1 <mark>Carbon stocks and soil sequestration rates of tropical riverine wetlands</mark>

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Abstract

Riverine wetlands are created and transformed by geomorphological processes that determine their vegetation composition, their 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 and mangroves) whose distribution spans from an environment dominated by riverine 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 MgC ha^{-1} and 722.2 ± 63.6 MgC ha^{-1}, respectively) were higher than those of marshes (336.5 ± 38.3 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 744-912 MgC ha^{-1}) compared to the intermediate and lower estuary (range 537-1,115 MgC ha^{-1}) probably as a result of a highly dynamic coastline. Soil C sequestration values were 1.3 ± 0.2 MgC ha^{-1}yr^{-1} and were similar across sites. Estimations of C stocks within large areas need to include spatial variability related to vegetation composition and geomorphological setting to accurately reflect variability within riverine wetlands.

49

1. Introduction

Deforestation and ecosystem degradation is, after fossil fuel combustion, the largest cause of carbon dioxide (CO_2) 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 saltmarshes 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 CO_2 to the atmosphere (Lovelock et al., 2011). To prevent the large emissions that result from wetland loss, programs such as REDD+ (Reducing Emissions from Deforestation and forest Degradation) have been proposed. In order to target coastal wetlands within REDD+ and other financing programs, 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, 1975). For example, sparse mangroves growing in an accreting riverbank could become tall, productive forests in fifty 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

73 destroy landforms, resulting in changes in vegetation, production, sedimentation, and

74 thus in C stocks (Adame et al. 2010, Alongi 2011).

75

76   Many forces contribute to the formation of riverine wetlands in deltaic-estuarine

77 landscapes, including: river run-off, wave action, tidal inundation and the incidence of

78 cyclones (Thom 1967, Woodroffe 1992). In the Southern Mexican Pacific (Fig. 1),

79 wetlands where freshwater input is constant, tidal inundation is negligible and wave

80 and storm damage is relatively low, are formed by a mosaic of marshes and peat

81 swamps. Lowland, mangroves dominate the vegetation from the upper to the lower

82 estuary. Upper estuarine mangroves have periodic input of freshwater and lower tidal

83 and wave influence compared to mangroves in the lower estuarine region (Thom

84 1975). In this study, we compared C stocks (trees, soil and downed wood) of riverine

85 wetlands of La Encrucijada Biosphere Reserve (LEBR) in the Pacific south coast of

86 Mexico. We compared C stocks of different vegetation types (mangroves, peat

87 swamps and marsh) and throughout a geomorphological gradient (upper to lower

88 estuary).

89

90   Wetlands are not only efficient at accumulating C, but also nitrogen (N) when

91 production exceeds N demand (Rivera Monroy et al., 1995). C and N cycles interact

92 closely, thus N stocks can increase with increments in C (Yimer et al., 2006). N

93 accumulation increases with rainfall, runoff, and production by organisms such as

94 cyanobacteria and algae (Alongi, 2009; Reef et al., 2010). Soil N accumulation is also

95 associated with large foliage cover and wood biomass (e.g. Hooker and Compton,

96 2003; Liao et al., 2007). In this study we compare the capacity of different types of

97   wetlands (mangroves, marshes and peat swamps) and geomorphologic settings

98   (upper and lower estuarine) to store N in the soil.

99

100   The high capacity of wetlands to store C and N is partly due to their high

101   productivity and low soil decomposition rates. Mangroves and marshes can store up to

102   three times more C than terrestrial ecosystems (Chmura et al., 2003; Donato et al.,

103   2011; McLeod et al., 2011). For example, mangroves in the Caribbean can store up to

104   987 MgC ha^{-1}, while in the Indo-Pacific, mangroves store 1,023 MgC ha^{-1} (Donato et

105   al., 2011; Adame et al., 2013). These values typically exceed those of tropical and

106   temperate forests (< 400 Mg ha^{-1}, IPCC, 2003). Similarly, soil C sequestration rates of

107   coastal wetlands (210 g C m^{-2} yr^{-1}) and freshwater wetlands (20 – 30 g C m^{-2} yr^{-1}) are

108   higher than those of terrestrial forests (~ 10 g C m^{-2} yr^{-1}) (Chmura et al., 2003; McLeod

109   et al., 2011). Long-term carbon sequestration rates of mangroves are very difficult to

110   obtain, but are required to participate in carbon payments (Alongi 2011). In this study,

111   we use a unique natural marker (ash horizon from a volcanic eruption in 1902,

112   Supplementary Fig.1) to calculate soil carbon sequestration rates during the last

113   century from a large number of locations (n = 36). We compared C sequestration rates

114   of mangroves across a geomorphological gradient, from mangroves in the upper

115   estuary to those in the lower estuary.

116

117   Riverine wetlands, especially mangroves, are one of the most extensive types of

118   wetlands and are predicted to have one of the largest C stocks on Earth (Ewel et al.,

119   1998). We expect that C stocks within the riverine wetlands of the South Mexican

120   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, 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 LEBR is located in Chiapas, in the south Pacific coast of Mexico (14° 43' N, 92° 26' W). The LEBR comprises an area of 144,868 ha. The Reserve 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; the forest is dominated by trees of *Rhizophora mangle* that range between 20 - 40 m in height, which 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 activity (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

6

144   In this study we sampled three types of wetlands: upriver, a peat swamp forest

145   and marsh and mangrove forests at the estuary. To determine a criteria for

146   stratification of mangroves, we used two SPOT 5 satellite images with geographical,

147   geometric and radiometric correction, and the Universal Transverse Mercator

148   projection system. From each image, the Normalized Difference Vegetation Index

149   (NDVI) was obtained with ERDAS Imagine. The NDVI values ranged from -1 to 1,

150   where negative values indicated areas without vegetation, values close to zero

151   indicated senescent vegetation or in a stressed condition, and values close to 1,

152   indicated green or healthy vegetation (Chuvieco, 2006). NDVI values were extracted

153   from the mangrove coverage map (CONABIO, 2013) and classified according to Ruiz-

154   Luna et al. (2010). The mangrove vegetation was divided in three classes: the most

155   vigorous vegetation was Class I (9,253 ha), the least vigorous vegetation was Class III

156   (11,467 ha), Class II (6,757 ha) had intermediate values of vegetation vigour. The

157   mangrove Classes along with the distance to the mouth of the estuary were used to

158   classify our sites into three categories: upper estuary mangroves with the most

159   vigorous vegetation, lower estuary mangroves with the least vigorous vegetation and

160   intermediate mangroves in terms of vigour and distance to the mouth of the estuary

161   (Fig. 1). Hereinafter, we will refer to our mangrove locations as "upper estuary",

162   "intermediate" and "lower estuary".

163

164   **2.3 Field and laboratory analyses**

165   Sampling was conducted during December 2012, where ecosystem C stocks,

166   soil N stocks and soil C sequestration rates were measured. We sampled 9 sites: a

167   peat swamp forest dominated by *Pachira aquatica*, a marsh dominated by the grass

168   *Typha dominguensis* and seven mangrove forests (three sites in the upper estuary,

169   two in the intermediate estuary and two in the lower estuary) (Fig. 1; Table 1). We

170   measured whole-ecosystem C stocks in six plots (radius of 7 m; 154 m^2) per site using

171   methodologies described in Kauffman et al. (2014a). The plots were established 25 m

172   apart along a 125 m transect set in a perpendicular direction from the water edge. At

173   each plot, we sampled C stocks within trees and shrubs, downed wood and the soil

174   profile. We also sampled soil N stocks and interstitial salinity. To estimate C

175   sequestration rates in mangroves, we used a natural horizon marker to calculate soil C

176   accumulation. The detailed methodology is explained below.

177

178   *2.3.1. Biomass and C stock within trees and shrubs*

179   Forest structure was measured at each plot through measurements of the

180   species and the diameter at 1.3 m height (DBH) of all trees. The diameter of trees of

181   *R. mangle* and *R. harrisonii* was measured at the main branch, above the highest prop

182   root (D_R). Aboveground biomass in the marsh communities was determined through

183   plant harvest within two 20 x 20 cm quadrants within each of the 6 plots. The wet mass

184   was determined in the field and then a subsample was collected from each quadrant

185   and oven-dried to determine its dry weight.

186

187   Tree biomass was calculated using allometric equations (Table 2). We used the

188   formula by Fromard et al. (1998), which was obtained for mangroves of French

189   Guiana, which is a location with similar characteristics than those found in LEBR

190   (riverine mangroves with a tropical hot humid climate). We compared the formulas of

191   Fromard et al. (1998) and Day et al. (1987), the latter obtained from mangroves in

192   Campeche, Mexico. The results using both formulas were not significantly different (t =

193   1.027; df = 2284; p = 0.30). We chose the formula by Fromard et al. (1998) because it

194   included trees with a DBH range similar to those found in LEBR (DBH $_{Max}$= 32 cm for

195   *R. mangle*, 9.6 cm for *Laguncularia racemosa* and 42 cm for *Avicennia germinans*).

196   Aboveground biomass of trees from the peat swamp (*P. aquatica*) were calculated with

197   the formula of van Breugel et al. (2011), while belowground biomass of *P. aquatica*

198   was determined with the equation of Cairns et al. (1997) for tropical forests.

199   Belowground root biomass for mangroves was calculated using the formula by

200   Komiyama et al. (2005) and wood density values (Chave et al. 2009, Zanne et al.

201   2009) using density values of comparable climatic regions as the LEBR (Table 2). Tree

202   C was calculated from biomass by multiplying by a factor of 0.48 for aboveground and

203   0.39 for belowground biomass; C content of marshes was calculated using a factor of

204   0.45 of the total biomass (Kauffman et al. 2014a).

205

206   Standing dead trees were also included in the tree C stocks estimations. Each

207   dead tree was assigned to one of three decay status (Kauffman et al. 2014a): Status

208   1- dead trees without leaves, Status 2- dead trees without secondary branches, and

209   Status 3- dead trees without primary or secondary branches. The biomass for each

210   tree status was calculated as a percentage of the total biomass using the values

211   provided by Fromard et al. (1998). For dead trees of Status 1, biomass was calculated

212   as the total dry biomass minus the biomass of leaves, equivalent to 2.8 % of the total.

213   The biomass of trees of Status 2 was calculated as the total biomass minus the

214   biomass of leaves (2.8% of the total) and minus secondary branches (equivalent to

215   18.7 % of the total). Finally, the biomass of trees of Status 3 was calculated as the

216   biomass of the main stem, which is equivalent to 76.6% of the total (Table 2).

217

218   *2.3.2. Downed wood*

219   The mass of dead and downed wood was calculated with the planar intersect

220   technique (Van Wagner, 1968) adapted for mangroves (Kauffman et al. 2014a). Four

221   14 m transects were established at the centre of each plot: the first one established at

222   45° off the direction of the main transect, the other three were established 90° off from

223   the previous transect. The diameter of any downed, dead woody material

224   (fallen/detached twigs, branches, prop roots or stems of trees and shrubs) intersecting

225   each transect was measured. Along the last 5 m of the transect, wood debris > 2.5 cm

226   but < 7.5 cm in diameter (hereafter "small" debris) was counted. From the second

227   meter to the end of the transect (12 m in total), wood debris > 7.5 cm in diameter

228   (hereafter "large" debris) was measured. Large downed wood was separated in two

229   categories: sound and rotten. Wood debris was considered rotten if it visually

230   appeared decomposed and broke apart when kicked. To determine specific gravity of

231   downed wood we collected ≈ 60 pieces of down wood of different sizes (small, large-

232   sound, and large-rotten) and calculated their specific gravity as the oven-dried weight

233   divided by its volume. Using the specific gravity for each group of wood debris,

234   biomass was calculated and converted to C using a conversion factor of 0.50

235   (Kauffman et al. 1995)

236

237   *2.3.3. Soil C and N*

238   Soil samples for bulk density and nutrient concentration were collected at each

239   plot using a peat auger consisting of a semi-cylindrical chamber of 6.4 cm-radius

240   attached to a cross handle (Kauffman et al., 1995). The core was systematically

241   divided into depth intervals of 0 - 15 cm, 15 - 30 cm, 30 - 50 cm, 50 -100 cm and > 100

242   cm. Soil depth was measured using a steel-2 m rod that was inserted in the ground at

243   each plot. Samples of a known volume were collected in the field and then dried to

244   constant mass to determine bulk density. Samples were sieved and homogenized and

245   treated with hydrochloric acid to eliminate the inorganic carbon portion before

246   analyses. Concentration of organic C and N were determined using a Costech

247   Elemental Combustion System 4010 (CA, USA, Michigan Technological University,

248   Forest Ecology Stable Isotope Laboratory).

249

250   *2.3.4 Soil C sequestration rates*

251   We estimated C sequestration rates in mangroves as the amount of C

252   accumulated in the soil profile. To date the soil cores, we used a natural marker that

253   consisted of a volcanic ash horizon that was clearly identified in all the cores

254   (Supplementary Fig. 1). This ash horizon is the remaining of the volcano Santa Maria's

255   eruption in 1902 that represented one of the four largest volcano eruptions of the 20th

256   Century (Volcanic Explosivity Index of 6 out of 7, Williams and Self, 1983). As a result

257   of the eruption, a recognizable plinian deposit of known date ashes can be established

258   in the Mexican Pacific coast, northwest of the volcano. We estimated soil C

259   sequestration within each plot of six of our mangrove sites by dividing the depth of the

260   ash horizon by years since the volcano eruption occurred and multiplying it by bulk

261   density and C content. Soil C sequestration rates are expressed in g C m^{-2} yr^{-1}. We

262 couldn't measure soil C sequestration rates of marsh and peats swamp forest, as

263 these vegetation types frequently suffer from fires and thus have confounding ash

264 horizons.

265

266 *2.3.5 Interstitial salinity*

267   Salinity was measured with an YSI-30 multiprobe sensor (YSI, Xylem Inc. Ohio,

268 USA) from water extracted from 30 cm deep. The water was obtained with a syringe

269 and an acrylic tube (McKee et al., 1988).

270

271 **2.4 Scaling up**

272   To scale up our field measurements to the LEBR we conducted different

273 approaches for each vegetation type. We relied on modelling approaches to predict

274 values of variables of interest in places where no information was available.

275

276   For mangroves, we first estimated aboveground C (trees) throughout the LEBR.

277 Data was spatially harmonized with vegetation-related remote sensing products and

278 the first three principal components of the SAGA GIS (http://www.saga-gis.org/)

279 standard terrain parameters derived from a digital elevation model (Supplementary

280 Table 1). A pixel size of 25 m was selected to resample remote sensing and

281 topographic layers given the coarser spatial resolution of ALOS Palsar products.

282 Upscaling of aboveground C was performed in R (Core Team 2015) by the means of a

283 machine learning random forest tree ensemble (Breiman, 2001). The number of

284 covariates to fit each tree (MTYR parameter) was tuned by ten-fold cross validation.

285 The number of trees to grow was 1000, which was enough to stabilize the error. For

286 external validation purposes, 20% of available data was randomly leaved out of the

287 model. Selection of external validation and modelling was repeated 400 times to

288 analyse the effects of the random split on error metrics by the correlation between

289 observed and modelled and the root mean squared error (RMSE). Additionally, we

290 implemented the quantile regression forest method proposed by Meinhausen (2006),

291 which allows the inference of the full conditional distribution of the response variable

292 as a function of its covariates. Having this information, prediction intervals (at 95%)

293 were identified and the range of them was used to provide a spatially explicit measure

294 of uncertainty, considering the number of data, the correlation among predictive

295 variables as well as the complexity and geographical dimensions of the study area.

296 The aboveground C was then extrapolated to total C stocks based the data collected

297 in the field. As a comparison exercise, we also estimated mean ecosystem C stocks

298 times the estimated area for each vegetation type on the basis of the NDVI

299 classification, which broadly represented mangroves in the upper, intermediate and

300 lower estuary (Fig. 1).

301

302   For the extrapolation of marsh also dominated by *T. dominguensis* to the whole

303 LEBR, we included a number of sites where aboveground, belowground biomass and

304 organic matter content have been measured (C. Tovilla, unpublished data, Fig. 1),

305 which together with our field measurements was used to roughly estimate C stocks

306 within the LEBR. The total area of marsh was calculated on the basis of the "other

307 wetlands" category obtained from the coastal vegetation map of the Pacific south

308 region (CONABIO, 2013), as well as from auxiliary cartographic (SERIE IV; INEGI,

309 2012) and our field experience. It is likely that the area of the marsh –and thus its C

310   stock– was over or underestimated, as the marsh area includes waterholes and

311   inundated vegetation ("popales") with unknown C stocks.

312

313   For peat swamps, we extrapolated our six sampling plots to the forest

314   surrounding our sampling area, which had an area of 844 ha (Fig. 1). The rest of the

315   area of peat swamp forest is not available for the LEBR. Therefore, the C stock

316   estimated for peat swamp forests was underestimated.

317

318   ***2.5 Statistical analyses***

319   One-Way Analysis of Variance (ANOVA) was performed to test differences of

320   above and belowground biomass and C stocks among wetland types (mangroves,

321   marsh and peat swamp), sites, and geomorphic setting (upper estuary, intermediate

322   and lower estuary mangroves). To avoid uncertainties associated to imbalance

323   designs, when comparing vegetation types (mangroves vs. peat swamps vs. marsh),

324   we used the mean for all mangrove sites for each of the five plots which represented a

325   range a vegetation from the water edge to the landward side of the forest. The mean

326   for the plots was compared against the plots laid in a similar way for peat swamp

327   forest and marsh (n= 5 plots per site). Differences in soil C and N concentrations by

328   depth were tested with a Two-Way ANOVA, with site as the fixed effect and depth as

329   the random effect of the model. Normality was assessed using Shapiro-Wilk tests.

330   When significant differences were found, pair-wise comparisons were explored using

331   Scheffé post-hoc tests. Analyses were performed using Prism ver 6.0 (GraphPad

332   Software, La Jolla, CA, USA) and SPSS Statistics (version 20, IBM, New York, USA).

333   Throughout the manuscript, data are reported as mean ± standard error.

334

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 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 (1,213-5,370 trees ha^{-1}) with tall trees (~20-40 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 than that of mangroves with a tree density of 2,469 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).

3.2 Tree biomass and C

Mean tree aboveground biomass of mangroves was 421.1 ± 67.8 Mg ha^{-1} and was higher than the biomass for the peat swamp and marsh, which was 162.2 ± 27.3 Mg ha^{-1} and 76.5 ± 11.6 Mg ha^{-1}, respectively. Thus, mean C stock in mangrove trees was significantly higher in mangroves (215.0 ± 44.4 MgC ha^{-1}) compared to swamp forests and marsh (95.1 ± 15.7 MgC ha^{-1} and 38.2 ± 5.8 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 significantly differences among sites with lowest C stocks measured in the

15

358 vegetation of Santa Chila (132.1 MgC ha^{-1}) (t= 2.54; *p* = 0.015) and highest at Las

359 Palmas (440.0 MgC ha^{-1}) (t= 2.03; *p* = 0.049), the only site dominated by *A. germinans*

360 and not *R. mangle*. The vegetation biomass and C stocks were quite similar among

361 sites within the upper estuary (range 211-243 MgC ha^{-1}), but highly variable among

362 sites within the intermediate and lower estuary (132-440C Mg ha^{-1}) (Table 3, Fig. 3).

363

364 *3.3 Downed wood C*

365   Downed wood C was low in peat swamp wetlands (12.5 ± 2.8 MgC ha^{-1}), but

366 considerable in some mangrove sites (mean of 29.4 ± 3.7 MgC ha^{-1}). The amount of

367 downed wood in mangroves had a wide range within sites, from 11 Mg ha^{-1} to 205 Mg

368 ha^{-1}, with a mean biomass of 59.4 ± 26.0 Mg ha^{-1} (Table 4, Fig. 3). Mangroves in the

369 lower estuary had the highest biomass and C stocks of downed wood ($F_{2,39}$ = 6.86; p =

370 0.0028), mainly due to large amounts of downed wood at Zacapulco (102.4 ± 27.0

371 MgC ha^{-1}) ($F_{7,47}$ = 8.147; p < 0.0001). Small downed wood comprised 10.2 % of the

372 total biomass (6.0 ± 0.8 Mg ha^{-1}); large sound wood the 55.4% (33.0 ± 13.9 Mg ha^{-1})

373 and large rotten wood comprised 34.4 % of the total (20.4 ± 15.2 Mg ha^{-1}).

374

375 *3.4 Soil C and N*

376   Soil C content (%) was higher in peat swamps (19.9 ± 3.4%) compared to

377 marsh (10.1 ± 2.5%); mangroves had intermediate values (14.6 ± 2.5%) ($F_{2,12}$ = 3.616;

378 p = 0.04). Soil N (%) was higher in peat swamps (1.2 ± 0.2%) compared to mangroves

379 and marsh (0.6 ± 0.1% and 0.6 ± 0.2%, respectively) ($F_{2,12}$ = 5.558; p = 0.019). Soil C

380 stock (MgC ha^{-1}) was significantly higher in mangroves (505.9 ± 72.6 MgC ha^{-1}) and

381 the peat swamp forest (620.4 ± 6.8 MgC ha^{-1}) compared to the marsh (298.3 ± 39.0

382 MgC ha^{-1}) (Fig. 2) ($F_{2,12}$ = 5.42; p = 0.02). Finally, soil N stocks were higher for peat

383 swamps (40.4 ± 5.5 Mg ha^{-1}) compared to mangroves (19.2 ± 2.7 Mg ha^{-1}) and

384 marshes (18.5 ± 1.7 Mg ha^{-1}) ($F_{2,12}$ = 11.51; p = 0.0016) (Table 5).

385

386 When comparing mangroves from the upper to the lower estuary we found that

387 the soil C stocks from the upper and intermediate estuary were significantly higher

388 than those from the lower estuary ($F_{2,12}$ = 25.43; p < 0.0001). Soil C stocks were also

389 significantly different among sites and depths (Site $F_{7,64}$ = 16.03, p < 0.0001; Depth

390 $F_{3,64}$ = 8.83; p < 0.001) (Table 5), with highest C density in the soil horizon > 50 cm.

391 Soil N stocks were higher in mangroves of the upper estuary (26.4 ± 0.5 Mg ha^{-1})

392 compared to mangroves in the intermediate and lower estuary (15.3 ± 1.6 Mg ha^{-1} and

393 12.3 ± 3.2 Mg ha^{-1}, respectively) ($F_{2,4}$ = 20.35; p = 0.008) (Table 5). We also found a

394 trend of the distribution of soil C with depth among mangroves from the upper to the

395 lower estuary. Soil C values increased with depth at Panzacola (upper estuary),

396 remained similar in depth in Teculapa and Paistalon (upper estuary) and decreased in

397 depth at the rest of the mangroves within the intermediate and lower estuary (Table 5).

398

399 Overall, C stocks were highest in mangroves and peat swamp forests, while N

400 stocks were highest in peat swamp forests. Soil C and N stocks were highest in the

401 upper estuary and decreased towards the lower estuary. Finally, the variation of site

402 replicates was different within the upper and lower estuary: inter site variability was

403 much lower in the upper estuary compared to the intermediate and lower estuary (Fig.

404 3).

405

3.5 Ecosystem C stocks

Mean C stocks of wetlands in the LEBR were significantly different, with highest stocks for mangroves (784.5 ± 73.5 MgC ha^{-1}) and peat swamps (722.2 ± 63.6 MgC ha^{-1}) and lowest for marsh (336.5 ± 38.3 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 ± 22.0 MgC ha^{-1}) and intermediate estuary (825.8 ± 289.2 MgC ha^{-1}) having higher C stocks compared to those in the lower estuary (659.5 ± 18.6 MgC ha^{-1}) ($F_{2,12}$ = 25.43; p < 0.0001). Largest C stocks were measured at Esterillo (1,114.9 ± 150.3 MgC ha^{-1}) and lowest at Santa Chila (536.6 ± 88.8 MgC ha^{-1}). The C stocks of mangroves 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 generated a model that was able to explain 34% of aboveground C variance, with a RMSE of 111.29 ton/ha. External validation had a higher correlation value (R^2= 0.73, RMSE = 60.28 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 18-567 MgC ha^{-1}, with a mean of 118 ± 54 MgC ha^{-1}, with an estimated total of 3.5 millions MgC for aboveground C for the LEBR (Fig. 4). However, the results had a large degree of uncertainty, mostly in mangroves at the water edge and mangroves close to the

estuary mouth or at the landward side of the reserve (Fig. 4), which were identified in the field as monospecific forests of *A. germinans*.

Although the prediction of the aboveground C was low, it allowed us to identify that most forests within the LEBR have less than 300 MgC ha^{-1}. Based on our field data, we identified that fringe forest dominated by *R. mangle* were between 300-400 MgC ha^{-1}, while forest of *A. germinans* had aboveground biomass > 400 MgC ha^{-1}, 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 forests 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 ± 31.6 MgC ha^{-1}, which extrapolated to the whole LEBR provides a rough estimate of 23.3 millions of MgC. The uncertainty of this estimation is highest mangroves in the lower estuary and mangroves close to water or the landward edge of the Reserve. As a comparison, if we extrapolated the C stocks of the mangroves by classes obtained from NDVI (upper, intermediate and lower estuary, respectively) the estimation is similar with 20.9 millions of MgC for the LEBR.

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

454 to be of at leas 0.6 millions of MgC. Summed up, the LEBR C stock is around 38

455 millions of MgC.

456

457 *3.7 Soil C sequestration rates*

458   Mean soil C sequestration rates in mangroves was 1.3 ± 0.2 Mg ha^{-1} yr^{-1}; soil C

459 sequestration was similar among all sites (upper, intermediate and lower estuary) ($F_{2,4}$

460 $= 0.78$; $p = 0.516$). Lowest values (0.4 ± 0.0 MgC ha^{-1} yr^{-1}) were measured in the site

461 Las Palmas, which was dominated by *A. germinans* (Table 8). Considering than less

462 than 10% of the mangroves in LEBR are dominated by *A. germinans*, we can estimate

463 that the C sequestration of mangroves in LEBR through soil accretion is close to

464 39,842 MgC every year.

465

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 MgC ha^{-1}, IPCC, 2003). C stocks of mangroves within LEBR were similar to other mangroves around the world (mean of 784.5 ± 73.5 MgC ha^{-1}; maximum of 1,115 MgC ha^{-1}) such as in Vietnam (762.2 ± 57.2 MgC ha^{-1}, Nguyen et al 2014), the Dominican Republic (853 MgC ha^{-1}, Kauffman et al., 2014b), Yucatan, Mexico (mean of 663 ± 176 MgC ha^{-1}; Adame et al., 2013) and Northwest Madagascar (367-593 MgC ha^{-1}; Jones et al., 2014). As hypothesised, C stocks of mangroves and peat swamps were higher than those of marshes (336.5 ± 38.3 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. On the contrary, 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).

490   As a result, mangroves in the lower estuary are a mosaic of old and young forests,

491   some of them with productivities and soil C similar to those in the upper estuary, but

492   others with low productivity, statures and soil C, and thus, C stocks.

493

494   The N stocks within mangroves also differed between mangroves, with highest

495   stocks in mangroves from the upper estuary. Upland mangroves receive high N inputs

496   due to agricultural activity in the catchment (UNESCO, 2014); lowland mangroves

497   probably receive lower N loads as oceanic water has usually lower nutrients than

498   riverine water. Differences in N content have also been associated to microbial activity

499   such as bacteria and protozoans, which are in turn linked to tidal flushing in

500   mangroves (Alongi, 1988). Higher nitrification and denitrification and lower N fixation

501   rates could further explain low N stocks in lowland mangroves; however, this remains

502   to be tested. The higher N inputs in mangroves in the upper estuary, coupled with

503   lower salinity values throughout the year probably contribute to higher productivity of

504   mangroves in the upper estuary compared to those in the lower estuary (Tovilla et al.

505   unpublished data).

506

507   Besides the differences in C and N stocks between upland and downland

508   mangroves, it stands out that the mangrove forest dominated by *A. germinans* (Las

509   Palmas) was notably different. This forest had the highest tree biomass, lowest soil C

510   and lowest C sequestration rates measured in this study. Lowest C stocks in soils *of A.*

511   *germinans* can be due to the lower C wood content that is buried in the soil. Wood

512   density of *A. germinans* is lower (0.67 g cm^{-3}– 0.90 g cm^{-3}) than wood density of *R.*

513   *mangle* (0.810 g cm^{-3}– 1.05 g cm^{-3}) (Chave et al. 2009, Zanne et al. 2009), which

514   dominated all other sites. Wood density is a major predictor of stored C in wood

515   biomass and could explain the low values of C buried in the soil (Flores and Coomes,

516   2011), and thus, the low C stocks in the mangrove forest dominated by *A. germinans.*

517

518   Most of the C stocks in mangroves is stored in the soil (Donato et al., 2011;

519   Adame et al., 2013), thus the potential of mangroves to sequester C is closely related to

520   their soil C sequestration potential. The soil C sequestration rates measured in

521   mangroves of LEBR (0.4 - 1.8 $MgC\ ha^{-1}\ yr^{-1}$) were similar throughout upper and lower

522   estuary mangroves, which suggests that over the long term, variability among sites in C

523   sequestration was not high enough to be detected with our method. However, C

524   sequestration rates within the site dominated by *A. germinans* was two to three times

525   lower than the forests dominated by *R. mangle.* The soil C sequestration estimates in

526   this study are within the range of those reported in the review by Chmura et al. (2003),

527   with lowest values in Rookery Bay, Florida (0.2 $MgC\ ha^{-1}$) and highest in Terminos

528   Lagoon, Campeche, Mexico (6.5 $MgC\ ha^{-1}\ yr^{-1}$), and are similar to those measured in

529   Moreton Bay, Australia (0.8 $MgC\ ha^{-1}\ yr^{-1}$; Lovelock et al. 2014). Long-term soil C

530   sequestration rates are difficult to obtain, thus the values obtained in this study are

531   valuable estimations of C sequestration rates of mangrove forests. For example, we can

532   roughly estimate that the sequestration rate of the mangrove soil of LEBR is 39,842

533      $MgC\ yr^{-1}$, which is equivalent to the annual emissions of approximately 10,348 Mexicans

534   (using emissions by country from IEA, 2014).

535

536   To include wetlands in REED+ projects and other financial incentives of climate

537   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 able to explain 2% of spatial variability (Cartus et al, 2014). Water level dynamics and the complexity of structural diversity are important sources of uncertainty when using remote sensing sources. It is important to distribute sampling efforts wisely as to include as much spatial variability as possible. Additionally, sampling variables such as pH and salinity, that 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, were 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 M ton C, which is equivalent to 139.5 Mton CO_2. 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.

561   The C stocks and sequestration values shown in this study can help provide

562   incentives into the reforestation and conservation projects of this reserve and

563   throughout similar wetland ecosystems. For example, marsh and swamp forests are

564   very susceptible to fire damage during the dry season (L. Castro, pers. comm). With

565   the C stocks calculated in this study, we estimated that if a fire consumes all the

566   vegetation and the top 15 cm of soil (Schmalzer and Hinkle 1992), every hectare of

567   burned marsh or peat swamp could emit 287 ton CO_2 and 567.4 ton CO_2, respectively.

568   Every year between 500 and 4,500 ha of marshes are burned within the reserve (L.

569   Castro pers. comm), which results in an annual mean emission of ~0.6 millions tons of

570   C or 4.6% of the emissions of the state of Chiapas (based on emissions reported by

571   IEA, 2014). This information can be used to emphasize the importance of managing

572   fires in the LEBR in order to maintain its large C stocks and avoid CO_2 emissions to

573   the atmosphere. Another example is to use the C stocks provided in this study to

574   negotiate for offsetting emissions within the country or abroad. For instance, California

575   USA has signed an agreement to import C credits from forests in Chiapas, the state

576   where this study takes place (Morris et al. 2011). To include mangroves and other

577   wetlands in similar agreements could be a cost-effective way to reduce C emissions

578   (Siikamäki et al. 2012), while at the same time protecting the biodiversity and the

579   ecosystem services they provide (Adame et al. 2014). Finally, our results have also

580   showed that extrapolation of C stocks to larger areas require to include not only

581   aboveground biomass, but also field measurements of soil C stocks and to consider

582   differences among vegetation types, species composition and geomorphological

583   setting.

584

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735

750
751 **Author contribution**

752 MFA designed the project, led the field campaign, collected the data and wrote the

753 manuscript. NSS designed the project, performed data analysis and participated in

754 writing and preparation of the manuscript. CT participated in field campaign, collected

755 data and contributed to the manuscript. AV prepared the geographical information

756 system data and map, and AV and MAGS performed data analysis and contributed to

757 the manuscript. LC participated in field campaign, collected data and contributed to the

758 manuscript.

759

760

761 Table 1. Characteristics of sampling sites within La Encrucijada Biosphere Reserve

762 (LEBR). Values are shown as mean (standard error). Max = maximum; DBH =

763 diameter at breast height; n.a. = not assessed; *Rm = Rhizophora mangle; Ag =*

764 *Avicennia germinans; Lr = Laguncunaria racemosa*

	Max height (m)	DBH (cm)	Tree density (trees ha^{-1})	Salinity (ppt)	Dominant species
MANGROVES					
Upper estuary					
Panzacola	40	10.5 (1.1)	1,213 (278)	n.a.	*Rm* (97.5%)
Teculapa	30	7.5 (1.0)	2,761 (398)	19.3 (5.3)	*Rm* (94.5%)
Paistalon	25	9.9 (0.9)	2,035 (134)	n.a.	*Rm* (100%)
Intermediate					
Esterillo	n.a.	8.8 (1.0)	3,346 (148)	37.6 (5.3)	*Rm* (87.7%), *Ag* (12.3%)
Sta Chila	22	9.9 (0.6)	2,371 (157)	37.5 (0.6)	*Rm* (68.9%), *Ag* (25.1%)
Lower estuary					
Zacapulco	n.a.	8.8 (0.8)	1,765 (274)	7.6 (0.4)	*Rm* (87.6%), *Lr* (10.6%)
Las Palmas	28	7.9 (0.4)	5,370 (388)	28.9 (0.6)	*Ag* (83.2%), *Lr* (13.9%)
PEAT SWAMP	22	14.5 (0.9)	2,469 (301)	0.0 (0.0)	*P.aquatica* (96.9%)
MARSH	3	-	-	n.a.	*T. dominguensis* (100%)

765

766 Table 2. Allometric equations used to calculate aboveground and belowground

767 biomass (kg) of mangrove and peat swamp trees. AGB= Aboveground biomass;

768 BGB= Belowground biomass; D_R = diameter above highest prop root (cm); DBH =

769 diameter at breast height. Wood density (g cm^{-3}) values used for calculating

770 belowground biomass were obtained from Chave et al. (2009) and Zanne et al. (2009)

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

771

772

773 Table 3. Aboveground biomass, belowground biomass (Mg ha^{-1}) and total carbon (C)

774 in vegetation (MgC ha^{-1}) within wetlands of La Encrucijada Biosphere Reserve. Values

775 are shown as mean (standard error). Different letters indicate significant differences

776 among sites ($p < 0.05$). The marsh was not included in analysis due to missing

777 belowground biomass.

	Biomass (Mg ha^{-1})		C (MgC ha^{-1})
Site	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}
Paistalon	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}
Sta Chila	198.8 (13.4)^{a}	93.9 (3.8)^{ab}	132.1 (7.8)^{a}
Zacopulco	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)

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779

780   Table 4. Biomass (Mg ha^{-1}) and C stocks (MgC ha^{-1}) of downed wood in La

781   Encrucijada Biosphere Reserve. Wood debris was calculated separately for small

782   wood (diameter > 2.5 and < 7.5 cm), and large sound and large rotten wood (diameter

783   > 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)
	Paistalon	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)
	Sta 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)

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787 Table 5. Soil carbon (C) and nitrogen (N) concentrations (%), and soil C and N stock

788 (Mg ha^{-1}) at different depths (0- 150 cm) of wetlands from La Encrucijada Biosphere

789 Reserve. Values are shown as mean (standard error). <mark>Different letters indicate</mark>

790 <mark>significant differences between sites ($p < 0.05$).</mark>

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]
Paistalon	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]

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794   Tabla 6. Ecosystem C stocks (MgC ha^{-1}) for wetlands of La Encrucijada Biosphere

795   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)
		Paistalon	865.6 (55.1)
		mean	871.0 (22.0)
	Intermediate	Esterillo	1,114.9 (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)

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799 Table 8. Soil carbon (C) sequestration rates (MgC ha^{-1} yr^{-1}) of mangroves within La

800 Encrucijada Biosphere Reserve, Mexico.

801

	Site	Soil C sequestration rate (Mg ha^{-1} yr^{-1})
Upper estuary	Panzacola	1.0 (0.1)
	Teculapa	1.4 (0.1)
	Paistalon	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)

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805 **Figure legends**

806

807 Fig. 1. Mangrove, peat swamp and marsh sampling sites within La Encrucijada

808 Biosphere Reserve, Mexico. Mangroves were classified according the NDVI (see

809 methods) in three classes, which broadly corresponded to a range of mangroves from

810 the upper to the lower estuary.

811

812 Fig. 2. Aboveground (A) (trees and shrubs and down wood) and belowground (B) (soil

813 at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves, peat swamp

814 and marsh wetlands within La Encrucijada Biosphere Reserve.

815

816 Fig. 3. Aboveground (A) (trees and shrubs and down wood) and belowground (B) (soil

817 at different depths and roots) carbon stocks (MgC ha^{-1}) of mangroves along a gradient

818 from the upper to the lower estuary within La Encrucijada Biosphere Reserve.

819

820 Fig. 4. Aboveground C stocks (trees) (Mg ha^{-1}) (A) estimated for the sampling

821 locations within La Encrucijada Biosphere Reserve; (B) uncertainty associated to

822 estimations; and (C) frequency of occurrence of estimated C stock values within

823 mangroves within La Encrucijada Biosphere Reserve
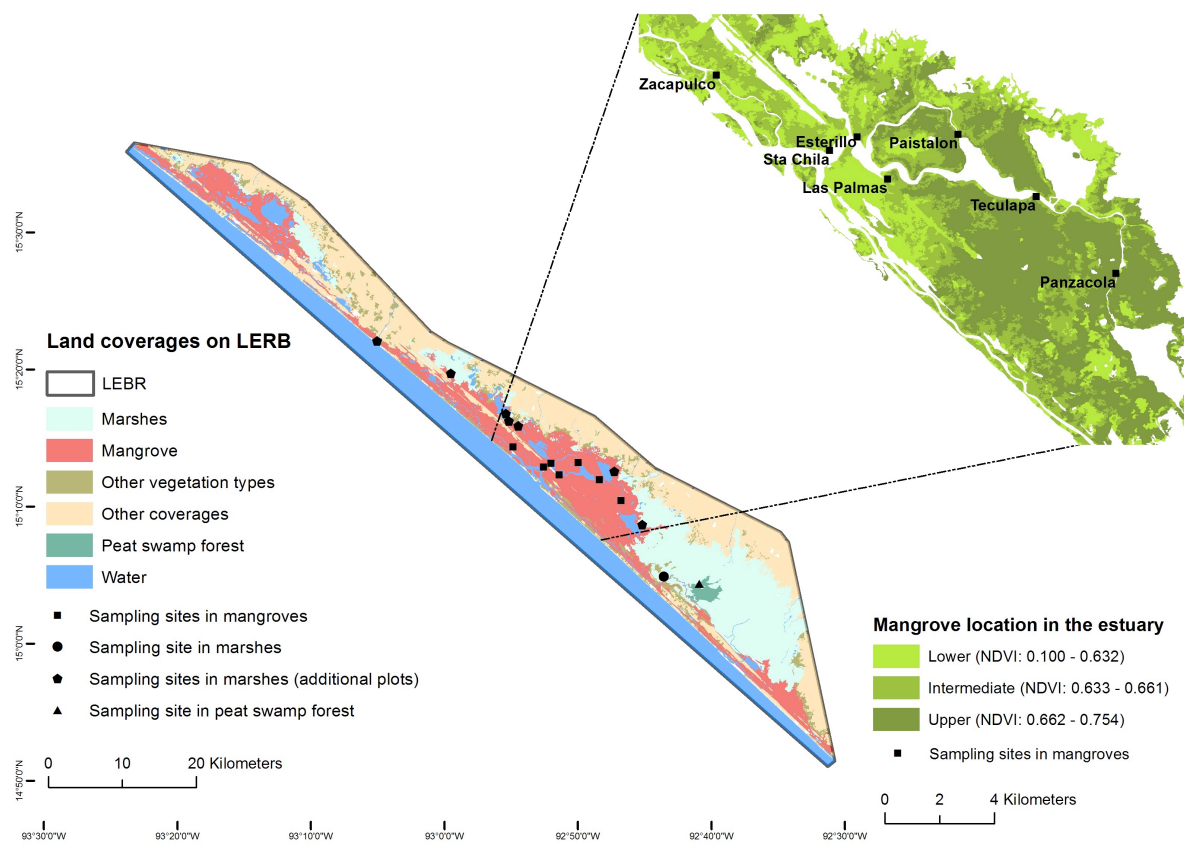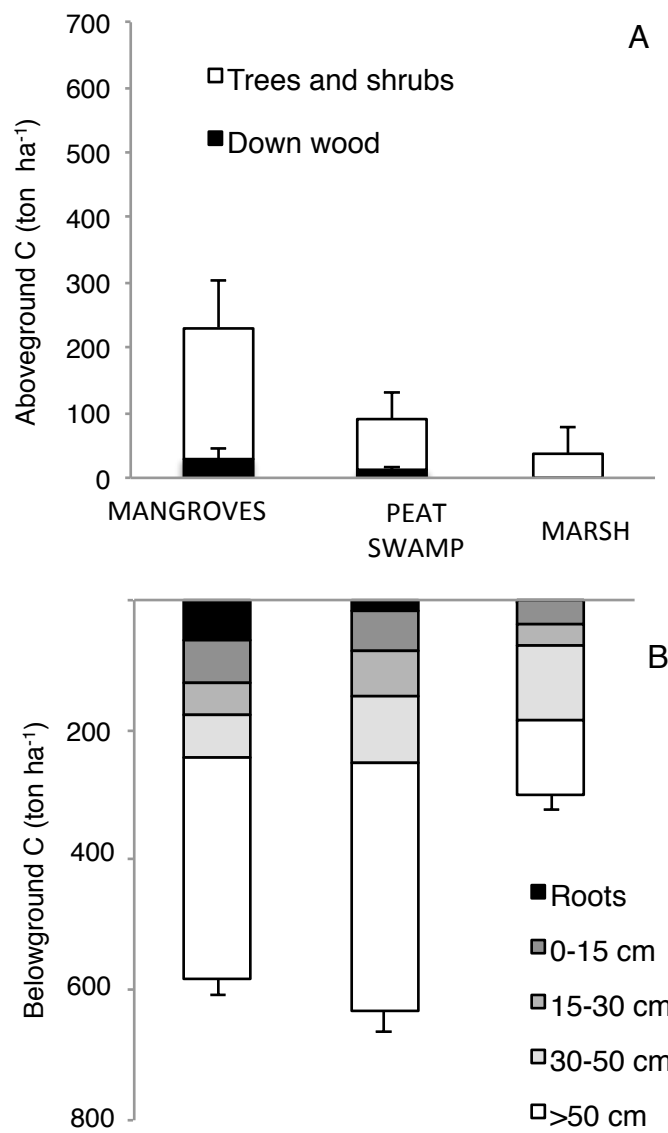
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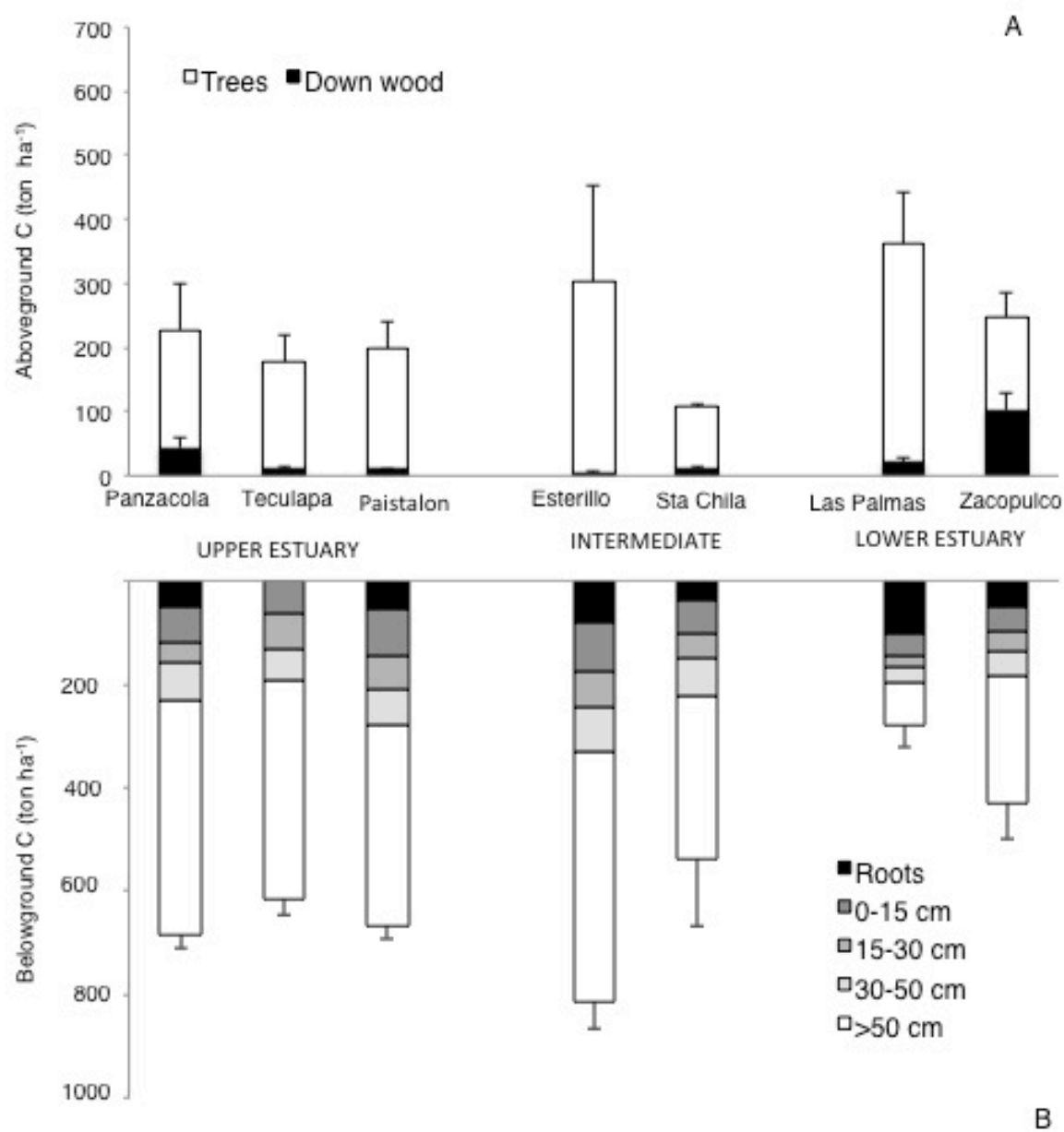
La Encrucijada Biosphere Reserve, Chiapas, Mexico

Land coverages on LERB

- ☐ LEBR
- Marshes
- Mangrove
- Other vegetation types
- Other coverages
- Peat swamp forest
- Water

- ■ Sampling sites in mangroves
- ● Sampling site in marshes
- ⬠ Sampling sites in marshes (additional plots)
- ▲ Sampling site in peat swamp forest

0   10   20 Kilometers

Mangrove location in the estuary

- Lower (NDVI: 0.100 - 0.632)
- Intermediate (NDVI: 0.633 - 0.661)
- Upper (NDVI: 0.662 - 0.754)
- ■ Sampling sites in mangroves

0   2   4 Kilometers

Zacapulco
Esterillo
Sta Chila
Paistalon
Las Palmas
Teculapa
Panzacola

Figure 1

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830   Figure 2

831

832   Figure 3

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841   Figure 4

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