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## **The effect of global warming on the establishment of mangroves in coastal Louisiana during the Holocene**

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26

## Abstract

27 Winter temperature and sea-level position are critical factors affecting the global  
28 distribution of mangroves and saltmarshes. The replacement of saltmarshes by  
29 mangroves is expected due to global warming, reflecting the long-term natural trends in  
30 the Holocene and anthropogenic impacts since the 20<sup>th</sup> century. We documented the  
31 Holocene history of wetlands dynamics in the boreal limits of the American mangroves,  
32 located at Bay Champagne, Louisiana (USA), by integrating sedimentological,  
33 palynological, geochemical ( $\delta^{13}\text{C}$  and  $\text{C/N}$ ), X-ray fluorescence (XRF) data, and  
34 radiocarbon chronology from two sediment cores. The results indicated a freshwater  
35 lake environment with herbs and wetland ferns, as well as  $\text{C}_3$  terrestrial plants, between  
36 ~8100 and ~6500 cal yr BP. This environment shifted into a lagoon and saltmarshes  
37 having sedimentary organic matter sourced from marine algae between ~6500 and  
38 ~1500 cal yr BP. In the final stage, washover sediments were deposited in the lagoon  
39 during the last ~1500 cal yr BP. Despite the increased marine influence over the last  
40 ~6500 cal yr BP, mangrove pollen were not recorded between ~8100 and ~1500 cal yr  
41 BP, suggesting that mangroves were absent in the study area during that time interval.  
42 Historical evidence and a comparative analysis of our multi-proxy data with other  
43 mangrove studies from the Gulf of Mexico, Caribbean, and eastern South America  
44 revealed a gradual mangrove expansion from tropical to subtropical coasts of South and  
45 North America during the mid-late Holocene. The mangrove colonies at their current  
46 boreal ( $29^\circ 09' \text{ N}$ ) and austral ( $28^\circ 29' \text{ S}$ ) limits were established in the early and mid  
47 20<sup>th</sup> century, respectively. This mangrove dynamics on a continental scale suggests that  
48 the poleward mangrove migration was likely caused by the warming climate during the  
49 Holocene. More importantly, the industrial-era warming has likely accelerated the

50 mangrove expansion, but it was not the primary force that drove the mangrove  
51 migration into temperate zones.

52 Keywords: Anthropocene; *Avicennia*; isotopes; palynology; Port Fourchon

### 53 **1.Introduction**

54 Mangroves are perhaps some of the most typical ecosystems of tropical coasts,  
55 consisting of valuable and productive intertidal forests (Food and Agriculture  
56 Organization of the United Nations., 2007; Ribeiro et al., 2019). The main products and  
57 services of mangroves include protection from storms and sea-level rise (Alongi, 2008);  
58 plant and animal productivity (Ewel et al., 1998); sources of organic matter for coastal  
59 ecosystems (Walsh and Nittrouer, 2004; Dittmar et al., 2006); and sequestration and  
60 storage of atmospheric and oceanic carbon, thereby mitigating climate change effects  
61 (Fisher and Huo, 2012; Taillardat et al., 2018).

62 Mangroves are also very useful indicators of climate and sea-level changes  
63 (Blasco et al., 1996; Fromard et al., 2004; Alongi, 2008) due to the high susceptibility to  
64 variations in air/water temperatures, subsidence, tidal flooding frequency, river  
65 discharge, estuarine salinity, and nutrient flux, as well as tropical cyclones intensified  
66 by climate changes (Amaral et al., 2006; McLeod and Salm, 2006; Cohen et al., 2012;  
67 Krauss et al., 2014; Liu et al., 2014; Alongi, 2015; Yao and Liu, 2017). However,  
68 depending on the latitude and proximity of large estuaries, some environmental drivers  
69 may operate more intensely in controlling the mangrove dynamics, such as winter  
70 temperatures on subtropical zones (Cohen et al., 2020b), and fluvial discharge, for  
71 instance, near the Amazon River (Cohen et al., 2012). Regarding the northern and  
72 southern limits of American mangroves, the air/water temperature becomes the most  
73 critical factor in controlling the establishment, expansion, and contraction of mangroves

74 (Cavanaugh et al., 2018; 2019). This ecosystem cannot develop under low temperatures,  
75 and then they occur mainly between latitudes 25° N and 25° S (Giri et al., 2011). Its  
76 distribution is limited to zones where the coldest-monthly temperature average is above  
77 20°C and the annual temperature range is less than 5°C (Walsh, 1974; Chapman, 1975;  
78 Duke, 1992). This restriction is associated with mangrove's low tolerance to low air  
79 temperature, usually inhibiting at around 5°C (Tomlinsom, 1986; Stuart *et al.*, 2007;  
80 Krauss *et al.*, 2014). A consequence of global warming is that mangroves can expand  
81 into temperate zones. Some studies have documented the influence of changes in air  
82 temperature in the latitudinal distribution of mangroves (Everitt et al., 1996; Stevens et  
83 al., 2006a; Perry and Mendelssohn, 2009a; Stokes et al., 2010; Osland et al., 2015,  
84 2017, 2018, 2019).

85         Records of mangrove species on Earth during the Tertiary (Sherrod and  
86 McMillan, 1985) and Quaternary (Cannon et al., 2009) revealed that the climate  
87 controlled their establishment and extinction in the northern hemisphere (Sun and Li,  
88 1999). Mangrove dynamics is generally associated with global climate and sea-level  
89 changes since the Last Glacial Maximum (LGM) (Alongi, 2008). In North America,  
90 there were alternations of mangrove expansion and contraction in response to  
91 pronounced changes in temperatures over the late Quaternary (Sherrod and McMillan,  
92 1985; Woodroffe and Grindrod, 1991; Sandoval-Castro et al., 2012a; Saintilian et al.,  
93 2014; Osland et al., 2017), and they were restricted to regions equatorward of their  
94 modern limits during the LGM. During this period, mangroves also decreased in Asia  
95 and Europe (Woodroffe and Grindrod, 1991; Cannon et al., 2009), being restricted to  
96 refuge areas with less impact of cold air temperature (Cannon et al., 2009). However, a  
97 poleward expansion was recorded in the Northern Hemisphere after 19000 years ago  
98 (Sandoval-Castro *et al.*, 2012b; Kennedy *et al.*, 2016). In the Caribbean, mangrove

99 northern limit retreated to more equatorial zones during the Pleistocene (Sherrod and  
100 McMillan, 1985). As a result of warmer climates and higher sea levels during the  
101 Holocene, mangroves expanded poleward, reaching Florida (Yao and Liu, 2017), Texas  
102 (Sherrod and McMillan, 1985), and Louisiana (McKee and Vervaeke, 2018) at different  
103 times.

104         According to pollen and isotopic studies from the South China Sea, mangroves  
105 would have replaced boreal forests and temperate grasslands due to a slight increase in  
106 air temperature and slow marine transgression at ~14000 cal yr BP (Sun and Li, 1999).  
107 Meanwhile, mangroves were not recorded in North America or Europe, probably due to  
108 the low temperatures (Sherrod and McMillan, 1985).

109         The increased winter temperatures during the last century (IPCC, 2014), mainly  
110 in boreal and temperate regions (Solomon et al., 2007), caused a mangrove expansion in  
111 the Gulf of Mexico (Cavanaugh et al., 2014), resulting in the replacement of salt marsh  
112 vegetation dominated by *Spartina alterniflora* (Sherrod and McMillan, 1985).

113         The ecological implications of global warming to the new biogeography of  
114 ecosystems adapted to tropical areas in the near future can be studied by reconstructing  
115 the long-term dynamics of mangroves, mainly along the northern and southern  
116 mangrove limits in the Americas. As such, a stratigraphic analysis of mangroves  
117 relative to sea-level and climate changes during the Holocene must be provided from  
118 various coastal environments to permit an inter-regional comparison. This work aims to  
119 discuss the influence of sea-level changes and global warming on American mangroves  
120 during the Holocene. We studied the Holocene changes in coastal depositional  
121 paleoenvironments, and the dynamics of temperate vegetation and mangroves in  
122 southern Louisiana, USA, representing the modern boreal limit of the American  
123 mangroves, by the integration of sedimentological, palynological, geochemical ( $\delta^{13}\text{C}$

124 and C\N), X-ray fluorescence (XRF) data, and radiocarbon chronology. These data are  
125 essential to evaluate and calibrate models that predict the fate of mangroves as the  
126 minimum winter temperatures continue to increase (Cavanaugh et al., 2014; 2015;  
127 2018).

## 128 **2. Study area**

### 129 *2.1 Geomorphology*

130 The Caminada-Moreau Headland is a complex mosaic of barrier islands formed by the  
131 transport of sediments by wind, waves, and tidal and longshore currents (Kulp et al.,  
132 2005). The study area in Bay Champagne (29° 6' 53, 10" N / 90° 10' 33, 38"W, Fig. 1)  
133 is located in the southwestern end of this headland, near Port Fourchon in the State of  
134 Louisiana. This site is part of the Lafourche complex delta lobes, formed ~3500 years  
135 ago, and remained active until 1600 to 600 cal yr BP. During this time, nutrient-rich  
136 sediments were deposited in floodplains along tributaries, contributing to establishing  
137 wetland systems across subdeltas (Blum and Roberts, 2012).

138 Bay Champagne (BC) is a semi-circular brackish lagoon (salinity: 32‰) (Fig. 1b,  
139 and c), with a maximum depth of 2.5 m (Liu et al., 2011). The lagoon is surrounded by  
140 cordgrass (*Spartina alterniflora*) and black mangrove (*Avicennia germinans*) vegetation  
141 (Naquin et al., 2014a). A sandy barrier, standing ~2 m above the mean relative sea-  
142 level, partially protects the backbarrier tidal flat wetlands from the impact of high  
143 energy waves and storm-forced winds (Dietz et al., 2018). Local barrier islands,  
144 including the Timbalier Island and Grand Isle (Penland, 1988), are strongly affected by  
145 erosion due to overwashing (Liu et al., 2011; Dietz et al., 2018). In addition, the decadal  
146 historical record from Bay Champaign indicates rapid shoreline retreat and coastal  
147 erosion in this area, especially during active periods of hurricanes, exacerbating the  
148 long-term trend of coastal subsidence and land loss (Dietz et al., 2018). A re-

149 nourishment project was initiated in 2012 and completed in 2014 (Coastal Engineering  
150 Consultants Inc., 2015), attempting to interrupt the rapid shoreline retreat process and  
151 sustain barrier beaches along the Caminada-Moreau headland (Jafari et al., 2018).

152 The coastal region in southern Louisiana is especially vulnerable to global  
153 climate change (Dietz et al., 2018; Johnson et al., 2020), resulting from the Holocene  
154 sea-level rise (Kjerfve, 1994). Traditional models have indicated a sea-level 3 to 4 m  
155 below present at 6,000 years BP, followed by a rise to 1.5 m below present at 5,000 BP  
156 (Saucier, 1994).

## 157 2.2 Physiography

158 The climate in the study area is humid subtropical, with mean monthly temperatures  
159 between 6°C and 30°C. The mean precipitation is about 1600 mm/year, with the wetter  
160 season from June to September and the drier season from September to June (National  
161 Climatic Data Center, 2018). During the last two centuries, the Louisiana coast has been  
162 subjected to climatic anomalies (Mock et al., 2007; Perry and Mendelssohn, 2009b).  
163 The Louisiana coast is frequently affected by severe weather phenomena, including  
164 hurricanes, heavy rainfall, flooding, drought, heatwaves, and freezing events (Vega,  
165 2012). Beach fronts and dunes along the Caminada coast support salinity tolerant  
166 vegetation, especially graminoid such as cordgrass (*Spartina alterniflora*), sea oats  
167 (*Uniola paniculata*), and bitter panicum (*Panicum amarum* var *amarum* 'Fourchon').  
168 Cordgrass is found on active overwash deposits (Brantley et al., 2014). Trees and shrubs  
169 are mainly represented by wax myrtle (*Myrica cerifera*), iva (*Iva imbricate*), vine  
170 (*Lycium barbarum*), eastern baccharis (*Baccharis halimifolia*), and black mangroves  
171 (*Avicennia germinans* L.) (Henry and Twilley, 2013). After the restoration project  
172 (Coastal Engineering Consultants Inc, 2015), the Caminda coastline has been used for  
173 vegetative plantations, including various native dune grass species. Data about the

174 modern American mangrove distribution were obtained at <http://data.unep->  
175 [wcmc.org/datasets/4](http://data.unep-wcmc.org/datasets/4).

### 176 **3. Materials and methods**

#### 177 *3.1. Remote sensing*

178 The spatial analysis was developed with high-resolution images obtained by the drone  
179 Phantom 4 Advanced DJI. This drone had a FC 6310 digital 4K/20MP (RGB), which  
180 provided images of high spatial resolution (2.6 cm) of the study area. The drone images  
181 were processed using the Agisoft Metashape Professional version 1.6.2 software. The  
182 vegetation was visually classified by photointerpretation using various tools in the  
183 Global Mapper Software 19. Details about the image processing may be obtained in  
184 Cohen et al. (2020a; 2020b).

185

#### 186 *3.2. Sampling and facies description*

187 Two sediment cores (BC81- 2,75 m, 29° 6' 53,10" N / 90° 10' 33,38"W and BC82 - 4  
188 m, 29° 6' 48,88' N / 90° 10' 40,83" W) were acquired via an aluminum push corer at the  
189 southern margin of the BC lagoon (Fig. 1b and 1c). The cores were measured and  
190 photographed in the field and kept in a cold room (4°C) at Louisiana State University.  
191 Grain size analysis (5 cm intervals) was determined by laser diffraction in the  
192 Laboratory of Chemical Oceanography of the Federal University of Pará UFPA  
193 (Brazil).

194 Sedimentary features, such as color, texture, lithology, and structure, were used to  
195 characterize the facies (Harper, 1984; Walker, 1992). The code of sedimentary facies  
196 was based on Miall (1978). The facies, pollen, isotopes, and elemental analyses were  
197 grouped into facies associations to determine a sedimentary environment (Reading,



198 1996). Cluster analysis of pollen grains supported the grouping of the facies  
199 associations.

### 200 *3.3. LOI and XRF data*

201 Loss-on-ignition (LOI) analysis was performed at 1 cm intervals. It involved heating  
202 sediment samples at 105°, 550°, and 1000°C to determine the contents of water, organic  
203 matter, and carbonates, respectively. XRF analysis was performed by scanning the core  
204 at 2 cm intervals using a handheld Innov-X Delta XRF. Only the major chemical  
205 elements in coastal sediments (ppm) representative of marine (e.g. Br, Ca, Cl, and Sr)  
206 and terrestrial (e.g. Fe, Ti, and Mn) origins were selected for this analysis (Yao et al.,  
207 2015).

### 208 *3.4. Palynological analysis*

209 The cores were sub-sampled at intervals of 5 cm, whereby 1 cm<sup>3</sup> of sediment was  
210 removed for pollen analysis. Before the sediment processing, one tablet of exotic  
211 *Lycopodium* spores was inserted into each sample to calculate the pollen concentration  
212 (grains/cm<sup>3</sup>) and pollen accumulation rates (grains/cm<sup>2</sup>/year). Sediment samples were  
213 treated following traditional pollen analytical procedures, using hydrochloric acid,  
214 hydrofluoric acid, and acetic anhydride/sulfuric acid (Fægri and Iversen 1989). The  
215 product of this treatment was fixed on slides in a glycerin gelatin medium. Pollen and  
216 spore morphology books were used as references (McAndrews *et al.*, 1973; Willard *et*  
217 *al.*, 2004), as well as the collections of the LSU Global Paleoecology Lab. A minimum  
218 of 300 pollen grains were counted for each sample. The total pollen sum did not include  
219 fern spores, algae, and foraminifers. Pollen diagrams are presented as percentages of the  
220 total pollen sum. The taxa were categorized into: herbs, trees and shrubs, and aquatics.

221 Cluster analysis and pollen diagram plotting were processed by the software TILIA  
222 (Version 1.7.16) (Grimm, 1990).

### 223 *3.5. Isotopic analysis and radiocarbon dating*

224 The isotopic composition ( $\delta^{13}\text{C}$ ) of modern organic matter was analyzed from 134  
225 samples (6-50 mg) taken at 5 cm intervals along the two cores. The stable carbon  
226 isotopes were determined at the Stable Isotopes Laboratory of the Center for Nuclear  
227 Energy in Agriculture (CENA/USP), using an ANCA SL2020 mass spectrometer (see  
228 further details in Pessenda et al. (2004)). Five sediment samples (~2 g each) were used  
229 for radiocarbon dating. The samples were physically cleaned using a microscope to  
230 prevent natural contamination at  $^{14}\text{C}$  Laboratory of CENA (Pessenda et al., 2004). The  
231 organic matter was chemically processed by treating with 2% HCl at 60°C over 4h,  
232 washed with distilled water, and dried (50°C) to eliminate young organic fractions  
233 (fulvic and/or humic acids) and carbonates (Pessenda et al., 2010; 2012). The sediment  
234 organic matter was analyzed by Accelerator Mass Spectrometry (AMS) at the  $^{14}\text{C}$   
235 Laboratory of CENA/USP, LACUFF (Fluminense Federal University, Brazil), and  
236 Center for Applied Isotope Studies (UGAMS) of the University of Georgia.  
237 Radiocarbon ages are reported in years before 1950 CE (yr BP). The radiocarbon ages  
238 were normalized to  $\delta^{13}\text{C}$  of  $-25\text{‰}$ VPDB, and are presented in cal yr BP, with a  
239 precision of  $2\sigma$  (Reimer et al., 2013).

## 240 **4. Results**

### 241 *4.1. Radiocarbon ages and sedimentation rates*

242 Radiocarbon ages and sedimentation rates are provided in Table 1. The ages recorded  
243 ranged from 8113 to 1470 cal yr BP (Figs. 2 and 3). Partial age inversions were  
244 observed between 350 (6286 - 6454 cal yr BP) and 300 cm (6406 - 6645 cal yr BP)

245 (Fig. 3). It can be attributed to high sedimentation rates and/or reworking of organic  
246 remains by storms or bioturbation by benthic organisms (Pessenda et al., 2012). The  
247 sedimentation rates ( $0.2$  to  $1 \text{ mm yr}^{-1}$ ) were within the range recorded in other cores  
248 sampled from tidal flats in the Gulf of Mexico (Naquin et al., 2014b; Yao et al., 2015).  
249 The sedimentation rates in the muddy segment ( $400 - 170 \text{ cm}$ ) of core BC82 were lower  
250 ( $0.6$  and  $0.26 \text{ mm/y}$ ) than in the sandy intervals ( $170 - 0 \text{ cm}$ ) of this core ( $1.11 \text{ mm/yr}$ )  
251 and core BC81 ( $0.77 \text{ mm/yr}$ ) (Figs. 2 and 3).

252

#### 253 *4.2. Facies description*

254 Three facies associations were recognized in the studied cores (Figs. 4, 5, and Table 2).  
255 Facies association A consisted of massive sand (facies Sm) and massive mud (facies  
256 Mm), related to a lacustrine environment. Facies association B consisted of lenticular  
257 and flaser heterolithic bedded deposits of facies Hl and Hf, respectively, related to a  
258 lagoonal environment. Facies association C, which included massive sand (Sm), and  
259 flaser heterolithic deposits (Hf), was attributed to washovers. These environments were  
260 interpreted based on the integration of sedimentary features with pollen, isotopic, C/N,  
261 LOI, and XRF data, as described in the following.

262

##### 263 *4.2.1. Facies association A (lacustrine)*

264 This facies association was represented by the  $400 - 310 \text{ cm}$  interval of core BC82,  
265 accumulated between  $\sim 8100$  and  $\sim 6500 \text{ cal yr BP}$ . It was characterized by massive mud  
266 (Mm) and lenticular heterolithic bedded deposits (Hl;  $40 - 80\%$  silt,  $20-60\%$  clay),  
267 ranging in color from dark brown ( $2.5/110Y$ ) to dark gray ( $3/1 10Y$ ). This facies  
268 association contained  $\sim 4\%$  of carbonate and  $\sim 7\%$  of organic matter. Two ecological  
269 groups characterized by herbaceous ( $25 - 65\%$ ) and tree and shrub pollen ( $30 - 55\%$ )

270 were present. The herbaceous taxa were predominantly composed of Amaranthaceae (0-  
271 20%), Asteraceae (0-18%), Poaceae (0-12%), *Amaranthus* (0-5%), and *Artemisia* (0-  
272 4%). Arboreal taxa were mainly represented by *Pinus* (0-35%), Fagaceae (0-3%),  
273 *Betula* (0-1%), and *Quercus* (0-1%). Fern pollen mainly consisted of Polypodiaceae  
274 (Fig. 3). XRF analysis indicated the highest concentration of Fe (14 k – 20 k ppm), K  
275 (8 k – 13 k ppm), Ti (1.5 k – 2 k ppm), and Mn (370 – 800 ppm), while the values for  
276 Cl (3.5 k – 12 k ppm), Ca (5.3 k – 8.6 k ppm), Br (184 - 248 ppm), and Sr (63 - 98  
277 ppm) were the lowest.  $\delta^{13}\text{C}$  values oscillated between -24.4‰ and -22.02‰ ( $\bar{x} = -$   
278 24‰), while the C/N ratio alternated between 12 and 52 ( $\bar{x} = 25$ ) (Fig. 5).

279

#### 280 4.2.2. Facies association B (lagoonal)

281 This facies association was evidenced in cores BC81 (270 – 170 cm) (Figs. 2 and 4),  
282 and BC82 (300 – 170 cm) (Figs. 3 and 5). The sediments were accumulated between  
283 ~6525 and ~1470 cal yr BP in core BC82 and up to ~2128 cal yr BP in core BC81.  
284 They consisted of dark gray (4/1 10Y) massive mud (Mm) and lenticular heterolithic  
285 bedded deposits (Hl; 0 - 80% sand, 15 - 80% silt, 5 - 60% clay). This facies association  
286 contained ~4% of carbonate and ~7% of organic matter. The bivalve *Rangia cuneata*  
287 was present in life position. The palynological analysis permitted the identification of  
288 three ecological groups, represented by pollen of herbs (50 – 70%), trees and shrubs (20  
289 – 55%) and aquatic plants (2 – 10%), in addition to marine markers, such as  
290 dinoflagellate cysts and foraminifera. Herbs were mainly represented by Poaceae (0-  
291 25%), Amaranthaceae (0-14%), Asteraceae (0-6%), *Amaranthus* (0-4%), *Ambrosia* (0-  
292 4%), *Bolboschoenus* (5%), Caryophyllaceae (2%), *Spartina* (0-3%) and  
293 Chenopodiaceae (0-2%). Arboreal pollen included mainly *Pinus* (0-20%), *Quercus* (0-  
294 3%), *Betula* (0-3%), and *Alnus* (0-2%). The group of aquatic plants was predominantly

295 composed of *Typha angustifolia* (0-14%) and *Typha latifolia* (0-3%) (Figs. 2 and 3).  
296 *Typha angustifolia* disperses as a reticulate, monoporate monad pollen ( $22.7 \pm 2.6 \mu\text{m}$ )  
297 (Fig. 1a and b, supplementary material), and *Typha latifolia* is reliably represented in  
298 the pollen record as perforate-reticulate, tetrads pollen ( $25.70 \pm 1.58$ ) (Finkelstein,  
299 2003; Hamdi et al., 2010; Skvarla and Larson, 1963) (Fig. 1c and d, supplementary  
300 material). XRF results revealed an increasing trend in Cl (3 k– 20 k ppm) and Br (190 –  
301 950 ppm) and a decreasing trend in Fe (7 k - 17.5 k ppm) and Mn (186 – 500 ppm)  
302 compared to facies association A. Facies association B presented more enriched  $\delta^{13}\text{C}$   
303 values ( $\sim -22\text{‰}$ ) than the facies association A ( $\sim -24\text{‰}$ ). C/N values decreased upward  
304 from  $\sim 25$  to  $\sim 11$  within this association (Figs. 4 and 5).

305

#### 306 4.2.3. Facies association C (washover)

307 These deposits were identified in both studied cores in the interval 170 – 0 cm, formed  
308 during the last  $\sim 1470$  cal yr BP (170 – 0 cm) and  $\sim 2100$  cal yr BP in the cores BC82  
309 and BC81, respectively. The cores consisted of dark gray (4/1 10Y) flaser heterolithic  
310 bedded deposits (facies Hf; 60 - 100% sand, 0-40% silt, 0- 10% clay); sandy layers were  
311 cross laminated. The upper part of facies association A was characterized by massive  
312 sand (Sm; 14% coarse, 73% medium, 13% fine); grain size increased gradually upward  
313 in this sandy facies. Shell fragments were frequent in this association. The carbonate  
314 concentration oscillated between 4 and 20%, while the organic matter decreased upward  
315 from 4 to 2%. A wide range of variation was recorded for the concentrations of Ca (2.7  
316 k – 130 k ppm), Sr (100 – 572 ppm), Zn (0 – 46 ppm), and Zr (44 – 422 ppm). The  
317 concentration of Ti (270 – 1134 ppm), and Fe (2100 – 7200 ppm) also varied largely,  
318 but with values that were lower than in facies associations A and B.  $\delta^{13}\text{C}$  and C/N

319 values oscillated between -20 and -27‰ and 3 and 28, respectively. No pollen grain was  
320 found in this facies association (Figs. 4 and 5).

321

### 322 *5.0. Discussion*

323 The sampling sites are accumulating washover sediments at present (Fig. 1b and 1c).  
324 These sites were chosen due to their position in the central portion of an old lake (Fig.  
325 7), with the potential to preserve the oldest lacustrine records. Depositional  
326 environments with a predominance of sandy sediments are not suitable for preserving  
327 pollen grains (Havinga, 1967). However, such environment may have evolved from an  
328 environment with low hydrodynamic flow that was favorable for the muddy (silt and  
329 clay) sedimentation (Reineck and Singh, 1980; Reading, 1996) and suitable for pollen  
330 preservation, as indicated by several pollen studies in tidal flats (Behling et al., 2001;  
331 2004; Cohen et al., 2005a; 2005b; 2012; 2020b, Guimarães et al., 2013; Moraes et al.,  
332 2017; Ribeiro et al., 2018), fluvial flood plains (Cohen et al., 2014; 2020a; Fontes et al.,  
333 2017; Lima et al., 2017; Silva et al., 2018), lagoons (Cohen et al., 2020b, 2016; Franca  
334 et al., 2016), and lakes (Lara and Cohen, 2009; Smith et al., 2011; Buso Junior et al.,  
335 2013). For example, oxbow lakes, developed after a channel abandonment, can be filled  
336 by muddy sediments and converted into a fluvial terrace or an active channel with sandy  
337 deposition (Cohen et al., 2014; Rossetti et al., 2014). In the case of the study area,  
338 evidence based on facies association indicated the development of a lake (~8100 -  
339 ~6500 cal yr BP), which subsequently evolved into a lagoon (6500 – 1470 cal yr BP).  
340 Relatively high pollen concentrations (50 k – 200 k pollen grains/cm<sup>3</sup>, Figs. 2 and 3) in  
341 the sediments from this period suggested that the land around the lake and lagoon was  
342 well-vegetated. Gradually over the last ~1470 cal yr BP, this coastal lake and lagoon at

343 the coring site has been filled by washover sandy sediment, which was not conducive to  
344 retention and preservation of pollen.

345

## 346 5.1. Depositional phases

### 347 5.1.1. Early Holocene (~8100 - ~6500 cal yr BP): lacustrine

348 The prevalence of muddy deposits in facies association A (i.e., basis of core BC82, 400  
349 – 310 cm) indicates a low energy depositional environment, most likely a freshwater  
350 lake. The  $\delta^{13}\text{C}$  and C/N, ranging from -24.4 to -22.02‰ and 12 to 52 respectively,  
351 recorded in these deposits support that C3 terrestrial plants were the source for the  
352 sedimentary organic matter (C3 plants  $\delta^{13}\text{C}$ : -32‰ to -21‰ and C/N: > 12; Deines,  
353 1980; Meyers, 1994; Tyson, 1995). The concentrations of K, Ti, Fe, and Mn in facies  
354 association A were compatible with values recorded in environments with a high input  
355 of terrestrial sourced sediment (Cuven et al., 2013; Yao et al., 2018). The presence of  
356 arboreal pollen from *Pinus*, *Quercus*, Fagaceae, and *Betula*, as well as herbs (mainly  
357 represented by Asteraceae and Amaranthaceae) and wetland ferns (represented by  
358 Polypodiaceae), conforms with a freshwater, terrestrial setting. Altogether, these  
359 characteristics are taken as evidence of a lacustrine environment for facies association  
360 A. The inferred lake developed in the study area during the early Holocene when the  
361 sea-level was ~8 m below the modern sea-level (Donoghue, 2011) (Fig. 7).

362

### 363 5.1.2. Mid-late Holocene (~6500 - ~1470 cal yr BP): lagoonal

364 This phase is recorded by facies association B, which is lithologically similar to the  
365 lacustrine deposits characterized by the prevalence of muddy components (facies Mm  
366 and Hl) indicating low energy environments. However, the presence of the bivalve  
367 *Rangia cuneate* attests to a connection to marine waters, as this species is typical of

368 brackish water environments (Tarver, 1972; Warzocha et al., 2016). This bivalve, native  
369 to the Gulf of Mexico (Benson, 2010), has often been used to indicate marine influence  
370 during the Holocene (Rodriguez et al., 2004; Wakida-Kusunoki, MacKenzie, 2004).  
371 Accordingly, we interpret facies association B to represent a lagoon. The slight  
372 enrichment of  $\delta^{13}\text{C}$  values in facies association B ( $\sim -22\text{‰}$ ) compared to the lacustrine  
373 deposits ( $-24\text{‰}$ ), and the decreasing C/N values from  $\sim 25$  to  $\sim 9$ , suggest the  
374 contribution of marine organic matter ( $\delta^{13}\text{C}$ :  $-24\text{‰}$  to  $-16\text{‰}$  and C/N:  $< 10$ ; Deines,  
375 1980; Meyers, 1994; Tyson, 1995) (Fig. 6), as expected in a lagoon. The upward  
376 increase of Cl (from 4 k to 13 k ppm) and Br (from 264 to 950 ppm) and decrease of Fe  
377 (from 16 k to 11 k ppm) and Mn (from 400 to 200 ppm) are also indications of a coastal  
378 environment with marine influence and lower input of terrestrial sediments. The pollen  
379 assemblage, marked by the increased abundance of brackishwater herbaceous  
380 (*Bolboschoenus*, *Spartina*) and brackishwater aquatic (*Typha angustifolia* and *Typha*  
381 *latifolia*) plants, is further consistent with the inferred lagoon environment. The aquatic  
382 macrophyte cattail (*Typha*) can tolerate environments with high salinity (Hameed et al.,  
383 2012; Akhtar et al., 2017) and variation in water level (Ladislas et al., 2012).  
384 Paleoecological studies in brackish lagoonal deposits from Mexico also indicated the  
385 establishment of *Typha*  $\sim 6000$  cal yr BP (Caballero et al., 2005). In addition, the  
386 occurrence of foraminifera and dinoflagellate cysts in this stratigraphic unit is further  
387 evidence for a marine-influenced environment, such as a lagoon.

388

### 389 5.1.3. Late Holocene (last $\sim 1470$ cal yr BP): shoreline retreat

390 This phase is recorded by facies association C, whereby the muddy deposits changed  
391 abruptly upward into heterolithic mud/sand and massive sand. It represents the modern  
392 washover sediments that are deposited inland of a beach by overwash. Overwash is the



393 flow of water and sediment over the beach's crest that does not return to the water body.  
394 Coastal overwash is mainly caused by hurricanes and winter storms along the Atlantic  
395 and Gulf Coasts of the United States (Liu, 2004; Donnelly et al., 2006). This  
396 sedimentary succession may reflect the gradual landward migration of sandy coastal  
397 barriers due to marine transgression (Fig. 7). This interpretation is based on the  
398 increased marine influence with respect to the lagoon deposits of the previous phase.  
399 This is evidenced by the lower input of terrestrially-sourced sediments evidenced by the  
400 decreasing trend of Ti (1700 to 400 ppm), Fe (from 12 k to 2 k ppm), and Mn (from 230  
401 to 75 ppm) and strong oscillations of Ca (2 k – 129 k ppm), Cl (5.6 k – 24 k ppm), Sr  
402 (100 – 572 ppm), Br (230 – 1200 ppm), Zn (0 – 46 ppm), and Zr (44 – 422 ppm). High  
403 Zn and Zr values are found in the sand fraction. Then, probably, oscillations of Zn and  
404 Zr values indicated phases of rock weathering carried by the action of the currents and  
405 tides and deposited as beach sand. Ca, Cl, Br, and Sr are constituents of  
406 biogeochemical cycling in marine systems (Yao and Liu, 2017; Joe-Wong et al., 2019).  
407 The significant decrease in C/N values, from ~10 to ~6, with respect to the lagoonal  
408 phase, and the  $\delta^{13}\text{C}$  values, between -20‰ and -27‰, are consistent with this  
409 interpretation (marine algae,  $\delta^{13}\text{C}$ : -24‰ to -16‰ and C/N: < 10) (Deines, 1980;  
410 Meyers, 1994; Tyson, 1995) (Fig. 6). Local oscillations of these values that were  
411 synchronized with Ca, Sr, Zn, and Zr peak concentrations are probably a result of storm  
412 events, since this coastline is notably affected by intense hurricanes and tropical storms  
413 (Dietz et al., 2018; Johnson et al., 2020).

414

## 415 5.2. Absence of mangrove pollen along the cores

416 The analyzed cores did not contain mangrove pollen grains, despite the dense  
417 occupation of *Avicennia* trees around the lagoon nowadays. Noteworthy is that lakes,

418 lagoons, tidal flats, and fluvial floodplains present suitable hydrodynamic conditions for  
419 muddy sedimentation with pollen derived from plants that lived at the times the  
420 sediments were deposited. Under this situation, lagoonal and lacustrine sediments  
421 preserve pollen grains transported by wind and from the flora surrounding the lake or  
422 lagoon. The spatial representation of lagoonal or lacustrine pollen records changes  
423 according to the wind intensities and the watershed area influencing the lake or lagoon  
424 (Cohen et al., 2008; 2014). In addition, the pollen percentage of each vegetation unit is  
425 distance-weighted, where the closer to the source, the greater the pollen signal from that  
426 plant (Davis, 2000; Xu et al., 2012). Thus, pollen accumulated in lagoon or lake  
427 sediments presents a wider spatial representation of the regional flora than tidal flats  
428 sediments. Pollen rain in tidal flats, mainly occupied by dense mangrove forests, should  
429 indicate local vegetation, while open canopy tends to present a higher proportion of  
430 long distance transport pollen rain (Weng et al., 2004; Gosling et al., 2009).

431         Considering the pollen grains can be transported by wind and currents mainly in  
432 open areas (Brush and Brush, 1972; Solomon et al., 1982; Weng et al., 2004), it is  
433 common to record <1% pollen grains that do not represent the local vegetation during  
434 the sediment accumulation. For instance, a core taken from a marsh in southwestern  
435 Louisiana revealed one or two *Avicennia* pollen grains in the 0, 210, and 280 cm depth,  
436 probably transported by currents or hurricanes (Yao et al., 2020). By contrast, cores  
437 taken from tidal flats occupied by mixed mangroves with *Rhizophora*, *Laguncularia*,  
438 and *Avicennia* in Florida contained pollen percentages of 30 – 60% of *Rhizophora*, 5 –  
439 20% of *Avicennia*, and 5 – 15% of *Laguncularia* (Yao et al., 2015; Yao and Liu, 2017).  
440 The lagoon and tidal flat sediments covered by *Avicennia* trees in Bay Champagne, the  
441 study area, accumulate between 6 and 9% of *Avicennia* pollen (Ryu, 2020). In  
442 Amazonian mangroves, pollen traps installed on tidal flats occupied only by *Avicennia*

443 trees present ~15% (~540 grains/cm<sup>2</sup>/yr) of *Avicennia* pollen (Behling et al., 2001).  
444 Accumulation rates of *Avicennia* pollen are also relatively elevated in a mangrove with  
445 *Rhizophora* and *Avicennia* trees (average 450 grains/cm<sup>2</sup>/yr). Even in mangroves  
446 dominated by *Rhizophora*, pollen grains of *Avicennia* may be found (average 120  
447 grains/cm<sup>2</sup>/yr) (Behling et al., 2001). In addition, *Avicennia* pollen grains have been  
448 found in thousands of stratigraphic pollen spectra obtained from cores sampled from the  
449 American coasts with *Avicennia* trees (e.g. Cohen et al., 2005a 2005b; 2009; 2012;  
450 2014; 2015; 2016, Vedel et al., 2006; Peros et al., 2007; Guimarães et al., 2011, 2013;  
451 Smith et al., 2011, 2012; França et al., 2014, 2016, 2019b; Yao et al., 2015b, 2017;  
452 Moraes et al., 2017; Ribeiro et al., 2018; Cordero-Oviedo et al., 2019; Jones et al.,  
453 2019).

454         These data suggest that sediments accumulated in tidal flats or lagoons with  
455 *Avicennia* or near *Avicennia* trees tend to have a significant *Avicennia* pollen  
456 representation. Therefore, the absence of *Avicennia* pollen grains in the sedimentary  
457 sequences formed during the lake (8100 – 6500 cal yr BP) and lagoon (6500 – 1470 cal  
458 yr BP) phases in our cores (Figs. 2 and 3) suggests that mangroves with *Avicennia* trees  
459 were absent at or near our study site during the Holocene.

460         The absence of mangroves in the modern northern limit of American mangroves  
461 between ~8100 and ~1470 cal yr BP is an important finding that contributes  
462 significantly to the discussions about the main forces driving the mangrove  
463 establishment on the American continent during the Holocene, as well as its poleward  
464 expansion in the Anthropocene (since the mid-twentieth century (Zalasiewicz et al.,  
465 2018)). Nevertheless, it is necessary to assess the effects of sea-level rise on the studied  
466 coastal vegetation and morphology, since the salinity gradients along the zones under

467 marine or estuarine influence need to be conducive to mangrove development (Lara  
468 and Cohen, 2006).

469

470

### 471 5.3. American mangrove establishment controlled by sea-level

472 Mangroves colonized the distal portion of the continental shelf during the Last Glacial  
473 Maximum (LGM) (~27 and ~ 20 k cal yr BP) due to the worldwide lowering of the  
474 eustatic sea-level (Murray-Wallace, 2007; Cohen et al., 2014). The continental shelf  
475 emerged almost completely, positioning the coastline at some sites ~100 km of its  
476 current location (Nittrouer et al., 1996; Clark et al., 2009; Harris et al., 2013). After the  
477 LGM low sea-level, melting ice sheets caused transgression between 16 and 4 ka in  
478 many areas of southern North America (Gischler, 2015) and, probably, a landward  
479 mangrove migration along the continental shelf (Cohen et al., 2012; 2014). A rapid  
480 relative sea-level rise was recorded on the eastern coast of South America during the  
481 early-middle Holocene. The sea-level in southeastern and northeastern Brazilian coast  
482 was between 5 and 1 m above the modern sea-level, at approximately 5500 cal yr BP,  
483 with a gradual fall during the middle to late Holocene (Angulo et al., 2006, 2016;  
484 Caldas et al., 2006; Lorente et al., 2013; Cohen et al., 2020a). Sea-levels comparable to  
485 the modern one were already reached between 6000 and 5000 cal yrs BP in the northern  
486 Brazilian coast (Cohen et al., 2005b; 2012). Several works have attributed the mangrove  
487 establishment in the middle Holocene along the tropical coasts to the lower rates of sea-  
488 level rise or a stable sea-level in the middle Holocene (Woodroffe et al., 1985, 2015;  
489 Toscano and Macintyre, 2003; Khan et al., 2017; Ribeiro et al., 2018; Cohen et al.,  
490 2020a) (Fig. 8). Then, mangroves were established in the tropical Brazilian littoral at  
491 ~7000 cal yr BP: Espírito Santo (19° S), Bahia (17° S), Rio Grande do Norte (5° S),

492 Pará (1° S), and Amapá (2° N) (Cohen et al., 2012; 2014; 2020a; Pessenda et al., 2012;  
493 França et al., 2013, 2015; Fontes et al., 2017; Ribeiro et al., 2018).

494 Similarly, transgressive events were also recorded in the northern Gulf of  
495 Mexico (Anderson and Fillon, 2004), with a high sea-level rise rate of  $7.4 \pm 0.7$  m/ka in  
496 the early Holocene, and a reduced rate of 2.3 mm/yr in the middle to late Holocene  
497 (Wanless et al., 1994; Khan et al., 2017). The relative stability of modern coastal  
498 systems along the Gulf of Mexico is primarily due to the stabilization of sea-level  
499 approximately 6,000 years ago (Donoghue, 2011). Blum et al. (2002) proposed that the  
500 middle Holocene sea-level along the Texas Gulf coast was at -9 m at ca. 7.8 ka, then  
501 rose rapidly to +2 m by ca. 6.8 ka. However, according to Khan et al. (2017), the  
502 relative sea-level did not exceed the present height during the Holocene, and around  
503 ~6.5 ka, sea-level was at 6.2 m below the modern sea-level (Willard and Bernhardt,  
504 2011). The sea-level, which was near the modern level during the middle Holocene,  
505 allowed mangrove establishment in the Caribbean and Gulf of Mexico coast, a tropical  
506 zone, at ~6100, ~5400, ~5300, and ~5500 cal yr BP, in Venezuela (9° N), Puerto Rico  
507 (18° N), Yucatan Peninsula-Mexico (18° - 21° N) and Cuba (22° N), respectively (Peros  
508 et al., 2007; Cohen et al., 2016; Aragón-Moreno et al., 2018; Montoya et al., 2019). In  
509 addition, mangroves were recorded in the western Gulf of Mexico coast (20° N) at  
510 ~6000 cal yr BP (Cordero-Oviedo et al., 2019).

511 In the study area (29° N), marine transgression caused the development of  
512 lagoons and saltmarshes with a strong contribution of marine organic matter after ~6500  
513 cal yr BP (Figs. 4, 5, 6, and 7). This sedimentary environment associated with  
514 vegetation and sedimentary organic matter suggests favorable physical-chemical  
515 conditions for mangrove establishment. Therefore, of the sea-level dependent factors,  
516 mangroves could have been established in the study area since ~6500 cal yr BP.

517 However, contrasting with the tropical coasts, there was no evidence of mangrove  
518 presence around the Bay Champagne lagoon, the current northern mangrove limit,  
519 between 6500 and 1470 cal yr BP. A similar situation occurred at the southern limit of  
520 American mangroves at Laguna, southern Brazilian coast (28° 29' S), where pollen  
521 studies also indicate the absence of mangroves during the Holocene. Mangroves were  
522 established at their current southern limit of South America only in the Anthropocene  
523 (Cohen et al., 2020b). Probably, despite the physical-chemical conditions suitable for  
524 mangrove establishment promoted by the sea-level rise, the temperature may not yet  
525 have been high enough to allow the growth of mangroves at their current northern and  
526 southern limits of American mangroves during the middle-late Holocene. In addition,  
527 biogeographic studies indicated that modern global distribution of mangroves is mainly  
528 controlled by temperature, hence being limited to tropical and subtropical regions (Lugo  
529 and Patterson-zucca, 1977; Sherrod and McMillan, 1985a; Duke et al., 1998; Stevens et  
530 al., 2006b; Stuart et al., 2007).

531

#### 532 5.4-Mangrove establishment controlled by climate

533 Considering that mangroves are susceptible to changes in sea-level and climate in a  
534 millennial timescale (Chapman, 1975; Duke, 1992; Blasco, 1996; Fromard et al., 2004b;  
535 Alongi, 2008), and to local factors in a secular/decadal time scale (Moraes et al., 2017;  
536 Ribeiro et al., 2018) the (1) presence or (2) absence of mangroves along their current  
537 northern and southern limits during the Holocene is essential to identify the reasons for  
538 the mangrove expansion to more temperate zones during the recent decades. Regarding  
539 the hypothesis of the (1) continuous presence of mangroves in the current northern (29°  
540 N) and southern (28° S) boundaries of the American continent (North and South  
541 America) during the middle-late Holocene, it would indicate relative stability of relative

542 sea-level and climate during that period. In this case, studies that show the poleward  
543 mangrove expansion during the most recent decades (e.g. Cavanaugh et al., 2014;  
544 Saintilan et al., 2014b; Osland and Feher, 2020) could be incorrectly attributing such  
545 mangrove dynamics to allogenic processes, for instance, global warming.  
546 Alternatively, it may be caused by autogenic mechanisms, for instance, related to the  
547 action of tides, storms, dynamics of beach-barrier, delta switching, and lateral migration  
548 of meandering fluvial channels, then creating and destroying mangrove substrates in a  
549 cyclical process with expansion and contraction phases of mangrove areas in a decadal  
550 time scale (Moraes et al., 2017). In this context, such mangrove expansion would be  
551 related to processes operated locally and intrinsic to the depositional system (Beebower,  
552 1964; Cecil, 2013).

553 By contrast, the (2) absence of mangroves in their current northern and southern  
554 limits in the Holocene indicates an allogenic process driving the mangrove expansion  
555 from tropical into temperate latitudes in a millennial time scale. In general, the  
556 geological record suggests equatorward contraction of mangroves during the LGM  
557 (Woodroffe and Grindrod, 1991; Cannon et al., 2009), when these forests occurred only  
558 in refuge areas more protected from the impact of cold air temperature (Cannon et al.,  
559 2009). In contrast, a poleward mangrove expansion occurred after the LGM (Sandoval-  
560 Castro et al., 2012a; Kennedy et al., 2016). During the early and middle Holocene, this  
561 trend may have been favored in tropical to subtropical areas by increasing the global  
562 mean surface temperature (O'ishi and Abe-Ouchi, 2011; Fig. 8).

563 There is a consensus about global warming between the LGM and early  
564 Holocene (Kaufman et al., 2020). However, less well understood is the climate between  
565 the mid and late Holocene (Sundqvist et al., 2014). The Antarctic Peninsula underwent  
566 an early-Holocene warm phase and stable temperatures between 9,200 and 2,500 years

567 ago (Mulvaney et al., 2012). Studies over land north of 40°N have indicated warming  
568 during the middle Holocene (O'ishi and Abe-Ouchi, 2011). Other proxy records  
569 indicated global cooling during the late Holocene (Marcott et al., 2013). However, with  
570 no direct net contribution from the orbitally-driven insolation, the global annual mean  
571 radiative forcing in the Holocene should be dominated by the retreating ice sheets and  
572 rising atmospheric greenhouse gases, with both favoring a globally averaged warming  
573 (Liu et al., 2014). Climate models simulate a robust global annual mean warming along  
574 the Holocene, mainly in response to rising CO<sub>2</sub> and the retreat of ice sheets (Liu et al.,  
575 2014). Other climate models suggest no change or warming during the mid-late  
576 Holocene (Braconnot et al., 2007; Timm and Timmermann, 2007; Lohmann et al.,  
577 2013). The increase of CO<sub>2</sub> and CH<sub>4</sub> concentrations after 7000 and 5000 years ago  
578 contributed to the late Holocene warmth, prolonging the natural interglacial warmth  
579 initiated by orbital variations. These mid-late Holocene greenhouse gas increases may  
580 be natural or anthropogenic in origin (Ruddiman, 2003; Broecker and Stocker, 2006;  
581 Kaplan et al., 2011; Ruddiman et al., 2016). A stable isotope record from ice wedges  
582 from the Arctic indicated a long-term winter warming trend during the mid-late  
583 Holocene (Meyer et al., 2015).  $\delta^{18}\text{O}$  of planktonic foraminifera from the western  
584 tropical South Atlantic Ocean on the northeast Brazilian margin showed a progressive  
585 warming trend of slightly more than 1°C during the transition from the mid- to late-  
586 Holocene (Santos et al., 2013). A record of Holocene sea-surface temperatures and sea-  
587 ice presence from the Polar Front of the East Atlantic Southern Ocean showed late  
588 Holocene warming and no abrupt Neoglacial cooling (Nielsen et al., 2004). Jomelli et  
589 al. (2011) proposed Holocene warming for the eastern tropical Pacific with increased  
590 atmospheric temperature and retreat of glaciers in the southern tropics in response to  
591 enhanced austral summer insolation. This Holocene climate trend indicated by the



592 climate models and proxy records is consistent with the hypothesis that climate  
593 warming permitted mangroves to expand from the tropics to subtropics during the mid-  
594 late Holocene (Fig. 8).

595         Although the coastal stabilization or low rates of sea-level change around the  
596 middle Holocene may have played a role in the establishment of northern and southern  
597 American mangroves in areas located between the latitude of 20°N and 20°S, the  
598 subtropical mangroves were established only in the mid-late Holocene in both  
599 hemispheres, probably as a result of global warming that caused a poleward mangrove  
600 expansion from the latitude of 20° to 29°. The mangroves in the subtropical Brazilian  
601 coast were established between ~2200 cal yr BP (São Paulo, 25° S) and ~1630 cal yr BP  
602 (Santa Catarina-Brazil, 26° S) (Pessenda et al., 2012; França et al., 2019), and the  
603 subtropical mangroves in North America appeared after ~ 4000 cal yr BP in the  
604 Everglades-Florida (25° N) (Willard and Bernhardt, 2011; Yao et al., 2015; Yao and  
605 Liu, 2017; Jones et al., 2019) (Fig. 8). Regional-scale droughts may have some  
606 influence in delaying the mangrove establishment in the subtropical mangroves of the  
607 Everglades (Willard and Bernhardt, 2011), but global warming in the mid-late  
608 Holocene must be considered as the main force favoring the mangrove expansion from  
609 tropical to subtropical areas in both hemispheres.

610         Our study shows the absence of mangroves between ~8100 and ~1500 cal yr BP  
611 in Port Fourchon (29° 09` N), USA. The first evidence of black mangroves in Louisiana  
612 was dated at approximately 1900 AD (Lloyd and Tracy, 1901). These authors described  
613 early mangrove stands short in stature (<0.6 m) growing on offshore islands, mainly in  
614 Breton Sound. In addition, a historical video of the U.S. Library of Congress  
615 (<http://www.loc.gov/item/mp76000363>) also exhibited black mangroves at the Breton  
616 National Wildlife Refuge in Louisiana in 1915. Similarly, in the southern limit of the

617 American mangroves at Laguna, Brazil (28° 29' S), even though physicochemical and  
618 hydrodynamic conditions were favorable for the establishment and expansion of  
619 mangroves since the middle Holocene, mangrove establishment occurred only between  
620 ~1957 and ~1986 AD (Cohen et al., 2020b). It is noteworthy that a subtropical  
621 Brazilian mangrove stand (26° S), established since ~1630 cal yr BP, contained  
622 *Rhizophora* trees only during the last decades (França et al., 2019). *Rhizophora* is less  
623 tolerant to low temperatures than *Laguncularia* and *Avicennia* (Duke et al., 1998;  
624 Quisthoudt et al., 2012). The presence of mangroves in Louisiana, even incipient and  
625 restricted to some islands since the beginning of the 20th century, suggests that this  
626 ecosystem was established only after appropriate climatic conditions were present since  
627 that time.

628         We propose that the establishment of *Avicennia* trees in the study area was  
629 related to the natural warming trend after the Little Ice Age (LIA). This cold climatic  
630 episode was attributed to solar activity fluctuations during the last six or seven centuries  
631 (Lean and Rind, 1999), ending between 1850 and 1890 AD (Bradley and Jones, 1992).  
632 Ongoing remote sensing work (unpublished) by Cohen and co-workers indicates a  
633 significant increase in the area and stature of Louisiana mangroves in recent decades,  
634 especially in the 21st century. Therefore, while our data suggest that a poleward  
635 mangrove migration occurred due to natural global warming during the late Holocene,  
636 the industrial-era warming must have intensified the mangrove expansion during the last  
637 few decades, when temperature increased at a higher rate in the boreal and temperate  
638 regions than in the tropics (Solomon et al., 2007).

639

640 6. Conclusions

641 Our integrated multi-proxy investigation based on sedimentology,  $^{14}\text{C}$  radiocarbon  
642 dating, pollen analysis, as well as X-ray fluorescence, isotope ( $\delta^{13}\text{C}$ ), and C/N data  
643 indicate a marine transgression at Bay Champagne, Louisiana-USA during the  
644 Holocene. This natural process changed the environment from a freshwater lake (~8100  
645 – ~6500 cal yr BP) to a brackish water lagoon (~6500 – ~1500 cal yr BP). During the  
646 last ~1500 cal yr BP, washover sand was deposited into the lagoon due to the relative  
647 sea-level rise and hurricanes. Physicochemical and hydrodynamic conditions suitable  
648 for mangrove development occurred in the study site over the last ~6500 cal yr BP.  
649 However, mangrove pollen were not recorded in sediments between ~8100 and ~1500  
650 cal yr BP, suggesting that mangroves were absent during the entire period. A  
651 comparative analysis of these multi-proxy data and historical records of mangrove  
652 establishment phases in the Gulf of Mexico, Caribbean, and eastern South America  
653 indicated that mangroves expanded gradually from the tropical to subtropical South and  
654 North American coasts during the mid and late Holocene. The modern boreal ( $29^{\circ} 09'$   
655 N) and austral ( $28^{\circ} 29' \text{ S}$ ) mangrove limits were established in the early and mid 20<sup>th</sup>  
656 century, respectively. This mangrove dynamics on a continental scale suggests that  
657 poleward mangrove migration was caused by natural Holocene global warming. The  
658 industrial-era warming must have intensified the mangrove expansion. However, the  
659 Anthropocene global warming was not a direct forcing that initiated the mangrove  
660 migration into temperate zones.

661

662

663

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673

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1333

1334 Figure captions

1335 Figure 1- a) Location of the study area, b) vegetation map with a stratigraphic profile  
1336 (a`-b`) exhibiting vegetation, geomorphology, and the facies associations, c) drone  
1337 image showing the coring sites along a sandy coastal barrier.,

1338 Figure 2- Stratigraphy of core BC81 exhibiting sedimentary characteristics, facies  
1339 associations, and pollen data with percentages of the ecological groups. Pollen diagrams  
1340 are presented as percentages of the total pollen sum.

1341 Figure 3- Stratigraphy of core BC82 exhibiting sedimentary characteristics, facies  
1342 associations, and pollen data with percentages of the ecological groups. Pollen diagrams  
1343 are presented as percentages of the total pollen sum.

1344 Figure 4- Summary of core BC81, presenting sedimentary characteristics, pollen  
1345 ecological groups, and geochemical data.

1346 Figure 5- Summary of core BC82, presenting sedimentary characteristics, pollen  
1347 ecological groups, and geochemical data.

1348 Figure 6- Binary diagram showing the source of the sedimentary organic matter for each  
1349 sedimentary facies associations based on the relationship between  $\delta^{13}\text{C}$  and C/N.

1350 Figure 7. Model of the geomorphology and vegetation development under the Holocene  
1351 relative sea-level rise.

1352 Figure 8. American mangrove distribution in the tropical and subtropical zones and time  
1353 of the mangrove establishment during the Holocene. The modern American mangrove  
1354 distribution was obtained at <http://data.unep-wcmc.org/datasets/4>.

1355

1356 Table 1. Samples of sedimentary organic matter selected for radiocarbon dating and  
1357 results with code site, laboratory number, depth (m),  $^{14}\text{C}$  ages (yr BP,  $1\sigma$ ), calibrated  
1358 ages (cal. yr BP,  $2\sigma$  deviation), sedimentation rate and median of calibrated ages (cal. yr  
1359 BP).

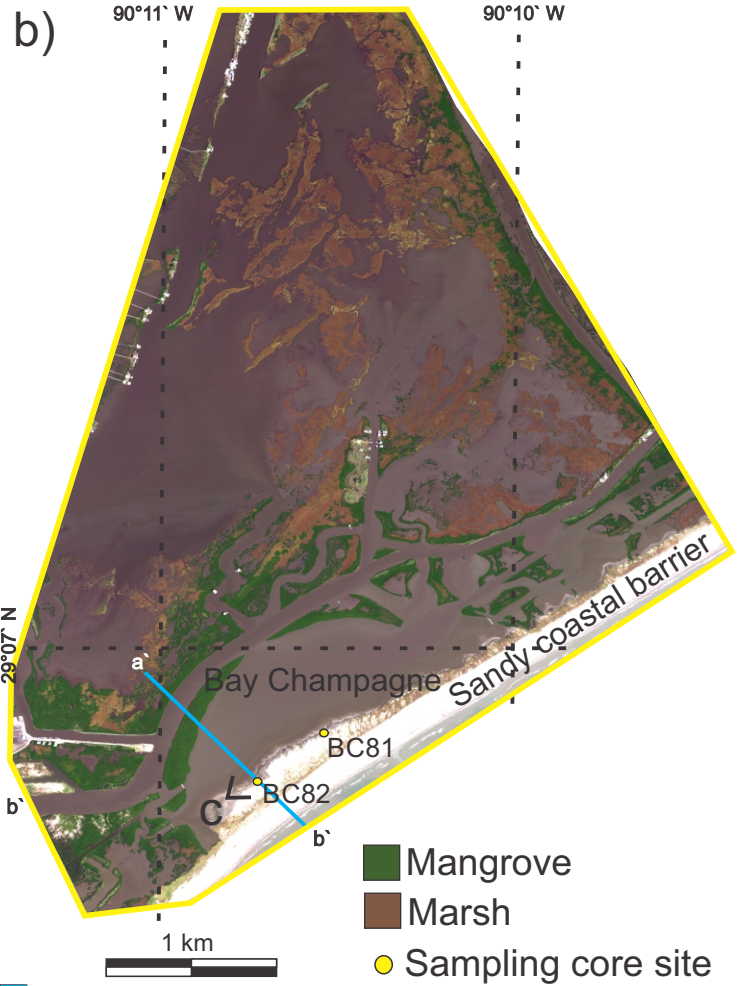
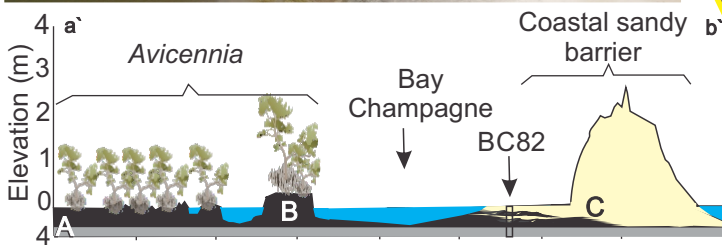
1360 Table 2. Characteristics of the three facies association.

1361

1362 Supplementary material

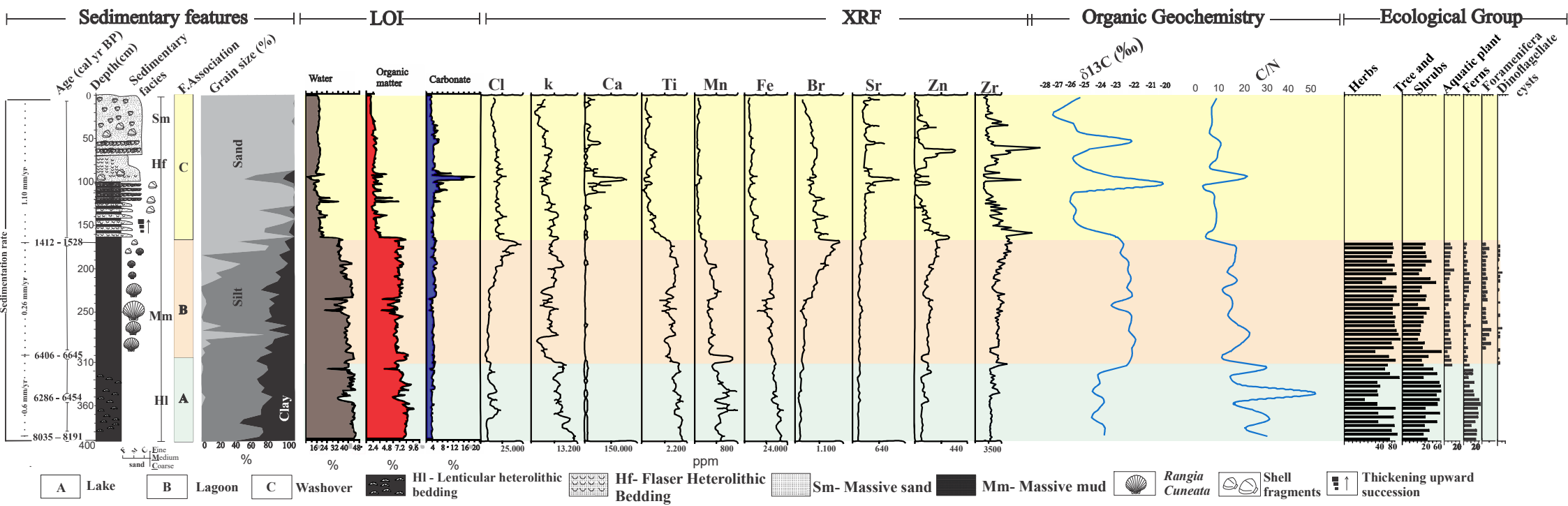
1363 Figure 1. Optical microscope photographs of *Typha* species with pollen in monad (a-b:  
1364 *Typha angustifolia*) and tetrad (c-d: *Typha latifolia*).

1365

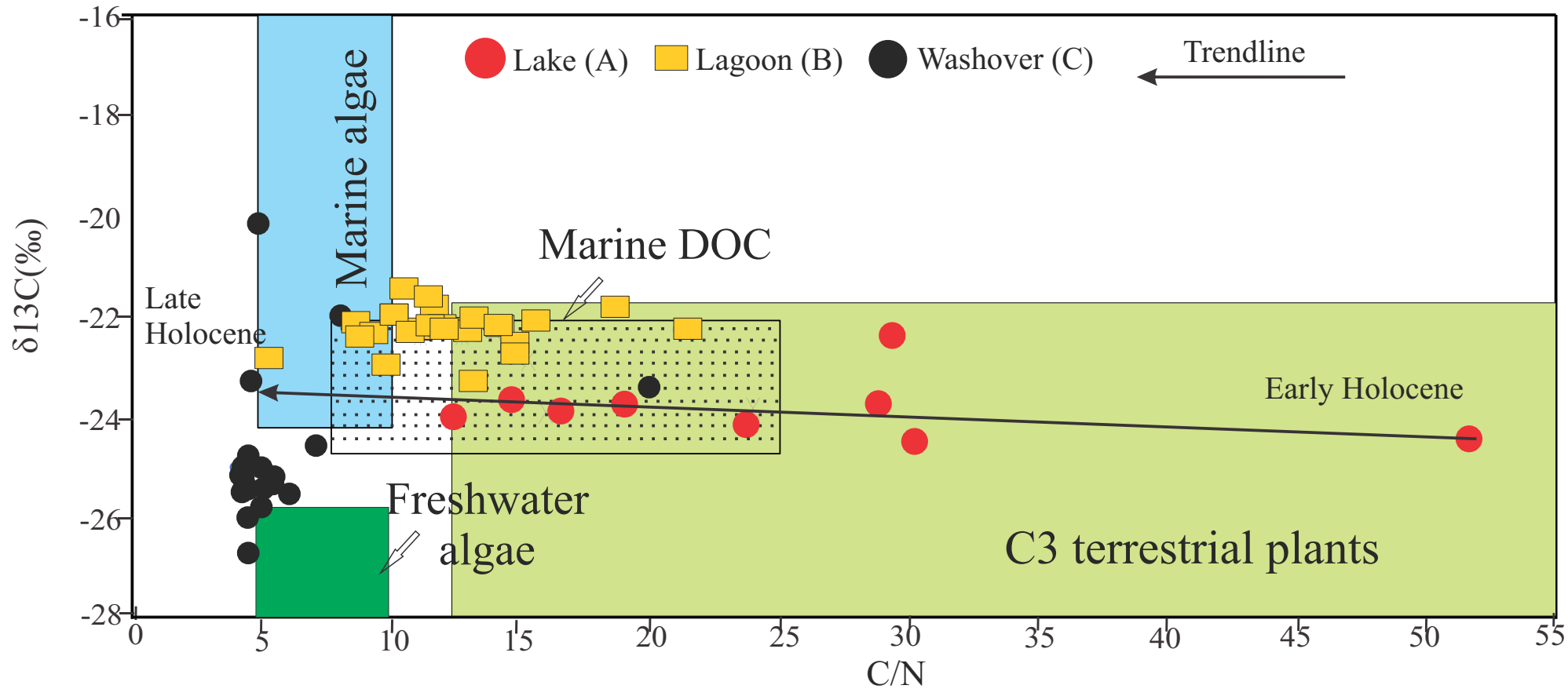












- Mangrove
- Saltmarshes
- Freshwater vegetation

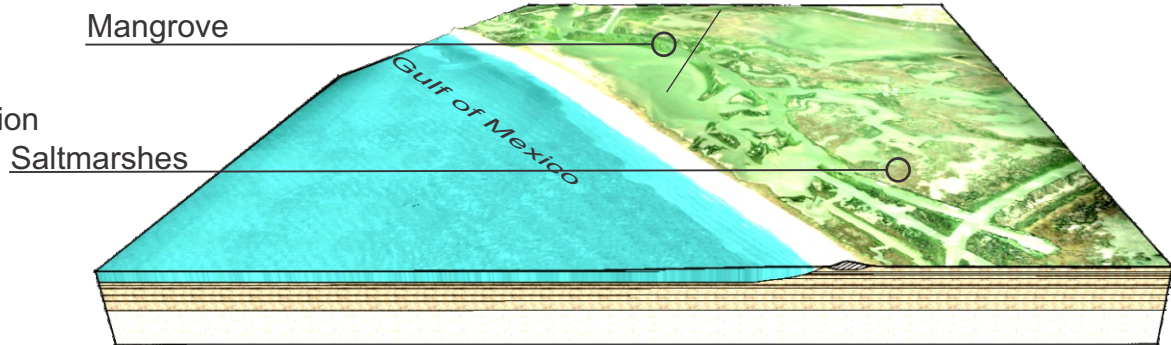
Freshwater



Marine influence

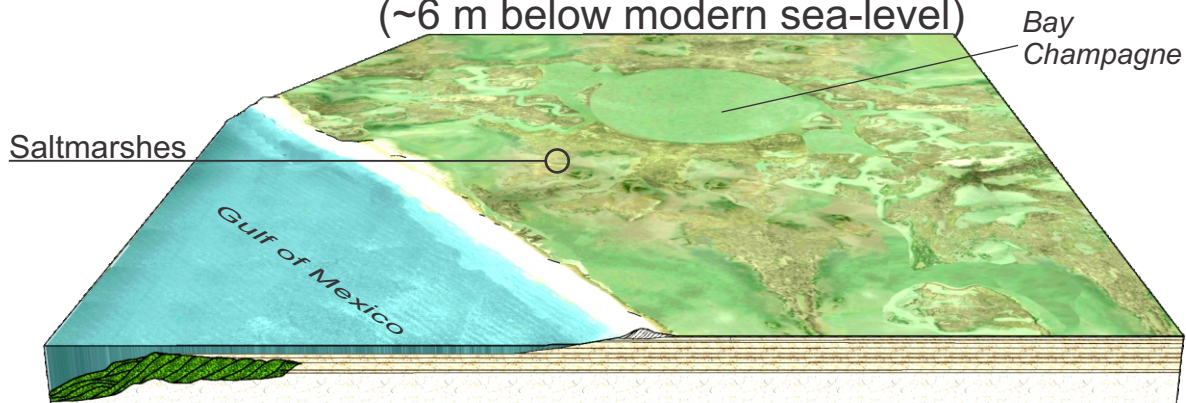
Marine

Today Bay Champagne



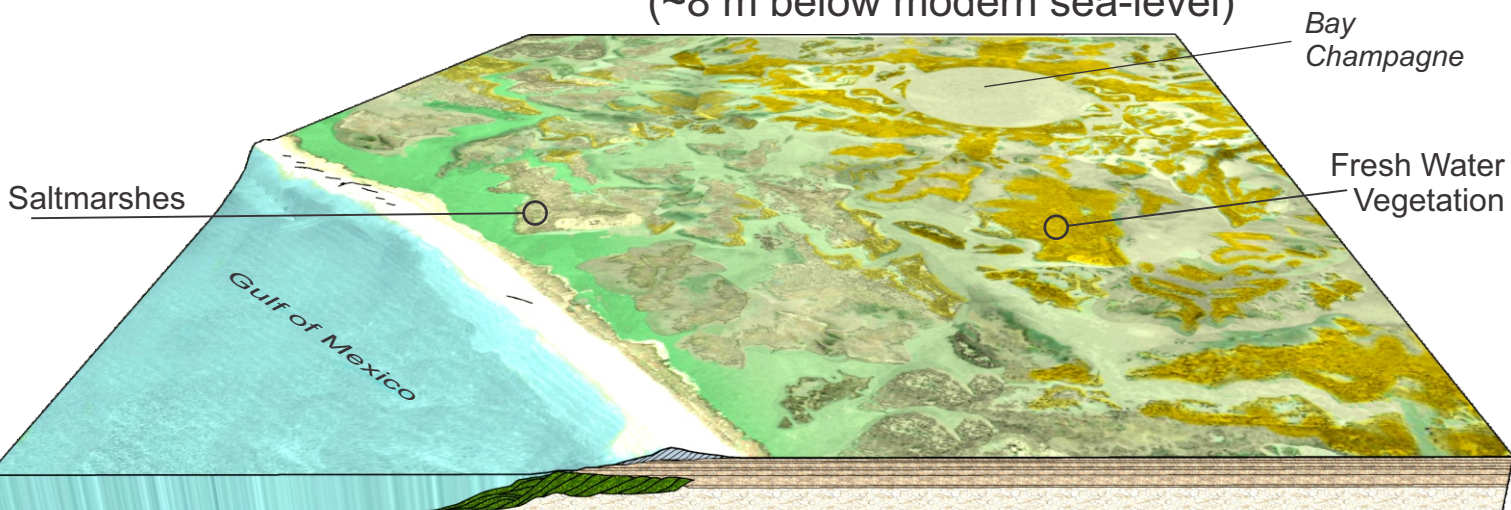
~6000 cal yr BP

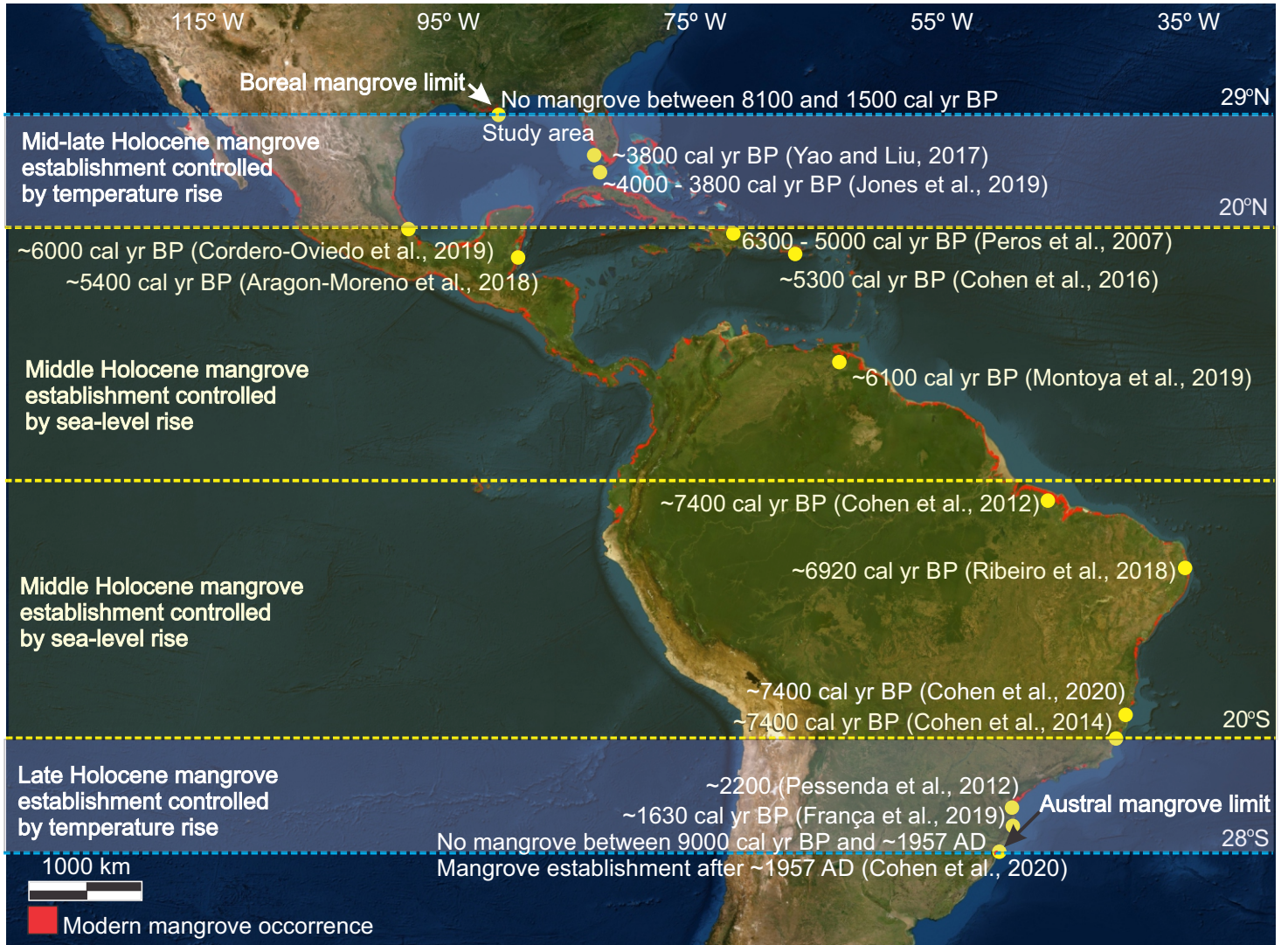
(~6 m below modern sea-level)



~8000 cal yr BP

(~8 m below modern sea-level)





<b>Sediment core</b>	<b>Code site and laboratory number</b>	<b>Depth (m)</b>	<b>Ages (<sup>14</sup>C yr BP, 1σ)</b>	<b>Ages (cal. yr BP, 2σ deviation)</b>	<b>Sedimentation rate (mm/yr)</b>	<b>Median of calibrated ages (cal. yr BP)</b>
BC81	UGAMS-34381	170	2150±20	2096 - 2160	0.76	2128
BC82	UGAMS-34379	170	1580±20	1412 - 1528	1.1	1470
BC82	LAC 190456	300	5766±48	6406 - 6645	0.26	6525
BC82	LAC 190457	350	5621±48	6286 - 6454-		6370
BC82	UGAMS-34380	400	7330±30	8035 – 8191	0.6	8113

Facies association	Facies description	Ecological group	Geochemical data	Elements predominance (ppm)	Interpretation
<b>A</b>	Lenticular heterolithic bedding (facies Hl)	Herbs, tree/shrubs, and ferns	$\delta^{13}\text{C} = -24.4 - -22\text{‰}$ C/N= 12 - 52	Fe: 14 k - 20 k K: 8 k - 13 k Ti: 1.5 k - 2 k Mn: 370 - 800	Lake
<b>B</b>	Massive mud (facies Mm) with <i>Rangia cuneate</i>	Herbs and aquatic plants from brackishwater. Foramenifera/ Dinoflagellate	$\delta^{13}\text{C} = -23 - -21\text{‰}$ C/N= 6 - 22	Cl: 3 k - 20 k Br: 190 - 950 Fe: 7 k - 17.5 k Mn: 186 - 500	Lagoon
<b>C</b>	Flaser heterolithic bedding (Hf), Massive sand (Sm) with shell fragments	No pollen/ferns	$\delta^{13}\text{C} = -27 - -20\text{‰}$ C/N= 5 - 20	Cl: 6 k - 24 k Ca: 2.7 k - 130 k Br: 230 - 1200 Sr: 100 - 572 Zr: 44 - 422	Washover