

Original article

Environmental changes during the last 1800 years in the Neguanje mangrove, Tayrona National Natural Park, Colombian Caribbean

Cambios ambientales en los últimos 1800 años en el manglar de Neguanje, Parque Nacional Natural Tayrona, Caribe colombiano

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Abstract

We reconstructed changes in vegetation and climate conditions during the last 1800 years in a column of sediment 4 m deep (Playa Pozo sector, Neguanje Bay, Tayrona National Natural Park, department of Magdalena, Colombia). We characterized the main components (mineral elements, organic matter), micro-stratigraphy (types of organic matter), humidity variations (%), organic and inorganic carbon, and palynological associations (specifically pollen grains), and counted spores of fungi, algae, ferns, plant debris, and insects. The palynological associations (dominant elements) were defined and related to the current types of vegetation. The definition of the dominant groups in the palynological spectrum and their relationship with the current vegetation types was associated with the stratigraphic conditions of the sediments to detect the changes that occurred during this period. In the reconstruction of the paleoenvironments, we determined the relationship between the defined palynological associations and the stratigraphy of the sediments, the humidity (precipitation), and the covered area. For this purpose, we used the temperature calibration curves of the last 2000 years proposed by various authors. We did not recover enough palynomorphs at the base of the column between 400 and 380 cm deep (2000-1693 years BP), but organic components of marine origin predominated in the sediment, a condition associated with a warm period in the central and eastern Colombian Caribbean coastal environments. In zone I (1693-1294 years B.P.), the mangrove was consolidated and in zone II (1294-1078 years A.P.), it expanded with the vegetation of flooded areas. In zone III (1078-654 years B.P.), we detected the occurrence of the greatest mangrove development, especially by the dominant species *Rhizophora mangle*. In zones IV and V (654 years A.P.-present), the mangrove cover decreased. This period was less warm than the previous ones, similar to the prevailing conditions in the *Ciénaga Grande de Santa Marta* and its surroundings.

Keywords: Mangroves; Late Holocene; Paleoecology; Coastal environments; Colombian Caribbean.

Resumen

Se reconstruyeron los cambios en la vegetación y en las condiciones del clima durante los últimos 1800 años en una columna de sedimento de 4 m de profundidad (sector Playa Pozo, bahía de Neguanje, Parque Nacional Natural Tayrona, Magdalena, Colombia). Se caracterizaron los componentes principales (elementos minerales, materia orgánica), la micro-estratigrafía (clases de materia orgánica), las variaciones de humedad (%), el carbono orgánico e inorgánico y las asociaciones palinológicas (específicamente granos de polen). También se contaron esporas de hongos, algas, helechos, y restos de plantas e insectos. Se definieron las asociaciones palinológicas (elementos dominantes) y se relacionaron con los tipos actuales de vegetación. En la reconstrucción de los paleoambientes se estableció la relación de las asociaciones palinológicas definidas y la estratigrafía de los sedimentos con la humedad (precipitación) y el área cubierta. Se utilizaron las curvas de calibración de temperatura de los últimos 2000 años propuestas por varios autores para este propósito. En la base de la columna, entre los 400 y 380 cm de profundidad (2000-1693 años A.P.) no se recuperaron suficientes palinomorfos, pero en el sedimento predominaron los componentes

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orgánicos de origen marino, condición que se asoció con un periodo cálido en ambientes costeros del Caribe colombiano. En la zona I (1693-1294 años A.P.) se consolidó el manglar y en la zona II (1294-1078 años A.P.) su extensión se amplió a la par con la vegetación de las zonas inundables. En la zona III (1078-654 años A.P.) se presentó el mayor desarrollo del manglar, especialmente de la especie dominante *Rhizophora mangle*. En las zonas IV y V (654 años A.P.-actual) disminuyó el cubrimiento del manglar y el período fue menos cálido que los anteriores, condición similar a la que prevaleció en la Ciénaga Grande de Santa Marta y alrededores.

Palabras clave: manglares; Holoceno tardío; paleoecología; ambientes costeros; Caribe colombiano.

Introduction

The physiography of the Colombian Caribbean is composed of geomorphic units associated with high coasts, such as hills and massifs, elevated abrasion platforms, marine terraces, eroded rock formations, and glacis or inclined planes, as well as units associated with coastal lowlands including coastal plains, floodplains, estuaries, coastal lagoons, mudflats, dunes, beaches, pins, rods, bars, and reef platforms (Ingeominas, 1996). Depending on rain annual amount and distribution, there are 14 climate units in three provinces: arid to dry in the north, dry to humid in the central area, and humid to very humid in the south. The Tayrona National Natural Park, Santa Marta, department of Magdalena, Colombia (between 11°18' and 11°21' N and 74°4' and 74°7' W) is a low massif with ecogeographic components such as estuaries, beaches and cliffs, lake environments, and hills (El Cielo at 500 m of altitude).

Geological formations in the study area comprise a representation of Tertiary material including Neogene sediments, Miocene and Pliocene rocks, Eocene plutonic and sedimentary rocks, and Paleocene-Eocene volcanic materials. Mesozoic materials are associated with metamorphic rocks from the Upper Cretaceous and Jurassic. The Quaternary sediments are recognizable in flat areas with valleys of colluvial and alluvial influence partly found in the maritime zone forming sedimentary lagoons behind the marine bars. Additional information on the Caribbean region of Colombia and the Tayrona National Natural Park study area can be accessed at www.colombiaversidadbiotica.com.

The soils have moderately coarse textures (loamy-sandy) on igneous or mixed materials and medium textures (loamy and loamy-silty) on metamorphic and mixed materials (Cortés, 1975). The humidity gradient varies from west to east: very dry (500 mm) near Taganga - Santa Marta, and humid (1400 mm) near Arrecifes - Cañaveral with a transition spot in the Bay of Cinto (Figure 1). The precipitation regime is bimodal and tetra-seasonal with two rainy periods (May to June and September to November) and two dry periods (December to April and July to August). The average annual temperature is 27 °C (Rangel & Carvajal, 2012).

Materials and methods

Study area

Neguanje Bay is located at the central-western coastal zone of the park bordered on the West and East by two South-North oriented hill ranges reaching up to 150 meters which separate it from the Gayraca and Cinto Bays, respectively (Figure 1). The southern limit is defined by high and low hills that gradually descend to the sea and are part of the maritime drainage system of the park hydrographic complex. These hills harbor small ravines and channels that reduced streams and remain dry for most of the year (Carbon-D. & García-Q., 2010).

Cortés-C. (2017) characterized the Caribbean mangrove vegetation and determined the phytosociological arrangement including the *Lagunculario racemosae-Avicennion germinantis* alliance present in the Neguanje area. The arboreal stratum of these forests is formed by *L. racemosa* and *Hilairanthus germinans* but *Rhizophora mangle* is very poorly represented while the fern *Acrostichum aureum* grows densely on the herbaceous

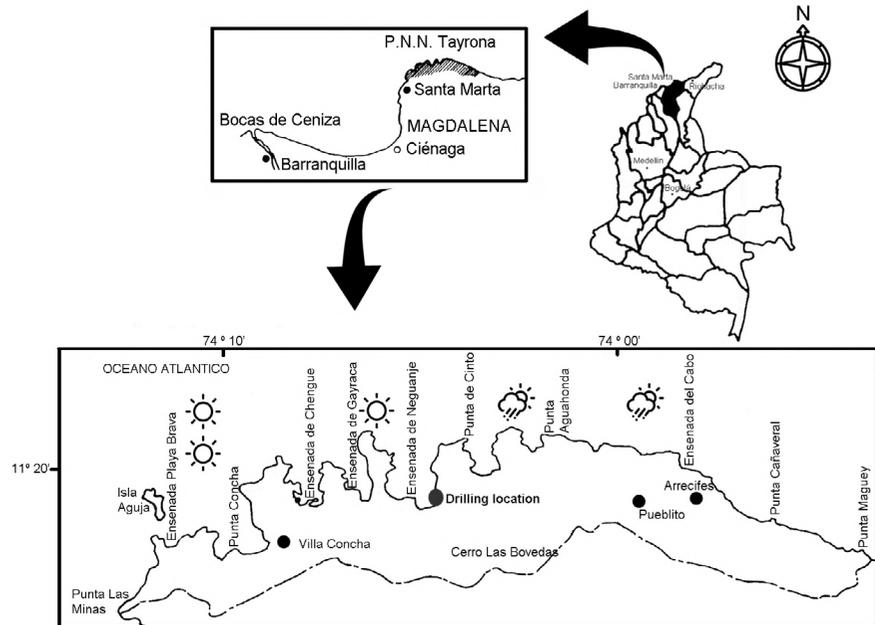


Figure 1. Location of Tayrona N.N.P. drilling at Neguanje bay and rainfall gradient on the study area

stratum. The *L. racemosae*-*A. germinantis* association also includes other species from the surrounding wet and dry forests, such as *Libidibia coriaria*, *Pithecellobium dulce*, *Ficus matiziana*, and *Maclura tinctoria*.

The beaches and flooded areas harbor larger thickets communities dominated by *Solanum campechiense* growing together with *Heliotropium indicum*, *Alternanthera paronychioides*, *Glinus radiatus*, *Portulaca oleracea*, *Mimosa dormiens*, *Euphorbia hirta*, and *Tarenaya (Cleome) spinosa*. The slopes are covered by forests composed of *Handroanthus billbergii*, *Libidibia punctata*, and *Capparis* (sensu lato) species, as well as communities dominated by *Astronium graveolens*, which is quite similar in its floristic composition to the forests located in the hills around Santa Marta (Carbonó & García, 2010; Rangel, 2012).

Landscape transformation events have occurred in the swamp including local ones: subsidence and uplift of blocks, ancient coral bars, and coastal terraces (Robertson & Martínez, 1999), as well as global ones: earthquakes and tsunamis in the Caribbean (Quintero, et al., 2020; Bolívar, et al., 2019), and fluctuations in the sea level, regressions and transgressions (Beltrán, 2015), which have influenced on the evolution of the territory. The effects of the tectonics, the variations in the sea surface temperature, and the precipitation have also been reflected in the changes in the stratigraphic and biostratigraphic sequences (Jaramillo, et al., 2012).

Fieldwork and laboratory analysis

In Neguanje (Playa Pozo sector at the Tayrona N.N.P.), we recovered a 4 m-deep column of sediment. We described the core stratigraphy in the field and then sealed and transported the sample in 50 x 5 cm plastic tubes to the palynology and paleoecology laboratory at the *Instituto de Ciencias Naturales, Universidad Nacional de Colombia*. A portion of the sediments was used for detailed stratigraphic and LOI (loss on ignition) analyses and carbon-14 dating.

We used the acetolysis methodology for the physicochemical preparation to extract the palynomorphs in the sample from the column and the two samples from the surface for recent pollen sedimentation analysis (Erdtman, 1986). The final part of the samples was subjected to flotation treatment with zinc chloride ($ZnCl_2$) (D'Antoni, 2008).

The slides samples for the palynological analysis were prepared using gelatin-glycerin according to the Kisser formula (**Brown, 1960**). Each sample was studied under a Zeiss Primo Star light microscope and we counted the maximum number of palynomorphs (grains, fungal spores, and ferns) and other palynomorphs (algae, plant, and insect remains). We made the taxonomic identification of the pollen grains based on the atlases of **Roubik & Moreno (1991)**, **Jiménez, et al. (2008)**, and **García-M., et al. (2011)** and comparing with the reference collections of the *Palinoteca del Instituto de Ciencias Naturales, Universidad Nacional de Colombia*. In some cases, the microscopic analysis effort included several sheets of one depth to reach a minimum number of palynomorphs (**Table 1**), which explains the lack of uniformity in the class intervals (depth).

A set of samples were selected and sent to the BETA Analytic Laboratory (Florida) and to the University of Colorado (USA) for carbon-14 dating. The dates (¹⁴C ages) supplied by the laboratories followed standardized protocols and were based on the

Table 1. Counts of palynomorphs per analyzed sample

Depth (cm)	Pollen grains + spores	Other palynomorphs (phytoclasts, fungiclasts, fungisporos)	Total palynomorphs	Included in pollen sum (grains and spores)
1	167	87	254	162
5	84	15	99	82
11	105	11	116	97
17	64	52	116	64
33	56	79	135	53
50	Loss of material			
55	94	67	161	94
60	82	33	115	81
65	58	26	84	58
70	103	108	211	102
80	130	71	201	130
87	112	75	187	111
95	95	73	168	95
100	150	101	251	150
105	116	64	180	116
110	116	49	165	116
115	101	82	183	101
120	140	31	171	139
125	160	139	299	160
130	169	179	348	169
135	117	176	293	117
140	107	110	217	107
147	67	289	356	67
155	84	142	226	84
160	82	189	271	79
167	59	152	211	58
175	81	75	156	81
182	97	301	398	97

Depth (cm)	Pollen grains + spores	Other palynomorphs	Total palynomorphs	Included in pollen sum (grains and spores)
190	93	262	355	93
195	60	244	304	60
200	71	81	152	71
212	65	266	331	65
220		Hiatus - No pollen recovery		
225		Hiatus - No pollen recovery		
230	108	157	265	106
235	104	275	379	104
240	115	280	395	113
245	91	117	208	91
252	45	189	234	44
260	63	66	129	61
265	50	91	141	50
270	82	119	201	82
275	99	320	419	97
280	115	62	177	113
285	121	236	357	119
290	100	314	414	98
295	86	299	385	84
302	57	155	212	56
310	76	85	161	76
322	93	172	265	91
332	107	129	236	107
340	90	221	311	90
345	139	308	447	137
350	97	126	223	94
355	63	120	183	63
362	101	180	281	99
372	99	246	345	98
380	99	411	510	96
385				
390		Very low amount of pollen recovered		
395				
400				

IntCal20 calibration (Reimer, *et al.*, 2020); they appear in the column marked with * in the palynological diagrams. Sedimentation rates were estimated according to the zonation of the palynological diagram. In all cases, both the depth at which the original sample was taken and the width of the intervals of each of the zones appear in the column (Table 2) We conducted sedimentological (microstratigraphic) and main components analyses for the bottom sediments (Jaramillo, *et al.*, 2012, Coronel, 2013).

To determine the reservoir capacity of the sediments, we used the loss of mass by calcination method (LOI) (Dean, 1974). We estimated LOI at 105°C (moisture %), LOI at 550°C (organic carbon %), and LOI at 950°C (inorganic carbon %) to establish the system's

Table 2. C¹⁴ ages, calibrated ages, and sedimentation rate, Playa Pozo-Neguanje

Deep (cm)	Laboratory	C ¹⁴ age	Calibrated age BP
123 (shells)	Colorado U.	1100 ± 20	1007
161 (shell/coral)		1120 ± 20	1011
197 (shells)	Beta Analytic	1120 ± 30	1039
305 (shells)		1270 ± 30	1120
377 (shells)	Colorado U.	1710 ± 20	1581
398 (shells)	Beta Analytic	2230 ± 30	1745
Estimated sedimentation rates			
Deep (cm)	Polen zone	Sedimentation rate (cm/year)	
33 – 1	V	0.12	
70 – 55	IV	0.12	
200 - 80	III	0.31	
310 - 230	II	0.90	
380 – 322	I	0.15	

organic reservoir capacity also by means of the LOI method (Dean, 1974). According to Eriksoon & Olsson (2015), the organic matter of continental origin comes from the vegetation near the study site. It may indicate high primary productivity related (in our case) to the extension or reduction of forest vegetation (flooded areas and mainland slopes). Therefore, the marine-origin organic matter is associated with mangrove vegetation; LOI values at 950 °C refer to the carbonate content in the sediments originating from elements of marine origin (corals, shells).

For the palynological diagrams, we used the Tilia software (version 1.7.16; Grimm, 2002) and the elements included in the pollen sum were those from reliable ecological and phytogeographic information sources while the spores of ferns, fungi, and other palynomorphs whose autecology and other ecological characteristics were not well documented were grouped under the name “elements not included in the pollen sum.” Finally, two surface sediment samples (recent pollen rain) were also analyzed.

For the phytoecological segregation of the palynomorphs (grains, spores) found in the sediments, we followed the recommendations of Rangel (2012), Cortés-C. & Rangel-Ch. (2013), and Cortés-C. (2017). We conducted surface sample or current pollen rainfall analyses throughout the entire column inside the palynological diagrams including the elements explained in the next section.

Elements included in the pollen sum

The following elements (genera, species), whose grains appear in the group included in the sum, were selected because their ecological characteristics and geographical distribution patterns reinforce the segregation.

Mangrove vegetation. *R. mangle*, *H. germinans*, *L. racemosa*, *Conocarpus erectus*, and *A. aureum*.

Aquatic and swamp vegetation. *Cyperus* sp., Poaceae, *Ambrosia peruviana*, and *Althernanthera* aff. *paronychioides*. Other elements with values below 1% clustered in the curve were tagged as diverse aquatic-swamp vegetation (*Cabomba* aff. *caroliniana*, *Ipomoea* sp., *Scleria* sp., *Eclipta* sp., *Persicaria* sp. (*Polygonum*) sp., *Amaranthaceae*, *Hibiscus* sp., and *Convolvulaceae*).

Floodplain vegetation included *Mascagnia macradena*, *Margaritaria nobilis*, *Phyllanthus* sp., *Cissus* aff. *biformifolia*, *Euphorbia* aff. *thymifolia*, *Solanum* sp., *S.* aff. *jamaicense*, *S.* aff. *umbellatum*, *Ficus* sp., *Bactris* sp., *Jacquemontia* sp., and *Sapium* sp. Other elements were gathered in diverse-floodable areas where their pollen representation

was less than 1%; these taxa were represented by *Cissus* aff. *fuliginea*, *Tournefortia* sp., *Euphorbia* aff. *hirta*, *Solanum* aff. *hayessii*, *Capsicum* sp., *Arrabidaea* sp., *Iseia* sp., *Hiraea* sp., *Alibertia* sp.

Slope vegetation of the mainland (tropical dry forest) was composed of *Celtis* sp., *Acalypha* sp., *Protium* sp., *Mabea* sp., *Anacardium* sp., *Handroanthus* sp., Fabaceae, Asteraceae, *Prestoea* sp., and Arecaceae. Other species were assembled in a curve under the name mainland-diverse slopes. The pollen representation of this group was below 1% and the taxa identified were *Spermacoce* sp., *Sabicea* sp., *Psychotria* sp., Rubiaceae (aff. *Psychotria*), *Alchornea* sp., *Casearia* sp., *Croton* sp., *Sida* sp., *Faramea* sp., *Faramea occidentalis*, *Maripa* sp., *Geophila* sp., *Justicia* sp., *Spondias* sp., *Schefflera* sp., *Tabebuia* sp., *Bursera* sp., *Cedrela* sp., *Jatropha* sp., *Chelonanthus* sp., *Peperomia* sp., Euphorbiaceae, Rubiaceae, Moraceae, Mimosaceae, Bignoniaceae, Boraginaceae, and Bombacoideae (Malvaceae).

Elements not included in the pollen sum

These were pollen grains: Asteraceae (indeterminate) type *Jacquemontia*, *Podocarpus* sp.; algae: *Pseudochizaea*; fern spores: *Polypodium* (Polypodiaceae); fungi spores: fungi spores, ascospores, and other palynomorphs: phytoclasts, zooclasts, and fungiclasts.

Here we document the major paleoenvironmental changes that occurred in the study area during the last 2000 years based on stratigraphic, sedimentological, and palynological analyses on a 4-m-deep borehole. Our research questions addressed the variations in the floristic composition of the vegetation types and their extension, especially the mangrove swamp, and their relationships with climatic characteristics (precipitation).

Results

Stratigraphy

In the 400-cm-deep core located in Playa Pozo (11°19' - 17.02" N; 74°04' - 35.99" W), the stratigraphic sequence corresponded mainly to clays with enriched levels of silt, sandy silt, and sands towards the middle of the column (**Figure 2**).

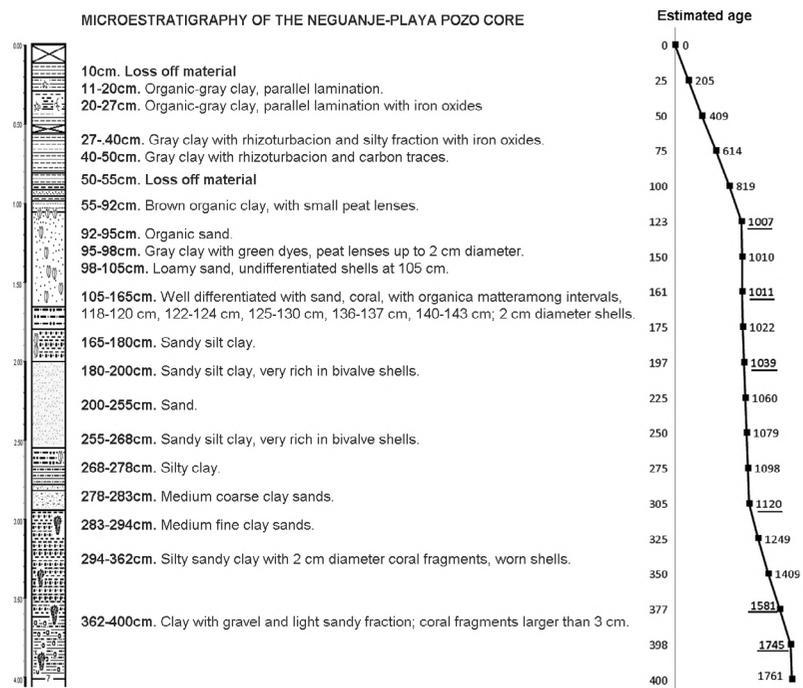


Figure 2. Microstratigraphy of the Neguanje nucleus (left) (Coronel, 2013). Age model (right)

Moisture-carbon-loss on ignition (LOI)

We differentiated four areas in the three figures that were used for the description.

Humidity (LOI at 105° C). In zone I, between 400 and 300 cm deep, the values fluctuated between 14% and 30% and up to 40%; in zone II, from 300 to 200 cm, variations were between 5% and 30% with a maximum value of 48%; in zone III, from 200 to 100 cm, values were between 10% and 20% and as high as 40% this being the zone with the lowest humidity in the entire core; in zone IV, between 100 and 1 cm, values ranged from 30% to 40% and up to a maximum of 54%, this being the zone with the highest humidity of the entire nucleus (**Figure 3A**).

Organic carbon (LOI at 550 ° C). In zone I, we registered values between 2% and 4% and as high as 36%, this being the zone with the lowest values; in zone II (300-200 cm), values ranged from 4% to 10% and reached as high as 24%; in zone III (200-100 cm), values were between 10% and 20% with up to 40%-54%, this being the highest value in this component; in zone IV (100 – 1 cm), values ranged from 4% to 6% and the extreme values reached 20% (**Figure 3B**).

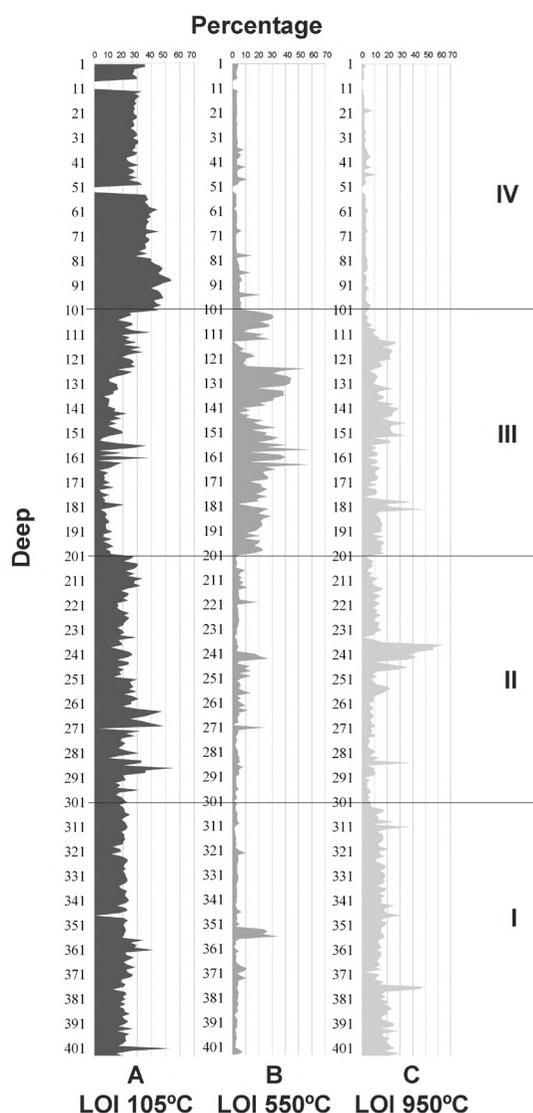


Figure 3. Moisture and organic and inorganic carbon values (LOI at 105°C, 550°C, and 950°C) from Neguanje core

Inorganic carbon (LOI at 950 ° C). In zone I, values were between 2% and 15% with extreme points of 30% and up to 48%; in zone II, we registered values from 10% to 14% and as high as 40% and 60%; zone III had the highest values ranging between 12% and 16% and as high as 32% and 40% while zone IV had the lowest values, between 4% and 10% (**Figure 3C**).

Main components and class (origin) of organic matter in sediment

Figure 4A shows the contents (%) of mineral and organic components throughout the sediment column. In the four differentiated zones (the entire nucleus), there is a high content of mineral fraction (between 60% and 80%) with the highest values in zone II.

The following was the distribution of organic matter components and their origin (continental or marine) (**Figures 4B, 4C**):

In zone I, 401 to 302-cm deep, marine origin components were predominant (corals, shells, jaws, fish bones, and an array of calcareous structures), with an average of 21% and extreme variations between 6% and a maximum of 46%, while the components of continental origin (peat, autochthonous and allochthonous coal, roots, stems, and wood) had an average value of 6.3% and values as low as 3%.

In zone II, 301 to 202 cm, there was a slight predominance of continental components with a mean of 9% and extremes of 20%, and an average of 7% with extremes of 12% in marine components.

Zone III, 201 to 102 cm, exhibited a shared domain with continental-origin components of 11.7% on average and maximum values of 23% and marine components with an average of 11.2% and maximum values of 31%.

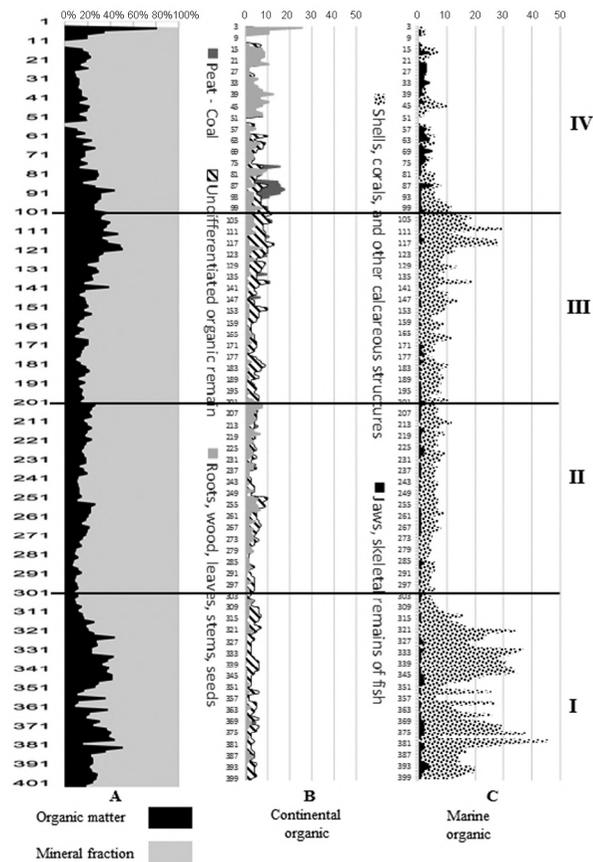


Figure 4. Main components of the Neguanje core - Playa Pozo. **A.** Main components = organic matter; mineral fraction. **B.** Continental organic components. **C.** Marine organic components

Finally, in zone IV, 101 to 1cm, continental components predominated with an average of 16% and maximum values of 80% while the marine components registered an average of 6% with extreme values of 14%.

Sedimentation rates

In the deepest part (zone I), the sedimentation rate was slightly higher than that from the superficial zones (IV-V). The highest value was registered in zone II followed by zone III, which was 2.3 and 3.5 times higher than that of the deepest zone (Table 1). These values were also part of the variation gradient (0.06 and 0.66 cm/year) in other mangrove environments such as Laguna Camarones in the department of La Guajira (Castaño, 2004), Cispatá in the department of Córdoba (Palacios, et al., 2012), and La Caimanera in the department of Sucre (Beltrán, 2015).

Recent pollen sedimentation

In the two samples analyzed, we identified 36 palynomorphs belonging to 22 families and 30 genera. Pollen representation was dominated by floodplain vegetation (38%), followed by mangroves (33%), and mainland forest (25%). The swamp vegetation (aquatic-swamp) was represented but in a very low proportion (4%).

As found in groups previously classified, floodplain vegetation included *E. aff. thymifolia* with an average pollen frequency of 6%, and *S. aff. jamaicense* and *S. aff. hirtum* with a value of 4%. *Rhizophora mangle* dominated in the mangrove swamp (20%) followed by *L. racemosa* (6%), *C. erectus* (5%), and *H. germinans* (2%). In the mainland forest, we found harbor taxa such as *Protium* (6%), *Celtis* (5%), and *Mabea* (3%), and in the swamp vegetation (aquatic-swamp) *C. aff. caroliniana*, *A. peruviana*, *Ipomoea* spp., *Cyperus*, and *Poaceae*, with less than 1% of the pollen frequency each (Figure 5).

Palynological diagram

In table 2 we present the palynomorphs (pollen grains, spores, and others) we counted. At some points, not enough materials were recovered and, therefore, the palynological diagrams show discontinuities as the intervals between samples were not constant. Between the surface and the 95-cm depth, the concentration of palynomorphs was low so it was necessary to extend the sampling interval while in most of the other sections of the column sampling was every 5 cm. There were sections in which palynomorphs were not recovered and in other their counts were very low. For example, between 380 and 400 cm, we found only four to seven grains, and, therefore, this material was not used in the analysis.

Zoning, description (palynological diagrams) and reconstruction of the vegetation changes.

Five zones were differentiated. From zones I to IV in the palynological spectrum there is a domain of mangrove-associated elements. In zone V, the outermost (recent) representation of the dry forests of the nearby slopes predominates (Figures 6A, B and 7). A detailed description offers us the following characteristics:

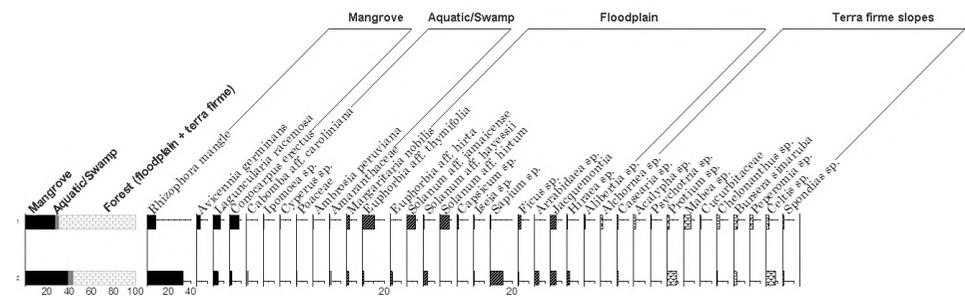


Figure 5. Recent pollen sedimentation in the Neguanje mangrove area, Playa Pozo

decreased its representation with *Mabea* sp. (5%), *Protium* sp. (5%), and three species of *Arecaceae* (10%). Aquatic-swamp vegetation was poorly represented with *Poaceae* (20%). The predominance of phytoclasts persisted among the elements not included.

Paleoenvironment: Estimated age: 1230-1064 years B.P. The distribution areas of the mangrove with *R. mangle* and the scrub-low forest of *S. aff. jamaicense*, *S. aff. umbellatum* and *Ficus* sp. vegetation in the floodplain increased while on the slopes, the area of forest dominated by *Acalypha*, *Protium*, and *Mabea* species decreased. Compared to the previous zone, humidity conditions (precipitation) were slightly lower and the marine organic components fewer.

Zone III. Depth: 230 - 80cm. The predominance of mangrove areas was represented by *R. mangle* reaching the highest values (80%) of the entire column followed by *H. germinans* (15%), *C. erectus* (5%), and *L. racemosa* (5%). The representation of flooded areas vegetation decreased with the presence of *E. aff. thymifolia* (10%), *S. aff. umbellatum* (40%), *S. aff. jamaicense* (10%), *Ficus* sp. (20%), *Bactris* sp. (10%), *Mabea* sp. (15%), and three *Arecaceae* species (20%). Aquatic vegetation in swamp areas decreased and they were dominated by *Poaceae* (10%) and *Cyperus* sp. (5%). Among the elements not included, phytoclast representation began to decrease towards the end of the zone.

Paleoenvironment: Estimated age: 1064 to 655 years B.P. Mangrove dominance and greatest extension were represented by *R. Mangle*, *H. germinans*, and *C. erectus*. The aquatic-swamp vegetation extension decreased significantly; both the scrub-low forest dominated by *Solanum* and *Ficus* species and the forests located on the slopes with *Mabea* maintained their distribution area. Humidity conditions (precipitation) in the lagoon surroundings were lower than those of the previous zone but the continental and marine organic components increased and their maximum points corresponded to the greatest coverage of the mangrove.

Zone IV. Depth: 80 - 33 cm. Although mangrove areas represented by *R. mangle* were predominant, they began to decrease drastically towards the top (10%), however, *H. germinans* (30%) and *L. racemosa* (10%) increased. Representation of hillside vegetation

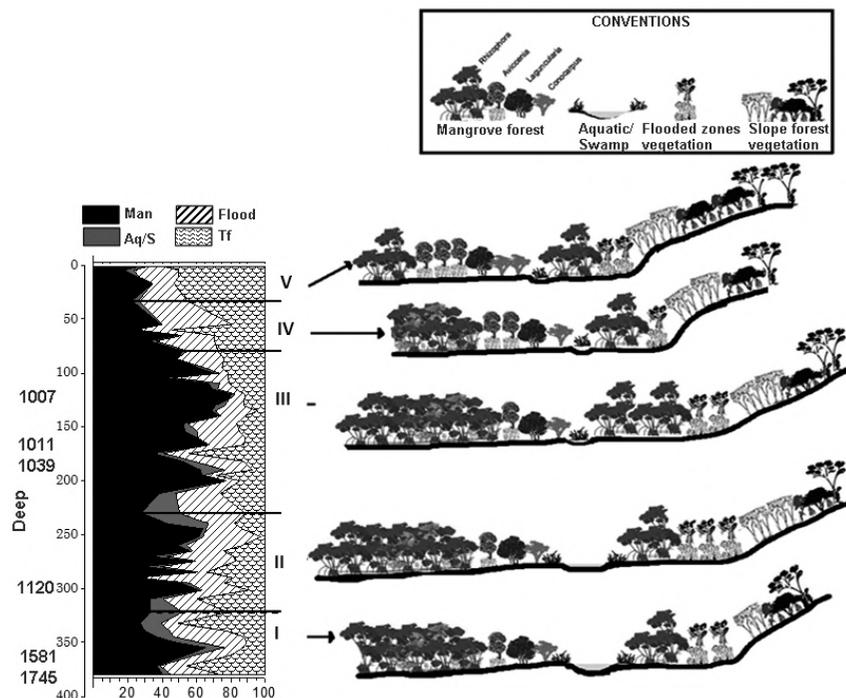


Figure 7. Reconstruction of the vegetation changes in the last 1800 years, Neguanje Bay.

(mainland) with species of *Protium* (15%) and *Mabea* (10%) increased considerably, as well as the flooded-area vegetation with *E. aff. thymifolia* (20%) and *S. aff. umbellatum* (10%). Aquatic-swamp vegetation was very poorly represented with *Cyperus* sp. and Poaceae elements (<5%). Among the elements not included, the predominance of phytoclasts prevailed, although their representation was lower compared to the previous sub-zone.

Paleoenvironment: Estimated age: 655 to 270 years B.P. The area occupied by the mangrove reduced, especially due to the strong decline of *R. mangle* while the representation of *H. germinans* and *C. erectus* increased, mainly towards the end when *A. aureum* appeared. The areas previously covered by the mangroves were occupied by scrub vegetation with *M. macradena*, *E. aff. thymifolia*, *M. nobilis*, and by floodplain vegetation. Firm land forests on the slope areas were dominated by *Protium* and *Anacardium* species extending to the flat areas adjacent to the mangrove. Organic matter of marine origin decreased (mangrove reduction) towards the end of the zone while that of continental origin increased associated with the extension of the flooded vegetation areas. Humidity conditions (precipitation) were lower than those of the previous zone.

Zone V. Depth: 33 - 0 cm. Representation of hillside vegetation (mainland) predominated with *Protium* sp. reaching up to 20%, *Mabea* sp. (20%), and other elements such as *Handroanthus* sp. (10%) and *Anacardium* sp. (5%). The representation of flooded vegetation areas with *E. aff. thymifolia* (20%), *M. macradena* (5%), and *Phyllanthus* sp. (20%) prevailed. In the mangrove community, *R. mangle* showed minimal values (15%) compared to those recorded in previous areas; the representation of *H. germinans* (25%) and *C. erectus* (20%) increased, and *A. aureum* (10%) appeared. The low representation of the aquatic and swamp vegetation persisted. Among the elements not included in the pollen sum, again phytoclasts dominated, although to a lesser extent compared to the initial zone (60%).

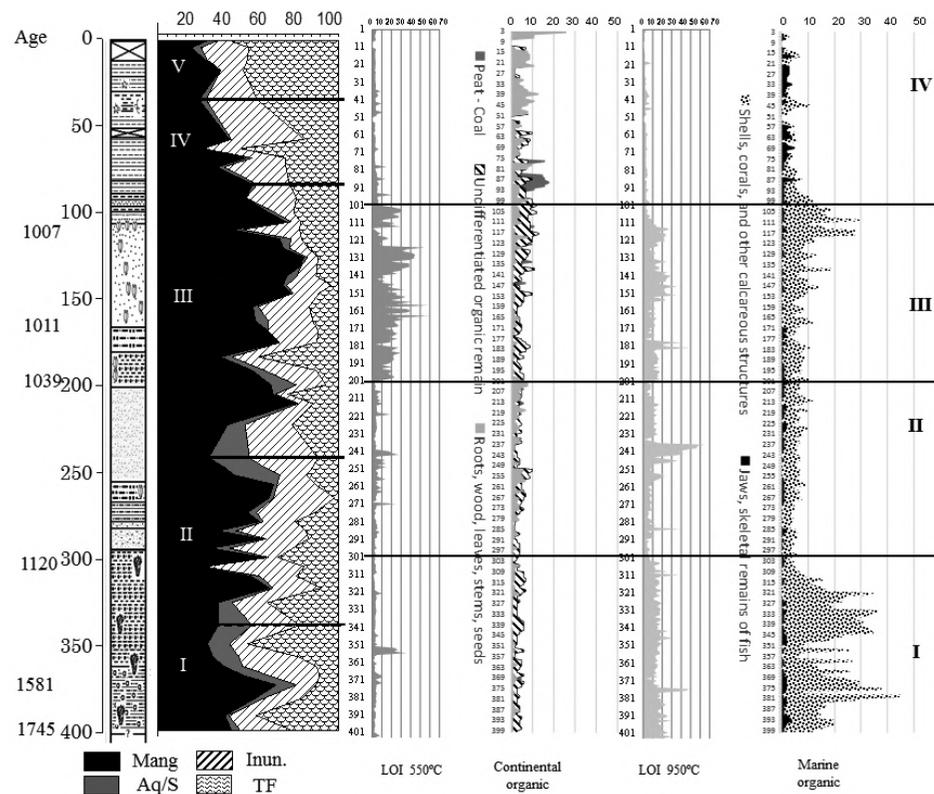


Figure 8. Summary of vegetation changes, main components, continental organic matter, and marine organic matter. Mang: Mangrove; Ac/P: Aquatic-swamp; Inun: Flood plain; TF: Mainland

Paleoenvironment: Estimated age: 270 years B.P. to present time. The area occupied by the mangrove drastically reduced due to the significant regression of *R. mangle* and *H. germinans* while *C. erectus* and *A. aureum* representation persisted. Hillside forests with *Protium*, *Mabea*, and *Handroanthus* increased their range and reached the basin. Current precipitation values (600-700 mm) qualify the region as very dry (Rangel & Carvajal, 2012). The organic matter of continental origin reached the highest values.

Organic matter components and main palynological diagram relationships

When comparing the LOI organic matter components curves and the main palynological diagram between 550 and 950°C it is possible to differentiate the following situations (Figure 8):

Zone I: Depth: 401 - 302cm. This includes zone I and the lower part of zone II in the palynological diagram. LOI values at 550 °C were between 2% and 4%, the lowest in the entire column. Marine components predominated, especially shells and other calcareous elements, which relate to LOI values at 950 °C with extreme points of 30% and up to 48%. Mangrove was the vegetation type with the greatest coverage (from 380 cm deep).

Zone II: Depth: 301 – 202 cm. This comprises three-quarters of zone II and the lower part of zone III in the palynological diagram. LOI contents were between 550 and 950° C, similar to the previous zone; organic matter decreased, especially marine components. The vegetation was dominated by mangroves communities.

Zone III: Depth: 201 - 102cm. This comprises three-quarters of zone III in the main palynological diagram. LOI values were at 550 °C (4% to 10%) and 950 °C (4% to 10%), the highest in the entire column. Compared to the previous zone, continental organic matter increased, as well as that of marine origin with an increase of calcareous remains towards the end of the zone. Regarding vegetation, here we found the mangrove area with the greatest coverage and development.

Zone IV: Depth: 101 - 1cm. This includes the upper part of zone III and zones IV and V in the palynological diagram. Compared to the previous zone, the LOI values between 550°C and 950°C decreased as seen in the reduction of marine origin organic matter. In centimeters 1 and 2, the values in continental components (differentiable plant remains) reached an extreme value of 76%. Regarding vegetation, the mangrove area reduced and the area the flooded forest increased.

Discussion

Palynological associations in sediments and affinities with current vegetation types

Table 3 shows the relationships between the palynological associations defined in this study based on their respective palynomorphs in the sediment and their correlation with current vegetation types according to their floristic composition. The correspondence grade between mangrove types dominated by *R. mangle* and by *H. germinans* was very significant as both types were associated with the same salinity conditions in the water column while the dry forest was dominated by *Mabea montana* and *Protium heptaphyllum*.

Palaeoenvironmental changes and their relationship with other Colombian Caribbean areas

For the period from 2000 to 500 years BP, **Jaramillo, et al.** (2012) and **Vélez, et al.** (2014) mentioned the presence of the vigorous development of mangrove communities in several localities of the Ciénaga Grande de Santa Marta (Boca de López, Hospitalito, La Ahuyama, Caño Perdiz, Bocas de Aracataca), and **Castaño** (2004) in Laguna Camarones, Guajira. These communities were dominated mainly by *Rhizophora* and significant values of *Hilairanthus* (*Avicennia*) were also measured. These associations were related to the dry conditions (low precipitation values) predominating in this period in the swamp sector and its surrounding areas.

Table 3. Relationship between the palynological associations detected in the sediment analysis and current vegetation types (Nevuanje)

Palynological associations (or dominant taxa) in sediments and pollen zones	Related current vegetation types in the Colombia Caribbean region (Rangel, <i>et al.</i> , 2010, 2013; Rangel, 2012; Cortés & Rangel, 2013)
<i>Mabea</i> sp. (zones V-IV-III)	Forests dominated by <i>Mabea montana</i> on Zapatos swamp (César) surrounding areas; associated species: <i>Cordia bicolor</i> and <i>Sterculia apetala</i>
<i>Protium</i> sp. (V-IV)	Forests dominated by <i>Protium heptaphyllum</i> and <i>Xylopia aromatica</i> on surrounding areas of Zapatos swamp; associated species: <i>Tapirira guianensis</i> , <i>Attalea butyracea</i> , <i>Dydimopanax morototoni</i>
<i>Euphorbia</i> aff. <i>thymifolia</i> + <i>Mascagnia macradena</i> and <i>Phyllanthus</i> sp. (V)	Thicket - <i>Phyllanthus elsiae</i> low forest. Shores of the Caribbean swamps
<i>Hilairanthus germinans</i> + <i>Laguncularia racemosa</i> + <i>Conocarpus erectus</i> with lowered values of <i>Rhizophora mangle</i> (V)	Mangrove dominated by <i>Hilairanthus germinans</i> and <i>Laguncularia racemosa</i> (<i>Lagunculario racemosae-Avicennietum germinantis</i> association)
<i>Rhizophora mangle</i> + <i>Hilairanthus germinans</i> , with high representation of <i>Laguncularia racemosa</i> (IV)	Mangrove dominated by <i>Rhizophora mangle</i> , <i>Hilairanthus germinans</i> and <i>Laguncularia racemosa</i> (<i>Lagunculario racemosae-Rhizophoretum manglis</i>)
<i>Solanum</i> aff. <i>umbellatum</i> + <i>Euphorbia</i> sp. (IV-II)	Thicket vegetation dominated by <i>Solanum campechensis</i> growing over Colombian Caribbean beaches
<i>Rhizophora mangle</i> + <i>Hilairanthus germinans</i> + <i>Conocarpus erectus</i> (III-II-I)	<i>Rhizophora mangle</i> mangrove (with total dominance of this species)
<i>Euphorbia</i> aff. <i>jamaicense</i> + <i>Solanum</i> aff. <i>umbellatum</i> + <i>Solanum</i> aff. <i>jamaicense</i> + <i>Ficus</i> sp. + <i>Bactris</i> sp. (III)	Thicket vegetation dominated by <i>Solanum campechensis</i> growing over Colombian Caribbean beaches
<i>Mabea</i> sp. + Arecaceae (II)	Forests dominated by <i>Mabea montana</i> on Zapatos swamp (César) surrounding areas; associated species: <i>Cordia bicolor</i> , <i>Sterculia apetala</i> , <i>Attalea butyracea</i>
<i>Acalypha</i> sp. + <i>Protium</i> sp. + Arecaceae (I)	Forests dominated by <i>Protium heptaphyllum</i> and <i>Xylopia aromatica</i> . Mixed palm forests

In the Nevuanje region, the largest mangrove development (*R. Mangle*) reached values up to 60% in the pollen spectrum occurring between 1078 and 654 years B.P. (see zone III of the palynological diagram). In the Ostional swamps, Cispatá Bay, this happened ca. 1380 years B.P. (Palacios, *et al.*, 2012), and 838 years A.P. in La Caimanera (Beltrán, 2015).

In the Ciénaga Grande de Santa Marta (C.G.S.M.), sediments were associated with a warming period between 1930 and 1660 years B.P. In Nevuanje, the predominance of organic components of marine origin can also be associated with warming conditions. Between 1660 and 900 years B.P., in the C.G.S.M., a shorter warm or “cold” period was detected, which differs from Nevuanje, as the presence of organic matter in its sediments of marine components predominated, and we identified a greater dominance and coverage of mangrove vegetation. In the C.G.S.M., Jaramillo, *et al.* (2012) classified as warm the period between 900 and 570 years B.P. According to Van der Hammen & Troncoso (1992) around 750 years B.P., dry conditions prevailed in the several localities of the lower Magdalena River. In Nevuanje, at the end of this period, an increase in organic components

of marine origin was observed, which would indicate warm conditions. Between 500 years A.P. and the present, warm or “cold” periods were detected in the CGSM. In this region, a high number of mineral components were found and, in some cases, shell deposition as well. In Neguanje, we identified high contents of the mineral component, a condition that can be present in cold conditions.

Based on the temperature calibration curves of the last 2000 years (D'Arrigo, *et al.*, 2006; Christiansen, *et al.*, 2012), and the precipitation and extension data, we adapted the interpretation of the types of vegetation to the Neguanje region as follows:

Zone I. Depth: 380 – 322 cm. Estimated age: 1605-1230 A.P. Compared to current climate variations (27.3°C temperature and 650 mm annual precipitation), the temperature and humidity conditions (precipitation) in the surroundings were slightly higher. Mangrove communities were established in swamp (marsh) areas highly dominated by *R. mangle*.

Zone II. Depth: 322 – 230 cm. Estimated age: 1230 to 1064 years A.P. Compared to zone I, the temperature was slightly lower and the humidity and precipitation conditions were slightly higher. The mangrove distribution area increased in the swamp (marsh) with *R. mangle* as the dominating species.

Zone III. Depth: 230 – 80 cm. Estimated age: 1064 to 655 years A.P. This was the zone with the warmest conditions according to the sequences set up in the sediment column. The humidity conditions (precipitation) in the areas surrounding the lagoon were lower than in zone II. We detected the effects of two climatic warming peaks: one towards the base of the area, ca. 1060 years B.P., with an approximate increase of 0.3°C above the global average estimated for the territory (27.3°C). The other peak was registered towards the top part, ca. 940 yr. B.P., with an increase of 0.5°C above the average related to the medieval climate optimum (records of maximum solar activity). In this zone, we recorded the largest extension of *R. mangle* mangrove. This period can be directly associated with a very strong marine influence as corroborated by an increase in transgression velocity rates.

Zone IV. Depth: 80 - 33 cm. Estimated age: 655 to 270 years B.P. The temperature decreased with respect to zone III. A marked decrease in the water levels was also observed in the swamp due to a lower entry of seawater, a decrease in precipitation around the swamp, and a slight drop in local temperature. It is possible that the decrease in marine influence is associated with a light regression process in the territory. The extension of the mangrove community was considerably reduced, and the exhumation of the territories facilitated the extension of the floodplain scrublands and the forests on the slopes (mainland) occupying areas contiguous to the mangrove.

Zone V. Depth: 0 - 33 cm. Estimated age: 270 years A.P. to the present. The upper part reflected the current conditions of temperature (27.3°C) and precipitation in the territory (650 mm annual precipitation). Compared to zone IV, the temperature was higher (1 to 1.2°C) and precipitation was less. In the swamp (marsh), the extension of the mangrove communities decreased drastically while the area covered by tropical dry forests on the slopes increased.

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