

Responses of the mangrove ecosystem to Holocene environmental change in the Sundarban Biosphere Reserve, India

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ABSTRACT. The Sundarban Mangrove Forest in the Sundarban Biosphere Reserve, located at the mouth of the Ganga–Brahmaputra Delta in India, is the most diverse mangrove ecosystem in the world. Sediment cores were taken from two widely separated islands in that reserve: Chamta (CMT) and Sudhyanyakhalai (SDK). Pollen analysis and radiocarbon dating were used to study the Holocene development and dynamics of this unique ecosystem. Modern pollen rain study reveals a strong relation between modern pollen rain and the present vegetation, as well as a high rate of *Phoenix palludosa* pollen production. The pollen records indicate that mangrove existed at CMT from ~5960 and at SDK from ~1520 cal yr BP. Changes in relative sea level, including the frequency and intensity of inundation as well as fluctuating precipitation, have been the major factors along with geomorphic processes that control the development and dynamics of the mangrove in the area during the Holocene. The mid Holocene mangrove at CMT declined, to be progressively replaced by successive communities, and eventually reached climax stage, while the SDK site is transitional in nature. The mangrove responds rapidly to changes in environmental conditions at both locations. Because of large-scale anthropogenic interventions, it is unlikely that similar rapid responses will occur in the future.

KEYWORDS: Delta, Holocene vegetation dynamics, pollen analysis, global change, sea level

INTRODUCTION

The Indian Sundarbans, located at 21°32'–22°40'N and 88°5'–89°10'E in the state of West Bengal, are famous for their extensive mangrove vegetation (Fig. 1) and are a Biosphere Reserve. The total area of the Indian Sundarbans is ~9630 km², of which 4264 km² is covered by mangrove, and 1738 km² by creeks, creeklets, estuaries and other waterways. The area has about 124 low-lying swampy islands formed by an intricate network of different types of water channels, 84 of which are inhabited by mangroves. This forest is unique as it is the most diverse mangrove ecosystem (Sanyal 1996, 2001a, Gopal & Chauhan 2006) and one of the two mangrove tiger lands in the world.

The Sundarban mangrove belongs to the category of littoral and swamp forest according to the vegetation mapping of the entire region (Das Gupta 1975). This littoral and swamp forest has been surveyed for vegetation types, plant distribution, plant associations, ecological succession (Rao & Sastry 1974, Chanda & Datta 1986, Naskar & Guha Bakshi 1989, Chaudhuri & Choudhury 1994, Blasco et al. 1996, Debnath & Naskar 1999, Naskar & Mandal 1999, Ellison et al. 2000, Gopal & Chauhan 2006, Giri et al. 2014, Ghosh et al. 2015, Barik et al. 2017, Danda et al. 2017, Mandal et al. 2019), modern pollen distribution (Pandey & Holt 2018, Pandey & Minckley 2019), change detection (Ghosh et al. 2015, Ghosh et al. 2016), impact of climate change and sea

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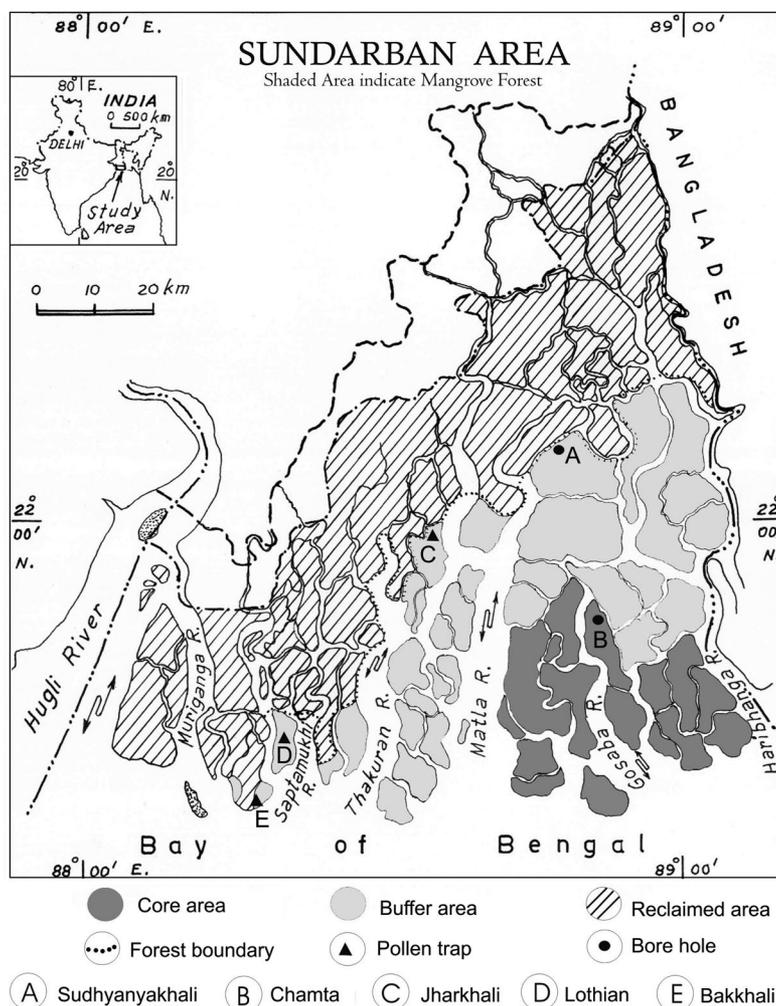


Fig. 1. Location map

level fluctuations on mangrove (Raha et al. 2012, Ellison 2015, Alongi 2015, Ward et al. 2016), biogeochemical and other studies (Ramanathan et al. 2009, Manna et al. 2010, Donato et al. 2011, Chowdhury & Maiti 2016, Majumder et al. 2016, Dutta et al. 2017).

Recent reviews by Sanyal (2001a) indicate the presence of 18 major mangrove species which are exclusively found in the inter-tidal zone and manifest typical mangrove adaptations such as pneumatophores, vivipary and salt glands. Fifteen other mangrove species (also found exclusively in the inter-tidal zone) and 51 species of back mangrove are found in the inter-tidal as well as beyond the tidal zone. The important tree taxa of the present-day Sundarban forest are *Avicennia* sp., *Excoecaria* sp., *Sonneratia* sp., *Rhizophora* sp., *Aegiceras* sp., *Bruguiera* sp., *Ceriops* sp., *Heritiera* sp., *Kandelia* sp. and *Xylocarpus* sp. The mangrove palm *Nypa* sp. and *Phoenix* sp., herbs like *Acanthus* sp., *Suaeda* sp. and *Porteresia* sp., and the mangrove fern *Acrostichum* sp.

are other important mangrove taxa present in the Sundarban forest.

This estuarine ecosystem has environmental, ecological and economic significance to the rapidly growing population of this region. The forest acts as a buffer and saves the hinterland from cyclones and storms during the monsoon, retaining sediment and thereby retarding coastal erosion. The ecosystem is very rich in nutrients and provides a habitat and breeding grounds for many species of fish and other economically important organisms. A large section of the population is also directly dependent on this forest for its livelihood (Chaudhuri & Choudhury 1994, Broadus 1996, Stanley & Hait 2000a, Gopal & Chauhan 2006).

Imbalances in this ecosystem have serious socio-economic and ecological implications. The delta was affected during the early and mid Holocene by natural factors such as an inclination towards the east and rising sea level (Blasco et al. 1996, Stanley & Hait 2000a, Gopal & Chauhan 2006, Hait & Behling 2009,

Barui 2011, Das 2014, Mishra et al. 2016, Sarkar & Sen 2019). In recent times, increasing human activity in the form of land reclamation and withdrawal of river water upstream has been responsible for habitat loss and enhanced salinity of both the water and soil (Milliman et al. 1989, Nazrul-Islam 1993, Alam 1996, Blasco et al. 1996, Allison 1998, Stanley & Hait 2000a, Gopal & Chauhan 2006, Zaman et al. 2013, Ghosh et al. 2015). Studies also indicate the presence of toxic material of anthropogenic origin in the soil, water and air of the Sundarban mangrove ecosystem (Santra 1994, Sikdar & Hait 1997, Sikdar et al. 1998, Saha et al. 2005, Gopal & Chauhan 2006, Manna et al. 2010, Ghosh et al. 2015, Chowdhury & Maiti 2016). Conservation of this unique ecosystem, which provides many benefits, is essential.

There have been many key advances in palaeobiological methodologies which may greatly improve the quality and relevance of palaeoenvironmental and palaeoecological studies for conservation biology. Palaeobiological studies can address questions about the biological vulnerability and resilience of a single taxon, a community, or a whole ecosystem facing environmental changes. This relates directly to conservation biology, including the design of biological reserves, the effect of biological and environmental change on ecosystem services, the stability of biogeochemical cycles, and the direct and indirect impacts of invasive species and extinction of species (Flessa & Jackson 2005, Willis & Birks 2006, Dietl & Flessa 2009, 2011, Jackson & Hobbs 2009, Willis et al. 2010, Birks 2012, Setyaningsih et al. 2019).

This study was undertaken to understand the biological, ecological and environmental changes that have taken place in and around study sites located in the core and buffer area of the Sundarban Biosphere Reserve, India, during the Holocene. This paper reports the first record of the Holocene vegetation and environmental history of the core and buffer area. The information obtained through this study can be used to formulate realistic conservation and management plans for this biologically unique ecosystem.

Another objective was to understand the relationship between the extant mangrove vegetation and modern pollen rain data, for better interpretation of fossil pollen data in studies of Holocene vegetation and palaeoenvironmental reconstruction.

STUDY AREA

LOCATION

The study sites are located inside the deltaic Sundarban mangrove forest (Fig. 1), which is a Biosphere Reserve. The forest forms the south-western part of the large Ganga–Brahmaputra Delta, between the Hugli River to the west and Haribhanga River to the east. The northern limit is demarcated by the Dampier–Hodges Line. The reserve is divided into core and buffer areas for management and conservation purposes. No human activity is allowed inside the core area. The area is further demarcated into three Wildlife Sanctuaries (Sajnekhali, Haliday, Lothian) and one National Park. The entire area of the National Park and the Sajnekhali Wildlife Sanctuary are included in the Project Tiger Area. This whole Biosphere Reserve has 22 forest blocks, of which the Sudhanyakhali (SDK) forest campsite of the Pirkhali forest block in the buffer area and the Chamta (CMT) forest campsite of the Chamta forest block in the core area of the Biosphere Reserve were selected for sediment coring.

GEOLOGY AND GEOMORPHOLOGY

The Ganga–Brahmaputra delta represents a late Quaternary sedimentation history (Stanley & Hait 2000a, Sarkar et al. 2009) and is underlain as well as bounded on three sides (east, north and west) by Precambrian metamorphic and Gondwana sediments and Mesozoic trap volcanics (Chanda et al. 1999). It is open to the sea on the south. Late Quaternary neotectonic activity that induced tilting of the delta region to the east altered the course of the Ganga–Brahmaputra–Meghna River system, resulting in an eastward shift in delta progradation (Sanyal 1990, Chaudhuri & Choudhury 1994, Blasco et al. 1996, Stanley & Hait 2000a).

The general lithology of the Holocene deposits of the coastal areas comprises fine to medium sand, silt and clay. Peat layers are also found in the north and northwest of the areas outside the present-day mangrove forest (Stanley & Hait 2000a, Stanley et al. 2000). The elevation is gentle, and most of the area is not more than 1 m above the present-day mean sea level (Delft Hydraulics 1989, Milliman et al. 1989, Jelgersma 1994, Broadus 1996).

Geomorphologically, the area is a set of tide-dominated estuaries with numerous linear tidal

sand bars and an extensive network of tidal channels, of which the larger channels (often 1.5 to 20 km wide) run north–south (Gopal & Chauhan 2006). The mouth of the estuary is funnel-shaped because of the high tidal amplitude of ~3.5 to 5.0 m (Chaudhuri & Choudhury 1994). A variety of habitats occur, including beaches, estuaries, swamps, tidal flats, tidal creeks, creek lets, coastal dunes and back dunes, and many of these are covered by dense mangrove (Sanyal & Ball 1986, Paul 1987a, b, Naskar & Guha Bakshi 1989, Gopal & Chauhan 2006).

STUDY SITES

Two different areas within the mangrove forest were selected for subsurface sediment sampling (Fig. 1). The first site, Sudhyanyakhali (SDK [A]: 22°06'09"N, 88°54'50"E) in the Pirkhali forest block, is located towards the north of the forest in the buffer area, and is part of the Sajnekhali Wildlife Sanctuary. The core was taken from an area which is apparently stable and not inundated regularly by tides. *Ceriops decandra*, *Excoecaria agallocha* and *Xylocarpus mekongensis* are the most common mangrove taxa in this block. *Bruguiera gymnorhiza* and *Avicennia* sp. are common along the creeks and creeklets. This forest block has a thick undergrowth of *Phoenix paludosa*.

The second site, Chamta (CMT [B]: 21°51'40"N, 88°54'56"E) of the Chamta forest block, is located in the core area of the Reserve, belongs to the category of National Park, and is remote and inaccessible during most times of the year. The block is characterized by high representation of low dense stands of *Ceriops decandra*, followed by *Excoecaria agallocha*. Species of *Xylocarpus* are also found scattered in this block. Other mangrove species are also present but in very low numbers. The core was collected from an area of *Ceriops* stands ~300 meters from the nearest active channel, which is not regularly flooded by tidal water.

Pollen traps were installed for collection of modern pollen rain data in three different areas in the buffer area of the Reserve (Fig. 1). The first site (Jharkhali [C] 22°00'N, 88°42'E) is towards the western part of the Reserve, where the vegetation is heterogeneous, with predominance of *Avicennia*, followed by *Excoecaria*. The second site is in the middle of a wildlife sanctuary (Lothian [D] 21°38'N,

88°19'E) within the Reserve, which is an isolated island. The site has profuse growth of *Avicennia* sp. *Ceriops decandra*, *Bruguiera gymnorhiza* and *Excoecaria agallocha* are found scattered in this block, with very low representation of other mangrove taxa. The third site (Bakkhali [E] 21°37'N, 88°18'E) is close to the coast; there, the predominant vegetation is *Excoecaria agallocha*, followed by *Aegiceras corniculatum* and *Phoenix paludosa*.

MATERIALS AND METHODS

FIELD SAMPLING

Sediment samples were collected from two different areas inside the Sundarban mangrove forest (Fig. 1), using a Russian sampler. Both cores (SDK, CMT) are 300 cm in length. Lithological descriptions were made and subsampling for palynological analysis was done immediately after recovery of the core.

Modern pollen rain data were collected with the type of pollen traps used by Behling et al. (2001) from three different locations (C, D & E; Fig. 1). Trapping of airborne pollen grains and spores was done using plastic tubes (h 11.5 cm, diam. 2.7 cm) filled with 5 cm³ glycerin and a few drops of phenol to avoid fungal growth. The tubes were covered with nylon mesh to avoid insects and debris. A set of five traps was installed ~15 m apart in each location. In the area inhabited by *Phoenix paludosa*, which is less inundated, the traps were installed 50 cm above the surface. In the swampy mangrove areas the traps were installed at ~2 m height to avoid tidal inundation. The collection period lasted one year from September 2002 to August 2003.

POLLEN ANALYSIS

For palynological study, 0.5 cm³ sediment was taken at 5 cm intervals along the cores. Prior to processing of the sediment and pollen rain samples, one tablet of exotic *Lycopodium* spores was added for calculation of pollen concentration (grains/cm³) and pollen accumulation rate (grains/cm²/yr). Palynological preparations were made following standard pollen analytical techniques (Erdtman 1969, Faegri & Iversen 1989). Slides were prepared with sample residues mounted in glycerin jelly medium. Published pollen morphological descriptions were consulted for identification of pollen grains and spores (Thanikaimoni 1987). The reference collection of the second author was also consulted for identification purposes. On the basis of ecological requirements and life form, taxa were grouped in the following categories: mangrove, non-mangrove (NM), herb, hypersaline herb (HSB), aquatics, fern, mangrove fern (MF), fungi, marine. Most of the samples were counted to a minimum of 300 pollen grains, including arboreal and nonarboreal pollen. This pollen sum excludes aquatic pollen, fern and fungal spores and marine taxa. The palynological data are presented in pollen diagrams as percentages of the pollen sum.

TILIA was used for calculations and CONISS was used for cluster analysis of pollen taxa. Cluster analysis is based on stratigraphically constrained pollen percentage data included in the pollen sum. TGVIEW was used to plot the pollen diagrams (Grimm 1987). The zonation of both cores is based on the cluster analysis and on conspicuous changes in the pollen assemblages.

RESULTS

STRATIGRAPHY

The general lithological unit in both cores is silt and clay. No peat was recorded in any of the cores. The lower part of the Chamta (CMT) core is black, sticky clay (300–290 cm). The next part of the core (290–0 cm) is grey silty clay with frequent occurrence of decomposed wood fragments.

The lower part (300–190 cm) of the Sudhyanyakhali (SDK) core is grey silty clay; a decomposed wood fragment was noted in the 300–230 cm interval of this sequence. The middle section (190–90 cm) is grey sticky clay. The lithology changes from clayey silt (90–45 cm) to silty clay (45–0 cm) in the top of the core.

CHRONOLOGY

Two organic-rich sediment samples (1 cm thick) from each location were taken and dated by accelerator mass spectrometry (AMS) at the Leibnitz laboratory of Christian-Albrecht-Universität in Kiel, Germany (Tab. 1). Only organic bulk sediments could be taken for dating. The dates were calibrated using Cal Pal (Weninger et al. 2004).

Two radiocarbon dates for the CMT core indicate deposits of mid and late Holocene age. The extrapolated age of the core base at 300 cm of the CMT core is 6083 cal yr BP. Sediment accumulation seems to be continuous,

probably without any gaps until the top of the core; this is probably modern in age.

The SDK core is younger. It began to accumulate at ~1520 cal yr BP (1635 + 30 ¹⁴C yr BP) at 295 cm core depth. The radiocarbon date from the upper section of this core at 120 cm shows a very old age of 9960 + 60 ¹⁴C yr BP. The record of an old age in a younger sequence in Holocene deltaic sediments probably is related to the remobilization of sediment that prevails in fluvial and deltaic plain (Stanley & Hait 2000b). To some extent the possible contamination of the sequence with older pollen and spores has to be taken into account. This old radiocarbon date has been excluded from the age calculations of each pollen zone. The age calculations for the zones of the SDK core are therefore somewhat limited and should be considered an approximation.

DESCRIPTION OF THE MODERN POLLEN RAIN DATA

Ten pollen trap samples from three different locations (C–E) were used for the modern pollen rain study. Three other samples from location C (Jharkhali) and two other samples from location E (Bakkhali) were contaminated, due to tidal inundation. Palynological study revealed 13 pollen types and 1 fern spore. Ten of the 13 pollen types belonged to mangrove (*Avicennia*, *Phoenix*, *Excoecaria*, *Acanthus*, *Aegiceras*, *Bruguiera*, *Ceriops*, *Rhizophora*, *Sonneratioa* and *Xylocarpus*), 1 to non-mangrove (*Borassus*), 1 to a hypersaline herb (*Suaeda*) associated with the mangrove environment, and 1 to Poaceae. The only spore type was assignable to the mangrove fern *Acrostichum aureum*. The percentages of the most frequent pollen taxa and the pollen influx rates are shown in Figure 2. The sum of each group and the fern spore *Acrostichum aureum* are also included in the diagram.

The three locations are inhabited by different types of mangrove plants. Locations C and D have higher representation of *Avicennia*, while *Phoenix* is dominant at location E, followed by *Excoecaria* and *Aegiceras*. Non-mangrove tree taxa are almost absent except in one sample at location C. Herb pollen are common in most of the locations except E. The dominance of *Avicennia* in the modern pollen rain is directly related to the higher representation of this plant in locations C and D. Regarding the domination of *Phoenix* at location E, we

Table 1. List of AMS radiocarbon dates of CMT and SDK core

Lab. no.	Depth cm	Age ¹⁴ C yr BP	Age cal yr BP	Material dated
Location: CMT				
KIA23357	103	2830 ± 40	2935 ± 51	Organic-rich sediment
KIA23358	295	5195 ± 35	5955 ± 31	Organic-rich sediment
Location: SDK				
KIA23360	120	9960 ± 60	11,404 ± 125	Organic-rich sediment
KIA23359	295	1635 ± 30	1519 ± 40	Organic-rich sediment

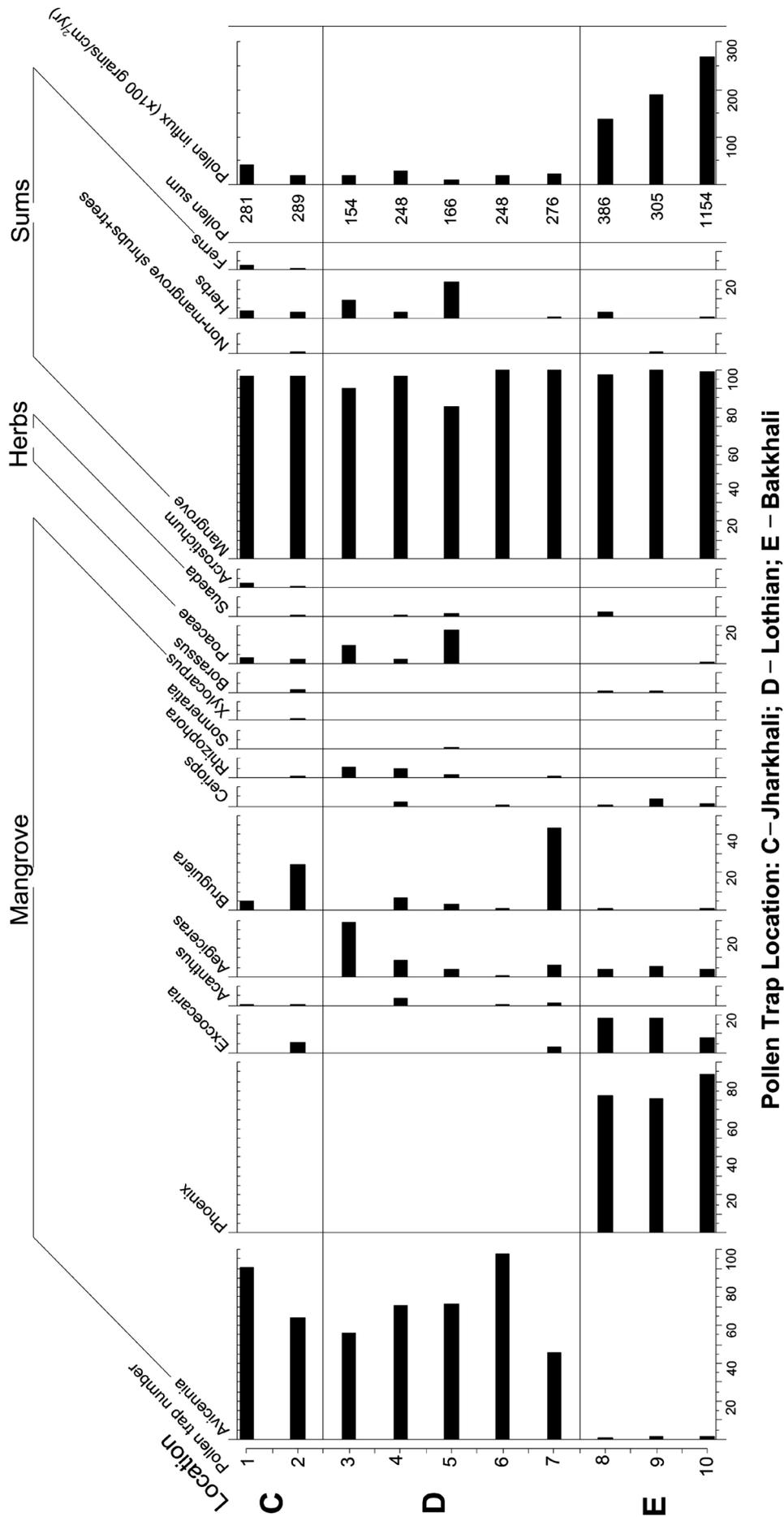


Fig. 2. Modern pollen rain data of Jharkhali, Lothian and Bakkhali in the Sundarbans

note that *Phoenix* is a high producer of pollen, while *Avicennia*, *Excoecaria* and *Aegiceras* are relatively low producers.

Pollen influx shows marked variation between sites **C–D** and **E**. It is very high (avg. 20 200 grains/cm²/yr) for the *Excoecaria*/*Phoenix*-dominated forest at location **E** and very low for the *Avicennia*-dominated mixed mangrove forest at locations **C** and **D** (2450 grains/cm²/yr).

Description of the Chamta (CMT) Pollen Diagram

The whole CMT pollen record is marked by abundant (80–90%) pollen types of different mangrove taxa. Non-mangrove and aquatic pollen is absent, while herbs, including hypersaline herbs, fungi and marine taxa, are rare in the analyzed core (Figs 3, 4).

Zone CMT-I (295–277 cm; ~5960–5660 cal yr BP; important taxa: *Phoenix–Excoecaria–Acrostichum*): This pollen zone is characterized by very high representation of the mangrove palm *Phoenix paludosa* (65–70%). Pollen of *Bruguiera*, *Excoecaria*, *Heritiera*, *Ceriops*, *Rhizophora*, *Avicennia* and *Sonneratia* is also present but in lower amounts. The hypersaline herb *Suaeda* is represented by some pollen. Other herbs are represented by some Poaceae and Cyperaceae pollen. Spores of the mangrove fern *Acrostichum* are frequent (5–20%) and increase through this zone. Other fern spores are represented in moderate percentages in this zone. Marine taxa are represented by some foraminifera (cf. *Ammonia*).

Zone CMT-II (277–205 cm; ~5660–4500 cal yr BP; important taxa: *Excoecaria–Avicennia–Nypa–Acrostichum*): This pollen zone is marked by a decrease of *Phoenix* pollen (30–55%), while *Excoecaria* (20–40%) increases significantly. *Avicennia* pollen is more frequent than in the previous zone. Other mangrove pollen types such as *Ceriops*, *Xylocarpus*, *Acanthus*, *Heritiera*, *Kandelia* and *Nypa* are present. Among the herbs, pollen of Poaceae, Cyperaceae and hypersaline *Suaeda* is present. *Acrostichum* spores (20–30%) are most frequent in this zone.

Zone CMT-III (205–90 cm; ~4500–2650 cal yr BP; important taxa: *Rhizophora–Ceriops–Bruguiera–Heritiera*): This pollen zone is characterized by high representation of *Rhizophora* (20–75%) and *Ceriops* (5–50%) and a marked decrease of *Phoenix* (0–3%). Other important mangrove pollen in this zone includes *Heritiera*

(2–20%), *Bruguiera* (0–40%) and *Excoecaria* (2–40%). Aquatic and non-mangrove pollen is totally absent. Pollen of the hypersaline herb *Suaeda* and spores of the mangrove fern *Acrostichum* are common to rare. Fungi are present in insignificant numbers at one level, while the foraminifera cf. *Ammonia* is almost consistent throughout.

Zone CMT-IV (90–0 cm; ~2560 cal yr BP – recent; important taxa: *Ceriops–Rhizophora*): The dominance of *Rhizophora* among the mangrove pollen grains is replaced by another mangrove taxon, *Ceriops* (45–90%). The decline of *Excoecaria* (0–5%) and *Heritiera* (0–7%) pollen is also noticed in this zone. Other mangrove pollen is rare. Non-mangrove taxa are absent, and pollen of plant groups including the hypersaline herb *Suaeda* and herbs are present in insignificant amounts. Fern spores, including those of mangrove ferns, are present but not common. An increase in the percentage of marine foraminifera is noticed in the upper part of the sequence.

Description of the Sudhyanyakhali (SDK) Pollen Diagram

Different mangrove pollen taxa are represented, with varying percentages (5–95%), in the SDK pollen record. The record is marked by the overwhelming representation of the hypersaline herb *Suaeda* (2–90%) during some restricted periods (Figs 5, 6).

Zone SDK-I (295–190 cm; ~1520–980 cal yr BP; important taxa: *Sonneratia–Excoecaria–Avicennia–Suaeda*): Mangrove pollen is dominant (50–95%) in this zone, followed by hypersaline herbs *Suaeda* (5–30%) and other herbs. Non-mangrove pollen is rare (0–2%). Fern spores are common. Fungi and aquatics are rare and are present at few levels. Marine taxa are common in the upper part of this zone. Among the mangrove taxa, *Sonneratia* is dominant (25–70%), followed by *Excoecaria* (5–30%), *Avicennia* (2–10%) and *Acanthus* (1–5%) pollen. Other mangrove taxa are present but in insignificant amounts. The mangrove fern spore *Acrostichum* is present through almost the whole zone and is abundant at two levels. The hypersaline herb *Suaeda* is also conspicuous (5–30%). Pollen of Cyperaceae is dominant among the other herbs. Aquatics are represented by *Typha* pollen.

Zone SDK-II (190–120 cm; ~980–480 cal yr BP; important taxa: *Suaeda–Sonneratia–Excoecaria*): The overall dominant pollen

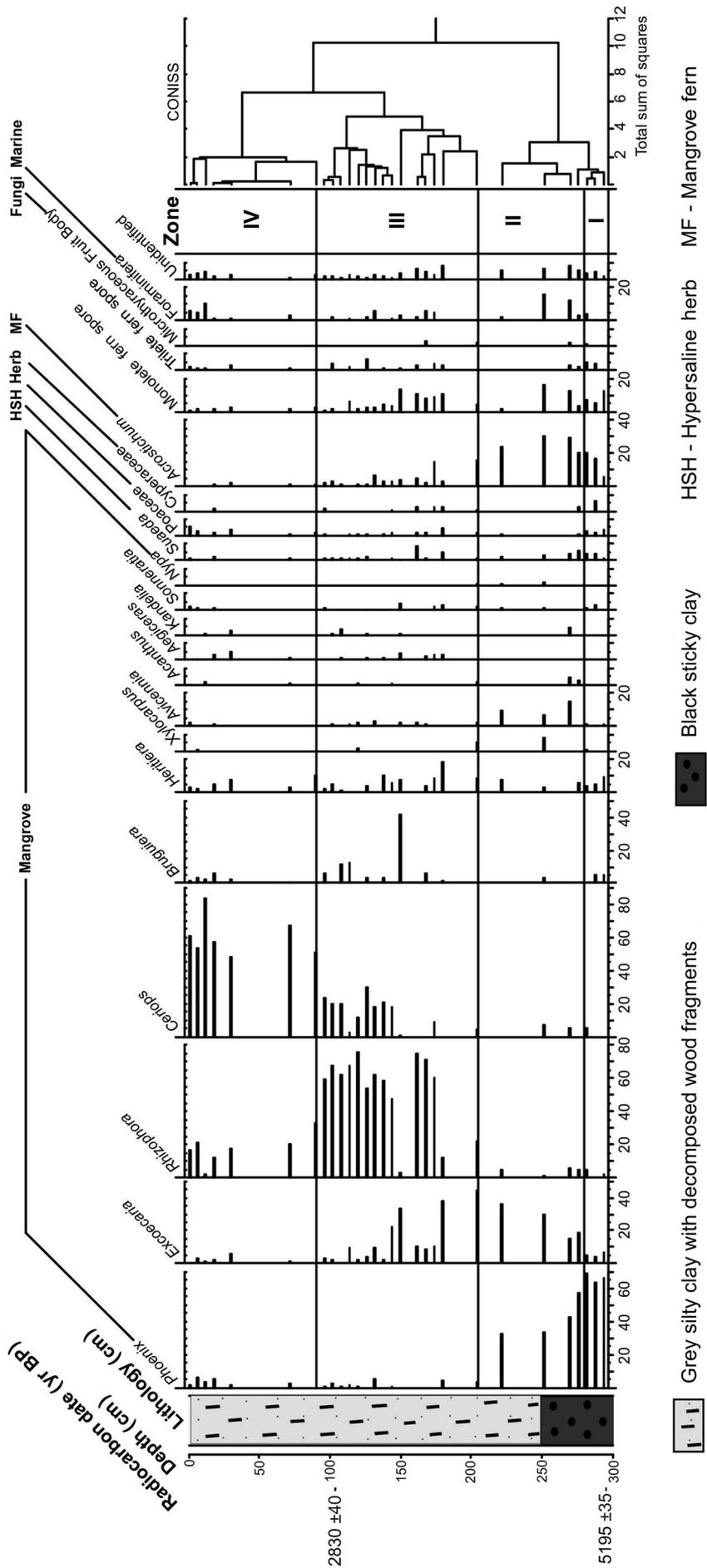


Fig. 3. Percentage diagram of the CMT core

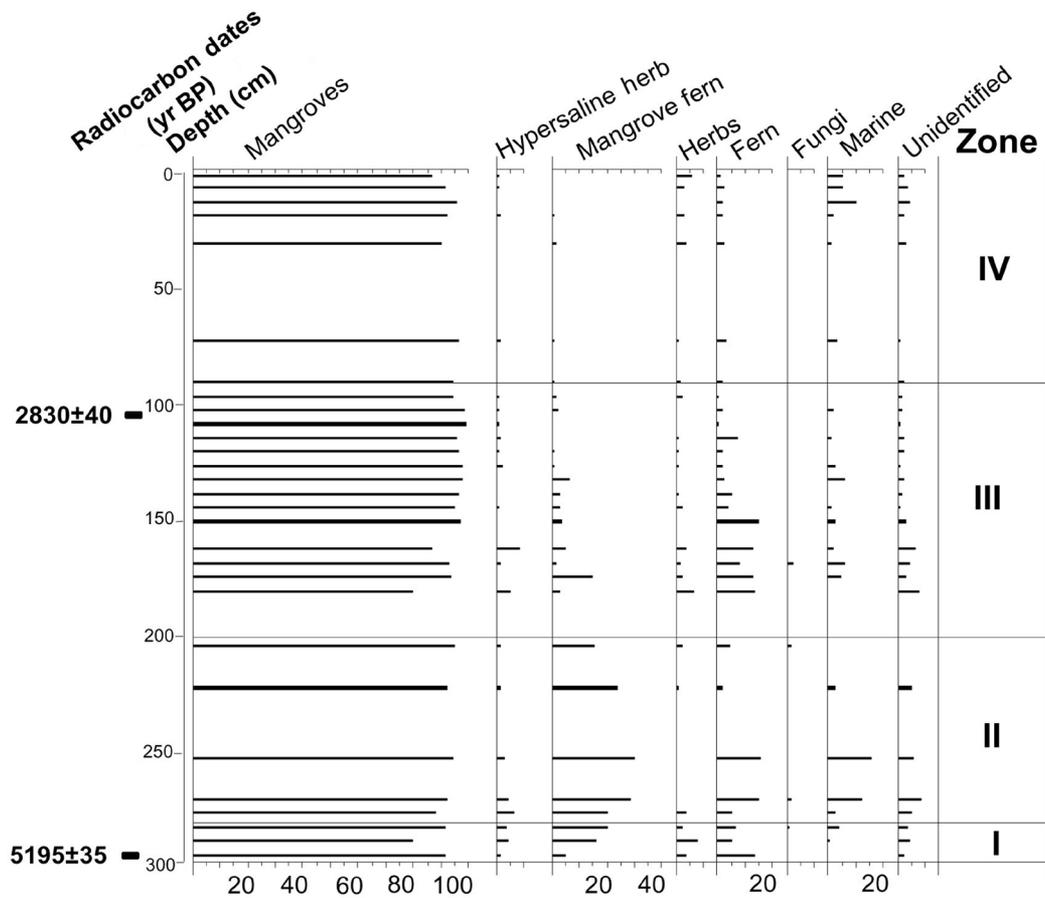


Fig. 4. Sums of different ecological groups and zones of the CMT core

taxon in this zone is *Suaeda* (40–90%). Non-mangrove and herb pollen, fern spores, fungi and marine taxa are common to rare in this zone. The frequent mangrove pollen in this zone consists of *Excoecaria* (2–30%) and *Sonneratia* (2–16%). The other mangrove pollen present in this zone includes *Acanthus*, *Avicennia*, *Aegiceras*, *Bruguiera*, *Heritiera*, *Phoenix* and *Rhizophora*.

Zone SDK-III (55–0 cm; ~480 cal yr BP – recent; important taxa *Avicennia*–*Excoecaria*–*Rhizophora*–*Bruiguiera*–*Sonneratia*): This zone is separated from the previous zone by a sequence of sediment having insignificant shares of pollen grains. Higher representation of mangrove pollen (80–95%) is noted in this zone, followed by pollen of hypersaline herbs. Non-mangrove pollen is insignificant and present at one level only. Members of other groups such as herbs, ferns and fungi are present. This zone is marked by a higher share of marine foraminifera (cf. *Ammonia*). The dominant mangrove pollen is *Avicennia* (20–50%), followed by *Excoecaria*, *Rhizophora*, *Bruguiera* and *Sonneratia*. Pollen grains of *Aegiceras*, *Cerriops* and *Xylocarpus* are also

recorded in this zone. *Suaeda* pollen is present but in a much lower amount (1–10%) than in the previous zone.

ENVIRONMENTAL CHARACTERISTICS OF THE SUNDARBAN MANGROVE

A variety of habitats are available in the Sundarbans, of which the shallow estuarine, deltaic and coastal mudflats are the preferred habitats of halophytic mangrove vegetation. These are the areas with the least disturbance of tidal currents and waves. This condition facilitates the growth, development and proliferation of mangrove plants (Sanyal & Ball 1986, Paul 1987a, b, Naskar & Guha Bakshi 1989, Danda et al. 2017, Mandal et al. 2019).

The modern distribution of mangrove vegetation is controlled by tidal magnitude, besides other factors like the physiography of the area, the nature of the substrate and the salinity gradient (Lugo & Snedaker 1974, Sanyal & Ball 1986, Naskar & Guha Bakshi 1989, Woodroffe 1990, Nazrul Islam 1993, Chaudhuri & Choudhury 1994, Paul 1996, Blasco et al. 1996, Duke et al. 1998, Ellison et al.

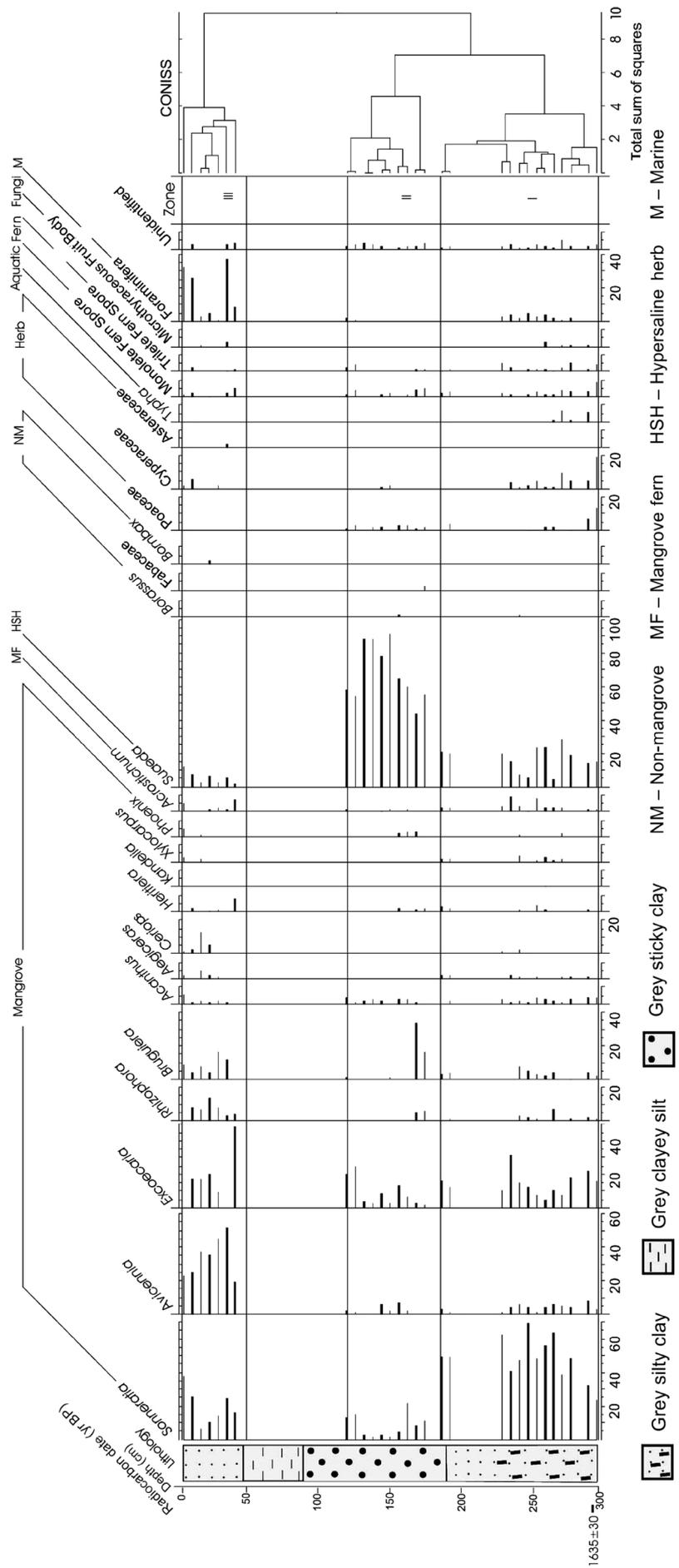


Fig. 5. Percentage diagram of the SDK core

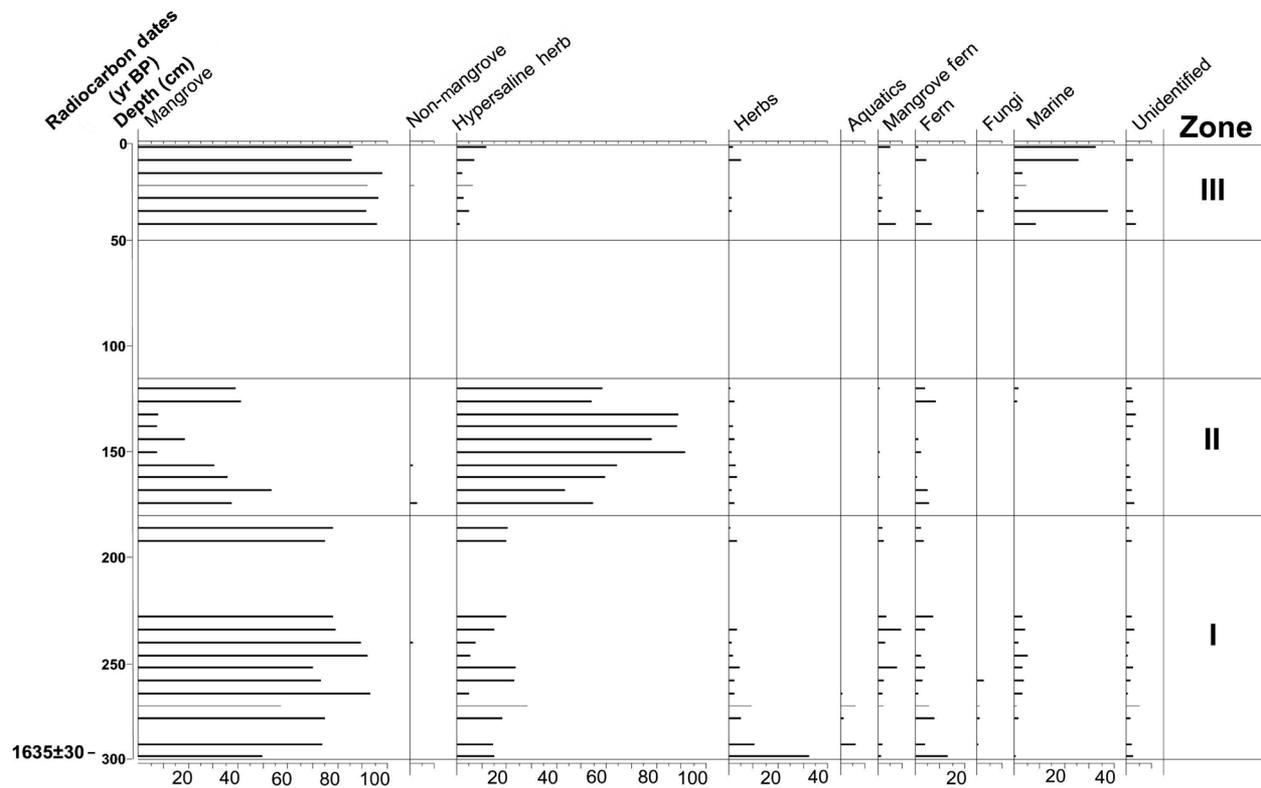


Fig. 6. Sums of different ecological groups and zones of the SDK core

2000, Grindrod et al. 2002, Anthony 2004, Ellison 2005, 2008, Gopal & Chauhan 2006, McKee et al. 2007, Gilman et al. 2008, Zaman et al. 2013, Ghosh et al. 2015, Lovelock et al. 2015, Barik et al. 2017). These plants are not common to all parts of the forest, and their distribution along the flooding gradient is often discussed in the context of zonal or successional stages (Johnstone 1983, Untawale 1987, Naskar & Guha Bakshi 1987, Chaudhuri & Choudhury 1994, Naskar & Mandal 1999, Gopal & Chauhan 2006). Studies on mangroves based on statistical analyses have, however, failed to detect any zonation pattern with respect to edaphic factors that co-vary with elevation (Ellison et al. 2000).

In general, *Rhizophora* forms the outermost zone, subjected to maximum salinity and regular submergence. This outer zone is followed by mixed stands of *Bruguiera*, *Heritiera*, *Xylocarpus*, *Excoecaria* and *Phoenix*, with a landward zone of *Ceriops*. *Avicennia* is the dominant plant in recently formed areas along with *Sonneratia*. Increasing salinity is responsible for an increase in both *Excoecaria* and *Ceriops*, gradually replacing other species in the area. Dense thickets of the mangrove palm *Phoenix paludosa* are also a common forest type in the dry soils of the Sundarbans (Chaudhuri

& Choudhury 1994, Blasco et al. 1996, Naskar & Mandal 1999, Gopal & Chauhan 2006). Table 2 presents a consolidated account of the ecological and environmental requirements of the mangrove and mangrove-associated taxa found in the pollen record.

INTERPRETATION AND DISCUSSION

EXTANT VEGETATION AND MODERN POLLEN RAIN

The primary objective of this study was to evaluate whether the pollen rain data obtained from pollen trap samples can serve as a reliable tool for inferring the vegetation assemblages growing at the sampled locations. In general, the pollen data recorded by the pollen traps in this study are mainly restricted to the local vegetation. There are many records of pollen grains of mangrove taxa such as *Avicennia*, *Excoecaria* and *Bruguiera* in location C (Jharkhali); *Avicennia*, *Aegiceras* and *Bruguiera* in location D (Lothian); *Phoenix paludosa*, *Excoecaria* and *Aegiceras* in location E (Bakkhali). Other mangrove taxa such as *Ceriops*, *Rhizophora*, *Sonneratia* and *Xylocarpus* show a strong connection between modern pollen rain taxa and the present vegetation of the

studied area. This means that the modern pollen rain obtained with pollen traps is strongly related to the proximity of source vegetation. Similar findings have been reported from other mangrove areas (Behling et al. 2001, Urrego et al. 2010) including the Sundarbans (Pandey & Holt 2017, Pandey & Minckley 2018); except for the first-mentioned work, however, these studies analyzed pollen of surface sediment. Behling et al. (2001) studied both pollen traps and surface samples. The high presence of local pollen in the pollen rain data and the very small input of pollen from farther away could also be correlated with the pattern of wind direction. In these areas the wind blows from the southeast to the mainland for most of the year except for a brief period during winter. Hence, transport of non-mangrove pollen grains from the adjacent hinterland is rare, as evidenced by the occasional presence of strictly freshwater non-mangrove taxa in the modern pollen spectra (Fig. 2).

The results on pollen influx indicate that *Phoenix* is a strong pollen producer, while *Excoecaria*, *Avicennia* and *Aegiceras* are relatively low pollen producers. The low representation of *Excoecaria*, *Avicennia* and *Aegiceras* could be due to the fact that these genera are insect-pollinated (Tomlinson 1986, Raju et al. 2012).

HOLOCENE POLLEN RECORD

The pollen diagrams of the **CMT** and **SDK** cores show the presence of qualitatively important and quantitatively significant mangroves throughout the recorded mid and late Holocene (Figs 3–6). This indicates that the two core sites, located in widely separated forest areas, developed in an estuarine mangrove setting throughout the deposition period. The modes of development differed, however.

RESPONSES OF THE MANGROVE ECOSYSTEM TO HOLOCENE ENVIRONMENTAL CHANGE

Chamta location (CMT): The bottom sediments of the CMT core record the presence of mangrove pollen grains, indicating the existence of a mangrove forest close to the study site. The period between ~5960 and 5660 cal yr BP (Zone CMT-I) was inhabited by mixed mangrove vegetation including *Phoenix*, *Excoecaria*, *Bruguiera* and *Heritiera*. This zone is marked by a very high percentage of

Phoenix pollen. The pollen production of *Phoenix* is very high, as indicated by the modern pollen rain data (Fig. 2). The modern analogue of this zone is characterized by clumps of *Phoenix* with *Excoecaria*. This type of climax forest with dominance of *Phoenix* is found in different parts of the present-day Sundarbans, which are just above the mean tide level and not inundated regularly (Naskar & Guha Bakshi 1989, Chaudhuri & Choudhury 1994, Naskar & Mandal 1999, Mandal et al. 2019).

After ~5660 cal yr BP a change in lithology is noted, with an increase in *Excoecaria*. Between ~5660 and 4500 cal yr BP (zone CMT-II), more or less the same combination of plants continues, but the dominance of *Excoecaria* over *Phoenix* and the stronger presence of intertidal mangrove plants (viz. *Avicennia*) and marine foraminifera (cf. *Ammonia*) indicate the frequent influence of inundation and a consequent increase in salinity.

After ~4500 cal yr BP (zone CMT-III), the composition of the vegetation changes; the area was covered by intertidal *Rhizophora*, with significant shares of *Bruguiera* and *Ceriops*. *Rhizophora* forms the outermost zone and with *Bruguiera* and *Ceriops* prefers relatively saline and frequently inundated habitats (Chaudhuri & Choudhury 1994, Blasco et al. 1996, Naskar & Mandal 1999, Gopal & Chauhan 2006).

The composition changes again from *Rhizophora* to *Ceriops*-dominated mangrove forest after 2560 cal yr BP (zone CMT-IV). *Ceriops* grows landward and appears as the climax stage in the relatively moderate- to high-saline areas of the Sundarban Biosphere Reserve (Chaudhuri & Choudhury 1994, Gopal & Chauhan 2006). *Ceriops*-dominated forest still occurs in the area today. The modern mangrove forest with 2–3 m tall *Ceriops* is generally inundated by tides (Tab. 2).

Sudhyanyakhali location (SDK): The mangrove was well established from the beginning of records at ~1520 cal yr BP, dominated by intertidal *Sonneratia*, *Avicennia* and *Excoecaria* (Zone SDK-I). *Avicennia* and *Sonneratia* were the dominant plants in newly built-up areas (Mandal et al. 2015). This species combination is found in different parts of the present-day forest, on the mud flats and below the tide level (Naskar & Guha Bakshi 1989, Chaudhuri & Choudhury 1994, Naskar & Mandal 1999).

The following period between ~980 and 480 cal yr BP (zone SDK-II), with dominance of the

Table 2. Ecological and environmental requirements of the mangrove and mangrove-associated taxa found in the pollen record (after Sanyal & Ball 1986, Paul 1987b, Sen & Bannerjee 1990, Naskar & Guha Bakshi 1989, Chaudhuri & Choudhury 1994, Naskar & Mondal 1999, Behling et al. 2001, 2004, Gopal & Chauhan 2006, Mandal et al. 2019)

Taxon	Ecology/Habitat
<i>Sonneratia</i>	Seaward fringes of the outer estuary, and best adapted in areas with regular inundation and normal salinity. Also found in newly accreted areas.
<i>Rhizophora</i>	Mouths of creeks, creeklets and small rivers in the middle part of the estuary with regular inundation and moderate to high salinity.
<i>Avicennia</i>	Common in intertidal river flats and slopes with normal salinity. Also found in newly accreted areas.
<i>Aegiceras</i>	Less saline and newly silted inner estuarine areas with regular inundation.
<i>Bruguiera</i>	Common on riverbanks and ridges in the middle estuarine region with frequent inundation.
<i>Excoecaria</i>	Common in slightly elevated and well-drained inner estuarine areas with moderate to low salinity.
<i>Xylocarpus</i>	Common in well-drained areas in the middle estuarine region with fewer than 10 inundations per month.
<i>Phoenix</i>	Inner estuarine areas on mature dry soil along rivers that flood only during spring tides.
<i>Heritiera</i>	Less saline inner estuarine area along rivers that flood only during spring tide and that receive sufficient freshwater from upstream.
<i>Ceriops</i>	Moderate- to high-saline middle estuarine areas with regular inundation in general.
<i>Nypa</i>	Less saline wet and flat river banks in the inner estuarine region receiving regular supply of freshwater.
<i>Acanthus</i>	Common in regularly inundated intertidal inner estuarine areas.
<i>Suaeda</i>	Slightly raised and less inundated areas, sometimes on denuded surfaces where soil salinity is particularly high.
<i>Acrostichum</i>	Found particularly in disturbed habitats with irregular inundation.

hypersaline herb *Suaeda*, indicates slightly raised substrate and consequently less inundation (Tab. 2). However, the surrounding area was low and influenced by tides, as indicated by the record of the mangrove taxa *Sonneratia*, *Avicennia*, *Aegiceras*, *Excoecaria* and *Rhizophora*. The less frequent inundation at the site during this period caused dryness and increased salinity of the substrate, which was colonized by the hypersaline herb *Suaeda*. In the Sundarbans the modern analogue of this type of vegetation is found in slightly raised areas of hypersaline soil vegetated by *Suaeda*, with tidal and intertidal taxa in the low-lying vicinity (Naskar & Guha Bakshi 1989, Chaudhuri & Choudhury 1994, Naskar & Mandal 1999, Mandal et al. 2019).

During the last period, after ~480 cal yr BP (zone SDK-III), intertidal mangrove reappeared to a significant extent, represented mainly by *Sonneratia*, *Avicennia*, *Excoecaria*, *Rhizophora* and *Bruguiera*. The higher occurrence of foraminifera (cf. *Ammonia*) is also indicative of a higher frequency of inundation during this period. At present the site is inundated only during spring tides, and it appears to be somewhat degraded. Adjoining areas are covered by mixed mangrove plants including *Phoenix*. This is also reflected in the upper part of the pollen diagram as the reappearance of *Phoenix* pollen

and the abundance of the hypersaline *Suaeda* and the mangrove fern *Acrostichum*.

COMMENTS ON THE MODE OF HOLOCENE MANGROVE DEVELOPMENT AND DYNAMICS

The mangrove ecosystems of the two islands – Chamta (CMT) in the core area and Sudhyanyakhal (SDK) in the buffer area of the Biosphere Reserve, both in the Sundarban mangrove forest and both within a similar regional environment – differ in their Holocene dynamics. This is due to local differences in ecological and geomorphological conditions. The mangrove responds to changes in relative sea level as well as to geomorphological processes at the two locations.

The pollen record of CMT indicates that the mangroves kept pace with sedimentation and relative sea level in the area from 5960 cal yr BP. The mid Holocene mangrove vegetation (5960 cal yr BP) was replaced by successive mangrove communities as ecological conditions changed and eventually reached the climax stage at this location in the late Holocene. This is evident from the pollen record, where the top pollen zone (CMT-IV) is dominated by the landward *Ceriops*. This site is important in view of the continuous presence of *Heritiera* along with *Nypa* pollen in some sequences. These two

genera require a regular supply of fresh water for their optimum growth and development (Sanyal 1990, 2001b, Chaudhuri & Chaudhury 1994, Naskar & Mandal 1999, Gopal & Chauhan 2006). Their presence in the pollen record is indicative of the balance between fresh and brackish water during the mid to late Holocene at this location. In recent times, however, the balance has been altered; less fresh water is getting into the system (Milliman et al. 1989, Sanyal 1990, Nazrul-Islam 1993, Alam 1996, Blasco et al. 1996, Allison 1998, Stanley & Hait 2000a, Gopal & Chauhan 2006, Ghosh et al. 2015, Mandal et al. 2019). This has resulted in a declining trend of *Heritiera* noted in the upper part (CMT–IV) of the pollen record of CMT.

The SDK site experienced a period of less frequent inundation and hypersaline conditions from ~980 to 480 cal yr BP, seen in the high frequency of pollen of *Suaeda* (zone SDK-II), a highly salt-tolerant shrub forming scattered patches in salt-encrusted areas among mangrove shrubs (Blasco & Aizpuru 2002). Local geomorphological processes were responsible for the formation of raised substrate, eventual lowering of relative sea level, less inundation, and hypersaline conditions. The following period shows the frequent occurrence of seaward mangrove genera such as *Sonneratia* and *Avicennia*, which indicates that an intertidal habitat was restored at the study site and that the site was in a transitional stage. This site is characterized by very low occurrence of *Heritiera*, the complete absence of *Nypa* pollen and high abundance of the hypersaline *Suaeda*. All this indicates more saline conditions during the deposition of late Holocene sediment at this location. Sedimentation at this location was also influenced by processes responsible for deposition of older sediments in a much younger sequence (Tab. 1); contamination from some older pollen is possible.

The mid and late Holocene changes in vegetation illustrate the dynamic nature of the forest in response to changes in environmental factors at the two locations during the late Holocene, continuing until recent times. At present both areas are sheltered, away from major estuaries, and the influence of direct tidal currents is feeble, but CMT is inundated by tidal water more than SDK is.

The sediment cores used for reconstructing the vegetation development and dynamics in the core and buffer areas of the Sundarban

Biosphere Reserve (India) yielded ages up to 5960 cal yr BP and exhibited sufficient signatures for palaeoclimatic reconstruction. The pollen profiles are represented by both C3 and C4 types of plants. C4 plants are better adapted to dry, water-stressed conditions than are C3 plants (Bond et al. 2005, Sarkar et al. 2009). In general, the regional vegetation record between 5960 cal yr BP (CMT site) and 980 cal yr BP (SDK site) is dominated by warm humid climate-loving C3 plants represented by different species of mangroves. However, the vegetation record from 5960 to 5660 cal yr BP (Location CMT) is dominated by *Phoenix* (C3 plant), a taxon that generally grows in higher, less inundated areas (Tab. 2), indicating lower precipitation during this period. The period between 5660 cal yr BP (CMT site) and 980 cal yr BP (SDK site) is represented by different species of intertidal C3 types of mangrove plants in different successive stages, indicating more humid conditions from increased precipitation. However, the strong signatures of the hypersaline taxon *Suaeda*, a C4-type indicator of dry to arid conditions, in pollen zone SDK-II (980–480 cal yr BP) is indicative of a weaker monsoon and consequent water-stressed conditions during this period. Studies on the Indian summer monsoon using different proxies also indicate that the amount and intensity of the monsoonal rains have fluctuated since the early Holocene on the Indian subcontinent (Gupta et al. 2006, Thamban et al. 2007, Clift & Plumb 2008, Sarkar et al. 2009, Singhvi et al. 2012, Shah et al. 2017, Ali et al. 2018). In general the early Holocene has been characterized by monsoon intensification followed by largely arid conditions since the mid Holocene, with intermittent short periods of strengthened monsoonal periods. The present study of the past vegetation history of core and buffer areas of the Sundarban mangrove forest also broadly corroborates the past climate record.

CONCLUSIONS

Our palynological analysis of radiocarbon-dated cores recovered from core and buffer sites in the Sundarban mangrove forest provides a basis for understanding the development and dynamics of the mangrove ecosystem in the area during the mid and late Holocene. It revealed that changes in relative sea level, including the frequency and intensity of

inundation and precipitation, have been the major factors in addition to the geomorphic processes that controlled mangrove development and dynamics in the area during the Holocene. The mangrove exhibits resilience, responding rapidly to changes in environmental conditions at both locations since the mid Holocene. Modern pollen rain data shows the predominance of mangrove taxa in the pollen spectra, demonstrating a close connection between modern pollen rain and the present-day vegetation.

Currently, anthropogenic factors prevail over natural factors. The coastal environment is being altered due to reduced inflow of fresh water to the system, increased input of pollutants, and large-scale removal of the mangrove for settlement, agriculture and aquaculture (Milliman et al. 1989, Nazrul-Islam 1993, Santra 1994, Alam 1996, Blasco et al. 1996, Sikdar & Hait 1997, Sikdar et al. 1998, Allison 1998, Stanley & Hait 2000a, Saha et al. 2005, Gopal & Chauhan 2006). Increased salinity due to reduced flow of fresh water has been the subject of much discussion recently. It is causing recolonization of species, stunted growth, and both qualitative and quantitative changes in the forest ecosystem (Sanyal & Ball 1986, Sanyal 2001b, Gopal & Chauhan 2006). The ecological impacts of pollution are uncertain because detailed information is lacking.

More recently the mangrove ecosystem is being threatened by global climate change. Of all the outcomes of climate change, rising sea level may be the greatest threat to the mangrove (Ellison & Stoddart 1991, Ellison 1994, 2015, Gilman et al. 2008, Krauss et al. 2014, Ward et al. 2016, Setyaningsih et al. 2019). As said above, the Holocene mangrove vegetation of the two studied sites exhibits resilience, responding to changes in the environmental condition at both locations since the mid Holocene, but it is unlikely that similar rapid responses will occur in the future. The mangrove's ability to respond is compromised by large-scale anthropopression in the hinterland as well as inside the Biosphere Reserve.

To advance our knowledge of landscape-scale changes in mangrove vegetation diversity through time and space, we need to reconstruct the past vegetation history of evenly distributed, radiometrically dated cores from core and buffer areas, and to generate data from more pollen traps in different mangrove

forest types. Surface samples are also needed. Such work will have important implications for management, conservation and habitat restoration in this economically important, ecologically sensitive, unique mangrove tiger land.

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