Catena 143 (2016) 187–200

Contents lists available at ScienceDirect

Catena

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

Effects of sea-level rise and climatic changes on mangroves from southwestern littoral of Puerto Rico during the middle and late Holocene

Marcelo Cancela Lisboa Cohen [a,b,*], Rubén José Lara [c], Elvira Cuevas [d,e], Eneilis Mulero Oliveras [d,e], Leonel Da Silveira Sternberg [f]

[a] Laboratory of Coastal Dynamics, Graduate Program of Geology and Geochemistry, Federal University of Pará, Augusto Correa Av. 01, 66075-110 Belém, PA, Brazil
[b] Faculty of Oceanography, Federal University of Pará, Augusto Correa Av. 01, 66075-110 Belém, PA, Brazil
[c] Instituto Argentino de Oceanografía, 8000 Bahía Blanca, Argentina
[d] Center for Applied Tropical Ecology and Conservation, University of Puerto Rico, PO Box 23360, San Juan, PR 00931-3360, United States
[e] Department of Biology, University of Puerto Rico, PO Box 23360, San Juan, PR 00931-3360, United States
[f] Department of Biology, University of Miami, Coral Gables, FL 33124, United States

ARTICLE INFO

Article history:
Received 14 October 2015
Received in revised form 18 February 2016
Accepted 30 March 2016
Available online xxxx

Keywords:
Carbon and nitrogen isotopes
C/N
Climatic changes
Palynology
Puerto Rico
Sea-level rise

ABSTRACT

We evaluated the response to sea level rise and climatic changes of the northeastern Caribbean by establishing a palaeoenvironmental reconstruction of the Flamenco Lagoon, located in the coastal side of the Guanica Dry Forest, a MAB/UNESCO reserve in the semi-arid southwestern coast of Puerto Rico (17°57′10.31″N, 66°50′39.30″W). The reconstruction was based on pollen records, sediments analysis, $\delta^{13}C$, $\delta^{15}N$, C/N data and AMS ^{14}C dating of one sediment core. The geology of the area is rocky calcareous karst with rocky outcrops and canyons, with intermittent streams that move water during periods of high run-off conditions. The present lagoon is surrounded by rocky outcrops where dry forest vegetation is present on the terrestrial sides, and sand dunes on the coastal side. We propose that the studied lagoon developed after the stabilization of sea level rise in the region following three main stages: (1) before ~5400 cal yr BP, sediments were accumulated according to small channels dynamics and trees, shrubs and herbs were present. The sedimentary organic matter was mainly sourced from terrestrial C_3 and C_4 plants. (2) Between ~5400 and ~4400 cal yr BP, tidal flats were established and mangroves, mainly represented by *Rhizophora* trees, migrated landward with sea level rise and established in the area, and the sedimentary organic matter was sourced from terrestrial C_3 plants. (3) Around 4400 cal yr BP, sea level was near the stabilization, the endorheic minibasin was closed when a coastal sand dune was established as a result of drier climatic conditions. Mangroves were eliminated from the system as a result of the closure of the area by sand dunes and increased salinity in water due to high evaporative demand of the climate. The pollen dominance of herbaceous and shrubby vegetation prevails until present. Throughout the lagoon development, sedimentary organic matter was sourced from C_3 and C_4 plants, as well as phytoplankton organic matter. The closure of the lagoon and the drier conditions prevalent in the region during the late Holocene, which lasts until the present day, and increased the contribution of salinity tolerant phytoplankton that characterizes the current conditions of the Flamenco Lagoon.

1. Introduction

Sea level rise (SLR) has affected widespread physical and ecological coastal ecosystems along the Caribbean (Bellard et al., 2014; Hubbard et al., 2005; Lane et al., 2013; Rangel-Buitrago et al., 2015; Toscano and Macintyre, 2003) during the Holocene. The dominant depositional systems under SLR are barrier islands, estuaries, lagoons and bays (e.g. Swift, 1975; Cohen et al., 2014). Over a range of SLR scenarios, coastal wetlands adjust toward an equilibrium with sea level (D'Alpaos et al., 2008; Kirwan and Murray, 2007). Equilibrium models predict that coastal wetlands have a number of feedbacks that allow them to maintain their positions relative to the mean tidal range (Cohen et al., 2005; McKee et al., 2007). For example, surface accretion, often through sediment inputs, increases with the depth of tidal inundation (French and Stoddart, 1992; Furukawa and Wolanski, 1996), leading to increments in surface elevation that allow the wetland to keep pace with SLR (Cahoon et al., 2006). When present, mangroves may be used as indicators of coastal dynamics, as their positions within the intertidal zone are strongly influenced by SLR (Woodroffe, 1995; Woodroffe et al., 1989). Fringe mangroves have kept up and could accommodate eustatic SLR rates of 4 mm/yr. If eustatic rates exceed 5 mm/yr, then the mangroves would likely not persist (McKee et al., 2007). Some studies indicate that mangroves are unlikely to keep

---

* Corresponding author at: Faculty of Oceanography, Federal University of Pará, Augusto Correa Av. 01, 66075-110 Belém, PA, Brazil.
E-mail address: mcohen80@hotmail.com (M.C.L. Cohen).

http://dx.doi.org/10.1016/j.catena.2016.03.041
0341-8162/

pace with the highest SLR scenarios between 0.52 and 0.98 m by 2100 (IPCC, 2013; Koch et al., 2015; Sasmito et al., 2015).

Regarding the Western Atlantic Holocene sea level curves based on coral and intertidal *Rhizophora mangle* peat from the Florida Keys, Belize, and the wider Caribbean indicate the SLR during the Holocene was ~5.2, ~1.47 and ~0.93 mm/yr during the early, middle and late Holocene, respectively (e.g. Toscano and Macintyre, 2003). Details of Holocene western Atlantic sea-level curves are debated, but all curves are transgressive and display a rapid rise in the early Holocene and a reduced rate of rise in the late Holocene (Gischler, 2015). According to a palynological record of an Early-Mid Holocene mangrove in eastern Venezuela, a rapid rise in sea levels up to 8000 years BP occurred, with a slower rate between 8000 and 4000 years BP, and stable levels after 3000 years BP (Rull et al., 1999). Differences in the Holocene sea-level curves between Florida Keys/Belize and the eastern Caribbean may be attributed to a shift in the Inter Tropical Convergence Zone that regionally affects the Caribbean sea (Haug, 2001).

In the Caribbean islands, such as Puerto Rico, the rates of SLR are the product of the relation between eustatic sea level rise and local tectonic movements. The geomorphology and distribution of late Quaternary marine terraces and beach ridges in south-central Puerto Rico suggest stability or slow late Quaternary uplift along the south-central part of the coast, while the coastline of southwestern Puerto Rico exhibits no late Quaternary coastal sediments and a pattern of long-term drowning of coastal features (Mann et al., 2005). The relative small presence of mangrove areas along the eastern side of the coastal plateau in the Guánica Dry Forest UNESCO/MAB Biosphere Reserve (Fig. 1a) may be a consequence of this drowning of coastal system. However, the establishment and maintenance of mangroves also depend on other environmental factors such as topography (Cohen and Lara, 2003; Cohen et al., 2009, 2015; Gornitz, 1991), wave and current energy (Woodroffe et al., 1989), and coastal morphology (Blasco et al., 1996; Fromard et al., 2004; Lara and Cohen, 2009) and mainly the input of nutrients, sediment and freshwater (Cohen et al., 2014; Cohen et al., 2012; Krauss et al., 2008; Lara and Cohen, 2006; Stevens et al., 2006; Stuart et al., 2007). The availability of nutrient/sediment and freshwater along the coastal system depend mainly on the river runoff. Regarding the climatic changes and its effects in the Caribbean region during the Holocene (Banner et al., 1996; Higuera-Gundy et al., 1999; Malaize et al., 2011; Mangini et al., 2007), the contribution of sediments, nutrients and freshwater to the littoral must have changed significantly during this period and influenced, together with the SLR, the mangrove development.

Reconstructed past climate changes and SLR effects on coastal mangrove environments have been used to predict the current and future effects of anthropogenic climate forcing and SLR (Cohen and Lara, 2003; Ellison and Stoddart, 1991; Ellison, 1993; Field, 1995; Graus and Macintyre, 1998; Lara et al., 2002; Parkinson et al., 1994). In semi-arid environments, with calcareous karstic geology, the presence of mangroves along a stratigraphic record would indicate how sea level rise and paleoclimate changes have affected the coastal environment. In this context, the main objectives of this study is 1) to propose a palaeoenvironmental reconstruction of the Flamenco Lagoon, southeastern Puerto Rico, during the middle and late Holocene, considering the changes in sedimentary environment, vegetation, and source of sedimentary organic matter. The interpretations are based on sediment analysis, pollen records, δ^{15}N, δ^{13}C, C/N data and AMS dating. 2) Evaluate the main driving forces controlling the mangrove dynamics on the study site. Noteworthy is that multiple proxies analysis enable to assess the compatibility between the sedimentary environment and its aquatic and terrestrial plants, mainly considering the mangroves, according to SLR and climatic changes.

2. Study site

Flamenco Lagoon, located in the Guánica littoral along the southwestern coast of Puerto Rico, is a small (~300/150 m) saline water lagoon (Fig. 1b and c). The saline intrusion occurs by permeable sandy sediment and during periodic overflowing of sand barrier by equinoctial and storms tides. Water depths in the lagoon range from ~0.5 to 3 m.

2.1. Geomorphology and geology

The lagoon bottom consists of sand and mud of marine and terrigenous origin near the coastal plains skirted by limestone hills with interior central cordilleras primarily containing mixed complexes of metamorphic, intrusive and volcanic deposits of Jurassic to Miocene age (e.g. Laffoon et al., 2012). The study area presents elevation ranges from 0 to 228 m above sea level (Fig. 1b) (Murphy et al., 1995). The lagoon receives runoff from the uplands that immediately surround the lagoon following rainfall events. These rainfall events can alter the water salinity of the lagoon.

2.2. Climate

In southwestern Puerto Rico, the average rainfall is 796 mm/yr, with the lowest amount of rain in January and February and the highest rainfall in September and October (http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?pr3532). Guánica Forest is mainly represented by a subtropical dry forest (Fig. 1), which typically receives <200 mm of rain from December through March, designated as a UNESCO Man and Biosphere Reserve in 1981.

2.3. Vegetation

The 4400 ha forest occurs as upland forest with mature stands of native trees, 40–80 year-old secondary forest stands dominated by introduced legume trees, and mangrove (*R. mangle*; *Laguncularia racemosa*) forest (Murphy and Lugo, 1986; Lugo et al., 1978). Most of the forest is semi-deciduous with <5 m in height and occasional larger emergent trees in favorable microsites (Murphy and Lugo, 1986).

The dry forests tend to occur at low elevations and often on limestone (Lugo et al., 2006). Many of the dry forests found today in Puerto Rico are dominated by young small-diameter trees. Dominant families include Capparidaceae, Cactaceae, Erythroxylaceae, Zygophyllaceae, Anacardiaceae, Asteraceae, Malvaceae, Lamiaceae, and Fabaceae. Common genus include *Acacia*, *Caesalpinia*, *Cassia*, *Mimosa*, *Tabebuia*, *Capparis*, *Byrsonima*, *Lysiloma*, *Ceiba*, *Aspidosperma*, *Erythroxylon*, *Pictetia*, *Plumeria*, and *Bursera* (Huggins et al., 2007). A detailed description of the dry forest from Puerto Rico is provided in Table 1.

Tropical dry forests are particularly susceptible to invasion by non-native species owing to extensive human disturbance including land clearing and fire (Fine, 2002). These novel ecosystems (Colón et al., 2011; Lugo and Helmer, 2004; Martinuzzi et al., 2013) with a legacy of human activity are widespread in Puerto Rico. In addition, naturalized, introduced species are an important component of forests regenerating on abandoned cropland and pastures (Brandeis and Turner, 2013; Colón et al., 2011). It includes non-native *Leucaena leucocephala* (Fabaceae), *Prosopis pallida* (Fabaceae), *Tamarindus indica* (Fabaceae), which is a planted and naturalized fruit tree, *Acacia farnesiana* (Fabaceae) and *Pithecellobium dulce* (Fabaceae), which is potentially invasive leguminous trees (Franklin et al., 2015). Surrounding the study lagoon was identified Anacardiaceae, Asteraceae, *Byrsonima* (Malpiguiaceae), Cactaceae, Coccoloba (Polygonaceae), Combretaceae, Cyperaceae, Fabaceae, Malpiguiaceae, Mimosa (Fabaceae), Poaceae and Rubiaceae.

2.3.1. Mangroves

The Puerto Rico mangroves, with approximately 83 km^2 (Gould et al., 2008) are subject to a tidal range of 0.2 m (Fornshell and Spina, 2000), and are classified into two groups based on contrasting environmental settings. The northern-coast mangroves are subject to high wave energy, high precipitation, and river runoff. The southern-coast

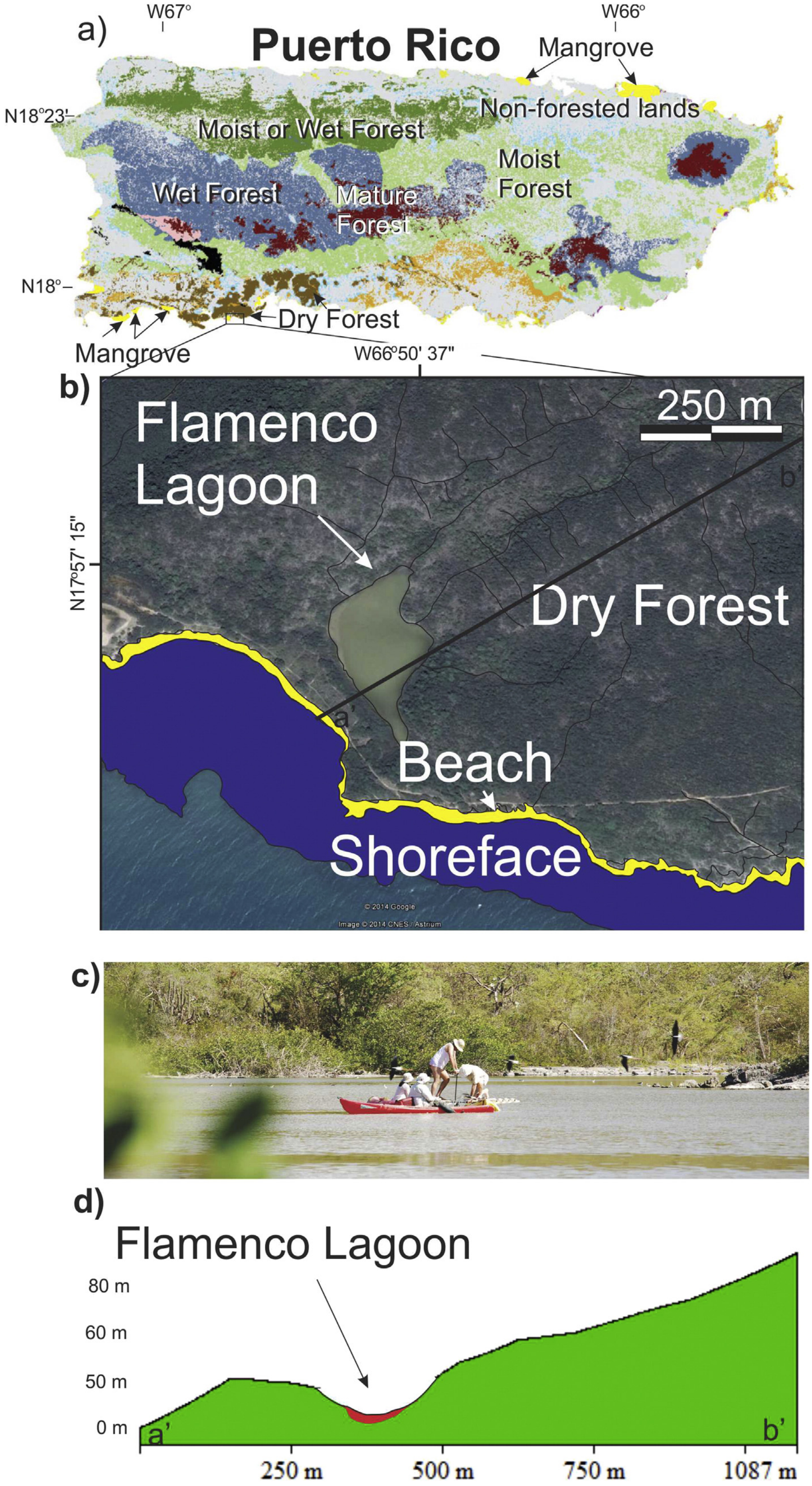

Fig. 1. a) Vegetation map of Puerto Rico (Martinuzzi et al., 2013), b) location of Flamenco Lagoon, c) photography of Flamenco Lagoon and d) topographic profile of the study site.

mangroves are subject to low wave energy regime, low precipitation and low river runoff due to the rain shadow effect of the Central Range (Daly et al., 2003). Basin and riverine mangroves predominate on the northern-coast type mangroves, while fringe mangroves predominate on the southern-coast type mangroves (Lugo and Cintrón, 1975).

Table 1
Taxa identified in Dry Forest from Puerto Rico (Murphy and Lugo, 1986; Colón and Lugo, 2006; Huggins et al., 2007; Franklin et al., 2015).

Family, genus and species	Family, genus and species	Family, genus and species
Anacardiaceae	Euphorbiaceae	Oleaceae
Comocladia dodonata	*Gymnanthes lucida*	*Forestiera segregate*
Metopium toxiferum	Fabaceae	*Linociera holdridgei*
Apocynaceae	*Acacia*	Polygonaceae
Aspidosperma	*Caesalpinia*	*Coccoloba*
Plumeria alba	*Cassia*	*Coccoloba diversifolia*
Arecaceae	*Lysiloma*	Rhamnaceae
Thrinax morrisii	*Mimosa*	*Krugiodendrom ferreum*
Asteraceae	*Pictetia aculeate*	*Reynosia guama*
Bignoniaceae	Lamiaceae	Rubiaceae
Tabebuia heterophylla	Lauraceae	*Antirhea acutata*
Boraginaceae	*Nectandra coriacea*	*Erithalis fruticosa*
Bourreria succulenta	Malvaceae	*Exostema caribaeum*
Burseraceae	*Ceiba*	*Guettarda elliptica*
Bursera simaruba	Malpighiaceae	*Guettarda krugii*
Cactaceae	*Byrsonima*	Rutaceae
Cephalocereus royenii	Meliaceae	*Amyris elemifera*
Leptocereus quadricostatus	*Swietenia mahagoni*	*Zanthoxylum flavum*
Capparidaceae	Myrtaceae	Sapindaceae
Capparis	*Eugenia foetida*	*Exothea paniculata*
Celastraceae	*Eugenia xerophytica*	*Hypelate trifoliata*
Cassine xylocarpa	*Pictetia aculeate*	*Thouinia portoricensis*
Crossopelalum rhacoma	Myrtaceae	Theophrastaceae
Combretaceae	*Eugenia foetida*	*Jacquinia berterii*
Bucida buceras	*Eugenia xerophytica*	Zygophyllaceae
Erithroxylum rotundifolium	Nyctaginaceae	
Ehretiaceae	*Guapira fragrans*	
Rochefortia acanthoplora	*Guapira obtusata*	
Erythroxylaceae	*Pisonia albida*	
Erythroxylum rotundifolium		

Agricultural activity did not occur on areas occupied by mangrove forest due to salinity. Loss of mangrove area was mainly a secondary result of agricultural activity due to drainage and changes in hydrology or excessive sedimentation. Draining was common in permanently flooded mangroves in the humid coasts, but not in the dry coast. Then, agricultural use was possible when soil salinity was reduced by rainfall and low seawater penetration (Martinuzzi et al., 2009).

3. Materials and methods

3.1. Remote sensing

The morphological aspects of the study area were characterized based on the analysis of images provided by Google Earth acquired on 03/12/2011. The topographic profile is based on the digital elevation model acquired during the Shuttle Radar Topography Mission-SRTM undertaken by the National Aeronautics and Space Administration-NASA. The software Global Mapper 9 (Global Mapper Software LLC, Olathe, KS, USA, 2009) was used to process the topographic data (Fig. 1d).

3.2. Sampling and facies description

One sediment core with 2.6 m long was sampled from Flamenco Lagoon (17°57′10.31″N, 66°50′39.30″W) in a sector with 1 m depth in southwestern coast of Puerto Rico using a Russian Sampler with the geographical position determined by GPS. Considering the water level of the Flamenco Lagoon during the sampling was equivalent to the modern sea-level, with a tidal range of 20 cm to the study area, the sampling site is 1 ± 0.1 m below the mean sea-level. Following the proposal of (Walker, 1992), facies analysis included descriptions of color, lithology, texture and structures. The sedimentary facies was codified following (Miall, 1978). The studied stratigraphic profile was divided into facies associations, which is a group of sedimentary facies used to define a particular sedimentary environment (Reading, 1996). X-ray radiographs aided the identification of internal sedimentary structures and some reworking of sediments by animals and plants that may cause age inversions by mixture of carbon of different ages along the studied core (Boulet et al., 1995; Gouveia and Pessenda, 2000).

3.3. Palynological analysis

The core was sub-sampled at intervals of 5 cm and 1 cm^3 of sediment was taken for palynological analysis. Samples were prepared using standard techniques for the extraction of palynomorphs, including acetolysis (Faegri and Iversen, 1989). Handbooks of pollen and spores morphology were consulted (Hesse et al., 2008; Roubik and Moreno, 1991) as well as the reference collections of the “Laboratory of Coastal Dynamics – UFPa”, ^{14}C Laboratory of the Center for Nuclear Energy in Agriculture (CENA/USP) and of Hermann Behling to identify pollen grains and spores.

A minimum of 300 pollen grains were counted per sample. Microfossils consisting of spores and algae were also counted, but they were not included in the sum.

The *taxa* were grouped according to source: mangrove, trees and shrubs, herbs, ferns and aquatics. The software TILIA and TILIAGRAF were used for calculation and to plot the pollen diagram (Grimm, 1987). CONISS was used for cluster analysis of pollen *taxa*, permitting the zonation of the pollen diagram. CONISS is a program for stratigraphically constrained cluster analysis by incremental sum of squares. It has been used widely for unconstrained analyses and has proved particularly satisfactory for pollen frequency data (Grimm, 1987).

Noteworthy is the fact of the composition of a fossil pollen flora in sediments depends on several different factors, such as the composition of the vegetation from which the pollen originates, pollen production of the individual plant species, pollen dispersion, sedimentation and preservation. Considering the low pollen preservation in sediments, it may be caused by various external factors (sediment grain size, microbial attack, oxidation and mechanical forces), as well as factors inherent to the pollen grains themselves (sporopollenine content, chemical and physical composition of the pollen wall) (Havinga, 1967). However, anaerobic conditions (low Eh value) in the fine-grained sediment of mangroves provide a suitable environment for pollen to be preserved (Bryant et al., 1994; Ellison, 2008; Grindrod, 1988; Tschudy, 1969). Sediment with high salinity and low Eh and pH values seems to be ideal for pollen preservation (Bryant et al., 1994; Campbell and Campbell, 1994; Dimbleby, 1957; Phuphumirat et al., 2009), but in other substrates, including unweathered rock platforms, coral rubble, and sandy sediments also occupied by mangroves are not suitable for pollen preservation (Grindrod, 1988). For instance, pollen tend to rapidly decay in sandy sediment because a better drainage in sand caused by large interstitial pores allows pollen grains to be abraded by a mobile inorganic matrix as well as to be oxidized during soil hydration-dehydration cycles (Faegri, 1971; Grindrod, 1988).

According to Phuphumirat et al. (2015) experiments developed in mangrove sediments from Thailand indicated that pollen deterioration must also be considered as a crucial taphonomic factor distorting the original pollen signal in mangrove sediments. Based on this study, spores and pollen deteriorated more slowly in mangrove sediments, compared with those in other tropical environments, due to anaerobic and hypersaline conditions. However, decreasing numbers of palynomorphs were registered even after a short interval of burial. Alkaline condition, a low salinity, and a longer period of subaerial exposure is responsible for rapid palynomorph deterioration, while high content of organic matter, fine sediments, and depletion of oxygen, increase the fossilization potential. >90% and extraordinarily high concentrations of pollen from *Rhizophora apiculata* recovered from the R. community tend to be indicative of *Rhizophora*-dominated forest due to a good preservation of their pollen in the parent plant community. Quantitative compositional of *Avicennia* pollen seemed to be lessened by progressive pollen degradation and poor pollen preservation. Then, the reduction in their pollen numbers within a sediment core might not necessarily reflect changes in vegetation or environmental conditions through time, but rather the poor fossilization potential of these pollen species.

Considering the studied core, sampled along different sedimentary environments and vegetation, it presents changes in sedimentation rates and in relationship between sand/mud sediments. Then, probably, the pollen concentrations were affected by pollen oxidation mainly in sandy intervals. Hence, the pollen analysis was based on pollen percentage, since it is more appropriate to attenuate the effects this pollen deterioration associated to sandy sediments.

The intervals 5–25 cm, 75–85 cm and 250–255 cm present eight samples with pollen concentrations lower than 10,000 g/cm^3, and two samples exhibit absolute absence of pollen grains (Fig. 2). Probably, the low pollen concentration, along these intervals, has been caused by low pollen preservation by pollen oxidation. These levels were considered in CONISS analysis, but the levels with absolute absence of pollen grains have been removed and these levels are not considered by the cluster analysis. Stratigraphic levels with intense pollen oxidation may cause a differentiated preservation for each pollen type, consequently distorting the original pollen signal (Phuphumirat et al., 2015). Obviously, it may cause a misinterpretation of the palaeovegetation, and then these zones were excluded from the diagram.

3.4. C/N, carbon and nitrogen isotopes

The δ^{13}C, δ^{15}N and elemental C and N (C/N) concentrations were analyzed from samples (6–50 mg) taken at 5 cm intervals along the core. The stable carbon and nitrogen isotopes as well as the total organic carbon (TOC) and nitrogen (TN) were determined at the Center for Tropical Marine Ecology – Bremen University, using a Continuous Flow Isotopic Ratio Mass Spectrometer (CF-IRMS). Further details may be found in Lara et al. (2010).

3.5. Radiocarbon dating

Four bulk samples of ~2 g each were used for radiocarbon dating (Table 2). Samples were checked and physically cleaned under the microscope to avoid natural contamination (Goh, 1978). The organic matter was chemically treated to remove the eventual presence of a younger organic fraction (fulvic and/or humic acids) and carbonates. This process consisted of extracting residual material with 2% HCl at 60 °C over 4 h, washed with distilled water until pH was neutral and dried (50 °C). The sediment organic matter was analyzed by Accelerator Mass Spectrometry (AMS) at the Leibniz Laboratory of Isotopic Research at Christian-Albrechts University in Kiel (Germany). Radiocarbon ages are reported in years before 1950 CE (yr BP) normalized to δ^{13}C of $-25‰$ VPDB and in cal yr BP with a precision of 2σ (Reimer et al., 2009).

4. Results and discussion

4.1. Radiocarbon date and sedimentation rates

Radiocarbon dating at depths of 260, 236, 174 and 122 cm produced ages of ~5660 cal yr BP, ~5370 cal yr BP and ~4480 cal yr BP and ~3650 cal yr BP, respectively, and no age inversions were observed (Table 2). Based on the ratio between the depth intervals (mm) and the mean time range, the sedimentation rates are about 0.8 mm/yr (260–236 cm), 0.7 mm/yr (236–174 cm), 0.6 mm/yr (174–122 cm) and 0.3 mm/yr (122–0 cm) (Fig. 2). The recorded sedimentation rates are within the vertical accretion range from 0.1 to 10 mm yr^{-1} of mangrove forests reported by other authors (Alizadeh et al., 2015; Bird and Barson, 1977; Buso Junior, 2013; Cohen et al., 2014, 2015; França et al., 2012, 2013, 2015; Guimarães et al., 2012, 2013; Smith et al., 2011; Xia et al., 2015) (Table 3). In addition, the recorded rates are not discrepant and show an upward decreasing trend. Similar trend has been found along many other deposits accumulated during the Holocene (Cohen et al., 2014; França et al., 2013, 2015).

4.2. Facies association descriptions

The sediment core consists mostly of lenticular heterolithic beddings (Hl), wavy heterolithic beddings (Hw), massive mud (Mm) and massive sandy (Sm) sediments with some levels presenting fining upward successions (Fig. 2). Pollen and spore records, δ^{13}C, δ^{15}N, Total Organic Carbon (TOC), Total Nitrogen (TN) and C/N values were added to facies characteristics in order to define three facies association: Channel, tidal flat with mangrove, and lagoon.

The highest pollen concentrations were obtained along the facies association tidal flat with mangrove (20–60,000 g/cm^3), while the channel and lagoon presented the lowest values (12–30,000 g/cm^3) (Fig. 2). It is noteworthy that some depositional environments such as lakes, tidal flats and fluvial floodplains provide suitable conditions for muddy accumulation and preservation of pollen grains sourced from vegetation living at the time that the sediment was deposited. Lacustrine sediments preserve pollen carried by wind and from vegetation surrounding the lake. The spatial representation of the lacustrine pollen signal depends on wind strengths and the extent of the drainage system feeding the lake. The proportion of the pollen signal provided by each vegetation type is distance-weighted (Davis, 2000; Xu et al., 2012), with closer sources usually being greater.

In addition, several other interacting factors determine the degree to which the pollen assemblages reflect each plant community. The most

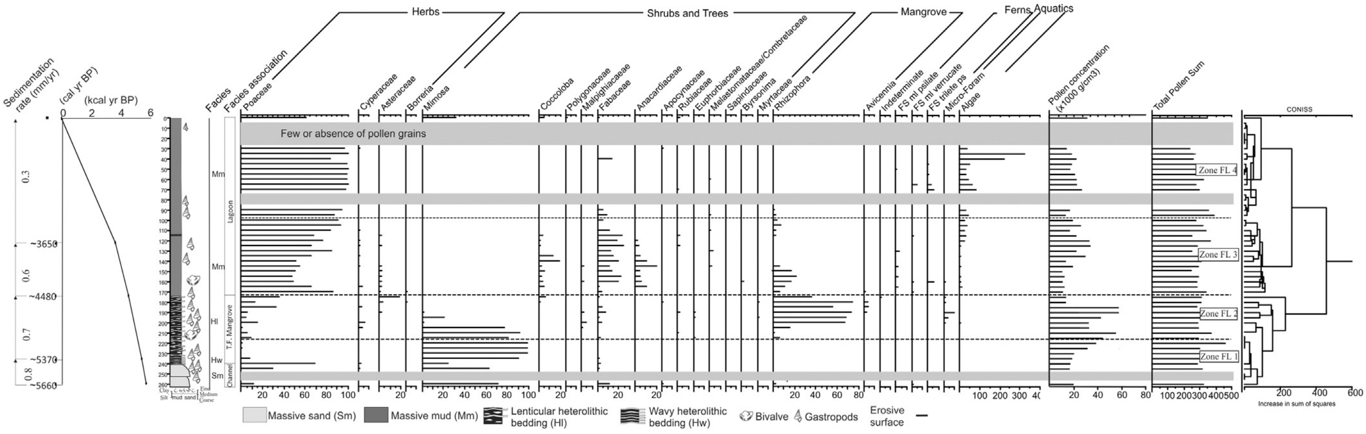

Fig. 2. Chronological profile with sedimentary facies and pollen diagram with zones based on cluster analysis.

Table 2
AMS ^{14}C dating of samples derived from sedimentary deposits.

Lab. Number	Depth (cm)	Dated material	Ages (14C yr BP, 1σ)	Ages (cal yr BP, 2σ)	Mean (cal yr BP, 2σ)
KIA42440	122	Sed. org. matter	3415 ± 30	3724–3580	~3650
KIA42441	174	Sed. org. matter	4022 ± 30	4537–4422	~4480
KIA42442	236	Sed. org. matter	4704 ± 31	5420–5322	~5370
KIA42443	260	Sed. org. matter	4884 ± 55	5739–5578	~5660

important are pollen productivity and dispersal characteristics of the species, the local-scale patterns of the species distribution at each community, and the representation of local and extra-local pollen rain. Considering the mangroves and associated vegetation, the plant parameters play important roles in pollen abundance. For example, plant cover may have the greatest significance for pollen percentages, while plant percentage may have greater impact on pollen abundance. In some cases, the type of flower pollination has less significant effect on pollen representation than the plant frequency. On the other hand, environment effects such as deposition conditions, hydrodynamics, and water table depth also influence the pollen representation (Li et al., 2008).

Mangrove pollen taxa have prevailed over pollen from other taxa in intertidal zones occupied by mangroves. In general, the pollen rain has maximum value of mangrove pollen in the low intertidal zone. In contrast, samples from high intertidal zone, where the back-mangrove types grow well and amounts of pollen from the terrestrial plants are easily transported by wind and deposited in the sediments, are characterized by the lowest mangrove percentages and the highest non-mangrove arboreal pollen (Li et al., 2008).

A study about the pollen rain in the northern Brazilian littoral indicated highest percentage values of *Rhizophora* pollen grains in the mixed *Rhizophora*/*Avicennia* and on the *Rhizophora* dominated forest area (90–100%). Markedly lower are the *Rhizophora* percentages from the *Avicennia* dominated forest area (60–85%), the herbaceous flat area (35–40%) and the restinga area (15–25%). Percentages of *Avicennia* pollen are high in the *Avicennia* dominated forest area (15–35%), and low in the mixed *Rhizophora*/*Avicennia* area (2–5%). Pollen traps of the other three sites show in average <1%. Traps from the herbaceous flat site are dominated by Cyperaceae pollen (55–60%) (Behling et al., 2001).

Open vegetation is likely to have a higher proportion of long distance transport pollen rain, but under a relatively closed canopy the pollen rain should indicate local deposition (Gosling et al., 2009). Then, the pollen grains preserved in sediments of lower intertidal zone occupied by mangroves must represent a smaller vegetation area than pollen assemblages accumulated on a lake. For this reason, we consider the pollen studies combined with the facies analysis highly relevant to assess the meaning of pollen signal along a stratigraphic profile.

In addition, the multiple proxies analysis allows to discuss, in an integrated way, the evolution of the depositional environment and changes in the source of sedimentary organic matter and in the dominant vegetation according to climate and sea level changes. Obviously, a certain deficiency of temporal synchrony between the physical, biological and biogeochemical indicators along the studied sediment core may occur, because mangroves are able to resist to all types of adverse physical and chemical conditions (Alongi, 2015; Kathiresan, 2011).

Table 3
Sedimentation rates for mangrove vegetation.

Authors	Sed. rates (mm/yr)
França et al. (2015)	0.5–7.7
Alizadeh et al. (2015)	0.3–2.4
Cohen et al. (2015)	0.1–0.7
Xia et al. (2015)	3.2–3.7
França et al (2014)	0.1–10
Cohen et al. (2014)	0.5–9.4
Buso Junior et al (2013)	0.03–5
Guimarães et al. (2013)	0.07–0.08
França et al. (2013)	0.2–16
França et al. (2012)	0.1–10
Guimarães et al. (2012)	0.22–3
Smith et al. (2011)	0.03–0.47
Bird and Barson (1977)	1–8

4.3. Facies association A (channel)

This facies association occurs in the lowest part of the stratigraphic sequence from ~5660 cal yr BP until ~5400 cal yr BP (Fig. 2). The sediment is composed mostly of greenish gray or dark brown massive sand (Sm) with fining upward successions. This deposit is typically bounded at the base by a sharp erosional surface. These characteristics are typical of a channel deposition (Rossetti et al., 2007). Considering the size of these sandy layers (15 cm), probably these sediments were accumulated by small channels. Besides these structures, this facies association presents many gastropods. The pollen assemblages of this facies association correspond partly to Zone FL 1 (Fig. 2). This zone is characterized by the predominance of shrubs and herbs pollen mainly constituted by *Mimosa* (60–70%) and Poaceae (10–30%).

Total organic carbon (TOC) oscillated between 3 and 15%, while total nitrogen (TN) oscillated between 0.4 and 1.1%. The sediment $\delta^{13}C$ values ranges between −23 and −19‰ (mean = −21‰) and the C/N values increase from 29 to 43 indicating an increased trend in organic matter sourced from C_3 to C_4 plants (Deines, 1980). The $\delta^{15}N$ presents values between 5.5 and 6‰. It may suggest an aquatic and terrestrial organic matter (Meyers, 1997; Thornton and McManus, 1994). According to Montes et al. (2013) high $\delta^{15}N$ values (>4.5‰) detected in sediments deposited in the Cariaco Basin-Venezuela could be indicative of higher inputs of terrigenous organic matter that result from more direct riverine discharge into the basin.

4.4. Facies association B (tidal flat with mangrove)

This facies association occurs between ~5400 and ~4400 cal yr BP. These deposits present lenticular heterolithic bedding (Hl) and wavy heterolithic bedding (Hw) and many gastropods and bivalves shells. Heterolithic beddings are sedimentary structures made up of interbedded deposits of sand and mud. Heterolithic bedding forms in response to alternations in sediment supply and tidal velocity. Depending on these factors some differences in beddings may be found, such as (1) wavy bedding that occurs when mud and sand deposits are equal. (2) Lenticular bedding occurs when sand ripples are deposited in mud in an isolated distribution pattern. Ripples in lenticular bedding are both laterally and horizontally discontinuous. In addition, lenticular and wavy heterolithic beddings indicate a vertical accretion following a alternation of energy flow with predominance of mud deposition from suspension and periodic sand inflows (Reineck and Singh, 1980). The pollen assemblages correspond to part of the Zone FL1 and Zone FL2 (Fig. 2). The Zone FL1 presents in this facies association *Mimosa* (90–100%) and Poaceae pollen (0–10%). The Zone FL2 is characterized by the predominance of mangrove (10–80%) pollen, represented by *Rhizophora* (2–75%) and *Avicennia* (0–5%). The herbaceous (10–90%) pollen are represented by Poaceae (1–85%), Asteraceae (0–20%) and Cyperaceae (0–6%). Some micro foraminifera have also been recorded.

Although the *Laguncularia* trees are present in mangroves from Puerto Rico, along the studied core was not possible record this genus.

Probably, pollen grains of *Laguncularia* are present at least along the stratigraphic intervals where *Rhizophora* and *Avicennia* pollen grains have been found. However, some pollen grains with morphological characteristics that could be associated with *Laguncularia* do not present suitable position to ensure that it is a *Laguncularia* pollen. The *Laguncularia* pollen presents morphological characteristics shared by *Rhizophora* pollen. Determining whether a grain belongs to *Rhizophora* or *Laguncularia* in fossil material are problematic since these pollen grains are quite similar in polar view. In such cases, a distinction may be made on exine thickness, exine pattern and endoapertural details. *Rhizophora* tends to have a slightly thicker exine and is more densely pitted than *Laguncularia*. In badly corroded grains these criteria may not be applicable and identification impossible (Bertrand, 2009).

Total organic carbon (TOC) and total nitrogen (TN) present a strong increase at the beginning of this facies association with 65% and 1.7%, respectively, but they show an decreasing trend to the top (24% and 0.9%). The sediment $\delta^{13}C$ values decrease from −19% to −23‰ and the C/N values range between 33 and 57 indicate organic matter from C_3 plants (−32‰ to −21‰; Deines, 1980). The $\delta^{15}N$ values decrease from 6 to 2.5‰. The decrease in $\delta^{15}N$ indicates nitrogen biological fixation, which is the mechanism that brings the $\delta^{15}N$ levels close to the atmospheric values that is around 0‰ (Meyers, 1997; Thornton and McManus, 1994). Changes in the sedimentary $\delta^{15}N$ over the last 580 kyr in the Cariaco Basin-Venezuela indicate that $\delta^{15}N$ was 5‰ during sea level low-stand and 2‰ during sea level high-stands periods. Probably, the $\delta^{15}N$ signal preserved in the basin reflects changes in water column denitrification. Then, the low $\delta^{15}N$ (2‰) during sea level high-stands indicates an increase in N_2 fixation rates as a result of the removal of nitrate by denitrification (Meckler et al., 2007), and intense denitrification occurs in mangrove sediments due to its reducing sediments (Fernandes et al., 2012).

4.5. Facies association C (lagoon)

This facies association has accumulated massive mud (Mm) with some gastropods during the past ~4400 cal yr BP. The pollen assemblages of association C correspond to Zone FL 3 and FL 4. These zones are characterized by the predominance of herbs (55–100%) pollen, mainly represented by represented by Poaceae (1–85%), Asteraceae (0–3%) and Cyperaceae (0–2%). In the Zone FL 3 the scrubs and trees (0–35%) pollen mainly exhibit Fabaceae (5–25%), *Anacardium* (0–20%) and *Coccoloba* (0–20%). The mangrove (0–20%) pollen are represented only by *Rhizophora* (0–20%) in the lowest part of this zone. Regarding the Zone FL 4, besides the herbaceous (60–100%) pollen, some *Mimosa* (0–30%), Fabaceae (0–15%), *Coccoloba* (0–5%) and Poligonaceae (0–2%) pollen occur. Algae and ferns are recorded only along the lagoon stage.

The $\delta^{13}C$ values exhibit an enrichment trend from −26 to −17‰ (mean = −21‰) along the Zone FL 3. The $\delta^{15}N$ values oscillate between 2.5 and 3.2‰ (mean = 2.8‰). Total organic carbon and total nitrogen along this facies association show lower values than tidal flat with mangrove, oscillating mainly between 5% and 38%, and 0.5% and 1.3%, respectively. Noteworthy is the fact of TOC and TN present an increasing trend in the surface from 40 cm (4% and 0.5%) to 0 cm (21% and 2.3%). The C/N values showed considerable variation between 21 and 35 (mean = 28) along this facies association. These data suggest sedimentary organic matter sourced from terrestrial C_3 plants with influence of terrestrial C_4 plants and aquatic organic matter, as indicated by the binary diagram between the $\delta^{13}C$ and C/N rate (Fig. 4). The Zone FL 4 presents an enrichment trend to $\delta^{13}C$ values from −25‰ to −21‰, and the $\delta^{15}N$ values (2.8–5.0‰, mean = 4.2‰) increased relative to the Zone FL 3. The C/N values present a significant decrease from 40 to 12. The binary diagram of $\delta^{13}C$ vs. C/N ratio reveals an increase in contribution of marine organic matter to the top of this sedimentary sequence (Figs. 3 and 4). The increasing trend of $\delta^{15}N$ values to the top may be explained also by marine primary production, which is based on nitrate (NO_3^-) supply. The $\delta^{15}N$ values of phytoplankton in marine regions reflect main two factors: the $\delta^{15}N$ value of NO_3^- supplied to the euphotic zone, and the degree of NO_3^- uptake by phytoplankton. Under such conditions, the biomass of phytoplankton will have a $\delta^{15}N$ similar to that of the nitrogen substrate: $\delta^{15}N \approx +5‰$ from dissolved NO_3^- versus $\delta^{15}N = +1$ for N_2. Then, most marine phytoplankton presents a $\delta^{15}N$ more like +5‰ (Emerson and Hedges, 2008).

4.6. Palaeoenvironmental interpretation

The data suggest three main stages to the Flamenco Lagoon development (Fig. 5): (1) before ~5400 cal yr BP, small channels drainage were active, and it accumulated muddy and sandy sediments with many gastropods reworked. Trees, shrubs and herbs were present. Mangroves were not close enough to disperse their pollen grains and preserve it in these sediments (Fig. 5). (2) The next stage is characterized by the establishment of a bay with tidal flats. This environment accumulated many gastropods and bivalves shells, and the mangrove expanded according to the sea-level rise between ~5400 and ~4400 cal yr BP. The presence of micro foraminifera reveals a marine influence during this time, since the majority live on or within the seafloor sediment (i.e., are benthic) while a smaller variety are floaters in the water column at various depths (i.e., are planktonic) (Giere, 2008). In addition, the geochemical data showed strong influence of terrestrial C3 plants. Likely, the significant increase in TOC and TN in sediments of the tidal flat with mangrove is associated to high productivity and capacity of the mangroves to store organic matter in its sediments (Giri et al., 2011). Donato et al. (2011) and Kauffman et al. (2011) demonstrated that carbon storage in mangroves is about 4 times higher than in terrestrial forests. (3) During the past 4400 cal yr BP, the stratigraphic records evidence the formation of an endorheic minibasin closed and a lagoon was established with accumulation of muddy sediments, few shells and the shrinkage and disappearance of mangroves. During this stage, the influence of arboreal, herbaceous vegetation and ferns increase in the pollen diagram, as well as the presence of algae recorded only during the lagoon stage.

The presence of ferns during the lagoon stage may be related to the capacity of ferns often fill in gaps caused by tree death in a mangrove forest (Hogarth, 1999). Acrostichum is one of the few understory plants in the mangrove forest (Janzen, 2009). However, it tends to be limited to the less saline areas of a mangrove site (Lugo, 1986). In some disturbed mangrove forests, Acrostichum is considered a weed that may impede the natural regeneration of mangrove tree species (Srivastava et al., 1987). Studies about the mortality of mangrove forest during the last decades in Puerto Rico revealed the salinities in excess as the cause for the loss of mangrove areas. In addition, the fern characteristics were sensitive indicators of stress, and individuals of *Acrostichum danaeifolium*, under adverse conditions of hypersalinity, were able to maintain the total number of leaves plant and leaf production rates (Sharpe, 2009).

Considering this upward increase of algae in the studied core, the density of microalgae increase with decrease in distance from the low tide line (Essien and Ubom, 2003), and some studies have highlighted the importance of monotypic stands formed by the alga in tidal flats directly and indirectly influencing the abundances of other algae and invertebrates (Bishop et al., 2009).

The binary diagram between the $\delta^{13}C$ and C/N rate (Fig. 4) confirms this palaeoenvironment, as they recorded terrestrial C_3 plants with influence of terrestrial C_4 plants and marine algae (Fig. 4). The enrichment trend of $\delta^{13}C$ values from −25 to −21‰ and decreasing trend of C/N from 35 to 11 between 80 and 0 cm (Figs. 3 and 4) indicates that during the late Holocene occurred an increase in contribution of organic matter sourced of salinity tolerant phytoplankton, which characterizes the current conditions of the Flamenco Lagoon.

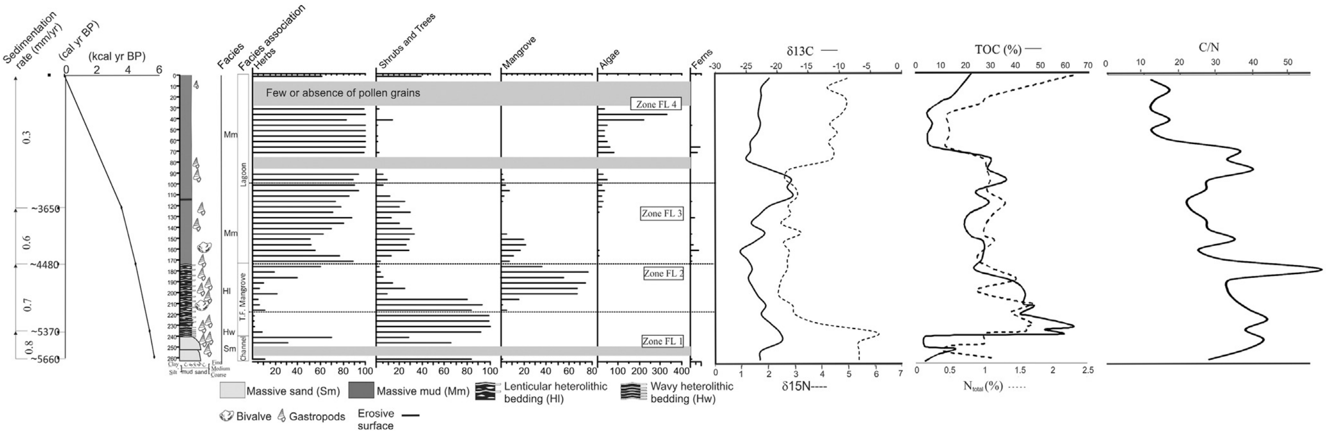

Fig. 3. Chronological profile with ecological groups and organic geochemical variables.

Noteworthy is the dominance of *Mimosa* on newly formed tidal flat (stage 1) and then mangrove expansion (stage 2). Subsequently, the mangrove shrank, while the herbaceous plain, mainly characterized by Poaceae, expanded (stage 3). This vegetation succession (Berger et al., 2006) must represent the migration of zones with mangroves and associated vegetation according to sea-level rise. Paleoecology studies in mangroves of the Cispata lagoon system (Colombian Caribbean) indicated a colonization of herbaceous pioneer vegetation started between 1142 and 1331 CE and mangrove colonization only took place since 1717 CE (Castaño et al., 2010).

The spatial patterns of mangroves and associated vegetation are controlled by interaction of important key factors that cause a species zonation (Jiménez and Sauter, 1991; McKee, 1993; Raffaelli and Hawkins, 1999; Snedaker, 1982). This vegetation zone arises from the succession, and they have been frequently discussed (Berger et al., 2006; Fromard et al., 1998).

Important factors controlling this vegetation zone may be highlighted, such as local competition for photosynthetic light in the canopy (Clarke and Allaway, 1993; Khan et al., 2004), vegetation composition (Kairo et al., 2002), dispersal patterns (Clarke, 1993), the competitive ability of species (Berger and Hildenbrandt, 2000), microtopography (Di Nitto et al., 2008), tidal inundation frequency (Clarke and Myerscough, 1993; Cohen and Lara, 2003), sediment chemistry (Da Cruz et al., 2013; Mendoza et al., 2011) and porewater salinity (Krauss et al., 2008; Lara and Cohen, 2006).

In the study site, probably, the Holocene sea-level rise is mainly affecting the microtopography, tidal inundation frequency, sediment chemistry and porewater salinity. Most of these issues are discussed below.

4.7. SLR and sediment accretion

The stratigraphic sequence studied is compatible with the trends of SLR during the Holocene to the Caribbean region (Gischler, 2015; Rull et al., 1999; Toscano and Macintyre, 2003). Considering the water depth of 1 m in the sampling site, the position of the sedimentary deposits, which represent the small drainage channels (creeks), are positioned between 3.6 and 3.2 m below the current mean sea level. These sediments were accumulated between ~5660 and ~5400 cal yr BP. During this time interval, the sea level was between 5 and 3.8 m below the present mean sea level (Toscano and Macintyre, 2003). Consequently, a significant portion of the continental shelf was exposed, placing the coastline distant of the current position (Fig. 5). In this period, the sedimentation in the studied sector was controlled by the drainage channel dynamics with arboreal and herbaceous vegetation colonizing the margin of this channel. The upward succession, between ~5400 and 4400 cal yr BP, composed of the transition from the drainage channel into the tidal flat colonized by mangroves suggests an increase in marine influence and forms a transgressive event. The SLR caused a marine incursion with invasion of channels valleys. It favored the sedimentation into the channels and their progressive filling up that produced a tidal flat occupied by mangroves (Fig. 5). The Caribbean sea level during this interval was between 4 and 2 m below the current one (Toscano and Macintyre, 2003), and those deposits were accumulated between

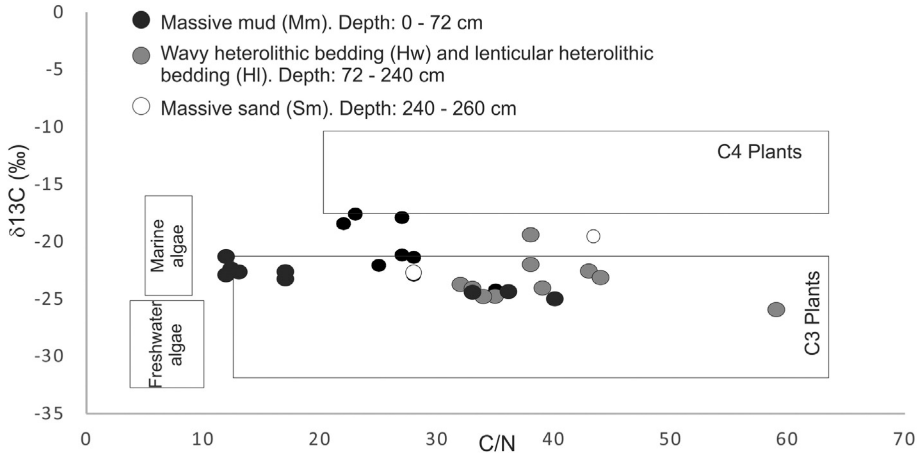

Fig. 4. Diagram illustrating the relation between $\delta^{13}C$ and C/N ratio for the different sedimentary facies, with interpretation according to data presented by Lamb et al. (2006) and Meyers (2003).

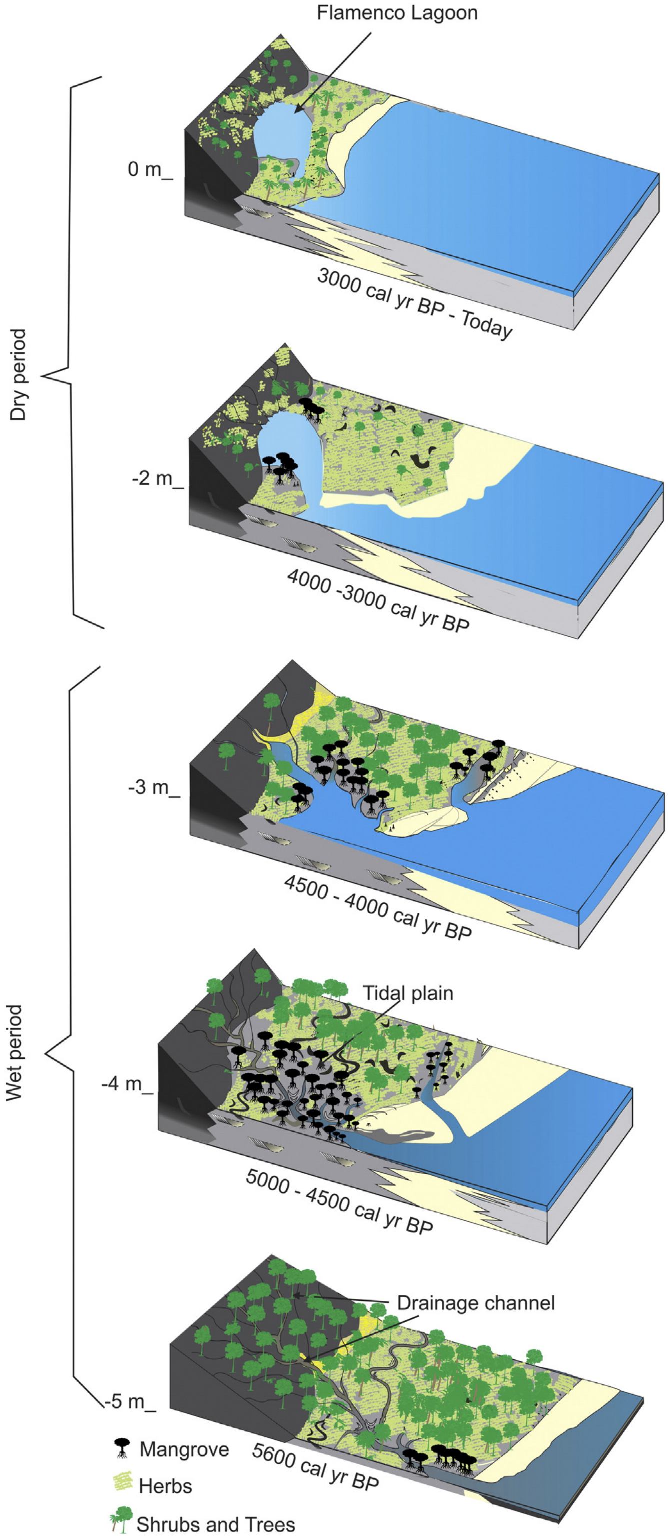

Fig. 5. Model of the geomorphology and vegetation development according to climatic and sea level changes during the middle and late Holocene.

3.1 and 2.6 m below the current mean sea level, then, under influence of the intertidal zone of the time interval of ~5400 and 4400 cal yr BP. During this time, the marine influence may be evidenced by mangrove pollen and the sedimentary structures formed by the action of tidal currents (Reineck and Singh, 1980). However, the sedimentary organic matter is mainly affected by the terrestrial C3 plants. Likely, this was caused by an elevated rainfall during that time (Fig. 5).

Between ~4400 and ~3000 cal yr BP, the sediments from the lagoon system were deposited between 2.6 and 2.0 m below the current mean sea level, when the old sea level to that time was between 3 and 1 m below the current sea level. During this stage, the arboreal and herbaceous vegetation expanded, whereas the mangroves shrank and disappeared from the study site. The sedimentary organic matter was influenced by terrestrial C_3 and C_4 plants, as well as marine organic matter.

During the past ~3000 cal yr BP, the sea level reached the current sea level (Toscano and Macintyre, 2003), and the studied lagoon accumulated sediments with predominantly marine organic matter. Today, herbaceous and arboreal vegetation is observed around the lagoon as recorded along this stage in pollen diagram (Figs. 2 and 3).

Therefore, the recorded succession of facies association A, B and C indicates significant changes in the coastal morphology under a marine transgression due to the SLR during the Holocene. The facies association A presents sedimentation rate (0.8 mm/yr) higher than the B (0.7 mm/yr) and C facies association (0.6–0.3 mm/yr) over the past ~5660 cal yr BP (Fig. 2). During the early Holocene in the Florida Keys, Belize, and the wider Caribbean, the relative sea level rose about 5.2 mm/yr, whereas in the middle and late Holocene the rates of SLR decreased to 1.47 mm/yr and 0.93 mm/yr, respectively (Toscano and Macintyre, 2003). At first, these data suggest a relation of cause and effect between the rates of SLR and sediment accretion, when more space was created to accommodate new sediments during the early Holocene than late Holocene. However, as discussed below, other factors may be affecting the sedimentation rates and consequently the mangrove dynamics in the studied area.

4.8. Mangrove and SLR

Generally, the mangroves migrate to higher topography following the topographic gradient according to SLR trend (Cohen and Lara, 2003; Cohen et al., 2015). Regarding the zone near the Flamenco Lagoon, the shoreface (submersed zone below the low tide level, but that is shallow enough to be agitated by everyday wave action) and the current intertidal zone (Fig. 1b), a significant soft topographic surface has been suitable to mangrove development according to the Holocene SLR. However, in the study site, an establishment, expansion and contraction of mangroves occurred, with the disappearance of this vegetation in the late Holocene.

The exact response of mangrove shorelines to SLR depends on the balance between sedimentation and sea level change (Woodroffe, 1995). Palaeoenvironmental studies in Belize indicate mangrove colonization about 8000 cal yr BP, with a significant decrease in the peat accumulation rate from ~6000 to 1000 cal. yrs BP (Monacci et al., 2009). During the early Holocene, the rise in sea level in the nearby coasts of Guyana caused the replacement of savannah by mangrove vegetation (Van der Hammen, 1988). Mangrove in Venezuela was established at about ~7800 cal yr BP (Rull et al., 1999). Since then, a relative SLR of about 1.3 mm/yr has been the most important natural disturbance suffered by the mangrove community (Vilarrúbia and Rull, 2002).

Holocene stratigraphic records from Bermuda show that mangroves maintain the same pace as SLR at rates up to 0.9 mm/yr (Ellison and Stoddart, 1991). Stratigraphy indicates that before 4000 yr BP sea level rose at a rate of 2.5 mm/yr; from 4000 to 1000 years BP the rate of SLR declined to 0.6 mm/yr during which time mangroves established, and in the last 1000 years there was an increase to 1.4 mm/yr, during which time the mangroves died back. The largest mangrove area in Bermuda has for the last 2000 years been building peat at a rate of 0.8 to 1.1 mm/yr (Ellison, 1993). In Laguna Grande, northeastern Puerto Rico, stratigraphic records indicate that its basin began accumulating sediment ~3600 cal yr BP, and the sedimentation began in Mangrove Lagoon ~3300 cal yr BP coincident with regional SLR (Lane et al., 2013). Regarding the stratigraphic sequence to Flamenco Lagoon, in southwestern Puerto Rico, the mangrove vegetation occurred only between ~5000 and ~4000 cal yr BP, when the sedimentation rates were about 0.7–0.6 mm/yr, and the sea level rose about 1.5 mm/yr (Toscano and Macintyre, 2003), more than double of the local sedimentation rate. After this period, the mangroves disappeared from the study site, when the sedimentation rates decreased to 0.3 mm/yr and the sea level rose 0.93 mm/yr.

The significant lower sedimentation rate than SLR may have caused the drowning of mangroves. However, the low sedimentation rates recorded along the studied core, mainly during the last 3600 cal yr BP, is consequence of erosive events due to the SLR. Mostly when mangroves are not occupying the littoral, the erosive effects of the SLR are more severe and it may have intensified the marine transgression (Temmerman et al., 2013). During mangrove development, physical and biological settings promote the increase of sedimentation rate (Furukawa and Wolanski, 1996; McKee et al., 2007). Then, low sedimentation rates along a stratigraphic sequence may be also interpreted as an effect of the loss of mangrove area.

Changes in nutrient and/or sediment supply to coastal zone related to the natural wetland dynamics may have caused the loss of mangrove area in the study site. These variables are controlled by oceanographic and meteorological factors that compose an integrated system that cannot be analyzed in isolation. Therefore, such variables will be presented in an integrated approach to propose possible causes to mangrove disappearance along the studied littoral during the late Holocene.

4.9. Mangrove and nutrient/sediment supply

Caribbean mangrove forests are often underlain by deep peat deposits formed by the gradual accumulation of organic matter (Macintyre et al., 2004; Mckee and Faulkner, 2000; Middleton and McKee, 2001; Parkinson et al., 1994; Toscano and Macintyre, 2003). These mangrove forests are different from those receiving mineral sediment, such as the mangroves near the mouth of the Amazon River (e.g. Cohen et al., 2012).

Generally, mangroves from Caribbean region have adjusted to changing sea level mainly through subsurface accumulation of refractory mangrove roots. Without root and other organic inputs, submergence of these tidal forests is inevitable due to peat decomposition, physical compaction and eustatic SLR (McKee et al., 2007).

Some works described the contribution of mangrove roots to peat formation and soil accretion (Krauss et al., 2014; Lovelock et al., 2015; Mckee and Faulkner, 2000; McKee et al., 2007; Parkinson et al., 1994). The indirect effects of plants on sedimentation in mangrove have also been demonstrated (Furukawa and Wolanski, 1996; Krauss et al., 2003; Morris et al., 2002; Spenceley, 1977), through the physical effects of vegetation on the trapping of mineral sediments. Then, likely, the decrease of sediment and organic matter accumulation influenced on the mangrove development, as well as the loss of mangrove areas also affected the sedimentation rates, and consequently the marine transgression.

The term “transgression” describes an advance of the sea over the land. Regarding a littoral occupied by mangroves, the transgression occurs when nutrient and/or sediment flux delivered to the shoreline results in sediment and/or organic matter vertical accretion lower than the amount of space added by relative SLR. In this case, the equilibrium profile between the relative sea level and surface of the substrate is moved landward, because mangroves were not able to accumulate sediment and/or organic matter to keep pace with the relative SLR. However, in a situation of sufficient nutrient and/or sediment is entering into the coastal system for that mangroves accumulate sediment and/or organic matter so as to equalize or overwhelm the amount of space available, the shoreline remains stable or a marine regression occurs, respectively. It means the mangroves are producing sufficient accretion rates to keep pace with or exceed the relative sea level. This situation can occur during stillstands or rises of relative sea level (which is a function of sea surface movement, i.e., eustasy and sea floor movement, the latter due to tectonics, thermal cooling, loading by sediments or by water, and sediment compaction (Posamentier and Morris, 2000). Therefore, since this littoral presented suitable river runoff to support sediment/nutrient input to the coast and, consequently, sufficient sediment and/or organic matter accretion compared to the relative SLR, the mangroves could keep their position.

4.10. Mangrove and climatic changes

Considering that absence of mangroves in the study site was caused by a decrease in nutrient and/or sediment input to coast area during the late Holocene, a relatively lower rainfall rates in the Puerto Rico during that time may have triggered or contributed to the process that caused the loss of mangrove area. Reconstruction of climate change over the past 10,500 years based on $^{18}O/^{16}O$ ratios in ostracod shells from Lake Miragoane, Haiti, indicates that water level in the lake rose at the end of the last deglaciation (~10–7 kyr BP), reflecting the wetter conditions of the early Holocene which persisted for nearly 4000 years. Lake level declined at ~3.2 kyr BP with the onset of a drier climate, which generally prevailed throughout the late Holocene (Hodell et al., 1991). These results were corroborated by a vegetation reconstruction from the same lake, which identified the middle Holocene as a period characterized by a greater relative abundance of moist forest taxa. Climatic drying began ~3200 14C yr BP (Higuera-Gundy et al., 1999). Records of stalagmite from Barbados indicate increased rainfall intensity between 6.7 and 3 ka BP (Mangini et al., 2007). Banner et al. (1996) also identified this wet period during the mid-Holocene through strontium-isotope analysis of calcite layers from Barbados speleothems. A multiproxy analysis of lacustrine sediments cored in Grand-Case Pond at Saint-Martin indicate severe drought events from 3700 to ~2500 yr cal BP and from 1150 yr cal. BP to the present (Malaize et al., 2011). Combined foraminiferal and XRF element analysis of sediment cores from Punta de Cartas and Playa Bailen, Cuba, indicates arid conditions developing since 4 kyr BP and a pronounced drying over the last ~1200 years (Gregory et al., 2015). A multiproxy analysis in an sediment core from Laguna Saladilla, Dominican Republic indicate drier conditions since 2500 cal yr BP (Caffrey et al., 2015).

Then, a decrease in rainfall rates during the late Holocene may have caused a reduction of moist/wet forest area and the expansion of dry forest in Puerto Rico coupled with a decrease of sediment and nutrient supply to the coast. Probably, this climatic event associated to the SLR influenced the mangrove dynamics, and it may have caused its disappearance at about 4000 cal yr BP. This process may have contributed to the marine transgression with an upward and landward migration of the shoreline.

4.11. Mangroves and water salinity

In addition to the mechanisms described above, mangrove dynamics may also be affected by the morphological evolution of the littoral, because the different species of mangrove tree, which colonize and grow in specific tidal zones, depending on inter-related factors such as the pore-water salinity (Matthijs et al., 1999; Tomlinsom, 1986). The distribution of mangrove trees species within the intertidal zone has been discussed by a number of authors (Feller, 1995; Lovelock et al., 2005; Satyanarayana et al., 2002; Ukpong, 2000). Studies carried out along the northern Brazilian littoral reported mangrove trees on intertidal zones with porewater salinity between 7 and 85‰ (Cohen and Lara, 2003; Cohen et al., 2008; Lara and Cohen, 2006). Studies indicate that species of the genus *Avicennia* are more salt tolerant and may thus be able to colonize areas with relatively high levels of interstitial salinity, whereas *Rhizophora* predominate in less saline sediments, in the lower terrain, and where fresh or brackish water is more common (Sherman et al., 1998, 2003).

Therefore, regarding the Flamenco Lagoon, the mangrove trees may have been eliminated from the system as a result of the closure of the area by the sand dune and the increased salinity in the water above the tolerance limit of mangroves due to the high evaporative demand of the climate. Then, the closure of the lagoon and the drier conditions prevalent in the region during the late Holocene, that lasts until the present day, may have inhibited the mangrove development and increased the contribution of salinity tolerant phytoplankton that characterizes the current conditions of the Flamenco Lagoon.

The studied stratigraphic sequence suggests that the Flamenco Lagoon has morphologically evolving to an increase of isolation from the open ocean (Figs. 1b and 3). Probably, this closure is associated to a pre-existing morpho-structural characteristics (Pelletier, 2003) of the studied littoral with coastal incisions and bays that traps the sediments (Fontoura et al., 2013). Later, coastal sand dune was established, and it completed the isolation of the lagoon. This process has been favored by the increased trade wind intensities that results in an increase in sediment transport within the longshore current along the southwestern margin of the Puerto Rico. Similar process was described to the Laguna Grande in northeaster of the Puerto Rico, where it becomes fully enclosed about 575 cal yr BP (Lane et al., 2013).

5. Conclusion

Considering the previous literature about sea level fluctuations (e.g. Gischler, 2015; Toscano and Macintyre, 2003) and climate changes (e.g. Caffrey et al., 2015; Gregory et al., 2015; Mangini et al., 2007) on Caribbean region during the Holocene and the multiple proxies analysis presented in this study, the Flamenco Lagoon was developed following mainly three stages: (1) before ~5400 cal yr BP, small channels drainage were active during a low relative sea level and elevated rainfall. Trees, shrubs and herbs were present, but mangrove trees were not close enough to disperse their pollen grains on the analyzed sediments. (2) The next stage, between ~5400 and ~4300 cal yr BP, is characterized by the establishment and expansion of mangrove trees under strong influence of terrestrial C_3 plants on tidal flats according to the sea-level rise and increased rainfall. (3) During the past 4300, the stratigraphic records evidence the formation of an endorheic minibasin closed and a lagoon was established due to a pre-existing morpho-structural characteristics associated to the sediment transport within the longshore current. The mangroves disappeared during this stage, and the herbaceous and arboreal vegetation predominated. Sedimentary organic matter was sourced from terrestrial C_3 and C_4 plants with some influence of marine organic matter. In the late Holocene, an increase in contribution of marine organic matter occurred, which characterizes the current conditions of the Flamenco Lagoon.

Generally, the literature proposes for the mangroves of the Caribbean region an adjustment of subsurface accretion according to rates of SLR, where depending on the rates of SLR the mangrove may persist or it can be drowned. In the southwestern littoral of the Puerto Rico, a marine transgression occurred during the middle and late Holocene and caused changes from terrestrial to marine influence with a transition stage of establishment, expansion and contraction of mangrove area. Probably, the mangroves were eliminated from the system as a result of combined action of stabilization of the sea level, and a drier period with a reduction of sediment transport along the coast. The closure of the studied area by sand sediments transported by littoral drift currents, and the increased salinity in the water above the tolerance limit of mangroves due to the high evaporation caused by the late Holocene dry period affected significantly the survivability of mangroves.

Acknowledgements

We would like to thank the members of the Laboratory of Coastal Dynamics-Federal University of Pará, Center for Applied Tropical Ecology and Conservation, University of Puerto Rico and Leibniz Centre for Tropical Marine Ecology, Bremen, Germany. This study was financed by the Center for Applied Tropical Ecology and Conservation of the University of Puerto Rico, NSF-HRD 0734826 and the Project DFG.LA 868/5 from the German Research Society.

References

Alizadeh, K., Cohen, M., Behling, H., 2015. Origin and dynamics of the northern south American coastal savanna belt during the Holocene — the role of climate, sea-level, fire and humans. Quat. Sci. Rev. 122, 51–62.

Alongi, D.M., 2015. The impact of climate change on mangrove forests. Curr. Clim. Chang. Rep. 1, 30–39.

Banner, J.L., Musgrove, M., Asmerom, Y., Edwards, R.L., Hoff, J.A., 1996. High-resolution temporal record of Holocene ground-water chemistry: tracing links between climate and hydrology. Geology 24, 1049–1053.

Behling, H., Cohen, M.C.L., Lara, R.J., 2001. Studies on Holocene Mangrove Ecosystem Dynamics of the Bragança Peninsula in North-eastern Pará, Brazil. Bosque Vol. 167 pp. 225–242.

Bellard, C., Leclerc, C., Courchamp, F., 2014. Impact of sea level rise on the 10 insular biodiversity hotspots. Glob. Ecol. Biogeogr. 23, 203–212.

Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecol. Model. 132, 287–302.

Berger, U., Adams, M., Grimm, V., Hildenbrandt, H., 2006. Modelling secondary succession of neotropical mangroves: causes and consequences of growth reduction in pioneer species. Perspect. Plant Ecol. Evol. Syst. 7, 243–252.

Bertrand, R., 2009. Pollen from four common new world mangroves in jamaica. Grana 22, 147–151.

Bird, E.C.F., Barson, M.M., 1977. Measurement of physiographic changes on mangrove-fringed estuaries and coastlines in Australia. International Symposium on the Ecology and Management of Some Tropical Shallow Water Communities: Coral Reefs, Tidal Forests and Estuaries. Jakarta (Indonesia). 28 Jun–3 Jul 1976.

Bishop, M., Morgan, T., Coleman, M., Kelaher, B., Hardstaff, L., Evenden, R., 2009. Facilitation of molluscan assemblages in mangroves by the fucalean alga *Hormosira banksii*. Mar. Ecol. Prog. Ser. 392, 111–122.

Blasco, F., Saenger, P., Janodet, E., 1996. Mangroves as indicators of coastal change. Catena 27, 167–178.

Boulet, R., Pessenda, L.C.R., Telles, E.C.C., Melfi, A.J., 1995. Une évaluation de la vitesse de l'accumulation superficielle de matière par la faune du sol à partir de la datation des charbons et de l'humine du sol. Exemple des latosols des versants du lac Campestre, Salitre, Minas Gerais, Brésil. C. R. Acad. Sci. Paris 320, 287–294.

Brandeis, T.J., Turner, J.A., 2013. Puerto Rico's forests, 2009. Resour Bull. SRS-191. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville.

Bryant, V.M.J., Holloway, R.G., Jones, J.G., Carlson, D.L., 1994. Sedimentation of Organic Particles. Cambridge University Press, Cambridge.

Buso Junior, A.A., 2013. Late Pleistocene and Holocene vegetation, climate dynamics, and Amazonian taxa in the Atlantic rainforest of Linhares, Southeastern Brazil. Radiocarbon 55, 1747–1762.

Buso Junior, A.A., Pessenda, L.C.R., Oliveira, P.E., Giannini, P.C., Cohen, M.C.L., Volkmer-Ribeiro, C., Barros de Oliveira, S.M., Favaro, D.I.T., Rossetti, D.F., Lorente, F., Borotti Filho, M.A., Schiavo, J.A., Bendassolli, J.A., França, M.C., Guimaraes, J.F., Siqueira, G., 2013. From an Estuary to a Freshwater Lake: A Paleo-Estuary Evolution in the Context of Holocene Sea-Level Fluctuations, Southeastern Brazil. Radiocarbon 55, 1735–1746.

Caffrey, M.A., Horn, S.P., Orvis, K.H., Haberyan, K.A., 2015. Holocene environmental change at Laguna Saladilla, coastal north Hispaniola. Palaeogeogr. Palaeoclimatol. Palaeoecol. 436, 9–22.

Cahoon, D.R., Hensel, P.F., Spencer, T., Reed, D.J., McKee, K.L., Saintilan, N., 2006. Coastal wetland vulnerability to relative sea-level rise: wetland elevation trends and process controls. In: Verhoeven, J.T.A., Beltman, B., Bobbing, R., Whigham, D.F. (Eds.), Wetlands and Natural Resource Management. Springer-Verlag, Berlin, pp. 271–292.

Campbell, I.D., Campbell, C., 1994. Pollen preservation: experimental wet–dry cycles in saline and desalinated sediments. Palynology 18, 5–10.

Castaño, A., Urrego, L., Bernal, G., 2010. Dinámica del manglar en el complejo lagunar de Cispatá (Caribe colombiano) en los últimos 900 años. Rev. Biol. Trop. 58, 1347–1366.

Clarke, P.J., 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in Southeastern Australia. Aquat. Bot. 45, 195–204.

Clarke, P.J., Allaway, W.G., 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. Oecologia 93, 548–556.

Clarke, P.J., Myerscough, P.J., 1993. The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: the effects of physical conditions, interspecific competition, and predation on propagule establishment and survival. Austral Ecol. 18, 307–315.

Cohen, M.C.L., Lara, R.J., 2003. Temporal changes of mangrove vegetation boundaries in Amazônia: application of GIS and remote sensing techniques. Wetl. Ecol. Manag. 11, 223–231.

Cohen, M.C.L., Souza Filho, P.W.M., Lara, R.J., Behling, H., Angulo, R.J., 2005. A model of Holocene mangrove development and relative sea-level changes on the Bragança Peninsula (Northern Brazil). Wetl. Ecol. Manag. 13, 433–443.

Cohen, M.C.L., Lara, R.J., Smith, C.B., Angélica, R.S., Dias, B.S., Pequeno, T., 2008. Wetland dynamics of Marajó Island, northern Brazil, during the last 1000 years. Catena 76, 70–77.

Cohen, M.C.L., Behling, H., Lara, R.J., Smith, C.B., Matos, H.R.S., Vedel, V., 2009. Impact of sea-level and climatic changes on the Amazon coastal wetlands during the late Holocene. Veg. Hist. Archaeobot. 18, 425–439.

Cohen, M.C.L., Pessenda, L.C.R., Behling, H., de Fátima Rossetti, D., França, M.C., Guimarães, J.T.F., Friaes, Y., Smith, C.B., 2012. Holocene palaeoenvironmental history of the Amazonian mangrove belt. Quat. Sci. Rev. 55, 50–58.

Cohen, M.C.L., França, M.C., Rossetti, D.F., Pessenda, L.C.R., Giannini, P.C.F., Lorente, F.L., Buso Junior, A., Castro, D., Macario, K., 2014. Landscape evolution during the late Quaternary at the Doce River mouth, Espírito Santo State, Southeastern Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 415, 48–58.

Cohen, M.C.L., Alves, I.C.C., França, M.C., Pessenda, L.C.R., Rossetti, D. de F., 2015. Relative sea-level and climatic changes in the Amazon littoral during the last 500 years. Catena 133, 441–451.

Colón, S.M., Lugo, A.E., 2006. Recovery of a Subtropical Dry Forest After Abandonment of Different Land Uses1. Biotropica 38, 354–364.

Colón, S.M., Lugo, A.E., Ramos González, O.M., 2011. Novel dry forests in southwestern Puerto Rico. For. Ecol. Manag. 262, 170–177.

D'Alpaos, A., Lanzoni, S., Marani, M., Rinaldo, A., 2008. Landscape Evolution in Tidal Embayments. Model. Interplay Erosion, Sedimentation. Veg. Dyn. 112, 1–17.

Da Cruz, C.C., Mendoza, U.N., Queiroz, J.B., Berrêdo, J.F., Da Costa Neto, S.V., Lara, R.J., 2013. Distribution of mangrove vegetation along inundation, phosphorus, and salinity gradients on the Bragança Peninsula in Northern Brazil. Plant Soil 370, 393–406.

Daly, C., Helmer, E.H., Quiñones, M., 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. Int. J. Climatol. 23, 1359–1381.

Davis, M.B., 2000. Palynology after Y2K — understanding the source area of pollen in sediments. Annu. Rev. Earth Planet. Sci. 28, 1–18.

Deines, P., 1980. The isotopic composition of reduced organic carbon. In: Fritz, P., Fontes, J.C. (Eds.), Handbook of Environmental Isotope Geochemistry. The Terrestrial Environments. Elsevier, Amsterdam, pp. 329–406.

der Hammen, Van, 1988. South America. In: Huntley, B., Webb, T. (Eds.), Vegetation History. Kluwer Acad. Pub, The Netherlands, pp. 307–337.

Di Nitto, D., Dahdouh-Guebas, F., Kairo, J., Decleir, H., Koedam, N., 2008. Digital terrain modelling to investigate the effects of sea level rise on mangrove propagule establishment. Mar. Ecol. Prog. Ser. 356, 175–188.

Dimbleby, G.W., 1957. Pollen analysis of terrestrial soils. New Phytol. 56, 12–28.

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, 293–297.

Ellison, J.C., 1993. Mangrove retreat with rising sea-level, Bermuda. Estuar. Coast. Shelf Sci. 37, 75–87.

Ellison, J.C., 2008. Long-term retrospection on mangrove development using sediment cores and pollen analysis: a review. Aquat. Bot. 89, 93–104.

Ellison, J.C., Stoddart, D.R., 1991. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. J. Coast. Res.

Emerson, S., Hedges, J., 2008. Chemical Oceanography and the Marine Carbon Cycle. Cambridge University Press.

Essien, J.P., Ubom, R.M., 2003. Epipellic algae profile of the Mixohaline mangrove swamp of Qua Iboe River estuary (Nigeria). Environmentalist 23, 323–328.

Faegri, K., 1971. The preservation of sporopollenin membranes under natural conditions. In: Brooks, J., Grant, P.R., Muir, M., Gijzel, P.V., Shaw, G. (Eds.), Sporopollenin. Academic Press, London, New York, pp. 256–270.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analyses. John Wiley and Sons.

Feller, I.C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecol. Monogr. 65, 477–505.

Fernandes, S.O., Michotey, V.D., Guasco, S., Bonin, P.C., Bharathi, P.A.L., 2012. Denitrification prevails over anammox in tropical mangrove sediments (Goa, India). Mar. Environ. Res. 74, 9–19.

Field, C.D., 1995. Impact of expected climate change on mangroves. Hydrobiologia 295, 75–81.

Fine, P.V.A., 2002. The invasibility of tropical forests by exotic plants. J. Trop. Ecol. 18, 687–705.

Fontoura, J.A.S., Almeida, L.E., Calliari, L.J., Cavalcanti, A.M., Möller, O., Romeu, M.A.R., Christófaro, B.R., 2013. Coastal hydrodynamics and longshore transport of Sand on Cassino Beach and on Mar Grosso Beach, Southern Brazil. J. Coast. Res. 289, 855–869.

Fornshell, J.A., Spina, P.M., 2000. Internal wave observations off Punta Tuna, Puerto Rico. Oceans Conference Record (IEEE). IEEE, pp. 1189–1193.

França, M.C., Francisquini, M.I., Cohen, M.C.L., Pessenda, L.C.R., Rossetti, D.F., Guimarães, J.T.F., Smith, C.B., 2012. The last mangroves of Marajó Island — Eastern Amazon : impact of climate and/or relative sea-level changes. Rev. Palaeobot. Palynol. 187, 50–65.

França, M.C., Cohen, M.C.L., Pessenda, L.C.R., Rossetti, D.F., Lorente, F.L., Buso Junior, A.Á., Guimarães, J.T.F., Friaes, Y., Macario, K., 2013. Mangrove vegetation changes on Holocene terraces of the Doce River, southeastern Brazil. Catena 110, 59–69.

França, M.C., Francisquini, M.I., Cohen, M.C.L., Pessenda, L.C.R., 2014. Inter-proxy evidence for the development of the Amazonian mangroves during the Holocene. Veg. Hist. Archaeobot. 23, 527–542.

França, M.C., Alves, I.C.C., Castro, D.F., Cohen, M.C.L., Rossetti, D.F., Pessenda, L.C.R., Lorente, F.L., Fontes, N.A., Junior, A.Á.B., Giannini, P.C.F., Francisquini, M.I., 2015. A multi-proxy evidence for the transition from estuarine mangroves to deltaic freshwater marshes, Southeastern Brazil, due to climatic and sea-level changes during the late Holocene. Catena 128, 155–166.

Franklin, J., Ripplinger, J., Freid, E.H., Marcano-Vega, H., Steadman, D.W., 2015. Regional variation in Caribbean dry forest tree species composition. Plant Ecol. 216, 873–886.

French, J.R., Stoddart, D.R., 1992. Hydrodynamics of salt marsh creek systems: implications for marsh morphological development and material exchange. Earth Surf. Process. Landf. 17, 235–252.

Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.L., Cadamuro, L., 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115, 39–53.

Fromard, F., Vega, C., Proisy, C., 2004. Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana. A case study based on remote sensing data analyses and field surveys. Mar. Geol. 208, 265–280.

Furukawa, K., Wolanski, E., 1996. Sedimentation in mangrove forests. Mangrove Salt Marshes 1, 3–10.

Giere, O., 2008. Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments. Springer Science & Business Media.

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.

Gischler, E., 2015. Quaternary reef response to sea-level and environmental change in the western Atlantic. Sedimentology 62, 429–465.

Goh, K.M., 1978. Removal of contaminants to improve the reliability of radiocarbon dates of peats. J. Soil Sci. 29, 340–349.

Gornitz, V., 1991. Global coastal hazards from future sea level rise. Palaeogeogr. Palaeoclimatol. Palaeoecol. 89, 379–398.

Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between neotropical rainforest, dry forest, and Savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev. Palaeobot. Palynol. 153, 70–85.

Gould, W.A., Alarcón, C., Fevold, B., Jiménez, M.E., Martinuzzi, S., Potts, G.,.M.,.Q., Solórzano, M., Ventosa, E., 2008. The Puerto Rico gap analysis project. Land cover, Vertebrate Species Distributions, and Land Stewardship. Gen. Tech. Rep. IITF-GTR-39 Vol. 1. U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Río Piedras.

Gouveia, S., Pessenda, L.C.R., 2000. Datation par le C-14 de charbons inclus dans le sol pour l'étude du rôle de la remontée biologique de matière et du colluvionnement dans la formation de latosols de l'état de São Paulo, Brésil. Vol. 330 pp. 133–138.

Graus, R.R., Macintyre, I.G., 1998. Global warming and the future of Caribbean coral reefs. Carbonates Evaporites 13, 43–47.

Gregory, B.R.B., Peros, M., Reinhardt, E.G., Donnelly, J.P., 2015. Middle–late Holocene Caribbean aridity inferred from foraminifera and elemental data in sediment cores from two Cuban lagoons. Palaeogeogr. Palaeoclimatol. Palaeoecol. 426, 229–241.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35.

Grindrod, J., 1988. The palynology of holocene mangrove and saltmarsh sediments, particularly in Northern Australia. Rev. Palaeobot. Palynol. 55, 229–245.

Guimarães, J.T.F., Cohen, M.C.L., Pessenda, L.C.R., Franca, M.C., Smith, C.B., Nogueira, A.C.R., 2012. Mid- and late-Holocene sedimentary process and palaeovegetation changes near the mouth of the Amazon River. The Holocene 22, 359–370.

Guimarães, J.T.F., Cohen, M.C.L., França, M.C., Alves, I.C.C., Smith, C.B., Pessenda, L.C.R., Behling, H., 2013. An integrated approach to relate Holocene climatic, hydrological, morphological and vegetation changes in the southeastern Amazon region. Veg. Hist. Archaeobot. 22, 185–198.

Haug, G.H., 2001. Southward migration of the Intertropical Convergence zone through the Holocene. Science 293, 1304–1308 (80-.).

Havinga, A.J., 1967. Palynology and pollen preservation. Rev. Palaeobot. Palynol. 2, 81–98.

Hesse, M., Halbritter, H., Zetter, R., Weber, M., Buchner, R., Frosch-Radivo, A., Ulrich, S., 2008. Pollen Terminology: An Illustrated Handbook. Springer, New York.

Higuera-Gundy, A., Brenner, M., Hodell, D.A., Curtis, J.H., Leyden, B.W., Binford, M.W., 1999. A 10,300 14C yr record of climate and vegetation change from Haiti. Quat. Res. 52, 159–170.

Hodell, D.A., Curtis, J.H., Jones, G.A., Higuera-Gundy, A., Brenner, M., Binford, M.W., Dorsey, K.T., 1991. Reconstruction of Caribbean climate change over the past 10,500 years. Nature 352, 790–793.

Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, Oxford.

Hubbard, D.K., Zankl, H., Van Heerden, I., Gill, I.P., 2005. Holocene reef development along the northeastern St. Croix Shelf, Buck Island, U.S. Virgin Islands. J. Sediment. Res. 75, 97–113.

Huggins, A.E., Keel, S., Kramer, P., Òez, F.N., Schill, S., Jeo, R., Chatwin, A., Thurlow, K., McPherson, M., Libby, M., Tingey, R., Palmer, M., Seybert, R., 2007. Biodiversity Conservation Assessment of the Insular Caribbean Using the Caribbean Decision Support System.

Intergovernamental Panel on Climate Change, 2013. Climate Change: The Physical Science Basis. Cambridge University Press, Cambridge.

Janzen, D.H., 2009. Mangroves: where's the understory? J. Trop. Ecol. 1, 89.

Jiménez, J.A., Sauter, K., 1991. Structure and dynamics of mangrove forests along a flooding gradient. Estuaries 14, 49–56.

Kairo, J.G., Dahdouh-Guebas, F., Gwada, P.O., Ochieng, C., Koedam, N., 2002. Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? Ambio 31, 562–568.

Kathiresan, K., 2011. Eco-biology of mangroves. Mangroves: Ecology, Biology and Taxonomy. Nova Science Publishers, Inc., pp. 1–50.

Kauffman, J.B., Heider, C., Cole, T.G., Dwire, K.A., Donato, D.C., 2011. Ecosystem carbon stocks of Micronesian mangrove forests. Wetlands 31, 343–352.

Khan, M.N.I., Suwa, R., Hagihara, A., Ogawa, K., 2004. Interception of photosynthetic photon flux density in a mangrove stand of *Kandelia candel* (L.) Druce. J. For. Res. 9, 205–210.

Kirwan, M.L., Murray, A.B., 2007. A coupled geomorphic and ecological model of tidal marsh evolution. Proc. Natl. Acad. Sci. U. S. A. 104, 6118–6122.

Koch, M.S., Coronado, C., Miller, M.W., Rudnick, D.T., Stabenau, E., Halley, R.B., Sklar, F.H., 2015. Climate change projected effects on coastal foundation communities of the Greater Everglades using a 2060 scenario: need for a new management paradigm. Environ. Manag. 55, 857–875.

Krauss, K.W., Allen, J.A., Cahoon, D.R., 2003. Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. Estuar. Coast. Shelf Sci. 56, 251–259.

Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M.L., Sousa, W.P., 2008. Environmental drivers in mangrove establishment and early development: a review. Aquat. Bot. 89, 105–127.

Krauss, K.W., McKee, K.L., Lovelock, C.E., Cahoon, D.R., Saintilan, N., Reef, R., Chen, L., 2014. How mangrove forests adjust to rising sea level. New Phytol. 202, 19–34.

Laffoon, J.E., Davies, G.R., Hoogland, M.L.P., Hofman, C.L., 2012. Spatial variation of biologically available strontium isotopes ($^{87}Sr/^{86}Sr$) in an archipelagic setting: a case study from the Caribbean. J. Archaeol. Sci. 39, 2371–2384.

Lamb, A.L., Wilson, G.P., Leng, M.J., 2006. A review of coastal palaeoclimate and relative sea-level reconstructions using $\delta^{13}C$ and C/N ratios in organic material. Earth-Science Rev. 75, 29–57.

Lane, C.S., Clark, J.J., Knudsen, A., McFarlin, J., 2013. Late-Holocene paleoenvironmental history of bioluminescent Laguna Grande, Puerto Rico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 99–113.

Lara, R.J., Cohen, M.C.L., 2006. Sediment porewater salinity, inundation frequency and mangrove vegetation height in Bragança, North Brazil: an ecohydrology-based empirical model. Wetl. Ecol. Manag. 14, 349–358.

Lara, R.J., Cohen, M.C.L., 2009. Palaeolimnological studies and ancient maps confirm secular climate fluctuations in Amazonia. Clim. Chang. 94, 399–408.

Lara, R., Szlafsztein, C., Cohen, M., Berger, U., Glaser, M., 2002. Implications of mangrove dynamics for private land use in Bragança, North Brazil: a case study. J. Coast. Conserv. 8, 97.

Lara, R.J., Alder, V., Franzosi, C.A., Kattner, G., 2010. Characteristics of suspended particulate organic matter in the southwestern Atlantic: influence of temperature, nutrient and phytoplankton features on the stable isotope signature. J. Mar. Syst. 79, 199–209.

Li, Z., Zhang, Z., Li, J., Zhang, Y., Liu, L., Fan, H., Li, G., 2008. Pollen distribution in surface sediments of a mangrove system, Yingluo Bay, Guangxi, China. Rev. Palaeobot. Palynol. 152, 21–31.

Lovelock, C.E., Feller, I.C., McKee, K.L., Thompson, R., 2005. Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. Caribb. J. Sci. 41, 456–464.

Lovelock, C.E., Adame, M.F., Bennion, V., Hayes, M., Reef, R., Santini, N., Cahoon, D.R., 2015. Sea level and turbidity controls on mangrove soil surface elevation change. Estuar. Coast. Shelf Sci. 153, 1–9.

Lugo, A.E., 1986. Mangrove understory: an expensive luxury? J. Trop. Ecol. 2, 287–288.

Lugo, A.E., Cintrón, G., 1975. The mangrove forests of Puerto Rico and their management. In: Walsh, G., Snedaker, S., Teas, H. (Eds.), Proceedings of International Symposium on Biology and Management of Mangroves. Institute of Food and Agricultural Sciences, University of Florida, pp. 825–846.

Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. For. Ecol. Manag. 190, 145–161.

Lugo, A., Gonzales, J., Cintron, B., Dugger, K., 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10, 278–291.

Lugo, A.E., Medina, E., Rejo-Torres, J.C., Helmer, E., 2006. Botanical and ecological basis for the resilience of Antillean Dry Forests. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), Neotropical Savannas and Seasonally Dry Forests. CRC Press, Boca Raton, pp. 359–381.

Macintyre, I.G., Toscano, M.A., Lighty, R.G., Bond, G.B., 2004. Holocene history of the mangrove islands of Twin Cays, Belize, Central America. Atoll Res. Bull. 1–16.

Malaize, B., Bertran, P., Carbonel, P., Bonnissent, D., Charlier, K., Galop, D., Imbert, D., Serrand, N., Stouvenot, C., Pujol, C., 2011. Hurricanes and climate in the Caribbean during the past 3700 years BP. The Holocene 21, 911–924.

Mangini, A., Blumbach, P., Verdes, P., Spötl, C., Scholz, D., Machel, H., Mahon, S., 2007. Combined records from a stalagmite from Barbados and from lake sediments in Haiti reveal variable seasonality in the Caribbean between 6.7 and 3 ka BP. Quat. Sci. Rev. 26, 1332–1343.

Mann, P., Hippolyte, J.-C., Grindlay, N.R., Abrams, L.J., 2005. Special Paper 385: Active Tectonics and Seismic Hazards of Puerto Rico, the Virgin Islands, and Offshore Areas. Geological Society of America Special PapersGeological Society of America.

Martinuzzi, S., Gould, W.A., Lugo, A.E., Medina, E., 2009. Conversion and recovery of Puerto Rican mangroves: 200 years of change. For. Ecol. Manag. 257, 75–84.

Martinuzzi, S., Lugo, A.E., Brandeis, T.J., Helmer, E.H., 2013. Case study: geographic distribution and level of novelty of Puerto Rican Forests. In: Hobbs, J.R., Higgs, E.S., Hall, C.M. (Eds.), Novel Ecosystems: Intervening in the New Ecological World Order. John Wiley & Sons, Ltd., pp. 81–87 (Published).

Matthijs, S., Tack, J., van Speybroeck, D., Koedam, N., 1999. Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. Mangrove Salt Marshes 3, 243–249.

McKee, K.L., 1993. Soil physicochemical patterns and mangrove species distribution — reciprocal effects? J. Ecol.

Mckee, K.L., Faulkner, P.L., 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. Atoll Res. Bull. 47–58.

McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Glob. Ecol. Biogeogr. 16, 545–556.

Meckler, A.N., Haug, G.H., Sigman, D.M., Plessen, B., Peterson, L.C., Thierstein, H.R., 2007. Detailed sedimentary N isotope records from Cariaco Basin for Terminations I and V: local and global implications. Glob. Biogeochem. Cycles 21 (n/a–n/a).

Mendoza, U.N., da Cruz, C.C., Menezes, M.P., Lara, R.J., 2011. Flooding effects on phosphorus dynamics in an Amazonian mangrove forest, Northern Brazil. Plant Soil 353, 107–121.

Meyers, P.a., 1997. Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. Org. Geochem. 27, 213–250.

Meyers, P.A., 2003. Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. Org. Geochem. 34, 261–289.

Miall, A.D., 1978. Facies types and vertical profile models in braided river deposits: a summary. In: Miall, A.D. (Ed.), Fluvial Sedimentology. Canadian Society of Petroleum Geologists, Calgary, pp. 597–604.

Middleton, B.A., McKee, K.L., 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J. Ecol. 89, 818–828.

Monacci, N.M., Meier-Grünhagen, U., Finney, B.P., Behling, H., Wooller, M.J., 2009. Mangrove ecosystem changes during the Holocene at Spanish Lookout Cay, Belize. Palaeogeogr. Palaeoclimatol. Palaeoecol. 280, 37–46.

Montes, E., Thunell, R., Muller-Karger, F.E., Lorenzoni, L., Tappa, E., Troccoli, L., Astor, Y., Varela, R., 2013. Sources of $\delta^{15}N$ variability in sinking particulate nitrogen in the Cariaco Basin, Venezuela. Deep-Sea Res. II Top. Stud. Oceanogr. 93, 96–107.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. Ecology 83, 2869–2877.

Murphy, P.G., Lugo, A.E., 1986. Structure and biomass of a subtropical dry Forest in Puerto Rico. Biotropica 18, 89.

Murphy, P.G., Lugo, A.E., Murphy, A.J., Nepstad, D.C., 1995. The dry forests of Puerto Rico's south coast. In: Lugo, A.E., Lowe, C. (Eds.), Tropical Forests: Management and Ecology. Springer-Verlag, New York, pp. 178–209.

Parkinson, R.W., DeLaune, R.D., White, J.R., 1994. Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. J. Coast. Res. 10, 1077–1086.

Pelletier, J.D., 2003. Drainage basin evolution in the rainfall erosion facility: dependence on initial conditions. Geomorphology 53, 183–196.

Phuphumirat, W., Mildenhall, D.C., Purintavaragul, C., 2009. Pollen deterioration in a tropical surface soil and its impact on forensic palynology. Open Forensic Sci. J. 2.

Phuphumirat, W., Zetter, R., Hofmann, C.-C., Ferguson, D.K., 2015. Pollen degradation in mangrove sediments: a short-term experiment. Rev. Palaeobot. Palynol. 221, 106–116.

Posamentier, H.W., Morris, W.R., 2000. Aspects of the stratal architecture of forced regressive deposits. Geol. Soc. Lond. Spec. Publ. 172, 19–46.

Raffaelli, D., Hawkins, S., 1999. Causes of zonation. Intertidal Ecology SE — 3. Springer, Netherlands, pp. 71–97.

Rangel-Buitrago, N.G., Anfuso, G., Williams, A.T., 2015. Coastal erosion along the Caribbean coast of Colombia: magnitudes, causes and management. Ocean Coast. Manag. 114, 129–144.

Reading, H.G., 1996. Sedimentary Environments: Processes, Facies and Stratigraphy. 3a ed. Blackwell Science.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Burr, G.S., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., McCormac, F.G., Manning, S.W., Reimer, R.W., Richards, D.A., Southon, J.R., Talamo, S., Turney, C.S.M., van der Plicht, J., Weyhenmeyer, C.E., 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years CAL BP. Radiocarbon 51, 1111–1150.

Reineck, H.E., Singh, I.B., 1980. Depositional sedimentary environments, with reference to terrigenous clastics. Depos. Sediment. Environ. with Ref. to terrigenous clastics, Second edition (Textbook) (Second Ed. (Textb).

Rossetti, D.F., Valeriano, M.M., Thales, M., 2007. An abandoned estuary within Marajó Island: implications for late Quaternary paleogeography of northern Brazil. Estuar. Coasts 30, 813–826.

Roubik, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden.

Rull, V., Vegas-Vilarrubia, T., Espinoza de Pernia, N., 1999. Palynological record of an Early–Mid Holocene mangrove in Eastern Venezuela. Implications for sea-level rise and disturbance history. J. Coast. Res.

Sasmito, S.D., Murdiyarso, D., Friess, D.A., Kurnianto, S., 2015. Can mangroves keep pace with contemporary sea level rise? A global data review. Wetl. Ecol. Manag.

Satyanarayana, B., Raman, A.V., Dehairs, F., Kalavati, C., Chandramohan, P., 2002. Mangrove floristic and zonation patterns of Coringa, Kakinada Bay, East Coast of India. Wetl. Ecol. Manag. 10, 25–37.

Sharpe, J.M., 2009. Responses of the mangrove fern *Acrostichum danaeifolium* Langsd. & Fisch. (Pteridaceae, Pteridophyta) to disturbances resulting from increased soil salinity and Hurricane Georges at the Jobos Bay National Estuarine Research Reserve, Puerto Rico. Wetl. Ecol. Manag. 18, 57–68.

Sherman, R.E., Fahey, T.J., Howarth, R.W., 1998. Soil–plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. Oecologia 115, 553–563.

Sherman, R.E., Fahey, T.J., Martinez, P., 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems 6, 384–398.

Smith, C.B., Cohen, M.C.L., Pessenda, L.C.R., França, M.C., Guimarães, J.T.F., Rossetti, D. de F., Lara, R.J., 2011. Holocene coastal vegetation changes at the mouth of the Amazon River. Rev. Palaeobot. Palynol. 168, 21–30.

Snedaker, S., 1982. Mangrove species zonation: why? In: Sen, D., Rajpurohit, K. (Eds.), Contributions to the Ecology of Halophytes SE — 8, Tasks for Vegetation Science. Springer, Netherlands, pp. 111–125

Spenceley, A.P., 1977. The role of pneumatophores in sedimentary processes. Mar. Geol. 24.

Srivastava, P.B.L., Keong, G.B., Muktar, A., 1987. Role of Acrostichum species in natural regeneration of Rhizophora species in Malaysia. Trop. Ecol. 28, 274–288.

Stevens, P.W., Fox, S.L., Montague, C.L., 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl. Ecol. Manag. 14, 435–444.

Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M., Ball, M.C., 2007. The role of freezing in setting the latitudinal limits of mangrove forests. New Phytol. 173, 576–583.

Swift, D.J.P., 1975. Barrier-island genesis: evidence from the central atlantic shelf, eastern U.S.A. Sediment. Geol. 14, 1–43.

Temmerman, S., Meire, P., Bouma, T.J., Herman, P.M.J., Ysebaert, T., De Vriend, H.J., 2013. Ecosystem-based coastal defence in the face of global change. Nature 504, 79–83.

Thornton, S.F., McManus, J., 1994. Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter Provenance in estuarine systems: evidence from the Tay estuary, Scotland. Estuar. Coast. Shelf Sci. 38, 219–233.

Tomlinsom, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Toscano, M.A., Macintyre, I.G., 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated 14C dates from *Acropora palmata* framework and intertidal mangrove peat. Coral Reefs 22, 257–270.

Tschudy, R.H., 1969. Relationship of palynomorphs to sedimentation. In: Tschudy, R.H. (Ed.), Asp. Palynol.

Ukpong, I.E., 2000. Ecological classification of Nigerian mangroves using soil nutrient gradient analysis. Wetl. Ecol. Manag. 8, 263–272.

Vilarrúbia, T.V., Rull, V., 2002. Natural and human disturbance history of the Playa Medina mangrove community (Eastern Venezuela). Caribb. J. Sci. 38, 66–76.

Walker, R.G., 1992. Facies, facies models and modern stratigrahic concepts. In: Walker, R.G., James, N.P. (Eds.), Facies Models — Response to Sea Level Change. Geological Association of Canada, Ontario, pp. 1–14.

Woodroffe, C.D., 1995. Response of tide-dominated mangrove shorelines in Northern Australia to anticipated sea-level rise. Earth Surf. Process. Landf. 20, 65–85.

Woodroffe, C.D., Chappell, J., Thom, B.G., Wallensky, E., 1989. Depositional model of a macrotidal estuary and floodplain, South Alligator River, Northern Australia. Sedimentology 36, 737–756.

Xia, P., Meng, X., Li, Z., Feng, A., Yin, P., Zhang, Y., 2015. Mangrove development and its response to environmental change in Yingluo Bay (SW China) during the last 150 years: Stable carbon isotopes and mangrove pollen. Org. Geochem. 85, 32–41.

Xu, Q., Tian, F., Bunting, M.J., Li, Y., Ding, W., Cao, X., He, Z., 2012. Pollen source areas of lakes with inflowing rivers: modern pollen influx data from Lake Baiyangdian, China. Quat. Sci. Rev. 37, 81–91.