



Carbon stocks and soil sequestration rates of tropical riverine wetlands

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Abstract. Riverine wetlands are created and transformed by geomorphological processes that determine their vegetation composition, primary production and soil accretion, all of which are likely to influence C stocks. Here, we compared ecosystem C stocks (trees, soil and downed wood) and soil N stocks of different types of riverine wetlands (marsh, peat swamp forest and mangroves) whose distribution spans from an environment dominated by river forces to an estuarine environment dominated by coastal processes. We also estimated soil C sequestration rates of mangroves on the basis of soil C accumulation. We predicted that C stocks in mangroves and peat swamps would be larger than marshes, and that C, N stocks and C sequestration rates would be larger in the upper compared to the lower estuary. Mean C stocks in mangroves and peat swamps (784.5 ± 73.5 and $722.2 \pm 63.6 \text{ MgC ha}^{-1}$, respectively) were higher than those of marshes ($336.5 \pm 38.3 \text{ MgC ha}^{-1}$). Soil C and N stocks of mangroves were highest in the upper estuary and decreased towards the lower estuary. C stock variability within mangroves was much lower in the upper estuary (range $744\text{--}912 \text{ MgC ha}^{-1}$) compared to the intermediate and lower estuary (range $537\text{--}1115 \text{ MgC ha}^{-1}$) probably as a result of a highly dynamic coastline. Soil C sequestration values were $1.3 \pm 0.2 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ and were similar across sites. Estimations of C stocks within large areas need to include spatial variability related to vegetation composition and geomorpho-

logical setting to accurately reflect variability within riverine wetlands.

1 Introduction

Deforestation and ecosystem degradation is, after fossil fuel combustion, the largest cause of carbon dioxide (CO₂) emissions to the atmosphere (Van der Werf et al., 2009). Wetlands have one of the highest deforestation rates; one-third of the world's mangrove forests have been lost in the past 50 years, while one-third of salt marshes has disappeared since the 1800s (Alongi, 2002; McLeod et al., 2011 and references therein). Because wetlands are rich in carbon (C), deforestation or disturbance of these ecosystems results in large emissions of CO₂ to the atmosphere (Lovelock et al., 2011). To prevent the large emissions that result from wetland loss, programmes such as REDD+ (Reducing Emissions from Deforestation and forest Degradation) have been proposed. In order to target coastal wetlands within REDD+ and other financing programmes, accurate estimates of C stocks and sequestration rates are needed (Alongi, 2011).

C stocks within wetlands can be associated with forest structure, with largest stocks in tall and vigorous forests (Adame et al., 2013). However, this is not always the case, as in some locations mangrove C stocks do not reflect the aboveground structure (Kauffman et al., 2014b). This could

be partly because wetlands are highly dynamic and the existing vegetation might not reflect the wetland long-term condition (Thom, 1967; Thom et al., 1975). For example, sparse mangroves growing in an accreting riverbank could become tall, productive forests in 50 years, but the soil C will take longer to accumulate. Thus, tall mangrove forests might not necessarily have larger C stocks than shorter ones. Geomorphic processes will constantly create, transform and destroy landforms, resulting in changes in vegetation, production, sedimentation, and thus in C stocks (Adame et al., 2010, Alongi 2011).

Many forces contribute to the formation of riverine wetlands in deltaic–estuarine landscapes, including: river run-off, wave action, tidal inundation and the incidence of cyclones (Thom, 1967; Woodroffe, 1992). In the Mexican southeast coast, wetlands are formed by a mosaic of marshes and peat swamps where freshwater input is constant, tidal inundation is negligible and wave and storm damage is relatively low. Lowland, mangroves dominate the vegetation from the upper to the lower estuary. Upper estuarine mangroves have periodic input of freshwater and lower tidal and wave influence compared to mangroves in the lower estuarine region (Thom et al., 1975). In this study, we compared C stocks (trees, soil and downed wood) of riverine wetlands of La Encrucijada Biosphere Reserve (LEBR) in the Pacific south coast of Mexico. We compared C stocks of different vegetation types (mangroves, peat swamps and marsh) and throughout a geomorphological gradient (upper to lower estuary).

Wetlands are not only efficient at accumulating C, but also nitrogen (N) when production exceeds N demand (Rivera Monroy et al., 1995). C and N cycles interact closely; thus N stocks can increase with increments in C (Yimer et al., 2006). N accumulation increases with rainfall, runoff and production by organisms such as cyanobacteria and algae (Alongi, 2009; Reef et al., 2010). Soil N accumulation is also associated with large foliage cover and wood biomass (e.g. Hooker and Compton, 2003; Liao et al., 2007). In this study we compare the capacity of different types of wetlands (mangroves, marshes and peat swamps) and geomorphological settings (upper and lower estuary) to store N in the soil.

The high capacity of wetlands to store C and N is partly due to their high productivity and low soil decomposition rates. Mangroves and marshes can store up to 3 times more C than terrestrial ecosystems (Chmura et al., 2003; Donato et al., 2011; McLeod et al., 2011). For example, mangroves in the Caribbean can store up to 987 MgC ha^{-1} , while in the Indo-Pacific, mangroves store $1,023 \text{ MgC ha}^{-1}$ (Donato et al., 2011; Adame et al., 2013). These values typically exceed those of tropical and temperate forests ($< 400 \text{ Mg ha}^{-1}$, IPCC, 2003). Similarly, soil C sequestration rates of coastal wetlands ($210 \text{ g C m}^{-2} \text{ yr}^{-1}$) and freshwater wetlands ($20\text{--}30 \text{ g C m}^{-2} \text{ yr}^{-1}$) are higher than those of terrestrial forests ($\sim 10 \text{ g C m}^{-2} \text{ yr}^{-1}$; Chmura et al., 2003; McLeod et al., 2011). Long-term carbon sequestration rates of mangroves are very difficult to obtain, but are required to participate

in carbon payments (Alongi, 2011). In this study, we use a unique natural marker (ash horizon from a volcanic eruption in 1902, Fig. S1 in the Supplement) to calculate soil carbon sequestration rates during the last century from a large number of locations ($n = 36$). We compared C sequestration rates of mangroves across a geomorphological gradient, from mangroves in the upper estuary to those in the lower estuary.

Riverine wetlands, particularly mangroves, are one of the most extensive types of wetlands and are predicted to have one of the largest C stocks on Earth (Ewel et al., 1998). We expect that C stocks within the riverine wetlands of the south Mexican Pacific coast have large C stocks compared to any other terrestrial forest. We also predict that mangroves and peat swamps have higher C stocks compared to marshes. Finally, we expect that geomorphological setting will affect C and N stocks and C sequestration rates with higher values for mangroves in the upper estuary compared to those in the lower estuary.

2 Methodology

2.1 Study site

The Encrucijada Biosphere Reserve (LEBR) is located in Chiapas, in the south Pacific coast of Mexico ($14^{\circ}43' \text{ N}$, $92^{\circ}26' \text{ W}$; Fig. 1). The LEBR comprises an area of $144\,868 \text{ ha}$. The LEBR has five coastal lagoons connected to seven river systems. The LEBR is characterized by large areas of wetlands including mangroves, marsh and peat swamp forests. The LEBR has one of the most extensive mangrove areas of the region, with forests dominated by trees of *Rhizophora mangle* that range between $20\text{--}40 \text{ m}$ in height, and are believed to be the tallest in the country (Tovilla et al., 2007). The mangroves of LEBR support a high biodiversity, as well as fisheries and tourist activities (UNESCO, 2013).

The climate of the LEBR is warm, sub-humid with most precipitation occurring in the summer months (June–October). The mean annual temperature of the region is 28.2° C , with a mean annual minimum of 19.2° C and a mean annual maximum of 36.5° C ; mean annual precipitation is 1567 mm (Sistema Meteorológico Nacional – Comisión Nacional del Agua, station no. 7320, 1951–2010).

2.2 Site stratification

In this study, we sampled three types of wetlands: peat swamp forest, marsh and mangroves. To determine a criterion for stratification of mangroves, we used two SPOT 5 satellite images with geographical, geometric and radiometric correction, and the Universal Transverse Mercator projection system. From each image, the Normalized Difference Vegetation Index (NDVI) was obtained with ERDAS Imagine. The NDVI values ranged from -1 to 1 , where negative values indicates areas without vegetation, values close to zero indicate senescent or stressed vegetation, and values

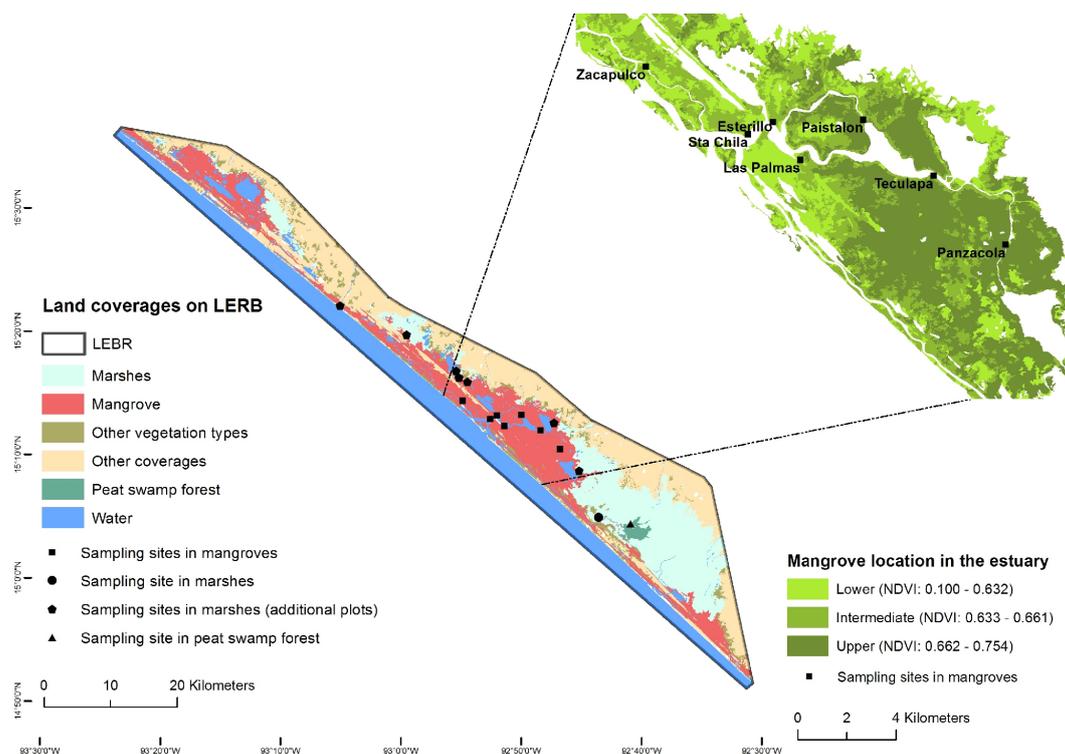


Figure 1. Mangrove, peat swamp and marsh sampling sites within La Encrucijada Biosphere Reserve, Mexico. Mangroves were classified according to the NDVI (see Sect. 2.2) into three classes, which broadly corresponded to a range of mangroves from the upper to the lower estuary.

close to 1 indicate green or healthy vegetation (Chuvienco, 2006). NDVI values were extracted from the mangrove coverage map (CONABIO, 2013) and classified according to Ruiz-Luna et al. (2010). The mangrove vegetation was divided into three classes: the most vigorous vegetation was Class I (9253 ha), the least vigorous vegetation was Class III (11 467 ha), and Class II (6757 ha) had intermediate values of vegetation vigour. The mangrove classes along with the distance to the mouth of the estuary were used to classify our sites into three categories: upper estuary mangroves with the most vigorous vegetation, lower estuary mangroves with the least vigorous vegetation and intermediate mangroves in terms of vigour and distance to the mouth of the estuary (Fig. 1). Hereafter, we refer to our mangrove locations as “upper estuary”, “intermediate” and “lower estuary”.

2.3 Field and laboratory analyses

Sampling was conducted during December 2012, where ecosystem C stocks, soil N stocks and soil C sequestration rates were measured. We sampled nine sites: a peat swamp forest dominated by *Pachira aquatica*, a marsh dominated by the grass *Typha domingensis* and seven mangrove forests (three sites in the upper estuary, two in the intermediate estuary and two in the lower estuary; Fig. 1; Table 1). We measured whole-ecosystem C stocks in six plots (radius of 7 m;

154 m²) per site using methodologies described in Kauffman et al. (2014a). The plots were established 25 m apart along a 125 m transect set in a perpendicular direction from the water edge. At each plot, we sampled C stocks within trees and shrubs, downed wood and the soil profile. We also sampled soil N stocks and interstitial salinity. To estimate C sequestration rates in mangroves, we used a natural ash horizon marker to calculate soil C accumulation. The detailed methodology is explained below.

2.3.1 Biomass and C stock within trees and shrubs

Forest structure was measured at each plot through measurements of the species and the diameter at 1.3 m height (DBH) of all trees. The diameter of trees of *R. mangle* and *R. harrisonii* was measured at the main branch, above the highest prop root (D_R). Aboveground biomass in the marsh communities was determined through plant harvest within two 20 × 20 cm quadrants within each of the six plots. The wet mass was determined in the field and then a subsample was collected from each quadrant and oven-dried to determine its dry weight.

Tree biomass was calculated using allometric equations (Table 2). We used the formula by Fromard et al. (1998), which was obtained for mangroves of French Guiana, which is a location with similar characteristics as those found in

Table 1. Characteristics of sampling sites within La Encrucijada Biosphere Reserve. Values are shown as mean (standard error). Max – maximum; DBH – diameter at breast height; n.a. – not assessed; Rm – *Rhizophora mangle*; Ag – *Avicennia germinans*; Lr – *Laguncularia racemosa*.

	Max height (m)	DBH (cm)	Tree density (trees ha ⁻¹)	Salinity (ppt)	Dominant species
Mangroves					
Upper estuary					
Panzacola	40	10.5 (1.1)	1213 (278)	n.a.	Rm (97.5 %)
Teculapa	30	7.5 (1.0)	2761 (398)	19.3 (5.3)	Rm (94.5 %)
Paixtalon	25	9.9 (0.9)	2035 (134)	n.a.	Rm (100 %)
Intermediate					
Esterillo	n.a.	8.8 (1.0)	3346 (148)	37.6 (5.3)	Rm (87.7 %), Ag (12.3 %)
Santa Chila	22	9.9 (0.6)	2371 (157)	37.5 (0.6)	Rm (68.9 %), Ag (25.1 %)
Lower estuary					
Zacapulco	n.a.	8.8 (0.8)	1765 (274)	7.6 (0.4)	Rm (87.6 %), Lr (10.6 %)
Las Palmas	28	7.9 (0.4)	5370 (388)	28.9 (0.6)	Ag (83.2 %), Lr (13.9 %)
Peat swamp	22	14.5 (0.9)	2469 (301)	0.0 (0.0)	<i>P. aquatica</i> (96.9 %)
Marsh	3	–	–	n.a.	<i>T. domingensis</i> (100 %)

LEBR (riverine mangroves with a tropical hot humid climate). We compared the formulas of Fromard et al. (1998) and Day et al. (1987), the latter obtained from mangroves in Campeche, Mexico. The results using both formulas were not significantly different ($t = 1.027$; $df = 2284$; $p = 0.30$). We chose the formula by Fromard et al. (1998) because it included trees with a DBH range similar to those found in LEBR (DBH_{Max} = 32 cm for *R. mangle*, 9.6 cm for *Laguncularia racemosa* and 42 cm for *Avicennia germinans*). Above-ground biomass of trees from the peat swamp (*P. aquatica*) was calculated with the formula of van Breugel et al. (2011), while belowground biomass of *P. aquatica* was determined with the equation of Cairns et al. (1997) for trees of tropical forests. Belowground root biomass for mangroves was calculated using the formula by Komiyama et al. (2005) and wood density values (Chave et al., 2009, Zanne et al., 2009) of comparable climatic regions as the LEBR (Table 2). Tree C was calculated from biomass by multiplying by a factor of 0.48 for aboveground and 0.39 for belowground biomass; C content of marshes was calculated using a factor of 0.45 of the total biomass (Kauffman et al., 2014a).

Standing dead trees were also included in the tree C stocks estimations. Each dead tree was assigned to one of three decay status (Kauffman et al., 2014a): Status 1, dead trees without leaves; Status 2, dead trees without secondary branches; and Status 3, dead trees without primary or secondary branches. The biomass for each tree status was calculated as a percentage of the total biomass using the values provided by Fromard et al. (1998). For dead trees of Status 1, biomass was calculated as the total dry biomass minus the

biomass of leaves, equivalent to 2.8 % of the total biomass. The biomass of trees of Status 2 was calculated as the total biomass minus the biomass of leaves (2.8 % of the total) and minus secondary branches (equivalent to 18.7 % of the total biomass). Finally, the biomass of trees of Status 3 was calculated as the biomass of the main stem, which is equivalent to 76.6 % of the total biomass (Table 2).

2.3.2 Downed wood

The mass of dead and downed wood was calculated with the planar intersect technique (Van Wagner, 1968) adapted for mangroves (Kauffman et al., 2014a). Four 14 m transects were established at the centre of each plot: the first one was established at 45° off the direction of the main transect, the other three were established 90° off from the previous transect. The diameter of any downed, dead woody material (fallen/detached twigs, branches, prop roots or stems of trees and shrubs) intersecting each transect was measured. Along the last 5 m of the transect, wood debris > 2.5 cm but < 7.5 cm in diameter (hereafter “small” debris) was counted. From the second metre to the end of the transect (12 m in total), wood debris > 7.5 cm in diameter (hereafter “large” debris) was measured. Large downed wood was separated into two categories: sound and rotten. Wood debris was considered rotten if it visually appeared decomposed and broke apart when kicked. To determine specific gravity of downed wood we collected ~ 60 pieces of downed wood of different sizes (small, large-sound, and large-rotten) and calculated their specific gravity as the oven-dried weight divided by its volume. Using the specific gravity for each group of wood

Table 2. Allometric equations used to calculate aboveground and belowground biomass (kg) of mangrove and peat swamp trees. AGB – aboveground biomass; BGB – belowground biomass; D_R – diameter above highest prop root (cm); DBH – diameter at breast height. Wood density (g cm^{-3}) values used for calculating belowground biomass were obtained from Chave et al. (2009) and Zanne et al. (2009).

Aboveground biomass		
<i>R. mangle</i>	$\text{AGB} = 0.1282 \times D_R^{2.6}$	Fromard et al. (1998)
<i>A. germinans</i>	$\text{AGB} = 0.140 \times \text{DBH}^{2.4}$	
<i>L. racemosa</i>	$\text{AGB} = 0.1023 \times \text{DBH}^{2.5}$	
<i>Pachira</i> sp.	$\ln\text{AGB} = -2.514 + 2.295 \times \ln\text{DBH}$	Van Breugel et al. (2011)
Belowground biomass		
<i>R. mangle</i>	$\text{BGB} = 0.199 \times (0.84^{0.899}) \times (D_R^{2.22})$	Komiyama et al. (2005)
<i>A. germinans</i>	$\text{BGB} = 0.199 \times (0.67^{0.899}) \times (\text{DBH}^{2.22})$	
<i>L. racemosa</i>	$\text{BGB} = 0.199 \times (0.60^{0.899}) \times (\text{DBH}^{2.22})$	
<i>P. aquatica</i>	$\text{BGB} = \text{Exp}(-1.0587 + 0.8836 \times \ln\text{AGB})$	Cairns et al. (1997)

debris, biomass was calculated and converted to C using a conversion factor of 0.50 (Kauffman et al., 1995)

2.3.3 Soil C and N

Soil samples for bulk density and nutrient concentration were collected at each plot using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm radius attached to a cross-handle (Kauffman et al., 1995). The core was systematically divided into depth intervals of 0–15, 15–30, 30–50, 50–100 and >100 cm. Soil depth was measured using a steel 2 m rod that was inserted in the ground at each plot. Samples of a known volume were collected in the field and then dried to constant mass to determine bulk density. Samples were sieved and homogenized and treated with hydrochloric acid to eliminate the inorganic carbon portion before analyses. Concentration of organic C and N were determined using a Costech Elemental Combustion System 4010 (CA, USA, Michigan Technological University, Forest Ecology Stable Isotope Laboratory).

2.3.4 Soil C sequestration rates

We estimated C sequestration rates in mangroves as the amount of C accumulated in the soil profile. To date the soil cores, we used a natural marker that consisted of a volcanic ash horizon that was clearly identified in all the cores (Fig. S1). This ash horizon marks the volcano Santa Maria's eruption in 1902 that represented one of the four largest volcano eruptions of the 20th century (Volcanic Explosivity Index of 6 out of 7, Williams and Self, 1983). As a result of the eruption, a recognizable Plinian deposit of known date ashes can be established in the Mexican Pacific coast, northwest of the volcano. We estimated soil C sequestration within each plot of six of our mangrove sites by dividing the depth of the ash horizon by years since the volcano eruption occurred and multiplying it by bulk density and C content. Soil C sequestration rates are expressed in $\text{g C m}^{-2} \text{yr}^{-1}$. We were

unable to measure soil C sequestration rates of marsh and peats swamp forest, as these vegetation types frequently suffer from fires and thus have confounding ash horizons.

2.3.5 Interstitial salinity

Salinity was measured with a YSI-30 multiprobe sensor (YSI, Xylem Inc. Ohio, USA) from water extracted from 30 cm deep. The water was obtained with a syringe and an acrylic tube (McKee et al., 1988).

2.4 Scaling up

To scale up our field measurements to the LEBR, we conducted different approaches for each vegetation type. We relied on modelling approaches to predict values of variables of interest in places where no information was available.

For mangroves, we first estimated aboveground C (trees) throughout the LEBR. Data were spatially harmonized with vegetation-related remote sensing products and the first three principal components of the SAGA GIS standard terrain parameters derived from a digital elevation model (Table S1 in the Supplement). A pixel size of 25 m was selected to resample remote sensing and topographic layers given the coarser spatial resolution of ALOS Palsar products. Upscaling of aboveground C was performed in R (Core Team, 2015) by the means of a machine learning random forest tree ensemble (Breiman, 2001). The number of covariates to fit each tree (mtyr parameter) was tuned by 10-fold cross-validation. The number of trees to grow was 1000, which was enough to stabilize the error. For external validation purposes, 20 % of available data was randomly left out of the model. Selection of external validation and modelling was repeated 400 times to analyse the effects of the random split on error metrics by the correlation between observed and modelled and the root mean squared error (RMSE). Additionally, we implemented the quantile regression forest method proposed by Meinhausen (2006), which allows the inference of

the full conditional distribution of the response variable as a function of its covariates. Having this information, prediction intervals (at 95 %) were identified and their range was used to provide a spatially explicit measure of uncertainty, considering the number of data, the correlation among predictive variables, as well as the complexity and geographical dimensions of the study area. The aboveground C was extrapolated to total C stocks based on the field-collected data. As a comparison exercise, we also estimated mean ecosystem C stocks times the estimated area for each vegetation type on the basis of the NDVI classification, which broadly represented mangroves from the upper, intermediate and lower estuary (Fig. 1).

For the extrapolation of marsh dominated by *T. dominguensis* to the whole LEBR, we included a number of sites where aboveground and belowground biomass and organic matter content have been measured (C. Tovilla, unpublished data, Fig. 1), which together with our field measurements, were used to roughly estimate C stocks within the LEBR. The total area of marsh was calculated on the basis of the “other wetlands” category obtained from the coastal vegetation map of the Pacific south region (CONABIO, 2013), as well as from auxiliary cartographic (SERIE IV; INEGI, 2012) and our field experience. It is likely that the area of the marsh – and thus its C stock – was over- or underestimated, as the marsh area included waterholes and inundated vegetation (*popales*) with unknown C stocks.

For peat swamps, we extrapolated our six sampling plots to the forest surrounding our sampling area, which had an area of 844 ha (Fig. 1). The rest of the area of peat swamp forest is not available for the LEBR. Therefore, the C stock estimated for peat swamp forests was underestimated.

2.5 Statistical analyses

One-way analysis of variance (ANOVA) was performed to test differences of above- and belowground biomass and C stocks among wetland types (mangroves, marsh and peat swamp forest), sites and geomorphological setting (upper estuary, intermediate and lower estuary mangroves). To avoid uncertainties associated with imbalance designs, when comparing vegetation types (mangroves vs. peat swamps vs. marsh), we used the mean for all mangrove sites for each of the five plots which represented a range a vegetation from the water edge to the landward side of the forest. The mean of the plots was compared against the plots laid in a similar way for peat swamp forest and marsh ($n = 5$ plots per site). Differences in soil C and N concentrations by depth were tested with a two-way ANOVA, with site as the fixed effect and depth as the random effect of the model. Normality was assessed using Shapiro–Wilk tests. When significant differences were found, pair-wise comparisons were explored using Scheffé post hoc tests. Analyses were performed using Prism v6.0 (GraphPad Software, La Jolla, CA, USA) and

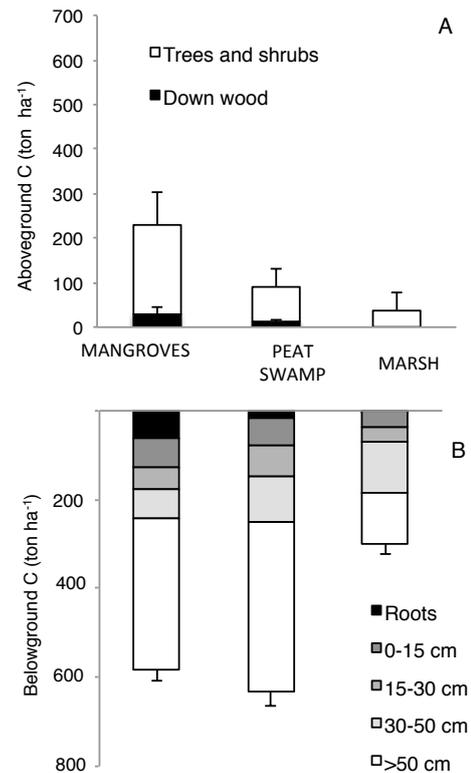


Figure 2. Aboveground (a) (trees and shrubs and down wood) and belowground (b) (soil at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves, peat swamp forests and marsh wetlands within La Encrucijada Biosphere Reserve.

SPSS Statistics v20 (IBM, New York, USA). Throughout the paper, data are reported as mean \pm standard error.

3 Results

3.1 Forest structure

Mangroves of the LEBR were dominated by trees of *R. mangle* with lesser contributions of *A. germinans*, *L. racemosa* and a few trees of *R. harrisonii* (in sites Panzacola and Teculapa). Only one of our study sites – Las Palmas – was dominated by a different species, *A. germinans*. All the sampling sites were characterized by relatively low tree density forests ($1213\text{--}5370$ trees ha^{-1}) with tall trees ($\sim 20\text{--}40$ m in height) of mean DBH of 8–11 cm (Table 1). The peat swamp forest was dominated by *P. aquatica* and had a similar structure to that of mangroves with a tree density of 2469 trees ha^{-1} , trees of up to 22 m in height and mean DBH of 14.5 cm. Finally, the marsh was dominated by tall grasses (2–3 m in height) of *T. dominguensis* (Table 1).

Table 3. Aboveground biomass, belowground biomass (Mg ha^{-1}) and total carbon (C) in vegetation (MgC ha^{-1}) within wetlands of La Encrucijada Biosphere Reserve. Values are shown as mean (standard error). Different letters indicate significant differences among sites ($p < 0.05$). The marsh was not included in analysis due to missing belowground biomass.

Site	Biomass (Mg ha^{-1})		C (MgC ha^{-1})
	Aboveground	Belowground	
Mangroves			
Panzacola	383.6 (153.6) ^{ab}	127.9 (47.6) ^{ab}	234.0 (92.3) ^{ab}
Teculapa	342.4 (87.0) ^{ab}	118.3 (20.4) ^{ab}	210.5 (49.4) ^{ab}
Paixtalón	391.6 (87.0) ^{ab}	140.0 (25.4) ^{ab}	242.6 (51.6) ^{ab}
Esterillo	621.3 (310.9) ^b	203.1 (85.1) ^b	377.4 (182.4) ^{bc}
Santa Chila	198.8 (13.4) ^a	93.9 (3.8) ^{ab}	132.1 (7.8) ^a
Zacapulco	303.5 (76.5) ^a	127.8 (29.9) ^a	195.5 (48.3) ^{ab}
Las Palmas	706.6 (172.6) ^b	268.7 (52.5) ^c	440.0 (103.1) ^c
Peat swamp	162.2 (27.3) ^a	43.5 (6.8) ^a	95.1 (15.7) ^a
Marsh	76.5 (11.6) ^a	n.a.	38.2 (5.8)

3.2 Tree biomass and C

Mean tree aboveground biomass of mangroves was $421.1 \pm 67.8 \text{ Mg ha}^{-1}$ and was higher than the biomass for the peat swamp and marsh, which was 162.2 ± 27.3 and $76.5 \pm 11.6 \text{ Mg ha}^{-1}$, respectively. Thus, mean C stock in mangrove trees was significantly higher in mangroves ($215.0 \pm 44.4 \text{ MgC ha}^{-1}$) compared to swamp forests and marsh (95.1 ± 15.7 and $38.2 \pm 5.8 \text{ MgC ha}^{-1}$, respectively; $F_{2, 12} = 167.4$; $p < 0.0001$; Table 3, Fig. 2).

Tree biomass and vegetation C stocks were not significantly different among upper, intermediate and lower estuary mangroves ($F_{7, 40} = 1.826$; $p = 0.109$). However, there were significant differences among sites with lowest C stocks measured in the vegetation of Santa Chila ($132.1 \text{ MgC ha}^{-1}$; $t = 2.54$; $p = 0.015$) and highest at Las Palmas ($440.0 \text{ MgC ha}^{-1}$; $t = 2.03$; $p = 0.049$), the only site dominated by *A. germinans* and not *R. mangle*. The vegetation biomass and C stocks were quite similar among sites within the upper estuary (range 211–243 MgC ha^{-1}), but highly variable among sites within the intermediate and lower estuary (132–440 MgC ha^{-1} ; Table 3, Fig. 3).

3.3 Downed wood C

Downed wood C was low in peat swamp wetlands ($12.5 \pm 2.8 \text{ MgC ha}^{-1}$), but considerable in some mangrove sites (mean of $29.4 \pm 3.7 \text{ MgC ha}^{-1}$). The amount of downed wood in mangroves had a wide range within sites, from 11 Mg ha^{-1} to 205 Mg ha^{-1} , with a mean biomass of $59.4 \pm 26.0 \text{ Mg ha}^{-1}$ (Table 4, Fig. 3). Mangroves in the lower estuary had the highest biomass and C stocks of downed wood ($F_{2, 39} = 6.86$; $p = 0.0028$), mainly due to large amounts of downed wood at Zaca-

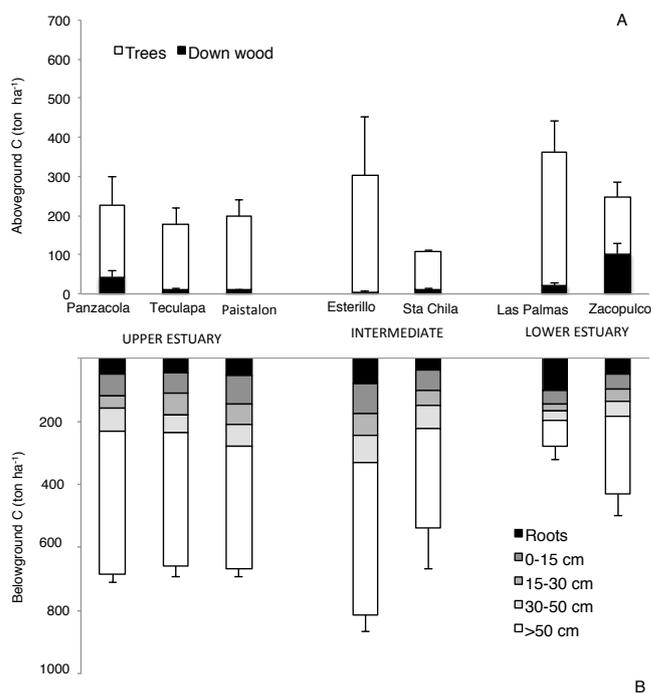


Figure 3. Aboveground (a) (trees and shrubs and down wood) and belowground (b) (soil at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves along a gradient from the upper to the lower estuary within La Encrucijada Biosphere Reserve.

pulco ($102.4 \pm 27.0 \text{ MgC ha}^{-1}$; $F_{7, 47} = 8.147$; $p < 0.0001$). Small downed wood comprised 10.2% of the total biomass ($6.0 \pm 0.8 \text{ Mg ha}^{-1}$); large sound wood the 55.4% ($33.0 \pm 13.9 \text{ Mg ha}^{-1}$) and large rotten wood comprised 34.4% of the total ($20.4 \pm 15.2 \text{ Mg ha}^{-1}$).

3.4 Soil C and N

Soil C content (%) was higher in peat swamps ($19.9 \pm 3.4\%$) compared to marsh ($10.1 \pm 2.5\%$); mangroves had intermediate values ($14.6 \pm 2.5\%$; $F_{2, 12} = 3.616$; $p = 0.04$). Soil N (%) was higher in peat swamps ($1.2 \pm 0.2\%$) compared to mangroves and marsh (0.6 ± 0.1 and $0.6 \pm 0.2\%$, respectively; $F_{2, 12} = 5.558$; $p = 0.019$). Soil C stock (MgC ha^{-1}) was significantly higher in mangroves ($505.9 \pm 72.6 \text{ MgC ha}^{-1}$) and the peat swamp forest ($614.6 \pm 85.7 \text{ MgC ha}^{-1}$) compared to the marsh ($298.3 \pm 39.0 \text{ MgC ha}^{-1}$; Fig. 2; $F_{2, 12} = 5.42$; $p = 0.02$). Finally, soil N stocks were higher for peat swamps ($40.4 \pm 5.5 \text{ Mg ha}^{-1}$) compared to mangroves ($19.2 \pm 2.7 \text{ Mg ha}^{-1}$) and marshes ($18.5 \pm 1.7 \text{ Mg ha}^{-1}$; $F_{2, 12} = 11.51$; $p = 0.0016$; Table 5).

When comparing mangroves from the upper to the lower estuary we found that the soil C stocks from the upper and intermediate estuary were significantly higher than those from the lower estuary ($F_{2, 12} = 25.43$; $p < 0.0001$). Soil C stocks were also significantly different among sites and depths (Site

Table 4. Biomass (Mg ha^{-1}) and C stocks (MgC ha^{-1}) of downed wood in La Encrucijada Biosphere Reserve. Wood debris was calculated separately for small wood (diameter >2.5 and <7.5 cm), and large sound and large rotten wood (diameter >7.5 cm). Values are shown as mean (standard error).

	Site	Small wood (<7.5 cm; Mg ha^{-1})	Large wood (>7.5 cm; Mg ha^{-1})		C stock (MgC ha^{-1})
			Sound	Rotten	
Mangroves	Panzacola	5.8 (1.0)	79.8 (24.0)	1.4 (0.6)	43.5 (15.5)
	Teculapa	10.3 (2.8)	14.0 (4.4)	3.4 (1.3)	11.9 (3.0)
	Paixtalon	5.3 (1.1)	7.7 (2.7)	5.8 (3.0)	9.4 (2.2)
	Esterillo	5.5 (0.9)	0.5 (0.4)	4.5 (1.4)	5.3 (0.4)
	Santa Chila	6.6 (1.9)	5.7 (1.7)	10.8 (3.5)	11.5 (1.9)
	Zacapulco	4.4 (1.3)	88.9 (26.7)	111.5 (45.2)	102.4 (27.0)
	Las Palmas	4.4 (0.9)	34.1 (11.1)	5.7 (2.1)	22.1 (6.6)
Peat swamp		9.2 (1.5)	3.0 (1.6)	20.4 (6.2)	12.5 (2.8)

$F_{7, 64} = 16.03$, $p < 0.0001$; Depth $F_{3, 64} = 8.83$; $p < 0.001$; Table 5), with highest C density in the soil horizon >50 cm. Soil N stocks were higher in mangroves of the upper estuary ($26.4 \pm 0.5 \text{ Mg ha}^{-1}$) compared to mangroves in the intermediate and lower estuary (15.3 ± 1.6 and $12.3 \pm 3.2 \text{ Mg ha}^{-1}$, respectively; $F_{2, 4} = 20.35$; $p = 0.008$; Table 5). We also found a trend of the distribution of soil C with depth among mangroves from the upper to the lower estuary. Soil C values increased with depth at Panzacola (upper estuary), remained similar in depth in Teculapa and Paixtalon (upper estuary) and decreased in depth at the rest of the mangroves within the intermediate and lower estuary (Table 5).

Overall, C stocks were highest in mangroves and peat swamp forests, while N stocks were highest in peat swamp forests. Soil C and N stocks were highest in the upper estuary and decreased towards the lower estuary. Finally, the variation of site replicates was different within the upper and lower estuary: inter-site variability was much lower in mangroves from the upper estuary compared to the mangroves from the intermediate and lower estuary (Fig. 3).

3.5 Ecosystem C stocks

Mean C stocks of wetlands in the LEBR were significantly different, with highest stocks for mangroves ($784.5 \pm 73.5 \text{ MgC ha}^{-1}$) and peat swamps ($722.2 \pm 63.6 \text{ MgC ha}^{-1}$) and lowest for marsh ($336.5 \pm 38.3 \text{ MgC ha}^{-1}$; $F_{2, 12} = 16.9$; $p = 0.0004$; Fig. 2, Table 6).

There was a significant difference among mangroves along the estuary, with mangroves from the upper ($871.0 \pm 22.0 \text{ MgC ha}^{-1}$) and intermediate estuary ($825.8 \pm 289.2 \text{ MgC ha}^{-1}$) having higher C stocks compared to those in the lower estuary ($659.5 \pm 18.6 \text{ MgC ha}^{-1}$) ($F_{2, 12} = 25.43$; $p < 0.0001$). Largest C stocks were measured at Esterillo ($1114.9 \pm 150.3 \text{ MgC ha}^{-1}$) and lowest at Santa Chila ($536.6 \pm 88.8 \text{ MgC ha}^{-1}$). The C stocks of man-

groves within the upper estuary were quite similar among sites (CV = 4.4 %), while the stocks from mangroves within the intermediate and lower estuary had large variability (CV = 34.4 %).

3.6 C stocks of LEBR

With the use of the cross-validated correlation from 400 realizations, we selected a model that was able to explain 34 % of aboveground C variance, with a RMSE of $111.29 \text{ MgC ha}^{-1}$. External validation had a higher correlation value ($R^2 = 0.73$, RMSE = $60.28 \text{ MgC ha}^{-1}$), but was less reliable since there were only 12 points (20 % of available data). Predicted aboveground C for the LEBR ranged between 18 and 567 MgC ha^{-1} , with a mean of $118 \pm 54 \text{ MgC ha}^{-1}$, with an estimated total of 3.5 million MgC for aboveground mangrove C for the LEBR (Fig. 4). However, the results had a large degree of uncertainty, mostly in mangroves at the water edge, at the landward side, and mangroves close to the estuary mouth (Fig. 4b), some of these sites identified as monospecific forests of *A. germinans*.

Although the prediction of the aboveground C was low, we were able to identify that most forests within the LEBR have less than 300 MgC ha^{-1} (Fig. 4c). Based on our field data, we identified that fringe forest dominated by *R. mangle* had between 300 and 400 MgC ha^{-1} , while forest of *A. germinans* had aboveground biomass $>400 \text{ MgC ha}^{-1}$, and most forests with aboveground values below 300 MgC ha^{-1} were basin forests dominated by *R. mangle*. According to the model, and agreeing with our field experience, this kind of forest comprises more than 90 % of the mangroves of the LEBR. On the basis of this result, we calculated the mean C stock for plots of mangroves with these characteristics and obtained a value of $848.0 \pm 31.6 \text{ MgC ha}^{-1}$, which extrapolated to the whole LEBR provides a rough estimate of 23.3 million MgC. The uncertainty of this estimation is highest in mangroves from the lower estuary and mangroves close

Table 5. Soil carbon (C) and nitrogen (N) concentrations (%), and soil C and N stock (Mg ha^{-1}) at different depths (0–150 cm) of wetlands from La Encrucijada Biosphere Reserve. Values are shown as mean (standard error). Different letters indicate significant differences between sites ($p < 0.05$).

Site	Depth (cm)	C (%)	N (%)	C stock (Mg ha^{-1})	N stock (Mg ha^{-1})
Panzacola	0–15	16.6 (1.5)	0.88 (0.08)	71.0 (4.2)	3.6 (0.2)
	15–30	14.6 (3.7)	0.76 (0.19)	37.9 (7.1)	1.9 (0.3)
	30–50	21.0 (2.8)	0.92 (0.13)	73.6 (7.8)	3.5 (0.5)
	> 50	26.8 (1.4)	1.04 (0.07)	451.6 (30.0)	17.5 (1.3)
	Total			634.0 (25.7) ^a	26.5 (1.1) ^{ac}
Teculapa	0–15	14.8 (4.0)	0.78 (0.20)	64.3 (9.1)	3.7 (0.4)
	15–30	20.1 (3.9)	0.76 (0.21)	68.6 (6.7)	2.6 (0.5)
	30–50	8.8 (3.7)	0.37 (0.16)	59.4 (11.8)	2.4 (0.5)
	> 50	15.9 (3.1)	0.67 (0.12)	421.2 (29.5)	18.4 (1.4)
	Total			613.6 (32.2) ^a	27.2 (2.0) ^{ac}
Paixtalón	0–15	22.3 (4.4)	0.82 (0.15)	91.6 (7.5)	3.6 (0.4)
	15–30	19.4 (4.0)	0.82 (0.16)	63.0 (6.5)	2.6 (0.2)
	30–50	13.0 (4.0)	0.50 (0.13)	69.6 (9.0)	2.9 (0.1)
	> 50	17.1 (3.9)	0.71 (0.17)	389.4 (21.1)	16.4 (1.3)
	Total			613.6 (23.6) ^a	25.4 (1.5) ^{ac}
Esterillo	0–15	20.4 (3.7)	0.95 (0.18)	98.1 (6.6)	4.8 (0.4)
	15–30	21.7 (4.2)	0.91 (0.17)	66.7 (8.2)	3.1 (0.4)
	30–50	16.5 (4.1)	0.65 (0.15)	88.1 (14.3)	3.1 (0.6)
	> 50	16.1 (3.4)	0.56 (0.11)	479.3 (44.6)	2.6 (0.2)
	Total			732.2 (53.8) ^b	13.6 (1.1) ^{ab}
Santa Chila	0–15	29.1 (1.3)	1.30 (0.06)	66.1 (6.2)	3.1 (0.4)
	15–30	23.2 (2.4)	1.08 (0.12)	47.2 (5.6)	2.8 (0.3)
	30–50	12.0 (2.6)	0.45 (0.09)	71.9 (8.8)	3.4 (0.4)
	> 50	14.8 (1.7)	0.49 (0.07)	317.7 (83.8)	11.7 (3.3)
	Total			393.0 (128.8) ^{ac}	16.9 (5.7) ^{ab}
Zacapulco	0–15	12.4 (2.9)	0.58 (0.15)	49.6 (8.1)	2.9 (0.6)
	15–30	11.8 (3.7)	0.58 (0.20)	37.9 (5.6)	3.8 (1.5)
	30–50	3.9 (1.6)	0.18 (0.06)	45.5 (10.9)	1.3 (0.5)
	> 50	8.5 (1.5)	0.34 (0.06)	247.2 (61.2)	12.7 (2.1)
	Total			380.1 (68.6) ^{ac}	15.5 (4.3) ^{ab}
Las Palmas	0–15	6.2 (1.2)	0.32 (0.07)	43.1 (5.5)	2.8 (0.3)
	15–30	1.7 (0.4)	0.09 (0.03)	20.3 (3.1)	1.3 (0.2)
	30–50	1.2 (0.2)	0.07 (0.01)	28.0 (5.5)	1.5 (0.2)
	> 50	0.8 (0.3)	0.04 (0.01)	83.4 (34.7)	3.5 (1.3)
	Total			174.8 (41.9) ^c	9.1 (1.7) ^b
Peat swamp	0–15	16.3 (5.5)	1.05 (0.32)	59.5 (15.13)	3.6 (0.1)
	15–30	19.2 (5.9)	1.18 (0.41)	70.3 (26.1)	3.6 (1.2)
	30–50	30.0 (7.2)	1.69 (0.35)	105.0 (21.8)	6.8 (1.4)
	> 50	16.7 (5.2)	1.02 (0.39)	379.8 (68.8)	26.4 (5.6)
	Total			614.6 (85.7) ^a	40.4 (5.5) ^c
Marsh	0–15	15.6 (4.0)	1.10 (0.28)	38.3 (7.9)	3.0 (0.5)
	15–30	6.9 (1.8)	0.42 (0.08)	32.0 (6.0)	2.8 (0.3)
	30–50	13.0 (3.0)	0.65 (0.17)	113.8 (19.2)	5.8 (0.8)
	> 50	4.7 (0.9)	0.24 (0.03)	114.1 (21.1)	6.8 (0.7)
	Total			298.3 (39.0) ^c	18.5 (1.7) ^{ab}

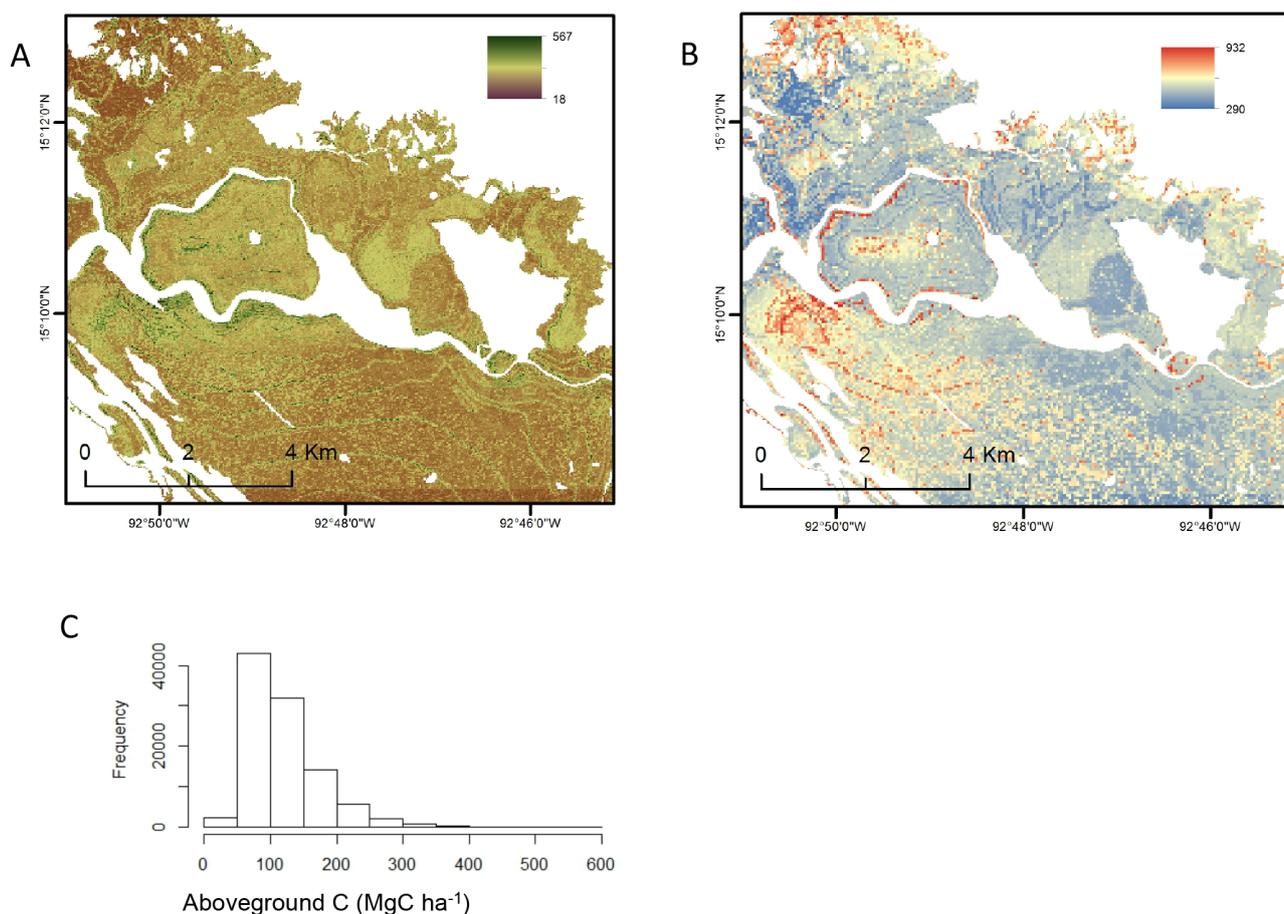


Figure 4. Aboveground C stocks (trees; MgC ha^{-1}) (a) estimated for the sampling region within La Encrucijada Biosphere Reserve; (b) uncertainty associated with estimations; and (c) frequency of occurrence of estimated C stock values of mangroves.

Table 6. Ecosystem C stocks (MgC ha^{-1}) for wetlands of La Encrucijada Biosphere Reserve. Values are shown as mean (standard error).

Vegetation	Site	C (MgC ha^{-1})	
Mangrove	Upper estuary	Panzacola	911.6 (74.5)
		Teculapa	835.8 (42.2)
		Paixtalon	865.6 (55.1)
		mean	871.0 (22.0)
	Intermediate	Esterillo	1114.9 (150.3)
		Santa Chila	536.6 (88.8)
		mean	825.8 (289.2)
	Lower estuary	Zacapulco	678.1 (115.7)
		Las Palmas	640.9 (114.8)
mean		659.5 (18.6)	
Mangrove mean		784.5 (73.5)	
Peat swamp		722.2 (63.6)	
Marsh		336.5 (38.3)	

to water or the landward edge. As a comparison, if we extrapolated the C stocks of the mangroves using the classes

obtained from the NDVI classification (upper, intermediate and lower estuary) the estimation is similar with 20.9 million MgC for the LEBR.

The C stock of marshes was estimated to vary between 37.1 and 720.4 MgC ha^{-1} across the LEBR. Using the mean value of 432.2 MgC ha^{-1} obtained from data from this study and from Tovilla et al. (unpublished data, Fig. 1), we estimated that the C stock of marshes within the LEBRE is close to 14.0 million MgC . Finally, peat swamps only cover a very small area of the LEBR and their C stocks were estimated to be of at least 0.6 million MgC . In summary, the approximate C stock value for the LEBR is 38 million MgC .

3.7 Soil C sequestration rates

Mean soil C sequestration rate in mangroves was $1.3 \pm 0.2 \text{ MgC ha}^{-1} \text{ yr}^{-1}$; soil C sequestration was similar among all sites (upper, intermediate and lower estuary; $F_{2, 4} = 0.78$; $p = 0.516$). Lowest values ($0.4 \pm 0.0 \text{ MgC ha}^{-1} \text{ yr}^{-1}$) were measured in the site Las Palmas, which was dominated by *A. germinans* (Table 7). Considering that less than 10% of the mangroves

Table 7. Soil carbon (C) sequestration rates ($\text{MgC ha}^{-1} \text{ yr}^{-1}$) of mangroves within La Encrucijada Biosphere Reserve, Mexico.

	Site	Soil C sequestration rate ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)
Upper estuary	Panzacola	1.0 (0.1)
	Teculapa	1.4 (0.1)
	Paixtalon	1.7 (0.1)
Intermediate	Esterillo	1.8 (0.1)
	Santa Chila	1.3 (0.1)
Lower estuary	Zacapulco	1.5 (0.0)
	Las Palmas	0.4 (0.0)
	Mean	1.3 (0.2)

in LEBR are dominated by *A. germinans*, we can estimate that the C sequestration of mangroves in LEBR through soil accretion is close to 39 842 MgC every year.

4 Discussion

The riverine wetlands measured in this study had large C stocks, with values for mangroves and peat swamps almost twice as high as those measured in terrestrial forests (typically $<400 \text{ MgC ha}^{-1}$, IPCC, 2003). C stocks of mangroves within LEBR (mean of $784.5 \pm 73.5 \text{ MgC ha}^{-1}$; maximum of $1,115 \text{ MgC ha}^{-1}$) were similar to other mangroves around the world, such as in Vietnam ($762.2 \pm 57.2 \text{ MgC ha}^{-1}$, Nguyen et al., 2014), the Dominican Republic (853 MgC ha^{-1} , Kauffman et al., 2014b), Yucatan, Mexico ($663 \pm 176 \text{ MgC ha}^{-1}$; Adame et al., 2013) and Northwest Madagascar ($367\text{--}593 \text{ MgC ha}^{-1}$; Jones et al., 2014). As hypothesized, C stocks of mangroves and peat swamps were higher than those of marshes ($336.5 \pm 38.3 \text{ MgC ha}^{-1}$).

In general, mangroves within the upper estuary had higher C stocks compared to mangroves in the lower estuary. However, the most striking difference was not related to C content, but to site variability. Mangroves from the upper estuary were quite similar in structure and C stocks within sites. In contrast, mangroves from the intermediate and lower estuary were much more variable. We also found differences in soil C with depth: soil C increased or was similar with depth at mangroves in the upper estuary, while soil C decreased with depth in mangroves from the lower estuary (similar to Donato et al., 2011). We suggest that differences in geomorphological forces explain the variation in C stocks and soil C distribution within the sediment column. Mangroves in the upper estuary have grown in a relatively stable environment that allowed C to be buried and forests to develop into a mature state. Comparatively, mangroves in the lower estuary are exposed to frequent changes in hydrology, sedimentology and are directly struck by tropical storms (Woodroffe, 1992). As

a result, mangroves in the lower estuary are a mosaic of old and young forests, some of them with productivities and soil C similar to those in the upper estuary, but others with low productivity, statures and soil C, and thus C stocks.

The N stocks within mangroves also differed among sites, with highest stocks in mangroves from the upper estuary. Upland mangroves receive high N inputs due to agricultural activity in the catchment (UNESCO, 2014); lowland mangroves probably receive lower N loads as oceanic water has usually lower nutrients than riverine water. Differences in N content have also been associated with microbial activity such as bacteria and protozoans, which are in turn linked to tidal flushing in the mangrove soil (Alongi, 1988). Higher nitrification and denitrification and lower N fixation rates could further explain low N stocks in lowland mangroves; however, this remains to be tested. The higher N inputs in mangroves in the upper estuary, coupled with lower salinity values throughout the year, probably contribute to the higher productivity of mangroves in the upper estuary compared to those in the lower estuary (Tovilla et al., unpublished data).

Besides the differences in C and N stocks between upland and downland mangroves, it stands out that the mangrove forest dominated by *A. germinans* (Las Palmas) was notably different. This forest had the highest tree biomass, lowest soil C and lowest C sequestration rates measured in this study. Lowest C stocks in soils of *A. germinans* can be due to the lower C wood content that is buried in the soil. Wood density of *A. germinans* is lower ($0.67\text{--}0.90 \text{ g cm}^{-3}$) than wood density of *R. mangle* ($0.810\text{--}1.05 \text{ g cm}^{-3}$; Chave et al., 2009, Zanne et al., 2009), which dominated all other sites. Wood density is a major predictor of stored C in wood biomass and could explain the low values of C buried in the soil (Flores and Coomes, 2011), and thus, the low C stocks in the mangrove forest dominated by *A. germinans*.

Most of the C stock in mangroves is stored in the soil (Donato et al., 2011; Adame et al., 2013); thus the potential of mangroves to sequester C is closely related to their soil C sequestration rates. The soil C sequestration rates measured in mangroves of LEBR ($0.4\text{--}1.8 \text{ MgC ha}^{-1} \text{ yr}^{-1}$) were similar throughout upper and lower estuary mangroves, which suggests that over the long term, variability among sites in C sequestration was not high enough to be detected with our method. However, the C sequestration rate of the site dominated by *A. germinans* was two to three times lower compared to forests dominated by *R. mangle*. The soil C sequestration estimates in this study are within the range of those reported in the review by Chmura et al. (2003), with lowest values in Rookery Bay, Florida (0.2 MgC ha^{-1}) and highest in Términos Lagoon, Campeche, Mexico ($6.5 \text{ MgC ha}^{-1} \text{ yr}^{-1}$), and are similar to those measured in Moreton Bay, Australia ($0.8 \text{ MgC ha}^{-1} \text{ yr}^{-1}$; Lovelock et al., 2014). Long-term soil C sequestration rates are difficult to obtain; thus the values obtained in this study are valuable estimations of C sequestration rates of mangrove forests. For example, we can roughly estimate that the sequestration rate of the mangrove

soil of LEBR is $39\,842\text{ MgC yr}^{-1}$, which is equivalent to the annual emissions of approximately 10 348 Mexicans (using emissions by country from IEA, 2014).

To include wetlands in REED+ and other financial incentives for climate change mitigation, it is usually necessary to estimate C stocks and sequestration data for large areas of wetlands. Extrapolation of field data was challenging, with models showing poor agreement between external and cross-validation, and high uncertainty in some areas of mangroves. Other studies have faced similar problems, with previous reports at a national level only being able to explain 2 % of spatial variability (Cartus et al., 2014). Water level dynamics and the complexity of structural diversity of mangroves are important sources of uncertainty when using remote sensing sources. It is important to distribute sampling efforts wisely so as to include as much spatial variability as possible. Additionally, sampling variables such as pH and salinity, which could further explain vegetation variability, could be helpful (Vaiphasa, et al, 2006). In this study, we identified that species composition is an important variable as well as geomorphic location (upper and lower estuary) to explain spatial variability within C stocks. Our results also show that the most variable, and thus where field sampling should be concentrated, are mangroves close to the mouth of the estuary and in the landward and water edges.

Mangroves in riverine deltas are the most extensive and developed forests (Woodroffe, 1992). Thus, the results in this study contribute to the C budgets of riverine wetlands, which are likely to be one of the most C rich ecosystems in the world. The wetlands of LEBR store about 38.0 Mton C, which is equivalent to 139.5 Mton CO₂. Degradation of wetlands in the region due to increased sediment loads derived from upriver dredging, fires, hydrological modifications and illegal harvesting threaten the potential C storage of these wetlands.

The C stocks and sequestration values shown in this study can help provide incentives into the reforestation and conservation projects of this reserve and throughout similar wetland ecosystems. For example, marsh and swamp forests are very susceptible to fire damage during the dry season (L. Castro, personal communication, 2013). With the C stocks calculated in this study, we estimated that if fire consumes all the vegetation and the top 15 cm of soil (Schmalzer and Hinkle, 1992), every hectare of burned marsh or peat swamp could emit 287 ton CO₂ and 567.4 ton CO₂, respectively. Every year, between 500 and 4500 ha of marshes are burned within the LEBR (L. Castro, personal communication, 2013), which results in an annual mean emission of ~ 0.6 million tons of C or 4.6 % of the emissions of the state of Chiapas (based on emissions reported by IEA, 2014). This information can be used to emphasize the importance of managing fires in the LEBR in order to maintain its large C stocks and avoid CO₂ emissions to the atmosphere. Another example is to use the C stocks provided in this study to negotiate for offsetting emissions within the country or abroad. For instance,

California USA has signed an agreement to import C credits from forests in Chiapas, the state where this study takes place (Morris et al., 2011). To include mangroves and other wetlands in similar agreements could be a cost-effective way to reduce C emissions (Siikamäki et al., 2012), while at the same time protecting the biodiversity and the ecosystem services they provide (Adame et al., 2014). Finally, our results have also shown that extrapolation of C stocks to larger areas requires the inclusion of not only aboveground biomass, but also field measurements of soil C stocks and to consider differences among vegetation types, species composition and geomorphological setting.

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Author contributions. M. F. Adame designed the project, led the field campaign, collected the data and wrote the paper. N. S. Santini designed the project, performed data analysis and participated in writing and preparation of the paper. C. Tovilla participated in the field campaign, collected data and contributed to the paper. A. Vázquez-Lule prepared the geographical information system data and map, and A. Vázquez-Lule and M. A. Guevara performed data analysis and contributed to the paper. L. Castro participated in the field campaign, collected data and contributed to the paper.

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