The non-Haplochromis fish fauna in Uganda: an update on the distribution and a review of data gaps

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Abstract

Freshwater fishes are the second most threatened group of vertebrates after amphibians. In most developing countries, the conservation of freshwater fishes is largely hampered by limited information and data. The Red List assessments by the International Union for Conservation of Nature (IUCN) provide a benchmark for conservation and planning, but these assessments require, *inter alia*, quantitative information on the species range in the wild. This information is largely missing for many species that face extinction threats. In this paper, we combined species occurrence data, expert knowledge, and literature to review and update the distribution of non-*Haplochromis* fish species native to Uganda and determine their geographical extent relative to the global range. Results showed that (i) at least 110 non-*Haplochromis* species occur in Uganda, (ii) the current status in the entire native range for more than 60% of these species is unknown; (iii) five species previously known to occur in Uganda: *Amphilius kivuensis, Bagrus degeni, Marcusenius macrolepidotus, Petrocephalus catostoma*, and *Lacustricola pumilus* lack a native locus and hence not Ugandan fishes, (iv) 17 species occur in areas beyond their previously known range, and therefore, their presence needs further investigations, preferably by examining specimen collections, and (v) majority of the non-*Haplochromis* species native to Uganda have a wide distribution outside the national boundaries. We anticipate this information to be relevant both for the national and global IUCN Red List assessments for the non-*Haplochromis* fishes in Uganda. Furthermore, the identified data gaps will be relevant in prioritizing limited resources during surveys and collections.

Introduction

Freshwater fishes are the second most threatened group of vertebrates after amphibians (Darwall & Freyhof, 2016). The threat level is likely to worsen in future as demand for aquatic food and animal protein continues to increase. Efforts by governments globally to reduce biodiversity loss have not prevented many habitats and their associated freshwater fish species from being lost or degraded at an alarming rate (Dudgeon et al., 2006; Darwall et al., 2018). Moreover, fish species are also being overexploited due to the perception that they are renewable 'agricultural products' with no intrinsic biodiversity value (Wadewitz, 2011). Furthermore, native fisheries have been greatly impacted by invasive species through predation, competition and habitat alteration (e.g., Ogutu-Ohwayo, 1990; Kaufman, 1992)

Conservation of freshwater fishes is partly being hampered by limited information and data that are needed to guide conservation planning. *Ex-situ* conservation, for instance, requires information on their current status in the wild and the condition of the natural habitat. This information is largely missing for many species that face extinction risk. For instance, on the International Union for Conservation of Nature (IUCN) Red List database of threatened species, which is the world's widest benchmark for conservation and development planning processes (Hoffmann et al., 2008), the majority of the freshwater fish species remain unassessed due to lack of data (IUCN, 2017).

Uganda is endowed with freshwater fish species diversity: up to 18% of the surface area is covered by lakes, rivers and swamps, where over 500 fish species dwell (Natugonza & Musinguzi 2022). There are five major lake basins in Uganda that lie in two ichthyofaunal provinces, i.e., Victoria, Kyoga, and Edward systems (East Coast Ichthyofaunal province) and Albert system (Nilo-Sudan Ichthyofaunal province) (Fig. 1, Decru et al., 2019). In addition, there are about 160 small lakes and numerous rivers. These lakes and rivers harbor a great diversity of fishes, which are largely endemic (Greenwood, 1966).

To date, Greenwood (1966) is still the most widely used reference for the distribution of non-*Haplochromis* fishes in Uganda. In total, 94 non-*Haplochromis* fish species in 17 families are documented in Greenwood (1966). Yet, taxonomic discoveries as well as revisions of previously described species have been on the rise since the work of Greenwood (1966). For example, between 2003 and 2022, approximately 250 new fish species were described globally per year (Fricke et al., 2022a). This observation suggests that new fish species description is a remarkably active area of species discovery, and therefore, Greenwood (1966) is likely out of date, requiring more recent reviews, based on numerous studies and surveys that have been conducted since then.

Recently, online databases such as FishBase (https://www.fishbase.org), the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), and the Freshwater Biodiversity Portal for Uganda (FWB) (https://freshwaterbiodiversity.go.ug/) have served as key reference tools for more recent data and information. FishBase is the most comprehensive of these reference tools and has served as an alternative to Greenwood (1966) for the updates on the fishes of Uganda. However, FishBase also has limitations. First, FishBase derives most of the distributional information on non-*Haplochromis* fishes in Uganda from Greenwood (1966). Second, FishBase tends to be ambiguous when there is no precise information on the species range. For example, a species such as *Garra hindii* (cyprinidae) is documented in FishBase to occur in "Uganda, Kenya, Cameroon, and the Congo basin"; yet, *Garra* species are mostly endemic (Jos Snoeks, *pers. comm*. 2022), and such a large country distribution, spanning more than four ichthyofaunal provinces is unlikely. Third, FishBase collates distribution information from published literature, leaving out enormous information from unpublished surveys and gray literature. Other reference databases such as GBIF and FWB, which host occurrence data from surveys, require some analytical skills to deduce distributional information, but these skills are not common with most potential data users such as policymakers.

When precise information on a species' location is lacking, local conservation planning is greatly affected. Decru et al. (2020) sought to bridge this information gap by comprehensively reviewing the distribution of non-*Haplochromis* fishes in Uganda, but only focusing on the Lake Edward system. Decru et al., (2020) evaluated the occurrence of the species found in the Lake Edward system by examining occurrences in three ichthyofaunal provinces: Nilo-Sudan, East Coast and Congo ichthyofaunal provinces. These authors found that the Lake Edward system alone hosted 34 non-*Haplochromis* species, belonging to 10 families and 21 genera, registering six new species that were not listed by Greenwood (1966) and the online databases such as FishBase. Similarly, there were several species in Greenwood (1966) that were no longer valid due to taxonomic revisions. These findings further underscore the need to review and update the distribution of fishes in other hydrological basins.

Besides, both the online databases (such as FishBase, GBIF, and FWB) and systematic reviews such as Decru et al. (2020) only provide qualitative information on the species distribution, which is insufficient for assessing the conservation status of the species. The IUCN Red List of Threatened Species, which is the global benchmark for the conservation status of species, currently relies on quantitative information either on population trends or the geographical extent to designate a species as threatened or "Least Concern" (IUCN, 2019a). Because information on population trends is scanty, most assessments in IUCN rely on the geographical extent of the species. The Extent of Occurrence (EOO) and Area of Occupancy (AOO) are by far the most commonly used metrics to infer the geographical extent of species used in IUCN assessments (IUCN, 2019a). When estimated at a scale that is biologically relevant to a species, EOO and AOO can provide insights into the species' habitat requirements, threats and limitations, and if data are available over time, valuable trend information (IUCN, 2019a). However, this information is largely missing for many freshwater species.

The absence of information on EOO and AOO in most studies on species distributions could be one of the reasons most freshwater fish species have remained unassessed. In Uganda, for instance, 117 non-*Haplochromis* fishes were listed on IUCN website in different Red List categories by the end of 2021. However, the assessments for more than 50% of these fishes were out of date, while an additional 14 species have never been assessed. Because of the recent changes in the red listing criteria, where quantitative information either by population or geographic extent must be present to designate a species' Red List category (IUCN, 2019a), these assessments may never be updated without information on EOO and AOO.

The purpose of this study, therefore, is twofold: first; to review the distribution and occurrence of non-*Haplochromis* fishes in Uganda, building on Decru et al. (2020); second, to estimate the extent and range for the non-*Haplochromis* fish species in Uganda in relation to the global range. This information is needed for updating IUCN Red List assessments as well as conducting new assessments for the unevaluated species.

Decru et al. (2020) relied on information from literature, distribution notes in Fishbase, museum collections, and field expeditions. In this study, field expeditions and access to museum specimens are not possible. However, occurrence records in the GBIF and FWB, supplemented by information from FishBase and other literature sources are deemed sufficient to provide a valuable update on the current status of fishes in Uganda, which can inform further detailed investigations and data collection.

Figure 1 shows that fish species native to Uganda live in two major ichthyofaunal provinces: The Nilo-Sudan and the East-Coast provinces. However, these two ichthyofaunal provinces span many countries, i.e., from the Indian Ocean (East Africa) to the Atlantic Ocean (West Africa) to the Mediterranean Sea (North Africa). This large extent suggests that fishes that are not endemic to a specific waterbody could have a very wide distribution and range (in terms of EOO and AOO). Consequently, one would expect the proportion of national EOO and AOO to the global range to be substantially smaller (probably less than 10% for the fishes in the bigger Nilo-Sudan ichthyofaunal province, and less than 50% for the fishes in the relatively smaller East Coast ichthyofaunal province). To investigate this hypothesis, one needs to map both global and national range of every fish species under consideration to estimate the values of EOO and AOO at global and national levels. This task is cumbersome, but possible and highly recommended (IUCN, 2019a). When complete, this information is indispensable when conducting national Red List assessments, which have recently become popular (Brito et al. 2010), but still lacking for the fishes in Uganda.

Material And Methods

Study area and scope

In this study, we examined fish species distribution in all waterbodies across Uganda. There are five major lakes (Victoria, Kyoga, Albert, Edward and George) and over 160 small lakes spread across the country in six major drainage basins (Fig. 2), covering about 18% of the total country surface area (Nsubuga et al., 2014). Some of the major rivers include the Nile, Katonga, Kagera, Sio, and Aswa (Fig. 2). Decru et al. (2020) evaluated the occurrence of the species found in the Lake Edward system by examining occurrences in three ichthyofaunal provinces: Nilo-Sudan, East Coast and Congo ichthyofaunal provinces. Given that most of the remaining water bodies in Uganda are not shared with the Congo ichthyofaunal province, this study only considered the Nilo-Sudan and East Coast provinces (Fig. 1).

In terms of taxonomic coverage, we focused on non-*Haplochromis* fish species that are native to Uganda. Most water bodies in Uganda contain large assemblages of endemic haplochromine cichlids; however, these fishes are largely understudied and many remain undescribed. Also, morphologically, the identification of *Haplochromis* species is not obvious, and as a result, data on occurrence is scanty.

Data sources

Without additional field expeditions and museum collections, this study sought to rely on the approach used by IUCN, by using distribution maps that display occurrence of a species within its extent, which is based on past observations and occurrences, knowledge of habitat preferences, and remaining suitable habitats (IUCN, 2019b). This information was derived from the literature (both published and unpublished), expert knowledge, online databases such as FishBase (Froese & Pauly, 2022), Eschmeyer's catalogue of fishes (Fricke et al., 2022b), the GBIF (GBIF.org, 2022), the FWB (Natugonza & Musinguzi, 2022), and institutional archives, especially from the National Fisheries Resources Research

Institute (NaFIRRI). These distribution maps are useful in identifying priority conservation areas, identifying data gaps, and informing management decisions (Jetz et al., 2012).

Updating the species list

A preliminary list of non-*Haplochromis* fishes in Uganda was downloaded from FishBase, a global online database of fishes, from the country-specific page (https://www.fishbase.se/Country/CountryChecklist.php?showAll=yes&what=list&trpp=50&c_code=800&cpresence=present&sortby=alpha2&ext_CL=on&ext_pic=on&vhabitat=all2 The taxonomic status of the names was checked using the Eschmeyer's Catalog of Fishes (Fricke et al., 2022b), which is also an on-line database that references work on the scientific names of fish species and genera.

Fish species occurrence data were downloaded from the GBIF (filtered by country) (GBIF.org, 2022) and the FWB. Data from these databases follow Darwin Core attributes, which facilitate easy use (Wieczorek et al., 2012). Therefore, all the occurrence data acquired from non-standard Darwin Core formats such as those of NaFIRRI archives was first mobilized into similar formats. These records were rigorously compared with the species list from FishBase to identify any inconsistencies in the distribution of known species and to ascertain where new species may have been recorded in recent surveys. Also, the records were checked against a host of literature sources, especially FishBase (Froese & Pauly, 2022), Eschmeyer’s catalogue of fishes (Fricke et al., 2022b), Greenwood (1966), and Decru et al. (2020) for inconsistencies in taxonomy as well as taxonomic updates, uncertainty over the identity or authenticity of the records, and the accuracy of the locations. Whenever the distribution of a species was in doubt, appropriate species occurrence designation was applied following the IUCN standard attributes for spatial data (Table 1).

Table 1
IUCN standard attributes for spatial data. Adopted from IUCN (2019a). Only extant ranges are used in the estimation of EOO and AOO.

Code	Presence	Definition
1	Extant	The species is known or thought very likely to occur presently in the area, which encompasses localities with current or recent (last 20–30 years) records where suitable habitat at appropriate altitudes remains.
2	Probably Extant	Phased out.
3	Possibly Extant	There is no record of the species in the area, but the species may possibly occur, based on the distribution of potentially suitable habitat at appropriate altitudes, or the records exist but are more than 30 years old and the present status cannot easily be ascertained. Identifying Possibly Extant areas is useful to flag up areas where the taxon should be searched for.
4	Possibly Extinct	The species was formerly known or thought very likely to occur in the area (post 1500 AD), but it is most likely now extirpated from the area due to habitat loss and/or other threats, and there have been no confirmed recent records despite searches.
5	Extinct	The species was formerly known or thought very likely to occur in the area (post 1500 AD), but it has been confirmed that the species no longer occurs because exhaustive searches have failed to produce recent records, and the intensity and timing of threats could plausibly have extirpated the taxon.
6	Presence Uncertain	A record exists of the species' presence in the area, but this record requires verification or is rendered questionable owing to uncertainty over the identity or authenticity of the record, or the accuracy of the location.

Before use, occurrence data was cleaned to make it fit for purpose by removing or correcting inaccurate, unreasonable, or incomplete data (García-Roselló et al., 2014). These included records with localities that were not in Uganda and all the records without specific epithets. Fields with data that were not relevant to the study were deleted to simplify data cleaning. Occurrences that had no coordinates were georeferenced where possible, based on information in the recorded field notes, locality, waterbody, and location remarks, using Google Earth Pro. These coordinates were in decimal degrees.

Other occurrence data obtained from the institution archives were mobilized following the Darwin core attributes, where higher taxonomy for taxa in the data was generated using the GBIF species name matching tool (https://www.gbif.org/tools/species-lookup). This tool is used to normalize species names from a *.csv* file against the GBIF backbone. Canadensys coordinate conversion tool (http://data.canadensys.net/tools/coordinates) was used to convert the geographic coordinates from other formats to decimal degrees.

All the occurrence datasets were changed from GBIF standards to IUCN standards using IUCN standard attributes for spatial data, which contain the core and optional fields (IUCN 2019a). The core fields are the required or recommended attributes such as binomial, origin, presence, compiler, citation and year compiled, whereas the optional fields are attributes that may or may not be included in the dataset such as record number, recorder, country code, verbatim Latitude and verbatim Longitude. Among the core spatial fields, species presence is the most important attribute as it determines whether the species range can be quantitatively ascertained or not (IUCN, 2019a). This attribute has five fields (Table 1), but only three fields were used: 'extant', 'possibly extant', and 'presence uncertain'. Most of the species had occurrence records, but these records were too old to ascertain the present status of the species in the area (i.e., more than 30 years). These species with older records were presumed possibly extant on assumption that not enough field searches for these species have been done (Snoeks, *pers. Comm.* 2022). Other fishes had records that extended beyond their known and expected range, based on various literature sources listed above. These fishes were designated as presence uncertain (Table 1) until specimens are obtained to confirm their validity. For the attributes such as presence, origin, seasonal and basis of the record, records were filled in using IUCN lookup codes (Table 1; IUCN, 2019a). The codes for the origin of each taxon were recorded based on information from FishBase (Froese & Pauly, 2022), Greenwood (1966), and Decru et al. (2020).

Modelling the species range

An updated species list (Table 2) was sent to the IUCN Freshwater Unit to create a Species Information Service (SIS) account. The SIS is the central database used by IUCN to store and manage species accounts and assessments for publication on the IUCN Red List database. In SIS, a new working dataset was created, comprising all the fish species to be mapped. Creation of the SIS account enabled access to the IUCN Freshwater Mapping Application (FWMA) used for mapping species distributions and calculating EOO and AOO (IUCN 2019b). FWMA is a web-based mapping application that is widely used, as part of assessments for the IUCN Red List of Threatened Species, to produce distribution maps of freshwater species based on hydro-basin layers (Lehner & Grill, 2013; IUCN, 2019b). This application also provides an online platform to produce new distribution maps or update existing distribution maps for species published on the IUCN Red List.

Table 2
National distribution and range—Extent of occurrence (EOO) and Area of occupancy (AOO)—of selected fish species in relation to global occurrence.

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Alestidae					
Alestes baremoze	Lake Albert, Murchison and lower Victoria Niles, and River Aswa. Possibly extant Albert Nile and affluent of Lake Albert.	12971.29	1–5	4785	1–5
A. dentex	Lake Albert and Murchison Nile. Possibly extant in Albert Nile and some affluent rivers of Lake Albert	6170.48	1–5	3738	1–5
Brycinus macrolepidotus	Lake Albert and Murchison Nile; possibly extant Albert Nile and Aswa river	7385.69	1–5	4036	1–5
B. jacksonii	Lakes Victoria and Kyoga basins	179992.85	46.8	92275	42.9
B. nurse	Lake Albert and Murchison Nile; possibly Albert Nile and Aswa river	11498.31	86.3	4346	57.9
B. sadleri	Lakes Victoria and Kyoga basins; possibly Aswa river basin	173974.66	28.6	87080	57.3
Hydrocynus forskahlii	Lake Albert and Murchison Nile. Possibly extant in Albert Nile.	6170.48	1–5	3738	1–5
H. vittatus	Lake Albert, Murchison and Albert Niles. There are no recent records, but the species is possibly extant (Wandera & Balirwa, 2010)				
Amphiliidae					
Amphilius jacksonii	Lake Edward drainage; possibly Kagera river drainage within Lake Victoria basin. Uncertain in Kyoga drainage as records are likely to be of *Amphilius lujani* (Froese & Pauly, 2022). Also uncertain in the Southern parts of Lake Albert.	28366.754	41.3	18992	71.1
A. lujani	Kyoga drainage and northeastern affluent rivers of Lake Victoria (Thomson et al., 2015).	7197.66	>70	4212	>70
A. cf. *kivuensis*	Lake Edward system (Decru et al., 2020)				

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
A. sp. "Bwindi"	Lake Edward system (Decru et al., 2020)				
Zaireichthys rotundiceps	Lakes Victoria, Edward, and Kyoga basins (both in rivers and lakes) (Decru et al., 2020; Seegers et al., 2003)	185801.45	12.6	93608	21
Anabantidae					
Microctenopoma damasi	Affluent rivers of the Lake Edward system and the Semliki River, but has not been found in other affluents of the Lake Albert system (Decru et al., 2020)	94054.08	62.6	52703	58.02
Ctenopoma muriei	Lakes Victoria, Kyoga, Edward and Albert and their affluent rivers	213697.27	6.2	161496	25.7
Bagridae					
Bagrus bajad	Lake Albert and Muzizi river mouth, Murchison and lower Victoria Niles, and River Aswa. Possibly extant in Albert Nile.	19000.97	1–5	5004	1–5
Bagrus docmak	Lakes Victoria, Victoria Nile, Kyoga, Nabugabo, Albert (including Albert and Murchison Niles), Edward and George, Kazinga channel, Bisina, and River Kagera	188858.98	1.2	49884	3.4
Cichlidae					
Astatoreochromis alluaudi	Victoria, Kyoga and Edward lake basins, including Semuliki river (but not reaching Lake Albert)	185255.024	42.5	122648	40.5
Oreochromis leucostictus	Lakes Edward, George and Albert, and affluent rivers and streams of these lakes and of the Semliki River; introduced in Lakes Victoria and Kyoga basins	136067.44	70.5	75667	64.6
Oreochromis niloticus	Lakes Edward, George and Albert, and many crater lakes in Western Uganda. Introduced in many localities in Lakes Victoria and Kyoga basins. Possibly in Aswa river basin, but origin is uncertain.	130223.68	< 1	86141	< 1

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Oreochromis esculentus	Lakes Victoria and Kyoga basins. Virtually extirpated in the main lakes, but still present in satellite lakes of these basins	109909.25	40.8	80211	37.9
Oreochromis variabilis	Lakes Victoria and Kyoga basins, and River Ayago. Virtually extirpated in the main lakes, but still present in satellite lakes of these basins	156277.9	49.1	109234	43.8
Coptodon zillii	Lake Albert and the Nile river; introduced in Lakes Victoria and Kyoga basins	6170.48	1–5	3738	1–5
Sarotherodon galilaeus	Lake Albert, including the delta of Murchison Nile	6170.48	< 1	3738	< 1
Pseudocrenilabrus multicolor	All major lake basins in Uganda. The current status in Albert Nile basin is not known as there no recent records, but is possibly extant	224076.37	46.9	188437	45.7
Citharinidae					
Citharinus citharus	Lake Albert and Murchison. Possibly extant in Albert Nile.	6170.48	1–5	3738	1–5
Citharinus latus	Lake Albert, including the Delta of Murchison Nile	6171.48	< 1	3739	< 1
Clariidae					
Clariallabes petricola	Lake Victoria and Victoria Nile, and Lake Kyoga. The current status is unknown due to lack of recent data, but possibly extant				
Clarias werneri	Lakes Victoria, Kyoga, Edward, Albert basins	49928.89	30–40	21788	30–40
Xenoclarias eupogon	Endemic to Lake Victoria (deep waters)				
Clarias liocephalus	Widespread in all major and minor water systems in Uganda	249945.519	5–10	161436	18.3
Clarias alluaudi	Widespread in all major and minor water systems in Uganda, excluding the Albert drainage	196065.03	30–40	163468	30–40
Clarias gariepinus	Widespread in all major and minor water systems in Uganda	267697.37	< 1	217946	5.0

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Heterobranchus longifilis	Lake Edward and Murchison Nile				
Claroteidae					
Auchenoglanis occidentalis	Lake Albert and Murchison and affluent of Lake Kyoga. Possibly Albert Nile and Nile basin.	44464.78	1–5	4443	1–5
Cyprinidae					
Labeo horie	Drainage basin of Nile river and Lake Kyoga, including Aswa river	11498.31	86.3	4346	57.9
Labeo victorianus	Lakes Victoria and Kyoga basins, both in lakes and rivers.	143376.75	37	82282	40
Labeo coubie	Lakes Albert and Murchison Nile; possibly Albert Nile drainage. Uncertain in Lake Victoria as it extends outside the known native range shown in Greenwood (1966)	9973.85	1–5	4814	1–5
Labeobarbus ruwenzorii	Rwenzoria area in the upper Lake Edward system (Sibwe, Mubuku, Rwimi). Current status is not known due to lack of data, but possibly extant. Uncertain in the lower Edward system (Ihihizo, Ishasha rivers in Bwindi Impenetrable National Park) (Decru et al., 2020).				
Labeobarbus altianalis	Lakes Victoria, Edward, and Kyoga basins (both in rivers and lakes)	185834.97	39.1	101099	41.3
Labeobarbus bynni	Lake Albert and Murchison Nile. Possibly extant in Albert Nile.	11498.31	1–5	4346	14
Labeo forskalii	Lake Edward and Albert drainage systems, and Aswa river	57738	76.1	24489	63.5
Labeobarbus alluaudi	Lake Edward system (Rivers Mubuku and Sibwe, and Ruimi), but it has not been observed recently.				

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Labeobarbus huloti	Lake Albert, but there is insufficient information on distribution as it only known from the type locality (Zega on the Vuda River)				
Labeobarbus somereni	Rwenzori area (Sibwe, Mubuku, Rwimi, and Kirimia Rivers). No recent records from these areas, which could be attributed to limited sampling of the area (Decru et al., 2020).				
Enteromius Pellegrini	Lake Edward basin	25708.9	58.1	18818	55.3
Enteromius nyanzae	Lake Victoria basin. Current status unknown due to lack of recent data. Records from Lake Kawi are uncertain and likely to be misidentification				
Enteromius jacksoni	Lake Victoria and Kyoga basins	74350.487	10–20	38182	10–20
Enteromius profundus	Endemic to Lake Victoria (Tweddle et al., 2006). Occurrence records from Lake Kyoga basin are uncertain and likely to be misidentifications	33755.071	38.4	29454	58.7
Enteromius alberti	Lakes Edward and George and their affluent rivers; possibly in affluent rivers of Lake Victoria. Presence in Albert drainage is uncertain and needs confirmation	25708.9		18818	
Enteromius radiatus	Lake Victoria basin. Possibly Aswa River basin. Records from Lake Kyoga basin are uncertain	44313.81	5–10	20384	5–10
Enteromius sexradiatus	Lake Victoria (possibly in nearshore).				
Enteromius yongei	Aswa river and Lake Kyoga affluent (Greenwood, 1966) and affluent of Lake Victoria in the North East (Whitehead, 1960). There are no recent records, but the species is possibly extant				
Enteromius paludinosus	Lakes Victoria and Kyoga basins	157218.71	1.7	95592	3.4

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Enteromius apleurogramma	Aswa River, Lake Victoria basin, Lake Edward-George system, and Lake Kyoga basin. Presence in Lake Albert system is uncertain as it is outside the known native range	185834.97	5–10	110258	5–10
Enteromius kerstenii	Lakes Victoria, Kyoga, Edward-George basins. Presence in Lake Albert system is uncertain as it is outside the known native range				
Enteromius magdalenae	Lakes Victoria and Nabugabo. Current status unknown due to lack of recent data. Records from Lake Kyoga basin are uncertain and could be misidentifications				
Enteromius neumayeri	Lakes Victoria and Kyoga basin. Possibly extant in Lake Albert watershed (Greenwood, 1966). Records from Lake Edward system are uncertain as they are likely to be *Enteromis pellegrin* (Decru et al., 2020).	157218.71	10–20	93083	10–20
Enteromius perince	Lake Albert, and Aswa River systems. There are no recent records, but the species is possibly extant (Greewood, 1966).				
Garra dembeensis	Lake Victoria and affluent and Victoria Nile	33755.071	< 1	29454	1–5
Danionidae					
Rastrineobola argentea	Lakes Victoria and Kyoga basins	70840.23	35.7	35275	22.6
Engraulicypris bredoi	Lake Albert, including the delta of Murchison Nile	6170.48	77.16	3738	55.42705
Leptocypris niloticus	Lake Albert and Murchison Nile	6170.48	< 1	3738	< 1
Raiamas senegalensis	Aswa river. There are no recent records, but the species is possibly extant (Greenwood, 1966). Records from Lake Albert affluent are uncertain and needs verification.				
Distichodontidae					

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Distichodus nefasch	Lake Albert, Murchison Nile, and Albert Nile. The present status in Albert Nile needs to be ascertained with more recent sampling	5024.97	64.3	3253	49.8
Nannocharax niloticus	Murchison Nile; also possibly extant in Lake Albert and Albert Nile (Daget & Gosse, 1984)	739.41	70–80	555	70–80
Distichodus rostratus	Murchison Nile; also possibly extant in Lake Albert and Albert Nile.				
Latidae					
Lates macrophthalmus	Lake Albert, including the delta of Murchison Nile	6170.48	77.16	3738	55.4
Lates niloticus	Lake Albert, Albert and Murchison Niles. Introduced in Victoria Nile, Lake Victoria and Kyoga basins	23201.84	< 1	7199	< 1
Malapteruridae					
Malapterurus electricus	Lake Albert and affluent; possibly extant in Albert Nile	26153	< 1	16410	< 1
Mastacembelidae					
Mastacembelus frenatus	Lakes Victoria and Kyoga basins. Possibly extant in Aswa River. Recent surveys suggest that the distribution extends to the Lower Victoria Nile.	133720.41	1–5	76679	5–10
Mochokidae					
Synodontis khartoumensis	Lake Albert and Albert Nile. Present status unknown due to lack of recent data				
Synodontis victoriae	Lake Victoria and its affluent rivers, Lakes Nabugabo and Kyoga; Victoria Nile	100468.542	28.5	22820	18.4
Synodontis afrofischeri	Lake Victoria and its affluent rivers, Lake Nabugabo, Kyoga basin; Victoria Nile. Records from the delta of Murchison Nile are uncertain.	167781.96	31.4	83680	42.6

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Synodontis nigrita	Lakes Albert and Murchison Nile. Possibly extant in Albert Nile. Presence in rivers affluent to Lake Albert is uncertain.	9797.807	1–5	6344	1–5
Synodontis schall	Lake Albert and Murchison Niles. Possibly extant in Albert Nile and Semiliki river	11831.394	1–5	7088	1–5
Synodontis frontosus	Lake Albert and Murchison. Possibly extant in the Albert Nile	12677.511	1–5	6904	1–5
Synodontis macrops	Aswa river. Current status unknown due to lack of data, but possibly extant				
Synodontis serratus	Lake Albert and lower Nile. It has not been recorded in the Ugandan side, but the presence in the DRC side suggests it possibly occurs in Uganda (Jos Snoeks, *Pers. Comm*)				
Mormyridae					
Mormyrus macrocephalus	Lake Kyoga basin; also possibly extant in Aswa river (Greenwood, 1966).	75859.84	97.7	56908	98.1
Mormyrus caschive	Lake Albert and the delta of Murchison Nile; also possibly extant in Albert Nile (Greenwood, 1966). Records in Aswa river and Elgon region are uncertain.	6170.48	10–20	3738	42.1
Mormyrops anguilloides	Lake Albert and Murchison Nile (including the delta). Possibly extant the affluent of Lake Albert and Albert Nile (Greenwood, 1966).	6170.48	1–5	3738	1–5
Mormyrus kannume	Lakes Victoria, Kyoga, Albert, George, and Edward. Not common in most affluent rivers of these lakes apart from Victoria and Murchison Niles, Kagera, and Kazinga channel.	136849.16	3.7	29659	5.4

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Marcusenius cyprinoides	Originally known from Albert Nile and Aswa river (Greenwood 1966), but no recent data to ascertain the current status. Recent records suggests the species is present in Lake Albert (Wandera & Balirwa, 2010), but this needs verification				
Mormyrus niloticus	Lake Albert, including the delta of Murchison Nile; also possibly in the Albert Nile	6170.48	75–80	3738	55–60
Marcusenius victoriae	Lakes Victoria and Kyoga basins	119611.164	38.2	75051	41.2
Pollimyrus petherici	Lake Albert and Murchison Nile; also possibly in Albert and lower Victoria Nile	6170.48	77.1	3738	55.4
Gnathonemus longibarbis	Lake Victoria and Kagera system, Victoria Nile and Lake Kyoga system	180621.83	43.2	91875	42.0
Marcusenius rheni	Lake Victoria. There are no recent records for this species				
Petrocephalus degeni	Lakes Victoria and Kyoga basins. This includes all records previously identified as *Petrocephalus catostoma* (Kramer et al., 2012).	119611.164	50–60	75051	50–60
Pollimyrus nigricans	Lakes Victoria, Nabugabo, Albert, George, Edward and Kyoga and affluents of the lakes	154791.29	26.5	56775	18.6
Hippopotamyrus grahami	Lakes Victoria and its affluent rivers, and Kyoga basin. Possibly extant in lower Victoria Nile. Records from Murchison Nile and River Muzizi (on Lake Albert) are uncertain and need verification	143376.75	60–70	82282	670
Hyperopisus bebe	Lake Albert, Albert and Murchison Niles. Possibly extant in Aswa river (Greenwood, 1966)	6170.48	1–5	3738	1–5
Nothobranchiidae					
Nothobranchius taeniopygus	Affluent of Lake Victoria and Aswa river drainage (Greenwood, 1966)				

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Nothobranchius robustus	Drainage basins of Lake Victoria and Albert.	145188.97	87.5	77405	> 80
Nothobranchius ugandensis	Drainages of Lakes Victoria, Albert and Kyoga. Possibly extant in Aswa river drainage (Wildekamp, 1995).	781.79	> 80	676	> 80
Nothobranchius elucens	Aringa system, south of Madi Opei township, Aswa drainage (Nagy, 2021). Possibly in other parts of the Aswa river basin	1760.13	93.5	1550	95.7
Nothobranchius taiti	Apapi river system, Lake Kyoga basin (Nagy 2019)				
Polypteridae					
Polypterus senegalus	Lake Albert and affluents; Possibly extant in Albert Nile and affluents	26749.26	1–5	16878	1–5
Procatopodidae					
Lacustricola kassenjiensis	Lake Albert, including the delta of the Semliki River and the Victoria Nile River below Murchison Falls.				
Lacustricola centralis	Lake Victoria and Kyoga basins (Wildekamp, 1995; Seegers, 1997)	143376.75	20.9	82282	28.6
Lacustricola vitschumbaensis	Lakes Edward and George; Kazinga Channel, and affluent rivers; northern parts of Lake Victoria, and Lake Kyoga drainage (Wildekamp, 1995; Decru et al., 2020).	25708.9	29.4	18818	37.3
Lacustricola bukobanus	Lakes Kyoga, George, Edward, Albert and adjacent river systems, and Lake Victoria drainage	147394.5	33.5	98447	35.6
Lacustricola margaritatus	Lakes Victoria and Kyoga basins (Nagy and Watters, 2022). This includes all records previously identified as *Lacustricola pumilus*.	119611.164	50–60	75051	50–60
Laciris pelagica	Endemic to Lake Edward; occurrence records in Lake George are unverified (hence uncertain)	782.18	29.2	638	24.5

Species	Distribution	National EOO	Percentage of global (%)	National AOO	Percentage of global (%)
Micropanchax loati	Nile river and the Lake Victoria system (including Kyoga and Aswa drainages) (Wildekemp, 1995).				
Platypanchax modestus	Affluent rivers of Lakes Edward and George	29517.86	81.9	16514	88.3
Protopteridae					
Protopterus aethiopicus	All major water bodies (Victoria, Edward, Kyoga, Albert) and affluent rivers. Possibly extant in Aswa river basin and Albert Nile and affluent.	213663.73	3.7	160449	16.5
Schilbeidae					
Schilbe intermedius	Lakes Victoria (including Kagera river) and Nabugabo, Kyoga basin, Albert and affluent; Murchison and Victoria Niles; possibly extant in Aswa river.	202198.44	1–2	108165	1–2
Schilbe mystus	Lakes Albert, Murchison Nile, and Semliki river. Possibly extant in Albert Nile	26284.02	1–5	16420	1–5

The FWMA uses point data on species' location to create a map, encompassing all possible hydro-basins where a species can be found. Species were mapped in the FWMA using hydro-basin level 8; after, the EOO, which is the smallest area that encompasses all the known, inferred or projected sites where a species is extant, was estimated by the minimum convex polygon method, while the AOO, which is the area inside the EOO occupied by the species, was estimated using the grid cell method. The two methods are described in detail in IUCN (2019b). Only hydro-basins where the species was extant (Table 1) were used in the estimation of EOO and AOO.

Initially, all mapping was done in the FWMA. The FWMA uses standardized base layers and follows the standard IUCN methods for mapping freshwater species and automatically calculates EOO and AOO. While the FWMA is quick and straightforward, it is not possible to complete the maps by connecting hydro-basins without point data (i.e., where the occurrence of a species is based on expert knowledge of suitable habitat). Connecting hydro-basins without point data is possible in QGIS, but this approach is cumbersome and time-consuming. Nonetheless, expert users of both tools suggest that there are advantages to combining the two frameworks: FWMA and QGIS (Laban Musinguzi *pers. Comm.* 2022). Therefore, we believed that using both tools could help derive the most precise estimates of EOO and AOO. Whenever it was not possible to complete maps in FWMA, the map shape files were transferred and completed in QGIS. In QGIS, EOO was estimated as the area of a convex layer encompassing basins where the presence of the species was extant, while AOO was estimated as the area of the basins where the species was extant. Both FWMA and QGIS are expected to give comparable estimates of EOO and AOO (IUCN 2019b). All the maps for the species included in this study can be found at https://freshwaterbiodiversity.go.ug/.

Results

Fish species diversity and distribution

A review of the 13,656 non-*Haplochromis* occurrence records from GBIF and FWB, combined with literature, resulted in a total of 110 non- *Haplochromis* fish species belonging to 21 families and 48 genera (Table 2). This number includes all species that were recognized as "extant" and "possibly extant". Out of this total, 21 species were found only in the rivers and streams, which is likely to be an underestimate as rivers are not as widely sampled as large lakes, and therefore, more sampling could reveal more species. Generally, among the major lakes, species richness was highest in Lake Victoria followed by Albert and least in the Lake Edward system (Fig. 3). A total of 12 non-*Haplochromis* fishes were found to be endemic: five in Lake Victoria; one in Lake Albert; one in Aswa river, two in Lake Edward; and three in the Rwenzori area (Table 2).

Approximately 60% of all fishes were recognized as "possibly extant", either in part or their entire native range (Table 2), as their occurrences were more than 30 years old; these fishes were considered "possibly extant" due to the presence of their native habitats and limited sampling in their native range. Five species previously listed in Uganda: *Amphilius kivuensis, Bagrus degeni, Marcusenius macrolepidotus, Petrocephalus catostoma*, and *Lacustricola pumilus* have no native locus; two species previously listed in the Lake Edward system: *Enteromius cercops* and *Enteromius perince* are not extant in the system; while 17 other species occur in areas beyond their known native range, and therefore, their presence in those areas, is also uncertain (Table 1). A summary of this review is shown below by family.

Amphilidae: One Amphilid species, *Amphilius jacksonii*, was recorded in Uganda by Greenwood (1966), but three other species have subsequently been recorded: *A. kivuensis*, *A. lujani*, and *Zaireichthys rotundiceps* (Seegers et al., 2003; Thomson & Page, 2010; Thomson et al., 2015). However, the presence of *A. kivuensis* in Uganda has not been confirmed e. Morphologically, *A. kivuensis*, which is more of a Congo ichthyofaunal province species, although also reported in upper Kagera drainage in Rwanda (Froese & Pauly, 2022), shares a close resemblance with *A. uranoscopus*, which is reported to be widespread in East and Central Africa (Froese and Pauly 2022). Whereas *A. uranoscopus* too has not been confirmed in Uganda, with its earlier specimens considered in Decru et al. (2020) as *A.* cf. *kivuensis*, in terms of biogeography, it is closer than *A. kivuensis*, and fishes in Uganda previously attributed *A. kivuensis* might turn out to be *A. uranoscopus* (Decru et al., 2020), but this needs further investigation. Meanwhile, two new possible amphilids from the Lake Edward system are considered in this study: *A*. sp. Bwindi and *A*. cf. *kivuensis* (Decru et al., 2020), bringing the total possible number of amphilids in Uganda to five species

Bagridae: Greenwood (1966) listed only two species under this family: *Bagrus docmak* and *B. bayad*, but also noted the likelihood of a third species, *Bagrus degeni*, in Lake Victoria, except that it closely resembled *B. docmak* and considered the two species to be one. Recently, Ferraris (2007) listed *B. degeni* as a distinct species occurring in Lake Victoria, which was subsequently adopted by FishBase (Froese & Pauly, 2022), but with no new observations or additional specimens. Given that there is no single record of this species from Lake Victoria apart from the type specimens, and considering the numerous surveys conducted on the lake, its presence appears questionable and the specimens are likely to be those of *B. docmak.*

Cyprinidae: Greenwood (1966) listed several *Enteromius* species under the genus *Barbus*, before it was split into the large hexaploid barbs in the genus *Labeobarbus* (Vreven et al., 2016) and small diploid barbs in the genus *Enteromius* (Van Ginneken et al., 2017). This study found that the records from surveys previously attributed to *Enteromius cercops* and *E. perince* need to be reconciled in line with the recent taxonomic updates. The former was previously recorded in the affluents of Lakes Victoria, Kyoga and Edward (Greenwood, 1966). However, the work of Decru et al. (2020) showed that records previously attributed to this species in the Lake Edward system were *E. perince*, which were latter re-identified as

E. cf. *mimus*, while *E. cercops* was synonymized with *E. alberti* (Maetenes et al., 2020). It is not known whether the records from Lake Kyoga basin previously attributed to *E. cercops* conform to *E. alberti*.

Mormyridae: Greenwood (1966) recorded 13 species under this family. In this study, we found occurrence records for species that were doubtful, such as *Marcusenius macrolepidotus* from Lakes Kyoga and Nakuwa. This species has a native distribution in the Zambezi ichthyofaunal province (Froese & Pauly, 2022). Whereas fish species can be shared by two ichthyofaunal provinces, as is the case for *Ctenopoma damasi, Pseudocrenilabrus multicolor*, and *Oreochromis leucostictus* that occur in both the East Coast and Nile-Sudan possibly via River Semiliki (Decru et al., 2020), M. *macrolepidotus* may not be shared with fishes in the East Coast province (Kyoga and Nakuwa). Similarly, *Petrocephalus catostoma* has a native distribution in the Zambezi ichthyofaunal province. It is listed by Greenwood (1966) to occur in Lake Victoria and Nabugabo and the Victoria Nile (East Coast Ichthyofaunal province), while other occurrence records from GBIF extend the distribution to Lakes Albert, Kyoga, George, Nabugabo, Kagera, and Nyaguo, which span two Ichthyofaunal provinces (Fig. 1). Such a distribution is not likely for lacustrine species, and therefore, the records in Uganda can be considered *Petrocephalus degeni* (Kramer et al., 2012).

Procatopodidae: This family represents the riverine killifishes, commonly known as the African lampeyes, originally attributed in old literature to family cyprinidontidae (e.g., Greenwood, 1966). In this family, *Lacustricola pumilus* was originally (and is still) identified in many surveys as *Aplocheilichthys pumilus.* A revision of the genus *Aplocheilichthys* and its synonymization with the genus *Lacustricola* (Huber, 1999) implies that *A. pumilus* lacks a native locus in Uganda because *L. pumilus* is endemic to Lake Tanganyika drainage (Froese & Pauly, 2022). In the Lake Edward system, most of the records previously attributed to *A. pumilus* have been re-identified as *Lacustricola bukobanus* (Decru et al., 2020), while those in the Lakes Victoria and Kyoga systems have been re-identified as *Lacustricola margaritatus* (Nagy & Watters, 2022).

Extent and range of the non-*Haplochromis* species

The estimates of EOO and AOO for the non-*Haplochromis* fishes are shown in Table 2. Generally, the EOO and AOO for most species (59) were less than 50% of the global range; in fact, 29 species had EOO and AOO values less than 10% of the global range implying that most of the species have a relatively wider distribution outside Uganda. According to the IUCN red listing criterion B, the minimum EOO for a species to trigger extinction threat category is 20,000 km^2 (IUCN 2019a). Table 2 shows that only 29 fish species (26%) had EOO values less than 20,000 km^2. The EOO and AOO for 25 fish species (about 22% of the total non-*Haplochromis* fishes) could not be quantitatively ascertained because their presence was designated as possibly extant, requiring intense surveys to ascertain the current status of these species in their native habitats.

The family Cichlidae had representatives with the largest geographical extent (e.g., *Pseudocrenilabrus multicolor*, *Oreochromis leucoustictus*, and *Oreochromis niloticus*), followed by claridae (e.g., *Clarias gariepinus*) (Table 2). Families with the most restricted range were Citharinidae, Danionidae, and Distichodontidae. These families mostly have individual species endemic to Lake Albert. Generally, water bodies within the Nilo-Sudan ichthyofaunal province, i.e. Lake Albert and Murchison Nile had more species with restricted range (e.g., *Pollimyrus petherici*, *Mormyrus caschive*, *Mormyrops anguilloides, Engraulicypris bredoi, Leptocypris niloticus, Labeo coubie, Citharinus citharus, Citharinus latus, Alestes dentex, and Hydrocynus forskahlii*) compared to water bodies in the East Coast ichthyofaunal province: i.e. Edward (e.g., *Laciris pelagica*) and Aswa drainage (e.g., *Nothobranchius elucens*).

Discussion

The purpose of this study was to review and update the literature on the distribution and range of non-*Haplochromis* fishes in Uganda, building on the recent work by Decru et al. (2020) for the Lake Edward system. Although no new field survey was conducted, this study was possible because of the large amounts of data that have recently been made available through GBIF and the Freshwater Biodiversity portal for Uganda. This study recorded a total of 110 non-*Haplochromis* species to occur in Uganda in different hydro-basins. This number implies 20 additional species to the original list by Greenwood (1966), given that four species previously listed by Greenwood (1966) do not have a native distribution in Uganda. The study also revealed a total of 17 non-*Haplochromis* species that occur within Uganda, but extending to areas outside their known native range documented in Greenwood (1966), FishBase (Froese & Pauly, 2022), and Eschmeyer's catalogue of fishes (Fricke et al., 2022b). This finding is not necessarily surprising given the recent (especially within the last two decades) numerous studies and surveys, which largely remained unpublished until the work of Natugonza & Musinguzi (2022). Given that these are new records that have not been affirmed by examination of their specimens, their occurrence in the new areas is still uncertain. Generally, the specimens for these species from these new habitats are not available. The NaFIRRI has conducted most of these surveys, but without systematic preservation of these specimens. This is a huge gap, and a systematic search and collection of specimens from these new habitats and a follow-up study to confirm this distribution are urgent. This study provides a foundation from which future surveys and field expeditions can be prioritized.

In terms of diversity, more species were recorded in large waterbodies or hydro-basins, which is also expected. Distribution and diversity, among others, are influenced by the size of the waterbody, surface area of the drainage basin, and topographical features (Franklin, 2010; Pelayo-Villamil et al., 2015; Trigal & Degerman, 2015). The higher species richness observed in Lake Victoria, for example, is expected because of its size and habitat heterogeneity, with fish being able to evolve and adapt to the different habitats. However, it is also important to note that these large waterbodies have been the major focus for numerous fisheries investigations and surveys, with limited attention to small waterbodies such as swamps, rivers, streams and minor lakes. These small ecosystems have been shown to harbor large assemblages of fish (Tibihika et al., 2015), and therefore, it is possible that with extended sampling and targeted surveys covering these systems, more species could be recorded beyond what is listed in this study.

Aside from species diversity, limited investigations on small ecosystems can also be seen in the estimated geographical range for some species. Table 2 shows many species without values of EOO and AOO because these species were designated as possibly extant due to a lack of recent data. IUCN guidelines for mapping species suggest that a species should only be designated as 'extant' if it has been observed or recorded within the last 30 years (Table 1; IUCN 2019a). Some non-*Haplochromis* species were described from their type localities and have not been recorded since then. Nevertheless, these fishes were designated as possibly extant as fish may not just disappear or move to another area, but instead, there have not been targeted searches for these species (Jos Snoeks, *pers. comm.* 2022). This delimitation will have implications for the red listing as these fishes whose range could not be quantitatively ascertained can only be listed as Data Deficient (IUCN, 2019a). This means, even with the large amounts of data in GBIF and FWB, more than 50% of non-*Haplochromis* fishes are generally still Data Deficient. Still, this designation is important as it points researchers to areas that are in need of data collection (IUCN, 2019a).

The national EOO and AOO for most fishes was less than 50% of their global range, a finding that was consistent with expectation. It was generally expected that since Uganda shares a small portion of both the Nile-Sudan and East Coast Ichthyofaunal provinces (Fig. 1), the proportion of the species' national range to the global range would be substantially low. This expectation was consistent with fishes especially from the Lake Albert system, i.e., Lake Albert, Murchison and Albert Nile, which, apart from the few endemic species, shares similar fish fauna with Western and Northern Africa (Nile-Sudan Ichthyofaunal province). For the East Coast fauna, the proportion of national range to global range partly deviated from expectation, where majority of the fishes had national EOO and AOO greater than 50% of the global range. This finding was unexpected, but also not entirely surprising because the fish fauna of Lake Victoria resembles that of the Lakes Kyoga and Edward systems. For instance, all fish families occurring in the Lake Edward system occur in Lake Victoria, although four families that are native to Lake Victoria (i.e., Alestidae, Mastacembelidae, Mochokidae and

Schilbeidae) are absent in the Edward system (Decru et al., 2020). The three systems are often collectively referred to as the Lake Victoria region (e.g., Greenwood, 1966; Natugonza et al., 2021). The connection between Lake Victoria and Kyoga is clear: the two systems are directly connected by Victoria Nile. However, the connection between Lake Victoria and the Lake Edward system is not straightforward, although it is suggested that the two systems could be connected through the marshy areas on the Katonga and Ruizi rivers (Decru et al., 2020). Therefore, the large extent of the Lake Victoria region, coupled with a high species endemism, may explain why the Ugandan non-*Haplochromis* fishes of the East Coast province have a big national distribution and range approaching the global range.

Conclusion

This study used species occurrence data, integrated with expert knowledge and literature, to review and update the distribution of non-*Haplochromis* fish species native to Uganda and determine their geographical extent relative to the global range. The review suggests that (i) at least 110 non-*Haplochromis* species occur in Uganda, (ii) five non-*Haplochromis* species previously considered to be native to Uganda: *Amphilius kivuensis, Bagrus degeni, Marcusenius macrolepidotus, Petrocephalus catostoma*, and *Lacustricola pumilus* lack a native locus, while (iii) 17 species occur in areas beyond their known native range, requiring further investigation to assess their taxonomic correctness, preferably by examining the specimen collections. This study highlights areas and species that need to be prioritized during surveys and collections, thereby providing a strong foundation for filling data gaps. The information in this study will also be useful in updating IUCN Red List assessments as well as conducting new assessments for the unevaluated species. The geographical restrictedness of the majority of the non-*Haplochromis* species native to systems in the East Coast ichthyofaunal province underscores the importance of actions to halt degradation of fish habitats and overexploitation, which pose a faster extinction risk as these fishes may have a limited chance to be conserved elsewhere.

Declarations

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Ethical Approval

Not applicable.

Competing interests

The authors declare no conflicts of interest.

Authors' contributions

Vianny Natugonza and Laban Musinguzi conceived the idea and designed the study; Dorothy Akoth, Vianny Natugonza and Laban Musinguzi assembled and analysed all the data and generated species distribution maps; Dorothy Akoth, Vianny Natugonza, Jackson Efitre, Fredrick Jones Muyodi, and Laban Musinguzi wrote and revised the manuscript.

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Availability of data and materials

All data used here are freely available at GBIF.org https://doi.org/10.15468/dl.48xwy3 and Freshwater Biodiversity Data for Uganda: https://freshwaterbiodiversity.go.ug/. A cleaned dataset is available from the corresponding author upon request.

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Figures

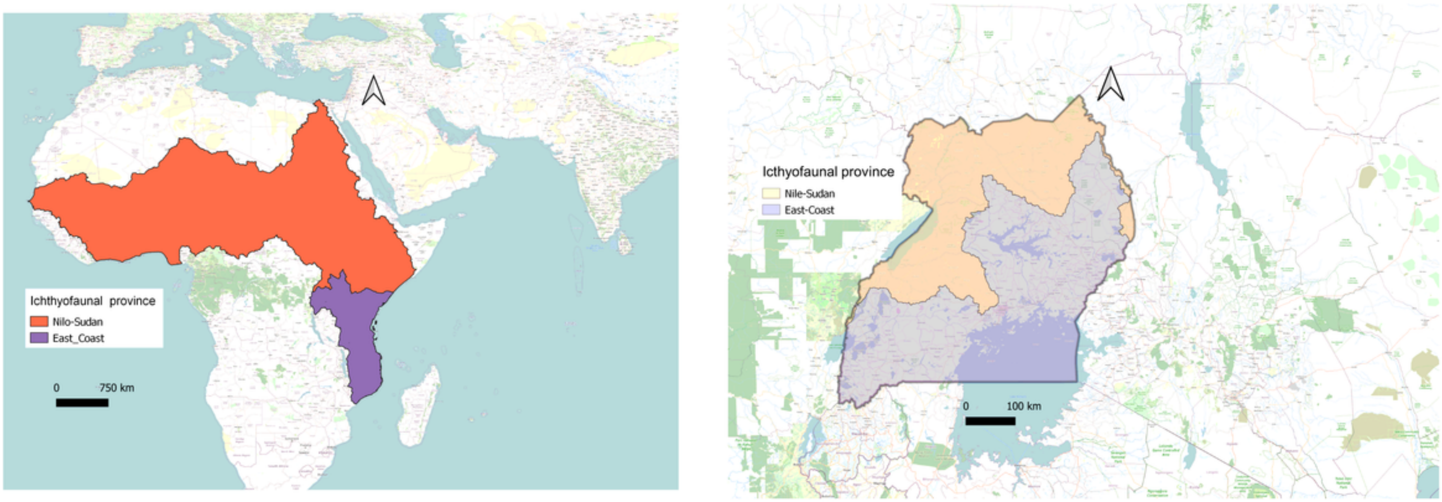

Figure 1

Extent of two ichthyofaunal provinces in Africa (left panel) and Uganda (right panel).

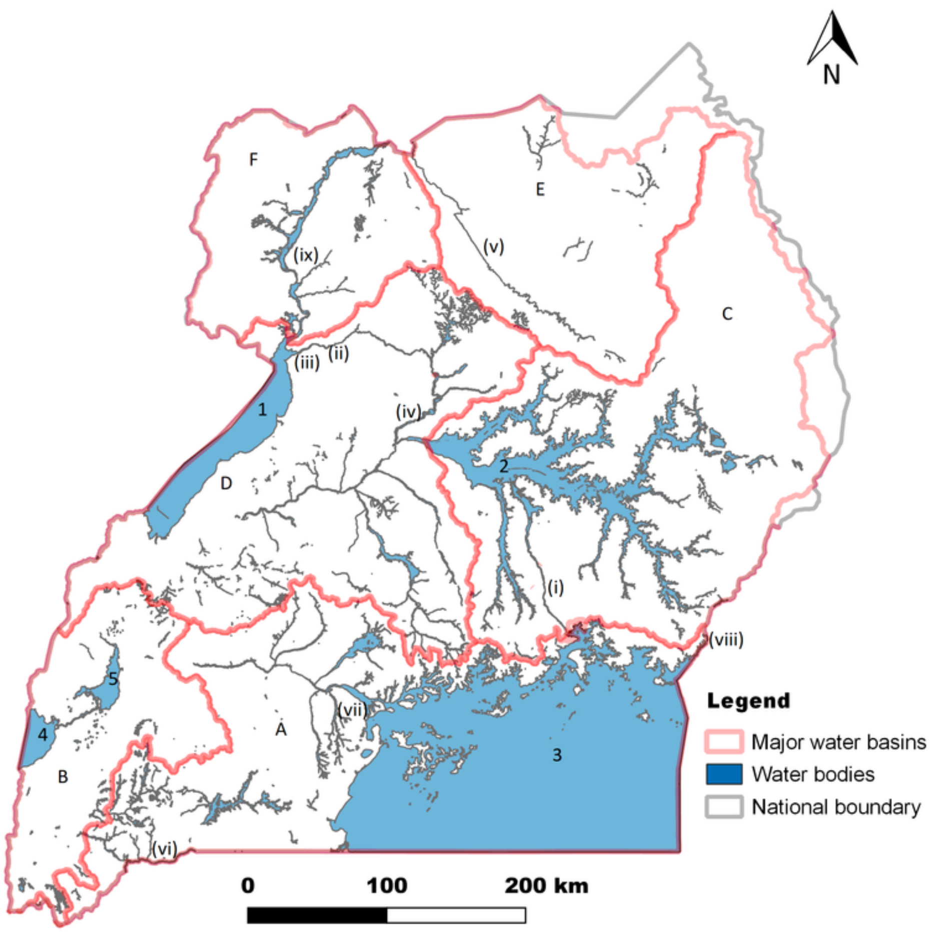

Figure 2

Location of major drainage basins in Uganda, with the major lakes and rivers. Letters denote major basins: A (Victoria), B (Edward), C (Kyoga), D (Albert), E (Aswa River), F (Albert Nile). Numbers denote major lakes: 1 (Albert), 2 (Kyoga), 3 (Victoria), 4 (Edward), 5 (George). Roman numerals denote major rivers: (i) Upper Victoria Nile, (ii) Murchison Nile, (iii) Murchison Nile Delta, (iv) Lower Victoria Nile, (v)Aswa, (vi) Kagera, (vii) Katonga, (viii) Sio, (ix) Alber Nile.

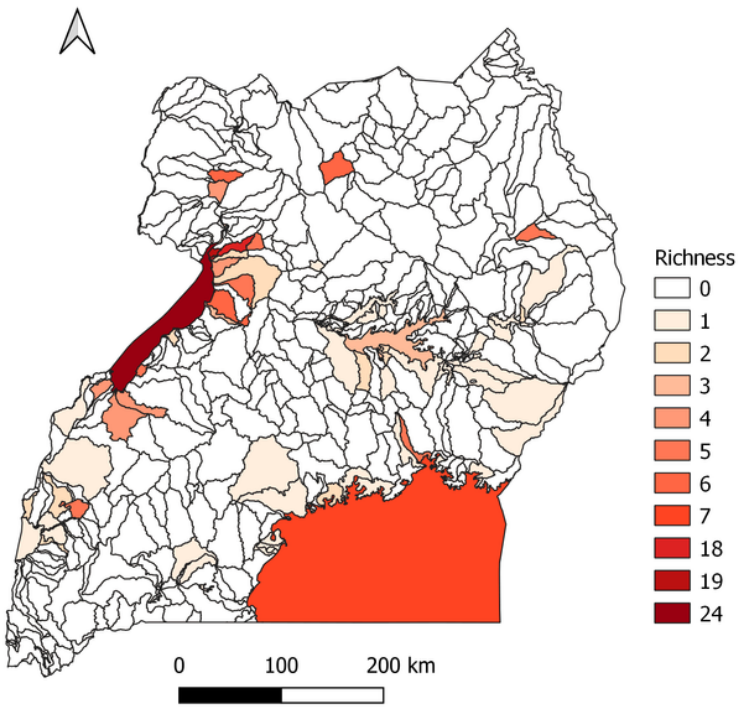

Figure 3

Fish species richness in Uganda in different hydro-basins.