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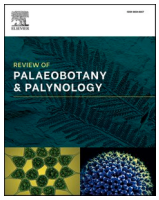

Mid-Late Holocene palynological development at Lake St Lucia, KwaZulu-Natal

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ABSTRACT

Palynological studies were done on lacustrine core sediments in the Indian Ocean Coastal Belt Biome of KwaZulu-Natal, eastern South Africa, that were deposited during the last ~6300 cal yrs BP in the Mkuze River delta that drains into the northern-most part of Lake St Lucia. The aim was to reconstruct the past vegetation and to infer past climate fluctuations as well as human disturbances to complement growing evidence from other disciplines about these aspects in the area. Palynological results show a dominance of Poaceae (20–50%) suggesting the consistent presence of grassy woodland. *Podocarpus* pollen dominated the arboreal spectra from 6300 to 2600 cal yrs BP. Thereafter *Spirostachys* pollen dominated the arboreal pollen spectra for the last 2600 cal yrs BP indicating a change from a forested environment to a more open woodland environment caused by a drop in moisture content (humidity). The results also show that the mid Holocene was humid and warm with high precipitation (freshwater conditions) coinciding with raised sea levels. The late Holocene was warm and dry with some marine influence with more seawater flowing into the estuary and lake due to high evaporation and low fresh water supply caused by drought. Similar pollen fluctuations were observed in records from Lakes Eteza and Sibaya, also located within the Indian Ocean Coastal Belt Biome. The presence of *Pinus* pollen at the top of the profiles suggests the onset of European settlement when pines were introduced for timber production.

1. Introduction

Past environmental and anthropogenic studies of the east coast of South Africa include palynology of sediment and peat sequences (Neumann et al., 2008, 2010; Finch and Hill, 2008), complemented by other proxies such as geochemical evidence, diatoms, charcoal, isotopes and leaf wax studies, etc. (Humphries et al., 2019, 2020; Miller et al., 2019; Strobel et al., 2022; House et al., 2022). With an area of about 30,520 ha, St. Lucia is the largest estuary in South Africa (Moll et al., 1971; Turpie et al., 2012). It is part of the iSimangaliso Wetland Park, which is South Africa's first UNESCO World Heritage Site and located in the Maputaland coastal plain of the Indian Ocean Coastal Belt Biome (IOCB) of South Africa (Fig. 1). Grundling (2004) reported on radiocarbon dates of deposits in Lake Saint Lucia that are of Holocene and late Pleistocene age, while the geological evolution of the lake system is discussed in Benallack et al. (2016), Botha et al. (2018) and Dladla et al. (2019). Using different approaches, seismic profiling of incised valleys (Benallack et al., 2016; Dladla et al., 2019) and physical mapping of the barrier dunes with OSL dating (Botha et al., 2018), they determined that the oldest beach ridge was formed about 6240–6350 years ago.

Although many peatlands and other sedimentary environments have been identified within the Maputaland coastal plain (Grundling et al., 1998), very little is known about the palynology of the greater area. Important studies at Lake Eteza to the south of Lake St Lucia, and Lake Sibaya and Mfabeni peatland to the North (e.g., Neumann et al., 2008, 2010; Finch and Hill, 2008) have revealed pollen records (Fig. 2). Moreover, variability in rainfall in southern Africa during the late Quaternary has been debated because individual studies using different proxies give different information about the variability in rainfall, hence, there is some discrepancy in the timing of events. Humphries et al. (2020) using geochemical proxies of sediments transported to the Lake St Lucia system in the IOCB, reported that a series of drought phases occurred between 4700 and 4200 and 3700–2600 cal yrs BP. In contrast, Neumann et al. (2010) indicated that palynomorphs of Lake

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Eteza in the IOCB suggested a drought phase between 3600 and 250 cal yrs BP that became severe around 700–250 cal yrs BP (Little Ice Age). Miller et al. (2019) used stable carbon and hydrogen isotopes of plant-wax proxies, reported that drier conditions generally prevailed in the past 5000 cal yrs BP with sharp variations in the conditions over this period that culminated in drier conditions in the last 2000 cal yrs BP. Hence, there is little general agreement on the time periods when there was low rainfall leading to drought. Since the diverse ecosystems in the IOCB and surroundings have significant spatial heterogeneity in vegetation with uneven distributions of plant species, additional well-dated palaeoenvironmental records from diverse settings are needed to obtain a comprehensive overview of the of the evolution of climate and vegetation in the region.

Focussing on the past vegetation from pollen studies some key taxa have been highlighted. Mazus (2000) studied *Podocarpus* sequences in KwaZulu-Natal (Maputaland) during the Quaternary and concluded that there was a northward migration of *Podocarpus* forest along the Maputaland coastal plain during the Holocene. Neumann et al. (2010) reported that the increase in *Podocarpus* pollen during the middle Holocene at Lake Eteza occurred during the mid-Holocene phase of high sea levels and decreased during the late Holocene. A corresponding increase in Amaranthaceae and grass pollen was found later indicating drier conditions when sea levels were lower. Finch and Hill (2008) studied a pollen sequence from the Mfabeni peatland close to St. Lucia covering >40,000 years. A radiocarbon date of c. 9580 ± 70 yr BP at 2.75m suggests that forest expansion after this level was probably during the early Holocene and indicates warm, relatively moist conditions. They interpreted a *Podocarpus* decline as evidence of deforestation

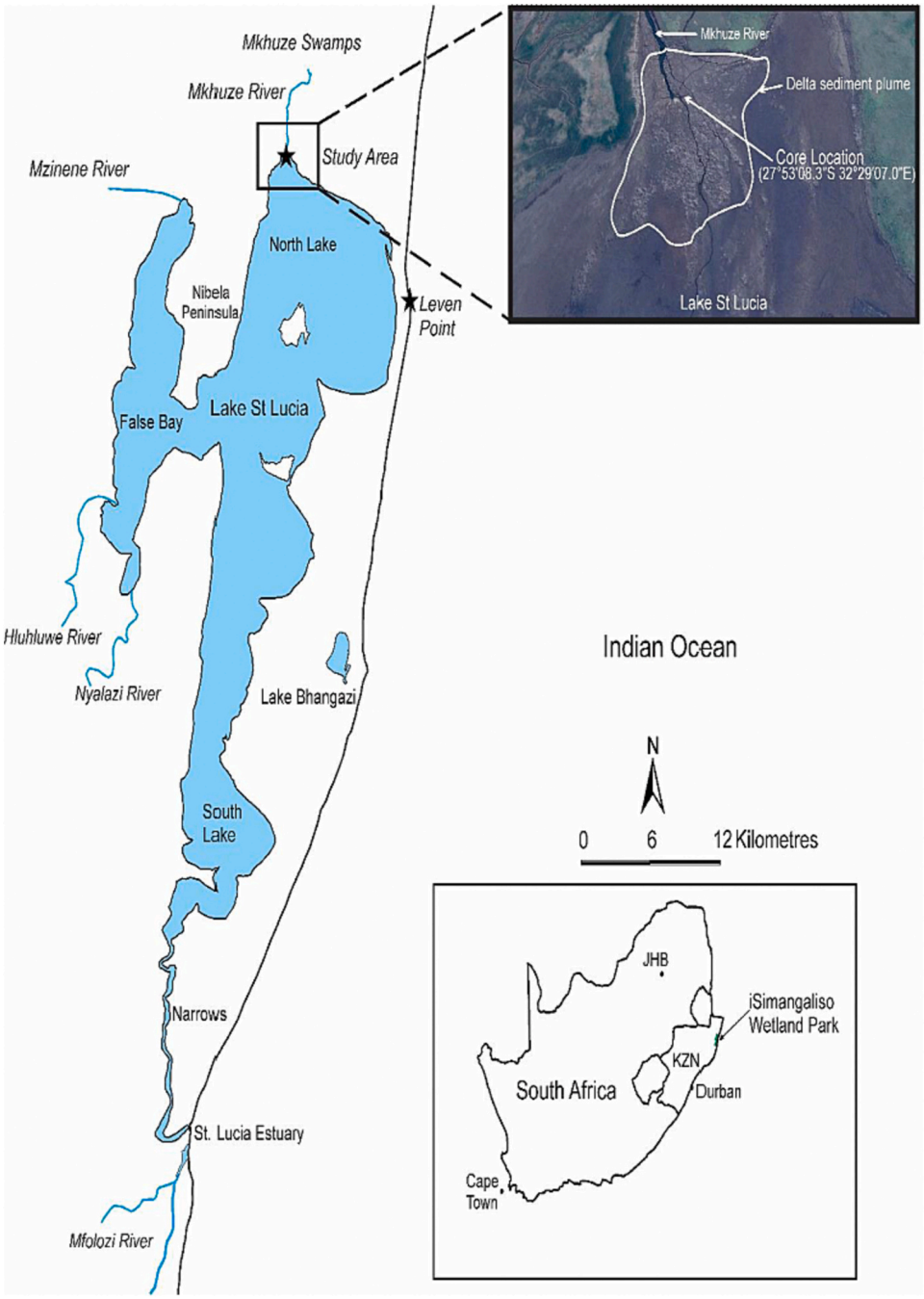

Fig. 1. Map indicating the study area and core location after Higgs (2017).

during the mid-Holocene and that it is supported by the appearance of *Morella serrata,* suggesting a shift towards more open grassland/ savanna, possibly due to burning. Neumann et al. (2008) in their study at Lake Sibaya suggested that the middle Holocene had warm humid conditions while the early Iron Age had a moist climate based on the increase in algae and cereal pollen from 300 to 150 cal yrs BP. They too suggested that this reflects human activities.

Scott et al. (2012), in review of Quaternary vegetation and climate changes in South Africa using Principal Components Analysis (PCA) reported that during the Holocene, marked but non-parallel moisture changes occurred in the sub regions. Hence, late Quaternary palaeoenvironmental studies of Lake St Lucia and comparison with relevant palynological sites with robust chronology in the region will further help to improve the understanding of the palaeoenvironment of the IOCB. Also, the estuarine lake has experienced several salinity fluctuations caused by wet and dry cycles, which in turn controls the occurrence and growth of plants at a given time and locality (Taylor, 1993). Hence, a pollen study of the past vegetation of Lake St Lucia can be compared with that at Lake Eteza and Sibaya to establish if the wet and dry cycles were experienced regionally and how these cycles influenced regional

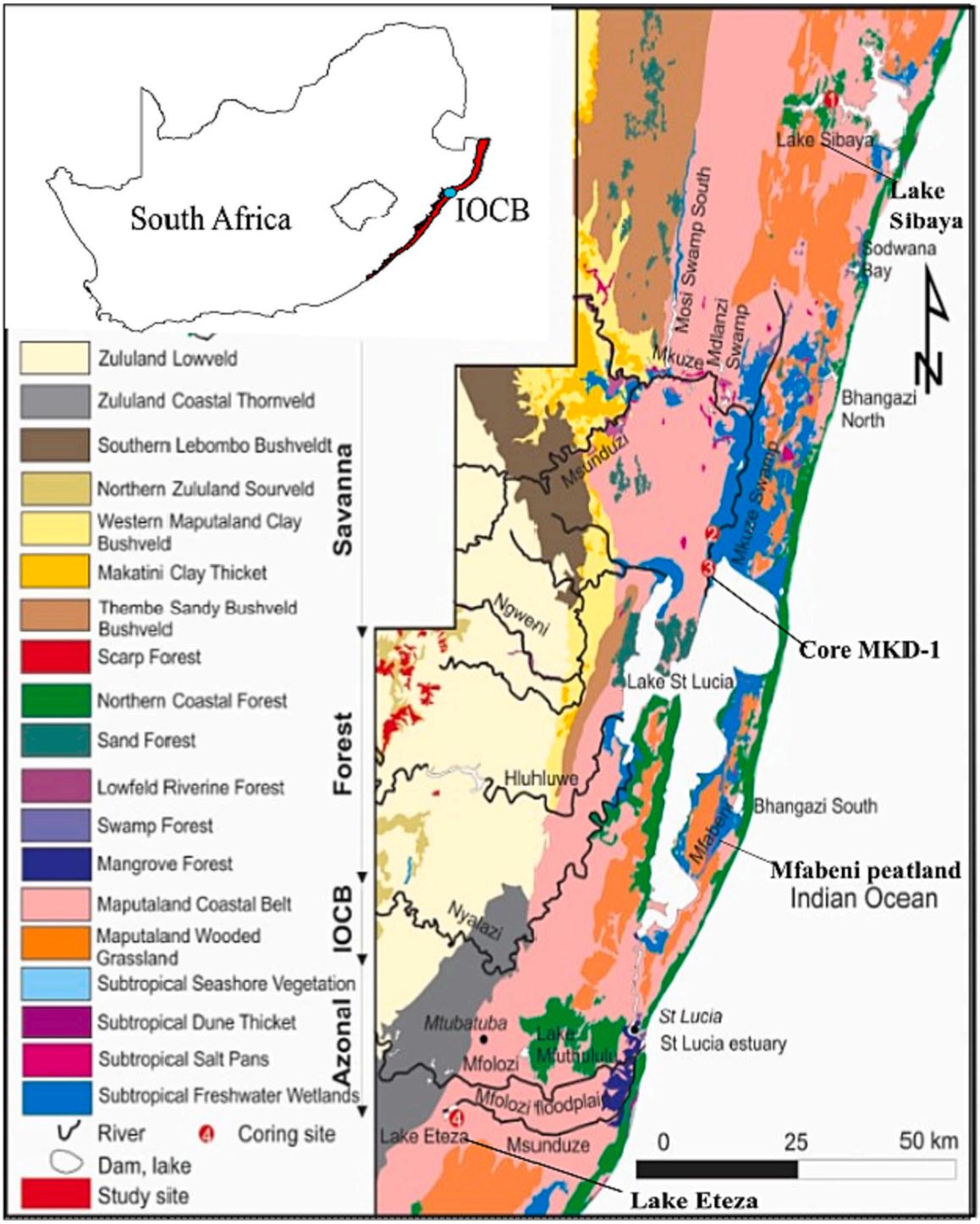

Fig. 2. Regional map showing the Indian Ocean Coastal Belt Biome (IOCB), core MKD-1 and other palynological sites in the region (Lake Eteza, Sibaya and Mfabeni peatland), after Mucina et al. (2006).

vegetation development.

1.1. Study site

1.1.1. Location and climate

The Lake St. Lucia estuarine or connected lake system is located at the southern end of the Maputaland coastal plain, which extends from northern KwaZulu-Natal to southern Mozambique up to Maputo (see Fig. 1). The estuary is situated between 32^0 41′E and 28^0 23'S, and covers about 350 km^2, along a length of 60 km, with a width of 1–20 km, and an average depth of 0.9 m (Orme, 1990).

The climate at St Lucia is subtropical and lies in the summer rainfall region of South Africa with 60% of the rainfall in summer and 40% in winter (Porter and Blackmore, 1998; Taylor et al., 2006). It has warm, moist summers (mean annual temperatures exceed 21 °C), and mild dry winters. Rainfall at the coast varies from 1200 to 1300 mm per annum but drops to only 900 mm per annum 10 km to the west at Fanies Island (Taylor et al., 2006). This temporal variability of rainfall gives rise to severe wet and dry periods in Maputaland (Taylor et al., 2006) which in turn affects the hydrology and salinity of the estuarine lake.

1.1.2. Hydrology and geology

Five river systems supply the estuarine lake with freshwater. These rivers are the Mkhuze, Hluhluwe, Mzinene, Impate and Nyalazi (Taylor et al., 2006). The estuary is open to the sea at times but closed to the sea at other times by a natural sand barrier. Variation in rainfall regionally and temporally affects hydrology and salinity at the St Lucia estuarine system (Taylor et al., 2006). Due to high surface area (350 km^2) to volume ratio (about 0.9 m average depth) in the estuarine lake (Orme, 1990), it is very sensitive to the impact of evaporation (Hutchison and Midgley, 1978). Hence, the hydrology of the lake changes. The quantity of water lost by evaporation exceeds the quantity received from rainfall even in years of moderate or above average precipitation (Porter and Blackmore, 1998). Fresh water received from the streams and rivers mainly regulates the salinity of the overall system (Porter and Blackmore, 1998). In periods where the amount of rainfall is moderate or above average, the salinity gradient ranges from a freshwater state near the river mouths to that of sea water (35 parts per thousand) in the estuary. In periods of drought, more water is lost from evaporation than enters the lake from river-flow and if the lake is open to the sea at the mouth, then more sea water flows in resulting in an increase in salinity (Porter and Blackmore, 1998). Hence, during extended periods of drought, the lake becomes hypersaline.

The geology within the St Lucia System comprises Cretaceous sedimentary rocks of the St Lucia Formation that are covered by the Maputaland Group sedimentary rocks of Neogene and Quaternary age (Porter and Blackmore, 1998). The Indian Ocean is bordered by a Pleistocene–Holocene coastal barrier dune complex that today is densely forested and stabilized (Benallack et al., 2016; Botha et al., 2018; Dladla et al., 2019; Porat and Botha, 2008; Porter and Blackmore, 1998).

1.1.3. Vegetation

Porter and Blackmore (1998) gave an elaborate classification of the vegetation at Lake St Lucia and divided it into six major groups based on habitat and growth form. These groups are as follows: (a) Wetland types (b) Grassland types (c) Swamp (d) Mangroves (e) Woodland types and (f) Forest types. Vegetation in the region is classified as Coastal Bushveld-Grassland (Low and Rebelo, 1996), which comprises a mixture of forest patches within a matrix of grassland and open savanna. The floodplain is characterized by open grassland dominated by *Echinochloa pyramidalis*, while *Acacia xanthophloea* fringes many of the floodplain lakes. The permanently wet areas are dominated by various reeds and sedges such as *Phragmites australis* and *Cyperus papyrus* (Patrick and Ellery, 2007), while the Mkhuze River is fringed by fragmented patches of riverine forest characterized by trees such as *Ficus sycomorus, Rauvolfia caffra, Voacanga thouarsii* and *Blighia unijugata* (Stormanns, 1987; Patrick and Ellery, 2007) (Fig. 2).

2. Materials and methods

The present study was carried out on core materials from north of Lake St Lucia. Results were obtained from core MKD-1 (27.8856 °S, 32.4853 °E), drilled in 2015 on the Mkhuze River Delta (Humphries et al., 2020). It spans ~7000 years from base to top. Dating, sedimentation rate and lithology of core MKD-1 are reported by Higgs (2017) and Humphries et al. (2020). The radiocarbon ages from Humphries et al. (2020) were calibrated here to calendar years using the Southern Hemisphere calibration SHCal20 (Hogg et al., 2020); a Bayesian age-depth model was developed using Bacon 2.2 software (Blaauw and Christen, 2011) (Fig. 3). The core was sub sampled for pollen analysis (total 80 samples). Samples above depth 770 cm (~6300 cal yrs BP) were not subsampled for pollen analysis. The samples were processed according to Erdtman, 1969 and Faegri and Iversen, 1966 method. The samples were treated with 40% HF overnight to dissolve silicates. Treatment with 10% KOH to remove humic acid as well as other organic matter followed. Mineral separation with $ZnCl_2$ (specific gravity 2.0) was carried out before acetolysis. Acetolysis is the removal of lipids and proteins including the inner organic pollen wall (intine) and cytoplasm using acetic anhydride and sulfuric acid in the ratio of 9:1 (Erdtman, 1960). The residue was mounted on microscopic slides in glycerine jelly. An Olympus BX51 photomicroscope was used for the pollen analysis. For each sample studied under the microscope, 100–250 grains were counted. If there were insufficient grains in a sample a second slide was prepared from the residue. Identification of the palynomorphs was done by comparing them with modern pollen reference collections at the Evolutionary Studies Institute, University of the Witwatersrand, and the Department of Plant Sciences, University of the Free State. Other pollen atlases were also consulted, such as Bonnefille and Riollet (1980), Scott (1982), Gosling et al. (2013), Schueler and Hemp (2016), Chevalier et al. (2022), as well as diverse online pollen databanks (e.g., https://globalpollenproject.org/, https://africanpollendatabase.ipsl.fr/#/pollen-atlases). The pollen diagram was calculated using strat.plot in rioja, which is designed for managing and graphing stratigraphic data especially paleontological data (Juggins, 2012; Juggins and Juggins, 2019). The pollen diagram was divided into Zones based on the internal variation within and between groups of palynomorphs at different depth/age using Constrained Incremental Sums of Squares (**CONISS,** R studio: http://www.rstudio.com/**).** This helped to identify pollen assemblages and abundance or sparsity zones which in turn gives information about the changes in vegetation in the different cores (see Fig. 4). Finally, using PAST version 4.13. Principal component analysis (PCA) was carried out as the record was explored for any fluctuations of the pollen assemblage due to biotic and/ or abiotic factors with the goal of understanding overall trends within the pollen profile which might infer major drivers of the system (see Figs. 5, 6).

3. Results

3.1. Dating and sedimentation rate

The radiocarbon ages from Humphries et al. (2020) were calibrated here to calendar years using the Southern Hemisphere calibration SHCal20 (Hogg et al., 2020); a Bayesian age-depth model was developed using Bacon 2.2 software (Blaauw and Christen, 2011) (see Fig. 3 & Table 1). Sedimentation rate for MKD-1 averaged ~0.8 cm yr^{-1} from 385 yrs. cal BP to 1598 yrs. cal BP, 0.2 cm yearly from 1598 yrs. cal BP to 1882 yrs. cal BP and from 4897 yrs. cal BP to 6316 yrs. cal BP, 0.4 cm yearly from 1882 yrs. cal BP to 3095 yrs. cal BP, 0.3 cm yearly from 3095 yrs. cal BP to 4179 yrs. cal BP and 0.1 cm yearly from 4179 yrs. cal BP to 4897 yrs. cal BP. The sedimentation rates should be treated with caution because there has been loss of sediments due to erosion and incision (Dladla et al., 2019).

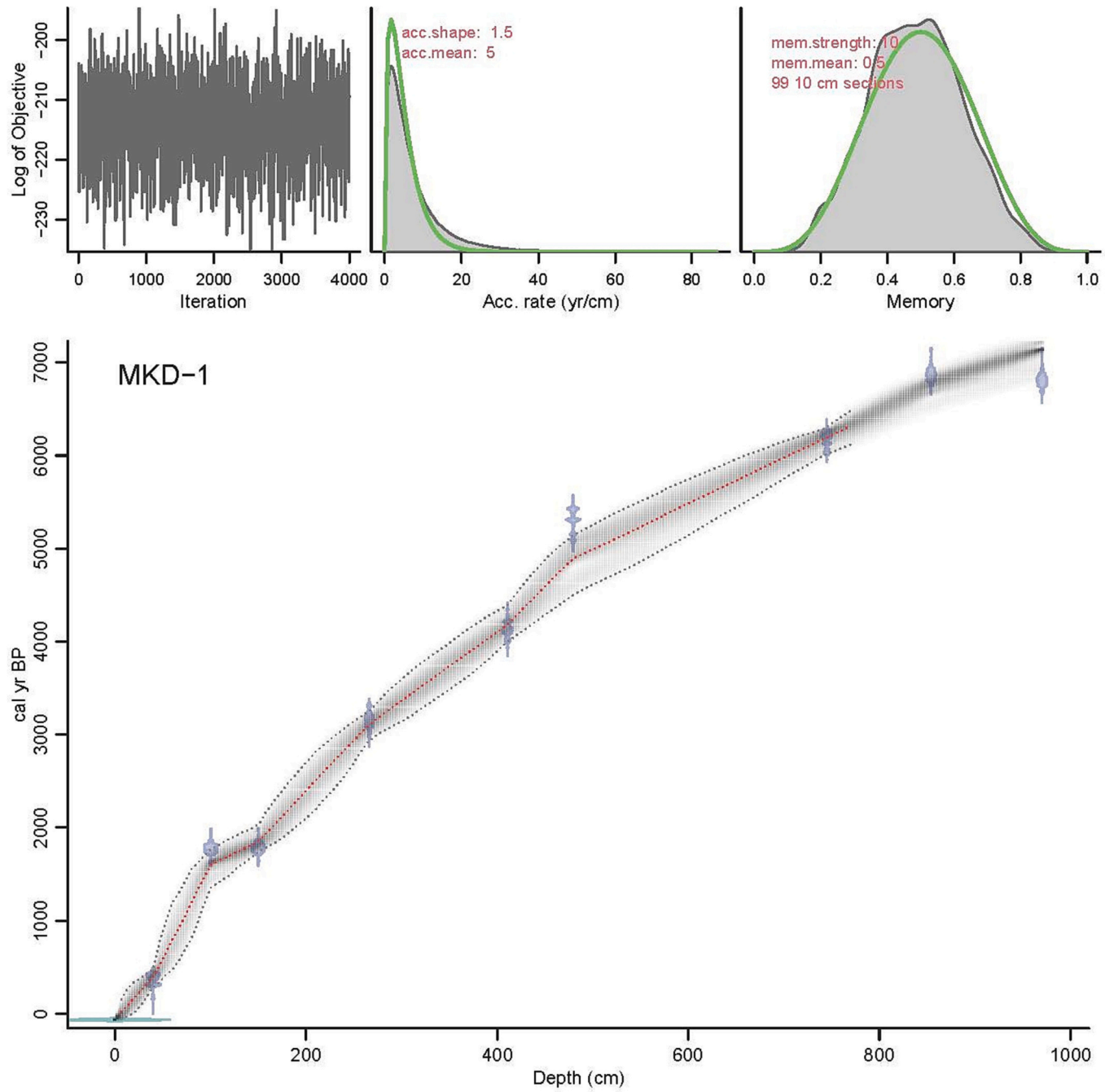

Fig. 3. Age model using Bayesian statistics (Bacon software v2.2) for core MKD-1.

3.2. Pollen analysis for core MKD-1

Generally, the sediment from 700 to 300 cm depth had poor pollen preservation when compared to the sediment between 350 and 770 cm but overall, there was a high diversity of palynomorphs. Using CONISS (Juggins, 2020), six pollen zones were generated. From the base, Zone 6 differs from Zone 5 as pollen of Amaranthaceae peaked with marine elements in Zone 6 while Zone 5 recorded an increase in *Podocarpus* and decline in the Amaranthaceae. Zone 4 recorded a peak in *Podocarpus* pollen, other forest elements and Cryptogam spores while Zone 3 recorded a peak in the pollen of *Spirostachys* at the beginning with that of Poaceae taking over at the middle, Zone 2 recorded the peak of *Phragmites,* foraminiferal linings and decline in Poaceae and fungal spores. Finally, Zone 1 records the presence of *Pinus*, increase in fungal spores and presence of wetland elements.

3.3. Pollen and spore zonation for MKD-1

Six pollen CONISS zones reflect changes in composition and abundance of individual species (see Fig. 4).

3.3.1. Zone 6 Podocarpus, Poaceae, Amaranthaceae, Cyperaceae and Scolecodonts. (6300–5900 cal yrs. BP)

This zone recorded the peak of Amaranthaceae, high *Podocarpus*, Poaceae, Cyperaceae, and scolecodonts, with few ryptogams (Pteridophytes and bryophytes).

3.3.2. Zone 5 Podocarpus, Poaceae, Pseudoschizaea and Cryptogams (5900–4900 cal yrs. BP)

An increase in *Podocarpus*, Poaceae, scolecodonts and cryptogams (Pteridophytes and bryophytes) was recorded. Also, *Pseudoschizaea*

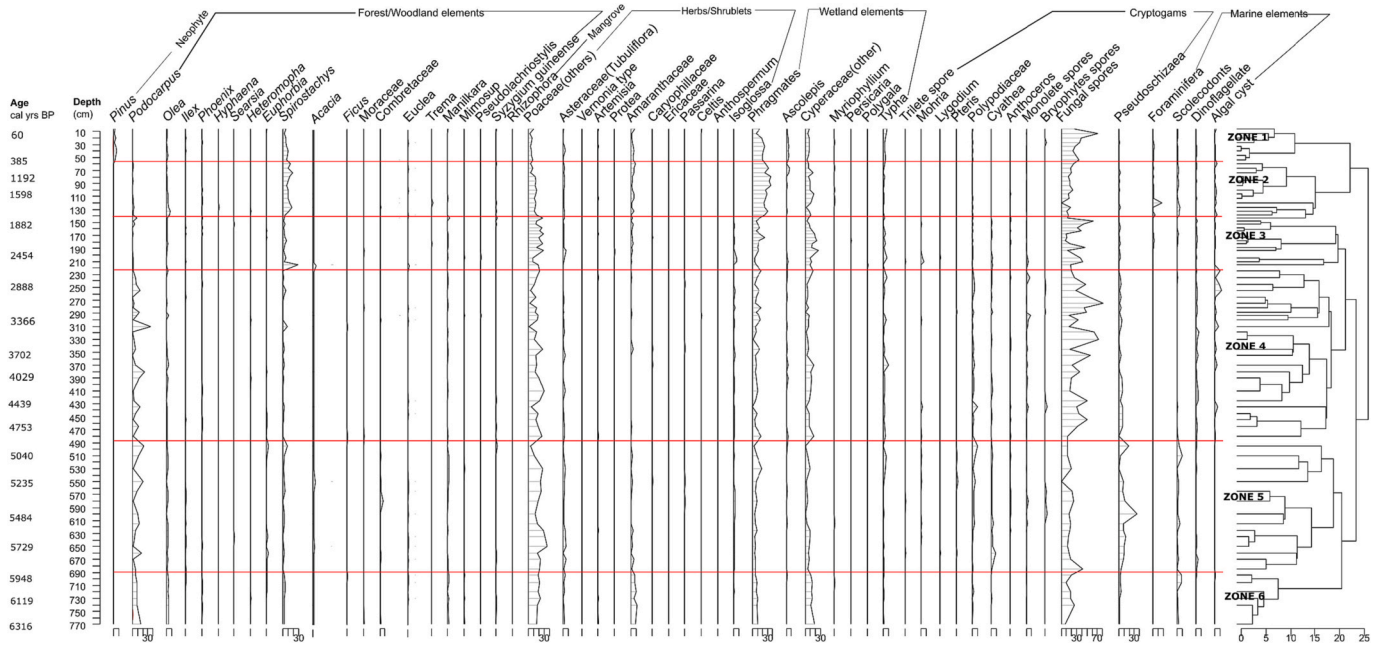

Fig. 4. Pollen percentage diagram for MKD-1 according to depths showing six pollen zones (CONISS).

reached its peak, and Ericaceae was also recorded in this zone.

3.3.3. Zone 4 Podocarpus, Typha, Poaceae, and Fungal spores (4900–2600 cal yrs. BP)

This zone recorded the peak of *Podocarpus* and fungal spores, high cryptogams and Poaceae, increased *Typha* and little to no marine elements.

3.3.4. Zone 3 Spirostachys,Cyperaceae, Poaceae and Fungal spore (2600–1800 cal yrs. BP)

In this zone, *Podocarpus* declined and disappeared at the beginning as *Spirostachys* increases and reached its peak but later declined as *Podocarpus* reappeared. Also, Poaceae decreased at the beginning as *Spirostachys* reached its peak but latter increased as *Spirostachys* declined. *Typha* was abundant in this zone and foraminiferal linings were first recorded in this zone.

3.3.5. Zone 2 Spirostachys, Phragmites and Foraminiferal linings (1800–800 cal yrs. BP)

In this zone, *Spirostachys* and Amaranthaceae increased as Poaceae declined. *Phragmites* and foraminiferal linings increased and reached its peak while fungi declined and little to no cryptogam spores (Bryophyte and pteridophyte) were recorded.

3.3.6. Zone 1 Neophyte, Spirostachys, Phragmites, Ascolepis and Fungal spore (800–17 cal yrs. BP)

This zone recorded the presence of *Pinus* (Neophyte) at the top of the core (last 400 Cal yrs. BP), high abundance of fungal spores, pollen of *Phragmites*, *Spirostachys* and Amaranthaceae was present, low Poaceae pollen percentages, decline and disappearance of foraminiferal linings.

3.4. Principal component analysis

Using PCA which allows visual exploration of data, a 1% sample threshold was used as pollen grains and spores were subjected to Principal Component Analysis, a representation of the principal component analysis is shown in Figs. 5, 6 (Table S1).

PC1 accounts for 12.4% while PC2 accounts for 9.7% of variance in pollen and spore composition throughout the core. PC1 reveals strong positive loading of ≥ 0.2 for *Podocarpus, Cyathea,* Polypodiaceae, *Isoglossa*, monolete spores, bryophytes, *Mohria*, fungal spores, trilete spores, *Pteris, Anthoceros, Euphorbia, Acalypha, Passerina, Ilex, Polygala, Acacia, Euclea, Ericaceae, Ficus* and a strong negative loading of ≥ -0.2 for *Phragmites,* Amaranthaceae, Cyperaceae, *Crassula, Pinus, Persicaria, Spirostachys*, *Olea, Trema, Phoenix, Myriophyllium, Ascolepis, Sparganium, Hyphaenae, Pseudolachnostylis, Celtis,* Caryophyllaceae, *Syzygium, Heteromopha*, Asteraceae, Moraceae, *Manilkara*, Poaceae suggesting a change from a humid forested environment to a dry open environment. Similar trends were reported for Lake Eteza and Sibaya (see Fig. 6).

4. Discussion

4.1. Vegetation history

Generally, the core (MKD-1) had a low pollen preservation in terms of quantity but was good in terms of diversity of palynomorphs. This may be due to the nature of the depositional environment as the core was taken at the northern end of the estuarine lake so may have been a good repository because the materials are not just from the immediate environment but also from a larger catchment area as the Mkhuze River discharges into the northern part of the lake thus, the higher diversity. The lake has experienced series of wet and dry cycles as discussed above that may have affected the preservation of pollen in the cores due to salinity fluctuations (Campbell and Campbell, 1994).

The pollen record of the northern end of Lake St Lucia is dominated by Poaceae (20–50%) suggesting an influence of grassy woodland. Similar trends were described at Lake Sibaya and Eteza (Neumann et al., 2008, 2010). *Podocarpus* pollen dominated the arboreal pollen spectra from 6300 to 2600 Cal yrs. BP then *Spirostachys* pollen dominated the arboreal spectra from 2600 to 17 cal yrs BP. *Spirostachys* are trees found in woodland and *Podocarpus* are forest trees, but *Podocarpus* is fire-sensitive (Scott, 1999; Coates-Palgrave, 2002; Finch and Hill, 2008). Pollen of *Phoenix* and *Hyphaene* palms also occurred in the sequence with *Phoenix* occurring more frequently than *Hyphaene.* The palm can be found along rivers, in coastal forest and grassland (Pooley, 1993; Neumann et al., 2010). Ericaceae and *Passerina* are fynbos elements and were present although scanty with *Passerina* pollen occurring more abundantly in the sequence (see Fig. 4). This could be the coastal *Passerina* species (*Passerina rigida*) Pooley, 1993. Aquatics and semi-aquatic plants such as *Phragmites*, Cyperaceae, *Persicaria* and *Typha* dominated

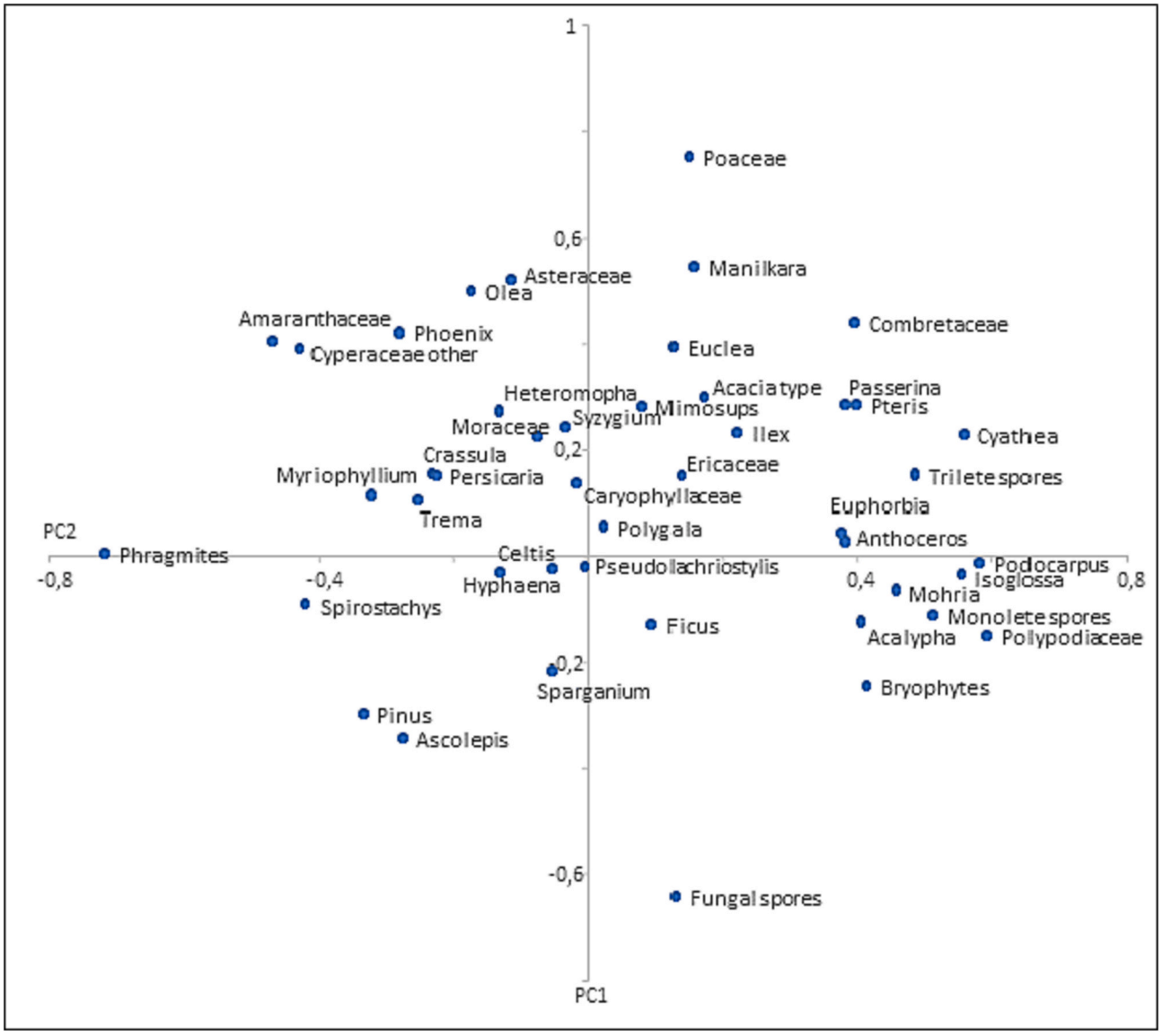

Fig. 5. PCA Biplots for MKD-1 using PAST version 4.1.

the topmost profiles.

4.2. Paleoenvironmental interpretations for Lake St Lucia (core MKD-1)

4.2.1. Zone 6 (6300–5900 cal yrs. BP)

Near the base of the MKD-1 core forest trees such as *Podocarpus, Olea* and *Manilkara* were present with *Spirostachys* pollen occurring in very low quantities. An Amaranthaceae pollen peak, Cyperaceae, *Phragmites*, Scolecodonts, low abundance of cryptogam spores (Bryophyte and Pteridophyte) and fungal spores were present during this period indicating a relatively warm and sub-humid forest with a wetland mosaic. The peak in Amaranthaceae points to a dry environment (local evaporation) or saline microenvironment such as coastal salt marshes (Dyer, 1975; Scott, 1999; Pooley, 2005). Cooper et al. (2018) reported a high sea level during the Holocene in southern Africa between 6000 and 7000 Cal yrs. BP. Botha et al. (2018) also reported that the oldest beach ridge at Lake St Lucia formed around 6240 years BP with a sequence of beach ridges having accumulated during the period of 4000 to 1500 years BP reflecting coeval accretion around the lake. This explains the presence of scolecodonts because the increase in sea level as reported by Cooper et al. (2018) would have led to a marine incursion as the beach ridges were just beginning to develop. The marine incursion led to increased water table and salinity of the soil hence, the presence of wetland plants such as Cyperaceae and *Phragmites*, and halophytic plants such as Amaranthaceae.

4.2.2. Zone 5 (5900–4900 cal yrs. BP)

Podocarpus, cryptogams (Pteridophytes and Bryophytes), and Poaceae increased; Ericaceae and *Passerina* were present in this zone. *Pseudoschizoaea* increased and reached its peak, fungal spores were also present, *Typha* type became prominent. The presence of Ericaceae during this period suggests a cold and sub-humid condition with a relatively seasonal moisture condition (Scott, 1999). As cryptogams increased, *Pseudoschizoaea* peaked and *Typha* became prominent at around 5000 cal yrs. BP indicating a shift from a saline wetland to a freshwater condition (Scott, 1999; Neumann et al., 2010; Freitas et al., 2015).

4.2.3. Zone 4 (4900–2600 cal yrs BP)

Podocarpus reached a peak of about 30% at around 3380 cal yrs. BP but declined at 2600 cal yrs. BP. Abundant forest elements, increased cryptogams and *Typha* with little or no marine elements and Amaranthaceae suggesting a sub-tropical (relatively warm, moist and

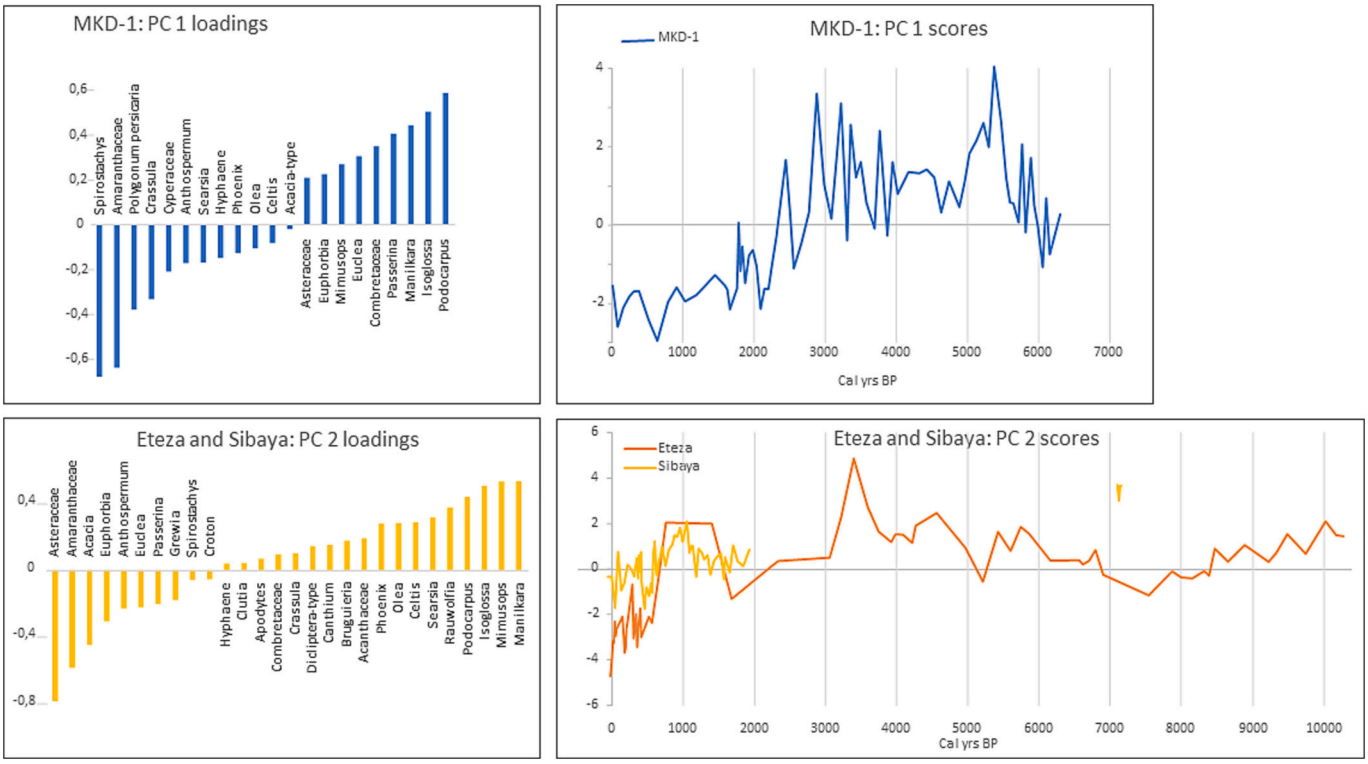

Fig. 6. Graphs of PCA loadings and scores for Core MKD-1, Lake Eteza and Sibaya. PC2 was used for Lake Eteza and Sibaya as it gives strong loadings on a combination of taxa that are better regional moisture indicators.

Table 1
AMS radiocarbon analyses of material from core MKD-1. Calibrated ages (cal yrs BP) and probability (%) from clam (Blaauw, 2010; Hogg et al., 2020).

Lab-Code	Depth (cm)	^{14}C age (yr BP)	Calibrated Age and prob. (cal yrs BP, %)
Beta-481891	40	320 +/− 30	462–307 (94.8%)
Beta-481892	100.5	1880 +/− 30	1838–1716 (89.9%)
Beta 439022	150	1890 +/− 30	1844–1719 (85.8%)
Beta 439023	266	3020 +/− 30	3271–3144 (69%)
Beta-481893	410.5	3800 +/− 30	4290–4089 (95%)
Beta 416422	479	4630 +/− 30	5463–5373 (71.3%)
Beta 416423	745	5420 +/− 30	6291–6188 (92.5%)
Beta 416424	854	6060 +/− 30	6994–6837 (87.8%)
Beta 439024	970	6010 +/− 30	6941–6782 (91.7%)

freshwater condition) (Finch and Hill, 2008) typified this zone. This zone is wetter and more humid as compared to Zone 5 which corresponds with the proposed 5–10% increase in precipitation in Maputaland during this period (Partridge, 1997).

4.2.4. Zone 3 (2600–1800 cal yrs. BP)

Podocarpus declined at about 2600 cal yrs. BP and finally disappeared at around 2390 cal yrs. BP. This decline was accompanied with a decline in other forest elements and cryptogams with a corresponding increase and peak of *Spirostachys* at around 2600–2390 cal yrs BP. *Spirostachys* later declined after 2390 cal yrs BP with a corresponding increase in Poaceae, Amaranthaceae, *Isoglossa* and Cyperaceae. *Podocarpus* resurfaced again in very low quantity of less than 8% at around 1700 cal yrs BP as *Spirostachys* pollen levels were still low. Foraminiferal linings appeared in this zone suggesting marine influence that may be due to high sea levels leading to marine incursion hence the increase in Amaranthaceae which might have spread along the shores of the lake. The decline in forest elements and cryptogams during this period and a corresponding increase in Poaceae and *Isoglossa* signals to a change from a forested environment to a more open ecosystem that may be due to a drop in moisture level (droughts). Similar *Podocarpus* forest retreat has been reported by Mazus (2000) at around 3100 cal yrs. BP in the Maputaland coastal area and Neumann et al. (2010) reported a similar *Podocarpus* retreat at around 3600 cal yrs. BP at Lake Eteza. Hence, it is suggested that this vegetation trend is a regional trend in the coastal area of the IOCB biome (see Fig. 7). PCA results agree with the changes reported as they show a strong positive loading of ≥ 0.02 for *Podocarpus* and cryptogams (forest and humid condition indicator) and a strong negative loading of ≥ -0.02 for *Spirostachys* and Poaceae

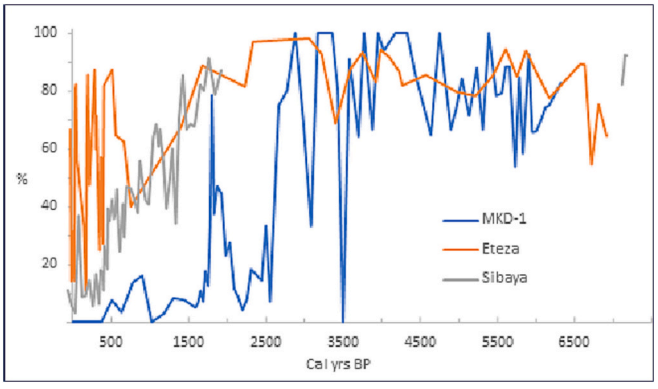

Fig. 7. Percentage of *Podocarpus* to *Spirostachys* pollen in the IOCB showing a decline in *Podocarpus* in the late Holocene.

(woodland/ savanna indicator) see Table 2. This means that an increase in *Spirostachys* indicates a reduction in the forest plants (e.g. *Podocarpus*) and cryptogams hence, a change from a humid forested environment to a dryer open woodland vegetation.

4.2.5. Zone 2 (1800–800 cal yrs. BP)

Spirostachys pollen increased as Poaceae declined and *Podocarpus* declined and disappeared. Amarathaceae also increased and *Phragmites* increased and reached its peak. Foraminiferal linings increased and reached a 20% peak at around 1700 cal yrs BP. During this period, Pteridophytes and Bryophytes declined and disappeared, and fungal spores declined suggesting low moisture level (humidity) which signals a severe drought and marine influence leading to increased salinity in the environment. The marine influence is due to more sea water flowing into the lake which was a lagoon at the time when the youngest beach ridge was formed, around 1500 yrs. BP (Botha et al., 2018). The presence and peak of benthic foraminiferal linings in this zone could be due to severe drought leading to increased evaporation of water from the lake as it is very sensitive to evaporation due to its very shallow depth (Orme, 1990; Hutchison and Midgley, 1978). Hence, as water is lost from the lake through evaporation, and less fresh water was incoming due to drought, more sea water flowed into the estuarine lake. The overall low moisture level experienced by the ecosystem might have led to the disappearance of *Podocarpus* which is moisture loving (Scott, 1999; Finch and Hill, 2008) and does not survive in highly saline environments. Zou et al. (2021) working on De novo transcriptome analysis of *P. macrophyllus* reported that salt treatment of *P. macrophyllus* significantly affected the photosynthesis system of the seedlings in the way of decreased chlorophyll content, altered chloroplast ultra-structure and reduced photosynthesis. Severe drought was reported by Humphries et al. (2019) working on diatoms for Lake Muzi during this period 2100–1400 and 850–550.

4.2.6. Zone 1 (800–17 cal yrs. BP)

Typha increased together with fungal spores as fungal spores reached 60% with little to no foraminiferal linings in the last 300 cal yrs BP suggesting a warm, sub-humid, less saline to freshwater environment in the last 300 cal yrs BP, but 800–300 cal yrs. BP was still dry and hypersaline. *Pinus* pollen appeared in the last 385 cal yrs BP indicating disturbance by the European settlers (Neumann et al., 2008). This is because *Pinus* was introduced to South Africa by the Europeans hence is not indigenous. The date of 385 cal yrs BP might look too early as Marwick (1973) and Thamm et al. (1996) reported that the Europeans introduced and grew large Pine plantations in coastal areas of the Indian Ocean Coastal Belt biome since 1928–1929 and in the St. Lucia region since 1957. The older pollen date may be due to bioturbation as Lake St Lucia is inhabited by large hippos which often times are on the floor of the lake and their activities can mix up the sediments. The increase and composition of fungal spores in the last 300 cal yrs BP also signals anthropogenic activities (Gelorini et al., 2012; Kettner et al., 2017. See Table 3 for a summary of palaeoenvironmental interpretation of core MKD-1.

4.3. Regional comparison

The Early Holocene period 10,200—7000 cal yrs. BP that precedes the sequence we study here, is characterized by moist climate as *Podocarpus* and other forest elements were present and abundant in Mfabeni peatland and Lake Eteza (Finch and Hill, 2008; Neumann et al., 2010). In the Mid-Holocene, regionally vegetation history varies among the various sites, but Lake Eteza, Lake Sibaya, Mfabeni peatland and Lake St. Lucia (MKD-1) shared a similar vegetation history as they are in the Maputaland Coastal Belt (Mucina et al., 2006). Other available sites are inland except the coastal forest and Miombo woodland of Vilankulo in Mozambique (Ekblom, 2008; Ekblom et al., 2014). Considering that

Table 2
Fossil pollen taxa and their environmental indications (after Scott, 1999; Finch and Hill, 2008).

Pollen types	Vegetation	Environment
Podocarpus	Forest	Relatively moist conditions
Isoglossa	Forest floor	
Proteaceae	Upland or mesic savanna	Wide range of temperature, sub-humid condition
Olea		
Combretaceae	Microphyllous or plains savanna	Relatively warm conditions, wide range of moisture condition; *Senegalia/ Vachelia* associated with relatively local deep soils
Spirostachys		
Euphorbia-type		
Peltophorum		
Senegalia/ Vachelia		
Ficus		
Tarchonanthus	Kalahari thornveld savanna	Relatively dry conditions
Asteraceae	Shrubland	Relatively even seasonal moisture distribution
Artemisia		
Ericaceae	Fynbos	Cool, sub-humid conditions, relatively seasonal moisture distribution
Passerina		
Cliffortia		
Stoebe type		
Aizoaceae	Succulents	Relatively warm and/ or dry conditions
Aloe type		
Amaranthaceae	Halophytes	Local? Evaporation
Persicaria	Semi-aquatics	Moist to damp or wet soil, indicates disturbances
Typha	Aquatics	Shallow freshwater conditions
Cyperaceae	Semi-aquatics	Local swamp, shallow water or damp soil
Poaceae	Grassland or savanna	Generally indicative of summer rainfall
Cyathea	Forest edges	Relatively warm and moist conditions (humid)
Polypodiaceae		
Monolete/ Trilete		

Table 3
Summarized paleoenvironmental interpretation for MKD-1.

	Pollen character	Age (calyrs. BP)	Climate interpretation
Zone 6	*Podocarpus*, *Olea, Manilkara,* and cryptogams present High Amaranthaceae, Scolecodonts	6300–5900	Warm, moist with marine influence
Zone 5	Increased *Podocarpus,* Poaceae, cryptogams appeared, presence of Ericaceae and *Passerina* Peak of *Pseudoschizaea,* and increase *Typha*	5900–4900	Cool, sub-humid with freshwater conditions
Zone 4	*Podocarpus* peak at 3500 cal yrs. BP. Increased cryptogams, *Typha*	4680–2600	Relatively warm, moist with freshwater condition. Wetter and more humid than zone 5
Zone 3	Decline in *Podocarpus* and cryptogams, Increase *Spirostachys initially* but later declined as Poaceae increased.	2600–1800	Warm, drop in moisture level (drought) and *Podocarpus* and cryptogams retreat
Zone 2	Increase *Spirostachys* as cryptogams and *Podocarpus* declined then disappeared. Amaranthaceae, Scolecodont and foraminiferal lining increased, the latter peaking at 1700 cal yrs. BP	1800–800	Warm and dry (drought) (drier than zone 3) with intense marine influence at 1700 cal yrs. BP
Zone 1	Decrease in *Spirostachys* and Poaceae in the last 500 cal yrs BP, increase in *Typha* in the last 300 cal yrs BP, fungal spores increased and presence of *Pinus* in the last 385 cal yrs. BP	800–17	Relatively warm and dry (800–300 cal yrs BP) with increased precipitation in the last 300 cal yrs BP and disturbance from human activities

local biogeography is influenced by elements other than climate, such as soil nutrients, soil type, topography, etc., the vegetation history varies locally, but a consistent overall climate sequence is suggested by palynological data at various sites over time (see Tables 4, 5). Other paleoenvironmental proxies in the area that extends to the South African summer rainfall zone provide varying climate deductions on drought phases but are consistent in suggesting that moist and wet climate prevailed between 7000 cal yrs BP to 4700 cal yrs BP. Drought phases were reported to last about 4700–2800 cal yrs BP based on geochemical studies in Lake St Lucia (MKD-1) and diatom studies Lake Muzi (Humphries et al., 2020; Humphries et al., 2019). However, drought phases were also recorded around 2100–1400 and 850–550 cal yrs BP

Table 4
Summary of vegetation dynamics and climate inferences in palynological sites in the IOCB.

	Southern Mozambique (Nhaucati lake) Ekblom (2008)		Coastal forest and Miombo woodland of Vilankulo (Mozambique) Ekblom et al. (2014)		Mfabeni Peatland (south of MKD-1 core) Finch and Hill (2008)		Lake Eteza (far south of MKD-1 core) Neumann et al. (2010)		Lake Sibaya (north of MKD-1 core) Neumann et al. (2008)	
Age (cal yrs BP)	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation dynamics	Climate inferences	Vegetation	Climate inferences
0–250	Moraceae, *Celtis*, T*rema* and *Dialium* type declined by	Drought during the little ice age at Ca. 550 cal yrs. BP	Herbs and aquatic increased while grasses declined also,	Cold dry periods			Neophytes, Poaceae, *Protea, Cliffortia*	Climate change induced by human activities and the onset of little ice age in Ca. 700 cal yrs. BP	Neophyte, *Zea mays*, Ericaceae grains	Vegetation change induced by human activities
250–550	5–10% *Alchornea* and *Cassine* types are in higher number.		*Brachystegia* declined and disappeared						*Spirostachys, Celtis, Stoebe, Manilkara* and *Searsia*	Humid climate
550–800	*Alchornea* type, Savanna is moderately represented by *Sclerocarya*, grassea and sedges also have their peak	Warm period	Increase in tree/shrubs and Cyperaceae, N*ymphaea*, *Typha* (riparian forest)						*Phoenix*, *Hyphaene*, monolete spores, Poaceae	
800–1200	Forest and riverine forest vegetation (*Celtis, Dialium* type, Moraceae and *Trema)*	Warm period	Myrtaceae (*Syzygium* and *Eugenia*), *Phyllanthus*, *Nymphaea*, *Brachystegia* is represented in low numbers.				*Phoenix*, Poaceae and Asteraceae	Drier, continued gradual decrease of SST, Sea levels drop. Mangrove swamp forest decline	*Olea, Manilkara, Celtis, Bruguiera*	
1200–1600	Asteraceae, *Nymphaea* (dry bushveld savanna vegetation)	Dry period	Sterospermum, Combretaceae, *Myrsine africana*, *Alchornea*, Moraceae, *Trema* and *Brachystegia*	Dry periods					*Podocarpus,* Moraceae, *Morella, Ilex* and Asteraceae	
1600–3600										
3600–4600					*Acacia,* Cyanthaceae, *Ficus, Morella,* Myrtaceae, *Protea,* Rosaceae, *Podocarpus* declined		*Podocarpus, Isoglossa,* Mangroves, Aquatic ferns	High precipitation, High SST, relatively high sea level		
4600–6800										
6800–8000							*Isoglossa, Olea and Phoenix* declines,	Relatively wet Ca. 10,000 cal yrs. BP becoming dry	*Phoenix, Isoglossa, Manilkara, Celtis*	Warm moist conditions
8000–10,200					*Podocarpus* abundant forest, Anacardiaceae, Apocynaceae, Celastraceae, Fabaceae, Rosaceae, Rubiaceae	Moist cool climate	Poaceae increases and *Acacia gerardii* is represented	Ca. 8000–7000 cal yrs. BP increase SST/ sea level		

Table 5
Summarized regional paleoenvironmental results.

Periods	Southern Mozambique (Nhaucati lake) Mozambique) Ekblom (2008)	Coastal forest and Miombo woodland of Vilankulo (Mozambique) Ekblom et al. (2014)	Mfabeni Peatland Finch and Hill (2008)	Lake Eteza Neumann et al. (2010)	Lake Sibaya Neumann et al. (2008)	Lake St Lucia Core MKD-1
Late Holocene (last 2000) cal yrs. BP	Warm and dry	Cold and dry		dry		Warm and dry with marine influence
Middle Holocene (7000–2000) cal. yrs. BP				High precipitation/ High sea levels		High precipitation/ High sea levels
Early Holocene (10,200—7000) cal. yrs BP			Moist, cool climate	Moist climate	Moist climate	

for Lake Muzi (Humphries et al., 2019) but in contrast, drought phases for Lake St Lucia suggested by palynomorphs were recorded between 2600 and 300 cal yrs BP with intense drought between 800 and 300 cal yrs BP.

Mid Holocene (7000–2600 cal. yrs BP): The mid Holocene climate is characterized by high sea levels (Cooper et al., 2018), leading to a marine incursion in Lake St Lucia as the beach ridges began forming in the mid Holocene and a sequence of beach ridges continued to form until the late Holocene (Botha et al., 2018). High precipitation (fresh water conditions) and high moisture content were also characteristic of the Mid-Holocene which is seen by the presence of moisture loving plants (*Podocarpus* forest, cryptogams and fungi), marine elements such as scolecodonts (worm jaws) and freshwater indicators such as *Pseudoschizoaea* and *Typha*.

Late Holocene (Last 2600 cal. yrs BP): Regional vegetation characteristics during the last 2600 cal. yrs. BP are said to denote a warm and dry climate because the *Podocarpus* forest retreated as *Spirostachys* increased in Lake Sibaya, Lake Eteza (Neumann et al., 2008, 2010) and Lake St Lucia (Core MKD-1). Additionally, in Mozambique from the Nhaucatic Lake, Coastal forest, and Miombo woodland, an increase in bushveld savanna pollen, Asteraceae, and *Brachystegia* was noted (Ekblom, 2008; Ekblom et al., 2014). It became drier regionally leading to drought around 800–250 cal. yrs. BP hence, the decline in *Brachystegia* in Miombo woodland, decline in bushveld trees in Nhaucatic Lake, and corresponding reduction in *Spirostachys* in Lake St Lucia (Core MKD-1) and Lake Eteza (Ekblom, 2008; Ekblom et al., 2014; Neumann et al., 2010). The marine influence was seen in MKD-1 between 1700 and 300 cal yrs BP as foraminferal linings were recorded. This can be explained as an increase in the flow of seawater into the estuary due to the drying out of the lake (evaporation) and less supply of freshwater from the rivers caused by drought. This was possible as the youngest beach ridge was formed only around 1500 cal yrs BP (Botha et al., 2018).

4.3.1. Podocarpus/Spirostachys trend in the Indian Ocean Coastal Belt Biome (IOCB)

Lake Eteza and Lake St. Lucia exhibit high *Podocarpus* percentages, despite fluctuations between 7000 and 2600 cal yrs BP (see Fig. 7). *Podocarpus* decreased as *Spirostachys* increased in Lake Eteza, Sibaya, and Lake St. Lucia between 2600 and 670 cal yrs BP. This inverse relationship is as a result of a drop in moisture content in the last 2600 cal yrs BP. *Podocarpus* was forced to retreat because of its sensitivity to changes in moisture content and so the distribution is restricted to areas of high moisture availability (Chevalier et al., 2022). This interpretation is confirmed by other proxies such as used by Miller et al. (2019) and House et al. (2022).

During the past 800 cal yrs BP, *Podocarpus* remained present in Lake Eteza and Lake Sibaya as they attempted to recover, but it vanished from the Lake St. Lucia pollen record (MKD-1) (see Fig. 7). The disappearance of *Podocarpus* in core MKD-1 could be due to the soil in the surrounding environment becoming hypersaline as a result of the extreme drought. *Podocarpus* can only survive in slightly saline environments as studies like those by Abiti (2019) and Zou et al. (2021) have demonstrated where hypersaline soils kill or impede the germination and growth of *Podocarpus* seedlings.

In conclusion, the Indian Ocean Coastal Belt Biome (IOCB) experienced high moisture availability during the mid-Holocene (7000–2600 cal yrs BP), as demonstrated by the abundance of *Podocarpus* in Lake Eteza, Sibaya, St. Lucia, and even Mfabeni peatland. The late Holocene witnessed low moisture availability as shown by *Podocarpus* retreating and in the last 800 cal yrs BP, with extreme drought in Lake St Lucia leading to the disappearance of *Podocarpus* (see Fig. 7).

The neophyte, *Pinus*, is present in the Lake St Lucia profile from 385 cal yrs BP but historical records show that pine plantations were established only in the 1920s. Bioturbation of the shallow lake waters by hippos might account for the rather early occurrence of this northern hemisphere tree.

5. Conclusion

According to the pollen analysis of the Lake St. Lucia core, the environment was warm, sub-humid to dry with high local evaporation or a saline microenvironment, such as coastal salt marshes, between 6300 and 5900 cal yrs. BP. This was interpreted from an increase and peak in Amaranthaceae and very low numbers of cryptogams (pteridophytes and bryophytes). Based on the occurrence of Scolecodonts coinciding with periods of high sea level as well as the beginning of the formation of beach ridges, there was a marine incursion 1700–300 cal yrs BP. Cryptogams, *Ericaceae, Passerina, Typha*, and *Pseudoschizaea*—the latter of which was common—are evidence that the environment between 5900 and 4900 cal years BP became cooler, sub humid, with freshwater conditions. Cryptogams and *Podocarpus* proliferated and peaked when the climate warmed and became more humid between 4900 and 2600 cal yrs BP. Between 2600 and 800 cal yrs BP, the environment became warmer, there were low moisture levels (drought), and there was a greater influx of sea water into the estuarine Lake as a result of the lake's high rate of evaporation and low freshwater input caused by drought. Hence, the presence of foraminferal linings around 1700 cal yrs BP and the retreat of *Podocarpus* in the last 2600 cal yrs BP. A relatively warm environment with high precipitation, wetland mosaic and human disturbances was evident in the last 200 cal yrs. BP which is seen with the presence and increase in *Typha, Persicaria*, *Pinus*, *Phragmites* and Cyperaceae.

In conclusion, findings show a change from a humid forested environment with high precipitation and high sea levels (6300–2600 cal yrs BP) to a warm and dry open woodland environment (2600–300 cal yrs BP), with Principal Component Analysis (PCA) confirming this assertion.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Angela Effiom reports financial support was provided by

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

Abiti, M.F., 2019. Effects of Salt Solution Concentration on the Germination Success of *Podocarpus latifolius* Seeds. Doctoral dissertation. Makerere University.
Benallack, K., Greena, A.N., Humphries, M.S., Cooper, J.A.G., Dladla, N.N., Finch, J.M., 2016. The stratigraphic evolution of a large back-barrier lagoon system with a nonmigrating barrier. Mar. Geol. 379, 64–77.
Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512–518.
Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6 (3), 457–474.
Bonnefille, R., Riollet, G., 1980. Pollens of the East African Savanna. Centre National de la 800 Recherche Scientifique, Paris.
Botha, G.A., Porat, N., Haldorsen, S., Duller, G.A., Taylor, R., Roberts, H.M., 2018. Beach ridge sets reflect the late Holocene evolution of the St Lucia estuarine lake system, South Africa. Geomorphology 318, 112–127.
Campbell, I.D., Campbell, C., 1994. Pollen preservation: Experimental wet-dry cycles in saline and desalinated sediments. Palynology 18 (1), 5–10.
Chevalier, M., Chase, B.M., Quick, L.J., Scott, L., 2022. An atlas of southern African pollen types and their climatic affinities. Palaeoecol. Africa 35, 239–257.
Coates-Palgrave, M., 2002. Keith Coates Palgrave Trees of Southern Africa, 3rdedn. Struik, Cape Town.
Cooper, J.A.G., Green, A.N., Compton, J.S., 2018. Sea Level Change in Southern Africa since the Last Glacial Maximum. Quat. Sci. Rev. 201, 303–331.
Dladla, N.N., Green, A.N., Cooper, J.A.G., Humphries, M.S., 2019. Geological inheritance and its role in the geomorphological and sedimentological evolution of bedrock-hosted incised valleys, lake St Lucia, South Africa. Estuar. Coast. Shelf Sci. 222, 154–167.
Dyer, R.A., 1975. The genera of Southern African flowering plants. In: Dicotyledons, vol. 1. Department of Agricultural Technical Services, Pretoria.
Ekblom, A., 2008. Forest–savanna dynamics in the coastal lowland of southern Mozambique since c. AD 1400. The Holocene 18 (8), 1247–1257.
Ekblom, A., Risberg, J., Holmgren, K., 2014. Coastal forest and Miombo woodland history of the Vilankulo region, Mozambique. The Holocene 24 (3), 284–294.
Erdtman, G., 1960. The acetolysis method-a revised description. Sven. Bot. Tidskr. 54, 516–564.
Erdtman, G., 1969. Handbook of palynolgy: morphology, taxonomy, ecology. In: An Introduction to the Study of Pollen Grains and Spores. Hafner, New York, 486 p.
Faegri, K., Iversen, J., 1966. Textbook of Pollen Analysis, Second ed. Munksgaard, Copenhagen. 237 p.
Finch, J.M., Hill, T.R., 2008. A Late Quaternary pollen sequence from Mfabeni Peatland, South Africa: reconstructing forest history in Maputaland. Quatern. Res. 70, 442–450.
Freitas, A.G.D., Carvalho, M.D.A., Toledo, M.B.D., Mendonça, C.B.F., Gonçalves-Esteves, V., 2015. Bryophyte and pteridophyte spores and other palynomorphs in quaternary marine sediments from Campos Basin, southeastern Brazil: Core BU-91-GL-05. Acta Bot. Brasil. 29, 161–174.
Gelorini, V., Verbeken, A., Lens, L., Eggermont, H., Odgaard, B.V., Verschuren, D., 2012. Effects of land use on the fungal spore richness in small crater-lake basins of western Uganda. Fungal Divers. 55, 125–142.
Gosling, W.D., Miller, C.S., Livingstone, D.A., 2013. Atlas of the tropical West African pollen flora. Rev. Palaeobot. Palynol. 199, 1–135.
Grundling, P.L., 2004. The role of sea-level rise in the formation of peatlands in Maputaland. In: AquaDocs. The Impact of Mega-Floods, Mozambique. Maputo, pp. 58–67. http://hdl.handle.net/1834/703.
Grundling, P., Mazus, H., Baartman, L., 1998. Peat resources in northern KwaZulu-Natal wetlands: Maputaland, Department of Environmental Affairs and Tourism Report no. A25/13/2/7, Pretoria, South Africa, 102 pp.
Higgs, C.G., 2017. Geochemical Insights into the Influence of Holocene Sea Level Change on the Evolution of the Mkhuze River delta, Lake St Lucia, Northern KwaZulu-Natal. MSc dissertation. University of the Witwatersrand, Faculty of Science, School of Chemistry.
Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Ramsey, C.B., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L., 2020. SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. Radiocarbon 62 (4), 759–778.
House, A., Bamford, M.K., Chikumbirike, J., 2022. Charcoal from Holocene deposits at Wonderwerk Cave, South Africa: a source of palaeoclimate information. Quat. Int. 614, 73–83.
Humphries, M.S., Kirsten, K.L., McCarthy, T.S., 2019. Rapid changes in the hydroclimate of southeast Africa during the mid-to late-Holocene. Quat. Sci. Rev. 212, 178–186.
Humphries, M., Green, A., Higgs, C., Strachan, K., Hahn, A., Pillay, L., Zabel, M., 2020. High-resolution geochemical records of extreme drought in southern Africa during the past 7000years. Quat. Sci. Rev. 236, 1–11.
Hutchison, I.P.G., Midgley, D.C., 1978. Modelling the water and salt balance in a shallow lake. Ecol. Model. 4 (2–3), 211–235.
Juggins, S., 2012. rioja: Analysis of Quaternary Science Data. Version 0.7-3.
Juggins, S., 2020. rioja: Analysis of Quaternary Science Data. R Package Version 0.9-26. https://cran.r-project.org/package=rioja.
Juggins, S., Juggins, M.S., 2019. Package 'rioja'.
Kettner, M.T., Rojas-Jimenez, K., Oberbeckmann, S., Labrenz, M., Grossart, H.P., 2017. Microplastics alter composition of fungal communities in aquatic ecosystems. Environ. Microbiol. 19 (11), 4447–4459.
Low, A.B., Rebelo, A.G., 1996. Vegetation Map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs, Pretoria, South Africa.
Marwick, C.W., 1973. Kwamahlati. Die verhaal van bosbou in Zululand. Bulletin, 49. Department of Environment and Forestry. Pretoria.
Mazus, H., 2000. Clues on the history of *Podocarpus* forest in Maputaland, South Africa, during the Quaternary, based on pollen analysis. Africa Geosci. Rev. 7 (1), 75–82.
Miller, C., Finch, J., Hill, T., Peterse, F., Humphries, M., Zabel, M., Schefuß, E., 2019. Late Quaternary climate variability at Mfabeni peatland, eastern South Africa. Clim. Past 15 (3), 1153–1170.
Moll, E.J., Ward, C.J., Steinke, T.D., Cooper, K.H., 1971. Our mangroves threatened. African Wildlife 26, 103–107.
Mucina, L., Scott-Shaw, C.R., Rutherford, M.C., Kemp, K.G.T., Matthews, W.S., Powrie, L. W., Hoare, D.B., 2006. Indian Ocean coastal belt. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland, Strelitzia, vol. 19. South African National Biodiversity Institute, Pretoria, pp. 569–583p.
Neumann, F.H., Stager, J., Scott, L., Hendrik, J., Weyhenmeyer, C., 2008. Holocene vegetation and climate records from Lake Sibaya, KwaZulu-Natal (South Africa). Rev. Palaeobot. Palynol. 152, 113–128.
Neumann, F.H., Scott, L., Bousman, C., Van As, L., 2010. A Holocene sequence of vegetation change at Lake Eteza, Coastal KwaZulu-Natal, South Africa. Rev. Palaeobot. Palynol. 162, 39–53.
Orme, A.R., 1990. Wetland morphology, hydrodynamics and sedimentation. In: Williams, M. (Ed.), Wetlands: A Threatened Landscape. Blackwell, Basil, pp. 42–94.
Partridge, T.C., 1997. Cainozoic environmental change in southern Africa, with special emphasis on the last 200 000 years. Prog. Phys. Geogr. 21 (1), 3–22.
Patrick, M.J., Ellery, W.N., 2007. Plant community and landscape patterns of a floodplain wetland in Maputaland, Northern KwaZulu-Natal, South Africa. Afric. J. Ecol. 45 (2), 175–183.
Pooley, E., 1993. The Complete Field Guide to Trees of Natal, Zululand and Transkei. Natal Flora Publication Trust, Durban.
Pooley, E., 2005. A Field Guide to Wildflowers KwaZulu-Natal and the Eastern Regions. Natal Flora Publication Trust, Durban.
Porat, N., Botha, G.A., 2008. The luminescence chronology of dune development on the Maputaland coastal plain, southeast Africa. Quat. Sci. Rev. 27 (9), 1024–1046.
Porter, R.N., Blackmore, A.C., 1998. St Lucia System (forming a part of the Greater St Lucia Wetland Park). In: Information Sheet on Ramsar Wetland (RIS).
Schueler, L., Hemp, A., 2016. Atlas of pollen and spores and their parent taxa of Mt Kilimanjaro and tropical East Africa. Quat. Int. 425, 301–386.
Scott, L., 1982. Late Quaternary fossil pollen grains from the Transvaal, South Africa. Rev. Palaeobot. Palynol. 36, 241–278.
Scott, L., 1999. Palynological analysis of the Pretoria Saltpan (Tswaing Crater) sediments and vegetation history in the bushveld savanna biome, South Africa. In: Tswaing, Investigations into the Origin, Age and Palaeoenvironments of the Pretoria Saltpan, Edited by: Partridge. TC, Council of Geoscience (Geological Survey of South Africa), Pretoria.
Scott, L., Neumann, F.H., Brook, G., Bousman, C., Norstrom, E., Metwally, A., 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in Southern Africa. Quat. Sci. Rev. 32, 100–118.
Stormanns, C.H., 1987. An Inventory and Assessment of the Conservation Value of the Mkuze Swamp System. Institute of Natural Resources.
Strobel, P., Bliedtner, M., Carr, A.S., Struck, J., du Plessis, N., Glaser, B., Meadows, M.E., Quick, L.J., Zech, M., Zech, R., Haberzettl, T., 2022. Reconstructing Late Quaternary precipitation and its source on the southern Cape coast of South Africa: a multi-proxy paleoenvironmental record from Vankervelsvlei. Quat. Sci. Rev. 284, 107467.
Taylor, S., 1993. Dryland Salinity—Introductory Extension Notes. Department of Conservation and Land Management, Bathurst. New South Wales.

Taylor, R., Kelbe, B., Haldorsen, S., Botha, G., Welden, B., Vaeret, L., Simonsen, M., 2006. Groundwater-dependent ecology of the shoreline of the subtropical Lake St Lucia estuary. Environ. Geol. 49, 586–600.
Thamm, A.G., Grundling, P., Mazus, H., 1996. Holocene and recent peat growth on theZululand Coastal Plain. J. African Earth Sci. 23 (1), 119–124.
Turpie, J.K., Wilson, G., Van Niekerk, L., 2012. National Biodiversity Assessment 2011: National Estuary Biodiversity Plan for South Africa – Technical Report. In: Anchor Environmental Consultants Report No. AEC2012/01, Cape Town.
Zou, L., Li, T., Li, B., He, J., Liao, C., Wang, L., Xue, S., Sun, T., Ma, X., Wu, Q., 2021. De novo transcriptome analysis provides insights into the salt tolerance of *Podocarpus macrophyllus* under salinity stress. BMC Plant Biol. 21 (1), 1–17.