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

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29 **Abstract**

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

54 prevalent in the region during the late Holocene, which lasts until the present day, and
55 increased the contribution of salinity tolerant phytoplankton that characterizes the
56 current conditions of the Flamenco Lagoon.

57 **KEY-WORDS:** carbon and nitrogen isotopes, C/N, climatic changes, palynology,
58 Puerto Rico, sea-level rise

59

60 **Introduction**

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

78 highest SLR scenarios between 0.52 and 0.98 m by 2100 (IPCC, 2013; Koch et al.,
79 2015; Sasmito et al., 2015).

80 Regarding the Western Atlantic Holocene sea level curves based on coral and
81 intertidal *Rhizophora mangle* peat from the Florida Keys, Belize, and the wider
82 Caribbean indicate the SLR during the Holocene was ~5.2, ~1.47 and ~0.93 mm/yr
83 during the early, middle and late Holocene, respectively (e.g. Toscano & Macintyre
84 2003). Details of Holocene western Atlantic sea-level curves are debated, but all curves
85 are transgressive and display a rapid rise in the early Holocene and a reduced rate of rise
86 in the late Holocene (Gischler, 2015). According to a palynological record of an Early-
87 Mid Holocene mangrove in eastern Venezuela, a rapid rise in sea levels up to 8000
88 years BP occurred, with a slower rate between 8000 and 4000 years BP, and stable
89 levels after 3000 years BP (Rull et al., 1999). Differences in the Holocene sea-level
90 curves between Florida Keys/Belize and the eastern caribbean may be attributed to a
91 shift in the Inter Tropical Convergence Zone that regionally affects the Caribbean sea
92 (Haug, 2001).

93 In the Caribbean islands, such as Puerto Rico, the rates of SLR are the product of
94 the relation between eustatic sea level rise and local tectonic movements. The
95 geomorphology and distribution of late Quaternary marine terraces and beach ridges in
96 south-central Puerto Rico suggest stability or slow late Quaternary uplift along the
97 south-central part of the coast, while the coastline of southwestern Puerto Rico exhibits
98 no late Quaternary coastal sediments and a pattern of long-term drowning of coastal
99 features (Mann et al., 2005). The relative small presence of mangrove areas along the
100 eastern side of the coastal plateau in the Guánica Dry Forest UNESCO/MAB Biosphere
101 Reserve (Fig. 1a) may be a consequence of this drowning of coastal system. However,
102 the establishment and maintenance of mangroves also depend on other environmental

103 factors such as topography (Cohen and Lara, 2003; Cohen et al., 2015, 2009; Gornitz,
104 1991), wave and current energy (Woodroffe et al., 1989), and coastal morphology
105 (Blasco et al., 1996; Fromard et al., 2004; Lara and Cohen, 2009) and mainly the input
106 of nutrients, sediment and freshwater (Cohen et al., 2014; Cohen et al., 2012; Krauss et
107 al., 2008; Lara and Cohen, 2006; Stevens et al., 2006; Stuart et al., 2007). The
108 availability of nutrient/sediment and freshwater along the coastal system depend mainly
109 on the river runoff. Regarding the climatic changes and its effects in the Caribbean
110 region during the Holocene (Banner et al., 1996; Higuera-Gundy et al., 1999; Malaize et
111 al., 2011; Mangini et al., 2007), the contribution of sediments, nutrients and freshwater
112 to the littoral must have changed significantly during this period and influenced,
113 together with the SLR, the mangrove development.

114 Reconstructed past climate changes and SLR effects on coastal mangrove
115 environments have been used to predict the current and future effects of anthropogenic
116 climate forcing and SLR (Cohen and Lara, 2003; Ellison and Stoddart, 1991; Ellison,
117 1993; Field, 1995; Graus and Macintyre, 1998; Lara et al., 2002; Parkinson et al., 1994).
118 In semi-arid environments, with calcareous karstic geology, the presence of mangroves
119 along a stratigraphic record would indicate how sea level rise and paleoclimate changes
120 have affected the coastal environment. In this context, the main objectives of this study
121 is 1) to propose a palaeoenvironmental reconstruction of the Flamenco Lagoon,
122 southeastern Puerto Rico, during the middle and late Holocene, considering the changes
123 in sedimentary environment, vegetation, and source of sedimentary organic matter. The
124 interpretations are based on sediment analysis, pollen records, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, C/N data and
125 AMS dating. 2) Evaluate the main driving forces controlling the mangrove dynamics on
126 the study site. Noteworthy is that multiple proxies analysis enable to assess the

127 compatibility between the sedimentary environment and its aquatic and terrestrial
128 plants, mainly considering the mangroves, according to SLR and climatic changes.

129

130 **2. Study site**

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

135 2.1- Geomorphology and geology

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

143 2.2-Climate

144 In southwestern Puerto Rico, the average rainfall is 796 mm/yr, with the lowest amount
145 of rain in January and February and the highest rainfall in September and October
146 (<http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?pr3532>). Guánica Forest is mainly
147 represented by a subtropical dry forest (Fig. 1), which typically receives less than
148 200 mm of rain from December through March, designated as a UNESCO Man and
149 Biosphere Reserve in 1981.

150 2.3-Vegetation

151 The 4,400 ha forest occurs as upland forest with mature stands of native trees, 40–80 year-old
152 secondary forest stands dominated by introduced legume trees, and mangrove
153 (*Rhizophora mangle*; *Laguncularia racemosa*) forest (Murphy & Lugo 1986; Lugo et
154 al., 1978). Most of the forest is semi-deciduous with less than 5 m in height and
155 occasional larger emergent trees in favorable microsites (Murphy and Lugo, 1986).

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

164 Tropical dry forests are particularly susceptible to invasion by non-native
165 species owing to extensive human disturbance including land clearing and fire (Fine,
166 2002). These novel ecosystems (Colón et al., 2011; Lugo and Helmer, 2004; Martinuzzi
167 et al., 2013) with a legacy of human activity are widespread in Puerto Rico. In addition,
168 naturalized, introduced species are an important component of forests regenerating on
169 abandoned cropland and pastures (Brandeis and Turner, 2013; Colón et al., 2011). It
170 includes non-native *Leucaena leucocephala* (Fabaceae), *Prosopis pallida* (Fabaceae),
171 *Tamarindus indica* (Fabaceae), which is a planted and naturalized fruit tree, *Acacia*
172 *farnesiana* (Fabaceae) and *Pithecellobium dulce* (Fabaceae), which is potentially
173 invasive leguminous trees (Franklin et al., 2015). Surrounding the study lagoon was
174 identified Anacardiaceae, Asteraceae, *Byrsonima* (Malpigiaceae), Cactaceae,

175 Cocoloba (Polygonaceae), Combretaceae, Cyperaceae, Fabaceae, Malpigiaceae,
176 Mimosa (Fabaceae), Poaceae and Rubiaceae.

177 *2.3.1-Mangroves*

178 The Puerto Rico mangroves, with approximately 83 km² (Gould et al., 2008) are subject
179 to a tidal range of 0.2 m (Fornshell and Spina, 2000), and are classified into two groups
180 based on contrasting environmental settings. The northern-coast mangroves are subject
181 to high wave energy, high precipitation, and river runoff. The southern-coast mangroves
182 are subject to low wave energy regime, low precipitation and low river runoff due to the
183 rain shadow effect of the Central Range (Daly et al., 2003). Basin and riverine
184 mangroves predominate on the northern-coast type mangroves, while fringe mangroves
185 predominate on the southern-coast type mangroves (Lugo and Cintrón, 1975).

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

192

193 **3. Materials and methods**

194 *3.1 Remote sensing*

195 The morphological aspects of the study area were characterized based on the analysis of
196 images provided by Google Earth acquired on 03/12/2011. The topographic profile is
197 based on the digital elevation model acquired during the Shuttle Radar Topography
198 Mission-SRTM undertaken by the National Aeronautics and Space Administration-

199 NASA. The software Global Mapper 9 (Global Mapper Software LLC, Olathe, KS,
200 USA, 2009) was used to process the topographic data (Fig. 1d).

201

202 *3.1 Sampling and facies description*

203 One sediment core with 2.6 m long was sampled from Flamenco Lagoon
204 (17°57'10.31"N, 66°50'39.30"W) in a sector with 1 m depth in southwestern coast of
205 Puerto Rico using a Russian Sampler with the geographical position determined by
206 GPS. Considering the water level of the Flamenco Lagoon during the sampling was
207 equivalent to the modern sea-level, with a tidal range of 20 cm to the study area, the
208 sampling site is 1 ± 0.1 m below the mean sea-level. Following the proposal of (Walker,
209 1992), facies analysis included descriptions of color, lithology, texture and structures.
210 The sedimentary facies was codified following (Miall, 1978). The studied stratigraphic
211 profile was divided into facies associations, which is a group of sedimentary facies used
212 to define a particular sedimentary environment (Reading, 1996). X-ray radiographs
213 aided the identification of internal sedimentary structures and some reworking of
214 sediments by animals and plants that may cause age inversions by mixture of carbon of
215 different ages along the studied core (Boulet et al., 1995; Gouveia and Pessenda, 2000).

216

217 *3.2 Palynological analysis*

218 The core was sub-sampled at intervals of 5 cm and 1 cm³ of sediment was taken for
219 palynological analysis. Samples were prepared using standard techniques for the
220 extraction of palynomorphs, including acetolysis (Faegri and Iversen, 1989).
221 Handbooks of pollen and spores morphology were consulted (Hesse et al., 2008;
222 Roubik and Moreno, 1991) as well as the reference collections of the “Laboratory of

223 Coastal Dynamics – UFPA”, ^{14}C Laboratory of the Center for Nuclear Energy in
224 Agriculture (CENA/USP) and of Hermann Behling to identify pollen grains and spores.

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

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

234 Noteworthy is the fact of the composition of a fossil pollen flora in sediments
235 depends on several different factors, such as the composition of the vegetation from
236 which the pollen originates, pollen production of the individual plant species, pollen
237 dispersion, sedimentation and preservation. Considering the low pollen preservation in
238 sediments, it may be caused by various external factors (sediment grain size, microbial
239 attack, oxidation and mechanical forces), as well as factors inherent to the pollen grains
240 themselves (sporopollenine content, chemical and physical composition of the pollen
241 wall) (Havinga, 1967). However, anaerobic conditions (low Eh value) in the fine-
242 grained sediment of mangroves provide a suitable environment for pollen to be
243 preserved (Bryant et al., 1994; Ellison, 2008; Grindrod, 1988; Tschudy, 1969).
244 Sediment with high salinity and low Eh and pH values seems to be ideal for pollen
245 preservation (Bryant et al., 1994; Campbell and Campbell, 1994; Dimbleby, 1957;
246 Phuphumirat et al., 2009), but in other substrates, including unweathered rock
247 platforms, coral rubble, and sandy sediments also occupied by mangroves are not

248 suitable for pollen preservation (Grindrod, 1988). For instance, pollen tend to rapidly
249 decay in sandy sediment because a better drainage in sand caused by large interstitial
250 pores allows pollen grains to be abraded by a mobile inorganic matrix as well as to be
251 oxidized during soil hydration-dehydration cycles (Faegri, 1971; Grindrod, 1988).

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

269 Considering the studied core, sampled along different sedimentary environments
270 and vegetation, it presents changes in sedimentation rates and in relationship between
271 sand/mud sediments. Then, probably, the pollen concentrations were affected by pollen
272 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 thousand g/cm³, 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.

3.3 C/N, Carbon and Nitrogen isotopes

The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ 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).

3.4. 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 hours, 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 AD 1950 (yr BP) normalized to $\delta^{13}\text{C}$ of -25‰ VPDB and in cal yr BP with a precision of 2σ (Reimer et al., 2009).

Results and discussion

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., 2015, 2014; França et al., 2015, 2013a, 2012; Guimarães et al., 2013, 2012; 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., 2015, 2013b).

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

323 some levels presenting fining upward successions (Fig. 2). Pollen and spore records,
324 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Total Organic Carbon (TOC), Total Nitrogen (TN) and C/N values were
325 added to facies characteristics in order to define three facies association: Channel, tidal
326 flat with mangrove, and lagoon.

327 The highest pollen concentrations were obtained along the facies association tidal
328 flat with mangrove (20 – 60,000 g/cm³), while the channel and lagoon presented the
329 lowest values (12 – 30,000 g/cm³) (Fig. 2). It is noteworthy that some depositional
330 environments such as lakes, tidal flats and fluvial floodplains provide suitable
331 conditions for muddy accumulation and preservation of pollen grains sourced from
332 vegetation living at the time that the sediment was deposited. Lacustrine sediments
333 preserve pollen carried by wind and from vegetation surrounding the lake. The spatial
334 representation of the lacustrine pollen signal depends on wind strengths and the extent
335 of the drainage system feeding the lake. The proportion of the pollen signal provided by
336 each vegetation type is distance-weighted (Davis, 2000; Xu et al., 2012), with closer
337 sources usually being greater.

338 In addition, several other interacting factors determine the degree to which the
339 pollen assemblages reflect each plant community. The most important are pollen
340 productivity and dispersal characteristics of the species, the local-scale patterns of the
341 species distribution at each community, and the representation of local and extra-local
342 pollen rain. Considering the mangroves and associated vegetation, the plant parameters
343 play important roles in pollen abundance. For example, plant cover may have the
344 greatest significance for pollen percentages, while plant percentage may have greater
345 impact on pollen abundance. In some cases, the type of flower pollination has less
346 significant effect on pollen representation than the plant frequency. On the other hand,

347 environment effects such as deposition conditions, hydrodynamics, and water table
348 depth also influence the pollen representation (Li et al., 2008).

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

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

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

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

379

380 *Facies association A (Channel)*

381 This facies association occurs in the lowest part of the stratigraphic sequence from
382 ~5660cal yr BP until ~5400 cal yr BP (Fig. 2). The sediment is composed mostly of
383 greenish gray or dark brown massive sand (Sm) with fining upward successions. This
384 deposit is typically bounded at the base by a sharp erosional surface. These
385 characteristics are typical of a channel deposition (Rossetti et al., 2007). Considering the
386 size of these sandy layers (15 cm), probably these sediments were accumulated by small
387 channels. Besides these structures, this facies association presents many gastropods. The
388 pollen assemblages of this facies association correspond partly to Zone FL 1 (Fig. 2).
389 This zone is characterized by the predominance of shrubs and herbs pollen mainly
390 constituted by *Mimosa* (60-70%) and Poaceae (10-30%).

391 Total organic carbon (TOC) oscillated between 3 and 15%, while total nitrogen
392 (TN) oscillated between 0.4 and 1.1%. The sediment $\delta^{13}\text{C}$ values ranges between -23
393 and -19‰ (mean= -21 ‰) and the C/N values increase from 29 to 43 indicating an
394 increased trend in organic matter sourced from C_3 to C_4 plants (Deines, 1980). The $\delta^{15}\text{N}$
395 presents values between 5.5 and 6‰. It may suggest an aquatic and terrestrial organic
396 matter (Meyers, 1997; Thornton and McManus, 1994). According to Montes et al.

397 (2013) high $\delta^{15}\text{N}$ values ($>4.5\%$) detected in sediments deposited in the Cariaco Basin-
398 Venezuela could be indicative of higher inputs of terrigenous organic matter that result
399 from more direct riverine discharge into the basin.

400

401 *Facies association B (Tidal flat with mangrove)*

402 This facies association occurs between ~5400 and ~4400 cal yr BP. These deposits
403 presents lenticular heterolithic bedding (Hl) and wavy heterolithic bedding (Hw) and
404 many gastropods and bivalves shells. Heterolithic beddings are sedimentary structures
405 made up of interbedded deposits of sand and mud. Heterolithic bedding forms in
406 response to alternations in sediment supply and tidal velocity. Depending on these
407 factors some differences in beddings may be found, such as (1) wavy bedding that
408 occurs when mud and sand deposits are equal. (2) Lenticular bedding occurs when sand
409 ripples are deposited in mud in an isolated distribution pattern. Ripples in lenticular
410 bedding are both laterally and horizontally discontinuous. In addition, lenticular and
411 wavy heterolithic beddings indicate a vertical accretion following a alternation of
412 energy flow with predominance of mud deposition from suspension and periodic sand
413 inflows (Reineck and Singh, 1980). The pollen assemblages correspond to part of the
414 Zone FL1 and Zone FL2 (Fig. 2). The Zone FL1 presents in this facies association
415 *Mimosa* (90-100%) and Poaceae pollen (0-10%). The Zone FL2 is characterized by the
416 predominance of mangrove (10-80%) pollen, represented by *Rhizophora* (2-75%) and
417 *Avicennia* (0-5%). The herbaceous (10-90%) pollen are represented by Poaceae (1-
418 85%), Asteraceae (0-20%) and Cyperaceae (0-6%). Some micro foraminifera have also
419 been recorded.

420 Although the *Laguncularia* trees are present in mangroves from Puerto Rico,
421 along the studied core was not possible record this genus. Probably, pollen grains of

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

433 Total organic carbon (TOC) and total nitrogen (TN) present a strong increase at
434 the beginning of this facies association with 65% and 1.7%, respectively, but they show
435 an decreasing trend to the top (24% and 0.9%). The sediment $\delta^{13}\text{C}$ values decrease from
436 -19‰ to -23‰ and the C/N values range between 33 and 57 indicate organic matter
437 from C_3 plants (-32‰ to -21‰; Deines, 1980). The $\delta^{15}\text{N}$ values decrease from 6 to
438 2.5‰. The decrease in $\delta^{15}\text{N}$ indicates nitrogen biological fixation, which is the
439 mechanism that brings the $\delta^{15}\text{N}$ levels close to the atmospheric values that is around 0‰
440 (Meyers, 1997; Thornton and McManus, 1994). Changes in the sedimentary $\delta^{15}\text{N}$ over
441 the last 580 kyr in the Cariaco Basin-Venezuela indicate that $\delta^{15}\text{N}$ was 5‰ during sea
442 level low-stand and 2‰ during sea level high-stands periods. Probably, the $\delta^{15}\text{N}$ signal
443 preserved in the basin reflects changes in water column denitrification. Then, the low
444 $\delta^{15}\text{N}$ (2‰) during sea level high-stands indicates an increase in N_2 fixation rates as a
445 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).

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 $\delta^{13}\text{C}$ values exhibit an enrichment trend from -26 to -17‰ (mean= -21‰) along the Zone FL 3. The $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and C/N rate (Fig. 4). The Zone FL 4 presents an enrichment trend to $\delta^{13}\text{C}$ values from -25‰ to -21‰ , and the $\delta^{15}\text{N}$ values ($2.8 - 5.0\text{‰}$,

mean= 4.2‰) increased relative to the Zone FL 3. The C/N values presents a significant decrease from 40 to 12. The binary diagram of $\delta^{13}\text{C}$ vs. C/N ratio reveals an increase in contribution of marine organic matter to the top of this sedimentary sequence (Fig. 3 and 4). The increasing trend of $\delta^{15}\text{N}$ values to the top may be explained also by marine primary production, which is based on nitrate (NO_3^-) supply. The $\delta^{15}\text{N}$ values of phytoplankton in marine regions reflects main two factors: the $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ similar to that of the nitrogen substrate: $\delta^{15}\text{N} \approx +5\text{‰}$ from dissolved NO_3^- versus $\delta^{15}\text{N} = +1$ for N_2 . Then, most marine phytoplankton presents a $\delta^{15}\text{N}$ more like +5‰ (Emerson and Hedges, 2008).

481

482 *Palaeoenvironmental interpretation*

483 The data suggest three main stages to the Flamenco Lagoon development (Fig. 5): (1)
484 before ~5400 cal yr BP, small channels drainage were active, and it accumulated muddy
485 and sandy sediments with many gastropods reworked. Trees, shrubs and herbs were
486 present. Mangroves were not close enough to disperse their pollen grains and preserve it
487 in these sediments (Fig. 5). (2) The next stage is characterized by the establishment of a
488 bay with tidal flats. This environment accumulated many gastropods and bivalves
489 shells, and the mangrove expanded according to the sea-level rise between ~5400 and
490 ~4400 cal yr BP. The presence of micro foraminifera reveals a marine influence during
491 this time, since the majority live on or within the seafloor sediment (i.e., are benthic)
492 while a smaller variety are floaters in the water column at various depths (i.e., are
493 planktonic) (Giere, 2008). In addition, the geochemical data showed strong influence of
494 terrestrial C3 plants. Likely, the significant increase in TOC and TN in sediments of the
495 tidal flat with mangrove are associated to high productivity and capacity of the

496 mangroves to store organic matter in its sediments (Giri et al., 2011). Donato et al.
497 (2011) and Kauffman et al. (2011) demonstrated that carbon storage in mangroves is
498 about 4 times higher than in terrestrial forests. (3) During the past 4400 cal yr BP, the
499 stratigraphic records evidence the formation of an endorheic minibasin closed and a
500 lagoon was established with accumulation of muddy sediments, few shells and the
501 shrinkage and disappearance of mangroves. During this stage, the influence of arboreal,
502 herbaceous vegetation and ferns increase in the pollen diagram, as well as the presence
503 of algae recorded only during the lagoon stage.

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

515 Considering this upward increase of algae in the studied core, the density of
516 microalgae increase with decrease in distance from the low tide line (Essien and Ubom,
517 2003), and some studies have highlighted the importance of monotypic stands formed
518 by the alga in tidal flats directly and indirectly influencing the abundances of other algae
519 and invertebrates (Bishop et al., 2009).

520 The binary diagram between the $\delta^{13}\text{C}$ and C/N rate (Fig. 4) confirm this
521 palaeoenvironment, as they recorded terrestrial C_3 plants with influence of terrestrial C_4
522 plants and marine algae (Fig. 4). The enrichment trend of $\delta^{13}\text{C}$ values from -25 to
523 -21‰ and decreasing trend of C/N from 35 to 11 between 80 and 0 cm (Figs. 3 and 4)
524 indicates that during the late Holocene occurred an increase in contribution of organic
525 matter sourced of salinity tolerant phytoplankton, which characterizes the current
526 conditions of the Flamenco Lagoon.

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

535 The spatial patterns of mangroves and associated vegetation are controlled by
536 interaction of important key factors that cause a species zonation (Jiménez and Sauter,
537 1991; McKee, 1993; Raffaelli and Hawkins, 1999; Snedaker, 1982). This vegetation
538 zone arise from the succession, and they have been frequently discussed (Berger et al.,
539 2006; Fromard et al., 1998).

540 Important factors controlling this vegetation zone may be highlighted, such as
541 local competition for photosynthetic light in the canopy (Clarke and Allaway, 1993;
542 Khan et al., 2004), vegetation composition (Kairo et al., 2002), dispersal patterns
543 (Clarke, 1993), the competitive ability of species (Berger and Hildenbrandt, 2000),
544 microtopography (Di Nitto et al., 2008), tidal inundation frequency (Clarke and

545 Myerscough, 1993; Cohen and Lara, 2003), sediment chemistry (Da Cruz et al., 2013;
546 Mendoza et al., 2011) and porewater salinity (Krauss et al., 2008; Lara and Cohen,
547 2006).

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

551

552 *SLR and sediment accretion*

553 The stratigraphic sequence studied is compatible with the trends of SLR during the
554 Holocene to the Caribbean region (Gischler, 2015; Rull et al., 1999; Toscano and
555 Macintyre, 2003). Considering the water depth of 1 m in the sampling site, the position
556 of the sedimentary deposits, which represent the small drainage channels (creeks), are
557 positioned between 3.6 and 3.2 m below the current mean sea level. These sediments
558 were accumulated between ~5660 and ~5400 cal yr BP. During this time interval, the
559 sea level was between 5 and 3.8 m below the present mean sea level (Toscano and
560 Macintyre, 2003). Consequently, a significant portion of the continental shelf was
561 exposed, placing the coastline distant of the current position (Fig. 5). In this period, the
562 sedimentation in the studied sector was controlled by the drainage channel dynamics
563 with arboreal and herbaceous vegetation colonizing the margin of this channel. The
564 upward succession, between ~5400 and 4400 cal yr BP, composed of the transition from
565 the drainage channel into the tidal flat colonized by mangroves suggests an increase in
566 marine influence and forms a transgressive event. The SLR caused a marine incursion
567 with invasion of channels valleys. It favored the sedimentation into the channels and
568 their progressive filling up that produced a tidal flat occupied by mangroves (Fig. 5).
569 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 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 C3 and C4 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,

595 respectively (Toscano and Macintyre, 2003). At first, these data suggest a relation of
596 cause and effect between the rates of SLR and sediment accretion, when more space
597 was created to accommodate new sediments during the early Holocene than late
598 Holocene. However, as discussed below, other factors may be affecting the
599 sedimentation rates and consequently the mangrove dynamics in the studied area.

600 *Mangrove and SLR*

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

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

619 Holocene stratigraphic records from Bermuda show that mangroves maintain
620 the same pace as SLR at rates up to 0.9 mm/yr (Ellison and Stoddart, 1991).
621 Stratigraphy indicates that before 4000 yr BP sea level rose at a rate of 2.5 mm/yr; from
622 4000 to 1000 years BP the rate of SLR declined to 0.6 mm/yr during which time
623 mangroves established, and in the last 1000 years there was an increase to 1.4 mm/yr,
624 during which time the mangroves died back. The largest mangrove area in Bermuda has
625 for the last 2000 years been building peat at a rate of 0.8 to 1.1 mm/yr (Ellison, 1993).
626 In Laguna Grande, northeastern Puerto Rico, stratigraphic records indicate that its basin
627 began accumulating sediment ~3600 cal yr BP, and the sedimentation began in
628 Mangrove Lagoon ~3300 cal yr BP coincident with regional SLR (Lane et al., 2013).
629 Regarding the stratigraphic sequence to Flamenco Lagoon, in southwestern Puerto Rico,
630 the mangrove vegetation occurred only between ~5000 and ~4000 cal yr BP, when the
631 sedimentation rates were about 0.7 – 0.6 mm/yr, and the sea level rose about 1.5 mm/yr
632 (Toscano and Macintyre, 2003), more than double of the local sedimentation rate. After
633 this period, the mangroves disappeared from the study site, when the sedimentation
634 rates decreased to 0.3 mm/yr and the sea level rose 0.93 mm/yr.

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

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

650 *Mangrove and nutrient/sediment supply*

651 Caribbean mangrove forests are often underlain by deep peat deposits formed by the
652 gradual accumulation of organic matter (Macintyre et al., 2004; McKee and Faulkner,
653 2000; Middleton and McKee, 2001; Parkinson et al., 1994; Toscano and Macintyre,
654 2003). These mangrove forests are different from those receiving mineral sediment,
655 such as the mangroves near the mouth of the Amazon River (e.g. Cohen et al. 2012).

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

660 Some works described the contribution of mangrove roots to peat formation and
661 soil accretion (Krauss et al., 2014; Lovelock et al., 2015; McKee and Faulkner, 2000;
662 McKee et al., 2007; Parkinson et al., 1994). The indirect effects of plants on
663 sedimentation in mangrove have also been demonstrated (Furukawa and Wolanski,
664 1996; Krauss et al., 2003; Morris et al., 2002; Spenceley, 1977), through the physical
665 effects of vegetation on the trapping of mineral sediments. Then, likely, the decrease of
666 sediment and organic matter accumulation influenced on the mangrove development, as
667 well as the loss of mangrove areas also affected the sedimentation rates, and
668 consequently the marine transgression.

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

687

688 *Mangrove and climatic changes*

689 Considering that absence of mangroves in the study site was caused by a decrease in
690 nutrient and/or sediment input to coast area during the late Holocene, a relatively lower
691 rainfall rates in the Puerto Rico during that time may have triggered or contributed to
692 the process that caused the loss of mangrove area. Reconstruction of climate change
693 over the past 10,500 years based on $^{18}\text{O}/^{16}\text{O}$ ratios in ostracod shells from Lake

694 Miragoane, Haiti, indicates that water level in the lake rose at the end of the last
695 deglaciation (~10-7 kyr BP), reflecting the wetter conditions of the early Holocene
696 which persisted for nearly 4,000 years. Lake level declined at ~3.2 kyr BP with the
697 onset of a drier climate, which generally prevailed throughout the late Holocene (Hodell
698 et al., 1991). These results were corroborated by a vegetation reconstruction from the
699 same lake, which identified the middle Holocene as a period characterized by a greater
700 relative abundance of moist forest taxa. Climatic drying began ~3200 14C yr BP
701 (Higuera-Gundy et al., 1999). Records of stalagmite from Barbados indicate increased
702 rainfall intensity between 6.7 and 3 ka BP (Mangini et al., 2007). Banner et al. (1996)
703 also identified this wet period during the mid-Holocene through strontium-isotope
704 analysis of calcite layers from Barbados speleothems. A multiproxy analysis of
705 lacustrine sediments cored in Grand-Case Pond at Saint-Martin indicate severe drought
706 events from 3700 to ~2500 yr cal BP and from 1150 yr cal. BP to the present (Malaize
707 et al., 2011). Combined foraminiferal and XRF element analysis of sediment cores from
708 Punta de Cartas and Playa Bailen, Cuba, indicates arid conditions developing since 4
709 kyr BP and a pronounced drying over the last ~ 1200 years (Gregory et al., 2015). A
710 multiproxy analysis in an sediment core from Laguna Saladilla, Dominican Republic
711 indicate drier conditions since 2500 cal yr BP (Caffrey et al., 2015).

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

719 *Mangroves and water salinity*

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

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

741 The studied stratigraphic sequence suggests that the Flamenco Lagoon has
742 morphologically evolving to an increase of isolation from the open ocean (Figs. 1b and
743 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).

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 C3 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 C3 and C4 plants with some influence of marine organic matter. In the late

769 Holocene, an increase in contribution of marine organic matter occurred, which
770 characterizes the current conditions of the Flamenco Lagoon.

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

783

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Figure 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.

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

Figure 3 - Chronological profile with ecological groups and organic geochemical variables.

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

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

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

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

Table 3- Sedimentation rates for mangrove vegetation.

Table 1

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

Table 2

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

Table 3

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 Jr 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

Figure 1

Figure 1 BW

Figure 2

Figure 3

Figure 4

Figure 5

Figure 5 BW