

Unlocking Nile tilapia (*Oreochromis niloticus* Linn., 1758) selective breeding programmes in Uganda through geographical genetic structure mapping

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Abstract

Nile tilapia (*Oreochromis niloticus*), native to Africa and the Levant, is an important species for both aquaculture and capture fisheries. Despite these attributes, Nile tilapia has been negatively impacted by anthropogenic activities ranging from over-fishing and habitat destruction to translocations. These human-mediated activities have threatened the genetic evolutionary integrity of native populations of Nile tilapia and congeneric species through admixture, demographic bottlenecks and introgressive hybridization. In this context, the genetic contrast between farmed/bred strains and wild Nile tilapia populations in the major lakes of Uganda remains understudied. Understanding the genetic structure of Nile tilapia populations in the major water bodies of Uganda (lakes Victoria, Kyoga, Edward, George, Albert and Nile River) is a key resource to guide selective breeding programmes, thus minimizing the effects of maladaptation under both aquaculture and natural stocks. Although the population genetics of Nile tilapia in Uganda's major lakes have been studied, this was based on limited sampling scope, especially in the wild, and the key information on the species could have been overlooked. We fill this knowledge gap by genotyping 756 Nile tilapia individuals from multiple populations for each major water body of Uganda using a panel of 34 microsatellite loci based on the microsatellite genotyping-by-sequencing (SSR-GBS) technique. The results indicate two discrete gene pools/stocks: the Edward-George system and the Albert-Kyoga system-Victoria. Evidence of loss of genetic diversity and admixture of some Nile tilapia stocks was found, most likely resulting from anthropogenic perturbations. This study contributes useful information key for understanding the potential Nile tilapia broodstock sources for selective breeding programmes, aimed at improving aquaculture production in Uganda.

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KEYWORDS

genetic structure, major lakes of Uganda, Nile tilapia, selective breeding programmes

1 | INTRODUCTION

The East African Great Lakes are well-known biodiversity hotspots and constitute an important fisheries resource for the rapidly growing human population through the provision of food protein and employment (Scullion, 2007; Tibihika et al., 2022). In Uganda, the fisheries subsector is predominantly supported by the six major freshwater bodies, including lakes Victoria, Kyoga, Edward, George, Albert and the Nile River (Ntiba et al., 2001; Ogutu-Ohwayo et al., 1997). The capture fisheries from L. Victoria alone contribute between \$250,000 and \$500,000 annually to the three greater East African States of Uganda, Kenya and Tanzania from exports and support a population of over 42 million people (Ntiba et al., 2001; Nyamweya et al., 2023). In Uganda, the available aquatic resources not only demonstrate enormous potential for aquaculture and capture fisheries but also support the livelihood of more than 3.5 million people (Cai et al., 2017). Uganda's fish account for more than 63% of the protein consumed locally, with an annual per capita consumption of 12.5 kg in 2013, higher than the continental average of 10.1 kg (Adeleke et al., 2020). Based on the Ministry of Agriculture, Animal Industry and Fisheries (MAAIF, 2017), the overall production of capture fisheries is predominantly anchored on three major fish species notably Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*) and the small cyprinid silver fish locally referred to as Mukene (*Rastrineobola argentea*). Over time, the total production from capture fisheries has remained constant at 410,000 metric tons (mt) between 2005 and 2015 against the anticipated potential of 700,000 mt (MAAIF, 2017). Although 700,000 mt is projected from the capture fisheries, this figure also will not address the fish demand by Uganda's population and thus potentially inadequate to meet the global recommended per capita fish consumption of 20.5 kg by the year 2040 (Egessa & Sándor, 2022). Several factors hinder the production and productivity of capture fisheries in Uganda, including the dwindled fish stocks due to overfishing, predation pressure, species competition, habitat destruction, biological invasions, pollution and eutrophication, among others (Nyamweya et al., 2023; Odada et al., 2004). The unlimited anthropogenic activities in Ugandan water bodies have potentially led to a massive decline, if not extinction, of the native ichthyofauna and widely continue to pose further biodiversity threats (Balirwa et al., 2003; Ogutu-Ohwayo, 1990). For instance, the human-induced introduction of tilapiines, particularly Nile tilapia, into lakes Victoria, Kyoga, Victoria Nile, Nabugabo and several other satellite waterbodies is believed to have contributed to the dramatic stock decline of the native congeneric species: *Oreochromis esculentus* (Singida tilapia) and *Oreochromis variabilis* (Victoria tilapia) (Balirwa, 1992; Balirwa et al., 2003; Kaufman, 1992; Tibihika et al., 2020).

In Uganda, Nile tilapia is second only to Nile perch (*L. niloticus*) in terms of economic importance, playing a vital role in both aquaculture and capture fisheries (Balirwa, 2007). Nile tilapia significantly contributes to the country's economic development, by providing food security, protein source and employment opportunities, thereby improving livelihoods. Despite its importance, the prevailing dynamics and complexity of Nile tilapia introductions in Uganda complicate the delimitation of genetically sound strains for management, conservation and aquaculture. Nile tilapia introductions/translocations in Uganda began in the 1950s from their putative native habitat, L. Albert to lakes Victoria, Kyoga, Victoria Nile, Nabugabo and several other satellite water bodies in Uganda (Balirwa, 1992; Ogutu-Ohwayo, 1990; Tibihika et al., 2022). Since this time, it is also assumed that various direct and indirect Nile tilapia translocations and restocking have been surging mainly through the expansion of aquaculture practices in the country (Tibihika et al., 2022, 2020). For example, the rise in fish demand has led to the expansion of farming practices, most notably cage fish farming which is becoming increasingly popular in the major lakes of Uganda. It appears that the only hope required to bridge the fish deficit and lessen the dilapidated natural fish stocks in Uganda is through improved and upscaled aquaculture/fish farming productivity in the country.

Uganda is Africa's third largest aquaculture producer behind Egypt and Nigeria (Adeleke et al., 2020; Egessa & Sándor, 2022; FAO, 2022). Aquaculture in Uganda has been in practice since the 1940s and has gradually increased from 5000 mt in 2004 to around 100,000 mt in 2014 (MAAIF, 2017). Recently, aquaculture production in Uganda has been estimated at 138,558 mt as of 2021 (WorldBank, 2021). To meet the increasing internal and international fish demand, aquaculture is projected to generate 1000,000 mt per annum (Egessa & Sándor, 2022). However, this level will likely not be met as several constraints still drag on the expansion and productivity of the sector in Uganda, most especially the lack of adequate and quality fish seed, among others (MAAIF, 2017).

Pond fish culture is the most widely used aquaculture system with an estimated 20,000 ponds, of various sizes, across Uganda (MAAIF, 2017). Cage fish culture started in 2006 as an alternative system to boost aquaculture in the country (Adeleke et al., 2020). Presently, in L. Victoria alone, the number of fish cages is potentially over 12,000 (Adeleke et al., 2020; Musinguzi et al., 2019). Cage aquaculture increases fish production being perceived by the government of the Republic of Uganda as a reliable source of employment, income, revenue and livelihood for the communities (Musinguzi et al., 2019). The low-volume high-density cages (8 m³) are the most common systems in Uganda, and productivity (though dependent on management practices) ranges between 5 and 35 kg of fish m⁻³ (Adeleke et al., 2020).

Nevertheless, cage fish farming may cause several environmental and ecological constraints, especially by potential escapees which could impose negative impacts on the wild fish stock of the same and related species (Fraser et al., 2010; Naylor et al., 2005). This is particularly a concern for the mostly cultured Nile tilapia (*O. niloticus*), as this may compromise the genetic integrity of the wild tilapiines in the process of upscaling fish cages and other production systems. Usually, the farmed or hatchery-bred fish are associated with less fit genotypes that, if integrated into wild stocks, may lead to a shift or loss of genetic integrity with subsequent low genetic fitness (Ingram & Nguyen, 2014). This can subsequently result in reduced fecundity, egg hatch rates, growth rates, increased incidences of abnormalities and susceptibility to diseases (Ingram & Nguyen, 2014). These challenges may confound the growth and productivity (performance) of aquaculture, if the potential Nile tilapia broodstocks are not holistically investigated, particularly through genomic approaches.

Traditionally, the impacts of introduced fish species are approached from an ecological perspective, focusing, for instance, on predation and competition (Rhymer & Simberloff, 1996). However, other critical negative impacts that are often overlooked are introgressive hybridization and admixture between fish populations which are usually influenced by intentional or indirect introductions and can dissipate unique gene pools of native taxa (Largiadèr, 2007; Rhymer & Simberloff, 1996; Verhoeven et al., 2011). In this context, the use of molecular genetic tools may be pertinent to elucidating Nile tilapia delimitation in Uganda to gain insights into the processes that may have reshaped the stocks. Molecular genetic approaches have been widely used for monitoring anthropogenic disturbances by quantifying effective population size, genetic diversity, hybridization and so on (Brown et al., 2005; Laikre et al., 2010; Luikart et al., 2020), population structure, inbreeding and gene flow (Kardos et al., 2016; Momigliano et al., 2017), as well as hybridization/introgression and admixture (Araguas et al., 2004; Beaumont et al., 2001; Consuegra et al., 2011; Pavlova et al., 2017).

Although various molecular genetic research projects focused on Nile tilapia have been conducted in Uganda (Diedericks et al., 2021; Kariuki et al., 2021; Mwanja, 2000; Tibihika et al., 2020, 2019), the species genetic structure patterns in the country are still elusive. Although some evidence of genetic substructuring in Nile tilapia populations within certain lakes is known (Robledo et al., 2024; Tibihika et al., 2020), it is not fully explored, and all the major water bodies in Uganda, particularly the potential broodstock sources for aquaculture. This is attributed to the focus of the previous studies that covered mainly the patterns in fish farms thus leaving out the wider geographical scope. More detailed genetic structure patterns of Nile tilapia populations in Uganda would play a pivotal role in unlocking the risks related to unknown broodstocks for selective breeding programmes. This will contribute to the remedies for fish maladaptation consistently faced by fish farmers in the country. Generally, formal selective breeding programmes have taken any shape in Uganda, apart from the consistent rudimentary fish breeding practices by various hatchery operators coupled with unknown broodstocks (Mwanja et al., 2015). The challenge of continued underperformance of Nile tilapia in captivity is fundamentally attributed to poor fry/seed commonly bred with

a knowledge gap of the ideal and suitable fish broodstock (Mwanja et al., 2016). Therefore, this study aims to delineate geographically the genetic structure of Nile tilapia in Uganda through mapping references. Here, we extend the sampling scope from Tibihika et al. (2020) to new water bodies as well as investigate the variation within the same lakes that have not been fully explored. Therefore, this study builds on the previous works and targets to inform and guide the ongoing selective breeding practices by improving and enhancing Nile tilapia performance under captivity in the country.

2 | MATERIALS AND METHODS

2.1 | Study areas

Nile tilapia tissue samples (fin clips) were collected from Uganda's major water bodies, including lakes Edward, George, Albert, Victoria and the Kyoga system, as well as the farmed fish at the Aquaculture Research and Development Centre Kajjansi (ARDCK) (Table 1; Figure 1). Considering the vast sizes and complexity of the studied water bodies in Uganda, we sampled multiple locations to assess possible genetic heterogeneity within the ecosystems (Table 1; Figure 1). In particular, because of the complex nature of the L. Kyoga system, we sampled several satellite water bodies: the main L. Kyoga, Kyoga/Nile (also referred to as Victoria Nile as it stretches from L. Victoria to upper Murchison Falls through L. Kyoga), Kyoga/Kwania and Kyoga/Nakuwa (Kwania and Nakuwa are satellite lakes in L. Kyoga basin). In this study, we refer to each water body as a population and each sampling locality as a subpopulation. Samples were collected by local fishermen using recommendable gillnets of mesh size 127 mm. The field excursions were conducted between 2019 and 2021, and in total, 756 samples/fin clips were collected (Table 1) and preserved in absolute ethanol contained in 2 mL Eppendorf tubes. The samples were later stored in a freezer at -21°C until genotyping at the Institute for Integrative Nature Conservation Research-University of Natural Resources and Applied Life Sciences Vienna (BOKU), Austria. Sampling was conducted in collaboration/authorization from the respective authorities, and therefore, no special permission was required. Additionally, no special animal rights/welfare were observed during the fieldwork, as the fish were already dead when obtained from the fishermen.

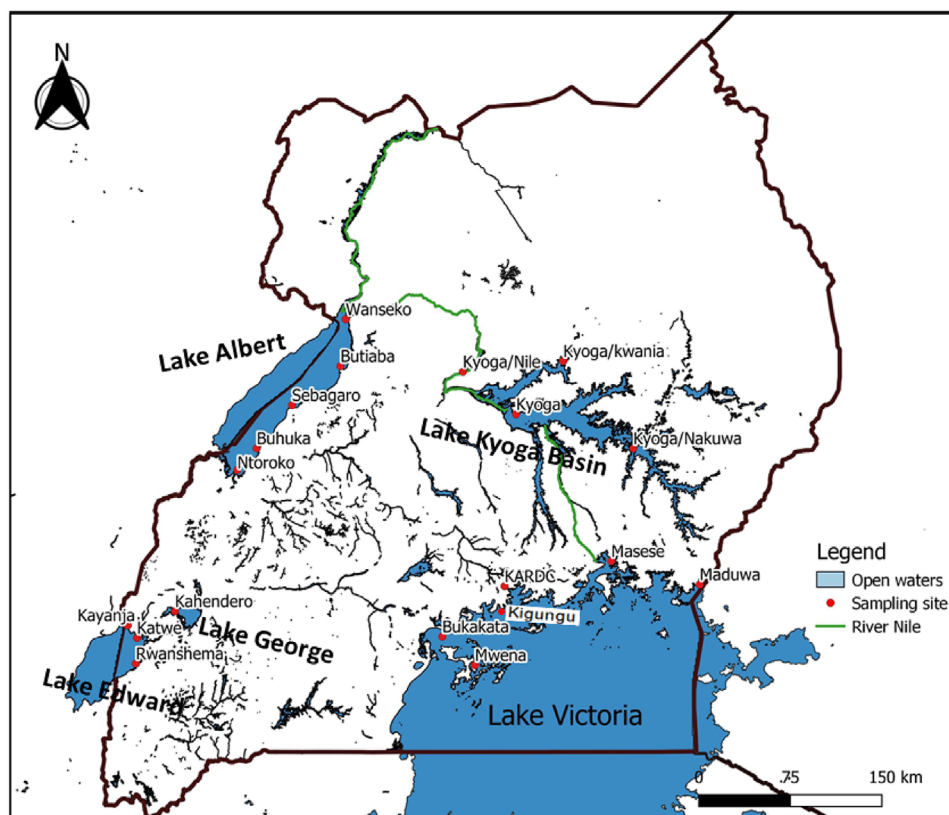
2.2 | DNA extraction and SSR-GBAS

Genomic DNA extraction was conducted using magnetic beads with a MagSi-DNA Vegetal kit (MagnaMedics) and a magnetic separator, SL-MagSep96 (Steinbrenner) (Curto et al., 2019; Tibihika et al., 2019). We amplified a panel of 34 microsatellite loci (SSR) previously developed by Tibihika et al. (2019). Screened primers were grouped into three multiplexes and used to prepare amplicon SSR-GBAS libraries using the protocol from Tibihika et al. (2019). These were then sent for paired-end sequencing (600 cycles) in Illumina MiSeq, at the Genomics Service Unit in Ludwig Maximilian Universität, München, Germany.

TABLE 1 Sampling sites, the number of fish individuals collected per water body, and location/site.

District	Landing site	Waterbody	ID	No.	Latitude	Longitude	Elevation (m)
Masaka	Bukakata	V_Bukakata	VBK	50	−0.14958	32.07606	1133
Kalangala	Mwena	V_Mwena	VKM	40	−0.35883	32.31658	1133
Jinja	Masese	V_Masese	VMS	25	0.405889	33.31972	1133
Busia	Maduwa	V_Maduwa	VMD	48	0.234778	33.97014	1139
Wakiso	Kigungu	V_Kigungu	VBU	27	1.077972	32.22897	1133
Palisa	Opetta	Kyoga/Nakuwa	KNO	47	1.243694	33.43761	1023
Dokolo	Dalaja	Kyoga/Kwania	KKD	32	1.848806	32.83703	1028
Kiryandongo	Kabonyi	Kyoga/Nile	KKN	47	1.798250	32.22047	1047
Amolator	Namasale	Kyoga	KNS	50	1.464389	32.64522	1030
Kikuube	Buhuka	A_Buhuka	ABK	44	1.223361	30.71008	623
Bulisa	Butiaba	A_Butiaba	ABU	41	1.818639	31.32339	622
Ntoroko	Ntoroko	A_Ntoroko	ANO	33	1.063000	30.54189	641
Kikuube	Sebagoro	A_Sebagoro	ASO	35	1.545611	30.94789	618
Bulisa	Wanseko	A_Wanseko	AWE	41	2.180194	31.36594	615
Kasese	Katwe	E_Katwe	EKW	40	0.164583	29.81781	777
Kasese	Kayanja	E_Kayanja	EKY	44	0.081472	29.73403	769
Rukungiri	Rwenshama	E_Rwenshama	ERS	41	−0.35258	29.82050	937
Kasese	Kahendero	George	GKH	27	0.052972	30.07083	914
Wakiso	ARDCK	Farm	ARDCK	44	0.222028	32.53436	1142
Total number of samples				756			

Abbreviations: A, L. Albert; ARDCK, Aquaculture Research and Development Centre Kajjansi; E, L. Edward; ID, sample identity; Nakuwa and Kwania, satellite lakes of L. Kyoga; No., number of samples; V, L. Victoria.

**FIGURE 1** Sample locations in Uganda's major water bodies.

The raw sequence data were deposited in the GenBank: Sequence Read Archive under the accession number PRJNA550300. Generated sequences were quality checked and controlled and subsequently used for alleles calling as described in Tibihika et al. (2019) and Curto et al. (2019) using the scripts from the SSR-GBS pipeline (<https://github.com/mcurto/SSR-GBS-pipeline>). For downstream analyses, only loci and specimens with less than 50% of missing genotypes were kept, leaving a total number of 28 markers and 749 samples.

2.3 | Genetic structure analysis

The genetic structure of Nile tilapia was first investigated using the STRUCTURE programme, Version 2.3.4 (Hubisz et al., 2009). STRUCTURE clusters individuals into hypothetical populations through the optimization of Hardy-Weinberg equilibrium (Porrás-Hurtado et al., 2013). STRUCTURE was run from $K = 1$ to 10 for 100,000 Markov chain Monte Carlo (MCMC) generations after a burn-in length of 10,000 iterations (Evanno et al., 2005), whereby each run was iterated 10 times. It is important to note that following the above STRUCTURE runs, longer burn-in lengths or MCMC generations did not change the outputs/results. Therefore, 100,000 MCMC generations and a burn-in length of 10,000 were sufficient. The programmes' default settings for the admixture model and allele frequencies correlated were implemented. Detection of the optimal K was done with STRUCTURE HARVESTER (Earl & vonHoldt, 2012) using the delta K (ΔK) statistic. Principally, this is the second-order rate of change ($\ln P(D)$) across successive K values (Chaluvadi et al., 2014; Evanno et al., 2005). Here, STRUCTURE HARVESTER uses ΔK to assess the multiple K values and henceforth identifies the best/optimal K . Results from multiple replicates were summarized using the online pipeline Clumpak programme (Kopelman et al., 2015) available at <http://clumpak.tau.ac.il/>. Similar analyses were performed within each lake system: Victoria, Kyoga system, Albert and Edward-George system. The genetic structure was later used to infer reference maps on the geographic major water bodies in Uganda. We further validated the Bayesian cluster analysis (STRUCTURE) using the Neighbour-Net and phylogenetic networks, implemented in SplitsTree4 version 4.14.8 (Huson & Bryant, 2006). This method uses distance information to group taxa without a hierarchical structure allowing for reticular patterns (Bryant & Moulton, 2002), which could be missed in systems with a high degree of admixture among populations such as Nile tilapia. This analysis was conducted based on Nei genetic distance matrices generated in the GenAlex programme Version 6.5 (Peakall & Smouse, 2006). We analysed the Nile tilapia population structure based on the discriminant analysis of principal components (DAPC) using the R 4.2.1 package adegenet (Jombart, 2008). The best number of groups was accessed with the function find.cluster with 150 principal coordinates retained. Finally, a phylogenetic tree was computed based on Nei genetic distance to enhance the visualization of the genetic structure of Nile tilapia populations using the GenePop programme (Raymond & Rousset, 1995).

3 | GENETIC DIVERSITY, DIFFERENTIATION AND NUMBER OF MIGRANTS

Genetic diversity and differentiation indices, including the number of different alleles (N_a), private alleles (P_a), allelic richness (A_r), expected and observed heterozygosity (H_e & H_o), unbiased expected heterozygosity (uH_e) and fixation index (F_{st}), were investigated. Apart from A_r , which was examined using the rarefaction algorithm implemented in the Hp-rare programme (Kalinowski, 2005), the other genetic diversity indices were calculated using the GenAlex programme Version 6.5 (Peakall & Smouse, 2006). The population pairwise genetic differentiation based on F_{st} analysis was used to complement the genetic structure analysis. The F_{st} results are presented as heatmaps in table format. We also estimated the number of migrants (N_m) as a proxy for gene flow between population pairs to expound on the genetic structure, using the GenAlex programme.

3.1 | Geographical mapping of genetic structure

The geospatial data of different sampling sites were cleaned and loaded into Quantum GIS, and an appropriate presentation was selected to identify the features and attributes to present (layer order, feature selection and frequent-used projections). We later defined data presentation (transparency-raster and vector), data classification and layer files. These were added to map components (geospatial data references) and illustrated into two categories: (i) genetic structure referenced on the Ugandan map covering the major freshwater body populations, and (ii) genetic structure within each major waterbody.

4 | RESULTS

4.1 | Nile tilapia genetic structure reference maps between populations

The Bayesian analysis implemented in STRUCTURE across the Ugandan Nile tilapia populations was depicted from the best/optimal K values (Figure S1). Here, for all the combined populations, the best K was 2 ($K = 2$), and for within populations; L. Victoria $K = 3$, L. Kyoga $K = 2$, L. Albert $K = 4$, and L. Edward-George system $K = 3$ (Figures 2, 5–7; Figure S1). For comparative purposes, we also present the Bayesian genetic structure assignments from $K = 3$ to $K = 9$ bearing the number of the studied populations (Figure S2). Considering all the combined populations, the genetic assignment patterns generally indicated two groups that mostly reflect the geographical proximity or water interconnection (Figure 2; see also $K = 3$ Figure S2). Lakes Edward-George system is exclusively assigned to one genetic cluster, whereas Lakes Albert-Kyoga system (Kyoga, Kyoga/Nile, Kyoga/Kwania and Kyoga/Nakuwa)-ARDCK and Victoria to the second genetic cluster (Figure 2). Lakes Victoria and Albert as well as the farm at ARDCK appear admixed, bearing major ancestral lineages from L. Albert and

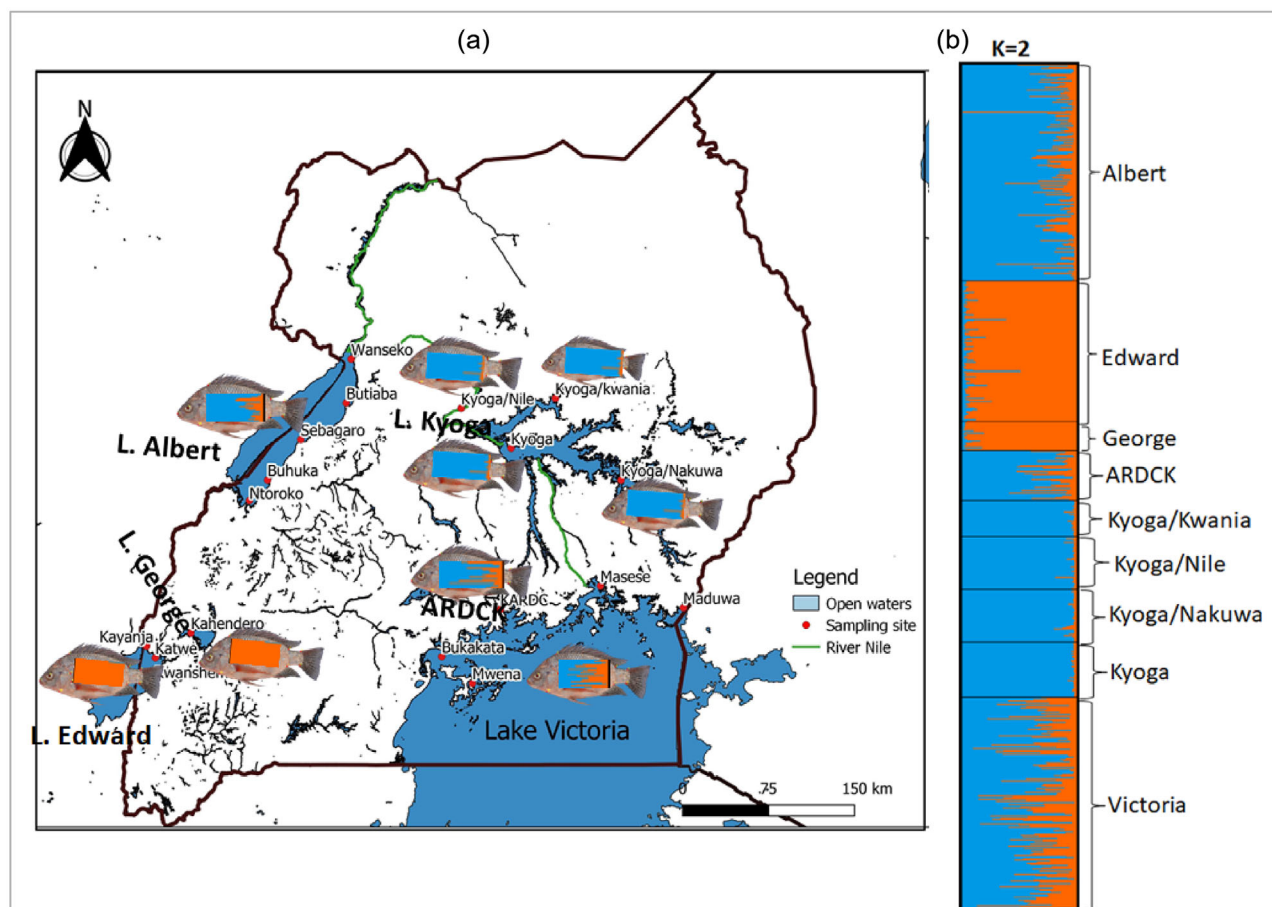


FIGURE 2 Bayesian clustering for genetic assignments of Nile tilapia populations between the major water bodies in Uganda based on STRUCTURE. Part (a) represents the map of Ugandan major water bodies, (b) Nile tilapia genetic structure. The various rectangular colour shapes embedded in Nile tilapia digital images in part (a) depict the species' genetic structure reference map/distribution in Ugandan major water bodies.

some indicators of gene flow potentially from the Edward-George system (Figure 2).

The Neighbour-network genetic structure demonstrated similar genetic structure patterns as the STRUCTURE analysis (Figure 3a). In this case, we show a better view of how the subpopulations from the various water bodies cluster together. For instance, although the subpopulations from the Edward-George system consistently appear genetically assigned together showing a high degree of divergence/isolation from the remaining subpopulations, the Kyoga subpopulations, Kyoga/Nakuwa and Kyoga/Kwania are genetically closer to the L. Victoria subpopulations: Maseke, Kigungu and Maduwa, than the remaining subpopulations in this system (Figure 3b). In fact, these form a divergent group from all the remaining subpopulations. Similarly, the two subpopulations in L. Victoria, Mwenya and Bukakata, group together and are genetically divergent from the remaining subpopulations within the same water body. In the same analysis, it is revealed that the population at ARDCK is genetically closer to the two subpopulations in L. Albert: Buhuka and Butiaba. Additionally, L. Kyoga and Kyoga/Nile are genetically close and appear intermediate between the L. Albert subpopulations: Ntoroko, Wanseko, Sebagoro, Butiaba and Buhuka (Figure 3b). Reticular patterns are found mostly within each of

the above-mentioned groups, especially within the lakes Victoria and the Edward-George system (Figure 3b).

DAPC resulted in six clusters consistent with the geographical location of the sampled waterbodies (Figure 4; Figure S3). Clusters 1–4 belong to lakes Victoria, Kyoga system, Albert and ARDCK; Cluster 5 to the L. Edward-George system; and Cluster 6 to a mixture of individuals from all waterbodies. This grouping is congruent with previous genetic structure results, whereas cluster 6 reflects the high degree of admixture found in Nile tilapia populations.

4.2 | Nile tilapia genetic structure reference maps within populations (lakes Victoria, Kyoga, Albert and the Edward-George system)

When genetic structure within specific water bodies/populations was investigated, generally no/shallow structure was observed in all the systems (Figures 5–8). However, Nile tilapia populations in these lakes, Victoria, Kyoga, Albert and Edward-George appear admixed/sub-structured. Within L. Albert, sub-structuring is not clear; however, Ntoroko (southern part of the lake), Sebagoro, Buhuka and Butiaba

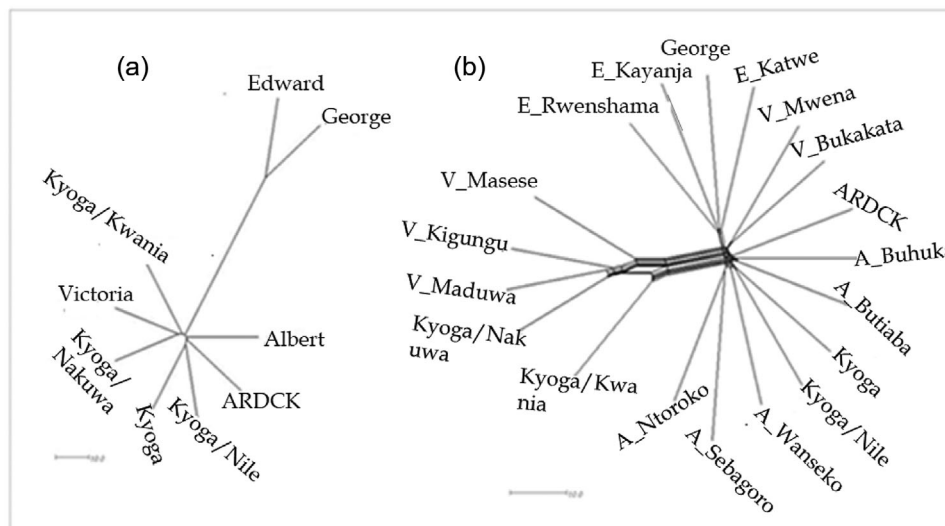


FIGURE 3 Genetic structure visualized on unrooted network tree implemented in SplitsTree4 programme illustrating population relationships based on genetic distance. Part (a) represents all the populations, and (b) for all populations but indicated as subpopulations. *E_* represents *L. Edward*; *V_* represents *L. Victoria*; *A_* represents *L. Albert*; *Ky_* represents *L. Kyoga*.

(central part of the lake) have higher genetic assignments than Wanseko (northern part of the lake) (Figure 7).

4.3 | Nile tilapia genetic structure visualized through a UPGMA tree

The results from the UPGMA phylogeny indicate a similar pattern with the structure based on Bayesian clustering and the unrooted Neighbour network tree. Although the UPGM analysis consistently indicates the genetic divergence nature of the Edward-George system from the other systems, the *L. Kyoga* system appears clustered together and relatively distant from another cluster of ARDCK, Victoria and *L. Albert* (Figure 9).

5 | GENETIC DIVERSITY AND DIFFERENTIATION

The mean genetic diversity (particularly the number of alleles) of Nile tilapia populations varied amongst the studied water bodies (Table 2). Lakes Albert and Edward showed the highest mean genetic diversity values (10.82 ± 1.34 and 10.29 ± 1.23 , respectively), followed by *L. Victoria* and ARDCK (7.18 ± 0.93 and 6.96 ± 0.79 , respectively). Notably, the *Kyoga* system: *L. Kyoga*, *Kyoga/Kwania*, *Kyoga/Nakuwa* and *Kyoga/Nile* demonstrated the lowest genetic diversity values. However, based on the expected heterozygosity results, we noted that Lakes Edward, George and ARDCK indicated higher values, followed by Albert, with generally lower values consistently shown in the *L. Kyoga* systems (Table 2). Similarly, Lakes Albert and Edward showed the highest number of private alleles (1.97 ± 0.09 and 1.95 ± 0.09 , respectively), with the subpopulations from the *L. Kyoga* complex system indicating the lowest (Table 2). Similar genetic diversity results

were consistent when Nile tilapia was analysed at the subpopulation level (Table 3). However, it was observed that although the *L. Kyoga* system (basin) steadily indicated lower genetic diversity values (particularly, N_a below 5 and H_e/uH_e below 0.5), also three subpopulations in *L. Victoria* (Kigungu, Maduwa and Masese) indicated lower genetic diversity values (Table 3). This trend was also consistent with the other genetic diversity indices: H_o , H_e , uH_e , N_o , P_a and A_r across the populations.

Regarding the genetic differentiations, populations were considered genetically similar when F_{st} indicated values equal or less than ($\leq$) 0.04 and N_m of equal or greater than ($\geq$) 5 (Tables 4–8; Tables S1–S5). Genetic differentiation between the studied populations based on F_{st} values and the number of migrants (N_m) was consistent with the genetic structure (Table 4; Table S1). For instance, all the populations that indicated structure or genetically clustered together demonstrated low F_{st} values with a high number of migrants (Table 4; Table S1). Here, *L. Albert* indicated low F_{st} values (≤ 0.04) and a high number of migrants with all the water bodies, except the Edward-George system, and *Kyoga/Nakuwa* (Table 4; Table S1). Similarly, ARDCK unveiled genetically undifferentiated genotypes from all the major water bodies, apart from *L. George*, and *Kyoga/Nakuwa*. Nevertheless, some comparisons between the Edward-George system and other lakes showed relatively low values of F_{st} (0.036) and moderately high values of N_m (>5), particularly between Edward and Victoria (Table 4; Table S1). Apart from *Kyoga/Nakuwa* and George, *L. Victoria* showed low F_{st} and high N_m values in all populations (Table 4; Table S1). Consistent with STRUCTURE, generally, all the F_{st} results indicated very low values, coupled with high N_m values when genetic differentiation was performed within populations (Tables 5–8; Tables S2–S5). The exception was *L. Kyoga* which showed high F_{st} values within the *Kyoga* system, particularly between *Kyoga/Nakuwa* and the other subpopulations (Table 6).

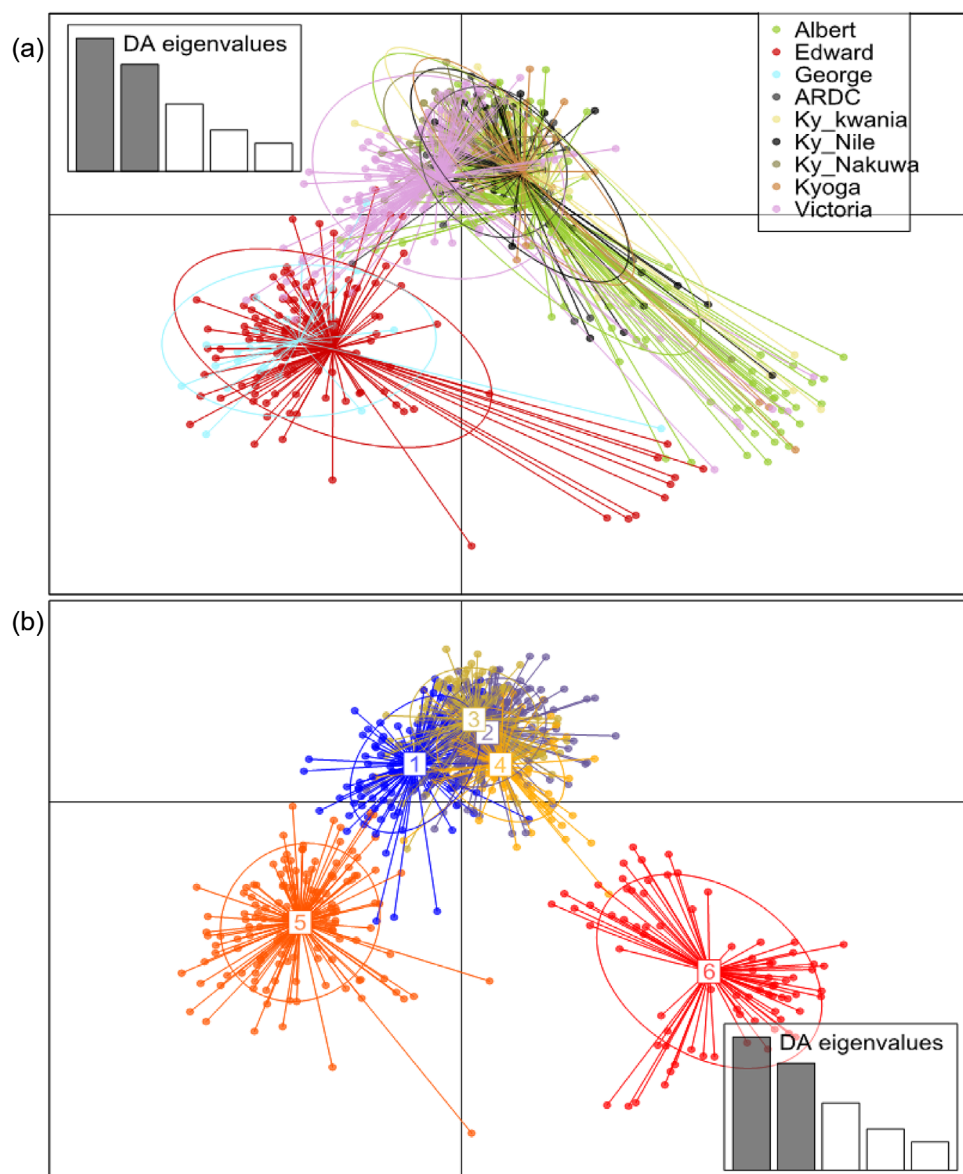


FIGURE 4 Discriminant analysis of principal components (DAPC) analysis of Nile tilapia populations. Part (a) shows pooled populations, and (b) shows the six clusters explaining the variance of the data. Numbers 1–4 represent lakes Victoria, Kyoga system, Albert and Aquaculture Research and Development Centre Kajjansi (ARDCK); 5 L. Edward-George system; and 6 a mixture of individuals from all waterbodies. The axes represent the first two Linear Discriminants (LD). Each circle represents a cluster, and each dot represents an individual.

6 | DISCUSSION

Deciphering the knowledge gap regarding the ideal Nile tilapia genotypes for selective breeding is crucial to the betterment of aquaculture practices in Uganda. Aquaculture development in Uganda is dated way back to the 1940s by the colonialists, and the focus primarily was on alien carp fish species (Adeleke et al., 2020; Dadzie, 1992). Despite the significant amount of time spent in the enterprise, the sector continues to struggle and is hugely constrained by the unexpectedly poor performance of the commonly cultured Nile tilapia (Mwanja et al., 2015). One of the key challenges that has hindered Nile tilapia culture in the country is the lack of knowledge regarding appropriate broodstock genotypes for quality fish seed generation.

We explored the geographic genetic structure and genotype differentiation of Nile tilapia to identify the brood stocks that can subsequently inform selective breeding programmes in Uganda. This study revealed two distinct genetic groups that can be used as reference founder stocks, (i) the Edward-George system and (ii) the Albert, Kyoga systems and Victoria. The Nile tilapia genotypes in L. Albert generally appear genetically undifferentiated from the ones in the Lakes Kyoga system and Victoria. These results may be elucidated by two factors: (i) natural factors/waterbody interconnectivity and (ii) the effects of anthropogenic activities (historical fish translocations and overfishing in Uganda). The first factor particularly is consistent with the genetic structure between lakes Edward and George and their high degree of divergence/isolation from the remaining lakes.

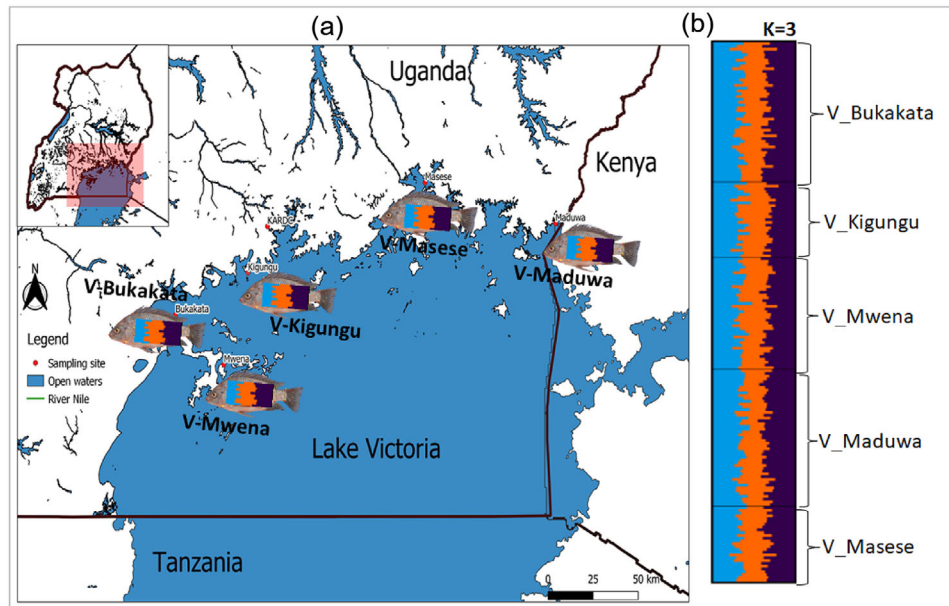


FIGURE 5 Bayesian clustering for genetic assignments of Nile tilapia populations within Lake Victoria based on STRUCTURE. Part (a) represents the map of Lake Victoria, (b) genetic structure. The various rectangular colour shapes embedded in Nile tilapia digital images in part (a) depict the species' genetic structure reference map/distribution within Lake Victoria.

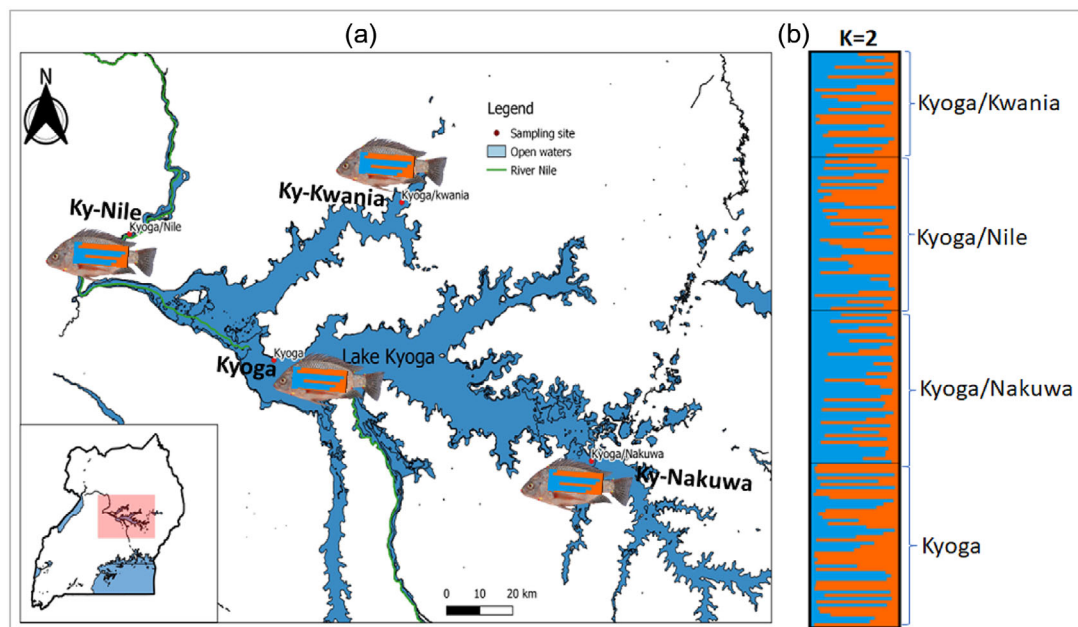


FIGURE 6 Bayesian clustering for genetic assignments of Nile tilapia populations within Lake Kyoga based on STRUCTURE. Part (a) represents the map of Lake Kyoga, (b) genetic structure. The various rectangular colour shapes embedded in Nile tilapia digital images in part (a) depict the species' genetic structure reference map/distribution within Lake Kyoga.

This pattern was supported by several analyses, including structure generated by the Neighbour network tree, F_{st} and N_m values. These results are congruent with the previous findings of Tibihika et al. (2020). Lakes Edward and George are interconnected by the Kazinga Channel, suggesting constant gene flow among the Nile tilapia popu-

lations that could explain their genetic homogeneity. Additionally, the genetic structure observed in the Lakes Edward-George system may be explained by potentially limited anthropogenic activities such as cage fish farming and fish translocations, among others. For instance, although various reports have indicated Nile tilapia invasion through

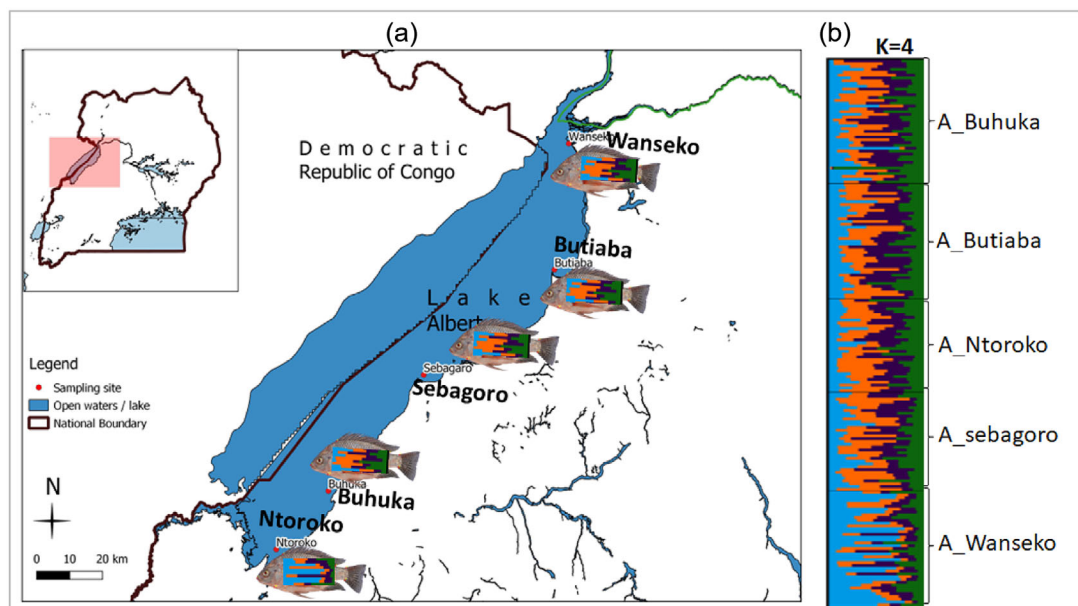


FIGURE 7 Bayesian clustering for genetic assignments of Nile tilapia populations within Lake Albert based on STRUCTURE. Part (a) represents the map of Lake Albert, (b) genetic structure. The various rectangular colour shapes embedded in Nile tilapia digital images in part (a) depict the species' genetic structure reference map/distribution within Lake Albert.

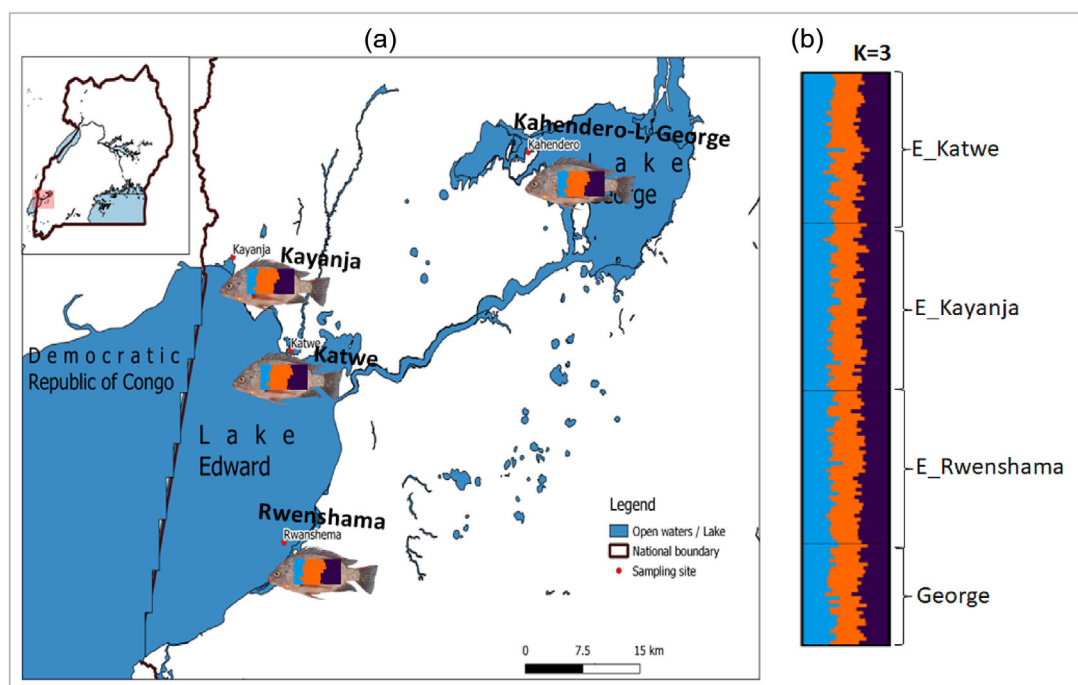


FIGURE 8 Bayesian clustering for genetic assignments of Nile tilapia populations within the Lake Edward-George system based on STRUCTURE. Part (a) represents the map of the Lake Edward-George system, (b) genetic structure. The various rectangular colour shapes embedded in Nile tilapia digital images in part (a) depict the species' genetic structure reference map/distribution within Lake Edward-George.

human-mediated translocations and fish farming that can propel gene flow and hence genetic relatedness, little or no information is available to show such forms of anthropogenic influx in the Edward-George system (Musinguzi et al., 2019; Ogutu-Ohwayo, 1990). Fundamentally, the

genetic homogeneity in the system may explain the likelihood of pure and discrete Nile tilapia strain in the Edward-George water body. The potentially unaltered genetic structure in the L. Edward-George system may be instrumental for future selective breeding programmes in

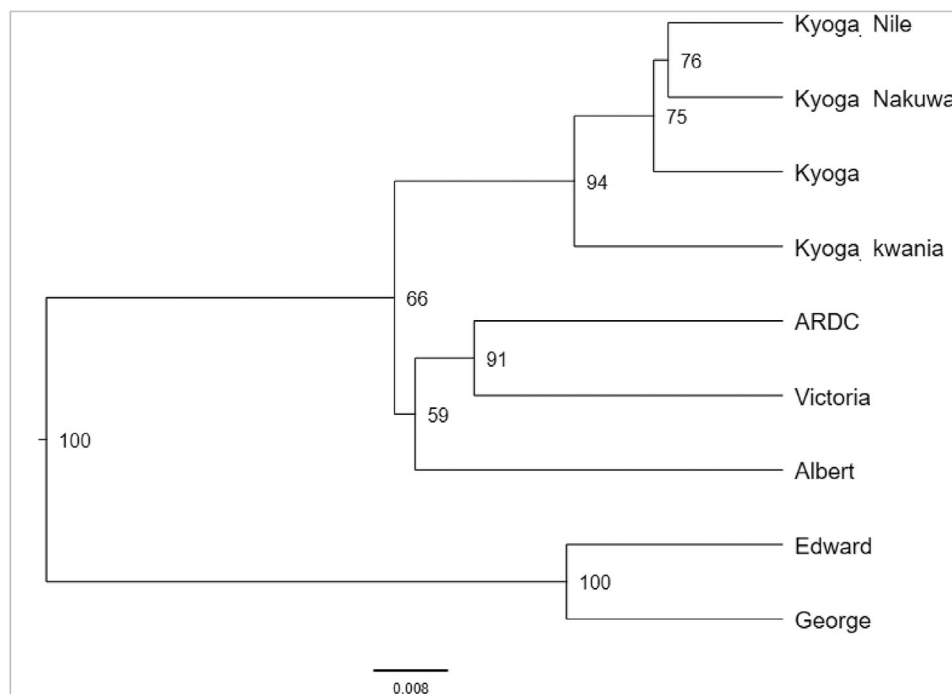


FIGURE 9 Phylogeny network visualized through UPGMA tree based on Nei distance and bootstrap values replicated over loci.

TABLE 2 Mean genetic diversity indices of Nile tilapia populations from Uganda's major water bodies.

Pop	Na	Ho	He	uHe	No. Pa	Ar
Albert	10.82 ± 1.34	0.44 ± 0.05	0.51 ± 0.06	0.52 ± 0.06	3.00 ± 0.50	1.91 ± 0.11
Edward	10.29 ± 1.23	0.51 ± 0.05	0.56 ± 0.05	0.56 ± 0.05	2.93 ± 0.50	1.97 ± 0.09
George	5.57 ± 0.50	0.46 ± 0.05	0.54 ± 0.05	0.55 ± 0.05	0.54 ± 0.14	1.95 ± 0.09
ARDCK	6.96 ± 0.79	0.45 ± 0.05	0.52 ± 0.06	0.53 ± 0.06	0.75 ± 0.17	1.92 ± 0.11
Kyoga/Kwania	4.39 ± 0.61	0.42 ± 0.05	0.47 ± 0.06	0.48 ± 0.06	0.07 ± 0.05	1.83 ± 0.11
Kyoga/Nile	4.57 ± 0.53	0.39 ± 0.05	0.47 ± 0.06	0.48 ± 0.06	0.00 ± 0.00	1.83 ± 0.11
Kyoga/Nakuwa	4.75 ± 0.70	0.38 ± 0.06	0.44 ± 0.07	0.44 ± 0.07	0.04 ± 0.04	1.71 ± 0.14
Kyoga	4.50 ± 0.54	0.41 ± 0.06	0.45 ± 0.06	0.45 ± 0.06	0.00 ± 0.00	1.79 ± 0.11
Victoria	7.18 ± 0.93	0.44 ± 0.05	0.50 ± 0.06	0.50 ± 0.06	0.54 ± 0.15	1.87 ± 0.10

Abbreviations: Ar, allelic richness; ARDCK, Aquaculture Research and Development Centre Kajjansi; He, expected heterozygosity; Ho, observed heterozygosity; Na, number of different alleles; No. Pa, number of private alleles; Pop, population; uHe, unbiased heterozygosity.

Uganda and conservation genetics. Although lakes Edward and George are connected to L. Albert by the Semliki River, the Nile tilapia genetic structure in the latter lake (Albert) is divergent from the former lakes. This is likely attributed to many factors, but most importantly to the prevailing physical features in the Semliki River (Dumont, 2009). The presence of strong rapids and falls in Semliki River appears to impede the potential gene flow between the Nile tilapia populations in lakes Edward-George and L. Albert which explains the observed degree of genetic divergence (Dumont, 2009; Tibihika et al., 2022). In the remaining sampled waterbodies (Victoria, Kyoga, Kyoga/Nile, Kyoga/Kwania and Kyoga/Nakuwa), Nile tilapia is not native, and the prevailing stocks may be associated with anthropogenic activities, par-

ticularly fish translocations potentially from L. Albert (Mwanja, 2000; Tibihika et al., 2020, 2019, 2022, 2018, 2023). Here, based on the high degree of genetic differentiation observed, the Edward-George system is unlikely to be the main contributor to the historical fish translocations. However, some contribution may exist since some indicators of gene flow were observed in other populations (e.g., some Kyoga and Victoria subpopulations). The genetic homogeneity and relatively high genetic diversity values observed in this water body system indicate that the Lake Edward-George system was also not affected by some of the anthropogenic threats assumed in the other lakes. Further scientific exploration is required, but these results support the idea that Nile tilapia in the L. Edward-George system may be one of the appropriate

TABLE 3 Mean genetic diversity indices of Nile tilapia subpopulations from Uganda's major water bodies.

Subpop	Na	Ho	He	uHe	No. Pa	Ar
A_Buhuka	8.07 ± 0.94	0.44 ± 0.05	0.53 ± 0.06	0.54 ± 0.06	1.21 ± 0.16	1.96 ± 0.11
A_Butiaba	6.82 ± 0.98	0.45 ± 0.06	0.49 ± 0.06	0.50 ± 0.06	0.43 ± 0.12	1.88 ± 0.11
A_Ntoroko	6.54 ± 0.88	0.43 ± 0.05	0.50 ± 0.06	0.51 ± 0.06	0.39 ± 0.13	1.90 ± 0.11
A_Sebugoro	6.21 ± 0.85	0.40 ± 0.05	0.48 ± 0.06	0.49 ± 0.06	0.29 ± 0.10	1.86 ± 0.11
A_Wanseko	6.29 ± 0.85	0.44 ± 0.06	0.50 ± 0.06	0.50 ± 0.06	0.18 ± 0.09	1.88 ± 0.12
E_Katwe	6.89 ± 0.76	0.52 ± 0.05	0.55 ± 0.05	0.56 ± 0.05	0.71 ± 0.19	1.97 ± 0.09
E_Kayanja	7.18 ± 0.77	0.50 ± 0.06	0.55 ± 0.05	0.56 ± 0.05	0.64 ± 0.17	1.96 ± 0.09
E_Rwenshama	7.36 ± 0.77	0.51 ± 0.05	0.56 ± 0.05	0.56 ± 0.05	0.82 ± 0.21	1.98 ± 0.09
George	5.57 ± 0.50	0.46 ± 0.50	0.54 ± 0.50	0.55 ± 0.50	0.54 ± 0.14	1.95 ± 0.09
ARDCK	6.96 ± 0.79	0.45 ± 0.05	0.52 ± 0.06	0.53 ± 0.06	0.75 ± 0.17	1.92 ± 0.11
Kyoga/Kwania	4.39 ± 0.61	0.42 ± 0.06	0.47 ± 0.06	0.48 ± 0.06	0.07 ± 0.05	1.83 ± 0.11
Kyoga/Nile	4.57 ± 0.53	0.39 ± 0.05	0.47 ± 0.06	0.48 ± 0.06	0.00 ± 0.00	1.83 ± 0.11
Kyoga/Nakuwa	4.75 ± 0.06	0.38 ± 0.06	0.44 ± 0.07	0.45 ± 0.07	0.04 ± 0.04	1.71 ± 0.15
Kyoga	4.50 ± 0.54	0.41 ± 0.06	0.45 ± 0.06	0.46 ± 0.06	0.00 ± 0.00	1.79 ± 0.11
V_Bukakata	5.39 ± 0.59	0.44 ± 0.05	0.48 ± 0.05	0.49 ± 0.06	0.04 ± 0.04	1.85 ± 0.10
V_Kigungu	4.39 ± 0.56	0.39 ± 0.06	0.44 ± 0.06	0.44 ± 0.06	0.04 ± 0.04	1.70 ± 0.14
V_Mwena	5.57 ± 0.65	0.44 ± 0.05	0.50 ± 0.05	0.51 ± 0.05	0.21 ± 0.10	1.88 ± 0.10
V_Maduwa	4.50 ± 0.57	0.38 ± 0.06	0.42 ± 0.06	0.43 ± 0.06	0.11 ± 0.06	1.67 ± 0.14
V_Masese	4.61 ± 0.55	0.45 ± 0.06	0.49 ± 0.06	0.51 ± 0.06	0.07 ± 0.05	1.88 ± 0.11

Abbreviations: A, L. Albert; ARDCK, Aquaculture Research and Development Centre Kajjansi; E, L. Edward; Subpop, subpopulations; V, L. Victoria.

TABLE 4 Pairwise matrix heatmap of population differentiation based on Nei Unbiased Genetic Distance.

Albert	Edward	George	ARDCK	Kyoga/Kwania	Kyoga/Nile	Kyoga/Nakuwa	Kyoga	Victoria	
-	-	-	-	-	-	-	-	-	Albert
0.121	-	-	-	-	-	-	-	-	Edward
0.133	0.000	-	-	-	-	-	-	-	George
0.030	0.111	0.124	-	-	-	-	-	-	ARDCK
0.032	0.161	0.175	0.027	-	-	-	-	-	Kyoga/Kwania
0.030	0.155	0.167	0.021	0.004	-	-	-	-	Kyoga/Nile
0.115	0.230	0.240	0.104	0.096	0.091	-	-	-	Kyoga/Nakuwa
0.036	0.162	0.170	0.027	0.014	0.005	0.102	-	-	Kyoga
0.045	0.036	0.101	0.023	0.041	0.040	0.123	0.043	-	Victoria

Abbreviation: ARDCK, Aquaculture Research and Development Centre Kajjansi.

sources for selective breeding programmes in Uganda, and the system may be regarded as conserved genes with unaltered genetic structure.

The observed genetic homogeneity and high gene flow among lakes Albert, Kyoga system (lakes Kyoga, Kyoga/Nile, Kyoga/Kwania and Kyoga/Nakuwa), Victoria and ARDCK may be attributed to the second factor, concerning the anthropogenic activities/historical fish translocations in Uganda. Nile tilapia is known to be an alien species in lakes Kyoga, Kyoga/Nile, Kyoga/Kwania, Kyoga/Nakuwa and Victoria, with its putative origins in L. Albert and L. Edward-George system (Balirwa, 1992; Ogutu-Ohwayo, 1990; Tibihiika et al., 2020, 2022; Trewavas, 1983; Welcomme, 1966). Therefore, the genetic similarity exhibited

between the native Nile tilapia in L. Albert and the non-native Nile tilapia in the Lakes Victoria and Kyoga systems may reflect the historical stocking events. Similarly, the lack of genetic structure between Nile tilapia in the fish farm at ARDCK and the lakes was expected as the brood stocks were potentially sourced from either L. Albert, Victoria or even L. Kyoga system. In addition to the historical fish translocations, the current upsurge in fish farming, which is characterized by constant fish movements across various waterbodies, may compel further gene flow among the Nile tilapia populations. This may be typically true because many fish farmers in Uganda particularly the local hatchery operators/breeders source fish from the wild and, in the long run, may

TABLE 5 Pairwise matrix heatmap of L. Victoria within-population differentiation based on Nei Unbiased Genetic Distance.

V_Bukakata	V_Kigungu	V_Mwena	V_Maduwa	V_Masese
–				V_Bukakata
0.015	–			V_Kigungu
0.004	0.011	–		V_Mwena
0.009	0.010	0.004	–	V_Maduwa
0.003	0.008	0.000	0.005	– V_Masese

TABLE 6 Pairwise matrix heatmap of L. Kyoga basin within-population differentiation based on Nei Unbiased Genetic Distance.

Kyoga/Kwania	Kyoga/Nile	Kyoga/Nakuwa	Kyoga
–			Kyoga/Kwania
0.005	–		Kyoga/Nile
0.096	0.093	–	Kyoga/Nakuwa
0.015	0.005	0.101	– Kyoga

find their way back or even in new environments through inevitable escapees.

The genetic relatedness demonstrated by Nile tilapia in lakes Albert, Kyoga system and Victoria is consistent with the high Nm values found between them reflecting high gene flow. The contemporary genetic structure of Nile tilapia in these water bodies may be a result of specific evolutionary and ecological processes, propelled by various anthropogenic (Tibihika et al., 2022; Trewavas, 1983; Welcomme, 1966). These processes could have subsequently influenced admixture as the key factors associated with the Nile tilapia structure in the water bodies. This is congruent with the previous various studies which indicate that Nile tilapia translocations/introductions into lakes Victoria and Kyoga system could have been from a similar source (Mwanja 2000; Tibihika et al., 2022, 2020; Trewavas, 1983). However, the evidence of admixture, particularly in Lakes Victoria and Albert, may suggest multiple Nile tilapia restocking from various sources. This explanation is supported by the significant recorded number of migrants as proxy gene flow between some subpopulations in Victoria/Albert and other systems. Similarly, the noted divergent genotypes of some subpopulations within L. Victoria (Mwena and Bukakata) may further support the notion of multiple introductions from different lineages other than L. Albert which is considered a putative source of fish introductions. Moreover, the issue of fish farming, particularly the practices within or in the periphery of the water bodies, may trigger continuous indirect restocking which can subsequently induce admixture.

Consistent with previous studies (Tibihika et al., 2020), Nile tilapia populations in L. Kyoga systems portrayed low genetic diversity, contrary to the other populations such as those in L. Victoria, Edward-George system and Albert. The low genetic diversity of Nile tilapia observed in the L. Kyoga basin may be a function of the second factor

regarding anthropogenic activities (overfishing) and other potential aspects such as climate change, predation pressure and habitat destruction. All these can drive fish stocks to decline, and consequently, bottleneck effects may be inevitable, resulting in low genetic diversity (Sonsthagen et al., 2017). For instance, some reports show that the land use and land cover changes in the L. Kyoga basin have led to the dwindling of fish stocks (Nambi et al., 2023). Similarly, the continued effects of overfishing in the L. Kyoga basin (Balirwa et al., 2003; Nambi et al., 2023; Ogutu-Ohwayo, 1990) may be among the key drivers contributing to low genetic diversity in the basin through founder effects as a consequence of reduced effective population size. Some studies indicate that overfishing or even fish harvesting may increase allele frequency fixation rates with subsequent low genetic diversity in fish populations (Allendorf et al., 2008). Overfishing is not news in Uganda. The impasse has been in the country since the 1920s following the importation of flux gill nets (Worthington, 1932). Relatedly, some reports indicate that the introduction of alien fish species in the Lakes Victoria and Kyoga system was partly to replace the overfished native fish stocks which had dwindled and could no longer support the fishing industry (Balirwa et al., 2003; Ogutu-Ohwayo, 1990). In this context, a significant decline in fish catches of L. Kyoga has been realized since the 1980s, with the total contribution of tilapines (Nile tilapia, *Coptodon zillii* and *Oreochromis leucostictus*) reducing from 80,960 t in 1985 to 37,148 t in 1989 (NaFIRRI, 2007). Several other key threats to the L. Kyoga fisheries have been reportedly associated with over-exploitation coupled with the use of destructive fishing gear such as beach and open lake seine nets, as well as drainage of the catchment/wetland for agricultural use (NaFIRRI, 2007). On the other hand, disturbances such as predatory pressure in the Kyoga system may have also contributed to founder effects and subsequent low genetic diversity in the fish stocks. Analogous to L. Victoria, following the introduction of the voracious predator; Nile perch (*L. niloticus*) into L. Kyoga (together with Nile tilapia) in the 1950s, threats to biodiversity have been a huge concern for the sustainability of fish stocks in the water bodies (Balirwa et al., 2003). Here, Nile perch is reported to have threatened its prey, including Nile tilapia, from the open waters, with some remnants displaced in refugial grounds; shallow aquatic vegetation/wetland areas, coupled with macrophytes (Balirwa, 1998; Balirwa et al., 2003; Ogutu-Ohwayo et al., 1999). The long adaptation in refugia by small populations may have influenced genetic drift with subsequent low genetic diversity (Gehri et al., 2021; Nosil et al., 2009). These processes may explain the degree of low genetic diversity observed in the L. Kyoga system. However, other factors such as extreme conditions that are unbearable for fish, for example, climate change, pollution and habitat destruction, among others, may trigger the fish dispersal/migrations/isolations and, hence, influence evolutionary biological shifts with subsequent low genetic diversity (Tamario et al., 2019). Therefore, the low genetic diversity of Nile tilapia in the L. Kyoga system may require management intervention options focused on regulating various anthropogenic activities in the basin to improve biodiversity protection.

TABLE 7 Pairwise matrix heatmap of L. Albert within-population differentiation based on Nei Unbiased Genetic Distance.

A_Buhuka	A_Butiaba	A_Ntoroko	A_Sebagoro	A_Wanseko	
-					A_Buhuka
0.003	-				A_Butiaba
0.001	0.005	-			A_Ntoroko
0.004	0.002	0.004	-		A_Sebagoro
0.014	0.011	0.018	0.013	-	A_Wanseko

TABLE 8 Pairwise matrix heatmap of L. Edward-George within-population differentiation based on Nei Unbiased Genetic Distance.

E_Katwe	E_Kayanja	E_Rwenshama	George	
-				E_Katwe
0.005	-			E_Kayanja
0.011	0.000	-		E_Rwenshama
0.010	0.000	0.000	-	George

7 | CONCLUSION AND RECOMMENDATIONS

This study reports two discrete gene pools of Nile tilapia populations that might serve as a base for future breeding programmes in Uganda. Among the genetic groups/clusters, the L. Edward-George system appears panmictic. The genetic clusters are potentially attributed to a combination of natural and anthropogenic processes that could have shaped the current observed groups. Additionally, the low genetic diversity in the L. Kyoga system could be an interplay of various stressors, particularly the various anthropogenic activities, including overfishing. The Kyoga basin is a large and complex system with numerous water bodies, and this study only sampled some of them. There is, therefore, a possibility that important Nile tilapia genetic resources could still be unexplored. Future studies may consider field expansion in the Kyoga basin to understand the extent of Nile tilapia genetic structure in the numerous satellite lakes. For the improvement of aquaculture practices, we recommend that specific parent stocks for selective breeding programmes be sourced from the Lakes Edward-George system (as one group) and Albert (another group). Each of these genetic groups may be considered genetically distant genotypes or strains and therefore potential broodstock sources. The genetic cluster in L. Edward-George may be bred with either Victoria or Albert, but the latter population may not be bred with Victoria. There is a concern about low genetic diversity in the L. Kyoga system and though breeding this group with Edward-George may suffice, considerably deeper thoughts should be observed.

AUTHOR CONTRIBUTIONS

Papius Dias Tibihika: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; supervision; writing—original draft; writing—review and editing. **Cassius Aruho and Richard Ddungu:** Conceptualization; data curation; fund-

ing acquisition; investigation; methodology; project administration; resources; writing—review and editing. **Victoria Namulawa:** Conceptualization; data curation; funding acquisition; project administration; resources; supervision; writing—review and editing. **Gertrude Atukunda:** Conceptualization; data curation; funding acquisition; methodology; project administration; resources; supervision. **Margaret Aanyu:** Data curation; funding acquisition; methodology; project administration; resources; supervision; validation. **Mujibu Nkambo:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources. **Thapasya Vijayan:** Conceptualization; formal analysis; methodology; software; validation; visualization; writing—review and editing. **Gerald Kwiriza:** Conceptualization; data curation; formal analysis; software; writing—review and editing. **Manuel Curto:** Conceptualization; formal analysis; methodology; software; visualization; writing—review and editing. **Harald Meimberg:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; supervision; validation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data were deposited in the GenBank, Sequence Read Archive (SRA), and are available under the accession number PRJNA550300.

ETHICS STATEMENT

The fish specimens used in this study were already dead when obtained from the fishermen. Therefore, no special animal rights/welfare were observed during the fieldwork.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/aff2.197>.

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SUPPORTING INFORMATION

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

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