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RESEARCH PAPER

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

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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. 1,200 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. 1,200-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 homogenization (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 homogenization, 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 to 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 fertilizers 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, and 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. 1,200 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 1,200 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 4000 m above sea level (asl), form part of the Virunga Conservation Area (Figure 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 2,300–3,000 m 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.

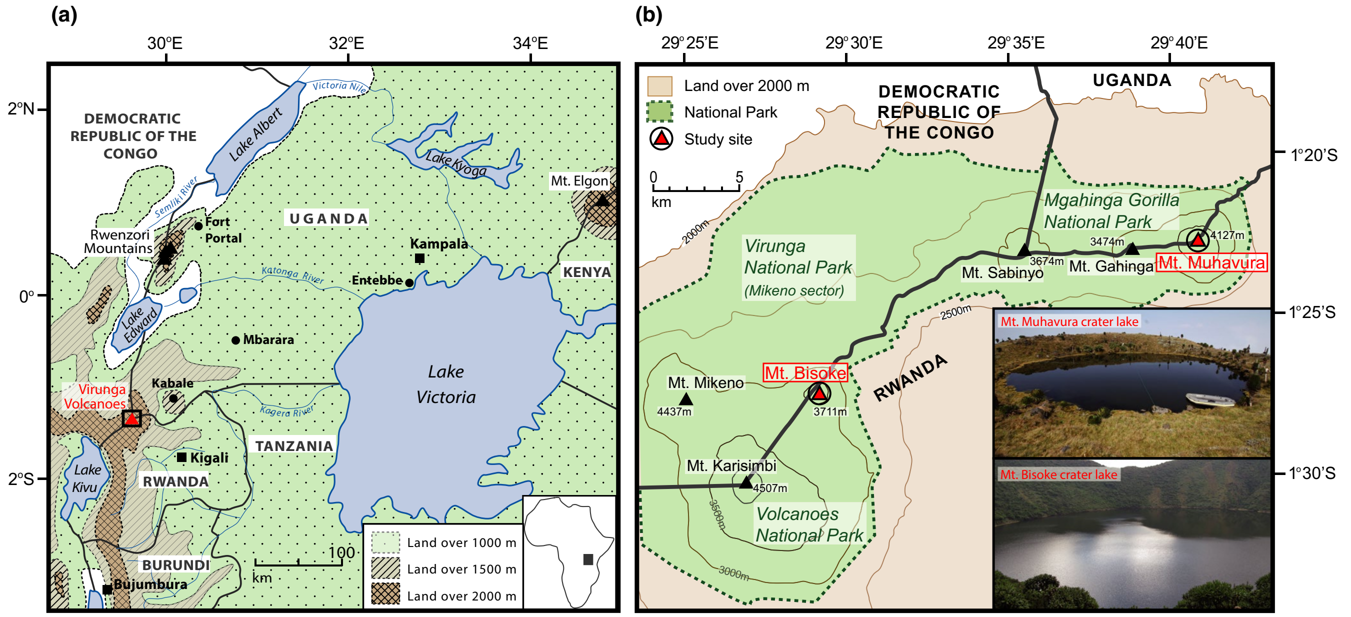


FIGURE 1 Location of the Virunga volcanoes in the Albertine Rift, which also accommodates the lakes of (from south to north) Tanganyika, Kivu, Edward and Albert, and forms the western boundary of eastern Africa (a). Location of Bisoke and Muhavura crater lakes on Mt Bisoke and Mt Muhavura within the 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) [Colour figure can be viewed at wileyonlinelibrary.com]

Vegetation on the volcanoes has a marked altitudinal zonation in response to altitude-related changes in climate conditions. Lower montane forest characterizes slopes up to an altitude of c. 2,500 m asl, and likely extended over much of the volcanic plain prior to the onset of Late Iron Age clearances in the region around 1,000 years ago (Taylor, 1990). Bamboo thickets are present above the lower montane forest, while Ericaceous vegetation occurs between c. 3,000 m asl and 3,600 m asl. Afroalpine vegetation is found on the highest mountains above c. 3,600 m 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 (4,127 m asl) has an elevation around 400m greater than Bisoke Lake. Vegetation in the crater on Mt. Bisoke is characterized 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 characterize the geomorphologically more subdued crater at the summit of Mt. Muhavura.

2.2 | Field sampling

Sediment core BIS3, 110 cm 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 1-cm-thick slices. The total depth of the longest of several sequences of sediments extracted from Muhavura Lake in 2008 was 247 cm. This paper focuses on the uppermost 120 cm of this sequence, comprising a short 37-cm-long core (MUH4) obtained using a Renberg gravity corer and the uppermost part of core MUH2. Core MUH2 was extracted in 1-m-long sections using a modified Livingstone piston corer, with each section offset to provide a c. 50 cm overlap between sections. Both BIS3 and MUH4 captured the sediment-water interface. Unfortunately, a 13-cm-long section of sediment between the base of MUH4 at 37 cm and the top of MUH2 at 50 cm below the surface was not collected. Core sections comprising MUH2 were packaged and shipped entire for subsampling in 1-cm-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

Chronological control and estimated sediment accumulation rates (SAR) were established using radiometric dating techniques and

TABLE 1 Geographical, physical and limnological information on Bisoke and Muhavura lakes (crater lakes at the summits of Mt Bisoke and Mt Muhavura)

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 (± 2σ)[a,b]	Atomic C:N ratio[a]	$\delta^{13}C$ (‰)[a]	$\delta^{15}N$ (‰)[a]
Bisoke	29° 29' 12" E/1° 27' 40" S	3,711	70,695	21	124,315	0.57	5.83 (0.43)	16.72	−24.86	+5.26
Muhavura	29° 40' 42" E/1° 23' 0" S	4,127	491	1.6	604	0.81	6.54 (0.45)	15.43	−20.08	+3.31

Abbreviation: asl = above sea level.

[a] Note that in the absence of lake water quality monitoring data, information from surface sediment measurements is referred to.

[b] Diatom-inferred value—see text for further information.

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 (9.5 cm in BIS3 and 15.5 cm 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 10-cm-thick tephra-rich layer (80–90 cm) 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 1-cm-thick, contiguous sediment slices for BIS3, and on 1-cm-thick sediment slices with at least a 2-cm resolution for MUH4/MUH2 (Heiri, Lotter, & Lemcke, 2001). Spheroidal carbonaceous particles (SCPs) were enumerated in 16 samples from BIS3 in accordance with Rose (1994, 2008) and are expressed as fluxes (n particles cm^{-2} yr^{-1}). SCPs, 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 and Lange-Bertalot (1986–1991), Krammer (1992), Lange-Bertalot and Moser (1994), Cocquyt (1998) and Cocquyt and 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 and 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 >250 µm, 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 <140 µm, 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 program 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 & 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 summarizing 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 (ter Braak & Prentice, 1988; Legendre & Birks, 2012). 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 homogenization, were determined based on a Sørensen distance metric and presence/absence data using the R package BETAPART and the function beta.multi (Anderson, 2006; Baselega & Orme, 2012), 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 summarized in Tables S2 and S3 and Figure 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 Figure 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 1-cm 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 120 cm 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. SAR increase in both sequences from the beginning of the 20th century and particularly from the 1960s in BIS3 (Figure S1).

3.2 | Sedimentary and numerical analyses

Down-core variations in sedimentary data for BIS3 and the uppermost 120 cm of sediment in MUH4/MUH2 are summarized in Figure 2. Figure 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). SCPs 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 to 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 19th century. PCA axes 1 and 2 sample scores in MUH4/MUH2 also exhibit an abrupt oscillation around 1,170–1180 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 characterized by increased diatom flux, continued relative abundance of *B. brebissonii*, increases in several *Eunotia* species and in *F. rhomboides* and the first appearance

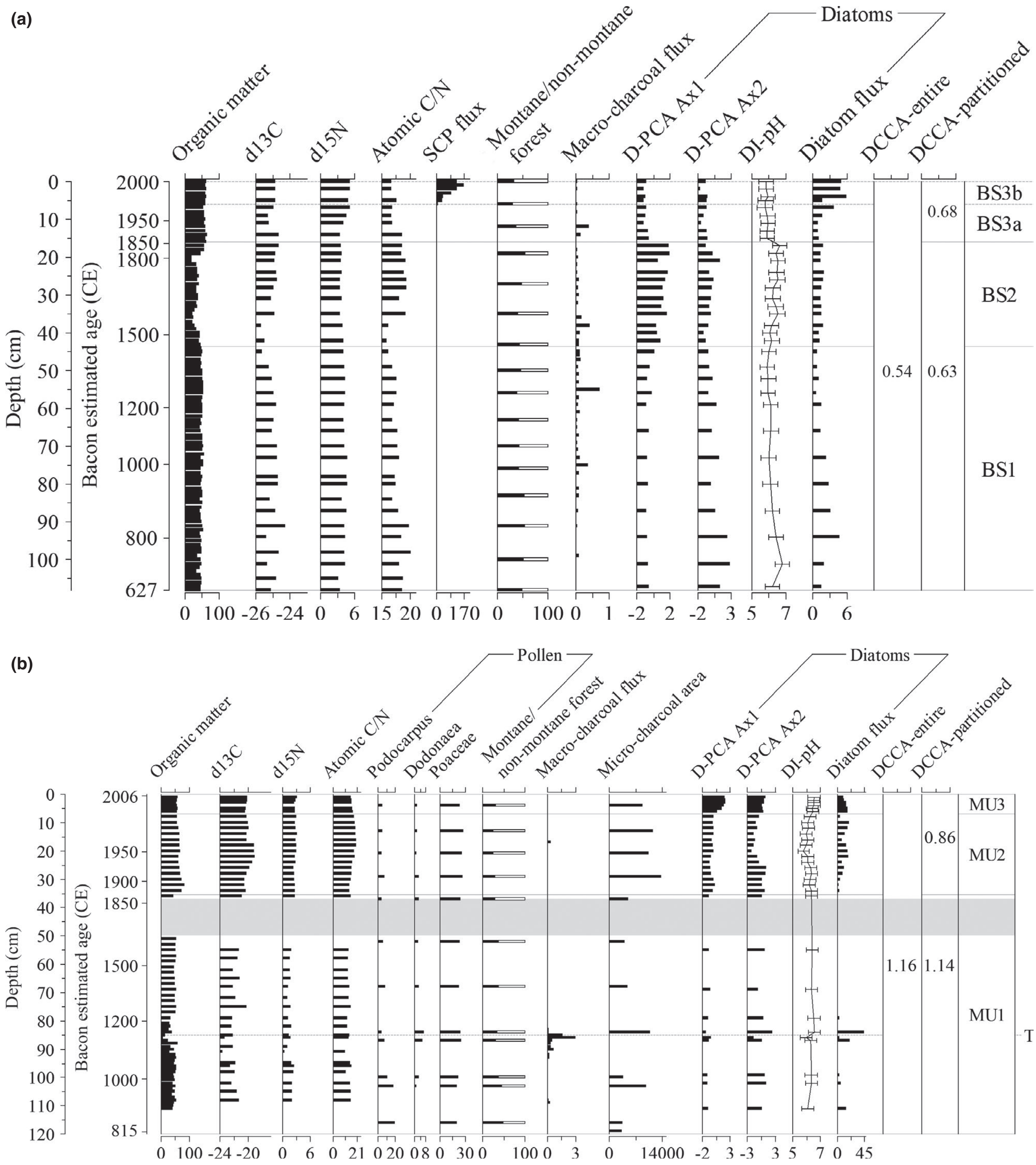


FIGURE 2 Selected sediment data for (a) Bisoke core BIS3 and (b) Muhavura cores MUH4-MUH2. Depth (cm) on the *Y*-axis is depth beneath the lake bed. Estimated ages (expressed as Common Era, CE) are from Bacon modelling based on AMS^{14}C, ^{210}Pb and ^{137}Cs activities (Table S4) (Blaauw & Christen, 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 $\times 10^6$ valves cm^{-2} yr^{-1}. SCPs = 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 summarize variations in subdominant taxa) (D-PCA A×1 and D-PCA A×2), 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

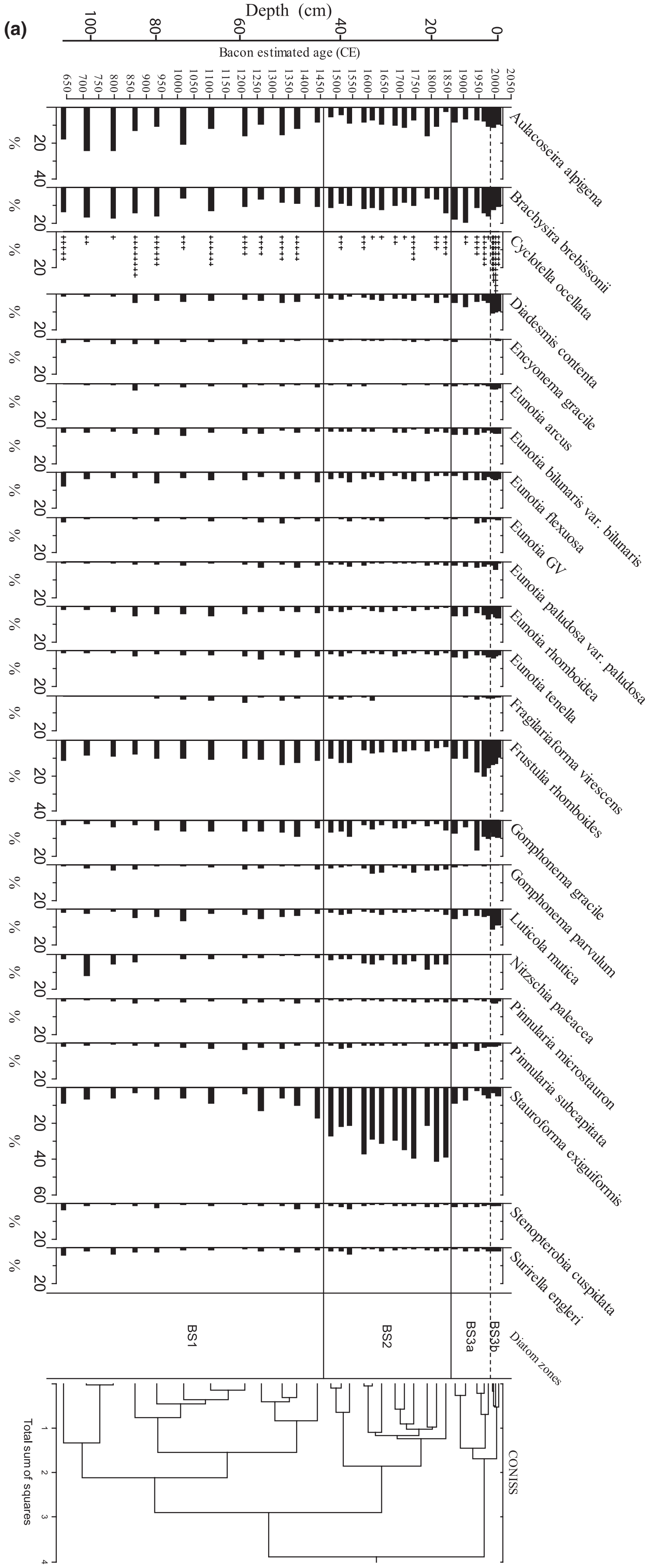


FIGURE 3 (Continued)

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, localized burning in the 1900s also exists, however, in the form of isolated peaks in macro-charcoal flux.

According to the results of CCA (Figure 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, Figure 2a) and 1.16 for MUH4/MUH2 (30 samples, 885 CE to 2005 CE, Figure 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 is 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.

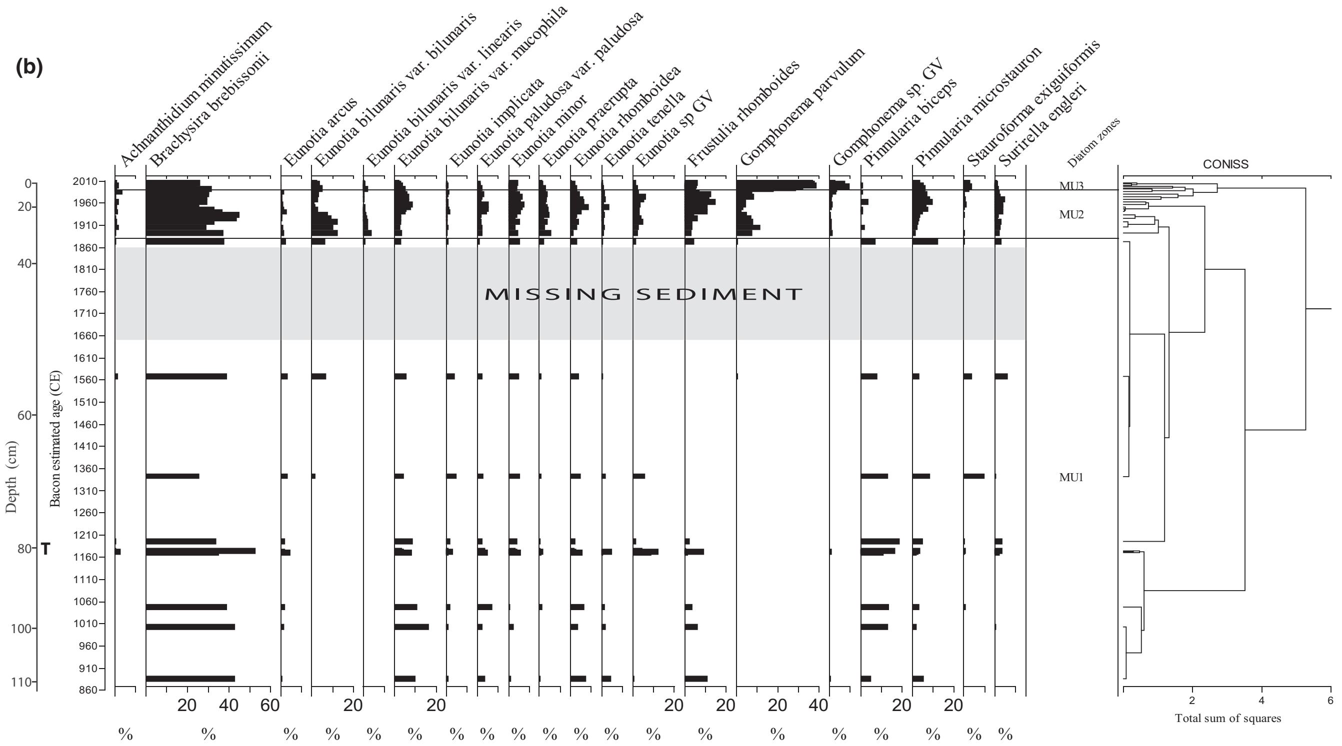


FIGURE 3 Variations in percent relative abundances of most common diatoms for a) BIS3 (minimum cut-off for inclusion ⩾ 2% in any one sample) and b) MUH4/MUH2 (minimum cut-off for inclusion ⩾ 1% in any one sample) cores, as well as for *Cyclotella ocellata* in (a). *C. ocellata* is found throughout BIS3, 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 program TILIA 2.0-41 (Grimm, 1987). Note the missing sediment interval in (b) between 1650 CE and 1860 CE (37–50 cm depth) owing to non-retrieval of sediment during coring. T = tephra

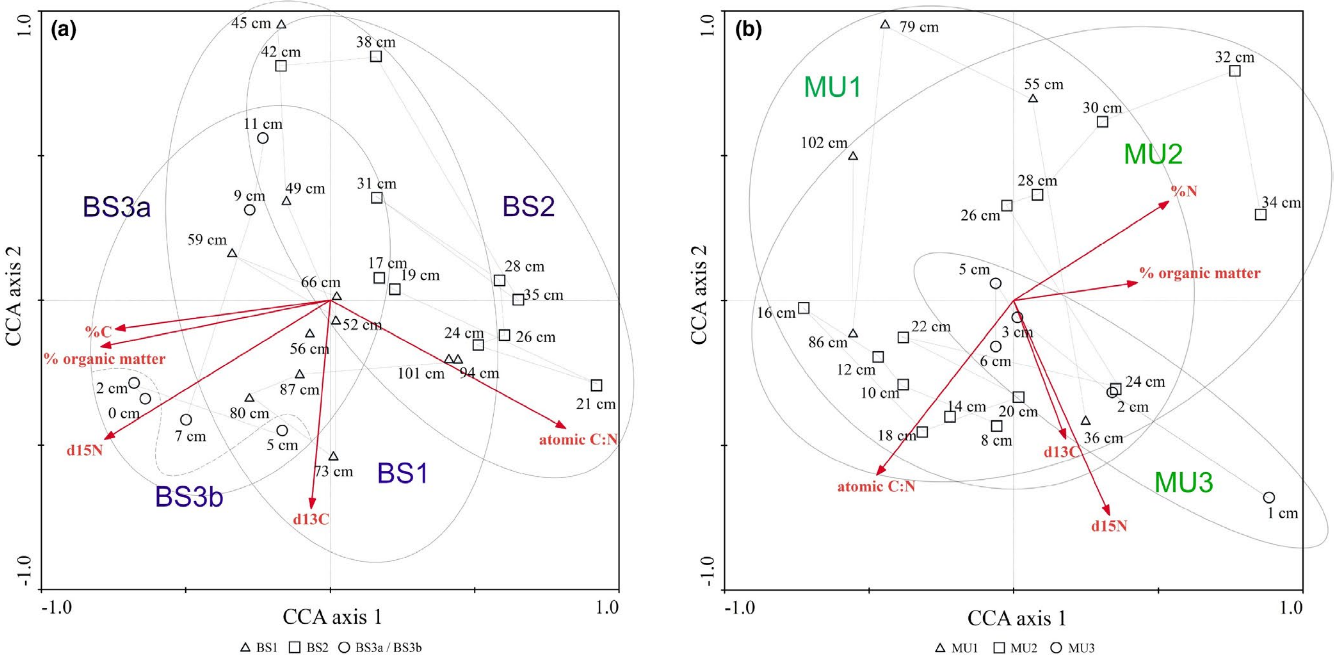


FIGURE 4 Results of Constrained Correspondence Analysis (CCA) using CANOCO 4.5 (ter Braak & Šmilauer, 2002) for diatom sediment sample data from (a) Bisoke core BIS3 [27 sample levels included] and (b) Muhavura cores MUH4/MUH2 [24 sample levels included]. Only diatom taxa that attained a level of > 1% 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 [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Atomic C/N ratios and δ^{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 (Michelutti et al., 2015; Rühland, Paterson, & Smol, 2008, 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 & 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 characterized by the presence of a 10-cm-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, for example, *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, 8-m-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 macrocharcoal 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).

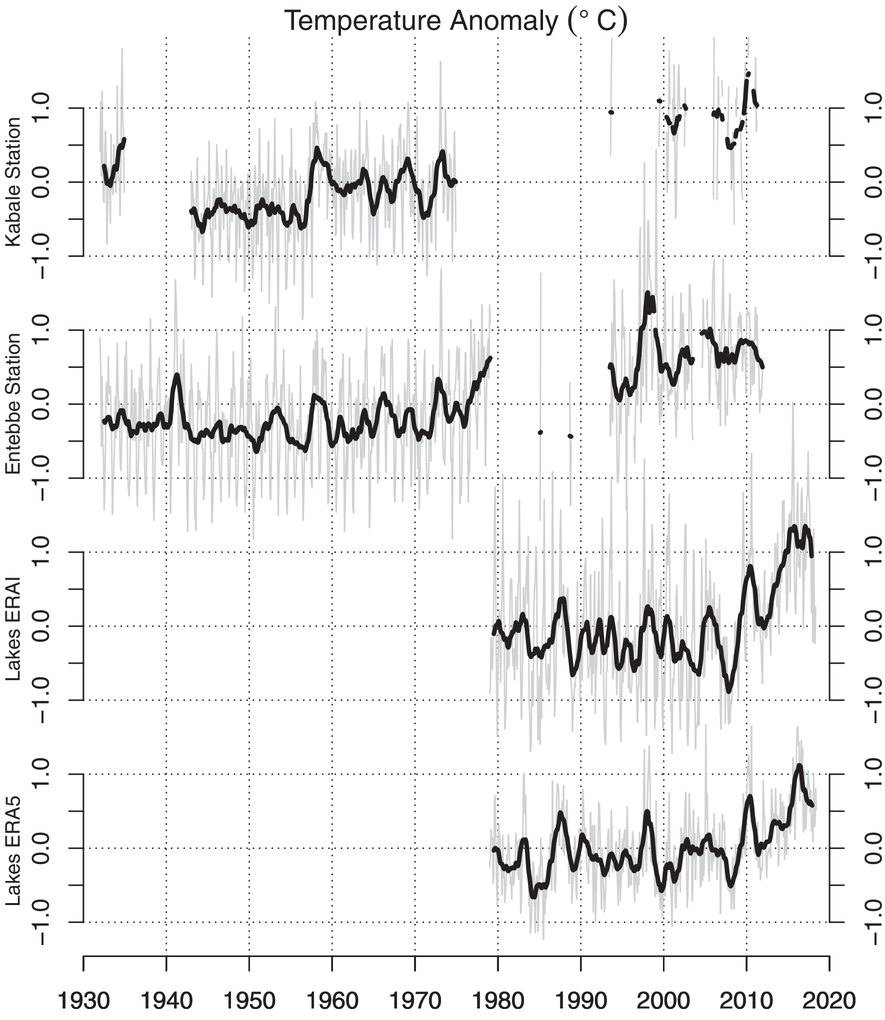
A change in conditions in Bisoke Lake is dated 1460 CE to 1860 CE (diatom zone BS2). The same period is not well covered in the sedimentary record from Muhavura Lake as it partially coincides with the gap in sediment between 1650 CE to 1860 CE. BS2 is characterized by relatively low diatom productivity together with increased PCA 1 axis sample scores and contributions of terrestrial plant material (based on relatively depleted $\delta^{13}C$ 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 characterizes 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 the timing of variations in diatom remains is evident at the two sites from the mid- to late 19th 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-Moreno & 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 30 km to the east and c.1900 m asl. Data from Kabale show a trend of increasing mean annual temperatures

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 75-km 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



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°C 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 0.2–0.6°C 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 (Figure 5).

Increases in aquatic productivity over the last 100 years or so, and particularly from the mid-1970s, are also evident at Lake Bujuku, 3960 m 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 δ^{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 δ^{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 δ^{15}N values (Holtgrieve et al., 2011). They are, however, in agreement with enriched δ^{15}N values in recently deposited sediments from Lake Wandakara, western Uganda (Russell, Mccoy, Verschuren, Bessems, & Huang, 2009).

Contrasting trends in δ^{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, and 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 δ^{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, characterized by high stocking densities and the use of large quantities of fertilizer, 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 to 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. 1,200 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.

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.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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