of the variation. The great variation in C stocks with similar precipitation regimes suggests that precipitation alone does not accurately predict ecosystem C stocks.

We hypothesized that TECS would decrease with increasing latitude, salinity, and tidal range. While there is a statistically significant relationship between TECS and each of these variables ($P \leq 0.02$), there was a very weak relationship (Figs 7A–C). Similar to precipitation, the great variation in the TECS of stands within similar tidal ranges, latitude, and salinity levels suggests that generalizations at the stand level based on such relationships are not tenable.

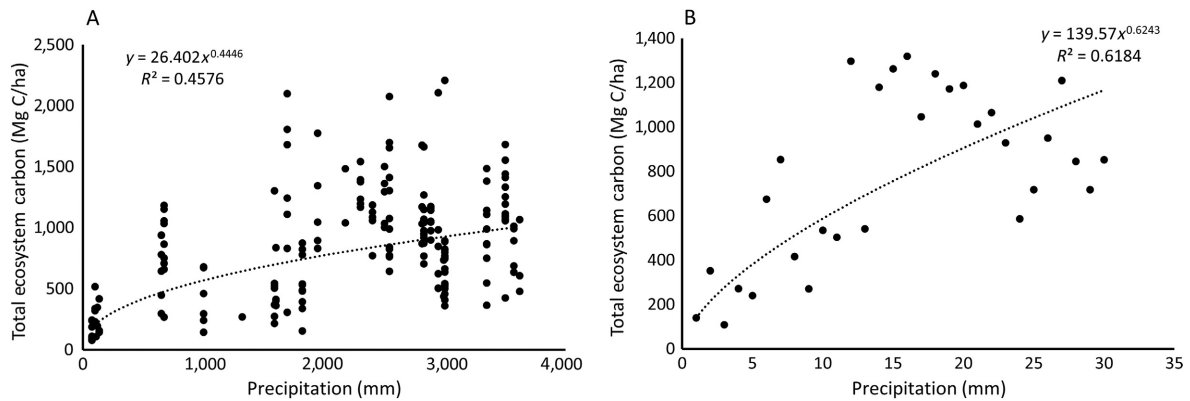


FIG. 6. The relationship of total ecosystem carbon stocks (Mg C/ha) with precipitation (mm) (A) where all sites are included and (B) where total stocks in locations with the same precipitation are averaged.

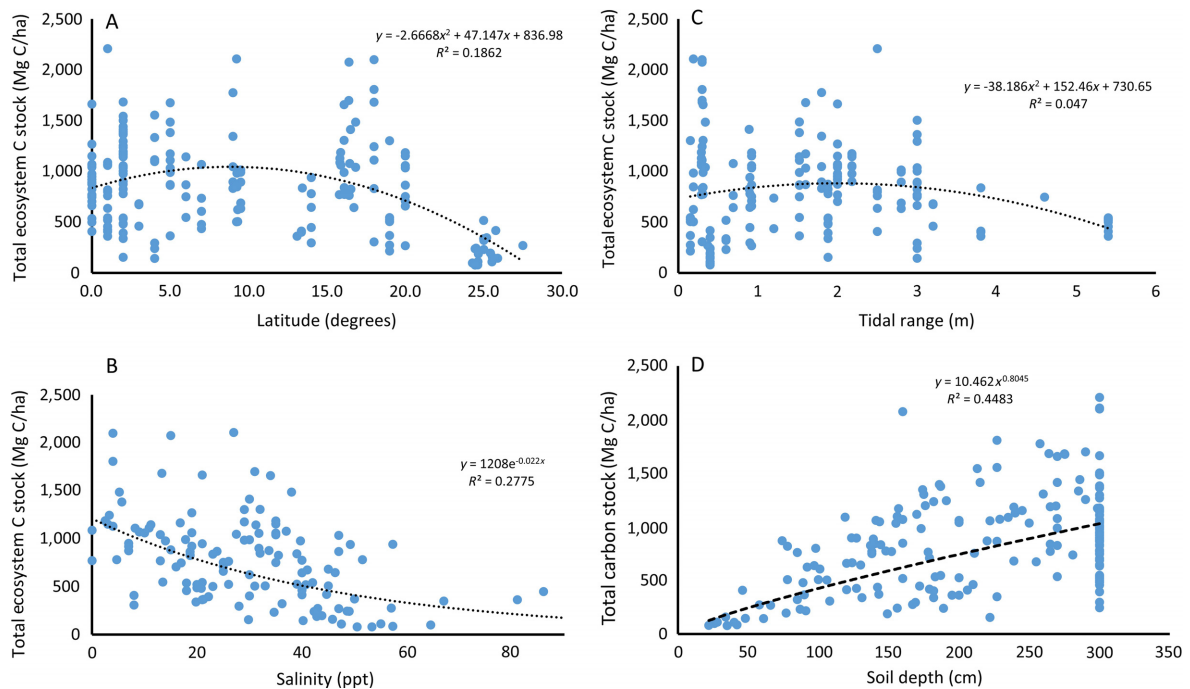


FIG. 7. The relationship of total ecosystem carbon stocks (Mg C/ha) with (A) latitude (degrees from the equator), (B) salinity (PSU), (C) tidal range (m), and (D) soil depth. Total ecosystem carbon stocks are best explained by a polynomial equation when latitude and tidal range are the explanatory variables. For salinity, total carbon stocks are best explained by an exponential equation, and soil depth is best explained by a power equation.

There were significant differences in TECS among mangroves on the basis of porewater salinity ($P < 0.0001$). The mean TECS in sites with salinity concentrations >40 PSU was 425 Mg C/ha while those in sites <40 PSU exceeded 826 Mg C/ha ($P < 0.05$). Similarly, mangroves of the highest latitudes ($>20^\circ$) had mean TECS significantly lower than those at lower latitudes (i.e., 423 vs. >908 Mg C/ha).

In developing practical multivariate predictive equations of TECS based on climate, physiochemical and vegetation parameters, we detected multicollinearity

only between the variables of precipitation and porewater salinity. We therefore only included precipitation, rather than porewater salinity in the models. First, we developed a predictive equation using variables that could be readily obtained via nearby weather stations, remote sensing or with a geographic positioning system (i.e., precipitation, tidal range, and latitude). This equation accounted for about 28% of the variation (adjusted $R^2 = 0.27$; Table 3). Next, we added tree biomass to the equation, which is a variable that can be obtained through field measurements (inventories) or may be

obtained via remote sensing (e.g., Simard et al. 2018). This resulted in a predictive model with an $R^2 = 0.39$ (adjusted $R^2 = 0.38$). An equation using latitude, precipitation, and soil depth as variables (parameters measured in all 190 sites) accounted for 37% of the variation (Adjusted $R^2 = 0.36$). Adding tree biomass to this equation improved the model moderately ($R^2 = 0.51$). The variables within this model showed a clear relationship with TECS (Fig. 8). However, these variables exhibited a large degree of heteroscedasticity as variation around the trend line increased with increasing TECS. Finally, including tidal range and soil pH with the variables above yielded an equation accounting for the greatest amount of variation ($R^2 = 0.67$, and an adjusted $R^2 = 0.64$). However, the sample size for development of this model was only 96 (Table 3).

Including tree biomass, latitude, precipitation and soil depth to predict TECS resulted in a large scatter around the trend line suggesting uncertainty in using this model for predicting TECS for individual sites (Fig 9). Nevertheless, the model does provide a reasonable mean estimate at global and continental scales when a large number of sites are included to determine the estimate. For example, using the predicted TECS from all of the sampled sites yields mean global estimate of 856 Mg C/ha (Fig. 9). The predicted mean estimates at continental scales were within 28% of that of the measured results with the exceptions of the Middle East and South America; the sites with the lowest mean ecosystem stocks. The predictive equations grossly overestimated TECS of Middle East sites by 161% (i.e., 217 Mg C/ha for the

actual and 567 Mg C/ha for the predicted). While not likely to yield satisfactory estimates for individual stands, the reasonable estimates of TECS at the continental scales (except for the arctic sites of the Middle East) suggest that these models can be used to predict the mean TECS at large scales if the analysis includes data collected at multiple sites in the region (such as an inventory where such data would be collected).

DISCUSSION

In a review of ecosystem C stocks of forest and marine ecosystems on an area-specific basis, Alongi (2014) concluded that mangrove forests store more C than many other forested ecosystems, especially in their soils. Our study supports this observation. Mangroves have a global mean TECS of 853 Mg C/ha (this study), compared with ~197–518 Mg C/ha for upland tropical forests, 593 Mg C/ha for salt marshes, and 142 Mg C/ha for seagrasses (Jobse 2008, Donato et al. 2012, Fourqurean et al. 2012).

The mean aboveground C stocks reported here are lower than that reported by Donato et al. (2011) and Pendleton et al. (2012) but higher than modeled estimates given by Hutchison et al. (2014) and Simard et al. (2018) (Table 4). Our estimated mean TECS are also somewhat lower than that of Donato et al. (2011) for mangroves of the Indo-Pacific region (1,023 Mg C/ha) but slightly higher than their scaled estimate of global mean mangrove C stocks (~800 Mg C/ha). Our estimate is also lower than that of Alongi (2014;

TABLE 3. Predictive equations for total ecosystem carbon stocks of mangroves based on variables possible to collect via remote sensing, weather stations, or simple measurements in the field.

Variables in the model	R^2	Adj R^2	SE	MAE	N	Equation
All mangroves						
Tree mass, Latitude, Precipitation, Tidal range, Soil pH, Soil depth,	67	64	277	185.5	96	$-1077.3 + 1.59 \times \text{Tree mass} + 9.18 \times \text{Latitude} + 0.21 \times \text{Precipitation} - 115.23 \times \text{Tidal range} + 127.57 \times \text{Soil pH} + 2.23 \times \text{Soil depth}$
Tree mass, Latitude, Precipitation, soil depth	51	50	313	228.1	190	$-437.8 + 1.89 \times \text{Tree mass} + 20.28 \times \text{Latitude} + 0.19 \times \text{Precipitation} + 2.30 \times \text{Soil depth}$
Latitude, Precipitation, Soil depth	37	36	354	266.2	190	$-192.00 + 12.94 \times \text{Latitude} + 0.20 \times \text{Precipitation} + 2.23 \times \text{Soil depth}$
Tree mass, Latitude, Precipitation, tidal range	40	38	346	257.0	167	$440.40 + 2.14 \times \text{Tree mass} - 1.55 \times \text{Latitude} + 0.21 \times \text{Precipitation} - 142.03 \times \text{Tidal range}$
Latitude, Precipitation, tidal range	28	27	376	280.4	168	$633.06 - 5.77 \times \text{Latitude} + 0.22 \times \text{Precipitation} - 126.10 \times \text{Tidal range}$
<i>Rhizophora</i> spp.						
Tree mass, Latitude, Precipitation, Tidal range, Soil pH, Soil depth	63	59	263	173.3	65	$-1412.0 + 1.39 \times \text{Tree mass} + 21.88 \times \text{Latitude} + 0.14 \times \text{Precipitation} - 85.43 \times \text{Tidal range} + 175.24 \times \text{Soil pH} + 2.53 \times \text{Soil depth}$
<i>Avicennia</i> spp.						
Precipitation, Tidal range, Soil depth	87	85	129	95.4	29	$153.11 + 0.26 \times \text{Precipitation} - 124.44 \times \text{Tidal range} + 0.84 \times \text{Soil depth}$

Notes: R^2 denotes the percentage of the variability in total ecosystem carbon is explained by the equation. The adjusted R -squared statistic (Adj R^2), is more suitable for comparing models with different numbers of independent variables such as presented here. The standard error of the estimate is the standard deviation of the residuals. The mean absolute error (MAE) is the average value of the residuals. N denotes the total number of sampled mangroves used to develop equations.

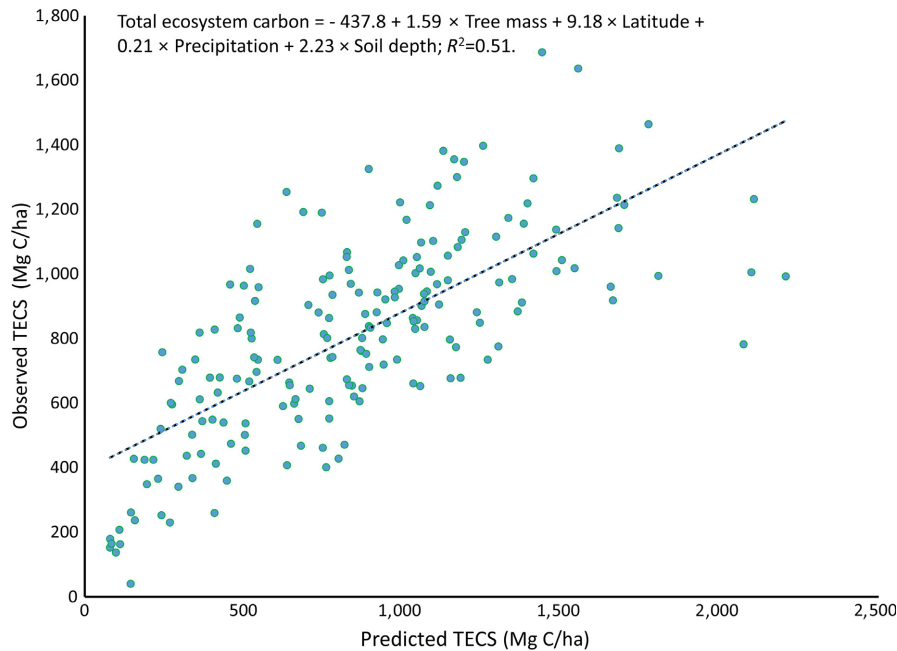


FIG. 8. The relationship between actual total ecosystem carbon stocks measurements and predicted ecosystem carbon stocks. The variables in the predictive model include precipitation (mm), aboveground tree carbon (Mg C/ha), soil depth (cm), and latitude (degrees from the equator); $n = 190$ observations.

956 Mg C/ha) and Pendleton et al. (2012; 933 Mg C/ha; Table 4). Their estimates were based on data largely collected from Oceania and Southeast Asia, which have larger ecosystem C stocks than other regions (Table 1; Fig. 9). In contrast, the present study encompassed a wide range of precipitation, tidal range, latitude, and composition in which mangroves occur, and therefore presents a more realistic estimate of the mean and variation in TECS of mangroves globally.

It is important to apply mean values cautiously (or default values such as those provided in IPCC 2014) as mangrove ecosystem C stocks at the site scale ranged from 79 to 2,208 Mg C/ha. Further, there were significant differences in TECS when testing for differences among both continents and countries (Fig. 9). However, multiplying the area of mangroves from the sampled continents (Spalding et al. 2010) by the mean continental values of TECS from this study only changed the global mean estimate by about 4.1% to 885 Mg C/ha. This suggests that our sample of 190 mangrove sites across the globe is a good representation of the range and mean TECS for this blue carbon ecosystem.

There are many compelling reasons for improved quantification of mangrove C stocks as well as other blue carbon ecosystems. They are among the most carbon-dense of tropical ecosystems, and when deforested and converted to agriculture or aquaculture, their cumulative GHG emissions far exceed that from uplands (Pendleton et al. 2012, Sanders et al. 2016, Kauffman et al. 2017a). The global estimates of GHG emissions

following land-use change, especially aquaculture, are likely underestimated due to use of low baseline estimates for soil C stocks and large underestimates of average emissions and C losses, which are as high as 85% of the TECS (Kauffman et al. 2017a, 2018b). For example, global soil GHG emissions from mangrove removal has been estimated to be 7.0 Tg CO₂e/yr (Atwood et al. 2017) at a rate of forest removal of 0.2% per yr (Hamilton and Casey 2016). However, global estimates of ecosystem C stocks (283 Mg C/ha; Duarte et al. 2013) and emissions following land-use change (43% of C remineralized at the top 1 m soils; Atwood et al. 2017) are less than half of what they would be using the mean global results based on TECS measurements (this study; Kauffman et al. 2017a).

Comparison with IPCC values

The large C stocks, high rates of mangrove deforestation, and subsequent high GHG emissions points to the relevance for inclusion of mangroves in nationally appropriate climate change mitigation and adaptation strategies, which necessitates accurate quantification of ecosystem C stocks (IPCC 2014). The methods utilized to quantify C stocks in this study would provide verifiable and reliable results for quantification. In addition, global default values at regional (Tier 2) and global (Tier 1) scales are in need of refinement given the paucity of published data prior to 2013. Mean C stocks presented here are substantially higher than the global default

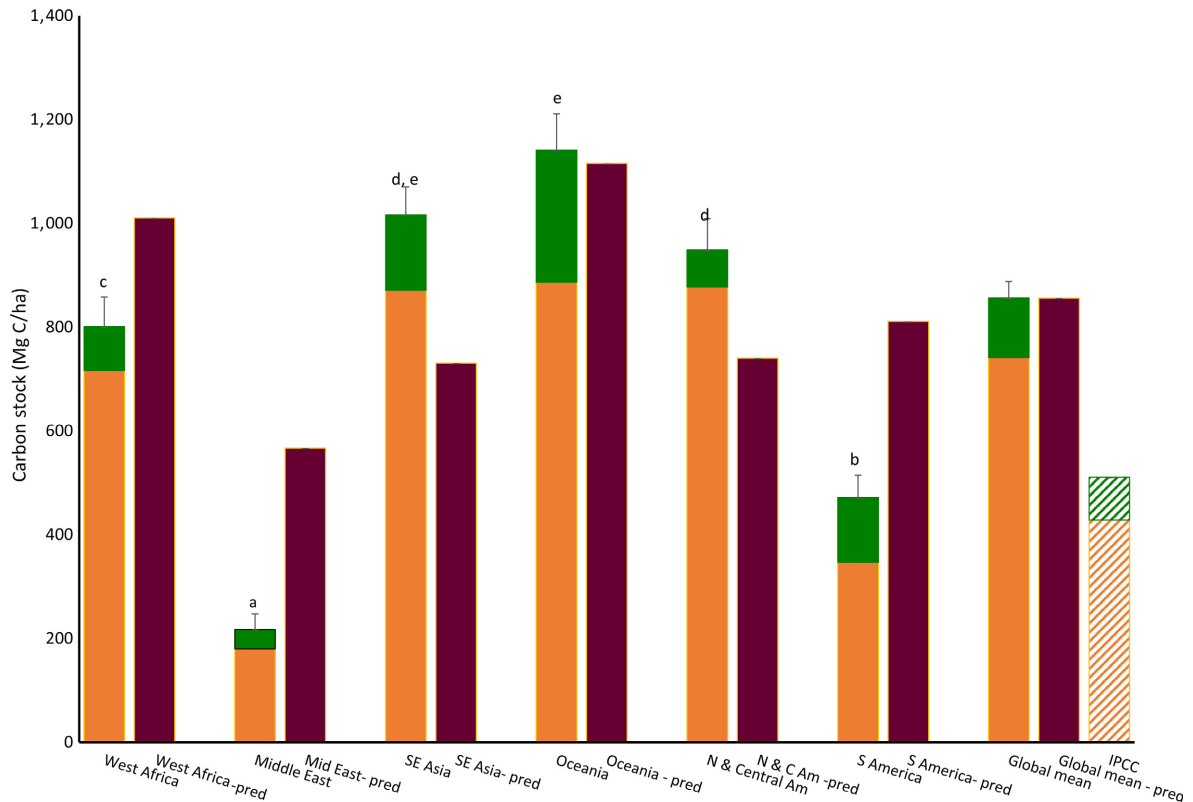


FIG. 9. Ecosystem carbon stocks (Mg C/ha) of intact mangroves from sampled continents and global means. Letters above the bars of measured ecosystem carbon stocks (green and brown bars) represent a significant difference ($P \leq 0.05$) between the continents. The violet bars are predicted (pred) ecosystem carbon stocks based on multiple regression analysis. SE, southeast; N & C Am, North and Central America. The hatched bar represents the current IPCC default values extracted from (Intergovernmental Panel on Climate Change (IPCC) 2014).

value given in Intergovernmental Panel on Climate Change (IPCC) (2014), which is ~ 511 Mg C/ha (Fig. 9; Table 4). Belowground C stocks comprised $\sim 84\%$ of the IPCC estimate (428 Mg/ha). The IPCC value is 341 Mg C/ha lower or only about 60% of our calculated global mean, and is much lower than results of mangrove ecosystem C stocks for Africa, Asia, Oceania, and the Americas (Fig. 9).

Given the larger sample size ($n = 190$) from a much wider range of environments and species dominance, this study suggests the global mean data presented here is more reflective of global conditions than that presented by Intergovernmental Panel on Climate Change (IPCC) (2014). In a study of land-use change in mangroves, mean GHG emissions from conversion of mangrove to shrimp ponds and cattle pastures were 2,033 Mg CO₂e/ha (Kauffman et al. 2017a). This C loss (equivalent to 554 Mg C/ha) exceeds the entire IPCC default value for ecosystem C stocks in mangroves (Intergovernmental Panel on Climate Change (IPCC) 2014). The sample size for the IPCC default values was 119 for soils and 72 for vegetation (Intergovernmental Panel on Climate Change (IPCC) 2014). We suggest using the mangrove ecosystem C stock

values in Table 1 to improve default values of mangroves at both regional and global scales.

Sampling approaches

Given that soils are the largest component of carbon pools and the greatest source of GHG emissions when disturbed their accurate measurement or representation is important. While belowground C comprised a mean of 85% of all mangroves, it frequently accounts for >96–99% of the ecosystem C stock, especially in medium- and low-stature mangroves (Fig. 3B). Sanders et al. (2016) also found that belowground C stocks accounted for $\sim 85\%$ of the TECS in mangroves.

The sampling protocol for all mangroves in this study included determining soil C to indurated layers/horizons (e.g., marine sands, coral gravels) or to a default value of 3 m when soils exceeded this depth. The mean depth of soils in this study was 216 cm (with a range of 22 cm to >300 cm) and only 26 sampled sites (13%) had a mean soil depth of ≤ 1 m. The mean soil depth of 68 sites (35%) exceeded 300 cm. This suggests that extrapolations to depths in order to estimate global stocks are going to be problematic. For example, we could not find

TABLE 4. Global estimates of mean ecosystem carbon stocks of mangroves at the site level (Mg C/ha) and global level (Pg C).

Source	Site level (Mg C/ha)			TECS	Global carbon stock estimate (Pg C)†	Notes
	Aboveground C	Soil OC limited to 1 m	Soil OC whole profile (or 3 m)			
This study	115	334	741	856	11.7	uniformly sampled plot data from five continents; measured soil horizon depths
Donato et al. (2011)	159	NR	864	1023	4.0–20	field data from the Indo-Pacific; only a range in global stocks provided
Pendleton et al. (2012)	NR	NR	NR	933	13.5	literature-derived carbon estimates
Sanderman et al. (2018)	NR	361	758	NR	12.6	model derived carbon estimates from literature values; soils limited to 2 m; global storage of 6.4 Pg to 1 m depth
Alongi (2012, 2014)	123	NR	814	937	NR	literature-derived carbon estimates limited to Australia and Southeast Asia
Hutchison et al. (2014)	89	NR	NR	NR	NR	only aboveground data reported
Jardine and Siikamaki (2014)	NR	369	NR	NR	5.0	limited to 1 m depth
Atwood et al. (2017)	NR	283	NR	NR	4.4	literature-derived carbon estimates; soils limited to 1 m depth
Simard et al. (2018)	62	NR	NR	NR	5.03	models based on remotely sensed forest heights; global estimate includes soils data from Atwood et al. (2017)
IPCC (2014)	83	428	NR	511	NR	literature-derived carbon estimates

Note: OC, organic carbon; NR, not reported or determined; TECS, total ecosystem C stocks.

† In addition to the above citations Sanders et al. (2016) reported global carbon stock estimate of 11.2 Pg C extrapolating to 2 m soil depth. Additional studies limiting soil stocks to a 1 m depth include Rovai et al. (2018; 2.3 Pg C) and Hamilton and Friess (2018; 4.19 Pg C).

any strong relationship of depth with the other biotic and physical variables measured. Depth was only weakly correlated with porewater salinity ($r^2 = 0.17$), latitude ($r^2 = 0.14$) and precipitation ($r^2 = 0.17$; Appendix S1: Table S2).

Some of the differences in the mangrove soil C mass reported in the literature are reflective of the varying arbitrary depths to which soil C pools were measured or modeled. Some studies of mangrove C stocks and losses by land use have limited C stock measurements to the top 1 m of soils (e.g., Twilley et al. 2018, Hamilton and Friess 2018; Table 4). We found the mean soil carbon stock to be 741 Mg C/ha, which is similar to other studies that have either directly measured soil carbon stocks or extrapolated them to ≥ 2 m. (Table 4) Carbon pool estimates limited to a 1 m depth are less than half (i.e. <261 Mg C/ha; Table 4) of those estimated that included the entire profile.

Is the C below 1 m vulnerable to loss and therefore important to consider in terms of C accounting? When mangroves are converted to other land uses, the C losses are high because large quantities of C formerly stored in their suboxic/anoxic soils are subjected to accelerated rates of aerobic decomposition resulting in potentially large GHG emissions (Pendleton et al. 2012, Kauffman et al. 2017a, b). Land use in mangroves has been shown

to affect soil properties, including C contents, at depths of 1–3 m (Ong 1993, Kauffman et al. 2014, 2016). For example, soils >1 m depth in both cattle pastures and shrimp ponds converted from mangroves were found to be higher in bulk density but lower in C concentration, C density, and C mass (Kauffman et al. 2014, 2016, Arifanti et al. 2019). Soil C losses from depths >1 m can be quite significant. Kauffman et al. (2016) reported that soil C losses from conversion of mangrove to cattle pasture in Mexico totaled 399 Mg C/ha when sampling was limited to the top 1 m of soil. However, emissions were 889 Mg C/ha when losses included C in soils at depths up to 3 m. In other words, 55% of the soil C loss due to land-use change originated from soils >1 m depth. Arifanti et al. (2019) quantified the impact of disturbance on the loss of soil carbon in 10 paired mangrove/shrimp pond sites in Indonesia, and found that their estimates of C losses differed 8-fold depending on whether they measured the top 1 m of soil (44 Mg C/ha) or the top 3 m of soil (393 Mg C/ha).

Factors affecting ecosystem carbon stocks

At the global scale, the unexplained variation on the best multiple regression models ($R^2 \leq 0.67$) would suggest caution in using these models to predict TECS for

an individual site. However, the models reasonably predict the mean TECS of mangroves at larger scales when they include data from many sites (Fig. 9). Such data could be easily obtained from mangrove forest inventories where trees mass and soil depth would be measured in concert with data on precipitation, tidal range, and latitude. The utility of these models is not in estimating a single location, but in their capacity to provide a reasonable estimate at larger spatial scales based on inventory data from multiple sites.

Regression models provided reasonable estimates for all continents/regions with the exception of South America and the Middle East (Fig. 9). Here, the actual C stocks were much lower than the model estimates. The unifying similarities of these overestimated regions were a preponderance of coarse-textured soils. Texture is one of several factors that regulate organic matter preservation in soils, and has been hypothesized to be a primary explanation for relatively small C stocks in sandy soils (Schile et al. 2017). The single-most important factor required to preserve soil organic matter is anoxia, a condition that requires the microbial and plant O₂ consumption rate to exceed the O₂ resupply rate. Coarse-textured soils support rapid rates of water infiltration that allows porewater to rapidly drain and exchange with relatively O₂-rich floodwaters or air during tidal cycles. Rapid porewater exchange inhibits development of the reducing, anoxic conditions, and favors more complete oxidation of organic C to CO₂. Additionally, soil organic matter in coarse-textured soils are likely less protected by the soil mineral matrix and its stabilization mechanisms (e.g., interactions with minerals that protect organic matter against decomposition; see Baldock and Skjemstad 2000, Schmidt et al. 2011). Soil texture and influences on belowground C stocks remain a critical variable in need of further examination.

Latitude

A number of studies have examined relationships of mangrove C stocks and latitude with varying results (Sanders et al. 2016, Atwood et al. 2017, Twilley et al. 2018). Sanders et al. (2016) found a decrease in ecosystem C stocks when comparing tropical to subtropical sites. However, their subtropical data only included four sites from Australia. We found that mangroves occurring >20° N ($n = 28$) were significantly lower in ecosystem C stocks than those closer to the equator ($n = 165$; Fig. 7A). However, we interpret this to be an artifact of the fact that these high latitude sites were largely limited to the fringing mangroves on coarse-textured soils of the hyperarid Arabian Peninsula (Schile et al. 2017). There were no significant differences in equatorial mangroves (0°–2°), and those occurring within latitudinal bands of 2°–10° and 10°–20° where means for these latitudinal categories were all >900 Mg C/ha. Some of the lowest stocks were found in Gabon at 2° S (154 Mg C/ha) and Brazil at 4° S (145 Mg C/ha; Appendix S1: Table S1). In

contrast, some of the largest TECS were found in mangroves in Mexico at 18° N (2,099 Mg C/ha; Kauffman et al. 2016). Latitude only accounted for 17% of the variation in predicting TECS (Fig. 7A). Atwood et al. (2017) and Twilley et al. (2018) also found a poor relationship between latitude and soil organic C stocks. The small sample sizes for mangroves in subtropical zones coupled with interactions with rainfall and other factors, especially soil factors, suggest greater attention should be focused on the soil parameters that may influence C storage (e.g., redox conditions, clay mineralogy, and inorganic binding agents).

Global estimates of ecosystem carbon stocks

Given the importance of mangrove carbon stocks globally, several studies that have provided estimates (Table 4). These estimates are derived from both actual measurements and models based on climate, physical, and geopolitical boundaries (Table 4). Using the C stock means with the areal extent of mangroves by continent provided by Giri et al. (2011), we estimate that mangroves store about 11.7 Pg C. This includes an aboveground C stock of 1.6 Pg C and a global belowground C stock of 10.2 Pg C. Published global estimates of mangrove C storage range from 2.3 to 13.5 Pg C. (Table 4). It appears that the differences in estimates of total ecosystem carbon stocks based on climate, salinity, forest structure, geomorphology, or geopolitical boundaries is not as much of an influence as the choice of soil depth included in the estimate. Choosing to limit soils to a 1-m depth resulted in estimates of <5 Pg whereas those that included the soil profile >1-m depth resulted in global carbon stock estimates that exceeded 11.2 Pg C (Table 4).

Hutchison et al. (2014) estimated the total global mangrove aboveground biomass (AGB) to be 2.83 Pg, based on an average of 184.8 Mg/ha. In C stocks units, this would be approximately 1.36 Pg C based on mean aboveground of 88.7 Mg C/ha. Similarly, Simard et al. (2018) estimated the global mangrove AGB to be 1.75 Pg, based on an average AGB of 129.1 Mg/ha. These biomass estimates, based on modeling and remote sensing, are 13% and 46% lower than our global AGB estimate of 3.27 Pg (1.57 Pg C). These differences could be partially explained by our measurements of AGB that included all living and dead trees and downed wood. Our estimate of total AGB was 239 Mg/ha (114.9 Mg C/ha) and trees accounted for about 90% of this total (Appendix S1: Table S2). However, it is necessary to place these differences in the context of TECS. At least 85% of the total ecosystem stocks are belowground (Fig. 9), and the differences in these aboveground C stock estimates are less than the 95% confidence interval error term of the TECS (856 ± 64 Mg C/ha). In addition, the majority of GHG emissions resulting from land-use changes originates from losses of belowground C stocks. For example, Kauffman et al. (2017a) reported

that 84% of the estimated emissions from mangrove to shrimp pond conversion were attributed to declines in soil C pools. Thus, the use of aboveground C stocks alone is of limited value in determining ecosystem C stocks as well as emissions from land-cover change.

Geomorphic/coastal settings

In addition, to partitioning mangroves on the basis of geomorphology and forest stature, Twilley et al. (2018) and Rovai et al. (2018) examined soil C density on the basis of six coastal environmental settings, including deltas, estuaries, lagoons, composite deltas and lagoons, carbonate, and arheic settings. They reported that nearly one-half of the global mangrove area occurs as estuaries, followed by deltaic (small deltas and large rivers combined), lagoon, carbonate, and arheic coastal settings. For the most part, the estuarine mangroves of the present study fall into the deltaic tidal settings, while fringing mangroves would encompass the tidal settings lagoon, carbonate, and arheic. The estuarine mangroves of our study would have greater influences from rivers and flooding than fringing mangroves, which were not associated with rivers but still subject to tides and greater wave energy. Interestingly, Twilley et al. (2018) and Rovai et al. (2018) reported the greatest C densities in the carbonate and arheic (dry coastal) settings, with the lowest C densities in deltas. Using predictive equations rather than the actual measurements in our study resulted in TECS overestimates of 161% in the arheic sites (i.e., the Middle East sites in Fig. 9). This suggests that models derived from mangroves with different climates, soils, and hydrological features poorly predict TECS of mangroves from arheic settings. In contrast to model estimates, we found that the actual measurements of the arheic settings had the lowest ecosystem C stocks of all sites sampled (belowground C stocks = 180 and TECS = 217 Mg C/ha; Schile et al. 2017, Appendix S1: Table S1). Carbonate-dominated sites in the Yucatan, Mexico were also lower than the global mangrove mean (belowground C stocks = 491 Mg C/ha and TECS = 534 Mg C/ha; Adame et al. 2013, Appendix S1: Table S2). In contrast, the TECS of estuarine mangroves that included the large and small deltaic settings had the largest ecosystem C stocks (Appendix S1: Table S2; Fig. 3A; e.g., mangroves in deltas of the Pantanos de Centla, Mexico, and Indonesia). However, ecosystem C stocks of tall mangroves in those deltaic sites dominated by coarse-textured soils (south Gabon and Brazilian Amazon; Kauffman and Bhomia 2017, Kauffman et al. 2018b) had significantly lower C stocks suggesting caution in generalizing about C stocks on the basis of geomorphic position.

Partitioning mangroves on the basis of the coastal geomorphic and environmental settings would likely improve global estimates of the C stored in mangroves. However, measurements of C density alone are not sufficient to estimate ecosystem C stocks. To accurately

quantify ecosystem C stocks and emissions arising from these stocks as a consequence of land-use and climate change, measurements of soil depth, soil C density, and aboveground stocks are critical. Given the value of mangroves as global C sinks, the disproportionate GHG emissions when disturbed and the other important ecosystem services they provide, their conservation, restoration, and inclusion in adaptation and mitigation strategies are warranted.

ACKNOWLEDGMENTS

We wish to thank the landowners, fishers, and coastal inhabitants throughout the world who made this study possible by sharing their knowledge and understanding of the mangrove ecosystems in which they live. We also thank the numerous field and laboratory technicians who contributed to this paper. Many of the plots were established as part of the Sustainable Wetlands Adaptation and Mitigation Project (SWAMP) funded by the United States Agency for International Development (MTO 069018). T. O. Ferreira was supported by CNPq, grant number 308288/2014-9. A. F. Bernardino was supported by CAPES, CNPq, and FAPES grants N 441243/2016-9; 79054684/17; 301161/2017-8. This is contribution #05 from the PELD-HCES program. This is contribution #37 from the Smithsonian's MarineGEO Network. We also thank James Peterson (USGS) for advice and assistance with statistical analyses and predictive modeling. Finally, we acknowledge Chris Heider for initial collaboration on development of methodological approaches, and James Fourqurean and Sara Wilson, Florida International University for analyses of much of the soil organic C in this study.

LITERATURE CITED

- Adame, M. F., J. B. Kauffman, I. Medina, J. N. Gamboa, O. Torres, J. Caamal, M. Reza, and J. A. Herrera-Silveira. 2013. Carbon stocks of tropical coastal wetlands within the karstic landscape of the Mexican Caribbean. *PLoS ONE* 8:e56569.
- Adame, M. F., C. Teutli, N. S. Santini, J. P. Caamal, A. Zaldívar-Jiménez, R. Hernández, and J. A. Herrera-Silveira. 2014. Root biomass and production of mangroves surrounding a karstic oligotrophic coastal lagoon. *Wetlands* 34:479–488.
- Alongi, D. M. 2002. Present state and future of the world's mangrove forests. *Environmental Conservation* 29:331–349.
- Alongi, D. M. 2012. Carbon sequestration in mangrove forests. *Carbon Management* 3:313–322.
- Alongi, D. M. 2014. Carbon cycling and storage in mangrove forests. *Annual Review of Marine Sciences* 6:195–219.
- Arifanti, V. B., J. B. Kauffman, D. Hadriyanto, D. Murdiyarto, and R. Diana. 2019. Carbon dynamics and land use carbon footprints in mangrove- converted aquaculture: the case of the Mahakam Delta, Indonesia. *Forest Ecology and Management* 432:17–29.
- Atwood, T. B., et al. 2017. Global patterns in mangrove soil carbon stocks and losses. *Nature Climate Change* 7:523–528.
- Baldock, J. A., and J. O. Skjemstad. 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry* 31:697–710.
- Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81:169–193.
- Donato, D. C., J. B. Kauffman, R. Mackenzie, A. Ainsworth, and A. Pflieger. 2012. Whole-island carbon stocks in the

- tropical Pacific: implications for mangrove conservation and upland restoration. *Journal of Environmental Management* 97:89–96.
- Donato, D. C., J. B. Kauffman, D. Murdiyarto, S. Kurnianto, M. Stidham, and M. Kanninen. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature GeoScience* 4:293–297.
- Duarte, C. M., I. J. Losada, I. E. Hendriks, I. Mazarrasa, and N. Marba. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change* 3:1970.
- Duke, N. C., et al. 2007. A world without mangroves? *Science* 317:41–42.
- FAO. 2007. The world's mangroves 1980-2005. FAO Forestry Paper (Volume 153). Food and Agriculture Organization of the United Nations, Rome, Italy.
- Fourqurean, J. W., et al. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5:505–509.
- Fourqurean, J. W., et al. 2014. Coastal Blue Carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses. In J. Howard, S. Hoyt, K. Isensee, M. Telszewski, and E. Pidgeon, editors. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, Virginia, USA, 184 pp.
- Friess, D. A. 2016. Mangrove forests. *Current Biology* 26: R739–R755.
- Giesen, W., S. Wulffraat, M. Zieren, and L. Scholten. 2007. Mangrove guidebook for Southeast Asia. Food and Agricultural Organization and Wetlands International, Bangkok, Thailand.
- Giri, C. E., L. Ochieng, L. L. Tieszen, Z. Zhu, A. Singh, T. Loveland, J. Masek, and N. Duke. 2011. Status and distribution of mangrove forests of the world using Earth observation satellite data. *Global Ecology and Biogeography* 20:154–159.
- Giri, C., Z. Zhu, L. L. Tieszen, A. Singh, S. Gillette, and J. A. Kelmelis. 2008. Mangrove forest distributions and dynamics (1975-2005) of the tsunami-affected region of Asia. *Journal of Biogeography* 35:519–528.
- Hamilton, S. E., and D. Casey. 2016. Creation of a high spatio-temporal resolution global database of continuous mangrove forest cover for the 21st century (CGMFC-21). *Global Ecology and Biogeography* 25:729–738.
- Hamilton, S. E., and D. A. Friess. 2018. Global carbon stocks and potential emissions due to mangrove deforestation from 2000 to 2012. *Nature Climate Change*. <https://doi.org/10.1038/s41558-018-0090-4>
- Howard, J., A. Sutton-Grier, D. Herr, J. Kleypas, E. McLeod, E. Pidgeon, and S. Simpson. 2017. Clarifying the role of coastal and marine systems in climate mitigation. *Frontiers in Ecology and Environment*. <https://doi.org/10.1002/fee.1451>
- Hutchison, J., A. Manica, R. Swetnam, A. Balmford, and M. Spalding. 2014. Predicting global patterns in mangrove forest biomass. *Conservation Letters* 7:233–240.
- Intergovernmental Panel on Climate Change (IPCC). 2014. 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: Wetlands. T. Hiraishi, T. , Krug, , K. Tanabe, N. Srivastava, J. Baasansuren, M. Fukuda, and T. G. Troxler, editors. IPCC, Switzerland.
- Jardine, S. L., and J. V. Siikamäki. 2014. A global predictive model of carbon in mangrove soils. *Environmental Research Letters* 9:104013.
- Jobse, J. C. 2008. Impacts of forest-to-agriculture conversion on aboveground and soil carbon and nitrogen stocks along a bioclimatic gradient in Costa Rica. Dissertation. Oregon State University, Corvallis, Oregon, USA. <https://ir.library.oregonstate.edu/downloads/mp48sg125>
- Kauffman, J. B., V. B. Arifanti, A. F. Bernardino, T. O. Ferreira, D. Murdiyarto, M. C. Cifuentes, and J. Norfolk. 2018a. And details for land-use carbon footprints arise from quantitative and replicated studies. *Frontiers in Ecology and the Environment* 1749:12–13.
- Kauffman, J. B., V. B. Arifanti, H. Hernandez Trejo, M. C. Jesus Garcia, J. Norfolk, M. Cifuentes, D. Hadriyanto, and D. Murdiyarto. 2017a. The jumbo carbon footprint of a shrimp: carbon losses from mangrove deforestation. *Frontiers in Ecology and the Environment* 2017:15.
- Kauffman, J. B., A. F. Bernardino, T. O. Ferreira, N. W. Bolton, L. E. O. Gomes, and G. N. Nobrega. 2017b. Shrimp ponds lead to massive loss of soil carbon and greenhouse gas emissions in northeastern Brazilian mangroves. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.4079>
- Kauffman, J. B., A. F. Bernardino, T. O. Ferreira, L. R. Giovanoni, L. E. O. Gomes, D. Romero, L. C. Z. Jimenez, and F. Ruiz. 2018b. Carbon stocks of mangroves and salt marshes of the Amazon Region. Brazil. *Biology Letters* 14:20180208.
- Kauffman, J. B., and R. K. Bhomia. 2017. Ecosystem carbon stocks of mangroves across broad environmental gradients in West-Central Africa: global and regional comparisons. *PLoS ONE* 12:e0187749.
- Kauffman, J. B., and D. C. Donato. 2012. Protocols for the measurement, monitoring, & reporting of structure, biomass and carbon stocks in mangrove forests. Working Paper 86. Center for International Forest Research. CIFOR, Bogor, Indonesia.
- Kauffman, J. B., C. Heider, T. Cole, K. A. Dwire, and D. C. Donato. 2011. Ecosystem C pools of Micronesian mangrove forests: implications of land use and climate change. *Wetlands* 31:343–352.
- Kauffman, J. B., C. Heider, J. Norfolk, and F. Payton. 2014. Carbon stocks of intact mangroves and carbon emissions arising from their conversion in the Dominican Republic. *Ecological Applications* 24:518–527.
- Kauffman, J. B., H. Hernandez Trejo, M. C. Jesus Garcia, C. Heider, and W. Contreras. 2016. Carbon stocks of mangroves and losses arising from their conversion to cattle pastures in the Pantanos de Centla, Mexico. *Wetlands Ecology and Management*. <https://doi.org/10.1007/s11273-015-9453-z>
- Komiyama, A., S. Pongparn, and S. Kato. 2008. Common allometric equations for estimating the tree weight of mangroves. *Journal of Tropical Ecology* 21:471–477.
- Krauss, K. W., D. R. Cahoon, J. A. Allen, K. C. Ewel, J. C. Lynch, and N. Cormier. 2010. Surface elevation change and susceptibility of different mangrove zones to sea-level rise on Pacific high islands of Micronesia. *Ecosystems* 13:129–143.
- Lugo, A. E., and S. C. Snedaker. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5:39–64.
- McLeod, K. W., G. L. Chmura, S. Bouillon, R. Salm, M. Bjork, C. M. Duarte, C. E. Lovelock, H. Schlesinger, and B. R. Silliman. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment* 9:552–560.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C., USA.
- Murdiyarto, D., J. Purbopuspito, J. B. Kauffman, M. W. Warren, S. Sasmito, D. C. Donato, S. Manuri, H. Krismawati, S. Taberima, and S. Kurnianto. 2015. The potentials of Indonesian mangrove forests for global climate change mitigation. *Nature Climate Change*. <https://doi.org/10.1038/nclimate2734>
- Murray, M. R., S. A. Zisman, P. A. Furley, D. M. Munro, J. Gibson, J. Ratter, S. Bridgewater, C. D. Mity, and C. J. Place.

2003. The mangroves of Belize. Part 1: distribution, composition and classification. *Forest Ecology and Management* 174:265–279.
- Ong, J. E. 1993. Mangroves - a carbon source and sink. *Chemosphere* 26:10971107.
- Pendleton, L., et al. 2012. Estimating global “blue carbon” emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS ONE* 7:e43542.
- Polidoro, B. A., et al. 2010. The loss of species: mangrove extinction risk and geographic areas of global concern. *PLoS ONE* 5:e10095.
- Price, J. T., and R. F. Warren. 2016. Review of the potential of “blue carbon” activities to reduce emissions. 1104872/AVOID2 WPE.2 Report 1. Available at: <http://avoid-net-uk.cc.ic.ac.uk/wpcontent/uploads/delightfuldownloads/2016/03/Literature-review-of-the-potential-ofbluecarbon-activities-to-reduce-emissions-AVOID2-WPE2.pdf>
- Rovai, A. S., R. R. Twilley, E. Castañeda-Moya, P. Riul, M. Cifuentes-Jara, M. Manrow-Villalobos, P. A. Horta, J. C. Simonassi, A. L. Fonseca, and P. R. Pagliosa. 2018. Global controls on carbon storage in mangrove soils. *Nature Climate Change* 8:534–538.
- Sanderman, J., et al. 2018. A global map of mangrove forest soil carbon at 30 m spatial resolution. *Environmental Research Letters* 13:055002.
- Sanders, C. J., D. T. Maher, D. R. Tait, D. Williams, C. Holloay, J. Z. Sippo, and I. R. Santos. 2016. Are global mangrove carbon stocks driven by rainfall? *Journal of Geophysical Research: Biogeoscience* 121:2600–2609.
- Schile, L. M., J. B. Kauffman, S. Crooks, J. Fourqurean, J. Glavan, and J. P. Megonigal. 2017. Limits on carbon sequestration in arid blue carbon ecosystems. *Ecological Applications* 27:859–874.
- Schmidt, M. W., M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, and P. Nannipieri. 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478:49.
- Servino, R. N., L. E. O. Gomes, and A. F. Bernardino. 2018. Extreme weather impacts on tropical mangrove forests in the Eastern Brazil Marine Ecoregion. *Science of the Total Environment* 628–629:233–240.
- Siikamäki, J., J. N. Sanchirico, and S. L. Jardine. 2012. Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences USA* 109:14369–14374.
- Simard, M., L. Fatoyinbo, C. Smetanka, V. H. Rivera-Monroy, E. Castañeda-Moya, N. Thomas, and T. Van der Stocken. 2018. Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. *Nature Geoscience*. <https://doi.org/10.1038/s41561-018-0279-1>
- Sippo, J. Z., C. E. Lovelock, I. R. Santos, C. J. Sanders, and D. T. Maher. 2018. Mangrove mortality in a changing climate: an overview. *Estuarine Coastal and Shelf Science* 215:241–249.
- Snedaker, S. C., and E. J. Lahmann. 1988. Mangrove understory absence: a consequence of evolution? *Journal of Tropical Ecology* 4:311–314.
- Spalding, M. D., M. Kainuma, and L. Collins. 2010. *World atlas of mangroves*. Earthscan, London, UK.
- Twilley, R. R., A. A. Rovai, and P. Riul. 2018. Coastal morphology explains global blue carbon distributions. *Frontiers in Ecology and the Environment* 16:1–6.
- UNEP. 2014. *The importance of mangroves to people: a call to action* (J. van Bochove, E. Sullivan, and T. Nakamura, editors). United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, UK., 128pp.
- Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science* 14:20–26.
- Wolanski, E., Y. Mazda, and P. Ridd. 1992. Mangrove hydrodynamics. Pages 43–62 in A. L. Robertson, and D. M. Alongi, editors. *Tropical mangrove ecosystems*. American Geophysical Union, Washington, D.C., USA.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1405/full>