Linking land and lake: Using novel geochemical techniques to understand biological response to environmental change

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ABSTRACT

The exploitation of lakes has led to large-scale contemporary impacts on freshwater systems, largely in response to catchment clearance. Such clearance is causing changes to carbon dynamics in tropical lakes which may have significance for wider carbon budgets, depending on the changes in carbon sequestration and mineralisation driven by changing roles of terrestrial and aquatic carbon in lakes over time. Despite increasing awareness of the pivotal role of carbon source in carbon dynamics, discriminating the source of carbon from a palaeolimnological record is rarely undertaken. Here we use novel geochemical techniques (brGDGTs, n-alkanes, Rock-Eval pyrolysis), paired with traditional analyses (diatoms, pollen), to elucidate changing sources of carbon through time and ecosystem response.

Environmental changes at Lake Nyamogusingiri can be divided into three phases: Phase I (CE 1150 −1275), a shallow and productive lake, where a diverse terrestrial environment is, initially, the main carbon source, before switching to an aquatic source; Phase II (CE 1275−1900), variable lake levels (generally in decline) with increasing productivity, and carbon is autochthonous in source; Phase III (CE 1900−2007), lake level declines, and the carbon is of a mixed source, though the terrestrially derived carbon is from a less diverse source.

The organic geochemical analyses provide a wealth of data regarding the complexity of aquatic response to catchment and with-in lake changes. These data demonstrate that small, tropical lake systems have the potential to bury high quantities of carbon, which has implications for the disruption of local biogeochemical cycles (C, P, N, and Si) both in the past, and the future as human and climate pressures increase.

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1. Introduction

Although tropical lakes and their sedimentary archives have been the focus of study for several decades (Richardson and Richardson, 1972; Stager et al., 1986, 1997), few studies have successfully separated the major drivers of change observed in aquatic systems through time (Mills et al., 2014, 2017b). The challenge in discerning the climatic signal from the human-signal is largely impeded by the dominant signature of climate change at decadal to millennial timescales in tropical regions (Dubois et al., 2017; Gelorini and Verschuren, 2012), which effectively "masks" the visibility of more subtle human impact on lake systems as recorded in the palaeolimnological record.

There is a pressing need to understand the responsiveness of aquatic systems to the presence of humans, within a framework of climate variability. Lakes, by their very nature, are dynamic and responsive to changes in climate and land use (Gillson, 2015); understanding this variability and resilience over long timescales is essential in the management of aquatic systems. In tropical areas, land-use change is driven by an exponential increase in rural populations, and poor rural infrastructure and investment (e.g. tertiary sewage treatment and sanitation systems) which culminates in naturally occurring freshwater systems being heavily relied

upon to provide an array of ecosystem services (e.g. potable water, fish stocks) while ecosystem functioning (such as nutrient cycling) is often substantially impacted. The exploitation of quasi-permanent and perennial water resources has led to large-scale contemporary impacts on vulnerable freshwater systems, largely in response to catchment clearance.

One of the serious impacts of catchment change and anthropogenic clearance and/or alteration is that of degrading water quality with associated ecological deterioration and biodiversity loss. In remote tropical regions, such as western Uganda, rural communities rely on lakes as a source of potable water and their (often) steep sided catchments for intensive subsistence agriculture and large-scale plantations. Previous palaeolimnological studies of crater lakes in western Uganda (Mills et al., 2014; Ryves et al., 2011) suggest that catchment impact does not necessarily manifest as early in the lake system as suggested changes in vegetation communities from pollen studies; that is, the early catchment impact is not significant enough to alter the water quality and/or chemistry of the systems. The lakes appear to have a hydrological buffer to surrounding landscape changes, which may be mediated by groundwater hydrology. Recent work (Mills et al., 2014) suggests that diatom records from lakes in the region show a response to climate over much of the last 1000 years. A distinct switch in many western Ugandan lake ecosystems has occurred in the last 50—100 years and is attributed to anthropogenic catchment change rather than a climatic driver, however analytical data (either proxy or observed) able to separate these two drivers were not available to test the climate versus anthropogenic nature of the signal recorded in the lake sediments. We hypothesise that use of novel organic geochemical techniques will allow the separation of catchment versus climate drivers in the analysis of lake sediment cores from tropical lakes.

The ability to determine the driver(s) of lake aquatic change is also important for understanding biogeochemical cycling in tropical lakes, particularly in relation to the carbon cycle. Unpublished work (Mills et al., 2015, 2017a) suggests that carbon burial in the lakes of western Uganda is equivalent to that observed in the agricultural landscapes of the northern hemisphere ($>100 \, \text{g C m}^{-2} \, \text{yr}^{-1}$) (Anderson et al., 2013, 2014; Dietz et al., 2015). However, the source of the carbon in the sedimentary record (i.e. whether catchment derived [allochthonous] or derived from in-lake productivity [autochthonous]) is less clear, because rarely are analytical methods employed that can fingerprint the organic carbon source. This ambiguity contributes to difficulties in understanding the relative role of climate and people on tropical lake systems.

In response to climatic and land-use changes, tropical lakes are experiencing shifts in water balance, increased catchment soil erosion (mobilising carbon (C), nitrogen (N), and phosphorus (P) from terrestrial to aquatic systems), high sedimentation rates, and water pollution (leading to eutrophication driven by N and P loading). Whilst lakes store carbon generated by lake productivity (Cole et al., 2007), they are increasingly sequestering and mineralising considerable amounts of C received from the terrestrial environment, largely as a result of anthropogenic catchment alteration (Anderson et al., 2014; Downing et al., 2008; Hanson et al., 2015). Disruption of the C cycle is, therefore, a key indicator of anthropogenic impact and driver of ecological change in lake-catchment systems (McGowan et al., 2016). Tropical lakes are hypothesised to be disproportionately important for carbon processing and burial, but are recognised as under sampled (Raymond et al., 2013). Current research in tropical Africa focuses on the response of terrestrial biodiversity and biogeochemical cycling (especially C dynamics) to anthropogenic climate change (Midgley and Bond, 2015). Despite these ecosystems being classed as 'disturbance-driven', there is little acknowledgement of the role of people on the modification of the environment (Midgley and Bond, 2015). Given the long-term and widespread impact of humans on the African continent, and in particular on recent land-use change (Goldewijk, 2001), lake systems are increasingly playing a role as hotspots for C cycling.

To begin to address questions related to carbon sources and the drivers of these changes, we base our research on the previously published sediment record from Lake Nyamogusingiri (Mills et al., 2014). For the first time in a tropical lake system we apply multiple novel organic geochemical techniques (brGDGTs, *n*-alkanes, Rock-Eval pyrolysis), paired with more traditional palaeolimnological methods (palynology, organic stable isotopes) to derive an independent climate proxy (in this case temperature) and to identify the source of organic material (and hence carbon) within a tropical lake system. This novel multidisciplinary approach allows a more holistic understanding of the response of the lake ecosystem and primary producers (here represented by the diatom community) in the sediment record, and more robustly determine the drivers of the observed changes.

1.1. Analysis of organic compounds from lake sediments

Lake sediments contain a broad range of organic compounds and require an array of analytical approaches in order to provide the breadth and depth of information related to source organism(s), climate indicators, and in-lake alteration processes to understand environmental change recorded in lake sediment archives. The multi-layered approach used for this research includes analysing macromolecular changes using Rock-Eval(6); tracking variations in organic source using *n*-alkanes; bulk organic carbon isotopes (δ^{13}C), C/N ratios; and inferring temperature changes using highly specific organic biomarkers (Branched Glycerol Dialkyl Glycerol Tetraethers; brGDGTs).

1.1.1. Rock-Eval pyrolysis

Rock-Eval is a geochemical screening technique typically applied to hydrocarbon bearing shales (Slowakiewicz et al., 2015) that has begun to gain recent acceptance in the tracking of changes in organic matter source, degradation, and preservation in lake sediment archives (Engelhart et al., 2013; Khan et al., 2013; Lacey et al., 2015). Rock-Eval provides key palaeolimnological information on the provenance, pre- and post-depositional decay state as well as extent of burnt organic carbon entering the lake, which can serve as a marker for land-use change.

In lake sediments the principal Rock-Eval parameters: total organic carbon (TOC), free hydrocarbons (S1), and bound (polymeric) hydrocarbons (S2), describe the quantity and proportion of volatile hydrocarbons (S1) and cell wall biopolymers and their alteration products (S2). The related hydrogen index (HI) values provide a measure of the extent of organic matter hydrogenation, with high HI values corresponding to algal organic matter (OM) and low HI associated with terrestrial OM. Similarly, the oxygen index (OI) provides an estimate of the amount of oxygen-containing compounds, a parameter that increases with sediment transport, reworking, and direct aerobic biological decay. In addition, the amount of non-pyrolysable carbon has been correlated with black carbon, which in turn has utility as a proxy for burning (Iglesias et al., 2014; Schüpbach et al., 2015; van Marle et al., 2017).

1.1.2. Carbon isotopes

The geochemical composition of lacustrine sedimentary matter (e.g. carbon isotope ratios (δ^{13}C) and C/N concentrations) has been successfully and widely used for the reconstruction of palaeoenvironments. Bulk organic δ^{13}C analysis, in conjunction with other organic indicators (C/N ratios and pollen analyses) can

provide information about the source of organic material entering a lake system as well as productivity (Leng and Marshall, 2004; Meyers and Teranes, 2001). C/N ratios are used as a secondary indicator of the relative proportions of autochthonous and allochthonous sources of lacustrine organic matter (Talbot and Lærdal, 2000).

1.1.3. Normal alkanes (n-alkanes)

n-alkanes are a sub-class of wax lipid widely used to provenance organic matter in lake and river sediments (Lamb et al., 2009; Meyers, 2003). Aquatic algae and plankton mainly synthesise odd numbered short-chain homologues (C13-C25) maximising at about C15 or C17. In contrast, vascular plants biosynthesise odd numbered long-chain homologues (C23-C35) maximising at C29, C31, or C33 (Cranwell, 1985; Eglinton and Hamilton, 1967). These higher chain homologues are present at highest concentration in plant leaf tissues where they function as a waxy protective coating. Although identification of a specific floral source may be confounded by the ubiquity of C29, C31, and C33 in terrestrial systems, Ficken et al. (2000) showed that submerged and floating aquatic plants produce elevated abundances of C23 and C25 when compared to C29, C31, and C33 homologues. These compositional relationships are summarised by the aquatic proxy ($P_{aq} = (C23 + C25)/(C23 + C25 + C29 + C31)$) to distinguish *n*-alkanes from plants that grow in terrestrial environments (P_{aq} c. 0.09), to those that are emergent (P_{aq} c. 0.25) to floating/submerged ($P_{aq} > 0.50$) (Ficken et al., 2000; Filley et al., 2001; Lamb et al., 2009).

1.1.4. Branched Glycerol Dialkyl Glycerol Tetraethers (brGDGT)

The use of branched GDGTs for the inference of past mean annual air temperatures (MAAT) and pH is increasingly common in lakes, and a number of different calibration sets are available globally (Pearson et al., 2011) and regionally (e.g. eastern Africa) (Loomis et al., 2012, 2014; Tierney et al., 2010). These compounds are membrane lipids of soil bacteria that are transported to the lake system by rivers and wind. Previous studies show that variation in their molecular structure in soils is mainly controlled by MAAT and pH (Peterse et al., 2012), and can be expressed using the Methylation of Branched Tetraethers (MBT) and the Cyclization of Branched Tetraethers (CBT) indices. The combination of these two indices can then be used as a temperature proxy (Peterse et al., 2012). In lake systems it is not clear whether the brGDGTs are transported solely from catchment soils or whether they are also produced in the water column (Blaga et al., 2010; Tierney et al., 2010). The origin of the brGDGTs may have a bearing on whether the methodology is more suitable for the inference of air (MAAT) or water temperatures.

Nonetheless, tropical lakes are likely better suited to the application of MBT/CBT proxy because of the smaller differences between MAAT and water temperatures in comparison to higher latitude lakes. This strong correlation between the brGDGT distribution and MAAT has led previous studies to explore the optimal regional eastern Africa lacustrine calibration to reliably infer temperatures (Loomis et al., 2012; Tierney et al., 2010). Three key calibrations currently exist: (i) local MBT/CBT calibrations, (ii) MbrGDGT calibrations only based on the major brGDGTs, and (iii) the stepwise forward selection calibration that uses brGDGTs that explain the most variance in temperatures (Loomis et al., 2012; Tierney et al., 2010).

2. Regional setting

Small lakes are known to be hotspots of carbon processing and can dominate tropical landscapes, responding rapidly to climatic and other environmental changes within well-defined topographic catchments. The crater lake district of western Uganda is well suited to study the response of freshwater ecosystems to changes in carbon loading as the lakes in this region are subject to a range of intensities of human impact. One such lake, Lake Nyamogusingiri (0°17′4.5″ S, 30°0′46.7″ E), has been previously studied for its ecological response to environmental change over the last 1000 years. Lake Nyamogusingiri is an amalgamation of several smaller crater lakes and consists of a larger basin to the east which is c. 4 m deep, and a smaller, deeper crater (c. 12.5 m) to the extreme west (Fig. 1); the two basins are separated by a sill that is recorded at a depth of c. 2 m. The deeper crater was selected for the study. The lake is situated within the Maramagambo Central Forest Reserve on the ecotone between moist semi-deciduous forest and grass savannah (Langdale-Brown et al., 1964), and forms part of the Bunyaruguru crater lake cluster (Melack, 1978). Rainfall in the region is c. 1100 mm, and is seasonally bimodal with wet seasons occurring between March and May, and October−December. The rainfall pattern in the region is driven by the biannual migration of the Inter Tropical Convergence Zone, and there are strong links between the amount of precipitation received and the El Niño Southern Oscillation (Nicholson, 1996). Average annual air temperature for the Rubirizi District (in which the lake is situated) is c. 22 °C. Mean water temperatures are not available for the lake, and during sample collection water temperature data were not recorded due to an equipment malfunction. However, other deeper lakes in the same crater district, record surface water temperatures ranging from 24.3 to 25.8 °C, and bottom water temperatures of 22.7−24.6 °C (temperatures were obtained during the dry season in July 2006 and January 2007) (Mills, 2009; Mills and Ryves, 2012).

The vegetation of the southern-most crater lake region (Bunyaruguru) consists of a forest savannah mosaic and medium altitude moist semi-deciduous forest and moist evergreen forest. These forest types form close stands up to 30 or 40 m in height; lianas are abundant. In this region grasses are generally absent, or are broad-leaved and fire sensitive (Ugandan Government, 1962). Outside the protected areas, natural or secondary vegetation in the region has largely been replaced by an agricultural landscape and the establishment of villages. Lake Nyamogusingiri has a catchment of semi-natural forest, though the catchment experienced disturbance in the mid-to late 1990s with the building of the Jacana Safari Lodge (Fig. 1).

3. Material and methods

3.1. Core collection, correlation, dating, and diatom analysis

Information regarding the collection of sediments, dating of the Nyamogusingiri core, and the process of diatom analysis are described in full in Mills et al. (2014), therefore only a brief synopsis is provided here.

3.1.1. Core collection

Sediments from Lake Nyamogusingiri were collected from the 12.5 m-deep basin in January 2007. A HON-Kajak gravity corer was used to collect the upper unconsolidated sediments; these cores were sectioned in the field at 0.5 cm intervals and placed in polythene bags. Consolidated sediments were collected using a Russian peat corer in overlapping drives; the sediments were transferred into half drain pipes and wrapped in polyethylene film. All sediments were stored in dark refrigeration (4 °C), and subsampling was undertaken prior to analyses.

3.1.2. Core correlation, loss-on-ignition, and dating

Cores were correlated using loss-on-ignition (LOI) (Dean, 1974), magnetic susceptibility, and visual stratigraphy to form a composite
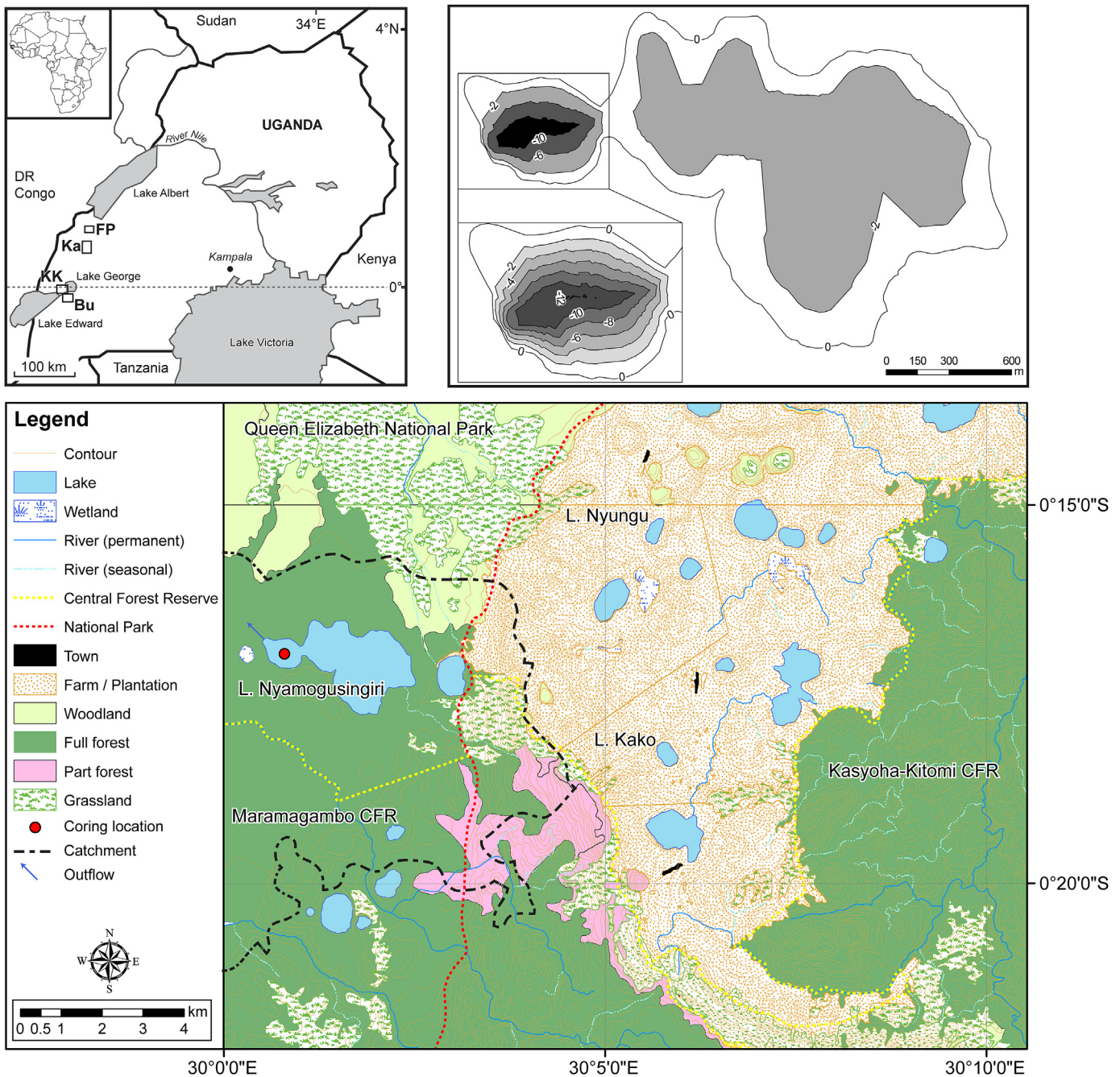
Fig. 1. Map of study region. Location of the crater lake clusters in western Uganda (FP: Fort Portal, Ka: Kasenda; KK: Katwe-Kikorongo; Bu: Bunyaruguru) (top left). Vegetation map of the Bunyaruguru lake cluster, showing the location of Lake Nyamogusingiri (main panel). The morphometry of Lake Nyamogusingiri (top right).

stratigraphy 127 cm in length. Sub-sampling for the different analyses were undertaken at differing intervals, and analyses were completed over a period of 9 years (Table 1). The loss-on-ignition data were converted to organic carbon burial rates (g C m^{-2} yr^{-1}) using a LOI to carbon correction factor (0.468) and multiplying by the dry mass accumulation rate. These data were then corrected for sediment focussing (using modern ^{210}Pb fallout data) following the methodology of Anderson et al. (2013). The sediment focussing correction factor for Lake Nyamogusingiri is 0.84.

The dating for the core sequence is based on ^{210}Pb and ^{137}Cs profiles (analysed at the University of Liverpool) and three AMS ^{14}C dates (SUERC). The dates were calibrated and modelled with a 0.5

smooth spline interpolation using CLAM for R (Blaauw et al., 2007).

3.1.3. Diatom analysis

The preparation of samples followed the methodology of Renberg (1990), with the digestion of organic matter, and removal of carbonates. A total of 133 samples were counted, with at least 300 valves per sample counted using an oil-immersion, phase-contrast light microscopy at x1000 magnification. All diatoms were identified to species level where possible using general (Krammer and Lange-Bertalot, 1986—1991) and regional floras (Cocquyt, 1998; Gasse, 1986). As published in Mills et al. (2014), the stratigraphic diatom data were divided into assemblage zones using

Table 1
Sampling intervals for each analysis presented in this paper (unless specified, sampling was non-contiguous), the year analysis was undertaken and by who/where sampling was completed.

Analysis	Interval (cm)	Year	Who/Where
Loss-on-ignition	0.5 (contiguous)	2007	Mills/LU
Carbon burial rates	0.5	2016	Mills & Ryves/BGS
Diatoms	1	2007/8	Mills/LU
Organic isotopes	1	2007	Mills & Leng/BGS
Pollen	2	2007	Ssemmanda/LU & MU
Rock-Eval (6)	1-2*	2016	Vane & dos Santos/BGS
brGDGTs	2-8**	2016	Vane & dos Santos/BGS

LU = Loughborough University, BGS = British Geological Survey, MU = Makerere University. *There are sections of the core where material was no longer available and could not be analysed. **Given the exploratory nature of the work, samples for organic geochemistry analysis were identified by using the existing δ^{13}C data to locate areas of interest or areas where the δ^{13}C were complacent, which is why sampling intervals vary.

optimal sum of squares partitioning.

The major patterns in the diatom data were analysed using an indirect ordination in CANOCO 4.5 (ter Braak and Šmilauer, 2002). Detrended correspondence analysis (DCA) was selected as the most appropriate response model for understanding changes in the diatom assemblage data. A lake level curve was determined using a matrix approach, where high percentages of both plankton and periphyton (benthic and epiphytic species) indicate a higher lake level. Lower lake levels are inferred by lower percentages of plankton and higher percentages of periphyton. Facultatively planktonic species were excluded from this calculation.

3.1.4. Pollen analysis

Pollen analysis followed the standard methodology of Fægri and Iversen (1975), with a *Lycopodium* spike added to enable the calculation of pollen concentrations (Stockmarr, 1972). In total 52 samples were analysed, of which 45 samples yielded a count of between 500 and 1000 terrestrial pollen grains and spores, six had a count of >400, and one a count of 259 (average count of 582). Pollen slides were counted using a Zeiss D-7082 microscope using x1000 magnification under oil-immersion. Pollen identification was based on comparisons with a reference collection of slides and photographs within the Department of Geology at Makerere University, and a variety of published sources from across Africa (Ssemmanda et al., 2005). The identified pollen taxa were assigned to major vegetation groups (high altitude trees, lowland forest, non-arboreal, and aquatics) to produce a summary of changes over the stratigraphic sequence.

3.2. Organic geochemistry

3.2.1. Glycerol dialkyl glycerol tetraether (GDGT) and n-alkanes

The analysis of GDGTs and *n*-alkanes follows the methodology of Lopes dos Santos and Vane (2016). In summary, freeze-dried sediment was extracted using an automated solvent extractor (Dionex 200) operated at 100 °C and 7.6×106 Pa with dichloromethane (DCM):MeOH (9:1, v:v) to provide a total lipid extract. The total lipid extract was then separated in an Al_2O_3 column into an apolar and a polar fraction using *n*-hexane and DCM:MeOH (1:1, v:v) respectively. The apolar fraction was analysed for *n*-alkanes on a Hewlett Packard 6890 series Gas Chromatograph. The polar fraction was filtered through a polytetrafluoroethylene filter and analysed for brGDGTs using a High Performance Liquid Chromatography-Mass Spectrometer (LC-MS) with a Thermo TSQ Quantiva MS instrument coupled to an Ultimate 3000 series HPLC instrument. GDGT distributions were determined by integrating the summed peak areas in the respective [M+H]+.

The MAAT and pH were estimated using MBT/CBT calibration of Tierney et al. (2010) with a calibration error of ±3 °C for temperature and ±0.66 for pH estimations. Additionally, MAAT was estimated using a second equation of Tierney et al. (2010) based on the fractional abundance of the 3 majors GDGTs (MbrGDGTs). This method has an error of ±2.2 °C. For comparison, the regional east Africa lake calibrations (MBT/CBT, MbrGDGTs and stepwise forward selection [SFS]) of Loomis et al. (2012) were also applied. The calibration error of these methods are ±2.8 °C, 2.7 °C, and 1.9 °C, respectively. The analytical error of all methods applied based on the average SD of duplicates was ±0.3–0.4 °C.

3.2.2. Rock-Eval pyrolysis

Sediments were analysed using a Rock-Eval(6) following the methodology reported for lake and wetland sediments (Lacey et al., 2015; Newell et al., 2016). Briefly, freeze-dried, powdered sediments (60 mg dry wt) were heated from 300 °C to 650 °C at 25 °C/min in an inert atmosphere of N_2, and the residual carbon oxidised from 300 °C to 850 °C at 20 °C/min. Resulting hydrocarbons were measured using a flame ionization detector and CO and CO_2 measured using an IR cell. The performance of the instrument was checked every eight samples against the accepted values of the Institut Français du Pétrole (IFP) standard (IFP 160 000, S/N1 5–081840), and instrumental error (standard deviation) was S1±0.1 mg HC/g rock, S2 ±0.77 mg HC/g rock, total organic carbon ±0.04 % wt, mineral carbon ±0.04% wt, maximum temperature (Tmax) ±1.4 °C.

3.2.3. Carbon isotopes and C/N ratios

$^{13}C/^{12}C$ analyses were performed by combustion in a Costech ECS4010 Elemental Analyser (EA) on-line to a VG TripleTrap and Optima dual-inlet mass spectrometer, with $\delta^{13}C$ values calculated to the VPDB scale using a within-run laboratory standards calibrated against NBS18, NBS-19 and NBS-22. Replicate analysis of well-mixed samples indicated a precision of ±<0.1‰ (1 SD). C/N ratios were measured at the same time, and these are calibrated against an acetanilide standard. Replicate analysis of well-mixed samples indicated a precision of <0.1.

4. Results

4.1. Previously published results

The original diatom record from Nyamogusingiri was divided into six assemblage zones. To account for the lower number of data points in some of the more recent analyses, and to allow a broader interpretation of the environmental history, the number of zones has been reduced and instead reflect three significant periods (phases) of change summarised and discussed in Mills et al. (2014). These are: Phase I (1150–1275; 127-100 cm), Phase II (1275–1900; 100-44 cm), and Phase III (1900–2007; 44-0 cm).

4.1.1. Age model

The age model applied to the Nyamogusingiri composite core is given in Fig. 2. High resolution ^{210}Pb, using a constant rate of supply (CRS) model constrained the upper 50 cm of the Nyamogusingiri core (last c. 150 years), and the raw CRS dates were corrected using the ^{137}Cs peak of 1963. Three radiocarbon dates (out of five) obtained from terrestrial macrofossils were retained for the age model (Table 2). The age model was produced in CLAM for R, using a 0.5 smooth spline function, which prevented age reversals in the model and allowed for a larger age uncertainty in the core chronology.

For detailed results, and information pertaining to the accepted and rejected radiocarbon dates, readers are directed to Mills et al.
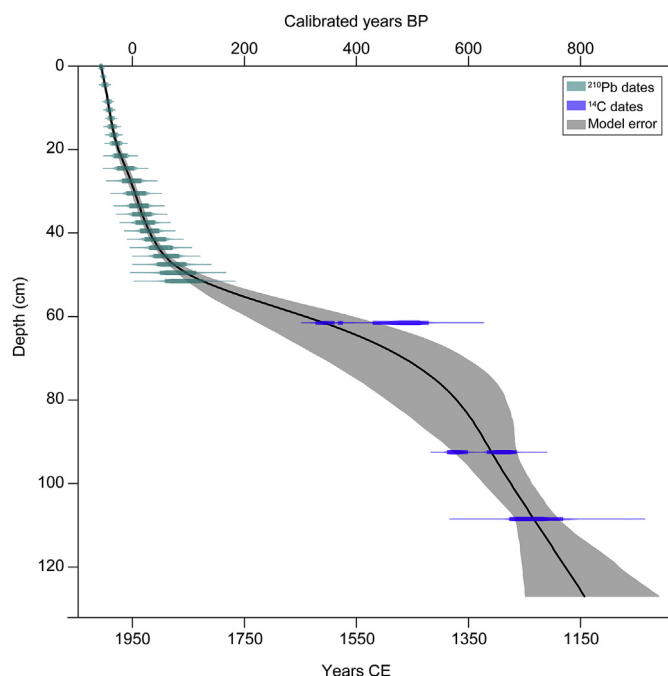
Fig. 2. Age model for the Lake Nyamogusingiri master core sequence based on ^{210}Pb and ^{14}C radiometric dates, modelled using CLAM (adapted from Mills et al., 2014). Data are available from: https://www.ncdc.noaa.gov/paleo-search/study/16791

(2014).

4.1.2. Diatom record

The diatom record shows the abundance of 12 species of >10% abundance in any one sample (Fig. 3a), a more detailed appraisal of the full diatom stratigraphy can be found in Mills et al. (2014).

In the early part of Phase I (CE 1150) the diatom assemblage is dominated by the planktonic *Cyclotella meneghiniana* (c. 55%). The presence of the salt-tolerant, littoral species *Amphora coffeaeformis* (13%) is also important. There are low abundances of other periphytic (littoral and benthic) taxa present during this phase, such as *Encyonema muelleri*, *Gomphonema pumilum*, and *Gomphonema parvulum*. The benthic, N-heterotrophic species *Nitzschia palea* also peaks in abundance. From CE 1150–1210, *C. meneghiniana* is present (10–15%) and there are also high abundances of the salt-tolerant taxa *Amphora veneta* and *A. coffeaeformis* (c. 13 and > 40%, respectively). By c. CE 1180 *C. meneghiniana*, *A. veneta*, and *A. coffeaeformis* almost disappear (<2%), and are replaced by a peak in the abundance of *Nitzschia lancettula* (which reaches a maximum of 50%). After this peak, *C. meneghiniana*, *A. veneta* and *A. coffeaeformis* increase once again; the littoral/benthic species *Achnanthidium minutissimum* also appears during this phase (CE 1220–1260).

Phase II is dominated by the rise and fall of the freshwater, planktonic *N. lancettula*, and the co-variance with *C. meneghiniana*;

when *N. lancettula* is higher in abundance, there is a decrease in the abundance of *C. meneghiniana* (and vice versa). During this phase, periphytic indicators such as *A. minutissimum*, *G. pumilum*, *G. parvulum*, *Amphora copulata*, and *E. muelleri* are consistently present in abundances >5%; though it is noted that both *A. minutissimum* and *Gomphonema* species are no longer represented in the record by CE 1760 and CE 1880, respectively. *Nitzschia palea* reappears at the start of Phase II, with an abundance of c. 18%, before decreasing to <5%, until CE 1430, where percentage abundance again increases to a minimum of 3% (and a maximum of 15%).

A distinct change is observed in the diatom record at the beginning of Phase III. The remaining periphytic species (*A. copulata*, *E. muelleri*) are no longer represented in the record from CE 1910, and whilst *A. copulata*, *E. muelleri*, and *Gomphonema* species do reappear from CE 1995 onwards, they are not consistently present, and their relative abundance is small (<2%). By CE 1930, the freshwater, planktonic *N. lancettula* is all but missing from the record, and is replaced by high percentages of *C. meneghiniana* (up to c. 85%), which is the dominant diatom during this phase. *Nitzschia palea* is also an important species, increasing in relative abundance where *C. meneghiniana* dips (CE 1910–1930). *Nitzschia lancettula* appears to recover from CE 1995, with c. 20% abundance. Phase III also contains two other key features, the presence of *Thalassiosira rudolfi* and *Nitzschia confinis*. The presence of the planktonic, alkaline indicative, and saline tolerant *Thalassiosira rudolfi* in abundances of c. 3–35% begins towards the end of Phase II (CE 1820), but then disappears from the record by CE 1975. *Nitzschia confinis* makes an appearance at CE 1980 in abundances ranging from 8 to 40%, before declining to <4% from CE 2000 until CE 2007.

4.2. New stratigraphic records: palynology and organic geochemistry

4.2.1. Pollen analysis

The stratigraphic results of the pollen analysis are shown in Fig. 3b. Only two pollen samples were counted from the top of the earliest zone (CE 1260–1270), and the samples are dominated by Poaceae (60–65%), with the remaining pollen community composed of Cyperaceae (c. 6%), Typha (c. 4%), Acalypha (c. 7%), and Celtis (c. 4%). This period is dominated by non-arboreal pollen, with lowland forest (e.g. low altitude species, including deciduous forest, savannah trees and evergreen trees) playing a role, and the persistent presence of aquatic pollen and spores.

During Phase II, Poaceae is still the dominant pollen type, with a relative abundance of >60% for the majority of the record. As with Phase I, Cyperaceae (>5%), Typha (>2%), Acalypha (>4%), and Celtis (>2%) comprise the rest of the community within this period. Phase II records two periods where the relative abundance of Poaceae decreases to values of c. 15%; these occur from c. CE 1330–1350 and c. CE 1540–1620. During these periods of lower Poaceae abundance, there is a concomitant increase in the proportion of Cyperaceae (c. 20%), Urticaceae (c. 5%), Typha (c. 6%), Celtis (c. 6%), and Acalypha (c. 12%). Towards to the top of Phase II (from c. CE 1850)

Table 2
Details of the accepted, calibrated radiocarbon dates for Lake Nyamogusingiri.

SUERC ID	Depth (cm)	Material	Conventional ^{14}C age (±1σ error)	Median probability (CE/BCE)	2σ calibrated ^{14}C age range (CE/BCE)	Relative Area (%)
18911	61.5	Leaf/charcoal	419 ± 37	1467	1422–1522	85.03
					1574–1585	1.53
19066	92.5	Leaf/charcoal	685 ± 35	1299	1587–1625	13.44
					1265–1319	64.48
					1351–1390	35.52
19067	108.5	Wood/charcoal	795 ± 35	1239	1180–1278	100

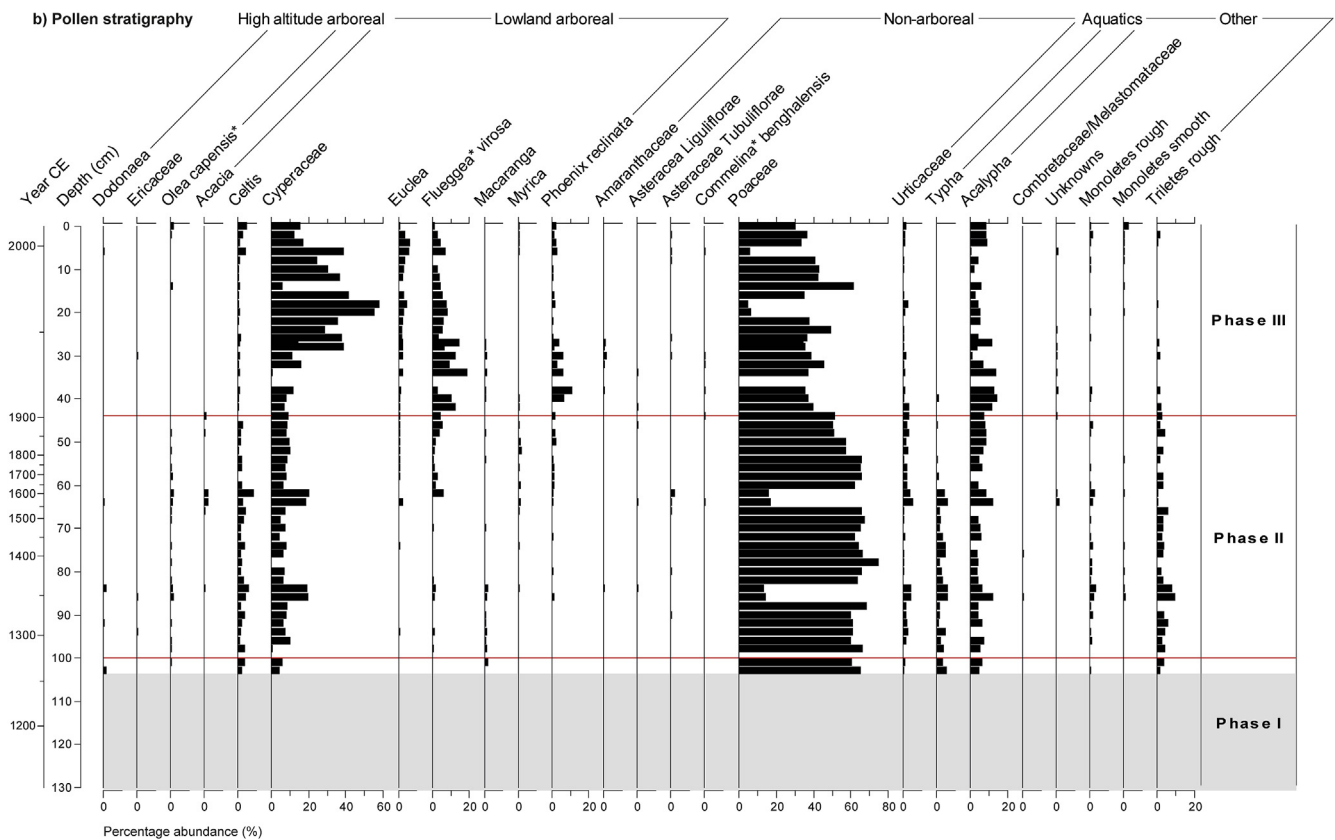## a) Diatom stratigraphy
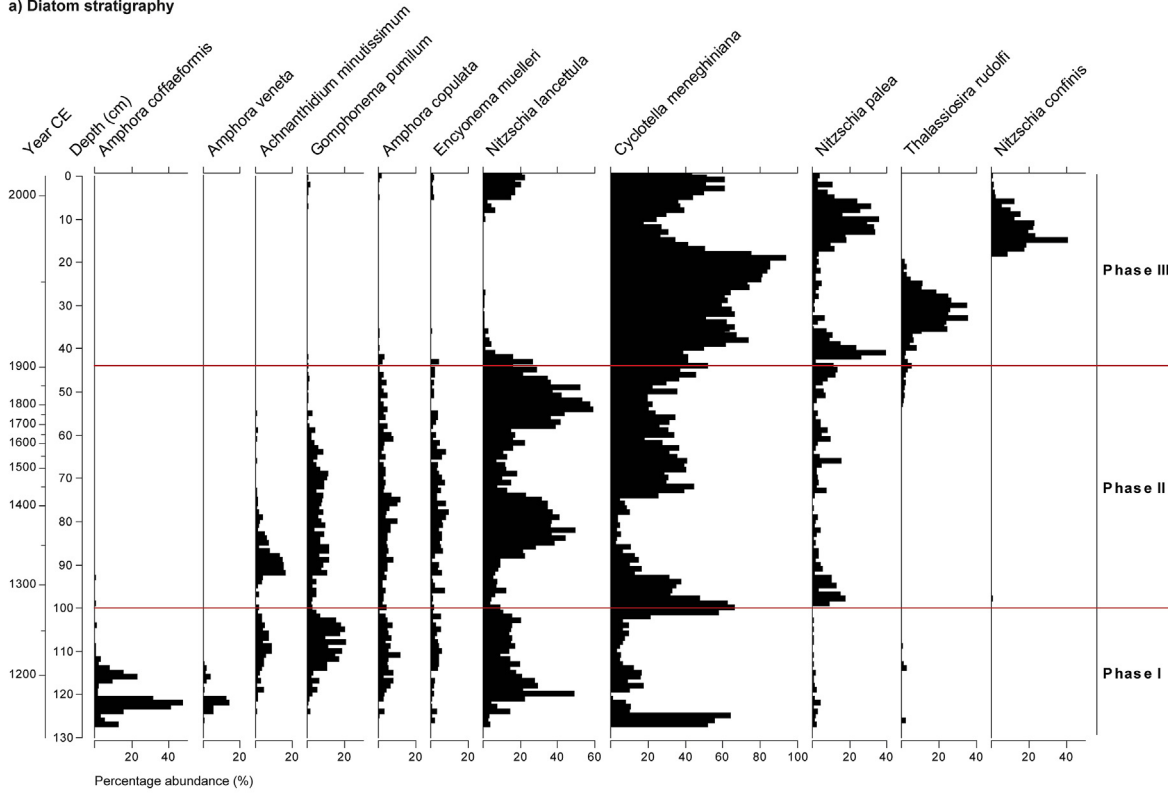
b) Pollen stratigraphy

Fig. 3. (a) Diatom stratigraphy from Lake Nyamogusingiri showing the 12 most common taxa (>10% abundance in anyone sample). Taxa are ordered using weighted-averaging optimum (ascending). Analyst: K. Mills, data available from: https://www.ncdc.noaa.gov/paleo-search/study/16791. **(b)** Pollen and spore taxa >1% relative abundance in any sample. Both digrams show the three phases (determined by optimal sum of squares partitioning). Note that pollen samples from the base of the Lake Nyamogusingiri core have not yet been analysed. Analyst: I. Ssemmanda, data available from: https://www.ncdc.noaa.gov/paleo-search/study/25550. All data were generated as part of a NERC standard grant (NE/ D000157/1).

Poaceae begins to decline, though the abundance of Cyperaceae and Urticaceae remains steady. *Typha* disappears from the record, and *Flueggea virosa* increases in abundance (c. 6%). The earliest part of Phase II (CE 1275–1400) is dominated by non-arboreal pollen, but lowland forest taxa becomes increasingly abundant, peaking between CE 1330–1350. Following this, lowland forest taxa once again decrease; aquatic pollen are persistent in the record, and spores are increasingly important peaking in tandem with the lowland forest taxa. From CE 1400 non-arboreal taxa dominate, though lowland forest taxa once again dominate between CE 1540–1620, and there is a concomitant increase (albeit slight) in aquatic pollen taxa and spore pollen. CE 1650–1900 shows a drop in lowland forest taxa, though percentages are higher than at the start of the record. There is a decrease in non-arboreal pollen, and aquatic pollen percentages are at their lowest on record so far.

During Phase III the relative abundance of Poaceae is generally lower than in earlier zones, and Cyperaceae becomes the dominant pollen type (increasing to a maximum of c. 60% by c. CE 1980, but declining thereafter towards the present (CE 2007)). *Acalypha* is still present in abundances of >5%; *Typha* is still "missing" from the record, and Urticaceae appears in abundances of <1%. *Flueggea virosa* peaks in abundance during this phase, rising from c. 5% at the onset, reaching a peak of 10–20% between CE 1915 and CE 1955 as does *Phoenix reclinata*-type (c. 6–12%). *Euclea* is also an important pollen type throughout this phase, occurring in abundances of c. 2–7%. From CE 1900–2007 lowland forest taxa are the most dominant, and high altitude tree taxa are at their lowest on record. Non-arboreal pollen is still an important contributor to the record, but reaches its lowest abundance at CE 1975 and CE 1998, when the percentage of lowland forest taxa peaks. Lowland forest taxa decline slightly towards to the top of the core, but remain strongly represented. Aquatic pollen taxa are more or less absent in the last 100 years.

4.2.2. Glycerol dialkyl glycerol tetraether (GDGT)

There was good recovery of brGDGTs from the lake sediments.

brGDGT concentration ranges from minimum values of 2 and 5 μg/gr at CE 1160 and CE 1940, to a maximum of 12 μg/gr at CE 1895 (Fig. 4). The MBT and MbrGDGT calibrations of Tierney et al. (2010) were applied, giving a surface sediment temperature inference of c. 21 °C and a pH 8.5; comparable to local reported air temperatures (21–24.5 °C) and pH (8) (Bwanika et al., 2004). Using the MBT and MbrGDGT calibrations described by Loomis et al. (2012), the inferred top-core temperatures were c. 1 °C lower in comparison to those inferred using the Tierney et al. (2010) calibration dataset. On the other hand SFS calibration showed 1 °C higher temperatures at the top of the core. Downcore, a similar trend between the calibrations was recorded with the 1 °C difference maintained.

Using the MbrGDGT calibration of Tierney et al. (2010), temperature variation across the sequence ranged from a minimum of c. 20.5 °C (CE 1990) to a maximum of 23.5 °C (CE 1160). Overall, the earlier part of the record (CE 1150–1400) recorded warmer temperatures than the upper core (CE 1400–2007). Phase I records the highest temperatures, c. 23.5 °C (CE 1160), before the temperature decreases by 2 °C (21 °C at CE 1220), and then increasing to 22 °C at CE 1270. The inferred pH during this zone fluctuates between 8.8 and 8.6, and the trend follows that of the temperature record. Phase II has a clear fluctuation in temperature; at the onset of the phase, temperature declines from 22 °C to 21 °C (CE 1280–1330), before peaking to values in the range of 22–23 °C between CE 1330–1520. Temperature decreases to 20.8 °C by CE 1675, before rising slightly (c. 21.5 °C) towards the top of the phase. Unlike earlier in the record, the pH during Phase II does not show such a strong coupling with the inferred temperature; overall, the inferred pH declines very slightly from 8.8 to 8.6. The most recent period (Phase III) exhibits a continuing decline in inferred temperatures, from a maximum of 21.5 °C at CE 1900 to a minimum of 20.5 °C at CE 1990. From CE 1990, temperatures increase slightly (by 0.5 °C) to the present. The trend observed in the pH is stronger than that observed in the temperature record, declining from pH 8.6 to a record minimum of pH 8.2 (CE 1995). The inferred pH increases slightly to 8.5 at the top of the core.
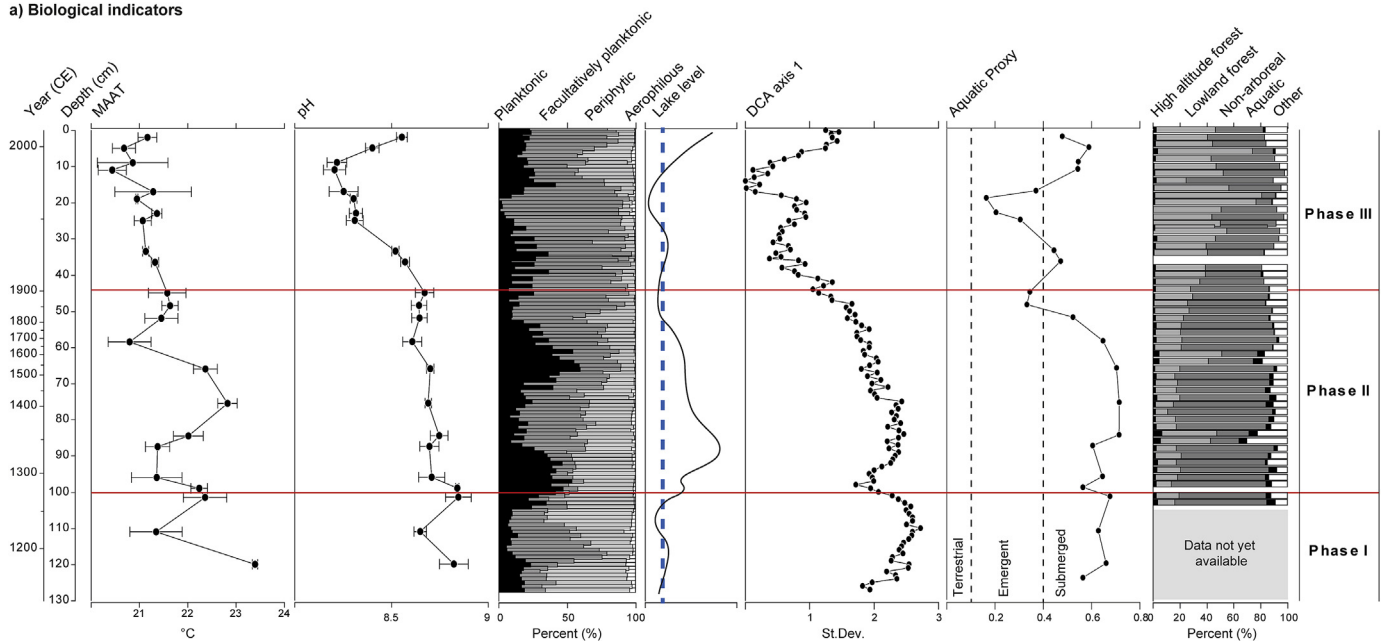

Fig. 4. Combined results from the analysis of brGDGTs (MAAT, pH) alongside a number of biological indicators, including a summary of the diatom habitat preferences, lake level inference (the dashed line represents when the lake level likely crossed the sill threshold), and the results of the DCA of the diatom assemblage data. The aquatic proxy of Ficken et al. (2000) is also shown, as is a summary of the main vegetation types. The diatom habitat preference, DCA, and lake level data are available from: https://www.ncdc.noaa.gov/paleo-search/study/16791. All other data are available from: https://www.ncdc.noaa.gov/paleo-search/study/25550.

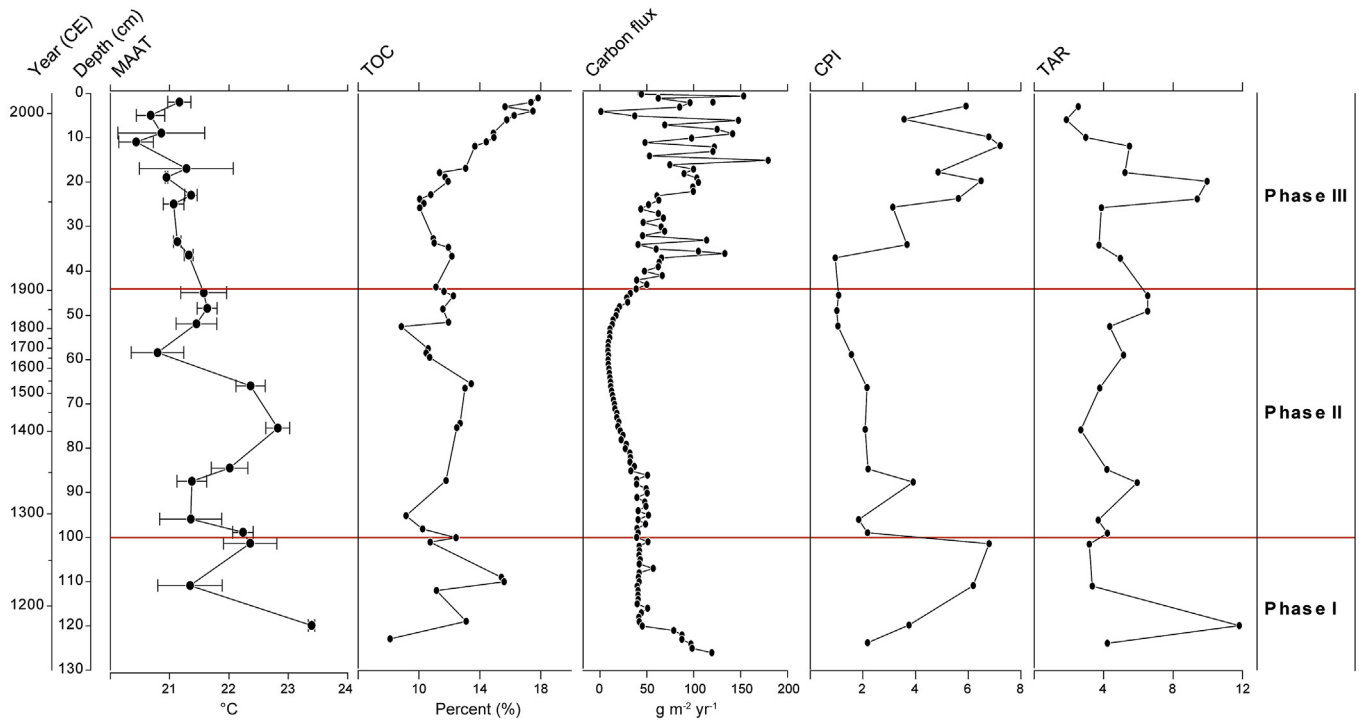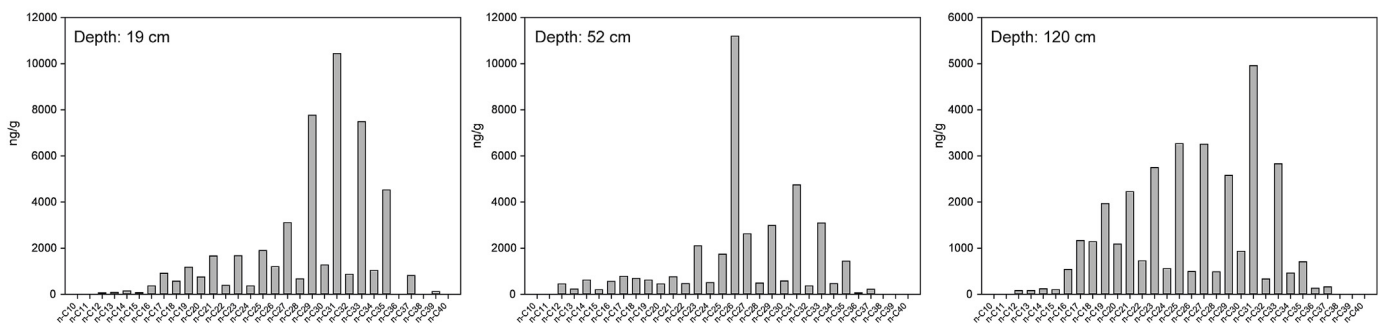## a) Indicators of carbon source

b) Example *n*-alkane histograme from each phase

Fig. 5. (a) Summary of data that are used to infer carbon source (plotted alongside MAAT), this includes total organic carbon (TOC), carbon burial rates (calculated from LOI data), the carbon preference index (CPI), and terrestrial: aquatic ratio (generated from *n*-alkanes). (b) Examples of the *n*-alkane profiles from each of the three phases indicating a switch between terrestrial signals (19 cm, 120 cm) to more of an aquatic signal (52 cm). Data are available from: https://www.ncdc.noaa.gov/paleo-search/study/25550.

4.2.3. Rock-Eval pyrolysis

The results from Rock-Eval include total organic carbon (TOC) (Fig. 5), and hydrogen Index (HI), oxygen index (OI), and percentage residual carbon (RC) (Fig. 6). Generally, throughout the record the HI tracks changes in TOC, and the OI records shows an opposite trend to the HI record.

During Phase I, TOC is variable and ranges from c. 8–16%. Similarly the HI shows strong fluctuations, co-varying with the TOC record, with values between c. 375 mgHC/gTOC (CE 1210) and 556 mgHC/gTOC (CE 1220). The OI increases from 92 mgCO$_2$/gTOC at CE 1155 to a maximum value of 119 mgCO$_2$/gTOC at CE 1210, before dipping and increasing towards the top of the phase. Residual carbon is low at CE 1155 (c. 4.5%), and rises to a maximum of c. 7% at CE 1230, before declining to c. 6% towards the top of the phase. Compared with the earliest part of the record, Phase II is generally less variable for TOC, with values declining to c. 9% between E 1275 and CE 1290), and increasing to a maximum of c. 13.5% by CE 1530.

TOC values decline to a c. 8.5% by CE 1810, before once again increasing to c. 12% at the top of the phase. The HI increases from a minimum value of c. 415 mgHC/gTOC at CE 1290 to a maximum of 555 mgHC/gTOC at CE 1330. The HI then declines again to a minimum of c. 420 mgHC/gTOC at CE 1650, before increasing to values c. 500 mgHC/gTOC at the top of the phase. The OI is relatively stable during Phase II, with an initial decline in values to 70 mgCO$_2$/gTOC (CE 1330), and then a general increase to values between 98 mgCO$_2$/gTOC and 110 mgCO$_2$/gTOC. Residual carbon is <7%, with minimum values occurring between CE 1290 and CE 1330 (c. 5.5%), and again at CE 1810 (4%). Most variables (with the exception of HI) increase during Phase III. TOC plateaus around 11% from CE 1900 to CE 1960, before increasing to c. 17.5% at the top of the core. The HI record is more variable, with values declining from c. 520 mgHC/gTOC (CE 1930) to low values of 417 mgHC/gTOC (CE 1965). The values are relatively stable until c. CE 1980, when they once again rise to >550 mgHC/gTOC towards the top of the phase. OI plateaus

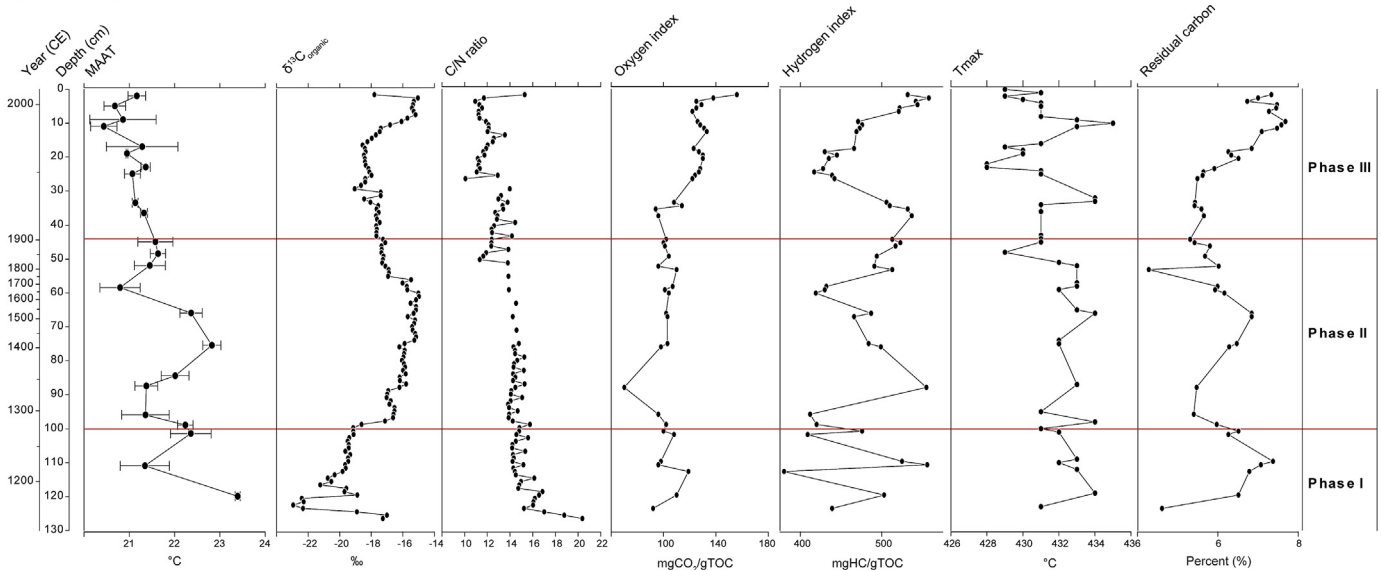**a) Carbon isotopes and Rock-Eval data**

Fig. 6. Data generated from carbon isotope analyses (C/N and δ^{13}C) and parameters from the Rock-Eval analysis. This latter dataset includes: hydrogen index (HI), oxygen index (OI), Tmax (temperature at which the maximum amount of polymerization occurs; higher values = terrestrial material), and percentage residual carbon (the amount of non-pyrolysable carbon). Data are available from: https://www.ncdc.noaa.gov/paleo-search/study/25550. The isotope data were generated as part of a NIGF Grant (IP/884/1105).

around 94 mgCO$_2$/gTOC, increasing from CE 1935 to maximum values of c. 140 mgCO$_2$/gTOC towards the top of the phase. Similarly, residual carbon is stable c. 5%, until CE 1965 where it increases to a c. 7.5% (CE 1990), and more or less remains at this value until the present.

4.2.4. n-Alkane analysis

The data from the analyses of n-alkanes are presented as the aquatic proxy (P_{aq}) (Ficken et al., 2000) (Fig. 4) and as a terrigenous: aquatic ratio (TAR), and the carbon preference index (CPI) (Fig. 5).

At the base of the record (CE 1150), the values of the P_{aq} is stable c. 0.5–0.6, suggesting that submerged macrophytes were dominant. Initially, both the TAR and CPI indicate that the n-alkanes are more affiliated to the terrestrial environment (CE 1180), before the TAR decreases and suggests the dominance of aquatic material (CE 1220). The CPI remains high (values peaking to c. 6.5; CE 1220 to 1275) suggesting a strong terrestrial component alongside the aquatic input. During Phase II, the record is relatively static (until CE 1815), with no large shifts in the data. All three datasets suggest that aquatic derived material is the dominant source, with the P_{aq} value of >0.5 indicating a dominance of submerged macrophytes. The TAR (values <4) and CPI (values of 2.5–5) suggest that the dominant source of material in the sediments is aquatic. By CE 1815, the P_{aq} values shift to those more indicative of emergent macrophytes (c. 0.3) and the TAR increases to values of 6.5, showing an increasing dominance of the terrestrial signal over the aquatic signature. The most recent period (Phase III) indicates large shifts in the data. The CPI values generally increase to between 3.5 and 7 (after CE 1930), indicating a terrestrial source of the n-alkanes. The P_{aq} record is more variable, with values of 0.3 and 0.45 between CE 1930 and CE 1960 indicating a switch from submerged to emergent macrophytes. Between CE 1960 and CE 1980, the P_{aq} values are at their lowest in the record (c. 0.15), suggesting that emergent macrophytes are important, but the values indicate a shift towards the dominance of the terrestrial environment (values of c. 0.12) (Ficken et al., 2000). At the same time as the decline in the P_{aq} value, the TAR record peaks to c. 9, suggesting that the terrestrial environment is the dominant source of the organic material deposited

within the lake. From CE 1980 the TAR values decline to <5, suggesting an aquatic source of material. Similarly, the P_{aq} values increase to >0.3, confirming once again that submerged macrophytes are important.

4.2.5. Carbon isotopes and C/N ratios

Overall, the δ^{13}C and C/N data from the lake are invariant (Fig. 6). The biggest change in the δ^{13}C record occurs in Phase I, with values at the base of the record c. −18‰ (CE 1150), decreasing to −23‰ at CE 1170, and then increasing to c. −19‰. C/N ratios fluctuate between 14 and 20, but overall show a steady decline during Phase I. During Phase II, C/N fluctuate slightly around values of 14–15, decreasing to 11 towards CE 1900. Whilst the C/N values look stable, there is a slightly decreasing trend through time. Values for δ^{13}C increase, reaching peak values of c. −15‰, but in general remaining stable with values between −16‰ and −15‰ from CE 1315 to CE 1780. From CE 1780, values begin to decrease to −17‰. Through Phase I, δ^{13}C continues to decrease slightly to a minimum of −19‰ by CE 1950; from here values steadily increase to the top of the core (−15‰). Similarly the C/N changes decrease to values around c. 10 (CE 1960), and then fluctuate between 10 and 13 until increasing again in the top few samples (CE 2007).

5. Discussion

5.1. Environmental change at Lake Nyamogusingiri over the last 1000 years

5.1.1. Phase I (CE 1150–1275; Mediaeval Climate Anomaly)

This period is concomitant with the northern hemisphere's Mediaeval Climate Anomaly (MCA). In eastern Africa this period is associated with drier conditions (CE 1000–1200); evidence is widespread with records from Ethiopia (Lake Hayq) (Lamb et al., 2007), Kenya (Naivasha) (Verschuren et al., 2000) and other lakes within Uganda, including Victoria (Stager et al., 2005), Edward (Russell and Johnson, 2005), Kitigata (Russell et al., 2007), and Kasenda (Ryves et al., 2011; Ssemmanda et al., 2005) indicating drier conditions. At Lake Nyamogusingiri, the evidence presented

herein suggests a shallow lake and a dominant terrestrial signal from the organic geochemistry data, though it is likely that this phase was punctuated by a wetter phase (e.g. c. 1180) (Mills et al., 2014). During this period, further evidence for a drier climate is also apparent around the northern crater lake cluster (Lake Kasenda; 80 km north of Lake Nyamogusingiri), with pollen data from Lake Kasenda suggesting the contraction of moist-deciduous forest and the expansion of grassland, concomitant with indicators of fire and increasing erosion (Ssemmanda et al., 2005).

Inferred air temperatures (brGDGTs) around Lake Nyamogusingiri are relatively high (c. 23.5 °C) during the earliest part of the phase, dropping to 21 °C by CE 1230, before once again increasing to 23 °C. The diatom record suggests a shallow lake system that is dominated by benthic and salt-tolerant species; Further, the aquatic proxy values are high, which confirms that submerged macrophytes are dominant (Ficken et al., 2000). With the prevalence of periphytic diatom taxa, this could also suggest a relatively clear lake with good light penetration that was able to sustain the aquatic ecosystem. The gently sloping nature of the crater lake, would also — at lower lake levels — provide an abundance of habitat for such plants. Such a lowering of lake levels would permit an increasing dominance of terrestrial inputs (as highlighted by the terrestrial: aquatic ratio [TAR], and the low $\delta^{13}C$). The typical n-alkane signature from Phase I is indicative of predominantly terrestrial material (Fig. 5), though given the n-alkane distributions it suggests (Fig. 5b) a more varied source of terrestrial vegetation (compared to the terrestrial signal from Phase III). This varied source is supported by both the high HI and low OI values, suggesting contributions from algal matter(Lacey et al., 2015).

From CE 1230 the input into the lake system appears to shift from a terrestrially-dominated source to an aquatic dominated source, reflected in part by the lower TAR values. The high values of the carbon preference index (CPI) coupled with the higher $\delta^{13}C$ and C/N values also suggest a strong contribution from terrestrially-sourced material into the lake, possibly derived from C_4 plants, but the absence of pollen data from this part of the record precludes further exploration of this notion. The limited pollen data from the top of this zone show the dominance of non-arboreal pollen (e.g. Poaceae, euphorbiacea [Acalypha]) and Typha (aquatic), and evidence for marsh-type vegetation around the shores of the lake (Fig. 7). Net carbon flux is high, suggesting large amounts of carbon burial in the system, though the source material is most definitely mixed.

Overall, during Phase I, Lake Nyamogusingiri is likely a shallow productive system, and is most probably disconnected from the main lake basin, allowing for an amplified response to a drying climate (implying a minimum lake level drop of c. 2 m). This is supported by the decreasing C/N signal and high $\delta^{13}C$ which suggests that algae contribute to in an increasingly closed lake system. However, as the lake did not dry out (whilst others in this region did during this period) (Bessems et al., 2008) it is possible that groundwater exchange plays a role in the lake hydrology at this time (via salt removal) (Ryves et al., 2011). The wet period of Mills et al. (2014) that punctuates Phase I (centred on CE 1180) may have caused the formation of a freshwater lens (N. lancettula) on more saline bottom waters (the periphytic A. coffeaeformis and A. veneta, and possibly the planktonic C. meneghiniana), which allowed the co-existence of both fresh and saline indicative diatom taxa. Further, such a water column conductivity gradient (as seen in many other lakes in the regions) (Mills, 2009), would allow for strong chemical stratification in the water column (which is stronger than thermal stratification in the Ugandan crater lakes). This in turn would provide the optimal conditions for freshwater, planktonic species to dominate the assemblage.

5.1.2. Phase II (CE 1275—1900)

With the MCA-LIA transition suggested to have culminated by c. CE 1400 (Maasch et al., 2005), the onset dates of the LIA in eastern Africa are widely reported as c. CE 1500 to CE 1800 (Russell et al., 2007; Stager et al., 2005; Verschuren et al., 2000). It is during this period that the majority of eastern African lake level records (Naivasha, Malawi, Turkana, Victoria) and Mount Kilimanjaro (Verschuren, 2004) suggest a return to much wetter conditions and higher lake levels from the end of the 13th century and into the 14th century. A long-lived wet period is likely confined to central eastern Africa, as lakes such as Tanganyika experienced a low stand from the late 14th century that persisted into the early CE 1800s; lake levels in western and southern Africa were also low at this time (Verschuren, 2004).

Inferred temperatures during Phase II fluctuate, with low temperatures at the onset and end of the phase (c. 21 °C), reaching a maximum of c. 23 °C between CE 1410 and CE 1540. During the main phase of the LIA (c. CE 1500—1800), temperatures were at their lowest. Inferred lake levels fluctuate during this period, though overall the lake level declines. The inferred lake level at the onset of Phase II is the highest on record, and the crater lake was likely connected to the main basin for the majority of this phase (Fig. 7), with the potential for the lake to outflow during the highest lake stand (CE 1275 to CE 1370). During high stands, the level of the lake within the crater is controlled by the outlet in the west that prevents lake levels surpassing c. 13—14 m. The diatom record, from which the lake level is inferred, indicates shifting conditions throughout this phase, with the planktonic Nitzschia lancettula representing periods of deeper, stratified fresh water, and the presence of Cyclotella meneghiniana representing periods of lower lake levels with greater mixing of deeper, nutrient-enriched water (Mills et al., 2014). Despite the fluctuating nature of the dominant species, the overall assemblage composition is stable, and little change is observed, though overall DCA axis 1 values decline through the zone (from 2.5 to 1.5). The presence of periphytic taxa is high towards the start of the record, likely as lake levels rise and marginal areas become inundated, supporting a strong littoral flora, and suggest that the lake water is clear with good light penetration. From CE 1465, periphytic taxa decline in importance and aerophilous species (those that can withstand intermittent drying) "disappear" from the record, suggesting that the littoral margins are inundated and the input of material from exposed, saturated margins are no longer important contributors to the record. This reduction in habitable littoral areas, coupled with high planktonic productivity, likely overrides the signal of any remaining periphyton and aerophilous taxa.

During this period the catchment appears to be far more stable, and contributing less source material to the lake than Phase I. Non-arboreal taxa (grasses) are still dominant in the pollen record, and lowland forest taxa (e.g. savannah trees) begin to increase in importance. During this phase, high and variable C/N and $\delta^{13}C$ suggest that there was a mixed source of carbon entering the lake, although the low C/N suggest a more algal influence on the sedimentary record. The high $\delta^{13}C$ values suggests a lake that was becoming evaporatively enriched or a system that was increasingly productive; though there is little evidence for saline tolerant taxa (Mills and Ryves, 2012), the other components of the organic geochemical record aid the understanding of where the material in the lake system is sourced.

The aquatic proxy (P_{aq}; Fig. 4a) suggests that submerged macrophytes were present and a large contributor to the organic component of the sediment record. Similarly, the TAR and CPI suggest that input from the terrestrial environment is at its lowest on record. The high HI indicates that algae are the main source of organic carbon in the record, and this is supported by the n-alkane
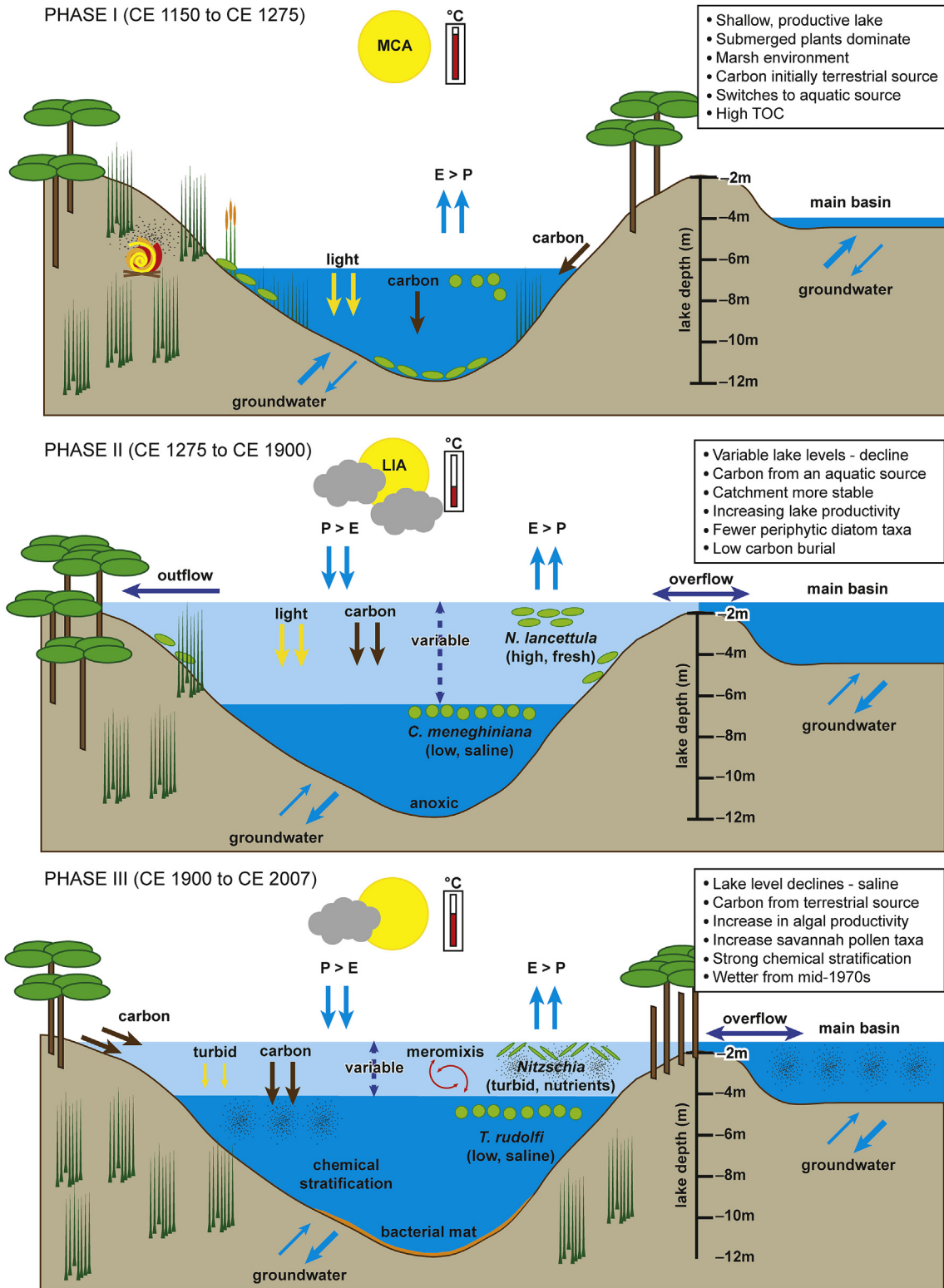
Fig. 7. A graphical overview of the major phases of environmental change at Lake Nyamogusingiri, highlighting the need to interpret changes in the lake system according to the catchment setting and basin morphometry at any given point in time, and the role antecedent conditions may play when interpreting changes.

histograms typical of this zone (Fig. 4b), which show a mixed algal/bacterial distribution overprinting the terrestrial signal. The terrestrial signal is still found during this phase, but represents a much lower proportion of the organic input.

During Phase II, sedimentation rates and TOC values are at their lowest (Mills et al., 2014) and the rate of carbon burial decreases to a minimum. However, values of >10% TOC are still indicative of a productive lake, supporting the interpretation that the δ^{13}C indicates an increasingly productive system, which as lake levels decline experience some degree of evaporative enrichment. This is

supported by modern lake water isotope data from Lake Nyamogusingiri which show that in drier months, the lake water becomes evaporatively enriched (Mills, 2009; Mills et al., 2014). This information in tandem with CPI, TAR, and P_{aq} suggest that autochthonous production is likely the source of organic material to the lake during this phase, given this tends to be preferentially accumulated in the deepest parts of lake basins (Yu et al., 2015).

5.1.3. Phase III (CE 1900—2007)

This final phase was a period originally associated with catchment instability, attributed to both climatic and cultural impacts, and the hypothesis that the response of the diatom flora is driven by changes in nutrients and light (turbidity) (Mills et al., 2014). The addition of new organic geochemical and pollen data allow a better understanding of a complex and dynamic lake system over the last 100 years.

Inferred temperatures during this phase are the lowest on record, varying between 20.5 °C to c. 21.5 °C (similar to modern day MAAT for this part of Uganda) (World Bank, 2018 CCKP). Inferred lake levels are low, only increasing from c. CE 1985. This inferred lowstand is in part driven by the complete disappearance of the freshwater, planktonic (*Nitzschia lancettula*), which reappears in the record from c. CE 1985 to the top of the record. This phase has the largest shift in the diatom assemblage, with a decline in DCA axis 1 sample scores; facultatively planktonic and aerophilous species are more abundant during this phase (and especially between CE 1900 and CE 1975). This lower lake level is also reflected in the aquatic proxy with a switch from submerged to emergent plants. The *n*-alkane record suggests that the terrestrial environment is an important source of material to the system (Fig. 5b); the terrestrial vegetation source is also less varied (compared to Phase III). Previous palaeolimnological studies from across eastern Africa either pre-date the CE 1970s (Russell and Johnson, 2005), or avoid climatic inferences from lakes of this age as they are presumed compromised by human impact. However, a reconnaissance to the crater lakes in western Uganda by Melack in CE 1971 mapped a number of the crater lakes, and recorded their lake levels and morphometry. In CE 2006 Lake Nyungu (in the same crater district as Lake Nyamogusingiri) was revisited (Mills, 2009), and new morphometric and depth data collected. By comparison to the results of Melack (1978), in CE 2006 Lake Nyungu was at least 8 m higher than in CE 1971. Further, the morphometry of the basin had also changed, with the inundation of land as lake levels have risen. Unpublished diatom stratigraphies from Lake Nyungu and Lake Kako (Mills, 2009) also shows the decline/disappearance of freshwater planktonic diatoms (*N. lancettula* in Nyungu, *Aulacoseira ambigua* in Kako) from the late CE 1960s, replaced by benthic species such as *Gomphonema pumilum* (Nyungu) and *Gomphonema gracile* (Kako). There is strong evidence that regional lake levels were lower in the CE 1970s (as seen at Lake Nyamogusingiri).

The decrease in C/N values during Phase III suggest that there is greater algal input into the sediments, although the small decline in $\delta^{13}C$ values suggest that productivity may be lower or there may be an increase in C cycling. Similarly, the decline in inferred pH (from 8.6 to 8.2) suggests lower photosynthesis and more respiration; this could in part be driven by an increase in TOC and carbon burial in the lake as a result of increased input from the terrestrial environment (as also reflected in the TAR and CPI).

In conjunction with lower lake levels, the pollen record suggests an increase in lowland forest taxa, which peaks c. CE 1975, from which a drier period may be inferred. This provides evidence for expanding savannah grassland; Pollen assemblages of wooded savannah are distinguished by high Poaceae with strong contributions of *Acalypha* and/or *Phoenix reclinata* type (Ssemmanda et al., 2014). The abundant Cyperaceae pollen during this phase

(highest abundance on record), suggests that marginal areas of the lake were occupied by a sedge swamp (Ssemmanda et al., 2014). The TOC increases during this phase to the highest values recorded (from CE 1965). Generally, C burial is also high (although variable) during this phase (with values similar to those observed in Phase I). The organic material deposited/buried in the lake may not be solely derived from the catchment, and we hypothesise that there is some increase in aquatic productivity related to algal blooms, and possible blooms of blue-green algae, which may also increase respiration in the system (as algal organic carbon is more labile). This is further supported by the TAR and CPI which suggest that input from the terrestrial environment is increasing, though it should be noted that towards the top of the core (from CE 1995), the aquatic component dominates (TAR only). The HI suggests that algae are the main component of the organic carbon record, but the increase in OI values during Phase III suggests that woody terrestrial plants are increasingly important. Lake levels show a recovery in the more recent part of the record (with the reappearance of *N. lancettula* from CE 1990), in tandem with the evidence from other nearby systems (Mills, 2009).

Phase III is the most dynamic phase of the lake's history, with a multitude of drivers impacting the biological and organic geochemical record. In the absence of robust hydroclimate data for the region, and the ambivalence of many previous studies when inferring hydrological change during the more recent period, the key drivers of change remain open to speculation. However, a number of indicators (e.g. diatoms, aquatic proxy) presented herein suggest that in the last c. 100 years there was another significant shift in the lake level of Nyamogusingiri, and that the crater lake was once again separated by the main basin between CE 1900 and CE 1965, permitting the appearance of the saline and planktonic diatom *Thalassiosira rudolfi*. Increasing depth of the lake from c. CE 1975 onwards caused by regionally wetter conditions (Ssemmanda et al., 2014) likely promoted the development of a freshwater lens overlaying more saline waters (as in Phase I), and allowed for strong stratification within the lake, allowing long, thin *Nitzschia* species to dominate but with *T. rudolfi* present. The increase in *Nitzschia palea* is likely a result of increased nutrients within the lake system. It is likely that the lower lake levels allow occasional mixing of nutrient rich deeper waters, providing an internal source of nutrients, which may have resulted in diatom blooms (reflected in the TAR), and even blue-green algal blooms which increased lake respiration at depth (decrease in pH).

5.2. The use of novel organic geochemical proxies

This paper, for the first time in the tropics, presents a unique combination of organic geochemical techniques for understanding changes in temperature (brGDGTs) and sources of organic material deposited in lake sediments (Rock-Eval, *n*-alkanes, carbon isotopes, C/N). At a time where there is increasing discussion surrounding lakes as hotspots of carbon cycling and sequestration, this study provides the first step toward disentangling the multiple sources of material contributing to carbon dynamics, through time, in a tropical lake system.

Lakes are known to store carbon generated by lake (autochthonous) productivity (Cole et al., 2007), and increasingly they are sequestering and mineralising large amounts of carbon received from the terrestrial environment. At present, much of this terrestrial material is mobilised to aquatic systems largely as a result of anthropogenic catchment alteration (Anderson et al., 2014; Downing et al., 2008), and the impact is particularly acute in small lakes (Hanson et al., 2015). Whilst disruption of the carbon cycle can be a key indicator of anthropogenic impact and driver of ecological change in lake-catchment systems (McGowan et al.,

2016), little attention is paid to longer term dynamics and the potential roles of climate in observed changes. Furthermore, most lake-carbon studies to date have focussed on northern hemisphere agricultural landscapes (Anderson et al., 2013, 2014; Heathcote et al., 2015; Sobek et al., 2007; Tranvik et al., 2009). In the tropics there has been little attention paid to the role of lakes (Raymond et al., 2013); the focus is on terrestrial carbon dynamics (Midgley and Bond, 2015).

5.2.1. Discriminating sources of carbon

Whilst existing palaeolimnological studies focus on understanding the quantity of carbon buried in differing landscapes (e.g. agriculture, boreal) (Anderson et al., 2013, 2014; Heathcote et al., 2015; Sobek et al., 2007) there has been little attention directed towards identifying the source of the material deposited in the lake system which is a key determinant for C burial or mineralisation (Sobek et al., 2007). Generally, increased carbon burial in lakes in anthropogenic landscapes is attributed to land use changes, and the increased delivery of organic carbon and nutrients from the terrestrial environment which drive the production of autochthonous carbon. Seldom do studies exist that connect the flow of material from the catchment and its impact on autochthonous production within the lake system. In palaeolimnological studies, carbon isotopes (often in tandem with pollen analysis) are often used to infer the source of material to the lake sediment record, and in many instances lake studies from eastern Africa have more readily been able to discriminate the source of material by using a biplot of the C/N and δ^{13}C values (Leng and Marshall, 2004), and in some cases this is enhanced by the analysis of modern catchment material.

Unfortunately, understanding the source of organic material using only C/N and δ^{13}C values from Lake Nyamogusingiri is difficult. The values generated from these analyses generally indicate a mixed source, and aside from the earliest part of the record, there were no major shifts observed in the relative abundance of, for example, C_3 and C_4 plants. On glacial timescales such changes are readily observed from lake sediments from across the eastern African rift lakes (Lamb et al., 2004; Talbot and Lærdal, 2000). However, in a small, productive lake catchment over a 1000 year time period, with relatively similar catchment vegetation throughout the record (even though relative abundance does change) and no large, long-lived changes in climate, it is perhaps expected that the δ^{13}C signal would not elucidate the source of OC. Carbon isotopes are useful for exploring in-lake processes, and the decreasing trend in C/N over time suggests an increasing dominance of algal matter. Therefore parallel changes in δ^{13}C can be used to understand in-lake productivity. This study demonstrates that bulk and molecular organic geochemistry (e.g. Rock-Eval(6) and *n*-alkane distribution ratios, brGDGT) provide an enhanced toolkit to discriminate organic matter source in tropical lakes.

Being able to understand the changing supply of material to the lake has allowed a more holistic understanding about the connection between the catchment and the lake system, and provided a more detailed appraisal as to how the lake system as a whole has changed through time (Fig. 7). It has provided the opportunity to decipher more complex signals than possible when interpreting lake system response using the diatom data alone.

5.2.2. Inferring temperature from lake sediments

Several studies have explored the potential for the application of brGDGTs to lakes in eastern Africa (Loomis et al., 2011; Tierney and Russell, 2009; Tierney et al., 2010). Compared to catchment soil (normalised to TOC), brGDGTs are often higher in concentration in lake sediments, which suggests a number of the compounds may be produced *in situ* in the lakes (Schouten et al., 2013). Often, the

MBT/CBT calibration suggests lower inferred temperatures (compared to other brGDGT calibration methods); however, generally the eastern African calibration set of Tierney et al. (2010) appears to show better correlation. This is indeed true of the record from Lake Nyamogusingiri. With little long-term monitoring data of local air temperatures in western Uganda, the climate-model derived temperature record for Uganda between 1901 and 2015 is c. 22 °C (World Bank CCKP); where local MAAT is recorded more recently, temperature ranges from 19 °C (Bushenyi) to 22.1 °C (Rubirizi). The agreement of the inferred temperature with that of modern measurements, and climate model data over the last 100 years, increases our confidence in the values reconstructed at Nyamogusingiri. Further, we see patterns in the inferred temperature that match more regional scale shifts, inferred from other studies. This includes higher temperatures between the beginning of the Nyamogusingiri record and CE 1200 – the period concomitant with the Mediaeval Climate Anomaly, and lower temperatures during the main time period concomitant with the Little Ice Age phenomenon in eastern Africa (CE 1500-CE 1800). The temperature and pH changes down the core are mostly smaller than the calibration error of the proxies. However, as the trend of the curves is comparable/in accordance to changes of the other proxies used (biological indicators, n-alkanes), we argue that the changes recorded are real.

Whilst we deem the application of the brGDGTs calibration of Tierney et al. (2010) a success, there are a number of factors that we do not yet fully understand, and as with other studies this largely applies to the systematics of the brGDGTs. As it stands, it is not clear whether the compounds are delivered from the surrounding catchment material (effectively recording MAAT), or whether a higher abundance is produced *in situ* (effectively recording lake water temperature). Where brGDGTs are formed in lakes, it is still unclear from which part of the water column they are derived (e.g. epilimnion, hypolimnion, or at the sediment-water interface) (Loomis et al., 2011). There is the potential for this fundamental unknown to be assessed by processing populations derived from endmembers (e.g. from the catchment and from sediment trap studies); however to date, this work has not been undertaken and is a gap in the knowledge base for the discipline. Further, the relative proportions of allochthonous vs autochthonous brGDGTs may well change through time (Loomis et al., 2011), and would be a product of not only changes in sediment focussing but also in changes in catchment vegetation (e.g. more human impact may expose bare soil surfaces which is then transported to the lake system) and also changes in catchment rainfall which would also impact the amount of terrestrial material delivered to the lake (Loomis et al., 2011). A larger, more detailed study is needed to maximise the techniques of discriminating sources of organic matter to quantify catchment versus aquatic input into the system, as would more fundamental understanding of changes in precipitation and its intricate link to lake hydrogeology.

5.3. The potential role of lake hydrology - the missing link?

In this paper we present a wealth of data relating to the interactions between a lake and its catchment; the response of the aquatic system and the origin of the material deposited in the lake. We also provide a temperature reconstruction, which can be used to understand a potential driver of change within the lake-catchment system. However, a key component of our work is missing, namely a robust reconstruction of changing hydroclimate through time. In areas such as western Uganda, whilst small changes in temperature have been linked to changes in dynamics of tropical crater lakes (Saulnier-Talbot et al., 2014), there is also a significant relationship between rainfall and terrestrial input into

lake systems; this was neatly demonstrated from a 20-year monitoring record from Lake Nkuruba by Saulnier-Talbot et al. (2014). It can be argued that in the tropics, even on glacial to interglacial timescales, temperature has only fluctuated between $\pm 4-7\,°C$ (Berke et al., 2014; Loomis et al., 2015), with lake waters suggesting temperatures of $>18\,°C$ (Berke et al., 2014) and this is likely to have minimal effect on lakes, specifically their thermal stratification (Mills, 2009). From a limnological perspective, the vertical thermal gradients within crater lakes are small, even though surface water temperatures can be in excess of $25\,°C$. Despite this small temperature difference, stratification is likely to be very stable once established (Beadle, 1966; Ruttner, 1931, 1932) due to the density of warmer waters. The difference in density between $22\,°C$ and $25\,°C$ is much greater than that between water of 5 and $10\,°C$, hence pronounced stratification can arise from only small temperature differences between top and bottom waters (Talling, 1963). In many of the deeper Ugandan crater lakes (>5 m), the density difference at depth is enhanced by chemical stratification (driven by conductivity) (Mills, 2009).

For Lake Nyamogusingiri, a difference in temperature of $20.5\,°C$ to $<23.5\,°C$ over 1000 years does not appear to be correlated with the changes observed in the biological and organic geochemical record. It is likely that a concomitant shift in rainfall presents the biggest contributor to changes observed in the lake record, specifically aiding the increased delivery of catchment material to the lake system. Furthermore, the depth of the lake water (and lake morphometry) is a crucial driver of sediment focussing in a lake system, and would cause carbon burial to be high at times of higher lake level and vice versa (Hilton, 1985; Hilton et al., 1986).

Closely coupled with this is understanding the hydrology of the lake system, including the major fluxes of water in the system (inflows and outflows). Shifts in hydroclimate impact lake levels in many of these crater lake systems (Mills et al., 2014; Ryves et al., 2011; Verschuren et al., 2000), altering lake levels directly through effective precipitation or more indirectly via groundwater recharge. Published and unpublished studies from the region suggest that even when some lake systems are known to be dry (Bessems et al., 2008), other lakes have persisted, during what appear to be long-lived periods of rainfall deficit, suggesting that groundwater can play a critical role in maintaining freshwater systems (Mills, 2009). The study of Lake Kasenda by Ryves et al. (2011) highlighted the potential role of groundwater as a possible point of ionic exchange that kept the lake fresh, even when lake levels were low and ionic concentration would be anticipated if this lake level lowering was largely due to evaporation without recharge. The oxygen isotope data from the lake carbonates (Ryves et al., 2011) also suggest some rapid shifts in lake hydrology through the last millennium, particularly to very negative values, often associated with increased groundwater inflow in such lakes. Both these lines of evidence suggest that groundwater is a critical component of Kasenda hydrology, and this has potential implications for the response of any aquatic system to meteorological drought.

6. Conclusions

The application of novel geochemical techniques, paired with more traditional palaeolimnological analyses, have permitted a more holistic understanding of the environmental change at Lake Nyamogusingiri through time. We demonstrated that it is possible to use sediments from smaller crater lakes to infer longer-term temperature changes, and for the first time, we discriminate sources of carbon delivered to a tropical lake system. The data generated from the organic geochemical and biological analyses all show good correspondence through time, and demonstrate the usefulness of indices such as the aquatic proxy by using multiple lines of validation. The wealth and complexity of the organic geochemical data has also provoked much thought when considering the changing functionality of a lake ecosystem through time, and the need to always view a lake within its catchment setting. In this case, each phase must be interpreted not only with regards to the lake basin morphometry, but also bearing in mind the catchment; the breadth of organic geochemical techniques offered a unique insight into the relative roles of autochthonous versus allochthonous drivers of change within a lake system that cannot borne from diatom and pollen data alone. As with all studies, we offer a caveat that we must be careful when interpreting the changes in the sediment as a real environmental change, whether this is in regards to the calibration errors of the methods used (e.g. temperature inference) or whether shifts in the organic geochemistry data are a result of changes in sediment degradation and transportation.

This research serves as a starting point for understanding interactions between climate, carbon, and ecosystem change in the tropics. Whilst restricted to a study of one lake, a relatively small lake system in Uganda, over the last 100 years, is burying quantities of carbon on a par with that observed in agricultural North America. These high C burial rates occur in a basin with minimal human impact, and Uganda alone offers >80 of these lakes, with some catchments heavily altered by people. This undoubtedly has implications for the disruption of local carbon cycles, and the links to other biogeochemical cycles (such as P, N, and Si) in the future as human and climate pressures increase in tropical regions.

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