



Recent climate-driven ecological changes in tropical montane lakes of Rwenzori Mountains National Park, central Africa

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Abstract Rwenzori Mountains National Park, which straddles the border between the Democratic Republic of Congo and Uganda, has experienced rapid glacier loss since the beginning of the twentieth century, yet there has been little investigation of aquatic biodiversity change in the park. This study presents a paleolimnological analysis from Lake Mahoma (2990 m asl), which is situated in the bamboo-forest transition zone. Diatom and organic geochemistry data from a 39-cm-long sediment core with a basal age of c. 1715 CE were compared with new analyses of previously published data from Lakes Bujuku (3891 m asl) and Lower Kitandara (3989 m asl), in the alpine zone. Comparisons were made to determine if aquatic ecosystem changes exhibited similar inter-lake patterns over the past ~ 150 years of climate warming and glacial recession, or if only local change was apparent. The diatom flora of Lake Mahoma is acidophilous, dominated by *Aulacoseira ikapoënsis* since at least the mid eighteenth century. In recent decades, the obligate nitrogen-heterotroph *Nitzschia palea* increased in importance, concurrent

with declining $\delta^{15}\text{N}_{\text{org}}$ values. We suggest that these late twentieth century changes were linked to regional warming and increased thermal stratification of Lake Mahoma. Regional comparisons of the Rwenzori lakes were done using existing organic geochemistry records (total organic carbon, C/N and $\delta^{13}\text{C}_{\text{org}}$) and through diatom compositional turnover analyses, and categorisation of species into one of four diatom growth morphology traits, or guilds: tychoplanktonic, high-profile, low-profile and motile. Over the past 150 years, all three lakes showed unidirectional, compositional diatom turnover, indicating that deterministic processes had affected diatom communities. Declining turnover at each site is broadly mirrored by an increase in tychoplanktonic taxa, along with concomitant declines in high-profile diatoms at Lake Mahoma, and low-profile diatoms at Lake Bujuku, and at least for the past 60 years, at Lower Kitandara. The interplay between diatom guilds at all sites is mainly a consequence of competition for available resources. Sediment organic carbon at all sites comes from both autochthonous and allochthonous sources, the relative abundances of which are influenced by the time elapsed since lakes had glaciers in their catchment.

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Introduction

Pronounced changes are occurring in high-altitude regions worldwide as a result of climate change and elevation-dependent warming (Pepin et al. 2015). This is evidenced by alpine temperature increases twice the northern hemisphere average (Gobiet et al. 2014), which have led to major hydrologic changes. For example, mountain glaciers are receding worldwide (Wouters et al. 2019), with substantial hydrologic impacts downstream, especially in relation to water storage and associated ecosystem services (Vuille et al. 2008; Huss and Hock 2018; Zhang et al. 2019). Elevation-dependent warming is particularly pronounced in the tropics (Bradley et al. 2006), and many tropical mountain glaciers are predicted to disappear entirely within the next few decades (Thompson et al. 2006; Prinz et al. 2018), including glaciers in the Andes (Vuille et al. 2008) and east Africa (Thompson et al. 2002; Taylor et al. 2006; Prinz et al. 2018). Although glacier loss in tropical African mountains, including Mount Kilimanjaro, Mount Kenya and the Rwenzori Mountains, has limited impacts on hydrology and water resources (Taylor et al. 2009; Prinz et al. 2018), the sensitivity of tropical montane regions to warming, coupled with their remoteness to direct anthropogenic influences, makes them important sentinels of global climate change. Furthermore, lakes can play an important role in understanding the consequences of such change because we can use their sediment records to decipher how aquatic and terrestrial montane ecosystems responded to past climate variability, even in places where monitoring and documentary records are rare or absent.

Paleolimnological studies in mountain lakes of tropical Africa have long been used to reconstruct Holocene climate and environments, and have included investigations of isotopically inferred periods of heavy convective precipitation on Mount Kenya (Barker et al. 2001), elevation-dependent temperature change (Loomis et al. 2017), diatom biogeography (Richardson 1968) and pollen-inferred vegetation change (Livingstone 1967) in the Rwenzori Mountains. More recently, the fluctuations of glaciers themselves have been inferred from lake sediment geochemistry (Karlén et al. 1999; Russell et al. 2009). We used lake sediments from the Rwenzori Mountains

to infer environmental change since the end of the Little Ice Age.

Rwenzori Mountains National Park (RMNP) is located on the border of Uganda and the Democratic Republic of Congo (Fig. 1). Alpine glaciers in the RMNP have shrunk considerably since the turn of the last century (Taylor et al. 2006), and several programmes have sought to understand potential relationships between glacier recession and aquatic ecosystem change (Eggermont et al. 2007; Taylor et al. 2007; Russell et al. 2009). Paleolimnological studies spanning recent centuries in the Rwenzori Mountains suggest that glacial lakes contain a record of glacier fluctuation through their siliciclastic content (Russell et al. 2009). There is only subtle evidence of glacier recession having a direct impact on either diatom assemblage composition or pollen-inferred vegetation change (Panizzo et al. 2008; McGlynn et al. 2010). There are, however, distinct differences in organic geochemical records between glacial and non-glacial lakes, both spatially (Russell et al. 2009), and over recent centuries (Panizzo et al. 2008; Russell et al. 2009; McGlynn et al. 2010), reflecting changing carbon dynamics, associated with within-lake productivity.

For this study, we focused on diatom and organic geochemical analyses of sediments from Rwenzori Mountain lakes. Diatoms are important primary producers in montane lakes worldwide and are sensitive to changes in climate and hydrology, and together with organic geochemical records they provide important context for underlying trends in lake ecosystem carbon dynamics. We specifically focused on Lake Mahoma, a moraine-dammed lake located in the bamboo-forest transition zone (~ 3000 m) (Fig. 1; Table 1). As there is no evidence of recent glacial activity in its catchment (Russell et al. 2009), our new sedimentary diatom record provides an interesting basis for comparison with diatom records published previously for alpine Lakes Bujuku and Lower Kitandara, which possess recently glaciated catchments (Panizzo et al. 2008; McGlynn et al. 2010). Although previous studies suggested that Lake Mahoma is meromictic, based upon a strong clinograde oxygen curve (5.36–0.45 mg/l) and conductivity gradient (11–41 $\mu\text{S}/\text{cm}$) (Table 2; Eggermont et al. 2007), recent temperature monitoring data show that the lake becomes homothermal for a few weeks in July, indicating it is weakly monomictic (Russell,

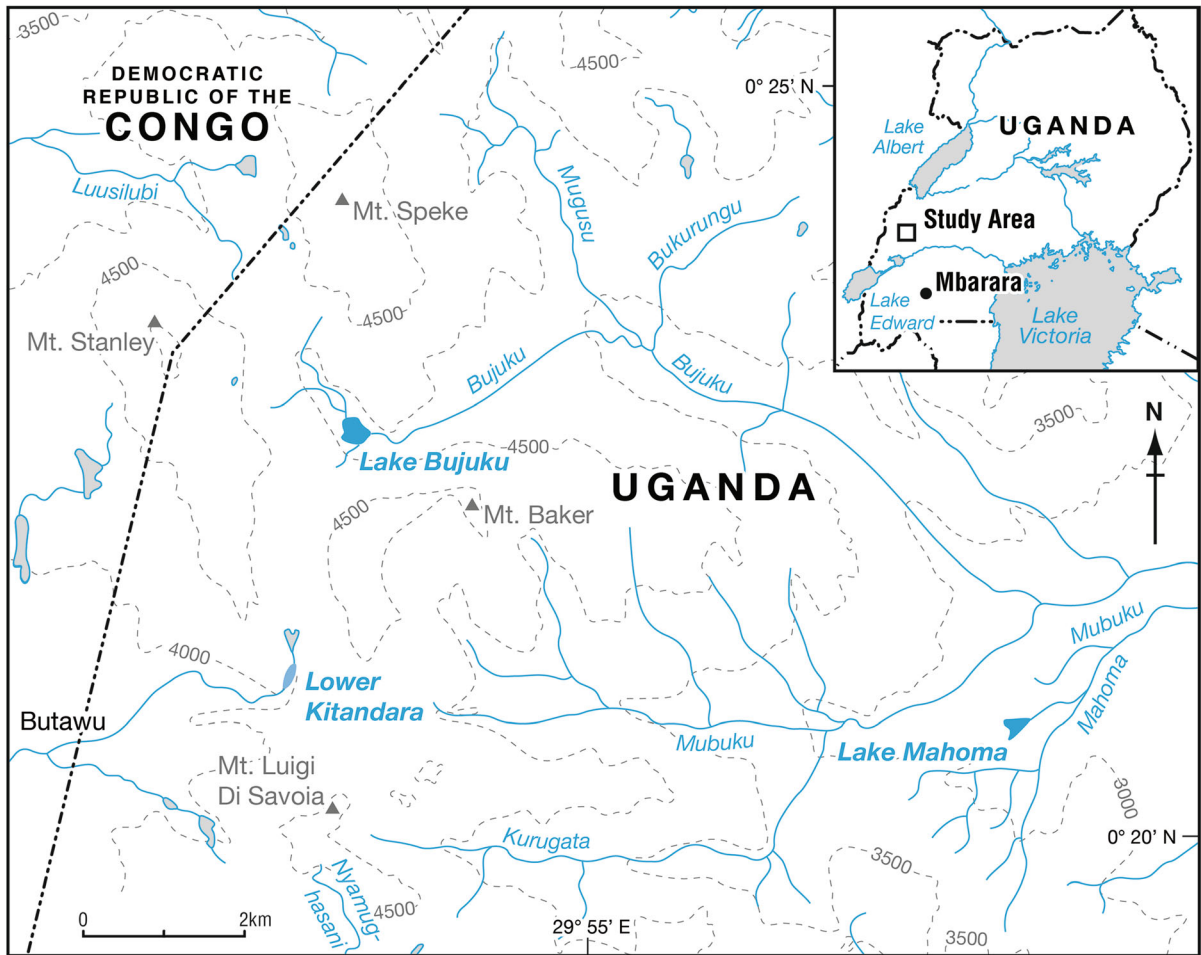


Fig. 1 Map of part of Rwenzori Mountains National Park (RMNP), showing relevant topography, locations of the three lakes highlighted in this study, and the Mbarara meteorological station. Elevation contours are metres (m)

Table 1 Summary of geographical lake characteristics of Mahoma, Bujuku and Lower Kitandara (Eggermont et al. 2007)

Lake	Latitude (N)	Longitude (E)	Altitude (m)	Max depth (m)	Lake origin	Catchment (type)
Mahoma	0° 20.734'	29° 58.102'	2990	25.6	Dammed (moraine)	Bamboo-forest
Bujuku	0° 22.688'	29° 53.576'	3891	13.5	Dammed (landslide)	Alpine
Lower Kitandara	0° 20.947'	29° 53.194'	3989	11	Dammed (moraine)	Alpine

unpublished data). This contrasts with higher-elevation Rwenzori lakes that are polymictic. Additionally, water temperatures in Lake Mahoma are much higher than other RMNP lakes because of its mid-elevation setting (Table 2; Eggermont et al. 2007). Mahoma’s unique characteristics, with respect to other RMNP lakes, make it an important site for understanding how

lakes in the region differ in their response to external drivers of environmental change. The aim of this study therefore, was to investigate how lake ecosystems at different altitudes in the RMNP responded to environmental change over the past few hundred years, with a special emphasis on Lake Mahoma. We note that few high-altitude lakes have been studied in the

Table 2 Summary of physical and chemical characteristics of Lakes Mahoma, Bujuku and Lower Kitandara (Eggermont et al. 2007). T = temperature (°C); TP = total phosphorus (µg/L); TN = total nitrogen (µg/L); Chl-a = chlorophyll a (µg/L)

Lake	Bottom T (°C)	Mixing regime	O ₂ surface (mg/L)	O ₂ bottom (mg/L)	pH bottom (units)	Secchi-disk depth (cm)	TP (µg/L)	TN (µg/L)	Chl-a (µg/L)
Mahoma	12.5	Weakly monomictic	5.36	0.45	5.10	82	10.2	343	2.1
Bujuku	7.0	Polymictic	7.40	0.24	5.88	180	6.2	227	2.6
Lower Kitandara	5.9	Polymictic	7.47	7.09	6.45	240	4.6	206	2.6

tropics in comparison to temperate and circumpolar montane regions, so our findings provide useful information about how these lakes have responded to global change since the end of the Little Ice Age.

Materials and methods

Core collection and dating

Two cores from different expeditions to Lake Mahoma were used in this study. The core used for diatom analysis (MAHO3; 39 cm) was collected in 2003 using a Glew gravity corer (Taylor et al. 2007), and sectioned in the field at 2.5-mm intervals for the top 2 cm, at 5-mm intervals between 2 and 20 cm, and then at 10-mm (1 cm) thereafter. The upper sediments of MAHO3 were dated using ²¹⁰Pb, ²²⁶Ra, ¹³⁷Cs and ²⁴¹Am analysis by non-destructive direct gamma assay on an ORTEC HPGe GWL series, well-type coaxial low-background intrinsic germanium detector at the UCL Environmental Radiometric Facility. The age-depth model was based on a 2nd-order polynomial regression fitted to the ²¹⁰Pb data. The core used for organic geochemical analysis was collected from the deepest part of the lake in 2006, using a UWITEC gravity corer (Russell et al. 2009). The age of the Mahoma core was estimated from a single radiocarbon date on bulk sediment taken from the base of the section (c. 1090 CE) and full details on the chronology can be found in Russell et al. (2009).

Diatom analysis

Following Battarbee et al. (2001), diatom analysis was carried out on 0.1 g of wet sediment from MAHO3, sub-sampled every 2 cm. Diatoms were counted and

identified to the lowest possible taxonomic resolution at 1000× magnification using a Zeiss Axiostar Plus light microscope under phase contrast and oil immersion. Counts were conducted along 1-mm transects until exactly 300 diatom valves were identified per slide with the aid of reference materials, including Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Camburn and Charles (2000), Gasse (1986), and Richardson (1968). Sedimentary diatoms were analysed using indirect ordination. An initial detrended correspondence analysis (DCA) revealed a linear data response of 0.68 SD (standard deviation units), so principal components analysis (PCA) was used to reveal major gradients in the dataset. Response of diatoms to changing available resources over recent centuries was inferred through their compositional turnover (Larson et al. 2016). Compositional turnover was estimated using detrended canonical correspondence analyses (DCCA), by constraining diatom data with estimated sample dates (Birks 2007). Species data were square-root transformed, but rare species were not down-weighted. Compositional turnover analyses were also undertaken on the diatom communities in the higher-altitude Lakes Bujuku (Panizzo et al. 2008) and Lower Kitandara (McGlynn et al. 2010). All ordinations were performed using Canoco5 (Šmilauer and Lepš 2014).

To infer further ecological information from the diatom communities observed, we categorised Lake Mahoma diatoms into four ecological guilds, according to their functional traits of growth morphologies (Passy 2007). Functional traits greatly influence the performance of species (McGill et al. 2006), and for diatoms these are commonly associated with disturbance (e.g. turbulence and grazing) and resource availability (e.g. nutrients, light) (Passy 2007; Rimet and Bouchez 2012). We classified diatoms into four

guilds: motile, low-profile, high-profile, and tycho-planktonic/planktic. Motile diatoms are relatively fast-moving diatoms, tolerant of siltation processes (Battagazzore et al. 2004) and relatively high amounts of nutrients (Passy 2007). Slow-moving diatoms are generally adapted to low-nutrient conditions, and these have been classified as low-profile diatoms, because they attach themselves to substrates in adnate, prostrate and erect forms (Passy 2007). Chain-forming, filamentous, or diatoms found in mucilage tubes are tall in stature, are generally adapted to low levels of disturbance and high amounts of nutrients, and we classified these as high-profile diatoms (Passy 2007). Finally, diatom species able to resist sinking through the water column were classified into the planktic guild (Rimet and Bouchez 2012). Analyses for ecological guild characterisation were also undertaken for the higher-altitude Lakes Bujuku and Lower Kitandara. Guild classification for lake diatoms, however, is not straightforward, as many species are tychoplanktonic, that is they usually grow in benthic habitats, but can also detach and live in open water. Rühland et al. (2015) defined tychoplankton as diatoms dependent on turbulence to remain in the water column, such as *Aulacoseira*, whose valves are generally silica-rich and heavy. Many *Aulacoseira* may also have part of their life cycle amongst the periphyton, and so may also be considered tychoplanktonic (Stoermer and Julius 2003). We therefore described the planktic guild to be tychoplanktonic, to include the small *Aulacoseira* species found at Mahoma, recognizing the guild contains both growth forms. The small *Fragilaria sensu lato* diatoms, consisting mainly of *Staurosirella*, *Staurosira* and *Pseudostaurosira* (collectively called fragilarioids) found at Lakes Lower Kitindara and Bujuka (Panizzo et al. 2008; McGlynn et al. 2010), are also tychoplanktonic. Whereas the use of ecological guilds is more commonly used to characterise growth morphologies of diatoms in rivers, we applied them in these lakes because they enable us to infer useful information about changing disturbance pressures and nutrient availability, which may not be so evident from subtle changes in individual species.

Organic geochemistry

Total organic carbon (TOC), $\delta^{13}\text{C}_{\text{org}}$, $\delta^{15}\text{N}_{\text{org}}$ and C/N ratio were measured on Mahoma sediments with a Carlo Erba Elemental Analyzer connected to a

Finnigan Delta Plus XL isotope-ratio mass spectrometer through a ConFlo II interface (see methods in Russell et al. 2009). TOC, $\delta^{13}\text{C}_{\text{org}}$ and C/N ratio data for Lakes Bujuku and Lower Kitandara were published previously by Panizzo et al. (2008) and McGlynn et al. (2010), respectively. Briefly, TN and TOC were determined using a Carlo Erba NA1500 (series 1), connected on-line to a VG TripleTrap and Optima dual-inlet mass spectrometer. $\delta^{13}\text{C}_{\text{org}}$ values were calculated to the VPDB scale using BROCC-1 laboratory standards. All stratigraphic plots were drawn using C2 v.1.7.7 (Juggins 2014).

Results

Lake Mahoma

Unsupported ^{210}Pb activity declines monotonically with depth and reaches equilibrium with the supporting ^{226}Ra (supported ^{210}Pb) at ~ 24 cm (Fig. 2). The ^{137}Cs activity has a relatively broad peak between 10 and 8 cm, whereas the ^{241}Am the peak is narrower, at 9.5 cm (Fig. 2). This suggests that sediments from this depth record the 1963/1964 CE fallout maximum from atmospheric testing of nuclear weapons. Using a constant rate of supply (CRS) model (Appleby 2008), the ^{210}Pb dates place 1963/1964 at 7–6 cm, whereas the constant initial concentration (CIC) model places 1963/1964 at about 10.5 cm, which is in better agreement with the artificial radionuclide peaks. Given that the simpler CIC model is appropriate to use in a lacustrine environment with minimal impact from anthropogenic activities (Dinsley et al. 2018), our final chronology for MAHO3 was calculated using the CIC model. Dates for remaining sample depths were estimated using a polynomial, second-order regression (Fig. 2), and we estimated that the base of the core was deposited c. 1715 CE.

Thirty-one diatom species were identified in Lake Mahoma sediments, with those present at $> 1\%$ relative abundance in at least one sample shown in Fig. 3. *Aulacoseira ikapoënsis* (O. Müll.) Simonsen, the sole representative of the tychoplanktonic guild (Richardson 1968), was the dominant species throughout the sediment core. *Aulacoseira ikapoënsis* fluctuates between 20% (c. 1740 CE) and 75% (1865 CE) over the length of the core with a gradual increase from c. 1760 to 1990 CE, and a decline of $\sim 25\%$ in

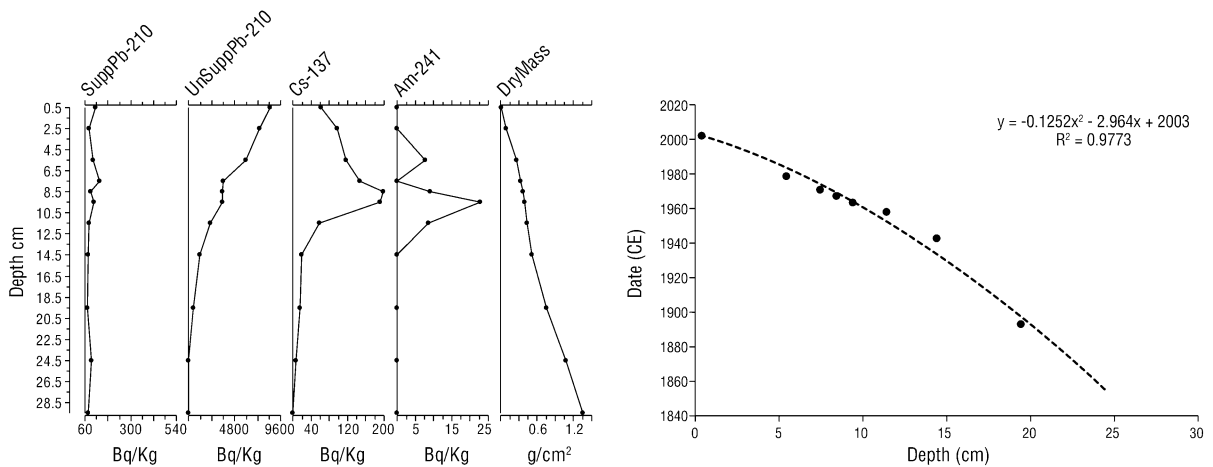


Fig. 2 Age-depth model for MAHO3 based on a second-order polynomial regression of dates obtained by ²¹⁰Pb analysis. Supported and unsupported ²¹⁰Pb concentrations (Bq/Kg) were also plotted against depth, alongside activities for radionuclides

¹³⁷Cs and ²⁴¹Am (Bq/Kg). The peak in ²⁴¹Am at 9.5 cm agrees well with ²¹⁰Pb-estimated age, using constant initial concentration (CIC) model (Dinsley et al. 2018), so this model was used to infer sediment ages

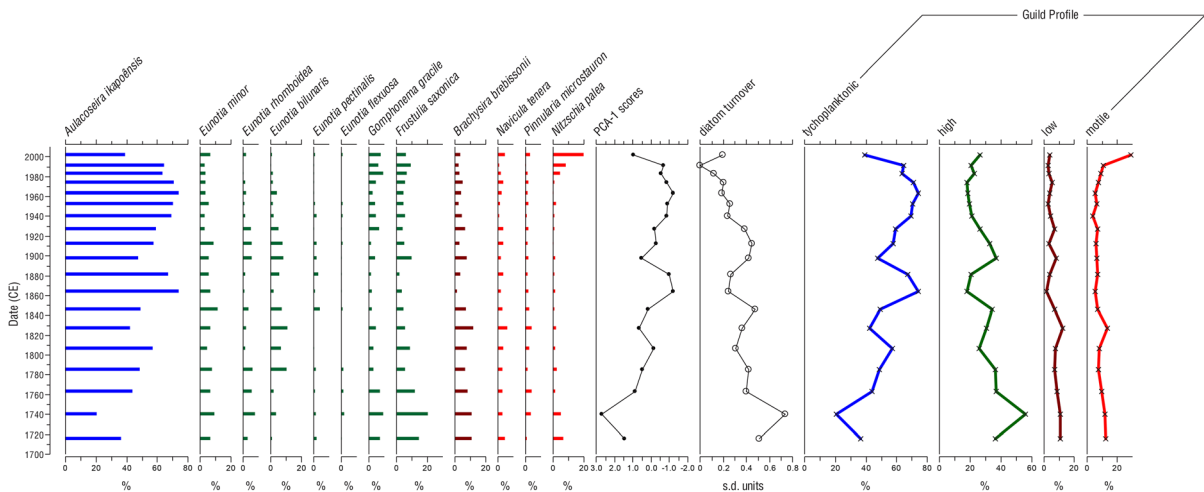


Fig. 3 Diatom relative abundances for common taxa (> 1%) found in MAHO3 plotted against date, given as ‘Date CE’, where CE = the common era. Species are colour-coded according to their designated guild (broadly after Rimet and Bouchez (2012)—see text for details) (blue = tychoplanktonic; green = high-profile; brown = low-profile; red = motile). In

addition, PCA and DCCA axes 1 sample scores are plotted, to show major composition change in the diatom flora. Diatom guild relative abundances for MAHO3 are colour-coded as for diatoms. Note that compositional sample scores and tychoplanktonic guild diatoms broadly follow complementary trends. (Color figure online)

the most recent sediment interval (Fig. 3). The low-profile guild also had only one representative, *Brachysira brebissonii* Ross in Hartley 1986. *B. brebissonii* was most abundant during the early part of the record, peaking at ~ 12% (c. 1825 CE), before declining to lower values, then fluctuating between 3 and 5% between c. 1950 and the top of the record. Important high-profile diatoms include *Frustulia*

saxonica Rabenhorst and *Eunotia bilunaris* (Ehr.) Schaarschmidt. *Frustulia saxonica* was most abundant (~ 20%) near the start of the record (c. 1740 CE), declining to lowest values of only ~ 2% at c. 1880 CE, before fluctuating at values < 10% for the remainder of the record. *Eunotia bilunaris* exhibited greatest abundance during the middle part of the record, between c. 1785 and 1925 CE. Motile diatoms

were fewer in number, but include *Nitzschia palea* (Kütz. W. Smith), which was present in highest abundances during the earliest and latest parts of the record, peaking at ~ 20% in the topmost sample. PCA axis 1 explains more than 40% of species variance. Species with highest axis 1 scores were *A. ikapoënsis* (−0.994), *F. saxonica* (+0.809) and *B. brebissonii* (+0.752). PCA axis 2 explains 28.1% of the variance in the dataset. Species with highest axis 2 scores included *E. bilunaris* (−0.881) and *N. palea* (+0.780). Diatom compositional turnover declines as the proportion of tycho planktonic diatoms increases (Fig. 3).

Organic geochemical analysis of Mahoma sediments reveals distinct changes in carbon and nitrogen dynamics, especially after 1960 CE (Fig. 4). TOC values range between 44 and 54%, with lowest values occurring in most recent decades. C/N ratios range from 9.1 to 14.6 and show an overall gradual decline from the base of the core until c. 1985 CE, after which they show a small increase. $\delta^{13}C_{org}$ values fluctuate between − 26.4 and − 25.4‰ for most of the record, but then show a marked decline, from about − 26.1 to − 28.4‰ between 1985 CE and the top of the core. $\delta^{15}N_{org}$ values fluctuate between − 1.9 and − 0.4‰.

After an initial decline, $\delta^{15}N$ values increase from c. 1770 CE to a maximum value of − 0.4‰ at 1890 CE, where they remain high until they decline from the early 1970s to the top of the profile (Fig. 4).

Regional comparisons

Temporal trends in diatom assemblages for Lakes Bujuku and Lower Kitandara were previously published by Panizzo et al. (2008) and McGlynn et al. (2010), respectively, and here we assign these species to their morphological guilds. The dominant taxa in both lakes were tycho planktonic fragilarioids (including *Staurosira construens*, *S. construens* var. *venter*, *Staurosirella pinnata*, and *Stauroforma exiguiformis*), with the low-profile diatom *Achnanthisidium minutissimum* present in all samples at lower abundance. Diatoms in the tycho planktonic guild dominate the flora of all three study lakes, whereas motile diatoms are least abundant (Fig. 5). The low-profile diatom guild is sub-dominant in the two glacial lakes, whereas high-profile diatoms form the sub-dominant guild at Lake Mahoma. At Lake Mahoma, tycho planktonic diatoms increased from the early eighteenth century to the late 20th century at the expense of high-profile

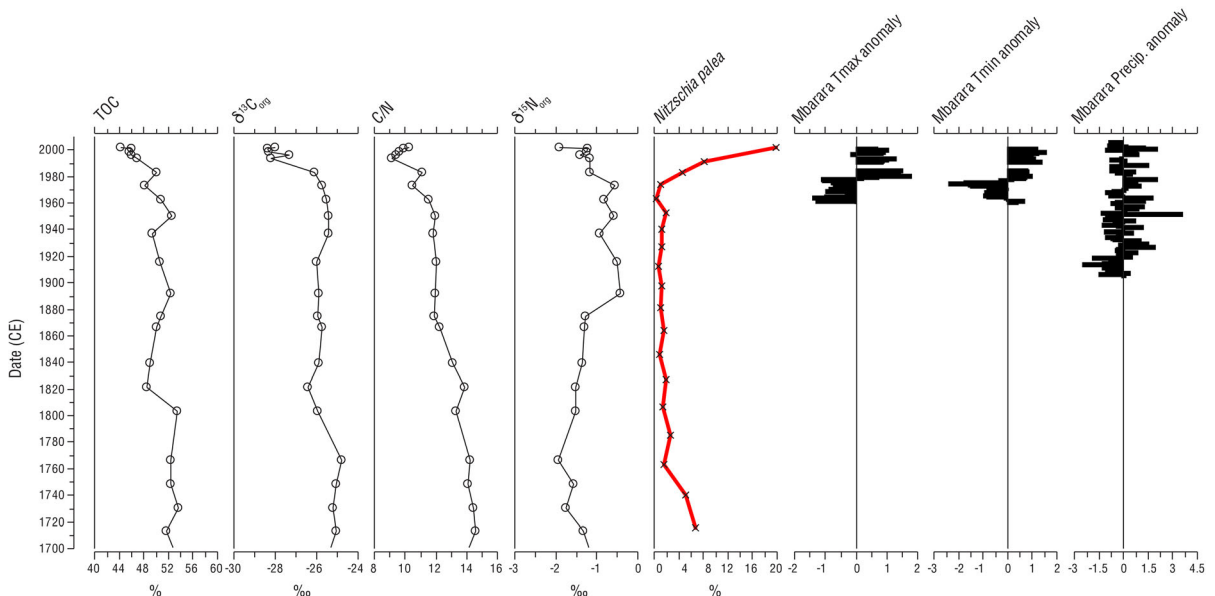


Fig. 4 Geochemical profiles of total organic carbon (TOC), $\delta^{13}C_{org}$, C/N ratios and $\delta^{15}N_{org}$, for Lake Mahoma, with all data from Russell et al. (2009). Plotted alongside the organic geochemical records are relative abundances of the obligate nitrogen-heterotrophic diatom *Nitzschia palea*. To the right of

the figure, standardised anomalies in annual mean maximum and mean minimum air temperature (Taylor et al. 2006), and annual mean precipitation (Taylor et al. 2009), from Mbarara meteorological station in western Uganda [0° 36' S, 30° 41' E] for the late twentieth century

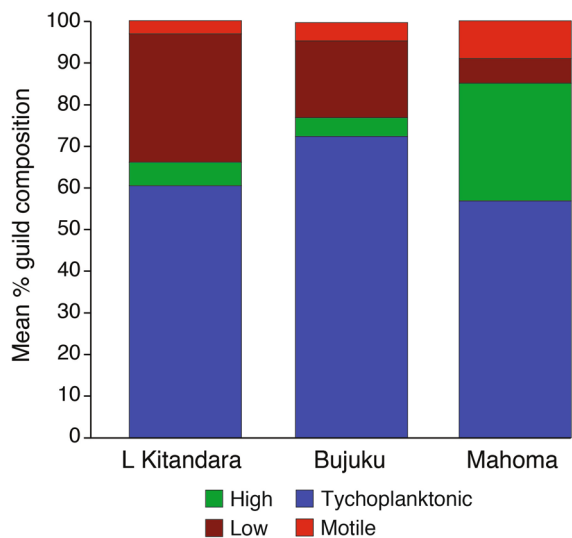


Fig. 5 Mean relative abundance for each diatom guild for each lake, calculated from samples in each of the three diatom cores. Original diatom data for Lakes Lower Kitandara and Bujuku are taken from McGlynn et al. (2010) and Panizzo et al. (2008), respectively. Tychoplanktonic taxa dominate each core, although for Lake Mahoma, this guild consists solely of *Aulacoseira ikapoënsis*, whereas small *Fragilaria sensu lato* tychoplanktonic species dominate the two alpine lakes. High-profile diatoms form the sub-dominant guild at Lake Mahoma, whereas low profile diatoms form the sub-dominant guild at Lakes Lower Kitandara and Bujuku

diatoms (Fig. 6). In the glacial lakes, however, as tychoplanktonic diatoms increased from the late nineteenth century to the early twenty-first century, this was generally at the expense of declining low-profile diatoms. Motile diatoms showed little change at Lakes Bujuku and Lower Kitandara, but tended to decline at Lake Mahoma between the early eighteenth century until c. 1940 CE, before increasing in the most recent decades, especially in the uppermost sample (Fig. 5).

Compositional turnover, estimated as weighted averages of the diatom scores for each sample (Felde et al. 2019), shows an overall decrease at all three lakes, although at Lower Kitandara turnover also increased temporarily during the middle of the last century (Fig. 7). All lakes exhibited lowest turnover between 1980 and 1990 CE (Fig. 5). Because we constrained the samples using only their ^{210}Pb -modeled ages, the gradient length of DCCA axis 1 represents the total amount of compositional change along each temporal gradient (standard deviation (SD) units), estimated by taking the range of CaseE values, *sensu ter Braak and Šmilauer (2012)*, presented in CANOCO5.

$\delta^{15}\text{N}_{\text{org}}$ values at Lake Mahoma initially decrease at the base of the profile, before increasing from c. 1770

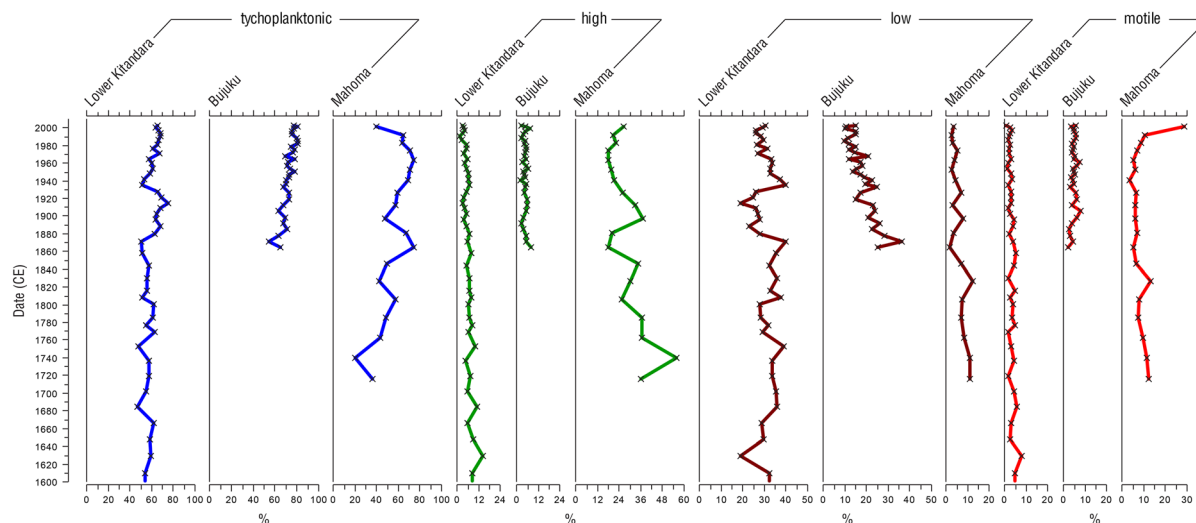


Fig. 6 Trends in relative abundance of each of the four diatom guilds plotted for each of the three lakes, against time (Date CE). Main trends highlighted include increasing tychoplanktonic guild through time, against declining high-profile guild diatoms

in Lake Mahoma, and declining low-profile guild diatoms in the two alpine lakes. Motile guild diatoms are generally low at all three sites, but show a marked increase at Lake Mahoma during the late twentieth century

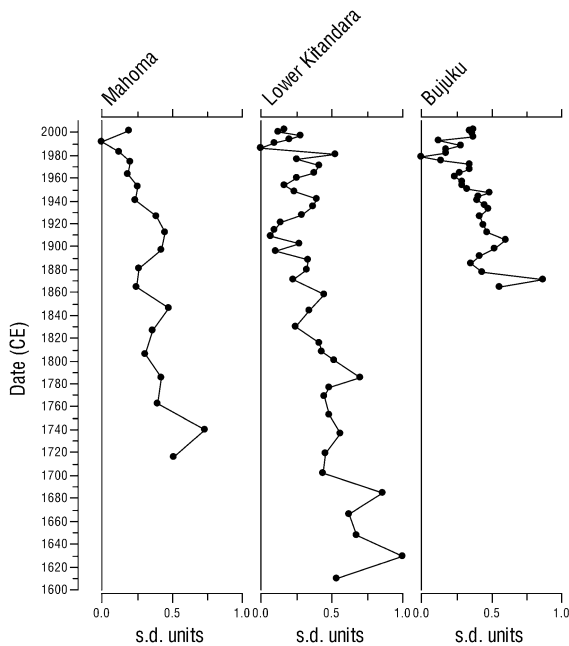


Fig. 7 Trends in diatom compositional turnover at each of the three study sites using detrended canonical correspondence analysis (DCCA). Individual sediment sample scores are weighted averages of the diatom scores (Felde et al. 2019). Since c. 1865 CE, compositional turnover broadly declines at each lake, although at Lower Kitandara turnover increases once more during the middle of the last century. All lakes exhibit a minimum in turnover between 1980 and 1990 CE

to 1890 CE (Fig. 4). Highest $\delta^{15}\text{N}_{\text{org}}$ values were observed from c. 1890 to 1975 CE, before declining to the lowest value, -1.9‰ , at the top of the profile. C/N

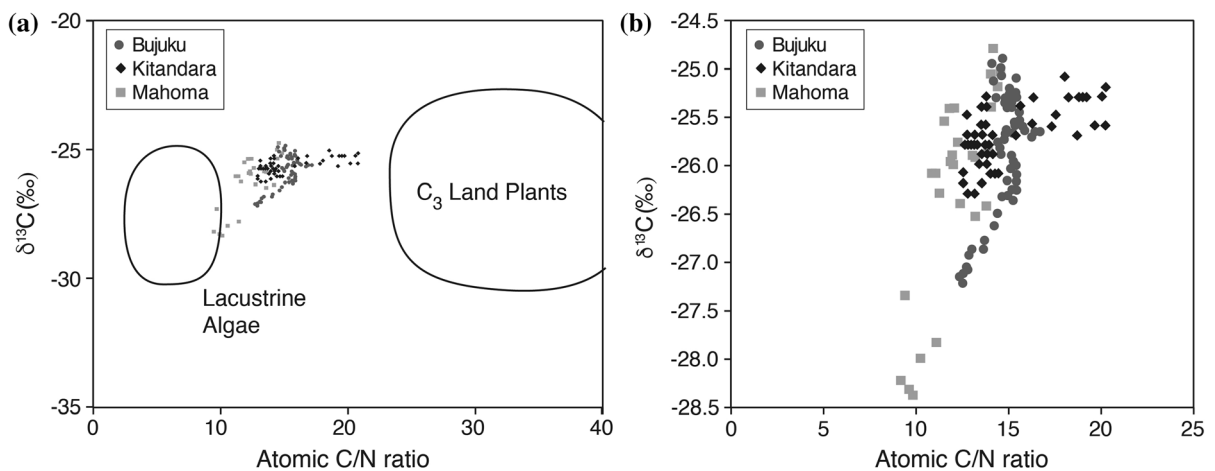


Fig. 8 C/N ratios versus $\delta^{13}\text{C}$ values for Lakes Mahoma, Bujuku and Lower Kitandara. Data highlight autochthonous and allochthonous sources of carbon. The older sediments of the

ratios for sediments from all three lakes range from 9.1 to 20.4, and $\delta^{13}\text{C}_{\text{org}}$ values range from -28.4 to -24.8‰ (Fig. 8). The oldest sediments from highest-altitude Lower Kitandara, has highest C/N ratios, whereas the youngest sediments from lowest-altitude Lake Mahoma have the lowest $\delta^{13}\text{C}_{\text{org}}$ values.

Discussion

Lake Mahoma

The diatom flora of Lake Mahoma is consistent with it being an acid, possibly dystrophic lake (Richardson 1968; Eggermont et al. 2007; Russell et al. 2009). For example, *Frustulia saxonica* and *Brachysira brebissonii* both grow well in the benthos of acid, humic-stained waters (Krammer and Lange-Bertalot 1986; Camburn and Charles 2000), whereas *Eunotia rhomboidea* Hustedt and *Eunotia bilunaris* are both acidophilous (Krammer and Lange-Bertalot 1991a; van Dam et al. 1994). The flora is dominated in particular by *Aulacoseira ikapoënsis*, a pan-tropical diatom found in warm, usually acidic lakes with low conductivity. Its dominance in Lake Mahoma has been known for more than half a century (Richardson 1968), and here we show for the first time that it has been a major component of the diatom flora since at least the eighteenth century (Fig. 3). Like many other *Aulacoseira* species, *A. ikapoënsis* forms filamentous

longest core from Lake Lower Kitandara have greatest allochthonous input, during the period of the Little Ice Age

chains that increase its buoyancy, which helps it to maintain position in the lake's photic zone. Autecological information for this species is sparse, although species in the genus *Aulacoseira* are known to have high silicon resource requirements, especially in African lakes (Kilham et al. 1986). However, as delivery of siliciclastic material to Lake Mahoma is low (as inferred from high TOC values), and did not vary much over this time period (Russell et al. 2009), demand for Si was likely met through remineralisation of Si in the water column, and groundwater sources. Periods when the abundance of *A. ikapoënsis* declined (e.g. 1860–1910 CE) may have been a consequence of resource limitation, e.g. when silica was being utilised by other species (*E. bilunaris*) or light was limiting because of high concentrations of humic-stained waters, as indicated by high abundances of *F. saxonica* at the base of the core. Trends in PCA axis 1 sample scores and the tychoplanktonic guild are highly correlated (Fig. 3) ($r = -0.735$), indicative of the close relationship between variation in Mahoma diatoms and the gradual shift away from high-profile guild diatoms to a tychoplanktonic flora, until the most recent decades, when *A. ikapoënsis* gave way to increasing *Nitzschia palea*. Although changes in individual species can be quite subtle, the decline in the high-profile guild suggests that either disturbance pressures in Mahoma increased, e.g. grazing (Passy 2007), or there was a gradual decline in nutrient and light availability for these high-stature diatoms (Bourassa and Cattaneo 2000). We tentatively suggest that increasing *A. ikapoënsis* either reflects deepening of Lake Mahoma, leading to the reduction in resources for many of the epilithic or epiphytic diatoms characteristic of members of the high-profile guild (Kramer and Lange-Bertalot 1991a; Passy 2007), or the availability of remineralised silica in the water column was increasing, allowing *A. ikapoënsis* to proliferate. In oligotrophic lakes such as Mahoma (Table 2; Eggermont et al. 2007), light can play as important a role in structuring algal communities as inorganic nutrients (Karlsson et al. 2009), and light may become limiting if lake depth increases. Evidence for higher lake levels may be supported by a small, but statistically significant trend in increased precipitation recorded at Mbarara meteorological station, just east of the Rwenzoris (Fig. 1) during the twentieth century (Fig. 4; Taylor et al. 2009), coincident with highest *A. ikapoënsis* abundances.

During the most recent decades, the increase in the motile species *N. palea* suggests nutrient concentrations are increasing in surface waters. As an obligate nitrogen-heterotrophic species, *N. palea* requires elevated concentrations of organically bound nitrogen to grow (van Dam et al. 1994). *N. palea* may therefore be responding to increased levels of nitrogen in the lake, which we discuss in more detail below, related to concomitant changes in the $\delta^{15}\text{N}_{\text{org}}$ record (Fig. 4). Given that certain *Nitzschia* species, including *N. palea*, have been found growing as epiphytes on the cyanobacterium *Microcystis* (Gessner 1956 in Richardson 1968; Flower 1982), they may obtain their N resources from this relationship. Motile species are generally more tolerant of nutrient-rich waters (Passy 2007), which ties in with observations of increased concentrations of nitrogen. If *N. palea* were indeed associated with increasing cyanobacteria, we may be observing competitive exclusion linked to high nutrient availability, as algae shifted from siliceous to non-siliceous communities (Larson et al. 2016).

Organic geochemical records in lake sediments are complex, and reflect long-term interactions between lakes and their catchments. Sediment total organic carbon (TOC) provides a first-order estimate of the amount of bulk organic matter that escapes remineralization (Meyers and Teranes 2001). TOC concentrations in Lake Mahoma sediments are very high, most likely because of a combination of very low rates of clastic mineral delivery to the lake (Russell et al. 2009), low remineralisation rates in the water column, and short oxygen exposure times at the sediment–water interface, linked to very low oxygen concentrations measured at depth in the lake (Eggermont et al. 2007). Together, these result in excellent burial efficiency (Sobek et al. 2009). TOC/total nitrogen (C/N) ratios can be used to discriminate among carbon sources. C/N values between 9 and 14 are indicative of mixed autochthonous and allochthonous carbon sources (especially from wetland soils) (Meyers and Teranes 2001), and the gradual decline in C/N values at lake Mahoma (Fig. 4) suggests that within-lake sources are increasingly important. This ties in with low, invariable inputs of siliciclastic material being delivered to the lake in recent centuries (Russell et al. 2009).

$\delta^{13}\text{C}$ analyses can also help us decipher carbon sources. The mean $\delta^{13}\text{C}_{\text{org}}$ value for Mahoma of -26.2‰ suggests TOC in the lake sediments was

derived mainly from C_3 plants, including algae (Leng and Marshall 2004). The decline in $\delta^{13}C_{org}$ values of almost 2.3‰ during the past few decades (Fig. 4) is greater than the potential Suess-effect decline of ~ 1.4 ‰, associated with fossil fuel emissions alone (Schelske and Hodell 1995). We rule out an enhanced supply of $\delta^{13}C$ -depleted dissolved CO_2 from increased soil respiration, because increases in catchment inputs are not supported by the C/N record (Fig. 4), or by previous measurements of siliciclastic inputs (Russell et al. 2009). Furthermore, unlike other montane regions in tropical Africa, phyto-sociological analyses have shown that human impact on forest ecosystems in the Rwenzori Mountains is low (Jacob et al. 2015), so we can rule out catchment vegetation change as well. The availability of CO_2 can also influence $\delta^{13}C_{org}$ of aquatic autotrophs, especially when productivity is enhanced (Leng and Marshall 2004), leading to higher $\delta^{13}C_{org}$ values, at least in large, deep lakes (Hodell and Schelske 1998). Although we can see from Fig. 4 that temperatures at the Mbarara meteorological station show a shift to positive anomalies during the past few decades (Taylor et al. 2006), in an acid, relatively low-productivity lake like Mahoma, CO_2 is abundant, so small changes in productivity may not result in a detectable change in the $^{13}C/^{12}C$ of the residual dissolved CO_2 pool, and will therefore not be evident in the $\delta^{13}C_{org}$ record. Alternatively, if concentrations of respired CO_2 in the lake are high, then depleted $\delta^{13}C_{org}$ values may come about as relative delivery of terrestrial organic matter declines, as suggested by declining C/N ratios. Different algal groups also have different $\delta^{13}C_{org}$ values. Therefore, because of the relative increase in *N. palea* during the past few decades (Fig. 4), it is possible that picoplankton such as cyanobacteria have increased in abundance as well. Carbon fractionation by picoplankton gives $\delta^{13}C_{org}$ ranges between -30 and -22 ‰ (Sakata et al. 1997), which is well within the values observed in our study, and may have helped drive $\delta^{13}C_{org}$ to lower values.

$\delta^{15}N_{org}$ records in recent lake sediments are widely used to reconstruct changes in the global nitrogen cycle associated with increases in atmospheric reactive nitrogen from fossil fuel combustion and agricultural activities. Atmospheric deposition fertilisation (e.g. by reactive nitrogen) has impacted the $\delta^{15}N_{org}$ of lakes worldwide (Holtgrieve et al. 2011), and may drive diatom changes observed in many alpine lakes (Hobbs et al. 2010; Catalan et al. 2013). The $\delta^{15}N_{org}$

signature is complex, with many interpretations (Botrel et al. 2014), but based on the low average sediment $\delta^{15}N_{org}$ values (mean = -1.2 ‰), Russell et al. (2009) suggested that the main source of N in Mahoma was *in situ* N-fixation. The increase in $\delta^{15}N_{org}$ at ~ 1880 may be consistent with enrichment observed in remote Northern Hemisphere lakes, caused by atmospheric N inputs (Holtgrieve et al. 2011). The recent (~ 1980) shift toward lower $\delta^{15}N_{org}$ values, however, could be linked to indirect evidence of increasing N-fixing cyanobacteria populations. The decline in $\delta^{15}N_{org}$ values is also concurrent with warmer air temperatures (Fig. 4), which may have led to increasing water temperatures and potentially strengthened stratification of the water column, both conducive to the growth of non-N-fixing *Microcystis* colonies (Jöhnk et al. 2008; Harke et al. 2016). The development of such conditions may explain the decline in planktonic diatoms and increase in motile species (*N. palea*), more commonly associated with cyanobacteria. These changes are likely influenced by climate-driven processes in lake stratification patterns, and a subsequent increase in autochthonous productivity from changing primary producers.

Regional comparisons

Previous limnological studies on lakes in RMNP demonstrated that they fall into two broad environmental categories: high-altitude, weakly acidic-neutral lakes with varying degrees of input from glacier meltwaters, and lower-altitude, acid, rather humic lakes, remote from any direct glacier input (Eggermont et al. 2007; Russell et al. 2009). Lakes Lower Kitandara and Bujuku are in the former group, situated in the Afro-alpine vegetation zone. Both are warm, polymictic lakes, exposed to strong diurnal temperature fluctuations, but which nevertheless stratify for short periods of time, i.e. several weeks or even months (Eggermont et al. 2007). Lower Kitandara and Bujuku are shallower than Mahoma (Table 1), and more oligotrophic (Table 2). They are also very transparent, so light is unlikely to limit diatom growth. Given their tropical, high-altitude location, however, photoinhibition from ultraviolet radiation may play a role in structuring their aquatic communities, especially when circulation is weak (Kinzie et al. 1998; Sommaruga 2001). For example, high UV radiation likely explains higher abundance of deeply pigmented

Cladocera in these lakes (Eggermont et al. 2007). The impact from UV radiation on these two alpine lakes is greater than at Lake Mahoma, in terms of amount of UV radiation hitting the lake, and because the higher-altitude lakes are above the tree line and so contain lower concentrations of protective dissolved organic carbon compounds (Sommaruga 2001), and have greater Secchi disc depths (Table 2). Continuous fluctuating conditions in both alpine lakes in an ecologically stressful environment, likely contribute to the dominance by small tychoplanktonic *Fragilaria* species *sensu lato* because they are *r*-strategists, well adapted to rapidly changing environments (Lotter and Bigler 2000).

Many small fragilarioid diatoms, such as *Staurrosirella pinnata* and *Staurrosira construens* that dominate lakes Bujuku and Lower Kitandara, are also classified as high-profile species because they initially form ribbon-like colonies, enabling them to access resources not available to low-profile species (Passy 2007), and in lakes, these colonies can break off and live freely as plankton in the water column. These ribbon-like colonies, however, make species with this growth form more susceptible to damage in benthic habitats, e.g. through strong currents or wind action. Their dominance at the higher-altitude sites may also reflect low grazing pressure, common in alpine lakes (Passy and Larson 2019), along with attenuated physical disturbance (Kingsbury et al. 2012). In both lakes, the increase in tychoplanktonic fragilarioid taxa during the twentieth century comes at the expense of the low-profile guild (Fig. 4), dominated by *Achnanthydium minutissimum* Kütz. Czarnecki (Panizzo et al. 2008; McGlynn et al. 2010), which suggests persistent, easier access to resources (e.g. light and nutrients) alongside declining disturbance (Passy 2007) during much of the twentieth century. Low-profile diatoms such as *A. minutissimum*, however, have been shown to be particularly sensitive to UV radiation (Vinebrook and Leavitt 1996), so an alternative hypothesis for this change in guild structure could be a response to changing UV in these lakes, perhaps linked to regional climate change, after the Little Ice Age.

All three lakes show unidirectional compositional turnover in the past 150 years, indicating that diatom communities were influenced by deterministic processes (Larson et al. 2016), possibly climate change since the end of the Little Ice Age. Given the nature of

the lake types involved, a deeper understanding of both the autoecology of key taxa is required, especially *A. ikapoënsis*, and of how resources (light and nutrients) are controlled by thermal stratification processes (Saros and Anderson 2015). At Mahoma, when abundance of *A. ikapoënsis* increases, species turnover declines (Fig. 3), which may be linked to a reduction in available resources for other species, as detailed above. An alternative explanation may be that if the lake has become deeper over the past few centuries, light may have become limiting for benthic communities. At Bujuku and Lower Kitandara, compositional turnover largely reflects gradual changes within the fragilarioid communities, and given that they comprise the same ecological guild, this suggests that although ecological function persisted through an “insurance effect,” species exhibiting stabilizing roles also demonstrate redundancy (Yachi and Loreau 1999). The very recent increase in compositional turnover at all three sites may indicate increasing resource availability.

Diatom turnover in the Rwenzori Lakes is rather minor, however (0.40–0.56 standard deviation (SD) units), in comparison to records from other alpine regions. Hobbs et al. (2010) reviewed a broad suite of alpine, arctic and forested boreal-montane lakes across North America and Greenland, and found that twentieth century diatom turnover in the 15 alpine lakes investigated ranged from 0.52 to 2.00 SD units, with a mean value of 1.01. Lin et al. (2018) investigated diatom compositional change in Lake Kanas, a large alpine lake in the Altai Mountains (NW China), and found very high diatom turnover during the past c. 100 years (1.72 SD units), whereas Wischniewski et al. (2011) investigated diatom changes in two alpine lakes on the southeastern Tibetan Plateau over the past

Table 3 Summary table for axes 1 results from detrended canonical correspondence analyses (DCCA) performed on each of our three study lakes

	Mahoma	Lower Kitandara	Bujuku
<i>Full profiles</i>			
Gradient length	0.41	0.56	0.40

Gradient lengths shown are based on the range of *CaseE* scores, *sensu* ter Braak and Šmilauer (2012), and measured in standard deviation (SD) units. A SD = 4 represents complete turnover of species composition

200 years, where diatom turnover ranged between 0.55 and 0.94 SD units. Diatom turnover in RMNP is likely low (Table 3) because these other lakes all experience strong seasonal gradients, linked to annual ice cover and summer stratification. There is extensive evidence to show that global warming is leading to reductions in ice cover worldwide, causing widespread, significant changes in diatom communities across cold regions, including the Arctic (Smol et al. 2005; Rühland et al. 2015), alpine regions in South America (Michelutti et al. 2015) and Europe (Catalan et al. 2013). The snow and ice fields of Kilimanjaro and the Rwenzori Mountains themselves are of course being severely impacted by global warming, although our data suggest that the Rwenzori lakes are only just beginning to show ecological responses, since the 1980s.

Finally, differences in carbon dynamics amongst the three lakes can be explained not only by differences in altitude, exposure and subsequent stratification, but also the time elapsed since lakes had glaciers in their catchment; lower amounts of TOC in sediments from Lakes Bujuku and Lower Kitandara are primarily associated with substantial amounts of siliciclastic input they receive from catchment glaciers (Russell et al. 2009). When we plot C/N ratios against $\delta^{13}\text{C}_{\text{org}}$ values for all three lakes (Fig. 8), some distinct features emerge. The oldest sediments from Lower Kitandara have highest C/N ratios, indicative of greater terrestrial carbon input during the seventeenth century. In contrast, Lake Mahoma had lowest $\delta^{13}\text{C}_{\text{org}}$ values of all the samples analysed, possibly caused by climate-enhanced lake stratification and inferred increases in cyanobacterial populations (Sakata et al. 1997). Unfortunately, we do not as yet have $\delta^{15}\text{N}_{\text{org}}$ records for Lakes Bujuku and Lower Kitandara, so interpretations are currently restricted to Mahoma.

Conclusions

The primary aim of this research was to investigate how lake ecosystems of different altitude in RMNP responded to environmental change over the past few hundred years. Diatoms appear to differ according to the two broad lake typologies identified by previous workers. Lower-altitude, deeper Lake Mahoma was dominated by pan-tropical *Aulacoseira ikapoensis*, whereas small *Fragilaria sensu lato* species

dominated the two alpine lakes. Nevertheless, all three lakes showed broadly similar directional compositional turnover regardless of altitude, which we suggest was caused by deterministic processes, such as regional climate change. At Lake Mahoma, lower recent values of both $\delta^{15}\text{N}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{org}}$ may be indicative of recent changes in algal composition in the lake, linked to higher surface water temperature and lake stratification. A more critical appreciation is needed regarding the range of non-siliceous algae taxa in these lakes. As of the 2003, the higher-altitude lakes had yet to cross a threshold leading to major change in the structure of their diatom communities. In the subsequent 17 years since cores were collected, however, global warming has proceeded apace and renewed research of these high-altitude sites is warranted to determine if the extent of Afro-alpine warming has yet affected the structure and function of these high-altitude aquatic ecosystems.

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