

# Ecosystem carbon stocks of mangrove forests along the Pacific and Caribbean coasts of Honduras

Rupesh K. Bhomia · J. Boone Kauffman · Tyler N. McFadden

Received: 23 January 2015 / Accepted: 1 February 2016 / Published online: 8 February 2016  
© Springer Science+Business Media Dordrecht 2016

**Abstract** Among the many ecosystem services provided by mangrove ecosystems, their role in carbon (C) sequestration and storage is quite high compared to other tropical forests. Mangrove forests occupy less than 1 % of tropical forested areas but account for approximately 3 % of global carbon sequestration by tropical forests. Yet there remain many areas where little data on the size and variation of mangrove C stocks exist. To address this gap and examine the range of C stocks in mangroves at landscape scales, we quantified C stocks of Honduran mangroves along the Pacific and Caribbean coasts and the Bay Islands. We also examined differences in ecosystem C stocks due to size and structure of mangrove vegetation found in Honduras. Ecosystem C stocks ranged from 570 Mg C ha<sup>-1</sup> in the Pacific coast to ~1000 Mg C ha<sup>-1</sup> in Caribbean coast and the Bay Islands. Ecosystem C stocks on the basis of mangrove structure were 1200, 800 and 900 Mg C ha<sup>-1</sup>, in low, medium and tall mangroves, respectively. We did not find significant differences in ecosystem C stocks on the basis of location (Pacific coast, Caribbean coast and Bay Islands) or mangrove type (low, medium and tall).

Mangrove soils represented the single largest pool of total C in these ecosystems, with 87, 81 and 94 % at the Pacific coast, Caribbean coast and the Bay Islands, respectively. While there were no significant differences in total ecosystem stocks among mangrove types, there were differences in where carbon is stored. Mangrove soils among low, medium and tall mangroves contained 99, 93 and 80 % of the total ecosystem C stocks. In addition, we found a small yet significant negative correlation between vegetation C pools and pore water salinity and pH at the sampled sites. Conversion of mangroves into other land use types such as aquaculture or agriculture could result in losses of these soil C reserves due to mineralization and oxidation. Coupled with their other ecosystem services, an understanding of the size of mangrove ecosystem C stocks underscores their values in the formulation of conservation and climate change mitigation strategies in Central America.

**Keywords** Coastal ecosystems · Land use · Shrimp ponds · Organic soils · Climate change mitigation · Carbon dynamics · REDD+

---

R. K. Bhomia (✉) · J. B. Kauffman · T. N. McFadden  
Department of Fisheries and Wildlife, Oregon State  
University, Corvallis, OR 97331, USA  
e-mail: rbhomia@ufl.edu

R. K. Bhomia · J. B. Kauffman  
Center for International Forestry Research (CIFOR),  
Bogor 16115, Indonesia

## Introduction

Coastal wetlands, particularly mangrove forests, provide a broad array of benefits that span the realm of regulating, provisioning, cultural and supporting

ecosystem services (Millennium Ecosystem Assessment 2005). In fiscal terms, mangrove ecosystem services are estimated to provide 14,000–16,000 USD  $\text{ha}^{-1} \text{y}^{-1}$  (Barbier et al. 2011), totaling 1.6 billion USD annually for all global mangrove areas combined (Polidoro et al. 2010). These services emanate from a wide range of characteristics that are found in mangroves. Mangrove vegetation assemblages provide habitats for terrestrial, estuarine and marine species and function as fish nurseries while supporting invaluable biodiversity (Nagelkerken et al. 2008; Luther and Greenberg 2009; MacKenzie and Cormier 2012). It is estimated that mangroves are the source of 10 % of the essential organic C inputs to the global oceans (Dittmar et al. 2006), which sustain complex biogeochemical processes and food dynamics within marine ecosystems. Mangroves also provide protection to coastal zones from erosion by dissipating tidal wave energy and functioning as natural barrier against the force of tropical storms (McIvor et al. 2012a, b; Sandilyan and Kathiresan 2015).

Mangrove forests cover <1 % of tropical forested areas but because of high rates of productivity, sequester an estimated 24 Tg C  $\text{y}^{-1}$ , which represents about 3 % of global C sequestration by tropical forests (Alongi 2012). Mangrove ecosystems have among the largest C stocks per unit area in the world, and majority of this C is stored in mangrove soils (Donato et al. 2011), where anoxic conditions due to presence of water prevent oxidation and encourage long-term storage of C. Mangroves' capacity to capture atmospheric C and store it for extended periods suggest they could be valuable ecosystems for inclusion in climate change adaptation and mitigation strategies.

Despite the many ecosystem services mangrove provide, deforestation and land conversion pressures on these coastal ecosystems are high because approximately 44 % of global population resides within 150 km of the coastline (Cohen et al. 1997; Duarte et al. 2008). Approximately 20–35 % of global mangrove area has been lost since 1980 (FAO 2007). An immediate effect of such extensive habitat loss is an elevated risk of extinction for approximately 40 % of endemic animal species (e.g. Proboscis monkey *Nasalis larvatus*, Pygmy three-toed sloth *Bradypus pygmaeus*) that are found exclusively in mangrove habitats (Luther and Greenberg 2009). The most common pressure that mangrove ecosystems

experience is conversion into other land-use regimes such as aquaculture, agriculture and urban development (Valiela et al. 2001; Spalding et al. 2010). Mangrove deforestation also results in release of greenhouse gases, which may be as high as 1–9 % of global emissions arising from tropical deforestation (Donato et al. 2011). If remained unchecked, ongoing decline in global mangrove areas will lead to loss in ecosystem functionality over the next 100 years (Polidoro et al. 2010), causing negative environmental and economic consequences, with the most severe impacts occurring in the developing countries where significant proportions of mangroves exist. Recent studies revealing the massive amounts of C storage in mangroves (Donato et al. 2012) have brought the role of mangroves in climate change mitigation and adaptation programs into sharper focus and highlighted the urgent need to stall global mangrove decline (IPCC 2014; UNEP 2014). Quantification of mangrove C stocks is necessary for their inclusion in nationally appropriate climate change mitigation activities (NAMAs) such as Reduced Emissions from deforestation and degradation (REDD+) (Murdiyarso et al. 2012).

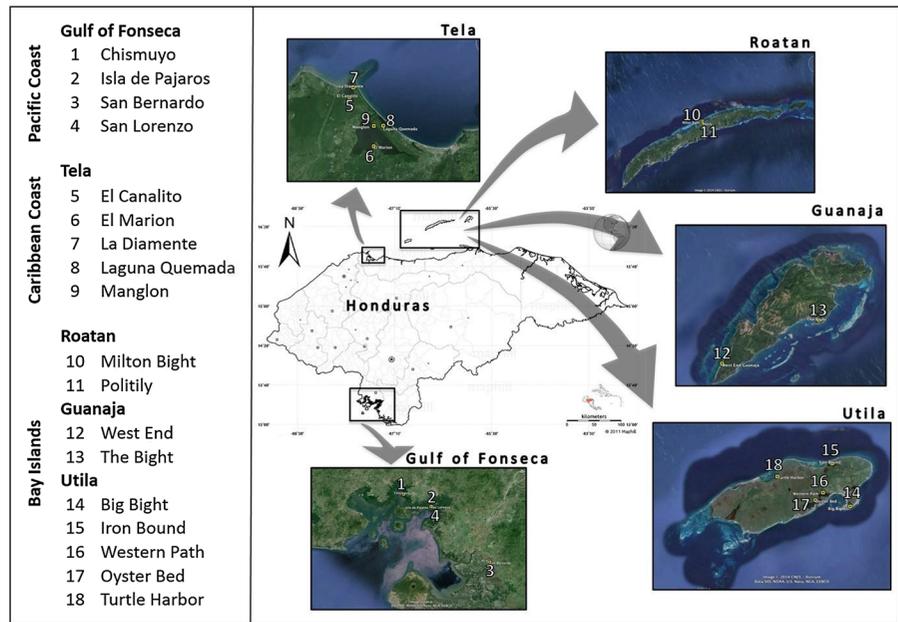
The focus of our study was to quantify C stocks in the mangroves across the country of Honduras encompassing a wide range of varying tidal, climatic, and geomorphic conditions. We examined differences in C storage in different locations/regions and the wide array of geomorphic settings resulting in varying mangrove structure and composition. This includes sites from the Caribbean and Pacific coasts on the Honduran mainland as well as the three Bay Islands located in the Caribbean. The mangrove stands at these locations were categorized as low, medium and tall based on the estimated height of mangrove trees. We hypothesized that variability in total C stocks from one location to another will be a function of above-ground structure, climate and soil properties (salinity, pH, etc.).

## Materials and methods

### Study area

In 2013, we sampled 18 coastal sites along the Pacific and Caribbean coasts and the three Bay Islands of Honduras (Fig. 1). Honduras was an ideal location to

**Fig. 1** Mangrove sampling locations in Honduras along Pacific coast, Caribbean coast and the three Bay Islands. (Image source: Google Earth ©2014)



examine the differences in mangrove C stocks due to differing oceanic influences (Atlantic vs. Pacific), variable geomorphic settings (coastal vs. island), and a range of tidal and climatic conditions. The spatial expanse of sampling sites also allowed quantification and comparison of mangrove C stocks in three types of mangrove vegetation: (a) Tall mangroves with a mean height >10 m (7 sites); (b) Medium mangroves with a mean height ranging from 3 to 10 m (8 sites); and c) Low mangroves with a mean height <3 m (3 sites; Table 1). The sampling sites were in the Gulf of Fonseca on the Pacific coast, Los Micos Lagoon in the Jeannette Kawas National Park, Tela on the Caribbean coast, and three Bay Islands (Roatán, Guanaja and Utila) located north of mainland Honduras within the Caribbean Sea. In this article, these three locations are identified as the Pacific coast, the Caribbean coast and the Bay Islands, respectively.

The Pacific coast has a tropical wet and dry climate with a distinct dry season from November through April. The Gulf of Fonseca is a large bay on the Pacific coasts of Honduras, El Salvador and Nicaragua. Annual precipitation in Gulf of Fonseca ranges from 1500 to 2000 mm and mean annual air temperature is about 30 °C (Vergne et al. 1993). The region contains a diverse variety of coastal ecosystems, including mangroves, marshes, mudflats, and lagoons. Approximately 70,000 ha of the Honduran Gulf of Fonseca

was designated as a Ramsar Wetland of International Importance in 1999.<sup>1</sup> Total mangrove area within the Gulf of Fonseca was estimated at 47,800 ha in 1999 (Rivera-Monroy et al. 2002) however this region has experienced widespread conversion of mangroves into aquaculture (shrimp) farms. During 1985–2013, approximately 5800 ha of mangrove forests were lost to aquaculture development (Dewalt et al. 1996; Chen et al. 2013).

The 753 km Caribbean coast of northern Honduras stretches from the border with Guatemala in the west to the border with Nicaragua in the east and also encompasses a number of offshore islands systems—the Bay Islands. The mangroves in the northern coast of Honduras are located around coastal lagoons and riverine deltas. Our sampling sites were located around Los Micos Lagoon, Jeannette Kawas National Park, where predominantly tall dense mangroves were found. The Caribbean coast and the Bay islands have a tropical wet climate with consistently high temperatures and humidity, and rainfall fairly evenly distributed throughout the year. Monthly mean air temperatures around Tela ranges from daily highs of 28–32 °C to daily lows of 20–24 °C and annual rainfall range is about 2800–3000 mm.

<sup>1</sup> <http://www.ramsar.org/wetland/honduras>.

**Table 1** Characteristics of sampling locations within Honduras (mean  $\pm$  SE of the mean)

Location	Site	Forest type	Latitude longitude	pH	Salinity (ppt)	Soil depth (cm) <sup>a</sup>	Dominant species	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Tree density (live trees ha <sup>-1</sup> )
Pacific Coast	Chismuyo	Tall	N 13°25.655' W 87°36.691'	7 $\pm$ 0.2	22.3 $\pm$ 0.7	>270	<i>Rhiz</i>	11.5 $\pm$ 3.3	1856 $\pm$ 572
	Isla de Pajaros	Medium	N 13°22.011' W 87°28.231'	6.6 $\pm$ 0.2	33 $\pm$ 0.8	182	<i>Rhiz/Lag</i>	3.8 $\pm$ 0.7	689 $\pm$ 93
	San Bernardo	Tall	N 13°05.868' W 87°11.017'	7.5 $\pm$ 0.1	87 $\pm$ 1.8	>200	<i>Avi</i>	4.8 $\pm$ 1.7	3573 $\pm$ 1307
	San Lorenzo	Medium	N 13°22.057' W 87°28.538'	6.8 $\pm$ 0.1	36.5 $\pm$ 1.5	120	<i>Rhiz</i>	3.3 $\pm$ 0.7	2274 $\pm$ 1008
Caribbean Coast	El Canalito	Tall	N 15°52.452' W 87°38.440'	6.9 $\pm$ 0	3.3 $\pm$ 0.5	>270	<i>Lag/Rhiz</i>	23.8 $\pm$ 6.7	520 $\pm$ 111
	El Marion	Tall	N 15°47.123' W 87°35.743'	7 $\pm$ 0.1	–	>270	<i>Lag</i>	17.7 $\pm$ 4.4	1104 $\pm$ 228
	La Diamante	Medium	N 15°53.475' W 87°38.007'	6.4 $\pm$ 0.2	6.3 $\pm$ 2.5	200	<i>Rhiz/Lag/Avi</i>	22.2 $\pm$ 2.6	1072 $\pm$ 154
	Laguna Quemada	Tall	N 15°49.331' W 87°34.681'	5.8 $\pm$ 0.1	2.2 $\pm$ 1	240	<i>Rhiz/Lag</i>	48.6 $\pm$ 7.9	476 $\pm$ 83
	Manglon	Tall	N 15°49.335' W 87°35.710'	5.5 $\pm$ 0.1	0.3 $\pm$ 0.3	235	<i>Rhiz/Lag</i>	32.9 $\pm$ 4.5	498 $\pm$ 72
Bay Islands	Milton Bight	Medium	N 16°24.254' W 86°23.929'	7.7 $\pm$ 0.2	22.5 $\pm$ 3.9	160	<i>Rhiz</i>	9 $\pm$ 2.7	1321 $\pm$ 175
	Politily	Tall	N 16°24.078' W 86°23.915	8.1 $\pm$ 0	31.2 $\pm$ 0.3	>270	<i>Rhiz</i>	20.5 $\pm$ 2.7	574 $\pm$ 61
	West End	Medium	N 16°25.101' W 85°56.639'	7.2 $\pm$ 0.2	27.3 $\pm$ 1	178	<i>Rhiz</i>	9.6 $\pm$ 2.3	1082 $\pm$ 263
	The Bight	Low	N 16°27.286' W 85°51.788'	7.3 $\pm$ 0	39.3 $\pm$ 0.7	>270	<i>Rhiz</i>	1.4 $\pm$ 0.3	1857 $\pm$ 393
	Big Bight	Low	N 16°05.312' W 86°53.311'	8.4 $\pm$ 0	30 $\pm$ 0	>270	<i>Rhiz</i>	7 $\pm$ 3.4	44,299 $\pm$ 17,217
	Iron Bound	Medium	N 16°07.152' W 86°54.092'	7.2 $\pm$ 0	41.8 $\pm$ 1.3	148	<i>Avi</i>	13.3 $\pm$ 1.5	1029 $\pm$ 166
	Western Path	Medium	N 16°05.899' W 86°54.532'	8.4 $\pm$ 0.1	31.3 $\pm$ 0.3	260	<i>Avi</i>	5.6 $\pm$ 1.8	3049 $\pm$ 1088
	Oyster Bed	Low	N 16°05.559' W 86°54.852'	7.5 $\pm$ 0.1	33.3 $\pm$ 1.3	>270	<i>Rhiz</i>	10.7 $\pm$ 1.7	28,914 $\pm$ 1081
	Turtle harbor	Medium	N 16°06.602' W 86°56.505'	7.9 $\pm$ 0.2	39.8 $\pm$ 0.5	140	<i>Rhiz</i>	4.1 $\pm$ 1.4	574 $\pm$ 146

Estimated height for tall mangroves was >10 m (7 sites), medium mangroves 3–10 m (8 sites), and low mangroves <3 m (3 sites). Dashes (–) indicates absence of data

*Rhiz* = *Rhizophora mangle*, *Lag* = *Laguncularia racemosa*, *Avi* = *Avicennia germinans*

<sup>a</sup> Soil depth measured using a 270 cm long depth probe. Data shown here from sub-plot 3, approximate midway of the sampling transect

The Bay Islands—Roatán, Guanaja, and Utila lie 30–50 km north of the Caribbean coast of Honduras. Roatán is the largest island (133 km<sup>2</sup>) and contains approximately 400 ha of mangrove forests on the

eastern extension of the island. Guanaja is smaller (57 km<sup>2</sup>) with approximately 300 ha of mangrove forests prior to 1998 when Hurricane Mitch impacted this island (McKee et al. 2007). Mangroves on

Guanaja were severely damaged by storm surges, flooding and high velocity winds that accompanied Hurricane Mitch. However impacts were relatively limited in the other two Bay islands and Caribbean and Pacific coast mangroves (Cahoon and Hensel 2002). The smallest of the three Bay Islands is the island of Utlia, which has mangroves along its northern coastline, interior areas and a few fragmented patches on the southern side along two lagoons (Jaxion-Harm et al. 2012). Air temperatures in the Bay Islands range from daily highs of 28–32 °C in the summer season to daily lows of 19–23 °C in winter season. Annual rainfall is about 2200–2500 mm. The tidal range was greater in the Pacific [1.8–2.3 m] than the Caribbean coast [0.35–0.5 m] (Harborne et al. 2001; Cahoon and Hensel 2002).

### Field sampling

Within each of the 18 sampled mangroves, we measured total ecosystem C stocks following methodologies outlined by Kauffman and Donato (2012). At each sampled site, six 7 m radius sub-plots were established 20 m apart along a 100 m transect in a perpendicular direction from the mangrove-ocean interface. At each sub-plot, we collected data necessary to calculate total C stocks derived from standing tree biomass, downed woody debris (dead wood on forest floor), belowground vegetation mass, and soils.

We determined vegetation mass and plant C pools through measurement of main stem diameter of the trees inside each of the six circular sub-plots at each sampling site. Trees >5 cm in diameter at 1.3 m in height (diameter at breast height, dbh) were measured inside the 7 m radius sub-plot, while trees <5 cm dbh were measured in a 2 m radius nested plot within the larger 7 m radius sub-plot. Main stem diameters of trees with prop roots (*Rhizophora* spp.) were measured at 30 cm above the highest prop root. Dead trees were categorized into specific classes (I, II and III) depending on decay status of the tree (Kauffman and Donato 2012). Class I dead trees were recently dead tree with majority of primary and secondary branches still intact, while class III dead tree contained only the main trunk with all of its branches lost. Class II category was assigned to a dead tree which showed presence of primary branches attached to the main trunk.

Downed wood debris were measured using the planar intercept technique (Brown 1974; Kauffman et al. 1995). In each of the 6 sub-plots at each site, we established 4 transects to determine the mass of downed wood. Downed wood  $\geq 7.6$  cm in diameter at the point of intersection was classified as 'large' and measured along the entire length of a 12 m long transect. Large wood debris were separated in two decay categories: sound and rotten. Wood debris that were  $\geq 2.5$  cm but  $< 7.6$  cm in diameter at the point of intersection were measured along the last 5 m of the transect. We did not measure wood debris smaller than 2.5 cm diameter as the total C contribution from this pool is relatively minimal. The understory or litter mass in mangroves is generally negligible (Snedaker and Lahmann 1988; Kauffman et al. 2011) and was not collected during this study.

At each sub-plot, soil samples were collected using an open faced peat auger consisting of a semi-cylindrical chamber with 22.95 cm<sup>2</sup> cross sectional area. The soil core was divided into five sections with depth intervals of 0–15, 15–30, 30–50, 50–100 and >100 cm. A relatively uniform 5 cm section of soil from these depth intervals was collected and brought to the laboratory for further analysis. Soil depth to parent material (marine sediments or rock) was measured at three locations around each sub-plot center by inserting a graduated aluminum pole. At sites where parent material was not encountered after inserting full length of the depth probe (270 cm), depth was recorded as >270 cm. The pore water which filled the cavity in the ground after removal of soil core was used for determining interstitial salinity and pH of mangrove soils. A portable handheld refractometer (VEE GEE STX-3, range 0–100 parts per thousand) and pH meter (Milwaukee Instruments, Inc, pH56, pH—Temperature meter) was used for measurements in the field.

### Ecosystem carbon stocks

The total ecosystem C stocks was defined as the sum of total organic C in vegetation, downed woody debris and soils to the bottom of the mangrove peat or 270 cm.

### *Vegetation and downed wood carbon stocks*

We computed aboveground tree biomass using species specific allometric equations developed in French

New Guinea by Fromard et al. (1998). Belowground tree mass was calculated by using a general allometric equation developed for mangroves by Komiyama et al. (2008). Species specific wood density ( $\text{g cm}^{-3}$ ) was obtained from the wood density database (Zanne et al. 2009) for belowground biomass calculations. We used  $0.776 \text{ g cm}^{-3}$  for *Avicennia germinans*,  $0.600 \text{ g cm}^{-3}$  for *Laguncularia racemosa* (Little and Wadsworth 1964) and  $0.840 \text{ g cm}^{-3}$  for *Rhizophora mangle* and *Rhizophora racemosa* (Malavassi 1992). The biomass of dead trees was calculated based upon its decay class. Biomass of status I dead trees was estimated to be 97.5 % of a live tree, status II was estimated to be 80 % of a live tree, and status III trees were estimated to represent 50 % of a live tree (Kauffman and Donato 2012). We converted dry biomass of trees, understory, and downed wood to C mass using biomass to carbon conversion ratios. Tree C was calculated by multiplying biomass by a factor of 0.47 for aboveground and 0.39 for belowground biomass (Kauffman and Donato 2012).

We used the specific gravity of downed wood as a measure of wood density for different wood classes based on Caribbean mangroves from Yucatan, Mexico as reported by Adame et al. (2013). For our calculations we used  $0.68 \pm 0.03$  and  $0.72 \pm 0.03 \text{ g cm}^{-3}$  respectively for sound medium and large wood debris and  $0.47 \pm 0.03 \text{ g cm}^{-3}$  for rotten large wood debris (Adame et al. 2013). Biomass calculations were carried out following the equations and biomass to total C conversion factor (0.50) as suggested in Kauffman and Donato (2012).

#### Soil carbon stocks

Each 5 cm of soil sample from various depth classes had a constant volume ( $114.74 \text{ cm}^3$ ) and was dried to a constant weight at  $60 \text{ }^\circ\text{C}$  using an oven in the lab. Dry sample weight was used to determine soil bulk density. Dry soil samples were ground using mortar and pestle after removing any large wood pieces or root fragments. Total C and nitrogen concentrations were then determined using a Thermo Flash EA 1112 series NC Soil Analyzer.

The geomorphic setting, higher pH, proximity of coral reefs and apparent shell fragments in the samples from the Bay Islands prompted us to test a subset of soil samples from three Bay Islands for presence of

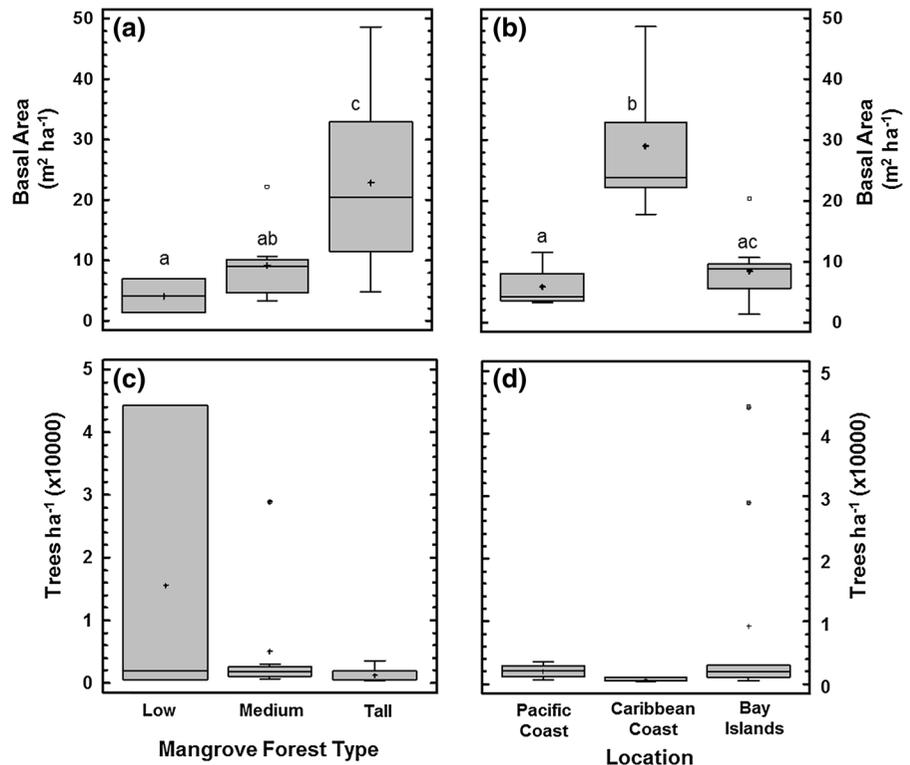
carbonates. Given the geomorphic settings and apparent fluvial and allochthonous origin of the soils for the Pacific and Caribbean coastal site as well as their low pH, and apparent absence of marine fragments this was not necessary at these sites. Inorganic C was absent in the surface 30 cm of the Bay Island mangrove soils but a considerable amount was detected in lower soil depths (up to 7 % of the total carbon in soils below 100 cm depth; Appendix Table 4). Mean inorganic C (%) was subtracted from the soil C concentration (%) to report only organic C in mangrove soils from Bay Islands. We subtracted 2.9, 3.5 and 7.4 % of the total soil C (%) for 30–50, 50–100 and >100 cm depth interval soil samples.

Soil C pools were obtained as the product of soil carbon concentration, bulk density, and plot specific soil depth measurements. Carbon mass from each soil section were added up to determine total C stocks at each sampling location. We used 270 cm as the maximum soil depth for calculating soil C stocks at sites where mangrove soils were deeper than the depth limit of our probe (270 cm).

#### Statistics

Differences in basal area, tree density and ecosystem C stocks among different locations (Pacific coast, Caribbean coast and Bay Islands) and mangrove types (low, medium and tall) were separately tested with one-way analysis of variation (ANOVA). In the first case mangrove type was the fixed effect while in second case, location was the fixed effect, while sampling site (nested in 'mangrove type' or 'location') and sub-plot (nested in site) were the random effects of the model. Data normality was assessed by Kolmogorov–Smirnov or Shapiro–Wilk tests. Tukey's honestly significant difference (HSD) procedure was performed to identify significantly different means where ANOVA results were significant. Correlation between soil pore water salinity and pH and vegetation C stocks was determined and significance was tested by a Durbin–Watson test. Also, correlation between mangrove soil bulk density and C concentration was determined using samples across all sites and all depth horizons. All statistical analyses were performed using STATGRAPHICS Centurion (XVI version). Data in this article are reported as mean  $\pm$  SE, else noted otherwise.

**Fig. 2** Basal area ( $\text{m}^2 \text{ha}^{-1}$ ) and tree density ( $\text{tree ha}^{-1}$ ) differences between mangrove forest type (low, medium and tall) and location (Pacific coast, Caribbean coast and Bay Islands). Basal area was significantly higher in tall mangroves (a) and in the Caribbean coast mangroves (b). Tree density was not significantly different among different mangrove types or locations (c and d) (Tukey's HSD;  $p < 0.05$ )



## Results

### Structural composition of mangrove forests

The most common mangrove species that we encountered were *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia germinans* (L.) Stearn (Avicenniaceae) and *Laguncularia racemosa* (L.) Gaertn (Combretaceae) (Table 1). The Pacific coast sites were dominated by medium and tall mangroves, while Caribbean coast had predominantly tall mangroves. The Bay Islands mainly had medium and low mangroves. Mean basal area for tall mangrove ( $22.8 \pm 5.4 \text{ m}^2 \text{ha}^{-1}$ ) was significantly higher than small ( $4.1 \pm 1.6 \text{ m}^2 \text{ha}^{-1}$ ) and medium mangroves ( $9.1 \pm 2.1 \text{ m}^2 \text{ha}^{-1}$ ;  $F_{2, 15} = 5.06$ ,  $p = 0.020$ ; Fig. 2). Basal area of Caribbean mangroves was significantly higher ( $29.1 \pm 5.5 \text{ m}^2 \text{ha}^{-1}$ ) than the Pacific coast ( $5.8 \pm 1.9 \text{ m}^2 \text{ha}^{-1}$ ) and Bay Island mangroves ( $8.5 \pm 1.8 \text{ m}^2 \text{ha}^{-1}$ ;  $F_{2, 15} = 14.3$ ,  $p = 0.000$ ; Fig. 2). The highest basal area was found at tall mangrove—Laguna Quemada ( $48.6 \text{ m}^2 \text{ha}^{-1}$ ) located on the Caribbean coast while the lowest basal area was observed at medium mangrove—San Lorenzo ( $3.3 \text{ m}^2 \text{ha}^{-1}$ ) located on the Pacific coast (Table 1).

Mangrove tree densities at Bay Islands' sites were close to the high range of distribution encountered in Honduras however no significant difference was found in tree densities among mangrove types ( $F_{2, 15} = 1.7$ ,  $p = 0.214$ ) or three sampling locations ( $F_{2, 15} = 1.07$ ,  $p = 0.368$ ; Fig. 2). Mangrove tree density ranged from 500 trees  $\text{ha}^{-1}$  in a tall mangrove site, Laguna Quemada on Caribbean coast to  $>40,000$  trees  $\text{ha}^{-1}$  in a low mangrove site, Big Bight in Bay Islands. Tree densities in tall, medium and low mangroves ranged from 3570, 690–3050, and 1860–44,300 trees  $\text{ha}^{-1}$ , respectively (Table 1).

### Vegetation carbon stocks

Mean total vegetation C stocks (including above-ground and below-ground pools) from the Pacific coast, Caribbean coast and Bay Islands were  $71 \pm 36$ ,  $196 \pm 54$  and  $53 \pm 16 \text{ Mg C ha}^{-1}$ , respectively (Table 2). The aboveground vegetation C pools at Caribbean coast ( $147 \pm 43 \text{ Mg C ha}^{-1}$ ) were significantly higher than the aboveground vegetation C pools at Bay Islands ( $36 \pm 12 \text{ Mg C ha}^{-1}$ ;  $F_{2,15} = 5.5$ ,  $p = 0.015$ ). The fraction of total ecosystem C

**Table 2** Carbon stocks in the measured ecosystem compartments from three different type of mangroves and from three locations in Honduras

Mangroves	Number of sites	Carbon stocks in various ecosystem compartments (Mg C ha <sup>-1</sup> )					Fraction of total ecosystem C (%)		
		Tree	Downed wood	Soil (0–100 cm depth)	Soil (below 100 cm)	Total ecosystem (tree + downed wood + soil)	Trees	Downed wood	Soils
Type									
Low	3	15 ± 6	3 ± 1	537 ± 87	667 ± 119	1222 ± 210	1.2	0.2	98.5
Medium	8	54 ± 12	4 ± 1	411 ± 45	352 ± 91	798 ± 138	6.7	0.5	92.8
Tall	7	179 ± 41	9 ± 1	322 ± 44	427 ± 93	933 ± 159	19.2	1.0	79.8
Location									
Pacific coast	4	70 ± 37	5 ± 2	258 ± 46	242 ± 64	570 ± 128	12.3	0.9	86.8
Caribbean coast	5	196 ± 54	9 ± 2	381 ± 53	481 ± 126	1060 ± 193	18.5	0.8	80.8
Bay Islands	9	52 ± 16	5 ± 1	468 ± 44	492 ± 89	1000 ± 129	5.2	0.5	94.3

stocks contributed by vegetation at Pacific coast, Caribbean coast and Bay Islands was 12, 19 and 5 %, respectively (Table 2). In terms of mangrove types, the fractions of total ecosystem C stock contributed by vegetation was 1, 7 and 19 % for low, medium and tall mangroves, respectively (Table 2).

At the Pacific coast, two tall mangrove sites (Chismuyo and San Bernardo) showed large differences in total vegetation C (Chismuyo = 178 Mg C ha<sup>-1</sup> and San Bernardo = 52 Mg C ha<sup>-1</sup>; Appendix Table 5). Mangrove stand at Chismuyo were dominated by *Rhizophora mangle* whereas San Bernardo had a dominance of *Avicennia germinans*. Interstitial salinity at San Bernardo was 87 ppt whereas the salinity at Chismuyo mangroves was 22 ppt. We found a significant negative correlation between vegetation biomass and pH (Pearson correlation coefficient,  $R = -0.53$ , Durbin–Watson statistic = 1.05;  $p = 0.00$ ) and soil water salinity ( $R = -0.49$ , Durbin–Watson statistic = 0.92;  $p = 0.00$ ). Low salinity indicates influx of fresh water from rivers, which could explain higher vegetation C stocks observed at Caribbean coast mangroves. Among Caribbean mangroves, one site—El Marion did not have high vegetation C stocks (77 Mg C ha<sup>-1</sup>; Appendix Table 5). The El Marion mangrove site was at the mouth of a small river where active deposition of silt and sediments was observed and the mangrove stand appeared to be composed of relatively smaller and young trees.

The widest range in biomass and structure of mangroves was observed in the Bay Islands. Vegetation biomass had a 50-fold range from 163 Mg C ha<sup>-1</sup>

at a tall mangrove site (Politily) to 3.7 Mg C ha<sup>-1</sup> at a low mangrove site (The Bight). Contribution of vegetation to the total ecosystem C stocks was highest at a tall mangrove site—Laguna Quemada (30 %) and lowest at a low mangrove site—The Bight (0.4 %) [See Appendix Table 5 for individual sites].

#### Downed wood carbon stocks

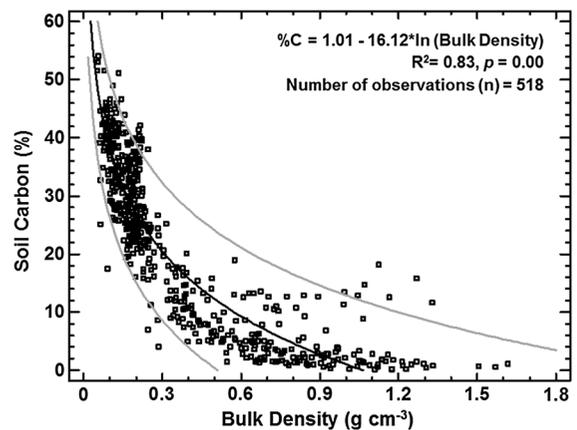
The overall contribution of downed wood to the mangrove ecosystem C stocks was minimal, ranging from about 0.5 % in Bay Islands to about 1 % in Pacific coast and Caribbean coast mangroves (Table 2). Similarly, downed wood C stocks contributed less than 1 % of total ecosystem C stocks in the low, medium and tall mangroves, with greatest proportion in the tall mangroves. The mean C stocks ranged from  $3 \pm 1$  Mg C ha<sup>-1</sup> in low mangroves to  $9 \pm 1$  Mg C ha<sup>-1</sup> in tall mangroves (Table 2; See Appendix Table 5 for individual sites). There was considerable variation in C in the form of downed wood across sampling sites and mangrove types. Across all sites, large sound and large rotten wood constituted 37 and 34 % of the downed wood C stocks respectively, while medium woody debris comprised 29 % of this pool.

#### Mangrove soils

Mean depths of the mangrove soils ranged from 120 to >270 cm (Table 1). Depth of soils varied across mangrove types (tall, medium and low) and location of sampling sites, however there was no apparent relation

between aboveground mangrove stature and soil depth. Soil depths along Pacific coast mangroves ranged from 120 to >270 cm, while soil depths at the Caribbean coast mangroves ranged from 200 to >270 cm. Soil depths across the Bay Islands sites ranged from 140 cm to >270 cm. The pH ranged from 6.0 to 8.7 while salinity ranged from 0 to 94 ppt across all sampled sites.

Bulk density of mangrove soils were higher in the Pacific coast in comparison to the Caribbean coast and Bay Islands except for two locations (El Marion and West end; Table 3). El Marion mangroves were located at the mouth of a small river and the soils predominantly consisted of heavy textured silt deposited by the river whereas high soil bulk density at West end on the island of Guanaja could be due to erosion and coastal sedimentation from the impacts of Hurricane Mitch. A significant and strong negative correlation between mangrove soil bulk density and C concentration in soils was observed when soil samples collected from all sites and all depth horizons ( $n = 518$ ) were included in the analysis (regression coefficient,  $r^2 = -0.82, p = 0.00$ ; Fig. 3). By fitting a



**Fig. 3** Relationship between bulk density ( $\text{g cm}^{-3}$ ) and soil carbon concentration (%) in mangrove soils. Samples from all sampling sites and soil horizons were used for this analysis. Outer gray lines indicate model prediction limits

logarithmic model, 82.6 % of the variability in soil C % could be explained by bulk density ( $p = 0.00$ ). Soils with higher bulk density and low C % were predominantly from Pacific coast and two sites from the Bay Islands (El Marion and Westend).

**Table 3** Mangrove soil bulk density ( $\text{g cm}^{-3}$ ) along soil profile from all sampling locations in Honduras

Location	Site name	Forest type	Bulk density for soil section depth ( $\text{g cm}^{-3}$ )				
			0–15 cm	15–30 cm	30–50 cm	50–100 cm	>100 cm
Pacific Coast	Chismuyo	Tall	$0.74 \pm 0.07$	$0.65 \pm 0.08$	$0.64 \pm 0.05$	$0.64 \pm 0.08$	$0.54 \pm 0.06$
	Isla de Pajaros	Medium	$1.06 \pm 0.06$	$1.02 \pm 0.11$	$0.92 \pm 0.13$	$0.77 \pm 0.1$	$0.85 \pm 0.19$
	San Bernardo	Tall	$0.83 \pm 0.04$	$0.84 \pm 0.06$	$0.75 \pm 0.05$	$0.68 \pm 0.01$	$0.71 \pm 0.04$
	San Lorenzo	Medium	$0.57 \pm 0.09$	$0.62 \pm 0.12$	$0.55 \pm 0.1$	$0.54 \pm 0.04$	$0.77 \pm 0.09$
Caribbean Coast	El Canalito	Tall	$0.08 \pm 0.01$	$0.09 \pm 0.01$	$0.11 \pm 0.01$	$0.1 \pm 0$	$0.14 \pm 0.01$
	El Marion	Tall	$0.5 \pm 0.14$	$0.45 \pm 0.12$	$0.86 \pm 0.17$	$1.09 \pm 0.07$	$1.19 \pm 0.04$
	La Diamante	Medium	$0.11 \pm 0.01$	$0.13 \pm 0.01$	$0.15 \pm 0.02$	$0.14 \pm 0.01$	$0.2 \pm 0.02$
	Laguna Quemada	Tall	$0.11 \pm 0.01$	$0.11 \pm 0.01$	$0.09 \pm 0.01$	$0.1 \pm 0.01$	$0.09 \pm 0.01$
	Manglon	Tall	$0.1 \pm 0.01$	$0.1 \pm 0.01$	$0.1 \pm 0.01$	$0.19 \pm 0.04$	$0.32 \pm 0.14$
Bay Islands	Milton bight	Medium	$0.16 \pm 0.01$	$0.12 \pm 0.01$	$0.29 \pm 0.08$	$0.7 \pm 0.1$	$1.08 \pm 0.03$
	Politically	Tall	$0.39 \pm 0.02$	$0.4 \pm 0.02$	$0.39 \pm 0.03$	$0.38 \pm 0.02$	$0.78 \pm 0.04$
	West end	Medium	$0.43 \pm 0.08$	$0.88 \pm 0.07$	$1.11 \pm 0.07$	$1.4 \pm 0.11$	$0.94 \pm 0.13$
	The Bight	Low	$0.22 \pm 0.01$	$0.21 \pm 0.01$	$0.2 \pm 0.01$	$0.2 \pm 0.01$	$0.2 \pm 0.01$
	Big bight	Low	$0.18 \pm 0.01$	$0.19 \pm 0.01$	$0.2 \pm 0.02$	$0.18 \pm 0.02$	$0.21 \pm 0.01$
	Iron bound	Medium	$0.18 \pm 0.01$	$0.22 \pm 0$	$0.22 \pm 0.02$	$0.3 \pm 0.03$	$0.41 \pm 0.06$
	Western path	Medium	$0.21 \pm 0.01$	$0.2 \pm 0.01$	$0.2 \pm 0.01$	$0.19 \pm 0.01$	$0.21 \pm 0.01$
	Oyster bed	Low	$0.2 \pm 0.01$	$0.21 \pm 0.01$	$0.19 \pm 0.01$	$0.19 \pm 0.01$	$0.18 \pm 0.01$
	Turtle harbor	Medium	$0.16 \pm 0.01$	$0.18 \pm 0.02$	$0.17 \pm 0.03$	$0.21 \pm 0.03$	$0.65 \pm 0.04$

There were no statistical differences in mangrove soil C stocks among various locations (Pacific coast, Caribbean coast and Bay Islands) and among mangrove types (low, medium and tall). The fraction of total ecosystem C stock contributed by soils at Pacific coast, Caribbean coast and Bay Islands were 87, 81 and 94 %, respectively while those from low, medium and tall mangrove soils were 99, 93, and 80 %, respectively (Table 2). A marked variation in soil C pools was observed across the sites. Lowest C stocks were found at San Bernardo (tall mangrove,  $347 \pm 17 \text{ Mg C ha}^{-1}$ ) on the Pacific coast, and highest stocks were observed at Oyster Bed (low mangrove,  $1600 \pm 45 \text{ Mg C ha}^{-1}$ ) in the Bay Islands. Soil C contribution to ecosystem C stocks was lowest at a Caribbean coast site—Laguna Quemada (tall mangrove, 69 %) and highest at a Bay Island site—The Bight (low mangrove, 99.5 %).

#### Total ecosystem carbon stocks

Aboveground mangrove structure was not a good indicator of ecosystem carbon stock, and no differences in total ecosystem C stocks were observed between low, medium and tall mangroves ( $p = 0.31$ ; Fig. 4). Similarly, location did not seem to have an effect on the total ecosystem carbon stocks, since no difference was observed between the Pacific coast, Caribbean coast and Bay Island mangroves ( $p = 0.14$ ; Fig. 4).

The mean ecosystem C stocks among low, medium and tall mangroves were 1222, 798 and 933  $\text{Mg C ha}^{-1}$ , respectively (Table 2). The mean total ecosystem C stock of the Pacific coast, Caribbean coast and Bay Islands mangroves were 570, 1060 and 1000  $\text{Mg C ha}^{-1}$ , respectively (Table 2).

$\text{C ha}^{-1}$ , respectively (Table 2). Across all sampled mangrove sites in Honduras, mangrove C stocks ranged from 306  $\text{Mg C ha}^{-1}$  at El Marion (tall mangrove) in the Caribbean coast to 1632  $\text{Mg C ha}^{-1}$  at Oyster Bed (low mangrove) in the Bay Islands.

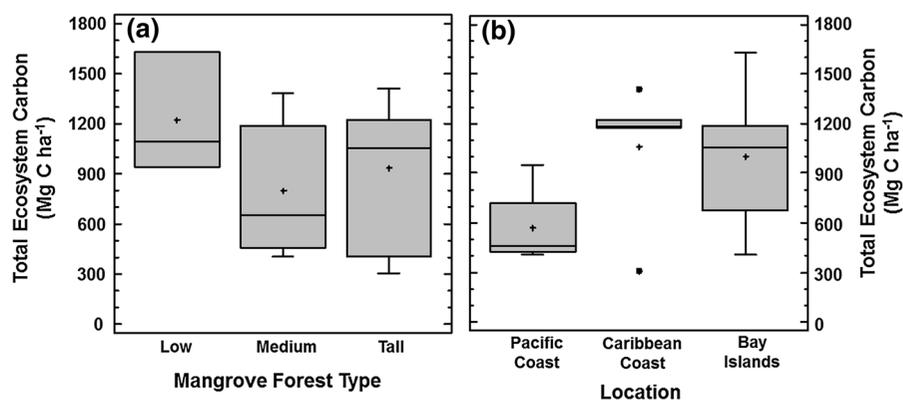
## Discussion and conclusions

### Vegetation biomass, mangrove soils and ecosystem carbon pools

We measured a large range and variability in the aboveground forest structure and biomass in the Honduran mangrove ecosystems. Mangrove tree densities from Honduran sites fell within the range reported from the Neotropics (Adame et al. 2013; Kauffman et al. 2014). Mangroves in the Dominican Republic had tall and medium tree densities of 900 and  $>40,000 \text{ ha}^{-1}$ , respectively (Kauffman et al. 2014). Tree density in the Yucatan region of Mexico were  $\sim 3000$  to  $7000 \text{ trees ha}^{-1}$  for tall mangroves and  $\sim 9000$  to  $11,000 \text{ trees ha}^{-1}$  for medium mangroves (Adame et al. 2013). The variability in mangrove tree density and structure represents differences in the characteristics of sampled locations such as geomorphic settings, rainfall, tides and the availability of fresh water and nutrients (Odum et al. 1982; Krauss et al. 2008).

In Honduras, the mangrove site where vegetation had the highest proportion of total ecosystem C (Laguna Quemada; 30 %) was associated with a fresh water source (river) and with low soil pore water salinity. The significant negative correlation between mangrove vegetation C and salinity indicated the

**Fig. 4** Total ecosystem carbon stocks of mangrove forest type (low, medium and tall) and location (Pacific coast, Caribbean coast and Bay Islands). Carbon stocks were not different among mangrove forest types (a;  $p = 0.32$ ) and locations (b;  $p = 0.14$ ; Tukey's HSD;  $p < 0.05$ )



positive role of fresh water in mangrove growth and stature. Low fresh water inputs resulting in higher soil salinity and/or accumulation of toxic substances (e.g. hydrogen sulfide; McKee et al. 1988) results in increased stress and lower productivity (Twilley and Day 1999). This association of the high plant biomass in tall mangroves with a higher occurrence of fresh water was also observed for Mexican mangroves by Adame et al. (2013). This suggested that high mangrove C stocks were attributed to fresh water and soil nutrient (specifically phosphorus) availability. Mangrove productivity has also been linked to availability of fresh water and essential nutrients in mangroves elsewhere (Twilley and Day 1999). The low biomass C (<4 % of total ecosystem C stocks) in the mangrove vegetation of Bay Islands could therefore be indicative of limited availability of terrigenous nutrients and fresh water.

The pH and salinity measurements obtained during our sampling represents only a single time point in the series of diurnal and seasonal fluctuations that these mangroves experience due to changing tides, rainfall and availability of dissolved ions. A robust analysis to explore relationships between environmental variables and mangrove C stocks will be possible when more information on the annual variability of pH and pore water salinity at these mangrove sites is available. However, this relationship is likely real, as the temporal variability in pH and salinity is likely lower than the spatial variability that we measured across the Honduran mangroves. The vegetation biomass of the mangroves in Bay islands was low but deeper soil depths and high concentration of C in the soil horizons resulted in relatively large ecosystem C stocks. Low aboveground biomass of Bay Island mangroves could also be a consequence of higher incidences of tropical storms (or hurricanes), which can cause tree mortality and reduction in the number of mature trees (Twilley and Day 1999). Although the mean ecosystem C stocks in mangrove stands of Caribbean coast (1060 Mg C ha<sup>-1</sup>) were similar to those sampled at the Bay Islands (1000 Mg C ha<sup>-1</sup>), contribution of vegetation biomass C was much higher in the Caribbean coast (19 %) in comparison to the Bay Islands (5 %).

Mangrove soils were the largest repository of C stocks in Honduran mangroves as also seen in mangroves found elsewhere (Donato et al. 2011; Kauffman et al. 2011; Alongi 2012; Donato et al.

2012; Ajonina et al. 2014; Kauffman et al. 2014; Tue et al. 2014). Mangrove forests are known to have high C burial rates, and a recent analysis of burial rates from different mangrove systems suggested a global mean value of 163 g C m<sup>-2</sup> y<sup>-1</sup> (Breithaupt et al. 2012). The prevailing anoxic conditions in saturated mangrove environments offer long-term preservation to buried C against oxidation resulting in high C concentrations in mangrove soils. With increasing C content in the soils its bulk density decreases in a non-linear fashion. Specifically, we found low bulk density and high C content in the mangrove soils from Caribbean coast sites while higher bulk density and low C density in sampled mangrove soils in the Pacific coast of Honduras (Fig. 3). Although soil bulk density is an important factor for estimating the C density and the C pool in mangrove soils, only a few studies simultaneously provide this information. The relationship between C content and bulk density that we obtained may offer a practical, cost effective solution to quantify C in mangrove soils where high laboratory costs or unavailability of analytical equipment presents a major challenge in mangrove C stock determination. At regional scales this relationship is apparently strong ( $r^2 = 0.83$ ). However, more research on mangrove soils from different locations and geomorphic settings is needed to determine if a robust relationship can be applied across a variety of mangrove ecosystems at global scales.

The total ecosystem C stocks among different types of mangroves (low, medium and tall) in Honduras were not significantly different. This is in contrast to mangrove C stock measurements from Mexico where tall mangroves had highest total C (987 Mg C ha<sup>-1</sup>; Adame et al. 2013) and Dominican Republic where higher total C was found in medium mangroves (1131 Mg C ha<sup>-1</sup>; Kauffman et al. 2014). This variation in relationship between total C stocks and mangrove stature is a result of relatively higher proportion of C stored in mangrove soils, which causes the sites with deeper organic C rich soils to have greater ecosystem C stocks regardless of the mangrove vegetation size. In Honduras, low and medium mangroves had deep and C dense soils which made their C stocks comparable to tall mangroves, hence we did not find differences in ecosystem C stocks based on the mangrove types.

The broad range of total ecosystem C stocks of Honduras (570–1060 Mg C ha<sup>-1</sup>) reflects the broad

array of sites and different geomorphic settings sampled in this study. These ranges were comparable to the variation in C stocks reported from this region, such as from Yucatan, Mexico (381–987 Mg C ha<sup>-1</sup>; Adame et al. 2013) and from Monte Cristi, Dominican Republic (741–1131 Mg C ha<sup>-1</sup>; Kauffman et al. 2014). Pacific coast mangroves (570 Mg C ha<sup>-1</sup>) were lower while Caribbean coast mangroves (1060 Mg C ha<sup>-1</sup>) and Bay Islands mangroves (1000 Mg C ha<sup>-1</sup>) were similar to the average global mangrove C stock (956 Mg C ha<sup>-1</sup>; Alongi 2012). Although not significantly different, the variation in C stocks among Pacific coast and the Caribbean coast and Bay Islands can be attributed to varying geomorphic, edaphic and climatic factors. The Pacific coast has a relatively dry climate in comparison to the Caribbean coast and Bay Islands; and the mangroves in Gulf of Fonseca were established in inter-distributary dendritic tidal channels formed by the sediment deposits from two major rivers—the Choluteca and Negro Rivers. Pacific coast soils appeared to have a higher mineral content because of higher bulk densities which resulted in low total ecosystem C (570 Mg C ha<sup>-1</sup>). Higher rainfall and the availability of fresh water due to proximity of rivers in the Caribbean coast mangroves possibly enhanced vegetative productivity. Significantly higher basal areas of Caribbean mangroves (Fig. 2) indicated large trees and larger vegetation C pools in comparison to the lower plant C pools in the Pacific coast mangroves. Higher total ecosystem C stocks in the Bay Island mangroves (400–1630 Mg C ha<sup>-1</sup>) was mainly due to large soil C stocks, while aboveground C pools (vegetation and dead wood debris) were relatively smaller, this again could be related to lower availability of fresh water and available nutrients in the Bay Islands.

#### Mangroves carbon stocks and risks due to climate change

Coastal ecosystems and mangroves in particular are critical to the resilience and vitality of many coastal social-ecological systems (UNEP 2014). In the long-term, the goods and services (e.g., carbon storage, increased fisheries production, or water purification) provided by mangrove forests are likely to be more valuable than low-term gains from unsustainable agriculture or aquaculture systems, even without including their coastal protection services (Feagin

et al. 2010). The C sequestered in mangroves and salt marshes, either in the form of plant biomass or as organic soils, can be derived from local production (autochthonous) or laterally imported from other sources (allochthonous), depending on tidal range, wave action and physiography of a location (Middelburg et al. 1997; Bouillon et al. 2003). The large amount of C stored in the mangroves of Honduras (570–1060 Mg C ha<sup>-1</sup>) reflects the outcomes of such processes. These C stocks are extremely vulnerable to loss by human induced disturbances such as deforestation and land conversion, sea level rise, or disruption in quantity and timing of fresh water availability. Furthermore, these ecosystems are prone to impacts from natural phenomena such as hurricanes or severe droughts which could result in the loss of stored C.

Globally, mangrove deforestation has occurred at a rate of 1–2 % per year, but losses of as much as 30–50 % have already been reported (Donato et al. 2011). The largest immediate threat is conversion to aquaculture which may have contributed up to 52 % of global mangrove loss (Valiela et al. 2001). The existing 36,000 ha of mangroves in the Pacific coast of Honduras are currently threatened by conversion into shrimp aquaculture. With >500 Mg C ha<sup>-1</sup>, any loss of mangrove forests, either by land use change or effects due to global climate change, will result in increased emissions of greenhouse gases to the atmosphere. In addition to land conversion pressure, the mangroves in the Caribbean coast and the Bay Islands are vulnerable to climate change impacts such as sea level rise, increased salinity and increased severity of tropical storms and surges. These increases in disturbance and stress-related processes could challenge the integrity of coastal vegetation communities and compromise their C storage function. Given the large quantity of C stocks in the Caribbean coast and Bay Island mangroves (>1000 Mg C ha<sup>-1</sup>), concerted efforts in conservation planning and mangrove area management are needed to prevent conversion and destruction of mangrove forests and minimize the loss of C to the atmosphere.

The quantification of the large C stocks of Honduran mangroves is valuable for the process of policy formulation with regards to mangrove conservation and restoration of abandoned and degraded coastal sites. Mangrove ecosystems are increasingly recognized as important for inclusion in climate change

mitigation and adaptation strategies due to their high C storage, C sequestration rates, and vulnerability to human induced disturbances. Carbon payment programs such as REDD+ (Murdiyarso et al. 2012) can provide necessary incentives and resources needed to conserve these areas and maintain C stocks while providing other ecosystem values that mangroves provide to local communities.

**Acknowledgments** This study was carried out under the Sustainable Wetlands Adaptation and Mitigation Program (SWAMP), a collaborative effort by the Center for International Forestry Research (CIFOR), Oregon State University, and the United States Forest Service (USFS), with support from the United States Agency for International Development (USAID). We wish to thank Ian Drysdale, Luis Turcios, Pamela Ortega, Wendy Naira and Claudia Vallejo for their logistical support, as well as Johnathon Lainez and the Honduran Secretariat of Natural Resources and the Environment

(SERNA) for their collaboration. We are grateful to the team of hardworking and committed participants who enabled data collection in the field. We also acknowledge the Seagrass Lab, Florida International University, Miami, USA where the soil nutrient analyses were performed. We are thankful to three anonymous reviewers for their useful comments and suggestions which helped significantly to improve the quality of this article.

**Funding** This work was part of the Sustainable Wetlands Adaptation and Mitigation Program (SWAMP), a collaborative effort by the Center for International Forestry Research (CIFOR), Oregon State University, and the United States Forest Service, with financial support from the United States Agency for International Development (USAID) and CIFOR.

## Appendix

See Tables 4 and 5.

**Table 4** The total and inorganic Carbon (%) in the mangrove soils from select Bay Island sites, Honduras (Avg.  $\pm$  SE)

Soil depth (cm)	Number of samples	Total C (%)	Inorganic C (%)
0–15	7	26.1 $\pm$ 3.3	0 $\pm$ 0
15–30	7	28.9 $\pm$ 2	0 $\pm$ 0
30–50	3	18.3 $\pm$ 5.4	2.9 $\pm$ 1.6
50–100	9	22.7 $\pm$ 3.4	3.5 $\pm$ 1.2
>100	12	18.5 $\pm$ 2.7	7.4 $\pm$ 2.1

**Table 5** Carbon stocks in the measured ecosystem compartments from all sampling locations in Honduras (Avg.  $\pm$  SE)

Location/site	Type	Carbon stocks in various ecosystem compartments					Fraction of total ecosystem C		
		Tree	Downed wood	Soil (0–100 cm depth)	Soil (below 100 cm depth)	Total ecosystem (tree + downed wood + soil)	Trees	Downed wood	Soils
Pacific coast		Mg C ha <sup>-1</sup>					%		
Chismuyo	Tall	178.3 $\pm$ 27.6	8.2 $\pm$ 1.5	336.3 $\pm$ 27.8	428.9 $\pm$ 52.2	951.6 $\pm$ 65.4	18.7	0.9	80.4
Isla de Pajaros	Medium	22.4 $\pm$ 4.7	4 $\pm$ 0.7	295.9 $\pm$ 47.9	144.1 $\pm$ 28.6	441.9 $\pm$ 69	5.3	0.9	94.1
San Bernardo	Tall	52.2 $\pm$ 19.3	8.3 $\pm$ 1.1	125 $\pm$ 12.3	222 $\pm$ 21.9	408 $\pm$ 29.2	12.8	2.0	85.0
San Lorenzo	Medium	27.6 $\pm$ 5.3	1.5	276.5 $\pm$ 11.7	173.4 $\pm$ 67	478.4 $\pm$ 59.4	6.1	0.3	94.0
Mean		<b>70.8 <math>\pm</math> 36.4</b>	<b>5.5 <math>\pm</math> 1.7</b>	<b>258.4 <math>\pm</math> 46.2</b>	<b>242.1 <math>\pm</math> 64.3</b>	<b>570 <math>\pm</math> 128</b>	<b>12.4</b>	<b>1.0</b>	<b>86.8</b>
Caribbean coast									
El Canalito	Tall	149 $\pm$ 41.2	15.4 $\pm$ 1.5	404.5 $\pm$ 13.7	842.3 $\pm$ 87.7	1410.4 $\pm$ 69.1	10.6	1.1	88.4
El Marion	Tall	77.4 $\pm$ 23.2	16.9 $\pm$ 4	190.7 $\pm$ 56.6	58.7 $\pm$ 14.8	306.3 $\pm$ 57.7	25.3	5.5	71.8
La Diamante	Medium	116.1 $\pm$ 16.1	2.6 $\pm$ 0.2	514.5 $\pm$ 37.9	548.3 $\pm$ 43.6	1180.9 $\pm$ 63.1	9.8	0.2	90.0
Laguna quemada	Tall	372.2 $\pm$ 65.7	8.7 $\pm$ 1.7	413.4 $\pm$ 34.9	432.3 $\pm$ 49.1	1226.2 $\pm$ 65.3	30.4	0.7	69.0
Manglon	Tall	263.7 $\pm$ 43.3	8.8 $\pm$ 1.2	381.9 $\pm$ 19.5	523.2 $\pm$ 59.9	1174.4 $\pm$ 71.6	22.5	0.7	77.1
Mean		<b>195.7 <math>\pm</math> 54.0</b>	<b>10.5 <math>\pm</math> 2.6</b>	<b>381 <math>\pm</math> 53</b>	<b>481 <math>\pm</math> 126</b>	<b>1060 <math>\pm</math> 193</b>	<b>18.5</b>	<b>1.0</b>	<b>80.8</b>

**Table 5** continued

Location/ site	Type	Carbon stocks in various ecosystem compartments					Fraction of total ecosystem C		
		Tree	Downed wood	Soil (0–100 cm depth)	Soil (below 100 cm depth)	Total ecosystem (tree + downed wood + soil)	Trees	Downed wood	Soils
Bay Islands									
Milton bight	Medium	70.1 ± 15	5.9 ± 1	563.6 ± 58.1	744 ± 200.2	1383.1 ± 205.7	5.2	0.4	94.5
Politically	Tall	163 ± 23	6.6 ± 0.3	403.6 ± 22.9	479.1 ± 110.3	1052.6 ± 113.9	15.5	0.6	83.9
West end	Medium	52 ± 6.9	6.3 ± 0.3	233.2 ± 20.6	234.7 ± 24.7	408.4 ± 66.7	13.5	1.5	85.8
The Bight	Low	3.7 ± 0.8	1.0	402.7 ± 12.1	532.4 ± 24.2	939.8 ± 33.8	0.4	0.1	99.5
Big Bight	Low	17.1 ± 9.5	6.3 ± 0.8	507.2 ± 28.1	564.9 ± 61.3	1093.4 ± 73.1	1.6	0.6	98.1
Iron bound	Medium	70.4 ± 6.7	5.8 ± 0.5	533.7 ± 15.6	101.3 ± 44.6	675.7 ± 42.6	10.7	0.9	89.0
Western path	Medium	52.9 ± 16.7	11.5 ± 2	471.7 ± 18.8	660.9 ± 20.4	1190.6 ± 40.2	4.4	1.0	95.1
Oyster bed	Low	23.7 ± 4.3	3.7 ± 1.3	700.4 ± 20.9	904.5 ± 39.4	1632.1 ± 47.5	1.5	0.2	98.3
Turtle harbor	Medium	17 ± 6.6	5.5 ± 0.7	397.3 ± 27	205.7 ± 43.5	625 ± 67.4	2.7	0.9	96.5
Mean		<b>52.9 ± 16.1</b>	<b>5.8 ± 0.9</b>	<b>468 ± 44</b>	<b>492 ± 89</b>	<b>1000 ± 129</b>	<b>3.7</b>	<b>0.4</b>	<b>94.3</b>

The significance of bold is to highlight that these values are mean of the preceding data in the rows above it

## References

- Adame MF et al (2013) Carbon stocks of tropical coastal wetlands within the karstic landscape of the Mexican Caribbean. *PLoS One* 8:e56569. doi:[10.1371/journal.pone.0056569](https://doi.org/10.1371/journal.pone.0056569)
- Ajonina G, Kairo J, Grimsditch G, Sembres T, Chuyong G, Diyouke E (2014) Assessment of mangrove carbon stocks in Cameroon, Gabon, the Republic of Congo (RoC) and the Democratic Republic of Congo (DRC) including their potential for reducing emissions from deforestation and forest degradation (REDD+). In: Diop S, Barousseau J-P, Descamps C (eds) *The Land/Ocean Interactions in the Coastal Zone of West and Central Africa*. Estuaries of the World. Springer International Publishing, Cham, pp 177–189. doi:[10.1007/978-3-319-06388-1\\_15](https://doi.org/10.1007/978-3-319-06388-1_15)
- Alongi DM (2012) Carbon sequestration in mangrove forests. *Carbon Manag* 3:313–322. doi:[10.4155/cmt.12.20](https://doi.org/10.4155/cmt.12.20)
- Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. *Ecol Monogr* 81:169–193
- Bouillon S, Dahdouh-Guebas F, Rao AVVS, Koedam N, Dehairs F (2003) Sources of organic carbon in mangrove sediments: variability and possible ecological implications. *Hydrobiologia* 495:33–39. doi:[10.1023/A:1025411506526](https://doi.org/10.1023/A:1025411506526)
- Breithaupt JL, Smoak JM, Smith TJ, Sanders CJ, Hoare A (2012) Organic carbon burial rates in mangrove sediments: strengthening the global budget. *Glob Biogeochem Cycles* 26(3):1–11
- Brown JK (1974) Handbook for inventorying downed woody material. General Technical Report GTR-INT-16. Missoula
- Cahoon DR, Hensel P (2002) Hurricane mitch: a regional perspective on mangrove damage, recovery, and sustainability. USGS Open File Report 03-183. US Department of the Interior, US Geological Survey
- Chen C-F et al (2013) Multi-decadal mangrove forest change detection and prediction in Honduras, Central America, with Landsat Imagery and a Markov chain model. *Remote Sens* 5:6408–6426
- Cohen JE, Small C, Mellinger A, Gallup J, Sachs J (1997) Estimates of coastal populations. *Science* 278:1209–1213. doi:[10.1126/science.278.5341.1209c](https://doi.org/10.1126/science.278.5341.1209c)
- Dewalt BR, Vergne P, Hardin M (1996) Shrimp aquaculture development and the environment: people, mangroves and fisheries on the Gulf of Fonseca, Honduras. *World Dev* 24:1193–1208
- Dittmar T, Hertkorn N, Kattner G, Lara RJ (2006) Mangroves, a major source of dissolved organic carbon to the oceans. *Global Biogeochem Cycles* 20:GB1012. doi:[10.1029/2005GB002570](https://doi.org/10.1029/2005GB002570)
- Donato DC, Kauffman JB, Murdiyarto D, Kurnianto S, Stidham M, Kanninen M (2011) Mangroves among the most carbon-rich forests in the tropics. *Nat Geosci* 4:293–297
- Donato DC, Kauffman JB, Mackenzie RA, Ainsworth A, Pflieger AZ (2012) Whole-island carbon stocks in the tropical Pacific: implications for mangrove conservation and upland restoration. *J Environ Manag* 97:89–96. doi:[10.1016/j.jenvman.2011.12.004](https://doi.org/10.1016/j.jenvman.2011.12.004)
- Duarte C, Dennison W, Orth RW, Carruthers TB (2008) The Charisma of coastal ecosystems: addressing the imbalance. *Estuar Coast* 31:233–238. doi:[10.1007/s12237-008-9038-7](https://doi.org/10.1007/s12237-008-9038-7)
- FAO (2007) *The World's Mangroves 1980–2005*. FAO, Rome
- Feagin RA et al (2010) Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. *Conserv Lett* 3:1–11. doi:[10.1111/j.1755-263X.2009.00087.x](https://doi.org/10.1111/j.1755-263X.2009.00087.x)
- Fromard F, Puig H, Mougou E, Marty G, Betoulle JL, Cadamuro L (1998) Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* 115:39–53. doi:[10.2307/4221977](https://doi.org/10.2307/4221977)

- Harborne AR, Afzal DC, Andrews MJ (2001) Honduras: Caribbean Coast. *Mar Pollut Bull* 42:1221–1235. doi:[10.1016/S0025-326X\(01\)00239-9](https://doi.org/10.1016/S0025-326X(01)00239-9)
- IPCC (2014) 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. IPCC, Genève
- Jaxion-Harm J, Saunders J, Speight (2012) Distribution of fish in seagrass, mangroves and coral reefs: life-stage dependent habitat use in Honduras. *Revis Biol Trop* 60:683–698
- Kauffman JB, Donato D (2012) Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests Center for International Forestry Research Center (CIFOR) Working paper 86
- Kauffman JB, Cummings D, Ward D, Babbitt R (1995) Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397–408
- Kauffman JB, Heider C, Cole TG, Dwire KA, Donato DC (2011) Ecosystem carbon stocks of Micronesian mangrove forests. *Wetlands* 31:343–352
- Kauffman JB, Heider C, Norfolk J, Payton F (2014) Carbon stocks of intact mangroves and carbon emissions arising from their conversion in the Dominican Republic. *Ecol Appl* 24:518–527. doi:[10.1890/13-0640.1](https://doi.org/10.1890/13-0640.1)
- Komiyama A, Ong JE, Pongpam S (2008) Allometry, biomass, and productivity of mangrove forests: a review. *Aquat Bot* 89:128–137. doi:[10.1016/j.aquabot.2007.12.006](https://doi.org/10.1016/j.aquabot.2007.12.006)
- Krauss KW, Lovelock CE, McKee KL, López-Hoffman L, Ewe SM, Sousa WP (2008) Environmental drivers in mangrove establishment and early development: a review. *Aquat Bot* 89:105–127
- Little EL Jr, Wadsworth FH (1964) Common trees of Puerto Rico and the Virgin Islands. Superintendent of Documents, US Government Printing Office, Washington, DC
- Luther DA, Greenberg R (2009) Mangroves: a global perspective on the evolution and conservation of their terrestrial vertebrates. *Bioscience* 59:602–612. doi:[10.1525/bio.2009.59.7.11](https://doi.org/10.1525/bio.2009.59.7.11)
- MacKenzie RA, Cormier N (2012) Stand structure influences nekton community composition and provides protection from natural disturbance in Micronesian mangroves. *Hydrobiologia* 685:155–171
- Malavassi IMC (1992) Maderas de Costa Rica: 150 Especies forestales. Editorial de la Universidad de Costa Rica
- McIvor AL, Möller I, Spencer T, Spalding M (2012a) Reduction of wind and swell waves by mangroves. The Nature Conservancy and Wetlands International, Cambridge
- McIvor AL, Spencer T, Möller I, Spalding M (2012b) Storm surge reduction by mangroves. The Nature Conservancy and Wetlands International, Cambridge
- McKee KL, Mendelsohn IA, Hester MW (1988) Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *Am J Bot* 75:1352–1359
- McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob Ecol Biogeogr* 16:545–556
- Middelburg J, Nieuwenhuize J, Lubberts R, Van de Plassche O (1997) Organic carbon isotope systematics of coastal marshes. *Estuar Coast Shelf Sci* 45:681–687
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being, vol 5. Island Press, Washington, DC
- Murdiyarto D, Kauffman JB, Warren M, Pramova E, Hergoualc'h K (2012) Tropical wetlands for climate change adaptation and mitigation: science and policy imperatives with special reference to Indonesia. Center for International Forest Research, Bogor
- Nagelkerken I et al (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat Bot* 89:155–185
- Odum W, McIvor C, Smith TI (1982) The ecology of the mangroves of South Florida: a community profile vol FWS/OBS-81/24. Washington, DC
- Polidoro BA et al (2010) The loss of species: mangrove extinction risk and geographic areas of global concern. *PLoS One* 5:e10095
- Rivera-Monroy VH, Twilley RR, Castañeda E (2002) Hurricane Mitch: integrative management and rehabilitation of mangrove resources to develop sustainable shrimp mariculture in the Gulf of Fonseca, Honduras vol 03-177. USGS Open File Report
- Sandilyan S, Kathiresan K (2015) Mangroves as bioshield: an undisputable fact. *Ocean Coast Manag* 103:94–96. doi:[10.1016/j.ocecoaman.2014.11.011](https://doi.org/10.1016/j.ocecoaman.2014.11.011)
- Snedaker SC, Lahmann EJ (1988) Mangrove understory absence: a consequence of evolution? *J Trop Ecol* 4:311–314
- Spalding M, Kainuma M, Collins L (2010) World Atlas of Mangroves. A collaborative project of ITTO, ISME, FAO, UNEP-WCMC, UNESCO-MAB, UNU-INWEH and TNC. Earthscan, London
- Tue NT, Dung LV, Nhuan MT, Omori K (2014) Carbon storage of a tropical mangrove forest in Mui Ca Mau National Park. *Vietnam Catena* 121:119–126. doi:[10.1016/j.catena.2014.05.008](https://doi.org/10.1016/j.catena.2014.05.008)
- Twilley RR, Day JW (1999) The productivity and nutrient cycling of mangrove ecosystem. In: *Ecosistemas de manglar en América Tropical*. Instituto de Ecología, AC México, UICN/ORMA, Costa Rica, NOAA/NMFS, Silver Spring, MD, pp 127–151
- UNEP (2014) The importance of mangroves to people: a call to action. World Conservation Monitoring Centre, Cambridge
- Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. *Bioscience* 51:807–815
- Vergne P, Hardin M, Dewalt B (1993) Environmental study of the Gulf of Fonseca. Tropical Research & Development, Washington, DC
- Zanne AE et al (2009) Global wood density database. Data from: a worldwide wood economics spectrum. Dryad Data Repository. *PLoS One*. doi:[10.5061/dryad.234](https://doi.org/10.5061/dryad.234)