Forest Ecology and Management 442 (2019) 135–147

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Mangrove wetland productivity and carbon stocks in an arid zone of the Gulf of California (La Paz Bay, Mexico)

Jonathan G. Ochoa-Gómez[a], Salvador E. Lluch-Cota[a], Víctor H. Rivera-Monroy[b], Daniel B. Lluch-Cota[a], Enrique Troyo-Diéguez[a], Walter Oechel[c,d], Elisa Serviere-Zaragoza[a,*]

[a] Centro de Investigaciones Biológicas del Noroeste, Av. Instituto Politécnico Nacional 195, Playa Palo de Santa Rita Sur, La Paz, B.C.S. 23096, Mexico
[b] Department of Oceanography and Coastal Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, LA 70803, USA
[c] Global Change Research Group, San Diego State University, San Diego, CA 92182, USA
[d] College of Life and Environmental Sciences, University of Exeter, Exeter, UK

ARTICLE INFO

Keywords:
Anthropogenic impact
Ecosystem services
Peri-urban mangroves
Structural properties
Biomass
Blue carbon

ABSTRACT

Mangroves provide multiple ecosystem services (ESs), including fish and wildlife habitat, protection from coastal erosion and flooding impacts, food resources, water quality, carbon sequestration and storage. However, most of the mangrove wetlands structural and functional information useful to evaluate the quality, quantity and monetary value of its ESs has been obtained from studies at tropical latitudes usually dominated by large deltas and extensive coastal lagoon and estuaries. Thus, there is a major data gap for mangrove wetlands located in arid and semi-arid regions due to their limited land cover and location at the boundary of transitional climate gradients. Here we analyze the spatial distribution of mangrove wetlands carbon stocks and net primary productivity (i.e., litterfall and root productivity) in La Paz Bay, an arid coastal region in the Gulf of California, Mexico, where mangrove wetlands are spatially distributed in conspicuously extensive patches. We used this information to qualitatively rank ESs. Three peri-urban mangrove wetland sites (Balandra, Enfermeria, and Zacatecas) were characterized by different degrees of anthropogenic impact. Aboveground biomass (interval: 13.6 to 31.6 $Mg\,C\,ha^{-1}$) was in the lower range when compared globally. The average C storage in mangrove soils (at 45 cm depth) in La Paz Bay is 175 $Mg\,C\,ha^{-1}$, which is higher than the values reported for other arid zones ($\geq$1 m soil depth: 43–156 $Mg\,C\,ha^{-1}$). Belowground root biomass and productivity values (roots range: 0.22–0.31 $Mg\,C\,ha^{-1}$; fine roots NPP: 0.06–0.09 $Mg\,C\,ha^{-1}\,yr^{-1}$) were in the lower range. We found distinct differences in aboveground C storage values among sites where mangrove species formed monospecific stands across the landscape within each site. Areas dominated by the species *Rhizophora mangle* reflected the highest soil C density values (208.9 $\pm$ 144.6 $Mg\,C\,ha^{-1}$), followed by *Laguncularia racemosa* (181.4 $\pm$ 118.2 $Mg\,C\,ha^{-1}$) and *Avicennia germinans* (155.5 $\pm$ 72.1 $Mg\,C\,ha^{-1}$). We identified ESs provided by each of the sites, including both cultural (i.e., ecotourism; especially in Balandra), and provisioning (fisheries) services. Our study is a first step in the quantitative assessment of functional and structural properties as ESs of arid mangrove wetlands in La Paz Bay that could be readily translated into robust economic estimates for this arid coastal region.

1. Introduction

Mangroves occupy 13,760,000 ha of coastal areas around the world (Bunting et al., 2018), and store 10–15% (24 $Tg\,C\,y^{-1}$) of the organic carbon (C) found in coastal sediments (Alongi, 2014) while exporting 11% (i.e., outwelling) of the terrestrial particulate C to the ocean (Jennerjahn and Ittekkot, 2002). The great potential for C storage (i.e., Blue Carbon; Alongi, 2018a), as one of the most recognized ecosystem services (ESs) in the context of climate change, is partially the result of high mangrove Net Primary Productivity (NPP) and variable C export rates. In this context, mangrove forest NPP is considered a valuable ES due to its potential role for C sequestration to mitigate excess atmospheric CO_2 throughout photosynthesis and long-term C storage in soils (Mcleod et al., 2011).

The relative magnitude of C storage, NPP, and sequestration rates are associated with the interaction of local (e.g., fertility and salinity gradients), regional (e.g., geomorphology), and global/latitudinal variables (e.g., temperature, precipitation) (Alongi, 2014; Rivera-

* Corresponding author.
E-mail address: serviere04@cibnor.mx (E. Serviere-Zaragoza).

https://doi.org/10.1016/j.foreco.2019.03.059
Received 10 January 2019; Received in revised form 27 March 2019; Accepted 29 March 2019

Monroy et al., 2017a; Simard et al., 2019; Rivera-Monroy et al., 2019). Mangrove soils are the primary organic C storage in these ecosystems (Donato et al., 2011). Microbial biomass has an important role in C storage in such ecosystems, as symbiotic microbiota in the plant roots can partially compensate for low soil nutrients availability in addition to its key role in decomposing and mineralization of organic matter (Duarte and Cebrián, 1996; Alongi, 2009; Holguín et al., 2001).

Mangroves have higher capacity as C reservoirs than most other tropical or temperate forests (Donato et al., 2011), even at the northern limit of mangrove distribution in the neotropics, where their structure and productivity are limited by the interaction of low annual air temperature and limited precipitation (Giri et al., 2011; Osland et al., 2017a; Osland et al., 2018; Yando et al., 2016). It has been observed that despite these environmental limitations in arid zones on the southwestern Gulf of California in the Pacific coast of Mexico, mangrove C stocks and litterfall productivity are relatively similar, or in some cases, higher than those reported for lower tropical latitudes (Ezcurra et al., 2016; López-Medellín and Ezcurra, 2012). Mangrove trees in arid regions have typically a height < 3 m (i.e., scrub ecotype; Lugo and Snedaker, 1974; Cintron et al., 1978), and grow under suboptimal conditions due to high water loss during CO_2 uptake, especially during the hot summer periods (López-Medellín and Ezcurra, 2012). However, they are physiologically and morphologically adapted and able to maintain high photosynthetic and low transpiration rates (Snedaker and Araujo, 1998), coping with hypersaline conditions (Dood et al., 1999; Ball, 1988).

Mangroves along the arid coastal region of the southwestern Gulf of California, including La Paz Bay, encompass the largest area that is dominated by scrub and fringe mangrove forests (Aburto-Oropeza et al., 2008; Ochoa-Gómez et al., 2018), distributed in fourteen well delimited patches with a total extension of 270 ha (Ávila-Flores, 2014). Human impacts directly influence some of the mangrove patches since the urban center of La Paz is adjacent to mangrove areas; in addition, this coastal region has the second highest population growth rate and urban development in Mexico (INEGI, 2015), where mangrove area has decreased in as much as 50% in some locations (Ochoa-Gómez et al., 2018).

Human impacts cause biological and ecological changes of different intensities and spatial extension in coastal ecosystems (Alongi, 2008; Collins et al., 2011) affecting functional and structural attributes such as the reduction of aboveground biomass and forest structural complexity (Alongi, 2008; Lugo, 1980). Although mangrove wetlands have different levels of resilience to major structural damages when are impacted by large-scale natural disturbances (e.g., tropical cyclones; Danielson et al., 2017; Rivera-Monroy et al., 2019), human impacts, such as deforestation or major alterations of hydrological regimes, are persistent and therefore can be considered some of the major causes of mangrove mortality and area reduction at global scale (Rivera-Monroy et al., 2017b; Simard et al., 2019). In fact, the level of disturbance is higher in mangrove forests close to urban centers (i.e., peri-urban mangroves; Lee et al., 2014), where pollution and urban development directly affect a number of functional properties and result in a negative impact (e.g., due to limited freshwater input) or positive in some cases (e.g., nutrient inputs increasing productivity) (Alongi, 2018b). This impact could change the quality and quantity of the ESs, such as the provision of fish habitat (López-Rasgado et al., 2012; Ochoa-Gómez et al., 2018) and C storage (Bhomia et al., 2016; Hemati et al., 2015; Hong et al., 2017; Kauffman et al., 2016; Rozainah et al., 2018).

Most of the published C storage estimates in mangrove wetlands have been performed in forests with relatively high canopies including riverine, fringe, and basin ecotypes in both tropical and subtropical regions (e.g., Adame et al., 2015; Bhomia et al., 2016; Kauffman et al., 2016; Kauffman and Bhomia, 2017), where water and nutrients availability is higher than in arid and semi-arid zones (Hickey et al., 2018). The limited number of studies in arid and semiarid environments have mostly focused on the estimation of aboveground biomass and soil C (Woomer et al., 2004; Eid and Shaltout, 2015; Almahasheer et al., 2017; Kauffman and Bhomia, 2017; Schile et al., 2017; Jacotot et al., 2018). Furthermore, there is limited information on the relative importance of the interaction between coastal geomorphology (Rovai et al., 2018; Simard et al., 2019; Twilley et al., 2018) and environmental settings defined by different regimes in environmental variables such as river discharge, salinity, and nutrient fertility gradients (Twilley and Rivera-Monroy, 2009). Therefore, it is uncertain how the degree of human impacts alters the long-term mangrove NPP and carbon storage in the arid coastal geomorphic-environmental setting typical of the Gulf of California.

The objective of this study was to estimate the above and belowground C stocks in three peri-urban mangrove wetlands representing three different levels of anthropogenic impact based on the distance from the city of La Paz, and local hydrological alterations due to road construction: low (Balandra), moderate (Zacatecas) and high (Enfermeria) (López-Rasgado et al., 2012; Mendoza-Salgado et al., 2011). These mangroves are physiographic units well-defined by local topography and surface/ground water availability; they are also part of the largest extension of arid mangrove area in the southwestern coastal area of the Baja California Peninsula, Mexico, which is hydrologically connected to the Gulf of California. We hypothesized that above and belowground organic C stocks and NPP (litterfall and fine roots) were significantly different among sites and characterized by major differences in structural development associated with the total basal area, tree height, and structural complexity. The particular objectives were to: (1) estimate above and belowground C storage and NPP values along disturbance gradients in the La Paz Bay, (2) evaluate and compare C stocks among arid and semi-arid mangrove wetlands, and 3) determine the magnitude and relative importance of mangroves C storage as an ecosystem service (ES) in arid climates. We also qualitatively assessed the functional role of ecosystems services (ESs) such as C storage as related to the provision of other services (e.g., aesthetic value, fisheries) by this scrub mangrove.

2. Material and methods

2.1. Study sites

Three peri-urban mangroves were selected along La Paz Bay, Baja California Sur, (Balandra, Enfermeria, and Zacatecas) (Fig. 1, Table 1). These wetlands represent three levels of human impact: low (Balandra), moderate (Zacatecas) and high (Enfermeria) (López-Rasgado et al., 2012; Mendoza-Salgado et al., 2011), and are characterized by the provision of different ESs to fishes (Ochoa-Gómez et al., 2018). The total area comprising the study sites is 44.1 ha and represents approximately 20% of the total mangrove area in La Paz Bay.

A comprehensive description of these sites can be found in Ochoa-Gómez et al. (2018). Briefly, Balandra (Natural Protected Area) is a coastal lagoon (30 ha) characterized by 180 m wide inlet and a mangrove area of 24.2 ha. Tree basal area is 13.7 ± 7.3 $m^2 ha^{-1}$ and average interstitial salinity is 44.9 ± 6.6 psu. Mangrove extension in the Zacatecas site is ~18 ha and distributed along a 6-ha tidal channel with a 36-m wide inlet; the basal area is 9.7 ± 7.3 $m^2 ha^{-1}$. Monthly interstitial salinity in this site is 47.0 ± 2.8 psu. The Enfermeria site includes a 5-ha artificial lagoon built as result of road construction in the 1970s; it has a direct connection to the La Paz Bay through a 6-m wide inlet; the mangrove extension is 1.9 ha and the mean forest basal area is 6.8 ± 3.8 $m^2 ha^{-1}$ where interstitial salinity is 44.7 ± 4.9 psu (Ochoa-Gómez et al., 2018).

Mangroves in this region are located on top of a large phosphorite deposit that extends by approximately 100 km up to the volcanic belt of northwestern Mexico (Fischer et al., 1995). The average rainfall and temperature of the region during the sampling period (from May 2015 to May 2016) were 225.2 mm and 25.1 ± 3.9 °C, respectively (CONAGUA, 2018). A defined mangrove zonation was observed where

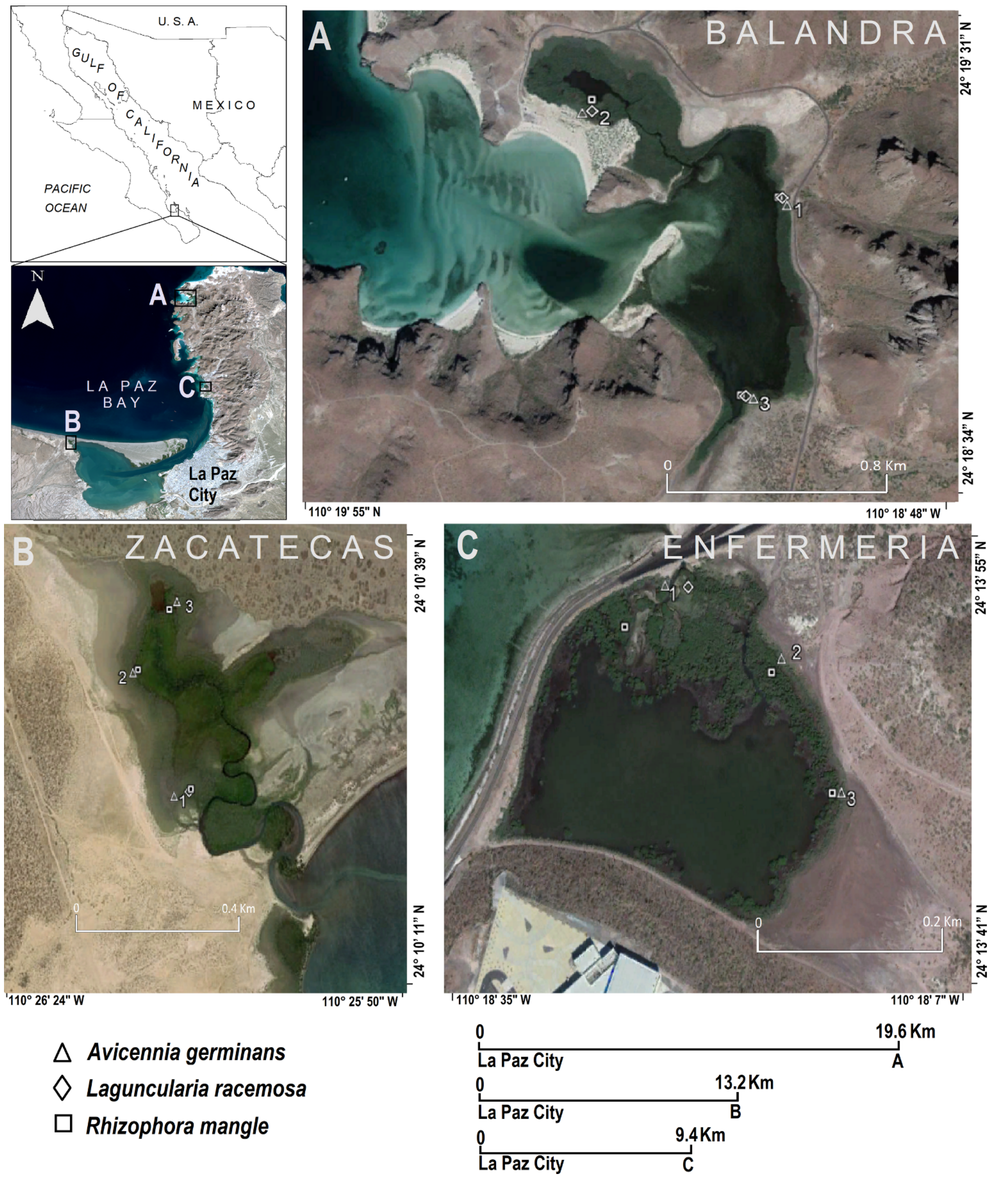

Fig. 1. Study sites location and delimitation of forested mudflat in each mangrove community. The numbers indicate the sampling areas and the figures the dominant species in the plot such described by Ochoa-Gómez et al. (2018).

the species *Rhizophora mangle* was generally located next to the bay/tidal channels while *Avicennia germinans* extended inland; the species *Laguncularia racemosa* was located between vegetation patches of the other species along an elevation gradient (Ochoa-Gómez et al., 2018).

2.2. Field sampling

Three sampling zones, characterized by the dominant species (i.e., *R. mangle, A. germinans, L. racemosa*), were selected along a transect from the largest adjacent waterbody (La Paz Bay) inland in each study site as described in Ochoa-Gómez et al. (2018) (Fig. 1); these transects varied from ~12 m to ~120 m depending on the location of the dominant species along the transect. At each transect, two or three 28.2 m^2 circular plots (radius = 3 m) were deployed according to the dominant species zones; nine plots were located in Balandra, and seven in both Enfermeria and Zacatecas sites (N = 23).

The following forest structural variables were measured in each circular plot: standing tree biomass, pneumatophores biomass, downed wood (i.e., dead wood on top forest floor and dead trees). Roots were also collected to a depth of 45 cm using a metallic core (diameter: 10 cm; height: 50 cm replicates). Direct and indirect C stocks values were estimated (above and belowground) following standard methods by Kauffman and Donato (2012). Additionally, both litterfall (litter baskets) and root productivity (ingrowth cores; Castañeda-Moya et al., 2013; Gleason and Ewel, 2002) were measured at each site from May 2015 to May 2016. C stock values were then used to estimate a total value for each study site and extrapolated for the total mangrove area in La Paz Bay.

2.2.1. Mangrove soil organic C estimation and physicochemical properties

Soil total organic C was determined at each site. One sediment core (ID: 10 cm diameter 45 cm length; volume = 3534 cm^3) was collected per plot in May 2015. Each core was divided into three 15 cm slices (0–15 cm, 15.1–30 cm and 30.1–45 cm). A subsample from the cores was sieved and homogenized using a 0.5 mm mesh to determine organic matter content with the method of chemical oxidation (Walkley and Black, 1934). The soil total organic C was converted to equivalent C units using a conversion factor (1.86) (Kauffman and Donato, 2012); these values were integrated over the three depths and extrapolated to the plot and site levels (Mg C ha^{-1}).

Table 1
Structural properties and characteristics of mangroves wetlands in the southwestern Gulf of California included in this study (Amador et al., 2008; Calderón et al., 2008; Mendoza-Salgado et al., 2011; López-Rasgado et al., 2012; Ochoa-Gómez et al., 2018; Pérez-Estrada et al., 2012).

Site Name	Forest complexity index	Tree density (average height)	Area	Water exchange	Level of impact and characteristics	Ecosystem services
Balandra	11.9	12, 924 Ind ha^{-1} (3.3 m)	24.2 ha (66% forested mudflat)	1.5 days	**Low:** Natural reserve with aesthetic value and economic importance	Nursery, aesthetic value
Enfermería	1.9	5, 775 Ind ha^{-1} (2.4 m)	1.9 ha (14% forested mudflat)	20–26 days	**High:** with press and pushing anthropogenic (modifications and highway's construction)	Artisanal fisheries (i.e., potential fish biomass)
Zacatecas	4.5	11, 094 Ind ha^{-1} (2.1 m)	18 ha (77% forested mudflat)	1–6 days	**Moderate:** bird refuges and feeding zone of birds Higher microbial biomass	Artisanal fisheries (especially macrobenthic)

Ind = individuals.

In each plot per site, pH, electric conductivity, bulk density and soil texture were measured monthly from May 2015 to May 2016 at 10 cm soil depth. The soil was collected (~600 g) using a core (internal diameter, ID: 10 cm; height: 10 cm), stored in labeled plastic bags, and transported to the laboratory for chemical analyses. In the laboratory, samples were dried at room temperature to constant mass (~20 °C) and then sieved using a 2 mm mesh size. Soil samples were homogenized, and an extract (1:2) was prepared with deionized water (50 g of dry soil sample with 100 ml of deionized water) and stirred for 30 min, to measure electrical conductivity and pH using a Hanna HI1288 sensor probe. Also, a sample of soil was analyzed for soil texture using a laser auto-analyzer Partica Horiba LA-950V2. Bulk density was determined using core volume (Kauffman and Donato, 2012).

2.2.2. Forest biomass

Aboveground biomass was estimated using Diameter at Breast Height (DBH) measurements of each tree located within each plot and published allometric equations (Komiyama et al., 2005). Since there are no available *in situ* allometric equations for our study sites, we used a generic model proposed by Komiyama et al. (2005), which provides robust estimations in a wide number of environmental settings (e.g., Ishihara et al., 2015; Rojas-García et al., 2015; Rovai et al., 2016). DBH measurements were recorded at a different tree height per species: 1.3 m in the case of *A. germinans* and *L. racemosa* and 0.3 m above the last main prop root for the species *R. mangle* (Dahdouh-Guebas and Koedam, 2006). We used published species-specific wood densities to estimate biomass (*A. germinans*: 0.67 g cm^{-3}, *L. racemosa*: 0.60 g cm^{-3}; *R. mangle*: 0.84 g cm^{-3}) (Chave et al., 2009; Zanne et al., 2009). Different structural variables were ranked per DBH class, species, and site including tree biomass, and total stem density. To determine the number and range of diametric classes to construct histograms, we used the formula proposed by Sturges (1926). We estimated biomass of pneumatophores in plots where the species *A. germinans* and *L. racemosa* were dominant: three quadrants (25 × 25 cm) were randomly deployed within each plot, and all the pneumatophores were harvested. Finally, total biomass (Mg ha^{-1}) was estimated in each plot per dominant species. Additionally, we converted the total biomass to equivalent C units using a conversion factor of 0.46 (Kauffman and Donato, 2012).

2.2.3. Downed wood

Downed woody material biomass was estimated using the planar intersections method in each circular plot (Brown, 1974 modified by Sánchez and Zerecero (1983)). Four transects lines (4 m length) were systematically placed from the center of each circular plot along North, East, South, and West directions. This kind of material (i.e. twigs, branches, prop roots and stems) intersecting the transect line were counted and measured by classifying wood debris in four categories according to their diameter: fine (0.0 to 0.6 cm), small (0.7 to 2.5 cm), medium (2.6 to 7.5 cm) and large (> 7.5 cm). Further, in the case of larger diameters, they were also classified based on their state of decay (sound or rotten) (Brown, 1974 modified by Sánchez and Zerecero (1983)). Downed wood biomass (Mg ha^{-1}) was estimated using the method proposed by Brown (1974; modified by Sánchez and Zerecero (1983)) and converted to organic carbon units using a factor of 0.50 (Kauffman and Donato, 2012).

2.2.4. Litterfall productivity

These values were originally obtained by Ochoa-Gómez et al. (2018) and used here to evaluate organic C fluxes from the forest canopy to the forest floor. Briefly, two 0.25 m^2 litterfall traps (screen mesh size: 1.0 mm) in each circular plot per zone and site; the traps were placed above the highest water level. The number of traps per site was variable (Balandra, n = 18; Zacatecas and Enfermeria, n = 14 in each site). Litterfall was collected monthly from April 2015 to May 2016. Litterfall productivity (Mg dw ha^{-1} $year^{-1}$) is reported by species at each site

Table 2
Soil physicochemical properties in mangrove study sites, La Paz Bay (± SD).

Mangrove	Electric conductivity (mS cm^{-1})	Bulk density (g cm^{-3})	pH	Sands (%)	Silts (%)	Clays (%)
Balandra	49.1 (29.7)	0.8 (0.5)	6.4 (0.5)^a	76.9 (17.0)^a	23.1 (16.9)^b	0.0 (0.2)^b
Enfermeria	38.2 (16.8)	0.9 (0.4)	6.5 (0.6)^a	69.1 (24.6)^b	30.7 (24.4)^a	0.2 (0.4)^a
Zacatecas	35.1 (19.8)	1.0 (0.4)	6.0 (0.3)^b	80.6 (16.6)^a	19.3 (16.6)^b	0.1 (0.2)^b
Average	40.8 ± 22.1	0.9 ± 0.1	6.3 ± 0.6	75.6 ± 19.4	24.4 ± 19.3	0.1 ± 0.3

*Letters indicate significant differences P (*perm*) < 0.05.

(see Ochoa-Gómez et al., 2018 for laboratory sample processing and statistical analysis).

2.2.5. Root biomass and productivity

Belowground root biomass was estimated by collecting two soil cores (diameter: 10 cm; length: 45 cm; total volume: 3534 cm^3) per plot/site and close to the dominant species (~60 cm of distance) in May 2015. These values were compared with values obtained with the general allometric equation of Komiyama et al. (2005) for belowground biomass. Model parameters were the same used in the calculation of forest above ground biomass (see Section 2.2.2).

Root productivity was also estimated in each plot using the ingrowth technique (Castañeda-Moya et al., 2013; Gleason and Ewel, 2002). Two galvanized and waterproofed cylinders (mesh: 1 cm; diameter: 10 cm; length: 45 cm), were deployed close (~60 cm distance) to trees with similar height and diameter of the dominant species in each plot. Root cylinders were deployed the same month (i.e., May 2015) when root biomass samples were obtained. All cylinders were retrieved one year after deployment.

All root material was stored separately in bags until processed to measure root biomass and productivity. Samples were processed by washing and separating root material from the soil using a 1 mm sieve, all roots were placed in paper bags and dried in an oven at 70 °C for 48 h to obtain dry weight (dw) (± 0.001 g). Roots values are reported per unit area and root productivity per unit area and time (Castañeda-Moya et al., 2013). Dry root organic material was converted to organic C units using a stoichiometry conversion factor 0.39 (Kauffman and Donato, 2012).

All C stocks were converted to equivalent CO_2 units using the molecular proportion of CO_2 and C by multiplying the C stock by 3.67 (Kauffman and Donato, 2012). These estimations are conservative and represent potential CO_2 emissions as a result of disturbance/deforestation (Kauffman and Donato, 2012).

2.2.6. Statistical analysis

Means and standard deviations (SD) were calculated for all variables to evaluate trends per plot and site including normality properties. Kolmogorov–Smirnov's normality test and Levene's homoscedasticity test were performed for each data set before statistical analyses. When normality criteria was not met, a permutational multivariate analysis of variance (perMANOVA) (Anderson, 2001) was applied to evaluate differences among main factors in a factorial design (site and species) and interactions. The response variables included in the analyses were: soil properties, aboveground and belowground forest C stocks, and NPP (litter and root productivity). Also, a perMANOVA analysis was also used to evaluate significant differences in NPP (*sensu* Danielson et al., 2017) among each mangrove species and their interaction. When significant differences were observed, a *post-hoc* pair-wise test was used to determine differences among main factors and interactions. All analyses were performed at 95% confidence using the statistical software SPSS Statistics Version 24 and PRIMER 6 software (Clarke and Warwick, 1994).

2.3. Perspective of ESs biomass and organic C

Some of the ESs provided by these three and by the three species on a regional scale were analyzed from a qualitative perspective of the organic C mass and spatial distribution. ESs criteria such as NPP and C storage were compared to other studies including bird and/or fish refuges or fisheries potentially influenced by C input (Amador et al., 2008; López-Rasgado et al., 2012; Ochoa-Gómez et al., 2018). We also considered cultural services such as ecotourism or landscape sighting at the study sites (Calderón et al., 2008; López-Rasgado et al., 2012; Mendoza-Salgado et al., 2011) or aesthetic value related to the structural complexity (at the mangrove wetland scale) and/or biomass (Ochoa-Gómez et al., 2018). These parameters were qualitatively classified according to the intensity by which they provide ESs at a regional scale (La Paz Bay): low (+), moderate (+ +) and high (+ + +).

3. Results

3.1. Physicochemical properties of soil sustaining mangrove ecosystems

We found no significant differences in any soil physicochemical properties sites dominated by different species. Average electrical conductivity (EC) at 10 cm depth, a proxy of soil salinity, ranged between 35 and 49 mS cm^{-1} (Table 2), show significant differences when considering the site-species interaction ($p < 0.00$), but not sites (Table 3). Similarly, no significant differences were observed in bulk density among sites, species, or their interaction. pH values were similar in both sites, Enfermeria (6.4 ± 0.5) and Balandra (6.5 ± 0.5), which were significantly higher than in the Zacatecas site (6.0 ± 0.3) (Table 2); perMANOVA results also suggest significant differences when considering the site-species interaction. Soil texture analysis revealed that the highest average percentage of sands and the lowest of silts were found in Zacatecas (80.6 ± 16.6%, 19.3 ± 16.3) and Balandra (76.9 ± 17.0%, 23.1 ± 16.9), which were significantly different from Enfermeria values (69.1 ± 24.6%, 30.7 ± 24.2) (Table 2); significant differences were also observed for the site-species interaction. The presence of clays was low in all sites (range: 0.0–0.2%). Despite the observed statistical differences among soil texture components (Table 3), all values are within the range reported for mangrove soils that are considered as fine sandy loam soils, which are typical of dry and dune dominated coastal areas.

3.2. Above and belowground C stocks

3.2.1. Aboveground

Aboveground carbon stock contribution by living trees was 31.6 ± 16.6 Mg C ha^{-1} in Balandra, 13.6 ± 7.8 Mg C ha^{-1} in Enfermería and 23.8 ± 23.7 Mg C ha^{-1} in Zacatecas (Table 4). On the other hand, C stock from dead wood and dead trees was between 1.2 and 1.8 Mg C ha^{-1} in Balandra and Zacatecas, and from 0.6 to 6.2 Mg C ha^{-1} in Enfermeria (Table 4). Trees in the 6 to 7.2 cm DBH range showed the highest biomass and C stock, with the exception of the Zacatecas site, where high C allocation was also measured in trees with a DBH ranging from 12.0 to 13.2 cm (Fig. 2); tree biomass in this

Table 3
perMANOVA of soil properties in mangrove study sites, La Paz Bay.

Soil properties Factor	Main factor and Interaction	df	SS	MS	Pseudo-F	p-Value
Electric Conductivity ($mS\ cm^{-1}$)	Site	2	571.11	285.55	1.70	0.19
	Species	2	786.58	393.29	2.35	0.10
	Site × Species	4	10,638	2659.6	15.90	0.00*
Bulk Density ($g\ cm^{-3}$)	Site	2	0.09	0.04	0.58	0.60
	Species	4	0.07	0.03	0.50	0.63
	Site × Species	4	0.40	0.10	1.30	0.40
pH	Site	2	2.14	1.07	8.38	0.00*
	Species	2	0.32	0.16	1.28	0.28
	Site × Species	4	4.72	1.18	9.23	0.00*
Sands (%)	Site	2	3908.4	1954.2	9.56	0.00*
	Species	2	21.40	10.70	0.05	0.95
	Site × Species	4	6035.1	1508.80	7.38	0.00*
Silts (%)	Site	2	3813.9	1906.9	9.42	0.00*
	Species	2	20.61	10.30	0.05	0.95
	Site × Species	4	6052.4	1513.1	7.48	0.00*
Clays (%)	Site	2	0.57	0.28	4.03	0.02*
	Species	2	0.00	0.00	0.40	0.66
	Site × Species	4	0.00	0.00	0.28	0.88

* Significant differences.

Table 4
Above-belowground carbon pools ($Mg\ C\ ha^{-1}$) and NPP (litter and fine roots) ($Mg\ C\ ha^{-1}\ year^{-1}$) (± SD) at each study site.

Partition Carbon Pools	Balandra	Enfermeria	Zacatecas
Aboveground			
Trees (Alive)	31.6 ± 16.6	13.6 ± 7.8	23.8 ± 23.7
DW + SDT*	1.8 ± 1.1	3.4 ± 2.8	1.2 ± 1.0
Pneumatophores	0.06 ± 0.09	0.03 ± 0.05	0.06 ± 0.07
NPP_{Litter}	0.5 ± 0.2	0.4 ± 0.2	0.3 ± 0.1
Belowground			
Roots	0.27 ± 0.07	0.22 ± 0.13	0.31 ± 0.08
$NPP_{Fine\ roots}$	0.08 ± 0.02	0.09 ± 0.03	0.06 ± 0.03
Soil (0–45 cm depth)	238.9 ± 121.5	185.5 ± 118.5	100.3 ± 13.4

* DW + SDT; Dead Wood plus Standing Dead Trees biomass.

site represented 18.9% of the total C stock followed by Balandra (11.6%) and Enfermeria (6.7%). The largest C stock for downed wood (including standing dead trees) was registered in Enfermeria (3.4 ± 2.8 Mg C ha^{-1}), representing 20% of the aboveground C stock measured in this site (Table 4; Table 5). The highest downed wood value was measured in plots dominated by *A. germinans* (3.0 Mg C ha^{-1}) (Table 6).

Integrated aboveground C stocks were highest in Balandra (33.5 ± 16.8 Mg C ha^{-1}), followed by Zacatecas (25.1 ± 24 Mg C ha^{-1}) and lowest in Enfermeria (17.0 ± 8.1 Mg C ha^{-1}) site (Table 7); mean C stocks were significantly different between Balandra and Enfermeria (*p (perm) < 0.05*) while the mean value in Zacatecas (25.1 ± 24.1 Mg C ha^{-1}) was no significant differently from those sites (Table 7).

When comparing aboveground living trees biomass per species across all sites we found that sites dominated by *R. mangle* (31.4 ± 18.0 Mg C ha^{-1}) and *L. racemosa* (28.8 ± 23.1 Mg C ha^{-1}) had higher C values (Table 6). For the total aboveground C stock, significant differences were only registered between *R. mangle* and *A. germinans*, with intermediate values for *L. racemosa* (Table 7). The highest biomass value was species-specific and was measured in trees ranging in DBH from 4.8 to 6.0 cm (*R. mangle)*, 8.4 to 9.6 cm (*L. racemosa)* and 6 to 7.2 cm (*A. germinans)* (Fig. 3). Habitats dominated by the species *L. racemosa* had the highest pneumatophores biomass (0.09 ± 0.1 Mg C ha^{-1}; Table 6) probably due to the high biomass storage capacity for this specie and oxygen supply requirements.

3.2.2. Belowground

Although biomass values (< 1 Mg C ha^{-1}) and annual root productivity rates were overall low in the La Paz Bay region, the Zacatecas mangrove forests had the highest root C stock (0.31 Mg C ha^{-1}; Table 4), and nominally representing 0.3% of the total belowground C stock; C root stock in Balandra and Enfermeria are even lower than 0.1% of the total belowground C stock.

Similar to the belowground C stock, the zones within each site dominated by *R. mangle* also show the highest root stock and total belowground C (Table 6). When belowground C stocks are compared per site, the highest value was measured in the Balandra site (239.2 ± 121.6 Mg C ha^{-1}) and statically similar to the value observed in Enfermeria (185.7 ± 118.6 Mg C ha^{-1}) (Table 7). When proportionally comparing the belowground carbon stock among sites, the Enfemeria site showed the highest percentage of C stock belowground (91.4%) while values for the sites Balandra (87.6%) and Zacatecas (79.8%) were slightly lower. No significant differences in total C belowground among species ($P > 0.05$) were observed overall (Table 8) and among soils depths (pseudo $F = 0.00$, $P = 0.99$).

3.3. Net primary productivity: Litterfall (NPP_L) and root productivity (NPP_R)

Mean litterfall rates were higher in Balandra (0.5 ± 0.2 Mg C ha^{-1} $year^{-1}$) than in Enfermeria (0.4 ± 0.2 Mg C ha^{-1} $year^{-1}$) and Zacatecas (0.3 ± 0.2 Mg C ha^{-1} $year^{-1}$) sites (Table 4). However, root productivity was relatively higher in Enfermeria: 0.09 ± 0.03 Mg C ha^{-1} $year^{-1}$ (Balandra: 0.08 ± 0.02 Mg C ha^{-1} $year^{-1}$; Zacatecas: 0.06 ± 0.03 Mg C ha^{-1} $year^{-1}$), yet despite this difference, litter productivity was one order of magnitude higher than root productivity (Table 4). Both NPP in Balandra (0.6 ± 0.2 Mg C ha^{-1} $year^{-1}$) and Enfermeria (0.5 ± 0.1 Mg C ha^{-1} $year^{-1}$) were not statistically different and contribute similarly to the NPP regional coastal C budget ($P > 0.05$; Table 7).

At a regional level, the highest litterfall rate was observed in habitats dominated by the species *L. racemosa* (0.5 ± 0.2 Mg C ha^{-1} $year^{-1}$), followed by areas dominated by *R. mangle* (0.4 ± 0.1 Mg C ha^{-1} $year^{-1}$) and *A. germinans* (0.3 ± 0.1 Mg C ha^{-1} $year^{-1}$) (Table 6). Root productivity rates in areas dominated by *A. germinans* and *R. mangle* were the highest, evidencing the same magnitude (0.08 Mg C ha^{-1} $year^{-1}$), while habitats dominated by *L. racemosa* reflected the lowest value (0.06 ± 0.03 Mg C ha^{-1} $year^{-1}$) (Table 6). In total, *L. racemosa* had the most significant annual contribution to coastal C budgets (0.6 Mg C ha^{-1} $year^{-1}$), followed by *R. mangle* and *A. germinans* (Table 7).

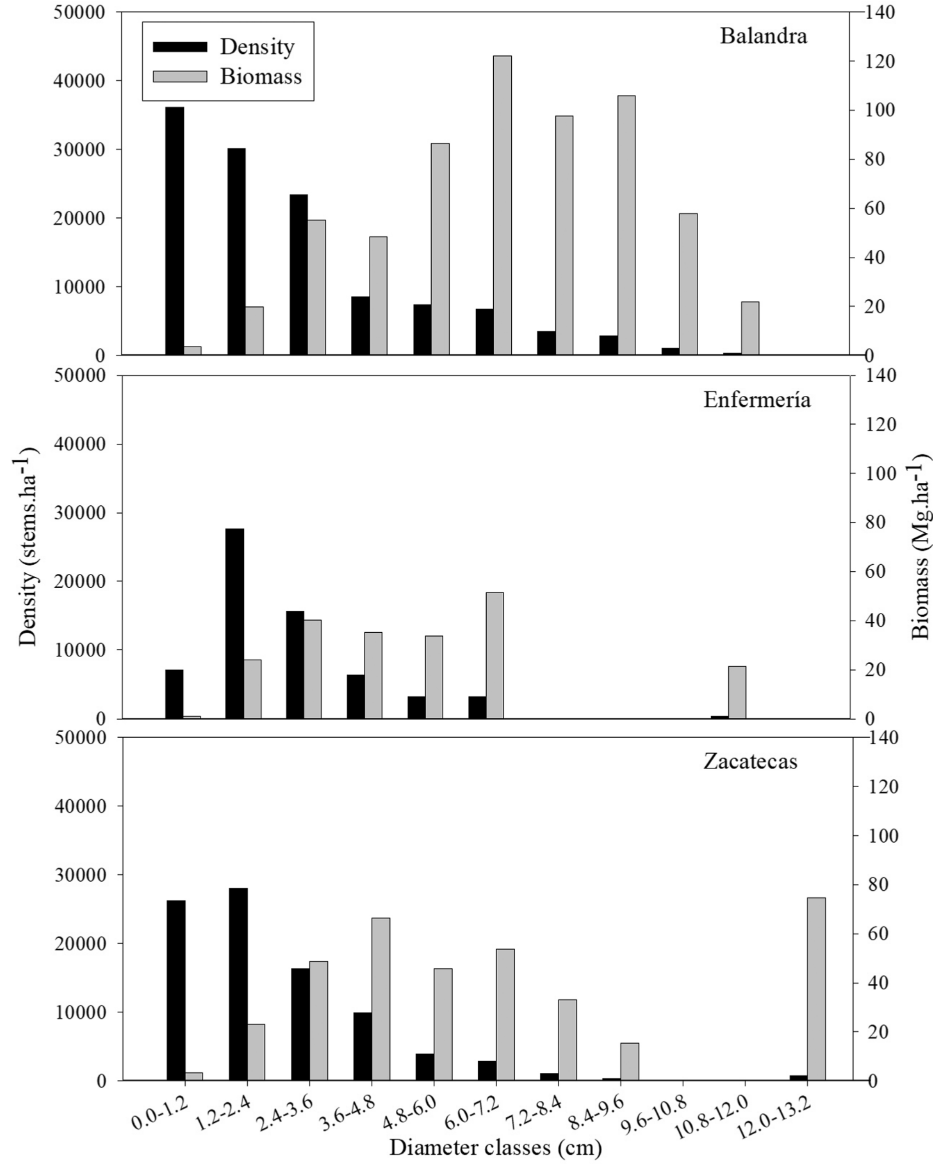

Fig. 2. Total biomass and total stem density by diameter class at each study site.

Table 5
Downed wood (Mg C ha^{-1}) by diameter class (cm) in each mangrove.

Downed Wood	Balandra	Enfermeria	Zacatecas
Diameter			
0–0.6	0.3	0.3	0.1
0.6–2.5	0.5	1.0	0.3
2.5–7.5	0.6	1.2	0.7
> 7.5 (sound)	0.4	0.5	0.1
> 7.5 (rotten)	0.0	0.0	0.0
Dead trees	0.0	0.4	0.0

Annual C litterfall rates ranged from 0.2 to 0.7 Mg C ha^{-1} year^{-1} and about 1.0 to 2.3% of the aboveground C stock. The annual belowground C root productivity is regionally low on average (< 0.09 Mg C ha^{-1} year^{-1}) ranging from 0.03 to 0.06% of the total belowground C stock.

3.4. Total organic C stock

The average total C stock in mangrove wetlands of the La Paz Bay was 200.4 Mg C ha^{-1}; Balandra had the highest value (272.7 Mg C ha^{-1}) followed by Enfermeria (202.7 Mg C ha^{-1}) and Zacatecas (125.7 Mg C ha^{-1}). No significant differences were found in the total C storage in high (i.e., Enfemeria) and low (i.e., Balandra) impacted sites (Table 7).

The total C stock in habitats dominated by *R. mangle* had the highest value (242.2 Mg C ha^{-1}) followed by *L. racemosa* (211.9 Mg C ha^{-1}) and *A. germinans* (172.2 Mg C ha^{-1}) (Table 7). When analyzing the total mean C stock and the interaction between sites and species some significant differences were observed (Table 8), however, given the low replication, it was not possible to determine the specific combination of each treatment level (Table 8).

3.5. Perspective of study sites as ESs

Biomass, structural complexity and organic carbon as ESs are different among sites and across species. Balandra biomass and net primary productivity shows high availability of ESs due to its structural complexity, followed by Zacatecas and Enfermería (Table 9). Because of their higher biomass, sites dominated by the species *R. mangle* y *L. racemosa* provide ecosystem services such the ecotourism or aesthetic

Table 6
Mean (± SD) Above-belowground carbon pools ($Mg\,C\,ha^{-1}$) and NPP (litter and fine roots) ($Mg\,C\,ha^{-1}\,year^{-1}$) in habitats dominated by different mangrove species in the La Paz Bay.

Partition Carbon Pools	*Habitat-dominance*		
	A. germinans	*L. racemosa*	*R. mangle*
Aboveground			
Trees (Alive)	13.4 ± 10.4	28.8 ± 23.1	31.4 ± 18.0
DW + SDT*	3.0 ± 2.7	1.3 ± 1.0	1.6 ± 1.0
Pneumatophores	0.08 ± 0.1	0.09 ± 0.1	–
$NPP_{Litterfall}$	0.3 ± 0.1	0.5 ± 0.2	0.4 ± 0.1
Belowground			
Roots	0.24 ± 0.10	0.26 ± 0.05	0.29 ± 0.11
$NPP_{Fine\ roots}$	0.08 ± 0.03	0.06 ± 0.03	0.08 ± 0.02
Soil (0–45 cm depth)	155.5 ± 72.1	181.4 ± 118.2	208.9 ± 144.6

* DW + SDT; Dead Wood plus Standing Dead Trees biomass.

value (Table 9). *A. germinans,* is the most important species in potentially provisioning organic carbon to regional food webs (Table 9).

4. Discussion

4.1. Biomass, C storage and NPP values along disturbance gradients in La Paz Bay

Despite the prevailing arid climate and low precipitation (< 250 mm $year^{-1}$) and irregular water discharge (i.e., runoff, groundwater), La Paz Bay in the Gulf of California is inhabited by an extensive area of mangroves typical of arid zones (Fig. 1). Mangrove spatial distribution in this area forms distinct patches in the landscape that are delineated by the availability of groundwater and surface water flow exchange next to coastal waters influenced by semidiurnal tides (Sandoval and Gómez-Valdés, 1997). Our analysis of C stocks and NPP throughout La Paz Bay show that these extensive mangrove patches are also significantly influenced by human activities, hence their classification as peri-urban wetlands (Lee et al., 2014; Ochoa-Gómez et al., 2018). We selected three locations to evaluate how mangrove structural composition and productivity patterns are influenced by the interaction between this arid environmental setting and the level of anthropogenic impact (Table 1). In sites with low (Balandra) or moderate (Zacatecas) impact, there was a quasi-normal distribution in biomass per DBH (not considering DBH outliers in Zacatecas). In contrast, above mangrove biomass in Enfermeria (highest impact) shows non-symmetrical DBH distribution due to logging and direct anthropogenic disturbances, especially hydrological alterations (Mendoza-Salgado et al., 2011) (Fig. 2). Regardless of the differences in biomass distribution per DBH class, the three sites showed approximately the same magnitude in NPP_{Litter}, NPP_{Roots} and belowground C storage. In Enfermeria, the site with the lowest complexity index and total extension, we also registered the lowest tree density (Table 1); this is most probably as result of stressful conditions driven by higher seasonal hypersalinity conditions in combination with nutrient limitation (e.g., Castañeda-Moya et al., 2013).

Another indicator of disturbance in the study sites was the relative contribution of downed wood to organic C (Kauffman and Donato, 2012). The values of downed wood stock in sites with low (Balandra) or moderate (Zacatecas) impact in La Paz Bay region were similar to those reported for other semi-arid regions of the world (1.2 $Mg\,C\,ha^{-1}$; Kauffman and Bhomia, 2017). We measured approximately twice the C stock in downed wood in Enfermeria than in the other sites underscoring the landscape level interactions of both natural (drought, storms) and human disturbances (e.g., direct removal, hydrological alterations). Further, this site was the only location where we identified dead standing trees indicating possible changes in groundwater level thus impacting salinity regimes in the long term, particularly since this area was impacted by road and infrastructure construction that might have affected water exchange and storage (Fig. 1C).

The use of allometric equations to estimate belowground biomass has been useful to determine the contribution of this soil component given the limited availability of field studies in different environmental settings (e.g., Rivera-Monroy et al., 2013). Yet, these values should be considered with caution when comparing sites along latitudinal gradients (Adame et al., 2017) since belowground values could be overestimated up to > 95% of the actual value, thus influencing total soil C stock estimates. In the case of our study sites, both below and

Table 7
Average values (± SD) and statistical analysis (perMANOVA) of above-belowground carbon stocks and NPP (litter + fine roots) by site, species, and interactions between both in mangroves of La Paz Bay. (*The statistical analysis was not performed due to sample size).

Sites	*n*	Aboveground ($Mg\,C\,ha^{-1}$)	Belowground ($Mg\,C\,ha^{-1}$)	NPP ($Mg\,C\,ha^{-1}\,year^{-1}$)
Balandra	9	33.5 ± 16.8^{a}	239.2 ± 121.6^{a}	0.6 ± 0.2^{a}
Enfermería	7	17.0 ± 8.1^{b}	185.7 ± 118.6^{a}	0.5 ± 0.1^{a}
Zacatecas	7	25.1 ± 24.1^{ab}	100.6 ± 13.4^{b}	0.4 ± 0.1^{b}
		p (perm) < 0.05	*p (perm) < 0.05*	*p (perm) < 0.05*
Species				
Avicennia geminans	9	16.5 ± 11.3^{b}	155.7 ± 72.1	0.4 ± 0.1^{b}
Laguncularia racemosa	5	30.2 ± 23.9^{ab}	181.7 ± 118.2	0.6 ± 0.3^{ab}
Rhizophora mangle	9	33.0 ± 18.0^{a}	209.2 ± 144.6	0.5 ± 0.1^{a}
		p (perm) < 0.05	*p (perm) = 0.21*	*p (perm) < 0.05*
Sites × species				
Balandra				
Avicennia germinans	3	19.3 ± 14.5	212.12 ± 95.3	0.4 ± 0.1
Laguncularia racemosa	3	43.5 ± 20.5	138.07 ± 34.9	0.7 ± 0.2
Rhizophora mangle	3	37.5 ± 3.8	367.30 ± 88.1	0.6 ± 0.1
Enfermeria				
Avicennia germinans	3	22.8 ± 10.2	137.2 ± 50.8	0.5 ± 0.1
*Laguncularia racemosa**	1	17.3	387.0	0.5
Rhizophora mangle	3	11.2 ± 2.5	167.2 ± 123.6	0.5 ± 0.1
Zacatecas				
Avicennia germinans	3	7.6 ± 2.4	106.0 ± 14.3	0.2 ± 0.0
*Laguncularia racemosa**	1	3.0	107.2	0.4
Rhizophora mangle	3	50.2 ± 9.1	92.9 ± 13.2	0.5 ± 0.0
		p (perm) < 0.05	*p (perm) < 0.05*	*p (perm) = 0.20*

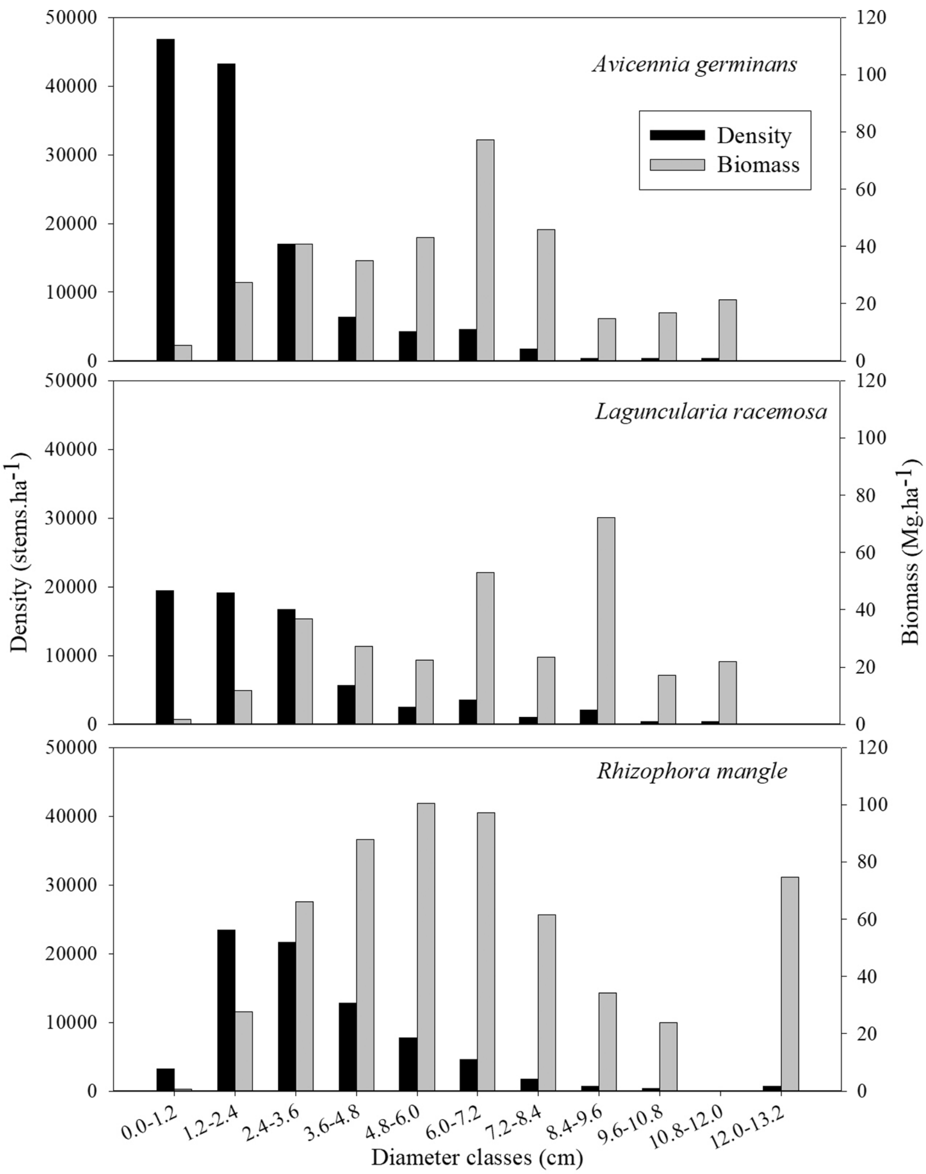

Fig. 3. Total biomass and total stem density by diameter class and species in study sites.

Table 8
perMANOVA of carbon stocks and NPP_{L+R} (i.e., litterfall + root productivity) in mangroves of La Paz Bay.

Factor	Interaction	df	SS	MS	Pseudo-F	p-Value
Aboveground	Site	2	1094.7	547.33	4.53	0.04*
	Species	2	1249.4	624.72	5.17	0.01*
	Site × Species	4	3226.7	806.68	6.68	0.00*
Belowground	Site	2	70,647	35,323	6.81	0.00*
	Species	2	17,719	8859.6	1.70	0.21
	Site × Species		113,790	28,449	5.48	0.00*
NPP_{L+R}	Site	2	0.18	0.09	6.71	0.01*
	Species	2	0.32	0.07	5.77	0.01*
	Site × Species	4	4.72	0.02	1.76	0.19

* Significant differences.

aboveground biomass values were at the lower limit of observed global patterns (Adame et al., 2017; Rivera-Monroy et al., 2013). This lower range is also comparable with values in mangroves ecosystems located in arid or semi-arid regions in the Arabian Gulf (aboveground: 7.3–243.6 Mg ha^{-1}; Schile et al., 2017), the Red Sea (Aboveground: 17–96.5 Mg C ha^{-1}; Mashaly et al., 2016), West Australia (aboveground: 55–115 Mg C ha^{-1}; Alongi, 2012; 45 Mg C ha^{-1}; Hickey et al., 2018) and Senegal (aboveground: 52 Mg C ha^{-1}; Kauffman and Bhomia, 2017). Overall, belowground biomass (roots) is considered one of the most important C pools (Komiyama et al., 2005), representing in some cases more than 50% of the belowground stock in tropical mangroves, (Santos et al., 2017). In our study, root belowground values represented < 3% of the soil biomass in all sites, which contrast with the relative importance in other tropical latitudes where roots can be up to 50% of total belowground biomass. This finding suggests that in the arid settings in the Gulf of California, Mexico, mangroves are able to maintain a comparable root production and biomass across all sites regardless of the level of disturbance. This similarity in root biomass and NPP values regardless of forest structure in La Paz Bay supports the hypothesis that belowground C accumulation in mangrove wetlands growing in desert inlets are accreting on their own accumulated peat; this process results in large C storage comparable to the tallest tropical mangroves in river-dominated settings in the Mexican Pacific (i.e., Ezcurra et al., 2016) as reflected by our total soil organic C values (Table 4, Table 7).

Given the distinct arid landscape surrounding each study site

Table 9
Ecosystem services of three mangroves in the southwestern Gulf of California with the intensity in each ecosystem function and services (Low: +; Moderate: + +; High: + + +).

Site	Supporting		Provisioning		Regulation	Cultural	
	NPP_L	NPP_R	Fisheries	Nursery	Carbon storage	Ecotourism	Aesthetic value
Balandra	+ + +	+ +	+	+ + +	+ + +	+ + +	+ + +
Zacatecas	+	+	+ +	+ +	+	+ +	+ +
Enfermería	+ +	+ + +	+ + +	+	+ +	+	+
Habitat sp. dominance							
A. germinans	+	+ +	+ + +	+	+	+	+
L. racemosa	+ + +	+	+ +	+ + +	+ +	+ +	+ +
R. mangle	+ +	+ + +	+	+ +	+ + +	+ + +	+ + +

NPP_L = Net Primary Productivity Litterfall; NPP_R = Net Primary Productivity Roots.

(Fig. 1), it is possible that the current patchy local distribution is an indicator of historical environmental conditions where mangrove plant establishment is recurrent as suggested by the similar soil organic C storage values reported for other arid areas in the Baja California Peninsula (Fig. 1; e.g., Ezcurra et al., 2016). Mangrove wetlands in La Paz Bay grow in soil that is spatially variable due to different physiographic, hydrological and geomorphic conditions. The relative importance of these drivers per location influence the presence of coastal vegetation adapted to major fluctuations in hydroperiod, soil salinity, and water availability; these conditions provide mangrove plants a competitive advantage over other herbaceous vegetation (e.g., *Salicornia* sp., *Batis* sp., *Spartina* sp.). Indeed, the high proportion of forested mudflat together with a higher water exchange rate in Zacatecas (Mendoza-Salgado et al., 2011; Ochoa-Gómez et al., 2018), might contribute to higher C export and facilitate organic matter decomposition, as previously reported (e.g., Ochoa-Gómez et al., 2018) resulting in lower carbon accumulation in the soil (Table 4). Soil C storage is generally higher under anoxic conditions controlled by long periods of inundation (e.g., Enfermeria) (Nguyen et al., 2004). Although we did not measure hydroperiod (flooding duration and frequency, water depth), we qualitatively observed how flooding duration and frequency during sampling campaigns were associated to observed pattern in soil C storage in our study sites (Zacatecas < Enfermeria < Balandra; Table 4). Our results are similar to other studies in semi-arid and arid regions where both the extension of mangrove patches and C storage capacity is inversely correlated with the distance to adjacent waterbodies (Hickey et al., 2018). This relationship is partially the result of an increase in oxygen diffusion into the soil that fuels organic matter decomposition as flooding duration diminish with distance from the waterbody (Hickey et al., 2018).

4.2. Global comparative evaluation among arid and semi-arid mangrove sites

Since the report of the first regional *in situ* C assessment indicating that mangrove forest store large amount of C (1023 Mg C ha^{-1}; Donato et al., 2011), a number of studies have published a wide range of values at different latitudinal ranges, particularly in tropical latitudes (Atwood et al., 2017; Rovai et al., 2016; Simard et al., 2019). Although C storage spatial patterns and magnitudes have been explained based on climatic factors (i.e., precipitation, air temperature) using statistical models at the global scale (Osland et al., 2017b; Simard et al., 2019), it is apparent that there are limitations in the predictions of C storage at corresponding regional and local scales (Simard et al., 2019). The main reasons for this discrepancy are the confounded effect of the interaction among coastal geomorphology, local climate, and fertility gradients (Rovai et al., 2018; Twilley et al., 2018) along with data gaps to upscale or downscale at regional scales (Cavanaugh et al., 2018; Simard et al., 2019). Thus, most of the databases used to construct C global statistical models (e.g., Simard et al., 2019) do not include relatively small areas of mangrove wetlands in different geomorphic settings (Twilley et al., 2018), especially at latitudinal boundaries between tropical, subtropical and temperate latitudes where arid regions are located (Cavanaugh et al., 2018; Jacotot et al., 2018). For instance, C aboveground in Southwestern Florida USA, a karstic environment located in higher latitudes (southwestern Everglades; 25.376949°N; Jerath et al., 2016) is double that in our sites at a lower latitude (24.142198°N) (Table 4). Indeed, regional climate between these two areas is distinct, with higher precipitation in the Gulf of Mexico than in the Northern Pacific coast of Mexico and the Gulf of California, even when they are impacted by the same seasonal and interannual variability in tropical storms (Zhang et al., 2008; Camacho-Ibar and Rivera-Monroy, 2014; Farfan et al., 2014).

From a comparative viewpoint, our estimates for C in soils of the La Paz Bay sites (e.g., Balandra: 239 Mg C C ha^{-1}; Enfermeria: 185 Mg C ha^{-1}) were higher than soil values reported for other semi-arid and arid regions in Senegal (90 Mg C ha^{-1}, at 40 cm; Woomer et al., 2004), the Red Sea (43 Mg C ha^{-1}; Almahasheer et al., 2017; 85 Mg C ha^{-1}; Eid and Shaltout, 2015), the Arabian Gulf (102–156 Mg C ha^{-1}; Schile et al., 2017; 76 Mg C ha^{-1}) and New Caledonia (100 Mg C ha^{-1}; Jacotot et al., 2018). Our values are similar to those reported for karstic coastal regions in the Yucatan Pensinsula, Mexico (286 Mg C ha^{-1}, La Raya: Adame et al., 2013) and river dominated lagoon environments (174.8 Mg C ha^{-1}, Las Palmas: Adame et al., 2015) in Chiapas, Mexico; these sites are located at lower latitudes where mangrove extension is larger and aboveground biomass is higher. This lack of association between mangrove latitudinal location and C storage values has been explained based on differences in specific attributes (e.g., Cardona-Olarte et al., 2006; Naidoo, 2010; Tognella et al., 2016) that characterize coastal environmental settings (Twilley and Rivera-Monroy, 2005). In this framework, global variations in mangrove soil organic C are driven by specific regional C dynamics (Rivera-Monroy et al., 2013; Twilley et al., 2018), as is apparently the case of arid mangrove wetlands in La Paz Bay where their total area is reduced (Fig. 1), but NPP (litter and root) and C storage is relatively high.

4.3. Mangrove structural properties and ESs

Two of the most conspicuous ESs provided by mangrove wetlands in our study sites are fisheries (provision) and C storage (regulation; *sensu* MEA, 2005). Despite their small extension, these wetlands provide shelter and nursery for fish assemblages that are associated to a habitat heterogeneity defined by mangrove structural complexity and species zonation (Ochoa-Gómez et al., 2018). For example, mangroves with lower structural complexity and higher dominance of the species *A. germinans* provide a higher potential for artisanal fisheries in the southwestern Gulf of California (Ochoa-Gómez et al., 2018). In fact, given the regional interannual variation in water availability and high evaporation rates, high soil salinity values could become prevalent and species adapted to withstand soil hypersalinity conditions (> 40 ups) (i.e., *A. germinans*) can form monospecific mangrove patches/stands. Similarly, areas close to the water edge in lagoons and channels (e.g., Balandra and Zacatecas sites) where water and nutrient exchange is higher along relative lower elevation gradients, both *R. mangle and L. racemosa* can also form both monospecific and mix species forest stands providing distinct habitats where fish and other animals (e.g., invertebrates and vertebrates) can find food, shelter and nursery based on the quality and quantity of organic matter production (e.g., high foliar nitrogen concentration) and forest structural attributes (e.g., density, tree height). Even with a limited extension and patchy spatial distribution, arid and semi-arid mangrove forest are areas of high biodiversity (Brusca et al., 2005) directly linked to ESs quality and quantity.

Carbon storage values, as a regulatory ES, illustrate the commonalities and relative functional differences in the availability of ESs when considering habitats dominated by one mangrove species or by mix-species stands interacting with disturbance level (Table 9). For example, the total C stock measured in Balandra and Enfermería sites were similar despite different anthropogenic impacts. Yet, when including the interaction among specific structural attributes, including complexity index, NPP (root, litterfall), and aboveground biomass, the Balandra study site provides *high quality* ESs within each of the ESs categories (supporting, provisioning, regulation, cultural; Table 9). Similarly, when considering the specific landscape level distribution of habitats dominated by *R. mangle* or *L. racemosa* in La Paz Bay, we found that these habitats show the highest capacity for C storage above and below ground (Table 6), as reported for other regions globally (*Laguncularia* sp.: $424 \pm 262\,\mathrm{Mg\,C\,ha^{-1}}$; *Rhizophora* sp.: $388 \pm 227\,\mathrm{Mg\,C\,ha^{-1}}$; Atwood et al., 2017). Although our ESs ranking (low, moderate, high; Table 9), based on expert opinion and published information from other regional and global studies (López-Medellín and Ezcurra, 2012; López-Rasgado et al., 2016; Himes-Cornell et al., 2018b), does not include monetary valuation due to lack of data, it represents a first-rate classification to establish priorities for mangrove conservation and management plans, which are currently lacking in La Paz Bay. Indeed, our C storage capacity estimates, if considered as a proxy of the potential removal of CO_2 from the atmosphere (i.e., ~198 Gg CO_2e), could be reflecting the high efficiency of CO_2 capture by scrub mangrove trees growing under stressful environmental conditions (e.g., hypersalinity and nutrients limitation; Snedaker and Araujo, 1998), thus underscoring the ecological and economic importance of mangrove wetlands not only in tall riverine mangroves (e.g., Jerath et al., 2016), but also in scrub mangroves (< 3 m tree height) in arid and semi-arid regions. Specifically, peri-urban mangroves in la Paz Bay can provide an essential ES to compensate for La Paz city CO_2 emissions in the context of climate change, thus providing some key criteria to be considered in developing management plans to protect and conserve mangrove wetlands as proposed in other regions where mangrove extension is the highest (Indonesia, Malaysia, Thailand; Atwood et al., 2017; Lee et al., 2014). This compensation criteria for La Paz Bay could be based, for example, in the conversion of our regional NPP_L estimates (~0.1 Gg C) to carbon dioxide equivalent representing ~0.4 Gg CO_2e. Although this CO_2 equivalent value is ~0.02% of the total value estimated for the city of La Paz for the year 2020 (1933 Gg CO_2e; Ivanova and Bermudez-Contreras (2014)), it provides a baseline for the economic valuation of this and other ESs. Since mangrove wetlands provide multiple ESs, it is critical to rank and assign a monetary value to fully account for relative role of each service to advance the conservation and management of wetlands globally (Osland et al., 2018; Lee et al., 2014).

There are major data gaps when assessing the diversity of mangrove ESs due to the lack of comparative studies, especially within a common framework. Although, monetary values have been tentatively assigned to a number of provisioning services (e.g., soil C stocks; Jerath et al., 2016), there is still major issues regarding other ESs, including cultural services such as spiritual and aesthetic values (Himes-Cornell et al., 2018a; Himes-Cornell et al., 2018b). This is the case for mangrove in La Paz Bay where we identified a wide availability of cultural services including potential ecotourism activities at different levels, especially in the Balandra site (high value; Table 9). Given the unique arid geomorphic setting of La Paz Bay, mangrove areas here represent a unique tourism destination that combined with educational activities can help promote the conservation of these peri-urban mangrove areas close to the city of La Paz (Fig. 1). This qualitative value per site can also be extrapolated to specific locations where species dominance provides relatively differences in importance value where habitats dominated by *A. germinans* offer high value for fisheries (provisioning) while locations where monospecific stands of *R. mangle* provide high value in regulation (C storage) and cultural ESs (aesthetic value). However, the lack of a regional monetary value assessment underscoring the potential economic loss if mangroves areas were to be replaced (deforestation) or impacted by urban development is a major regional risk that needs to be addressed in the short term. Our study represents a first step in the quantitative assessment of functional and structural properties as ESs of arid mangrove wetlands in La Paz Bay that could be readily translated into robust economic estimates in this extensive arid coastal region. This information should contribute to the development of a comprehensive ESs valuation framework where at least benefit transfer values (Himes-Cornell et al., 2018a), currently lacking for mangrove wetlands in arid/semi-arid regions, could be applied. This is particularly true in the case of the Baja California Peninsula and the Northern Pacific coasts of Mexico, where arid/ semi-arid climate is prevalent and mangrove extension is 15.5% of total area currently estimated for Mexico (Valderrama-Landeros et al., 2017).

5. Conclusions

We evaluated functional and structural properties of three peri-urban mangrove forests in La Paz Bay, Mexico, an arid coastal region in the Gulf of California to initiate a regional economic assessment of mangrove ESs. We found that despite different levels of natural and human disturbance, the mangrove sites were comparatively similar in NPP values. In contrast, we found differences in soil C storage and aboveground carbon values. There were also distinct differences in aboveground C storage values among locations where mangrove species forming monospecific stands across the landscape are delineated by differences in relative elevation and distance from the adjacent water bodies. Areas dominated by the species *R. mangle* had the highest soil C density values followed by *L. racemosa* and *A. germinans*. Although scrub mangroves were the dominant ecotype in all sites, functional differences may be explained by species-specific traits. We proposed that these structural and potential eco-physiological differences translate into the quality and quantity of ESs when separately considering habitats dominated by one mangrove species or by mix-species stands at different levels of disturbance (natural and anthropic), as currently proposed for differences among mangrove ecotypes (Ewel et al., 1998).

There are major data gaps to assess the monetary valuation for all type of ESs in arid and semi-arid regions due to the lack of comparative studies, especially within a common theoretical framework (Hickey et al., 2018; Himes-Cornell et al., 2018a). Although monetary values have been tentatively assigned to a number of provisioning services in mangrove wetlands (e.g., soil carbon stocks), there is still major shortcomings regarding other ESs, including cultural services such as spiritual and aesthetic values (Himes-Cornell et al., 2018a) which are greatly underestimated in La Paz Bay and of high potential economic importance for the region. Our study represents a first step in the quantitative assessment of functional and structural properties of mangrove forest in La Paz Bay that could be translated into benefit transfer values in the case of the Baja California Peninsula and the Northern Pacific coasts of Mexico.

Acknowledgments

This research was funded by the Mexican Consejo Nacional de Ciencia y Tecnología (CONACYT) agency through a research grant to ESZ and SELlC and a doctoral scholarship to JGOG (grant # 388919). The Centro de Investigaciones Biológicas del Noroeste (CIBNOR) provided laboratory support. VHRM was partially supported by the Department of the Interior South-Central Climate Adaptation Science Center (Cooperative Agreement #G12AC00002) and the Florida Coastal Everglades-LTER international collaboration initiative funded the US National Science Foundation-FCE-LTER program (Grant No. DEB-1237517). We are grateful to Sofía Grimaldi Calderón, Obdulia Gómez Domínguez, and Horacio Bervera León for their technical assistance. Special thanks to Joanna Acosta-Velázquez for assistance in the preparation of the map. All fieldwork was performed under SEMARNAT scientific collecting permit SGPAlDGVSI 05102/15. This paper is based on a PhD dissertation submitted to CIBNOR by JGOG.

References

Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., Sala, E., 2008. Mangroves in the Gulf of California increase fishery yields. PNAS. USA 105 (30), 10456–10459. https://doi.org/10.1073/pnas.0804601105.
Adame, M.F., Kauffman, J.B., Medina, I., Gamboa, J.N., Torres, O., Caamal, J.P., Herrera-Silveira, J.A., 2013. Carbon stocks of tropical coastal wetlands within the karstic landscape of the Mexican Caribbean. Plos One 8 (2), e56569.
Adame, M.F., Santini, N.S., Tovilla, C., Vázquez-Lule, A., Castro, L., Guevara, M., 2015. Carbon stocks and soil sequestration rates of tropical riverine wetlands. Biogeosciences 12 (12), 3805–3818.
Adame, M.F., Cherian, S., Reef, R., Stewart-Koster, B., 2017. Mangrove root biomass and the uncertainty of belowground carbon estimations. Forest Ecol. Manage. 403, 52–60.
Almahasheer, H., Serrano, O., Duarte, C.M., Arias-Ortiz, A., Masque, P., Irigoien, X., 2017. Low Carbon sink capacity of Red Sea mangroves. Sci. Rep. 7 (1), 9700.
Alongi, D.M., 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. Estuar. Coast. Shelf Sci. 76 (1), 1–13.
Alongi, D.M., 2009. The Energetics of Mangrove Forests. Springer, New York.
Alongi, D.M., 2012. Carbon sequestration in mangrove forests. Carbon Manage. 3 (3), 313–322.
Alongi, D.M., 2014. Carbon cycling and storage in mangrove forest. Annu. Rev. Mar. Sci. 6, 195–219.
Alongi, D.M., 2018a. Blue Carbon Coastal Sequestration for Climate Change Mitigation. Springer Briefs in Climate Studies. eBook, Switzerland.
Alongi, D., 2018b. Impact of global change on nutrient dynamics in mangrove forests. Forests 9 (10), 596.
Amador, E., Mendoza-Salgado, R., Palacios, E., 2008. Manejo de un sitio de anidación para la conservación de Sternula antillarum (Charadriiformes: Laridae) en Baja California Sur, México Rev. Mex. Biodivers. 79 (1), 271–274.
Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral. Ecol. 26 (1), 32–46.
Atwood, T.B., Connolly, R.M., Almahasheer, H., Carnell, P.E., Duarte, C.M., Lewis, C.J.E., Serrano, O., 2017. Global patterns in mangrove soil carbon stocks and losses. Nat. Clim. Change. 7 (7), 523–528.
Ávila-Flores, G., 2014. Diagnosis of the state of conservation of the mangroves in La Paz Bay México. Mastefs Thesis. UABCS. 104.
Ball, M.C., 1988. Ecophysiology of mangroves. Trees 2, 129–142.
Bhomia, R.K., Kauffman, J.B., McFadden, T.N., 2016. Ecosystem carbon stocks of mangrove forests along the Pacific and Caribbean coasts of Honduras. Wetl. Ecol. Manage. 24 (2), 187–201.
Brown, J.K., 1974. Handbook for inventorying downed woody material. USDA Forest Service. General Technical Report INT 16. Utah, USA. 24.
Brusca, R.C., Findley, L.T., Hastings, P.A., Hendrickx, M.E., Cosio, J.T., van der Heiden, A.M., 2005. Macrofaunal diversity in the Gulf of California. In: Cartron, J.E., Ceballos, G., Felger, R. (Eds.), Biodiversity, Ecosystems, and Conservation in Northern Mexico. Oxford University Press, New York, pp. 179–202.
Bunting, P., Rosenqvist, A., Lucas, R., Rebelo, L.M., Hilarides, L., Thomas, N., Hardy, A., Itoh, T., Shimada, M., Finlayson, C.M., 2018. The global mangrove watch—a new 2010 global baseline of mangrove extent. Remote Sens. 10 (10), 1669.
Calderón, C., de la Anaya, G., Cueva, M.A., Aburto, O., 2008. Balandra: El bosque costero de La Paz. CONABIO. Biodiversitas 78, 1–7.
Camacho-Ibar, V.F., Rivera-Monroy, V.H., 2014. Coastal lagoons and estuaries in Mexico: processes and vulnerability. Estuaries Coast. 37, 1313–1318.
Cardona-Olarte, P., Twilley, R.R., Krauss, K.W., Rivera-Monroy, V., 2006. Responses of neotropical mangrove seedlings grown in monoculture and mixed culture under treatments of hydroperiod and salinity. Hydrobiologia 569, 325–341.
Castañeda-Moya, E., Twilley, R.R., Rivera-Monroy, V.H., 2013. Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. Forest Ecol. Manage. 307, 226–241.
Cavanaugh, K.C., Osland, M.J., Bardou, R., Hinojosa-Arango, G., Lopez-Vivas, J.M., Parker, J.D., Rovai, A.S., 2018. Sensitivity of mangrove range limits to climate variability. Glob. Ecol. Biogeogr. 27, 925–935.
Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12 (4), 351–366.
Cintron, G., Lugo, A.E., Pool, D.J., Morris, G., 1978. Mangrove in arid environments in Puerto Rico and adjacent Islands. Biotropica 10, 110–112.
Clarke, K.R., Warwick, R.M., 1994. An approach to statistical analysis and interpretation. Change Marine Commun. 2, 117–143.
Collins, S.L., Carpenter, S.R., Swinton, S.M., Orenstein, D.E., Childers, D.L., Gragson, T.L., Grimm, N.B., Grove, J.M., Harlan, S.L., Kaye, J.P., Knapp, A.K., Kofinas, G.P., Magnuson, J.J., McDowell, W.H., Melack, J.M., Ogden, L.A., Robertson, G.P., Smith, M.D., Whitmer, A.C., 2011. An integrated conceptual framework for long-term social-ecological research. Front. Ecol. Environ. 9 (6), 351–357.
CONAGUA (National Water Commission), 2018. Climatological information by state. http://smn.cna.gob.mx/es/climatologia/informacion-climatologica (accessed 06 July 2018).
Dahdouh-Guebas, F., Koedam, N., 2006. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): solutions to ambiguous field situations and description of the PCQM+ protocol. Forest Ecol. Manage. 229, 1–18.
Danielson, T.M., Rivera-Monroy, V.H., Castañeda-Moya, E., Briceño, H., Travieso, R., Marx, B.D., Gaiser, E., Farfán, L.M., 2017. Assessment of Everglades mangrove forest resilience: implications for above-ground net primary productivity and carbon dynamics. Forest Ecol. Manage. 404, 115–125.
Dood, R.S., Blasco, F., Rafii, Z.A., Torquebiau, E., 1999. Mangroves of the United Arab Emirates: ecotypic diversity in cuticular waxes at the bioclimatic extreme. Aquat. Bot. 63, 291–304.
Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4 (5), 293.
Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41 (8), 1758–1766.
Eid, E.M., Shaltout, K.H., 2015. Distribution of soil organic carbon in the mangrove *Avicennia marina* (Forssk.) Vierh. along the Egyptian Red Sea Coast. Reg. Stud. Mar. Sci. 3, 76–82.
Ewel, K.C., Twilley, R.R., Ong, J.E., 1998. Different kinds of mangrove forests provide different goods and services. Glob. Ecol. Biogeogr. 7, 83–94.
Ezcurra, P., Ezcurra, E., Garcillán, P.P., Costa, M.T., Aburto-Oropeza, O., 2016. Coastal landforms and accumulation of mangrove peat increase carbon sequestration and storage. PNAS. USA 113 (16), 4404–4409.
Farfan, L.M., D'Sa, E.J., Liu, K.-B., Rivera-Monroy, V.H., 2014. Tropical cyclone impacts on coastal regions: the case of the yucatan and the baja california peninsulas, Mexico. Estuaries Coast. 37, 1388–1402.
Fischer, R., Galli-Olivier, C., Gidde, A., Schwennicke, T., 1995. The El Cien Formation of southern Baja California, Mexico: stratigraphic precisions. Newsl. Stratigr. 32 (3), 137–161.
Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Glob. Ecol. Biogeogr. 20, 154–159.
Gleason, S.M., Ewel, K.C., 2002. Organic matter dynamics on the forest floor of a Micronesian mangrove forest: an investigation of species composition shifts. Biotropica 34 (2), 190–198.
Hemati, Z., Hossain, M., Emenike, C.U., Rozainah, M.Z., 2015. Rate of carbon storage in soil of natural and degraded mangrove forest in peninsular Malaysia. CLEAN–Soil Air Water 43 (4), 614–619.
Hickey, S.M., Callow, N.J., Phinn, S., Lovelock, C.E., Duarte, C.M., 2018. Spatial complexities in aboveground carbon stocks of a semi-arid mangrove community: a remote sensing height-biomass-carbon approach. Estuar. Coast. Shelf Sci. 200, 194–201.
Himes-Cornell, A.H., Grose, S.O., Pendleton, L., 2018a. Mangrove ecosystem service values and methodological approaches to valuation: where do we stand? Front. Mar. Sci. 5 (376), 15 p.
Himes-Cornell, A.H., Pendleton, L., Atiyah, P., 2018b. Valuing ecosystem services from blue forests: a systematic review of the valuation of salt marshes, sea grass beds and mangrove forests. Ecosyst. Serv. 30, 36–48.
Holguín, G., Vazquez, P., Bashan, Y., 2001. The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview. Biol. Fert. Soils 33 (4), 265–278.
Hong, L.C., Hemati, Z.H., Zakaria, R.M., 2017. Carbon stock evaluation of selected mangrove forests in peninsular malaysia and its potential market value. JESAM 20 (2), 77–87.
INEGI (National Institute of Statistic and Geography), 2015. Main results of the Intercensal survey. Mexico. 122.
Ishihara, M.I., Utsugi, H., Tanouchi, H., Aiba, M., Kurokawa, H., Onoda, Y., Hiura, T., 2015. Efficacy of generic allometric equations for estimating biomass: a test in Japanese natural forests. Ecol. Appl. 25 (5), 1433–1446.
Ivanova, A., Bermudez-Contreras, A., 2014. Climate Action Plan for the City of La Paz, BCS, Mexico: a tool for public policy in a Coastal City. Current Urban Studies. 2 (03), 249–262.
Jacotot, A., Marchand, C., Rosenheim, B.E., Domack, E.W., Allenbach, M., 2018. Mangrove sediment carbon stocks along an elevation gradient: influence of the late Holocene marine regression (New Caledonia). Mar. Geol. 404, 60–70.
Jennerjahn, T.C., Ittekkot, V., 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. Naturwissenschaften 89 (1), 23–30.
Jerath, M., Bhat, M., Rivera-Monroy, V.H., Castaneda-Moya, E., Simard, M., Twilley, R.R., 2016. The role of economic, policy, and ecological factors in estimating the value of carbon stocks in Everglades mangrove forests, South Florida. USA. Environ. Sci. Policy 66, 160–169.
Kauffman, J.B., Donato, D.C., 2012. Protocols for the measurement, monitoring, and

reporting of structure, biomass, and carbon stocks in mangrove forests. Bogor, Indonesia: CIFOR. Working paper. No. 86, pp. 50.
Kauffman, J.B., Hernández-Trejo, H., Jesús-García, M.D.C.J., Heider, C., Contreras, W.M., 2016. Carbon stocks of mangroves and losses arising from their conversion to cattle pastures in the Pantanos de Centla, Mexico. Wetl. Ecol. Manage. 24 (2), 203–216.
Kauffman, J.B., Bhomia, R.K., 2017. Ecosystem carbon stocks of mangroves across broad environmental gradients in West-Central Africa: global and regional comparisons. Plos One 12 (11), e0187749.
Komiyama, A., Poungparn, S., Kato, S., 2005. Common allometric equations for estimating the tree weight of mangroves. J. Trop. Ecol. 21 (4), 471–477.
Lee, S.Y., Primavera, J.H., Dahdouh-Guebas, F., McKee, K., Bosire, J.O., Cannicci, S., Mendelssohn, I., 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Global Ecol. Biogeogr. 23 (7), 726–743.
López-Rasgado, F.J., Herzka, S.Z., Del-Monte-Luna, P., Serviere-Zaragoza, E., Balart, E.F., Lluch-Cota, S.E., 2012. Fish assemblages in three arid mangrove systems of the Gulf of California: comparing observations from 1980 and 2010. B. Mar. Sci. 88 (4), 919–945.
López-Rasgado, F.J., Lluch-Cota, S.E., Balart, E.F., Herzka, S.Z., 2016. Variation in isotopic trophic structure and fish diversity in mangrove systems subject to different levels of habitat modification in the Gulf of California. Mexico. Bull. Mar. Sci. 92, 399–422.
López-Medellín, X., Ezcurra, E., 2012. The productivity of mangroves in northwestern Mexico: a meta-analysis of current data. J. Coast. Conserv. 16 (3), 399–403.
Lugo, A.E., 1980. Mangrove ecosystems: successional or steady state? Biotropica 12 (2), 65–72.
Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. 5, 39–64.
Mashaly, I.A., Hegazy, A.K., Aal, M.A., El-Hussieny, S.A., 2016. Habitat based estimate of carbon content in mangrove *Avicennia marina* (Forssk.) Vierh. of South Sinai, Egypt. IOSR-J. Environ. Sci. Toxicol. Food Tech. 10 (11), 8–14.
Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. 9 (10), 552–560.
Mendoza-Salgado, R.A., Lechuga-Devéze, C.H., Amador, E., Pedrín-Aviles, S., 2011. The environmental quality of mangroves in Baja California Sur. In: Félix-Pico, E.F., Serviere-Zaragoza, E., Riosmena, R., León de la Luz, J.L. (Eds.), Los manglares de La Península de Baja California. CICIMAR-CIBNOR-UABCS, La Paz, Baja California Sur, México, pp. 9–26.
MEA (Millennium Ecosystem Assessment), 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.
Naidoo, G., 2010. Ecophysiological differences between fringe and dwarf Avicennia marina mangroves. Trees-Struct. Funct. 24, 667–673.
Nguyen, H.T., Yoneda, R., Ninomiya, I., Harada, K., Van Dao, T., Sy, T.M., Phan, H.N., 2004. The effects of stand-age and inundation on carbon accumulation in mangrove plantation soil in Namdinh, Northern Vietnam. Tropics 14 (1), 21–37.
Ochoa-Gómez, J.G., Serviere-Zaragoza, E., Lluch-Cota, D.B., Rivera-Monroy, V.H., Oechel, W., Troyo-Diéguez, E., Lluch-Cota, S.E., 2018. Structural complexity and biomass of arid zone mangroves in the southwestern Gulf of California: key factors that influence fish assemblages. J. Coastal Res. 34 (4), 979–986.
Osland, M.J., Day, R.H., Hall, C.T., Brumfield, M.D., Dugas, J.L., Jones, W.R., 2017a. Mangrove expansion and contraction at a poleward range limit: climate extremes and land-ocean temperature gradients. Ecology 98, 125–137.
Osland, M.J., Feher, L.C., Griffith, K.T., Cavanaugh, K.C., Enwright, N.M., Day, R.H., Stagg, C.L., Krauss, K.W., Howard, R.J., Grace, J.B., Rogers, K., 2017b. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecol. Monogr. 87 (2), 341–359.
Osland, M.J., Feher, L.C., López-Portillo, J., Day, H.R., Suman, D.O., Guzmán-Menéndez, J.M., Rivera-Monroy, V.H., 2018. Mangrove forests in a rapidly changing world: global change impacts and conservation opportunities along the Gulf of Mexico coast. Estuar. Coast. Shelf. Sci. 214, 120–140.
Pérez-Estrada, C.J., León-Tejera, H., Serviere-Zaragoza, E., 2012. Cyanobacteria and macroalgae from an arid environment mangrove on the east coast of the Baja California Peninsula. Bot. Mar. 55 (2), 187–196.
Rivera-Monroy, V.H., Castañeda-Moya, E., Barr, J.G., Engel, V., Fuentes, J.D., Troxler, T.G., O'Halloran, T.L., 2013. Current methods to evaluate net primary production and carbon budgets in mangrove forests. In: DeLaune, R.D., Reddy, K.R., Richardson, C.J., Megonigal, J.P. (Eds.), Methods in Biogeochemistry of Wetlands. Soil Science Society of America Inc., USA, pp. 243–288.
Rivera-Monroy, V.H., Lee, S.Y., Kristensen, E., Twilley, R.R., 2017a. Introduction. In: Rivera-Monroy, V.H., Lee, S.Y., Kristensen, E., Willey, R.R. (Eds.), Mangrove Ecosystems: A Global Biogeographic Perspective: Structure, Function, and Services. Springer, Switzerland, pp. 1–16.
Rivera-Monroy, V.H., Osland, M.J., Day, J.W., Ray, S., Rovai, A., Day, R.H., Mukherjee, J., 2017b. Advancing mangrove macroecology. In: Rivera-Monroy, V.H., Lee, S.Y., Kristensen, E., Willey, R.R. (Eds.), Mangrove Ecosystems: A Global Biogeographic Perspective: Structure, Function, and Services. Springer, Switzerland, pp. 347–381.
Rivera-Monroy, V.H., Danielson, T.M., Castañeda-Moya, E., Marx, B.D., Travieso, R., Zhao, X., Gaiser, E.E., Farfan, L.M., 2019. Long-ter demography and stem productivity of Everglades mangrove forests (Florida, USA): resistance to hurricane disturbance. Forest Ecol. Monogr. 440, 79–91.
Rojas-García, F., De Jong, B.H., Martínez-Zurimendí, P., Paz-Pellat, F., 2015. Database of 478 allometric equations to estimate biomass for Mexican trees and forests. Ann. For. Sci. 72 (6), 835–864.
Rovai, A.S., Riul, P., Twilley, R.R., Castañeda-Moya, E., Rivera-Monroy, V.H., Williams, A.A., Simard, M., Cifuentes-Jara, M., Lewis, R.R., Crooks, S., Horta, P.A., Schaeffer-Novelli, Y., Cintrón, G., Pozo-Cajas, M., Pagliosa, P.R., 2016. Scaling mangrove aboveground biomass from site-level to continental-scale. Global Ecol. Biogeogr. 25 (3), 286–298.
Rozainah, M.Z., Nazri, M.N., Sofawi, A.B., Hemati, Z., Juliana, W.A., 2018. Estimation of carbon pool in soil, above and below ground vegetation at different types of mangrove forests in Peninsular Malaysia. Mar. Pollut. Bull. 137, 237–245.
Rovai, A.S., Twilley, R.R., Castañeda-Moya, E., Riul, P., Cifuentes-Jara, M., Manrow-Villalobos, M., Horta, P.A., Simonassi, J.C., Fonseca, A.L., Pagliosa, P.R., 2018. Global controls on carbon storage in mangrove soils. Nat. Clim. Change. 8, 534–538.
Sánchez., J., Zerecero L.G., 1983. Practical method to calculate the amount of woody fuels and litter. Disclosure Note. Num. 9. CIFONOR. INIF. SFF. SARH. Mexico.
Sandoval, F.J., Gómez-Valdés, J., 1997. Tides and tidal currents in Ensenada de La Paz Lagoon, Baja California Sur, México. Geofís. Int. UNAM 36 (1), 37–47.
Santos, D.M.C., Estrada, G.C., Fernandez, V., Estevam, M.R., De Souza, B., Soares, M., 2017. First assessment of carbon stock in the belowground biomass of Brazilian Mangroves. An. Acad. Bras. Cienc. 89 (3), 1579–1589.
Schile, L.M., Kauffman, J.B., Crooks, S., Fourqurean, J.W., Glavan, J., Megonigal, J.P., 2017. Limits on carbon sequestration in arid blue carbon ecosystems. Ecol. Appl. 27 (3), 859–874.
Simard, M., Fatoyinbo, L., Smetanka, C., Rivera-Monroy, V.H., Castaneda-Moya, E., Thomas, N., Van der Stocken, T., 2019. Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. Nat. Geosci. 12, 40–45.
Snedaker, S.C., Araujo, R.J., 1998. Stomatal conductance and gas exchange in four species of Caribbean mangroves exposed to ambient and increased CO_2. Mar. Freshwater Res. 49 (4), 325–327.
Sturges, H., 1926. The choice of a class-interval. J. Amer. Statist. Assoc. 21, 65–66.
Tognella, M.M.P., Soares, M.L.G., Cuevas, E., Medina, E., 2016. Heterogeneity of elemental composition and natural abundance of stables isotopes of C and N in soils and leaves of mangroves at their southernmost West Atlantic range. Braz. J. Biol. 76, 994–1003.
Twilley, R.R., Rivera-Monroy, V.H., 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. J. Coast. Res. 79–93.
Twilley, R.R., Rivera-Monroy, V.H., 2009. Ecogeomorphic models of nutrient biogeochemistry for mangrove wetlands. In: Perillo, G.M.E., Wolanski, E., Cahoon, D.R., Brinson, M.M. (Eds.), Coastal Wetlands: An Integrated Ecosystem Approach. Elsevier, Amsterdam, pp. 671–683.
Twilley, R.R., Rovai, A.S., Riul, P., 2018. Coastal morphology explains global blue carbon distributions. Front. Ecol. Environ. 16 (9), 503–508.
Valderrama-Landeros, L.H., Rodríguez-Zúñiga, M.T., Troche-Souza, C., Velázquez-Salazar, S., Villeda-Chávez, E., Alcántara-Maya, J.A., Vázquez-Balderas, B., Cruz-López, M.I., Ressl, R., 2017. Mangroves of Mexico: Update and Exploration of the Data of the Monitoring System 1970/1980–2015. National Commission for the Knowledge and Use of Biodiversity, Mexico, pp. 128.
Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37 (1), 29–38.
Woomer, P.L., Tieszen, L.L., Tappan, G., Touré, A., Sall, M., 2004. Land use change and terrestrial carbon stocks in Senegal. J. Arid Environ. 59 (3), 625–642.
Yando, E.S., Osland, M.J., Willis, J.M., Day, R.H., Krauss, K.W., Hester, M.W., 2016. Salt marsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant-soil interactions and ecosystem carbon pools. J. Ecol. 104, 1020–1031.
Zanne, A.E., Lopez-Gonzalez G., Coomes, D.A., Ilic J., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemannn M.C. Chave J., 2009. Global wood density database. Dryad Data Repository. Available: http://hdl.handle.net/10255/dryad.235 (accessed September 2018).
Zhang, K.Q., Simard, M., Ross, M., Rivera-Monroy, V.H., Houle, P., Ruiz, P., Twilley, R.R., Whelan, K.R.T., 2008. Airborne laser scanning quantification of disturbances from hurricanes and lightning strikes to mangrove forests in Everglades National Park, USA. Sensors 8, 2262–2292.