Aquatic ecosystem changes in a global biodiversity hotspot: evidence from the Albertine Rift, central Africa

[1]McGlynn, G., [2]Lejju, J., [3]Dalton, C., [4]Mooney, S.D., [5]Rose, N.L., [6]Tompkins, A.M., [7]Bannister, W., [7]Tan, Z. D., [4]Zheng, X., [8]Rühland, K. and [7,9]*Taylor, D

[1]Department of Geography, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.

[2]Department of Biology, Mbarara University of Science and Technology, P.O. Box 1410, Mbarara, Uganda

[3]Department of Geography, Mary Immaculate College, University of Limerick, Limerick, Ireland.

[4]School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney 2052, NSW

[5]Environmental Change Research Centre, Department of Geography, University College London, London, WC1E 6BT, UK

[6]Abdus Salam International Centre for Theoretical Physics, Trieste, Italy

[7]Department of Geography, National University of Singapore, Singapore 117570

[8]Department of Biology, Queen's University, Kingston, Ontario, Canada, K7L 3N6.

[9]Current address: School of Geography, University of Melbourne, Carlton, Victoria, Australia, 3053.

***Corresponding author:** David Taylor; Tel: +65 6516 7394; Fax: +65 6777 3091; email: geodmt@nus.edu.sg

Type of paper: Research Paper

Abstract

Aim

Determine the extent to which remote, high-altitude (Afroalpine) aquatic ecosystems in tropical Africa have been impacted by global and regional-scale environmental change processes.

Location

Two volcanic crater lakes (Bisoke and Muhavura) in the Afroalpine zone, Albertine (Western) Rift, central Africa.

Methods

Sediment cores were collected from Bisoke and Muhavura lakes and dated using radiometric techniques. A range of sediment based-proxies was extracted from the cores and quantified. Sedimentary data were subjected to statistical analyses that contributed to the identification of influential environmental variables and their effects on diatom assemblages, the determination of variations in spatial beta diversity and estimates of the rate of compositional turnover over the last c. 1200 years.

Results

Sediments from the two sites provide evidence of the sensitivity of remote, Afroalpine aquatic ecosystems to perturbation. Climate variability has been a major driver of ecological change, particularly at Bisoke Lake, throughout the c. 1200 year-long record, while Muhavura Lake has been directly impacted by and recovered from at least one volcanic eruption during this time. The effects of climatic warming from the mid- to late-19th century and especially from the late-20th century, possibly accentuated by atmospheric deposition-driven nutrient enrichment, appear increasingly in lockstep. Effects include changes in diatom community composition, increased productivity and compositional turnover, and biotic homogenisation (reduced spatial beta diversity) between the two sites.

Main conclusions

The two Afroalpine sites record changes in atmospheric conditions and their effects on diatom assemblage composition, particularly over the last c. 150 years. Drivers of these changes have the potential to disrupt ecosystems at lower altitudes in the Albertine Rift, including biodiverse areas of forest, and across tropical Africa more widely.

KEYWORDS: Afroalpine, atmospheric deposition, biotic homogenisation, climate change, eutrophication, pollution

1. INTRODUCTION

Global warming poses a significant threat to mountainous regions (Steinbauer et al., 2018). More rapid rates of temperature increase at higher altitudes when compared with lower elevations (MRI, 2015), together with substantial losses in range area as climates warm, pose significant risks to montane taxa (Moritz & Agudo, 2013). Although alpine ecosystems globally are at risk, those located in the tropics may be particularly sensitive and vulnerable to climate change (Zimmer et al., 2018).

Climate change is just one of several pressures faced by montane areas at low latitudes. Productivity in high-altitude ecosystems is typically strongly nutrient limited (Cárate-Tandalla, Camenzind, Leuschner, & Homeier, 2018) and is thus sensitive to changes in the availability of nutrients (Gütlein et al., 2017). One means through which nutrients might become more available in remote high-altitude locations is through increased atmospheric depositions of, for example, nitrogen (N) arising from human-induced disruptions to the global N cycle. Disruptions to the global N cycle can occur via the conversion of largely unreactive molecular N to a reactive state (reactive N [Nr]) that is available to biota before being returned to the atmosphere by microbial denitrification. The industrial-scale conversion of N into ammonia (NH_3)-based fertilisers has severely disrupted the global N cycle and led to dramatically increased environmental levels of Nr (Fowler et al., 2013), as have anthropogenic emissions of N_2O. Biomass burning is another, often overlooked, potential source of Nr (Benedict et al., 2017).

Despite their vulnerability, tropical high-altitude ecosystems are among the most poorly studied on Earth (Buytaert, Cuesta-Camacho, & Tobón, 2011). Consequently, little knowledge exists of the actual extent to which montane taxa are being impacted by global-and regional-scale drivers of change. One exception is the discovery that recent increases in air temperature may have driven ecological changes in tropical Andean lakes (Michelutti et al., 2015), although Fritz, Benito & Steinitz-Kannan (2019) suggest that the effects may be less evident in larger lakes, particularly when viewed in the context of sedimentary evidence spanning a millennium or more. Lakes can be sentinels of changing atmospheric conditions and their effects (Catalan et al., 2013), especially when located in small, isolated catchments above the treeline and with minimal direct anthropogenic disturbance. Even relatively small changes in temperature and nutrient availability can have profound impacts on key physical and biological processes that go on to be recorded in lake sediments. As Michelutti et al. (2015) demonstrate, lake sediment records can be particularly valuable in the absence of, or as a complement to, direct measurements of environmental changes and their effects.

Here we present new sedimentary evidence of aquatic ecological changes over the last c. 1200 years from the Afroalpine zone in the highly biodiverse Albertine, or Western, Rift that forms the western perimeter to equatorial eastern Africa. The Albertine Rift supports one of 35 global biodiversity hotspots (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011) and has become an important focus for biodiversity conservation efforts (Plumptre et al., 2007). Aside from climate change (Ponce-Reyes et al., 2017), high levels of species diversity and endemism are directly threatened by human activity, with human population densities more than 300% greater than the mean for sub-Saharan Africa (Burgess et al., 2007). More insidious processes, such as variations in land values, declining agricultural productivity and political insecurity, also pose a significant threat to biodiversity in the region (Ayebare, Plumptre, Kujirakwinja, & Segan, 2018; Hochleithner, 2017; Salerno et al., 2018). To date, however, there is little if any empirical evidence of biotic responses to current environmental changes at high-altitude in the Albertine Rift, or indeed cool- and low-nutrient adapted taxa associated with the Afroalpine belt more widely.

This paper provides evidence of the extent to which climate change and possibly also pollution from atmospheric deposition, are impacting aquatic biota in two remote, high-altitude crater lakes in the Virunga volcanoes, Albertine Rift, within the context of the last 1200 years or so of ecological variability. The remains of diatoms (Bacillariophyceae) preserved in sediment are a particular focus; diatoms have been widely used to track changes in water quality and as indicators of biological condition more broadly (Battarbee et al., 2001; Hausmann, Charles, Gerritsen & Belton, 2016). The sediment records obtained provide a basis for assessing biodiversity trends over an expanded period of time that extends to before the onset of the current period of significant, widespread human impacts, or the proposed Anthropocene Epoch (McGill, Dornelas, Gotelli & Magurran, 2015; Steffen, Grinevald, Crutzen, & McNeil, 2011). In addition to being important in their own right, the two high-elevation lakes may also be viewed as sentinels of broader-scale, atmosphere-transmitted ecological pressures in the Albertine Rift.

2. MATERIALS AND METHODS

2.1 Study area and sites

The Virunga volcanoes, rising steeply from a relatively undulating volcanic plain to elevations well over 4000m above sea level (asl), form part of the Virunga Conservation Area (Fig. 1). Located close to the Equator, variations in day length and monthly mean temperatures are relatively minor. Significant seasonal variations in rainfall exist, reflecting the annual migration of the tropical rain belt and the position and strength of the Congo Air Boundary. The main wet season usually occurs during April-June, when airflows from the

Atlantic Ocean predominate, and is followed by a second, shorter, wet season in November-December, during which the Indian Ocean has a greater influence. Temperature decreases with altitude, while rainfall levels peak at about 2300-3000m and low clouds and mist are common occurrences on mountain summits (Hedberg, 1964; Spinage, 1972). At the highest elevation strong diurnal variations in temperature occur, with day-night differences dampened at times by relatively high humidity.

Vegetation on the volcanoes has a marked altitudinal zonation in response to altitude-related changes in climate conditions. Lower montane forest characterises slopes up to an altitude of c. 2500m asl, and likely extended over much of the volcanic plain prior to the onset of Late Iron Age clearances in the region around 1000 years ago (Taylor, 1990). Bamboo thickets are present above the lower montane forest, while Ericaceous vegetation occurs between c. 3000m asl and 3600m asl. Afroalpine vegetation is found on the highest mountains above c. 3600m asl with more sheltered locations hosting the most mesic, shrubby vegetation cover. Short alpine grassland and areas of bare rock are found on the highest, exposed slopes.

The two study sites are crater lakes at the summits of Mount (Mt.) Bisoke and Mt. Muhavura, hereafter referred to as, respectively, Bisoke Lake and Muhavura Lake. Both are located above the treeline in the Afroalpine zone in small, clearly defined and topographically-closed catchments that are largely undisturbed by the direct effects of human activity. Bisoke Lake has a much greater volume and is set within a far larger crater than Muhavura Lake (Table 1). Moreover, Muhavura Lake (4127 m asl) has an elevation around 400m greater than Bisoke Lake. Vegetation in the crater on Mt. Bisoke is characterised by a dense cover of shrubby Afroalpine vegetation, notably giant lobelia (e.g. *Lobelia stuhlmannii* Schweinf. ex Stuhlmann and *L. wollastonii* Baker f.) and groundsels (*Dendrosenecio johnstonii* (Oliv.) B.Nord). Alpine grasses (members of the Pooideae), sparse giant lobelia and groundsels and areas of bare rock characterise the geomorphologically more subdued crater at the summit of Mt. Muhavura.

2.2 Field sampling

Sediment core BIS3, 110cm long, was extracted from the deepest part of Bisoke Lake in 2010 using a tapper corer (Chambers & Cameron, 2001). BIS3 was sampled in the field in 1cm-thick slices. The total depth of the longest of several sequences of sediments extracted from Muhavura Lake in 2008 was 247cm. This paper focuses on the uppermost 120cm of this sequence, comprising a short 37cm-long core (MUH4) obtained using a Renberg gravity corer and the uppermost part of core MUH2. Core MUH2 was extracted in 1m-long sections using a modified Livingstone piston corer, with each section off-set to provide a c. 50cm overlap between sections. Both BIS3 and MUH4 captured the sediment-water interface. Unfortunately a 13cm-long section of sediment between the base of MUH4 at 37cm and the top of MUH2 at 50cm below the surface was not collected. Core sections comprising MUH2 were packaged and shipped entire for subsampling in 1cm-thick slices in the laboratory. Overlaps between sections were verified, post collection, using sedimentary data (McGlynn, Mooney, & Taylor, 2013). All cores and core samples were stored at 2 °C prior to laboratory analyses.

2.3 Sedimentary analyses

2.3.1 Chronological control and estimated sediment accumulation rates (SAR)

Chronological control and estimated SAR were established using radiometric dating techniques and BACON, software that enables the systematic establishment of sediment age-depth relationships using a Bayesian, hierarchical model with autoregressive gamma processes (Blaauw & Christen, 2011). Down-profile variations in ^{210}Pb and application of the Constant Rate of Supply (CRS) model (Appleby & Oldfield, 1978) were used to date the uppermost parts of the sediment sequences from both sites. Measurements of ^{137}Cs activity, and what is assumed to be the 1963 CE peak (9.5cm in BIS3 and 15.5cm in MUH4), provided independent validation of the CRS model. Changes in abundances of the isotopes were established for MUH4 and the upper part of BIS3 by direct gamma assay using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector (Appleby, 2001). Thirteen AMS ^{14}C dates were obtained on plant macrofossil fragments (initially identified as terrestrial in origin) extracted from BIS3 and MUH2. All conventional ^{14}C dates, expressed along with their 2σ errors, were calibrated using INTCAL13 (Reimer et al., 2013). Bayesian models can take into account prior knowledge. This allowed the age-depth model for Muhavura Lake to take account of a 10cm thick tephra-rich layer (80-90cm) in MUH2, which was regarded as having been deposited within a single year. Thus sediment deposited between 80 and 90 cm in MUH2 was given the same age.

2.3.2 Sediment proxies

Percentage organic matter was measured via loss-on-ignition on 1cm-thick, contiguous sediment slices for BIS3, and on 1cm-thick sediment slices with at least a 2cm resolution for MUH4/MUH2 (Heiri, Lotter, & Lemcke, 2001). Spheroidal carbonaceaous particles (SCP) were enumerated in 16 samples from BIS3 in accordance with Rose (1994, 2008), and are expressed as fluxes (n particles cm^{-2} yr^{-1}). SCP, a component of black carbon, are released during the industrial-scale combustion of coal and fuel oil (Rose, Harlock & Appleby, 1999). The atmospheric deposition of SCP is generally assumed to be coherent over relatively small areas (Rose, Juggins, Watt, & Battarbee, 1994) and has been used as a proxy of acidifying substances associated with emissions from power stations and other power-intensive industries dependent upon coal and fuel oils (Heard et al., 2014). Samples from MUH4/MUH2 were not subjected to SCP analysis.

Percentage total organic carbon (%TOC), percentage total nitrogen (%TN) and ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes provide an indication of the source of organic matter fraction of sediments (Meyers, 2003; Talbot, 2001) and were determined for 55 and 29 samples from, respectively, BIS3 and MUH4/MUH2. Samples were analysed on either a Finnegan Delta plus XP gas source mass spectrometer (BIS3 and MUH4) or a Thermo Deltaplus Continuous Flow Isotope Ratio Mass Spectrometer (MUH2). Atomic C/N ratios were calculated based on %TOC and %TN. $\delta^{13}C$ values were calculated to the VPDB scale using a within-run laboratory standard, while $\delta^{15}N$ values were calculated relative to atmospheric N.

Diatom remains were concentrated in sediment samples in accordance with standard procedures (Battarbee et al., 2001); a total of 33 samples from BIS3 and 30 from MUH4/MUH2 were analysed. A minimum of 400 valves was counted in each sample (Battarbee et al., 2001). Diatoms were identified primarily in accordance with Gasse (1986), Krammer & Lange-Bertalot (1986-1991), Krammer (1992), Lange-Bertalot & Moser (1994), Cocquyt (1998) and Cocquyt & Jahn (2007) and are expressed in percentage terms (sum = total number of valves counted in each sample). Total diatom counts are also expressed as flux (number of frustules cm^{-2} year^{-1})

Preparation of pollen preserved in sediment samples, here used as a guide to changes in local and regional vegetation, followed Bennett & Willis (2001). Pollen data from a total of 28 samples were determined; 16 from BIS3 and 12 from MUH4/MUH2. At least 500 pollen grains and spores were identified for each sediment sample and expressed as percentages (sum = total pollen and spores, excluding damaged grains). Sediment samples were analysed for charcoal content, a proxy for vegetation fires. Fluxes in macro-charcoal (area of fragments >250µm, mm^2 cm^{-2} yr^{-1}), which may largely reflect local burning (Conedera et al., 2009), were quantified in 52 and 21 sediment samples from, respectively, BIS3 and MUH2/MUH4, using a modification of the wet-sieving method (Mooney & Tinner, 2011). Variations in micro-charcoal (area of fragments <140µm, cm^2 cm^{-3}), generally assumed to include material of long-distance origin and therefore to represent the burning of biomass over a wide area, were also determined on 12 samples from MUH4/MUH2 using a modification of the size-classing technique (Waddington, 1969).

2.4 Numerical analysis

Diatom-based biostratigraphic zones were identified by cluster analysis using constrained incremental sum of squares (CONISS) in the programme Tilia v 2.0-41 (Grimm, 1987) with chord distance (Cavalli-Sforza & Edwards, 1967) as the dissimilarity measure, and a broken-stick model to determine the optimum number of diatom zones (Bennett, 1996). Diatom remains were also used to infer past variations in pH (diatom-inferred pH, DI-pH) at both sites using a transfer function approach (Birks, 1995). A classic weighted averaging model with tolerance down weighting and inverse deshrinking was deployed. Since no diatom training set specific to Afroalpine lakes is available, the European Diatom Database (EDDI; http://craticula.ncl.ac.uk/eddi) was used as a basis for DI-pH estimations. EDDI includes alpine lakes in Europe, and sub-alpine lakes in eastern Africa, including medium altitude crater lakes in western Uganda (Mills & Ryves, 2012). Reconstructions of pH were performed using the software ERNIE (Environmental Reconstruction using the EDDI diatom database) v. 1.2. The use of transfer functions to infer individual environmental variables from among a complex of interacting forces has increasingly been questioned (Davidson, Bennion, Reid, Sayer & Whitmore, 2018). Here DI-pH is viewed cautiously in the absence of monitoring data and as one of several components of reconstructed variations in water quality.

Multivariate ordination was carried out on the diatom and selected environmental proxy data (% organic matter, %TN, %TOC, atomic C/N and $\delta^{13}C$, $\delta^{15}N$) (Constrained Correspondence Analysis, CCA) and solely on diatom data (Principal components analysis, PCA) from both sites using CANOCO 4.5 (ter Braak and Šmilauer, 2002). Only taxa that attained an abundance of 1% or greater in at least one sample were included in the CONISS, CCA and PCA analyses. Data were not transformed prior to analysis. CCA allows the fitting of possible gradients of environmental influences to ecological data (ter Braak, 1986), while PCA provides a means of summarising major trends in data. Because of the fragmented nature of meteorological records in the region and difficulties in accurately matching-up those data that are available with sedimentary evidence, variations in temperature and precipitation were not included in the analysis as potential environmental influences. All of the environmental variables included in the first CCA run scored Variation Inflation Factor (VIF) values > 20, with %N and %C scoring highest in, respectively, BIS3 and MUH4/MUH2. A second run of CCA with %N (BIS3) and %C (MUH4/MUH2) excluded resulted in VIF values < 20 for both sites.

CANOCO 4.5 was also used to carry out Detrended Canonical Correspondence Analysis (DCCA) on diatom data from both sites, including rarely occurring taxa. Diatom data were square root transformed. DCCA can be used to generate an estimate of total compositional turnover, measured as beta diversity and scaled in standard deviation (SD) units (Birks, 2007), where a SD of 4.0 represents a 100% turnover of taxa (Legendre & Birks, 2010; ter Braak & Prentice, 1988). Differences in diatom compositional turnover (i.e. beta diversity) at the two sites were estimated by DCCA within the entire stratigraphical record, and for intervals representing time periods before and after the mid-19th century (Birks, 2007; Smol et al., 2005). The latter division, which roughly marks the boundary between the pre-industrial and the industrial ages (Waters, Zalasiewicz, Williams, Ellis & Snelling, 2014) was included to determine the effects, if any, of anthropogenic activity. Aquatic acidification and eutrophication become widespread in northern Europe and North America from the mid-19th century (Battarbee et al. 2011; Wilkinson, Poirier, Head, Sayer & Tibby, 2014), while climatic warming and its effects on lake stratification and productivity over the last 150 years or so are recorded in Lake Tanganyika sediments (Cohen et al., 2016). In addition, variations in spatial beta diversity, or the degree of homogenisation, were determined based on a Sørensen distance metric and presence/absence data using the R package BETAPART and the function beta.multi (Anderson, 2006; Baselga & Orme, 2002), and following the method outlined in Wengrat et al. (2018). This involved first dividing the diatom data into pairs of samples, one from each site, in which the estimated age range of one sample overlapped with the other in the same pair. The latter requirement resulted in some data not being included in the analysis and a total of 16 pairs of samples (Table S1). A simple linear regression was used to estimate the relationship between estimated age of the sample pairs and their corresponding Sørensen distance metric using EXCEL.

3. RESULTS

3.1. Chronology

Results of all AMS ^{14}C, ^{210}Pb and ^{137}Cs analyses, the latter including the 1963 CE ^{137}Cs peak, were used as input to the age-depth modelling and are summarised in Tables S2 and S3 and Fig. S1. The seven AMS ^{14}C dates from Muhavura were reported in McGlynn et al. (2013), while the six from BIS3 have not previously been published. Results from the age-depth modelling are shown in Fig. S2. For the remainder of this paper, only the mean of the estimated range of ages for the sample depth, rounded to the nearest multiple of five, is quoted. Full information on the actual estimated ages and errors (2σ) of all sample depths, at 1cm resolution, is provided for both BIS3 and MUH4/MUH2 in Table S4. Accordingly, the estimated age of the base of BIS3 is 610 CE, while 120cm in MUH4/MUH2 corresponds to 805 CE. The gap in the sediment record between MUH4 and MUH2 equates to c. 200 years, from 1650 CE to 1860 CE. Sediment accumulation rates increase in both sequences from the beginning of the 20th century and particularly from the 1960s in BIS3 (Fig. S1).

3.2 Sedimentary and numerical analyses

Down-core variations in sedimentary data for BIS3 and the uppermost 120cm of sediment in MUH4/MUH2 are summarised in Fig. 2. Fig. 3 illustrates changes in relatively abundant and ecologically-significant diatom taxa referred to below.

Sediment cores from both lakes were largely dark-coloured, organic, fine grained with occasional inclusions of plant macrofossils. Their largely organic nature is supported in the laboratory measurements; levels of organic matter are generally above 40%: BIS3 mean = 48.5 ± 9.6%, range = 20.2 to 65.3%; MUH4/MUH2 mean = 50.9 ± 13.0%, range = 8.4 to 84.8 %. Levels of organic matter in BIS3 are noticeably higher, in general, in the uppermost part of the core (above c. 1860 AD) than lower in the sequence. Lowest organic matter values at both sites are from periods of accumulation of relatively inorganic sediment, dated 1530 CE to 1815 CE (Bisoke Lake) and 1170 CE to 1195 CE (Muhavura Lake) - the latter included a brown-coloured, tephra-rich layer. The tephra had a sugary textured appearance, either a blocky or flatter sharp/angular morphology and contained numerous micro-inclusions.

Mean atomic C/N ratios for BIS3 and MUH4/MUH2 are, respectively, 15.5 ± 2.5, ranging from 10.6 to 20.0, and 17.9 ± 1.1, ranging from 16.0 to 20.1. Levels of $\delta^{13}C$ vary throughout both sequences, although no trends are evident, with less variability in the data for BIS3 compared with the generally less depleted levels for MUH4/MUH2; BIS3 mean = -25.0 ± 0.3‰, range = -25.7 to -24.3‰: MUH4/MUH2 mean = -21.0 ± 1.16‰, range = -23.5 to -19‰. Values of $\delta^{15}N$ are generally a little more enriched in BIS3 than in MUH4/MUH2; BIS3 mean = 4.2 ± 0.5‰, range = 3.2 to 5.3‰: MUH4/MUH2 mean = 2.3 ± 0.7‰, range = 0.5 to 3.3‰. They also gradually increase up-core at both sites, and particularly from 1890 CE in BIS3 ($\delta^{15}N$ values show a similar trend in MUH4/MUH2). In both cases, $\delta^{15}N$ enrichment is particularly conspicuous from the 1960s to the present, where BIS3 mean = 5.0 ± 0.3‰ (based on five measurements, and representing a c. 20% increase over the overall mean) and MUH4/MUH2 mean = 2.9 ± 0.2‰ (based on nine measurements, and representing a c. 25% increase over the overall mean). SCP were not enumerated in any of the samples analysed from before 1985 CE in BIS3, after which they increase rapidly in the overlying five samples to peak at 169 particles cm^{-2} yr^{-1} at 2005 CE, before declining slightly again at the surface.

Diatom remains are well-preserved and abundant throughout both BIS3 and MUH2/MUH4. A total of 59 diatom taxa were enumerated in sediment samples from BIS3, with CONISS identifying zone boundaries at 1460 CE (BS1-BS2) and 1860 CE (BS2-BS3). Zone BS3 was further subdivided into two sub-zones (BS3a and BS3b), with the boundary dated 1985 CE. For MUH4/MUH2, 52 taxa were enumerated. Benthic diatoms, such as several *Eunotia* spp., are much more prominent throughout MUH4/MUH2 when compared with BIS3. CONISS identified three zones in the diatom record, with boundaries at 1880 CE (MU1-MU2) and 1990 CE (MU2-MU3). Both BIS3 and MUH4/MUH2 record substantial changes in diatoms over the last 150 years or so, particularly from the mid 1980s to the present. PCA axes 1 and 2 sample scores and DI-pH values also exhibit sharp changes in the late 19^{th} century. PCA axes 1 and 2 sample scores in MUH4/MUH2 also exhibit an abrupt oscillation around 1170-1180 CE, coincident with the aforementioned brown-coloured tephra-rich layer, a peak in macro-charcoal flux, and relatively low $\delta^{13}C$ and C/N values, ranging from -1.38 to -0.39.

Remains of *Aulacoseira alpigena* (Grunow) Krammer, *Brachysira brebissonii* R. Ross, *Frustulia rhomboides* (Ehrenberg) De Toni and *Eunotia* spp are relatively abundant throughout zone BS1 in BIS3. *B. brebissonii* is the most common taxon in zone MU1 in MUH4/MUH2, along with the benthic species *Pinnularia biceps* Greg and several small *Eunotia* species. Planktonic *Cyclotella ocellata* Pantocsek is not present in shallow Muhavura Lake prior to 1890 CE, and thereafter only sporadically and in low abundances (<1%) when it does occur. The taxon is, however, virtually omnipresent throughout BIS3, and initially increases in abundance in zone BS1 between 850 and 1150 CE. Marked changes in diatom composition occur across the BS1-BS2 zone boundary that are not evident in the diatom data in MUH4/MUH2, where the sampling resolution in this part of the sequence is relatively coarse; both *Stauroforma exiguiformis* (Lange-Bertalot) Flower, V.J. Jones & Round and *Nitzschia paleacea* Grunow becomes more abundant, while *A. alpigena* and *B. brebissonii* both decline. Overall diatom productivity in BS2 increases by c 50% across the BS1-BS2 boundary, but remains relatively low.

Several abrupt changes in diatoms occur across the BS2/BS3a boundary, dated 1860 CE. *S. exiguiformis* declines, while *F. rhomboides* and *B. brebissonii* show an initial increase in BS3a, and then a decline in BS3b. *N. paleacea* and *Gomphonema parvulum* (Kützing) disappear completely at the beginning of BS3a, and do not reappear. The abundances of

Luticola mutica (Kützing) D.G.Mann and *Diadesmis contenta* (Grunow ex Van Heurck) D.G.Mann increase in BS3a and still further in BS3b, the latter along with a second rise in *C. ocellata*, while overall diatom productivity shows a major increase from 1980 CE.

Zone MU2, beginning 1880 CE, is characterised by increased diatom flux, continued relative abundance of *B. brebissonii*, increases in several *Eunotia* species and in *F. rhomboides* and the first appearance of *G. parvulum*. The most marked change in diatoms in MUH4/MUH2 occurs across the MU2-MU3 zone boundary, dated 1990 CE, with an abrupt increase in *G. parvulum*, and a relative decline in most other taxa. Diatom accumulation rates remain relatively high throughout MU3.

More than 90 pollen and spore types were enumerated in BIS3 and MUH4/MUH2. Pollen data from the latter are described in full in McGlynn et al. (2013). The most substantial change in vegetation evident in the MUH4/MUH2 part of the record occurred at 1010 CE and comprises a decline in pollen from montane forest taxa. An increased abundance of micro-charcoal also occurs around the same time. The pollen record in BIS3 indicates similar changes in vegetation and fire activity more-or-less contemporaneously, from around 940 CE. BIS3 also records reduced abundance of pollen from some montane forest taxa during the period 1400 to 1760 CE, and concomitant increases in pollen indicating more open vegetation (notably Poaceae and *Dodonaea*). A peak in macro-charcoal flux around 1540 CE indicates burning of vegetation, possibly close to the lake. Further reductions in forest cover are evident in BIS3 over the last 150 years or so, while being more muted in MUH4/MUH2. Increased biomass burning in the region is also evident from the early 1900s, according to a steep rise in abundance of micro-charcoal in MUH4/MUH2. Evidence of sporadic, localised burning in the 1900s also exists, however, in the form of isolated peaks in macro-charcoal flux.

According to results of CCA (Fig. 4, Table S5), $\delta^{15}N$ and the atomic C/N ratio are the most influential of the selected environmental variables considered. When applied to the complete sets of diatom data, DCCA generated SD scores of 0.54 for BIS3 (33 samples, 640 CE to 2010 CE, Fig. 2a) and 1.16 for MUH4/MUH2 (30 samples, 885 CE to 2005 CE, Fig. 2b). A comparison of diatom compositional turnover between pre and post-industrial (~1850 CE) assemblages yielded DCCA gradient lengths of 0.63 SD (20 samples) and 0.68 SD (9 samples) for BIS3, respectively. A similar comparison for MUH4/MUH2 yielded DCCA gradient lengths of 1.14 SD for pre-industrial assemblages (20 samples) and 0.86 SD for post-industrial assemblages (10 samples). Sørensen distance metrics decline over time (R^2 = 0.7072, $p < 0.001$), indicating that diatom flora at the two lakes are becoming increasing similar (more homogenous) (Table S6). A step change (fall) in Sørensen distance metrics is evident between samples dating to before (7 pairs, mean = 0.52) and those dating to after (9 pairs, mean = 0.39) the mid-19th century.

4. DISCUSSION

Atomic C/N ratios and $\delta^{13}C$ values indicate a mixed plant source for the organic fraction of sediments accumulating at both Bisoke and Muhavura lakes, with algae, which are relatively N-enriched compared with more woody aquatic macrophytes and terrestrial plants, generally more prominent contributors to organic matter in BIS3 than MUH4/MUH2 (Meyers & Lallier-Vergès, 1999). Overall, diatom assemblages from the two sites indicate the maintenance of slightly acidic, low conductivity, oligotrophic conditions throughout the last c 1200 years (Holmgren, Ljung & Björck, 2012; Kilroy, Biggs, Vyverman, & Broady, 2006; Soeprobowati, Suedy, Hadiyanto, Luis & Gell, 2018). That said, sedimentary sequences from both Bisoke and Muhavura lakes record variations in aquatic conditions and their potential drivers that have important implications for biodiversity conservation, including the protection of remote sites and their biota.

Benthic diatoms are relatively prominent in MU1, and indeed throughout much of MUH4/MUH2, which is in keeping with the much shallower depth of Muhavura Lake. Two excursions in diatom assemblages are evident during the early part of the sedimentary record. The first, 850 CE to 1150 CE, consists of an increased relative abundance of *Cyclotella ocellata* in Bisoke Lake but not in the much shallower Muhavura Lake. Increases in the relative abundance of small planktonic, cyclotelloid taxa, such as *C. ocellata,* at the expense of small, benthic fragilarioid taxa and larger-celled diatom taxa have been widely linked to recent warming-induced, enhanced thermal stability and attendant changes in resource availability in deep alpine lakes (Rühland, Paterson & Smol, 2008, 2015; Michelutti et al., 2015; Saros, Northington, Anderson, & Anderson, 2016; Yan et al., 2018). Small cyclotelloid taxa have a high surface area to volume ratio that results in lower sinking rates (Ptacnik, Diehl & Berger, 2003), greater efficiency in nutrient uptake and light harvesting (Litchman, Klausmeier, Miller, Schofield & Falkowski, 2006) and, under ideal conditions, are often capable of prolific reproduction (Jewson 1992), providing them with a competitive advantage during prolonged periods of stratification (Winder and Hunter 2008; Yang, Stenger-Kovács, Padisák, & Pettersson, 2016). Increased abundances of *C. ocellata* in BS1 could thus reflect the effects of warmer temperatures associated with the Medieval Warm Period (MWP), which was a period of widely experienced warming and other climate-related anomalies in the region from about 950 CE to 1250 CE (Mann et al., 2009), including aridity (Alin & Cohen, 2003; Verschuren, Laird & Cumming, 2000). Hypothesized increased stability during the MVP, however, does not appear to have resulted in meromixis-induced, increased preservation of organic matter. The very shallow depth of Muhavura Lake and a greater propensity of mixing of the water column explains the absence of a peak in *C. ocellata* from this site.

The second excursion is dated c. 1180 CE at Muhavura Lake and is characterised by the presence of a 10cm-thick tephra-rich deposit, abrupt oscillations in PCA axes 1 and 2 sample scores, highly variable rates of diatom flux, large peak in macro-charcoal flux, dip in the proportion of pollen from montane forest taxa, e.g. *Podocarpus*, and relatively depleted $\delta^{13}C$ values, including the lowest measurement (-23.54‰) for the entire sequence. Collectively the data represent the effects of volcanic activity and deposition of a thick, tephra-rich layer in the crater at the summit of Muhavura, including vegetation fires. Deposition of tephra appeared to have little or no long-term impact on diatom assemblages at Muhavura Lake, based on similarities in composition of sediment samples that bracket the tephra-rich layer. The tephra is not evident in sediments recovered from Bisoke Lake. A brown-coloured tephra with a similar morphology to that recovered from Muhavura Lake was, however, recorded at c. 1150-1180 CE in a well-dated, 8m-long core of peat sediment from the crater swamp at the summit of Mt. Gahinga, fewer than 5km to the west of Mt. Muhavura, but only in much smaller amounts (<5% concentration). Several peaks in macro-charcoal flux clustered around 1200 CE (McGlynn et al., 2013) suggest that vegetation fires could have extended to Mt. Gahinga. The distribution of the tephra could reflect prevailing wind patterns at the time of eruption, which resulted in transportation of the majority of the volcanic debris to the east and south, rather than to the west. Lake Kivu to the south has a rich record of volcanic activity, in the form of thick layers of tephra that suggest an interval of around 500 years between major eruptions of Virunga volcanoes over the last c. 12,000 years (Wood & Scholz, 2017).

A change in conditions in Bisoke Lake is dated 1460 CE to 1860 CE (diatom zone BS2). The same period is not well covered in the sedimentary record from Muhavura Lake as it partially coincides with the gap in sediment between 1650 CE to 1860 CE. BS2 is characterised by relatively low diatom productivity together with increased PCA 1 axis sample scores and contributions of terrestrial plant material (based on relatively depleted δ^{13}C and enhanced C/N data) and inorganic matter to sediments. An increased relative abundance of *Stauroforma exiguiformis* and *Nitzschia paleacea*, and declines in the planktonic taxa *Aulacoseira alpigena* and *C. ocellata*, also characterise the zone. *S. exiguiformis* and *N. paleacea* are both benthic, periphytic taxa, while *A. alpigena*, is tolerant of low-light conditions often associated with deep water (Dalton et al., 2018). A fall in water level in Bisoke Lake, resulting in an expansion of littoral and benthic habitats, is indicated, and may have been linked to a period of climatic aridity in the region associated with the main phase of the Little Ice Age (LIA). This commenced in Africa from around 1500 CE (Nash et al., 2016), and was associated with reduced rainfall and lower lake levels throughout western parts of eastern Africa (Mills, Ryves, Anderson, Bryant & Tyler, 2014; Russell, Verschuren & Eggermont, 2007). Increased aridity may have arisen from a change in location and/or a weakening of convergence associated with the Congo Air Boundary (Nash et al., 2016). Climatically drier conditions from around the beginning of the 16th century have been suggested as a driver of changes in the pattern of human settlement and land use in what is now central and western Uganda (Taylor, Marchant & Robertshaw, 1999; Taylor, Robertshaw & Marchant, 2000).

Some coherence in timing of variations in diatom remains is evident at the two sites from the mid to late 19thth century, marked by the BS2-BS3a (1860 CE) and MU1/MU2 (1880 CE) zone boundaries, and from the late 1980s. Substantial changes in PCA axis 1 sample scores during the mid- to late-19th century track the most pronounced diatom assemblage shifts expressed in the sedimentary records of both lakes. A marked decline in the relative abundance of *S. exiguiformis* from 1860 CE suggests a deepening of Bisoke Lake, which accords with evidence from the region for generally increased rainfall, punctuated with occasional, prolonged droughts, from the late 19th century into the early 20th century (Nash et al., 2016). In addition to an increase in precipitation, an increase in the relative abundance of *C. ocellata* provides evidence of recent climatic warming from c. 1900 CE. This is consistent with findings from Lake Tanganyika (Cohen et al. 2016; Tierney et al., 2010). The effects of warming are less evident in the sediments from Muhavura Lake, where in addition to a continued predominance of *Brachysira brebissonii* and other benthic taxa indicative of slightly acidic waters, *Frustulia rhomboides* increases in abundance and *Gomphonema parvulum* makes its first appearance. Both *F. rhomboides* and *G. parvulum* are cited as tolerant of nutrient enrichment (Abarca, Jahn, Zimmermann & Enke, 2014; Bellinger, Cocquyt & O'Reilly, 2006; Montoya & Aguirre-Ramírez, 2013). Warmer conditions and a greater availability of nutrients may have brought about an increase in diatom productivity at Bisoke Lake that along with reduced decomposition, owing to a strengthening of stratification (Littke, 1985), could explain an increased contribution of organic matter to sediments from c. 1860 AD. Changes in pollen and micro-charcoal recorded at the two sites indicate a reduction in extent of montane forest at lower elevations and an increase in vegetation fires in the region.

Climate warming, possibly in tandem with increases in nutrient availability, appears to be the main driver of changes in the composition of diatom taxa in the late 1980s, highlighted by the BS3a-BS3b sub-zone (1985 CE) and MU2-MU3 zone (1990 CE) boundaries, with neither site showing evidence of the effects of a continent-wide reduction in rainfall from the 1980s (Nicholson, Funk & Fink, 2018). The abundances of *C. ocellata*, *Diadesmis contenta* and

Luticola mutica increase in the uppermost part of the sediment sequence from Bisoke Lake, while at Muhavura Lake *G. parvulum* rises to prominence. Diatom flux, while remaining high at both sites, increases at Bisoke Lake. As with *G. parvulum*, increases in abundances of *D. contenta* and *L. mutica* and relatively high diatom productivity and increased rate of sediment accumulation could represent responses to increased nutrient availability. *D. contenta*, characteristic of good water quality in general, is tolerant of low levels of pollution and has been recorded in mesotrophic to eutrophic waters in Brazil (Bere & Tundisi, 2011), while *L. mutica* is regarded as indicative of elevated nutrient levels (Gell, Sluiter, & Fluin, 2002).

Meteorological data, although scarce and often highly discontinuous when available, support recent warming in the region. The closest meteorological station to Bisoke and Muhavura lakes is located at Kabale, Uganda, around 30km to the east and c.1900m asl. Data from Kabale show a trend of increasing mean annual temperatures since the 1960s-1970s. A longer, more complete record from the meteorological station at Entebbe, even farther to the east in central Uganda, reveals an increase in mean annual temperatures of around 0.8-1.0 ºC since the 1930s. Recent warming in the Albertine Rift is also evident in satellite-derived proxy data from lakes Albert, Rukwa and Tanganyika, indicating a 0.2 to 0.6 ºC decade^{-1} increase in temperature of surface waters between 1985 and 2005 (O'Reilly et al., 2015), and in ERA-Interim and ERA-5 reanalysis data centred upon the Virunga volcanoes (Fig. 5).

Increases in aquatic productivity over the last 100 years or so, and particularly from the mid 1970s, are also evident at Lake Bujuku, 3960m asl on Mt. Rwenzori, also part of the Albertine Rift (Panizzo et al., 2008). Nitrogen can play an important role in limiting primary productivity in lakes in the tropics (Abell, Özkundakci, Hamilton, & Jones, 2012), and increasingly enriched $\delta^{15}N$ values, evident at both Bisoke and Muhavura lakes in the 20th

century, and particularly from the 1960s, may represent an increased availability of Nr and consequent relaxation of N-limitations on productivity. Such a scenario is supported by the results of CCA, which identified $\delta^{15}N$ as an important environmental influence over diatom variations at the two sites, particularly Bisoke Lake. This coherence is at variance with sediment records from some lakes in temperate latitudes, however, which show recent declines in $\delta^{15}N$ values (Holtgrieve et al., 2011). They are, however, in agreement with enriched $\delta^{15}N$ values in recently deposited sediments from Lake Wandakara, western Uganda (Russell et al., 2009).

Contrasting trends in $\delta^{15}N$ values between Bisoke and Muhavura lakes and lakes in more temperate latitudes could reflect differences in the main sources of N. Hu, Anderson, Yang & McGowan (2014) describe four main pathways through which nutrient enrichment of remote, alpine lakes can occur. Of these, and given their isolated location and the very small size of the catchments relative to lake surface area, enhanced, direct atmospheric deposition of Nr on the lake surface is the most likely cause of $\delta^{15}N$ enrichment in Bisoke and Muhavura lakes. The presence of SCP in sediments from Bisoke Lake from the mid-1980s is evidence of the importance of both long-distance transport and atmospheric deposition at these remote, mountain-top sites, with the nearest sources potentially several thousand km away. Moreover, SCP accumulation has been linked to eutrophication at a remote lake caused by N deposition from fossil-fuel sources (Pla, Monteith, Flower & Rose, 2009). Biomass burning in the region is, however, perhaps the most obvious source of atmospheric depositions of Nr at Bisoke and Muhavura lakes, in addition to fragments of charcoal. Vegetation fires occur annually on the African continent (van der Werf et al., 2017), and are an important source of atmospheric N, which dominates the N cycle in tropical Africa (Bauters et al., 2018; Galy-Lacaux & Delon, 2014). Biomass burning in the region has a long history (Jolly et al., 1997; Taylor, 1990), with sedimentary data from mid-altitude western Uganda indicating a sustained increase in vegetation fires from the mid-20th century (Colombaroli, Ssemmanda, Gelorini & Verschuren, 2014). Evidence from Muhavura Lake, and from the northern part of Lake Tanganyika (Cohen et al., 2005), places the onset of the most recent period of increased burning in the region even earlier, to the late 19th/early 20th centuries. The increasingly enhanced $\delta^{15}N$ values towards the top of the sediment records from Bisoke and Muhavura lakes also implicate increased biomass burning as an important source. Emissions from highly productive agriculture, characterised by high stocking densities and the use of large quantities of fertiliser, and from the combustion of fossil fuel – two other potential sources – tend to be associated with relatively depleted levels of $\delta^{15}N$ when compared with those from biomass burning (Felix, Elliott, Gish, McConnell, & Shaw 2013; Felix, Elliott, & Shaw, 2012; Kawashima & Kurahashi, 2011; Wang et al., 2017).

Major ecological changes are evident at both Bisoke and Muhavura lakes throughout the last c. 1200 years, and appear increasingly in lockstep from the mid 19th century and especially from the 1980s. Climate change has been and remains an important driver of variations in aquatic ecological conditions at Bisoke Lake in particular, perhaps because the higher elevation and much smaller size of Muhavura Lake have resulted in shorter-term (e.g. diurnal) and extreme episodic (e.g. volcanic activity) processes having a much greater influence on aquatic biota than climate pressures developing over a longer duration. The sedimentary evidence also suggests nutrient enrichment at both sites, and possibly also variations in pH. The release of CO_2 along with other magmatic gases directly into the water column together with the occurrence of products of weathering of volcanic material may have been local sources of acidification pressures (Balagizi et al., 2015; Pérez et al., 2011), in addition to atmospheric depositions of acidifying material originating in far more distant locations

According to the results of DCCA, ecological changes at Bisoke Lake include an acceleration in the rate of compositional turnover in diatom assemblages over the last c. 150 years that is less evident at Muhavura Lake. Results from Bisoke Lake are thus in keeping with increased diatom turnover rates reported for the same period for arctic and alpine lakes in the Northern Hemisphere, with Smol et al. (2005) attributing increased turnover primarily to climate warming, while Hobbs et al. (2010) propose increased deposition of Nr as a possible, additional, contributing factor. Furthermore, the distinctiveness of diatom flora at Bisoke and Muhavura lakes also appears to have reduced over time, experiencing a stepped fall when compared with conditions pre mid-19th century. Reduced spatial beta diversity is an increasing concern at present (Dornelas et al., 2014), and has been linked to both climate change and nutrient enrichment (Monchamp et al., 2018; Wengrat et al., 2018; Zwiener, Lira-Noriega, Grady, Padial & Vitule, 2018).

The ecological effects of recent warming, possibly in combination with increased availability of nutrients, presented here have coincided with a ramping-up of conservation efforts in the Virunga volcanoes (Robbins et al., 2011). The effects are unlikely to be restricted to Bisoke and Muhavura lakes, given the potential geographic scope of the drivers. Future research will determine the extent to which anthropogenic climate change and other large-area effects of transboundary pollution are impacting the Albertine Rift, including biodiverse-rich areas of forest at lower altitudes, and indeed tropical Africa more widely.

ACKNOWLEDGEMENTS

This research was funded by the Irish Research Council, with additional support provided by the National Geographic Society (research grant ‘Climate change, fire and ecosystem response on the Virunga volcanoes') and Mary Immaculate College, University of Limerick. Research permission was provided by the Uganda Wildlife Authority (UWA/TDO/33/02), the Ugandan National Council for Science and Technology (NS196) and the Rwanda Development Board. Thanks to Elaine Doyle (charcoal) and Patrick Carroll (pollen) for assistance with laboratory analysis of core BIS3, to Poonam Saksena-Taylor for assistance with figures, and to Prosper Uwingeli, Glenn Bush, May Murungi, Stephen Taylor and Yonah Okoth for help in the field.

Table 1: Geographical, physical and limnological information on Bisoke and Muhavura lakes (crater lakes at the summits of Mt Bisoke and Mt Muhavura). *asl = above sea level. +Note that in the absence of lake water quality monitoring data, information from surface sediment measurements is referred to. **Diatom-inferred value ~ see text for further information.

Lake	Latitude/ Longitude	Altitude (m asl*)	Lake surface area (m^2)	Max depth (m)	Lake catchment area (m^2)	Lake area:catchment area ratio	pH ($\pm 2\sigma$) $^{+, **}$	Atomic C:N ratio^{+}	$\delta^{13}C$ (‰)$^{+}$	$\delta\,^{15}N$ (‰)$^{+}$
Bisoke	29° 29’ 12” E/ 1° 27’ 40” S	3711	70695	21	124,315	0.57	5.83 (0.43)	16.72	-24.86	+5.26
Muhavura	29° 40’ 42” E/ 1° 23’ 0’’ S	4127	491	1.6	604	0.81	6.54 (0.45)	15.43	-20.08	+3.31

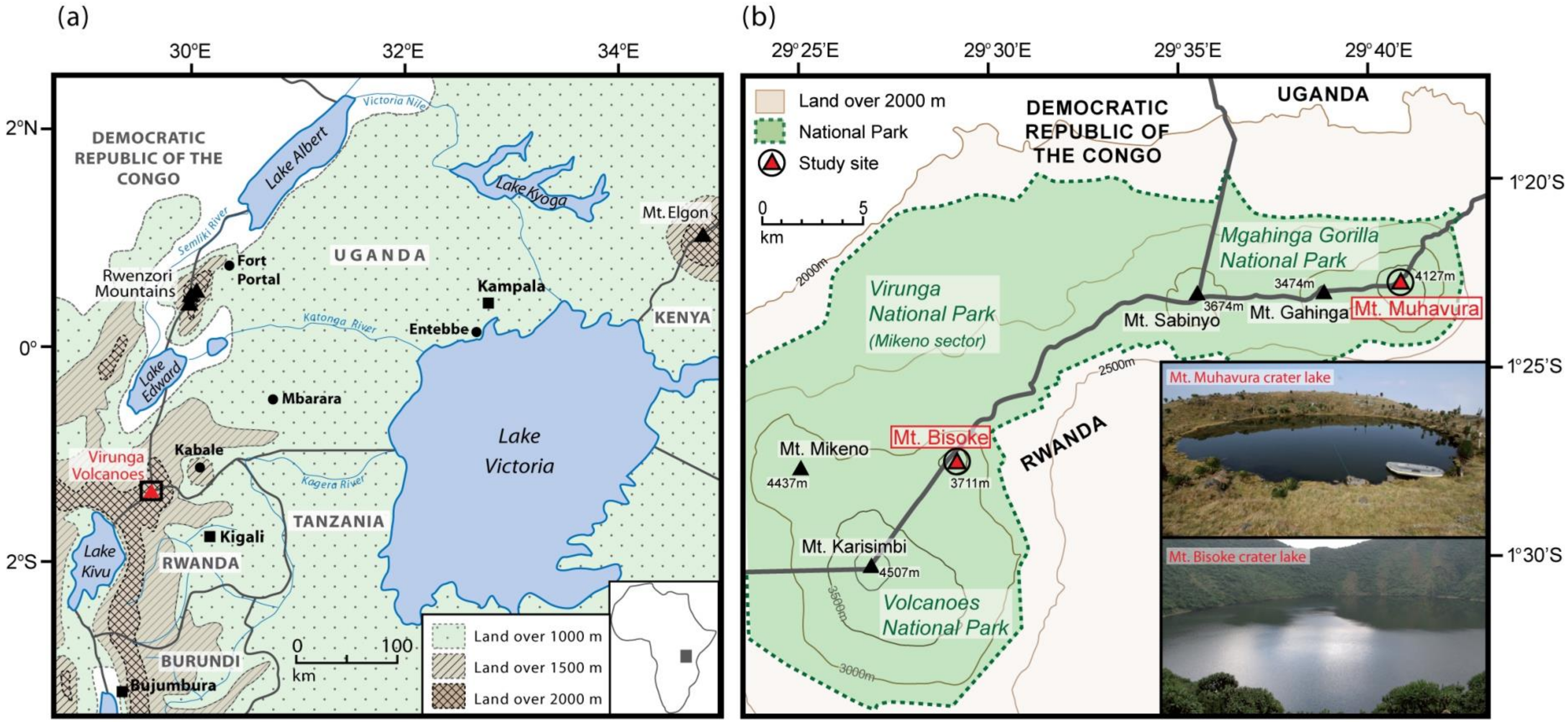
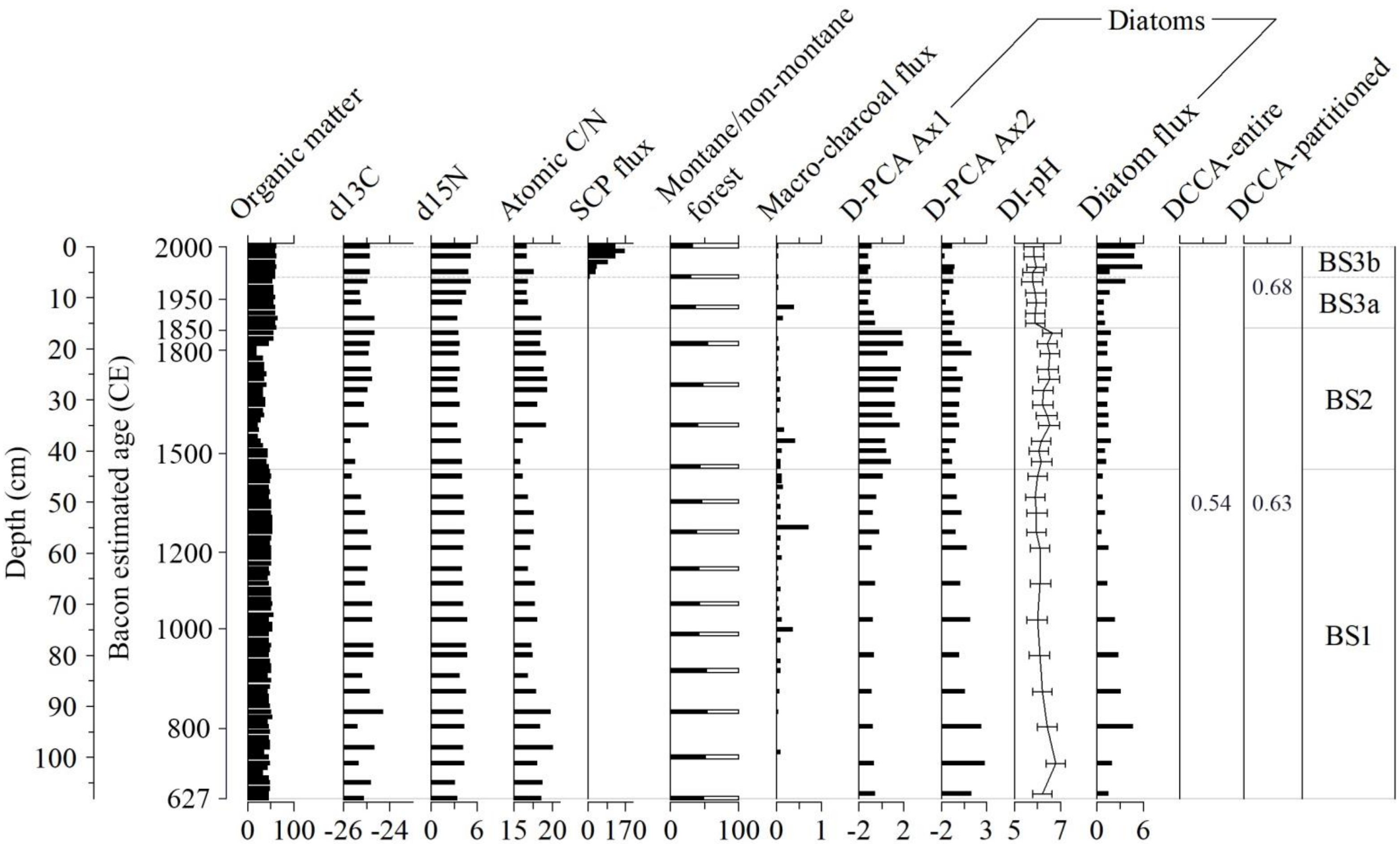


Figure 1: Location of the Virunga volcanoes in the Albertine Rift, which also accommodates the lakes of (from south to north) Tanganyika, Kivu, Edward and Albert, and forms the western boundary of eastern Africa (a). Location of Bisoke and Muhavura crater lakes on Mt Bisoke and Mt Muhavura within the Virunga Conservation Area, which comprises three national parks. All altitudes shown are in metres above sea level (m asl). The two photographs show the sample sites on Mt Muhavura (upper photograph) and Mt Bisoke (lower photograph). Note the very different sizes and vegetation cover in the two craters. Sediment cores were collected during several periods of fieldwork in 2008 (Mt Muhavura) and 2010 (Mt Bisoke).

a)



Diatoms
Organic matter
d13C
d15N
Atomic C/N
SCP flux
Montane/non-montane forest
Macro-charcoal flux
D-PCA Ax1
D-PCA Ax2
DI-pH
Diatom flux
DCCA-entire
DCCA-partitioned
Depth (cm)
Bacon estimated age (CE)
0
10
20
30
40
50
60
70
80
90
100
2000
1950
1850
1800
1500
1200
1000
800
627
0 100 -26 -24 0 6 15 20 0 170 0 100 0 1 -2 2 -2 3 5 7 0 6
0.68
0.54
0.63
BS3b
BS3a
BS2
BS1

b)

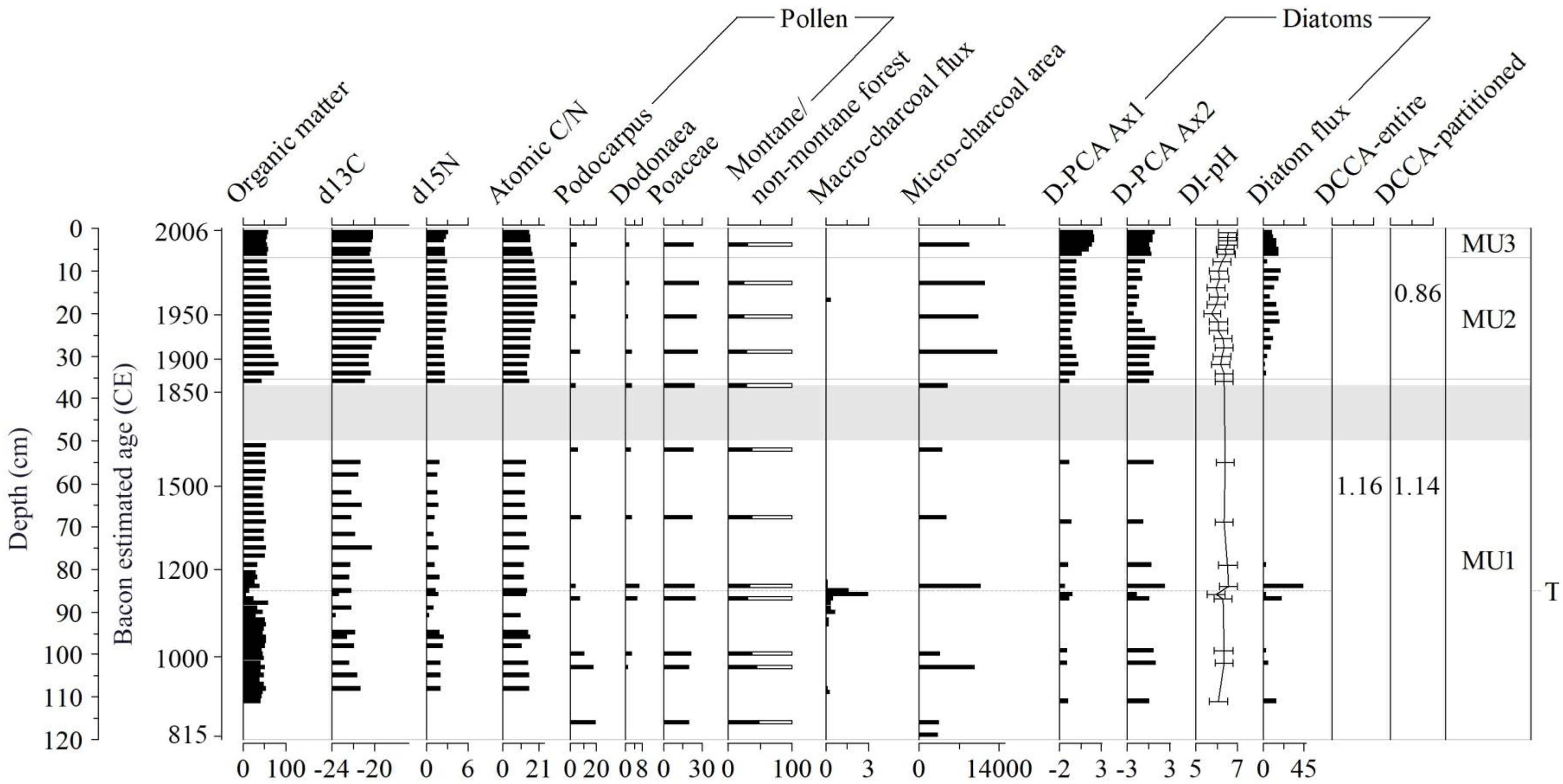
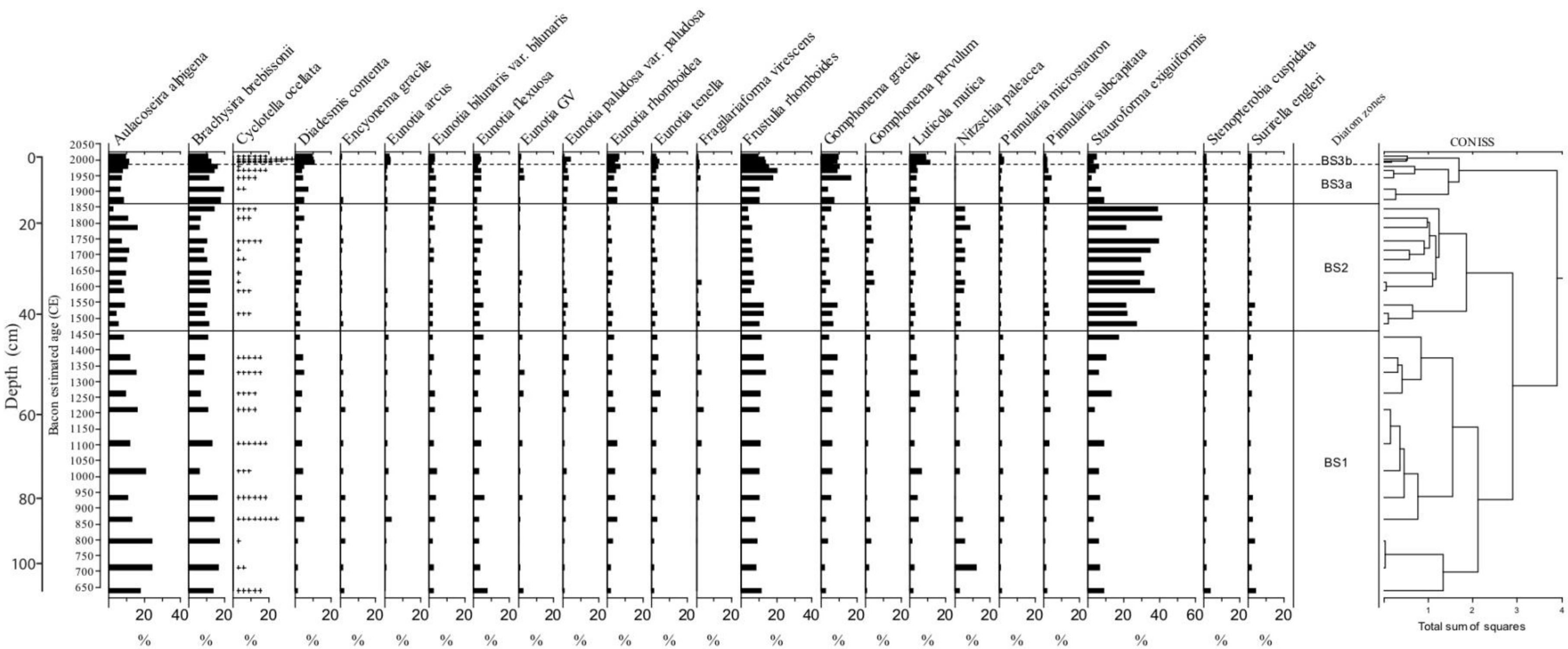


Figure 2: Selected sediment data for a) Bisoke core BIS3 and b) Muhavura cores MUH4-MUH2. Depth (cm) on the Y axis is depth beneath the lake bed. Estimated ages (expressed as Common Era, CE) are from BACON modelling based on AMS^{14}C, ^{210}Pb and ^{137}Cs activities (Table S4) (Blaauw & Christen, 2011). Note that units for organic matter and pollen data = %, d15N and d13C represent, respectively, δ^{15}N and δ^{13}C (units = ‰), units for diatom flux are x10^{6} valves cm^{-2} yr^{-1}. SCP = Spheroidal carbonaceous particles (flux = number of particles cm^{-2} yr^{-1}). Charcoal abundances are represented as Macro-charcoal (flux = mm^{2} cm^{-3} yr^{-1}) and Micro-charcoal (area = cm^{2} cm^{-3}). Results of data analysis are also

included in both a) and b) in the form of Principal components analysis (PCA) axes 1 and 2 diatom sample scores (axis 1 scores mainly reflect variations in the predominant diatoms, while axis 2 scores summarise variations in subdominant taxa) (D-PCA Ax1 and D-PCA Ax2), diatom-inferred pH (DI-pH) values, the results of Detrended Canonical Correspondence Analysis (DCCA) and diatom zone boundaries (BS1-BS3 and MU1-MU3) based on the results of constrained incremental sum of squares (CONISS) (Grimm, 1987) (see Figure 3). DCCA beta diversity results (standard deviation, SD, units) are provided for the full core (DCCA-entire), and for pre- and post-mid 19th century (DCCA-partitioned), and provide an estimate of compositional turnover. T = tephra. Note the missing sediment interval in b) between 1650 CE and 1860 CE (37cm to 50cm depth) and highlighted as grey-shading owing to non-retrieval of sediment during coring.

a)



Aulacoseira alpigena
Brachysira brebissonii
Cyclotella ocellata
Diadesmis contenta
Encyonema gracile
Eunotia arcus
Eunotia bilunaris var. bilunaris
Eunotia flexuosa
Eunotia GV
Eunotia paludosa var. paludosa
Eunotia rhomboidea
Eunotia tenella
Fragilariaforma virescens
Frustulia rhomboides
Gomphonema gracile
Gomphonema parvulum
Luticola mutica
Nitzschia paleacea
Pinnularia microstauron
Pinnularia subcapitata
Stauroforma exiguiformis
Stenopterobia cuspidata
Surirella engleri
Diatom zones
CONISS
Depth (cm)
Bacon estimated age (CE)
BS3b
BS3a
BS2
BS1
Total sum of squares
%

b)

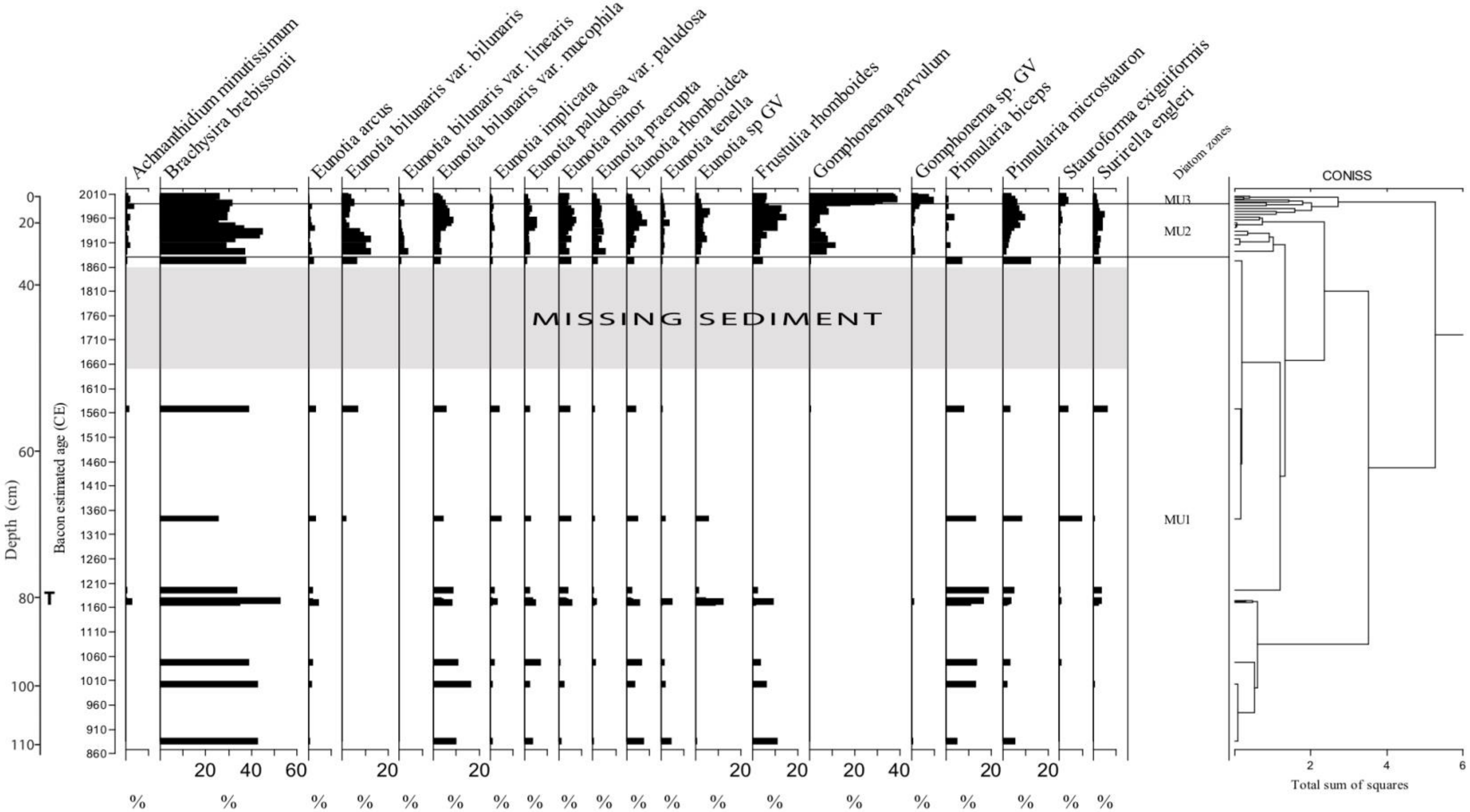


Figure 3: Variations in percent relative abundances of most common diatoms for a) BIS3 (minimum cut-off for inclusion ⩾ 2% in any one sample) and b) MUH4/MUH2 (minimum cut-off for inclusion ⩾ 1% in any one sample) cores, as well as for *Cyclotella ocellata* in (a). *C. ocellata* is found throughout BIS3, but reaches a peak of 2.5% in subzone BS3b. In b), relative abundances of *C. ocellata* (%s, levels marked with a "+") are shown x 10. Estimated ages on the Y axis are from BACON modelling, shown as year Common Era (CE), and are based on

AMS^{14}C, ^{210}Pb and ^{137}Cs activities (and see Table S4). X axis is % abundance. GV = Girdle View. Also shown are the results of constrained incremental sum of squares (CONISS) generated along with the Figure using the programme TILIA 2.0-41 (Grimm, 1987). Note the missing sediment interval in b) between 1650 CE and 1860 CE (37cm to 50cm depth) owing to non-retrieval of sediment during coring. T = tephra.

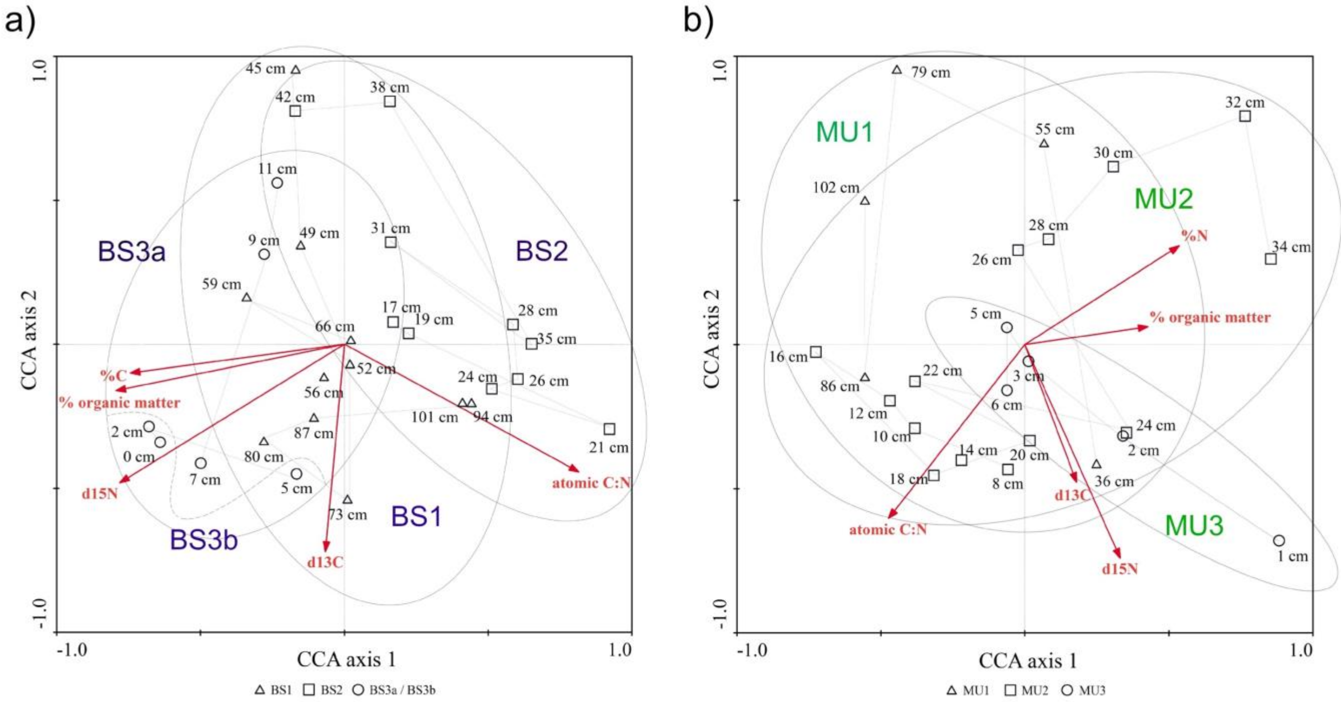


Figure 4: Results of Constrained Correspondence Analysis (CCA) using CANOCO 4.5 (ter Braak and Šmilauer, 2002) for diatom sediment sample data from a) Bisoke core BIS3 [27 sample levels included] and b) Muhavura cores MUH4/MUH2 [24 sample levels included]. Only diatom taxa that attained a level of >1% in at least one sample were included, along with selected environmental proxy data (% organic matter, % Total Nitrogen [TN], %Total Organic Carbon [TOC], atomic C:N, δ^{13}C (d13C) and δ^{15}N (d15N)). Diatom zones are shown. Stratigraphically contiguous samples are joined by a line. Note that %N and %C were excluded from, respectively a) BIS3 and b) MUH4/MUH2. See Table S5 for information on eigenvalues and explained variation.

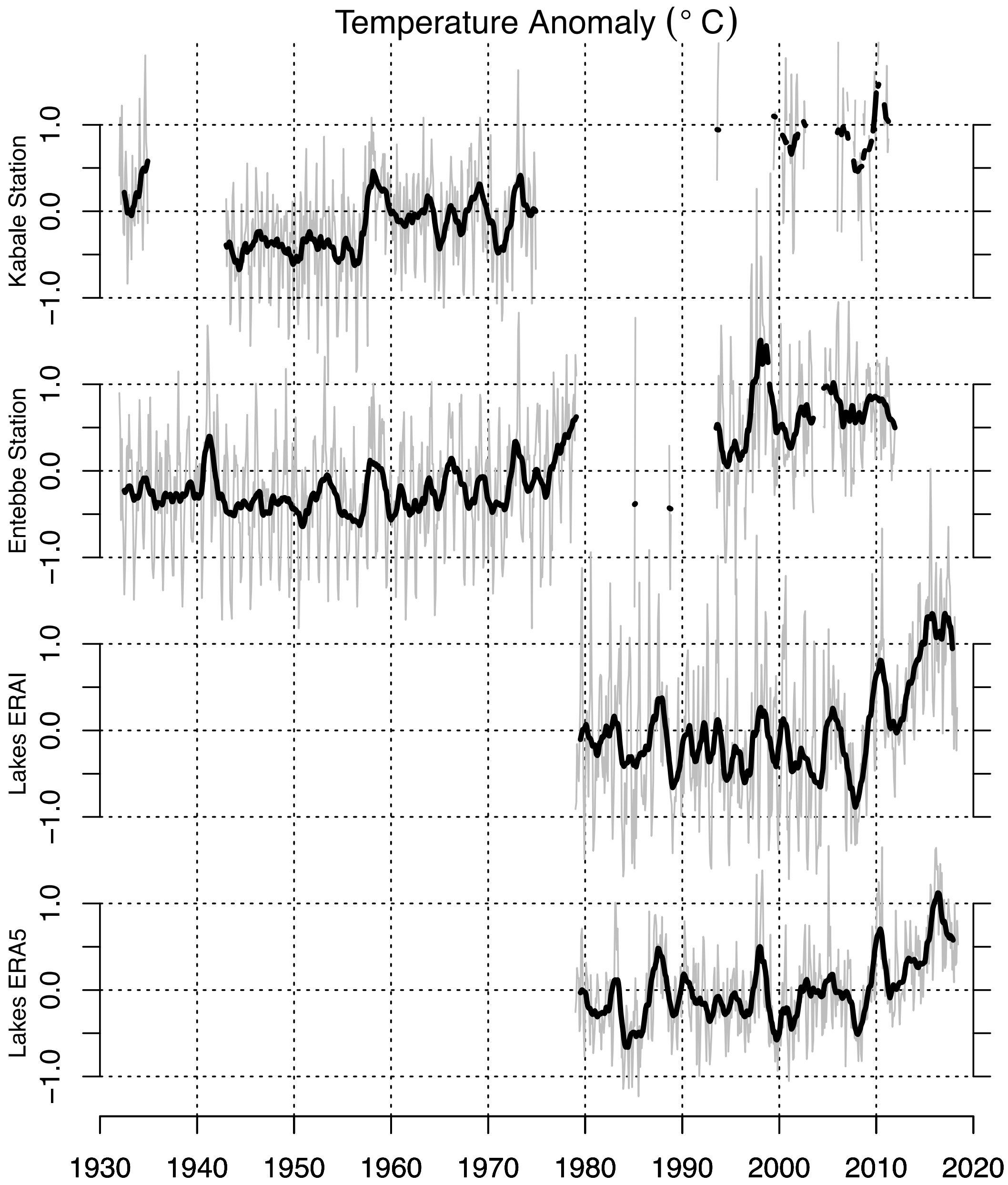


Figure 5: Panels are described from the uppermost down. Monthly average temperature anomalies calculated with respect to series mean recorded at Kabale station, western Uganda, c. 30 km to the east of Mt. Muhavura with de-seasonalized trend (bold line) calculated using the zoo package of the R software; same for Entebbe station, central Uganda, on the northern shoreline of Lake Victoria, and with the most complete available record for the 20th century for a meteorological station close to the study area; the two lowermost panels show European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim (ERAI, Dee et al., 2011) and ERA5 reanalysis monthly average temperature anomalies for the respective 75km and 35 km grid-cells that contain Bisoke and Muhavura lakes, with de-seasonalized trend shown (bold line). Note the significant gaps in the record and that the more complete record from Entebbe indicates c. 0.8-1.0 °C of warming since the 1930s.

REFERENCES

Abarca, N., Jahn, R., Zimmermann, J. & Enke, N. (2014) Does the cosmopolitan diatom *Gomphonema parvulum* (Kützing) Kützing have a biogeography? *PLoS ONE*, 9: e86885

Abell, J.M., Özkundakci, D., Hamilton, D.P. & Jones, J.R. (2012) Latitudinal variation in nutrient stoichiometry and chlorophyll-nutrient relationships in lakes: A global study. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 181, 1–14.

Alin, S.R. & Cohen, A.S. (2003) Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracod-inferred water-depth reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 199, 31-49

Anderson, M.J. (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245-253

Appleby, P.G. (2001) Chronostratigraphic techniques in recent sediments. In: W.M. Last & J.P. Smol (Eds.) *Tracking environmental change using lake sediments. Volume 1: Basin analysis, coring, and chronological techniques* (pp. 171–203). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Appleby, P.G. & Oldfield, F. (1978) The calculation of 210Pb dates assuming a constant rate of supply of unsupported 210Pb to the sediment. *Catena*, 5, 1–8.

Ayebare, S., Plumptre, A.J., Kujirakwinja, D. & Segan, D. (2018) Conservation of the endemic species of the Albertine Rift under future climate change. *Biological Conservation*, 220, 67-75.

Balagizi, C. M., F. Darchambeau, S. Bouillon, M. M. Yalire, T. Lambert & Borges, A.V. (2015) River geochemistry, chemical weathering, and atmospheric CO_2 consumption rates in the Virunga Volcanic Province (East Africa). *Geochemistry. Geophysics, Geosystems*, 16, doi:10.1002/ 2015GC005999.

Baselega, A. & Orme, D.L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3, 808-812.

Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., & Juggins, S. (2001) Diatoms. In: J.P. Smol, H.J.B. Birks & W.M. Last (Eds.) *Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal, and siliceous indicators* (pp. 155–205). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Battarbee, R.W., Morley, D., Bennion, H., Simpson, G.L., Hughes, M. & Bauere, V. (2011) A palaeolimnological meta-database for assessing the ecological status of lakes. *Journal of Paleolimnology*, 45, 405-414

Bauters, M., Drake, T.W., Verbeeck, H., Bodé, S., Hervé-Fernández, P., Zito, P., … Boeckx, P. (2018) High fire-derived nitrogen deposition on central African forests. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 549-554

Bellinger, B.J., Cocquyt, C. & O'Reilly, C.M. (2006) Benthic diatoms as indicators of eutrophication in tropical streams. *Hydrobiologia*, 573, 75–87.

Benedtict, K.B., Prenni, A.J., Carrico, C.M., Sullivan, A.P., Schichtel, B.A. & Collett Jr., J.L. (2017) Enhanced concentrations of reactive nitrogen species in wildfire smoke. *Atmospheric environment*, 148, 8-15.

Bennett, K.D. (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132, 155–170.

Bennett, K.D. & Willis, K.J. (2001). Pollen. J.P. Smol, H.J.B. Birks & W.M. Last (Eds.) *Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal, and siliceous indicators* (pp. 5–32). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Bere, T. & Tundisi, J.G. (2011) Influence of land-use patterns on benthic diatom communities and water quality in the tropical Monjolinho hydrological basin, São Carlos-SP, Brazil. *Water SA*, 37, 93-102

Birks, H.J.B. (1995) Quantitative palaeoenvironmental reconstructions. In: D. Maddy & J.S. Brew (Eds.) Statistical modelling of Quaternary science data (pp 161–254). Cambridge: Quaternary Research Association.

Birks, H.J.B. (2007) Estimating the amount of compositional change in late-Quaternary pollen-stratigraphical data. *Vegetation History and Archaeobotany*, 16: 197-202.

Blaauw M and Christen JA. (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis,* 6, 457-474.

Burgess, N.D., Balmford, A., Cordeiro, N.J., Fjeldså, J., Küper, W., Rahbek, C., … Williams, P.H. (2007) Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation*, 134, 164–177.

Buytaert, W., Cuesta-Camacho, F. & Tobón, C. (2011) Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecology & Biogeography*, 20, 19–33

Cárate-Tandalla, D., Camenzind, T., Leuschner, C. & Homeier, J. (2018) Contrasting species responses to continued nitrogen and phosphorus addition in tropical montane forest tree seedlings. *Biotropica*, 50, 234-245.

Catalan, J., Pla-Rabés, S., Wolfe, A.P., Smol, J.P., Rühland, K.M., … Renberg, I. (2013) Global change revealed by palaeolimnological records from remote lakes: a review. *Journal of Paleolimnology*, 49, 513–535.

Cavalli-Sforza, L.L. & Edwards, A.W.F. (1967) Phylogenetic analysis: models and estimation procedures. *Evolution*, 21, 550–570.

Chambers, J.W. & Cameron, N.G. (2001) A rod-less piston corer for lake sediments; an improved, rope-operated percussion corer. *Journal of Paleolimnology*, 25, 117–122.

Cocquyt, C. (1998) *Diatoms from the northern basin of Lake Tanganyika*. Berlin: J. Cramer.

Cocquyt, C. & Jahn, R. (2007) *Surirella Engleri* O. Müller: A study of its original infraspecific types, variability and distribution. *Diatom Research*, 22, 1–16.

Cohen, A.S., Gergurich, E.L., Kraemer, B.M., McGlue, M.M., McIntyre, P.B., Russell, J.M., … Swarzenski, P.W. (2016) Climate warming reduces fish production and benthic habitat in Lake Tanganyika, one of the most biodiverse freshwater ecosystems. *Proceedings of the National Academy of Sciences*, 113, 9563-9568.

Cohen, A.S., Palacios-Fest, M.R., Msaky, E.S., Alin, S.R., McKee, B., … Lezzar, K.E. (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IX. Summary of paleorecords of environmental change and catchment deforestation at Lake Tanganyika and impacts on the Lake Tanganyika ecosystem. *Journal of Paleolimnology*, 34, 125-145.

Colombaroli, D., Ssemmanda, I., Gelorini, V. & Verschuren, D. (2014) Contrasting long-term records of biomass burning in wet and dry savannas of equatorial East Africa. *Global Change Biology*, 20, 2903-2914.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F. & Krebs, P. (2009) Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews*, 28, 555–576.

Dalton, A.S., Patterson, R.T., Roe, H.M., Macumber, A.L., Swindles, G.T. … Falck, H. (2018) Late Holocene climatic variability in Subarctic Canada: Insights from a high-resolution lake record from the central Northwest Territories. *PLoS ONE*, 13, e0199872

Davidson, T.A., Bennion, H., Reid, M., Sayer, C.D. & Whitmore, T.J. (2018) Towards better integration of ecology in palaeoecology: from proxies to indicators, from inference to understanding. *Journal of Paleolimnology*, 60, 109-116.

Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S., … Vitart, F. (2011). The ERA-Interim reanalysis: confirmation and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society*, 137, 553-597

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., … Magurran, A.E. (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science, 296-299.

Felix, J.D., Elliott, E.M., Gish, T., McConnell, L. & Shaw, S. (2013) Characterizing the isotopic composition of atmospheric amonina emission sources using passive samplers and a combined oxidation-bacterial denitrifier isotope ratio mass spectrometer method. *Rapid Communication Mass Spectrometry*, 27, 2239-2246.

Felix, J.D., Elliott, E.M. & Shaw, S.L. (2012) Nitrogen isotopic composition of coal-fired power plant NO_x: influence of emission controls and implications for global emission inventories. *Environmental Science and Technology*, 46, 3528-3535.

Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., … Voss, M. (2013) The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20130164.

Fritz, S.C., Benito, X., Steinitz-Kannan, M. (2019) Long-term and regional perspectives on recent changes in lacustrine diatom communities in the tropical Andes. *Journal of Paleolimnology*, 61, 252-262

Galy-Lacaux, C. & Delon, C. (2014) Nitrogen emission and deposition budget in West and Central Africa. *Environmental Research Letters*, 9, 125002

Gasse, F. (1986) *East African diatoms: Taxonomy, ecological distribution*. Stuttgart: Cramer.

Gell, P.A., Sluiter, I.R & Fluin, J. (2002) Seasonal and interannual variations in diatom assemblages in Murray River connected wetlands in north-west Victoria, Australia. *Marine and Freshwater Research*, 53, 981–992.

Grimm, E.C. (1987) CONISS: a fortran 77 programme for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, 13, 13–35.

Gütlein, A., Zistl-Schlingmann, M., Becker, J.N., Cornejo, N.S., Detsch, F., Dannenmann, M, … Kiese, R. (2017) Nitrogen turnover and greenhouse gas emissions in a tropical alpine ecosytem, Mt. Kilmanjaro, Tanzania. *Plant Soil*, 411 243-259.

Hausmann, S., Charles, D.F., Gerritsen, J. & Belton, T.J. (2016) A diatom-based biological condition gradient (BCG) approach for assessing impairment and developing nutrient criteria for streams. *Science of the Total Environment*, 15, 914-927.

Heard, A.M., Sickman, J.O., Rose, N.L., Bennett, D.M., Lucero, D.M., Melack, J.M. & Curtis, J.H. (2014) 20th Century atmospheric deposition and acidification trends in lakes of the Sierra Nevada, California, USA. *Environmental Science and Technology*, 48, 10054-10061

Hedberg, O. (1964) Features of Afroalpine plant ecology. *Acta phytogeographica Suecica*, 49: 1-144

Heiri, O., Lotter, A.F. & Lemcke, G. (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology*, 25, 101–110.

Hobbs, W.O., Telford, R.J., Birks, H.J.B., Saros, J.E., Hazewinkel, R.R.O., Perren, B.B. … Wolfe, A.P. (2010) Quantifying recent ecological changes in remote lakes of North America and Greenland using sediment diatom assemblages. *PLoS ONE*, 5, e10026

Hochleithner, S. (2017) Beyond contesting limits: land, access and resistance at the Virunga National Park. *Conservation and Society*, 15, 100-110.

Holmgren, S.U., Ljung, K. & Björck, S. (2012) Late Holocene environmental history on Tristan da Cunha, South Atlantic, based on diatom floristic changes and geochemistry in sediments of a volcanic crater lake. *Journal of Paleolimnology*, 47, 221-232

Holtgrieve, G.W., Schindler, D.E., Hobbs, W.O., Leavitt, P.R., Ward, E.J., Bunting, L., … Wolfe, A.P. (2011) A coherent signature of anthropogenic nitrogen deposition to remote watersheds of the northern hemisphere. *Science*, 334, 1545–1548.

Hu, Z., Anderson, N.J., Yang, X. & McGowan, S. (2014) Catchment-mediated atmospheric nitrogen deposition drives ecological change in two alpine lakes in SE Tibet. *Global Change Biology*, 20, 1614-1628.

Jewson, D.H. (1992) Size reduction, reproductive strategy and the life cycle of a centric diatom. *Philosophical Transactions of the Royal Society*, B, 335:191–213

Jolly, D., Taylor, D., Marchant, R, Hamilton, A., Bonnefille, R., … Riollet, G. (1997) Vegetation dynamics in central Africa since 18,000 yr BP: pollen records from the interlacustrine highlands of Burundi, Rwanda and western Uganda. *Journal of Biogeography*, 24, 492-512.

Kawashima, H. & Kurahashi, T. (2011) Inorganic ion and nitrogen isotopic compositions of atmospheric aerosols at Yurihonjo, Japan: implications for nitrogen sources. *Atmospheric Environment*, 45, 6309-6316.

Kilroy, C., Biggs, B.J.F., Vyverman, W. & Broady, P.A. (2006) Benthic diatom communities in subalpine pools in New Zealand: relationships to environmental variables. *Hydrobiologia*, 561, 95-110.

Krammer, K. (1992) *Pinnularia: Eine Monographie der europäischen Taxa*. Berlin: Cramer.

Krammer, K. & Lange-Bertalot, H. (1986-1991) *Susswasserflora von Mitteleuropa Bacillariophyceae*, *Teil 2-4*. Stuttgart: Gustav Fisher.

Lange-Bertalot, H. & Moser, G. (1994) *Brachysira: Monographie der Gattung*. Berlin: Cramer.

Legendre, P. & Birks, H.J.B. (2012). From Classical to Canonical Ordination. In: H.J.B. Birks et al. (Eds.), *Tracking Environmental Change Using Lake Sediments*, Developments in paleoenvironmental Research 5. (pp 201-248) Springer Science + Business Media B.V

Litchman, E., Klausmeier, C.A., Miller, J.R., Schofield, O.M. & Falkowski, P.G. (2006) Multi-nutrient, multi-group model of present and future oceanic phytoplankton communities. *Biogeoscience*, 3, 585–606

Littke, R. (1985) Deposition, Diagenesis and Weathering of Organic Matter-Rich Sediments. *Lecture Notes in Earth Sciences*. Volume 47, Springer, Berlin.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S. Hughes, M.K., Shinwell, D., … Ni, F. (2009) Global signature and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, 326, 1256-1260

McGill, B.J., Dornelas, M., Gotelli, N.J. & Magurran, A.E. (2015) Fifteen forms of biodiversity trend in the Anthroopocene. *Trends in Ecology & Evolution*, 30, 104-113

McGlynn, G., Mooney, S. & Taylor, D. (2013) Palaeoecological evidence for Holocene environmental change from the Virunga volcanoes in the Albertine Rift, central Africa. *Quaternary Science Reviews*, 61, 32–46.

Meyers, P.A. (2003) Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. *Organic Geochemistry*, 34, 261-289.

Meyers, P.A. & Lallièr-Vergès, E. (1999) Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. *Journal of Paleolimnology*, 21, 345-372

Michelutti, N., Wolfe, A.P., Cooke, C.A., Hobbsm W.O., Vuille, M. & Smol, J.P. (2015) Climate change forces new ecological states in tropical Andean lakes. *PLoS ONE* 10: e0115338

Mills, K. & Ryves, D. (2012) Diatom-based models for inferring past water chemistry in western Ugandan crater lakes, *Journal of Paleolimnology*, 48, 383-399.

Mills, K, Ryves, D.B., Anderson, N.J., Bryant, C.L. & Tyler, J.J. (2014) Expressions of climate perturbations in western Ugandan crater lake sediment records during the last 1000 years. *Climates of the Past*, 10, 1581-1601

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M. & Gascon, C. (2011) Global biodiversity conservation: the critical role of hotspots. In: F.E. Zachos & J.C. Habel (Eds.) *Biodiversity hotspots* (pp 3–22). Heidelberg, Germany: Springer-Verlag.

Monchamp, M-E., Spaak, P., Domaizon, I., Dubois, N., Bouffard, D. & Pomati, F. (2018) Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. *Nature Ecology and Evolution*, 2, 317-324

Montoya-Moreno, Y. & Aguirre-Ramírez, N. (2013) Knowledge to ecological preferences in tropical epiphytic algae to use with eutrophication indicators. *Journal of Environmental Protection*, 4, 27-35.

Mooney, S.D. & Tinner, W. (2011) The analysis of charcoal in peat and organic sediments. *Mires and Peat*, 7, 1–18.

Moritz, C. & Agudo, R. (2013) The future of species under climate change: resilience or decline? Science, 341, 504-508.

MRI (Mountain Research Initiative EDW Working Group) (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430.

Nash, D.J., Gijs, D.C., Chase, B.M., Verschuren, D., Nicholson, S.E., Shanahan, T.M., … Grab, S.W. (2016) African hydroclimatic variability during the last 2000 years. *Quaternary Science Reviews*, 154, 1-22

Nicholson, S.E., Funk, C., Fink, A.H. (2018) Rainfall over the African continent from the 19th through the 21st century. *Global and Planetary Change*, 165, 114-127

O'Reilly, C. M., Sharma, S., Gray, D.K., Hampton, S.E., Read, J.S., Rowley, R.J., … Zhang, G. (2015) Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters*, 42, 10773-10781

Panizzo, V.N., Mackay, A.W., Ssemmanda, I., Taylor, R., Rose, N. & Leng, M.J. (2008). A 140-year record of recent changes in aquatic productivity in a remote, tropical alpine lake in the Rwenzori Mountain National Park, Uganda. *Journal of Paleolimnology*, 40, 325-338.

Pérez, N.M., Hernández, P.A., Padilla, G., Nolasco, D., Barrancos, J., Melían, G. … Ibarra, M. (2011) Global CO_2 emission from volcanic lakes. *Geology*, 39, 235-238.

Pla, S., Monteith, D.T., Flower, R. J., Rose, N.L. (2009) The recent palaeolimnology of a remote Scottish loch with special reference to the relative impacts of regional warming and atmospheric contamination. *Freshwater Biology*, 54, 505-523.

Plumptre, A.J., Davenport, T.R.B., Behangana,M., Kityo, R., Eilu, G., Ssegawa, P., … Moyer, D., (2007) The biodiversity of the Albertine rift. *Biological Conservation*, 134, 178–194.

Ponce-Reyes, R., Plumptre, A.J., Segan, D., Ayebare, S., Fuller, R.A., Possingham, H.P. & Watson, J.E.M. (2017). Forecasting ecosystem responses to climate change across Africa's Albertine Rift. *Biological Conservation*, 209, 464-472.

Ptacnik, R., Diehl, S. & Berger, S. (2003) Performance of sinking and nonsinking phytoplankton taxa in a gradient of mixing depths. *Limnology & Oceanography*, 48, 1903–1912

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., … van der Plicht, J. (2013) IntCal13 and Marine13 radiocarbon age calibration curves, 0-50,000 years cal BP. *Radiocarbon*, 55, 1869-1887

Robbins, M.M., Gray, M., Fawcett, K.A., Nutter, F.B., Uwingeli, P., Mburanumwe, I., …Robbins, A.M.. (2011) Extreme conservation leads to recovery of the Virunga mountain gorillas. *PLoS ONE*, 6, e19788.

Rose, N. L. (1994). A note on further refinements to a procedure for the extraction of carbonaceous fly-ash particles from sediments. *Journal of Paleolimnology*, 11, 201-204.

Rose, N. L. (2008). Quality control in the analysis of lake sediments for spheroidal carbonaceous particles. *Limnology and Oceanography: Methods*, 6, 172-179.

Rose, N.L., Harlock, S. & Appleby, P.G. (1999) The spatial and temporal distributions of spheroidal carbonaceaous fly-ash particles (SCP) in the sediment records of European mountain lakes. *Water and Soil Pollution*, 113, 1-32.

Rose, N.L., Juggins, S., Watt, J. & Battarbee, R. (1994) Fuel-type characterisation of spheroidal carbonaceous particles using surface chemistry. *Ambio*, 23, 296-299.

Rühland, K., Paterson, A.M. & Smol, J.P. (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. *Global Change Biology*, 14, 2740–2754

Rühland, K.M., Paterson, A.M. & Smol, J.P. (2015) Lake diatom responses to warming: reviewing the evidence. *Journal of Paleolimnology*, 54, 1-35

Russell, J.M., Mccoy, S.J., Verschuren, D., Bessems, I. & Huang, Y. (2009) Human impacts, climate change, and aquatic ecosystem response during the past 2000 yr at Lake Wandakara, Uganda. *Quaternary Research*, 72, 315–324.

Russell, J.M., Verschuren, D. & Eggermont, H. (2007) Spatial complexity of 'Little Ice Age' climate in East Africa: sedimentary records from two crater lake basins in western Uganda. *The Holocene*, 17, 183-193.

Salerno, J., Chapman, C.A., Diem, J.E., Dowhaniuk, N., Goldman, A., MacKenzie, C.A., … Hartter, J. (2018) Park isolation in anthropogenic landscapes: land change and livelihoods at park boundaries in the African Albertine Rift. *Regional Environmental Change*, 18, 913-928.

Saros, J.E., Northington, R.M., Anderson, D.S. & Anderson, N.J. (2016) A whole-lake experiment confirms a small centric diatom species as an indicator of changing lake thermal structure. *Limnology and Oceanography Letters*, 1, 27-35

Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S.V., Jones, V.J., Korhola, A. … Weckström, J. (2005) Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 4397-4402.

Soeprobowati, T.R., Suedy, W.W.A, Hadiyanto, Luis, A.A. & Gell, P. (2018) Diatom assemblage in the 24cm upper sediment associated with human activities in Lake Warna Dieng Plateau Indonesia. *Environmental Technology and Innovation*, 10, 314-323.

Spinage, C.A. (1972) The ecology and problems of the Volcano National Park, Rwanda. *Biological Conservation*, 4, 194-204.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011) The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369, 842‑867

Steinbauer, M.J., Grytnes, J-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H. … Wipf, S. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. Nature, 556, 231-234

Talbot, M.R. (2001) Nitrogen isotopes in palaeolimnology. In: W.M. Last & J.P. Smol (Eds.) *Tracking environmental change using lake sediments. Volume 2: Physical and geochemical methods* (pp 401–439). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Taylor, D., Marchant, R.A. & Robertshaw, P. (1999) A sediment-based history of medium altitude forest in central Africa: a record from Kabata Swamp, Ndae volcanic field, Uganda. *Journal of Ecology*, 87, 303-315.

Taylor, D., Robertshaw, P. & Marchant, R.A. (2000) Environmental change and political-economic upheaval in precolonial western Uganda. *The Holocene*, 10, 527-536

Taylor, D.M. (1990) Late Quaternary pollen records from two Ugandan mires: evidence for environmental changes in the Rukiga Highlands of southwest Uganda. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 80, 283-300.

ter Braak, C. J. F. (1986) Canonical correspondence analysis – a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67, 1167–1179.

ter Braak, C.J.F. & Prentice, I.C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, 18, 271-317.

ter Braak, C. J. F. & Šmilauer, P. (2002) *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. New York: Microcomputer Power, Ithaca, pp. 352.

Tierney, J.E., Mayes, M.T., Meyer, N., Johnson, C., Swarzenski, P.W. Cohen, A.S. & Russell, J.M. (2010) Late-twentieth-century warming in Lake Tanganyika unprecedented since AD 500. *Nature Geoscience*, 3, 422-425

Van der Werf, G.R. Randerson, J.T., Giglio, L., van Leeuwen, T.T., Chen, Y., Rogers, B.M., … Kasibhatla, P.S. (2017) Global fire emissions estimates during 1997-2016. *Earth System Science Data*, 9, 697-720.

Verschuren, D., Laird, K.R. & Cumming, B.F. (2000) Rainfall and drought in equatorial east Africa during the past 1100 years. *Nature*, 403, 410-414.

Waddington, J.C.B. (1969) A stratigraphic record of the pollen influx to a lake in the Big Woods of Minnesota. *Geological Society of America Special Paper*, 123, 263–282.

Wang, Y-L., Liu, X-Y., Song, W., Yang, W., Han, B., Dou, X-Y., … Bai, Z-P. (2017) Source apportionment of nitrogen in $PM_{2.5}$ based on bulk $\delta^{15}N$ signatures and a Bayesian isotope mixing model. *Tellus B: Chemical and Physical Meteorology*, 69, 1299672

Waters, C.N., Zalasiewicz, J.A., Williams, M., Ellis, M.A. & Snelling, A.M. (2014) A stratigraphical basis for the Anthropocene? In: C.N. Waters, J.A. Zalasiewicz, M. Williams, M.A. Ellis & A.M. Snelling (Eds) A stratigraphical basis for the Anthropocene (pp 1-21). Geological Society, London, Special Publications, 395.

Wengrat, S., Padial, A.A., Jeppesen, E., Davidson, T.A., Fontana, L., Costa-Böddeker, S. & Bicudo, D.C. (2018) Paleolimnological records reveal biotic homogenization driven by eutrophication in tropical reservoirs. *Journal of Paleolimnology*, 60, 299-309

Winder, M & Hunter, D.A. (2008) Temporal organization of phytoplankton communities linked to physical forcing. *Oecologia*, 156, 179–192

Wilkinson, I.P., Poirier, C., Head, M.J., Sayer, C.D. & Tibby, J. (2014) Microbiotic signatures of the Anthropocene in marginal marine and freshwaer palaeoenvironments. In: C.N. Waters, J.A. Zalasiewicz, M. Williams, M.A. Ellis & A.M. Snelling (Eds) A stratigraphical basis for the Anthropocene (pp 185-219). Geological Society, London, Special Publications, 395.

Wood, D.A. & Scholz, C.A. (2017) Stratigraphic framework and lake level history of Lake Kivu, East African Rift. *Journal of African Earth Sciences*, 134, 904-916

Yan, Y., Wang, L., Li, J., Li., J., Zou, Y., Zhang, J., … Wan, X. (2018) Diatom response to climatic warming over the last 200 years: A record from Gonghai Lake, North China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 495, 48-59

Yang, Y., Stenger-Kovács, C., Padisák, J. & Pettersson, K. (2016) Effects of winter severity on spring phytoplankton development in a temperate lake (Lake Erken, Sweden). *Hydrobiologia*, 780, 47-57.

Zimmer, A., Meneses, R.I., Rabatel, A., Soruco, A., Dangles, O. & Antheleme, F. (2018) Time lag between glacial retreat and upward migration alters tropical alpine communities. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 89-102.

Zwiener, V.P., Lira-Noriega, A., Grady, C.J., Padial, A.A. & Vitule, J.R.S. (2018) Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography*, 27, 298-309.

BIOSKETCH

Gayle McGlynn is an Assistant Professor in the School of Natural Sciences, Trinity College, University of Dublin. She holds a PhD in environmental change and its impacts in eastern Africa. Gayle has carried out field-based research in Africa in Burndi, Kenya, Rwanda, Tanzania, Uganda and Zambia. David Taylor is Provost's Chair and Professor of Tropical Environmental Change in the Department of Geography at National University of Singapore. A tropical palynologist by training, he has more than 35 years of research experience in tropical Africa and Asia.

AUTHOR CONTRIBUTIONS

GMcG and DT were involved in all aspects of the paper and the research that underpins it, including fieldwork. CD and JL were involved in part of the fieldwork. AT, NR, SM, WB, ZT, XZ & KR provided data and/or helped with data analysis. All authors were involved in writing the paper, led by DT.

DATA ARCHIVING

Research data referred to in this paper will be kept for a minimum of 10 years, according to the Research Data Management Policy of the National University of Singapore.