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1	Mid to late Holocene sea-level rise and precipitation variability recorded in the fringe
2	mangroves of the Caribbean coast of Panama.
3	
4	Carlos Castañeda-Posadas ^{1,2} , Alex Correa-Metrio ^{2,3*} , Jaime Escobar ^{4,5} , J. Enrique
5	Moreno ⁵ , Jason Curtis ⁶ , Maarten Blaaw ⁷ , and Carlos Jaramillo ⁵
6	
7	¹ Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Coyoacán,
8	Ciudad de México 04510, Mexico.
9	² Instituto de Geología, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de
10	México 04510, Mexico.
11	³ Centro de Geociencias, Universidad Nacional Autónoma de México, Juriquilla, Querétaro
12	76230, Mexico.
13	⁴ Departamento de Ingeniería Civil y Ambiental, Universidad del Norte, Barranquilla,
14	Colombia.
15	⁵ Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute,
16	Box 0843-03092, Balboa, Panama.
17	⁶ Department of Geological Sciences, University of Florida, Gainsville, FL 32611, United States
18	of America.
19	⁷ School of Natural and Built Environment, Queen's University Belfast, Belfast BT7 1NN, United
20	Kingdom.
21	
22	* Corresponding author: acorrea@geociencias.unam.mx
23	
24	Abstract
25	Throughout the Holocene, two of the most important factors involved in the evolution of tropical
26	coastlines have been fluctuations in sea level and regional climates. The geological record
27	provides insightful realizations of the complex interaction between these two factors, improving
28	our understanding of the evolution of littoral zones. Here we present the sedimentary record of a
29	mangrove swamp located in Punta Galeta, Caribbean coast of Panama. Through the conjunction
30	of geochemical and biological sedimentary indicators, we reconstruct environmental dynamics of
31	the area for the last ~5200 years. Between ~5200 and ~1800 cal yr B.P., the progressive

32 dominance of carbonates and a decrease of mangrove pollen indicate increasing marine influence 33 in the area, probably facilitated by a progressively drier climate. Between 3100 and 1800 cal yr 34 B.P., the embayment was flooded by marine water resulting in a landward migration of 35 mangroves. From ~1800 cal yr B.P. to present, the pollen and organic matter records indicate 36 that mangrove vegetation belt recovered, contributing a large proportion of organic matter to the 37 sediment and advancing the shoreline seaward. The maturation of the mangrove forest has 38 resulted in a progradation process that offsets between 4 and 5 meters of sea level rise occurred 39 through the last ~5000 years. This process was facilitated by the progressive decrease in rates of 40 sea level rise and by increasing sedimentation rates resulting from a higher accumulation of 41 organic matter from the more vigorous vegetation and more terrigenic input associated with 42 higher regional precipitation. The record of Punta Galeta demonstrates that the evolution of 43 fringe mangroves throughout the Holocene has been mostly driven by sea level rise, which 44 effects are potentially offset by erosion during times of high precipitation. Thus, across the 45 Caribbean coast, precipitation regimes have played a pivotal role at defining the structure and 46 function of mangrove communities.

47

48 Keywords

49 Mangroves; sea level rise; precipitation variability; Caribbean; pollen analysis; geochemical50 analysis; Holocene.

51

52 **1. Introduction**

53 Regional coastal dynamics are defined by the differential strength of continental and 54 marine influences that act upon a specific area (Bird, 2011). The local geomorphology and the 55 balance between continental and marine influences define the physiognomy and complexity of 56 the resulting ecosystems, which range from coastal dune fields to exuberant mangrove forests 57 (Alongi, 2020; Ellison, 2004). These ecosystems intermediate the interchange of matter and 58 energy between continental and marine areas and largely define the physiognomy of the 59 coastlines (Alongi, 2020). Continental influences are mostly represented by the input of a 60 mixture of materials of minerogenic and organic origin, transported mostly by rain and wind or 61 produced *in situ*. Thus, these influences are mainly dominated by regional climates and the 62 nature of the depositional environments. Marine influences, on the other hand, manifest through 63 the erosive action of the waves and tides, and the control that sea level exerts on the hydraulic 64 and compositional properties of the coastal soils. Through the Holocene, regional climates of 65 Central America and sea level in the Caribbean have been variable (e.g. Khan et al., 2017; Stansell et al., 2020; Toscano and Macintyre, 2003; Winter et al., 2020), resulting a dynamic 66 67 coastal landscape where ecosystems have been in a constant process of reconfiguration. Regional 68 precipitation regimes, and thus sediment transport, have varied at time-scales from annual (e.g. 69 interannual varibility of the Pacific system, Conroy et al., 2008) to millennial (e.g. the 70 progressive southern dispalcement of the intertropical convergence zone, ITCZ, Haug et al., 71 2001). Sea level, on the other hand, has been rising at a progressively lower rate through time, 72 reaching relatively stable levels between ~6000 and 5000 cal yr B.P. (Khan et al., 2017; 73 Lambeck et al., 2014; Toscano and Macintyre, 2003). Thus, the modern landforms and 74 ecosystems are the result of a dynamic evolutive history highly dependent on local and regional 75 conditions.

76 Mangrove forests are probably the most exuberant ecosystem established in the intertidal 77 zone of tropical and subtropical regions, in settings usually protected from the direct action of the 78 waves (Lugo and Snedaker, 1974). Classified among the most productive ecosystems in the 79 world, mangrove forests offer goods and services such as protection of the coastline from 80 extreme weather events, storage of carbon, shelter for marine and terrestrial fauna, among others 81 (Ward et al., 2016). During times of marine transgressive events such as the Holocene, their 82 persistence over a given location largely depends on the input of lithogenic and organic materials 83 offsetting sea level rise (Jaramillo and Bayona, 2000; Soares, 2009), a process facilitated by high 84 precipitation regimes that associate with high erosion rates. Whereas sea level rises, mangroves 85 facilitate terrain accretion and promote progradation processes, which are only possible given a 86 reasonable input of sediments (Woodroffe, 1993). Thus, Holocene dynamics of mangroves 87 provide hints into their response to rising sea level, although the variability of the input of 88 continental can be an important source of variability. In this sense, the development of 89 mangroves along coastal settings characterized by the absence of major tributaries (fringe 90 mangroves, Lugo and Snedaker, 1974) offers a natural laboratory to identify vegetation 91 responses to rising sea level.

92 Fringe mangrove communities have long thrived behind beach ridges and in embayments
93 of the Caribbean (Ellison, 2004). In Panama, Punta Galeta is a good example of a setting

3

94 protected from the direct effect of the waves inhabited by mangroves since at least 7000 cal yr 95 B.P. (Macintyre and Glynn, 1976). The communities is composed of four mangrove species 96 (Avicennia germinans, Conocarpus erectus, Laguncularia racemosa, and Rhizophora mangle), 97 each one adapted to specific conditions of salinity and soil hydric regime, in turn defined by 98 local geomorphology and the spatial structure of the intertidal zone (Ellison, 2004; Lugo and 99 Snedaker, 1974; Sousa et al., 2007). Given the absence of major fluvial discharge into the area, 100 mangrove dynamics through the Holocene have probably been largely dominated by sea level 101 rise. We reconstruct the local and regional environmental history by analyzing geochemical and 102 biological indicators in a sediment core from an embayment. Our main goal is to identify the 103 effects of progressive sea level rise on the composition and structure of local mangrove 104 communities, and the possible modulating role of regional climate. Whereas geochemical 105 indicators provide insights on the environmental setting at local and regional spatial scales, 106 palynological indicators provide independent evidence on local vegetation dynamics.

107

108 2. Study area

109 Punta Galeta is located on the Caribbean coast of central Panama, on the eastern side of 110 the Panama Canal. It consists of a small peninsula surrounded by small islands (Fig. 1). The 111 regional basement rock is part of the Gatun Formation, a middle and upper Miocene geological 112 unit composed of massive siltstone to fine sandstone, and tuff, rich in molluscan fauna (Hendy, 113 2013; Woodring, 1957). The regional coastline is covered by deposits of marine carbonates that, 114 in the Galeta coral reef, reach depths of at least 14 m (Macintyre and Glynn, 1976) (Fig. 1). 115 Towards the embayments and behind the beach ridges, mangrove forests and swamps have 116 developed, producing deposits rich in organic matter. The swamps are protected from direct 117 wave action by a fringing reef flat that extends seaward, with its highest elevation in the fore reef 118 and decreasing height landward (Kilar and Norris, 1988). The tidal regime is semidiurnal, with a 119 mean diurnal range of 33.5 cm and a mean annual range of 21.3 cm (Cubit et al., 1986). Mean 120 monthly temperature is relatively constant throughout the year, with an annual mean of 27.2 °C, 121 and a daily temperature range of approximately 5 °C. Mean annual precipitation is ~2920 mm, 122 with the dry season extending from January to mid-April (Fig. 1). The landward limit of the 123 mangrove forests and swamps is determined by higher-elevation terrains occupied by tropical 124 forest (Schmidt, 2008). The canopy of the mangrove forests of Punta Galeta is dominated by

125 Avicennia germinans (hereafter Avicennia), Laguncularia racemose (hereafter Laguncularia),

126 and *Rhizophora mangle* (hereafter *Rhizophora*) (Sousa et al., 2007; Sousa and Mitchell, 1999).

127 These species are distributed according to the tidal influence, forming zones of different canopy

128 composition (Sousa et al., 2007). *Rhizophora* dominates the low intertidal areas, mixing with

129 Laguncularia at distances of 10-20 m from the water's edge. Avicennia is present in the mid-

130 intertidal areas, creating a canopy that has representatives of all three species. Additionally, there

131 is sparse presence of *Conocarpus erectus* (hereafter *Conocarpus*), mostly found around the

132 beach ridges and the transition zone from mangrove to tropical forest.

133

134 **3. Methods**

135 In October 2018, a 452-cm-long sediment core (GAL18) was retrieved from a mangrove forest in Punta Galeta, Caribbean coast of Panama (9.39°N 79.86°W, Fig. 1). The core was 136 137 recovered in 1-m-long increments, using a modified Livingstone piston corer (Colinvaux et al., 138 1999), under a stand of Avicennia germinans. After retrieval, the core was sealed and has been 139 stored at \sim 4 °C for preserving sedimentary evidence. Core sections were longitudinally open, and 140 the material was photographed and described in terms of color, texture, and content of macro 141 rests. Six depths along the core were sampled for radiocarbon dating on organic matter at the 142 ¹⁴CHRONO Centre for Climate, the Environment and Chronology of Queen's University 143 Belfast. Radiocarbon dates were calibrated using IntCal20 (Reimer et al., 2020), expressed in 144 calibrated years before present (cal yr B.P. hereafter), and interpolated using clam to construct an 145 age-depth model (Blaauw, 2010).

146 The core was sampled at 5-cm intervals for geochemical analyses, for a total of 88 147 samples. For this purpose, 3-cm³ subsamples were oven-dried and ground using a mortar and a 148 pestle. Concentrations of major and trace elements were determined using a handheld XRF 149 analyzer, with three repeated measurements per sample, and expressed in ppm. Confidence 150 intervals for each element in each sample were calculated using the mean and standard deviation 151 of the triplicate measurements. Only elements that showed concentrations statistically different 152 from zero and that showed significant variability throughout the record were included in further 153 analyses. Samples were also analyzed for total carbon (TC), total inorganic carbon (TIC), total 154 nitrogen (TN), and carbon and nitrogen isotopes (δ^{13} C and δ^{15} N) in bulk organic matter. Total 155 carbon and total nitrogen were measured using a Carlo Erba NA 1500 CNS elemental analyzer.

156 Total inorganic carbon was determined by acidification followed by coulometric titration using 157 an AutoMate Prep Device coupled with a UIC 5014 CO₂ coulometer. Percent total organic 158 carbon was calculated by subtraction of TIC from TC. Subsamples for carbon isotope analysis on 159 bulk organic matter were pretreated with 2N HCl to remove carbonate and later washed with 160 distilled water to remove chloride, prior to isotope measurement. Around 50 mg of carbonate-161 free sediment was loaded into tin sample capsules for stable carbon isotope measurement. 162 Nonacidified samples were used for nitrogen isotopes. Combustion gases were carried in a 163 helium stream through a Conflo II interface to a Thermo Electron DeltaV Advantage isotope 164 ratio mass spectrometer. Carbon and nitrogen isotope data are reported in per mil (‰) and expressed in standard delta notation. Carbon isotopes ($\delta^{13}C_{org}$) are reported relative to VPDB and 165 166 nitrogen isotopes are reported relative to AIR. A principal component analysis (Jolliffe, 1986) 167 was used to evaluate relationships among elements through a correlation biplot. Sample scores 168 across the principal components (PC) were used to summarize the total variability of the 169 geochemical record through time. TOC/TN ratios were calculated for each sample aiming to 170 assess relative contributions of terrestrial and aquatic organic matter to the sediment (Meyers, 171 2003).

172 The core was subsampled every ~8 cm for pollen analysis for a total of 54 samples. 173 Samples were prepared using standard techniques (Faegri and Iversen, 1989) and gravimetrically 174 separated for concentrating palynomorphs (Krukowski, 1988). Samples were analyzed under a 175 transmitted light microscope at magnifications of 400x and 1000x. Because of very low pollen 176 concentrations, palynomorphs were counted aiming to a pollen sum of 200 grains, which 177 included pollen of terrestrial plants and spores of Acrostichum, as this taxon is considered a 178 component of the vegetation in mangrove communities (Lee et al., 2017). Pollen from aquatic 179 plants was excluded from the pollen sum because they are probably transported from freshwater 180 streams that descend from the area occupied by the tropical forest. Pollen types were identified to 181 the finest possible taxonomic level using available reference pollen collections and specialized 182 literature (Bush and Weng, 2007; Roubik and Moreno, 1991; Willard et al., 2001). All 183 palynomorph abundances were transformed to percentages of the pollen sum. 184

- 185 **4. Results**
- 186

187 *4.1 Core stratigraphy and chronology*

188	The core was characterized by two main sections differentiated by their texture and the
189	presence of macrorests (Fig. 2). The lower section, from 452 to 250 cm below lagoon floor (blf
190	hereafter), was characterized by abundant bivalve and gastropod shells, low content of organic
191	matter, and a relatively coarse sediment texture dominated by lime and sand. The upper section
192	from 250 cm blf to the top of the core, was characterized by abundant vegetal macrorests, high
193	content of organic matter, and a finer sediment texture dominated by lime and clay (Fig. 2).
194	Radiocarbon dates resulted in stratigraphic order, except the sample taken at 331 cm blf that
195	showed an age reversal and was, therefore, excluded from the age-depth model (Fig. 2).
196	According to the age-depth model, the sediment sequence GAL18 spans the last ~5,200 years
197	(Fig. 2). Sedimentation rate showed a general increase towards present, going from ~ 0.05 cm/yr
198	from ~452 to 320 cm blf, to 0.2 cm/year in the uppermost ~100 cm of the record (Fig. 2).

199

200 Table 1. Radiocarbon and calibrated dates of core GAL18. 95% confidence intervals for

Laboratory ID	Depth (cm)	¹⁴ C Age	Error	Calibrated age (cal yr BP)
UBA-40771	45	138	23	136 (12-269)
UBA-40772	91	338	22	389 (317-469)
UBA-40773	195	1553	28	1441 (1363-1515)
UBA-40774	311	2269	25	2259 (2162-2340)
UBA-40935	330	892	20	2665 (2583-2737)
UBA-40776	435	4340	28	4908 (4850-4975)

201 calibrated ages are shown in parenthesis.

202

203 *4.2 Geochemical analyses*

204 Concentrations of Ca, Cu, Fe, K, Mo, Mn, Rb, S, Sr, Ti, Zn, and Zr, determined by XRF 205 analysis, were significantly different from zero and displayed significant variability through the 206 record (Fig. 3). Mo, Cu, and Rb were characterized by stable concentrations from the bottom of 207 the record to ~500 years cal yr B.P. Thereafter, concentrations increased, reaching a peak around 208 200 cal yr B.P. (Fig. 3). Fe, S, Ti, Zn, and Zr were characterized by relatively low and stable 209 concentrations from the bottom of the record to ~2000 cal yr B.P. These elements showed higher 210 and more variable values from ~2000 cal yr B.P. to the top of the core. K showed a long-term 211 decreasing trend throughout the record, whereas Mn remained stable from the bottom of the

212 record to ~2000 cal yr B.P., when it began to decrease towards present (Fig. 3). Ca and Sr

- 213 increased from the bottom of the record to ~3100 cal yr B.P., reaching a plateau of maximum
- 214 concentrations that lasted until ~2000 cal yr B.P. and subsequently decreasing towards present.

215 TC and TN were characterized by low and stable concentrations from the bottom of the

216 sediment core to ~2000 cal yr B.P. (Fig. 3). $\delta^{13}C_{org}$ values were relatively stable (-24.0‰) and

217 less negative from the bottom of the record to \sim 2000 cal yr B.P., when they started to decrease,

218 reaching their most negative values in the topmost sample (-29.0‰) (Fig. 3). $\delta^{15}N$ was

219 characterized by values around 2.0‰ between the bottom of the record and ~4000 cal yr B.P.

Values increased to ~2.5‰ between 4000 and 1500 cal yr B.P., and thereafter decreased towards
 present.

In the PCA, more than half of the total variance of the dataset was associated with PC1 (Fig. 4). The broken-stick model indicates that only the two first principal components were statistically significant, representing 51.1% and 14.9% of the total variance, respectively (Fig. 4). The positive end of PC1 is associated with Ca, Mn, Sr, TIC, δ^{15} N, and δ^{13} Corg, whereas the negative end was associated with Cu, Mo, Rb, S, Ti, TN, TOC, and Zr (Fig. 4). PC2 was mostly defined by K and Zr towards the positive end, and Fe and Zn towards the negative end.

228

229 4.3 Palynological analysis

230 Pollen sums varied between 92 and 781 grains per sample (mean = 260, Q1 = 194 and Q3 231 = 293). Samples in which the pollen sum was below the target of 200 grains were mostly from 232 below 330 cm blf. Pollen spectra were characterized by 57 morphotypes, 28 and 29 classified to 233 genus and family levels, respectively. Counts of fern spores other than Acrostichum ranged from 234 5 to 65 spores per sample (mean = 26, Q1 = 14 and Q3 = 30), and were represented by the 235 families Lycopodiaceae, Selaginellaceae, Aspleniaceae, Cyatheaceae, Polypodiaceae, and 236 Pteridaceae. The most abundant taxa were *Rhizophora* (mean 36.4%), Avicennia (17.6%), 237 Achrostichum (11.7%), cf. Laguncularia (6.9%), Polypodium (4.7%), Bombacopsis (4.5%), 238 Cecropia (4.3%), Asplenium (3.3%), Cyatheaceae (2.2%), Urticaceae-Moraceae (2.0%), Poaceae 239 (1.75%), and Arecaceae (1.6%) (Fig. 5). See full diagram in Appendix 1 of Supplementary 240 Material.

In the fossil pollen spectra, mangroves were represented by *Avicennia*, cf. *Laguncularia*,
and *Rhizophora*, with sporadic appearances of *Conocarpus* (Fig. 5). *Acrostichum* spores were

243 also an important component of the palynomorph counts, with higher percentages before 2000 244 cal yr B.P. Herbs were mostly represented by Urticaceae-Moraceae, Chenopodium, and 245 Amaranthaceae that better represented in samples older than ~3800 cal yr B.P. (Fig. 5). Aquatics 246 were represented by Cyperaceae, Nymphea, and Polygonum (Fig. 5). Other herbs such as 247 Ambrosia and Polygala were more abundant between ~3100 and 1500 cal yr B.P., whereas the 248 last 2000 years were characterized by relatively high abundances of Mimosa and Asteraceae 249 (Fig. 5). Trees and shrubs were present throughout the entire record, although their abundances 250 were higher between 3100 and 1800 cal yr B.P. Alnus and Podocarpus were more abundant in 251 samples older than 3000 cal yr B.P.

252

253 **5. Discussion**

254 Core GAL18 spans the last 5,200 years of the environmental history of Punta Galeta, 255 Caribbean coast of Panama (Fig. 2). Sedimentation rates resulted variable and were punctuated 256 by radiocarbon dates, implying that our age-depth model offers a rough approximation to the 257 temporal structure of the environmental history of the area during the last 5,200 years. Further, 258 the age-depth model must be interpreted in the light of a possible influence of old carbon, an 259 important source of chronological overestimation under environments with high marine 260 influence (Stuiver and Braziunas, 1993). Low sedimentation rates below 311 cm blf (before 261 \sim 2200 cal yr B.P.) could be reflecting a depositional hiatus previously reported for the area 262 (Schmidt, 2008) that roughly coincides with a drought reported for several coastal sites in the 263 Caribbean and surrounding regions (e.g. Giry et al., 2012; Haug et al., 2001; Stansell et al., 2020; 264 Velez et al., 2014). Differences in sediment composition and sedimentation rates between the 265 lower and upper part of the core reflect concomitant changes of both the depositional 266 environment and regional climatic conditions. Whereas depositional environments in costal 267 settings such as Punta Galeta show high spatiotemporal variability (Woodroffe, 1993), Holocene 268 changes in precipitation regime and human activities have been documented for the region (e.g. 269 Correa-Metrio et al., 2016; Piperno et al., 1991; Toth et al., 2015). In the following sections, we 270 first introduce the interpretation of the proxies analyzed for core GAL18 and then, present an 271 interpretation of the environmental history of the area.

272

273 5.1 Geochemical indicators

274 The composition of the sediments of core GAL18 reflects the balance between 275 continental and marine influences that define sediment sources as well as transport and 276 deposition patterns. The continental influence is associated with the input of detrital materials 277 eroded from the catchment basin. Punta Galeta lies on the Gatun Formation, a shallow marine 278 sequence rich in carbonates and in siliciclastic material of volcanic origin (Hendy, 2013; Hidalgo 279 et al., 2011). Thus, in our geochemical dataset, the continental influence is surely represented by 280 lithogenic elements such as Rb, Ti, and Zr, which concentrations reflect the dynamics of the 281 erosive agents (Boës et al., 2011; Rothwell and Croudace, 2015). Carbonates eroded from the 282 basin probably represent a substantial source of TIC and Ca, but the negative association of these 283 elements with lithogenics (Fig. 4) points to marine carbonates as their main source at the coring location. TIC and Ca are strongly correlated with Mn and Sr, and $\delta^{13}C_{org}$ (Figs. 3 and 4), 284 285 reinforcing the interpretation of their association with marine sources as marine organic matter carbon is isotopically heavier (Meyers, 1997; Schneider et al., 2006). High concentrations of Ca, 286 Sr, and TIC accompanied by less negative values of $\delta^{13}C_{org}$ are probably associated with subtidal 287 depositional environments where large amounts of marine carbonates precipitate. Overall, the 288 289 main variability of the geochemical record was reflected by the trends of two groups of 290 correlated elements: one associated with input of detrital material and the other associated with 291 deposition of marine carbonates (Figs. 3 and 4). 292 Accumulation of organic matter in the sediments is directly reflected by concentrations of

293 TOC (Meyers, 2003). In core GAL18, the positive correlation between concentrations of TOC, S 294 and Mo (Figs. 3 and 4) indicate organic matter that has accumulated under poorly oxygenated 295 conditions that inhibit oxidative processes. Under a reduced depositional environment, 296 concentrations of Mo increase because of its lower mobility (Smedley and Kinniburgh, 2017), 297 whereas bacterial activity favors the accumulation of S (Goldhaber, 2003). High concentrations 298 of Fe and Zn usually indicate oxygen availability (Tribovillard et al., 2006), but these elements 299 can also associate with the organic fraction of the sediment (Dean et al., 1997). Towards the 300 upper part of our record, concentrations are of Fe and Zn are in phase with those of TOC and Cu 301 (Fig. 3), suggesting that, in our record, these elements associate with changes in organic matter 302 productivity. The peaks of these elements that characterize the upper part of the record coincide 303 with substantial decreases of δ^{15} N (Fig. 3), which were probably associated with denitrification 304 caused by high bacterial activity under anoxic conditions (Hodell and Schelske, 1998).

305 PC1 indicates that the main mode of variability in core GAL18 is associated with changes 306 in the balance between terrigenic and marine sediments, and thus with the balance between 307 continental and marine influences in the area. While the negative end of the axis reflects 308 substantial input of organic matter and lithogenic elements (mainly Rb, Ti, and Zr), the positive 309 end is defined by elements associated with marine carbonates (mainly Ca, TIC, and Sr). 310 Dominant deposition of terrigenic materials indicated by negative scores along PC1 probably 311 took place under inter to supratidal environments. On the other hand, dominant deposition of 312 marine carbonates indicated by positive scores of PC1 probably took place under inter to 313 infratidal environments. PC2, on the other hand indicates a mode of variability probably 314 associated with the dominant sources of terrigenic material (lithogenic vs. organic) and with 315 oxygen availability in the water column. Whereas the positive end of PC2 was mostly defined by 316 K, Ti, and Zr (Fig. 4), all lithogenic conservative elements (Boës et al., 2011; Rothwell and 317 Croudace, 2015), the negative end was defined by Cu, Zn, and Fe, which associate with organic 318 matter and/or with oxygen availability in the depositional environment (Dean et al., 1997; 319 Tribovillard et al., 2006). The association of these elements with TOC indicates that the negative 320 end of PC2 is more related to the accumulation of organic matter.

321

322 5.2 Biological indicators

323 The pollen assemblages deposited in the sediments of Punta Galeta are dominated by 324 local components with mangrove taxa representing more than 40% of the pollen sum, as 325 commonly found in mangrove sediments (Behling et al., 2001; Urrego et al., 2009). This 326 overrepresentation pattern obscures the signal of pollen from trees and shrubs from the 327 surrounding tropical forests, impeding a detailed interpretation of their variability though the 328 record. On the other hand, the geomorphology of Punta Galeta offers very limited space for the 329 formation of back swamps and saltmarshes (Sousa et al., 2007), hindering the development of a 330 clear salinity-driven zonation of herbaceous taxa that characterize well-developed tidal flats 331 (Behling et al., 2001; Urrego et al., 2009). Thus, herbaceous taxa in the sedimentary record of 332 Punta Galeta probably reflect patterns of vegetation disturbance instead of changes in soil 333 salinity. Most of taxa represented in the palynological record are associated with herbaceous 334 vegetation and shrubs and trees from tropical forests, except for *Alnus* and *Podocarpus* that often 335 associate with forests from higher elevations (Marchant et al. 2002). In core GAL18, however,

these taxa occurred mostly in abundances below 1.5% probably resulting from long-distance transported pollen (Fig. 5). Overall, the variability of the pollen spectra from core GAL18 mostly reflects local vegetation dynamics. The progressive increase of pollen percentages from all mangrove taxa reflects the invigoration of this vegetation time through time. On the other hand, variability of individual mangrove taxa probably reflects changes in the spatial configuration of the community.

342 Through the last 5200 years, the most important pollen taxa of the mangrove of Punta 343 Galeta have been Avicennia, cf. Laguncularia, and Rhizophora, coinciding with the taxa that 344 dominate the modern canopy of the local mangrove forests (Sousa et al., 2007; Sousa and 345 Mitchell, 1999). The sporadic appearance of pollen of *Conocarpus* coincides with the minor 346 representation of this taxon in the modern vegetation (Schmidt, 2008). Contrastingly, whereas 347 Acrostichum is a relatively minor component of the modern forests, it seems to have been better 348 represented from the bottom of the record to \sim 700 cal yr B.P. (Fig. 5). Given the association of 349 this fern with rather sparse canopies (Medina et al., 1990), it is possible that this time period 350 were characterized by a more sparse mangrove canopy. In fact, from ~5000 to 2000 cal yr B.P., 351 percentages of Rhizophora were relatively low (between ~21 and 32%, Fig. 5), considering the 352 usual over-representation of this taxa in pollen spectra (e.g. Behling et al., 2001; Ramcharan and 353 McAndrews, 2006; Urrego et al., 2009). The coincidence of rising percentages of Rhizophora 354 and cf. Laguncularia through the last 2000 years likely indicates that the mangrove vegetation 355 that occupies Galeta today is a relatively novel community in the context of the last 5000 years. 356 From 5200 to 5000 cal yr B.P., percentages of *Rhizophora* and cf. *Laguncularia* were relatively 357 high, although the higher abundances of Avicennia suggest a mangrove community with a 358 structure different than that of today.

359

360 5.3 Environmental turnover in Punta Galeta through the last ~5200 years

During the last 5200 years, the environmental variability of Punta Galeta has been largely associated with the marine transgression that has characterized coastal settings during the Holocene. Regional climatic variability at interannual to millennial scale seem to have played an important role at amplifying the effects of sea-level rise on the mangroves of Punta Galeta. Thus, our record provides insights into the response of the shoreline to the rising sea level and the progradation process mediated by the mangrove community, constituting a typical sedimentary

367 parasequence (sensu Catuneanu and Zecchin, 2020). The general variability pattern is 368 summarized by the PCA, with PC1 representing the balance between continental and marine 369 influences on the depositional processes, and PC2 indicating the dominating nature of the 370 terrigenic sediments. The palynological record, on the other hand, reflects the local dynamics of 371 the mangrove forests in response to the geomorphological dynamics associated with sea level 372 rise and regional precipitation changes. Based on the geochemical and biological evidence, we 373 divide the history of the area into four main environmental stages. This discretization of the 374 record does not intend to provide a formal chronostratigraphy, but rather to facilitate the 375 interpretation of environmental variability in the area. Stage I (from 5200 to 5000 cal yr B.P.) 376 represents a depositional environment under supra to intertidal conditions covered by a mature 377 mangrove forest. Stage II (from ~5000 to 3100 cal yr B.P.) represents a inter tidal environment 378 submitted to a progressively higher water column, and probably progressively dryer conditions. 379 Rapidly increasing sea level rise and likely lower precipitation led to Stage III, characterized by 380 infratidal conditions that lasted from ~3100 to 1800 cal yr B.P. From 1800 cal yr B.P. to present, 381 the coring site was characterized by a rapid infilling, first with terrigenic materials that probably 382 reflect a precipitation rebound (Stage IV, from ~1800 to 700 cal yr B.P.) followed by organic 383 matter (Stage V, 700 cal yr B.P. to modern).

384 Stage I. (~5200 to 5000 cal yr B.P.). The lowermost 200 years of the record were 385 characterized by mangrove pollen percentages above 70%, with equitable representation of 386 Rhizophora, Avicennia, and cf. Laguncularia (Fig. 6), suggesting a well-established mangrove 387 community. The coring site was probably on the distal part of the coastline, which was migrating 388 landward given the progressive sea level rise that has characterized the Caribbean throughout the 389 Holocene (Toscano and Macintyre, 2003). High concentrations of TOC through these 200 years 390 (Fig. 6) indicate a relatively stable substratum with accumulation of organic matter. Percentages 391 of mangrove taxa above 60% (Fig. 6) suggest that the coring site was occupied by a mangrove 392 forest located towards the upper limit of the tidal range. PC1 sample scores indicate an intertidal 393 depositional environment, whereas PC2 indicates high deposition of organic matter that, 394 according to C/N ratios above 20, was mostly derived from terrestrial vegetation (Meyers, 2003; 395 Rovai et al., 2018). Relatively high precipitation that coincides with a more northerly position of 396 the Intertropical Convergence Zone (Haug et al., 2001) probably played a significant role at

maintaining a vigorous vegetation. Low concentrations of lithogenics probably result from thehigh concentration of organic matter in the sediment.

399 Stage II (~5000 to 3100 cal yr B.P.). A substantial decrease of mangrove pollen at ~5000 400 cal yr B.P. indicates a sparser mangrove stand. Increasing PC1 scores indicate a progressive 401 increase of marine influence in the area (Fig. 6), whereas decreasing concentrations of 402 lithogenics (Fig. 3) indicate a long-term trend towards drier conditions. Sedimentation rates were 403 exceeded by rates of sea level rise (Fig. 6), resulting in a progressive flooding of the coring site 404 and thus a higher precipitation of marine carbonates. Decreasing concentrations of lithogenics 405 indicate a trend towards drier conditions that coincides with an invigoration of the drying trend 406 reported for the Northern Hemisphere through the Holocene based on the record of Cariaco 407 Basin (Haug et al., 2001; Winter et al., 2020). Mangrove forests responded to this sea level rise 408 process by migrating landward, thus becoming sparser at the coring site. Higher abundances of 409 Acrostichum indicate a sparser canopy as this fern usually associates with disturbed mangrove 410 forests (Medina et al., 1990). PC2 indicates that terrigenic sediments were mostly lithogenic, 411 which reflects on the decreasing concentrations of TOC. Less negative $\delta^{13}C_{org}$ and C/N ratios between 16 and 18 indicate a higher contribution of marine phytoplankton to the organic matter 412 413 (Meyers and Lallier-vergès, 1999; Meyers, 2003). TOC values are, indeed, similar to those 414 reported for river deltas (Rovai et al., 2018) where substrate is relatively unstable. The deepening 415 of the lagoon together with the more open vegetation probably increased the energetic impact of 416 the tides around the coring location.

417 Stage III (~3100 to 1800 cal yr B.P.). Percentages of mangrove pollen ~40% indicate that 418 the forest around the coring site was still sparse (Figs. 5 and 6). This period was characterized by less negative $\delta^{13}C_{org}$ values that indicate organic matter production was dominated by marine 419 420 phytoplankton (Meyers and Lallier-vergès, 1999), and C/N ratios below 15 that are characteristic 421 of estuarine systems of brackish water (Rovai et al., 2018). High and stable values of PC1 422 indicate strong marine influence characterized by high concentration of carbonates, most likely 423 deposited under an infratidal environment. According to PC2, the terrigenic fraction became 424 progressively more organic, although high concentrations of Mn and increasing concentrations of 425 Fe and Zn indicate a well oxygenated water column (Tribovillard et al., 2006). These negative 426 PC2 scores are also related to the lowest concentrations of lithogenics throughout the record, 427 which could be indicating a relatively dry regional climate. Dry conditions have been reported

428 for other location in Central America and the western Atlantic during this time (Giry et al., 2012; 429 Stansell et al., 2020; Velez et al., 2014), suggesting a regional driver of precipitation variability. 430 According to evidence from the Galapagos Islands, El Niño events were frequent between ~4000 431 and 1500 cal yr B.P. (Conroy et al., 2008), which probably increased precipitation seasonality in 432 Punta Galeta. This time interval was also reportedly characterized by La Niña-like conditions 433 (Toth et al., 2015), which in Panama result in a higher precipitation variability (Fig. 1C). The 434 conjunction of El Niño and La Niña were likely associated with a higher both seasonality 435 interannual variability of precipitation, offering a plausible scenario for the low deposition of 436 lithogenic elements. Nevertheless, the high uncertainty of our age-depth model precludes definite 437 conclusions on the effect of the ENSO system on the climate and vegetation of Punta Galeta. 438 Additionally, decreasing PC2 scores coincide with a gradual southern displacement of the ITCZ 439 (Haug et al., 2001), which would associate with lower mean annual precipitation (Fig. 6). Higher 440 percentages of Arecaceae, Fabaceae, and Malvaceae (Fig. 5) offer further evidence of a relatively 441 high precipitation seasonality. Increasing percentages of Ambrosia suggest anthropogenic 442 influence, widely documented for Central Panama through this time interval (Cooke and Ranere, 443 1992; Piperno, 2006; Piperno et al., 1991), could have acted as an additional source of pressure 444 on vegetation. The evidence suggests that, during this stage, the water column in Punta Galeta 445 reached its maximum levels through the last ~5200 years, leaving the coring site in the subtidal 446 zone. These conditions indicate that rising sea level rates exceeded the accretion rates that were 447 diminished because of the low sediment input from pluvial erosion.

448 Stage IV (~1800 to 700 cal yr B.P.). Increasing percentages of mangrove taxa and TOC 449 concentrations indicate a recovery of mangrove vegetation accompanied by a monotonic trend of 450 organic carbon accumulation in the soil (Figs. 5 and 6). The increasing trend of PC1 scores 451 suggest a progressive increase of terrestrial influence (Fig. 6). Higher concentrations of 452 lithogenic elements summarized by the increasing scores of PC2 indicate a rebound of moisture 453 availability, which could be associated with higher sedimentation rates. Even though El Niño 454 events were still frequent (Conroy et al., 2008; Moy et al., 2002), the change in the hydroclimate 455 probably resulted from two main factors, both of them associated with lower seasonality: i) the 456 termination of the La Niña-like conditions (Fig. 6) (Toth et al., 2015), and ii) a decrease of 457 insolation seasonality driven by increasing insolation through the moths of higher moisture 458 deficit (January to April, Figs. 1 and 6). This trend towards wetter conditions has also been

reported for the Galapagos Islands (Conroy et al., 2008), highlighting the importance of the
Pacific system at modulating moisture availability patterns of Central Panama (Correa-Metrio et

461 al., 2016). Sedimentation rates increased over the rate of sea level rise, diminishing the depth of

462 the water column, leaving the coring site in the intertidal zone. The stage represents a seaward

463 progradation the terrain facilitated by increasing sedimentation rates, in turn associated with a

464 higher terrigenic input of sediments and a more vigorous mangrove.

- 465 Stage V (\sim 700 cal yr B.P. to Present). The mangrove vegetation through this stage was 466 characterized by increasing percentages of cf. Laguncularia (Fig. 6). This taxon in Galeta 467 represents the transition between the waterfront dominated by *Rhizophora* and the stands of 468 Avicennia that dominate the upper inter-tidal areas (Sousa et al., 2007). This stage probably 469 corresponds to the establishment of the modern mangrove forest with a well-developed zonation 470 of taxa. Whereas δ^{13} C and C/N values suggest that organic matter is mostly contributed by 471 terrestrial plants (Mevers, 2003), the latter values are characteristic of mangrove forests located 472 on carbonate settings (Rovai et al., 2018). The regional vegetation resulted enriched with 473 Annonaceae, Araceae, Cecropia, Machaerium, and Rubiaceae, suggesting a more diverse forest. 474 Although highly variable, PC1 scores reach their lowest values indicating high terrestrial 475 influence, which, according to PC2 consists mostly of organic matter (Fig. 6). Towards the upper 476 part of the stage, sea level rise rates for the Caribbean and sedimentation rates at Punta Galeta 477 equilibrate, coinciding with the highest accumulation of organic carbon in the soil (Fig. 6).
- 478

479 6. Conclusions

480 The development of mangrove communities is the result of an intricate network of 481 interactions between local and regional factors. In the Caribbean coast of Panama, sea level has 482 defined the baselines for erosion and deposition, whereas regional precipitation has been linked 483 to sedimentary input and vegetation vigor. The interaction between these two main factors 484 defines sediment accumulation and soil accretion, as well as substrate salinity, all of them in turn 485 associated with vegetation composition and structure. The sedimentary record of Punta Galeta 486 demonstrates that the monotonically increasing sea level of the Caribbean has played a major 487 role at defining the establishment of fringe mangroves in the area. According to the geochemical 488 evidence, more than half of the local environmental variability (50.3% of the variance reflected 489 in PC1) has been directly linked to the depositional processes, which reflects the balance the

490 between marine and terrestrial influences. The balance between these two sources of variability 491 defined the spatiotemporal distribution of the mangrove community, which from \sim 5200 to 1800 492 cal yr B.P. migrated landward, and from 1800 cal yr B.P. to present have led a seaward 493 progradation of the terrain. PC2 reflets a secondary mode of environmental variability reflected 494 in the main composition of the terrigenic fraction of the sediments probably associated with 495 precipitation variability. Through the last 5200 years, there has been a trend towards lower 496 concentrations of lithogenic conservative elements, indicating a trend towards drier conditions 497 and coinciding with the southward displacement of the intertropical convergence zone (Haug et 498 al., 2001). More important, however, has been the variability related to the ENSO system, with 499 high El Niño frequency associated with high precipitation variability. Overall, the establishment 500 and thriving of mangrove forests has been a result of the equilibrium between rates of sea level

- 501 rise and rates of soil accretion. Well-established mangroves coincided with the highest
- accumulation of TOC, highlighting the importance of mangrove vegetation for maintaining soilcarbon stocks.
- 504

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- 659
- 660

661 Figure captions

662

663	Figure 1. Study area. A. Core site location (red star) and geology of Punta Galeta, Caribbean
664	coast of Panama. B and C. Mean monthly precipitation and standard deviation of monthly
665	precipitation (Data from Galeta Meteorological Station from 1974 to 2020; Paton, 2019); months
666	were classified into El Niño, La Niña, and regular conditions, according to the Southern
667	Oscillation Index (SOI) (Ropelewski and Jones, 1987).
668	
669	Figure 2. Core GAL18 from the mangroves of Punta Galeta, Caribbean coast of Panama. From
670	left to right, photographs of the core, schematization of sediment texture, content of macro rests,
671	and depth-age model. The radiocarbon date in red was excluded from the age-depth model.
672	
673	Figure 3. The geochemical record of core GAL18 from Punta Galeta, Caribbean coast of
674	Panama. Environmental stages I to V, based on changes in element concentrations, are shown in
675	the column to the right. Indicators are classified according to the interpretation of the record.
676	
677	Figure 4. Principal component analysis of element concentrations in core GAL18, Caribbean
678	coast of Panama.
679	
680	Figure 5. The pollen record of core GAL18, Punta Galeta, Caribbean coast of Panama. Taxa are
681	grouped by growing habits (after Marchant et al., 2002), and organized according to depths
682	weighted by taxon abundance; only taxa present in five or more samples are shown; occurrences
683	of Conocarpus with abundances below 1% are indicated by asterisks. The last column shows
684	sampling effort, indicating number of pollen and/or spores in each category.
685	
686	Figure 6. The sedimentary record of Punta Galeta, Caribbean coast of Panama. a) The age-depth
687	model of core GAL18 in the context of the reconstructed sea level for the Caribbean through the
688	last 5200 years; the shaded area is bounded by the estimates of Khan el al. (2017) and Toscano
689	and Macintyre (2003); a modern mean elevation of the coring site of 0.3 m asl is assumed (datum
690	from Sousa et al., 2007). b) Stacked organic and inorganic carbon concentrations of core GAL18.
691	c) Stacked percentages of cf. Laguncularia, Rhizophora, and Avicennia; Conocarpus
692	appearances marked by circles. d) PC1 scores of the geochemical record of cores GAL18. e)
693	TOC/TN ratios for core GAL18; the threshold of C/N ratios characteristic of terrestrial vs.

- 694 marine organic matter is indicated by the dashed line (after Meyers, 2003); the gray band
- 695 represents the coral reef growth shutdown reported for Las Perlas archipelago, Panamanian
- 696 Pacific (Toth et al., 2015). f) Content of sand in El Junco record, Galapagos Islands (Conroy et
- al., 2008). g) PC1 scores of the geochemical record of cores GAL18. h) Ti content in the Cariaco
- Basin record (Haug et al., 2001). i) Environmental stages identified in the sedimentary record of
- 699 Punta Galeta. h) Schematic representation of the evolution of the fringe mangrove of Punta
- 700 Galeta.











