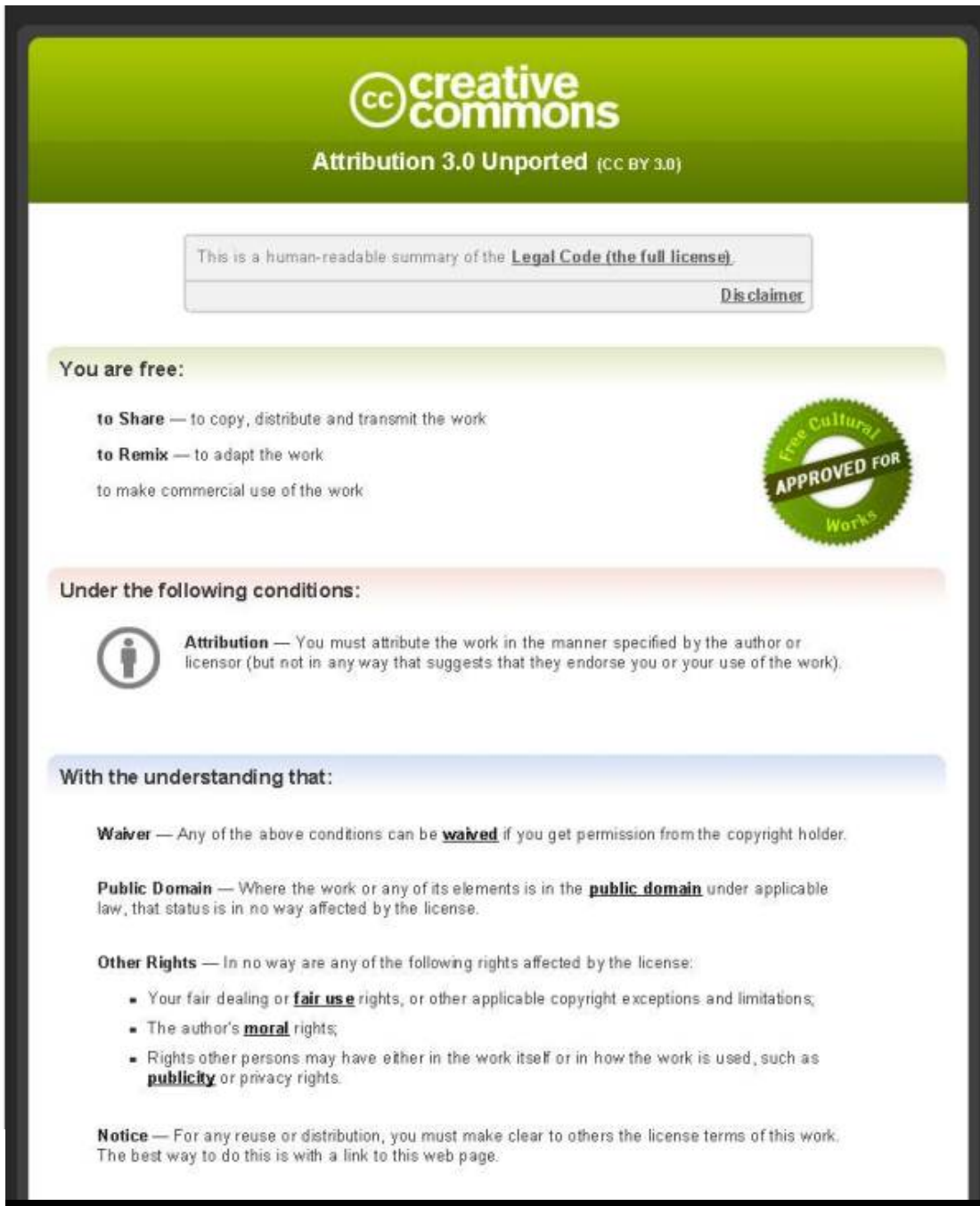


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Expressions of climate perturbations in western Ugandan crater lake sediment records during the last 1000 yr

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Abstract

Equatorial East Africa has a complex, regional patchwork of climate regimes, with multiple interacting drivers. Recent studies have focussed on large lakes and reveal signals that are smoothed in both space and time, and, whilst useful at a continental scale, are of less relevance when understanding short-term, abrupt or immediate impacts of climate and environmental changes. Smaller-scale studies have highlighted spatial complexity and regional heterogeneity of tropical palaeoenvironments in terms of responses to climatic forcing (e.g. the Little Ice Age [LIA]) and questions remain over the spatial extent and synchronicity of climatic changes seen in East African records.

Sediment cores from paired crater lakes in western Uganda were examined to assess ecosystem response to long-term climate and environmental change as well as testing responses to multiple drivers using redundancy analysis. These archives provide annual to sub-decadal records of environmental change. The records from the two lakes demonstrate an individualistic response to external (e.g. climatic) drivers, however, some of the broader patterns observed across East Africa suggest that the lakes are indeed sensitive to climatic perturbations such as a dry Mediaeval Climate Anomaly (MCA; 1000–1200 AD) and a relatively drier climate during the main phase of the LIA (1500–1800 AD); though lake levels in western Uganda do fluctuate. The relationship of Ugandan lakes to regional climate drivers breaks down c. 1800 AD, when major changes in the ecosystems appear to be a response to sediment and nutrient influxes as a result of increasing cultural impacts within the lake catchments.

The data highlight the complexity of individual lake response to climate forcing, indicating shifting drivers through time. This research also highlights the importance of using multi-lake studies within a landscape to allow for rigorous testing of climate reconstructions, forcing and ecosystem response.

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1 Introduction

The climate of East Africa exhibits high inter-decadal variability during the last 2000 yr, whilst high magnitude and abrupt climate events characterise the short instrumental record (e.g. rainfall variability as a result of short-term climatic perturbations, such as El Niño-Southern Oscillation; Nicholson, 1996, 2000; Nicholson and Yin, 2001; Conway, 2002). Previous studies within East Africa have shown that some of these past climatic events are synchronous across the region. However, a number of more recent studies have suggested spatial complexity (Verschuren et al., 2000; Ssemmanda et al., 2005; Stager et al., 2005; Ryves et al., 2011), and thus regional heterogeneity of tropical palaeoenvironments in terms of responses to climatic forcing (e.g. the Little Ice Age; Russell et al., 2007). Current palaeoclimatic research in Africa is of immense importance as it has the means to provide an historical and pre-colonial perspective on past variability (both natural and anthropogenic). The last 1000 yr is a crucial period in East African history during which time there were major societal transformations and political changes, which have often been linked to fluctuations in climatic conditions (e.g. Taylor et al., 2000; Robertshaw and Taylor, 2000; Verschuren et al., 2000; Robertshaw et al., 2004; Doyle, 2006). In addition to this, the last 1000 yr provides one of the most challenging time frames in which to understand regional climatic and environmental changes from lake sediment records in East Africa due to the issues associated with the dating of sediments spanning this period as well as increasing modification of many of the catchments by anthropogenic activity, especially in terms of agriculture (with the development of nucleated, permanent settlements) and the implementation of new technologies (e.g. iron technology and associated forest clearance for the production of charcoal).

More recently, research has focussed upon compiling continent wide, historical and proxy temperature records from a range of archives to understand past variations in climate of the last 2000 yr (Nicholson et al., 2013). However, given that equatorial East Africa has a complex, regional patchwork of climate regimes, with a general eastward

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trend of increasing aridity, there are clearly multiple interacting drivers that appear to have a causal relationship with long-term trends in temperature, rainfall and lake levels, but which are overlain by the cultural signals. The causes of century- to millennial-scale climate variability in tropical Africa and the drivers of some of the significant climatic perturbations (e.g. Mediaeval Climate Anomaly – MCA – and Little Ice Age – LIA) are poorly understood (Russell and Johnson, 2005), though several climatic scenarios (hypotheses) have been suggested. Recent high-resolution studies that have focussed on large lakes reveal signals that are smoothed in both space and time which whilst useful at a continental scale, are of less relevance when addressing short term, abrupt or immediate impacts of climate and environmental change at a scale that is relevant to people and policy.

There is a growing body of literature on high temporal resolution palaeolimnological records of Ugandan crater lakes spanning the last c. 1000 yr (Ssemmanda et al., 2005; Russell et al., 2007; Bessems et al., 2008; Ryves et al., 2011) which have suggested that some of these lakes are particularly sensitive to short-term (decadal to century-scale) rainfall variability (Russell et al., 2007; Bessems et al., 2008), due to the lake water-balance which is primarily driven by effective moisture (precipitation: evaporation ratio), even in open systems. In addition to this, the relatively small catchment to lake ratio increases the lake's sensitivity to shifts in precipitation (hydrological connectivity) as well as catchment changes (as a result of disturbance). However, whilst these studies explore regional coherence through paired lake reconstructions, they do not explicitly explore potential drivers of changes in a quantitative manner. The objective of this study was to use a paired-lake approach to test the sensitivity of lake sediment records in western Uganda to climatic and environmental perturbations (LIA, MCA, 18th century drought) not only contributing to the continuing debate about regional heterogeneity and complexity of known climatic events, but to highlight the need for such records to be integrated into continental-scale climate dynamics.

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2 Study sites

Lakes Nyamogusingiri and Kyasanduka ($0^{\circ}17'4.5''$ S, $30^{\circ}0'46.7''$ E and $0^{\circ}17'23.2''$ S, $30^{\circ}0.6''$ E) are two adjacent crater lakes located within the Bunyaruguru lake cluster (Melack, 1978; Fig. 1). These lakes are situated within the Maramagambo Central Forest Reserve on the ecotone between moist semi-deciduous forest and grass savannah (Langdale-Brown et al., 1964). Reported annual rainfall for Lakes Nyamogusingiri and Kyasanduka is in the range of 900–1300 mm (Lock, 1967). Whilst the two lakes sit within the same catchment geology, despite their close proximity, they differ greatly in both their physical and limnological attributes. Lake Nyamogusingiri is much larger (4.3 km^2), with a minimum catchment area: lake ratio (CA : L) of 11.6 and a higher conductivity ($554 \mu\text{S cm}^{-1}$) than Kyasanduka (0.55 km^2 ; $204 \mu\text{S cm}^{-1}$; CA : L = 4.1).

Lake Nyamogusingiri is the deeper of the two lakes. Kyasanduka has a maximum recorded depth of 2 m (Mills, 2009), whilst previous studies have reported that the maximum depth of Lake Nyamogusingiri is 4.6 m (Melack, 1978), Nyamogusingiri appears to be an amalgamation of several smaller craters, the majority of which form a broad, flat basin (with a depth of 3.9 m). To the extreme west of this basin, however, lies a smaller but deeper crater (12.5 m), which is currently connected to the main basin. A sill exists at a depth of 1.2 m between these two basins. If lake level was to lower sufficiently, the two adjoined basins would become two independent and isolated lakes. There is evidence within Nyamogusingiri's deep crater of previous lower lake levels. Situated around the present shoreline, several metres offshore are a series of dead trees and emergent tree stumps. These trees are rooted at a depth of c. 2 m and may be indicative of a long-term lower lake level in the recent past (Mills, 2009).

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3 Materials and methods

3.1 Coring, physical analyses and radiometric dating

Sediment cores were collected from the deepest, central areas of Lakes Nyamogusingiri and Kyasanduka in January 2007 using a HON-Kajak gravity corer to retrieve the uppermost, unconsolidated sediments and a Russian peat corer to collect the deeper, consolidated sediments. Multiple cores were taken in parallel drives to ensure overlap between adjacent core sections. The gravity cores were sectioned in the field (0.5 cm intervals) and the Russian cores were kept intact and placed in half drain-pipes, wrapped in cling-film immediately after collection and stored in the dark. After shipping to the UK (2–3 weeks after collection) the samples were kept in dark refrigeration (4°C) until required for analysis.

The cores from each lake were correlated using a combination of visual stratigraphy, loss-on-ignition (LOI; Dean, 1974) and magnetic susceptibility, and for Kyasanduka by high-resolution diatom analyses in the lower core sections (see Supplement). Composite sequences from both lakes include correlated samples from several individual cores, totalling 127 cm in Nyamogusingiri and 217 cm in Kyasanduka. Sampling density for physical analyses was completed on contiguous 0.5 cm intervals and diatom counts at 1 cm intervals (non-contiguous sampling).

The core sequences from both lakes were dated using a combination of ^{210}Pb and ^{137}Cs for recent sediments and AMS ^{14}C dating for the older core sequences. Lead-210 dates for each core were calculated using the constant rate of supply model (CRS; Appleby, 2001), and compared with stratigraphic dates determined from the ^{137}Cs record. AMS ^{14}C dating was carried out on terrestrial macrofossils or charcoal (both $> 250 \mu\text{m}$). Sixteen dates were obtained across the 2 cores (Table 1). A 1 cm thick sediment sample was taken from the selected horizon and wet sieved through a 250, 125 and $63 \mu\text{m}$ mesh with de-ionised water. The various residues were transferred into labelled petri-dishes, and samples were picked using metal tweezers under a Leica dissecting microscope. The picked samples were transferred into sterile glass bottles and dried at 40°C .

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All of the samples for radiocarbon dating were subject to an acid-alkali-acid (AAA) pre-treatment before analysis, combusted to CO₂ and reduced to an iron-graphite mixture (Slota et al., 1987) at the NERC Radiocarbon Facility before ¹⁴C analysis at the SUERC AMS laboratory. All dates were calibrated using CALIB 5.0 (Stuiver and Reimer, 1993) using the IntCal09 calibration curve (Reimer et al., 2009) and an age model was derived based upon 0.5 span smooth spline interpolation using the program CLAM for R (Blaauw, 2010).

3.2 Diatom analysis

Samples for diatom analysis were prepared following the waterbath method of Renberg (1990). A total of 133 and 278 samples from Nyamogusingiri and Kyasanduka respectively were counted. Strewn slides were mounted in Naphrax, and at least 300 valves per sample were counted in parallel transects under oil-immersion phase-contrast light microscopy (LM) at × 1000 magnification on a Leica DMRE research microscope. A variety of general (e.g. Krammer and Lange-Bertalot, 1986–1991; Patrick and Reimer, 1966, 1975) and regional floras (e.g. Gasse, 1986; Cocquyt, 1998) were consulted, and valves identified to species level where possible. The dissolution of the diatom valves was assessed using a two-scale system (pristine and dissolved; cf. Ryves et al., 2001). This ratio varies from 0 (all valves partly dissolved) to 1 (perfect preservation). Diatom concentrations were estimated by adding a known number of inert microspheres to the samples (Battarbee and Kneen, 1982).

3.3 Numerical methods

The stratigraphical diatom data from each core were divided into assemblage zones using optimal sum of squares partitioning (Birks and Gordon, 1985) by the program ZONE (version 1.2; Juggins, 2002). Diatom-inferred conductivity was calculated using the Ugandan crater lake model of Mills and Ryves (2012).

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3.3.1 Indirect ordinations

Ordination analyses were carried out using CANOCO 4.5 (ter Braak and Šmilauer, 2002) to identify the predominant trends within the diatom abundance data. Initially a Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) with detrending by segments, and down-weighting of rare species, was used to explore the main patterns of taxonomic variation among sites and to estimate the compositional gradient lengths of the first few DCA axes. The diatom percentage data were transformed using log transformation in an attempt to reduce clustering of abundant or common taxa at the centre of origin (Leps and Šmilauer, 2003). The gradient lengths allow the determination of the most appropriate response model for further analysis with thresholds of 1.5 s.d. units determining the choice of linear (< 1.5 s.d.) or unimodal models (> 1.5; ter Braak and Prentice, 1988).

3.3.2 Direct ordinations

To investigate the factors that might be driving changes in the aquatic environment a set of predictor (e.g. organic and minerogenic accumulation rates, sunspots, regional lake levels; Table S1 in the Supplement) and response (diatom taxa) variables were created. Redundancy analysis was undertaken using a combination of RDA (linear) and CCA (unimodal) response models in Canoco 4.5. Preliminary analyses showed sediment age was significantly correlated with the diatom response data (DCA axis 1; $p < 0.001$). As a result, sediment age was included as a covariable in subsequent ordinations to partial-out the variance resulting from this autocorrelation (Odgaard, 1994).

To explain changes in drivers through time, the core sequences were divided into groups of the same sample size (15 = Nyamogusingiri – 7 groups; 40 = Kyasanduka – 5 groups). Whilst these samples are even spatially (to allow for statistically viable results – $p < 0.01$), it should be noted that they are temporally uneven and overlaps were not used as has been used in other studies (e.g. Bradshaw et al., 2005).

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For each sample group, a DCA was applied to the diatom data to ascertain the gradient length and then partial RDA was undertaken (as gradient length was < 1.5 s.d.). Analyses used down-weighting of rare species and Bonferroni-adjusted forward selection to identify a subset of significant explanatory variables. Monte Carlo permutation tests ($n = 999$ unrestricted permutations) were used to test the significance of the remaining variables (Table 2; Bradshaw et al., 2005).

4 Results

4.1 Core correlation and chronological analysis

For both lakes a master core sequence was created from the overlapping core sequences. Initially, this correlation was derived using the coring depths as recorded in the field; further physical and stratigraphical analyses were employed to strengthen the correlation of both lake sequences. This correlation process was straightforward and involved the use of LOI for Lake Nyamogusingiri (Fig. S1 in the Supplement). However, the correlation of the overlapping core sections from Lake Kyasanduka was slightly more complex, and a final sequence was derived through the use of LOI profiles and detailed diatom analyses of the lower core sections (Figs. S2 and S3 in the Supplement).

Age models were constructed for both lakes using high-resolution ^{210}Pb and ^{137}Cs analyses of the upper sediments and AMS radiocarbon dating of terrestrial macrofossils for the lower core sequences (Table 1). The resulting age models are presented in Figs. 2 and 3. A small number of dates were rejected from the models (Table 1) the details of which, including a full discussion of core correlation and chronological analyses for both core sequences, are given in the Supplement (text).

Age models were constructed for both lakes. The calibrated radiocarbon ages are given in Table 1 and the resulting age models are presented in Figs. 2 and 3. A de-

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tailed discussion of correlation and chronological analysis for both core sequences is provided in the Supplement (text).

4.2 Diatom record

4.2.1 Lake Nyamogusingiri (Fig. 4a)

- 1145–1265 AD (102–127 cm) Initially the diatom assemblage is dominated by *Cyclotella meneghiniana* and low abundances of the salt-tolerant taxon *Amphora coffeaeformis*, indicating a shallow, saline environment (Gasse, 1986; Gasse et al., 1997). The appearance of *Aulacoseira ambigua* and an increase in the abundance of *Nitzschia lancettula* and a reduction in *A. coffeaeformis* and *C. meneghiniana* attest to a short-lived fresher phase. The increase in *A. coffeaeformis*, in conjunction with the salt-tolerant *A. veneta*, suggests periods of higher salinity. These two saline events are punctuated by a freshwater event (c. 1180 AD) characterised by a deepening of the lake, indicated by a rise in *Nitzschia lancettula* (Stager et al., 2005). A deepening and freshening of the lake is inferred by the higher abundance of *N. lancettula* and low *C. meneghiniana* although the dominance of benthic and periphytic species suggest that marginal lake areas are important.
- 1265–1900 AD (44–102 cm) Higher lake levels with a stratified water column are indicated by high abundances of *N. lancettula* (Stager et al., 2005). Lower lake levels, increased turbidity and nutrient rich phases are typified by high abundances and fluxes of *C. meneghiniana* and *Nitzschia palea* (Leland and Porter, 2000; Tuchman et al., 2006) and may attest to poor health of this aquatic ecosystem (Lange-Bertalot, 1979; van Dam et al., 1994; Charles et al., 2006). *Nitzschia palea* follows a similar pattern to *C. meneghiniana*, diverging only in the uppermost section. Periphytic taxa are also important, suggesting persistent aquatic vegetation (Stager and Johnson, 2000).

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– 1900–2007 AD (0–44 cm) During the last c. 100 yr, a major change is observed in the record. The increase in abundance of *N. palea* and *C. meneghiniana* is coincident with an increase in the influx of sediments and organic matter, perhaps as a result of catchment disturbance (Sabater, 2000; Mills, 2009). Studies have shown that *Nitzschia palea* thrives in habitats that are organically enriched and is capable of living and sustaining large populations in very turbid conditions (Tuchman et al., 2006).

Enhanced catchment destabilisation (vegetation removal) in response to climatic stressors (e.g. hydrological connectivity) and cultural impacts (clearance for agriculture) likely led to the delivery of a large quantity of nutrients to the lake increasing primary (diatom) productivity. The disappearance of littoral/periphytic taxa suggests conditions were unsuitable for the growth of aquatic vegetation, as a consequence of high turbidity and rising salinity (*Thalassiosira rudolfi*; Stager, 1984; Gasse, 1986); *Nitzschia lancetula* disappears almost completely from the record. Increasing nutrient inputs to the lake are a consequence of human induced catchment disturbance. For example, the construction of a safari lodge (Jacana, completed in 1998) on the shores of the larger basin would likely have delivered large amounts of catchment sediment to the lake system.

4.2.2 Lake Kyasanduka (Fig. 4b)

– 1100–1395 AD (180–217 cm) The presence of the aerophilous species in the earliest period suggests a very shallow lake or swampy/water-logged conditions (Gasse, 1986). Following this, the lake is dominated by aquatic vegetation as suggested by the high abundances of *Nitzschia amphibia* and other periphytic species. The presence of *Amphora veneta* and *Cyclotella meneghiniana* may attest to slightly more saline conditions at this time. There are three small perturbations in this relatively uniform phase, where there are short-lived peaks in the

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abundance of *Aulacoseira ambigua*, perhaps suggesting a rapid freshening of the lake system (Chalié and Gasse, 2002; Stager et al., 2005).

– 1395–1730 AD (135–180 cm) The appearance of *A. ambigua* and decline in periphytic species indicates an opening of the lake waters, and a reduction in the available habitat for littoral vegetation. *Aulacoseira ambigua* dominates the zone. This species has a high light requirement and is indicative of well-mixed, less turbid conditions. The availability of silica (in particular a high Si:P ratio) is also likely responsible for the dominance of *A. ambigua* (Kilham et al., 1986; Owen and Crossley, 1992; Fritz et al., 1993; Barker et al., 2002). *Aulacoseira granulata* is a poor competitor for Si, and in the absence of turbid waters, *A. ambigua* may simply outcompete *A. granulata* v. *angustissima*. A subsequent switch to *A. granulata* v. *angustissima* dominance suggests a shallower, well-mixed, turbid lake (Stager et al., 1997). The increase in turbidity is likely responsible for a decline in *A. ambigua* due to the reduction of light intensity.

– 1730–1860 AD (112–135 cm) This period marks a major change in the diatom flora. The abundance of *A. granulata* v. *angustissima* declines and there is an increase in *C. meneghiniana* and *Nitzschia palea*. The presence of *A. granulata* v. *angustissima* in conjunction with aerophilous and shallow water species suggest a turbid, shallow environment. The turbidity is likely caused by either the in-lake (internal) resuspension of sediments or the input of catchment sediments as a result of disturbance (e.g. vegetation removal).

– 1860–2007 AD (0–112 cm) The occurrence of *C. meneghiniana* is indicative of a shallowing of the lake system; the lake experienced rapid infilling from this point, with over a metre of sediment deposited in the last c. 150 yr. The co-dominance of *N. palea* and *C. meneghiniana* is indicative of waters with a heavy load of decomposed organic matter (Sabater, 2000). *Nitzschia palea* is a species highly tolerant of organic pollution (Sabater, 2000), as well as being suggestive of eutrophic/hyper-eutrophic conditions (van Dam et al., 1994). This may be the

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result of an increase in nutrients and organic matter from the catchment following deforestation and/or the onset of agriculture. *Nitzschia palea* is a species common in water bodies draining agricultural land (Leland and Porter, 2000). The appearance of *Navicula microrhombus* is also worthy of note and perhaps denotes the introduction of fish to the lake and the increasing impacts that humans are exerting on these ecosystems (Cholnoky, 1970).

5 Discussion

5.1 Lake level reconstructions from Lakes Nyamogusingiri and Kyasanduka

Relative lake levels for each of the core sequences were reconstructed using the diatom data. Reconstructions were based upon the known habitat preferences of the most dominant taxa. For example, in Nyamogusingiri, the presence of the fresh, deep water taxon *Nitzschia lancettula* was used as the main basis for lake level reconstruction. Similarly, *Aulacoseira* spp. (*A. ambigua* and *A. granulata*) were used as indicators of deeper water in Lake Kyasanduka. The dominance of benthic species was used as an indicator of lower lake level.

The reconstructed lake level records Lakes Nyamogusingiri and Kyasanduka (Fig. 5) are independent of reconstructed conductivity in these systems. There are clear fluctuations in lake levels (inferred from diatom habitat preferences) but not a corresponding change in conductivity, except, perhaps, at times of extreme aridity (e.g. c. 1940 AD in Nyamogusingiri), when it is possible that the smaller, deeper lake separated from main basin (sill) and operated as a closed system, allowing the hyper-saline species *Thalassiosira rudolfi* to dominate (Mills, 2009).

The discrepancy between the lake level inference and DI-conductivity may arise from three potential issues: (1) the conductivity optima of the main species included in the transfer function. *Cyclotella meneghiniana* is a problematic species in East Africa with broad conductivity tolerance (c. $200 \mu\text{S cm}^{-1}$; Mills and Ryves, 2012 to

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$> 10\,000 \mu\text{S cm}^{-1}$; European Diatom Database, 2013), although its distribution in contemporary western Ugandan crater lakes results in a low optimum in the model applied here (see Mills and Ryves, 2012, for a full discussion) in agreement with observations from other East African lakes; (2) the potential impact of regional groundwater hydrology in the crater lakes of western Uganda, where fresh groundwater may feed lakes during periods of lower lake levels, allowing the removal of salts and keeping water fresh (see Ryves et al., 2011) and (3) diatom-inferred conductivity may not be the primary controlling variable in the training set, and other variables may drive the diatom response (Juggins, 2013). This scenario is perhaps the likely source of error in these reconstructions, given the change in salinity appears to be correlated to DCA axis 2 (Fig. 4a and b), and rather it is changes in diatom habitat preference that is driving DCA axis 1 (Mills, 2009).

Lake Nyamogusingiri demonstrates a lake level response for much of the record (fluctuating abundance of *N. lancettula* and *C. meneghiniana*), Lake Kyasanduka appears to do so in the earlier part of record, but this shallow lake system appears to exhibit a switch in state c. 1880 AD. In fact, lake level reconstructions from both systems should be treated with caution post 1800 AD as it seems that the lakes are responding to influx of catchment sediments (drier climate coupled with human impacts) which overrides signals of lake level changes. Whilst human impacts on vegetation in the region are known to span the last 1000–2000 yr or more (Bessens et al., 2008; Russell et al., 2009; Ryves et al., 2011; Gelorini and Verschuren, 2013), the effects on freshwater aquatic ecosystems (such as Lakes Kyasanduka and Nyamogusingiri) are only apparent in the last 200 yr (when the ecosystems likely cross a turbidity threshold).

5.2 Drivers of diatom change over the last 1000 yr

Constrained ordinations were carried out to assess: (i) which of the specific drivers were explaining change in the fossil assemblages (e.g. sunspots, ENSO) and (ii) to explore whether the data shared similarities with other records of environmental change

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from across East Africa. The analyses highlight some of the main drivers behind the changes observed in the different records. The inclusion of other proxy lake level data also helps to illustrate similarities between the various records. These similarities could be interpreted as either regional scale events (e.g. MCA) or perhaps that the similar lake records share a similar driver (e.g. if similar to Lake Victoria levels, the lake may be responding to solar forcing). The CCA results are given in Table 2. The highlighted variables (Tables 3 and 4) are those that were selected as being statistically significant in “explaining” variation in the diatom data for each time period (Bradshaw et al., 2005).

The redundancy analysis suggests that different processes have influenced lake ecosystem response and that change in the aquatic ecosystem has had different triggers through time. The periods represented overlap and so only major trends are discussed. It should be noted that correlations are scale-dependent (Bradshaw and Anderson, 2003; Bradshaw, 2005). The correlations are complex and do not necessarily reflect cause and effect relationships, but do suggest a number of general patterns in the response of diatoms to impacts on the lake ecosystem. Where samples have high loadings with levels from other lake sequences (e.g. Wandakara and Kasenda), they tend to be linked to higher levels at those sites, equally samples at the opposite ends of the vector are linked to lower inferred lakes levels. The reverse is true for $\delta^{14}\text{C}$; higher loadings suggest a lower number of sunspots (due to the inverse relationship between $\delta^{14}\text{C}$ and sunspot numbers). Where the records bear similarities to other records from across Uganda, it can perhaps be inferred that the lake level fluctuations are a regional signal and where records bear similarities to the lake level from Naivasha, it is most likely an East African signal.

Both records suggest a link to $\delta^{14}\text{C}$ (a proxy for sunspot numbers), as well as similarities to other lake level records from western Uganda, suggesting some coherence of regional lake level fluctuations. Results from Nyamogusingiri also suggest a connection between the changes in Uganda and other areas of East Africa (e.g. Lake Naivasha levels). In the more recent past, the influx of minerogenic or organic matter appears

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to be important in explaining the variation in the diatom data (human impact in lake catchments).

The full core CCA identifies general trends within the two datasets, and suggests that some of the general patterns observed are comparable to trends observed elsewhere in East Africa (e.g. Lake Naivasha data), and such correlations may be interpreted as a response to a regional climatic driver. The results of the RDA moving window illustrate shifts in drivers of ecosystem change through time. Both lakes indicate a general trend from a sequence driven by sedimentary fluxes (organic flux, Kyasanduka; minerogenic flux, Nyamogusingiri) c. 1100 AD, to sections of the record driven by changes in $\delta^{14}\text{C}$ (sunspots) and showing similarities to lake levels from Kitigata, Kasenda (Nyamogusingiri), Naivasha and Kitigata (Kyasanduka). The more recent period shows a clear shift to sedimentary fluxes as the major driver of changes observed in the diatom records.

Redundancy analysis provides an insight into the data that would not be apparent in the direct comparison of the crater lake (level) records to other published work (e.g. Fig. 5). The correlations alluded to here are complex, and may not be the result of a “cause and effect” relationship, yet they do reflect the general patterns of response of the diatom assemblages to various impacts on the lake ecosystem over time (Bradshaw et al., 2005). The moving window RDA allows an understanding of changing drivers of ecosystem responses through time. Many of these drivers are contrasting, and not all are climate related. These analyses also indicate that drivers are not constant within a site or between sites, highlighting the potential issues of making direct climate inferences from complex ecosystems. In addition to this, the differences in the limnological and catchment properties of the two lakes (relatively deep lake, large catchment – Nyamogusingiri – versus shallow lake, smaller catchment – Kyasanduka) will, in itself, be a filter of the climate forcing record (Magnuson et al., 2004; Leavitt et al., 2009). Whilst paired lakes may be expected to respond in tandem to a similar driver, complex [immeasurable] interactions at the lake ecosystem scale renders this assumption problematic. Rather, it might be expected that where paired lakes show a

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synchronous response, these are a direct result of a regional-scale forcing mechanism; other non-synchronous changes are likely to be much more local in scale.

5.3 Coherence between records and regional comparison

The sediment sequences presented here were taken from a paired lake system located on the rift valley floor, within the Queen Elizabeth National Park. As the lakes are located in a similar geology and climate, it would be expected that broad trends in climate and environmental changes would manifest as similar patterns.

Whilst the two lakes differ in their diatom assemblages and therefore, ecological response, statistical zoning of the diatom data shows a number of coherent “time” zones (Fig. 5j and k). These chronozones common to both cores occur at c. 1200, 1300, 1500, 1700, 1900 AD and the late 20th century (c. 1990 AD; Fig. 5). By directly comparing a range of lake level records from across East Africa, together with inferred lake level curves from Lakes Nyamogusingiri and Kyasanduka (Fig. 5) the spatial and temporal (dis)similarities of lake level response to climate drivers can be observed.

There is general agreement that, prior to 1100 AD, the climate in Uganda showed a transition to drier conditions, which likely began earlier during the mid-Holocene (Gasse, 2002; Lejju et al., 2005). Lakes Nyamogusingiri and Kyasanduka confirm this period of aridity recorded across East Africa at the onset of the 2nd millennium (1000–1200 AD). The evidence for this arid phase is widespread elsewhere across East Africa, with records from Ethiopia (Lake Hayq, Lamb et al., 2007), Kenya (Naivasha, Verschuren et al., 2000) and from lakes within Uganda itself (Victoria: Stager et al., 2005; Edward: Russell and Johnson, 2005; Kitigata: Russell et al., 2007; Kasenda: Ssemmanda et al., 2005; Ryves et al., 2011). From 1000 to 1200 AD, historical summer Nileometer readings were at a minimum (Nicholson, 1998), Lake Victoria levels were high and Naivasha (Kenya) levels were low, coincident with the MCA.

The low-stand of c. 1100 AD in lakes Nyamogusingiri and Kyasanduka persists until the late 13th century in Nyamogusingiri and as late as 1450 AD in Kyasanduka. Lake Naivasha provides evidence that this arid phase was punctuated by a freshwa-

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ter event in the early 13th century (Verschuren et al., 2000). Within the errors of the core chronologies, both lakes record a shift to fresher (Nyamogusingiri) and/or deeper, open water (Kyasanduka) conditions c. 1210 AD, providing further evidence in East Africa for this freshwater phase that is also observed in Lakes Naivasha (Verschuren et al., 2001), Edward (Russell and Johnson, 2005) and Kasenda (Ryves et al., 2011) and suggesting that this could be the result of a regional climatic perturbation. Lake Nyamogusingiri also records a fresher event prior to this in the 12th century (c. 1140 AD), although there is no evidence for a similar event at Kyasanduka (perhaps a result of resolution of analysis).

East African records from larger lakes (Naivasha, Malawi, Turkana, Tanganyika, Victoria) suggest a return to wetter conditions and higher lake levels from the end of the 13th century and into the 14th century (Verschuren, 2004). This wetter phase is also evident in the records from Nyamogusingiri and Kyasanduka, with the latter experiencing its deepest (c. 3 m; the maximum depth attainable in Lake Kyasanduka due to level of outflow and depth on sediment infill), open water phase as a consequence of the conditions associated with the LIA (1270–1850 AD). At Lake Naivasha, the wetter conditions were punctuated by three persistent arid phases and corresponding lower lake levels (1380–1420, 1560–1620 and 1760–1840 AD; Verschuren et al., 2000) also recorded at Nyamogusingiri and Kyasanduka and broadly agree with the timings at Naivasha (Nyamogusingiri: 1380–1400, 1510–1600 and c. 1850 AD; Kyasanduka: 1530, 1610–1680 and c. 1810 AD). Conversely, lake levels at Tanganyika fell to their lowest levels and did not recover until the late 1800s. Similarly, Lake Chad water levels were high c. 1100 and 1600 AD, with lower levels during the 15–16th century (Verschuren, 2004). These results suggest that the wetter conditions and therefore higher lake levels associated with the LIA are restricted to East Africa; with lake levels in West and South Africa showing lower lake levels at this time.

Lake Nyamogusingiri has high lake levels centred on c. 1450 and 1750 AD and at Kyasanduka higher levels or open, freshwater phases occur c. 1500 AD, 1570 and 1740. Inferred lake levels from larger lakes across East Africa at all these times are

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high (e.g. Verschuren et al., 2001; Stager et al., 2005). It has been suggested that these high levels occur in response to rising atmospheric $\delta^{14}\text{C}$ residual series (sunspot activity; Stuiver and Braziunas, 1989). Stager et al. (2007) suggest that changes in sunspot activity are transmitted to lake systems through changes in rainfall activity; with higher lake levels are associated with an increased number of sunspots. This correlation is significant throughout the 20th century (Stager et al., 2007) and it is thought that the increased solar activity serves to enhance small thermal effects on surface water bodies (and likely tropical SSTs) by increasing humidity and therefore influences East African precipitation through changes in the ITCZ. $\delta^{14}\text{C}$ rose during the Wolf (1280–1350 AD), Spörer (1416–1534 AD) and Maunder sunspot minima (1645–1715 AD; Nesje and Dahl, 2000), which broadly correspond to the high lake levels at Nyamogusingiri and Kyasanduka. There is evidence from Lake Victoria that this relationship between sunspot minima and higher lake levels reversed during the late 19th and early 20th century (1890–1927 AD), coincident with the Dalton sunspot minimum (1790–1820 AD; Stager et al., 2005). This reversal caused low lake levels to occur coincident with the Dalton minimum. Lakes Nyamogusingiri and Kyasanduka both record lower lake levels broadly coincident with this period.

Similar to other lake level inferences from western Uganda, levels are high at Nyamogusingiri and Kyasanduka c. 1690–1800 AD (and until c. 1840 AD in Nyamogusingiri). Sedimentary archives from Lake Kasenda (diatoms) and Edward (Mg/Ca ratios) provide evidence for increasing lake levels, whilst Victoria, Abiyata (Legesse et al., 2004), Naivasha and Kibengo are all at high-stands. It is likely that wet conditions c. 1750 AD were confined to a narrow belt along the equatorial region of East Africa. This is further supported by inferred drought at Lakes Malawi (Brown and Johnson, 2005) and Tanganyika (Cohen et al., 2005), further south, at the same time.

Despite the generally high levels in Kyasanduka and Nyamogusingiri during the 1700s, there is diatom-inferred lake level evidence for the widely reported late 18th early/19th century drought in Lake Kyasanduka (Nicholson, 1995, 1998; Verschuren et al., 2000; Stager et al., 2005; Bessems et al., 2008; Fig. 5). Nyamogusingiri

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documents a decline in lake level several years after Kyasanduka (c. 1840 AD). It is possible that these two periods of lake level changes are a result of the same external driver; with Kyasanduka being the shallower lake system, with a smaller CA: L area, an immediate response to a shift in precipitation: evaporation ratio might be expected, whereas the deep lake Nyamogusingiri may be less sensitive to changes, thus displaying a delayed response to the same forcing mechanism (Fig. 5).

A return to wetter conditions since the early 1800s is seen in Kyasanduka (1840 AD) and Nyamogusingiri (1860 AD) as well as across east Africa (Lamb et al., 2007; Bessems et al., 2008; Ryves et al., 2011), and it is likely that this wet period, given the possible errors in the various chronologies, is simultaneous. From the late 19th century, written records and observations can supplement palaeolimnological data (Endfield et al., 2009). There is documentary evidence of a dry period c. 1890s AD and also evidence of low lake levels in Lake Victoria (Nicholson, 1998). These low levels are also observed in lakes Nyamogusingiri and Kyasanduka as well as lakes Edward, Kasenda and Wandakara (Ryves et al., 2011) suggesting that this short-lived perturbation was in fact a regional event. Lakes Nyamogusingiri and Kyasanduka show a general decline in lake level from c. 1850 AD onwards.

Increasing human impacts are also evident over the last 150–200 yr, with an increase in the delivery of organic matter to the lake ecosystems (Fig. 4a and b), driven by changes in catchment vegetation (and subsequently catchment hydrology). It is therefore likely that some responses observed in the diatom records are driven by nutrients and turbidity, rather than a result of climate changes and fluctuating lake levels (Battarbee, 2000; Becht and Harper, 2002; Verschuren et al., 2002; Legesse et al., 2003; Legesse et al., 2004; Cohen et al., 2005; Plater et al., 2006).

Regional drivers

Equatorial East Africa has a complex, regional patchwork of climate regimes, with a general eastward trend of increasing aridity. Over long timescales, there are multiple interacting drivers that appear to have a causal relationship with long-term trends

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in rainfall and lake levels. The causes of century- to millennial-scale climate variability in tropical Africa and the drivers of some of the significant climatic perturbations (e.g. MCA and LIA) are poorly understood (Russell and Johnson, 2005).

It is now well established that the drought c. 1200 AD, coincident with the MCA affected much of East Africa (Verschuren et al., 2001; Verschuren, 2004; Russell and Johnson, 2005; Russell et al., 2007; this study). The arid conditions are linked to a period of increased solar activity (Fig. 5x) and, potentially, changes in the North Atlantic thermohaline circulation (Broecker et al., 1999). A study by Ssemmanda et al. (2005) suggested wetter conditions prevailed in western Uganda during Mediaeval times, and given these findings contrast with other records, it was hypothesized that strong regional gradients must have existed across the East African plateau. Lakes to south of those studied by Ssemmanda et al. (2005; e.g. Lakes Victoria, Edward and Nyamogusingiri), show a decrease in lake levels c. 1150 AD, with levels dropping from a short-lived high-stand just prior to 1150 AD. It is possible both an east to west and north to south gradient may have existed at this time.

Unlike the relative simplicity and widespread aridity of the MCA, the manifestation of the LIA in East Africa appears to be much more complex, with increasing evidence for a climatic gradient during this time (Russell et al., 2007). Russell et al. (2007) suggest that 1500 AD marked the onset of arid conditions in western Uganda. The results from this study go some way to corroborating the hypothesis of Russell et al. (2007) and suggest common anti-phasing between western sites (Kibengo, Kitagata, Edward, Tanganyika, Nyamogusingiri and Kyasanduka) and sites from eastern equatorial Africa (Naivasha, Victoria; Russell et al., 2007). This supports the existence of an east-west gradient in which wet conditions in eastern equatorial East Africa were synchronous with arid conditions in western equatorial East Africa (Russell et al., 2007).

The patterns of climate variability across East Africa and their links to changes at higher latitudes is a question that still remains to be resolved (Barker and Gasse, 2003; Brown and Johnson, 2005; Russell and Johnson, 2005a,b). It has been suggested that mechanisms controlling rainfall anomalies during the LIA are unlike those occurring

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during the last 100 yr (Nicholson, 1986). The southward migration of the inter-tropical convergence zone (ITCZ) in response to cooling at higher latitudes is often cited as the main hypothesis for explaining the changes during the LIA (Baker et al., 2001; Haug et al., 2001; Brown and Johnson, 2005; Russell and Johnson, 2005a; Russell et al., 2007). However, changes in the Indian Ocean dipole (IOD; Marchant et al., 2006) coupled with El Niño-Southern Oscillation (ENSO) may be the cause of high rainfall anomalies (Nicholson et al., 1997). In addition to this, lake level fluctuations in Lake Victoria have long been linked to sunspots (Brooks, 1923; Stager et al., 2005), however the inconsistency of sun-rainfall associations (e.g. during the Dalton Minimum) questions this proposed relationship (Stager et al., 2005), unless sun-climate relationships in East Africa are subject to abrupt variability.

Russell and Johnson (2007) suggest that it is ENSO which is the key factor linking high-latitude cooling, the ITCZ, and moisture gradients within Africa, and models suggest that increased insolation in the Southern Hemisphere and southward migration of the ITCZ are associated with more intense ENSO years (Haug et al., 2001; Moy et al., 2002). Russell and Johnson (2007) suggest that it is therefore possible that interactions between the ITCZ and the ENSO system during the Little Ice Age may have triggered a shift toward El Niño-like conditions, increasing rainfall in easternmost Africa, while southward ITCZ migration led to increased aridity in the west.

6 Conclusions

The sedimentary archives from the Ugandan crater lakes provide high-resolution, annual to sub-decadal records of lake level fluctuations during the last 1000 yr. The lakes demonstrate an individualistic response to external (e.g. climatic) drivers. However, given the limnological variations between the systems (e.g. depth), reconstructed lake levels and independent statistical analyses indicate a regional coherence within these sediment archives, with the lakes responding to similar drivers through time. Furthermore, statistical analyses and the direct comparison of these archives to previous

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palaeolimnological work in Uganda and across East Africa suggest that the western Uganda crater lakes are indeed sensitive to climatic perturbations such as a major arid phase coincident with the northern hemispheric MCA (1000–1200 AD) and a drier LIA main phase 1500–1600 AD), though the latter is also characterised by fluctuating lake levels. The general trends support the hypothesis of an east to west (wet to dry) gradient across East Africa during the LIA, however, the relationship breaks down and is more complex towards the end of the LIA (c. 1700–1800 AD) when it appears that cultural disturbances within the catchment (causing increases in sediment and nutrient flux) over-ride the climate signals preserved within these systems.

It may be expected that paired lakes will respond in a similar fashion to the same driving force; where observed changes are synchronous, these are interpreted as a climate signal, but the two lakes clearly operate as independent systems. Whether such an outcome is problematic will depend on the approach used in the understanding of lake sedimentary archives. This research highlights the importance of avoiding single lake studies as an archive of regional environmental change, while the use of a multi-lake approach reduces the potential issues. It is critical that any approach to climate reconstructions from lake sediments, especially those pertaining to biological proxies, accounts for the multi-proxy aspect of diatom response to environmental forcing and climate effects when they exist (i.e. can be seen or are recorded in the sediment archive) are still filtered through the catchment and modified by the lake itself.

Taken together the data show the complexity of individual lake response to climate forcing and hence how single lake studies should be treated with caution. This research also highlights the importance of natural high-density lake areas, such as western Uganda, where lakes located in similar geology, climate and landscape allow for rigorous testing of climate reconstructions, forcing and ecosystem response.

Supplementary material related to this article is available online at <http://www.clim-past-discuss.net/9/5183/2013/cpd-9-5183-2013-supplement.pdf>.

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Table 1. Calibrated radiocarbon ages for all samples from Lakes Nyamogusingiri and Kyasanduka.

Lab. code	Depth (cm)	Dated material	Conventional ¹⁴ C age ± 1σ error	Median probability (AD/BC)	2σ calibrated ¹⁴ C age range (AD/BC)	Relative area (%)
Lake Nyamogusingiri						
SUERC-18911	61.5	Leaf/Charcoal	419 ± 37	1467	1422–1522 1574–1585 1587–1625	85.03 1.53 13.44
SUERC-190660	92.5	Leaf/Charcoal	685 ± 35	1299	1265–1319 1351–1390	64.48 35.52
SUERC-19067	108.5	Wood/Charcoal	795 ± 35	1239	1180–1278	100
SUERC-18396 ^{1*}	121.5	Wood	494 ± 37	1426	1326–1343 1394–1454	4.17 95.82
POZ-26361 ^{1*}	126.5	Charcoal	415 ± 30	1464	1429–1518 1594–1618	90.25 9.74
Lake Kyasanduka						
SUERC-16174	90.5	Leaf	227 ± 35	1750	1528–1551 1634–1685 1732–1808 1928–1952	2.76 41.6 44.06 11.72
SUERC-19070 ^{2*}	134.5	Charcoal	995 ± 35	1036	983–1058 1069–1071 1076–1154	61.75 0.29 37.96
SUERC-18397	167.5	Leaf	362 ± 37	1538	1449–1530 1538–1635	49.24 50.76
SUERC-16175	169	Charcoal	568 ± 37	1353	1300–1368 1381–1429	58.94 41.06
SUERC-16176	184	Wood	516 ± 37	1416	1319–1351 1390–1447	15.74 84.26
SUERC-18988	189.5	Wood	480 ± 37	1431	1332–1337 1397–1470	0.70 99.30
SUERC-19065	189.5	Charcoal	565 ± 35	1354	1302–1366 1383–1429	56.87 43.13
SUERC-19071	192.5	Wood	905 ± 35	1119	1037–1209	100
SUERC-18398 ^{3*}	192.5	Charred wood	2700 ± 37	–853	–914–802	100
SUERC-16173	202.5	Wood	792 ± 35	1240	1182–1279	100
POZ-26360 ^{2*}	206.5	Charcoal	1830 ± 30	182	86–107 120–252	3.62 96.38

* denotes date rejected from age model. ¹ Potentially modern contamination; ² charcoal – reworking; ³ uncertainty surrounding composition of dating material.

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Table 2. Results of CCA of the forward selected (FS) environmental variables at Lakes Nyamogusingiri and Kyasanduka (last 100 yr). The unique variance explained by each variable is also given. The *p* value for all variables is 0.001.

FS variable	Canonical eigenvalue	% variance
Lake Nyamogusingiri		
All (6)	0.394	23.9
Organic	0.071	6.8
Mineral	0.050	4.8
δ ¹³ C	0.041	4.0
δ ¹⁴ C	0.037	3.7
Kasenda	0.029	2.9
Kitigata	0.019	1.9
Lake Kyasanduka		
All (7)	0.433	24.6
Organic	0.094	8.7
CN ratio	0.041	4.0
δ ¹⁴ C	0.032	3.2
Kitigata	0.023	2.3
Kasenda	0.021	2.1
Naivasha	0.018	1.8
δ ¹³ C	0.016	1.6

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Table 3. Results of the moving window RDA from Lake Nyamogusingiri. The variance explained is a percentage of the constrained variance. “X” highlights the most statistically significant driver(s) correlated with a change in the diatom stratigraphy in each of the age groupings.

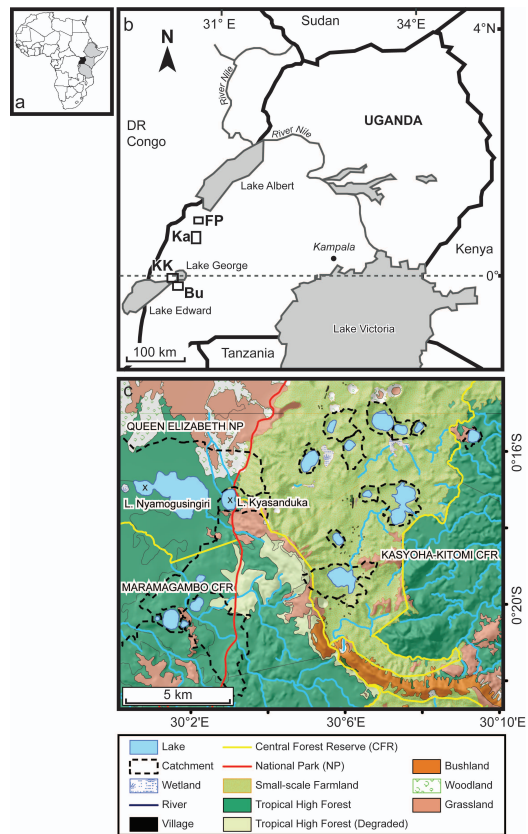
Year AD	Organic	Kasenda	Kitigata	$\delta^{13}\text{C}_{\text{org}}$	$\delta^{14}\text{C}$	% explained
2000–1980	X	X				18.7
1978–1940			X			11.6
1937–1882				X		11.9
1872–1620					X	9.0
1598–1431		X				11.8
1421–124			X		X	28.9
1242–1144	X	X				18.9

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Table 4. Results of the moving window RDA from Lake Kyasanduka. The variance explained is a percentage of the constrained variance. “X” highlights the most statistically significant driver(s) correlated with a change in the diatom stratigraphy in each of the age groupings.

Year AD	Mineral	Kitigata	Kasenda	$\delta^{14}\text{C}$	C/N	% explained
2000–1951	X					10.9
1950–1896		X				7.4
1896–1681			X			7.3
1672–1400				X	X	23.3
1394–1099	X		X		X	15.1

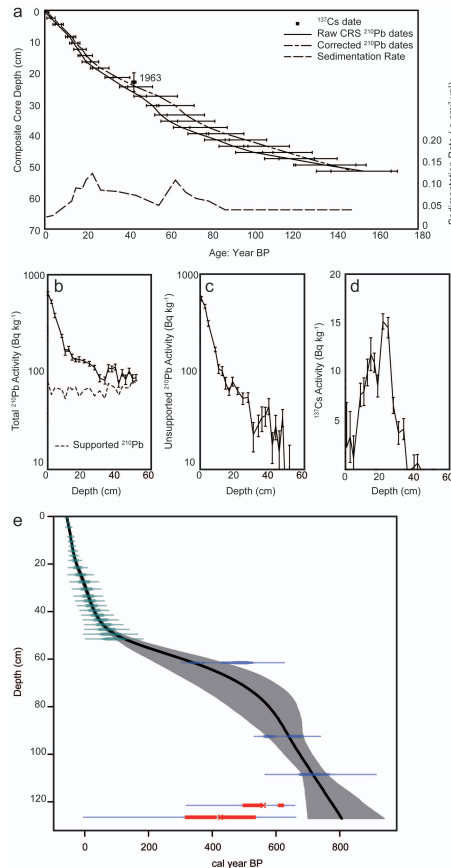
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Fig. 1. (a) Regional location of Uganda. (b) Map of Uganda showing the four crater lake clusters: Fort Portal (FP), Kasenda (Ka), Katwe-Kikorongo (KK) and Bunyaruguru (Bu) as described by Melack (1978). (c) The Bunyaruguru crater lake cluster showing Lakes Nyamogusingiri and Kyasanduka.

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Fig. 2. Radiometric dating of the Lake Nyamogusingiri sediment core **(a)** ^{210}Pb and ^{137}Cs chronology and sedimentation rate. Fallout radionuclides (versus depth) of **(b)** supported and unsupported ^{210}Pb , **(c)** unsupported ^{210}Pb and **(d)** ^{137}Cs concentrations. **(e)** Final age model; the grey envelope highlights the chronological uncertainty in the record.

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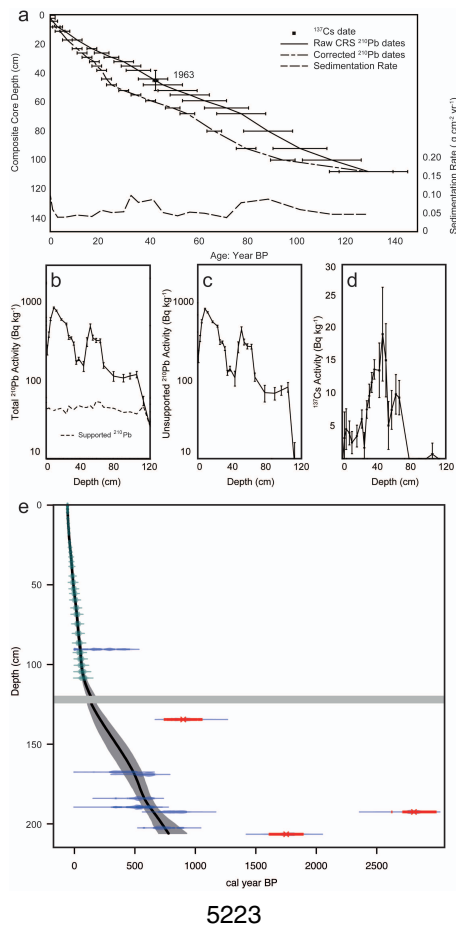


Fig. 3. Radiometric dating of the Lake Kyasanduka sediment core (a) ^{210}Pb and ^{137}Cs chronology and sedimentation rate. Fallout radionuclides (versus depth) of (b) supported and unsupported ^{210}Pb , (c) unsupported ^{210}Pb and (d) ^{137}Cs concentrations. (e) Final age model; the grey envelope highlights the chronological uncertainty in the record.

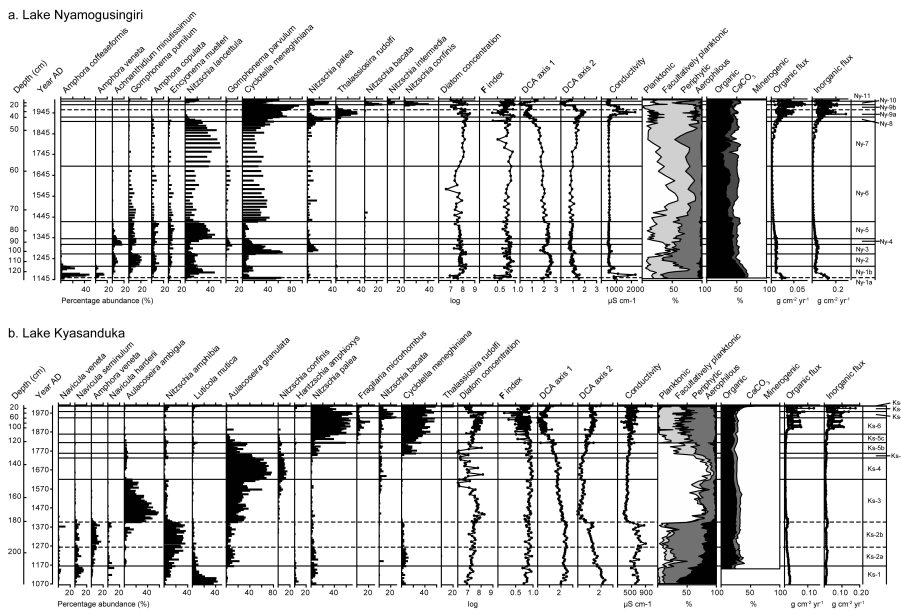


Fig. 4. Diatom stratigraphy from **(a)** Lake Nyamogusingiri and **(b)** Lake Kyasanduka showing selected taxa (> 10 % in any one sample), ordered by weighted-averaging (ascending). Diatom concentration, DCA axis scores and conductivity reconstructions are also shown alongside a diatom habitat summary and the results of LOI and calculated organic and mineralogenic flux rates.

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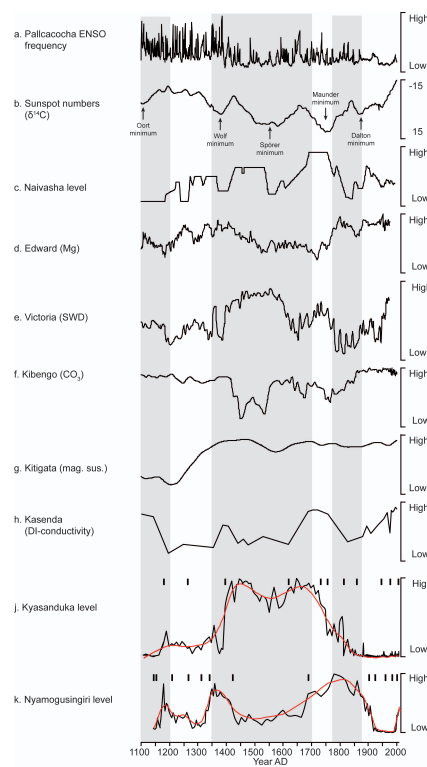


Fig. 5. Comparison of climate drivers **(a, b)** and regional lake levels in East Africa **(c–h)** to reconstructed lake levels from **(j)** Kyasanduka and **(k)** Nyamogusingiri (see also Table S1 in the Supplement).

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