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Title: Holocene establishment of mangrove forests in the western coast of the Gulf of Mexico

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Keywords: coastal environment; Gulf of Mexico; Holocene; mangroves; sea-level changes; pollen analysis

Corresponding Author: Dr. Alexander Correa-Metrio,

Corresponding Author's Institution:

First Author: Cecilia Cordero-Oviedo

Order of Authors: Cecilia Cordero-Oviedo; Alexander Correa-Metrio; Ligia Estela Urrego; Gabriela Vázquez-Hurtado; Maarten Blaauw; Jaime Esconar; Jason Curtis

Abstract: The successful establishment of mangrove ecosystems depends on an intricate network of interactions among physical and biological factors that are highly dynamic through time. At millennial to centennial time scales, regional climates, sea levels, and local geomorphology play critical roles in the establishment of mangroves. Whereas fluvio-marine dynamics define coastal sedimentary settings, regional precipitation and freshwater input modulate salinity and seasonal flooding patterns. We analyzed a ~7800-year-old, continuous sedimentary record from the western coast of the Gulf of Mexico to shed light on regional biophysical coastal processes and the history of the mangroves that occupy the region today. We used a systematic sampling of mud-water interface sediments to generate a modern reference frame for interpreting fossil pollen assemblages. Our results indicate that the cored location that is currently approximately at sea level, was below sea level from ~7800 to 4000 calibrated years before present (cal BP). The establishment of dense mangrove stands took place around 3700 cal BP, when regional sea levels stabilized, resulting in a substantial increase of organic matter and therefore carbon stored in the sediments. However, the mangrove ecological succession that started at ~6000 cal BP was interrupted by a regional drought that extended from ~5400 to 3700 cal BP. From 3700 cal BP to Present, the lagoon has been characterized by relatively stable both substratum and sea level, that together have facilitated the establishment of mangrove forests. Overall, our record demonstrates the complexity of the interactions between local and regional factors in the development and evolution of both coastal geomorphology and ecosystems.

Revision Notes
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Dear Dr. Cammeraat
We are happy to submit a revised version of the manuscript entitled "Holocene establishment of mangrove forests in the western coast of the Gulf of Mexico". We are very appreciative of the thorough review of the manuscript because it substantially improved it. The main change we made was including carbon and nitrogen analyses on both modern and fossil samples, giving more solid bases to our interpretations. We have included Jason Curtis and Jaime Escobar as coauthors because they very kindly contributed the C and N analysis and helped with the interpretation of results. Please find below the response to the queries from the reviewer, whereas the idiomatic suggestions marked on the pdf were directly attended on the word documents, which marked up copy we are attaching too. Please extend all our gratitude to the reviewer, he did a fantastic job at raising conceptual and stylistic concerns.
We feel that the new version is much better and stronger, we hope you find it suitable for publications in CATENA.
Sincerely yours,

Alex Correa-Metrio

Reviewer #1: This paper provides a reconstruction of change in the La Mancha lagoon, on Mexico's east coast, based on pollen analysis. In fact, it relies almost entirely on pollen, with only a passing reference to stratigraphy. As the authors themselves note, the evolution of these coastal systems involves the complex interplay of a number of factors, a challenge that really needs a multi-proxy approach. There are some hints that there might be some other information available, but it is not presented (see below).

We are aware of the importance of a multiproxy approach, and thus, we have decided to add analyses of total both carbon and nitrogen in modern and fossil samples. The inclusion of new data has strengthened our case, but we, however, would like to emphasize that the aim of our research, as clearly stated in the manuscript, is reconstructing vegetation dynamics, a goal that is achieved through pollen analysis. Mangrove forests develop under a precise combination of geomorphologic settings as well as fluvial and marine influences, thus the use of mangrove pollen has been recognized as a reliable and efficient means for reconstructing environmental dynamics in costal environments.

The water level reconstructions in particular seem really quite speculative based on pollen alone and the lack of information about the morphology of the modern lagoon.

We have added a basic bathymetry based on data points that were measured during the collection of modern samples.

There are a number of places where more detail is needed and more justification for some of the reconstructions made. This need for clearer justification feeds through to the Highlights listed. Although the quality of the English was generally good, there were a few places where the meaning was not clear (see annotated pdf uploaded).

The document was changed according to the comments on the pdf.

Study area. More about the morphology of lagoon (is there anything in Reassert, 1999?) would be useful.

We included a basic bathymetry. Also, in Section 2 (Study area), we abounded "La Mancha lagoon belongs to a geomorphic unit known as the Low Cumulative Plain that formed during the Quaternary (Geissert, 1999), allowing deposition of clayey-silt sediments. The lagoon formed at the margin of a volcanic mountain range that interrupts the coastal plain of the Gulf of Mexico (Geissert, 1999; Fig. 1). The current morphology of the area has been mostly shaped by Quaternary dynamics, going from an empty deep basin during times of sea-level low stands to a depositional coastal plain during times of sea-level high stands (Geissert, 1999; Kjerfve, 1994). The mountain ridge that connects La Mancha Hill with the adjacent western mountains divides La Mancha lagoon into two contrasting sub-basins (Fig. 1). Differences in freshwater input, marine influence, energy of the sedimentary environments, and human occupation have created two clearly distinct environments for mangrove forests, which today occupy ~3.55 km^2 around the lagoon"

What was transect in Fig. 1 based on?

The transect represented an arbitrary line that was drawn aiming to describe the morphology and likely evolution of the area. We have excluded the transect and replaced Fig. 1D.

More detail is needed here about canals (referred to later) and the nature and extent of human impact.

There was an idiomatic misunderstanding, we misused the word "canals" for referring to drainage channels. We have amended the text likewise. Also, we have reworded the last paragraph of Study Area, which now reads "Regional human occupation has been reported since at least ~4,600 BP, and the lagoon has apparently been an important source of resources for human populations (Moreno-Casasola, 2006). This factor has exerted direct pressure on the mangrove forest through deforestation for timber and fuel wood extraction, and more recently in the interruption of surface and subsurface flows in the by infrastructure of the oil industry. These local factors have been especially harsh on the northern sub-basin, where only sparse remnants of the mangrove forest survive today. Thus, whereas vigorous mangrove forests surround the southern sub-basin, the northern sub-basin is occupied by highly disturbed vegetation including sparse mangrove remnants. Regionally, growing human population and the parallel development of infrastructure apply further pressures to coastal ecosystems through pollution, accelerated erosion, increasing sea level, among other elements (Gilman et al., 2008)."

Methods. Were water depths measured when the surface sediment samples were taken?

Yes, we have added a bathymetric map of the lagoon.

Did you measure LOI for these samples to look at spatial variability? Grain size? This information would give an idea of basin bathymetry. Presumably there would be a clear river channel?

We added analyses of TIC, TOC, and TN on surface samples and demonstrated that there are significant differences between the northern and southern sub-basins, providing further, more solid elements for interpreting the fossil record "TC content in modern samples varied between 3.1 and 12.3%, with mean and median of 4.9 and 4.4%, respectively. Although mean values for the northern and southern sub-basins were not statistically differentiable ($t = 1.66$, p-value = 0.11), the northern sub-basin consistently showed lower values (Fig. 3). Differently, individual fractions of C resulted statistically differentiable, with a higher concentration of TOC in the southern sub-basin (3.56, p-value = 0.002) and a higher concentration of TIC in the northern sub-basin ($t = -2.47$, p-value = 0.023). TN range between 0.02 and 0.37% with mean and median of 0.23 and 0.24%, respectively (Fig. 3), with southern concentration statistically higher than the northern concentration ($t = 5.54$, p-value < 0.001). TC resulted statistically associated with TN, TIC, and TOC, although the magnitude of the correlation was substantially higher with the latter (Fig. 3). Whereas TIC resulted moderately associated only with TN, TOC was strongly associated with both TC and TN (Fig. 3)."

What evidence do you have to support claim of deep and bucket shape basin?

Where it read "Thus, the lacustrine basin of La Mancha was probably deep and bucket-shaped, impeding the establishment of mangrove forests", it now reads "Thus, the lacustrine basin of La Mancha was probably deeper than modern, impeding the establishment of mangrove forests".

Was anything else done on the core other than pollen? LOI? What were the shells, terrestrial? aquatic/ freshwater or marine? Do they tell you anything directly about salinity?

We have added TC and TN analyzed on modern and fossil samples, which greatly strengthened our interpretation. Biological indicators other than pollen provide a wealth of information on different environmental attributes. The goal of our research was reconstructing the evolution of the mangrove forest, which we did through the fossil pollen record, and the modern context provided by the spatial sampling. The shells we found were marine bivalves, and we then clarified in the discussion that their presence through the record evidences a constant marine influence through time. We added to the discussion "Additionally, the constant presence of marine shells through the sedimentary record (Fig. 2) demonstrates a permanent marine influence through the last ~7,800 year."

Results. Radiocarbon dates - need to add calibrated dates to Table 1.

Calibrated dates were added to Table 1.

Why bulk dates? What was OM content? See query above re LOI.

The material dated was bulk sediment since no other material such as macrofossils or charcoal could be found. We are aware of the possibility of a ^{14}C age offset but were not able to quantify this in the present study. We added TC and TN for the entire record,

making evident that the content of TC of points sampled for radiocarbon analyses varied between 2 and 7%. Although TC content is likely associated with the organic fraction, we did not quantify organic matter content for the fossil samples.

Add actual dates to Fig 2.
Actual dates are in Table 1, thus we considered it was not necessary repeating this information on Fig. 2 as the figure is already crowded.

What was/is human disturbance in N basin? When did it start? (see above).
In the study area it now reads "Regional human occupation has been reported since at least ~4,600 BP, and the lagoon has apparently been an important source of resources for human populations (Moreno-Casasola, 2006). This factor has exerted direct pressure on the mangrove forest through deforestation for timber and fuel wood extraction, and more recently in the interruption of surface and subsurface flows in the by infrastructure of the oil industry. These local factors have been especially harsh on the northern sub-basin, where only sparse remnants of the mangrove forest survive today. Thus, whereas vigorous mangrove forests surround the southern sub-basin, the northern sub-basin is occupied by highly disturbed vegetation including sparse mangrove remnants. Regionally, growing human population and the parallel development of infrastructure apply further pressures to coastal ecosystems through pollution, accelerated erosion, increasing sea level, among other elements (Gilman et al., 2008)."

Was NMDS run on core samples alone to improve discrimination between these?
No; as stated in the text, NMDS was run on both modern and fossil samples as our interest was to investigate the establishment of modern systems in the area.

Discussion. More about the % mangrove taxa in the surface sediment and core samples compared to modern % vegetation cover would be useful.
We don't have reliable quantitative data on the forest surrounding La Mancha. We discuss mangrove representation in the first two paragraphs of the discussion, where we demonstrate that although mangrove taxa percentages are generally high, there is a clear distinction of percentages between the two sub-basins.

Base of core - sea water flooding - text indicates this recorded at 12-13m below modern surface. How far below modern was sea level 8 - 6 Ka? Is it 6m (see bottom of p.23)? Is there any other evidence to support the idea of sea-water flooding and then a deep water body? (see above).
See level regional curves for the Gulf of Mexico and the Caribbean are shown in Fig. 7 (former Fig. 6), and their difference with sediment depth were used for estimating lagoon water depth. We explained better in the discussion that now reads "Through this time period, the mud-water interface was between 13 and 9 m below the modern surface, which today is at sea level. At the same time, average sea level was between 9 and 5 m below modern. The difference between mud-water interface depth and sea level can only be accounted by lagoon water depth, which was ~ 4 m below sea level (Fig. 6A)."

On Fig. 6 do the depths on the y axis relate to both core depth and the height of sea level relative to modern?

Fig. 7 (former Fig. 6) is meant to compare the depth and age scales of core depth and sea level, and thus they have to necessarily be the same. To avoid confusion, the y-axis label that read “Depth (m)”, now reads “Depth (m below modern surface)”.

6300-5400 Is there any clear evidence to support the claim of complete closure of the lagoon? Period of more silt deposition. Are these sediments more organic?
We tried to clarify through the manuscript that the establishment of mangroves (either true mangrove trees or marshland vegetation) requires depositional environments, which an open lagoon would not have provided given the high energy of direct sea influence. We hope to have strengthened our interpretation by adding the curves of TC and TN.

5400-3700 What's the real basis for identifying modern seasonal cycle?
This is just an interpretation based on the fact that sea level and sediment interface level apparently became similar. We explained better in the text that now reads “Whereas the rate of sea-level rise continued to decrease, relatively high sedimentation rates were evident in La Mancha sequence up to ~5000 cal BP, when apparently the rates of sediment deposition in the lagoon and those of sea level rise became similar (Fig. 6A). Such equilibrium between sediment deposition and sea-level rise implies the definition of a coastal erosive baseline that allowed the deposition of sand in the coast by the northerly currents during the dry season, creating the sandbar that dams the lagoon. Differently, during the wet season, the fluvial input would have the capacity to erode the sandbar, opening the direct contact between the lagoon and the sea and, thus, resulting in the modern seasonal flood cycle.”

Last 3700 what's the balance between climate, sea level and human disturbance? See note above re what is known about disturbance?
I hope this question has been addressed by the multiple changes we made through the document.

Holocene establishment of mangrove forests in the western coast of the Gulf of Mexico

Cordero-Oviedo, C[a]., A. Correa-Metrio[b,*], L.E. Urrego[c], G. Vázquez-Hurtado[d], M. Blaauw[e], J. Escobar[f,g], J.H. Curtis[h]

[a] Posgrado en Ciencias de la Tierra, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México 04510, ceciliacorderoviedo@gmail.com, [b] Instituto de Geología, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México 04510, acorrea@geologia.unam.mx, [c] Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Sede Medellín A.A. 568 Medellín, Colombia, leurrego@unal.edu.co, [d] Instituto de Ecología, A.C. Carretera antigua a Coatepec 351, El Haya, Xalapa 91070, Veracruz, México, gabriela.vazquez@inecol.mx, [e] School of Natural and Built Environment, Queen's University Belfast, Belfast, United Kingdom, maarten.blaauw@qub.ac.edu, [f] Departamento de Ingenieria Civil y Ambiental, Universidad del Norte, Km 5 Via Puerto Colombia, Colombia, jhescobar@uninorte.edu.co, [g] Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Panama, [h] Department of Geological Sciences, University of Florida, Gainesville, FL, 32611, USA, curtisj@ufl.edu

***Corresponding autor:** Alexander Correa-Metrio, acorrea@geologia.unam.mx

Abstract

The successful establishment of mangrove ecosystems depends on an intricate network of interactions among physical and biological factors that are highly dynamic through time. At millennial to centennial time scales, regional climates, sea levels, and local geomorphology

play critical roles in the establishment of mangroves. Whereas fluvio-marine dynamics define coastal sedimentary settings, regional precipitation and freshwater input modulate salinity and seasonal flooding patterns. We analyzed a ~7800-year-old, continuous sedimentary record from the western coast of the Gulf of Mexico to shed light on regional biophysical coastal processes and the history of the mangroves that occupy the region today. We used a systematic sampling of mud-water interface sediments to generate a modern reference frame for interpreting fossil pollen assemblages. Our results indicate that the cored location that is currently approximately at sea level, was ~~under~~ below sea level from ~7800 to 4000 calibrated years before present (cal BP). The establishment of dense mangrove stands took place around 3700 cal BP, when regional sea levels stabilized, resulting in a substantial increase of organic matter and therefore carbon stored in the sediments. However, the mangrove ecological succession that started at ~6000 cal BP was interrupted by a regional drought that extended from ~5400 to 3700 cal BP. From 3700 cal BP to Present, the lagoon has been characterized by relatively stable both substratum and sea level, that together have facilitated the establishment of mangrove forests. Overall, our record demonstrates the complexity of the interactions between local and regional factors in the development and evolution of both coastal geomorphology and ecosystems.

Keywords: coastal environment; Gulf of Mexico; Holocene; ~~pollen analysis~~mangroves; sea-level changes; pollen analysis

1. Introduction

Mangrove ecosystems are a large component of tropical and sub-tropical coastal landscapes. Occupying intertidal zones (Lugo and Snedaker, 1974), they ~~intermediate~~ regulate the relationship between continental ~~discharges~~discharge of sediments and water~~, mainly fluvial,~~ and sea level (Ellison, 1989). The main engineers of these ecosystems are a reduced group of plant species physiologically adapted to brackish-to-saline substrates (Ball, 2002; Vovides et al., 2014). The establishment of mangrove forests creates the conditions for complex food webs that incorporate marine and continental components. The entire mangrove ecosystem is fundamental for providing products and ecological services, ~~which reflect~~resulting in direct and indirect uses by human populations, mainly fuelwood, fisheries, sediment trapping, and carbon storage (Bouillon et al., 2008; Feller et al., 2017; Méndez et al., 2007; Ward et al., 2016).

Although they represent one of the most important carbon sinks worldwide (Bouillon et al., 2008), together with coral reefs and tropical forests, mangroves are among the most endangered modern ecosystems (Valiela et al., 2001). It has been estimated that through the last two decades of the 20th Century, 35% of the global mangrove area had been lost mostly because of direct and/or indirect anthropogenic causes (FAO, 2007). The main human-related causes of mangroves loss are the conversion to aquaculture and agriculture, urbanization, and pollution (Feller et al., 2017; Gilman et al., 2008; Thorhauga et al., 2017), which in Mexico have translated in a net loss ~240 ha/year through the last decades (Hamilton and Cassey, 2016). The rapid rate at which these threats to mangrove ecosystems are growing highlights the need ~~of~~ to understand~~ing~~ them in the context of their natural history and the intricate network of factors that interact to facilitate or impede their colonization and establishment.

A wide variety of factors interact to create the specific conditions under which mangrove communities thrive and persist through time (Gilman et al., 2008). Healthy vigorous mangrove forests, and therefore ecosystems, depend on a delicate balance between marine influences and freshwater and sediment input from continental areas acting upon specific geomorphologic settings (~~Chapman, 1976;~~ Lugo and Snedaker, 1974; Soares, 2009). Whereas marine influences on mangrove ecosystems materialize through tidal regimes and sea level changes that define base~~-level~~line for erosion and accumulation of sediments, regional climates and vegetation cover over the mainland control continental discharge of freshwater and sediments along the coast. Thus, through the Holocene, changes in precipitation, vegetation cover, geomorphologic dynamics, and sea levels have probably led to high environmental variability over the intertidal areas (Geissert Kientz, 1999). In the Gulf of Mexico and the Caribbean, regional sea levels have progressively risen since the deglaciation (Milliken and Anderson, 2008; Toscano and Macintyre, 2003), whereas annual precipitation has shown a wide variability associated with extraterrestrial forcings (e.g. solar activity and orbital cycles, Haug et al. 2001, Hodell et al. 2001) and higher frequency processes associated with complex internal systems (e.g. El Niño-Southern Oscillation, Moy et al. 2002). The balance between fluvial loads and sea-level rise modulates local geomorphologic and sedimentary processes, defining the formation of either depositional or erosional environments the balance of which ~~balance~~ is in turn critical for the establishment and persistence of mangroves (Parkinson et al., 1994). Indeed, modern net losses of mangrove cover have been widely associated with sea-level rises along unprotected coasts (Suárez et al., 2015). Thus, the definition of the context that led to the development of modern mangrove forests would provide important clues for identifying the limits of environmental pressure that these ecosystems can endure.

Sedimentary deposits that accumulate in coastal lagoons provide a natural record of the evolution of coastal landscapes through time. Understanding the natural development of mangrove ecosystems and the main factors involved in the process would give insights into the threat level that coastal zones face given modern environmental change (Lopez-Portillo et al., 2011; Thom, 1967). Here we use the pollen record of a 13-m-long ~8,000-year-old sedimentary sequence retrieved from La Mancha Lagoon, State of Veracruz, Mexico, to reconstruct the history of the local vegetation through the Holocene. By analyzing the history of vegetation assemblages as reflected by fossil pollen spectra, we aim to answer the following questions: i) what has been the role of sea-level rise and precipitation variability through the Holocene in the establishment and persistence of mangrove forests in the west coastline of the Gulf of Mexico? ii) when did the barrier-lagoon systems of the region consolidate in the context of Holocene environmental variability?

2. Study Area

La Mancha lagoon is located in the State of Veracruz, Mexico, on the western coasts of the Gulf of Mexico (19.579 N°, 96.387 W°, Fig. 1). With a north-to-south length of 3 km, the lagoon has an area of ~1.35 km^2 distributed in two sub-basins separated by a strait located ~~around~~ near the center of the water body (Fig. 1). Whereas the southern sub-basin is exposed to permanent freshwater input from the Caño Grande River that drains water from a basin of almost 2,500 km^2, the northern sub-basin more exposed to tidal influence through an ephemeral mouth that communicates seasonally with the sea ~~seasonally~~ (Fig.1) (Lankford, 1977; Moreno-Casasola, 2006). During the dry season, a sand bar accumulates closing the estuarine mouth and causing a damming of continental

freshwater. With the onset of the rainy season, freshwater starts to accumulate, eventually breaking the sandbar, opening the mouth, and creating a direct connection with the sea (Moreno-Casasola, 2006). Thus, lagoon dynamics are intimately linked to regional climate that is warm (temperatures from 22 to 26 °C), with an annual mean precipitation of 1222 mm, with 85% of the annual value falling between June and October (Fig. 1) (Servicio Meteorologico Nacional, 2018). The dry season is especially pronounced between December and April with mean monthly precipitation~~s~~ below 20 mm, ~~whereas~~ while November and May are characterized by a mean precipitation around 50 mm. By the end of the summer and early autumn, the area is exposed to tropical cyclones, although their incidence is relatively low compared with other areas of the Gulf of Mexico (Moreno-Casasola, 2006).

La Mancha lagoon belongs to a geomorphic unit known as the Low Cumulative Plain that formed during the Quaternary (Geissert Kientz, 1999), allowing deposition of clayey-silt sediments. The lagoon formed at the margin of a volcanic mountain range that interrupts the coastal plain of the Gulf of Mexico (Geissert Kientz, 1999; Fig. 1). The current morphology of the area has been mostly shaped by Quaternary dynamics, going from an empty deep basin during times of sea-level low stands to a depositional coastal plain during times of sea-level high stands (Geissert Kientz, 1999; Kjerfve, 1994). The mountain ridge that connects La Mancha Hill with the adjacent western mountains divides La Mancha lagoon into two contrasting sub-basins (Fig. 1). ~~The lagoon formed at the margin of a volcanic mountain range that interrupts the coastal plain of the Gulf of Mexico (Geissert, 1999) (Fig. 1).~~Differences in freshwater input, marine influence, and energy of the sedimentary environments have created two clearly distinct environments for mangrove forests, which today occupy ~3.55 km^2 around the lagoon.

Regional tides are mixed, mostly diurnal and of low amplitude (highest and lowest tidal levels at 22 cm and -30 cm from average sea level, respectively), preventing the formation of tidal currents. This feature together with the permanent input of fresh water and the sheltering of the lagoon from the energy of the waves by La Mancha Hill (Fig. 1) have probably played a critical role ~~at~~ in maintaining the morphology of the lagoon, avoiding the formation of tidal ~~coasts~~mudflats, marshes, and/or estuaries (Geissert Kientz, 1999). ~~Through the last~~Over recent decades, progressive loss of depth of the lagoon because of sediment accumulation suggests that sediment input surpasses local erosion (~~Matus~~ Moreno-Casasola~~et al.~~, ~~1994~~2006), although this might not have been the case through the entire history of the area.

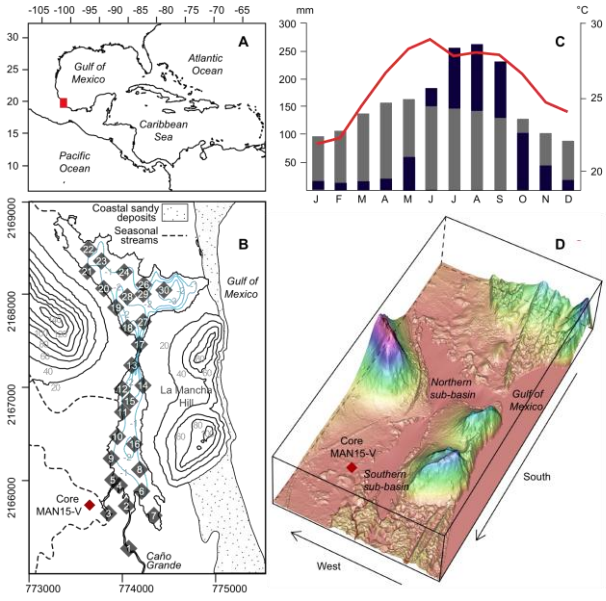

Figure 1. Study area. A. Location of La Mancha lagoon in the continental context. B. Locations sampled for modern and fossil sediments in the local context of La Mancha

coastal lagoon; elevation contours are shown in increments of 20 m asl (solid black lines), whereas a basic bathymetry based on field observations is shown as blue contours. C. Monthly precipitation (blue bars), evapotranspiration (gray bars), and monthly mean temperature (black line with dots) at La Mancha Meteorological Station (Servicio Meteorologico Nacional, 2018) D. Topographic ~~profile through~~representation of La Mancha coastal lagoon.

Pollen assemblages contained in sediments reflect parental vegetation and are therefore useful for reconstructing environmental dynamics through time (e.g. Carrillo-Bastos et al., 2010; Urrego et al., 2009; Urrego et al., 2018). Given the regional geomorphology, the large size of the catchment basin of Caño Grande River, and the proximity to high mountain ranges, the pollen spectra of sediments from La Mancha lagoon ~~might~~ contains regional and local taxa (Moreno-Casasola, 2006; Travieso-Bello, 2000). Whereas the former are transported by water and wind currents, the latter are produced by *in situ* vegetation (Hooghiemstra et al., 2006). Regional elements come mostly from montane forests that dominate the regional highlands (Rzedowski, 2006~~García-Franco et al., 2008~~; Williams-Linera, 2002) and are characterized by wind-pollinated ~~anemophyllous~~ taxa with long-distance pollen dispersal (e.g. *Alnus*, *Myrica*, Ulmaceae, *Quercus*, and *Pinus*), which ~~in turn result~~ tend to be overrepresented in the pollen spectra. From within these allochthonous elements, *Pinus* is worth noticing because of the opportunist nature of most of the parental species (Richardson, 1998), which results in a high representation of this taxon in pollen s~~e~~pectra when environmental conditions are suboptimal for other arboreal elements (e.g. during drughts, Correa-Metrio et al., 2013). Local elements of the pollen spectra are~~a~~ in turn associated with two main vegetation types, namely lowland and

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mangrove forests. The hills that surround the lagoon reach heights up to 300 m asl and are mostly occupied by species of *Desmodium, Inga, Machaerium, Psychotria, Protium, Bursera,* Moraceae-Urticaceae and *Acacia*. The salt marshes, coastal dunes, and beaches that characterize ~~local cumulative~~flood plains are mainly dominated by species of Cyperaceae, Amaranthaceae, *Typha*, Asteraceae, Chenopodiaceae, *Mimosa* and *Croton*. These vegetation types can be associated with the distal part of a marine transgression plain~~e~~, or be related to the first stage of a progradational pattern indicative of a typical ecological succession on intertidal habitats (González and Dupont, 2009).

The edges of the lagoon are occupied by species typical of mangrove forests, *Rhizophora mangle, Avicennia germinans, Conocarpus erectus* and *Laguncularia racemosa* (Travieso-Bello, 2000 ~~and Moreno-Casasola, 2006~~). The interplay of these species is modulated by their differential adaptation to the changing environmental conditions along a salinity gradient, which in turn defines the structure and composition of the forest (Lugo and Snedaker, 1974; Travieso-Bello, 2000; Urrego et al., 2009). Thus, these forests are highly sensitive to changes in sea-level, coastal progradation and/or erosion at different time scales (Ellison, 2008). Mangrove forest species are adapted to specific environmental conditions, with *R. mangle* tolerating high inundation levels, strong wave energy and shorter distances to the sea, *A. germinans* thriving in more saline environments, hurricane-disturbed or experiencing severe droughts, *L. racemosa* ~~is~~ being restricted to average minimum temperatures ~~of more than~~over 15.5 ºC and successional processes triggered by anthropogenic disturbance, and *C. erectus* being tolerant to higher sediment pH typical of supra-tidal waters close to well drained forests (González et al., 2010; Hogarth, 2007; Urrego et al., 2009; Urrego et al., 2010).

Regional human occupation has been reported since at least ~4,600 BP, and the lagoon has apparently been an important source of resources for human populations (Moreno-Casasola, 2006). This factor has exerted direct pressure on the mangrove forest through deforestation for timber and fuel wood extraction, and more recently in the interruption of surface and subsurface flows in the by infrastructure of the oil industry. These local factors have been especially harsh on the northern sub-basin, where only sparse remnants of the mangrove forest survive today. Thus, whereas vigorous mangrove forests surround the southern sub-basin, the northern sub-basin is occupied by highly disturbed vegetation including sparse mangrove remnants. Regionally, growing human population and the parallel development of infrastructure apply further pressures to coastal ecosystems through pollution, accelerated erosion, increasing sea level, among other elements (Gilman et al., 2008).

3. Methods

3.1 Field work and laboratory analysis

In autumn 2015, a 13-meter-long core was recovered from the southern part of La Mancha coastal lagoon (core MAN15V, Fig. 1), under an *A. germinans* stand, using a modified Livingston piston corer (Colinvaux et al., 1999). The core was longitudinally sectioned, stratigraphically described, and stored at ~ 4ºC to preserve the sedimentary evidence. The chronological control of the sedimentary sequence was based on eight accelerator-mass-spectrometer (AMS) radiocarbon dates of bulk sediment, ~~homogenously distributed along the core~~given that no other material such as macrofossils or charcoal could be found. Radiocarbon dates were calibrated to years before present (hereafter cal BP) using the

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IntCal13 curve (Reimer et al., 2013), and calibrated dates were used to build a Bayesian age-depth model using Bacon (Blaauw and Christen, 2011). The core was subsampled every ~ 12.5 cm for pollen analysis, aiming at a temporal resolution of ~75 years between contiguous samples. A total of 104 samples were processed for pollen analysis using standard pollen extraction techniques (Faegri and Iversen, 1989). Samples were analyzed under transmitted-light microscope at magnifications of x400 and x1000, aiming to reach a minimum pollen sum of 300 pollen grains. Grains of the family Cyperaceae and pteridophytes spores were excluded from the pollen sum, although they were counted and included in the interpretation. Pollen counts were transformed into percentages of the pollen sum and a stratigraphic pollen diagram was constructed.

Pollen taxa were classified into five groups according to their modern ecological affinities (ecological affinities after Lugo and Snedaker 1974, Ranwell 1972, Travieso-Bello 2000): i) mangroves represented by *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus*; although *Laguncularia racemosa* is an important component of the local mangrove forests, it was not found in the pollen spectra; ii) salt marsh vegetation represented by Cyperaceae, Amaranthaceae, *Croton*, *Typha*, Asteraceae, Chenopodiaceae, and *Mimosa*;~~,~~ iii) lowland forest represented by *Inga*, *Acacia*, *Machaerium*, *Protium*, *Bursera*, and Moraceae-Urticaceae; iv) montane regional forests represented by *Alnus*, *Myrica*, Ulmaceae, *Quercus*, *and Miconia*; and v) disturbance taxa represented by *Pinus* and Poaceae; these latter taxa were classified as representatives of disturbance because in Mexico they are distributed along environments unfavorable to vegetation development, usually associated with either natural or anthropogenic causes (Franco-Gaviria et al., 2018; Rzedowski, 2006). High abundances of *Pinus* pollen have been reported for areas ~~submitted~~

subjected to dry conditions and/or regimes of high disturbance (Correa-Metrio et al., 2013; Metcalfe et al., 2000), mostly associated with early succession colonizers (Ramirez-Marcial et al., 2001). Meanwhile, although Poaceae pollen is characteristic of successional processes of supratidal plains (Bush, 2002; Urrego et al., 2013), it is also found in pollen assemblages from all Mexican vegetation types, usually associated with disturbance (Correa-Metrio et al., 2013; Franco-Gaviria et al., 2018).

The fossil pollen record was complemented by sampling 30 locations homogeneously for modern mud-water interface (15 samples from each sub-basin) distributed ~~along~~ across the water body, using an Ekman dredge. This sampling was meant to cover the variability of the modern pollen spectra (Fig.1), especially the differences between depositional environments of the two sub-basins. Samples were treated and analyzed using the same techniques as the fossil samples.

Total both C (%TC) and N (%TN) were measured in fossil samples every 5 cm along the core and in modern samples. For this purpose, samples were freeze dried and crushed, and subsequently analyzed using a Carlo Erba NA1500 CNS elemental analyzer. Additionally, coulometric titration was used to determine carbonate carbon (%TIC) in modern samples, allowing the estimation of organic carbon (%TOC). The discrimination of TC into TIC and TOC in modern samples was used to infer the relationship between these two carbon sources in the system of La Mancha lagoon.

3.2 Statistical Analysis

A non-metric multidimensional scaling ordination (NMDS) was applied on pollen relative abundances, including both modern and fossil samples. The ordination was performed to summarize the temporal variability of the pollen spectra, and to evaluate vegetation temporal dynamics in the context of the modern lagoon. This technique ordinates samples on a *k*-dimensional space defined *a priori* by the analyst, aiming to maintain the original topologic relationships among samples (Legendre and Legendre, ~~1998~~2012). Although two-dimensional ordinations are readily used, we selected three dimensions to produce a relaxed ordination where the affinity among pollen spectra can manifest more freely. We used the Bray-Curtis metric to estimate dissimilarity among samples, a metric that relies more on compositional data than ~~in~~ on the abundance of individual taxa and has been proven monotonic to ecological distance (Faith et al., 1987).

Modern samples were classified into southern and northern sub-basins as representative of dense and sparse mangrove forests, respectively. Whereas the northern sub-basin has direct contact with the sea through the ephemeral mouth, which creates a more energetic environment, and has been ~~submitted~~ subjected to important human disturbances and modifications resulting in sparse mangrove cover, the southern sub-basin is more influenced by the entrance of the river and is occupied by a well-developed dense mangrove stand. Thus, pollen spectra from these two sub-basins should reflect contrasting mangrove-forest cover conditions, and their relative oceanic and fluvial influences. The statistical significance of the difference between NMDS sample scores of the two sub-basins were tested using a two-sample t-test (Zar, 1999). TIC, TOC, TC, and TN content in modern samples were compared using Pearson correlation coefficient, whereas comparisons of concentrations between the northern and southern sub-basins were also compared using two-sample t-test (Zar, 1999).

4. Results

4.1 Stratigraphy and chronology of the sedimentary record

Sediments from the La Mancha coastal lagoon were mostly brownish, shelly clays with low content of organic material, and some intermissions of brownish silt with shell fragments and organic material (Fig. 2A). From the base of the core up to 1200 cm below lagoon floor (blf hereafter), the sediments were brown ~~shellish~~ shelly clay, while from 1200 to 663 cm blf the color turned into a light brown matrix (clay and silt) with shell fragments and carbonates. From 663 to 615 cm blf the ~~claylish~~ clayey sediment~~s~~ was~~ere~~ brown with light brown bands. From 615 to 372 cm blf, the sediment showed brownish tones, and were mostly composed of clay with a thin layer of silt, ~~shellish~~ shelly and little organic material. The uppermost 327 cm were dark to very light brown, with a uniform ~~shellish~~ shelly clay composition (Fig 2A).

All radiocarbon dates resulted in stratigraphic order (Table 1). Although bulk sediment dates could lead to an ^{14}C age offset, we were not able to quantify ot because of the lack of other quantifiable materials. Nevertheless, the high correspondence between TC and TN along the sedimentary record (Fig. 2) suggests that inorganic carbon represents a relatively low proportion of the sedimentary material. According to the age-depth model, the core has a basal age of ~7840 cal BP, resulting in an average sedimentation rate of 1.96 mm/yr (Fig 2B). From the bottom of the sequence up to 5500 cal BP, sedimentation rates were high, with maximum values around 5500 cal BP (4.10 mm/yr). From c. 5500 cal BP to present, sedimentation rates showed a decreasing trend, reaching 0.89 mm/yr in the uppermost part of the core (Fig 2).

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Table 1. Radiocarbon dates of core MAN15V from La Mancha coastal lagoon. Depths in cm below lagoon floor (blf). Ages calibrated after the IntCal13 curve (Reimer et al., 2013).

Laboratory code	Depth (cm blf)	^{14}C Age	Error	Calibrated age (95% range; cal BP)
UBA-34340	109	1290	24	1181-1283
Beta-440367	175	1880	30	1730-1883
UBA-34341	282	3447	26	3637-3826
Beta-440368	373	3970	30	4300-4523
UBA-34342	564	4732	41	5326-5584
Beta-437078	649	4770	30	5334-5588
UBA-34343	979	5624	41	6312-6482
Beta-437079	1249	6700	30	7508-7616

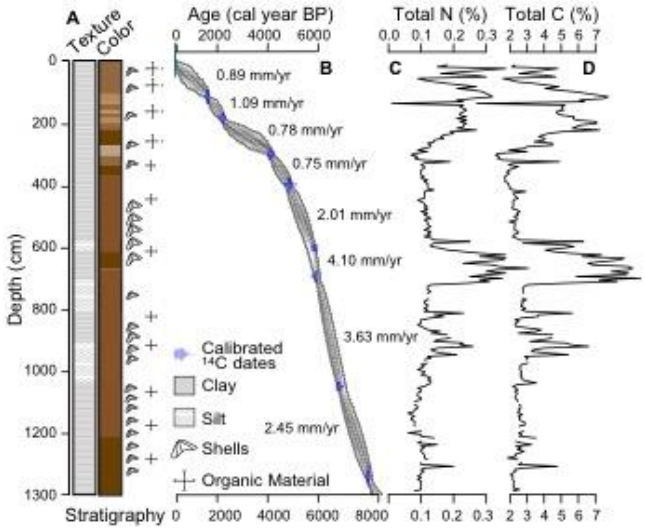


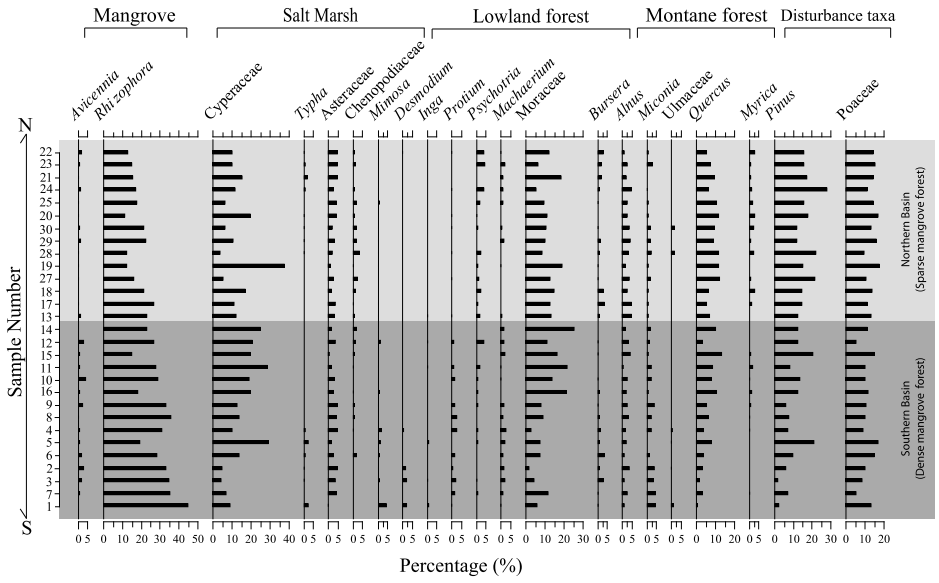
Figure 2. Core MAN15V from La Mancha coastal lagoon. A. Stratigraphy of the sedimentary sequence~~;~~: texture (left) ~~and,~~ color (right), and organic and shell content. B. Age-depth model; calibrated ages (blue silhouettes), 95% confidence intervals in grey (darker colors indicate higher probability), and sedimentation rates (mm/yr). C and D. Percentage of total nitrogen and total carbon content (TN and TC, respectively).

4.2 ~~Modern p~~Pollen spectra and C and N in modern samples

Modern samples were characterized by 49 taxa, 18 and 31 identified at family and genus levels, respectively. Pollen sums varied between 300 and 387, whereas pollen counts including Cyperaceae and pterodophytes were between 322 and 472 palynomorphs. *Rhizophora*, Cyperaceae, Moraceae-Urticaceae, *Quercus*, *Pinus*, and Poaceae dominated these samples (up to 45%), whereas taxa such as *Typha*, *Mimosa*, *Desmodium*, *Inga*, and Ulmaceae were poorly represented (less than 5%). One sample from the northern sub-basin ~~resulted~~ was barren of pollen (sample 26, Fig. 1).

Avicennia and *Rhizophora* showed high percentages (up to 5 and 45%, respectively) towards the southern sub-basin of the lagoon (Figs. 1 and 3). Contrastingly, other taxa such as *Quercus*, *Myrica*, and *Pinus* decreased southwards. Compositional differences between the northern and southern sub-basins of the lagoon were also ~~evidenced~~ indicated by taxa that occurred only at the latter, such as *Desmodium*, *Inga*, and *Protium* (Figs. 1 and 3). Samples from the middle area of the lagoon (samples 12,13,14,17 and 18) (Figs. 1 and 3) contained the highest percentages of Cyperaceae and Moraceae-Urticaceae (25% and 30%, respectively), and minima of *Typha*, Asteraceae, and *Psychotria*. In the northern sub-basin

345 (Figs. 1 and 3), *Quercus*, *Pinus*, and Poaceae dominated the pollen spectra with abundances
346 above 10%.
347



348

349 Figure 3. Pollen diagram of selected taxa from mud-water interface samples from La
350 Mancha coastal lagoon. Ecological affinities after Lugo and Snedaker (1974), Ramwell
351 (1972), and Travieso-Bello (2000). Samples are ordered from South to North with samples
352 from the southern (northern) sub-basin highlighted in dark (light) grey.
353
354 TC content in modern samples varied between 3.1 and 12.3%, with mean and median of 4.9
355 and 4.4%, respectively. Although mean values for the northern and southern sub-basins
356 were not statistically differentiable (t = 1.66, p-value = 0.11), the northern sub-basin
357 consistently showed lower values (Fig. 3). Differently, individual fractions of C resulted

statistically differentiable, with a higher concentration of TOC in the southern sub-basin (3.56, p-value = 0.002) and a higher concentration of TIC in the northern sub-basin (t = -2.47, p-value = 0.023). TN range between 0.02 and 0.37% with mean and median of 0.23 and 0.24%, respectively (Fig. 3), with higher mean concentration in the southern subbasin (t = 5.54, p-value < 0.001). TC resulted statistically associated with TN, TIC, and TOC, although the magnitude of the correlation was substantially higher with the latter (Fig. 3). Whereas TIC resulted moderately associated only with TN, TOC was strongly associated with both TC and TN (Fig. 3).

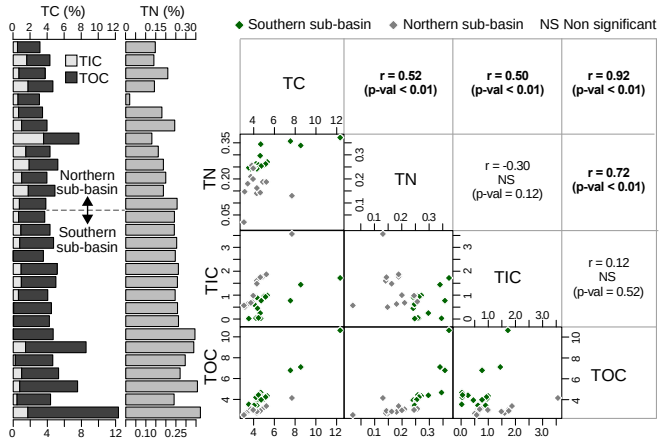


Figure 4. Content (%) of carbon and nitrogen in the modern samples of La Mancha coastal lagoon. Total C content (TC) discriminated into inorganic and organic fractions (TIC and TOC), and total N content (TN). Comparisons among sedimentary attributes are shown in the right side panels (biplots and correlation coefficients with their significance).

4.3 ~~Fossil pollen~~Fossil record

Fossil pollen types included 55 taxa classified into 24 families and 31 genera. Pollen sums varied between 300 and 349 grains per sample (average 306 grains), whereas pollen counts that included Cyperaceae and pterodophytes reached between 303 and 359 palynomorphs per sample (average 317). The highest abundances were shown by *Rhizophora*, Moraceae-Urticaceae, *Quercus* and *Pinus*, while the lowest abundances were shown by *Conocarpus, Inga, Bursera and Miconia.* From within the 55 identified taxa, only *Rhizophora*, Cyperaceae, *Typha*, Asteraceae, Chenopodiaceae, Moraceae-Urticaceae, *Alnus*, *Quercus*, *Pinus*, and Poaceae persisted throughout the entire record. The record was discretized into four main pollen zones (Fig. 4) to facilitate the description of the sedimentary sequence. Pollen zones were defined based on an inspection of the distribution of pollen percentages though time, aiming to identify time periods characterized by relatively stable pollen assemblages.

Pollen Zone I (from 1300 to 907 cm blf, c. 7840-6300 cal BP): The sediment showed TC concentrations between 1.84 and 4.78%, with mean of 2.54%, and TN concentrations between 0.06 and 0.20%, with mean 0.10% (Fig. 2). This zone showed high percentages of *Rhizophora* (up to 20%), Moraceae-Urticaceae (up to 50%), *Quercus* (up to 20%), *Pinus* (up to 50%), and Poaceae (up to 20%). Low percentages (less than 5%) were shown by *Avicennia*, Amaranthaceae, *Croton, Typha*, Asteraceae, Chenopodiaceae, *Mimosa, Inga, Acacia, Machaerium, Protium, Bursera*, Ulmaceae *and Miconia* (Fig.4).

Pollen Zone II (from 907 to 569 cm blf, c. 6300 - 5400 cal BP): The sediment showed highly variable concentrations of both TC and TN (Fig. 2). TC varied between 2.28 and 9.67% with mean of 4.6%, whereas TN varied between 0.09 and 0.43 with a mean of 0.19%. This zone was dominated by Cyperaceae (20%), *Croton* (10%), *Typha* (20%), Chenopodiaceae (15%), Moraceae-Urticaceae (50%), *Alnus* (~6%), Ulmaceae (10%), *Quercus* (20%), *Pinus* (50%) and Poaceae (20%). Percentages below 5% were shown by *Avicennia*, *Conocarpus*, Amaranthaceae, Asteraceae, *Mimosa*, *Inga*, *Machaerium*, *Protium*, *Bursera and Miconia* with less than 5%. The upper part of the zone was characterized by relatively low percentages of *Pinus* (~18%) and a substantial increase of Amaranthaceae, *Croton*, *Typha*, Asteraceae, Chenopodiaceae, and Cyperaceae (up to ~20%) (Fig. 4).

Pollen Zone III (from 569 to 280 cm blf, c. 5400 - 3700 cal BP): With lower variability, both TC and TN decreased substantially (Fig. 2). TC varied from 1.14 and 6.31% with mean of 2.45, and TN varied between 0.07 and 0.25% with mean of 0.12%. From 5400 BP *Rhizophora* abundances began to increase gradually, and *Avicennia* ~~showed~~ was less than 5%. *Pinus* reached the highest abundances throughout the record (up to 60%), while Amaranthaceae, *Croton*, *Mimosa*, *Inga*, *Machaerium*, *Bursera*, Alnus, Ulmaceae, Moraceae-Urticaceae, and *Miconia* showed their lowest percentages. Lastly, *Typha*, Asteraceae, and Chenopodiaceae showed abundances around 10% (Fig 4).

Pollen Zone IV (from 280 to 0 cm blf, c. 3700 cal BP - Present): TC and TN progressively reached high variable concentrations (Fig. 2). TC varied between 0.02 and 7.77% with mean of 4.45%, and TN varied between 0.01 and 0.36% with mean of 0.20%. Abundances of *Rhizophora* and *Avicennia* reached their highest values (up to 60% and 10%

respectively), and displayed an increasing trend towards the present. Amaranthaceae, *Croton*, *Typha*, Chenopodiaceae, *Myrica*, Ulmaceae, *Quercus*, and *Pinus* abundances decrease up to the present. Meanwhile *Acacia*, *Inga*, *Machaerium*, and *Protium* presented their highest abundances (up to 10%) (Fig. 4).

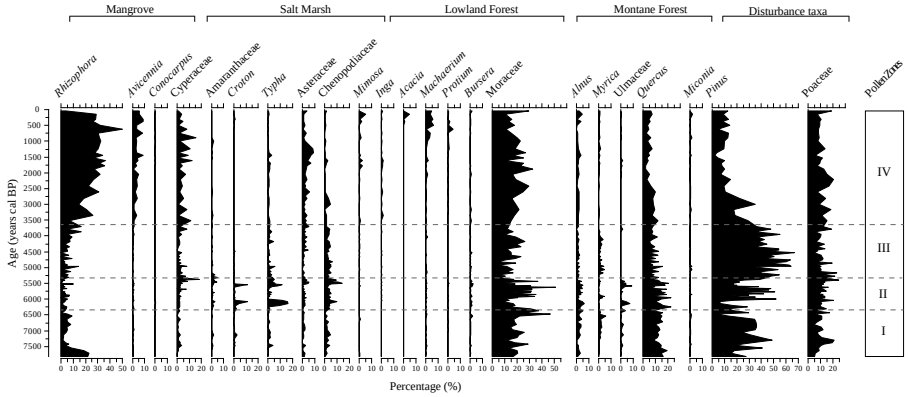


Figure 45. Fossil pollen diagram of selected taxa of core MAN15V from La Mancha coastal lagoon. (ecological affinities after Lugo and Snedaker 1974, Ramwell 1972, and Travieso-Bello 2000~~, and Castillo-Campos 2006~~).

4.4 Statistical analyses

The three-dimensional ordination of the modern and fossil pollen samples showed a stress of 0.144. Negative scores along Axis 1 characterized modern samples, whereas fossil samples were clearly divided into positive (negative) scores for samples older (younger) than ~ 5400 cal BP (Fig. 5 and 6.B). Along Axis 2, both modern and fossil samples were mostly located between –0.31 and 0.2, although fossil samples showed positive and

435 negative excursions (Fig. 5). NMDS Axis 3 was characterized by widespread scores for
436 fossil samples and almost exclusively negative scores for modern samples (Appendix 1).
437 The t-test for comparing NMDS scores of modern samples from the northern and
438 southern sub-basins yielded significant differences in terms of Axis 1 and 2, but non-
439 significant for Axis 3 (Table 2). Given the relatively flat behavior of Axis 2 and the lack of
440 significance of Axis 3 (Appendix 1), only the first axis of the ordination will be considered
441 for interpretations hereafter.
442
443 Table 2. Comparison of NMDS sample scores in the three axes for modern samples from
444 the northern and southern sub-basins, i.e scores from dense (D) vs. sparse (S) mangrove
445 areas. For the comparison of scores along each axis, t scores, degrees of freedom corrected
446 for variance differences between samples (d.f.), and p-value are shown.
447

Comparison	t	d.f.	p-value
Axis 1_D – Axis 1_S	-3.5184	18	0.0026
Axis 2_D – Axis 2_S	-2.7661	26	0.0103
Axis 3_D – Axis 3_S	1.3831	24	0.1796

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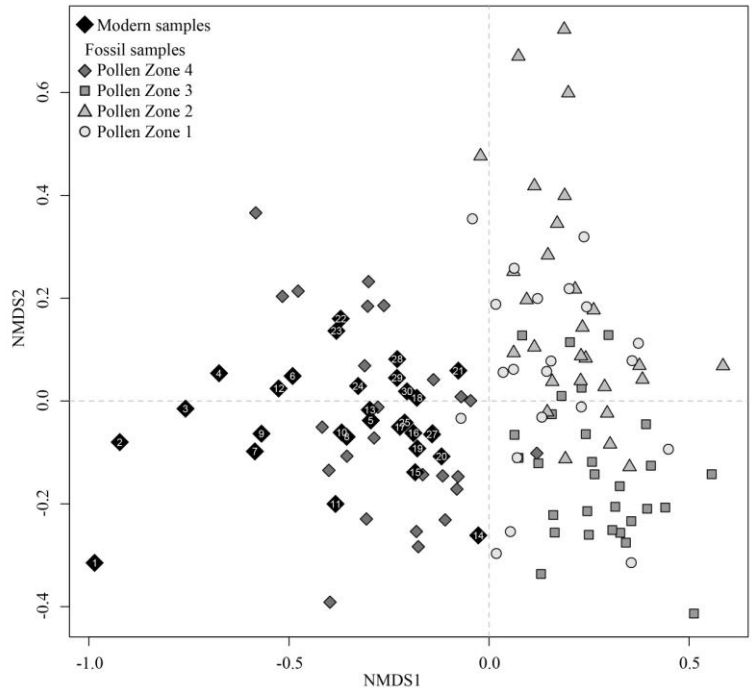

Figure ~~5~~6. Non-metric multidimensional scaling for modern and fossil pollen assemblages from La Mancha lagoon. Modern samples in black diamonds showing sample number, whereas fossil samples were symbol coded according to the declared legend.

5. Discussion

5.1 Modern ~~pollen spectra~~sediments of La Mancha coastal lagoon

Palynological composition of modern samples generally reflected the patterns of modern vegetation, incorporating vegetation elements from the surrounding mangroves and salt marshes (local vegetation), and nearby lowlands and highland forest (regional vegetation). Although the mangroves of La Mancha are dominated by *A. germinans* over *R. mangle* (Moreno-Casasola, 2006), modern pollen spectra were dominated by the latter (Fig. 3).

Given its pollination mechanism, *R. mangle* produces high amounts of pollen, dominating most of pollen spectra from mangrove forests. Contrastingly, *A. germinans* is an insect-pollinated species that produces low amounts of pollen (Hogarth, 2007), resulting in under-representation of the parental taxon in the pollen spectra where percentages as low as 5% implying an important share in the standing vegetation. However, the mean representation of *R. mangle* in modern samples from the densely mangrove-forested southern sub-basin (~25%) are low as compared to pollen spectra from stands dominated by this species which have been reported as high as 65% (e.g. Behling et al., 2001; Urrego et al., 2009). Although *C. erecta* and *L. racemosa* are components of the standing forest of La Mancha, they are not represented in the modern pollen spectra probably because of their low production, and also because of their distal position with respect to the sampled water body (~~Tovilla and De la Lanza, 1999~~Moreno-Casasola, 2006).

~~At~~ In the southern sub-basin of La Mancha, the high percentages of *Rhizophora* reflect the relatively good conservation statge of the mangroves (Moreno-Casasola, 2006), with the exclusive presence of taxa such as *Desmodium*, *Inga* and *Protium* indicating a well preserv~~ation of~~ed lowland vegetation as well (Franco-Gaviria et al., 2018). Pollen spectra from the northern sub-basin contained lower percentages of *Rhizophora*, and a substantial representation of regional pollen, possibly coming from the highlands of the catchment basin. ~~Through the last~~Over recent decades, the deleterious effects of human activities on mangrove cover have been more intense around the northern sub-basin of La Mancha lagoon (Lopez-Portillo et al., 2011; Moreno-Casasola, 2006), reflecting on pollen assemblages where the regional and disturbance elements are better represented (mainly Moraceae-Urticaceae, *Myrica*, *Pinus*, Poaceae, and *Quercus*) (Correa-Metrio et al., 2011;

Franco-Gaviria et al., 2018). Although *Rhizophora*, Moraceae-Urticaceae, *Pinus*, and *Quercus* do not dominate the shore vegetation of the most disturbed northern areas, they are represented by pollen percentages above 10 % each (Fig. 3), reflecting the sparse nature of mangrove forests over this area. This finding reflects the widely reported overrepresentation of these taxa in pollen spectra, derived from their high production of pollen and their long-distance pollen dispersal capacity, as reported for species of anemophyllous pollination (e.g. Correa-Metrio et al., 2013; Ellison, 2008; Hooghiemstra et al., 2006; Marchant et al., 2002).

Modern samples ~~resulted~~ were clustered in the NMDS (Fig. 5), implying more consistency among the modern pollen spectra than between modern and fossil samples. This finding demonstrates that the modern heterogeneity of the lagoon does not represent the ecological and environmental variability of the area over the last ~7800 years. Statistically significant differences between the NMDS Axis 1 scores of pollen assemblages from the two sub-basins demonstrate that density of mangrove forest cover can be identified though their pollen spectra. Overall, these findings ~~imply~~ indicate that i) pollen assemblages of La Mancha lagoon are systematically associated with physical and biological attributes of the region at a broad scale (regional vegetation), and ii) pollen spectra are highly sensitive to the modern environmental variability ~~that express~~ throughout La Mancha lagoon (local vegetation). Thus, as reported for other areas (e.g. Franco-Gaviria et al., 2018; Urrego et al., 2009; Urrego et al., 2010), modern pollen assemblages of our studied lagoon provide a robust framework for interpreting our fossil pollen sequence.

Higher concentrations of TOC and TN in the southern sub-basin were probably a result of differences in surrounding vegetation and energy of the depositional environment.

More vigorous vegetation in the southern sub-basin would produce higher amounts of organic matter rich in TOC and TN, whereas the lower energy of the depositional environment would prevent resuspension and, therefore, further oxidation of the sediments (Meyers, 1997). Differently, TIC resulted higher in the northern sub-basin, probably reflecting both higher contribution of marine particulate suspended matter and more oxidation of organic components (Bouillon et al., 2003). Overall, C and N analyses are consistent with higher organic matter storage in the sediments of the lagoon where mangrove forests are well preserved. The relationships that were found between the different components of C and N demonstrate that in the modern setting of La Mancha, TOC is the main component of TC. Although these relationships cannot be extrapolated to the fossil record, they demonstrate that TN is a good proxy for organic matter, and therefore it is used to offer further support to our pollen-based reconstruction of past environmental dynamics.

5.2 Vegetation history of La Mancha Lagoon

The pollen record of La Mancha lagoon reflects the complexities associated with the multiple factors that have intervened in the development toward the modern biotic and abiotic systems. Whereas highly variable abundances of regional vegetation suggest variability in freshwater input by precipitation and tributaries to the lagoon system, pollen from mangroves together with herbaceous vegetation offer insights into the successional patterns and development of the local vegetation (Urrego et al., 2013; Urrego et al., 2018). Additionally, the constant presence of marine shells through the sedimentary record (Fig. 2) demonstrates a permanent marine influence through the last ~7,800 year. Together, these

indicators illustrate the intimate interaction between sea levels and regional fresh water inputs (precipitation, sediments) that ultimately regulates the colonization, establishment, and development of mangrove ecosystems in the area. According to our pollen and geochemical data, the history of the vegetation that surrounds the lagoon and therefore the regional environmental history could be summarized in four main stages that will be discussed below.

From c.7800 to 6300 cal BP: sea-water flooding of valleys

Through this time period, the mud-water interface was between 13 and 9 m below the modern surface, which today is at sea level. At the same time, average sea level was between 9 and 5 m below modern. The difference between mud-water interface depth and sea level can only be accounted by lagoon water depth, which ~~The comparison of our age-depth model with the reported increase of regional sea levels suggests that throughout this time period the mud-water interface~~ was ~~around 6~~~ 4 m below sea level (Fig. 6A). La Mancha Hill, an andesitic rock of Neogene origin (~~García-Gil~~Moreno-Casasola, 2006; Geissert Kientz, 1999) (Fig. 1), probably acted as a barrier that protected the depositional environment from the erosive energy of the waves and winds. Through this period, even though sedimentation rates at La Mancha (~3.04 mm/year) were lower than the inferred rate of sea-level increase, they are among the highest through the record. High rates of both regional sea-level rise and sedimentation at La Mancha are likely a result of the regional geologic instability that characterized the conformation ~~processes~~ of the modern Gulf of Mexico in its final stages, up to 5000 cal BP (Davis, 2011~~; Pirazzoli, 1990~~). As sea level increased through the deglaciation and the early Holocene, sea-water flooded coastal plains and valleys at a speed that surpassed the accumulation of continental sediments. Thus, the

lacustrine basin of La Mancha was probably deeper than modern ~~and bucket shaped~~, impeding the establishment of mangrove forests (Fig. 6C). A peak of *Rhizophora* from the bottom of the record to ~7500 cal BP (Fig. 4) probably shows the colonization of mangroves during the initial stages of the lagoon and the sea-water flooding, which were subsequently displaced by the formation of a deep-water body.

In México, *Pinus* populations thrive under early post-disturbance successional stages, or under conditions that are not optimal for other taxa (Metcalfe et al., 2000; Ramirez-Marcial et al., 2001). Thus, the persistence of *Pinus* in high percentages from the bottom of the record to ~6500 cal BP (Fig. 5) indicates that regional conditions were likely dry, an interpretation that is further supported by the lowest concentrations of TN (Fig. 7) and therefore of organic matter. These dry conditions probably played a central role at maintaining sedimentation rates that did not offset sea-level rise, impeding the establishment of mangrove forests, as demonstrated by the NMDS Axis 1 scores that were outside the envelope defined by modern samples (Fig. ~~6B~~7C).

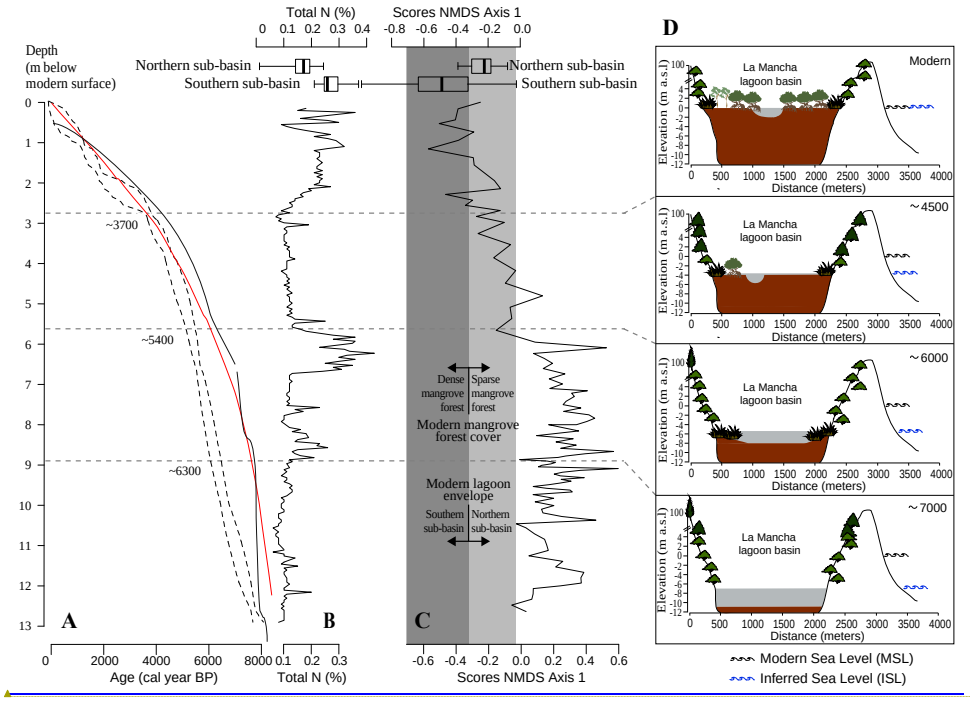

Figure ~~6~~7. Environmental history of La Mancha Lagoon through the last 7,800 years. **A.** Age-depth model of core MAN15V from La Mancha Lagoon (dashed lines show 95% confidence interval), compared with sea level rise curves for the Caribbean (red line, Toscano and Macintyre, 2003) and the northern Gulf of Mexico (black solid line, Milliken and Anderson, 2008). **B**. Sedimentary total nitrogen content (%); boxplots illustrate total nitrogen in modern samples form the northern (up) and southern (down) sub-basins of the lagoon (whiskers show minimum and maximum scores). **C**. NMDS Axis 1 scores through time; boxplots illustrate scores of modern samples ~~form the northern (up) and southern (down) sub-basins of the lagoon (whiskers show minimum and maximum scores)~~; scores of the modern environmental envelope represented by modern samples are highlighted in grey; scores of the interquartile range of samples from the well preserved southern sub-

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basin are in dark grey. ~~C~~D. Schematic development of La Mancha Lagoon, illustrated at ~7,000, 6000, 4,500 cal BP, and Modern.

From c. 6300 to 5400 cal BP: development of lagoon shores

Whereas the rate of sea-level rise started to decline through this period, sedimentation rates at La Mancha remained high (3.86 mm/yr, Fig. 6). This phenomenon could be explained by two critical factors: i) following the reported deceleration of sea-level rise at ~7000 cal BP (Toscano and Macintyre, 2003), sand bars started accumulating at the mouth of coastal lagoons (Davis, 2011), providing a more stable plain for sediment accumulation at La Mancha; and ii) a substantial decrease in the percentages of *Pinus*, and an increase of montane forest taxa (e.g. *Alnus*, *Quercus*, and Ulmaceae) indicate wetter conditions that would be in turn associated with higher river sediment discharge. These regional wetter conditions could be related to the final stages of the Holocene Thermal Maximum, which was in general characterized by higher than present precipitation and temperature in the Northern Hemisphere (Renssen et al., 2009).

The lagoon became shallower, and the development of muddy shores is evidenced by high percentages of salt marsh vegetation (Fig. 5), and high accumulation of organic matter revealed by the increasing TN (Fig. 7B). This state of local vegetation and the high accumulation of organic matter suggest ~~, a process also favored by the slowing rates of sea level rise (Fig. 6A), with dominance of pollen spectra by salt marsh taxa indicating also more tidal influence (González et al., 2010; Ranwell, 1972). T~~the closing of the ephemeral

mouth, ~~was~~ probably caused by lower energy associated with the shallowing of the lagoon, together with the intensification of the wind currents, and sea level changes reported for the Gulf of Mexico and the Caribbean (Balsille and Donoghue, 2004; González and Dupont, 2009; Urrego et al., 2013; Wooller et al., 2007). Pollen spectra suggest the early stages of a successional pattern of mangrove vegetation associated with the marine transgression, although NMDS Axis 1 sample scores demonstrate that mangrove forests were not established yet near the location where the core was retrieved.

From c. 5400 to 3700 BP: A regional drought

Whereas the rate of sea-level rise continued to decrease, relatively high sedimentation rates were evident in La Mancha sequence up to ~5000 cal BP, when apparently the rates ~~deposition~~ of sediment~~s~~ deposition in the lagoon and those of sea level rise became similar (Fig. 6A). Such equilibrium between sediment deposition and sea-level rise implies the definition of a coastal erosive baseline that ~~,~~allowed the deposition of sand in the coast by the northerly currents during the dry season, creating the sandbar that dams the lagoon. Differently, during the wet season, the fluvial input would have the capacity to erode the sandbar, opening the direct contact between the lagoon and the sea and, thus, resulting in the modern seasonal flood cycle ~~of the lagoon~~. During the dry season, the coastal bar would be closed by the action of the waves and the prevailing winds, whereas during the rainy season the bar would be opened by the energy of the fresh water discharge. The lagoon thus became a shallow water body (z_{max} ~1 m) mostly protected from the energy of the waves by La Mancha hill (Fig.1), and subjected to seasonal tidal and climatic fluctuations.

From c. 5400 to 3700 cal BP, the recurrent drainage of fresh water into the sea probably created a series of ~~canals~~ channels giving the lagoon a physiography very similar

to modern. However, according to the NMDS scores, vegetation at that time resembled the northern sub-basin today (Fig. 6B), an area characterized by poorly developed sparse mangrove stands. Thus, vegetation assemblages from this period were a result of suboptimal environmental conditions for mangrove forest development. High percentages of *Pinus* (up to 60%) through this period suggest that there was a regional drought in place, which likely maintained high substrate salinity by reducing freshwater river discharge to the lagoon. Thus, local vegetation consisted of a mixture of sparse mangrove trees with some salt marshes species, and a slow increase of mangrove pollen because of the prevailing dry conditions (Fig. 4). Although anthropogenic influence cannot be discarded as a plausible explanation for the sparse mangrove vegetation, the inference of a regional drought is supported by similar reports from Lake Petén Itzá between ~ 4500 up to ~3000 cal BP, Lake Tzib (Quintana Roo) at ~3500 cal BP (Carrillo-Bastos et al., 2010; Mueller et al., 2010), and also in the Cariaco Basin record, with a trend from ~5400 up to the present (Haug et al., 2001). Furthermore, the abrupt decrease of TN and its linear trend towards even lower concentrations (Fig. 7B) evidence rather oxidizing conditions, an environmental process that is difficult to explain from the perspective of human occupation.

From c. 3700 cal BP to Present: the establishment of modern mangrove forests

Mangrove pollen taxa showed the highest percentages (Fig. 5), ~~which~~ reflect~~ed~~ing an environment of relative stability where the exchange of saline and fresh water, and the input of sediments were balanced, producing an increase of mangrove forest biomass (Krauss et al., 2008). These conditions provided consolidated clay sediments, where as indicated by the NMDS scores, mangrove forests developed into mature forest stands of *Rhizophora* and *Avicennia*. Increasing concentrations of TN (Fig. 7B) indicate high

accumulation of organic matter probably associated with the establishment of the mangrove forest (Bouillon et al. 2003). Sea level continued to increase at slower rates (Balsille and Donoghue, 2004) that were matched by the rate of sediment accumulation in La Mancha (~0.92 mm/yr on average). These more stable conditions for coastal ecosystems have been reported for other localities in the Caribbean coinciding with other records (Urrego et al., 2013), where mangrove forests developed under a relatively stable sedimentation rate (1.09 to 0.89 mm/yr).

Pinus and salt marsh pollen in La Mancha showed substantial decreases caused by wetter conditions and higher representation of local mangrove pollen, implying a lower regional influence on pollen spectra, and the continuation of the successional processes that led to the establishment of the mangrove forest (González and Dupont, 2009). At this stage, the lagoon seems to have reached its modern configuration, with influences from local processes like the annual opening of the ephemeral mouth, fluctuating floods of salt water, input of fresh water from the streams, and anthropogenic activities (Moreno-Casasola, 2006). Indeed, the sharp decrease of *Rhizophora* is likely reflecting the terrestrialization of the cored site, which today is occupied by an *Avicennia germinans* forest that floods only when the ephemeral mouth is closed and the lagoon reaches its maximum water level through the year. This latter observation is further supported by the high variability of TN concentrations towards the top of the record.

6. Conclusion

The sedimentary record of La Mancha lagoon encompasses the history of ~~the~~ local and regional environmental conditions through the last ~8,000 years, including the

establishment of modern mangrove forest along the coast of Veracruz. The record shows the regional context under which the coastal lagoon formed, showing the transformation of the lagoon from a water body with permanent communication with the sea to the modern seasonally closed system. When sea level rise rates were higher than the rates of sediment infill of the lagoon's basin, the depositional environment was under sea level and pollen assemblages were dominated by regional taxa. The ecological succession towards the establishment of mangrove forest started at ~6,300 cal BP, but mangrove forests were sparse, resembling those of the modern northern sub-basin because of two main reasons: i) the water column was relatively deep and sedimentary plains for mangrove establishment were likely narrow, and ii) a regional drought lasting from ~5400 to 3700 BP probably caused extremely high substrate salinity that impeded mangrove forests expansion. Dense mangrove forests ~~a~~like those that occupy the southern sub-basin today established around ~3500 BP, and have dominated the area ever since.

The ~~pairing~~ matching of lagoon sediment and sea levels at ~4000 cal BP was likely associated with the development of the seasonally open mouth. This pairing of lagoon sedimentary accumulation and sea levels defined the latter as the base level for erosion, allowing the accumulation of material during the dry season, and therefore the formation of a damming bar, which would eventually be ~~eventually~~ open during the rainy season owing to the increased freshwater discharge. Concomitant to this process would be the linear erosion of ~~canals~~ channels through the sedimentary deposit, conforming the modern geomorphology of the area. The establishment of the mangrove forest implied a substantial increase of sedimentary organic matter, highlighting the role of these ecosystems at storing carbon. Overall, our record demonstrates the complexity of the interactions between local

and regional factors in the development and evolution of both coastal geomorphology and ecosystems.

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Holocene establishment of mangrove forests in the western coast of the Gulf of Mexico

Cordero-Oviedo, C[a]., A. Correa-Metrio[b,*], L.E. Urrego[c], G. Vázquez-Hurtado[d], M. Blaauw[e], J. Escobar[f,g], J.H. Curtis[h]

[a] Posgrado en Ciencias de la Tierra, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México 04510, ceciliacorderoviedo@gmail.com, [b] Instituto de Geología, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México 04510, acorrea@geologia.unam.mx, [c] Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Sede Medellín A.A. 568 Medellín, Colombia, leurrego@unal.edu.co, [d] Instituto de Ecología, A.C. Carretera antigua a Coatepec 351, El Haya, Xalapa 91070, Veracruz, México, gabriela.vazquez@inecol.mx, [e] School of Natural and Built Environment, Queen's University Belfast, Belfast, United Kingdom, maarten.blaauw@qub.ac.edu, [f] Departamento de Ingenieria Civil y Ambiental, Universidad del Norte, Km 5 Via Puerto Colombia, Colombia, jhescobar@uninorte.edu.co, [g] Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Panama, [h] Department of Geological Sciences, University of Florida, Gainesville, FL, 32611, USA, curtisj@ufl.edu

***Corresponding autor:** Alexander Correa-Metrio, acorrea@geologia.unam.mx

Abstract

The successful establishment of mangrove ecosystems depends on an intricate network of interactions among physical and biological factors that are highly dynamic through time. At millennial to centennial time scales, regional climates, sea levels, and local geomorphology

play critical roles in the establishment of mangroves. Whereas fluvio-marine dynamics define coastal sedimentary settings, regional precipitation and freshwater input modulate salinity and seasonal flooding patterns. We analyzed a ~7800-year-old, continuous sedimentary record from the western coast of the Gulf of Mexico to shed light on regional biophysical coastal processes and the history of the mangroves that occupy the region today. We used a systematic sampling of mud-water interface sediments to generate a modern reference frame for interpreting fossil pollen assemblages. Our results indicate that the cored location that is currently approximately at sea level, was below sea level from ~7800 to 4000 calibrated years before present (cal BP). The establishment of dense mangrove stands took place around 3700 cal BP, when regional sea levels stabilized, resulting in a substantial increase of organic matter and therefore carbon stored in the sediments. However, the mangrove ecological succession that started at ~6000 cal BP was interrupted by a regional drought that extended from ~5400 to 3700 cal BP. From 3700 cal BP to Present, the lagoon has been characterized by relatively stable both substratum and sea level, that together have facilitated the establishment of mangrove forests. Overall, our record demonstrates the complexity of the interactions between local and regional factors in the development and evolution of both coastal geomorphology and ecosystems.

Keywords: coastal environment; Gulf of Mexico; Holocene; mangroves; sea-level changes; pollen analysis

1. Introduction

Mangrove ecosystems are a large component of tropical and sub-tropical coastal landscapes. Occupying intertidal zones (Lugo and Snedaker, 1974), they regulate the relationship between continental discharge of sediments and water and sea level (Ellison, 1989). The main engineers of these ecosystems are a reduced group of plant species physiologically adapted to brackish-to-saline substrates (Ball, 2002; Vovides et al., 2014). The establishment of mangrove forests creates the conditions for complex food webs that incorporate marine and continental components. The entire mangrove ecosystem is fundamental for providing products and ecological services, resulting in direct and indirect uses by human populations, mainly fuelwood, fisheries, sediment trapping, and carbon storage (Bouillon et al., 2008; Feller et al., 2017; Méndez et al., 2007; Ward et al., 2016).

Although they represent one of the most important carbon sinks worldwide (Bouillon et al., 2008), together with coral reefs and tropical forests, mangroves are among the most endangered modern ecosystems (Valiela et al., 2001). It has been estimated that through the last two decades of the 20th Century, 35% of the global mangrove area had been lost mostly because of direct and/or indirect anthropogenic causes (FAO, 2007). The main human-related causes of mangroves loss are the conversion to aquaculture and agriculture, urbanization, and pollution (Feller et al., 2017; Gilman et al., 2008; Thorhauga et al., 2017), which in Mexico have translated in a net loss ~240 ha/year through the last decades (Hamilton and Cassey, 2016). The rapid rate at which these threats to mangrove ecosystems are growing highlights the need to understand them in the context of their natural history and the intricate network of factors that interact to facilitate or impede their colonization and establishment.

A wide variety of factors interact to create the specific conditions under which mangrove communities thrive and persist through time (Gilman et al., 2008). Healthy vigorous mangrove forests, and therefore ecosystems, depend on a delicate balance between marine influences and freshwater and sediment input from continental areas acting upon specific geomorphologic settings (Lugo and Snedaker, 1974; Soares, 2009). Whereas marine influences on mangrove ecosystems materialize through tidal regimes and sea level changes that define baseline for erosion and accumulation of sediments, regional climates and vegetation cover over the mainland control continental discharge of freshwater and sediments along the coast. Thus, through the Holocene, changes in precipitation, vegetation cover, geomorphologic dynamics, and sea levels have probably led to high environmental variability over the intertidal areas (Geissert Kientz, 1999). In the Gulf of Mexico and the Caribbean, regional sea levels have progressively risen since the deglaciation (Milliken and Anderson, 2008; Toscano and Macintyre, 2003), whereas annual precipitation has shown a wide variability associated with extraterrestrial forcings (e.g. solar activity and orbital cycles, Haug et al. 2001, Hodell et al. 2001) and higher frequency processes associated with complex internal systems (e.g. El Niño-Southern Oscillation, Moy et al. 2002). The balance between fluvial loads and sea-level rise modulates local geomorphologic and sedimentary processes, defining the formation of either depositional or erosional environments the balance of which is in turn critical for the establishment and persistence of mangroves (Parkinson et al., 1994). Indeed, modern net losses of mangrove cover have been widely associated with sea-level rises along unprotected coasts (Suárez et al., 2015). Thus, the definition of the context that led to the development of modern mangrove forests would provide important clues for identifying the limits of environmental pressure that these ecosystems can endure.

Sedimentary deposits that accumulate in coastal lagoons provide a natural record of the evolution of coastal landscapes through time. Understanding the natural development of mangrove ecosystems and the main factors involved in the process would give insights into the threat level that coastal zones face given modern environmental change (Lopez-Portillo et al., 2011; Thom, 1967). Here we use the pollen record of a 13-m-long ~8,000-year-old sedimentary sequence retrieved from La Mancha Lagoon, State of Veracruz, Mexico, to reconstruct the history of the local vegetation through the Holocene. By analyzing the history of vegetation assemblages as reflected by fossil pollen spectra, we aim to answer the following questions: i) what has been the role of sea-level rise and precipitation variability through the Holocene in the establishment and persistence of mangrove forests in the west coastline of the Gulf of Mexico? ii) when did the barrier-lagoon systems of the region consolidate in the context of Holocene environmental variability?

2. Study Area

La Mancha lagoon is located in the State of Veracruz, Mexico, on the western coasts of the Gulf of Mexico (19.579 N°, 96.387 W°, Fig. 1). With a north-to-south length of 3 km, the lagoon has an area of ~1.35 km^2 distributed in two sub-basins separated by a strait located near the center of the water body (Fig. 1). Whereas the southern sub-basin is exposed to permanent freshwater input from the Caño Grande River that drains water from a basin of almost 2,500 km^2, the northern sub-basin more exposed to tidal influence through an ephemeral mouth that communicates seasonally with the sea (Fig.1) (Lankford, 1977; Moreno-Casasola, 2006). During the dry season, a sand bar accumulates closing the estuarine mouth and causing a damming of continental freshwater. With the onset of the

rainy season, freshwater starts to accumulate, eventually breaking the sandbar, opening the mouth, and creating a direct connection with the sea (Moreno-Casasola, 2006). Thus, lagoon dynamics are intimately linked to regional climate that is warm (temperatures from 22 to 26 °C), with an annual mean precipitation of 1222 mm, with 85% of the annual value falling between June and October (Fig. 1) (Servicio Meteorologico Nacional, 2018). The dry season is especially pronounced between December and April with mean monthly precipitation below 20 mm, while November and May are characterized by a mean precipitation around 50 mm. By the end of the summer and early autumn, the area is exposed to tropical cyclones, although their incidence is relatively low compared with other areas of the Gulf of Mexico (Moreno-Casasola, 2006).

La Mancha lagoon belongs to a geomorphic unit known as the Low Cumulative Plain that formed during the Quaternary (Geissert Kientz, 1999), allowing deposition of clayey-silt sediments. The lagoon formed at the margin of a volcanic mountain range that interrupts the coastal plain of the Gulf of Mexico (Geissert Kientz, 1999; Fig. 1). The current morphology of the area has been mostly shaped by Quaternary dynamics, going from an empty deep basin during times of sea-level low stands to a depositional coastal plain during times of sea-level high stands (Geissert Kientz, 1999; Kjerfve, 1994). The mountain ridge that connects La Mancha Hill with the adjacent western mountains divides La Mancha lagoon into two contrasting sub-basins (Fig. 1). Differences in freshwater input, marine influence, and energy of the sedimentary environments have created two clearly distinct environments for mangrove forests, which today occupy ~3.55 km^2 around the lagoon.

Regional tides are mixed, mostly diurnal and of low amplitude (highest and lowest tidal levels at 22 cm and -30 cm from average sea level, respectively), preventing the

formation of tidal currents. This feature together with the permanent input of fresh water and the sheltering of the lagoon from the energy of the waves by La Mancha Hill (Fig. 1) have probably played a critical role in maintaining the morphology of the lagoon, avoiding the formation of tidal mudflats, marshes, and/or estuaries (Geissert Kientz, 1999). Over recent decades, progressive loss of depth of the lagoon because of sediment accumulation suggests that sediment input surpasses local erosion (Moreno-Casasola, 2006), although this might not have been the case through the entire history of the area.

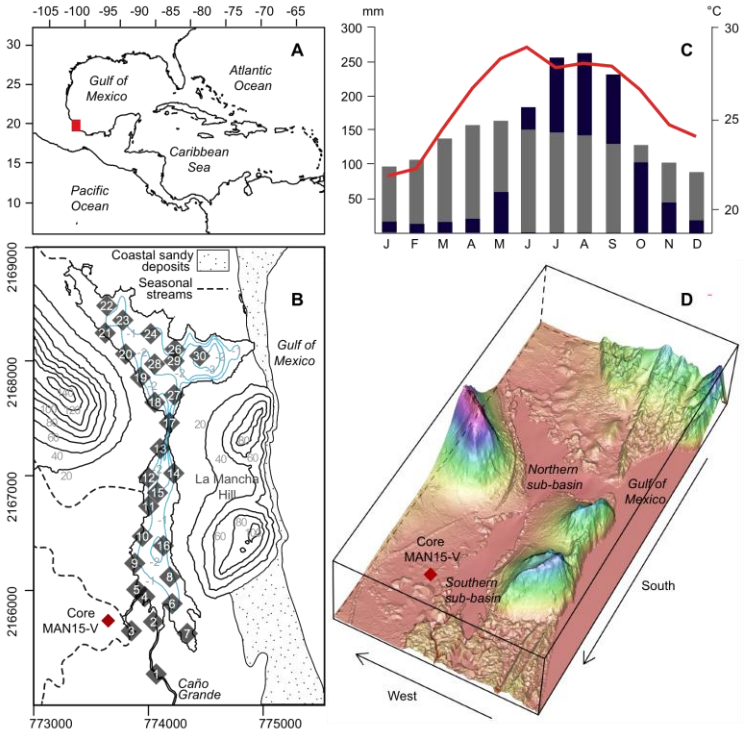


Figure 1. Study area. A. Location of La Mancha lagoon in the continental context. B. Locations sampled for modern and fossil sediments in the local context of La Mancha coastal lagoon; elevation contours are shown in increments of 20 m asl (solid black lines), whereas a basic bathymetry based on field observations is shown as blue contours. C. Monthly precipitation (blue bars), evapotranspiration (gray bars), and monthly mean

154 temperature (black line with dots) at La Mancha Meteorological Station (Servicio
155 Meteorologico Nacional, 2018) D. Topographic representation of La Mancha coastal
156 lagoon.
157
158 Pollen assemblages contained in sediments reflect parental vegetation and are
159 therefore useful for reconstructing environmental dynamics through time (e.g. Carrillo-
160 Bastos et al., 2010; Urrego et al., 2009; Urrego et al., 2018). Given the regional
161 geomorphology, the large size of the catchment basin of Caño Grande River, and the
162 proximity to high mountain ranges, the pollen spectra of sediments from La Mancha lagoon
163 contains regional and local taxa (Moreno-Casasola, 2006; Travieso-Bello, 2000). Whereas
164 the former are transported by water and wind currents, the latter are produced by *in situ*
165 vegetation (Hooghiemstra et al., 2006). Regional elements come mostly from montane
166 forests that dominate the regional highlands (Rzedowski, 2006; Williams-Linera, 2002) and
167 are characterized by wind-pollinated taxa with long-distance pollen dispersal (e.g. *Alnus*,
168 *Myrica*, Ulmaceae, *Quercus*, and *Pinus*), which tend to be overrepresented in the pollen
169 spectra. From within these allochthonous elements, *Pinus* is worth noticing because of the
170 opportunist nature of most of the parental species (Richardson, 1998), which results in a
171 high representation of this taxon in pollen spectra when environmental conditions are
172 suboptimal for other arboreal elements (e.g. during drughts, Correa-Metrio et al., 2013).
173 Local elements of the pollen spectra are in turn associated with two main vegetation types,
174 namely lowland and mangrove forests. The hills that surround the lagoon reach heights up
175 to 300 m asl and are mostly occupied by species of *Desmodium, Inga, Machaerium*,
176 *Psychotria, Protium, Bursera,* Moraceae-Urticaceae and *Acacia*. The salt marshes, coastal
177 dunes, and beaches that characterize flood plains are mainly dominated by species of

178 Cyperaceae, Amaranthaceae, *Typha*, Asteraceae, Chenopodiaceae, *Mimosa* and *Croton*.
179 These vegetation types can be associated with the distal part of a marine transgression
180 plain, or be related to the first stage of a progradational pattern indicative of a typical
181 ecological succession on intertidal habitats (González and Dupont, 2009).
182 The edges of the lagoon are occupied by species typical of mangrove forests,
183 *Rhizophora mangle, Avicennia germinans, Conocarpus erectus* and *Laguncularia*
184 *racemosa* (Travieso-Bello, 2000). The interplay of these species is modulated by their
185 differential adaptation to the changing environmental conditions along a salinity gradient,
186 which in turn defines the structure and composition of the forest (Lugo and Snedaker, 1974;
187 Travieso-Bello, 2000; Urrego et al., 2009). Thus, these forests are highly sensitive to
188 changes in sea-level, coastal progradation and/or erosion at different time scales (Ellison,
189 2008). Mangrove forest species are adapted to specific environmental conditions, with *R.*
190 *mangle* tolerating high inundation levels, strong wave energy and shorter distances to the
191 sea, *A. germinans* thriving in more saline environments, hurricane-disturbed or
192 experiencing severe droughts, *L. racemosa* being restricted to average minimum
193 temperatures over 15.5 ºC and successional processes triggered by anthropogenic
194 disturbance, and *C. erectus* being tolerant to higher sediment pH typical of supra-tidal
195 waters close to well drained forests (González et al., 2010; Hogarth, 2007; Urrego et al.,
196 2009; Urrego et al., 2010).
197 Regional human occupation has been reported since at least ~4,600 BP, and the
198 lagoon has apparently been an important source of resources for human populations
199 (Moreno-Casasola, 2006). This factor has exerted direct pressure on the mangrove forest
200 through deforestation for timber and fuel wood extraction, and more recently in the
201 interruption of surface and subsurface flows in the by infrastructure of the oil industry.

These local factors have been especially harsh on the northern sub-basin, where only sparse remnants of the mangrove forest survive today. Thus, whereas vigorous mangrove forests surround the southern sub-basin, the northern sub-basin is occupied by highly disturbed vegetation including sparse mangrove remnants. Regionally, growing human population and the parallel development of infrastructure apply further pressures to coastal ecosystems through pollution, accelerated erosion, increasing sea level, among other elements (Gilman et al., 2008).

3. Methods

3.1 Field work and laboratory analysis

In autumn 2015, a 13-meter-long core was recovered from the southern part of La Mancha coastal lagoon (core MAN15V, Fig. 1), under an *A. germinans* stand, using a modified Livingston piston corer (Colinvaux et al., 1999). The core was longitudinally sectioned, stratigraphically described, and stored at ~ 4ºC to preserve the sedimentary evidence. The chronological control of the sedimentary sequence was based on eight accelerator-mass-spectrometer (AMS) radiocarbon dates of bulk sediment, given that no other material such as macrofossils or charcoal could be found. Radiocarbon dates were calibrated to years before present (hereafter cal BP) using the IntCal13 curve (Reimer et al., 2013), and calibrated dates were used to build a Bayesian age-depth model using Bacon (Blaauw and Christen, 2011). The core was subsampled every ~ 12.5 cm for pollen analysis, aiming at a temporal resolution of ~75 years between contiguous samples. A total of 104 samples were processed for pollen analysis using standard pollen extraction techniques (Faegri and Iversen, 1989). Samples were analyzed under transmitted-light microscope at

magnifications of x400 and x1000, aiming to reach a minimum pollen sum of 300 pollen grains. Grains of the family Cyperaceae and pteridophytes spores were excluded from the pollen sum, although they were counted and included in the interpretation. Pollen counts were transformed into percentages of the pollen sum and a stratigraphic pollen diagram was constructed.

Pollen taxa were classified into five groups according to their modern ecological affinities (ecological affinities after Lugo and Snedaker 1974, Ranwell 1972, Travieso-Bello 2000): i) mangroves represented by *Rhizophora mangle*, *Avicennia germinans,* and *Conocarpus erectus*; although *Laguncularia racemosa* is an important component of the local mangrove forests, it was not found in the pollen spectra; ii) salt marsh vegetation represented by Cyperaceae, Amaranthaceae, *Croton*, *Typha,* Asteraceae, Chenopodiaceae, and *Mimosa*; iii) lowland forest represented by *Inga*, *Acacia*, *Machaerium*, *Protium*, *Bursera*, and Moraceae-Urticaceae; iv) montane regional forests represented by *Alnus*, *Myrica*, Ulmaceae, *Quercus*, *and Miconia*; and v) disturbance taxa represented by *Pinus* and Poaceae; these latter taxa were classified as representatives of disturbance because in Mexico they are distributed along environments unfavorable to vegetation development, usually associated with either natural or anthropogenic causes (Franco-Gaviria et al., 2018; Rzedowski, 2006). High abundances of *Pinus* pollen have been reported for areas subjected to dry conditions and/or regimes of high disturbance (Correa-Metrio et al., 2013; Metcalfe et al., 2000), mostly associated with early succession colonizers (Ramirez-Marcial et al., 2001). Meanwhile, although Poaceae pollen is characteristic of successional processes of supratidal plains (Bush, 2002; Urrego et al., 2013), it is also found in pollen assemblages

247 from all Mexican vegetation types, usually associated with disturbance (Correa-Metrio et
248 al., 2013; Franco-Gaviria et al., 2018).

249 The fossil pollen record was complemented by sampling 30 locations
250 homogeneously for modern mud-water interface (15 samples from each sub-basin)
251 distributed across the water body, using an Ekman dredge. This sampling was meant to
252 cover the variability of the modern pollen spectra (Fig.1), especially the differences
253 between depositional environments of the two sub-basins. Samples were treated and
254 analyzed using the same techniques as the fossil samples.

255 Total both C (%TC) and N (%TN) were measured in fossil samples every 5 cm
256 along the core and in modern samples. For this purpose, samples were freeze dried and
257 crushed, and subsequently analyzed using a Carlo Erba NA1500 CNS elemental analyzer.
258 Additionally, coulometric titration was used to determine carbonate carbon (%TIC) in
259 modern samples, allowing the estimation of organic carbon (%TOC). The discrimination of
260 TC into TIC and TOC in modern samples was used to infer the relationship between these
261 two carbon sources in the system of La Mancha lagoon.

262

263 *3.2 Statistical Analysis*

264 A non-metric multidimensional scaling ordination (NMDS) was applied on pollen relative
265 abundances, including both modern and fossil samples. The ordination was performed to
266 summarize the temporal variability of the pollen spectra, and to evaluate vegetation
267 temporal dynamics in the context of the modern lagoon. This technique ordinates samples
268 on a *k*-dimensional space defined *a priori* by the analyst, aiming to maintain the original

topologic relationships among samples (Legendre and Legendre, 2012). Although two-dimensional ordinations are readily used, we selected three dimensions to produce a relaxed ordination where the affinity among pollen spectra can manifest more freely. We used the Bray-Curtis metric to estimate dissimilarity among samples, a metric that relies more on compositional data than on the abundance of individual taxa and has been proven monotonic to ecological distance (Faith et al., 1987).

Modern samples were classified into southern and northern sub-basins as representative of dense and sparse mangrove forests, respectively. Whereas the northern sub-basin has direct contact with the sea through the ephemeral mouth, which creates a more energetic environment, and has been subjected to important human disturbances and modifications resulting in sparse mangrove cover, the southern sub-basin is more influenced by the entrance of the river and is occupied by a well-developed dense mangrove stand. Thus, pollen spectra from these two sub-basins should reflect contrasting mangrove-forest cover conditions, and their relative oceanic and fluvial influences. The statistical significance of the difference between NMDS sample scores of the two sub-basins were tested using a two-sample t-test (Zar, 1999). TIC, TOC, TC, and TN content in modern samples were compared using Pearson correlation coefficient, whereas comparisons of concentrations between the northern and southern sub-basins were also compared using two-sample t-test (Zar, 1999).

4. Results

4.1 Stratigraphy and chronology of the sedimentary record

Sediments from the La Mancha coastal lagoon were mostly brownish, shelly clays with low content of organic material, and some intermissions of brownish silt with shell fragments and organic material (Fig. 2A). From the base of the core up to 1200 cm below lagoon floor (blf hereafter), the sediments were brown shelly clay, while from 1200 to 663 cm blf the color turned into a light brown matrix (clay and silt) with shell fragments and carbonates. From 663 to 615 cm blf the clayey sediment was brown with light brown bands. From 615 to 372 cm blf, the sediment showed brownish tones, and were mostly composed of clay with a thin layer of silt, shelly and little organic material. The uppermost 327 cm were dark to very light brown, with a uniform shelly clay composition (Fig 2A).

All radiocarbon dates resulted in stratigraphic order (Table 1). Although bulk sediment dates could lead to an ^{14}C age offset, we were not able to quantify ot because of the lack of other quantifiable materials. Nevertheless, the high correspondence between TC and TN along the sedimentary record (Fig. 2) suggests that inorganic carbon represents a relatively low proportion of the sedimentary material. According to the age-depth model, the core has a basal age of ~7840 cal BP, resulting in an average sedimentation rate of 1.96 mm/yr (Fig 2B). From the bottom of the sequence up to 5500 cal BP, sedimentation rates were high, with maximum values around 5500 cal BP (4.10 mm/yr). From c. 5500 cal BP to present, sedimentation rates showed a decreasing trend, reaching 0.89 mm/yr in the uppermost part of the core (Fig 2).

Table 1. Radiocarbon dates of core MAN15V from La Mancha coastal lagoon. Depths in cm below lagoon floor (blf). Ages calibrated after the IntCal13 curve (Reimer et al., 2013).

Laboratory code	Depth (cm blf)	^{14}C Age	Error	Calibrated age (95% range; cal BP)
UBA-34340	109	1290	24	1181-1283
Beta-440367	175	1880	30	1730-1883
UBA-34341	282	3447	26	3637-3826
Beta-440368	373	3970	30	4300-4523
UBA-34342	564	4732	41	5326-5584
Beta-437078	649	4770	30	5334-5588
UBA-34343	979	5624	41	6312-6482
Beta-437079	1249	6700	30	7508-7616

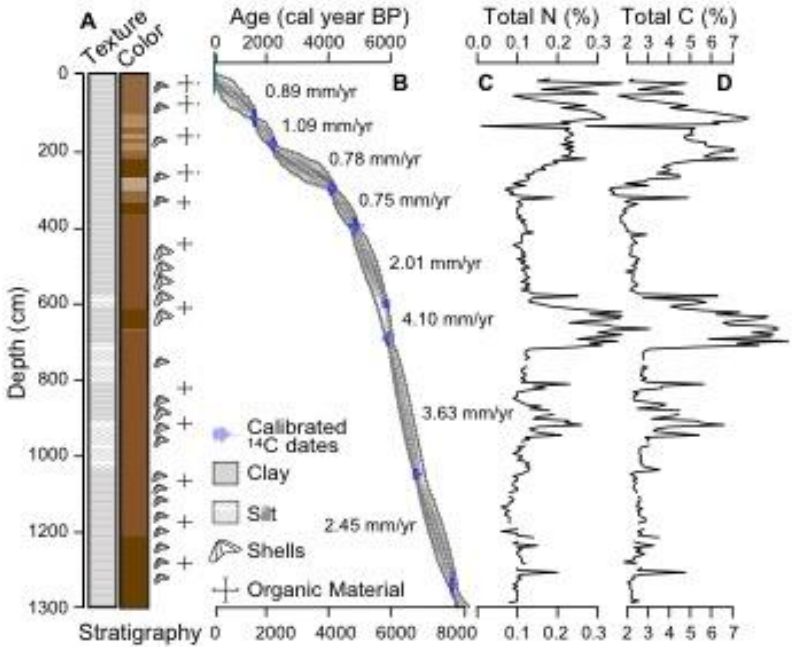


Figure 2. Core MAN15V from La Mancha coastal lagoon. A. Stratigraphy of the sedimentary sequence: texture (left), color (right), and organic and shell content. B. Age-depth model; calibrated ages (blue silhouettes), 95% confidence intervals in grey (darker colors indicate higher probability), and sedimentation rates (mm/yr). C and D. Percentage of total nitrogen and total carbon content (TN and TC, respectively).

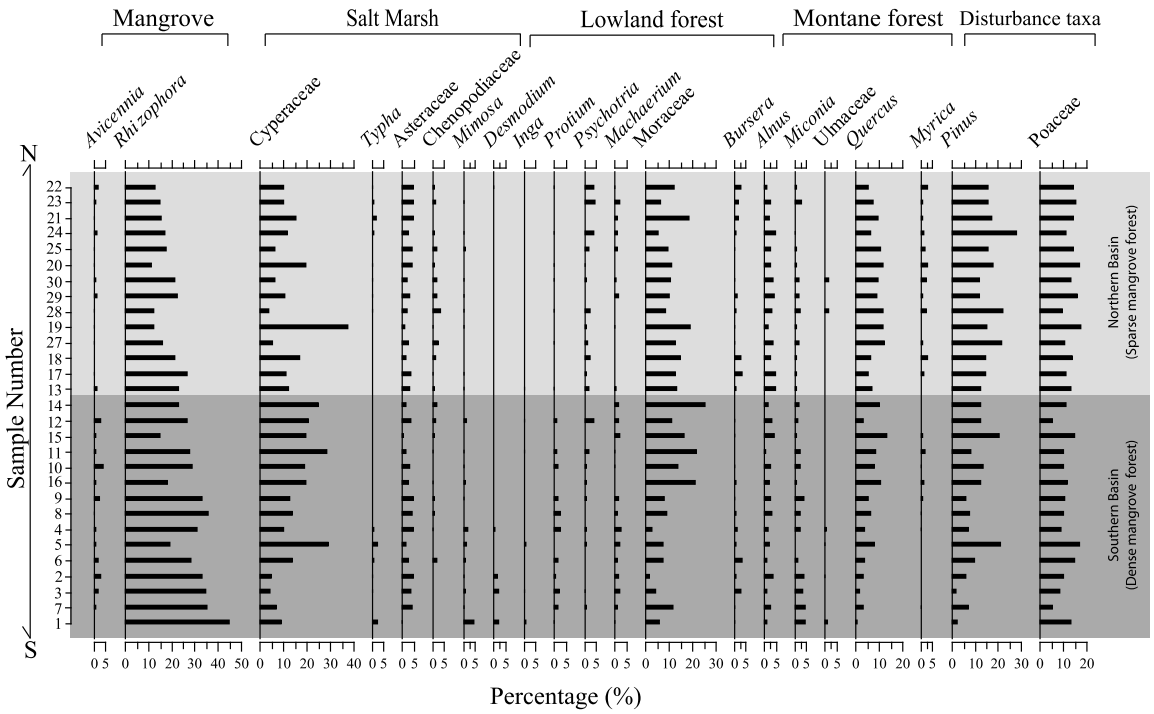
320

321 *4.2 Pollen spectra and C and N in modern samples*

322 Modern samples were characterized by 49 taxa, 18 and 31 identified at family and genus
323 levels, respectively. Pollen sums varied between 300 and 387, whereas pollen counts
324 including Cyperaceae and pterodophytes were between 322 and 472 palynomorphs.
325 *Rhizophora*, Cyperaceae, Moraceae-Urticaceae, *Quercus*, *Pinus*, and Poaceae dominated
326 these samples (up to 45%), whereas taxa such as *Typha*, *Mimosa*, *Desmodium, Inga*, and
327 Ulmaceae were poorly represented (less than 5%). One sample from the northern sub-basin
328 was barren of pollen (sample 26, Fig. 1).

329 *Avicennia* and *Rhizophora* showed high percentages (up to 5 and 45%, respectively)
330 towards the southern sub-basin of the lagoon (Figs. 1 and 3). Contrastingly, other taxa such
331 as *Quercus*, *Myrica*, and *Pinus* decreased southwards. Compositional differences between
332 the northern and southern sub-basins of the lagoon were also indicated by taxa that
333 occurred only at the latter, such as *Desmodium*, *Inga*, and *Protium* (Figs. 1 and 3). Samples
334 from the middle area of the lagoon (samples 12,13,14,17 and 18) (Figs. 1 and 3) contained
335 the highest percentages of Cyperaceae and Moraceae-Urticaceae (25% and 30%,
336 respectively), and minima of *Typha*, Asteraceae, and *Psychotria*. In the northern sub-basin
337 (Figs. 1 and 3), *Quercus*, *Pinus*, and Poaceae dominated the pollen spectra with abundances
338 above 10%.

339



340

341 Figure 3. Pollen diagram of selected taxa from mud-water interface samples from La
342 Mancha coastal lagoon. Ecological affinities after Lugo and Snedaker (1974), Ramwell
343 (1972), and Travieso-Bello (2000). Samples are ordered from South to North with samples
344 from the southern (northern) sub-basin highlighted in dark (light) grey.

345

346 TC content in modern samples varied between 3.1 and 12.3%, with mean and median of 4.9
347 and 4.4%, respectively. Although mean values for the northern and southern sub-basins
348 were not statistically differentiable (t = 1.66, p-value = 0.11), the northern sub-basin
349 consistently showed lower values (Fig. 3). Differently, individual fractions of C resulted
350 statistically differentiable, with a higher concentration of TOC in the southern sub-basin
351 (3.56, p-value = 0.002) and a higher concentration of TIC in the northern sub-basin (t = -
352 2.47, p-value = 0.023). TN range between 0.02 and 0.37% with mean and median of 0.23

and 0.24%, respectively (Fig. 3), with higher mean concentration in the southern subbasin ($t = 5.54$, p-value < 0.001). TC resulted statistically associated with TN, TIC, and TOC, although the magnitude of the correlation was substantially higher with the latter (Fig. 3). Whereas TIC resulted moderately associated only with TN, TOC was strongly associated with both TC and TN (Fig. 3).

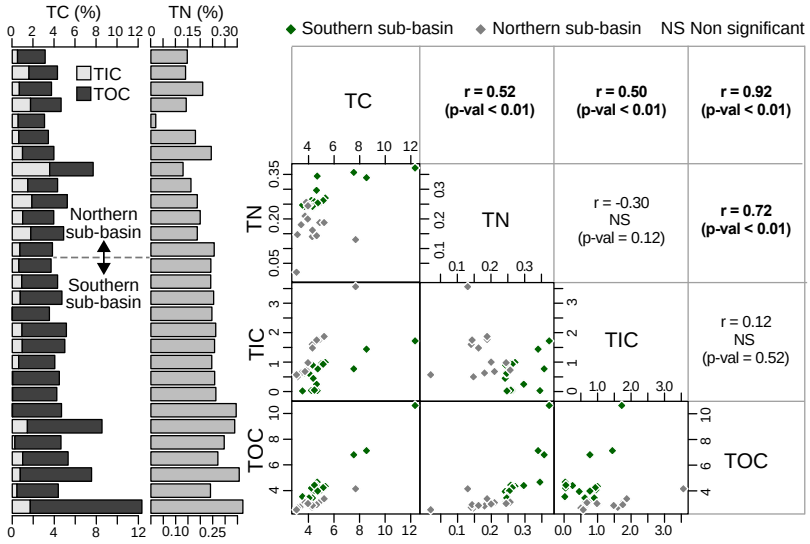


Figure 4. Content (%) of carbon and nitrogen in the modern samples of La Mancha coastal lagoon. Total C content (TC) discriminated into inorganic and organic fractions (TIC and TOC), and total N content (TN). Comparisons among sedimentary attributes are shown in the right side panels (biplots and correlation coefficients with their significance).

4.3 Fossil record

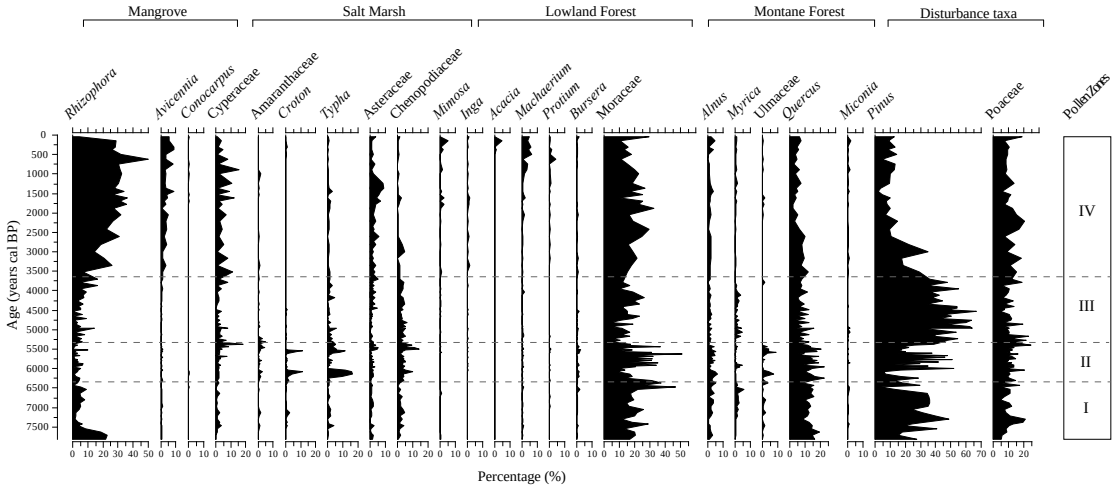
Fossil pollen types included 55 taxa classified into 24 families and 31 genera. Pollen sums varied between 300 and 349 grains per sample (average 306 grains), whereas pollen counts that included Cyperaceae and pterodophytes reached between 303 and 359 palynomorphs

per sample (average 317). The highest abundances were shown by *Rhizophora*, Moraceae-Urticaceae, *Quercus* and *Pinus*, while the lowest abundances were shown by *Conocarpus, Inga, Bursera and Miconia*. From within the 55 identified taxa, only *Rhizophora*, Cyperaceae, *Typha*, Asteraceae, Chenopodiaceae, Moraceae-Urticaceae, *Alnus, Quercus, Pinus,* and Poaceae persisted throughout the entire record. The record was discretized into four main pollen zones (Fig. 4) to facilitate the description of the sedimentary sequence. Pollen zones were defined based on an inspection of the distribution of pollen percentages though time, aiming to identify time periods characterized by relatively stable pollen assemblages.

Pollen Zone I (from 1300 to 907 cm blf, c. 7840-6300 cal BP): The sediment showed TC concentrations between 1.84 and 4.78%, with mean of 2.54%, and TN concentrations between 0.06 and 0.20%, with mean 0.10% (Fig. 2). This zone showed high percentages of *Rhizophora* (up to 20%), Moraceae-Urticaceae (up to 50%), *Quercus* (up to 20%), *Pinus* (up to 50%), and Poaceae (up to 20%). Low percentages (less than 5%) were shown by *Avicennia,* Amaranthaceae, *Croton, Typha,* Asteraceae, Chenopodiaceae, *Mimosa, Inga, Acacia, Machaerium, Protium, Bursera,* Ulmaceae *and Miconia* (Fig.4).

Pollen Zone II (from 907 to 569 cm blf, c. 6300 - 5400 cal BP): The sediment showed highly variable concentrations of both TC and TN (Fig. 2). TC varied between 2.28 and 9.67% with mean of 4.6%, whereas TN varied between 0.09 and 0.43 with a mean of 0.19%. This zone was dominated by Cyperaceae (20%), *Croton* (10%), *Typha* (20%), Chenopodiaceae (15%), Moraceae-Urticaceae (50%), *Alnus* (~6%), Ulmaceae (10%), *Quercus* (20%), *Pinus* (50%) and Poaceae (20%). Percentages below 5% were shown by

392 *Avicennia, Conocarpus,* Amaranthaceae, Asteraceae, *Mimosa, Inga, Machaerium, Protium,*
393 *Bursera and Miconia* with less than 5%. The upper part of the zone was characterized by
394 relatively low percentages of *Pinus* (~18%) and a substantial increase of Amaranthaceae,
395 *Croton, Typha,* Asteraceae, Chenopodiaceae, and Cyperaceae (up to ~20%) (Fig. 4).
396
397 **Pollen Zone III (from 569 to 280 cm blf, c. 5400 - 3700 cal BP):** With lower variability,
398 both TC and TN decreased substantially (Fig. 2). TC varied from 1.14 and 6.31% with
399 mean of 2.45, and TN varied between 0.07 and 0.25% with mean of 0.12%. From 5400 BP
400 *Rhizophora* abundances began to increase gradually, and *Avicennia* was less than 5%.
401 *Pinus* reached the highest abundances throughout the record (up to 60%), while
402 Amaranthaceae, *Croton, Mimosa, Inga, Machaerium, Bursera,* Alnus, Ulmaceae,
403 Moraceae-Urticaceae, and *Miconia* showed their lowest percentages. Lastly, *Typha,*
404 Asteraceae, and Chenopodiaceae showed abundances around 10% (Fig 4).
405
406 **Pollen Zone IV (from 280 to 0 cm blf, c. 3700 cal BP - Present):** TC and TN
407 progressively reached high variable concentrations (Fig. 2). TC varied between 0.02 and
408 7.77% with mean of 4.45%, and TN varied between 0.01 and 0.36% with mean of 0.20%.
409 Abundances of *Rhizophora* and *Avicennia* reached their highest values (up to 60% and 10%
410 respectively), and displayed an increasing trend towards the present. Amaranthaceae,
411 *Croton, Typha,* Chenopodiaceae, *Myrica,* Ulmaceae, *Quercus,* and *Pinus* abundances
412 decrease up to the present. Meanwhile *Acacia, Inga, Machaerium,* and *Protium* presented
413 their highest abundances (up to 10%) (Fig. 4).
414



415

416 Figure 5. Fossil pollen diagram of selected taxa of core MAN15V from La Mancha coastal
417 lagoon. (ecological affinities after Lugo and Snedaker 1974, Ramwell 1972, and Travieso-
418 Bello 2000).

419

420 *4.4 Statistical analyses*

421 The three-dimensional ordination of the modern and fossil pollen samples showed a stress
422 of 0.144. Negative scores along Axis 1 characterized modern samples, whereas fossil
423 samples were clearly divided into positive (negative) scores for samples older (younger)
424 than ~ 5400 cal BP (Fig. 5 and 6.B). Along Axis 2, both modern and fossil samples were
425 mostly located between –0.31 and 0.2, although fossil samples showed positive and
426 negative excursions (Fig. 5). NMDS Axis 3 was characterized by widespread scores for
427 fossil samples and almost exclusively negative scores for modern samples (Appendix 1).
428 The t-test for comparing NMDS scores of modern samples from the northern and
429 southern sub-basins yielded significant differences in terms of Axis 1 and 2, but non-
430 significant for Axis 3 (Table 2). Given the relatively flat behavior of Axis 2 and the lack of

significance of Axis 3 (Appendix 1), only the first axis of the ordination will be considered for interpretations hereafter.

Table 2. Comparison of NMDS sample scores in the three axes for modern samples from the northern and southern sub-basins, i.e scores from dense (D) vs. sparse (S) mangrove areas. For the comparison of scores along each axis, t scores, degrees of freedom corrected for variance differences between samples (d.f.), and p-value are shown.

Comparison	t	d.f.	p-value
Axis 1_D – Axis 1_S	-3.5184	18	0.0026
Axis 2_D – Axis 2_S	-2.7661	26	0.0103
Axis 3_D – Axis 3_S	1.3831	24	0.1796

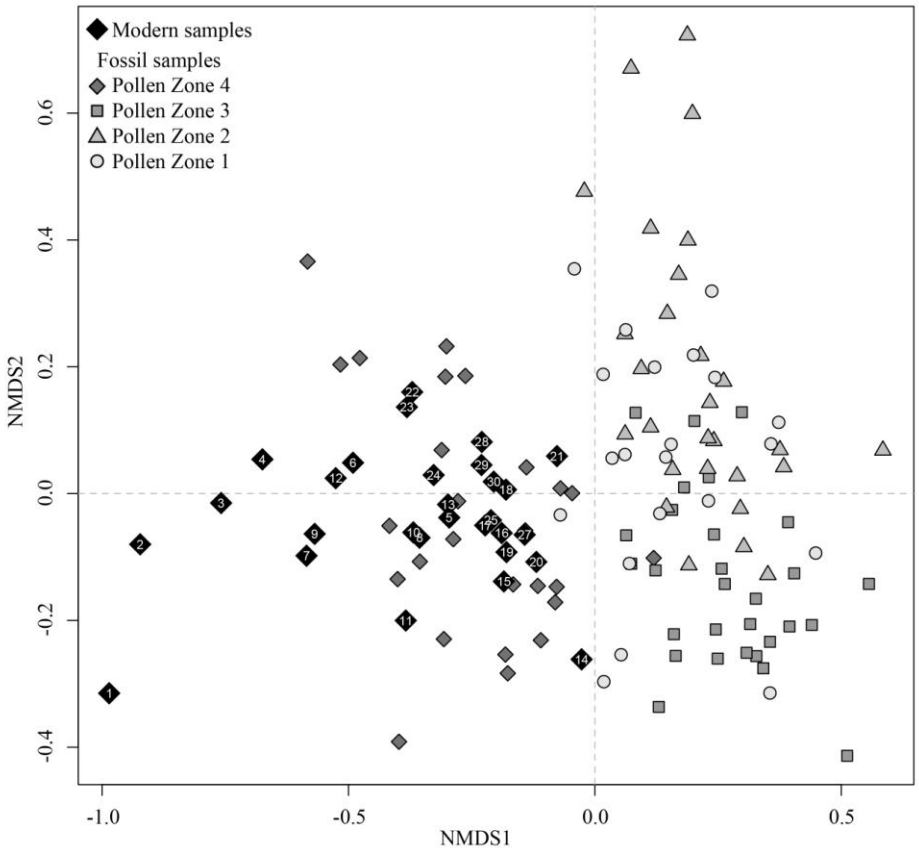


Figure 6. Non-metric multidimensional scaling for modern and fossil pollen assemblages from La Mancha lagoon. Modern samples in black diamonds showing sample number, whereas fossil samples were symbol coded according to the declared legend.

5. Discussion

5.1 Modern sediments of La Mancha coastal lagoon

Palynological composition of modern samples generally reflected the patterns of modern vegetation, incorporating vegetation elements from the surrounding mangroves and salt marshes (local vegetation), and nearby lowlands and highland forest (regional vegetation). Although the mangroves of La Mancha are dominated by *A. germinans* over *R. mangle* (Moreno-Casasola, 2006), modern pollen spectra were dominated by the latter (Fig. 3).

Given its pollination mechanism, *R. mangle* produces high amounts of pollen, dominating most of pollen spectra from mangrove forests. Contrastingly, *A. germinans* is an insect-pollinated species that produces low amounts of pollen (Hogarth, 2007), resulting in under-representation of the parental taxon in the pollen spectra where percentages as low as 5% implying an important share in the standing vegetation. However, the mean representation of *R. mangle* in modern samples from the densely mangrove-forested southern sub-basin (~25%) are low as compared to pollen spectra from stands dominated by this species which have been reported as high as 65% (e.g. Behling et al., 2001; Urrego et al., 2009). Although *C. erecta* and *L. racemosa* are components of the standing forest of La Mancha, they are not represented in the modern pollen spectra probably because of their low production, and also because of their distal position with respect to the sampled water body (Moreno-Casasola, 2006).

In the southern sub-basin of La Mancha, the high percentages of *Rhizophora* reflect the relatively good conservation state of the mangroves (Moreno-Casasola, 2006), with the exclusive presence of taxa such as *Desmodium*, *Inga* and *Protium* indicating a well preserved lowland vegetation as well (Franco-Gaviria et al., 2018). Pollen spectra from the northern sub-basin contained lower percentages of *Rhizophora*, and a substantial representation of regional pollen, possibly coming from the highlands of the catchment basin. Over recent decades, the deleterious effects of human activities on mangrove cover have been more intense around the northern sub-basin of La Mancha lagoon (Lopez-Portillo et al., 2011; Moreno-Casasola, 2006), reflecting on pollen assemblages where the regional and disturbance elements are better represented (mainly Moraceae-Urticaceae, *Myrica*, *Pinus*, Poaceae, and *Quercus*) (Correa-Metrio et al., 2011; Franco-Gaviria et al.,

2018). Although *Rhizophora*, Moraceae-Urticaceae, *Pinus*, and *Quercus* do not dominate the shore vegetation of the most disturbed northern areas, they are represented by pollen percentages above 10 % each (Fig. 3), reflecting the sparse nature of mangrove forests over this area. This finding reflects the widely reported overrepresentation of these taxa in pollen spectra, derived from their high production of pollen and their long-distance pollen dispersal capacity, as reported for species of anemophyllous pollination (e.g. Correa-Metrio et al., 2013; Ellison, 2008; Hooghiemstra et al., 2006; Marchant et al., 2002).

Modern samples were clustered in the NMDS (Fig. 5), implying more consistency among the modern pollen spectra than between modern and fossil samples. This finding demonstrates that the modern heterogeneity of the lagoon does not represent the ecological and environmental variability of the area over the last ~7800 years. Statistically significant differences between the NMDS Axis 1 scores of pollen assemblages from the two sub-basins demonstrate that density of mangrove forest cover can be identified though their pollen spectra. Overall, these findings indicate that i) pollen assemblages of La Mancha lagoon are systematically associated with physical and biological attributes of the region at a broad scale (regional vegetation), and ii) pollen spectra are highly sensitive to the modern environmental variability throughout La Mancha lagoon (local vegetation). Thus, as reported for other areas (e.g. Franco-Gaviria et al., 2018; Urrego et al., 2009; Urrego et al., 2010), modern pollen assemblages of our studied lagoon provide a robust framework for interpreting our fossil pollen sequence.

Higher concentrations of TOC and TN in the southern sub-basin were probably a result of differences in surrounding vegetation and energy of the depositional environment. More vigorous vegetation in the southern sub-basin would produce higher amounts of

498 organic matter rich in TOC and TN, whereas the lower energy of the depositional
499 environment would prevent resuspension and, therefore, further oxidation of the sediments
500 (Meyers, 1997). Differently, TIC resulted higher in the northern sub-basin, probably
501 reflecting both higher contribution of marine particulate suspended matter and more
502 oxidation of organic components (Bouillon et al., 2003). Overall, C and N analyses are
503 consistent with higher organic matter storage in the sediments of the lagoon where
504 mangrove forests are well preserved. The relationships that were found between the
505 different components of C and N demonstrate that in the modern setting of La Mancha,
506 TOC is the main component of TC. Although these relationships cannot be extrapolated to
507 the fossil record, they demonstrate that TN is a good proxy for organic matter, and
508 therefore it is used to offer further support to our pollen-based reconstruction of past
509 environmental dynamics.

510

511 *5.2 Vegetation history of La Mancha Lagoon*

512 The pollen record of La Mancha lagoon reflects the complexities associated with the
513 multiple factors that have intervened in the development toward the modern biotic and
514 abiotic systems. Whereas highly variable abundances of regional vegetation suggest
515 variability in freshwater input by precipitation and tributaries to the lagoon system, pollen
516 from mangroves together with herbaceous vegetation offer insights into the successional
517 patterns and development of the local vegetation (Urrego et al., 2013; Urrego et al., 2018).
518 Additionally, the constant presence of marine shells through the sedimentary record (Fig. 2)
519 demonstrates a permanent marine influence through the last ~7,800 year. Together, these
520 indicators illustrate the intimate interaction between sea levels and regional fresh water

inputs (precipitation, sediments) that ultimately regulates the colonization, establishment, and development of mangrove ecosystems in the area. According to our pollen and geochemical data, the history of the vegetation that surrounds the lagoon and therefore the regional environmental history could be summarized in four main stages that will be discussed below.

From c.7800 to 6300 cal BP: sea-water flooding of valleys

Through this time period, the mud-water interface was between 13 and 9 m below the modern surface, which today is at sea level. At the same time, average sea level was between 9 and 5 m below modern. The difference between mud-water interface depth and sea level can only be accounted by lagoon water depth, which was ~ 4 m below sea level (Fig. 6A). La Mancha Hill, an andesitic rock of Neogene origin (Moreno-Casasola, 2006; Geissert Kientz, 1999) (Fig. 1), probably acted as a barrier that protected the depositional environment from the erosive energy of the waves and winds. Through this period, even though sedimentation rates at La Mancha (~3.04 mm/year) were lower than the inferred rate of sea-level increase, they are among the highest through the record. High rates of both regional sea-level rise and sedimentation at La Mancha are likely a result of the regional geologic instability that characterized the conformation of the modern Gulf of Mexico in its final stages, up to 5000 cal BP (Davis, 2011). As sea level increased through the deglaciation and the early Holocene, sea-water flooded coastal plains and valleys at a speed that surpassed the accumulation of continental sediments. Thus, the lacustrine basin of La Mancha was probably deeper than modern, impeding the establishment of mangrove forests (Fig. 6C). A peak of *Rhizophora* from the bottom of the record to ~7500 cal BP (Fig. 4) probably shows the colonization of mangroves during the initial stages of the lagoon and

544 the sea-water flooding, which were subsequently displaced by the formation of a deep-
545 water body.

546 In México, *Pinus* populations thrive under early post-disturbance successional
547 stages, or under conditions that are not optimal for other taxa (Metcalfe et al., 2000;
548 Ramirez-Marcial et al., 2001). Thus, the persistence of *Pinus* in high percentages from the
549 bottom of the record to ~6500 cal BP (Fig. 5) indicates that regional conditions were likely
550 dry, an interpretation that is further supported by the lowest concentrations of TN (Fig. 7)
551 and therefore of organic matter. These dry conditions probably played a central role at
552 maintaining sedimentation rates that did not offset sea-level rise, impeding the
553 establishment of mangrove forests, as demonstrated by the NMDS Axis 1 scores that were
554 outside the envelope defined by modern samples (Fig. 7C).

555

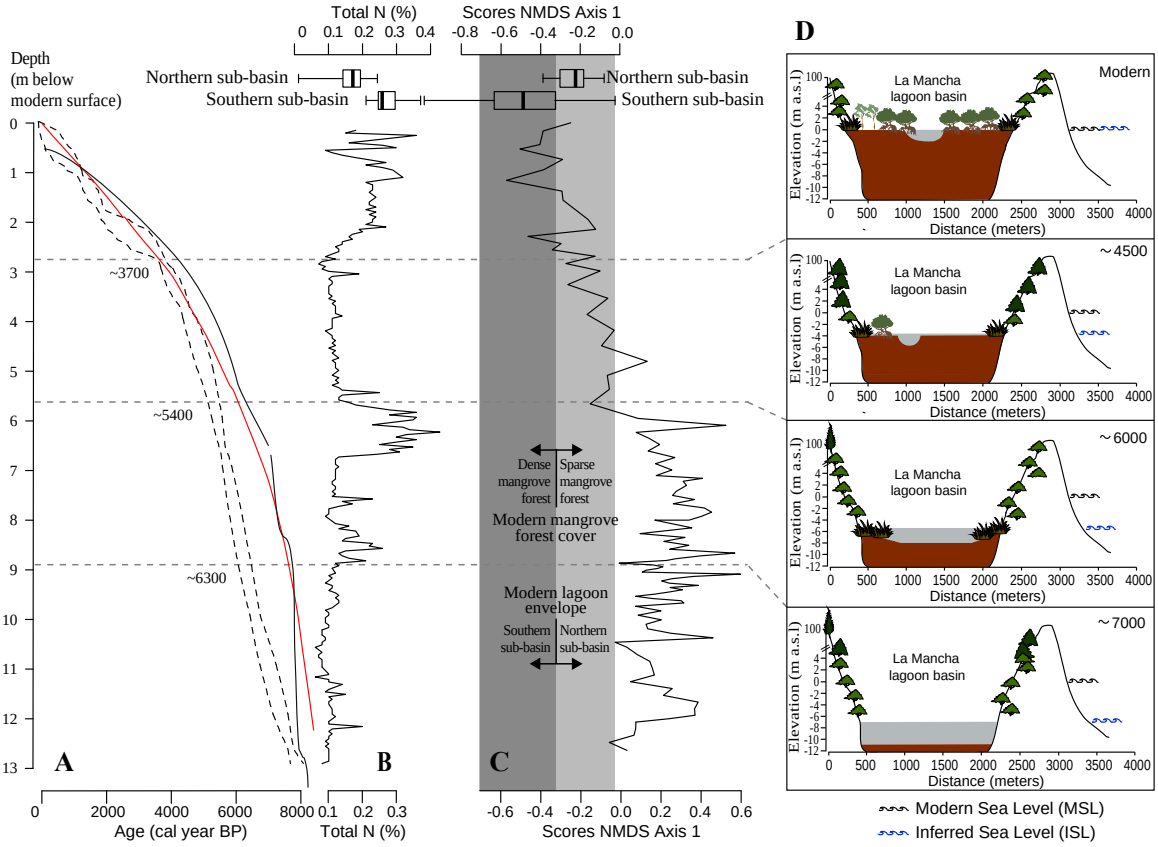


Figure 7. Environmental history of La Mancha Lagoon through the last 7,800 years. **A.** Age-depth model of core MAN15V from La Mancha Lagoon (dashed lines show 95% confidence interval), compared with sea level rise curves for the Caribbean (red line, Toscano and Macintyre, 2003) and the northern Gulf of Mexico (black solid line, Milliken and Anderson, 2008). **B**. Sedimentary total nitrogen content (%); boxplots illustrate total nitrogen in modern samples form the northern (up) and southern (down) sub-basins of the lagoon (whiskers show minimum and maximum scores). **C**. NMDS Axis 1 scores through time; boxplots illustrate scores of modern samples; scores of the modern environmental envelope represented by modern samples are highlighted in grey; scores of the interquartile range of samples from the well preserved southern sub-basin are in dark grey. **D**. Schematic development of La Mancha Lagoon, illustrated at ~7,000, 6000, 4,500 cal BP, and Modern.

From c. 6300 to 5400 cal BP: development of lagoon shores

Whereas the rate of sea-level rise started to decline through this period, sedimentation rates at La Mancha remained high (3.86 mm/yr, Fig. 6). This phenomenon could be explained by two critical factors: i) following the reported deceleration of sea-level rise at ~7000 cal BP (Toscano and Macintyre, 2003), sand bars started accumulating at the mouth of coastal lagoons (Davis, 2011), providing a more stable plain for sediment accumulation at La Mancha; and ii) a substantial decrease in the percentages of *Pinus*, and an increase of montane forest taxa (e.g. *Alnus, Quercus,* and Ulmaceae) indicate wetter conditions that would be in turn associated with higher river sediment discharge. These regional wetter conditions could be related to the final stages of the Holocene Thermal Maximum, which was in general characterized by higher than present precipitation and temperature in the Northern Hemisphere (Renssen et al., 2009).

The lagoon became shallower, and the development of muddy shores is evidenced by high percentages of salt marsh vegetation (Fig. 5), and high accumulation of organic matter revealed by the increasing TN (Fig. 7B). This state of local vegetation and the high accumulation of organic matter suggest the closing of the ephemeral mouth, probably caused by lower energy associated with the shallowing of the lagoon, together with the intensification of the wind currents, and sea level changes reported for the Gulf of Mexico and the Caribbean (Balsille and Donoghue, 2004; González and Dupont, 2009; Urrego et al., 2013; Wooller et al., 2007). Pollen spectra suggest the early stages of a successional pattern of mangrove vegetation associated with the marine transgression, although NMDS

590 Axis 1 sample scores demonstrate that mangrove forests were not established yet near the
591 location where the core was retrieved.

592 *From c. 5400 to 3700 BP: A regional drought*

593 Whereas the rate of sea-level rise continued to decrease, relatively high sedimentation rates
594 were evident in La Mancha sequence up to ~5000 cal BP, when apparently the rates of
595 sediment deposition in the lagoon and those of sea level rise became similar (Fig. 6A).
596 Such equilibrium between sediment deposition and sea-level rise implies the definition of a
597 coastal erosive baseline that allowed the deposition of sand in the coast by the northerly
598 currents during the dry season, creating the sandbar that dams the lagoon. Differently,
599 during the wet season, the fluvial input would have the capacity to erode the sandbar,
600 opening the direct contact between the lagoon and the sea and, thus, resulting in the modern
601 seasonal flood cycle. During the dry season, the coastal bar would be closed by the action
602 of the waves and the prevailing winds, whereas during the rainy season the bar would be
603 opened by the energy of the fresh water discharge. The lagoon thus became a shallow water
604 body (z_{max} ~1 m) mostly protected from the energy of the waves by La Mancha hill (Fig.1),
605 and subjected to seasonal tidal and climatic fluctuations.

606 From c. 5400 to 3700 cal BP, the recurrent drainage of fresh water into the sea
607 probably created a series of channels giving the lagoon a physiography very similar to
608 modern. However, according to the NMDS scores, vegetation at that time resembled the
609 northern sub-basin today (Fig. 6B), an area characterized by poorly developed sparse
610 mangrove stands. Thus, vegetation assemblages from this period were a result of
611 suboptimal environmental conditions for mangrove forest development. High percentages
612 of *Pinus* (up to 60%) through this period suggest that there was a regional drought in place,

613 which likely maintained high substrate salinity by reducing freshwater river discharge to
614 the lagoon. Thus, local vegetation consisted of a mixture of sparse mangrove trees with
615 some salt marshes species, and a slow increase of mangrove pollen because of the
616 prevailing dry conditions (Fig. 4). Although anthropogenic influence cannot be discarded as
617 a plausible explanation for the sparse mangrove vegetation, the inference of a regional
618 drought is supported by similar reports from Lake Petén Itzá between ~ 4500 up to ~3000
619 cal BP, Lake Tzib (Quintana Roo) at ~3500 cal BP (Carrillo-Bastos et al., 2010; Mueller et
620 al., 2010), and also in the Cariaco Basin record, with a trend from ~5400 up to the present
621 (Haug et al., 2001). Furthermore, the abrupt decrease of TN and its linear trend towards
622 even lower concentrations (Fig. 7B) evidence rather oxidizing conditions, an environmental
623 process that is difficult to explain from the perspective of human occupation.
624
625 *From c. 3700 cal BP to Present: the establishment of modern mangrove forests*
626 Mangrove pollen taxa showed the highest percentages (Fig. 5), reflecting an environment of
627 relative stability where the exchange of saline and fresh water, and the input of sediments
628 were balanced, producing an increase of mangrove forest biomass (Krauss et al., 2008).
629 These conditions provided consolidated clay sediments, where as indicated by the NMDS
630 scores, mangrove forests developed into mature forest stands of *Rhizophora* and *Avicennia*.
631 Increasing concentrations of TN (Fig. 7B) indicate high accumulation of organic matter
632 probably associated with the establishment of the mangrove forest (Bouillon et al. 2003).
633 Sea level continued to increase at slower rates (Balsille and Donoghue, 2004) that were
634 matched by the rate of sediment accumulation in La Mancha (~0.92 mm/yr on average).
635 These more stable conditions for coastal ecosystems have been reported for other localities

636 in the Caribbean coinciding with other records (Urrego et al., 2013), where mangrove
637 forests developed under a relatively stable sedimentation rate (1.09 to 0.89 mm/yr).
638 *Pinus* and salt marsh pollen in La Mancha showed substantial decreases caused by
639 wetter conditions and higher representation of local mangrove pollen, implying a lower
640 regional influence on pollen spectra, and the continuation of the successional processes that
641 led to the establishment of the mangrove forest (González and Dupont, 2009). At this stage,
642 the lagoon seems to have reached its modern configuration, with influences from local
643 processes like the annual opening of the ephemeral mouth, fluctuating floods of salt water,
644 input of fresh water from the streams, and anthropogenic activities (Moreno-Casasola,
645 2006). Indeed, the sharp decrease of *Rhizophora* is likely reflecting the terrestrialization of
646 the cored site, which today is occupied by an *Avicennia germinans* forest that floods only
647 when the ephemeral mouth is closed and the lagoon reaches its maximum water level
648 through the year. This latter observation is further supported by the high variability of TN
649 concentrations towards the top of the record.
650

651 **6. Conclusion**

652 The sedimentary record of La Mancha lagoon encompasses the history of local and regional
653 environmental conditions through the last ~8,000 years, including the establishment of
654 modern mangrove forest along the coast of Veracruz. The record shows the regional
655 context under which the coastal lagoon formed, showing the transformation of the lagoon
656 from a water body with permanent communication with the sea to the modern seasonally
657 closed system. When sea level rise rates were higher than the rates of sediment infill of the
658 lagoon's basin, the depositional environment was under sea level and pollen assemblages

were dominated by regional taxa. The ecological succession towards the establishment of mangrove forest started at ~6,300 cal BP, but mangrove forests were sparse, resembling those of the modern northern sub-basin because of two main reasons: i) the water column was relatively deep and sedimentary plains for mangrove establishment were likely narrow, and ii) a regional drought lasting from ~5400 to 3700 BP probably caused extremely high substrate salinity that impeded mangrove forests expansion. Dense mangrove forests like those that occupy the southern sub-basin today established around ~3500 BP, and have dominated the area ever since.

The matching of lagoon sediment and sea levels at ~4000 cal BP was likely associated with the development of the seasonally open mouth. This pairing of lagoon sedimentary accumulation and sea levels defined the latter as the base level for erosion, allowing the accumulation of material during the dry season, and therefore the formation of a damming bar, which would eventually be open during the rainy season owing to the increased freshwater discharge. Concomitant to this process would be the linear erosion of channels through the sedimentary deposit, conforming the modern geomorphology of the area. The establishment of the mangrove forest implied a substantial increase of sedimentary organic matter, highlighting the role of these ecosystems at storing carbon. Overall, our record demonstrates the complexity of the interactions between local and regional factors in the development and evolution of both coastal geomorphology and ecosystems.

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***Highlights (for review)**

- During the mid Holocene, sedimentation rates were lower than sea level rise rates
- Modern barrier-lagoon systems of the Gulf of Mexico appeared ~5000 years ago
- A drought between 5400 and 3700 years ago impeded mangrove forest establishment
- Modern coastal lagoons of the western Gulf of Mexico established ~3700 years ago
- The establishment of mangroves caused an increase of sedimentary organic matter

Table 1

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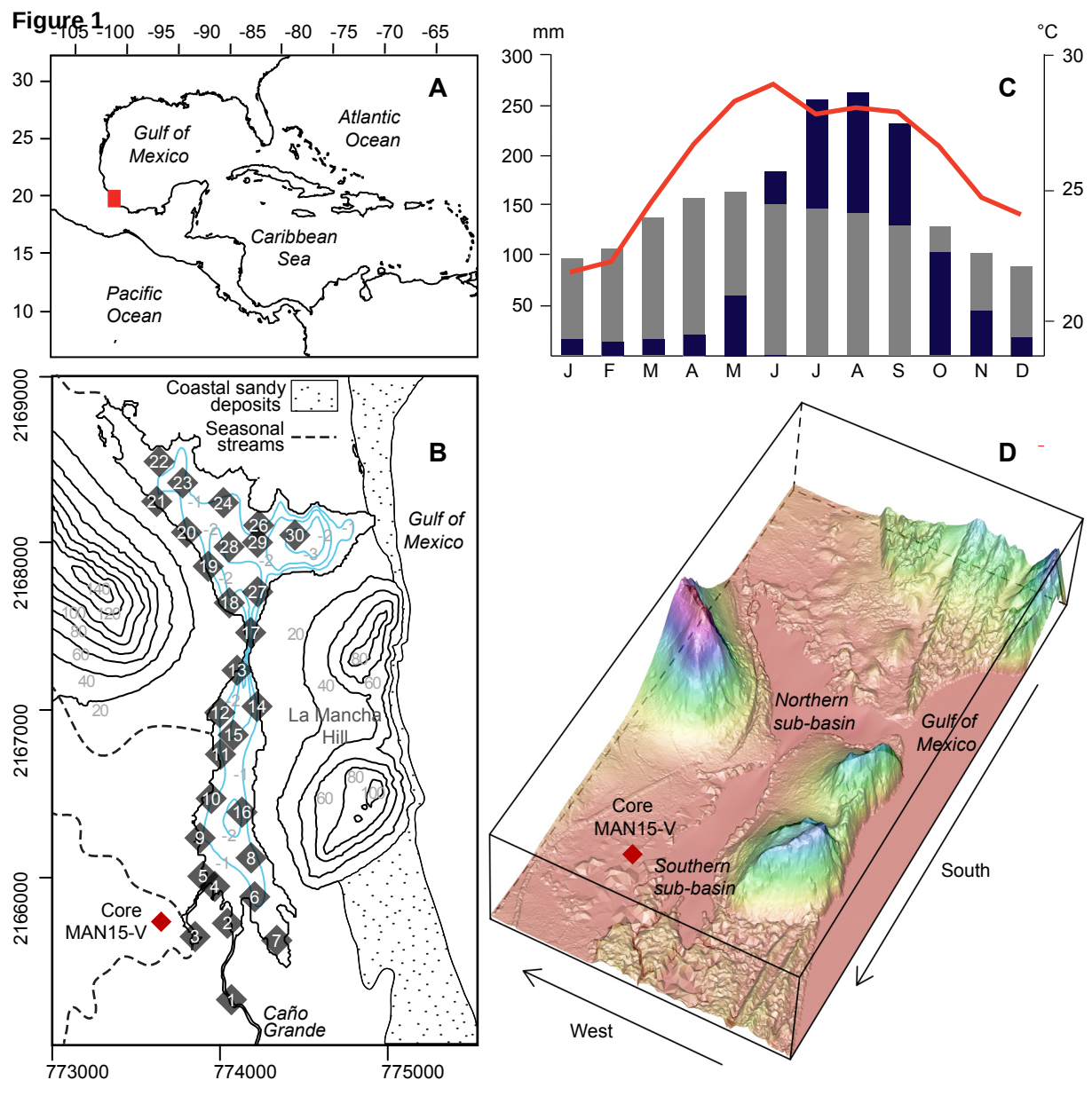
Table 1. Radiocarbon dates of core MAN15V from La Mancha coastal lagoon. Depths in cm below lagoon floor (blf). Ages calibrated after the IntCal13 curve (Reimer et al., 2013).

Laboratory code	Depth (cm blf)	^{14}C Age	Error	Calibrated age (95% range; cal BP)
UBA-34340	109	1290	24	1181-1283
Beta-440367	175	1880	30	1730-1883
UBA-34341	282	3447	26	3637-3826
Beta-440368	373	3970	30	4300-4523
UBA-34342	564	4732	41	5326-5584
Beta-437078	649	4770	30	5334-5588
UBA-34343	979	5624	41	6312-6482
Beta-437079	1249	6700	30	7508-7616

Figure 1


A
Gulf of Mexico
Atlantic Ocean
Caribbean Sea
Pacific Ocean
B
Coastal sandy deposits
Seasonal streams
Gulf of Mexico
La Mancha Hill
Core MAN15-V
Caño Grande
C
mm
°C
J F M A M J J A S O N D
D
Northern sub-basin
Gulf of Mexico
Core MAN15-V
Southern sub-basin
South
West

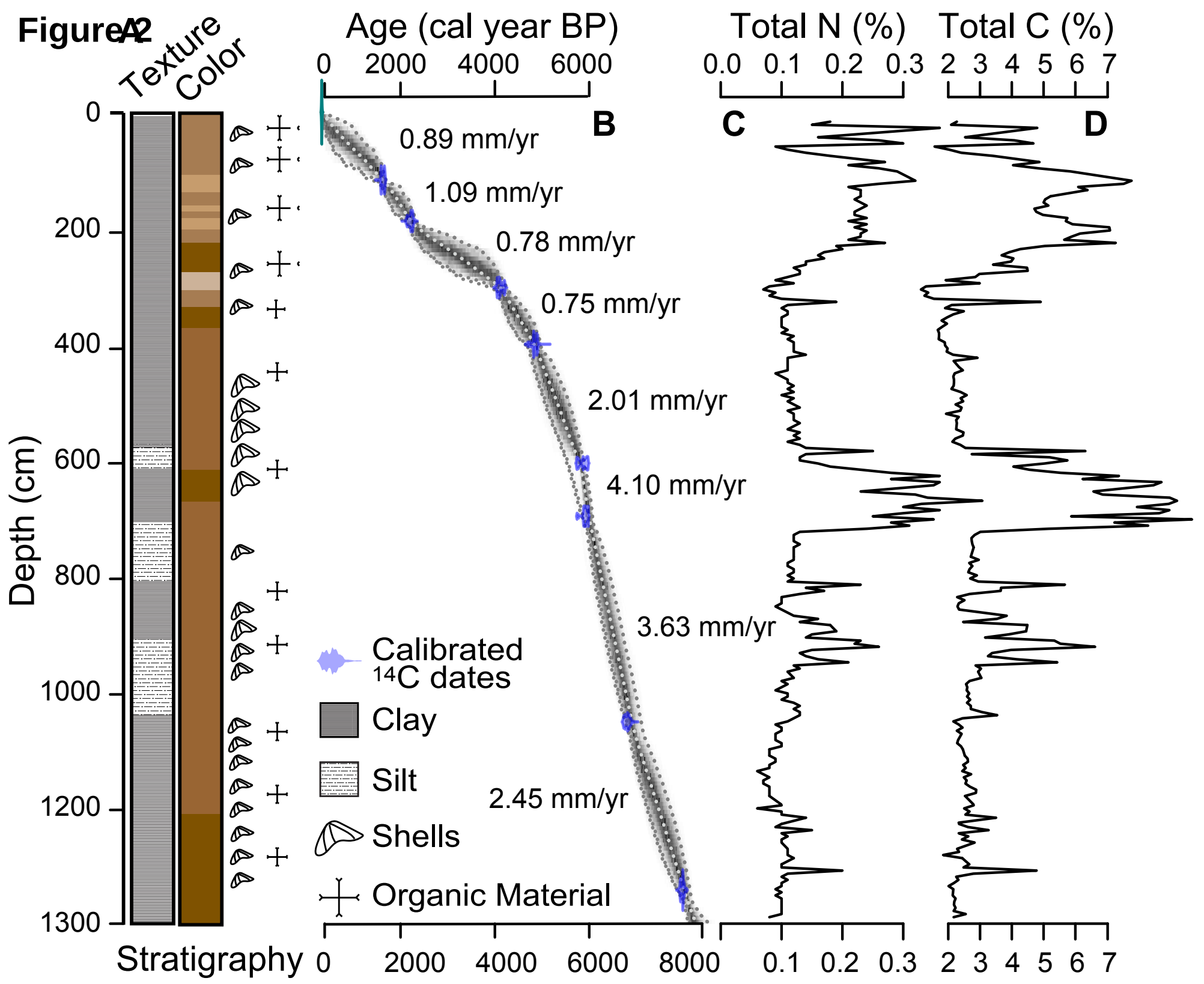


Figure A2
Texture
Color
Age (cal year BP)
0
2000
4000
6000
Total N (%)
0.0
0.1
0.2
0.3
Total C (%)
2
3
4
5
6
7
B
C
D
0.89 mm/yr
1.09 mm/yr
0.78 mm/yr
0.75 mm/yr
2.01 mm/yr
4.10 mm/yr
3.63 mm/yr
2.45 mm/yr
Depth (cm)
0
200
400
600
800
1000
1200
1300
Calibrated
14C dates
Clay
Silt
Shells
Organic Material
Stratigraphy
0
2000
4000
6000
8000
0.1
0.2
0.3
2
3
4
5
6
7

Figure 3

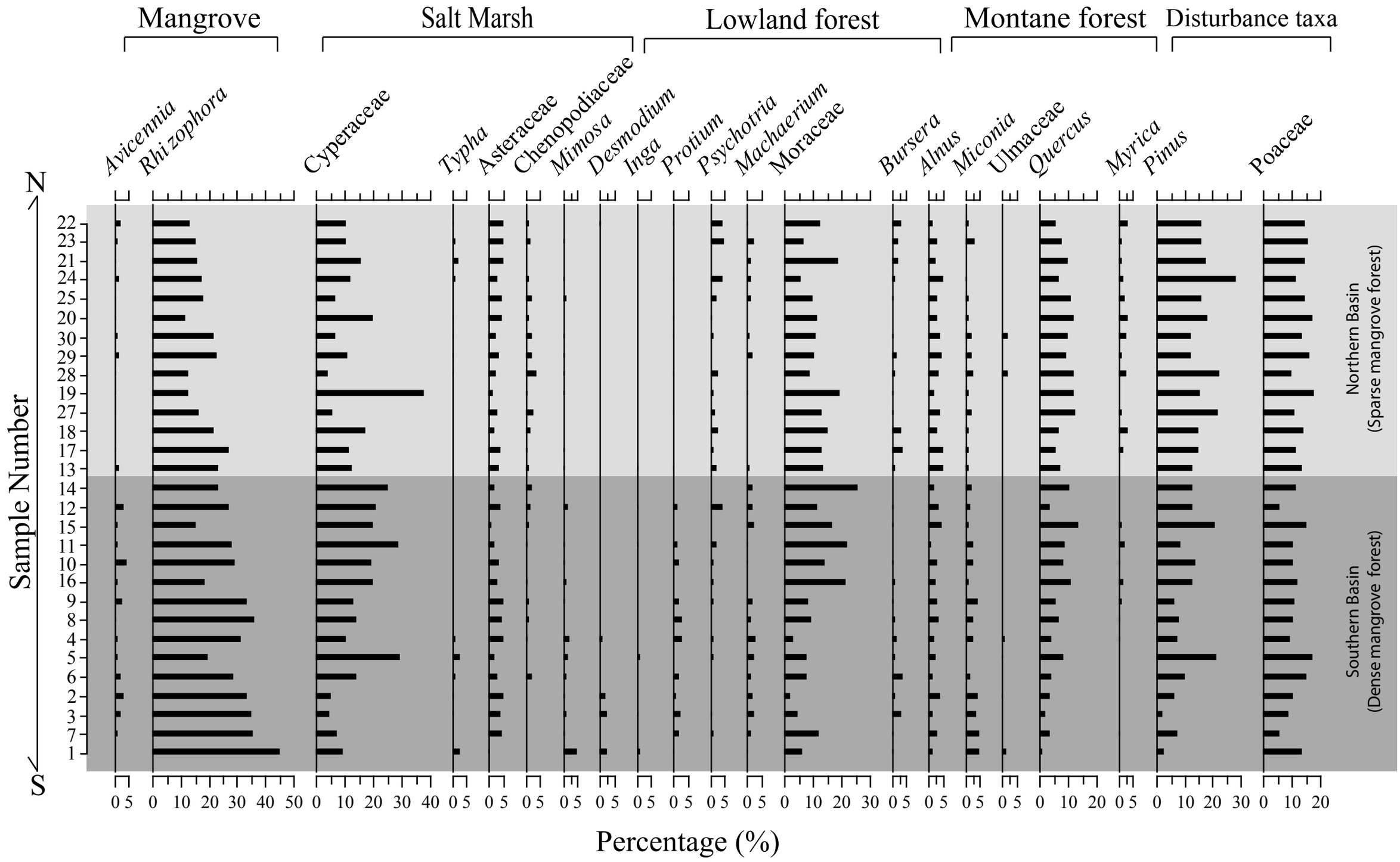

Mangrove
Salt Marsh
Lowland forest
Montane forest
Disturbance taxa
Avicennia
Rhizophora
Cyperaceae
Typha
Asteraceae
Chenopodiaceae
Mimosa
Desmodium
Inga
Protium
Psychotria
Machaerium
Moraceae
Bursera
Alnus
Miconia
Ulmaceae
Quercus
Myrica
Pinus
Poaceae
N
S
Sample Number
Northern Basin
(Sparse mangrove forest)
Southern Basin
(Dense mangrove forest)
Percentage (%)

Figure 4

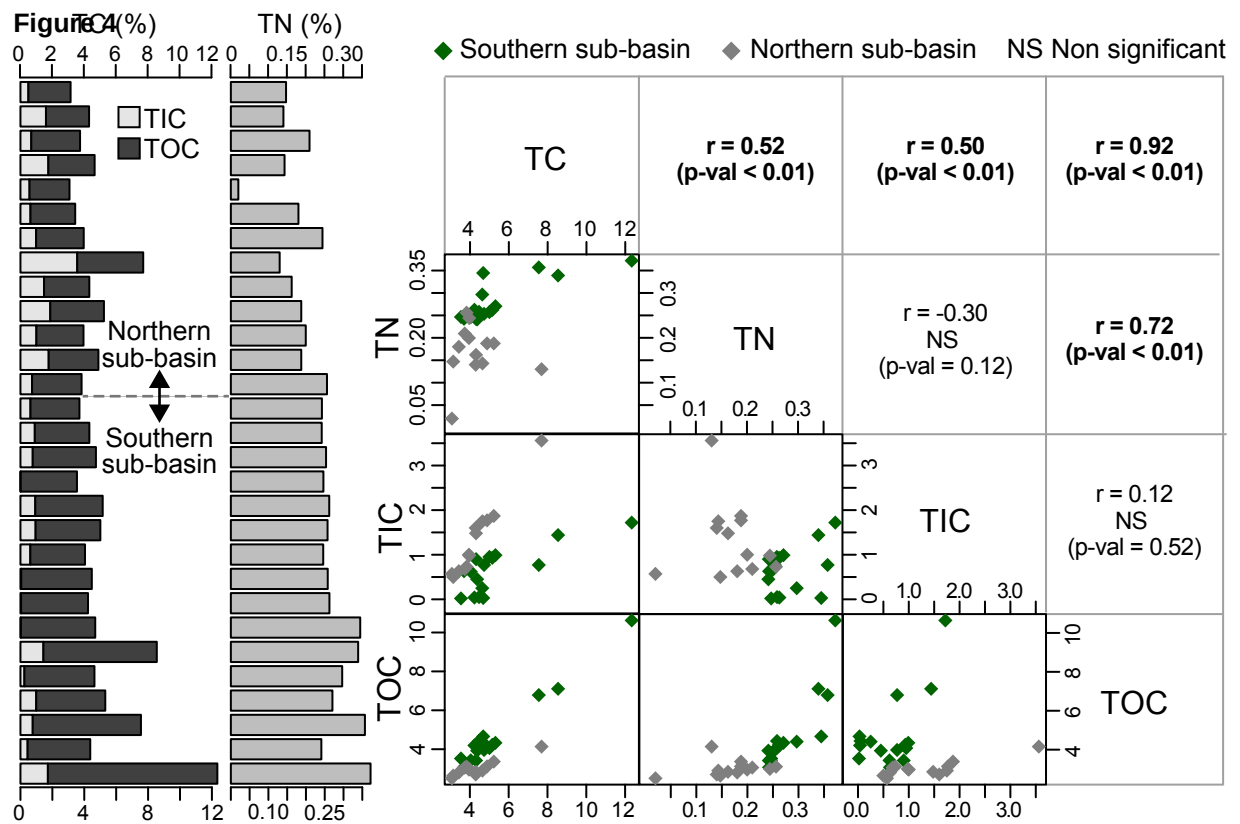

TC (%)
TN (%)
TIC
TOC
Northern sub-basin
Southern sub-basin
Southern sub-basin
Northern sub-basin
NS Non significant
TC
TN
TIC
TOC
r = 0.52 (p-val < 0.01)
r = 0.50 (p-val < 0.01)
r = 0.92 (p-val < 0.01)
r = -0.30 NS (p-val = 0.12)
r = 0.72 (p-val < 0.01)
r = 0.12 NS (p-val = 0.52)

Figure 5

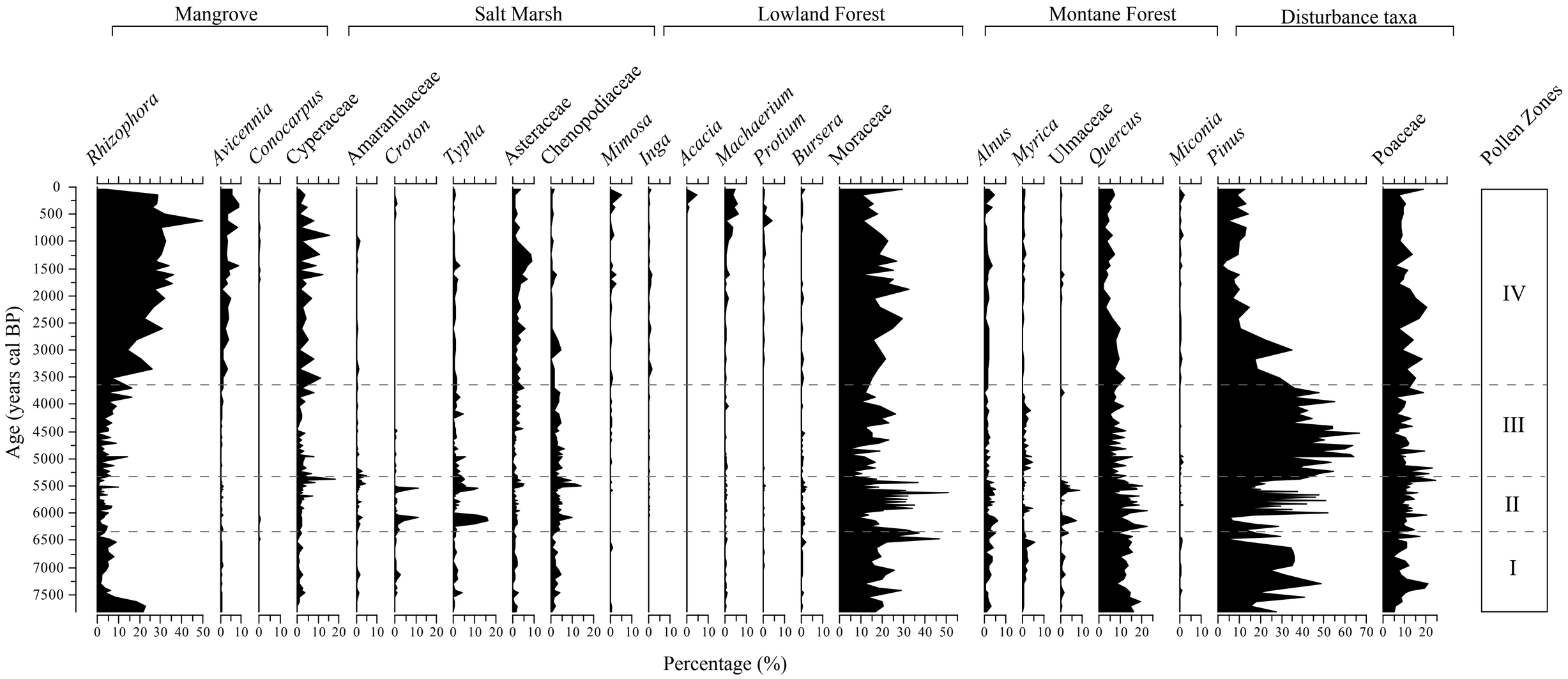

Mangrove
Salt Marsh
Lowland Forest
Montane Forest
Disturbance taxa
Rhizophora
Avicennia
Conocarpus
Cyperaceae
Amaranthaceae
Croton
Typha
Asteraceae
Chenopodiaceae
Mimosa
Inga
Acacia
Machaerium
Protium
Bursera
Moraceae
Alnus
Myrica
Ulmaceae
Quercus
Miconia
Pinus
Poaceae
Pollen Zones
IV
III
II
I
Age (years cal BP)
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5500
6000
6500
7000
7500
Percentage (%)

Figure 6

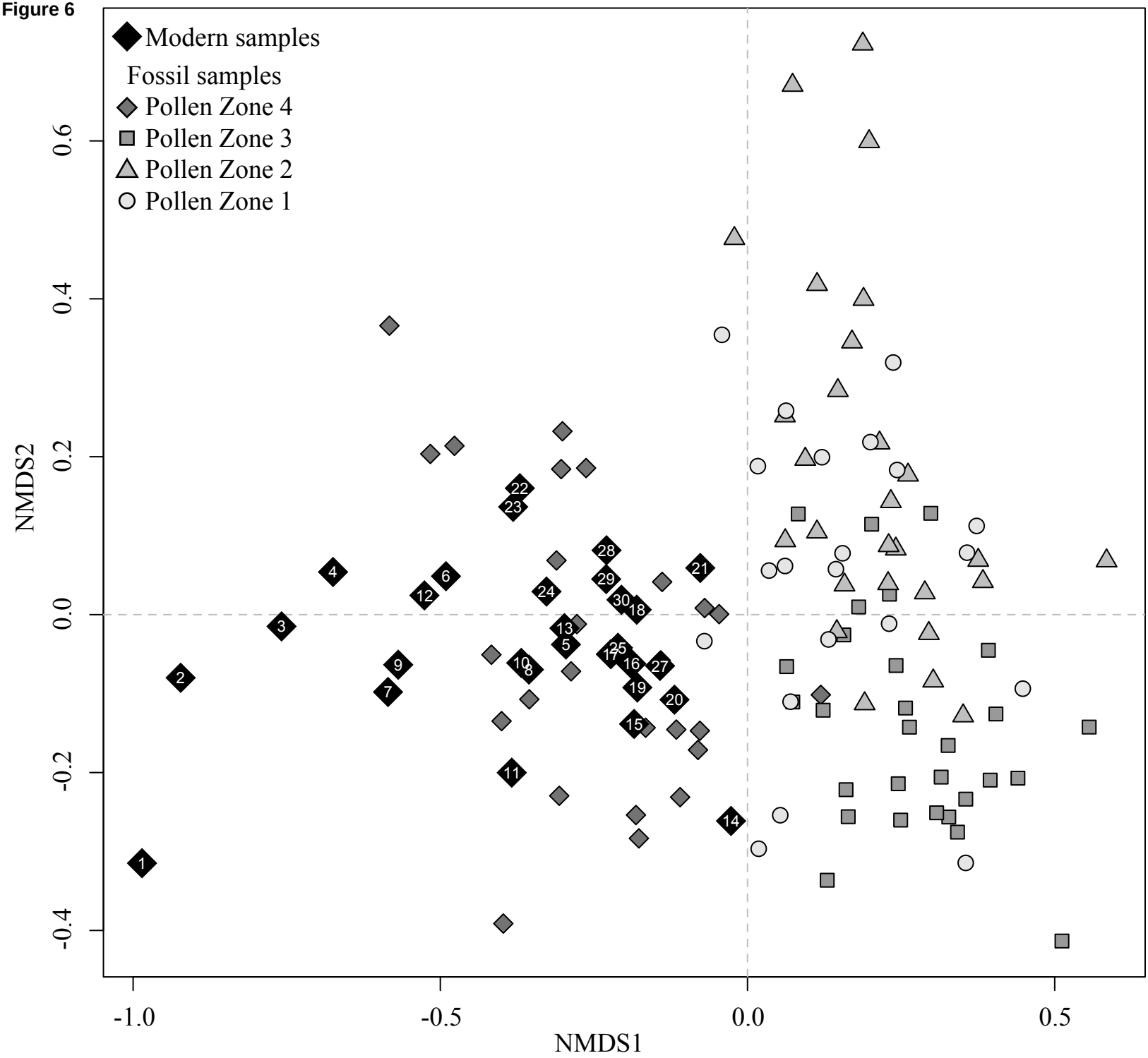

Modern samples
Fossil samples
Pollen Zone 4
Pollen Zone 3
Pollen Zone 2
Pollen Zone 1
NMDS2
NMDS1
0.6
0.4
0.2
0.0
-0.2
-0.4
-1.0
-0.5
0.0
0.5
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
27
28
29
30

Figure 7

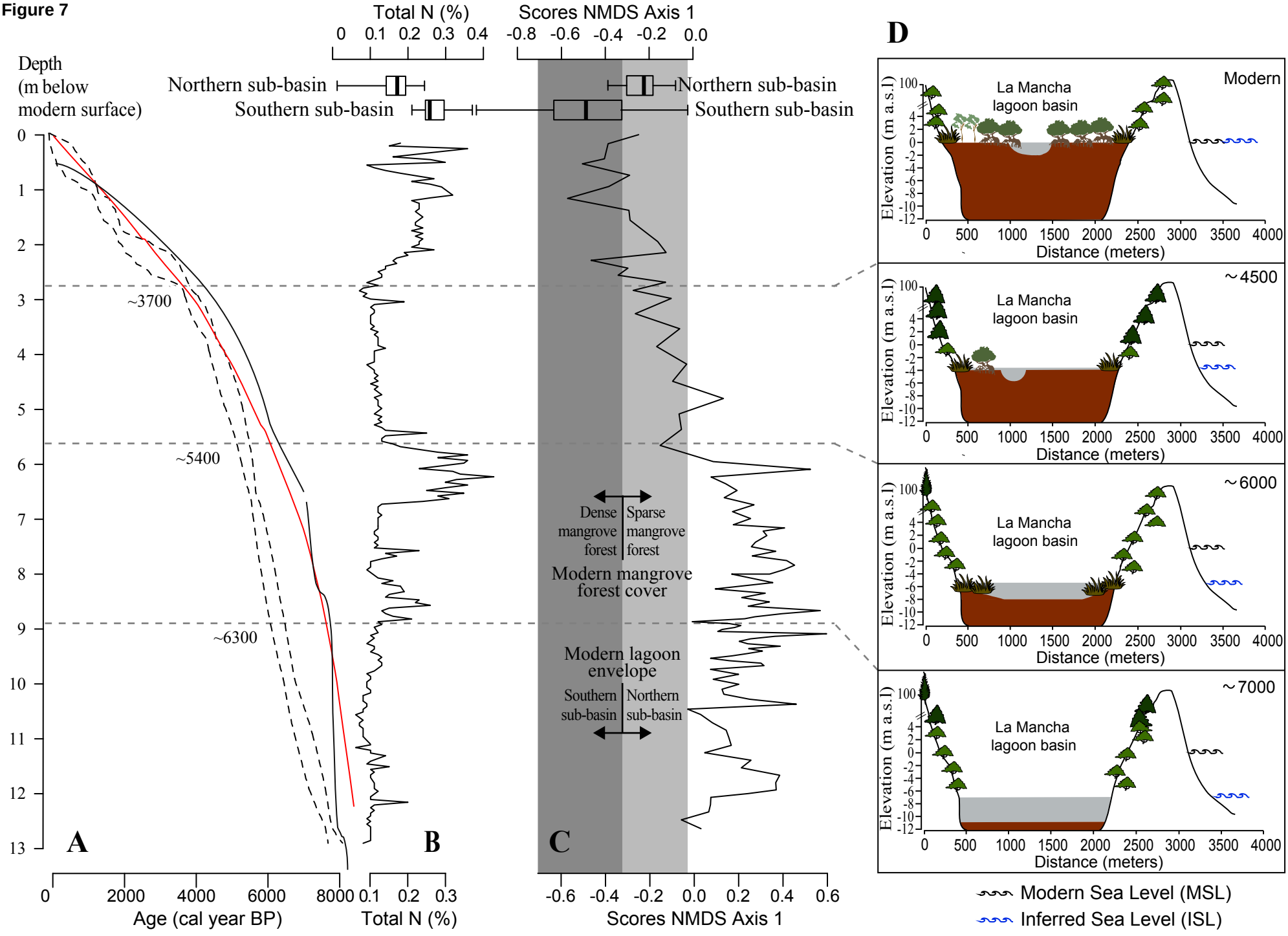

Total N (%)
0 0.1 0.2 0.3 0.4
Scores NMDS Axis 1
-0.8 -0.6 -0.4 -0.2 0.0
Depth (m below modern surface)
Northern sub-basin
Southern sub-basin
Northern sub-basin
Southern sub-basin
~3700
~5400
~6300
Dense mangrove forest
Sparse mangrove forest
Modern mangrove forest cover
Modern lagoon envelope
Southern sub-basin
Northern sub-basin
A
B
C
D
Age (cal year BP)
Total N (%)
Scores NMDS Axis 1
Elevation (m a.s.l)
Distance (meters)
La Mancha lagoon basin
Modern
~4500
~6000
~7000
Modern Sea Level (MSL)
Inferred Sea Level (ISL)

Figure Captions

Figure 1. Study area. A. Location of La Mancha lagoon in the continental context. B. Locations sampled for modern and fossil sediments in the local context of La Mancha coastal lagoon; elevation contours are shown in increments of 20 m asl (solid black lines), whereas a basic bathymetry based on field observations is shown as blue contours. C. Monthly precipitation (blue bars), evapotranspiration (gray bars), and monthly mean temperature (black line with dots) at La Mancha Meteorological Station (Servicio Meteorologico Nacional, 2018) D. Topographic representation of La Mancha coastal lagoon.

Figure 2. Core MAN15V from La Mancha coastal lagoon. A. Stratigraphy of the sedimentary sequence: texture (left), color (right), and organic and shell content. B. Age-depth model; calibrated ages (blue silhouettes), 95% confidence intervals in grey (darker colors indicate higher probability), and sedimentation rates (mm/yr). C and D. Percentage of total nitrogen and total carbon content (TN and TC, respectively).

Figure 3. Pollen diagram of selected taxa from mud-water interface samples from La Mancha coastal lagoon. Ecological affinities after Lugo and Snedaker (1974), Ramwell (1972), and Travieso-Bello (2000). Samples are ordered from South to North with samples from the southern (northern) sub-basin highlighted in dark (light) grey.

Figure 4. Content (%) of carbon and nitrogen in the modern samples of La Mancha coastal lagoon. Total C content (TC) discriminated into inorganic and organic fractions (TIC and

TOC), and total N content (TN). Comparisons among sedimentary attributes are shown in the right side panels (biplots and correlation coefficients with their significance).

Figure 5. Fossil pollen diagram of selected taxa of core MAN15V from La Mancha coastal lagoon. (ecological affinities after Lugo and Snedaker 1974, Ramwell 1972, and Travieso-Bello 2000).

Figure 6. Non-metric multidimensional scaling for modern and fossil pollen assemblages from La Mancha lagoon. Modern samples in black diamonds showing sample number, whereas fossil samples were symbol coded according to the declared legend.

Figure 7. Environmental history of La Mancha Lagoon through the last 7,800 years. **A.** Age-depth model of core MAN15V from La Mancha Lagoon (dashed lines show 95% confidence interval), compared with sea level rise curves for the Caribbean (red line, Toscano and Macintyre, 2003) and the northern Gulf of Mexico (black solid line, Milliken and Anderson, 2008). **B**. Sedimentary total nitrogen content (%); boxplots illustrate total nitrogen in modern samples form the northern (up) and southern (down) sub-basins of the lagoon (whiskers show minimum and maximum scores). **C**. NMDS Axis 1 scores through time; boxplots illustrate scores of modern samples; scores of the modern environmental envelope represented by modern samples are highlighted in grey; scores of the interquartile range of samples from the well preserved southern sub-basin are in dark grey. **D**. Schematic development of La Mancha Lagoon, illustrated at ~7,000, 6000, 4,500 cal BP, and Modern.

Supplementary material for on-line publication only

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