The oldest Holocene Caribbean mangroves and the postglacial sea level rise: biogeographical implications

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May 10, 2024

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The Neotropical mangroves originated in the southern Caribbean region (Fig. 1) during the Eocene (50-40 Ma), underwent a major evolutionary turnover in the Eocene/Oligocene transition (~34 Ma), and diversified during the Neogene (~23 to 2.6 Ma), to attain their present biogeographical and taxonomic configuration in the Quaternary (Rull, 2024). Due to their transitional sea-land nature, these tidal forested ecosystems have been considered to be excellent proxies for sea-level position in past paleoenvironmental reconstructions (Muller, 1959; Ellison, 1989; Khan et al., 2017). For the same reason, mangroves are expected to be significantly affected by the predicted future sea-level rise that, in combination with anthropogenic deforestation, are the main threats for the conservation of these singular tropical/subtropical coastal forests. In the Caribbean region, it has been estimated that, under current deforestation rates, what has taken evolution ~50 million years to build, could disappear in barely three centuries (Rull, 2023).
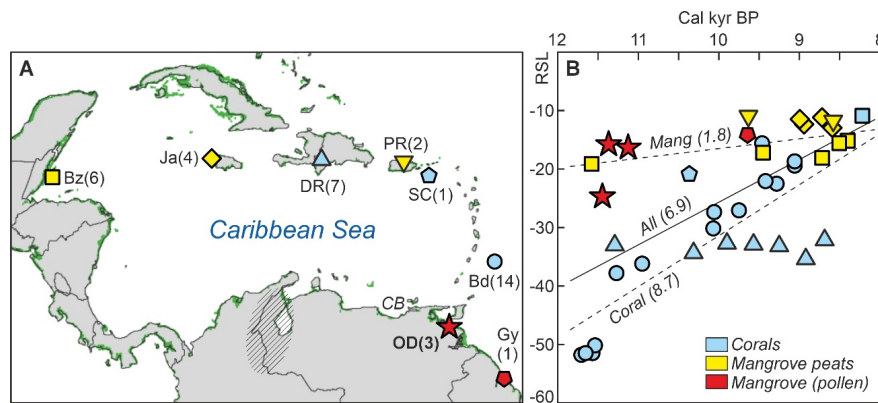
Figure 1. Location map and sea-level trends. A) Map of the Caribbean region (current mangrove areas in green) indicating the locations used for reconstructing the relative sea level (RSL) and the number of dates measured in parenthesis. Bd, Barbados; Bz, Belize; CB, Cariaco Basin; DR, Dominican Republic; Gy, Guyana; Ja, Jamaica; OD, Orinoco Delta; PR, Puerto Rico; SC, St Croix. The dashed area in the southern Caribbean coasts is the region of origin of Caribbean mangroves (Rull, 2024). B) RSL trends, in m below

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the present, corresponding to the Early Holocene. Raw data from Khan et al. (2017), except for OD (see Table 1). Linear regression lines and RSL rates (in m/1000 yr) are also indicated for the totality of records (All), the coral records (Coral) and the mangrove records (Mang).

At the beginning of the Quaternary (the last ~2.6 Ma), the Caribbean mangrove forests have already attained their present-day plant composition and dominance patterns. Therefore, Quaternary records of mangrove responses to natural and anthropogenic drivers of ecological change are often utilized as past analogs for predictive purposes in the face of future global change. The incompleteness of Quaternary pollen records, however, is a handicap for a thorough appreciation of these changes and their biogeographical expression. Indeed, Pleistocene mangrove records are almost lacking and most reconstructions using pollen correspond to the Holocene (the last 11.7 kcal yr BP). The Holocene mangrove record is also incomplete, as the only continuous sequences correspond to the Mid-Late Holocene (~8 cal kyr BP onward), and the Early Holocene is virtually absent (Rull, 2022). Indeed, a single isolate Early Holocene mangrove date (8590±65[14]C BP; 9465-9715 cal yr BP) from Guyana is available (Van der Hammen, 1961, 1963), which prevents the assembly of a reliable chronostratigraphic model for the Early Holocene Caribbean mangroves.

A palynological reconstruction that has just been published provides additional dates that extends the Holocene Caribbean mangrove record to around the Pleistocene/Holocene (P/H) boundary, which marks the end of the last glaciation (Pocknall & Jarzen, 2024). These dates are provided in ^{14}C years BP and have been calibrated here (Table 1) for homogeneity with the available Caribbean-wide mangrove review (Rull, 2022). Another date (11,090±50 ^{14}C yr BP at 7.62 cm depth) was considered as anomalous by these authors, possibly due to the presence of reworked material from older sediments. Pollen analysis revealed that samples corresponding to the 50.90-60.05 m sampling interval (Pollen Zone II), which include the dated samples of Table 1, were deposited within a mangrove environment dominated by *Rhizophora* and *Avicennia*, the two major mangrove trees of the Caribbean region.

Table 1. Sample depths (SD) and radiocarbon ages (RA) provided by Pocknall & Jarzen (2024) for the borehole BH-1 at Punta Pescador (first two columns). Here, SD have been corrected by the water depth at the boring site (3.66 m±2) (SD_w) and these new depths have been corrected by subsidence rates estimated for Punta Pescador (2.8 mm/yr; Warne et al., 2002) (CD_{ws}). TS, total subsidence. RA have been calibrated here (RA_c) with IntCal20 (Reimer et al., 2020) using CALIB 8.20 (*http://calib.org/calib/*).

SD (m)	RA (^{14}C yr BP)	SD_w (m)	TS (m)	SD_{ws} (m)	RA_c (2σ cal yr BP)	Median
50.90	9690±50	47.24±2	31.12	16.12±2	10797-11228	11114
51.05	9950±50	47.39±2	31.86	15.53±2	11242-11686	11378
60.05	9920±230	56.39±2	32.08	24.31±2	10699-12447	11457

To estimate the corresponding sea-level position from these mangrove age-depth data, the sample depths still need some corrections. First, the core was drilled at 12' (3.66 m) of water depth (Pocknall, pers. comm.); however, it is not known at which tide situation, which in the delta coasts has a diurnal amplitude of 2 m (Warne et a., 2020). Therefore, 3.66±2 m should be subtracted from the original samples depths (SD) to obtain the water-corrected sample depths (SD_w). Second, according to Kuhn et al. (2017), local tectonics and subsidence – i.e., the lowering of the land surface relative to a topographic datum – due to sediment compaction and dewatering, may be important in the Orinoco delta. No corrections for local tectonics is needed, as the delta is seismically quiescent (Warne et al., 2020). However, At Punta Pescador, near the coring site, subsidence rates are 2.88 mm/y (Warne et al., 2002). Therefore, the depth of the sample should be multiplied by this rate to obtain the total subsidence (TS), which should be subtracted from SD_w to obtain the actual sea level corrected by water depth and subsidence (SD_{ws}). See Table 1 for calculations.

The resulting age-depth points for mangroves, deduced from pollen analysis, are compared with the available Early Holocene relative sea level (RSL) trends for the Caribbean region (sensu lato). The most complete RSL curve available, with almost 500 index points and 240 limiting dates, estimated rising rates between

approximately 7.5 and 11 m/millennium (Khan et al., 2017) for sea levels between ~50 and ~10 m below the present (Fig. 1). The majority of dates for this reconstruction were obtained in coral reefs (~60%) with the rest derived from organic sediments identified as mangrove peats based on sedimentary features. Only one of these peats, from the above-mentioned Guyana record (Van der Hammen, 1963), was positively identified as a mangrove peat using pollen analysis. The new Orinoco delta samples fit well within this trend (Fig. 1) and represent the oldest mangrove samples analyzed palynologically available for the Early Holocene and the Lateglacial, up to 14 cal kyr BP, as all samples analyzed before the Holocene correspond to corals (Khan et al., 2017).

From a biogeographical perspective, the work by Pocknall & Jarzen (2024) not only contributes to the reconstruction of past sea levels, but it also aids in the geographical delimitation and expansion of Caribbean mangroves during the Early Holocene, when sea levels were rising fast after the ~120-m lowstand of the Last Glacial Maximum, attained ~20 cal kyr BP (Rull, 2022). During the LGM, the continental shelf was fully exposed and the coasts were close to the continental slope, which is less favorable for mangrove development due to the steep topography. Indeed, these ecosystems require shallow waters and protection from strong waves, which is usually provided by coral reefs. Therefore, the most suitable environments for mangrove growth occur in highstand conditions, when the flooded continental shelf provides flat, shallow and quiet tidal environments, and favor the development of corals in front of the coasts. During the LGM, mangroves were likely restricted to small favorable microrefugia (Rull, 2009) from where they expanded progressively until reaching their present extent. This is supported by the small amounts of mangrove pollen (<4%) recovered in the Cariaco Basin (Fig. 1) sediments corresponding to the last glaciation (68 to 28 cal kyr BP), just before the LGM, when sea levels were falling (González et al., 2008). These microrefugia were located offshore of present coasts, where the sea level was situated at those times.

Prior to the publication of the Early Holocene Orinoco delta record, the Guyana record suggested that mangroves would have begun to colonize coasts situated ~14m below the present sea level by 9.7-9.5 cal kyr BP (Fig. 1). The Orinoco data suggest that this colonization occurred before that, by 11.5 cal kyr BP, when mangroves established at sea levels ~25 m below the present. Interestingly, mangrove records, either confirmed palynologically or inferred sedimentologically, are as older as coral records but they are present at significantly shallower depths, and define different RSL rates. Indeed, the overall RSL rising rates (6.9 mm/yr) are similar to the rates estimated using only corals (8.7 mm/yr) and both fit with the Khan et al. (2017) rates for the Early Holocene mentioned above. However, using only mangrove samples, the RSL rising rates are significantly lower (1.8 mm/yr). Notably, the differences in depth between corals and mangroves of similar ages are maximal at the beginning and minimize with time. This could be linked to differences in habitat requirements and colonization patterns between these two ecosystems.

On one hand, corals are submerged marine organisms, whereas mangroves are restricted to the tidal coastal fringe, essentially at sea level itself. The preferred corals used in the Caribbean-wide reconstruction are *Acropora palmata* , which lives between 0 and 5 m depth, but also include other taxa that can live up to 30 m depth (Khan et al., 2017). This is more or less the difference that exists between coral and mangrove samples at the beginning of the Holocene, between 12 and 11 cal kyr BP (Fig. 1), and this coexistence under the same water-level conditions, is not surprising and is common in present-day Caribbean coasts. This does not mean that corals are not suitable indicators of sea-level position but, in multiproxy reconstructions of this type, the particular biological features of each proxy should be considered with care and in combination with others.

On the other hand, the absence of mangrove samples during the Lateglacial and their first appearance in the Early Holocene, as seen in the Orinoco delta record commented here, may be partly due to a delay in the colonization of Caribbean coasts under rising sea levels. It is possible that the postglacial colonization of the Caribbean coasts by mangroves from the small and restricted LGM microrefugia, which were living approximately 120 m below present sea levels, was not a quick process, especially under relatively rapid RSL rising trends. The Early Holocene mangroves recorded in the Orinoco delta by the P/H boundary could constitute a critical point beyond which mangroves initiated the full colonization of the coasts of the

Caribbean region and surrounding areas. This would have favored by slower RSL rising rates, as compared to former times (Khan et al., 2017). In summary, the work by Pocknall & Jarzen (2024) not only provide new data to improve our understanding of Caribbean mangroves in eustatic and biogeographical contexts, but also reinforces the utility of palynological records of mangroves as the best suited proxies for reconstructing the sea-level trends over time and space.

Acknowledgments

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