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Two contrasting swamp forest succession pathways in central Congo Basin peatlands

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Abstract

The central Congo Basin (CCB) contains one of the world's most extensive regions of tropical peat swamp forest, occupying interfluves and floodplains surrounding the Congo River and its tributaries. The region is dominated by hardwood and *Raphia*-palm forests. Little is known about how and when these forests developed. We investigate peatland ecosystem and forest development via pollen and

$\delta^{13}C_{TOC}$ analysis on peat cores from four study sites, two on floodplains to the east of the Congo River, and two on interfluves to the west of the Congo River. We present 81 ^{14}C dates on bulk peat samples from four peat cores to show that peat initiation and forest establishment occurred at three sites before or during the Last Glacial Maximum (LGM), at 26,750 calendar years before present (cal yr BP) (Bolengo), 19,600 cal yr BP (Ekolongouma) and 19,400 cal yr BP (Bondamba), and later at 13,350 cal yr BP (Boboka) at a fourth site. The three oldest dates support earlier hypotheses that the CCB may have been a dynamic refuge for rainforest taxa during the LGM. The pollen records from the four sites show two contrasting patterns of vegetation succession following peat initiation: the interfluvial peatlands developed from an open herbaceous wetland; the river floodplain peatlands developed from a hardwood swamp forest. All four sites eventually transitioned to a mixed swamp forest containing *Raphia* and *Uapaca* trees. Differences in the timing of vegetation transitions between sites suggest that autogenic (within-site) processes are important drivers of vegetation succession in these peatlands, overlain to varying degrees by allogenic (climatic) drivers. Overall, the comparative analysis of pollen records from four sites within the CCB reveals two contrasting trajectories of forest development—one associated with interfluves and the other with river floodplains—driven by a combination of autogenic and allogenic processes. Our findings highlight the biological diversity and complexity of the CCB peatlands, and their sensitivity to climatic change. Reduced precipitation in the Late Holocene affected peat accumulation and forest composition at all sites, with some sites being more sensitive than others. This study provides important context for efforts to protect and conserve the CCB peat swamp forests by demonstrating their sensitivity to environmental stress in the past.

Keywords

Swamp forest, Congo Basin, vegetation succession, Holocene, refugia, pollen.

1. Introduction

Recent mapping in the central Congo Basin (CCB) has shown that 167,600 km^2 of swamp forest is underlain by extensive deposits of peat, making it one of the world's largest tropical peatland areas (Crezee et al., 2022; Dargie et al., 2017). The CCB peatlands are globally important in terms of carbon storage, containing 29.0 petagrams of carbon (Pg C; or 29 billion tonnes of carbon; Crezee et al., 2022). This is more than the carbon storage of above-ground biomass in the entire Democratic Republic of Congo (~23.0 Pg C) (Xu et al., 2017). However, these carbon stocks and their overlying forests may be sensitive to climatic change. Initial palaeoenvironmental reconstructions have shown that a reduction in palaeo-precipitation from ~5000 to ~2000 cal yr ago resulted in drying of the peatlands, a substantial decline in peat carbon storage, and a change in forest structure (Garcin et al., 2022; Hawthorne et al., 2023). This finding raises the possibility that future climatic change could similarly threaten the peatlands.

Peat has so far been found in the CCB beneath three vegetation types: hardwood swamp forest (including *Uapaca mole* Pax, *Carapa procera* DC. and *Xylopia rubescens* Oliv.), and two types of palm-dominated swamp forest, a widespread type dominated by *Raphia laurentii* De Wild. (Dargie et al., 2017), and a much rarer type, confined to recently abandoned river channels, which is dominated by *Raphia sese* De Wild. (authors' observation). It remains to be established when these vegetation types developed, and whether and how their distributions are controlled by factors including climate, hydrological regime, geomorphological processes and/or peat thickness. Previous research on spatio-temporal patterns of swamp forest development in Southeast Asia and Amazonia has demonstrated the influence of such factors on vegetation succession on decadal to millennial timescales, with differences between sites and regions (Hapsari et al., 2017; Mlotha 2018; Philips et al., 1997; Roucoux et al., 2013). Establishing a similar understanding of spatial and temporal ecological patterns and their (abiotic and biotic) driving factors in the CCB peatlands will provide a foundation for ongoing attempts to conserve this globally significant ecosystem complex (CongoPeat Consortium, 2023).

Here, we reconstruct the palaeoenvironmental history of three unpublished peatland sites distributed across the CCB (Fig. 1 and Supplementary Table 1), building on previous palaeoecological research on a fourth peat core CEN-17.4 (Garcin et al., 2022, Hawthorne et al., 2023), to deliver a broad-scale assessment of the timing and pattern of peat and forest development across the CCB. Two of the sites, Bolengo (peat core BNG1-4) and Bondamba (BDM1-7), are located on the floodplains of the Busira river, part of the tributary network of the Ruki river which extends eastward from the south bank of the Congo River, approximately four hundred and eight kilometres across the basin. The other two sites are located on wide, low-lying interfluves between major rivers: Ekolongouma (CEN-17.4), the previously published record, lies between the Ubangi and the Likouala-aux-Herbes rivers; and Boboka (BOB-9) lies between the Ngiri and the Congo River. Peat cores were extracted from each site, radiocarbon dated to determine the basal peat age and analysed via pollen, loss on ignition (LOI) and $\delta^{13}C_{TOC}$ to establish how the vegetation and peat developed at each site from peat formation up to the present day. We use this data to discuss evidence for the presence of refugial forests during the Last Glacial Maximum (LGM, 26,000 – 19,000 cal yrs BP: Cohen and Gibbard 2019) and assess the likely drivers of ecological change over time.

2. Geographical setting

The CCB peatlands (Fig. 1) cover an area of 167,600 km^2 and extend across the eastern Republic of Congo and western Democratic Republic of Congo. At each of our four study sites, transects extended from the margin to the interior of the peatland. The peat along these transects at all sites was underlain by clays, silts and/or sands. All sites in this article are named informally after nearby villages.

The Bolengo peatland is located on the floodplain to the south of the Busira River (a major tributary of the Ruki River), adjacent to Bolengo village. Our study transect extends 8 km into the peatland from the banks of the river. Peat depths increase from the riverbank along the study transect to 6 km, after which peat depth decreases. The peat core, BNG1-4, was extracted from 4 km along the study transect (0.3187°S, 19.7994°E) to a depth of 4.10 m. The majority of the study transect is covered by hardwood

swamp forest (1.75 – 6.5 km), with species including *Entandrophragma palustre* Staner*, Uapaca pynaertii* De Wild*, Coelocaryon botryoides* Vermoesen and *Homalium africanum* (Hook.f.) Benth. The end of the transect (6.75 – 8 km) transitions out of swamp forest to cultivated manioc fields, *terre firme* (dry land) forest and secondary forest. Palm dominated swamp forest exists only close to the start of the transect, between 1 and 1.5 km, dominated by *R. laurentii*.

The Bondamba peatland is located on the floodplain to the north of the Busira River. Our study transect extends 7 km northwards into the peatland from the banks of the Busira in the south, adjacent to Bondamba village. Peat depth increases from the riverbank towards the centre of the site, reaching a maximum of 6.4 m at 6.5 km. Most of the study transect is covered by palm dominated swamp forest (up to 6.75 km), with species of *R. laurentii* and *R. sese*. The end of the transect and coring site (7 km) are dominated by palms (*R. laurentii* and *R. sese*) and hardwood trees, including *Cryptosepalum congolanum* (De Wild.) J.Léonard*, Syzygium sp.,* and *Englerophytum laurentii* (De Wild.) L.Gaut. The peat core, BDM1-7, was extracted from 7 km along the study transect (0.1734°S, 19.6960°E) to a depth of 5.70 m.

The Ekolongouma peatland is located on the interfluve between the Likouala-aux-Herbes and Ubangi rivers, in the Likouala department of the Republic of Congo. The study site consists of three nearly continuous transects across the interfluve: Itanga, Centre and Ekolongouma. The peatland is ~45 km wide from east to west, bounded by Itanga village in the west and Ekolongouma village in the east. Peat depths increase towards the peatland centre, reaching a maximum of 5.99 m at the coring site of CEN-17.4 (1.1835°N, 17.6399°E, 17.4 km along the Centre transect). The study transect is dominated by either hardwood swamp forest or *R. laurentii* dominated palm swamp, with gradations between the two. The coring site is dominated by a mix of the palm (*R. laurentii*) and hardwood trees including *C. procera*, *U. mole* and *Xylopia aethiopica* (Dunal) A.Rich.

The Boboka peatland is located on the interfluve between the Ngiri River (a tributary of the Ubangi River) to the north and the Congo River to the south, southwest of the town of Makanza. Our study

transect extends 11 km north into the peatland from the banks of the Congo River. The transect ends next to a channel and stream which are connected to Lake Libanda. Peat depths increase from the riverbank to the end of the transect. The peat core, BOB-9, was extracted from 9 km along the study transect (1.5162°N, 18.8475°E) to a depth of 2.50 m. Savannah vegetation dominates the start of the transect (0 – 0.75 km), transitioning to a mix of palm and hardwood at the forest edge. The majority of the transect is dominated by hardwood swamp forest, with species of e.g. *U. mole, C. Procera, Manilkara obovata* (Sabine & G.Don) J.H.Hemsl. and *Symphonia globulifera* L.f. The transect ends (9.25 – 11 km) in a mixed swamp forest of hardwood species and *R. laurentii* palms.

3. Methods

3.1 Peat coring

'Peat', defined here as material with loss-on-ignition (LOI, see below for method) >65%, was sampled at a single location at each of the four study sites. Cores were extracted with a 5 cm diameter, 50 cm long Russian-type corer in two parallel holes to collect a continuous sequence and minimise disturbance of the upper and lower ends of the core sections. Coring continued until the underlying clay substrate was encountered. Each core section was wrapped, transported under licence to the UK and refrigerated at 4°C. Where necessary, depths were corrected using linear interpolation to account for compaction of core sections during transportation from the core site (BNG1-4: max. 13 cm, BDM1-7: max. 7 cm, CEN17-4: max. 5 cm, and BOB-9: max. 1 cm correction). Core locations were recorded using a Garmin handheld GPS.

3.2 Loss on ignition

Loss on ignition (LOI) analysis was carried out using methods described by Heiri et al. (2001). Sub-samples (1 cm^3) extracted from peat cores (BDM1-7: 22 samples, BNG1-4: 45 samples, CEN-17.4: 87 samples, BOB-9: 18 samples) at varying depths, were first dried overnight at 105 °C, then weighed and returned to the furnace at 550 °C for 4 hours, before calculating organic content by loss on ignition.

3.3 Peat core chronology and ^{14}C dating

A total of 81 bulk peat samples (56 of which are previously unpublished) were dated by radiocarbon AMS (Supplementary Table 2) across the four peat cores (BDM1-7: 20 dates, BNG1-4: 19 dates, CEN-17.4: 22 dates, BOB-9: 20 dates). The samples were sieved at 180 µm to remove roots, then treated with acid-alkali-acid digestion; the remaining solids (humin) were retained and combusted to CO_2 with CuO and Ag in an evacuated quartz tube. Sample CO_2 was converted to graphite by Zn/Fe reduction and the ^{14}C content measured by AMS (Ascough et al 2023). All dates were calibrated using a 50:50 mix of the IntCal20 and SHCal20 calibration curves (Hogg et al., 2020) in the *IntCal* package in *R* v. 4.0.3 (R Core Team, 2021); for brevity, ages cited in the text are median calibrated ages unless otherwise stated. Radiocarbon dates are presented in full in Supplementary Table 2. The age models, presented in Fig 2, were constructed using the *R* package *rBacon* v.2.5.8 (Blaauw & Christen 2011), setting the priors to allow for low memory and a wide range of accumulation rates (acc.mean=40, acc.shape=1, mem.mean=0.1, ssize=15000, mem.strength=2).

3.4 $\delta^{13}C_{TOC}$

$\delta^{13}C_{TOC}$ was measured on bulk samples (BDM1-7: 537 samples, BNG1-4: 395 samples, CEN-17.4: 162 samples, BOB-9: 183 samples) using an elemental analyser (SerCon ANCA GSL) interfaced to a continuous flow isotope ratio mass spectrometer (Hydra 20–20). Precision on $\delta^{13}C$ was <0.1‰.

3.5 Pollen analysis

A total of 264 pollen samples were analysed across the four peat cores (BDM1-7: 72 samples, BNG1-4: 51 samples, CEN17-4: 109 samples, BOB-9: 32 samples) at a maximum 8 cm resolution. Sample preparation followed standard methods (Moore et al., 1991), substituting density separation (Nakagawa et al., 1998) for HF treatment. Two *Lycopodium* tablets (Lund University batch no. 201890, 11,267 ± 370 spores per tablet) were used as an exotic marker in each 1 cm^3 sample of peat. Samples were mounted in silicone oil and counted and identified at x1000 magnification using a Zeiss Axioskop microscope. Samples were counted to a minimum sum of 300 grains. Spores were excluded from the pollen sum and calculated as a percentage outside of the pollen sum, but the sum does include unidentified morphotypes, which never reach more than 5 % of the pollen sum. Identifications were made using a key compiled from the literature (e.g. Gosling et al., 2013, Van Campo et al., 1974, Ybert 1979), and from personal observations from reference collections at the University of Oxford and Aix-Marseille University's CEREGE, and photographs from reference collections at Goethe University Frankfurt, University of Montpellier II, Aix-Marseille University's CEREGE, and Pierre and Marie Curie University Paris. Pollen identifications were made to the lowest taxonomic level possible, either family (listed as e.g. Poaceae or Cyperaceae), genus (listed as e.g. *Raphia*) or species level (listed as e.g. *Symphonia globulifera).* Pollen grains have been listed as a 'type', e.g. *Alisma*-type, when other genera produce identical pollen but the named genus is a likely candidate for pollen identity because of the site's geographic or ecological context. The incomplete state of pollen taxonomy in central Africa means that any of these identifications and attributions may include other genera or species whose pollen has not yet been described in the literature.

Palaeoecological interpretations are based on ecological information derived from the African Plant Database v. 3.4.0 and on vegetation census data from the Ekolongouma site (Dargie, Bocko and Lewis, 2024, unpublished data) supplemented by information in the palaeoecological and ecological literatures (e.g. Elenga et al., 2000; Brncic et al., 2007; Kiahtipes et al., 2011; Moutsambote, 2012; Ifo

et al., 2016: Bocko et al., 2016), as well as conservation inventories (e.g. Hughes and Hughes 1992). The frequent inability to identify pollen morphotypes to species level, combined with the low rates of endemism, a high rate of environmental crossover (i.e. taxa found in a wide range of environments) and the limited research into the ecology of peatland taxa in CCB peat swamp forests, mean that our interpretations, while made with the best current knowledge, may be open to revision in the future as research in the region develops.

3.5 Data analysis

Local pollen assemblage zones (LPAZs), i.e. stratigraphically contiguous clusters of similar samples interpretable as representing distinct phases of vegetation succession in the past, were established in the pollen data at each site using a stratigraphically constrained cluster analysis (CONISS) and a Bray-Curtis dissimilarity matrix, including only taxa achieving >5 % abundance in at least one sample (Birks and Gordon, 1984). The choice of number of zones was informed by a broken stick model (Bennett, 1996) and visual examination of key vegetation transitions in the pollen data. Indicator species analysis (Dufrêne and Legendre, 1997) was performed to determine which taxa were characteristic of each zone, referred to here as indicator taxa. To allow comparison between sites, we qualitatively compared the pollen data (Fig 3 – 4) from each set of local zones and defined a simplified sequence of Regional Pollen Assemblage Zones (RPAZs), which represent pollen assemblage variations across a region with no assumption that the changes correlate in time: Cushing, 1967; Bennett, 1988). The major changes in the pollen data can be represented by three RPAZs for the sites to the east of the Congo River (Bolengo and Bondamba: RPAZs 1A, 2A and 3A) and three different RPAZs for the sites to the west of the Congo River (Ekolongouma and Boboka: RPAZs 1B, 2B and 3B; Supplementary Table 7). To support this qualitative summary of the dataset and identify ecologically meaningful structure in the pollen dataset, non-metric multidimensional scaling (NMDS) ordination (Legendre and Birks, 2012) using the

239 Bray-Curtis dissimilarity matrix was carried out (Fig. 7). These analyses were carried out in *R* using the
240 *rioja* (Juggins, 2017) and *vegan* (Oksanen et al., 2013) packages.

241

242 ## 4. Results

243 ### 4.1 Loss on ignition

244 Loss on ignition (LOI) data (>65% organic matter content, Fig. 3 – 4) was used to determine the
245 thickness of the peat at each site. The cores from the two river floodplain peatland sites east of the
246 Congo River, Bolengo and Bondamba both have high organic matter content (>65%, our definition of
247 peat), at the base of the cores (410 cm and 569 cm respectively). This suggests that in both cases coring
248 failed to capture the oldest basal peats (probably because the pointed end of the Russian corer could
249 not penetrate sufficiently deep into the underlying sediments). At Bondamba, a few samples between
250 562 and 564 cm show lower organic matter content (between 28 and 39%), probably indicating an
251 episode of substantial fluvial input of inorganic sediment. LOI fluctuates at both sites but increases
252 gradually upwards through the peat profile, suggesting repeated (seasonal or more episodic) but
253 diminishing low-energy flooding bringing inorganic sediment to the sites until 329 cm at Bolengo and
254 539 cm at Bondamba , after which LOI values are consistently above 90%.

255 At the two interfluvial sites to the west of the Congo River, Ekolongouma and Boboka, the transition
256 between the underlying inorganic sediment and peat is recorded in the cores. At Ekolongouma, there
257 is a sharp transition to peat at 599 cm. At Boboka, the transition is more gradual than at Ekolongouma,
258 occurring over 28 cm; LOI values reach >65% at 222 cm. Ekolongouma and Boboka were also likely to
259 have been repeatedly flooded after peat establishment (but to a lesser degree than Bolengo and
260 Bondamba), evidenced by minor decreases in the LOI increasing trend until 514 cm at Ekolongouma
261 and 189 cm at Boboka, after which LOI values are consistently above 90%.

4.2 Radiocarbon dating and age-depth models

The age-depth models (Fig. 2) provide age estimates for the base of peat cores and the initiation of peat formation at each site; 26,750 cal yr BP at Bolengo, 19,400 cal yr BP at Bondamba, 19,600 cal yr BP at Ekolongouma and 13,350 cal yr BP at Boboka.

Peat initiation at the river floodplain sites may have occurred slightly earlier, than the basal peat dates recorded (Bolengo: ~26,750 cal yr BP, Bondamba: 19,400 cal yr BP), given that the core appears not to have sampled the sediment/peat interface. One of the river floodplain sites, Bondamba returned a similar basal peat age (19,400 cal yr BP), to the interfluvial peatland Ekolongouma (19,600 cal yr BP), at similar depths, 569 cm and 599 cm respectively. The basal age estimates at both these sites should be treated with caution because dates near the core base (at 596 and 625 cm at Ekolongouma, and 504 cm at Bondamba) are out of stratigraphic sequence (younger or older than surrounding dates). This suggests that organic carbon from older sources (e.g. reworked soils) may have been introduced at the core base, perhaps via flooding during peat establishment. The Bayesian age model used here (Bacon), assumes that peat accumulates monotonically with depth and deeper layers are older, therefore any age inversions will affect the accuracy and reliability of the model, where accumulation rates are drawn from prior distributions (Blaauw & Christen 2011). The Bayesian age models implemented here attempt to balance all the available information, providing the most comprehensive view of peat age and accumulation, however, potentially increasing uncertainty and bias in the sections of the peat core with out of sequence dates. Alternatively, removing out of sequences dates or choosing to place more weight on the outlying dates could substantially alter the estimated age of peat initiation. At Ekolongouma, placing more weight on the dates at 596 and 625 cm would give a younger estimate (~17,500 cal yr BP), while placing more weight on the date at 599 cm, would give a slightly older estimate (~20,300 cal yr BP). At Bondamba the difference between the outlying date at 504 cm and the bounding upper and lower dates, at 425 and 516 cm, is 200 and 100 calibrated years respectively, which is less substantial than at Ekolongouma (for context, the average analytical

uncertainty on these dates is ~40 years: Supplementary Table 2) therefore placing more weight on the outlying date at 504 cm would not substantially change the age of peat initiation at this site. Therefore, the age models presented here include the out of sequence dates to accurately reflect real stratigraphic processes e.g. organic carbon introduced via flooding during peat establishment, and to highlight realistic uncertainty at the core base. The basal peat age at Boboka is substantially younger than the other sites examined, ~13,350 cal yr BP at a shallower depth of 221 cm, with no outliers at the core base.

All the age-depth models presented here (Fig. 2) show a similar pattern, starting with a shallow sloping age-depth relationship followed by a steep increase in the age-depth slope (i.e. consistent with rapid peat accumulation) during the early Holocene (Young et al., 2021). Holocene peat accumulation is interrupted by an interval with a substantially shallower age-depth slope, observed across all peat sequences (and indeed to other sites in the CCB, as reported in Garcin et al., 2022), between approximately 7500 and 2000 cal yr BP, with some slight temporal variation between study sites. Following this shallower age-depth interval, all sites show a steep gradient in the uppermost part of the sequence from ~2000 cal yr BP. The pattern is observed more clearly at Ekolongouma and Bondamba, than at Bolengo and Boboka which are shorter peat sequences and therefore less well resolved.

The substantially shallower age-depth slope observed at multiple sites likely represents a period of enhanced peat decomposition (Garcin et al., 2022). This Late Holocene period of enhanced peat decomposition has been discussed in detail in relation to the sequence from Ekolongouma, where between 7520 and 2090 cal yr BP the gradient of the age-depth profile is five to eight times shallower than in the peat above and below. By examining four palaeoenvironmental proxies (I-index from Rock-Eval pyrolysis, total organic carbon (TOC), carbon-to-nitrogen ration (C/N) and C-isotope composition of total organic carbon ($\delta^{13}C_{TOC}$)) it was established that this interval, named the 'Ghost Interval', consists of highly decomposed peat, consistent with contemporaneous and/or secondary decomposition during an interval of water table drawdown linked with climatic drying culminating

around 2000 cal yr BP (Garcin et al., 2022). The replication of the same pattern in age-depth models from across the region suggests that the climatic drying between 5000 and 2000 cal yr BP caused widespread peat decomposition across the CCB. Once conditions stabilised (~2000 cal yr BP) and wetter climatic conditions returned (evidenced by depleted δD*n*-C_{29} values from ~600 cal yr BP; Garcin et al., 2022) peat accumulation resumes at all our study sites, evidenced by a steeper age-depth profile from ~2000 cal yr BP.

4.3 $\delta^{13}C_{TOC}$

The C-isotope composition of total organic carbon ($\delta^{13}C_{TOC}$, Fig. 6) fluctuates around -29‰ and -30‰ (Bolengo: -28‰ to -31‰, Bondamba: -27‰ to -34‰) at the river floodplain sites, Bolengo and Bondamba, respectively, suggesting that these records are dominated by C3 plants (e.g., mosses, shrubs, and trees) throughout. By contrast, the interfluvial peatland sites, Ekolongouma and Boboka, show less negative values (between -20‰ and -25‰) at the base of their records, indicating a dominance of C4 plants (grasses, sedges). Both these sites gradually shift to a dominance of C3 plants, ~12,500 cal yr BP at Ekolongouma and ~7200 cal yr BP at Boboka, where values drop by 5-10‰ to an average of -30‰ at Ekolongouma and -29‰ at Boboka.

4.4 Pollen percentages

Two distinct successional patterns were observed in the pollen data, split between the river floodplain peatlands, Bolengo and Bondamba, to the east of the Congo River, which developed from a hardwood swamp forest, and the interfluvial peatlands, Ekolongouma and Boboka, to the west of the Congo River, which developed from an open herbaceous wetland. All four sites eventually transitioned to a mixed swamp forest containing *Raphia* palm and *Uapaca* trees. Here we describe the most prominent vegetation changes observed with respect to the comparable pollen assemblage zones established across sites (sites east of the Congo River – zones 1A, 2A and 3A, and sites west of the Congo River – zones 1B, 2B and 3B), described in detail in Supplementary Table 7. A detailed description of the local pollen assemblage zones at each site is presented in Supplementary Tables 3 – 6.

The two river floodplain sites located to the east of the Congo River (Bolengo and Bondamba), on the blackwater (sediment-poor) Busira River, were occupied by similar vegetation communities in the past with a similar pattern of vegetation change over time, represented here by (Regional) Pollen Assemblage Zones 1A, 2A and 3A (Fig. 3). The lowest part of these records, Zone 1A, is dominated by high percentages of *Macaranga* (mean 20.3% Bolengo, 17.3% Bondamba) and *Brazzeia* (7.9% Bolengo, 16.9% Bondamba) pollen. At a depth corresponding to ~10,500 cal yr BP, the Zone 1A taxa decline at both sites and are replaced by *Mitragyna* (mean 8.2%, Bolengo 19.2% Bondamba) and *Lophira* (17.5% Bolengo, 7.3% Bondamba) pollen (Zone 2A). The final pollen assemblage, Zone 3A, begins at a depth corresponding to ~8000 cal yr BP at both sites, dominated by *Raphia* (mean 13.3% Bolengo, 24% Bondamba) and *Uapaca* (mean 21.5% Bolengo, 16.5% Bondamba) pollen. In this zone, there is an increase in *Syzygium,* from ~4500 to ~2500 cal yr BP at Bolengo, and from ~6500 to ~2000 cal yr BP at Bondamba.

Sites located to the west of the Congo River, Ekolongouma (on the interfluve between the whitewater (sediment-rich) Ubangi and blackwater Likouala-aux-Herbes Rivers) and Boboka (on the interfluve between the whitewater Congo River and the blackwater Ngiri River), were likewise occupied by similar vegetation communities in the past with a similar pattern of vegetation change over time, but the sequence was different from the eastern sites and is represented here by (Regional) Pollen Assemblage Zones 1B, 2B and 3B (Fig. 4). The base of these records, Zone 1B, is dominated by high percentages of Cyperaceae (mean 34.5% Ekolongouma, 25.9% Boboka) and Poaceae (9.7% Ekolongouma, 10.3% Boboka) pollen. At ~12,000 and 6400 cal yr BP, at Ekolongouma and Boboka respectively, Zone 1B taxa decline and are replaced by a dominance of *Manilkara* (mean 26.5% Ekolongouma, 20.7% Boboka) and *Carapa*-type (8.2% Ekolongouma, 5.9% Boboka) (Zone 2B). The uppermost zone, Zone 3B, emerges at ~9800 cal yr BP at Ekolongouma only, dominated by *Pandanus* (mean 22.4%) and *Pycnanthus* (17.9%) pollen. Despite the fact that *Pandanus* and *Pycnanthus* do not expand towards the top of the Boboka sequence, the two sites do share a further palynological feature:

363 at ~2000 cal yr BP, there is an increase in *Lophira* and a decline in *Uapaca* at both sites (and additionally,
364 a decline in *Pandanus* and *Pycnanthus* at Ekolongouma).

365 ## 4.5 Non-metric multidimensional scaling (NMDS) ordination

366 The NMDS biplot (Fig. 7) for Bolengo and Bondamba (river floodplain sites, east of the Congo River)
367 shows a distinct overlap in pollen samples from zones 1A-3A, occupying positive Axis 1 scores in the
368 NMDS space. However, each zone is dominated by distinct swamp forest taxa, likely representing
369 different forest environments (discussed in detail in Section 4.2). In contrast, the NMDS biplot (Fig. 7)
370 for Ekolongouma and Boboka (interfluvial sites, west of the Congo River) highlights an overall trend
371 with increasing Axis 2 scores moving up the NMDS biplot and up-core from zones 1B to 3B. The NMDS
372 analysis also emphasizes the distinct species composition of zone 1B, which is characterised by
373 indicator taxa Cyperaceae and Poaceae. Zones 2B and 3B by contrast are characterised by indicator
374 taxa *Manilkara* and *Carapa* (2B) and *Pandanus* and *Pycnanthus* (3B), both representing swamp forest
375 environments and overlapping in the NMDS space. Finally, the Ghost Interval at Ekolongouma and
376 Boboka, characterised by *Lophira* and *Uapaca,* overlaps with pollen samples from Zones 2B and 3B. At
377 Bolengo and Bondamba, the Ghost Interval is characterised by an increase in *Syzygium* and at Bolengo
378 is partly distinct from the rest of the pollen samples in the NMDS space, whereas at Bondamba the
379 Ghost Interval samples overlap with samples from zones 3A, 2B and 3B in the NMDS space.

380

5. Discussion

Taken together, the data from the four sites provide evidence for peat accumulating in the CCB under a forest canopy at two river floodplain sites (Bolengo and Bondamba, east of the Congo River) and in open herbaceous wetland at two interfluvial sites (Ekolongouma and Boboka, west of the Congo River), well before the start of the Holocene; at three of these sites, peat persisted and formed even during the generally dry conditions of the LGM, at 26,750 cal yr BP (Bolengo), 19,600 cal yr BP (Ekolongouma) and 19,400 cal yr BP (Bondamba), and later at a fourth site at 13,350 cal yr BP (Boboka). The three oldest dates support earlier hypotheses that the CCB may have been a refuge for rainforest taxa during the LGM.

5.1 Peat initiation and forest development

Peat initiated at different times in two contrasting environments, one dominated by hardwood taxa typical of seasonally flooded forest, on floodplains adjacent to the Busira River, and the other by taxa indicating open herbaceous vegetation, on large interfluves bounded by rivers, as evidence by site chronologies (Fig. 2), pollen (Figs. 3 and 4) and $\delta^{13}C_{TOC}$ data (Fig. 6).

At the sites on the floodplains to the east of the Congo River, Bolengo and Bondamba, pollen and $\delta^{13}C_{TOC}$ data (Fig. 3 and Fig. 6) are interpreted as evidence for peat initiation under closed forest cover. The pollen assemblages are dominated by hardwood taxa characteristic of seasonally flooded forest: *Brazzeia* (7.9% & 16.9% respectively), *Macaranga* (20.3% & 17.3% respectively) and *Manilkara* (15.3% & <1% respectively). Peat was accumulating at Bondamba ~19,400 cal yr BP (Fig. 2), during what may have been the coolest and driest period of the LGM in central Africa (Schefuß et al., 2005; Weijers et al., 2007). At Bolengo, peat was accumulating even earlier at ~26,750 cal yr BP (Supplementary Table 2). The palaeoenvironmental evidence thus demonstrates that conditions were sufficiently wet on parts of the floodplain of the Busira river to support peat accumulation and swamp forest throughout the LGM. This finding supports earlier hypotheses that the CCB may have been a glacial refuge for rainforest taxa (Sowunmi 1999; Colyn et al., 1991).

406 The generalist nature of taxa observed in our palaeoecological data, the apparent absence of peatland
407 endemic species in present-day vegetation surveys, and the scarcity of peat sequences older than the
408 LGM, provides qualified evidence to support the hypothesis that parts of the CCB acted as a dynamic
409 refugium for hygrophilous generalist taxa during the LGM (Maley 1996; Hardy et al., 2013). Rather than
410 indicating stable, continuous peatland conditions across the region throughout the Quaternary, this
411 evidence suggests that peat-forming ecosystems persisted in localized, hydrologically favourable
412 settings, providing refugial habitats for moisture-demanding plants during many periods of regional
413 drying e.g. the LGM. However, the observations that (1) as yet, there are no documented peatland
414 endemics and (2) levels of plant endemism in the central Congo Basin are low by regional standards
415 (Dagallier et al., 2020), together suggest that peatland habitats occasionally disappeared entirely, or
416 were reduced to very small fragments, on evolutionary timescales (hundreds of thousands of years).
417 If extensive peatland habitat had persisted throughout the Quaternary, it seems likely that specialist
418 peatland species would have evolved. Future phylogeographical studies in the peatlands could help to
419 shed light on their role as museums (where species persist) or cradles (where species diversify)
420 (Dagallier et al., 2020) during the Quaternary.

421 At the sites on interfluves to the west of the Congo River, Ekolongouma and Boboka, pollen and $\delta^{13}C_{TOC}$
422 (Fig. 4 and Fig. 6) data provide evidence for peat initiation in open environments dominated by
423 Cyperaceae (mean pollen percentages of 34.5% and 25.9% respectively) and Poaceae (mean pollen
424 percentages of 9.7% and 10.3 % respectively). Low but persistent percentages of pollen from certain
425 tree taxa (e.g. *Lophira*, *Carapa*-type and *Macaranga*) likely represents scattered presence of these
426 trees within the pollen catchment of the sites, with somewhat higher percentages of *Macaranga*
427 (Vincens et al., 2006) indicating greater tree cover at Boboka than Ekolongouma. Peat initiation
428 occurred at Ekolongouma ~19,600 cal yr BP (a similar time to Bondamba, i.e. the LGM), coinciding with
429 a minor short-lived increase in precipitation (Hawthorne et al., 2023; Fig. 6). However, at Boboka peat
430 initiated 6,250 years later at ~13,350 cal yr BP. By this time, climatic conditions had probably become

warmer and wetter, with mean annual temperatures rising by ~2.5°C from 18,000 to 13,000 cal yr BP, following the generally cooler conditions of the LGM (Schefuß et al., 2005; Weijers et al., 2007).

Thus, this new data provides further evidence that peat accumulation and peat swamp forests in the CCB are not purely an interglacial or Holocene phenomena associated with very warm, wet climatic conditions, as previously thought (Dargie et al., 2017), but instead that peatland development has occurred under a range of climatic states — although the largest number of basal peat dates still occur during the warm, wet Holocene (Dargie et al., 2025; Dargie, 2015). These early peat initiation dates are much older than those reported from the vast majority of temperate/boreal peatlands (e.g. Gorham et al., 2007; Liu et al., 2025) and from peatlands in lowland Amazonia, which typically occur on geomorphologically dynamic floodplains (Lähteenoja et al., 2009a, b; Kelly et al., 2020), but there are similar and older peatlands in inland parts of SE Asia (e.g. Dommain et al., 2011; Ruwaimana et al., 2020). Peatlands in the CCB have formed in varying geomorphological settings; the cores studied here are, at the present day, located well away from the margins of the peatlands, in two different geomorphological contexts, two on large, almost flat interfluves between whitewater and blackwater rivers, and two on blackwater river floodplains confined by low hills. The survival of peat during intervals of dry glacial climate is not necessarily incompatible with the evidence for sensitivity to climatic drying during the Mid- to Late Holocene (Garcin et al., 2022). The cores studied here come from the deepest peats encountered at each site, likely to be situated in what were topographic low points before peat initiation. Such sites are likely to be fed by groundwater, floodwater and/or catchment runoff as well as rainfall, unlike the purely rain-fed peat domes that are thought to have accumulated in many places during the Holocene.

5.2 Peatland vegetation succession on the floodplains of the Busira River

The pollen records from Bolengo and Bondamba share similar patterns and timing of vegetation succession (Fig. 3; Supplementary Tables 3 – 4). Both sites were forested at the time of peat initiation (~26,750 cal yr BP at Bolengo and ~19,400 cal yr BP at Bondamba), with pollen assemblages dominated

by *Brazzeia* and *Macaranga*, representing a waterlogged hardwood forest (zone 1A). This forest assemblage persisted for ~10,000 years at Bondamba and for ~16,000 years at Bolengo.

Pollen assemblage zone 2A begins around ~10,500 cal yr BP at both sites, with an expansion of (among other taxa) *Mitragyna* and *Lophira*. *Lophira* pollen peaks at 29% at Bolengo ~9300 cal yr BP and 58.3% at Bondamba at ~8,250 cal yr BP, accompanied by reduced abundance of *Raphia*, possibly indicating an adaptation to drier seasonal conditions or opening of the forest canopy. Zone 2A is interpreted to represent a seasonally inundated hardwood swamp with a more open canopy than represented by the underlying zone.

Zone 3A, characterised by *Raphia* and *Uapaca* pollen, begins at ~8000 cal yr BP at both sites; we interpret the palynology of this zone as representing a mixed hardwood- and palm-dominated swamp forest. Notably, *Syzygium* pollen is abundant from ~4500 to ~2500 cal yr BP at Bolengo and from ~6500 to ~2000 cal yr BP at Bondamba. *Syzygium* is frequently considered an indicator of forest change (Mlotha, 2018), and while it is typically found in seasonally flooded forests and along rivers in the CCB, some species in this genus e.g. *Syzygium guineense* (Willd.) DC., indistinguishable in the pollen record, are more tolerant of lower water tables and can withstand intense dry seasons (Bidalia et al., 2018; Zigelski et al., 2019; Negash 2021). Therefore, the increase in *Syzygium* seen here may represent a local response to the drought episode that resulted in peat decomposition (between ~7500 and 2000 cal yr BP). As discussed above, this interval is thought to have been characterized by lowering water tables across the region which caused substantial peat decomposition (Garcin et al., 2022), involving the near-total mineralisation of several metres of peat and an associated change in the vegetation (Hawthorne et al., 2023) (see below). The age-depth models from core CEN-17.4 at Ekolongouma and the other three sites reported here (Fig. 2) all show a steep age-depth relationship (i.e. rapid peat accumulation) during the early Holocene followed by an interval where the slope of the age-depth curve is substantially shallower (a pattern which is consistent with the decomposition of some of the peat that had accumulated prior to ~2000 cal yr BP). The age-depth models from Bondamba and, less clearly, Bolengo, are consistent with recovery of peat accumulation after ~2000 cal yr BP. The drying trend

likely correlates with the proposed 'Late Holocene Rainforest Crisis', which is well supported by palaeoecological records across central Africa (Ngomanda et al., 2009; Maley et al., 2018; Giresse et al., 2020; Bayon et al., 2019; Garcin et al., 2018). This climatic event appears to have caused a vegetation change in all four of our pollen records from the CCB peatlands, expressed at both Bolengo and Bondamba as an expansion of *Syzygium*.

Other smaller variations throughout zone 3A in the abundance of *Raphia*, *Uapaca*, and less abundant tree taxa (e.g. *Macaranga, Lophira, Pandanus*) may reflect localised changes in canopy openness (e.g. patch dynamics, treefall events). While we cannot exclude human activity (e.g. selective harvesting, clearance for agriculture or fire) as a possible cause of these fluctuations, there is no direct evidence for human impact in our records.

The three pollen assemblage zones (1A, 2A and 3A) therefore represent three vegetation types and three stages of ecological succession, from permanently flooded forest (zone 1A) via seasonally flooded forest (zone 2A) to the mixed hardwood–palm swamp forest (zone 3A) observed today at Bolengo and Bondamba. As peat accumulated and the height of the peat column increased, there was a gradual reduction in the importance of river flooding over time and a transition towards ombrotrophy (i.e. accumulation of peat beyond the reach of flooding, leading to purely atmospheric supply of moisture and nutrients), evidenced by the vegetation succession and by a gradual increase in LOI values indicating reducing mineral sediment inputs throughout zone 1A. These trends are consistent with the pattern of successional change associated with basin infilling, upward peat accumulation, and a tendency towards ombrotrophy (the 'fen-bog transition', e.g. Loisel and Bunsen 2020) frequently observed in peatlands, including in similar topographic and climatic settings (Phillips et al., 1997; Roucoux et al., 2013; Kelly et al., 2020). The similarities in timing of changes at these two sites may simply be coincidental, but they hint at shared (allogenic) controls on peatland development (see Section 5.4 below).

5.3 Peatland vegetation succession on interfluves of the Ubangi River

In contrast to the sites to the east of the Congo River, at the interfluvial sites to the west of the Congo River (Ekolongouma and Boboka: Fig. 4 and Fig. 6), the pollen data suggest that peat initiated in open, herbaceous wetlands with scattered trees. In this respect they are markedly different from the Busira River sites but are similar to one another (Fig. 3 and Fig. 6).

The presence of occasional *Alisma*-type pollen in the basal peats at both Ekolongouma (~19,600 cal yr BP) and Boboka (13,350 cal yr BP), rich in Cyperaceae and Poaceae pollen (Zone 1B) (probably representing the aquatic plant(s) *Ranalisma* sp.: Léonard 1996), interpreted to represent patches of open water (shallow pools or river edges), and small amounts of pollen from heliophytic taxa such as *Pycnanthus* and *Macaranga*, are consistent with an open herbaceous wetland with sparse trees.

The pollen and $\delta^{13}C_{TOC}$ data (Fig. 4 and Fig. 6) indicate that forest developed first at Ekolongouma ~12,000 cal yr BP, with a dominance of *Manilkara* with *Carapa*-type, *Entandrophragma*, *Pandanus* and *Pycnanthus* pollen (zone 2B). A similar set of forest taxa developed at Boboka at ~6,400 cal yr BP, again with *Manilkara* and *Carapa*, but this time also with *Lophira* and *Uapaca* pollen. We interpret both sets of pollen assemblages to represent closed-canopy, seasonally-flooded hardwood swamp forest. This zone spans an interval of ~2200 years (~12,000 – 9800 cal yr BP at Ekolongouma), and considerably longer, ~5900 years at Boboka, only ending at ~500 cal yr BP.

The *Manilkara*-type flooded forest represented by zone 2B appears to have been replaced at Ekolongouma by a more diverse palynological assemblage ~9800 cal yr BP, dominated by *Pandanus* and *Pycnanthus* pollen, alongside smaller amounts of *Lophira*, *Syzygium* and *Uapaca* pollen (zone 3B), representing a seasonally flooded hardwood swamp forest.

Between ~2000 and ~1000 cal yr BP at Ekolongouma the palynology shows an increase in light-demanding taxa (*Alchornea* and *Macaranga)* and taxa tolerant of seasonal drying (*Lophira*), as well as an increase in *Syzygium* and declines in *Uapaca* and several swamp forest taxa (e.g. *Raphia*, *Pandanus*, *Pycnanthus*). These changes have previously been interpreted (Garcin et al., 2022; Hawthorne et al.,

2023) as an ecological response to the long-term drying causing peat decomposition. Comparable changes occur in the pollen record from Boboka, although the timing varies slightly: *Lophira* increases and *Uapaca* declines as the record approaches 2000 cal yr BP, then *Macaranga*, *Alchornea* and *Syzygium* increase ~1000 cal yr BP, followed at ~500 cal yr BP by a resurgence of *Lophira* and *Uapaca*.

By 1000 cal yr BP (following the driest phase) at Ekolongouma the vegetation appears to have returned to an abundance of *Pandanus* and *Pycnanthus* pollen (last dominant in zone 3B). At Boboka*, Manilkara* (zone 2B) pollen remains abundant to the top of the sequence and there is no indication that the site has ever witnessed an abundance of *Pandanus* and *Pycnanthus,* meaning that it has not yet or may never reach this successional phase (due e.g. to abiotic factors, disturbance or climate change).

5.4 Drivers of peat swamp forest succession

Our data provide evidence that autogenic processes were important in driving ecological succession at all study sites. Autogenic processes in peatland development include the immigration and establishment of taxa, and feedbacks between vegetation, the accumulating peat and the physical, chemical and hydrological characteristics of the habitat (Charman 2002). These processes can act in isolation without requiring any external forcing (e.g. climate changes) to account for observed changes in vegetation over time (Colyn et al., 1991). However, at our study sites there is evidence that climate change has also been important in driving succession, with three of the sites (Bolengo, Bondamba and Ekolongouma) apparently being more sensitive than Boboka to climatic changes during their development, while all were sensitive to Late Holocene climatic drying.

The two sites east of the Congo River, Bolengo and Bondamba, show stronger evidence for allogenic drivers. Despite different peat initiation dates, the transition between each vegetation type (represented by zones 1A, 2A and 3A) occurred at the same time, consistent with the changes being driven by an external factor – most plausibly regional changes in precipitation affecting the hydrology simultaneously at both sites. Peat began to form well before the beginning of the Holocene at these two sites, with the apparent rate of pre-Holocene peat accumulation being very low; nonetheless, the

site must have been (at least intermittently) waterlogged via permanent or seasonal flooding to allow 65 and 28 cm of peat accumulation at Bolengo and Bondamba respectively. Lower net primary productivity (NPP) at this time under relatively cooler and drier conditions may also have limited the rate of peat accumulation, although the proportion of arboreal pollen in assemblages remains fairly constant during the Late Pleistocene and early Holocene, which is consistent with continued forest cover and little change in litter input the to the peat. The transition from Zone 1A to 2A occurred during the early Holocene, at a time when independent proxy data indicate that regional precipitation increased following a drier period between ~12,500 and 11,500 cal yr BP (Schefuß et al., 2005; Bayon et al., 2012). The age-depth relationship at both sites shows an abrupt increase in the gradient of the slope around this time, and the pollen record shows a shift in the vegetation, consistent with wetter climatic conditions allowing rapid accumulation of peat above the zone of permanent river flooding, accompanied by a shift from permanently-flooded to seasonally-flooded forest types. The transition to Zone 3A vegetation occurs at ~8000 cal yr BP at both sites, during the period of peak Holocene climatic wetness (~10,000 – 6000 cal yr BP) (Schefuß et al., 2005; Bayon et al., 2012; Shanahan et al., 2015). Here we see the establishment of a mixed swamp forest dominated by *Raphia* and *Uapaca*, possibly indicating the continuing accumulation of the peat above the zone of regular flooding and hence the start of a transition towards ombrotrophic conditions, driven partly by Holocene climate change and autogenic succession.

In contrast, the data for the two sites on the interfluves to the west of the Congo River suggest that factors other than climate were locally important in determining the pattern and timing of vegetation change. At both these sites open herbaceous wetland (Zone 1B) persisted for about 8000 years, despite peat initiation at Ekolongouma happening much earlier than at Boboka. The vegetation transition to zone 2B (~12,000 cal yr BP) at Ekolongouma could have been driven by climate change, occurring close to the start of the Holocene when climatic conditions became warmer and wetter; but the Late Glacial-Holocene transition appears to have had no effect on the vegetation at Boboka, which persisted in zone 1B dominated by Cyperaceae and Poaceae, until ~6400 cal yr BP. Thus, different vegetation

582 communities occurred at different sites at the same time, and the Late Glacial/Holocene transition
583 appears to have coincided with substantial ecological change at three of the sites but not at the fourth.
584 We propose that different local conditions – differences in site topography, proximity to rivers, or the
585 different flooding regimes expected on different river floodplains – led to distinct ecological histories
586 at the four sites, and differing sensitivities to Late Glacial and early Holocene climatic change. A similar
587 explanation for between-sites variation in peatland histories has been invoked for example in relation
588 to floodplain peatlands in Amazonia (Roucoux et al., 2013; Kelly et al., 2017, 2020; Sassoon et al., 2023)
589 and for coastal and inland peatlands in SE Asia (e.g. Anderson and Muller, 1975; Morley, 1981; Hope
590 et al., 2005; Yulianto et al., 2005; Nguyen et al., 2024).

591 There is, however, one climatic event during which all four sites show evidence of vegetation change:
592 the late Holocene drying culminating around 2000 cal yr BP. Hiatuses in past peat accumulation have
593 previously been observed at some sites in Amazonia (Kelly et al., 2017; Swindles et al., 2018) and SE
594 Asia (e.g. Ruwaimana et al., 2024), but the late Holocene drying event in the CCB is unusual among
595 tropical peatlands in its ubiquity (documented at almost every site studied so far) and apparent
596 synchroneity. At Ekolongouma, palaeoclimatic proxy data provide clear evidence for pronounced
597 climatic drying, which was associated with substantial peat mineralization, and a change in forest
598 composition (Garcin et al., 2022, Hawthorne et al., 2023), with an increase in *Lophira*. The evidence
599 presented here is consistent with the same climatic drying having affected the peatlands at Bolengo,
600 Bondamba and Boboka in comparable ways, though with slight temporal variations (possibly within
601 the uncertainty of our age-depth models; Fig. 2) and with variable responses in vegetation
602 composition, e.g. an increase in *Lophira* at Boboka, and an increase in *Syzygium* at Bolengo and
603 Bondamba; Figs. 3 and 4). These varied responses to drying suggest that certain sites may be more
604 vulnerable than others to changes in precipitation, in terms of carbon accumulation and ecosystem
605 resilience. However, at all sites peat accumulation appears to have resumed following this event and
606 the palynology indicates varying degrees of forest recovery, which may still be ongoing at some sites
607 (i.e. Boboka, where the peat is comparatively shallow and *Lophira* remains abundant).

6. Conclusion

Our records demonstrate the temporal heterogeneity and diverse developmental histories expressed at four locations across the CCB peatlands. While the importance of autogenic processes varies between the study sites spatially and temporally, influencing these developmental patterns, water-table height and inundation from rivers is a key component of maintaining peat swamp forests in multiple locations in the CCB (Georgiou et al., 2023). Our results highlight different patterns of vegetation succession between the interfluvial and river floodplain peatland sites. However, it remains to be established how site-specific factors such as hydrology, catchment geology or topography influence the variation in vegetation structure and composition.

All four study sites were affected, to differing extents, by a critical allogenic factor, namely climatic change. Past changes in climatic conditions, particularly the reduction in precipitation during the mid- to late Holocene, caused basin-wide changes in vegetation composition, which were represented in different ways at different sites e.g. increases in *Syzygium* at the sites east of the Congo River, increases in *Lophira* pollen at the sites west of the Congo River. The palaeoenvironmental data thus show that the histories of individual sites within the CCB are consistent with a common set of processes that nonetheless resulted in a rich mosaic of environments in time and space. Major hydrological inputs in the region are at least in part climatically driven and are locally influenced by geomorphology, topography and geology which influences the vegetation succession and peat development in a range of different landscape settings, which in turn will result in different climate sensitivities (Georgiou et al., 2023).

Our palaeoenvironmental data provide a framework for understanding present-day diversity in the context of ecosystems that have changed, developed, and reacted to climatic change over millennia. The varying responses to climatic change observed at our study sites suggest that some of these complex and irreplaceable sites may be more vulnerable than others to climate change. Future

633 research could usefully focus on understanding how records of past change could yield insights into
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652 **Author Contributions:**

653 S.L.L., I.T.L., G.C.D., S.E.P., A.B., P.G., and P.J.M. conceived the study. S.L.L., I.T.L., G.D., B.C., and N.T.G.
654 collected the cores. D.H. and I.T.L. developed the study. D.H., W.H., A.B., G.T., and P.G. conducted the
655 laboratory analysis. D.H. and I.T.L. compiled and analysed the data. Y.G., and E.S., contributed data.
656 D.H. wrote the paper with significant inputs from I.T.L. All authors commented on and reviewed the
657 paper.

Statement on inclusion:

Our study brings together authors from a number of different countries, including scientists based in the Republic of Congo and Democratic Republic of Congo where the study was carried out. Authors from the region were consulted based on their knowledge of Congo Basin swamp forest taxa and vegetation dynamics in the peatlands. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

Data availability:

The data will be archived in PANGAEA; Data Publisher for Earth & Environmental Science (pangaea.de).

Figure Captions

Figure 1. Location of the study sites within the CCB peatlands, Ekolongouma located within the Republic of Congo and Boboka in the Democratic Republic of Congo, both west of the Congo River, Bolengo and Bondamba located east of the Congo River, within the Democratic Republic of Congo. Inset show's location of CCB peatlands within Africa. Map colours denote predicted landcover classes adapted from Crezee et al., 2022.

Figure 2. Age-depth models for peat cores from each study site (BNG1-4 Bolengo, BDM1-7 Bondamba, CEN-17.4 Ekolongouma and BOB-9 Boboka) modelled in rbacon v.2.5.8 (Blaauw and Christen, 2011) using a mixed calibration curve (50:50 mix of the IntCal20 and SHCal20 (Hogg et al., 2020) in the *IntCal* package in *R* v. 4.0.3 (R Core Team, 2021). Colours represent the age of each corresponding local pollen assemblage zone. Arrows represent the point of peat initiation.

Figure 3. Pollen percentage diagram for the peatlands east of the Congo River, Bolengo (peat core BNG1-4) and Bondamba (peat core BDM1-7) showing selected taxa >5% abundance and indicator taxa mentioned in the text (coloured by pollen assemblage zones), with loss on ignition (%), plotted against age (cal yr BP) and depth (cm). The diagram is divided into phases determined via CONISS analysis and visual examination of key vegetation transitions.

Figure 4. Pollen percentage diagram for the peatlands west of the Congo River, Ekolongouma (peat core CEN-17.4) and Boboka (peat coreBOB-9) showing selected taxa >5% abundance and indicator taxa mentioned in the text (coloured by pollen assemblage zones), with loss on ignition (%), plotted against age (cal yr BP) and depth (cm). The diagram is divided into phases determined via CONISS analysis and visual examination of key vegetation transitions.

Figure 5. Artistic schematic of peat and forest development at sites east of the Congo River (Bolengo and Bondamba, top) and west of the Congo River (Ekolongouma and Boboka, bottom) with each vegetation community representing a palynological assemblage (presented in Figs. 3 and 4). Age (cal yr BP) of each vegetation community/palynological zone presented at the base of the diagram.

Figure 6. Precipitation proxy ($\delta D_{n\text{-}C29}$ (‰), blue) from Ekolongouma and $\delta^{13}C_{bulk}$ (‰) from Bolengo, Bondamba, Ekolongouma and Boboka, plotted against age (cal yr BP).

Figure 7. Non-metric multidimensional scaling (NMDS) ordination of pollen data (>5% abundance) from the river-influenced peatlands Bolengo and Bondamba, top, and from the interfluvial peatlands Ekolongouma and Boboka, bottom. Taxa labels represent indicator taxa for each Regional Pollen Assemblage Zone (RPAZ) and match those presented in Figs. 3 and 4. Shapes represent the pollen data

from each core (BDM1-7, BNG1-4, CEN17-4 and BOB1-9). Colours represent each RPAZ discussed in the text and represented in Figs. 3 and 4, identified via CONISS analysis and visual examination of key vegetation transition.

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897 Supplementary Table 1. Study site and peat core characteristics.

Site	Co-ordinates	Peat core	Peat depth (m)	Hydrology	Distance along transect (km)	Basal peat age (median cal yr BP)
Bolengo	0.31869°S 19.79940°E	BNG1-4	4.10 m	River-influenced	4 km	26,750
Bondamba	0.17344°S 19.69599°E	BDM1-7	5.70 m	River-influenced	7 km	19,400
Ekolongouma	1.1835°N, 17.6399°E	CEN-17.4	5.99 m	Interfluvial	17.4 km	19,600
Boboka	1.51616°N 18.84751°E	BOB-9	2.50 m	Interfluvial	9 km	13.350

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900 Supplementary Table 2. ^{14}C dataset used for the age-depth models of peat cores BNG1-4, BDM1-7,
901 BOB-9 and CEN-17.4. (Note: a column citing the original publication for each date has been
902 temporarily removed to ensure author anonymity).

Core	Laboratory code	Depth (cm)	^{14}C age (yrs BP)	^{14}C age error (yr)	Median age cal.yr BP	Age range (95%)
BNG1-4	SUERC-105273	33.1	2022	39	1946	1834-2045
BNG1-4	SUERC-251362	49.4	4010	20	4476	4415-4521
BNG1-4	SUERC-105274	73.1	6742	39	7590	7510-7665
BNG1-4	SUERC-99643	93.7	6969	39	7775	7685-7915
BNG1-4	SUERC-105275	124.6	6831	40	7645	7580-7715
BNG1-4	SUERC-99633	149.1	8073	39	8930	8730-9085
BNG1-4	SUERC-105279	163.4	8176	41	9095	9005-9265
BNG1-4	SUERC-99638	191.8	8302	40	9285	9130-9425
BNG1-4	SUERC-105280	213.6	8643	40	9590	9535-9680
BNG1-4	SUERC-99639	247.8	8584	39	9535	9475-9655
BNG1-4	SUERC-105281	280.1	9277	43	10430	10285-10565
BNG1-4	SUERC-99640	297.6	9265	41	10415	10260-10555
BNG1-4	SUERC-105282	309.3	9108	46	10240	10185-10400
BNG1-4	SUERC-105283	325.2	8572	42	9525	9470-9595
BNG1-4	SUERC-99641	346.7	10991	43	12880	12770-13060
BNG1-4	SUERC-103978	373.3	12958	51	15470	15290-15640
BNG1-4	SUERC-105284	389.3	17621	79	21250	20960-21670
BNG1-4	SUERC-105285	399.9	21581	123	25860	25700-26020
BNG1-4	SUERC-99642	405.2	22886	140	27200	26500-27420
BDM1-7	SUERC-94360	49.5	749	35	670	569-725
BDM1-7	SUERC-103957	76.9	851	37	731	677-791
BDM1-7	SUERC-99647	120.5	1557	35	1413	1351-1520
BDM1-7	SUERC-103958	153.9	1879	37	1779	1704-1874

BDM1-7	SUERC-103962	167.5	3633	38	3925	3780-4082
BDM1-7	SUERC-99648	172.5	2507	37	2578	2371-2724
BDM1-7	SUERC-103963	185.5	4701	37	5400	5320-5565
BDM1-7	SUERC-103964	200.5	5426	38	6225	6015-6290
BDM1-7	SUERC-103965	225.5	6056	37	6880	6755-6985
BDM1-7	SUERC-99649	236.5	5987	38	6800	6675-6895
BDM1-7	SUERC-103966	270.5	6171	37	7055	6945-7160
BDM1-7	SUERC-94361	289.5	6225	37	7090	6990-7245
BDM1-7	SUERC-103967	340.5	7556	40	8355	8210-8410
BDM1-7	SUERC-99650	391.5	8495	39	9495	9445-9535
BDM1-7	SUERC-103972	425.5	9146	38	10280	10210-10475
BDM1-7	SUERC-99651	503.9	9346	42	10535	10385-10680
BDM1-7	SUERC-103973	516.2	9245	40	10385	10255-10500
BDM1-7	SUERC-103974	526.4	9908	42	11275	11205-11600
BDM1-7	SUERC-103975	540.5	10267	42	11940	11770-12425
BDM1-7	SUERC-94362	569.5	15980	65	19270	19100-19460
CEN-17.4	AWI-2567.1.1	0.5	565	170	540	0-899
CEN-17.4	AWI-1820.1.1	12.8	345	60	390	158-500
CEN-17.4	AWI-2255.2.1	53.6	835	25	713	676-768
CEN-17.4	AWI-2568.1.1	94.4	1240	75	1134	974-1282
CEN-17.4	AWI-2802.1.2	132.5	1760	70	1641	1427-1826
CEN-17.4	AWI-1821.1.1	151.5	2120	60	2069	1893-2306
CEN-17.4	AWI-2256.2.1	170.5	4450	30	5031	4872-5279
CEN-17.4	AWI-2569.1.1	190.5	6770	85	7610	7431-7776
CEN-17.4	AWI-2570.1.1	214.4	7630	95	8413	8197-8591
CEN-17.4	AWI-2571.1.1	235.6	7640	110	8424	8183-8635

CEN-17.4	AWI-2257.2.1	256.5	7570	35	8370	8213-8419
CEN-17.4	AWI-1677.2.1	296.5	8020	140	8864	8482-9286
CEN-17.4	AWI-2803.1.1	356.5	9140	50	10285	10196-10485
CEN-17.4	AWI-2258.2.1	396.5	8360	835	9361	9148-9473
CEN-17.4	AWI-2572.1.1	418.5	9930	40	11301	11215-11608
CEN-17.4	AWI-1822.1.1	460.5	10150	50	11751	11357-11936
CEN-17.4	AWI-2573.1.1	498.5	12450	40	14569	14293-14913
CEN-17.4	AWI-2259.1.1	540.5	13650	45	16463	16299-16637
CEN-17.4	AWI-2574.1.1	579.7	14750	85	18051	17824-18233
CEN-17.4	AWI-1823.1.1	596.4	11550	55	13401	13303-13567
CEN-17.4	AWI-2575.1.1	599.1	16850	85	20350	20116-20534
CEN-17.4	AWI-1824.1.2	625.2	14050	55	17071	16931-17330
BOB-9	SUERC-105289	25	351	123	362	0-547
BOB-9	SUERC-105290	32.1	423	39	464	324-517
BOB-9	SUERC-101833	49.5	443	37	484	329-529
BOB-9	SUERC-105292	64.5	1134	39	1012	929-1175
BOB-9	SUERC-105293	75.5	1382	39	1282	1178-1346
BOB-9	SUERC-105294	90.5	1994	39	1915	1829-1999
BOB-9	SUERC-101837	99.5	2395	37	2411	2333-2691
BOB-9	SUERC-105295	115.5	3129	36	3318	3215-3437
BOB-9	SUERC-105299	128.5	4864	40	5575	5480-5655
BOB-9	SUERC-105300	140.5	5930	39	6730	6645-6845
BOB-9	SUERC-101838	149.5	7543	37	8345	8205-8400
BOB-9	SUERC-105303	155.5	5074	39	5810	5665-5905
BOB-9	SUERC-105304	167.5	6296	37	7210	7025-7300
BOB-9	SUERC-101839	174.5	7556	39	8355	8210-8410

BOB-9	SUERC-105305	188.5	8944	43	10045	9905-10200
BOB-9	SUERC-101840	199.5	9829	41	11225	11175-11265
BOB-9	SUERC-105309	208.5	10793	44	12740	12705-12765
BOB-9	SUERC-105310	221.5	11475	46	13335	13195-13450
BOB-9	SUERC-105311	235.5	12765	50	15200	15020-15370
BOB-9	SUERC-105312	249.4	12706	51	15120	14965-15290
CEN-17.4	AWI-2567.1.1	0.5	565	170	540	0-899
CEN-17.4	AWI-1820.1.1	12.8	345	60	390	158-500
CEN-17.4	AWI-2255.2.1	53.6	835	25	713	676-768
CEN-17.4	AWI-2568.1.1	94.4	1240	75	1134	974-1282
CEN-17.4	AWI-2802.1.2	132.5	1760	70	1641	1427-1826
CEN-17.4	AWI-1821.1.1	151.5	2120	60	2069	1893-2306
CEN-17.4	AWI-2256.2.1	170.5	4450	30	5031	4872-5279
CEN-17.4	AWI-2569.1.1	190.5	6770	85	7610	7431-7776
CEN-17.4	AWI-2570.1.1	214.4	7630	95	8413	8197-8591
CEN-17.4	AWI-2571.1.1	235.6	7640	110	8424	8183-8635
CEN-17.4	AWI-2257.2.1	256.5	7570	35	8370	8213-8419
CEN-17.4	AWI-1677.2.1	296.5	8020	140	8864	8482-9286
CEN-17.4	AWI-2803.1.1	356.5	9140	50	10285	10196-10485
CEN-17.4	AWI-2258.2.1	396.5	8360	835	9361	9148-9473
CEN-17.4	AWI-2572.1.1	418.5	9930	40	11301	11215-11608
CEN-17.4	AWI-1822.1.1	460.5	10150	50	11751	11357-11936
CEN-17.4	AWI-2573.1.1	498.5	12450	40	14569	14293-14913
CEN-17.4	AWI-2259.1.1	540.5	13650	45	16463	16299-16637
CEN-17.4	AWI-2574.1.1	579.7	14750	85	18051	17824-18233
CEN-17.4	AWI-1823.1.1	596.4	11550	55	13401	13303-13567

CEN-17.4	AWI-2575.1.1	599.1	16850	85	20350	20116-20534
CEN-17.4	AWI-1824.1.2	625.2	14050	55	17071	16931-17330

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908 Supplementary Table 3. Local pollen assemblage zone descriptions for BNG1-4, Bolengo.

LPAZ	Pollen Summary
IV 132-0cm 8280 – 0 cal.BP	*Raphia* and *Uapaca* (indicator taxa) dominate this zone (mean 13.5 and 21.4 % respectively), accompanied by other indicator taxa *Anacolosa* (1.7%). *Pandanus* (75.7%) and *Syzygium* (48.3%) show distinct isolated peaks in the middle of this zone. The uppermost samples display a decline in *Raphia* and *Uapaca*, and an increase in *Lophira* and *Macaranga*.
III 261-132 cm 10,060-8280 cal.BP	Dominant indicator taxa in this zone include *Lophira* (mean 17.5%) and *Mitragyna* (8.2%) with *Treculia* (6%) and *Homalium* (2.5%). *Uapaca* (14.3%) increases in the second half of this zone, accompanied by a decline in *Mitragyna* and Melastomataceae/ Combretaceae. Several other taxa remain present in low abundance, including *Pandanus, Macaranga Carapa* and *Syzygium*.
II 318-261 cm 10,800-10,060 cal.BP	*Brazzeia*, *Macaranga*, *Oubanguia* and *Crotalaria*, indicator taxa for Zone I gradually decline. Indicator taxa for this zone include *Symphonia* (mean 4.2%), *Terminalia* (2.4%) and *Alchornea* (3.1%), representing a short-lived distinct assemblage. *Pandanus, Mitragyna* and *Lophira* increase in the second half of this zone.
I 410-318cm	The indicator taxa for this zone are *Macaranga* (mean 20.3%), *Manilkara* (15.3%), *Brazzeia* (7.9%), *Oubanguia* (5.5%) and

26,750-10,800 cal.BP	*Crotalaria* (1.9%). Several other taxa are present in smaller abundances, including *Carapa*, *Lophira*, *Syzygium*, *Raphia* and *Uapaca*.

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910 Supplementary Table 4. Local pollen assemblage zone descriptions for BDM1-7, Bondamba.

LPAZ	Pollen Summary
V 154-0 cm 2100-0 cal.BP	*Syzygium* gradually declines throughout this zone, accompanied by a general increase in *Raphia* (mean 21.9%) and *Uapaca* (19.5%). *Entandrophragma, Macaranga, Mitragyna* and *Pandanus* occur in higher proportions here (previously most abundant in Zone I). The uppermost samples display a large increase in *Raphia* and a decline in *Uapaca*.
IV 252-154 cm 2320-2100 cal.BP	Indicator taxa include *Syzygium*, *Triplochiton, Gaertnera* and *Klaineanthus* (means 32.2, 3.8, 4.3 and 1.8% respectively), accompanied by *Macaranga*, *Mitragyna*, *Pandanus*, and *Homalium* in smaller proportions. *Raphia* remains abundant, as does *Uapaca*, at the expense of *Syzygium*.
III 326-252 cm 9680-6770 cal.BP	*Raphia*, indicator taxa (mean 41.9%) increases dramatically in first half of this zone at the expense of *Pandanus* and *Uapaca.* After this, *Raphia* is largely replaced by *Uapaca* (indicator taxa, mean 22.2%), with a gradual increase in *Syzygium*. Several other taxa (*Macaranga*, *Pandanus, Triplochiton*) are also present in lower abundances.
II 438-326 cm 11,650-9680 cal.BP	At the base of the zone indicator taxa for Zone I rapidly decline, replaced by a distinctive assemblage of hardwood tree taxa; indicator taxa for this zone include the numerically-dominant *Mitragyna* (mean 19.2%) and, in smaller amounts, *Homalium*, *Carapa*, Lophira and *Sclerosperma* (means 3.3, 2.4, 8.9 and 2% respectively). *Raphia* increases in the first half of this zone before declining rapidly.

I 570-438 cm 19,400-11,650 cal.BP	The indicator taxa for this zone are *Macaranga* (mean 17.3%), *Brazzeia* (16.9%), *Pandanus* (13.8%) and *Entandrophragma* (3%). Several other taxa are important throughout this zone, including *Carapa*, *Mitragyna*, *Lophira*, *Homalium*, *Syzygium*, *Raphia* and *Uapaca*.

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912 Supplementary Table 5. Local pollen assemblage zone descriptions for CEN17-4, Ekolongouma.

LPAZ	Pollen Summary
V 81-0 cm 1020-0 cal.BP	*Raphia, Symphonia and Pycnanthus are* indicator taxa for this zone (means 11.3, 41.3 and 7% respectively. *Uapaca* is abundant in the uppermost sample, while *Pycnanthus* is abundant in the lower part of the zone. Indicator taxa for zone IV remain present here but in low abundance.
IV 154-81 cm 2320-1020 cal.BP	Dominant indicator taxa in this zone include *Syzygium* (mean 12.3%), *Lophira* (15.5%) and *Uapaca* (22.4%), with *Macaranga*, *Alchornea*, *Croton* and *Homalium* in lower abundances. *Pycnanthus* is less abundant here than in the zone below.
III 327-154 cm 9680-2320 cal.BP	Indicator taxa Pycnanthus (19.2%) and Gaertnera (1.1%), along with *Syzygium, Lophira, Uapaca, Raphia* and *Pandanus*, rapidly replace the *Manilkara* dominated forest of Zone II.
II 469-327 cm 12,650-9680 cal.BP	Cyperaceae and Poaceae rapidly decline, replace by indicator tree taxa Manilkara (25.2%), Khaya (1.6%), *Carapa*-type procera (8.2%), Sapotaceae undiff. (2.9%) and *Entandrophragma* (4.2%). Tree taxa expand to >70%, with *Pycnanthus*, *Pandanus*, *Raphia* and *Uapaca* also important in this zone.
I 629-469 cm	The indicator taxa for this zone are Cyperaceae (mean 37.6%), Poaceae (13.1%), *Alisma-type* (4.3%) and Asteraceae undiff. (1.5%), which covary, with greater abundance in Subzones 1a, c

20,400-12,650 cal.BP	and e. *Carapa*-type *procera*, *Manilkara*-type., *Pycnanthus*, *Macaranga*, *Syzygium*, *Lophira*, *Raphia* and *Pandanus* are also important.

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915 Supplementary Table 6. Local pollen assemblage zone descriptions for BOB1-9, Boboka.

LPAZ	Pollen Summary
V 20-0 cm 250-0 cal.BP	*Symphonia* is the single indicator taxa for this zone (mean 7 %). *Uapaca* peaks at the start of this zone (37%) before declining, while *Lophira* gradually increases. *Macaranga* and *Alchornea* (indicator taxa for zone IV) remain present here in low abundance. The uppermost samples display a decline in *Symphonia*, and an increase in *Lophira*.
IV 44-20 cm 465-250 cal.BP	Dominant indicator taxa in this zone include *Alchornea* (mean 11%) and *Macaranga* (40.5%). *Manilkara* declines in this zone, while *Lophira* and *Uapaca* which are initially low, gradually increase.
III 140.5-44 cm 6700-465 cal.BP	Cyperaceae and Poaceae, indicator taxa for Zone I disappear from the record in this zone. *Manilkara*, indicator taxa for this zone increases (mean 20.7%). *Lophira* and *Uapaca* are also present in significant abundance here (17.6 and 13.9% respectively. Lower percentages of *Entandrophragma, Raphia* and *Symphonia* are also present.
II 156.5-140.5 cm 6950-6700 cal.BP	The indicator taxa for zone I gradually decline in this zone. There is an isolated peak in *Triplochiton* (indicator taxa, 34%), and a gradual increase in *Manilkara, Lophira* and *Uapaca*.
I 250-156.5 cm	The indicator taxa for this zone are Cyperaceae (mean 27.4%), and Poaceae (11.3%). *Alisma-type* (0.63%) and *Nymphaea* (0.7%) are

15,200-6950 cal.BP	also present only in this zone. Several other taxa are present, including *Macaranga*, *Lophira*, *Raphia* and *Pandanus*.

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918 Supplementary Table 7. Regional pollen assemblage zone descriptions for each site

Zone	Site	Core	Timing (cal yr BP)	Description	Interpretation
3B	Ekolongouma	CEN17-4	9680 – 0	This zone at Ekolongouma is dominated by *Pandanus* (mean 22.4%) and *Pycnanthus* (17.9%) pollen, alongside lower amounts of *Lophira* (4.3%), *Syzygium* (6.8%) and *Uapaca* (11.9%). This zone is absent at Boboka.	Seasonally flooded hardwood swamp forest.
	Boboka	BOB1-9	-		-
3A	Bolengo	BNG1-4	8280 – 0	This zone is dominated by *Raphia* (mean 13.3% Bolengo, 24% Bondamba) and *Uapaca* (mean 21.5% Bolengo, 16.5% Bondamba) pollen, accompanied by an abundance of *Syzygium* from ~4500 to ~2500 cal yr BP at Bolengo, and from ~6500 to ~2000 cal yr BP at Bondamba.	Mixed hardwood and palm swamp forest.
	Bondamba	BDM1-7	7960 – 0		
2B	Ekolongouma	CEN17-4	12,650 – 9680	The RPAZ 1B open environment dominated by Poaceae and Cyperaceae is colonised by forest taxa dominated by *Manilkara* (mean 26.5% Ekolongouma, 20.7% Boboka) and *Carapa*-type (8.2% Ekolongouma, 5.9% Boboka), with *Entandrophragma* (4.4%), *Pandanus* (17.1%) and *Pycnanthus* (7.9%) at Ekolongouma, but with *Lophira* (mean	Seasonally flooded (closed canopy) hardwood swamp forest.
	Boboka	BOB1-9	6700 – 0		

				17.6%) and *Uapaca* (mean 13.9%) at Boboka.	
2A	Bolengo	BNG1-4	10,800 – 8280	The RPAZ 1A forest taxa decline and are replaced by dominant taxa *Mitragyna* (mean 8.2%, Bolengo 19.2% Bondamba) and *Lophira* (17.5% Bolengo, 7.3% Bondamba). *Homalium, Carapa* and *Sclerosperma* are present in small amounts (means <5%).	Seasonally flooded (open canopy) hardwood swamp forest.
	Bondamba	BDM1-7	9680 – 7960		
1B	Ekolongouma	CEN17-4	20,400 – 12,650	Cyperaceae (mean 34.5% Ekolongouma, 25.9% Boboka) and Poaceae (9.7% Ekolongouma, 10.3% Boboka) pollen dominate this zone, with occasional *Alisma*-type and small amounts of *Pycnanthus, Macaranga* and *Lophira* pollen.	Open herbaceous swamp
	Boboka	BOB1-9	15,200 – 6700		
1A	Bolengo	BNG1-4	26,750 – 10,800	This zone is dominated by *Macaranga* (mean 20.3% Bolengo, 17.3% Bondamba) and *Brazzeia* (7.9% Bolengo, 16.9% Bondamba) pollen. Several other taxa are important, notably *Pandanus* and *Manilkara*.	Waterlogged hardwood swamp forest.
	Bondamba	BDM1-7	19,400 – 9680		

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