




# Temporal dynamics of invertebrate community assembly in Lake Victoria since the late Pleistocene based on chitinous remains

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## Abstract

1. Preserved assemblages of invertebrate remains in lacustrine sediment reveal temporal variations of community composition and environmental conditions. However, records for large tropical lakes are scarce. Lake Victoria, the largest tropical lake, has a dynamic history of changes in water level, biogeochemistry and fish community composition over the past ~17,000 calyr BP.
2. In order to quantify changes in the invertebrate assemblage of Lake Victoria from the late Pleistocene throughout the Holocene, we examined chitinous remains of Cladocera and larval dipterans (Chironomidae and Chaoboridae) from a sediment core (37 m water depth) dated from ~13,700 calyr BP to present.
3. We identified four major phases in the invertebrate assemblage throughout this period of lake history. Firstly, Chironomidae and Chaoboridae appeared at low abundances during the earliest stages of lake inundation in the late Pleistocene, at a time when Cladocera were notably absent. Secondly, chaoborids and chironomids increased in abundance during the mid-Holocene, which coincided with high diatom production toward the end of the Holocene African Humid Period. Thirdly, starting ~4,700 calyr BP, *Alona*, a predominantly littoral cladoceran genus, consistently appeared in the invertebrate assemblage alongside changes in mixing regimes and persisted throughout the late Holocene to the present. Fourthly, the arrival of both *Chydorus* and *Bosmina longirostris* marked the establishment of an abundant cladoceran assemblage at ~1,350 calyr BP. The assemblage then gradually shifted toward the increasing dominance of *B. longirostris*, a planktonic cladoceran.
4. Several of the observed changes in the invertebrate assemblage occurred concurrently with changes in climatic conditions in East Africa and diatom productivity that have been previously recorded in Lake Victoria. This multi-millennial record

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of sedimentary invertebrate assemblages in Lake Victoria elucidates some of the temporal development of these communities throughout most of the dynamic modern history of the ecosystem.

#### KEYWORDS

*Chaoborus*, chironomids, Cladocera, East Africa, palaeolimnology

## 1 | INTRODUCTION

One of the major goals of community ecology is to understand covariation of environmental conditions and community composition (Vellend, 2010) over a wide range of timescales (Shurin, 2007; Tomasovych & Kidwell, 2010). Species turnover in communities is typically inferred from either among-site variation along broad environmental gradients (Leibold et al., 1997; Shurin et al., 2010), or from within-site variation over long records of ecosystem monitoring (typically decades; Korhonen et al., 2010). Palaeoecological records extend the timescale over which observations of covariation in communities and environmental processes can be made (Rillo et al., 2022). In lakes, long-term dynamics provide unique insights into how processes associated with community (dis)assembly (e.g., timing of species arrival, shifts in dominance) relate to changes in both regional climatic variability and catchment-scale dynamics at centennial and millennial timescales (Jackson & Blois, 2015; Mergeay et al., 2011). As such, these records can help to reveal how environmental change and species interactions jointly influence community dynamics (Gu et al., 2021; Jeppesen et al., 2005; Otake et al., 2021).

Microfossils isolated from lake sediment cores provide the opportunity to examine the temporal patterns of community assembly. In particular, aquatic invertebrate remains are useful biological indicators of past environmental change and to make inferences about trophic interactions within lake ecosystems (Frey, 1960; Hofmann, 1988; Korhola & Rautio, 2001; Walker, 2001). As aquatic invertebrates are sensitive to both bottom-up and top-down trophic controls, observed shifts in community composition are potentially indicative of changes in both the lake environment and food-web structure (Brahney et al., 2010; Eggermont & Heiri, 2012; Frolova et al., 2017; Heiri et al., 2003; Korponai et al., 2011; Labaj et al., 2021; Sweetman & Smol, 2006; Verschuren, Tibby, et al., 2000). Examining multiple invertebrate taxonomic groups in parallel, with different ecological affinities, strengthens inferences about the underlying causes of compositional change of communities (De Meester et al., 2023; Ursenbacher et al., 2020; Verschuren, Tibby, et al., 2000). For example, a previous study that included an analysis of both cladocerans (water fleas; Crustacea: Branchiopoda) and chironomid larvae (non-biting midges; Insecta: Diptera: Chironomidae), suggested that compositional change of cladoceran communities responded to vegetation and fish predation, whereas chironomids communities responded to fluctuating water levels (Płóciennik et al., 2020).

Palaeolimnological studies have disproportionately focused on temperate rather than tropical lakes based on global lake abundance

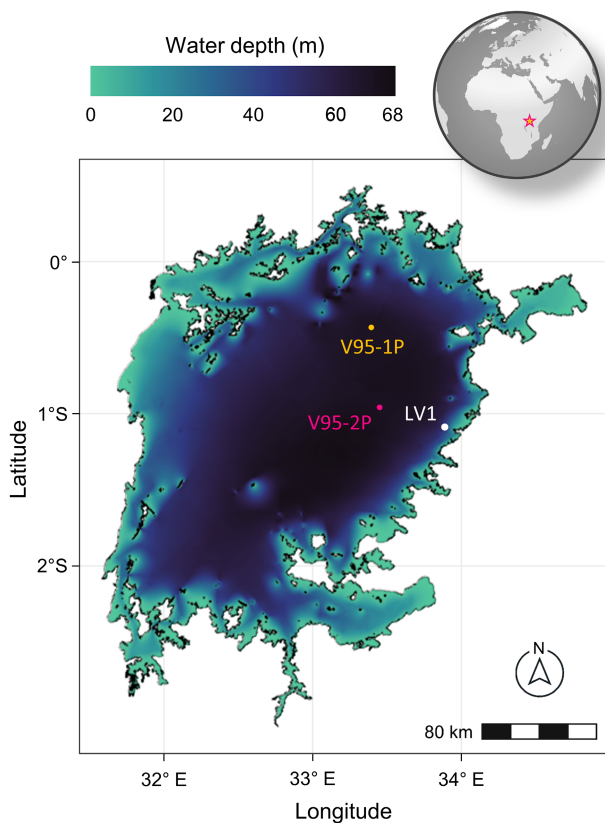
estimates (Escobar et al., 2020; Verpoorter et al., 2014). Many previous studies have documented the history of zooplankton assemblages in temperate lakes, providing important insights into the environmental drivers of changes in these ecosystems over decadal-to-centennial scales (Allen et al., 2011; Cáceres et al., 2005; Otake et al., 2021). However, few palaeoecological records from lakes in East Africa have documented the changes in invertebrate community composition from the initial lake formation and throughout the entire ontogeny of ecosystem development (Table 1). For example, tropical Lake Naivasha varied dramatically in water depth over the past 1,800 years (<5 to ~35-m-deep lake), and zooplankton remains were used to investigate the joint roles of priority effects and species sorting in determining the assembly dynamics of *Daphnia* communities (Mergeay et al., 2011). Invertebrate studies of Lake Victoria have only previously examined changes over the past 200 years (Bridgeman, 2001; Verschuren et al., 2002) despite the modern lake having formed over ~17,000–15,000 cal yr BP (0 cal yr BP = 1950 CE; Johnson et al., 1996, 2000; Temoltzin-Loranca et al., 2023). Additionally, most invertebrate assemblage studies within the region have focused solely on one or two taxonomic groups (Table 1). Therefore, there remains a major gap in our understanding of the long-term successional patterns of invertebrate community assembly in response to environmental variation in large tropical lakes.

Located in East Africa, Lake Victoria (Figure 1) covers an area of ~69,000 km<sup>2</sup> within Kenya, Uganda and Tanzania. As the world's largest freshwater fishery, it supports an estimated 35 million people within the region who rely on the lake as a source of food, employment and water (Njiru et al., 2018). Lake Victoria is of particular interest for the study of community assembly owing to its relatively young geological age (~17,000–15,000 years; Table 1), extraordinary biodiversity and dynamic ecosystem history (Figure 2; Seehausen, 2002). For example, the Lake Victoria ecosystem has not only experienced dynamic periods of climatic variation, water-level fluctuation and ecosystem productivity (Berke et al., 2012; Beuning, Kelts, et al., 1997; Johnson et al., 1996, 1998, 2000; Kendall, 1969; Ngoepe et al., 2023; Stager & Johnson, 2000, 2008; Talbot & Lærdal, 2000; Wienhues et al., 2023), but also has generated a spectacular adaptive radiation of >500 species of haplochromine cichlid fish (Goldschmidt & Witte, 1992; Greenwood, 1974; Meier et al., 2017; Seehausen, 2002). To date, however, no previous study has analysed the fossil invertebrate assemblages of Lake Victoria for a time period spanning more than a few centuries. Here, we examine sedimentary invertebrate remains from a new Lake Victoria sediment core (Figure 1; LVC18\_S1, hereafter LV1, located at 01°06.914' S,

TABLE 1 Palaeolimnological studies within the African Great Lakes region that analysed sedimentary invertebrate remains (X indicates that the taxonomic group was included).

Lake	Age of last refilling (calyr BP unless specified)	Time covered (calyr BP unless specified)	Mean sample resolution (years/samples)	Cladocera	Chaoborus	Chironomids	Ostracods	Study
Lake Victoria	~17,000–15,000 (Temoltzin-Loranca et al., 2023)	~13,700 <sup>a</sup> 200 80	125 8 4	X X X	X X X	X X X	-	LV1 (this study) Verschuren et al. (2002) Bridgeman (2001)
Lake Tanganyika	~12–9 Ma (Cohen et al., 1993)	~8,000 ~4,550 ~2,500 <100 <10 Present	235 270 60 15 1 1	X X X X X X	X X X X X X	X X X X X X	X X X X X X	Kamulali et al. (2022) Palacios-Fest et al. (2005) Alin and Cohen (2003) Park et al. (2003) Eggermont and Verschuren (2003a) Eggermont and Verschuren (2003b)
Lake Malawi	~8.6–4.5 Ma (Delvaux, 1995)	1.2 Ma ~145,000	620 310	X X	X X	X X	X X	Ivory et al., 2016 Cohen et al. (2007) Park and Cohen (2011) Scholz et al. (2011)
Lake Albert	~15,000–14,000 ( <sup>14</sup> C) (Beuning, Talbot, & Kelts, 1997)	~75,000 (±250) <100	6 15	X	X	X	X	Jackson et al. (2015) Park et al. (2003) Cohen (1987)
Lake Nakuru	~12,800 (Richardson & Dussinger, 1986)	~28,000 <sup>a</sup>	280	X	X	X	X	Cohen et al. (1983)
Lake Edward	~18–15,000 (?) (McGlue et al., 2006)	~11,000	n/a	X	X	X	X	Russell et al. (2003)
Crescent Island Crater (Lake Naivasha basin)	~1,800 (Van der Meer et al., 2019)	~1,100	7	X	X	X	X	Verschuren, Laird, and Cumming (2000) Mergeay et al. (2011) Van der Meer et al. (2019)
Lake Turkana	~17,000 (Morrissey & Scholz, 2014)	~500	7	X	X	X	X	Beck et al. (2021)
Lake Oloidien (Lake Naivasha basin)	~200 (Verschuren, 1999)	~120	7	X	X	X	X	Verschuren, Tibby, et al. (2000)
52 low- to mid-elevation lakes (Uganda, Kenya, Tanzania, Ethiopia)	n/a	<10	1	X	X	X	X	Eggermont et al. (2006)

<sup>a</sup>Sediment records that cover the duration of lake ontogeny, and dashes indicate that sediments were analysed for the invertebrate group but no remains were found. Shaded row highlights this study.



**FIGURE 1** Bathymetric map of Lake Victoria, adapted from Hamilton et al. (2022), showing the coring locations of LV1 (white; 01°06.914' S, 33°55.146' E at 37 m water depth), V95-2P (pink; 00°58.67' S, 33°27.32' E at 67 m water depth; Stager & Johnson, 2000) and V95-1P (orange; 00°27.630' S, 33°25.090' E at 68 m water depth; Berke et al., 2012).

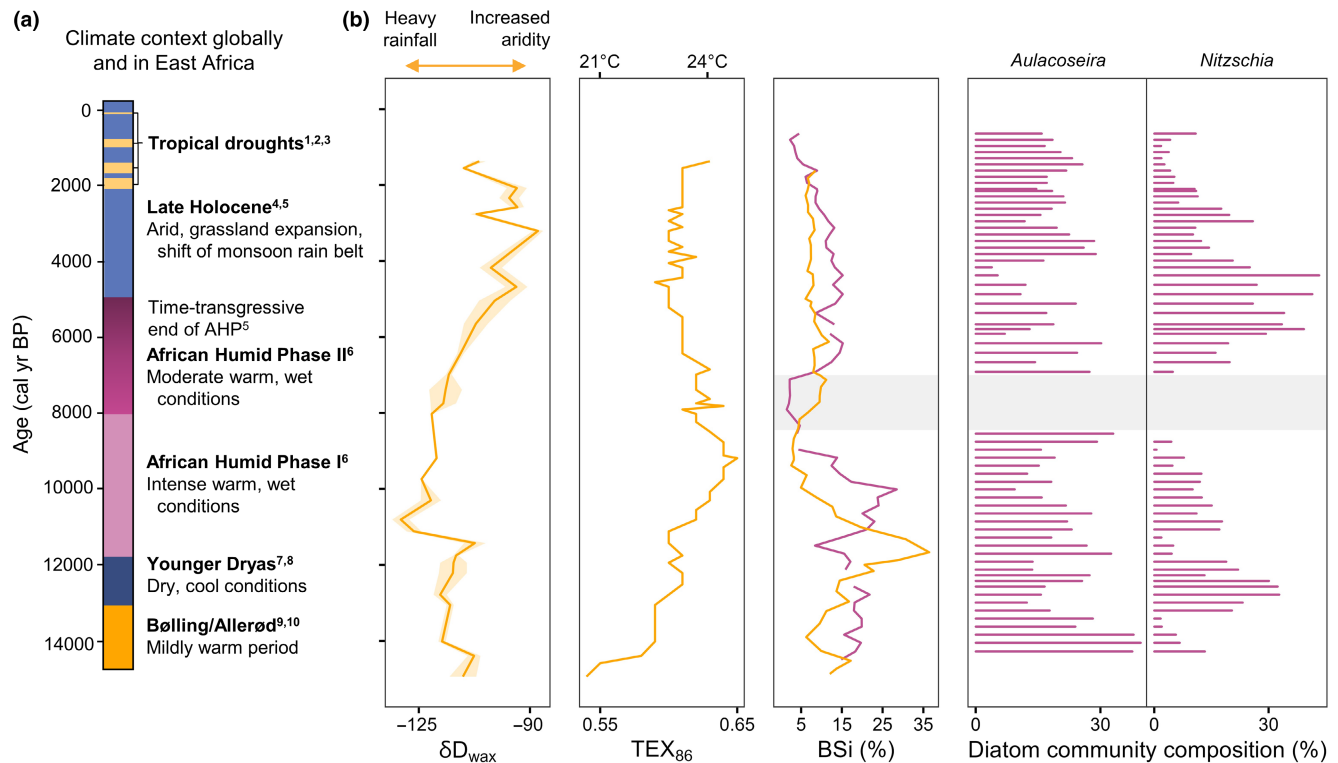
33°55.146' E at a 37 m water-column depth, ~9 km from the nearest shore) to explore changes in invertebrate community composition over ~14,000 years of the lake's history.

The dynamic nature of hydroclimatic and other environmental conditions in East Africa over the past ~17,000 calyr BP (Figure 2) lends itself to multiple research objectives regarding the invertebrate assemblage of Lake Victoria. Firstly, we examine if the timing of arrival and establishment of invertebrate groups coincides with changing regional climatic conditions (e.g., Holocene African Humid Period; AHP). Secondly, we investigate whether changes in species abundances co-vary with proxies of environmental change within the lake inferred from geochemical analysis of previously collected sediment cores described by Stager and Johnson et al. (2000) and Berke et al. (2012). Thirdly, we explore how compositional change over the whole record might provide insight into invertebrate community assembly processes (e.g., rise of a pelagic environment). Additionally, we discuss our results in relation to other environmental changes in the Lake Victoria region; including the timing of lake filling, the radiation of cichlids, the decline of diatom production in the mid-Holocene and changes in wind-driven mixing inferred from diatoms (Berke et al., 2012; Greenwood, 1974; Johnson et al., 2000; Seehausen, 2002; Stager & Johnson, 2000).

## 2 | METHODS

### 2.1 | Study site

Situated in a depression between the eastern and the western branch of the East African Rift, Lake Victoria is moderately shallow (mean depth 40 m, maximum depth 68 m; Johnson et al., 2000) with an extensive surface area of ~68,800 km<sup>2</sup>. As a consequence of the shallow nature of the lake, its large size and its positioning along the equator under variable environmental conditions, the ecological dynamics of Lake Victoria are exceptionally sensitive to climatic changes in the region (Figure 2; Beuning, Kelts, et al., 1997; Johnson et al., 2000; Kendall, 1969; Stager et al., 1986; Stager & Johnson, 2000). The lake is at the intersection of savanna, rainforest and Afromontane biomes; thus, minor climatic changes (e.g., precipitation or temperature) can cause major lake-level fluctuations and shifts in the major terrestrial biome surrounding the lake (Temoltzin-Loranca et al., 2023). Previous work has speculated that the formation of the lake basin ~400,000 years ago was followed by several lake level regressions and transgressions that may have occurred corresponding to a combination of high- and low-latitude climate forcing, and catchment hydroclimate and ecosystem variability (Johnson et al., 2000). The most recent major desiccation of the modern lake basin is estimated at ~17,000 calyr BP (Johnson et al., 1996, 2000; Temoltzin-Loranca et al., 2023), contemporaneous with other lakes in the region (Beuning, Talbot, & Kelts, 1997; Gasse, 2000). Following the late Pleistocene desiccation, the lake began to fill at ~16,600 calyr BP and modern lake levels were established ~14,000–10,000 calyr BP (Wienhues et al., 2023). Thus, the coring location of LV1 was continuously inundated over the period which our core encompasses. During this past history of the modern lake, the region experienced alternating wetter and drier periods, most notably during the AHP from ~11,500 to 5500 calyr BP (Berke et al., 2012; de Menocal et al., 2000), associated with changes from savannah to rainforest and back to savannah, as inferred from pollen data (Kendall, 1969; Temoltzin-Loranca et al., 2023). Additionally, Berke et al. (2012) measured two geochemical proxies, TEX<sub>86</sub> and  $\delta D_{\text{wax}}$ , indicative of lake water temperature and precipitation, respectively (Castañeda & Schouten, 2011), from V95-1P (Figure 1) to examine the surrounding climatic changes.  $\delta D_{\text{wax}}$  values are generally inversely correlated with rainfall amount in the tropics (Rozanski et al., 2013), and have been shown to be a useful indicator of hydroclimate variability throughout Africa (Tierney et al., 2008). Previous research has posited that such changes in monsoonal circulation and precipitation–evaporation relationships could be important drivers of community change across the entire food web. For example, previous work has inferred four phases of diatom production based on biogenic silica (BSi) and diatom microfossils preserved in a previously examined sediment core, V95-2P (Figures 1 and 2; Stager & Johnson, 2000). Furthermore, within this relatively short geological history of the modern lake the adaptive radiation of haplochromine cichlid fish produced >500 endemic species spanning 14 different trophic groups (Greenwood, 1974, 1980; Kaufman, 1992; Seehausen et al., 1997; Seehausen, 2002).



**FIGURE 2** Summarised climate context globally and in East Africa over the past ~14,000 cal yr BP (a), as well as geochemical and diatom proxies analysed from two previously collected sediment cores from Lake Victoria, V95-2P (pink lines and bars) and V95-1P (orange lines), plotted along the associated age-depth models (b; adapted from Berke et al., 2012, Johnson et al., 2000, and Stager & Johnson, 2000). Berke et al. (2012) measured TEX<sub>86</sub> temperature proxy values in V95-1P, to reconstruct down-core records of lake water temperatures, and ice-volume corrected  $\delta D_{wax}$  of the C<sub>28</sub> leaf wax fatty acid methyl ester (orange shading indicates the mean error of replicated analyses for each sample), to investigate regional rainout history. Stager and Johnson (2000) counted diatom community composition (%; only dominant taxa shown) in deep-water sediments from V95-2P. Biogenic silica (BSi, %) was measured for both cores, with grey shaded area indicating the relative absence of preserved diatom remains in V95-2P. References for human and climate summary include: <sup>1</sup>Russell and Johnson (2005), <sup>2</sup>Marchant (2022), <sup>3</sup>Battistel et al. (2017), <sup>4</sup>Gasse (2000), <sup>5</sup>Shanahan et al. (2015), <sup>6</sup>Liu et al. (2017), <sup>7</sup>Gasse et al. (2008), <sup>8</sup>Carlson (2013), <sup>9</sup>Alley and Clark (1999), <sup>10</sup>Tierney et al. (2008).

## 2.2 | Sediment core analyses

Sediment cores were collected from Lake Victoria (Figure 1; LV1) in October 2018 using an UWITEC piston corer (Mondsee, Austria) on a floating platform located ~9 km offshore at a water depth of 37 m. Given the relative agreement between BSi profiles of LV1 and other deep-water sediment cores from Lake Victoria over the same age range (V95-2P,  $r=0.54$ ,  $p<0.001$ ; V95-1P,  $r=0.56$ ,  $p<0.001$ ), our record represents a spatial region toward the eastern sector of the lake that is unlikely to be completely anomalous to deepwater representations of planktonic versus littoral invertebrate assemblages. The LV1 composite stratigraphy of 723 cm sediment depth was created from nine core segments from two parallel coring locations, which were correlated based on X-ray fluorescence element profiles of Zr, Ti and K/Ti because lithological markers were not present in the core. The core consisted of uniform fine organic mud with no erosional unconformities and a sand layer at 720 cm (~13,800 cal yr BP) indicating the inundation of LV1 as lake levels rose (Wienhues et al., 2023). A robust and reproducible chronology for LV1 was established using 30 radiocarbon dates (Figure S1) measured with accelerator mass

spectrometry; see Temoltzin-Loranca et al. (2023) for more details on the coring campaign and chronology. Age estimates were rounded to the nearest 50 years and the error represents the 95% confidence interval (CI), which on average represents  $\pm 520$  years (Figure S1). We extracted the BSi content of LV1 sediments using the procedure by Ohlendorf and Sturm (2008) and then measured it with inductively coupled plasma mass spectrometry. Before leaching, organic material was removed from the sample with hydrogen peroxide (Mortlock & Froelich, 1989). BSi is reported as accumulation rate (mg BSi cm DW<sup>-2</sup> year<sup>-1</sup>; DW, dry sediment weight) for LV1 to account for variable sedimentation rate (Figure S1).

## 2.3 | Sediment preparation

Invertebrate remains were isolated from lake sediment subsamples by chemical digestion and wet sieving ( $\geq 38$ - and  $\geq 100$ - $\mu$ m size fractions) and prepared for microscopy analyses by mounting on microscope slides for identification (Brooks et al., 2007; Korhola & Rautio, 2001; Szeroczyńska & Sarmaja-Korjonen, 2007; Walker & Paterson, 1985).



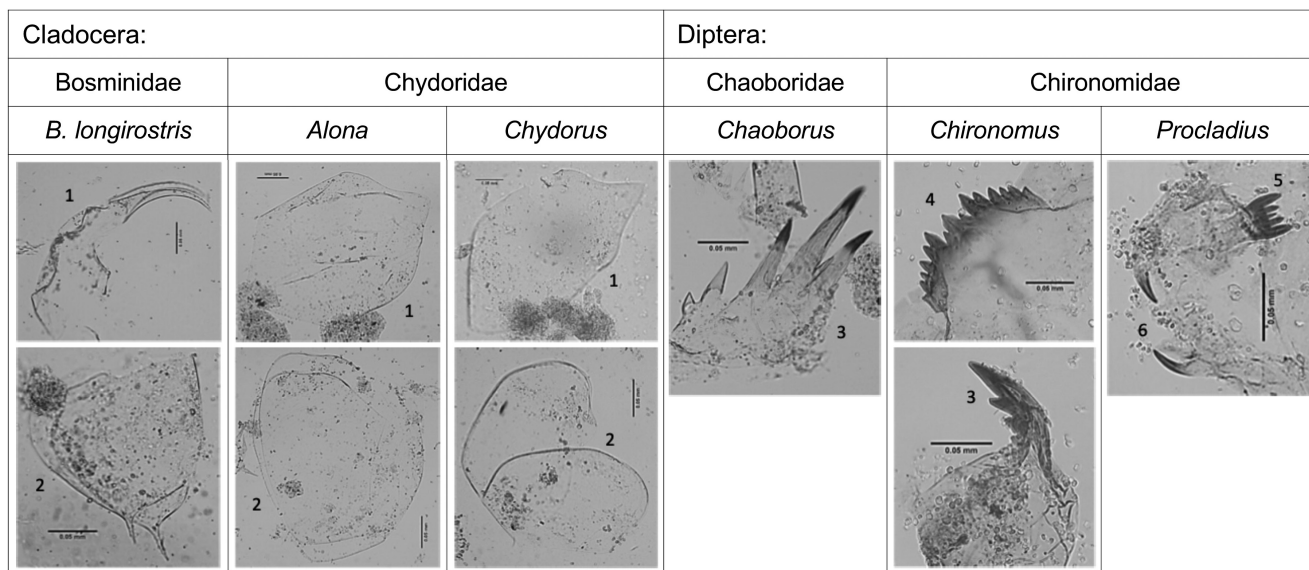


FIGURE 3 Representative images of invertebrate remains identified in Lake Victoria sediments: (1) headshield, (2) carapace, (3) mandible, (4) mentum, (5) ligula and (6) dorsomentum. Scale bars represent 0.05 mm.

All subfossil remains of cladocerans and aquatic dipterans (e.g., carapaces, headshields, mandibles, head capsules) were tabulated separately and used to determine the minimum number of individuals as this method is less likely to overestimate the significance of individual taxa (Zharov et al., 2022). Individual remains were identified to the most detailed taxonomic level possible (Figure 3). Microscope slides were examined in their entirety to avoid bias arising from a non-random distribution of remains under the coverslip. Published identification literature for aquatic invertebrate remains focus on temperate rather than tropical regions (Brooks et al., 2007; Korosi & Smol, 2012a, 2012b); therefore, many of the remains could only be identified to the genus level consistent with identifications of contemporary taxa (e.g., Ngupula et al., 2010; Vincent & Mwebaza-Ndawula, 2012). Taxa that did not occur in more than three samples at  $\geq 1\%$  relative abundance were not included in our analyses (Bredesen et al., 2002).

### 2.3.1 | Identification and enumeration of Cladocera

Sediment subsamples ( $\sim 1 \text{ cm}^3$ ) of 1-cm thickness for Cladocera analysis were collected along the length of the core ( $n=103$ ; sampling intervals typically ranged from every 2 cm upcore to 15 cm downcore). The sediment was mixed with a 10% potassium hydroxide solution and heated to  $\sim 70^\circ\text{C}$  for 10 min with gentle mixing to adequately separate cladoceran remains from other sediment particles and minimise further fragmentation (Frey, 1959; Matveev, 1986; Verbruggen et al., 2010). The mixture was subsequently washed through a 38- $\mu\text{m}$  mesh to remove finer materials. The retained material was rinsed with tap water into labelled vials and a small amount of ethanol was added to prevent fungal growth. In order to calculate the concentration of individuals in each sample, one *Lycopodium clavatum* spore tablet containing a known amount of marker spores (Department

of Geology, Lund University, Batch 3862, manufactured October 2015, mean number of spores per tablet = 9,666,  $\sigma = 671$ ; Supporting Information S1) was dissolved in each sample vial.

Following sediment preparation, the cladoceran solution ( $\sim 75 \mu\text{l}$ ) for each sample was mounted on glass slides while ensuring that the sample was adequately mixed. The solution was mounted on glass slides that were examined at  $\times 200$ – $400$  magnification via bright-field illumination using a compound microscope. *Lycopodium* marker spores were counted simultaneously to microfossils in order to calculate the concentration of individuals in each sample, and a photo library of microfossil remains was compiled in a data repository for further analyses.

The taxonomic resolution of our analyses was limited by the preservation of conspicuous diagnostic features. All *Bosmina* headshields that displayed a clear lateral headpore were identified as *B. longirostris*, which is further supported by contemporary zooplankton samples that identify it as the only *Bosmina* species in Lake Victoria (Mwebaza-Ndawula et al., 2005; Ngupula et al., 2010; Vincent & Mwebaza-Ndawula, 2012; Waya & Mwambungu, 2004; Yongo & Outa, 2017). Headshields and carapaces of *Alona* and *Chydorus* could not be reliably identified to species.

### 2.3.2 | Identification and enumeration of Chaoborus and chironomids

Sediment subsamples ( $\sim 4$ – $7 \text{ cm}^3$ ) intended for chironomid & *Chaoborus* analysis were collected approximately every 10 cm throughout the composite core ( $n=83$ ). Subsamples were wet-sieved with no chemical preprocessing into two size fractions: 100–200  $\mu\text{m}$  (intermediate) and  $\geq 200 \mu\text{m}$  (larger). Chironomid and *Chaoborus* remains were picked individually from both sieved

fractions using a stereomicroscope ( $\times 5\text{--}60$  magnification) and placed on a microscope slide (Brooks et al., 2007). The slides were allowed to air-dry and then permanently affixed using Euparal (Carl Roth), and examined with a compound microscope at  $\times 100\text{--}400$  magnification. The sum of the remains found in the two sieved fractions was used for analyses.

Similar to Cladocera, Diptera remains were reliably identifiable only to the genus level (based on Brooks et al., 2007; Courtney-Mustaphi et al., 2024). However, previous work on short cores in Lake Victoria identified two species of *Chaoborus*: the large, offshore *C. edulis* and the smaller, littoral *C. anomalous* (Bridgeman, 2001). Earlier sediment core analyses of Lake Victoria identified *Procladius* remains as *P. brevipetiolatus*, which are widely distributed throughout East Africa (Eggermont et al., 2008; Freeman and Cranston, 1980), and the *Chironomus* taxon as *C. imicola* (Verschuren et al., 2002).

## 2.4 | Data analyses

The influx of individuals to the sediment was calculated by dividing the total number of individuals per  $\text{cm}^3$  (concentrations) by the number of years per cm of depth (sedimentation rate; Temoltzin-Loranca et al., 2023). For cladoceran subsamples, the volume of sediment screened for microfossils (Figure S2) was determined by multiplying the volume of the entire subsample by the proportion of marker spores counted relative to the total number of marker spores added (Szeroczyńska & Sarmaja-Korjonen, 2007). The influx of *Chaoborus* was calculated from the sum of *Chaoborus* and sediment volume from both sieve fractions. Influxes were square-root transformed for visualisation purposes. Additionally, we calculated the ratio of benthic to planktonic Cladocera taxa ( $[\textit{Alona} + \textit{Chydorus}]/\textit{Bosmina}$ ) to examine the succession from a benthic to planktonic community.

Multivariate nonparametric change point analysis (Matteson & James, 2014) was used to detect significant changes in the cladoceran and dipteran assemblages, respectively, as well as environmental variables (Figure 1). The number and location of change points was estimated using the E-Aggl method (*ecp* package, version 3.1.3; James & Matteson, 2023) in R version 4.2.2 (R Development Core Team, 2021). This method performs a hierarchical agglomerative estimation of multiple change points of both the mean and variance ( $\alpha = 1$ ; BSi change point based only on mean) of a time series by optimizing a goodness-of-fit statistic. It uses an initial segmentation of the data (member = number of observations) with the assumption that the observations are independent with a finite moment index. Change points with fewer than three observations on either side were omitted. We completed a linear interpolation of the chironomid taxa time series, to substitute missing values when paired with the *Chaoborus* time series, using the “interpTs” function (*wql* package, version 1.0.0; Jassby et al., 2022) in R version 4.2.2 (R Development Core Team, 2021). Additionally, we performed a permutation test (*wPerm* package, version 1.0.1; Weiss, 2022) for relationships between environmental variables

(BSi,  $\text{TEX}_{86}$  and  $\delta D_{\text{wax}}$ ; values were linearly interpolated when necessary) and dipteran taxa, using Pearson correlation coefficients. Correlations were not possible for cladoceran taxa because of limited overlap between datasets.

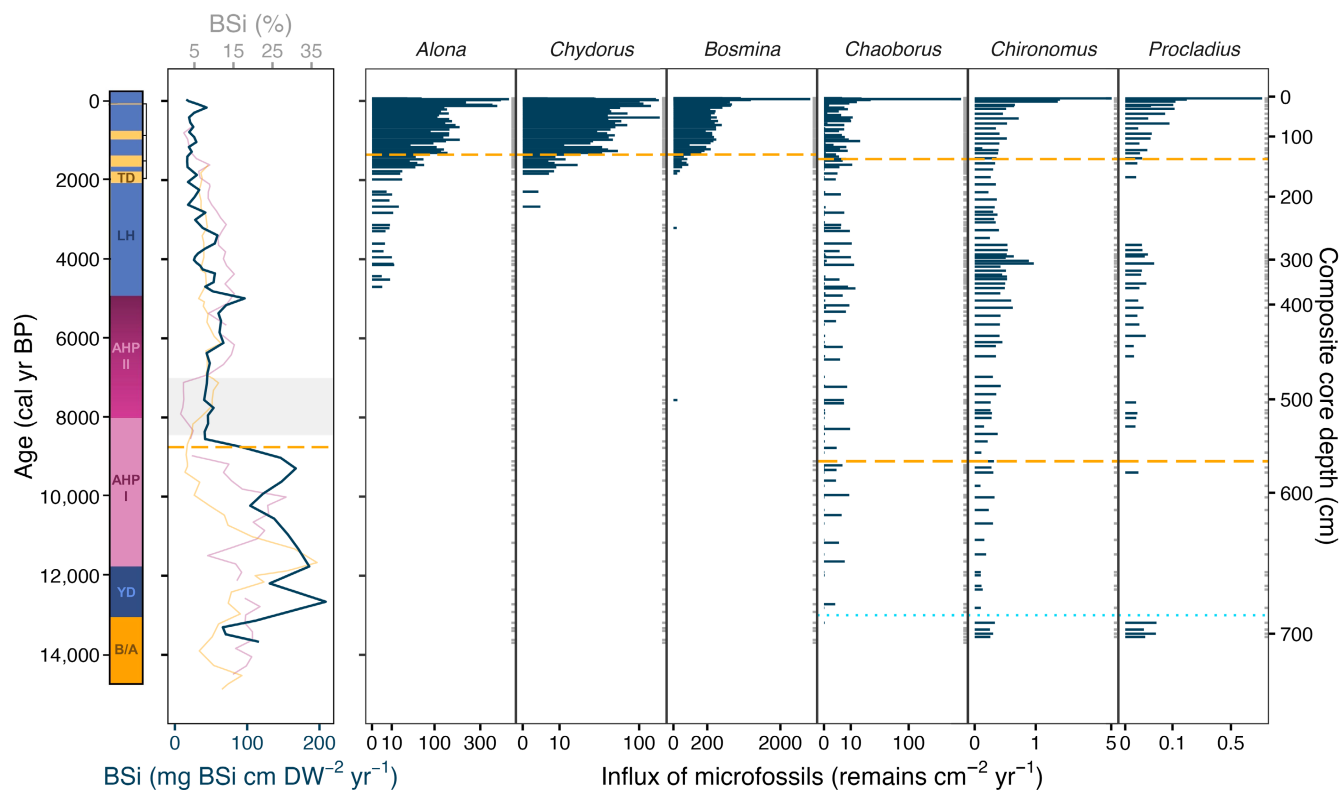
## 3 | RESULTS

Cladoceran microfossils comprised three major taxonomic groups: *Bosmina longirostris*, *Alona* and *Chydorus* (Figures 4 and S3). Likewise, three main taxa were identified among dipteran microfossils: *Chaoborus*, *Chironomus* and *Procladius* (Figures 4 and S3). Count sizes were relatively low (Figure S2) in comparison to previous analyses in small lakes and in temperate biomes (Kurek et al., 2010). A minimum count threshold was not reached for samples below 140cm core depth, corresponding to sediments older than  $\sim 1,420$  calyr BP, owing to microfossil scarcity; however, sampling effort was consistent, if not greater, downcore in terms of the number of samples and sediment volume examined (Figure S2). Additionally, the number of cladoceran taxa found throughout LV1 is consistent with the number of taxa identified in previous short core analyses from Lake Victoria (Bridgeman, 2001). Likewise, although total counts (ranging from 0 to 87 individuals) of chironomids in each sample were well below the typical recommended number, the total volume of sediment picked was much greater relative to most published analyses (Figure S2; mean =  $8\text{cm}^3$ ). Sididae ( $n = 9$ ), *Cricotopus/Orthocladius* ( $n = 11$ ) and *Tanytarsus* ( $n = 13$ ) remains were rarely and intermittently observed, and thus were not included in our statistical analyses (Figure S3). Additionally, other aquatic microfossils were observed throughout the core (Figure S4) and included two groups of algae (siliceous remains of Bacillariophyceae [*Nitzschia* and *Cymatopleura*] and Chlorophyceae [*Pediastrum* spp.; (Millington & Gawlik, 1967)]), as well as organic remains of flatworm oocytes (Platyhelminthes: Rhabdozoela; Haas, 1996).

The overall patterns of LV1 BSi throughout the late Pleistocene and Holocene record of Lake Victoria is strongly correlated with cores V95-1P and V95-2P (correlation with V95-2P,  $r = 0.54$ ; correlation with V95-1P,  $r = 0.57$ ) despite some temporal and spatial offset (Figure 4). Accumulation rates of BSi in LV1 sediments ranged from  $\sim 16$  to  $210\text{mg BSi cm DW}^{-2}\text{year}^{-1}$ , displaying maximum values during lake refilling, a subsequent period of low accumulation marked by a significant change point at  $\sim 8,750$  calyr BP, and then a slight increase—although not to early Holocene values—near the end of the AHP. Two significant change points were identified in  $\text{TEX}_{86}$  values throughout the lake's history at  $\sim 9,200$  and  $\sim 11,100$  calyr BP, as well as a change point at  $\sim 5,050$  calyr BP in  $\delta D_{\text{wax}}$ .

### 3.1 | Invertebrate community of the late Pleistocene to early Holocene ( $\sim 13,700\text{--}9,100$ calyr BP)

The bottom-most sediments of LV1, representing  $\sim 13,700\text{--}13,200$  calyr BP, contained remains of *Chironomus* and *Procladius*, with *Chaoborus* emerging shortly thereafter at  $\sim 13,200$  calyr BP



**FIGURE 4** Biogenic silica (BSi) concentrations throughout LV1 (dark blue;  $\text{mg BSi g SW}^{-1} \text{ year}^{-1}$ ), V95-1P (orange; %; Johnson et al., 2000) and V95-2P (pink; %; Stager & Johnson, 2000) plotted along their original age–depth scales, as well as the square-root transformed influx of invertebrate microfossils ( $\geq 38$  and  $\geq 100 \mu\text{m}$  size fractions) observed throughout LV1. Grey tick marks on the right axis indicate sampling depths along the core. Orange dashed lines indicate the location of multivariate change points of the cladoceran and dipteran assemblages. The grey shaded zone represents the relative absence of preserved diatom remains in V95-2P (Stager & Johnson, 2000) and the blue dotted line indicates the end of first stage of rapid lake-level rise (Wienhues et al., 2023). Climate zones are referenced in Figure 2 and include: B/A, Bølling/Allerød; YD, Younger Dryas; AHP, African Humid Period (phases I & II); LH; late Holocene; TD, tropical droughts.

(Figure 4). Notably, cladoceran remains were absent during the late Pleistocene and into the Holocene ( $\sim 13,700$ – $4700$  cal yr BP) at LV1. *Chironomus* remains were consistently present at low abundances starting from the inundation of LV1 throughout the entire remaining history of the lake. Meanwhile, *Procladius* abundances fell below detection limits through much of this phase. Despite few *Procladius* observations,  $\text{TEX}_{86}$  palaeotemperature was negatively correlated with *Procladius* throughout this phase ( $r = -0.53$ ; Table S1). *Tanytarsus* and *Cricotopus/Orthocladus* remains were not present during this early phase of the lake (Figure S3).

### 3.2 | Rise of Chironomidae and Chaoborus during the African Humid Period ( $\sim 9,100$ – $1450$ cal yr BP)

Chironomidae and *Chaoborus* remains were present at relatively low abundances throughout the sediment record with small, yet significant, increased influxes from  $\sim 9,100$  to  $1,450$  cal yr BP as indicated by multivariate change point analysis. *Procladius* appeared consistently in the LV1 record starting at  $\sim 6,500$  cal yr BP and remained present at low abundances until  $\sim 3650$  cal yr BP when abundances fell below detection limits. Additionally, *Tanytarsus* and *Cricotopus/*

*Orthocladus* individuals were first observed during this phase of increased Diptera abundances (Figure S3). During this phase, *Chironomus*, but not *Procladius*, was correlated with  $\delta D_{\text{wax}}$  ( $r = 0.36$ ) and  $\text{TEX}_{86}$  ( $r = -0.38$ , Table S1).

### 3.3 | Rise of Cladocera in the late Holocene ( $\sim 4,700$ – $1,350$ cal yr BP)

Although individual cladoceran remains were occasionally observed during the first ten millennia of the lake's history (unidentifiable Chydoridae postabdomen:  $n = 5$ , *B. longirostris* carapace:  $n = 1$ ), Cladocera remains were largely absent throughout the LV1 sediment core prior to the appearance of *Alona* at  $\sim 4700$  cal yr BP (Figure 4). *Alona* remained at relatively low abundances for the following few millennia until the appearance of *Chydorus* and *Bosmina* consistently in the sediment record at  $\sim 1,850$  cal yr BP. This appearance was followed by the establishment of an abundant cladoceran assemblage, which is indicated by the multivariate change point detected at  $\sim 1,350$  cal yr BP (Figure 4). Another notable feature of this phase included increased influxes of the diatom genera *Cymatopleura* and *Nitzschia*, as well as oocytes of the flatworm Rhabdocoela (Figure S4).



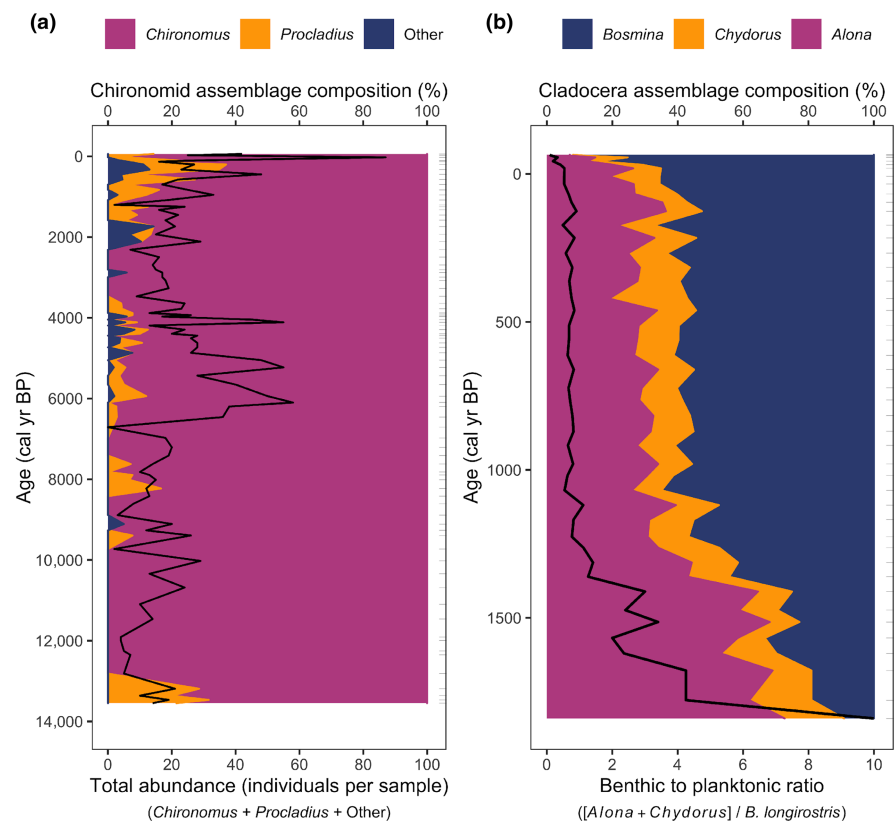
### 3.4 | Rise of an abundant cladoceran assemblage with planktonic dominance in the late Holocene (~1,350 cal yr BP–present)

All cladoceran taxa displayed substantial increases in abundance following the establishment of the new abundant cladoceran assemblage at ~1,350 cal yr BP, indicated by multivariate change point analysis (Figure 4). The appearance of *B. longirostris* in the sediment record was followed by a rapid decrease in the proportion of benthic to planktonic cladoceran taxa, and *B. longirostris* quickly became the dominant species within the last ~1,200 years (Figure 5b). Following the transition to *B. longirostris* dominance, the community composition of cladoceran taxa, and thus the proportion of benthic to planktonic taxa, remained relatively stable until the past few 100 years. In the most recent sediments, a dramatic increase in the abundance of *B. longirostris* coincided with decreases in benthic cladoceran taxa (Figure 5b). However, this increase may be an artefact of the increased sedimentation rate in the uppermost samples of LV1 rather than an ecological indicator. Likewise, *Chaoborus*, *Procladius* and *Chironomus* displayed steadily increasing abundances in the top sediment layers, with remains approximately two times greater in surface sediments than other sediment subsamples (Figure 4). BSi accumulation was positively correlated with both *Chironomus* ( $r=0.76$ ) and *Procladius* ( $r=0.68$ ) during this phase (Table S1). *Tanytarsus* and *Cricotopus/Orthocladius* individuals continued to be occasionally observed during this phase (Figure S3). The influx of *Nitzschia*, *Pediastrum* spp. and Rhabdozoela oocytes also remained relatively higher

than before the late Holocene with major increases in surface sediments (Figure S4).

## 4 | DISCUSSION

Our results demonstrate multiple major invertebrate assemblage changes related to the first appearance and establishment of taxa for the eastern region of Lake Victoria in Tanzania during the late Pleistocene and Holocene. Firstly, *Chaoborus*, *Chironomus* and *Procladius* were all present at low abundances in the early history of LV1 (i.e., late Pleistocene–early Holocene, ~13,700–9,100 cal yr BP): a period when Cladocera remains were notably absent from the record. Secondly, all dipteran larvae exhibit a phase of increased abundance during the mid-Holocene (~9,100–1,450 cal yr BP) that corresponds with rising diatom production (BSi) after a period of low productivity during the early- to mid-Holocene. Thirdly, cladoceran taxa were largely absent from the sediment record until the appearance of *Alona* at ~4,700 cal yr BP, which coincided with the end of the AHP (Liu et al., 2017; Shanahan et al., 2015). Lastly, the arrival of *Chydorus* and *B. longirostris* in the late Holocene at ~1,850 cal yr BP was followed by the initial establishment of an abundant cladoceran assemblage at ~1,350 cal yr BP. We then observe a progressive shift over the following 500 years toward conditions that continued to favour all cladocerans, particularly planktonic taxa, which has been sustained for the past ~1,200 years. Many species of the plankton community are not preserved in lake sediments (e.g., copepods, rotifers), and only typically well-preserved cladoceran taxa (Bosminidae



**FIGURE 5** Community composition of Chironomidae over the past ~13,700 cal yr BP (a) and Cladocera over the past ~1,850 cal yr BP (b) from LV1. Black lines indicate the total abundance (number per sample) of chironomid individuals (a) and the ratio of benthic to planktonic cladoceran taxa (b).

and Chydoridae; Hann, 1989) were observed in Lake Victoria sediments (consistent with results of short cores; Bridgeman, 2001) compared to the full suite of genera encountered in modern water-column samples (*Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Moina* and *Macrothrix*; Waya & Mwambungu, 2004; Ngupula et al., 2010) that are often not as well-preserved. Therefore, we recognise that the remains of cladoceran and dipteran taxa provide only limited insights into the entire planktonic food web of Lake Victoria. Nevertheless, we present the first study of cladoceran and dipteran assemblages over the modern history of Lake Victoria at a relatively high temporal resolution compared to other studies in the region. The patterns observed indicate major shifts in the invertebrate community that occur concomitant with major regional changes in climate and are consistent with inferences made from previous palaeolimnological proxies from Lake Victoria. Differences between the spatial and temporal uncertainty of the various Lake Victoria sediment cores collected over the years leads to some difficulties integrating our results with those of previous studies (e.g., Berke et al., 2012; Stager & Johnson, 2000). For example, the chronology of V95-2P was based on only three radiocarbon dates, excluding dates between ~1,450 and ~10,300 calyr BP, compared to the chronology of LV1 based on 30 radiocarbon dates (Temoltzin-Loranca et al., 2023). Therefore, further efforts examining lake conditions throughout the lake's history will be necessary to elucidate the specific drivers of the observed changes in the invertebrate assemblage beyond those examined here. However, this study still provides a valuable contribution by discussing the first long-term record of invertebrate assemblage dynamics in Lake Victoria within the ecological context provided by previous studies, which subsequent studies with greater spatial analyses can build upon further.

#### 4.1 | Invertebrate community of the late Pleistocene to early Holocene (~13,700–9,100 calyr BP)

During the early dynamic period of level change and subsequent stabilization, chironomid remains were consistently present at low abundances starting from the inundation of LV1 at ~13,700 calyr BP, with *Chaoborus* then appearing ~13,200 calyr BP. Subsequently, both *Chironomus* and *Chaoborus* are then consistently present into the Younger Dryas and AHP. Although, *Procladius* remains disappear between ~12,800 and ~9,700 calyr BP, abundances are likely to have fallen just below the detection limits. The oldest sediments at LV1 would have been deposited ~13,700 calyr BP, almost contemporaneous with a period of very dynamic lake-level variations (Wienhues et al., 2023). Therefore, our record at LV1 may not capture the earliest stage of community succession in Lake Victoria ~17,000–13,700 calyr BP when the modern lake basin would have consisted of an extensive landscape of wetlands with fluctuating extents of inundation by variation in lake levels (Temoltzin-Loranca et al., 2023; Wienhues et al., 2023). *Chironomus* and *Procladius* are

known to be early colonisers, surviving even in temporary pools of water from rainfall (Frouz et al., 2003; Layton & Voshell Jr., 1991; Verschuren, 1997); thus, it is unsurprising that they are established at the base of LV1 immediately following inundation. They tend to predominate in sediments characterised by fine sand or silt with high organic content (Pinder, 1986), which is typical for contemporary Lake Victoria wetlands and sheltered vegetated embayments. Likewise, *Cricotopus/Orthocladius* are commonly found in littoral areas (Coffman & Ferrington, 1996). As lake levels continued to rise as a result of intensification of monsoon systems during the Bølling/Allerød (Wienhues et al., 2023), the appearance of pelagic *Chaoborus* and disappearance of benthic *Procladius* coincided with the transition to open lacustrine conditions at LV1 when water levels would have risen by >30m within a few centuries. Establishment of a permanent outflow by ~13,200 calyr BP (Wienhues et al., 2023) coincides with the temporary disappearance of *Procladius* in LV1, indicating that the accompanying environmental shifts (e.g., water depth, nutrient cycling) did not favour high abundances of *Procladius*. In other tropical African Lakes, *Procladius* tends to be less common with increasing salinity (Verschuren, Tibby, et al., 2000) suggesting that lake freshening (i.e., decreased salinity) was not a driver of the decreased abundances. Additionally, *Procladius* was negatively correlated with lake temperature throughout this phase ( $r = -0.53$ ), no major deviations in lake temperature coincided with the disappearance of *Procladius* in the sediment record. Despite climatic changes throughout the rest of this phase, *Chironomus* and *Chaoborus* continued to persist at relatively low abundances concurrent with consistently high diatom production and gradually increasing temperatures.

A notable feature of this early phase is the veritable absence of Cladocera. Cladoceran remains are composed of essentially the same chitinous material as Chironomidae and *Chaoborus*. Therefore, the presence of *Chaoborus* and chironomid remains throughout the lowermost portion of the core suggests that the preservation environment within the sediment column would likely have been suitable for the preservation of cladoceran microfossils as well. Although we cannot exclude the role of taphonomic processes (e.g., degradation) definitively because cladoceran remains may not be as robust in terms of skeletal thickness as other chitinous remains (i.e., *Chaoborus* and Chironomidae remains), we did not observe substantial changes in preservation quality of the remains across the core. Therefore, we proceeded under the assumption that the absence of Cladocera in lower sediment intervals was not likely to have been the result of differential preservation. This is further supported by the presence of a few cladoceran remains before their initial appearance and community establishment, which suggests that Cladocera were likely to have been present at very low abundance below the detection limit. Owing to their intermediate position in the food web, abundances of cladoceran taxa would have been limited by climatic factors influencing habitat conditions (e.g., water chemistry) and food availability, competition with other zooplankton, or predation pressures (de Bernardi et al., 1987; Dodson et al., 2010). For example, large zooplankton herbivores have been observed to suppress abundances

of small cladocerans (Vanni, 1986). However, given the ubiquitous nature of Cladocera across almost all freshwater, including in the tropics (Dumont, 1994), their relative absence throughout this time is notable. Their rarity upon first occurrence in the core also leads to some uncertainty over our inference about the precise arrival time in the lake and the dynamics of their rise in abundance.

#### 4.2 | Rise of Chironomidae and Chaoborus during the African Humid Period (~9100–1450 calyr BP)

During the AHPI, increased abundances of *Chaoborus*, *Chironomus*, and *Procladius* occurred around ~9,100 calyr BP. This timing coincided well with both the decrease in diatom production inferred from BSi, which exhibited a significant change point at ~8,750 calyr BP with decreases observed even earlier and the  $TEX_{86}$  lake temperature change point at ~9,200 calyr BP. Although *Chironomus* and *Procladius* co-varied throughout this phase ( $r=0.6$ ,  $p=0.001$ ), *Chironomus* were consistently more abundant than *Procladius*. Both taxa are known to be abundant in warm water lakes (Heiri et al., 2011) and lake temperatures were consistently within the optimal range for both *Chironomus* and *Procladius* (16–26°C; Eggermont et al., 2010). Taxon-poor assemblages that are dominated by *Chironomus* and *Procladius*, are commonly indicative of oxygen limitation (Brooks et al., 2007; Quinlan & Smol, 2001). Whereas *Chironomus* is one of the most tolerant genera of low oxygen conditions as a result of their high haemoglobin concentrations (Nagell & Landahl, 1978; Panis et al., 1996), *Procladius* are typically less tolerant of anoxic conditions (Verschuren et al., 2002). Thus, the ratio of *Procladius* to *Chironomus* has previously been used in palaeolimnological research in Lake Victoria to make inferences about hypolimnetic oxygen (short core V96-5MC representing the past 20 years, 68 m water depth; Verschuren et al., 2002). Increasing relative contributions of *Procladius* to the chironomid assemblage during the AHPII through much of the late Holocene, as well as *Tanytarsus* and *Cricotopus/Orthocladus*, may be indicative of increased water-column mixing promoting oxygenation of bottom waters. This is supported by the diatom record of V95-2P in which Stager and Johnson et al. (2000) attributed the transitions in the diatom assemblage, particularly increased BSi and replacement of *Aulocoseira granulata* with the more buoyant *A. nyassensis*, to a shift in seasonally restricted water-column mixing that allowed increased diatom resuspension at the end of the AHPII (~5,000 calyr BP). *Procladius* then drop below the detection limit around ~3,500 calyr BP, which again coincides with a change in diatom deposition indicating progressive reduction of monsoonal wind activity (Stager & Johnson, 2000). Assuming that changes in diatom deposition were driven by water-column mixing (Stager & Johnson, 2000), the concurrent timing of changes in both diatoms and chironomids, as well as the moderate BSi correlation between influxes of *Chironomus* and *Procladius* suggests that the increase in chironomid abundance is influenced by water-column mixing.

By contrast, the transition between phases of the AHP is reported to have exhibited reduced duration and intensity of monsoonal wind activity that led to stronger lake stratification and considerable reduction in offshore diatom production, indicated by the low BSi concentrations observed in all three cores and the absence of diatoms in V95-2P (Stager & Johnson, 2000). The reappearance of *Procladius* during this period of reduced diatom production suggests that other factors in addition to water-column mixing influence their abundances in Lake Victoria. Next to oxygen concentrations, food quality and availability also may have favoured increased *Procladius* abundances given the (marginally significant) positive correlation with BSi. The consistent presence of *Procladius* occurred concurrently with the increased diatom production toward the end of the AHPII. *Procladius* larvae are omnivores, and are known to engulf Cladocera, copepods, oligochaetes, and other chironomids, as well as algae (Antczak-Orlewska et al., 2021), and are considered to be more selective feeders than *Chironomus* (Hershey, 1986; Macdonald, 1956). Comparatively, *Chironomus* larvae are filter-feeders of sedimenting algal material (Walshe, 1947) and/or non-selective deposit feeders (Kelly et al., 2004; Ptatscheck et al., 2017).

Similar to chironomids, *Chaoborus* abundances are regulated by both abiotic and biotic factors, including habitat structure (Luoto & Nevalainen, 2009), hypolimnetic oxygen (Quinlan & Smol, 2010; Ursenbacher et al., 2020), fish predation pressure (Sweetman & Smol, 2006; Uutala, 1990) and the zooplankton community (Sarmaja-Korjonen, 2002). *Chaoborus* also displayed a mid-Holocene increase in abundance at the end of the AHPII. The observed increase of *Chaoborus* coincided with the period of increased diatom production around 5,000 calyr BP, inferred from the BSi profile of LV1, which may have indirectly promoted the increase in *Chaoborus* through increased food availability for their zooplankton prey. However, this is difficult to assess because *Chaoborus* often prefer feeding on copepods rather than cladocerans (Swift & Fedorenko, 1975), and only the latter preserve in lake sediments. In addition, *Chaoborus* are known to tolerate low oxygen conditions (Jager & Walz, 2002), which enables diel vertical migration to optimise predator avoidance and foraging opportunities (Dawidowicz et al., 1990; Dodson, 1990; Irvine, 1997). Abundances of *Chaoborus* remains have been reported to be primarily driven by changes in hypolimnetic oxygen (Quinlan & Smol, 2010). Thus, their persistence in the deep-water lake conditions of Lake Victoria throughout its history suggests the presence of bottom water refugia that limited visual predation, particularly by insectivorous and zooplanktivorous pelagic haplochromines (Witte et al., 1995). However, the concurrent increase in *Procladius* and changes in the diatom assemblage suggests increased oxygenation during this phase. The insignificant correlations between *Chaoborus* and the environmental proxies investigated here suggests that other factors, such as predation, influence changes in *Chaoborus* abundance. Disentangling the (potentially interacting) effects of changes in hypolimnetic oxygen and predation pressure over millennial timescales will require further inference about the timing of trophic

guild emergence and changes in relative abundance of the fish haplochromine community over time, which is potentially attainable from future morphological and ancient DNA analyses of fish bone and tooth fossils (Muschick et al., 2023).

### 4.3 | Rise of Cladocera in the late Holocene (~4,700–1,350 calyr BP)

As the AHP came to a gradual end, and drier, cooler conditions prevailed over Lake Victoria (Berke et al., 2012; Shanahan et al., 2015), *Alona* was the first cladoceran taxon to emerge at ~4,700 calyr BP. The appearance coincided with the late Holocene BSi maximum at ~5,000 calyr BP and the significant change point in  $\delta D_{wax}$  at ~5,050 calyr BP driven by increased aridity suggesting that climatic changes in the region indirectly facilitated habitat conditions that favoured *Alona*. Following its appearance, *Alona* persisted at relatively low abundances for the following three millennia. Although typically known to be littoral, *Alona* species segregate spatially across the littoral zone based on water depth, macrophytes, total organic carbon, conductivity and pH (Adamczuk, 2014). Thus, it is difficult to make additional inferences into their environmental tolerances owing to taxonomic uncertainty related to differentiating species in understudied tropical regions.

The appearance of *Alona* at the end of the AHP may have been influenced by changes in both abiotic (e.g., hypolimnetic oxygen) and biotic (e.g., lake food-web structure) factors. For instance, increased oxygenation of bottom waters, resulting from the return of seasonally-restricted wind mixing as suggested by the diatom assemblage following the mid-Holocene diatom decline, would have fostered a more suitable environment for benthic *Alona* because they have been observed to disappear if bottom waters become hypoxic (Sakuma et al., 2004). The concurrent increase of *Procladius*, *Tanytarsus* and *Cricotopus/Orthocladus*, which are typically less tolerant of anoxic conditions (Verschuren et al., 2002), further suggests increased oxygenation that favoured *Alona*. Alternatively, the late Holocene increase in diatom production, at ~5,000 calyr BP, may have shifted the competitive outcomes in favour of small-bodied *Alona*. Stager and Johnson et al. (2000) reported increased abundances of *Nitzschia fonticola*, a diatom taxon that is often epiphytic on cyanobacteria in African lakes (Kilham et al., 1986). In turn, cyanobacterial blooms would have benefitted *Alona* as they are often associated with increased dominance of small-bodied zooplankton (Jiang et al., 2017). A further possibility, although speculative, is that predation on Cladocera by both vertebrate and invertebrate predators altered the competitive interactions between *Alona* and other zooplankton taxa. Abundances of invertebrate predators (e.g., *Chaoborus* and *Rhabdocoela*, some of which are predatory) remained relatively stable throughout the early history of modern Lake Victoria, exhibiting a small increase in abundance concurrent with the appearance of *Alona*. Moreover, the influence of predation pressures of zooplanktivorous fish on *Chaoborus*, cladocerans and

copepods throughout history remains a major question to be addressed for the Lake Victoria ecosystem.

### 4.4 | Rise of an abundant cladoceran assemblage with planktonic dominance in the late Holocene (~1,350 calyr BP–present)

The final major phase of change was the transition to an abundant cladoceran assemblage at ~1,350 calyr BP following the appearance of *B. longirostris*, *Chydorus* and Sididae. All cladoceran taxa were consistently more abundant throughout this phase compared to their absence throughout the early Holocene, indicating a major change in lake conditions that favoured all cladocerans. The timing of this rise is consistent with increased late Holocene aridity as indicated by increasing phytolith and diatom abundances since ~1,400 calyr BP (Stager & Johnson, 2000); however, BSi remained relatively stable at LV1 during this time. Overall, the regional climate was becoming increasingly arid following the end of the AHP (Temoltzin-Loranca et al., 2023), culminating in a severe drought between ~2,050 and 1,850 calyr BP (Russell & Johnson, 2005). Subsequent arid periods occurred from ~1,700 to 1,400, ~1,000–800, and ~150–100 calyr BP (Battistel et al., 2017; Marchant, 2022). Although these climatic changes led to lake-level fluctuations throughout the past millennium (Tierney et al., 2013), the magnitude of changes in water depth for Lake Victoria is unclear, although certainly minor (<5 m) compared to its earliest stages of refilling (i.e., ~60 m; Wienhues et al., 2023). Rainfall and lake temperature proxies do not extend into this part of the lake's history. Furthermore, the relative error associated with our age-depth model makes inferring the precise timing difficult, particularly given the rapidly changing climate and intensification of human activities over the past millennia (Marchant, 2022).

In addition to the increased abundances of all cladocerans, a relatively quick transition to planktonic dominance suggests that the shift within the lake environment favoured dominance of planktonic cladocerans. Within the cladoceran community, *B. longirostris* was the only planktonic species observed, whereas both *Alona* and *Chydorus* typically represent littoral taxa (Frey, 1988). Previous studies have revealed that the replacement of benthic Cladocera by pelagic ones has been observed in response to increasing phytoplankton abundance (Otake et al., 2021). Furthermore, *B. longirostris* has been reported to dominate cladoceran assemblages following their invasion (Nevalainen et al., 2014; Nevalainen & Luoto, 2012). Ngoepe et al. (2023) observed an increase in pelagic haplochromine cichlid abundance, and a return of cyprinids, preceding the rise of the abundant cladoceran assemblage observed here. Changes in the fish community within the past century have led to shifts in abundances of small-bodied Cladocera (Van Zwieten et al., 2016). Thus, this transition may rather be linked to a restructuring of the lake food web through a combination of increased food availability (despite declines in diatom abundance) and change



in predation pressure. However, given the unknown changes in primary production and the extent of zooplanktivory associated with the emergence of the Lake Victoria cichlid fish radiation, it is unclear what food-web effects there may have been on the invertebrate community at this time. Size structure analyses of key morphological features of *B. longirostris* might provide additional insight into potential changes in zooplanktivorous fish predation during this phase (Korosi et al., 2013).

The expansion of all invertebrate taxa in the most recent surface sediments may be related to recent ecological changes in Lake Victoria, yet the age uncertainties of the topmost sediments of LV1 limit our ability to identify specific drivers. Recent ecological changes to the Lake Victoria ecosystem have been caused by anthropogenic pressures that occurred in short succession over the past century, including increases in phytoplankton production starting in the 1930s that parallel human-population growth and agricultural activity in the catchment (Hecky, 1993; Mugidde, 1993; Verschuren et al., 1998), the explosion of the population of the introduced Nile perch in the 1980s (*Lates niloticus*) (Ogutu-Ohwayo, 1990; Pringle, 2005), the major population declines of many native haplochromine cichlids (Barel et al., 1985; Witte et al., 1992) and the recent recovery of a subset of these (Witte et al., 2012). For such questions and analyses, short cores collected from key areas of Lake Victoria and examined at a higher temporal resolution are needed to assess how recent ecosystem changes coincide with compositional changes in the invertebrate assemblage.

## 5 | CONCLUSIONS

Few multi-millennial records of invertebrate population and assemblage dynamics exist in the African Great Lakes region, of which many focus on only one taxonomic group (e.g., chironomids) rather than the broader invertebrate community. Our late Pleistocene and Holocene record of the invertebrate assemblage preserved in a sediment core of Lake Victoria provides novel insights into the temporal dynamics of invertebrate community assembly, as well as the long-term nature of ecosystem change in the world's largest tropical lake. We observed long phases of relative stability and minor changes in chironomids followed by a very dynamic late Holocene phase with the appearance of several cladoceran groups and the expansion of Cladocera, *Chaoborus* and chironomids. Several of the observed changes in the invertebrate assemblage occurred concurrently with changes in climatic conditions of East Africa and diatom productivity that had been previously recorded in Lake Victoria. However, a key question that remains is how the observed changes in the invertebrate assemblage are related, or not, to the adaptive radiation of endemic haplochromine cichlid fish in Lake Victoria. Palaeolimnological archives can help reveal how the temporal development of past ecological environments may be related to evolutionary change within the lake community (Cuenca-Cambronero et al., 2022). In order to achieve progress toward that goal, a multi-proxy approach of multiple sediment cores is needed to help make inferences about changes

in organism–environment interactions that have culminated in the unique community composition of Lake Victoria today.

## AUTHOR CONTRIBUTIONS

Conceptualisation: LK, BM, OS. Developing methods: LK, BM, CCM, OH, OS. Conducting the research: LK, GW, MCC, CCM. Data analysis: LK. Preparation of figures and tables: LK. Data interpretation and writing: All authors.

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## CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

## DATA AVAILABILITY STATEMENT

All data are available in Zenodo: <https://doi.org/10.5281/zenodo.10090595>.

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