# Environmental perturbations and anthropogenic disturbances determine mollusc biodiversity of Africa's explosive Lake Kivu

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## ARTICLE INFO

## ABSTRACT

Lake Kivu (Rwanda and Democratic Republic of Congo) is known to be unique among the African Great Lakes due to its peculiar history as a volcanic barrier lake and the frequent environmental pertubations caused by limnic eruptions. This lake is a major resource for riparian people but is also characterized by a depauperate fauna. For molluscs, available information is scarce and spatio-temporally restricted. We studied the freshwater molluscs of the lake and its tributaries and their biogeographical affinities, for the first time via genetic characterization. Our study revealed that the malacofauna of Lake Kivu, though admittedly poor compared to other African Great Lakes, is significantly more diverse than previously anticipated. The occurrence of living populations is restricted to a narrow fringe of littoral substrates, but some of the total of eight species occur much deeper than the immediate margins of the lake, i.e. down to a maximum of 15 m. The fauna displays 'Nilotic' biogeographic connections though widespread forms dominate. Differences in diversity occur in the North vs. South of Lake Kivu in species richness and abundance measures. This pattern can be attributed to recent volcanic eruptions and geochemical stressors in the north, but also to current and ongoing anthropogenic effects. A detailed study of schistosomiasis and fasciolosis with high spatial resolution along the local communities and their livestock is recommended since several potential intermediate host snails are present in Lake Kivu and its tributaries.

## 1. Introduction

Lake Kivu is one of the great lakes in the western branch of the East African Rift System and it is infamous as a dangerous "explosive" lake because of its limnological peculiarities and history of lacustrine volcanic eruptions (Jones, 2021). The lake hosts very substantial fisheries and other natural resources that support the livelihoods of millions of people in the two riparian countries, the Democratic Republic of Congo (DRC) and Republic of Rwanda (Rwanda) (Amisi et al., 2022). Lake Kivu is ancient, as it has existed since the middle Pleistocene, when it formed by uplift of the Virunga Mountains to the north (Degens et al., 1973). Previously, Lake Kivu drained to the north into Lake Edward. However,

~20,000 years ago, volcanic eruptions and resulting lava flows in the Virunga Volcanic Province (VVP) impounded this outlet (Hecky and Degens, 1973; Ross et al., 2014). This barrier led to a lake level rise and a new outlet, the Ruzizi River, was formed in the South which drains to Lake Tanganyika (Degens et al., 1973; Ross et al., 2014). Since its formation, Lake Kivu has been heavily influenced by volcanic activity, particularly that within the VVP (e.g. Smets et al., 2010; d'Oreye et al., 2011; Ross et al., 2014). Lava flows from Nyiragongo and Nyamulagira, the two active volcanoes located north of Lake Kivu in the Virunga Mountains, have repeatedly entered Kabuno Bay and the main basin of Lake Kivu, particularly during the 1938–40 Nyamulagira and 2002 Nyiragongo eruptions (Balagizi et al., 2018). Beyond volcanic eruptions,

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Lake Kivu is exposed to earthquakes and degassing events, which may result in limnic overturns (Balagizi et al., 2018). The methane reservoir in Lake Kivu is a valuable energy resource for neighboring Rwanda and DRC, but also a looming threat to millions of people in the surrounding area if the stability of the lake is disrupted and the gasses are released into the atmosphere. Several researchers have suggested that methane gas exploitation could reduce the risks of dangerous limnetic eruptions due to supersaturation or subaqueous volcanic eruption (Balagizi et al., 2018; Ross et al., 2014; Schmid et al., 2021, 2005).

There are four major cities along Lake Kivu: Goma (DRC) and Rubavu (formerly Gisenyi, Rwanda) straddling the border in the north, Bukavu (DRC) and Rusizi (formerly Cyangugu, Rwanda) in the south. Livelihoods around the lake include hotel operations, fishing, agriculture, boating, methane gas extraction, mineral mining, and local sand mining. Industrial activities are rather limited but include two breweries, mining facilities, as well as tea drying and coffee cleaning factories (Wronski et al., 2015). The waste products of these activities could release organic or mineral contaminants, and their management would need further evaluation. Gas extraction may pose the most risk to destroy aquatic life in the mixolimnion as uncontrolled toxic gas emission may render the lakeshore and waters uninhabitable and, therewith, cause extensive habitat destruction and fragmentation. Methane-producing plants could also cause local pollution with solid waste that may affect water chemistry (Hirslund and Morkel, 2020; Amisi et al., 2022).

The low biodiversity of Lake Kivu likely reflects the unstability of its environments. Compared to other lakes in the East African Rift, Lake Kivu has a relatively low species diversity (Salzburger et al., 2014). Fish diversity in the lake is remarkably low, with only 29 species from the families Cichlidae, Clariidae, Cyprinidae, and Clupeidae (Snoeks et al., 2012). Biodiversity research in Lake Kivu has mainly focused on fish ecology and biology, due to the needs of the fishery (Sarmento et al., 2007). Knowledge of macroinvertebrates in Lake Kivu is still in an early stage of development (Dartevelle and Schwetz, 1947; Verbeke, 1957; Richard et al., 2020), and genetic characterizations have been undertaken for hardly any groups. The combination of genetic assessments in addition to classical morphology-based diversity assessments have considerably improved the knowledge of biodiversity in other tropical lakes including those of the African Great Lakes (e.g. Schultheiß et al., 2009; Van Bocxlaer et al., 2021). Despite their recognized importance to the functioning of aquatic ecosystems and numerous applications to water quality assessment (Doric et al., 2021; Dusabe et al., 2019), macroinvertebrates are generally poorly understood, and little is known about their ecology, diversity, and distribution. This state of affairs is exemplified by the molluscs of Lake Kivu for which very spatially restricted data were presented by Pilsbry and Bequaert (1927), Dartevelle & Schwetz (1947), and Gillet (1960). In a short summary by Brown (1994), Lake Kivu is reported to have seven species of gastropods, including one endemic taxon, *Gabbiella humerosa kivuensis* (Bithyniidae). It should be noted that the available data, collected over the last ~ 100 years, were spatially and temporally very restricted and reflect the lack of a comprehensive mollusc dataset for Lake Kivu. Documenting the diversity and distribution of molluscs is important because of their role in the aquatic food web. They contribute greatly to the processes of nutrient exchange, primarily by controlling algal growth, maintaining water quality, and providing clean substrates for other bottom-dwelling animals such as insects (Johnson, 2009). In addition, some molluscs are intermediate hosts of infectious diseases such as those caused by trematode parasites of the genera *Schistosoma* (blood flukes) and *Fasciola* (liver flukes). The extent of spread of these diseases depends on the availability of snail intermediate hosts in the area of concern and their susceptibility to infection. Understanding the occurrence and distribution of intermediate host snails is an important step towards implementing cost-effective measures to control and monitor schistosomiasis, and complements such efforts by Kagabo et al. (2023) in Rwanda.

Based on extensive field sampling and the use of mitochondrial DNA markers for a genetic assessment of the fauna, we aim to gain new insights into the biodiversity of molluscs in Lake Kivu and its basin. With the present study, we specifically aim to: (a) assess current molluscan species diversity and how this diversity is spatially distributed in Lake Kivu; (b) determine ecological insularity by contrasting tributaries, and lacustrine habitats; (c) evaluate the differences in communities across basins in the lake; and (d) assess effects of anthropogenic disturbances on the diversity and abundances of molluscs. Additionally, we discuss the current status of the mollusc fauna, including their conservation, and their potential role as bioindicators and/or vectors for diseases.
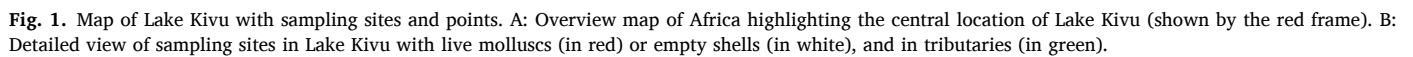
## 2. Materials and methods

### 2.1. Study area

Lake Kivu is shared by the DRC and Rwanda (Fig. 1). The lake lies in the centre of the axis of the western branch of the East African Rift and is, with an elevation of 1,463 m above sea level, at highest altitude lake within this branch (Degens et al., 1973). Lake Kivu has a surface area of 2,370 km$^2$ (Muvundja et al., 2014), a volume of 549 km$^3$, a catchment area of ~ 7,140 km$^2$ (Stoffers and Hecky, 1978), and reaches a maximum depth of ~ 485 m in its northern basin (Lahmeyer and OSAE, 1998). The lake consists of four basins (Wong and Herzen, 1974; Schmid and Wuest, 2012): the northern or main basin (off Goma and Gisenyi: max. depths of 485 m), the southern basin (max. depths of ~ 180 m off Ishungu and 100 m off Bukavu Bay and Kamembe), the eastern basin (max. depths 400 m) and the western basin (max depths of ~ 230 m). Kabuno Bay off Minova (max. depths of 150 m) in the northwestern part of the lake is connected to the northern basin by a narrow channel and can be considered to be a pseudo-satellite lake (Fig. 1). The most important water sources of Lake Kivu include direct rainfall (average 1,404 mm/year) and inflows from various streams and rivers. In particular, the Sebeya River and the Koko River, which originate in the Rwandan mountains (Ross, 2014), contribute significantly to the lake's water balance. The only outflow is via the Ruzizi River, which flows south into Lake Tanganyika. The climate is humid with a bimodal precipitation regime (~1,400 mm/year$^{-1}$ over the lake catchment; Muvundja et al., 2009). The long rainy season extends from Febuary to May and short rains from October to December (Bergonzini, 1998). The average water temperature at the surface is about 24 °C (Snoeks, 1994). Lake Kivu has the tenth largest inland island in the world, Idjwi, which is located in the centre of Lake Kivu and is home to ~ 320,000 people (Nyamalyongo et al., 2022).

The catchment of Lake Kivu is relatively small as its shorelines are generally steep, except along the northern shore, where the slope rises more gradually toward the Nyiragongo and Nyamuragira volcanoes. Current land use around Lake Kivu is dominated by subsistence agriculture and cropping, which means that only manure is used for fertilization and comparatively few agrochemicals are used (Muvundja et al., 2009), though there might be significant use of pesticides, too. The main industrial activities in the watershed area are two breweries and a few processing plants for agricultural products such as tea, coffee, and quinine (Wronski et al., 2015; Houbraken et al., 2017). Deforestation in the surroundings of Lake Kivu to meet the increasing demand for fuelwood, given the lack of alternative energy sources for households (Jones, 2003), results in more soil erosion, landslides and sediment influx to the lake (Moeyersons et al., 2004). More than 100 small tributaries, with varying degrees of deforestation along their course, feed the lake (Muvundja et al., 2009) creating a mosaic of impacts.

### 2.2. Sampling

An extensive field campaign for the collection of mollusc species was carried out from October to November 2022 in northern, central, and southern parts of Lake Kivu by M. C. Dusabe and B. L. Hyangya. Previously sampled material from 2019 (northern basin, Rwanda; C.

**Fig. 1.** Map of Lake Kivu with sampling sites and points. A: Overview map of Africa highlighting the central location of Lake Kivu (shown by the red frame). B: Detailed view of sampling sites in Lake Kivu with live molluscs (in red) or empty shells (in white), and in tributaries (in green).

Albrecht, M. C. Dusabe, B. L. Hyangya), 2018 (south-western Lake Kivu, DRC; B. L. Hyangya), and 2010 (south-eastern part of the lake, Rwanda; R. Schultheiß) were also included in this study. In total, we surveyed 34 sites with 64 collecting points (Fig. 1). These points represent different collecting depths (Table 1). In addition, the material collected by M. C. Dusabe in 2014 and used by Wronski et al. (2015) from 19 tributaries on the Rwandan side of Lake Kivu was also included for comparative purposes.

Samples from the shore (0–0.5 m depth) were collected using a scoop net (diameter: 20 cm, mesh size: 1 mm) and a Surber net (250 μm mesh size). At the shoreline, sites were selected to reflect different micro-habitat types: pristine sites, lowly disturbed, moderately disturbed and highly disturbed (Table 1). Site utilization (boating, fishing, swimming, digging etc.) was recorded. The depth, geographical coordinates, and substrate type (vegetation, rocks, stones, sand, mud, detritus, sapropel, artificial substrates) of each site were noted (Table 1).

Lake sampling (0.6–33 m depth) was done using an Ekman's bottom grab from a motorized boat. The depth was measured with an echo sounder (Plastimo Handecholot Echotest II*)*. All sampled materials were sieved in a bucket with a 250 μm Surber sampler and the collecting net was rinsed after each sample. All samples were preserved in 80% ethanol and labelled accordingly. The material was brought to the University of Giessen Systematics and Biodiversity collection (UGSB), Germany or to UMR 8198 - Evo-Eco-Paleo (CNRS, Univ. Lille).

Specimens were identified to species level if possible, but in some cases only to genus level based on shell morphology according to Brown (1994). For each site, two specimens of each species were selected and photographed using a Keyence digital microscope system (KEYENCE VHX-2000; Keyence Deutschland GmbH, Neu-Isenburg, Germany) before processing them in the lab.

### 2.3. DNA extraction, amplification and sequence analysis

We selected 96 specimens from 9 genera namely *Biomphalaria, Bulinus, Afrogyrorbis, Gabbiella, Sphaerium, Radix, Pisidium, Physella,* and *Melanoides,* for DNA barcoding. Genomic DNA was extracted from a small piece of foot muscle using the CTAB protocol of Wilke et al. (2006) or with a DNeasy Blood and Tissue Kit (Qiagen). Gene fragments of the mitochondrial cytochrome *c* oxidase subunit I (COI) and the large

subunit of ribosomal RNA (LSU rRNA or 16S) were amplified with the primers LCO1490 and HCO2198 (Folmer et al., 1994) or COR722b (Wilke and Davis, 2000) for COI and 16Sar and 16Sbr for 16S (Palumbi, 1991) using the PCR conditions decribed in Electronic Supplementary Material (ESM) Appendix S1. Sanger sequencing was performed on an ABI 3730xl DNA analyzer using the BigDye Terminator Kit (Life Technologies, LGC Genomics GmbH, Berlin, Germany). All new sequences were deposited in NCBI GenBank (accession numbers are provided in Table 2).

DNA sequence errors at the beginning and end of the sequences were manually edited and aligned using BioEdit v7.2 (Hall, 1999). Unique haplotypes were calculated using TCS v1.2.1 (Clement et al., 2000; connection limit = 95 %), and were compared to the nucleotide database of NCBI GenBank with BLAST (BLASTn suite: megablast) to find similar sequences (Zhang et al., 2000). BLAST hits were sorted by max *score* (default setting) and the top two hits for each of our specimens were selected. This approach has several potential pitfalls, including that some sequences in GenBank might be wrongly labelled, i.e. based on misidentifications. Additionally, in some cases closely related species may not be present in GenBank yet. In a few of such cases, we used local BLAST searches to compare the sequences of our Kivu specimens with our internal sequence database (unpublished data).

### 2.4. Phylogenetic analysis

Whereas most recovered genera were monospecific, Biomphalaria was not, so we carried out a phylogenetic analysis of this genus using the COI marker. Additional sequences were downloaded from NCBI GenBank, resulting in a dataset with 48 ingroup specimens, and *Afrogyrorbis natalensis* was used as outgroup. The multi-sequence alignment for the Folmer region of cox1 was conducted using the ClustalW tool implemented in BioEdit. The final alignments comprised 655 bp. The software jModelTest v2.1.4 (Darriba et al., 2012) was used to select the best-fit substitution model for each of the three codon positions. Based on the Akaike information criterion (AIC) and Bayesian information criterion (BIC), the best-fit substitution model for the dataset was HKY + G. We used the software MEGA 11 (Tamura et al., 2021) to construct a phylogenetic tree using maximum likelihood (ML) and bootstrapping with 1,000 replicates. The final tree was visualized and edited in FigTree

**Table 1**
Information on sampling sites and points (N = 64) including depth, latitude and longitude, and habitat characterization: substrates, sites uzilitazation and degree of anthropogenic disturbance.

| Sampling points | Depth/ m | Latitude | Longitude | Substrates | Sites utilization | Level of disturbance |
|---|---|---|---|---|---|---|
| K1 | 0 | −1.73939 | 29.27028 | Detritus, sapropel and artificial (cloth) | Boating, fishing and swimming | high |
| K2 | 5 | −1.74006 | 29.27511 | Detritus and fine silt | Boating, fishing and swimming | medium |
| K3 | 10 | −1.74849 | 29.27708 | Detritus and fine silt | Boating and fishing | low |
| K4 | 20 | −1.74014 | 29.27461 | Detritus and fine silt | Boating and fishing | low |
| K5 | 30 | −1.74833 | 29.27650 | Detritus and fine silt | Boating and fishing | low |
| K6 | 0 | −1.70423 | 29.25916 | Stones and sand | Boating, fishing and swimming | medium |
| K7 | 5 | −1.69867 | 29.25355 | Detritus and fine silt | Boating and fishing | medium |
| K8 | 10 | −1.70026 | 29.25012 | Detritus and fine silt | Boating and fishing | medium |
| K9 | 15 | −1.74541 | 29.23054 | Detritus and fine silt | Boating and fishing | medium |
| K10 | 20 | −1.72982 | 29.23408 | Detritus and fine silt | Boating and fishing | medium |
| K11 | 30 | −1.73931 | 29.24282 | Detritus and fine silt | Boating and fishing | medium |
| K12 | 0 | −1.69798 | 29.24905 | Detritus, sand and silt | Swimming, baoting and fishing | medium |
| K13 | 0 | −1.81300 | 29.27903 | Stones and sand, rocks | Boating, fishing and swimming | medium |
| K14 | 0 | −1.81336 | 29.27950 | Stones and sand, rocks | Boating, fishing and swimming | medium |
| K15 | 0 | −1.70000 | 29.25000 | Detritus, sand and silt | Swimming, baoting and fishing | medium |
| K16 | 0 | −2.07361 | 29.35914 | Detritus, sapropel and artificial (cloth) | Boating and fishing | medium |
| K17 | 5 | −2.06036 | 29.33725 | Detritus and fine silt | Boating, fishing and cattle swimming | medium |
| K18 | 10 | −2.06222 | 29.34678 | Detritus and fine silt | Boating, fishing and cattle swimming | medium |
| K19 | 0 | −2.05329 | 29.34718 | Stones and sand, rocks | Boating, fishing and swimming | medium |
| K20 | 0 | −2.31239 | 29.13775 | Detritus and sapropel | Boating and fishing | medium |
| K21 | 0 | −2.47062 | 28.69626 | Detritus and fine silt | Boating and fishing | low |
| K22 | 0 | −2.47922 | 28.89847 | Detritus and fine silt | Boating and fishing | low |
| K23 | 3 | −2.48436 | 28.89408 | Detritus and fine silt | Boating and fishing | low |
| K24 | 15 | −2.48414 | 28.89387 | Detritus and fine silt | Boating and fishing | low |
| K25 | 30 | −2.48410 | 28.89351 | Detritus and fine silt | Boating and fishing | low |
| K26 | 0.5 | −2.48599 | 28.85234 | Detritus and fine silt | Boating and fishing | low |
| K27 | 5 | −2.46946 | 28.84277 | Detritus and fine silt | Boating | low |
| K28 | 20 | −1.74014 | 29.27461 | Detritus and fine silt | Boating | low |
| K29 | 30 | −2.46890 | 28.84514 | Detritus and fine silt | Boating | low |
| K30 | 0 | −2.47167 | 28.83972 | Detritus, sand and silt | Turbid river | low |
| K31 | 0 | −1.65472 | 29.02778 | Detritus, sand and silt | Boating | medium |
| K32 | 0 | −2.31361 | 28.97167 | Detritus and fine silt | No activity | pristine |
| K33 | 0 | −2.31028 | 28.96556 | Detritus, sand and silt | Boating and fishing | medium |
| K34 | 0 | −2.31028 | 28.96553 | Detritus, sand and silt | Boating and fishing | medium |
| K35 | 0 | −2.30000 | 28.97167 | Detritus, sand and silt | Boating | medium |
| K36 | 10 | −2.31056 | 28.96861 | Detritus and fine silt | No activity | pristine |
| K37 | 0 | −2.11065 | 28.91298 | Detritus and fine silt | No activity | pristine |
| K38 | 10 | −2.11040 | 28.91305 | Detritus and fine silt | No activity | pristine |
| K39 | 20 | −2.11051 | 28.91276 | Detritus and fine silt | No activity | pristine |
| K40 | 30 | −2.10991 | 28.91293 | Detritus and fine silt | No activity | pristine |
| K41 | 0 | −2.10750 | 28.92556 | Detritus, sand and silt | Movement of people, and a turbid river | high |
| K42 | 0 | −2.11222 | 28.91361 | Detritus and fine silt | Boating | medium |
| K43 | 0 | −2.48889 | 28.84500 | Detritus, sand and silt | Market for fish | high |
| K44 | 5 | −2.46890 | 28.84514 | Detritus, sand and silt | Boating | high |
| K45 | 0 | −2.18839 | 29.28014 | Detritus and sapropel | Boating, fishing and digging | high |
| K46 | 5 | −2.49665 | 28.86323 | Detritus and fine silt | Boating and fishing | low |
| K47 | 0 | −2.11861 | 28.90611 | Stones and gravel | No activity | pristine |
| K48 | 0 | −2.11667 | 28.90667 | Detritus and fine silt | No activity | pristine |
| K49 | 0 | −2.48528 | 28.87411 | Detritus, sand and silt | Boating | medium |
| K50 | 10.2 | −2.50278 | 28.88556 | Detritus and fine silt | Fishing | low |
| K51 | 0 | −2.48599 | 28.85234 | Detritus, sand and silt | Boating | high |
| K52 | 11.2 | −2.49889 | 28.86622 | Detritus and fine silt | Fishing | low |
| K53 | 30 | −2.46890 | 28.84514 | Detritus and fine silt | Fishing | low |
| K54 | 32.5 | −2.49662 | 28.86342 | Detritus and fine silt | Boating and fishing | low |
| K55 | 0 | −2.50250 | 28.85639 | Sand and gravel, rocks | Market, boating and big turbid river | high |
| K56 | 5 | −2.48528 | 28.85639 | Detritus and fine silt | Boating | low |
| K57 | 0 | −2.48488 | 28.85669 | Detritus and fine silt | Boating | low |
| K58 | 33 | −2.48519 | 28.85624 | Detritus and fine silt | Boating | low |
| K59 | 20.3 | −2.48528 | 28.85621 | Detritus and fine silt | Boating | low |
| K60 | 0 | −1.70722 | 29.02167 | Detritus and fine silt | Boating | low |
| K61 | 5 | −2.11500 | 28.91750 | Detritus and fine silt | Boating | medium |
| K62 | 10 | −1.70222 | 29.02500 | Detritus and fine silt | Boating | medium |
| K63 | 20 | −1.70278 | 29.02444 | Detritus and fine silt | Boating | medium |
| K64 | 30 | −1.6925 | 29.03583 | Detritus and fine silt | Boating | low |

v1.4.2 (Rambaut, 2014). (ESM Appendix S1; Figure S1).

### 2.5. Ecological analyses

To assess current molluscan species diversity and visualize its spatial distribution in Lake Kivu, we calculated two different diversity indices, Shannon-Wiener index and Pielou's evenness. Heatmaps were used to visualize the spatial distribution of molluscs in Lake Kivu. Descriptive statistics were used to summarize the environmental variables (See above and ESM Appendix S2) that had been collected. To determine the differences in the abundance of molluscs across sites, species, and basins, a non-parametric Kruskal-Wallis test was performed. Furthermore, the effect of environmental variables (See above and ESM Appendix S2) on mollusc abundance was determined using a generalized linear model

**Table 2**

Results of BLAST searches, indicating species, with voucher code, the associated BLAST hits with % similarity (in squared brackets) and NCBI GenBank accession numbers. UGSB – University of Giessen Systematics and Biodiversity collection. The three letter code indicated for BLAST results indicates the country of origin: CAN = Canada, DRC = DR Congo, KEN = Kenya, RWA = Rwanda, SDN = Sudan, TZA = Tanzania, UGA = Uganda, ZAF = South Africa, ZWE = Zimbabwe, EA = East Africa.

| Family | Species (morphological) | Voucher no. | BLAST results (COI) | local BLAST results (COI) | GenBank acc. numbers |
|---|---|---|---|---|---|
| **GASTROPODA** | | | | | |
| Bithyniidae | *Gabbiella humerosa* | UGSB 28063 | *Gabbiella* sp. UGA OP339805 [97.2 %] *Gabbiella humerosa* KEN OP339804 [97.2 %] | – | PP510644 |
| | | UGSB 28072 | *Gabbiella* sp. UGA OP339805 [96.9 %] *Gabbiella humerosa* KEN OP339804 [96.9 %] | – | PP510645 |
| | | UGSB 27879 UGSB 27868 UGSB 27901 | *Gabbiella* sp. UGA OP339805 [97.2 %] *Gabbiella humerosa* KEN OP339804 [97.2 %] | – | PP510646; PP510647; PP510648 |
| Lymnaeidae | *Radix natalensis* | UGSB 27333 | *Radix natalensis* ZWE MZ546834 [98.4 %] *Radix natalensis* ZWE MT888846 [98.4 %] | – | PP510649 |
| Bulinidae | *Bulinus* sp. | UGSB 27317 UGSB 27319 | *Bulinus truncatus* RWA MN551581 [99.5 %] *Bulinus truncatus* RWA MN551578 [99.5 %] | – | PP510650; PP510651 |
| | | UGSB 27318 | *Bulinus truncatus* TZA AM286313 [100.0 %] *Bulinus truncatus* SDN MN853656 [99.8 %] | – | PP510652 |
| | | UGSB 27894 UGSB 27898 UGSB 27908 UGSB 28051 UGSB 27905 | *Bulinus truncatus* DRC HQ121561 [100.0 %] *Bulinus truncatus* UGA MT707414 [99.7 %] | – | PP510653; PP510654; PP510655; PP510656; PP510657 |
| | | UGSB 27906 | *Bulinus truncatus* DRC HQ121561 [99.8 %] *Bulinus truncatus* UGA MT707414 [99.5 %] | – | PP510658 |
| | | UGSB 27907 | *Bulinus truncatus* DRC MT707423 [99.5 %] | – | PP510659 |
| | | UGSB 27865 | *Bulinus truncatus* UGA GU176748 [99.3 %] *Bulinus truncatus* UGA GU176748 [99.3 %] | – | PP510660 |
| | | UGSB 27883 | *Bulinus truncatus* UGA MT707423 [99.7 %] *Bulinus truncatus* UGA GU176748 [99.54 %] | – | PP510661 |
| Planorbidae | *Biomphalaria pfeifferi* | UGSB 23723; UGSB23709; UGSB23719; UGSB23720; UGSB23721; UGSB 23722 | *Biomphalaria pfeifferi* KEN NC_038059 [99.2 %] *Biomphalaria pfeifferi* KEN OL423116 [99.2 %] | – | PP510662; PP510666; PP510667; PP510668; PP510669; PP510670 |
| | *Biomphalaria* sp. MT1 | UGSB 28055; UGSB 28056; UGSB28880; UGSB28881; UGSB28882; UGSB28883; UGSB23771 | *Biomphalaria choanomphala* UGA HM768905 [99.7 %] *Biomphalaria* sp. EA HM769163 [99.5 %] | – | PP510663; PP510664; PP510673; PP510674; PP510675; PP510676; PP510672 |
| | *Biomphalaria* sp. MT2 | UGSB 27886 | *Biomphalaria smithi* UGA DQ084836 [99.2 %] *Biomphalaria* sp. EA HM769209 [99.1 %] | – | PP510665 |
| | *Biomphalaria* cf. *smithi* | UGSB23759 | *Biomphalaria smithi* UGA DQ084836 [99.5%] *Biomphalaria* sp. EA HM769209 [99.2%] | – | PP510671 |
| | *Afrogyrorbis kigeziensis* | UGSB 27892 UGSB 27892 UGSB 27900 | *Gyraulus chinensis* KEN AF199086 [96.6 %] *Gyraulus* sp. UGA OQ849997 [96.3 %] | *Afrogyrorbis* sp. COD UGSB 7770 [96 %] *Afrogyrorbis natalensis* ZAF UGSB 28782 [96 %] | PP510677; PP510678; PP510679 |

**Table 2** (*continued*)

| Family | Species (morphological) | Voucher no. | BLAST results (COI) | local BLAST results (COI) | GenBank acc. numbers |
|---|---|---|---|---|---|
| | | UGSB 27909 | *Gyraulus chinensis* KEN | *Afrogyrorbis* sp. COD | PP510679; |
| | | UGSB 27910 | AF199086 [96.6 %] | UGSB 7770 [96 %] | PP510680 |
| | | | *Gyraulus* sp. UGA | *Afrogyrorbis natalensis* ZAF | |
| | | | OQ849997 [96.3 %] | UGSB 28782 [96 %] | |
| | | UGSB 27895 | *Gyraulus* sp. UGA | *Afrogyrorbis natalensis* ZAF | PP510681 |
| | | | OQ849997 [96.8 %] | UGSB 28784 [96 %] | |
| | | | *Gyraulus chinensis* KEN | *Afrogyrorbis* sp. COD | |
| | | | AF199086 [99.6 %] | UGSB 7770 [96 %] | |
| | | UGSB 28067 | *Gyraulus chinensis* KEN | *Afrogyrorbis* sp. COD | PP510682 |
| | | | AF199086 [96.0 %] | UGSB 7770 [95 %] | |
| | | | *Gyraulus* sp. UGA | *Afrogyrorbis natalensis* ZAF | |
| | | | OQ849997 [95.8 %] | UGSB 28782 [95 %] | |
| | | UGSB 27897 | *Gyraulus* sp. UGA | *Afrogyrorbis natalensis* ZAF | PP510683 |
| | | | OQ849997 [96.5 %] | UGSB 28786 [96 %] | |
| | | | *Gyraulus chinensis* KEN | *Afrogyrorbis* sp. COD | |
| | | | AF199086 [96.2 %] | UGSB 7770 [95 %] | |
| **BIVALVIA** | | | | | |
| Sphaeriidae | *Sphaerium* cf. *hartmanni* | UGSB 27314 | *Sphaerium* sp. UGA | – | PP510684; |
| | | | KF483419 [94.2 %] | | PP510685 |
| | | UGSB 27315 | *Musculium partumeium* CAN | | |
| | | | MT324076 [93.9 %] | – | |

with a Poisson link function. However, using this model, we observed that the mean mollusc abundance was greater than the variance indicating over-dispersion. We further followed the poisson model with the *estat gof* function in Stata/SE version 18.0 but used the *glm* to obtain the deviance and Pearson's chi-square values. The deviance was greater than 1, thus making the poisson model unsuitable due to over-dispersion which often leads to underestimated SEs and inflated test statistics (Hilbe, 2014, Hilbe, 2011). Thus, the negative binomial model was used to model the effect of environmental variables (see above and ESM Appendix S2) on mollusc abundance. To test for differences in the diversity of fauna across basins in the lake, the presence or absence of molluscs across the sites was determined. Furthermore, to assess ecological insularity by contrasting tributaries, and lacustrine habitats, the differences in the diversity of tributaries and Lake Kivu (shorelines) were done using the non-parametric Wilcoxon rank-sum (Mann–Whitney).

## 3. Results

### 3.1. Sampling and species identification

Living molluscs were found at 40 collection depths from 26 sites, whereas at 24 collection depths from 8 sites we found empty gastropod shells only. For Lake Kivu (excluding the tributaries) we morphologically identified four nominal gastropod species: *Melanoides tuberculata* (Thiaridae), *Gabbiella humerosa* (Bithyniidae), *Radix natalensis* (Lymnaeidae), and *Afrogyrorbis kigeziensis* (Planorbidae), and one bivalve species: *Sphaerium* cf. *hartmanni* (Sphaeriidae). All other taxa were morphologically determined up to the genus level, namely: *Bulinus* sp. (Bulinidae) and *Biomphalaria* spp., for which we distinguished two different morphotypes, MT1, which resembles *Biomphalaria pfeifferi*, and MT2 (Planorbidae). In summary, eight species-level taxa from seven distinct genera were found in Lake Kivu proper. For the tributaries of Lake Kivu six species (representing five distinct genera) could be determined morphologically (ESM Table S1). *Biomphalaria* MT1 (cf. *pfeifferi*) and *Radix natalensis* were found in both the lake and the tributaries, but *Bulinus forskalii* (Planorbidae), *Physella acuta* (Physidae), *Pisidium kenianum* (Sphaeriidae), and *Pisidium* cf. *viridarium* (Sphaeriidae) exclusively occurred in the tributaries (ESM Table S2).

Our analysis of molecular identification focused on 52 specimens from 9 genera of molluscs whose sequences were successfully processed. In most cases, our BLAST searches confirmed at least the genera

identified based on shell morphology (Table 2). A seeming exception was for *Afrogyrorbis*, for which the closest BLAST hits related to a different genus, *Gyraulus* (Table 2), but there were no *Afrogyrorbis* sequences in GenBank when we performed these BLAST searches. We thus compared our sequences from Lake Kivu to unpublished sequences of *Afrogyrorbis natalensis* from KwazuluNatal, South Africa and *Afrogyrorbis* sp. from the DRC, which suggested close relationships. Further taxonomic work on *Gyraulus* and *Afrogyrorbis* is required to illucidate relationships, and for now, we retain our assignment of Lake Kivu specimens to *Afrogyrorbis kigeziensis*.

Five sequences of *Gabbiella humerosa* (646 bp length) represented three unique haplotypes. *Gabbiella* sp. (Uganda) and *G. humerosa* (Kenya) with around 97 % identity were the closest hits. For *Radix natalensis* only one COI sequence (468 bp length) could be successfully amplified and this sequence had > 98 % similarity to *R. natalensis* from Zimbabwe. A total of 13 sequences (652 bp length) resulted in 7 unique haplotypes for the *Bulinus* sp. studied. All of these haplotypes had > 99.3 % similarity with *Bulinus truncatus* specimens from various African countries in geographic proximity to Lake Kivu (see Table 5).

Of the five COI sequences of *Biomphalaria* MT1 (cf. *pfeifferi*, length 655 bp), one was an exact match (100 %) to *B. pfeifferi*, and the other four had high similarity (99.24–99.85 %) with *Biomphalaria pfeifferi* from Kenya. For *Biomphalaria* sp. MT2 we generated five sequences with a length of 655 bp, which represented two unique haplotypes. Four sequences could be identified as *Biomphalaria choanomphala* with matches of 99.7 and 99.34 % similarity to *B. choanomphala* from Uganda. The fifth sequence comes out as *Biomphalaria smithi* (99.2 % identity with one sequence of *B. smithi* from Uganda). Maximum Likelihood (ML) phylogenetic analysis of all *Biomphalaria* species revealed that there are only two distinct groups. *B. pfeifferi* clustered with specimens from Kenya, whereas *B. choanomphala* with specimens from Uganda. Branches were extremely short and poorly supported within that clade (ESM Appendix S1; Figure S1), highlighting the unresolved taxonomy within this particular group.

For *Afrogyrorbis kigeziensis,* the eight COI sequences we generated (lengths of 655 bp) represent five unique haplotypes that share appr. 96 % similarity with various *Gyraulus* spp. and *Afrogyrorbis natalensis*. A 16S sequence of *Bulinus forskalii* (16S GenBank accession no.: PP504869) (length of 428 bp) from the Kavungu stream in the Musogoro catchment matched 97.67 % with *Bulinus forskalii* from Tanzania, Tunduma. A sequence of *Physella acuta (16S GenBank accession no.: PP504870)* (length of 505 bp) from the Kiboga stream matched 98.99 % with

*Physella acuta* from the USA. *Sphaerium* cf. *hartmanni* (397 bp length) was 94 % identical with a *Sphaerium* sp. from DRC. Two *Melanoides tuberculata* samples from Lake Kivu (COI GenBank accession no.: KP774714 and KP774715) have been previously published by Van Bocxclaer et al. (2015). The sequneces of *Pisidium kenianum* (COI GenBank accession no.: OK663625 and OK663626) and *P.* cf. *viridarium* (COI GenBank accession no.: OK663621) from the tributary of Lake Kivu have already been analysed by Clewing et al. (2022).

### 3.2. Mollusc communities

Our combined morphological and genetic approach to identifying the freshwater molluscs of Lake Kivu revealed eight species (seven gastropod and one bivalve species), which belong to seven genera and six families (Table 3). *Sphaerium* cf. *hartmanni* was recorded for the first time in Lake Kivu from one sampling site (K1) located in Gisenyi region. *Biomphalaria choananomphala*, which was mentioned twice in Lake Kivu (Pilsbry and Bequaert, 1927; Dartevelle and Schwetz, 1947) was found at one sampling site in K22 (South Kivu Rwanda). *Afrogyrorbis kigeziensis* was for the first time mentioned from Lake Kivu by Brown (1994), and occurred at ten sampling sites in our study (Table 3). *Biomphalaria pfeifferi* was previously reported by Gillet et al. (1960) in the Bukavu region and later by Brown (1994) from Lake Kivu, and was obtained here from five sites. *Radix natalensis* was found at 4 sites, whereas *Bulinus truncatus* at 15 sites (Table 3). *Melanoides tuberculata* and *Gabbiella humerosa kivuensis* were found at 5 and 19 sites, respectively (Table 3).

In general, the Shannon-Wiener index was very low, ranging from 0 to 1.1 (ESM Table S3). Species richness at sites ranged from 1 to 5 (Fig. 2) while Pielou evenness ranged from 0 to 1 (Fig. 3). Richness was highest in shallow waters (0–0.5 m) with a mean of 2.45 ± 1.54 and it decreased to 1.33 ± 0.57 on deeper substrates (Fig. 2). Evenness increased with increasing depth (11–15 m: mean 0.94 ± 0.10), suggesting that the number of species obtained was more constant in deeper than in shallow waters (mean 0.80 ± 0.25) (Fig. 3). The northern basin had lower evenness (mean 0.77 ± 0.18) than the southern basin (mean

0.86 ± 0.23) (Fig. 3).

Results from the Wilcoxon rank-sum (Mann–Whitney) test comparing the diversity of the tributaries and Lake Kivu showed no statistically significant difference ($z = 1.593$; $p = 0.071$). The mean diversity for the tributaries was 0.21 (95 % CI: 0.071–0.343) whereas that for Lake Kivu was 0.388 (95 % CI: 0.259–0.515) (see Fig. 4.).

### 3.3. Mollusc biomass and depth distribution

In the 26 sites where living molluscs were collected, *Gabbiella humerosa,* a species endemic to Lake Kivu recognized as *Gabbiella humerosa kivuensis* (Mandahl-Barth, 1968), accounted for most of the density of gastropod species (31.17 %, 66.41 ± 13.25 indiv. m$^2$) and was found at 19 sampling sites. *Afrogyrorbis kigeziensis* and *Bulinus truncatus* contributed to 18.18 % (4.93 ± 2.97 indiv. m$^2$) and 22.08 % (5.49 ± 3.73 indiv. m$^2$), respectively, and were found at 10 and 15 sampling sites, respectively. *Biomphalaria choanomphala* and *Sphaerium* cf. *hartmanni* were each found at one site only (Table 3). Furthermore, we found no significant differences in the abundance of molluscs across sites (Krukal-Wallis test; $p = 0.4040$). On the other hand, significant differences were observed in the abundance of the various species ($p = 0.0009$).

Results from the nbGLM model suggested that site utilization (nbglm: Coeff: −0.180; $p = 0.001$, 95 % CI: −0.286 − -0.075), substrate types (nbglm: Coeff: −0.2081; $P = 0.041$, 95 % CI: −0.407 − -0.008), and depth (nbglm: Coeff: −0.839; $P = 0.007$, 95 % CI: −1.452 − -0.226) significantly influenced the abundance of molluscs. On another hand microhabitat type (nbglm: Coeff: 0.469; $p = 0.125$; 95 % CI: -0.130–1.068) had no statistically significant effect on snail abundance. In particular, sites with medium disturbance (nbglm: Coeff:-1.477; $p = 0.082$; 95 % CI:-3.141–0.186) and high disturbance (nbglm: Coeff:-1.879; $p = 0.214$; 95 % CI:-4.841–1.082) showed a decline in molluscs compared to sites with low or no disturbance, but these differences were not statistically significant. Compared to the detritus and fine silt, detritus and sapropel and detritus, artificial and sapropel substrates increased the abundance of molluscs by 3.10; $p = 0.001$ (95 % CI:

**Table 3**
Mollusca species recorded at each site sampled in Lake Kivu. The number of collecting points with live records are given. There are 26 sites and 40 sampling points. For details of the sampling points refer to Table 1.

| Site (number of points) | B. choanomphala | B. pfeifferi | B. truncatus | A. kigeziensis | G. humerosa | M. tuberculata | S. cf. hartmanni | R. natalensis |
|---|---|---|---|---|---|---|---|---|
| K1(4) | | 1 | 1 | 2 | 2 | 1 | | |
| K26(2) | | | | | 2 | | | |
| K30 | | | | | 1 | | | |
| K16(2) | | 1 | 1 | 1 | 1 | | | |
| K18 | | | | | 1 | | | |
| K55 | | | | 1 | 1 | 1 | | |
| K57 | | | | | 1 | | | |
| K31 | | | | 1 | 1 | | | |
| K12 | | 1 | 1 | | | | 1 | |
| K42 | | | | 1 | | | | 1 |
| K37 | | | | | 1 | | | |
| K43 (2) | 1 | | 1 | 1 | 1 | | | 1 |
| K21(3) | | 1 | 1 | | 1 | | | 1 |
| K23 | | | 1 | 1 | 1 | | | |
| K20 | | 1 | 1 | | | 1 | | |
| K16 | | | | | 1 | | | |
| K13 | | | 1 | | | | | |
| K14 | | | 1 | | | | | |
| K33 | | | | | | 1 | | |
| K34 | | | | 1 | | | | |
| K35(3) | | | 1 | | 1 | 1 | | 1 |
| K60 | | | | | 1 | | | |
| K45 (3) | | | 2 | 1 | 1 | 1 | | |
| K48 (3) | | | 2 | | | 1 | | |
| K51 | | | 1 | | | | | |
| K15 | | | | | 1 | | | |
| N points (40) | 1 | 5 | 15 | 10 | 19 | 7 | 1 | 4 |
| Frequency (%) | 2.5 | 12.5 | 37.5 | 25 | 47.5 | 17.5 | 2.5 | 10 |

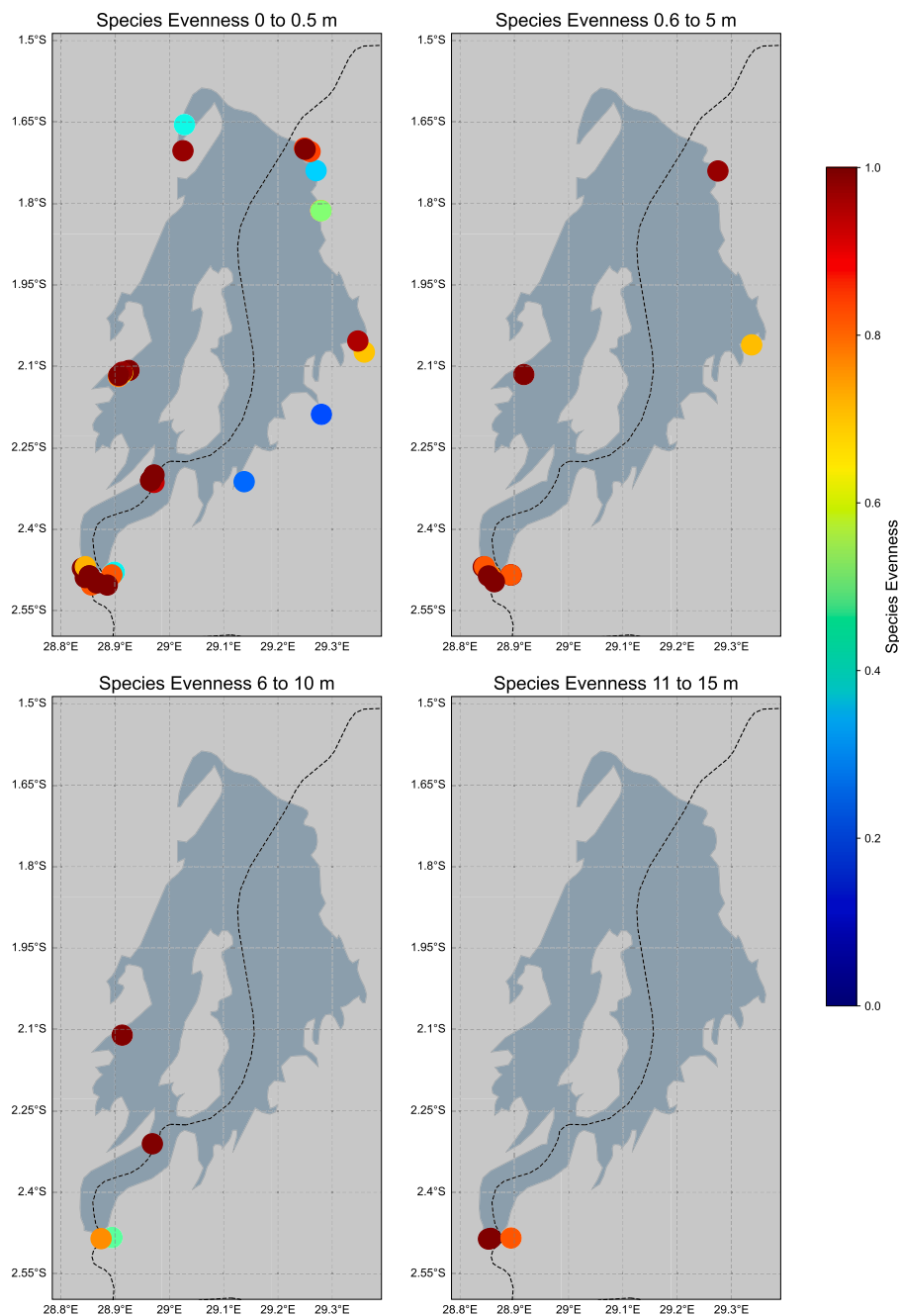# Lake Kivu Species Richness
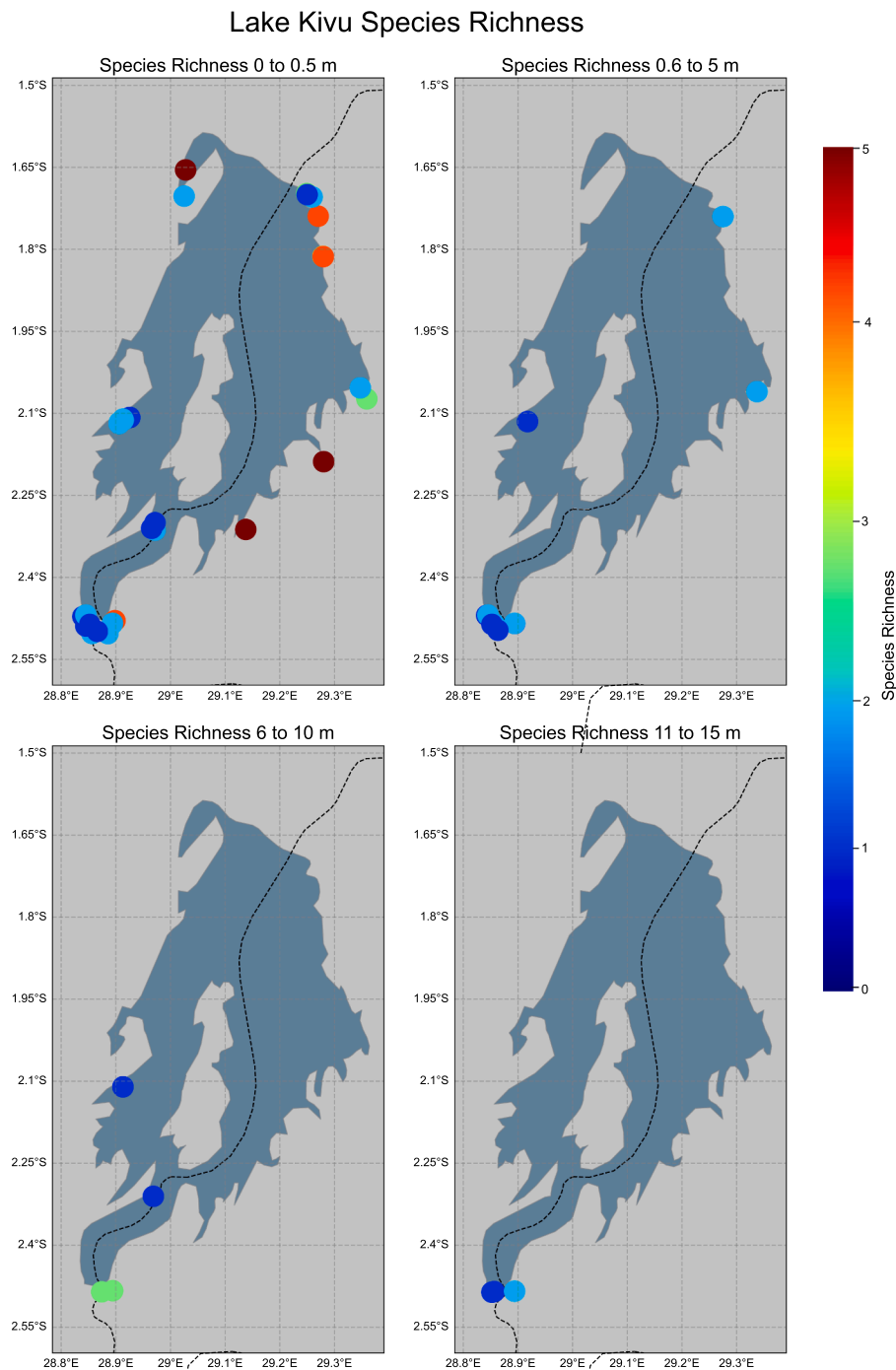


**Fig. 2.** Heatmap visualization of species richness of molluscs in Lake Kivu with subplots for the different sampling depths, A: 0 to 0.5 m; B: 0.6 to 5 m; C: 5 to 10 m; D: 11 to 15 m. The colour bar indicates the range of species richness in the different sites and depths.

1.202–5.016) and 2.51; $p = 0.003$ (95 % CI: 0.849–4.176) (ESM Appendix S2). Mollusc abundance generally decreased with increasing sampling depth with a notable statistical decrease observed particularly between 11 and 15 m depth (nbglm: Coeff: −2.226; $p = 0.021$, 95 % CI: −1.113 − -0.338).

All species were observed on nearshore substrates (0–0.5 m). *Radix natalensis*, *Sphaerium* cf. *hartmanni*, and *Bulinus truncatus* were found exclusively near the shoreline, whereas *Biomphalaria pfeifferi* and *Biomphalaria choanomphala* were found from the shoreline to a depth of 5 m (Fig. 5), *Afrogyrorbis kigeziensis* up to 11 m, and *Gabbiella humerosa* and *Melanoides tuberculata* up to 15 m. At deeper collecting depths (16–20 m and 26–33 m), we only found empty shells.

In total, we collected 1,983 living mollusc specimens of the various species. Of these, 1,243 individuals were collected from the southern basin, 377 from the eastern basin, 347 from the northern basin and 17 from the western basin. A Kruskal-Wallis test showed no statistically significant difference in the diversity of snails collected from the different basins (Chi 2 (3) = 5.775, $p = 0.138$). Furthermore, the northern basin had lower species richness compared to the southern basin (Fig. 6a). Also, the western basin had one snail species whereas 5 species were found in the eastern basin (Fig. 6b). In addition, there were many sites in the northern basin with empty shells, both near the shore and at all depths compared to other basins (Fig. 1). Of the 23 collecting points examined in the northern basin, only 8 collecting points

## Lake Kivu Species Evenness



**Fig. 3.** Heatmap visualisation of evenness of molluscs in Lake Kivu with subplots for the different sampling depths, A: 0 to 0.5 m; B: 0.6 to 5 m; C: 5 to 10 m; D: 11 to 15 m. The colour bar indicate the range of taxa evenness in the different sites and depths.

contained living molluscs, whereas all others had empty shells. In contrast, in the southern basin, we found 30 collecting points with living molluscs and 6 collecting points with only empty shells. In the northern basin, live specimens were found only to a depth of up to 5 m, whereas in the southern basin live species were found up to a depth of 15 m. Although species richness was lower in the northern basin compared to the southern basin, most species are more evenly distributed across sites in the northern basin than in the southern basin (see Figs. 2 & 3).

## 4. Discussion

### 4.1. Mollusc diversity and endemism

The mollusc fauna of Lake Kivu has been considered previously to be depauperate (Brown, 1994), reflecting a similar status as for other freshwater organisms (Beadle, 1981; Descy et al., 2012). Here, we present a comprehensive assessment of freshwater molluscs in the Lake Kivu Basin, in fact, one of the most spatially complete surveys of any of the large African lakes. As a result, we present considerable changes to the species list compared to historical records (Table 4). Changes in the list of recognized species relate to new findings during our survey (e.g.
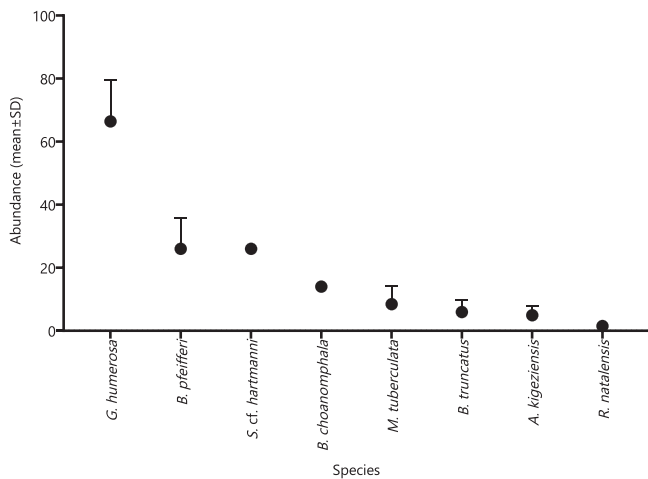
**Fig. 4.** Average abundances of live molluscs in Lake Kivu **.** This figure displays the average abundance of live molluscs collected from 26 sites across 40 collection points at varying depths in Lake Kivu. The standard deviation are also presented for reference.

*Sphaerium* cf. *hartmanni*) but also due to taxonomic changes (e.g. *Afro-gyrorbis kigeziensis*). Some taxa that had been previously reported could not be found during our survey (Table 4). Even though our sampling is comparatively dense, it cannot be excluded that a few rare species might have been overlooked, especially small planorbids. As we have complemented morphological examinations with genetic studies, especially for *Biomphalaria*, we consider it unlikely that cryptic but divergent

genetic lineages would have been present. Our study casts more doubt on the previous records of *Corbicula* and *Mutela* sp. (Dartevelle and Schwetz, 1947) as we have not been able to obtain any living nor fossil specimens of these taxa.

As in other large rift lakes (Schultheiß et al., 2011; Van Damme et al., 2018; Van Bocxlaer et al., 2012), we found rare and hyperdominant species in Lake Kivu. *Melanoides tuberculata*, *Radix natalensis* and *Gabbiella humerosa* belong to the latter category and are common throughout many places in Africa. Rare species were *Sphaerium* cf. *hartmanni*, and *Biomphalaria choanomphala*, which were each found in only one locality. Such findings outline the possibility of overlooked and/or cryptic species in the tropical regions of Africa as demonstrated for other mollusc genera (e.g. Elderkin et al., 2016). It can also be seen in *Pisidium kenianum* for which at least two different clades have been found in tributaries of Lake Kivu (Clewing et al., 2022) Fig. 7.

Recognizing the presence of cryptic species and illucidating their status requires more extensive surveys and classical taxonomic work. Understanding cryptic diversity is also needed to characterize the level of endemism among local faunas such as that of Lake Kivu, and to characterize patterns and processes of speciation accurately. Currently, the only proposed endemic taxon in Lake Kivu is *Gabbiella humerosa kivuensis* and its relation to other *Gabbiella* species warrants a detailed phylogeographic study covering the diversity and geographic range of the genus.

Our barcoding approach helped to clarify several questions as to species identification that cannot easily be solved with shell-morphological studies alone. Even though not new for studies of poorly known faunas in ancient lakes (Stelbrink et al., 2019; Wiese et al., 2020), a similar genetic characterization has not been used yet for any of the African lakes and should be implemented for other regional faunas of
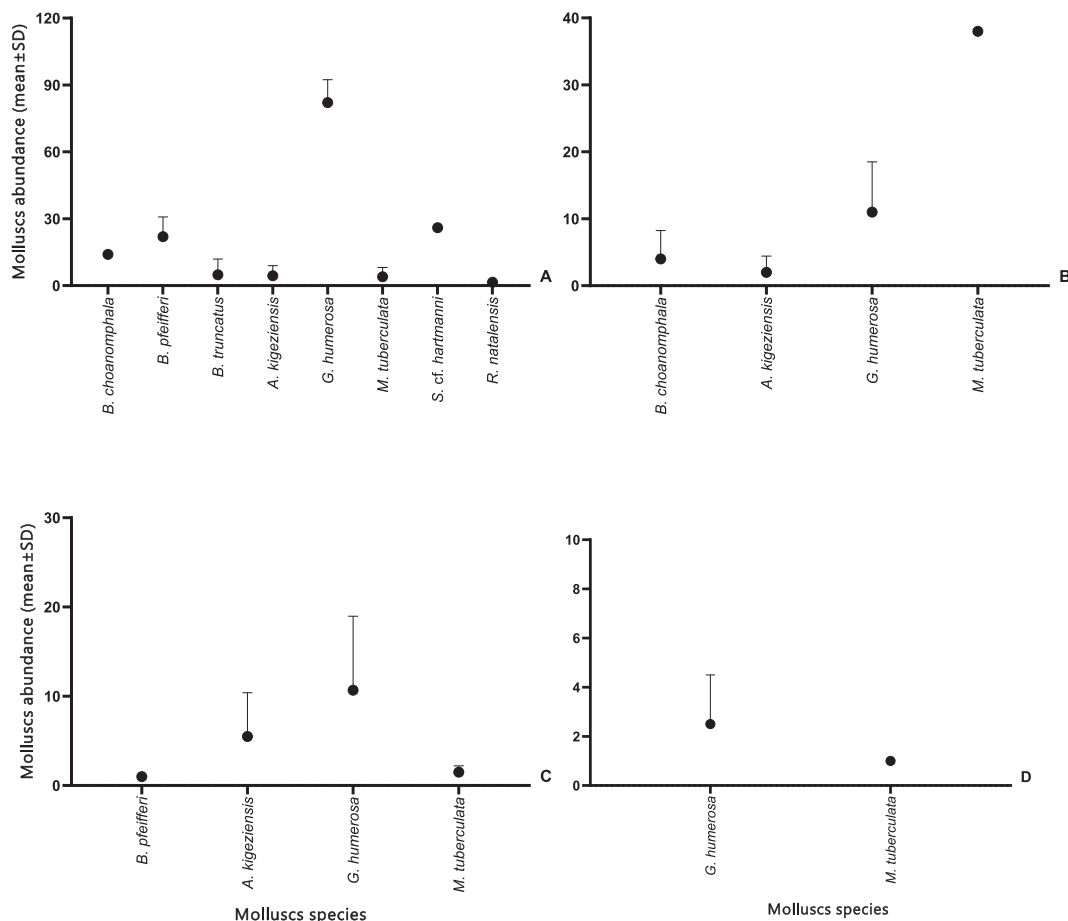


**Fig. 5.** Mean and standard deviation of snail abundances at different depths. The categories include A: 0 to 0.5 m, B: 0.6 to 5 m, C: 6 to 10 m and D: 11 to 15 m.
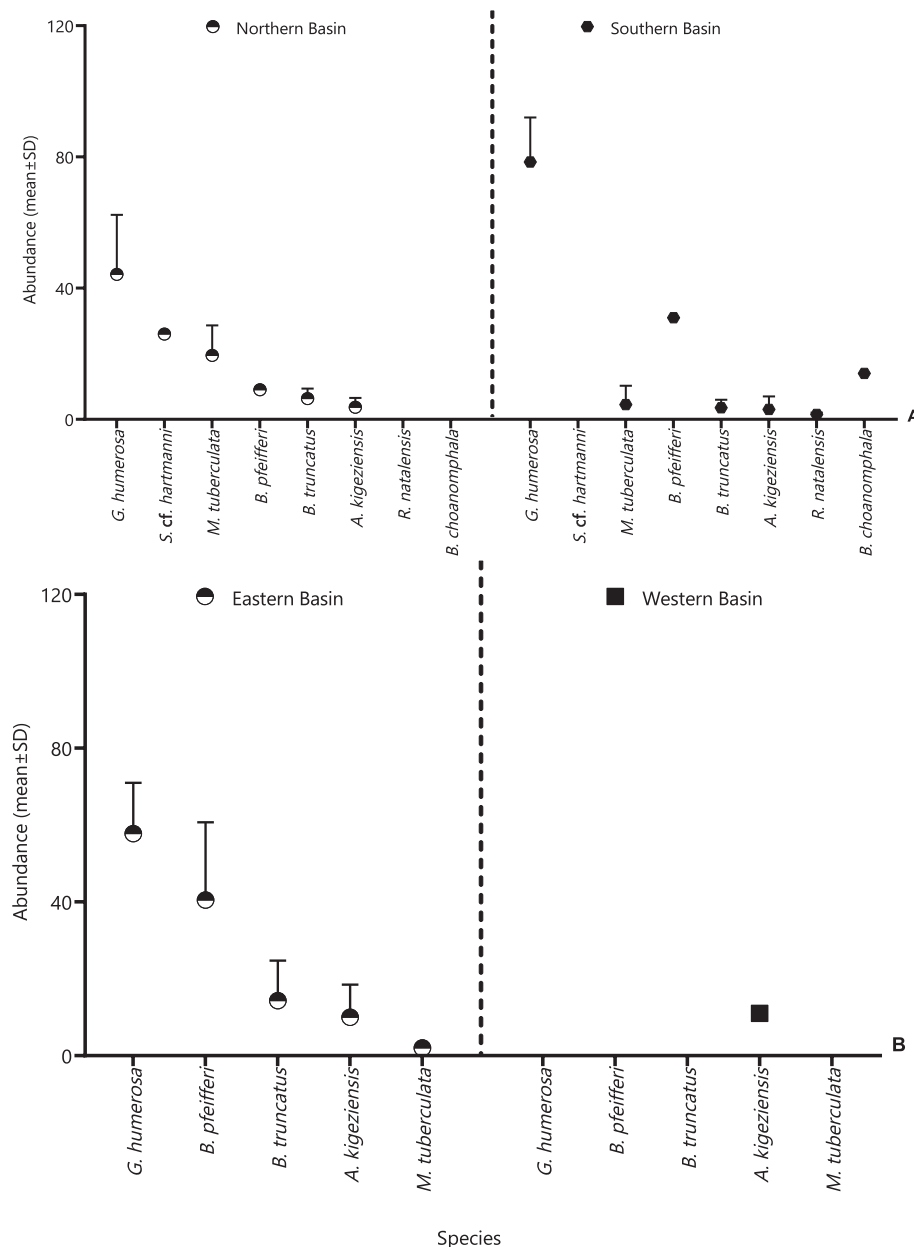
**Fig. 6.** Abundance and distribution of molluscs species in northern and southern Lake Kivu basin (A) and eastern and western Lake Kivu basin (B). The standard deviation are also presented for reference.

interest. Such approaches will also contribute to a growing reference library of African freshwater molluscs, which is a pre-requisite for studies of whole ecosystems employing technologies such as eDNA metabarcoding. Such studies are becoming more and more common (Schenekar, 2023) although they remain currently rare for Afrotropical lakes (but see Doble et al., 2020). Genetic characterization of species and local populations is also useful to trace faunal connections across scales.

*4.2. Biogeography and faunal origin*

The mollusc fauna of Lake Kivu resembles that of Lake Edward and as such suggests Nilotic biogeographical relationships. These affinities to Lake Edward likely result from its previous hydrographic connectivity with Lake Kivu (Beadle, 1981) and, as such, they provide evidence of faunal stability over extended time periods despite dramatic changes in the hydrological setting. It would be very interesting to address the faunal origin in a context that involves all Nilotic lakes and the

surrounding watersheds (Table 5). It is noteworthy that not a single species of Lake Kivu shows affinities to Congolese taxa or to those of Lake Tanganyika, despite the current hydrographic connectivity of Lake Kivu to Lake Tanganyika and, therefore, to the Congo drainage via the Ruzizi River. These faunal relationships have been observed previously based on morphological similarities (e.g. Pilsbry and Bequaert, 1927; Schultheiß et al., 2011; Van Damme and Van Bocxlaer, 2009).

Beyond geographically restricted species, widespread species may also provide information on faunal origins. For example, *Bulinus truncatus* is more common in northern Africa than elsewhere. Colonization may occur from connected waterbodies or less commonly via long-distance dispersal. For those species found in Lake Kivu which also occur in the studied tributaries, colonization likely took place directly. Interestingly, a significant number of species have not been found in Lake Kivu proper indicating differences in habitat structure or water parameters. *Pisidium* spp., *Physella acuta* and *Bulinus forskalii* were exclusively present in the tributaries whereas some other taxa are

**Table 4**
Historical account of the malacological exploration and established mollusc species list of Lake Kivu (x = live specimens/F = fossils) for the most comprehensive studies [S1: Pilsbry and Bequaert (1927); S2: Dartevelle and Schwetz (1947); S3: Gillet et al. (1960); S4: Brown (1994)] and our current study (ES). Nomenclature follows MolluscaBase (as of May 2023, except for Pisidium spp.). Previous names refer to names used in the consulted studies (S1–4). [1]Found only in tributaries.

| Species | Previous names | S1 | S2 | S3 | S4 | ES |
|---|---|---|---|---|---|---|
| **GASTROPODA** | | | | | | |
| **Viviparidae** | | | | | | |
| *Bellamya* sp. | *Viviparus* sp. | | F | | | |
| **Thiaridae** | | | | | | |
| *Melanoides tuberculata* (O.F. Müller, 1774) | | x | x/ F | x | x | x |
| **Bithyniidae** | | | | | | |
| *Gabbiella humerosa kivuensis* Mandahl-Barth, 1968 | *Bithynia alberti* | x | x | x | x | x |
| **Lymnaeidae** | | | | | | |
| *Radix natalensis* (Krauss, 1848) | *Lymnaea natalensis* | x | x | x | x | |
| **Bulinidae** | | | | | | |
| [1]*Bulinus forskalii* (Ehrenberg, 1831) | | | | | | x |
| *Bulinus truncatus* (Audouin, 1827) | *Bulinus coulboisi* | x | | | x | x |
| **Physidae** | | | | | | |
| [1]*Physella acuta* (Draparnaud, 1805) | | | | | | x |
| **Planorbidae** | | | | | | |
| *Afrogyrorbis kigeziensis* (Preston, 1912) | *Ceratophallus kigeziensis* | | | | x | x |
| *Afrogyrorbis natalensis* (Kraus, 1848) | *Ceratophallus natalensis, Gyraulus natalensis* | | | x | | |
| *Afrogyrorbis gibbonsi* (W. Nelson, 1878) | *Gyraulus gibbonsi, Afrogyrus coretus* | | x | | | |
| *Biomphalaria pfeifferi* (Kraus, 1848) | | | | x | x | x |
| *Biomphalaria alexandrina* (Ehrenberg, 1831) | *B. boissyi* | | F | | | |
| *Biomphalaria choanomphala* (E. v. Martens, 1879) | *B. ruppellii choanomphalus* | x | x/ F | | | x |
| *Biomphalaria smithi* Preston, 1910 | *B. ruppellii smithi* | | F | | | |
| *Biomphalaria sudanica* (E. v. Martens, 1870) | *Planorbis sudanicus* | | x/ F | | | |
| *Biomphalaria stanleyi* (E. A. Smith, 1888) | *B. ruppellii stanleyi* | | x/ F | | | |
| **BIVALVIA** | | | | | | |
| **Cyrenidae** | | | | | | |
| *Corbicula fluminalis* (O.F. Müller, 1774) | *Corbicula radiata* | | x/ F | | | |
| **Sphaeriidae** | | | | | | |
| *Sphaerium* cf. *hartmanni* (Jickeli, 1874) | | | | | | x |
| [1]*Pisidium kenianum* Preston, 1911 | | | | | | x |
| [1]*Pisidium viridarium* Kuiper, 1956 | | | | | | x |
| **Unionidae** | | | | | | |
| *Mutela* sp. | | | F | | | |

exclusively found in the lake, such as *B. choanomphala*, which might not be surprising given that it is a lacustrine species (Gouvras et al., 2017; Standley et al., 2011).

An interesting pattern relates to the presence (or absence) of invasive or non-indigenous species among the molluscs of Lake Kivu. Candidates would have been *Melanoides tuberculata* for which several independent Asian invasions occurred across Africa – including in lakes Malawi and Tanganyika (Van Bocxlaer et al., 2015). However, *Melanoides tuberculata* from Lake Kivu represents a lineage that is native to Africa. A candidate invasive taxon is the globally invasive *Physella acuta*, but so far it was

only found in tributaries. This species is known to occur elsewhere in the Lake Kivu region (Lawton et al., 2015; Brown, 1994) and is occasionally reported from sites with some anthropogenic disturbance such as in Lake Naivasha (Brown, 1994) and Lake Victoria (Albrecht et al., unpublished data). Despite historical (geographic) factors, ecological settings may underlie present-day occurrences of molluscs in Lake Kivu.

*4.3. Ecology and bioindication*

The N-S differences in species richness and the total absence of life molluscs in some northern localities can be linked to the Holocene history of Lake Kivu (Ross et al., 2014) when repeated lava intrusions into the lake occurred from the Virunga volcanoes. These intrusions created (underwater) heatwaves and complete overflow of vast parts of the littoral substrates that would have wiped out entire benthic communities. The latest major lava intrusion dates back to a period from 1938 to 1940 (Beadle, 1981), but similar events would have happened frequently throughout the Holocene (Ross et al., 2014). Additionally, sublacustrine volcanic eruptions also occurred repeatedly during the last 1000 years (Ross et al., 2014), which would have changed the limnological conditions at least temporarily and locally. These events may explain the substantial littoral deposits of subfossil shells, especially along the northern shorelines of the lake. Preservation of such shells (instead of dissolution) is supported furthermore by the high alkalinity of the lake in general. Currently, it is not clear whether ecosystem calamities have been affecting the total benthos of the whole lake or primarily populations in the northern Basin, but concordant patterns in other organisms indicate that effects are more severe in the North. Ash layers from subaerial eruptions sinking in the water column additionally could have caused extinction waves among all Lake Kivu mollusc populations. Such effects have been demonstrated in other lakes worldwide (e.g. Wagner et al., 2014; Jovanovska et al., 2016).

Benthic communities in other African Great Lakes have been shaped by Pleistocene lake level low stands (Schultheiß et al., 2009; Van Bocxlaer, 2017; Van Bocxlaer et al., 2021), and this might have also been the case in Lake Kivu to some extent (e.g. Ross et al., 2014). The more recent volcanic eruptions and the general physico-chemical peculiarities of the lake, including high salinity might have had a greater effect, however, on the composition of the depauperate communities existing today. As a result, macrophytes and soft substrates rich in organic-rich detritus are relatively scarce, so that habitat diversity is low, contributing further to the factors explaining why mollusc communities in Lake Kivu on average only contained 2.5 (1–5) species, which is lower than in the majority of other African rift lakes. Even though most Lake Kivu mollusc species are common, their total biomass remains comparatively small to that in the large Nilotic lakes (Verbeke, 1957; Lange et al., 2013). An interesting pattern relates to the abundance distribution of molluscs along the depth of the lake. Here, a significant extension of live populations has been found for all species compared to the data reported in Gillet et al. (1960) who found live snails (*Melanoides*) at a maximum depth of 7 m only. Here, we found living *Melanoides* down to 15 m and all other species also extend 2 to 3 times deeper than previously known (Fig. 5). The steep decline of mollusc diversity in deeper waters likely relates to oxygen availability and it has been shown that metazoan life is restricted to the upper 40 m of the lake (Richard et al., 2020). The data of Gillet et al. (1960) are from the 1950s and were restricted to the Bukavu region which, however, is one of the more diverse parts of the lake even nowadays. The contrast might be reflecting our sampling effort simply or might hint to the extension of mollusc populations. This has been shown in other African Rift lakes where multiple factors such as overfishing, eutrophication, habitat modification, and invasive plants have led to significant changes in benthic communities and much-extended molluscs abundances for common species and a decline of specialists (e.g. Beeton, 2002). This is significant since molluscs are an important, sometimes dominant component of benthic communities in tropical lakes. Interestingly, both species richness and abundance were
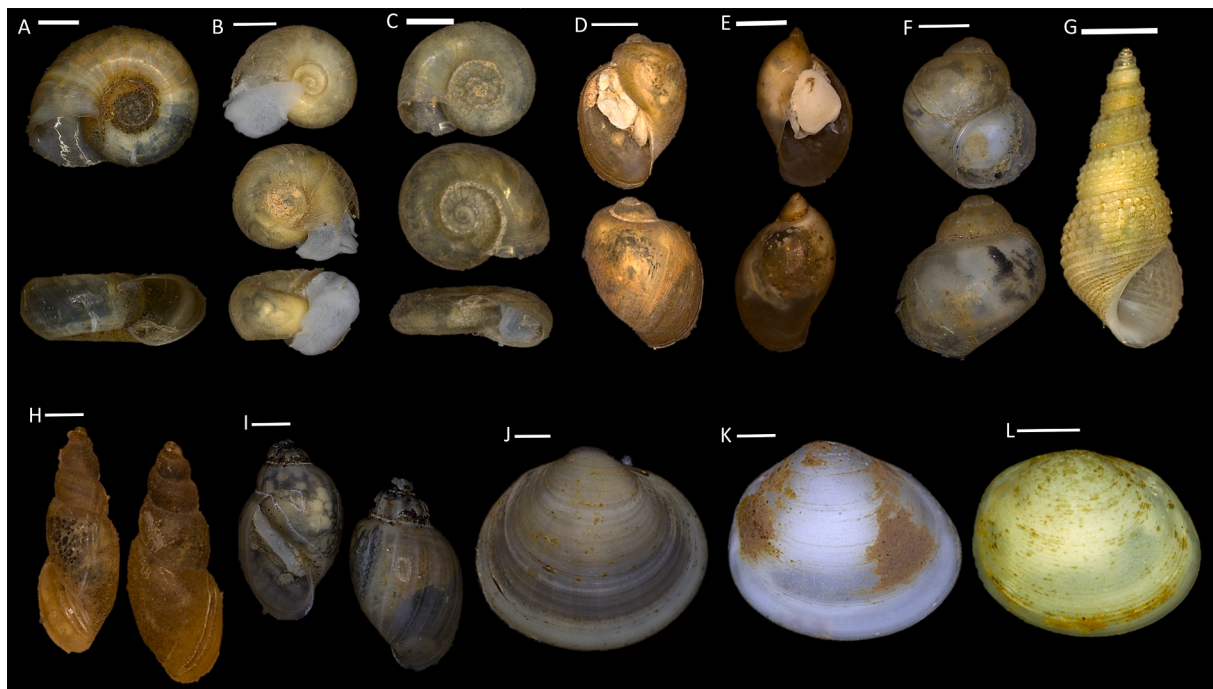
**Fig. 7.** Mollusc species collected in Lake Kivu and its tributaries (Rwandan side): (A) *Biomphalaria pfeifferi*; (B) *Biomphalaria choanomphala*; (C) *Afrogyrorbis kigeziensis*; (D) *Bulinus truncatus*; (E) *Radix natalensis*; (F) *Gabbiella humerosa*; (G) *Melanoides tuberculata*; (H) *Bulinus forskalii*; (I) *Physella acuta*; (J) *Sphaerium* cf. *hartmanni*; (K) *Pisidium kenianum*; (L) *Pisidium* cf. *viridarium*. Scale bar: 1000 μm.

related to depth (see above) because of a steep decline in oxygen, and changes in salinity but also related to the coarse anthropogenic disturbance measure we employed. This type of disturbance can be expected to even increase in the near future given the ever-growing urban centres at both ends of the lake (Bukavu, Goma-Gisenyi). Given that the anthropogenic impact is observed in even the species-poor mollusc communities of Lake Kivu, supports the potential of lacustrine mollusc species as bio-indicators of littoral conditions. Such indicators are mostly developed at the family level though, and they have been successfully used in lotic systems (Masese et al., 2023; Tumusiime et al., 2019; Dusabe et al., 2019; Wronski et al., 2015). Very recently, biodiversity indicators have been successfully developed for stretches of shoreline along the Congolese side of Lake Kivu (Hyangya et al., 2022), but similar efforts did not work in the Ruzizi River (Dusabe et al., 2022). Enhancing the taxonomic resolution to species level in species-poor communities may offer a solution and should be explored more systematically in other African lakes systems and across taxa. Another interesting factor to which molluscs react sensitively is climate change, specifically to rising temperatures in African lakes (Van Bocxlaer et al., 2012; Cohen et al., 2016). It would be worthwhile to monitor changes in the lake community given that a temperature rise has already been demonstrated in Lake Kivu (Katsev et al., 2014).

### 4.4. Biomedical implications

Our malacological survey has biomedical implications for both riparian people and their livestock because all genera that typically act as intermediate host species (IHS) for the parasites causing schistosomiasis and fasciolosis are prominently present in the study area. For *Bulinus*, *Bulinus truncatus* only has been identified genetically. This species is a prominent IHS in northern Africa, but it does not seem to be involved in schistosome transmission in equatorial regions, although this condition is to be verified (Brown, 1994). The very few studies available indicate absence of urogenital schistosomiasis in Rwanda (Kagabo et al., 2023; Rujeni et al., 2017), but a more comprehensive study is needed to verify its absence. It is noteworthy that in close geographical proximity,

several *Bulinus* species serve as intermediate hosts, namely in Tanzania, Uganda (Babbitt et al., 2023), and the Democratic Republic of Congo (Madinga et al., 2015). *B. truncatus* is also an intermediate host for bovine schistosomiasis (Brown, 1994).

Intestinal schistosomiasis is very common in the Lake Kivu basin and surrounding areas (Clark et al., 2019; Kagabo et al., 2023). We demonstrated the presence of at least two *Biomphalaria* species in the Lake Kivu catchment, namely *B. pfeifferi* and *B. choanomphala* which are often invoked in the transmission of *Schistosoma mansoni*. It has been thought that *B. chonaomphala* is endemic to Lake Victoria (Standley et al., 2011, 2014); however, here we reported it from Lake Kivu too. Identifying which species exactly are involved regionally in transmission is crucial to understand transmission dynamics and to develop potential targeted eradication strategies (Tabo et al., 2024). For example, there is discussion on whether *B. choanomphala* represents a separate species or whether it is synonymous with *B. sudanica* (Standley, 2011, 2014; Zhang et al., 2018). Overall, the findings of our study call for a detailed assessment involving parasitological studies on many of the *Biomphalaria* and *Bulinus* populations in the Kivu basin. Studies on other lakes such as Lake Malawi have shown that transmission patterns can change on short timescales and are often related to human ecosystem alterations (Van Bocxlaer et al., 2014). Our knowledge of IHS transmitting human diseases remains limited in the Lake Kivu catchment, but it is even scarcer for veterinary diseases such as fasciolosis, which is transmitted by lymnaeid snails (e.g. Ngcamphalala et al., 2022; Mahulu et al., 2019; Sun et al., 2020). It can be assumed that transmission occurs along the shoreline of Lake Kivu and its tributaries given the abundance of *Radix natalensis*, but to what extent it is a major burden requires further studies.

### 5. Conclusions

Our study revealed that the malacofauna of Lake Kivu, though admittedly comparatively poor, is more diverse than previously anticipated. The occurrence of living populations is restricted to a small ring of littoral substrates even though some species penetrate to a maximum

**Table 5**

Biogeographical relationships of the mollusks of Lake Kivu. The affinities listed a based on molecular studies of phylogenetic relationship of mollusc species wherever available. In cases where no phylogenies have been published or no molecular data are available the standard literature is referred to.

| Species | Phylogenetic relationship | Biogeographical affinity | Reference |
|---|---|---|---|
| **GASTROPODA** | | | |
| **Thiaridae** | | | |
| *Melanoides tuberculata* | African lineage of *M. tuberculata*, i.e. not Asian invasives | Widespread in tropical Africa | Brown (1994), Van Bocxlaer et al. (2015) |
| **Bithyniidae** | | | |
| *Gabbiella humerosa kivuensis* | n.a.; endemic subspecies | Large lakes from Albert, Tanganyika to Victoria for *Gabbiella humerosa* | Brown (1994), Mandahl-Barth (1968) |
| **Lymnaeidae** | | | |
| *Radix natalensis* | *Radix* s.str. | Wide-spread in African freshwaters, potentially Asian affinities | Aksenova et al. (2018), Albrecht et al. (2023), Brown (1994) |
| **Bulinidae** | | | |
| *Bulinus truncatus* | East Africa, Lake Victoria | Widespread throughout Africa but mainly in northern parts of the continent | Brown (1994), Tumwebaze et al. (2019) |
| **Planorbidae** | | | |
| *Ceratophallus kigeziensis* | n.a. | Lakes Victoria and Edward | Brown (1994) |
| *Biomphalaria choanomphala* | East Africa, Uganda lineage | Lakes Victoria and Albert, Albert Nile | Brown (1994), Joergensen et al., 2007 |
| *Biomphalaria pfeifferi* | East Africa, Kenya lineage | Tropical Africa | Brown (1994) |
| **BIVALVIA** | | | |
| **Sphaeriidae** | | | |
| *Sphaerium* cf. *hartmanni* | n.a. | East Africa | Mandahl-Barth (1988) |
| [1]*Pisidium kenianum* | *P. viridarium, P. pirothi, P. ethiopicum* | Ethiopia to Zambia | Clewing et al. (2022), Mandahl-Barth (1988) |
| [1]*Pisidium viridarium* | *P. kenianum, P. pirothi, P. ethiopicum* | Ethiopia to South Africa | Clewing et al. (2022), Mandahl-Barth (1988) |

depth of 15 m. The fauna displays 'Nilotic' biogeographic affinities although widespread taxa dominate. Species richness and abundance is more elevated in the south compared to the north, which can be attributed to recent historical ecosystem stresses (volcanic eruptions and associated disturbance) but also to current and ongoing anthropogenic effects. More molecular characterization of African freshwater molluscs is needed for intra- and supraregional comparisons and biodiversity estimates but also to characterize communities for future eDNA studies. A detailed study of schistosomiasis and fasciolosis at high spatial resolution along the shorelines and tributaries of Lake Kivu is recommended.

## CRediT authorship contribution statement

MCD collected data, performed laboratory identification, and wrote the draft article; CK performed ecological data analyses and contributed to the manuscript; CC contributed to the DNA data analyses and writing the MS; BH contributed to data collection; VB contributed to wiring and revising the MS; CA contributed to the conceptualization of the topic and writing and revising the manuscript. All authors read and approved the final version of the manuscript.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.jglr.2024.102339.

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