

1 **Long-term vegetation dynamics of a tropical megadelta: mid-Holocene palaeoecology of the**  
2 **Orinoco Delta (NE Venezuela).**

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13

14 **Abstract**

15 Coastal wetlands have been proposed as highly threatened by the ongoing and future climatic  
16 change, including projected sea-level changes as an additional forcing factor compared to more  
17 inland locations. The limited knowledge generated to date in this topic has been primarily  
18 focused on those areas attaining a high population density, and rarely deals with long-term (>50  
19 years) dynamics. Here we present the first Holocene palaeoecological study carried in the  
20 Orinoco Delta, in NE Venezuela. The record presented here contains sediments from the last  
21 6200 years and is located in a river-shore swamp dominated by the palm *Mauritia flexuosa*.  
22 Current human occupation is almost restricted to small settlements of the Warao indigenous  
23 culture, closely related to the use of *M. flexuosa* and other palm species present in the zone.

24 The results show the occurrence of three well-distinguished palynological zones: (i) from 6200  
25 to 5200 cal yr BP, characterised by mixed rainforest and other taxa related to salinity (coastal-  
26 like), low (negative) values of magnetic susceptibility and magnetic grain size, absence of  
27 transported clays, and the highest macrocharcoal particles abundance; (ii) from 5200 to 2950  
28 cal yr BP, marked by a replacement of the mangrove-like vegetation by a more inland mixed-  
29 swamp forest community with low levels of charcoal, and (iii) from 2950 cal yr BP to present-  
30 day, characterised by the establishment of the current vegetation community, dominated by *M.*  
31 *flexuosa*, and an increasing trend in the charcoal curve since the last 700 years. A combination  
32 of regional (climatic changes) and local (sediment ontogeny) has been proposed as the key  
33 drivers influencing the vegetation succession recorded. The stabilisation of the sea-level that  
34 occurred during the mid-Holocene would have favoured the transgression of the coastal line,  
35 with the migration of the coastal-like vegetation seawards. Synchronous to this event, a trend  
36 towards drier conditions has been reported in the close Cariaco record, that could have also  
37 influenced the vegetation replacement. Between 3800 and 2800 years ago, the increased ENSO  
38 variability registered in Cariaco may have played a key role in the expansion of the *Mauritia* palm  
39 community. It is suggested that in our location, the potential inhabiting human populations were  
40 differently influenced by these environmental changes. First, the disappearance of the coastal  
41 resources could have favoured land abandonment, whereas the increase in the abundance of  
42 the palm might be influential for the arrival of other inland cultures that were previously used  
43 to manage *Mauritia*. This sequence shows the importance of the ecosystem services for the  
44 location inhabitants, highlighting the abandonment of the mid-Holocene culture coeval with the  
45 disappearance of its ecosystem. These results also provide information about the sensitivity and  
46 resilience in facing external stressors of both humans and vegetation, and will be valuable tools  
47 for managing the future of this ecosystem.

48

49 **Keywords:** climate change, fire, indigenous cultures, *Mauritia*, soils ontogeny, sea-level  
50 changes.

51

## 52 **1. Introduction**

53 Current climate change is a global phenomenon that will have a devastating influence on the  
54 planet and the way we perceive it nowadays (IPCC, 2013). As an attempt of anticipating, the  
55 IPCC last report highlights the importance of studying the dynamics occurred in the past that are  
56 preserved in the fossil sedimentary records as analogues to infer potential future directions that  
57 the Earth system may take (IPCC, 2013). Within the study of climate change in the long-term  
58 (>50 years), the analysis of the biota responses to those changes is equally needed.

59         Studies of long-term vegetation dynamics through palynology have been performed for  
60 the last 100 years (von Post, 1916), however, this research has been and currently continues  
61 being geographically patchy. In this sense, research efforts in the tropics are qualitatively under-  
62 represented compared to more temperate locations such as Europe or North America (Grimm  
63 et al., 2007, Flantua et al., 2015). Some handicaps often lie in the accessibility, availability and  
64 suitability of the study sites among other potential impediments (e.g., Rull et al., 2008). Within  
65 tropical South America, tropical lowlands hold some of the most biodiverse ecosystems (Myers  
66 et al., 2000), so long-term vegetation dynamics' studies are needed to understand the  
67 functioning and conservation of these globally important areas. Moreover, recent advances in  
68 the increased number of both the techniques applied and locations studied in the region have  
69 highlighted a heterogeneous human occupancy pattern prior the European invasion. This lately  
70 observed occupancy may have played in some areas a key role in shaping the current landscapes  
71 and diversity (Koch et al., 2019; Montoya et al., in press), which might be important when  
72 analysing the resilience of a given ecosystem in facing perturbations. In this sense, studies of past

73 human occurrence and their subsistence style or landscape management are crucial to  
74 understand the past, current and future vegetation dynamics.

75           Within tropical lowlands, deltas are transitional terrestrial-aquatic systems in which the  
76 landform configuration, water budget, and ecosystems reflect the balance of inputs and outputs  
77 associated with interacting climatic, upland, river, and marine processes (Warne et al., 2002a).  
78 These transitional settings typically respond quickly and markedly to even modest changes in  
79 water and sediment inflow and throughflow, as well as to other environmental parameters'  
80 shifts (França et al., 2016, 2019). Human modifications can also disrupt the balance of natural  
81 processes (typically fresh water and sediment supply) and thereby initiate a series of adverse  
82 impacts on delta ecosystems (Warne et al., 2002a). Deltas and coastal wetlands in general have  
83 been proposed as highly threatened by the ongoing and future climatic change, including  
84 projected sea-level changes as an additional forcing factor compared to more inland locations  
85 (IPCC, 2013; Vegas-Vilarrúbia & Rull, 2016). The limited knowledge generated to date in this  
86 topic has been primarily focused on those megadeltas attaining a high population density in the  
87 present-day, and rarely deals with long-term dynamics (Vegas-Vilarrúbia et al., 2015; Vegas-  
88 Vilarrúbia and Rull, 2016). Here we present the first Holocene palaeoecological study carried out  
89 in the Orinoco Delta, in NE Venezuela, an underpopulated and not massively disturbed so far  
90 tropical megadelta (Vegas-Vilarrúbia and Rull, 2016). The long-term dynamics of the deltaic  
91 vegetation will be explored based on pollen analysis, and supported by charcoal and stable  
92 isotope analyses on bulk organic matter. Furthermore, geochemical (diffraction X-ray) and rock-  
93 magnetic data will be used to derive potential palaeoclimatic and palaeoenvironmental  
94 inferences. Emphasis will be placed on diversity and stability dynamics, as well as to identify the  
95 drivers that may have triggered such dynamism. The sensitivity and resilience of the deltaic  
96 vegetation as well as the nature of the forest components will be discussed framed within the  
97 ongoing climatic change scenario.

## 99 2. Study Area and Methodology

### 100 2.1. Study area

101 The Río Orinoco is amongst the largest rivers of South America, with headwaters in the Guiana  
102 Shield region of Sierra de Parima (in the Brazilian - Venezuelan border) and discharging into the  
103 Atlantic Ocean. The drainage basin area is widely known as Orinoquia, and comprises  $1.1 \times 10^6$   
104  $\text{km}^2$  mainly shared by Venezuela and Colombia (Warne et al., 2002a). In NE Venezuela, the Río  
105 Orinoco's mouth forms a wide triangular to trapezoidal delta that branches into hundreds of  
106 rivers and channels (locally known as *caños*) intermingled with vast extents of swampy forests  
107 composing the lower Orinoco (Figure 1). The Orinoco Delta is developed in the Eastern  
108 Venezuela Basin (EVB), and has a marked distinction of water and sediment discharges between  
109 the eastern and central-northwestern delta sections (Warne et al. 2002a,b). The delta is  
110 considered as a distinct geomorphological unit and it is located between the NE border of the  
111 Precambrian Guiana Shield, the Pleistocene deposits of Mesa formation to the west, the NE  
112 mountain system of the Mesozoic - Cenozoic Cordillera de la Costa and the Gulf of Paria (Figure  
113 1) (González, 2011). Climate in the Orinoco basin is controlled by the Intertropical Convergence  
114 Zone (ITCZ), with rainfall volumes typically ranging in the delta from 1500 to 2600  $\text{mm year}^{-1}$   
115 with a slight dry season from January to April, and temperatures between 25 and 28 °C  
116 throughout the year (Huber, 1995a; Warne et al., 2002a). Diurnal tides affect the entire delta  
117 plain, with tidal amplitudes between 0.7 and up to 1.1 m in the mid delta (where the study site  
118 is located), and perform the majority of geomorphic work within the channel network (Warne  
119 et al., 2002a). The Holocene Orinoco Delta is the latest of a series of stacked deltas that have  
120 infilled the EVB since the Oligocene (Warne et al. 2002b). Delta progradation has been  
121 accomplished by a combination of distributary avulsion and mudcape progradation, with  
122 substantial sediment input from as far as the Amazon system (Aslan et al., 2003). The channel

123 network is highly dynamic, with preliminary radiocarbon dating of major distributaries, such as  
124 Caño Mánamo system, resulting in no more than 1500 years old (Warne et al. 2002a; Aslan et  
125 al.2003). The coring site is located in the northwest sector, which is widely spaced with relatively  
126 straight channels and tide- and precipitation-dominated within the fluvial-marine influenced  
127 region of the delta (middle delta). Peat swamps formed by histosols are abundant in the  
128 interdistributary plains (Aslan et al., 2003; Vegas-Vilarrúbia et al., 2010). The variety of  
129 environmental processes operating in the Orinoco Delta results in a wide range of plant  
130 communities, including mangroves, lowland forests, and marshy (herbaceous) vegetation as the  
131 most abundant types (White et al. 2002; Vegas-Vilarrúbia et al., 2007; Vegas-Vilarrúbia and  
132 López-Laseras, 2008; González, 2011). Within forests, coastal and estuarine forests form dense  
133 mangroves that occur as the outermost vegetation type along the delta shoreline, as well as  
134 landward due to marine water incursions (Warne et al., 2002b). These mangroves are composed  
135 of just a few highly specialised tree species, namely *Rhizophora mangle* (Rhizophoraceae),  
136 *Avicennia schaueriana* (Acanthaceae) and *Laguncularia racemosa* (Combretaceae). In slightly  
137 more inland positions, mature mangrove stands are often mixed with palms (*Euterpe* spp.) and  
138 *Pterocarpus officinalis*. The zonation of (inland) forest vegetation in the Orinoco Delta is also  
139 influenced by the different regimes of flooding that occur, and the forests of the middle delta  
140 are characterised by evergreen, seasonally flooded marsh and palm forests dominated by:  
141 *Symphonia globulifera* (Clusiaceae), *Virola surinamensis* (Myristicaceae), *Carapa guianensis*  
142 (Meliaceae), *Pterocarpus officinalis* (Fabaceae), *Mora excelsa* (Caesalpinaceae), *Pachira*  
143 *aquatica* (Malvaceae), *Mauritia flexuosa*, *Manicaria saccifera*, *Euterpe oleracea* and *Bactris* sp.  
144 (Arecaceae), and *Phenakospermum guyannense* (Strelitziaceae), on periodically flooded ground.  
145 In some parts of the middle Orinoco Delta, large areas with seasonally flooded shrub and/or  
146 palm savannahs are also found. Their herbaceous layer is dominated by flood-resistant grasses  
147 such as *Leersia hexandra* and *Imperata brasiliensis*. Shrubs are scarce, whereas *Mauritia* palms  
148 are quite abundant and often form extensive colonies representing up to 80% of the canopy,

149 locally known as *morichales* (Huber, 1995b; Vegas-Vilarrúbia et al., 2007; González, 2011). This  
150 palm has been defined as an Amazonian hyperdominant species (ter Steege et al., 2013), and a  
151 post glacial expansion from several microrefugia (*sensu* Rull, 2009) has been suggested (Rull,  
152 1998a; Rull and Montoya, 2014).

153           Contrary to other megadeltas of tropical regions, the Orinoco Delta does not hold a large  
154 human population (Vegas-Vilarrúbia and Rull, 2016). Nevertheless, it is the homeland of the  
155 indigenous culture called Warao, with a total population of 21,125 people in the 1992-year  
156 census, and around 48,770 people in 2011, (Huber, 1995a; INE, 2015). This important indigenous  
157 group is skilled in fishing, hunting, and gathering and has an independent linguistic affiliation  
158 (Heinen 1988), and heterogeneous origin (Gassón and Heinen, 2012; Heinen and García-Castro,  
159 2013). They live dispersed in an intricate labyrinth of river channels and creeks of the Orinoco  
160 Delta, where they have developed a specialised lifestyle adapted to the frequently inundated  
161 and swampy environment (Wilbert and Mandazen Soto, 1997). They make extensive use of the  
162 abundant forest resources, particularly the palms *Mauritia flexuosa* (*moriche*), that they call "the  
163 tree of life" (Heinen et al., 1994-1996), and *Euterpe* sp. (*manaca*). Today the Warao are rather  
164 acculturated to Venezuelan society, especially in the northwestern sector of the delta, and their  
165 lifestyle has been affected strongly by the influences of outside settlers (Heinen, 1975; Huber,  
166 1995a; Huber & Zent, 1995), in some cases associated to extensive cattle exploitation. However,  
167 evidence of previous (pre-Columbian) settlements in the delta is very limited, although  
168 archaeological sites of past peoples have been found in the near Trinidad since the early  
169 Holocene (Rivera-Collazo, 2019).

170           Despite being a Biosphere Reserve and a National Park, the Orinoco Delta faces several  
171 threats. The construction of the dam El Volcán at Caño Mánamo (Fig. 1) in 1966 by Corporación  
172 Venezolana de Guayana (CVG) is considered amongst the more important human impacts in the  
173 area (García Castro and Heinen, 1999). The creation of the dam has resulted in increased

174 upstream tidal flow of marine waters and its cascade effects (expansion of mangrove and marine  
175 fish population upstream, increased rates of sediment entrapment), increase in water  
176 temperatures and decreased in dissolved oxygen in the *caños*, salinization and acidification of  
177 the soils, and clogging of the *caños* by weedy floating vegetation and its consequences (Warne  
178 et al., 2002b; Rondón de Rodríguez et al., 2012). Another important perturbation refers to oil  
179 prospection and extraction activities, which occur in the delta since 1930s (Vila, 1970). To a much  
180 lesser extent, tourism is also present in the region, but has been heavily reduced by the  
181 economic and political instabilities faced by the country in the last fifteen years.

182

## 183 2.2. Methodology

184 The coring site is located around 20 m inland in Caño Tigre (9° 30' 08.2'' N - 62° 40' 55.3'' W, 13  
185 m bsl), near Caño Buja in the boundary between Monagas and Delta Amacuro states (Figure 1).  
186 Currently, the vegetation is characterised by a monospecific palm stand of *M. flexuosa* with  
187 some other minor elements including climbing species of Mimosoidae, the palm *Desmoncus*  
188 *orthocanthos*, *Montrichardia* sp. and several grass species of Bambusoidae being abundant in  
189 the understory. A 141 cm-long sediment core called PATAM18\_A12 was extracted from the  
190 swamp in February 2012 using a Russian corer (Jowsey, 1966) (Figure 2). Five samples were  
191 selected through the entire sequence and sent to Beta Analytic (Beta) for radiocarbon analysis  
192 by accelerator mass spectrometry (Table 1). An age-depth model was constructed using the  
193 statistical package “clam” (Blaauw, 2010) in R (R Core Team, 2018), using the calibration curve  
194 IntCal.13.14c (Reimer et al., 2013), and the best fit was obtained with smooth spline (Figure 2).  
195 Four modern samples were also collected from different environments occurring in Caño Tigre  
196 along a transect to characterise their pollen content (Figure 1; Table 2). The site selection of  
197 these four modern samples was established to represent different plant communities present  
198 nowadays in the study area and will be used as modern analogues to compare with the



199 palynological assemblages obtained in the fossil record, in addition to previous studies in nearby  
200 locations (Hofmann, 2002; Rull, 1998b; Urrego et al., 2009,2010).

201 Samples for pollen analysis (1 cc of wet sediment and 1 cm thickness) were sampled  
202 every four cm in average and processed using standard methods including KOH, HCl, and HF  
203 digestions, acetolysis and mounting/storing in glycerin jelly (Faegri and Iversen, 1989).  
204 *Lycopodium* spores' tablets (University of Lund batch # 124961; 12,542 spores/tablet) were  
205 added before chemical processing (Stockmarr, 1971). Counting was conducted until a minimum  
206 of 300 pollen and spores and the saturation of diversity (Rull, 1987). The pollen sum included all  
207 pollen types with the exception of aquatic plants (Cyperaceae, *Ludwigia*, *Myriophyllum*,  
208 *Sagittaria*, *Utricularia*), considered azonal taxa. Identification was based on regional pollen  
209 atlases (Roubik and Moreno, 1991; Colinvaux et al., 1999; Bush and Weng, 2006). The plant  
210 nomenclature used in this paper follows the APG IV classification (APG IV, 2016), and ecological  
211 grouping of the taxa found followed local botanical inventories (Vegas-Vilarrúbia et al., 2007;  
212 González, 2011). Charcoal particles were analysed following two different protocols. Micro-  
213 charcoal particles were identified and counted in the same palynological slides under the optical  
214 microscope, only particles >5 µm were considered and two different classes were established  
215 based on size: (1) small particles (>5–100 µm), indicative of regional fires due to easy dispersion  
216 by wind, and (2) big particles (>100 µm), indicative of fires occurred at local scale (Whitlock and  
217 Larsen, 2001). Macro-charcoal analysis was also performed by first deflocculating 0.5 cc of  
218 sediment in 15 ml of a 0.1M solution of Na<sub>4</sub>P<sub>2</sub>O<sub>7</sub> in cold during 2-3 days and then washed through  
219 a sieve at 125 µm (Whitlock and Larsen, 2001). The remaining residue was then analysed under  
220 a low magnification (20×) microscope in a Bogorov tray and all charcoal particles were recorded,  
221 except in samples where the number of charcoal particles was too high, in which case the count  
222 was stopped after counting 2600 particles. Particles were identified by their angular form, brittle  
223 nature and high reflectivity (Clark and Royall, 1995).

224 Samples for rock-magnetic analysis were obtained by pushing plastic boxes (2x2x2 cm)  
225 continuously into each drive of the core. The analysis involved measurement of the low-field  
226 magnetic susceptibility ( $\chi$ ) and of the natural remanent magnetization (NRM) of all samples.  
227 Additional rock magnetic properties that were measured include the anhysteretic remanent  
228 magnetization (ARM) and three isothermal remanent magnetizations that were imparted at 0.1  
229 T (IRM<sub>0.1 T</sub>), 0.3 T (IRM<sub>0.3 T</sub>) and 1.2 T (IRM<sub>1.2 T</sub>).  $\chi$  was measured with a Kappabridge KLY-2  
230 (Geofyzica Brno) susceptibility bridge using a field of 0.1 mT at a frequency of 470 Hz. ARM  
231 experiments were conducted using a D-Tech 2000 (ASC Scientific) AF demagnetizer. The ARM  
232 was applied along the Z axis of the samples with a dc bias field of 0.05 mT parallel to a peak AF  
233 of 100 mT. IRM<sub>0.1 T</sub> and IRM<sub>1.2 T</sub> (SIRM) were imparted using an IM10-30 (ASC Scientific) pulse  
234 magnetizer. Magnetizations were measured using a SRM755R (2G Enterprises) three-axis  
235 cryogenic superconducting rock magnetometer. All magnetic properties were normalized by the  
236 dry weight of the samples. We used different magnetic properties and interparametric ratios to  
237 determine variations in the type, concentration, and grain size of magnetic minerals (Evans and  
238 Heller, 2003; Thompson and Oldfield, 1986). Magnetic susceptibility ( $\chi$ ) has been used as a first-  
239 order indicator of the concentration of magnetic (*sensu lato*) minerals. S-ratios, defined as IRM<sub>0.1</sub>  
240 T/IRM<sub>1.2 T</sub> and IRM<sub>0.3 T</sub>/IRM<sub>1.2 T</sub>, have been used to indicate the relative concentration of low  
241 versus high coercivity minerals and ARM and IRM<sub>0.1 T</sub> as proxies for the concentration of low  
242 coercivity minerals. IRM<sub>1.2 T</sub> - IRM<sub>0.1 T</sub>, which is equivalent to the “hard” IRM of Bloemendal et al.  
243 (1992) (hereafter referred to as HIRM), has been used as a proxy for the concentration of high  
244 coercivity minerals. Finally, the ARM/SIRM ratio has been used to make inferences about relative  
245 variations in magnetic mineral grain size, provided that a single magnetic mineral (in this case  
246 magnetite) is dominant (Thompson and Oldfield, 1986; Evans and Heller, 2003).

247 Samples for x-ray diffraction (XRD) were picked every four cm and dried at 60 °C in an  
248 oven for 48 h and ground manually using an agathe mortar. Mineralogical analyses were  
249 conducted using a SIEMENS D500 automatic x-ray diffractometer (Cu ka, 40 kV, 30 mA and

250 graphite monochromator). The identification and quantification of the relative abundances of  
251 the different mineralogical species present in the samples were conducted using standard  
252 procedure (Chung, 1974). The same samples employed for the XRD analysis were also used for  
253 the total carbon (TC), total nitrogen (TN) (relative standard deviation: 5% of the measurements),  
254  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses (0.2 ‰ analytical precision). These analyses were conducted using a  
255 Finnigan DELTAplus TC/EA-CF-IRMS spectrometer at the Centres Científics i Tecnològics of the  
256 Universitat de Barcelona (Barcelona, Spain). The carbonate content of the samples was below  
257 the detection limit (<1%) of the XRD analysis. Therefore, the total carbon (TC) was considered  
258 equivalent to the total organic carbon (TOC).

259 Statistical analyses were performed in R version 3.82 using the packages “vegan”  
260 (Oksanen et al., 2013), “rioja” (Juggins, 2017), and “analogue” (Simpson, 2007). For statistical  
261 analyses, biological data consisted of the percentages data squared root transformed, with  
262 downweight of rare taxa in the ordination analyses. Geochemical data (XRD, rock-magnetism)  
263 were standardised. Stratigraphic diagrams were plotted with R and Psimpoll 4.27  
264 (<http://chrono.qub.ac.uk/psimpoll/psimpoll.html>) and zonation was performed by “Optimal  
265 Splitting by Information Content” (OSIC), using the broken stick method to determine the  
266 significant zones (Bennett, 1996). Diversity measures include N0 (richness or species number,  
267 also called S), N1 (number of common taxa) and N2 (number of dominant taxa), calculated  
268 following Hill (1973), and the evenness ratio N2/N0 after Finsinguer et al. (2017). For calculating  
269 these indices, the dataset used was the percentage data without downweight of rare taxa in  
270 order to capture the total diversity values. A Principal Component Analysis (PCA) was performed  
271 considering only the XRD data to characterise the main sedimentary processes that have ruled  
272 the sedimentation in the coring site that has not been included in the present paper (scores of  
273 axis 1 represented in Figure 8).

274

### 275 3. Results

#### 276 3.1. Sediment description, chronology and geochemical data

277 The retrieved sediments are composed by greyish to black clays and silty clays with variable  
278 proportions of organic matter, which can form brownish centimetre-thick peat layers (Figure 2).  
279 These sediments have been deposited within a floodplain environment. Locally, fine sand  
280 centimetre-thick layers have been found, mostly related to punctual avulsion episodes.  
281 According to the age-depth model, this sedimentary record contains the environmental history  
282 for the last 6200 cal. years BP (Figure 2). Sedimentation rate varies between 0.016 and 0.067 cm  
283 yr<sup>-1</sup>, providing a sample resolution of 78-154 years per sampling interval.

284 Figure 3 shows the geochemical analyses (including different interparametric ratios  
285 based on rock-magnetism properties) and will be explained following the statistically significant  
286 zones found based on the XRD results. As expected, rock-magnetism indicates that the dominant  
287 magnetic mineralogy in the entire sequence is magnetite, as suggested by the IRM/K values  
288 obtained and the different concentration parameters' trends observed (Figure 3), with some  
289 punctual inputs of a high-coercivity minerals (most probably hematite) around 25 and 45 cm of  
290 core depth. The coincidence of illite trends with the magnetite content confirms the detrital  
291 origin of the second mineral. The base of the record (Zone OR18-A: 141-106.5 cm depth) is  
292 characterised by high values of kaolinite and chlorite and absence of illite. Negative values of  
293 magnetic susceptibility (MS), characteristic of organic-rich sediments dominated by diamagnetic  
294 minerals, is observed in this zone, confirming the geochemical data. Total Carbon (TC) and Total  
295 Nitrogen (TN) show the highest values of the entire sequence during this zone, especially from  
296 130 cm upwards the top of the zone. Together with the increase in TC content a sharp increase  
297 in the concentration of low-coercivity minerals (magnetite) is observed. Altogether the results  
298 indicate that the ARM (magnetite content) increase observed in the lower part of the sequence  
299 cannot be interpreted as a detrital magnetite. Zone OR18-B (106.5-0 cm depth) is marked, in the

300 lower section (106.5-82 cm), by a decrease in kaolinite and chlorite and increase in illite and  
301 quite homogeneous magnetic properties dominated by low-coercivity minerals (e.g. magnetite)  
302 of detrital origin. This is confirmed by the clear correlation between the illite content and  
303 magnetite concentration in the middle part of the section (Figure 3). This lower interval is also  
304 marked by very low values of TC, TN, and TOC/TN. The intermediate section of this zone (82-37  
305 cm) is marked by fluctuating trends of kaolinite, illite, chlorite and concentration of detrital  
306 magnetite, and a weak recovery, although with still low values of TC and TN. On the other hand,  
307 TOC/TN and the isotopic fractions analysed ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) show the highest values of the entire  
308 record. The observed variations in both concentration of magnetite and grain-size related  
309 parameters are probably related to changes in sediment supply and, hence, to environmental  
310 conditions. In the upper part of the zone there is a shift towards the values attained at the  
311 bottom of Zone OR18-B, with low values of chlorite, kaolinite, TC, TN and TOC/TN and high  
312 values of illite and MS. The uppermost 10 cm of the sequence are marked by an increasing trend  
313 of chlorite, quartz, concentration of low coercivity minerals, TC and TN. The opposite trends are  
314 observed in illite, which disappears, and in MS probably due to the increase in the TC content  
315 and the formation of magnetite of non-detrital origin.

316

## 317 3.2. Palynological data

### 318 3.2.1. *Modern samples*

319 The modern samples show distinct palynological assemblages that reflect the different  
320 environment and vegetation communities in which they were collected (Table 2; Figure 4). CT0  
321 is largely characterised by high values of *Rhizophora* and the fern spore *Monolote psilate*. Other  
322 taxa present are *Euterpe*, *Mauritia*, *Cecropia*, *Urticales* (now includes in *Rosales sensu* APG IV;  
323 hereafter named as *Urticales*), *Solanaceae* and *Cyperaceae*. CT1 is marked by high values of the  
324 palms *Mauritia* and *Euterpe*, and to a minor extent, *Rhizophora*, *Monolete psilate*, *Asteraceae*,

325 *Cecropia*, Combretaceae/Melastomataceae (Myrtales; hereafter referred as  
326 Combrataceae/Melastomataceae) and Cyperaceae. *Mauritia* pollen attains the maximum values  
327 in the modern sample CT2 and obscures the rest of palynological taxa signal; this sample was  
328 collected at the same location than the sedimentary sequence PATAM18\_A12. Sample CT3 is  
329 characterised by high values of Poaceae, Monolete psilate, *Ficus*, *Cecropia*, Asteraceae and  
330 Cyperaceae, with some input from *Alchornea*, *Anthurium* and the aquatic plants *Ludwigia* and  
331 *Sagittaria*. Microcharcoal values are average, being the lowest value obtained in sample CT2,  
332 and the highest value in CT3. In relation to the macrocharcoal analysis, values are almost  
333 negligible for three of the samples (CT0: 88, CT1: 20, and CT2: 30 particles cc<sup>-1</sup>), while CT3 attains  
334 a high value (2690 particles cc<sup>-1</sup>; Fig. 4).

335

### 336 3.2.2. Sedimentary record PATAM18\_A12

337 The fossil pollen assemblages obtained in the sedimentary record of PATAM18\_A12 delimits  
338 three significant zones (Figure 5). Microcharcoal values follow the same trends than the  
339 macrocharcoal analysis, and given the broader geographical provenance of the microcharcoal  
340 particles, only the small particles (indicative of fires occurring from a larger spatial scale) have  
341 been included in the diagram for comparison.

342 Zone OR18-1 (103-141 cm; eight samples): The lower zone is characterised, at the  
343 bottommost of the section, by high values of *Ficus*, Myrtaceae, and Asteraceae, which shortly  
344 after drop to almost disappear. This zone is then marked by high values of *Symphonia*, *Ilex*,  
345 *Rhizophora*, *Cassipourea*, Asteraceae and Urticales. Monolete psilate and *Polypodium* verrucate  
346 are the most abundant pteridophyte spores, and *Acrostichum* is, although with low values, only  
347 present in this zone throughout the record. The aquatic plants' record shows punctual peaks,  
348 such as *Sagittaria* at the bottom of the zone and Cyperaceae (semi-aquatic) in the upper section.

349 *Ludwigia* is also present in the upper half with low values. Macrocharcoal particles attain their  
350 maximum values during this zone (Figure 5).

351           Zone OR18-2 (63.5-103 cm; sixteen samples): This zone is marked by the disappearance  
352 of the previous dominant taxa, high values of Urticales, and the presence of several palms  
353 including *Euterpe*, *Mauritia* and *Desmoncus*, appearing the last two taxa for the first time in the  
354 record. *Alchornea* peaks at the middle of the zone, and other minor taxa contributing in a more  
355 regular, continuous way, are *Ilex* (though with lower values than in the previous zone),  
356 Asteraceae, *Amanoa* and *Herrania*. Besides *Ilex*, other taxa that show decreased abundances  
357 compared to Zone OR18-1 are Myrtaceae and *Symphonia*, whereas *Crudia*, Loranthaceae and  
358 *Paullinia* appear in the record at the beginning of the zone. Although with lower values than in  
359 the previous zone, Monolete psilate, *Polypodium* verrucate and Cyperaceae are the more  
360 representative taxa outside of the pollen sum, with some punctual appearance of *Salvinia*-t and  
361 *Actinotaenium*. The charcoal values are very low, and a subtle increase is observed at the upper  
362 half of the zone.

363           Zone OR18-3 (0-63.5 cm; twenty-six samples): The upper zone is marked by the lowest  
364 values of taxa previously abundant like Urticales and *Ilex*, and the dominance of *Mauritia*. This  
365 zone is divided into two subzones: OR18-3a (18.5-63.5 cm; eighteen samples) and OR18-3b (0-  
366 18.5 cm; eight samples). Sub-zone OR18-3a is defined by a sudden and marked increase in  
367 *Mauritia* abundances that reach up to 60% of the total pollen sum. Other taxa contributing to a  
368 minor extent include *Anthurium*, *Euterpe* and Asteraceae. Towards the upper half of the  
369 subzone, there is an increase in the abundance of taxa related to water, such as *Salvinia*-t, and  
370 the algae *Actinotaenium* and *Mougeotia*. The split of this upper zone responds to the marked  
371 appearance of several taxa only in the sub-zone OR18-3b, such as  
372 Combretaceae/Melastomataceae and *Spathiphyllum*. The uppermost sub-zone is also

373 characterised by a marked increase in the charcoal record and a decrease in the algal remains  
374 that appeared in the previous subzone OR18-3a.

375

### 376 3.3. Statistical analyses

377 The similarity between the pollen assemblages obtained in the modern and fossil samples has  
378 been tested with three different statistical analyses (Figure 6: analogue matching and close  
379 analogues (AMCA), Detrended Correspondence Analysis (DCA), and timetracker). The AMCA  
380 technique defines the occurrence of analogues based on the similarities found between the  
381 modern and the fossil assemblages' composition (Simpson, 2012). DCA biplot shows the fossil  
382 and modern samples data treated as being the same dataset. In the timetracker ordination  
383 analysis the modern samples are used for defining the spatial framework where to display the  
384 fossil samples, and those fossil samples are connected following the stratigraphical order  
385 (Simpson, 2007). AMCA plot shows all the fossil samples that have one or two modern samples  
386 analogues, which are mostly restricted to the upper zone OR18-3. In the DCA analysis the fossil  
387 samples are clustered and well defined following the palynological zones observed. Regarding  
388 the display of the samples in the DCA plot, it is noteworthy that the palynological zones OR18-1  
389 and OR18-2 do not have any modern sample related. The same is also shown in the timetracker  
390 ordination analysis, where modern samples CT-0 and CT-3 appears much farer to the fossil  
391 sequence samples than CT-1 and CT-2. Altogether the three analyses interpretation shows that  
392 only the upper samples from the sedimentary record have modern analogues. Considering the  
393 range of modern samples presented (Figure 4), samples CT-1 and CT-2 act as modern analogues  
394 whereas CT-0 and CT-3 do not share enough similarities with any of the fossil samples analysed.

395 The geochemical data have been plotted as environmental variables in a Redundance  
396 Analysis (RDA) against the biological data (fossil pollen) in Figure 7. The XRD analysis shows illite  
397 and quartz at the left of the first axis and chlorite and kaolinite to the right, whereas the second



398 axis splits illite towards the positive values and the rest of variables located at the negative side  
399 (Figure 7A). Within the space defined, the biological data are displayed along the first axis, with  
400 samples from the palynological zone OR18-3 located at the left with negative values, followed  
401 to the right by the samples belonging to Zone OR18-2 and towards the more positive values of  
402 axis one are the oldest samples of OR18-1. Such distribution of the pollen samples is also  
403 observed in the RDA analysis of the rock-magnetic data (Figure 7B). In this case, besides the  
404 ordination from negative (younger samples) to positive (older samples) values of axis one, there  
405 is a difference in the distribution pattern of the samples according axis 2. Whereas the pollen  
406 samples from OR18-1 and OR18-2 are located close to zero or negative values of the axis, the  
407 younger samples from OR18-3 are widely distributed along the entire axis. Regarding the  
408 environmental variables considered, high coercivity minerals, MS and low coercivity minerals  
409 are located to the left of axis 1 and the grain size and the high/low coercivity ratio to the right.  
410 The second axis divides MS, high coercivity minerals and grain size, located in the positive side  
411 of the axis, from low coercivity minerals and the ratio (plotted in the negative side of axis two).  
412 Finally, following Meyers (1994), we have plotted the samples according to their values in  
413 TOC/TN and  $\delta^{13}\text{C}$  to observe the nature of the biological remains found in the sediment. Most  
414 of the samples attain TOC/TN ratio values higher than 20 and  $\delta^{13}\text{C}$  values between -28 and -30.5  
415 ‰, which indicates that the organic matter is mainly related to  $\text{C}_3$  terrestrial plants, except for  
416 the samples of zone OR18-1 representing the last 1400 years of the sedimentary record that  
417 contain lower values, indicating some algal contribution to the organic matter present in this  
418 sequence.

419

## 420 **4. Interpretation & Discussion**

### 421 **4.1. Long-term dynamics of deltaic vegetation**

422 The Mid-Holocene record of the sedimentary archive PATAM18\_A12 has shown the high  
423 dynamism of the deltaic vegetation of Caño Tigre during the last 6200 years. Although forested  
424 through the entire record, the taxa composition has greatly varied through time showing  
425 different forest types.

426 From 6200 to 5200 cal yr BP, the presence of several salinity tolerant taxa (*Rhizophora*,  
427 *Cassipourea* and the fern *Acrostichum*) can be interpreted as the occurrence of a mixed  
428 rainforest or swamp forest with mangrove elements (or mangroves occurring nearby), similar to  
429 other coastal plant communities found in the Amazon in the recent past (Behling & Lima da  
430 Costa, 2000,2001; Vedel et al., 2006), and today in the lower delta (Vegas-Vilarrúbia and López-  
431 Laseras, 2008). The area was likely subjected to some tidal influence as indicated by the  
432 abundance of *Rhizophora* and Chenopodiaceae/Amaranthaceae (Urrego et al., 2013), with  
433 inundation events being rare as shown by the presence of rainforest elements (Vedel et al.,  
434 2006; Vegas-Vilarrúbia et al., 2007). This ancient coastal-like community also presented some  
435 disturbance as revealed by the presence of pioneer taxa such as *Cecropia*, Poaceae, Cyperaceae  
436 and Monolete psilate that could indicate some brackish waters or the opening of the understory  
437 (Rull, 1998b; França et al. 2012). The presence of *Acrostichum* (and  
438 Chenopodiaceae/Amaranthaceae) on Colombian and Venezuelan mangroves has been  
439 previously interpreted as indicative of early successional stages (Vegas-Vilarrúbia, 2000; Urrego  
440 et al. 2013), but in the present study both taxa maintained their abundances during a  
441 millennium. In addition, the differences between the plant dynamics of pure mangroves and our  
442 plant community, currently located at around 50 km from the coast line, need to be considered  
443 when comparing results. Despite the long-dispersion by wind and water of its pollen (Behling et  
444 al., 2001), the presence of *Rhizophora* individuals in the coring site or nearby during this time  
445 interval should not be completely ruled out, as mangrove forests have been previously reported  
446 in the area since at least 7000 cal yr BP (Rull et al., 1999). In Caño Tigre, we hypothesise the local  
447 occurrence of *Rhizophora* trees, even at low abundances, due to the occurrence of *Rhizophora*

448 trees in the surroundings of the coring site nowadays (Table 2 & Figure 4). Nevertheless, this  
449 ancient plant community differed from the current assemblages growing nearby, as it shown by  
450 the absence of modern analogues within the samples analysed (Figure 6). On the contrary, some  
451 of the abundant taxa found in this zone are also common elements in today's swamp forest  
452 closer to the delta mouth (Vegas-Vilarrúbia and López-Laseras, 2008).

453         Around 5200 cal yr BP, a vegetation succession took place, dominated by the  
454 appearance and establishment of *Mauritia*. The marked decrease of previously abundant taxa  
455 (*Symphonia*, *Ilex*, *Rhizophora*, *Cassipourea*, *Amaranthaceae/Chenopodiaceae*, *Coursetia*) and  
456 the increase of others including *Urticales*, *Alchornea*, *Amanoa*, *Virola*, *Anthurium*, *Euterpe* and  
457 *Herrania* showed the change towards a different assemblage of mixed swamp forest. This forest  
458 composition evidenced the occurrence of at least sporadically inundation events (Behling & Lima  
459 da Costa, 2000) and was not transitional, as it lasted for more than 2000 years, until  
460 approximately 2900 cal yr BP. Similar trends and vegetation composition were found in a close  
461 record of French Guiana mangroves and in the N Brazilian coasts (Tissot & Marius, 1992; Behling  
462 2001; Behling & Lima da Costa 2001). The disappearance of coastal-like communities has been  
463 reported for other coastal records during the mid-Holocene. However, these sequences have  
464 often registered a replacement by herbaceous vegetation forming marshes instead of a mixed-  
465 swamp forest (Behling et al., 2001; Urrego et al. 2013). Some exceptions to this herbaceous  
466 replacement are found in more inland records of the N Brazilian coast, showing a mangrove-like  
467 vegetation being replaced by palms (Behling, 2001; Behling & Lima da Costa 2001). The forest  
468 taxa composition found in Zone OR18-2 has been previously reported also as a palm-swamp  
469 community, but given the evenness of the zone compared to the next one (Figure 8: ratio  
470  $N2/N0$ ), we argue that a numerically intermediate importance of *Mauritia* will be best defined  
471 as a mixed-swamp forest (González, 2011; Tissot & Marius, 1992). In this sense, our classification  
472 as a mixed-swamp forest agrees with previous botanical surveys of present-day plant  
473 communities in the lower Orinoco Delta plain (Vegas-Vilarrúbia and López-Laseras, 2008;

474 González, 2011). Altogether, the community replacement nature and dynamics found are in  
475 agreement with the hypothesis by Vedel et al. (2006), that highlights that the differences  
476 between the successions recorded can rely in the distance of the coring site to the sea.

477         Since 2950 cal yr BP onwards, the vegetation of Caño Tigre is represented by a *Mauritia*-  
478 dominated swamp, which is the present-day plant community (indicated by the similarity to the  
479 modern samples; Figure 6). However, once established, several shifts have occurred maintaining  
480 the dynamism of the plant community until shaping the present landscape. Noteworthy are: i)  
481 the appearance and increase of aquatic elements during the last 1400 years (Figure 5), high  
482 enough to change the isotopic and magnetic signals of the sediment (Figure 7), and ii) the  
483 increase in Combretaceae/Melastomataceae and *Spathiphyllum* 700 cal yr BP. coeval to the  
484 increment in the fire occurrence (Figure 5). Such synchrony points to a possible causal  
485 relationship, especially regarding the last taxon, inhabitant of the understory, that will be  
486 discussed in the last section of the discussion.

487         Caño Tigre has shown three different stable plant communities, in the sense of being  
488 present in the location without major structural changes during several millennia. It is  
489 noteworthy that although the changes occurred were dramatic and probably had profound  
490 consequences in the forest structure or ecosystem services provided, they were neither abrupt  
491 nor fast. Thus, the coastal-like forest was replaced by a mixed forest between 5400 and 4900 cal  
492 yr BP, whereas the expansion of *Mauritia* and the establishment of the palm swamp took almost  
493 1000 years, between 3800 and 2900 cal yr BP. Nevertheless, these long-term changes are  
494 referred to plant community shifts. Regarding individual taxa responses, it can be observed the  
495 abruptness in the appearance and expansion of *Mauritia*, Combretaceae/Melastomataceae or  
496 *Spathiphyllum*, and in the disappearance of *Rhizophora*, *Cassipourea* or Urticales, all faster than  
497 the centennial sampling resolution performed (Figure 2). These results are in agreement with  
498 previous studies highlighting the need of long-term research in order to observe real plant

499 communities' dynamics applicable to answer today's ecological and conservation questions (Rull  
500 et al., 2013; Vegas-Vilarrúbia et al., 2011). Within the dynamics observed, the expansion of  
501 *Mauritia* occurred around 3000 years ago and the establishment of the current landscape  
502 resulted in a less diverse plant community. This is clearly appreciated in the diversity indices  
503 included (Figure 8), where despite the total number of species being regular through the entire  
504 record (N0), the almost monospecific character of the palm-swamp drastically reduced the  
505 evenness of the plant community (N2/N0). Local conditions have been proposed as key drivers  
506 of the shift from mixed mangrove-like communities to monospecific assemblages in Colombian  
507 coastal records (Urrego et al., 2013), although referred to changes towards mangrove species  
508 dominance, not *Mauritia's* as in the present study. In the following sections, we will infer some  
509 of the key drivers responsible for the observed vegetation responses.

510

#### 511 4.2. Ecological consequences of Holocene geomorphology, sea-level and climate changes

512 The onset of the Holocene was characterised by an eustatic sea-level around 60 m below  
513 present, and rose at a relatively stable rate until 7000 cal yr BP, with a progressive decrease  
514 afterwards to present (Khan et al., 2017). Holocene sea-level changes in the Caribbean show  
515 that for the Orinoco region, there was a rapid relative sea-level rise (SLR) in the early to mid-  
516 Holocene (from  $-6.8 \pm 3$  m at 7.8 cal kyr BP to  $-1 \pm 0.9$  by 5.9 cal kyr BP), remaining relatively  
517 constant afterwards (Khan et al., 2017). Most of coastal Amazonian palaeoecological studies  
518 highlight the importance of Holocene sea-level trends in the past vegetation responses observed  
519 (Cohen et al., 2012). Due to the proximity of the coring site to the present coastline (Figure 1),  
520 it is logical to explore the potential effects of sea-level rise on the vegetation dynamics, as it has  
521 been highlighted by Behling & Lima da Costa (2000) for Amazonian wetlands not strictly coastal.  
522 We suggest that our coring site was located closer to the coastline prior the stabilisation of the  
523 sea-level and thus during the occurrence of the coastal-like plant community, according to

524 previous geomorphologic works that have suggested that the northwest region of the Orinoco  
525 Delta prograded around 20-30 km during the late Holocene (Aslan et al., 2003). The stabilisation  
526 of the sea-level likely provoked the transition from marine-dominated sedimentation  
527 environment to a fluvial floodplain one with the formation of new soils and the progradation of  
528 the coast shoreline (Yulianto et al., 2005). This environmental shift was probably involved in the  
529 migration of the coastal-like elements seawards as it has been previously reported (Behling &  
530 Lima da Costa, 2001; Tissot & Marius, 1992). Considering the potential effect of the sea-level  
531 change, there was a delay or time-lag between the driver (sea-level stabilisation) and the  
532 ecological response (migration of the coastal-like taxa and appearance and establishment of  
533 *Mauritia*) of about 500 years in Caño Tigre (from 5900 to 5400 cal yr BP). However, it is highly  
534 unlikely that the sea-level change acted as the sole force driving the vegetation change. Under  
535 this scenario of sea-level and soil stabilisation, regional climatic trends were likely also involved.  
536 The Cariaco basin record has proven its usefulness and accuracy in registering supra-continental  
537 past climatic trends, and is located very close to our study area (Figure 1). The titanium (Ti) curve  
538 of Cariaco shows a decreasing trend in precipitation and strong El Niño signal around mid-  
539 Holocene starting around 5400 cal yr BP (Haug et al., 2001), coinciding with the onset of the  
540 vegetation replacement. This is also observed more locally in the scores of PCA first axis of the  
541 XRD data (Figure 8) as well as the geochemical and rock-magnetic data (Figure 3), that shows  
542 the absence of Illite and can be interpreted as some humidity in the soils and negative MS values  
543 related to organic-rich sediments. The absence of transported clays and the observed enhanced  
544 magnetite content in the lowermost part of the core suggests the presence of authigenic  
545 magnetite. We suggest that the replacement of coastal-like elements by a mixed-swamp forest,  
546 with the arrival and establishment of *Mauritia* was influenced by the joint action of at least two  
547 interconnected, scale-dependent processes: i) sea-level stabilisation promoting stable  
548 conditions for new soil formation (local process), suitable for the arrival of new taxa, and ii)  
549 registered precipitation decrease with strong El Niño acting as a trigger (regional process),

550 favouring its establishment with regards to other species (Urrego, 2018). As already mentioned,  
551 mid-Holocene mangroves colonisation has been reported in many Caribbean works highlighting  
552 the importance of local factors compared to regional sea-level rise in the establishment of  
553 coastal plant communities (Urrego et al., 2013). In this sense, Emilio et al. (2014) showed the  
554 importance of soil conditions to explain site-to-site variability in the observed current plant  
555 communities. These authors revealed in a macro-study that young, weakly structured and poor  
556 soils favour higher palm basal area compared to trees (Emilio et al., 2014). The importance of  
557 the soils has been also proved in a local scale by Vegas-Vilarrúbia and López-Laseras (2008) who  
558 tested the importance of edaphic conditions to interpret the large  $\beta$ -diversity of the lower  
559 Orinoco Delta plain that can be observed today. It is possible that the nature and quality of the  
560 formed soils favoured the arrival of *Mauritia* and the increase of *Euterpe*. In this sense, finer-  
561 grain sediments accumulation resulted from the delta progradation could have formed water-  
562 saturated (or poorly drained) sediments, and the combination with a decrease in organic matter  
563 (Figure 3) might have favoured the *Mauritia* establishment (Aslan et al., 2003; Urrego, 2018).  
564 Whatever the nature of the sediment prior and after the sea-level stabilisation, a change in its  
565 characteristics is evident by the zonation resulted in the geochemical data (Figure 3). The  
566 potential socioeconomic and ecological threats of current and future sea-level rise to deltas have  
567 been already highlighted by Vegas-Vilarrúbia and Rull (2016). Our study shows the local habitat  
568 disappearance resulted at least partially from the Holocene sea-level rise, which could be used  
569 as past analogue for future scenarios (Vegas-Vilarrúbia et al., 2011; Rull et al., 2013).

570         After the disappearance of coastal-like elements, another dramatic event in the Caño  
571 Tigre record was registered with the expansion of *Mauritia* at the expenses of the mixed-forest  
572 between 3800 and 2900 cal yr BP. Based on the Cariaco Ti curve, this period registered the  
573 maximum amplitude of the climatic trends during the Holocene caused by an increased ENSO  
574 variability that included several precipitation minima during this period, and was preceded by a  
575 strong El Niño (Haug et al., 2001). According to Haug et al. (2001), such amplitudes are

576 comparable to the difference between the Younger Dryas and the Holocene Thermal Maximum,  
577 and it is striking that the *Mauritia* expansion occurred exactly coeval to this climatic event (Figure  
578 8). These results are in agreement with Urrego (2018), which has suggested a positive  
579 relationship between ENSO driven short-duration droughts and *Mauritia*. Similar palm swamp  
580 flourishing as the one occurred in the present study has been also previously reported and  
581 interpreted as evidence of relatively high water table (Behling & Lima da Costa, 2001). Thus, a  
582 potential influence of the soil type present (water-saturated or poorly drained) should be taken  
583 into account. Moving onwards on the temporal frame, the Cariaco record is characterised by  
584 wetter conditions during the Medieval Warm Period (MWP: 1.05-0.7 cal kyr BP), and this is also  
585 reflected in Caño Tigre record, although more subtly, by the synchronous increase in aquatic  
586 elements (Figures 5, 7 & 8). However, the trends observed in the PCA axis scores do not agree  
587 with the climatic conditions inferred by the Cariaco record (Figure 8). It is suggested that once  
588 the *Mauritia* swamp expanded around 3800 cal yr BP, the clays trend is responding to the fine  
589 sediment captured by the *Mauritia* roots, obscuring any regional climate signal. The importance  
590 of the soils ontogeny (and therefore, of the local processes) in the present record is also shown  
591 in the RDAs made with the XRD and rock-magnetism data, with the biological samples (fossil  
592 pollen) ordered by age (Figure 7). Our data are also in agreement with geomorphological studies  
593 showing the onset of Caños Mánamo and Pedernales as the principal distributaries of the  
594 northwest delta by distributary avulsion around 3000 cal yr BP, coeval to the final establishment  
595 of *Mauritia*-dominance (Aslan et al., 2003).

596         Around 700 cal yr BP, a shift towards drier conditions started in Cariaco that culminated  
597 with several precipitation minima during the Little Ice Age (LIA; Haug et al., 2001). The present  
598 record is marked at this time snapshot by the sudden appearance and increase of several taxa  
599 that altered the composition and possibly the structure of the plant community (Figure 5). This  
600 period is also characterised in Caño Tigre by an increase in the charcoal record and in the  
601 concentration of low-coercivity minerals, which would agree with the climatic scenario inferred



602 from Cariaco (Figure 8). Besides Cariaco, other palaeoecological studies show shifts in climatic  
603 conditions around 700 cal yr BP (e.g., Behling et al., 2001; Carrillo-Bastos et al., 2010). Apart  
604 from the climatic trends, in the Orinoco Delta, Muller (1959) mentioned a previous work that  
605 evidenced a shift of the main Orinoco discharge from the eastern Delta towards Macareo and  
606 Boca Vagre estuaries at that time.

607

#### 608 4.3. Human occupancy in the NW Orinoco Delta

609 The presence of large indigenous populations in the Orinoco region was noticed by the earliest  
610 European explorers in the 16th and 17th centuries (Huber, 1995a). Even nowadays, Orinoquia is  
611 the homeland of 26 different Amerindian groups (Gassón, 2002). Palaeoecological studies can  
612 provide important evidence of past human presence or activities, and this information is  
613 especially valuable for those regions where archaeological research is limited (Montoya, 2018),  
614 as it is the Orinoco Delta. Amongst the most used proxies to infer past human impact in  
615 palaeoecological research is the fire record, even in the absence of impacts on the vegetation  
616 (Behling & Lima da Costa, 2000). Nevertheless, human presence and impact in the landscape  
617 has also been evidenced in the absence of fire use in coastal savannah environments (Iriarte et  
618 al., 2012). In this sense, multi-proxy studies (including for instance phytoliths, macro-fossils, or  
619 biomarkers) providing independent lines of anthropic evidence are encouraged to avoid too  
620 simplistic or even wrong inferences, as fire can have a climatic origin too (Siegel et al., 2015). An  
621 exception to this climatic origin of fires would be the wettest regions of northwestern Amazonia,  
622 where fire ignition is often undoubtedly human-made (Montoya et al., in press).

623 Last 700 yr were characterised in the Caño Tigre record by a high fire incidence. As  
624 already mentioned, this increase coincided with a climatic shift towards drier conditions so a  
625 climate role should not be disregarded. Given the high charcoal values attained in the record  
626 and the current precipitation regime in the zone ( $>1500$  mm yr<sup>-1</sup> without a marked dry season),

627 we propose that the drier conditions could have favoured the fuel biomass availability. However,  
628 as showed by the continuous and increasing trend, we suggest that the ignition source of these  
629 fires was probably human occupation, with the burning of the plant material being favoured by  
630 the drier climatic conditions. Our suggestion of coupled human and climatic forces as  
631 responsible for the fire increase is also in agreement with the research performed so far in  
632 nearby ancient sites. In this sense, archaeological literature shows an important movement for  
633 eastern South American peoples starting at 500 Common Era (CE), with the Arauquinoid peoples  
634 migrating from Middle Orinoco towards the delta, the Antilles and the Guianas coast around  
635 600-700 CE (Navarrete, 2008). Once the Arauquinoid started their migration down through the  
636 river, they mixed with Cedeñoid groups in the Delta, and mixed Cedeñoid-Arauquinoid-Valloid  
637 groups sailed toward Trinidad and the Antilles (Rostain, 2008). Closer to the present study area,  
638 the Mora site in central Delta was characterised by integrated elements of the Barrancoid and  
639 Arauquinoid traditions dated around 1000-1500 CE (Voorhies et al., 1981).

640 On the contrary, the oldest interval registered in the Caño Tigre record was related to  
641 more stable climatic conditions, and the presence of a mixed forest with coastal-like vegetation  
642 and some disturbance elements (i.e., *Chenopodiaceae/Amaranthaceae*, *Cecropia*, *Monolete*  
643 *psilate*). The most likely driver of such vegetation opening or clearing recorded on Zone OR18-1  
644 is fire, as this period is characterised by the highest values of macrocharcoal of the entire  
645 sequence (Figure 5). Despite the lack of additional proxies, it is suggested that this fire record  
646 was highly likely human-made, as it coincided with the wettest period of the interval studied  
647 (Figure 8). The southeastern Caribbean (including southern islands and the mainland coast of  
648 Venezuela) has provided some evidence of ancient peoples (Siegel et al., 2015). The Archaic  
649 period has been described as a period of sparse but continuous inhabitation of the coastal areas  
650 forming an Archaic arc that included the southern Caribbean islands and the Venezuelan  
651 mainland coast (including the Gulf of Paria) until at least the Guianas and Brazil at the South  
652 (Antczak et al. 2019; Sanoja & Vargas, 1999). It has been suggested that the Archaic period in

653 the coastal areas could have lasted longer than in the more inland locations due to geographic  
654 isolation (with stepped slopes and hills in the Venezuelan coast and islands). However, they  
655 might have had sporadic or even regular contacts with (inland) pottery-makers depending on  
656 the proximity. During the Mesoinian period (7000-5000 yr BP, equivalent to Archaic) there was  
657 a transition from mammals' hunters to socio-economic tribal formation, defining diverse  
658 economic and sociocultural strategies. Within the subsistence strategies described for the  
659 eastern Venezuelan coast during the Archaic period, the following could have been adopted by  
660 the potential inhabitants of Caño Tigre: (i) gathering of endemic species in the Sucre coast  
661 mangroves (7000-4000 yr BP), (ii) fishermen and hunters related to eastern Venezuelan coast  
662 gatherers, or (iii) sea shore and deep water fishermen and sea shell gatherers, although the first  
663 remains for this last type appeared later (Navarrete, 2008). Towards the south, palaeoindian and  
664 archaic shell mounds were commonly found in western Guiana littorals, especially between the  
665 Orinoco Delta and Essequibo river, with relatively sparse inhabitation during the initial period  
666 and main subsistence based on shellfish, fishing and hunting, but also using a wide range of  
667 plants including palms (Plew, 2009; Rostain, 2008,2009). In addition, previous palaeoecological  
668 records in N Brazil have argued possible Archaic human occupancy based on the charcoal record  
669 in similar environments to the present study site (Behling & Lima da Costa, 2001). It is suggested  
670 that in Caño Tigre record, coastal peoples were likely occupying the location, and once the  
671 seaward progradation of the sediment started, these ancient people abandoned the area.  
672 However, more multi- and interdisciplinary research is needed in order to validate or reject this  
673 working hypothesis. In case the coastal-peoples occupation is proved, the land abandonment  
674 following the combination of drivers including sea-level rise and drier conditions would have  
675 profound consequences in terms of the projected climatic scenarios and the current inhabitants  
676 of the delta (IPCC, 2013; Vegas-Vilarrúbia and Rull, 2016). On the other hand, based on the  
677 evidence obtained so far, a causal link in the synchronicity between the disappearance of fires

678 (land abandonment) and the appearance and establishment of *Mauritia* in the surroundings  
679 remains elusive (Rull and Montoya, 2014).

680           Given the abundance of archaeological remains near the study site altogether, it is  
681 proposed that Caño Tigre location was probably populated at least in the mid-Holocene and  
682 during the last millennium by different cultures with diverse subsistence strategies. The above  
683 suggestions of human presence and their relationship between their dynamics and the  
684 environment are not examples of environmental determinism, as formerly proposed for some  
685 lowland South American cultures (Meggers, 1954; Lathrap 1970). Such interpretation should be  
686 taken as a working hypothesis of some of the potential strategies used by past peoples when  
687 facing environmental events and the interplay with the natural dynamics of the ecosystems in  
688 where they lived. Nevertheless, given the absence of shell mounts or other archaeological  
689 evidence, this hypothesis should be considered with caution.

690

## 691 **5. Conclusions**

692 The palaeoecological study of the mid-Holocene dynamics of Caño Tigre vegetation has shown  
693 the forested nature of the landscape for the last 6200 years. However, this forest dramatically  
694 changed its composition twice during the interval studied, showing a rapid response of the  
695 individual species, but more gradual shifts as plant community. Swamp or rainforest with  
696 coastal-like elements characterised the location until approximately 5400 cal yr BP, when drier  
697 conditions were inferred from Cariaco and the sea-level was already stabilised, which promoted  
698 sediment accumulation and the transition to a fluvial floodplain environment. The shoreline  
699 progradation favoured seaward migration of the coastal-like elements of the forest, and the  
700 nature of the sediment formed likely allowed the arrival and establishment of *Mauritia* stands  
701 and the occurrence of a mixed-swamp forest in this floodplain. Between 3800 and 2900 cal yr  
702 BP, during a period of climatic instability, *Mauritia* undertook an expansion that culminated with

703 its absolute dominance upon the vegetation, establishing a less diverse palm-swamp in the study  
704 site. This community was completely established around 3000 yr ago, when the present-day  
705 main tributaries of the northwestern sector of the delta (i.e., Mánamo) appeared. Although  
706 similar to the present-day community, additional plant elements arrived to the study site around  
707 700 years ago that finally shaped the current landscape. This last period was also marked by an  
708 increase in the fire regime. Archaeological evidence and the climatic inferences made from  
709 previous works point to a likely human contribution to the origin of this fire trend, possibly the  
710 arrival of the Arauquinoid culture to the study site. An ancient human occupancy in the area has  
711 been also suggested for the Mesoindian or Archaic period, between 6200 and 5400 cal yr BP,  
712 when the coastline was about 30 km closer than nowadays, which would probably have had  
713 some coastal affinities and subsistence lifestyle. Nevertheless, more research with multi-proxy  
714 and interdisciplinary approach is mandatory in order to validate these working hypotheses.  
715 Given the importance of local conditions including delta ontogeny in both present and previous  
716 works on wetlands, careful must be taken before extrapolating results of a given wetland/delta  
717 to a supra-regional scale in terms of palaeoclimate and biological responses. Concerning climate  
718 during the 6200 yr interval studied, it is remarkable the lack of significant delays of Caño Tigre's  
719 plant communities showing fast ecological responses to the climatic events or shifts registered  
720 in Cariaco. This research shows the high dynamism and sensitivity of these tropical plant  
721 communities in facing climatic shifts, so special attention to the potential responses they may  
722 develop in the near future as consequences of the ongoing climate change scenario should be  
723 paid. In this sense, the inferred socio-ecological shifts of increased ENSO and sea-level changes  
724 have been noteworthy. Finally, the present study shows the importance of undertaking multi-  
725 proxy approaches and frame them in an interdisciplinary context for acquiring a more precise  
726 picture of past landscape dynamics.

727

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742

743 **7. References**

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1024 **Table 1.** AMS radiocarbon dates used for the age-depth model. WA: weighted average.

Laboratory	Sample	Depth (cm)	Sample type	Age (yr C <sup>14</sup> BP)	<sup>13</sup> C/ <sup>12</sup> C ratio (‰)	Age (cal yr BP) 2σ	Age (cal yr BP) estimation (WA)
Beta- 347774	PATAM18D1/40	40	Pollen residue	1820±30	-29	1694- 1825	1763
Beta- 347775	PATAM18D2/80	80	Pollen residue	3450±30	-28.5	3637- 3779	3952
Beta- 347776	PATAM18D3*/10	100	Pollen residue	4680±30	-27.9	5319- 5429	5123
Beta- 342033	PATAM18D3/46	127	Pollen residue	5290±30	-28.7	5990- 6181	6013
Beta- 342044	PATAM18D3*/49	140	Pollen residue	5280±30	-26.6	5987- 6128	6229

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1032 **Table 2.** Main features of the modern samples collected in different environments along Caño  
 1033 Tigre (CT).

Sample	Coordinates	Elevation	Vegetation community	Major taxa
CT0	9°32'44.3"N - 62°38'53.8"W	6 m asl	Disturbed delta; abandoned Warao settlement	<i>Mauritia flexuosa</i> , <i>Montrichardia arborescens</i> , <i>Blechnum</i> sp., Poaceae, <i>Rizophora mangle</i> , <i>Eichhornia crassipes</i> , Cyperaceae
CT1	9°30'28.0"N - 62°40'50.1"W	10 m bsl	Palm forest	<i>Mauritia flexuosa</i> , <i>Euterpe</i> <i>oleracea</i> , <i>Chusquea</i> sp., <i>Montrichardia arborescens</i>
CT2	9°30'08.2"N - 62°40'55.3"W	13 m bsl	Deltaic monoespecific palm stand	<i>Mauritia flexuosa</i> , Mimosoidae, <i>Desmoncus</i> <i>orthocanthos</i> , <i>Montrichardia</i> sp.
CT3	9°29'31.7"N - 62°41'55.2"W	3 m asl	Monoespecific palm stand; close to a current Warao settlement	<i>Mauritia flexuosa</i> , <i>Ficus</i> sp., <i>Montrichardia</i> <i>arborescens</i> , Bignoniaceae, <i>Eichhornia crassipes</i>

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1038 **Figure 1.** Study area. A: North of South America showing the locations mentioned in the text (1:  
1039 Cariaco Basin, 2: Gulf of Paria, 3: Trinidad, 4: Guianas coastal region, and 5: Amazon mouth). B:  
1040 Orinoco Delta region, with main towns shown in yellow and main river channels or *caños* named  
1041 in blue and italics. EVD: El Volcán Dam, 6: Mora archaeological site (Voorhies et al., 1981). C:  
1042 Specific location of the study site, showing the closest village (in white) and the name of the  
1043 main *caños* (blue and italics). Black dots and numbers in yellow refer to the location of the  
1044 samples collected, being 15: modern sample CT0, 16: Modern sample CT3, 17: modern sample  
1045 CT1, and 18: modern sample CT2 and sedimentary archive PATAM18A-12. Images modified from  
1046 Google Earth.

1047 **Figure 2.** Sediment description, radiocarbon ( $^{14}\text{C}$ ) dates, and age-depth model of the  
1048 sedimentary record PATAM18\_A12. Colour legend used in the sediment description refers to  
1049 subtle differences in the facies (composed by clays and peat) found, being silty clays with high  
1050 content of organic matter (black), grey clay without peat (grey), peaty clay (brown), and light  
1051 coloured clay with some peat (white).

1052 **Figure 3.** Geochemical analyses. A: Identified mineral species and their temporal evolution. Data  
1053 expressed in percentage with respect to dry weight (% wt). From B to F: Downcore variation of  
1054 concentration of low- and high-coercivity magnetic minerals together with the S and the  
1055 ARM/SIRM ratios that are proxies of the relative concentration of low versus high-coercivity  
1056 magnetic minerals and of the magnetic grain size, respectively. G: Total carbon and nitrogen as  
1057 well as their respective stable isotope composition of the bulk organic matter present in the  
1058 studied record. Data expressed in per thousand (‰). Two values of  $\delta^{13}\text{C}$  were too high and  
1059 saturated the curve (shown in grey bars).

1060 **Figure 4.** Diagram of the palynomorphs registered in the modern samples analysed, expressed  
1061 in percentages, and including macro- and microcharcoal particles expressed in concentration

1062 (particles  $\text{cc}^{-1}$ ) values. All the taxa percentages are shown with the same scale (equal width  
1063 means equal % values). Only taxa with percentages higher than 5% have been represented.

1064 **Figure 5.** Pollen diagram of the sedimentary record PATAM18\_A12 expressed in percentages,  
1065 including the stratigraphic column and charcoal particles expressed in concentration (particles  
1066  $\text{cc}^{-1}$ ) values: referring macro- and microcharcoal to the different methodologies explained in  
1067 section 2.2. Only taxa occurring at percentages higher than 10% are represented. All the taxa  
1068 percentages are shown with the same scale (equal width means equal % values) and outline  
1069 values represent x10 exaggeration. Colours refer to features of the taxa (Green: trees; Orange:  
1070 palms; Purple: treelets, lianas or vines; Yellow: herbs; Brown: pteridophytes; Blue: algal and  
1071 aquatic plants; Black: undefined).

1072 **Figure 6.** Modern analogues analysis. A: AMCA, B: DCA, and C: Timetracker (in PCA). Sample  
1073 colours in B refers to the main palynological zones and associated forest types: Blue (Zone OR18-  
1074 1; swamp or rainforest with coastal-like elements; Green (Zone OR18-2; mixed swamp forest);  
1075 and Orange (Zone OR18-3; *Mauritia* palm-swamp).

1076 **Figure 7.** RDA plot of the geochemical data (A: XRD; B: rock-magnetism) as environmental  
1077 variables with biological data (fossil pollen samples), and C: Meyers (1994) plot for stable  
1078 isotopes. Samples' colours follow Figure 6.

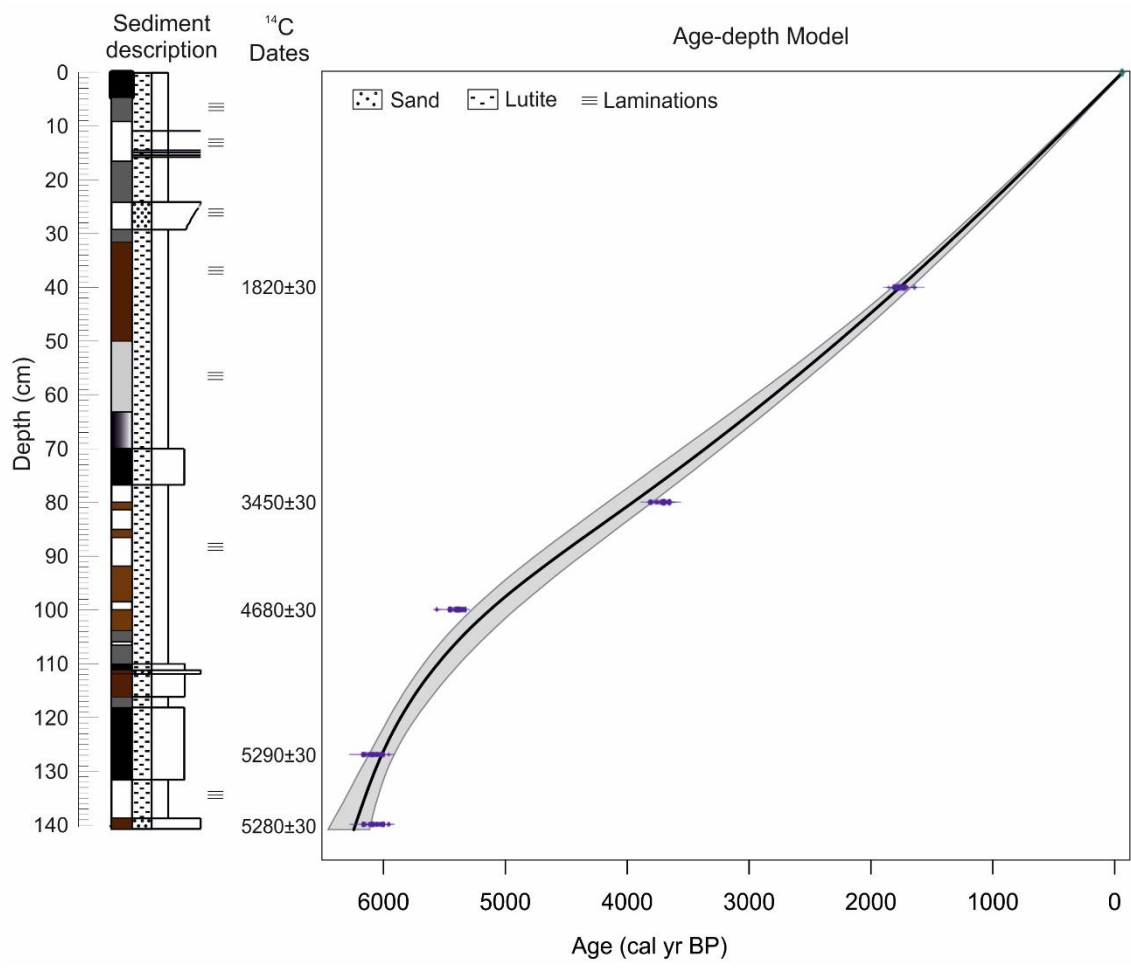
1079 **Figure 8.** Discussion-summary figure that includes: (A) the pollen zones obtained for the  
1080 sedimentary archive PATAM18\_A12; (B) the Ti curve obtained in the Cariaco basin record,  
1081 previously published in Haug et al. (2001) (data downloaded from NOAA database). LIA: Little  
1082 Ice Age; (C) the diversity values calculated following Hill (1973); (D) the scores obtained for the  
1083 PCA first axis of the XRD data, which represents the relationship between kaolinite and chlorite  
1084 (K+C; positive) and illite (negative) values; (E) the macrocharcoal curve expressed in influx values  
1085 (particles  $\text{cm}^{-2} \text{yr}^{-1}$ ); and (F) the pollen sum of terrestrial pollen taxa (in %), with colours legend  
1086 following Figure 6.



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Figure 1

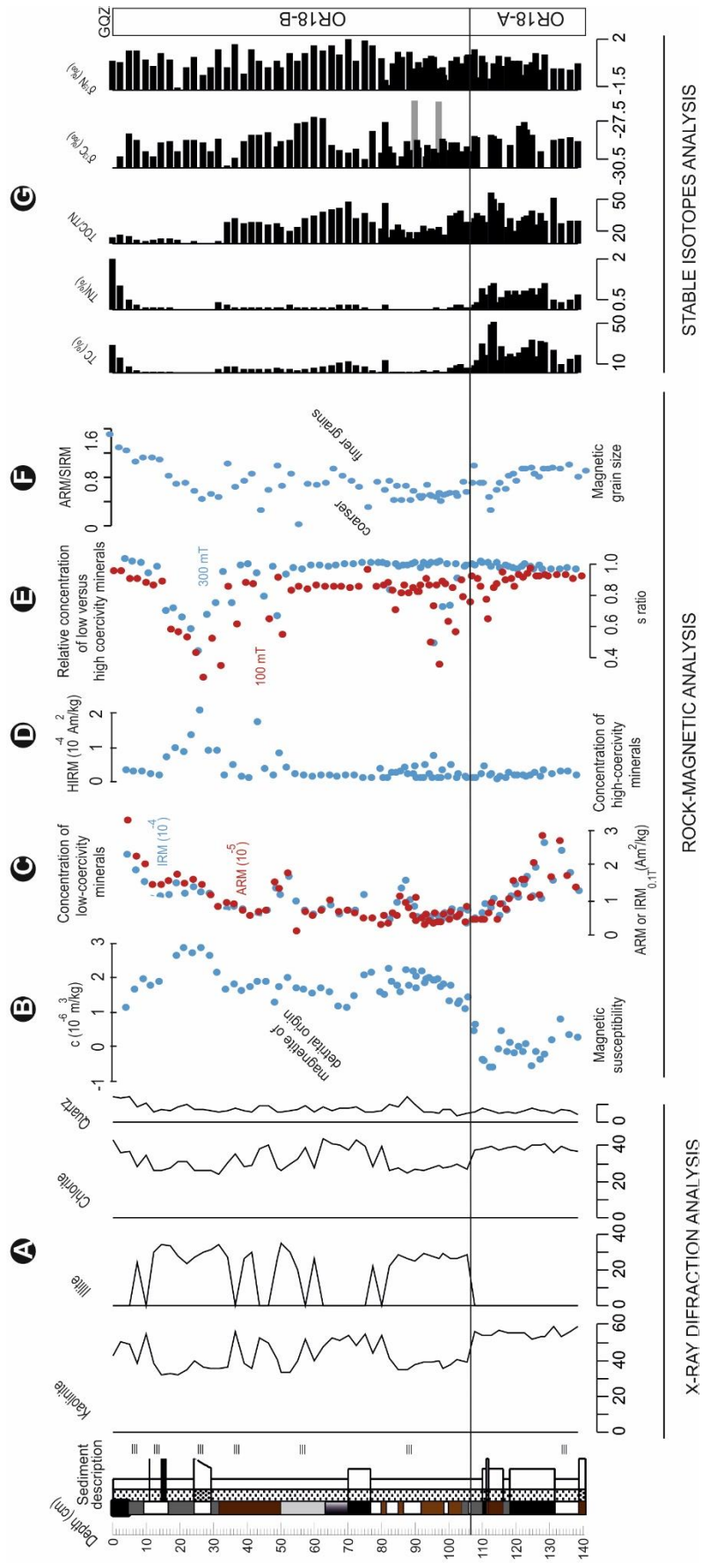


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Figure 2





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Figure 3

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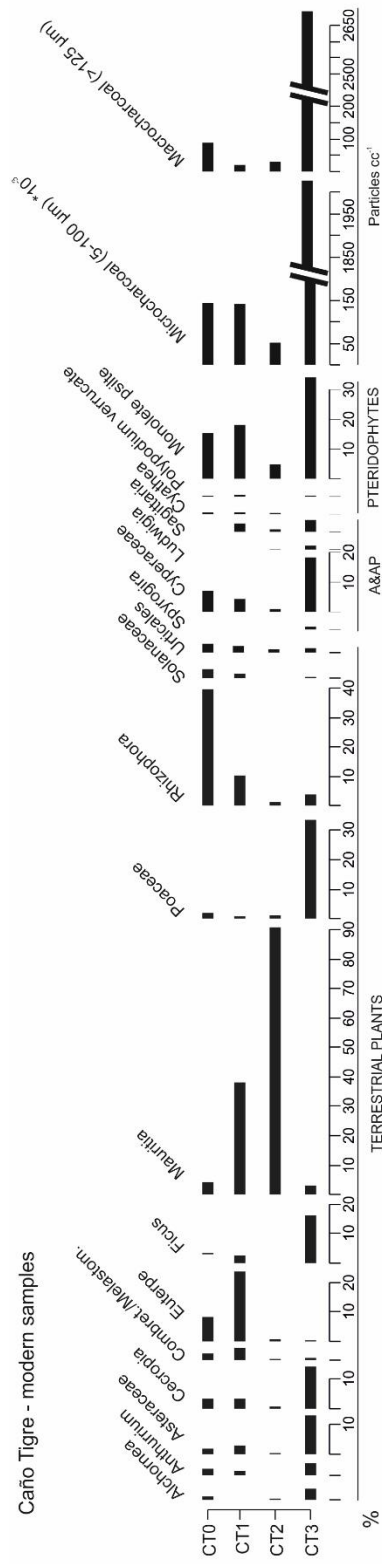
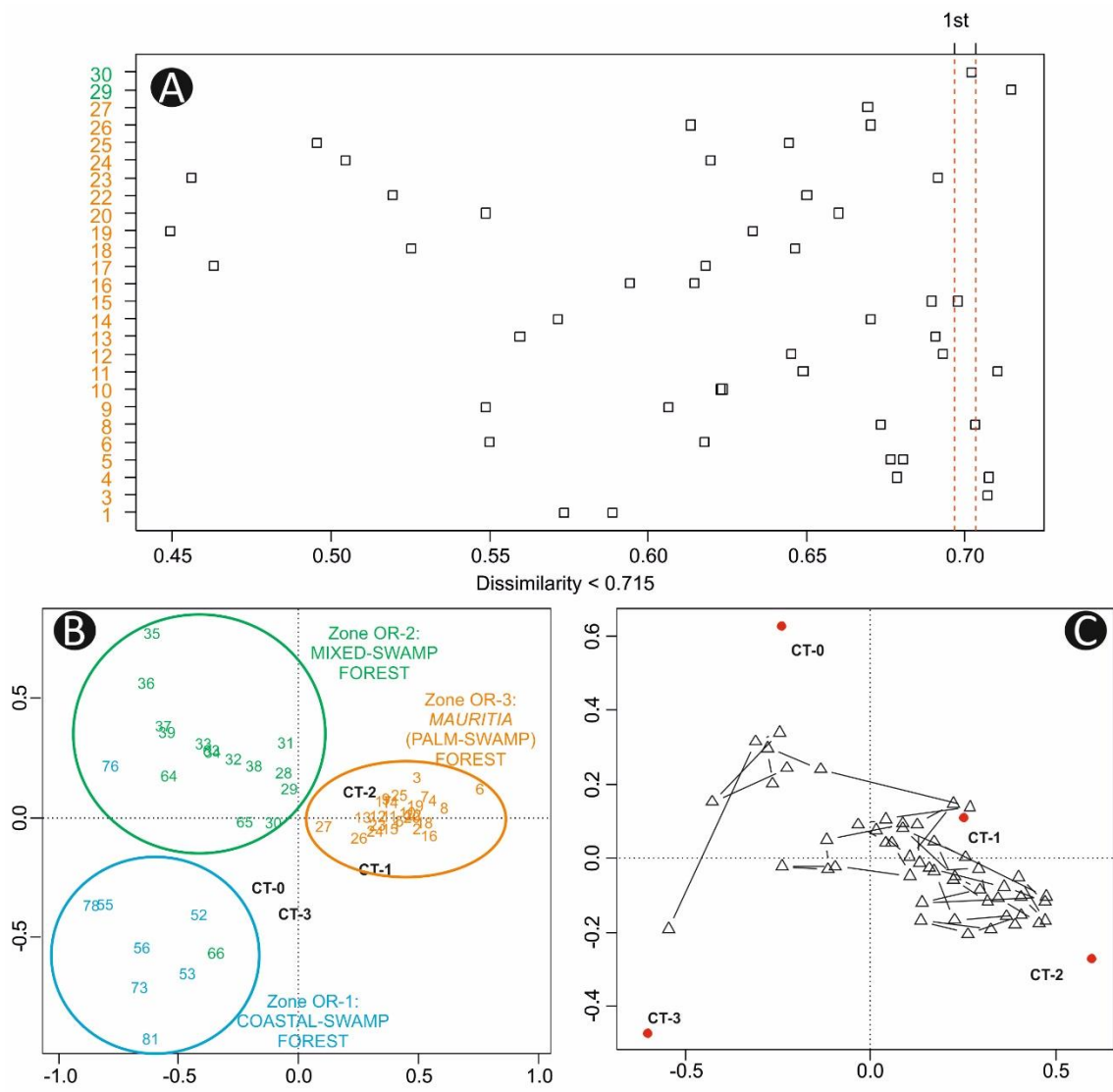


Figure 4

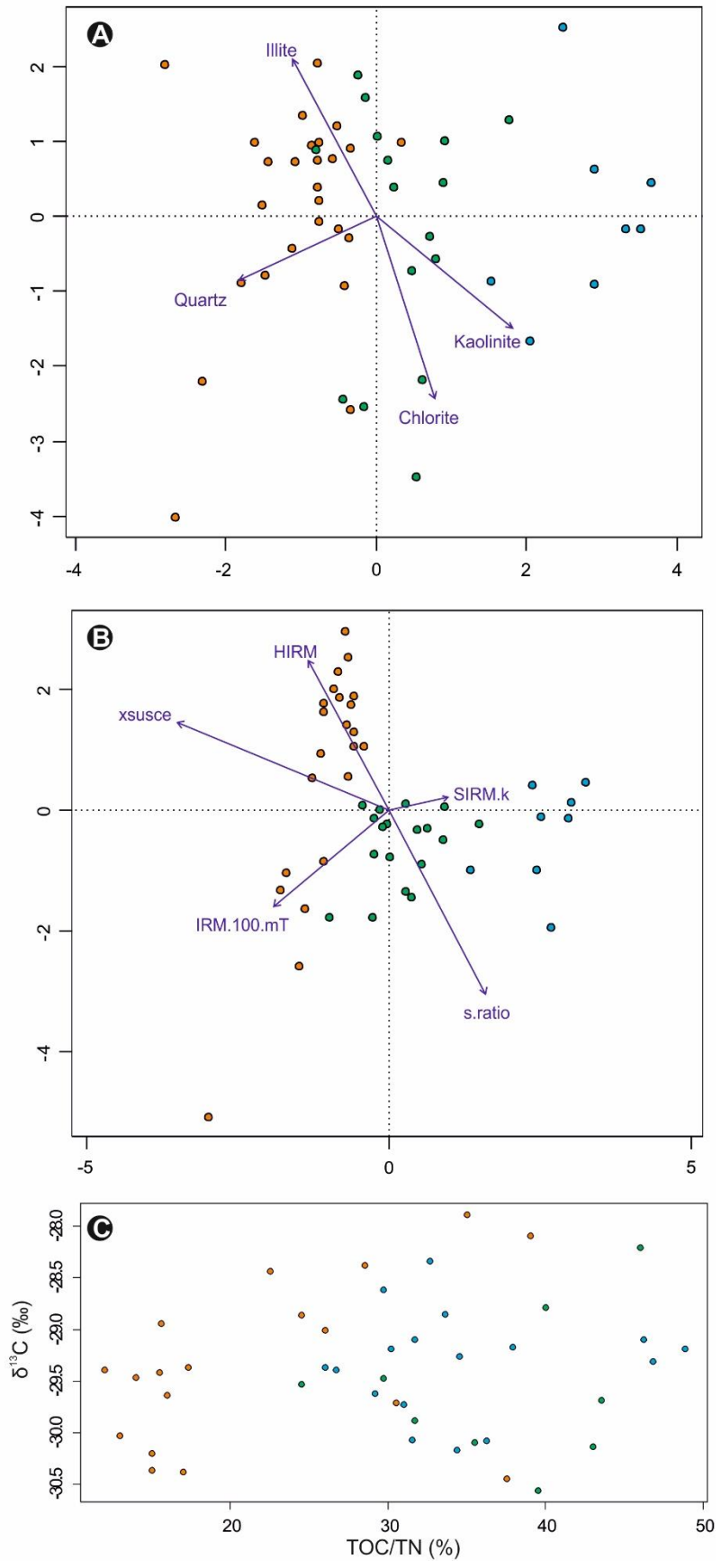




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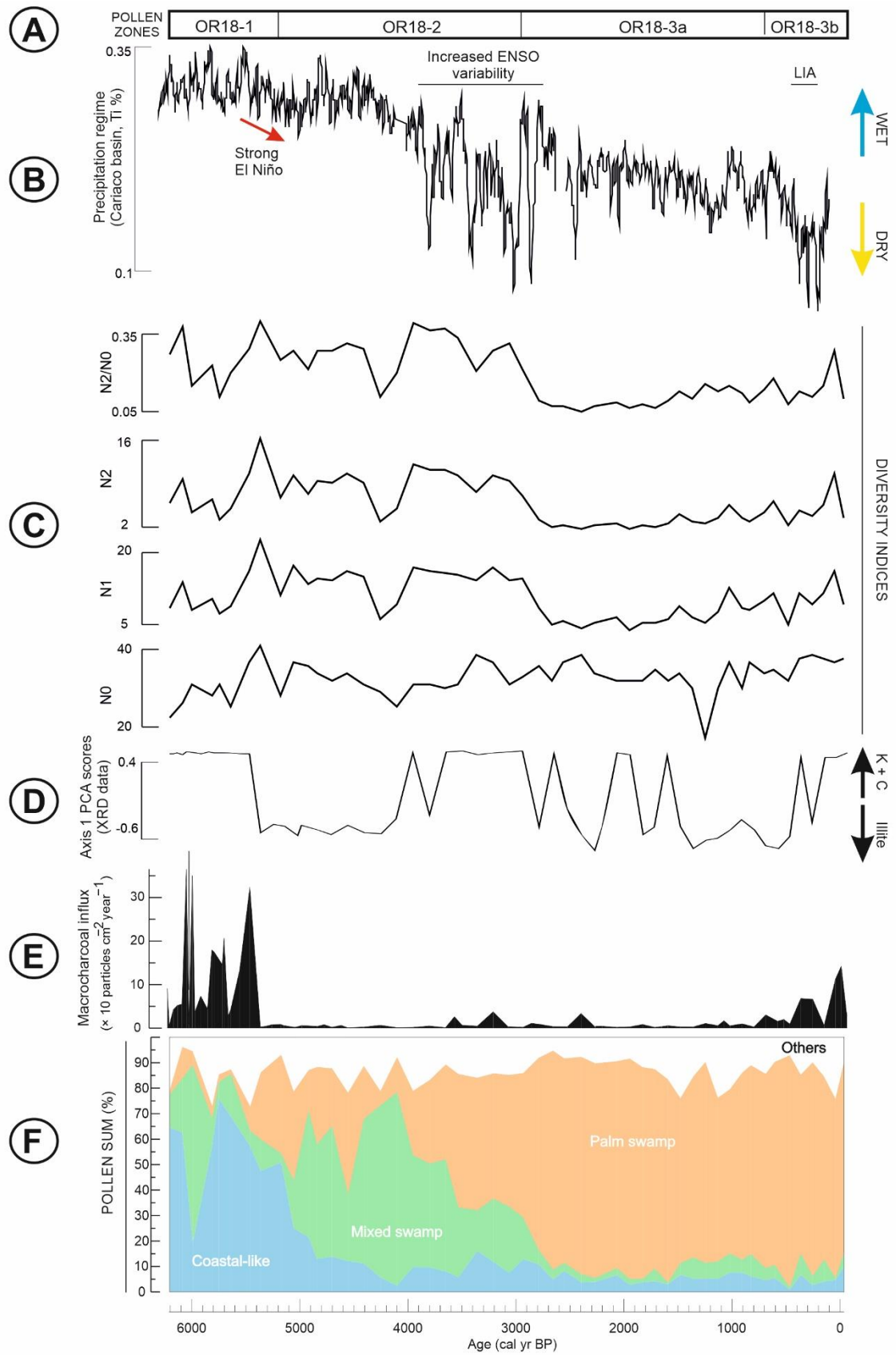
Figure 6



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Figure 7



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Figure 8