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The Upemba National Park (Upper Congo Basin, DR Congo): An Updated Checklist Confirming Its Status as an African Fish Biodiversity Hotspot

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Abstract: An annotated checklist of the ichthyofauna of the Upemba National Park, draining part of the Upper Lualaba basin and situated in the southern part of the Democratic Republic of the Congo, is presented, based on a literature review, a re-examination of museum collections, and a study of recent collections (2012–2020). In total, 247 native and 1 introduced species, *Heterotis niloticus*, are reported. The native species belong to 78 genera, 26 families, and 15 orders. Of these, 45 species (18%) are endemic to the park, 35 species (14%) await formal description, and 5 taxa (2%) need further study to clarify their status. With 51 species, the Cyprinidae is by far the most species-rich family, followed by the Mormyridae (26), Mochokidae (26), Alestidae (18), Distichodontidae (18), Amphiliidae (17), and Cichlidae (16). The remaining families are represented by less than 15 species. Comments about the species distribution and the fish fauna shared with adjacent ecoregions are provided. Although the park provides some protection for the fish species living within its borders by limiting human access to the core zone, the annex and buffer zones are both subject to strong anthropogenic pressure. These observations underscore the need for the implementation and further elaboration of fish-related preservation guidelines and plans to enable better protection/conservation of the park's ichthyofauna.

Keywords: systematics; conservation; protection; endemicity; ichthyofauna; Upper Lualaba

1. Introduction

The Upemba National Park (UNP) is located in the south-eastern part of the Democratic Republic of the Congo (DR Congo) (~8°45′–9°5′S, 26°0′–27°10′E) (Figure 1). It was created on 15 May 1939, to protect mainly the mammalian diversity [1], and the spectacular landscapes [2]. With an estimated surface area of 17,730 km^2, the UNP is the second largest park in the DR Congo, after the Salonga National Park (360,000 km^2) [3]. The UNP is drained by two major basins, the Upper Congo River, also called Lualaba, in the Kamalondo Depression, and the Lufira River, its major right-bank tributary, which divides the park into a so-called northern and a southern sector [4] (Figure 1). These two rivers receive their water from many tributaries that originate from the Kibara Plateau in the north-east (max. altitude 1890 m) and the Biano Plateau in the south-east (max. altitude

1700 m) [2,5]. The entire park lies within the Upper Lualaba Ecoregion [6] in the Upper Congo Basin [7].

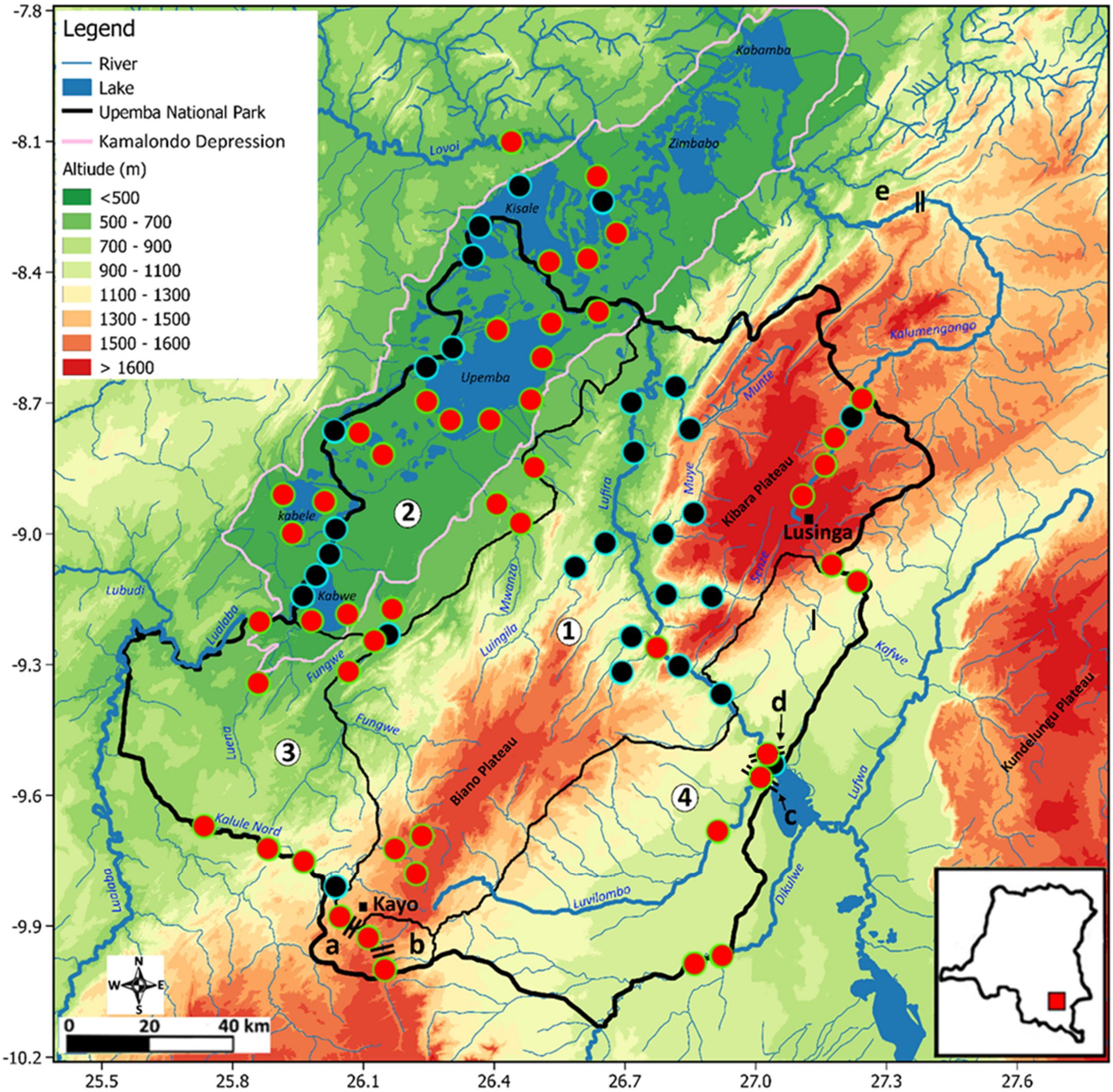

Figure 1. Map of the Upemba National Park and its surroundings. Sites sampled prior to this study are indicated by black circles and those of this study (2012–2020) by red circles. (**1**) core zone, (**2**) annex zone, (**3**) and (**4**) buffer zones: Bena Mulumbu Hunting Area (**3**) and Lubudi-Sampwe Hunting Area (**4**). Double bars indicate major falls: (**a**) Kamwanga Falls, (**b**) Kayo Falls, (**c**) Luvilombo Falls, (**d**) Kyubo Falls, and (**e**) Kalumengongo Falls.

The published information on fishes of the UNP includes: (i) checklists from (occasional) explorations [8–11] and (ii) the description of new species [12–15]. The only currently available fish inventory of the park lists a total of 116 species and was compiled mainly based on de Witte's expeditions between 1946 and 1949 [16]. However, since large parts of the UNP remained unexplored (Figure 1), the actual distribution of several species within the park remained unknown. In addition, for most of the families and genera cited in previous studies, a detailed systematic revision has since been completed, which therefore also requires updating the currently available list of fish taxa.

The UNP is located in a post-conflict region occupied by armed groups in the core zone until 2018 and by mostly unemployed populations in the buffer zone. This, combined with human population growth, resulted in increasing pressure on the fish fauna of the UNP, especially through illegal fishing with mosquito nets distributed as part of the fight against malaria by the government in partnership with various NGOs, and the use of ichthyotoxins derived from *Amblygonocarpus andongensis* (Welw. ex Oliv.) Exell and Torre and *Tephrosia vogelii* Hook. F. (both Fabaceae).

In this context of increasing threats, documenting species diversity and their distribution is crucial. This, together with the identification of threats, will help in the formulation of protection/conservation guidelines and sustainable management measures. A first step in this direction and the main objective of the present paper is to provide an updated, annotated list of the fish species diversity and distribution according to the major hydrographic units recognised in the UNP. The affinities between the UNP fish fauna and those of the neighbouring ecoregions are also discussed. Finally, some protection/conservation issues are highlighted.

2. Materials and Methods

In order to obtain an as complete as possible picture of the species diversity of the UNP, different fishing techniques were used, including angling, dip nets, fyke nets, traditional traps, ichthyotoxins, trammel nets, gill nets, and beach seines in various habitats and in many sub-basins of the UNP. Sampling expeditions were only organised during the dry season due to ease of access and to optimise sampling efficiency. Specimens of species not collected by us were purchased from local fishermen.

For each catch, fish were grouped by species and preliminarily identified or given cheironyms (working names). For each species, between 5 and 30 specimens in good condition were preserved, depending on the variability in size (age), and sex of the specimens. For small samples, all specimens were preserved. As such, reference specimens were deposited at the Unité de Recherche en Biodiversité et Exploitation durable des Zones Humides (BEZHU, Lubumbashi, DR Congo), the Centre de Surveillance de la Biodiversité (CSB, Kisangani, DR Congo), and the Royal Museum for Central Africa (RMCA, Tervuren, Belgium). In addition, depending on the species and size of the specimens collected, a fin-clip of at least two to five specimens was taken on the right side, stored in ethanol 95% for genetic analysis, and deposited at the RMCA for long-term storage. Subsequently, the specimens were fixed in formalin 10%. Collection data such as sampling site, river, GPS coordinates, date, fishing method, etc. were recorded. All sampling localities were mapped. If coordinates were lacking for historical collections, when possible, the gazetteer of the DR Congo was consulted [17].

If needed, the field and laboratory identifications made at BEZHU (DR Congo) were subsequently verified at the RMCA where voucher specimens were deposited (collection numbers: RMCA 2012-031; RMCA 2015-005; RMCA 2016-003; RMCA 2016-025; RMCA 2018-018; and RMCA 2021-020). The publications used for the identification of the studied specimens are the checklists of the fishes of the region or the revisions of the genera and families present in the UNP [11,16,18–27]. In addition, existing historical collections from the UNP, mainly housed at the RMCA, the Royal Belgian Institute of Natural Sciences (RBINS, Brussels, Belgium), and the Natural History Museum (NHM, London, United Kingdom), have been verified and, when necessary, re-identified. Orders and families are listed according to phylogenetic order [28], while the genera and species in each family are listed in alphabetical order. The spellings of species' names and years of publication are in accordance with 'Eschmeyer's Catalog of Fishes' [28]. Identification confidence was expressed by using the following open nomenclature qualifiers [29]: 'sp.' followed by a working name (cheironym) between simple quotation marks is used for specimens that do not correspond to any described species; and 'cf.' followed by a valid species name is used for specimens for which some morphological differences with the valid species have been observed but for which further studies are needed to evaluate their taxonomic status.

We examined the gradients of fish community change by qualitatively studying species' presence/absence data. The degrees of (dis)similarities of the ichthyofauna of the UNP, the Upper Lualaba Ecoregion, and the ichthyofauna of the four neighbouring ecoregions (Bangweulu-Mweru, Upper Congo, Kasai, and Upper Zambezi) (sensu [6]) were calculated using the Jaccard similarity index (J) [30]: $J = C/(N1 + N2 - C)$, with C being the number of common species between the two zones, while N1 and N2 represent the total number of native species in each of the two zones, respectively. Fish lists for the surrounding ecoregions were compiled from the data available on FishBase [31] and supplemented by relevant publications [32–36]. The conservation status of all reported species is based on the IUCN red list (www.iucnredlist.org, accessed on 04 July 2023). Abbreviations of museum collections follow Sabaj [37]. Other abbreviations: a.s.l., above sea level; DR Congo, Democratic Republic of the Congo; HL, head length; s.l., sensu lato; SL, standard length; and UNP, Upemba National Park.

3. Results

3.1. Fish Diversity

The distribution of the fish species in the various sub-basins of the UNP and in the neighbouring ecoregions, together with their IUCN red list status, is presented in Table 1 (see Appendix A in Figure A1 for an illustration of some representative species of the UNP). In total, 247 native species were reported, with 45 species (18%) endemic to the park and currently only known from their type localities. Only one introduced species, *Heterotis niloticus*, is reported. The species richness reported in this study represents more than double the number of fish species known from the park [16] and confirms that the species richness of the UNP was still seriously underestimated.

The native species belong to 78 genera, 26 families, and 15 orders. The order richest in species was Siluriformes (70 species or 28%), followed by Cypriniformes (60 species or 24%), Characiformes (39 species or 16%), Osteoglossiformes (27 species or 11%), Cichliformes (16 species or 7%), and Gonorynchiformes (11 species or 5%). In the other nine orders, the species numbers varied between five and one. The most diverse families are Cyprinidae (51 species or 20%), Mormyridae (26 species or 11%), Mochokidae (26 species or 11%), Alestidae (18 species or 7%), Distichodontidae (18 species or 7%), Amphiliidae (17 species or 7%), and Cichlidae (16 species or 6%). Thus, 172 species or 70% of the collected native species recorded during this study belong to only six families. The other 19 families are represented by less than 15 species each (Table 1).

Table 1. List of the fish species reported from the Upemba National Park (UNP), their IUCN red list status, and comparison of the UNP fish fauna with that of the neighbouring ecoregions. Family names are followed by the number of genera/species between brackets. +: present; -: absent; N: recently collected and not yet reported from the UNP; *: type locality; E: endemic; I: introduced. UNP protection/conservation zones: AZ, annex zone; CZ, core zone; BM, Bena Mulumbu Hunting Area; LS, Lubudi-Sampwe Hunting Area. Sub-basins in the UNP: Di, Dikulwe River; Fu, Fungwe River; Ln, Luena River; Lu, Lower Lufira Basin (excluding Lv and Kyubo area); Lv, Luvilombo River and Kyubo area; Ka, Kafwe River; KD, Kamalondo Depression; KM, Kalumengongo River; KN, Kalule Nord River; Mw, Mwanza River; Ng, Ngulungu River. IUCN red list status: LC, Least Concern; DD, Data Deficient; EN, Endangered; NE, Not Evaluated; VU, Vulnerable. Neighbouring ecoregions: UC, Upper Congo; BM, Bangweulu-Mweru; Kas, Kasai; UZ, Upper Zambezi.

Family (No. Genera/Species)	Upemba National Park															IUCN Status	Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area								
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Polypteriformes																				
Polypteridae (1/4)																				
Polypterus bichir (Geoffroy, 1802)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	-	-
Polypterus congicus Boulenger, 1898	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Polypterus ornatipinnis Boulenger, 1902	-	+	-	+	-	-	-	N	-	N	-	+	+	N	N	LC	+	-	+	-
Polypterus senegalus Cuvier, 1829	-	-	-	+	-	+	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Osteoglossiformes																				
Arapaimidae (1/1)																				
Heterotis niloticus (Cuvier, 1829)	-	-	-	N I	-	N I	-	-	-	-	-	-	N I	-	-	LC	+	-	+	-
Mormyridae (10/26)																				
Campylomormyrus elephas (Boulenger, 1898)	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Campylomormyrus rhynchophorus (Boulenger, 1898)	-	+	-	+	-	-	-	N	-	N	-	-	+	N	N	LC	+	-	+	-
Campylomormyrus sp. 'kadia'	-	-	-	N E	-	-	-	-	-	-	-	-	N E	-	-	NE	-	-	-	-
Campylomormyrus tamandua (Günther, 1864)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	+	+	-
Cyphomyrus discorhynchus (Peters, 1852)	-	+	-	N	N	+	-	N	-	-	-	+	N	N	-	LC	+	+	+	+
Cyphomyrus lufirae Mukweze et al., 2020	-	N E	-	-	-	-	-	-	N E	N	-	N E	-	-	N	NE	-	-	-	-
Genyomyrus donnyi Boulenger, 1898	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Gnathonemus sp. 'kamalondo'	-	N E	-	N E *	N E	N E	-	-	-	-	-	N E *	-	-	-	NE	-	-	-	-
Heteromormyrus tavernei (Poll, 1972)	-	-	-	-	-	-	-	-	-	-	+ *	-	-	-	+ *	LC	-	-	-	-
Heteromormyrus sp. 'dikulwe'	-	N E *	-	-	-	-	-	-	N	-	-	N E *	-	-	N	NE	-	-	-	-
Marcusenius greshoffi (Schilthius, 1891)	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Marcusenius macrolepidotus (Peters, 1852)	-	N	-	+	N	+	N	N	N	-	-	N	+	N	N	LC	+	+	-	+
Marcusenius monteiri (Günther, 1873)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	+	+	-
Marcusenius multisquamatus Kramer and Wink, 2013	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	NE	+	+	+	-
Marcusenius stanleyanus (Boulenger, 1897)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	-
Mormyrops anguilloides (Linnaeus, 1758)	-	+	-	N	-	-	-	N	-	N	-	+	N	N	N	LC	+	+	+	+
Mormyrus caballus Boulenger, 1898	-	+	-	-	-	-	-	-	-	N	-	+	-	-	N	LC	+	+	+	-
Mormyrus rume Valenciennes, 1847	-	N	-	+	-	-	-	-	-	-	-	N	+	-	-	NE	+	-	+	-

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park																Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Petrocephalus cf. *christyi* Boulenger, 1920	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	LC	+	+	+	-
Petrocephalus cf. *frieli* Lavoué, 2012	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	NE	-	+	-	-
Petrocephalus sauvagii (Boulenger, 1887)	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	NE	+	-	+	-
Petrocephalus simus Sauvage, 1879	-	-	-	-	N	+	-	-	-	-	-	-	+	-	-	LC	+	+	+	+
Pollimyrus cuandoensis Kramer et al., 2013	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	NE	-	-	-	-
Pollimyrus fasciaticeps (Boulenger, 1920)	-	N	-	-		N	-	-	-	-	-	N	N	-	-	LC	-	-	-	-
Pollimyrus osbornii (Nichols and Griscom, 1917)	-	N	-	N	N	N	-	-	-	N	-	N	N	-	N	NE	+	+	+	-
Pollimyrus tumifrons (Boulenger, 1902)	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Clupeiformes																				
Clupeidae (2/4)																				
Microthrissa congica (Regan, 1917)	-	-	-	+	-	-	-	N	-	-	-	-	+	N	-	LC	+	-	+	-
Microthrissa royauxi Boulenger, 1902	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	-	-	+	-
Microthrissa whiteheadi Gourène and Teugels, 1988	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Odaxothrissa losera Boulenger, 1899	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Gonorynchiformes																				
Kneriidae (2/11)																				
Kneria katangae Poll, 1976	-	$+^{*}$	-	-	-	-	-	-	-	-	-	$+^{*}$	-	-	-	LC	-	-	-	-
Kneria sp. 'kalule'	-	-	N^{E*}	-	-	-	-	N^{E*}	-	-	-	N^{E*}	-	N^{E*}	-	NE	-	-	-	-
Kneria sp. 'kalumengongo'	N^{E*}	-	-	-	-	-	-	-	-	-	-	N^{E*}	-	-	-	NE	-	-	-	-
Kneria sp. 'lusinga'	-	-	-	-	-	-	-	-	-	-	E^{*}	-	-	-	E^{*}	NE	-	-	-	-
Kneria sp. 'luena'	-	-	-	-	-	-	N^{E*}	-	-	-	-	-	-	N^{E*}	-	NE	-	-	-	-
Parakneria lufirae Poll, 1965	-	E^{*}	-	-	-	-	-	-	-	-	-	E^{*}	-	-	-	DD	-	-	-	-
Parakneria sp. 'kilwezi'	-	E^{*}	-	-	-	-	-	-	-	-	-	E^{*}	-	-	-	NE	-	-	-	-
Parakneria sp. 'fungwe'	-	-	-	-	-	N^{E*}	-	-	-	-	-	-	N^{E*}	-	-	NE	-	-	-	-
Parakneria sp. 'kalule'	-	-	-	-	-	-	-	N^{E*}	-	-	-	-	-	N^{E*}	-	NE	-	-	-	-
Parakneria sp. 'luvilombo'	-	-	-	-	-	-	-	-	-	N^{E*}	-	-	-	-	N^{E*}	NE	-	-	-	-
Parakneria thysi Poll, 1965	-	N^{E*}	-	-	-	-	-	-	N	N^{E*}	-	N^{E*}	-	-	N	DD	-	-	-	-
Cypriniformes																				
Cyprinidae (4/51)																				
Clypeobarbus congicus (Boulenger, 1899)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	-	-
Clypeobarbus pleuropholis (Boulenger, 1899)	-	-	-	+	N	N	N	-	-	-	-	-	+	N	-	LC	+	-	+	-
Clypeobarbus sp. 'mwanza'	-	-	-	-	N^{E*}	-	-	-	-	-	-	-	N^{E*}	-	-	NE	-	-	-	-
Enteromius afrovernayi (Nichols and Boulton, 1927)	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC		+		+
Enteromius eutaenia (Boulenger, 1904)	-	+	-	-	-	+	-	-	-	+	+	-	+	-	+	DD	-	+	+	+
Enteromius janssensi (Poll, 1976)	-	-	-	-	-	$+^{*}$	-	-	-	-	-	-	$+^{*}$	-	-	LC	-	-	-	-
Enteromius kamolondoensis (Poll, 1938)	-	+	-	-	-	N^{E}	-	N	-	-	-	+	N^{E}	N	-	LC	+	-	-	-
Enteromius kerstenii (Peters, 1868)	-	+	-	N	N	+	-	N	N	N	-	+	+	N	N	LC	+	+	+	+
Enteromius kessleri (Steindachner, 1866)	-	-	-	-	-	-	-	-	-	-	N	-	-	-	N	LC	+	+	+	+
Enteromius lineomaculatus (Boulenger, 1903)	-	-	-	-	-	-	-	-	N	N	-	-	-	-	N	LC	+	+	+	+
Enteromius lukusiensis (David and Poll, 1937)	-	N	-	N	-	+	-	-	-	-	-	N	+	-	-	LC	+	+	-	-
Enteromius luluae (Fowler, 1930)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	+	+	-

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park																Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Enteromius miolepis (Boulenger, 1902)	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	+	+	+
Enteromius cf. *mocoensis* (Trewavas, 1936)	-	-	-	-	-	-	-	N	-	-	-	-	-	N	-	DD	-	-	+	-
Enteromius multilineatus (Worthington, 1933)	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC	-	+	-	+
Enteromius neefi (Greenwood, 1962)	-	+	+	+	-	N	-	+	-	-	-	+	+	+	-	LC	+	+	+	+
Enteromius paludinosus (Peters, 1852)	-	N	-	-	-	N	-	-	+	+	+	N	N	-	+	LC	-	+	+	+
Enteromius radiatus (Peters, 1853)	-	+	-	-	-	-	-	-	N	N	-	+	-	-	N	LC	+	+	+	+
Enteromius taeniopleura (Boulenger, 1917)	-	+	-	-	-	+	-	-	-	-	-	+	+	-	-	LC	+	-	-	-
Enteromius trimaculatus (Peters, 1852)	-	+	-	-	-	-	-	-	+	+	-	+	-	-	+	LC	-	+	-	+
Enteromius sp. 'kalumengongo'	N^{E*}	-	-	-	-	-	-	-	-	-	-	N^{E*}	-	-	-	NE	-	-	-	-
Enteromius sp. 'ngulungu'	-	-	+*	-	-	-	-	+*	-	-	-	+*	-	+*	-	NE	-	-	-	-
Enteromius sp. 'luena'	-	+*	-	-	-	-	-	-	-	-	-	+*	-	-	-	NE	-	-	-	-
Enteromius thespesios Katemo Manda et al., 2020	-	-	-	-	-	-	-	N*	-	N	-	-	-	N*	N	NE	-	+	-	-
Enteromius unitaeniatus (Günther, 1867)	-	+	-	-	-	-	-	-	+	-	-	+	-	-	+	LC	+	+	+	+
Enteromius urostigma (Boulenger, 1917)	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	LC	-	-	-	-
Labeo annectens Boulenger, 1903	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	+	+	+
Labeo cylindricus Peters, 1852	-	N	-	-	N	-	-	N	-	-	-	N	N	N	-	LC	+	+	-	+
Labeo dhonti Boulenger, 1920	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	+
Labeo greeni Boulenger, 1920	-	N	-	N	-	-	-	-	-	-	-	N	N	-	-	LC	+	-	+	-
Labeo kibimbi Poll, 1949	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	-	-
Labeo lineatus Boulenger, 1898	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	+	+	-
Labeo longipinnis Boulenger, 1898	-	-	-	N	-	-	-	-	+	-	-	-	N	-	+	LC	+	-	+	-
Labeo lualabaensis Tshibwabwa, 1997	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	-	-
Labeo parvus Boulenger, 1902	-	N	-	-	-	N	-	N	N	N	-	N	N	N	N	LC	+	-	+	-
Labeo simpsoni Ricardo-Bertram, 1943	-	N	-	-	-	-	-	N		-	-	N	-	N		LC	+	+	+	-
Labeo rosae Steindachner, 1894	-	-	-	-	-	-	-	-	N	-	-	-	-	-	N	LC	-	-	-	-
Labeo weeksii Boulenger, 1909	-	+	-	+	-	-	-	N	-	-	-	+	+	N	-	LC	+	+	+	-
Labeobarbus altipinnis (Banister and Poll, 1973)	-	E*	-	-	-	-	-	-	-	-	-	E*	-	-	-	LC	-	-	-	-
Labeobarbus gestetneri (Banister and Bailey, 1979)	E*	-	-	-	-	-	-	-	-	-	-	E*	-	-	-	DD	-	-	-	-
Labeobarbus iphthimostoma (Banister and Poll, 1973)	-	E*	-	-	-	-	-	-	-	-	-	E*	-	-	-	DD	-	-	-	-
Labeobarbus sp. 'lower_lufira'	-	N^{E*}	-	-	-	-	-	-	-	-	-	N^{E*}	-	-	-	NE	-	-	-	-
Labeobarbus sp. 'middle_lufira'	-	N^{E*}	-	-	-	-	-	-	N^{E*}	N^{E*}	N^{E*}	N^{E*}	-	-	N^{E*}	NE	-	-	-	-
Labeobarbus sp. 'kalumengongo'	N^{E*}	-	-	-	-	-	-	-	-	-	-	N^{E*}	-	-	-	NE	-	-	-	-
Labeobarbus sp. 'kapepe'	-	-	-	-	-	-	-	N^{E*}	-	-	-	N^{E*}	-	-	-	NE	-	-	-	-
Labeobarbus sp. 'kayo'	-	-	N^{E*}	-	-	-	-	N^{E*}	-	-	-	N^{E*}	-	N^{E*}	-	NE	-	-	-	-
Labeobarbus sp. 'ngulungu'	-	-	N^{E*}	-	-	-	-	N^{E*}	-	-	-	N^{E*}	-	N^{E*}	-	NE	-	-	-	-
Labeobarbus sp. 'thick lip'	-	+	-	-	-	-	-	N	-	-	-	+	-	N	-	NE	+	+	+	-
Labeobarbus sp. 'nshila'	-	-	-	-	-	-	-	N^{E*}	-	-	-	-	-	N^{E*}	-	NE	-	-	-	-
Labeobarbus upembensis (Banister and Bailey, 1979)	E*	-	-	-	-	-	-	-	-	-	-	E*	-	-	-	DD	-	-	-	-
Labeobarbus wittei (Banister and Poll, 1973)	-	E*	-	-	-	-	-	-	-	-	-	E*	-	-	-	DD	-	-	-	-
Danionidae (4/9)																				
Chelaethiops congicus (Nichols and Griscom, 1917)	-	N	-	+	-	-	-	N	-	N	-	N	+	N	N	LC	+	+	+	-
Chelaethiops elongatus Boulenger, 1899	-	-	-	+	-	-	-	-	N	-	-	-	+	-	N	LC	+	-	+	-
Leptocypris lujae (Boulenger, 1909)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park															IUCN Status	Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area								
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Leptocypris modestus Boulenger, 1900	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Leptocypris weynsii (Boulenger, 1899)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Opsaridium leleupi (Matthes, 1965)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	DD	-	-	-	-
Opsaridium ubangiense (Pellegrin, 1901)	-	+	-	-	-	-	-	N	-	-	-	+	-	N	-	LC	+	+	+	-
Opsaridium zambezense (Peters, 1852)	-	N	-	-	-	-	-	-	N	N	-	N	-	-	N	LC	-	+	+	+
Raiamas marqueti Katemo Manda et al., 2018	-	-	-	-	-	-	-	N *	-	-	-	-	-	N *	-	NE	+	-	-	-
Characiformes																				
Citharinidae (1/3)																				
Citharinus congicus Boulenger, 1897	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Citharinus gibbosus Boulenger, 1899	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Citharinus macrolepis Boulenger, 1899	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Distichodontidae (7/18)																				
Distichodus antonii Schilthuis, 1891	-	N	-	+	-	-	-	-	-	-	-	N	+	-	-	LC	+	+	+	-
Distichodus fasciolatus Boulenger, 1898	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Distichodus lusosso Schilthuis, 1891	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Distichodus maculatus Boulenger, 1898	-	+	-	+	-	-	-	N	-	N	-	+	+	N	N	LC	+	+	+	-
Distichodus polli Abwe et al., 2019	-	N *	-	N *	-	-	-	-	-	-	-	-	N *	-	-	NE	-	-	+	-
Distichodus sexfasciatus Boulenger, 1897	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Eugnathichthys eetveldii Boulenger, 1898	-	+	-	-	-	N	-	-	-	N	-	+	N	-	N	LC	+	-	+	-
Eugnathichthys macroterolepis Boulenger, 1899	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	LC	+	-	+	-
Ichthyborus congolensis (Giltay, 1930)	-	-	-	N	-	N	-	-	-	-	-	-	N	-	-	NE	+	-	-	-
Mesoborus crocodilus Pellegrin, 1900	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Microstomatichthyoborus katangae David and Poll, 1937	-	-	-	+ *	-	-	-	-	-	-	-	-	+ *	-	-	LC	+	-	-	-
Nannocharax brevis Boulenger, 1902	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Nannocharax chochamandai Katemo Manda et al., 2023	-	+	-	-	N *	+	-	-	-	-	-	+	+	-	-	NE	+	-	-	-
Nannocharax elongatus Boulenger, 1900	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	-
Nannocharax hadros Katemo Manda et al., 2021	-	-	-	-	-	-	-	N [E] *	-	-	-	-	-	N [E] *	-	NE	-	-	-	-
Nannocharax sp. 'lovoi'	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	NE	-	-	-	-
Phago boulengeri Schilthuis, 1891	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Phago intermedius Boulenger, 1899	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	-	-
Alestidae (8/18)																				
Alestes liebrechtsii Boulenger, 1898	-	N	-	+	-	-	-	-	-	-	-	N	+	-	-	LC	+	+	+	+
Alestes macrophthalmus Günther, 1867	-	+	-	+	-	-	-	N	-	N	-	+	+	N	N	LC	+	+	+	+
Brachypetersius cadwaladeri (Fowler, 1930)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Brycinus bimaculatus (Boulenger, 1899)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Brycinus grandisquamis (Boulenger, 1899)	-	N	-	-	-	-	-	N	-	N	-	N	-	N	N	LC	+	+	+	-
Brycinus imberi (Peters, 1852)	-	+	-	+	-	+	-	N	-	-	-	+	+	N	-	LC	+	+	+	+
Brycinus lateralis (Boulenger, 1900)	-	N	-	-	-	-	-	-	+	-	-	N	-	-	+	LC	-	+	+	+
Brycinus macrolepidotus Valenciennes, 1850	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	+	+	-
Bryconaethiops boulengeri Pellegrin, 1900	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC	+	+	+	-
Bryconaethiops macrops Günther, 1873	-	N	-	-	-	-	-	-	-	-	-	-	-	-	-	LC	+		-	
Bryconaethiops microstoma Günther, 1873	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC	+	-	+	-
Hydrocynus vittatus Castelnau, 1861	-	+	-	+	-	-	-	N	-	-	-	+	+	N	-	LC	+	+	+	+
Micralestes acutidens (Peters, 1852)	-	+	-	N	-	-	-	N	-	N	-	+	N	N	N	LC	+	+	+	+

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park																Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Micralestes humilis Boulenger, 1899	-	N	-	+	N	+	-	-	-	-	-	N	+	-	-	LC	+	+	+	+
Micralestes lualabae Poll, 1967	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Micralestes stormsi Boulenger, 1902	-	+	-	-	-	-	-	N	N	N	-	+	-	N	N	LC	+	-	+	-
Phenacogrammus aurantiacus (Pellegrin, 1930)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	-
Rhabdalestes rhodesiensis (Ricardo-Bertram, 1943)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	-	+	-	-
Siluriformes																				
Bagridae (1/1)																				
Bagrus ubangensis Boulenger, 1902	-	+	-	-	-	-	-	N	-	-	-	+	-	N	-	LC	+	-	+	-
Clariidae (2/8)																				
Clarias buthupogon Sauvage, 1879	-	+	-	N	-	+	N	N	+	+	-	+	N	N	+	LC	+	+	+	-
Clarias cf. *dumerilii* Steindachner, 1866	-	-	N	-	-	-	-	N	-	-	-	N	-	N	-	LC	+	+	+	+
Clarias cf. *liocephalus* Boulenger, 1898	N	+	-	-	-	-	-	-	-	-	-	N	-	-	-	LC	+	+	+	-
Clarias gariepinus (Burchell, 1822)	-	N	-	+	+	+	-	-	+	+	-	N	+	-	+	LC	+	+	+	+
Clarias ngamensis Castelnau, 1861	-	-	-	-	-	-	-	-	-	N	-	-	-	-	N	LC	-	+	+	+
Claraias stappersii Boulenger, 1915	-	-	-	-	-	-	-	-	N	-	-	-	-	-	N	LC	-	+	+	-
Clarias theodorae Weber, 1897	-	-	-	+	+	-	-	-	+	-	+	-	-	-	+	LC	-	+	+	+
Heterobranchus longifilis Valenciennes, 1840	-	+	-	+	-	-	-	N	-	-	-	+	+	N	-	LC	+	+	+	+
Amphiliidae (5/17)																				
Amphilius cryptobullatus Skelton, 1986	-	N	-	-	-	-	-	-	-	-	N	N	-	-	N	NE	-	+	-	-
Amphilius frieli Thomson and Page, 2015	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	NE	-	+	-	-
Amphilius sp. 'lufira'	-	N	-	-	-	-	-	-	+	+	-	N	-	-	+	NE	-	-	-	-
Amphilius sp. 'kayo_above'	-	-	-	-	-	-	-	N [E] *	-	-	-	-	-	N [E] *	-	NE	-	-	-	-
Amphilius sp. 'kayo_below'	-	-	N [E] *	-	-	-	-	N [E] *	-	-	-	N [E] *	-	N [E] *	-	NE	-	-	-	-
Amphilius sp. 'kalumengongo'	N [E] *	-	-	-	-	-	-	-	-	-	-	N [E] *	-	-	-	NE	-	-	-	-
Amphilius sp. 'mwanza'	-	-	-	-	N [E] *	-	-	-	-	-	-	-	N [E] *	-	-	NE	-	-	-	-
Belonoglanis tenuis Boulenger, 1902	-	+	-	-	N	+	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Congoglanis cf. *alula* (Nichols and Griscom, 1917)	-	-	-	-	-	-	-	-	N	-	-	-	-	-	N	LC	-	-	-	-
Congoglanis sagitta Ferraris, Vari and Skelton, 2011	N	-	-	-	-	-	-	-	+	-	-	N	-	-	+	NE	-	+	+	-
Tetracamphilius notatus (Nichols and Griscom, 1917)	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	-	-	+	-
Zaireichthys brevis (Boulenger, 1915)	-	-	-	-	+	+	-	+	-	-	-	-	+	+	-	LC	+	+	-	-
Zaireichthys rotundiceps (Hilgendorf, 1905)	-	+	-	+	-	-	-	-	+	+	-	+	+	-	+	LC	-	+	-	+
Zaireichthys sp. 'upemba'	-	-	N [E] *	-	-	-	-	N E	-	-	-	N [E] *	-	N E	-	NE	-	-	-	-
Zaireichthtys sp. 'ngulungu'	-	-	N [E] *	-	-	-	-	-	-	-	-	N [E] *	-	-	-	NE	-	-	-	-
Zaireichthtys sp. 'mwanza'	-	-	-	-	N [E] *	-	-	-	-	-	-	-	N [E] *	-	-	NE	-	-	-	-
Zaireichthtys sp. 'dikulwe'	-	-	-	-	-	-	-	-	N [E] *	-	-	-	-	-	N [E] *	NE	-	-	-	-
Malapteruridae (1/3)																				
Malapterurus melanochir Norris, 2002	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Malapterurus microstoma Poll and Gosse, 1969	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Malapterurus monsembeensis Roberts, 2000	-	+	-	-	-	N	-	N	-	-	-	+	N	N	-	NE	+	-	+	-
Mochokidae (4/26)																				
Atopochilus christyi Boulenger, 1920	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	-	-	+	-

Table 1. *Cont.*

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	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Chiloglanis lufirae Poll, 1976	-	E *	-	-	-	-	-	-	-	-	-	E *	-	-	-	DD	-	-	-	-
Chiloglanis microps Matthes, 1965	-	E *	-	-	-	-	-	-	-	-	-	E *	-	-	-	LC	-	-	-	-
Chiloglanis msirii Kashindye et al., 2021	-	-	-	-	N [E] *	N [E]	-	-	-	-	-	-	N [E] *	-	-	NE	+	-	-	-
Chiloglanis pojeri Poll, 1944	-	N	-	-	-	-	-	-	-	-	-	N	-	-	-	LC	+	-	-	-
Chiloglanis sp. 'dikulwe'	-	-	-	-	-	-	-	-	N [E] *	-	-	-	-	-	N [E] *	NE	-	-	-	-
Chiloglanis sp. 'mwanza'	-	-	-	-	N [E] *	N [E]	-	-	-	-	-	-	N [E] *	-	-	NE	-	-	-	-
Chiloglanis sp. 'kalule'	-	-	-	-	-	-	-	N [E] *	-	-	-	-	-	N [E] *	-	NE	-	-	-	-
Chiloglanis sp. 'kalumengongo_1'	N [E] *	-	-	-	-	-	-	-	-	-	-	N [E] *	-	-	-	NE	-	-	-	-
Chiloglanis sp. 'kalumengongo_2'	N [E] *	-	-	-	-	-	-	-	-	-	-	N [E] *	-	-	-	NE	-	-	-	-
Euchilichthys royauxi Boulenger, 1902	-	+	-	-	-	-	-	N	-	N	-	+	-	N	N	LC	+	+	+	-
Synodontis acanthomias Boulenger, 1899	-	+	-	+	-	-	-	-	-	-	-	+	+	-	-	LC	+	-	+	-
Synodontis alberti Schilthuis, 1891	-	N	-	+	-	-	-	-	-	-	-	N	+	-	-	LC	+	-	+	-
Synodontis angelicus Schilthuis, 1891	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	-
Synodontis congicus Poll, 1971	-	N	-	N	-	+	-	-	-	-	-	N	N	-	-	LC	+	-	+	-
Synodontis decorus Boulenger, 1899	-	+	-	N	-	-	-	N	-	N	-	+	N	N	N	LC	+	-	+	-
Synodontis denticulatus Kasongo Ilunga et al., 2019	-	-	-	-	-	-	-	-	N *	-	-	-	-	-	N *	NE	-	-	-	-
Synodontis dorsomaculatus Poll, 1971	-	N	-	+	N	+	-	N	-	N	-	N	+	N	N	EN	+	-	-	-
Synodontis greshoffi Schilthuis, 1891	-	N	-	+	-	+	-	N	-	-	-	N	+	N	-	LC	+	-	+	-
Synodontis lufirae Poll, 1971	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	VU	-	-	-	-
Synodontis notatus Vaillant, 1893	-	-	-	+	-	N	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Synodontis nummifer Boulenger, 1899	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Synodontis pleurops Boulenger, 1897	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Synodontis polystigma Boulenger, 1915	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	-	+	-	-
Synodontis smiti Boulenger, 1902	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Synodontis sp. 'kifita'	-	-	-	N *	-	N *	-	-	-	-	-	-	N *	-	-	LC	-	+	-	-
Claroteidae (3/10)																				
Auchenoglanis occidentalis (Valenciennes, 1840)	-	+	-	+	-	-	-	N	-	-	-	+	+	N	-	LC	+	+	+	-
Chrysichthys congicus (Boulenger, 1899)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	NE	-	-	-	-
Chrysichthys cranchii (Leach, 1818)	-	N	-	+	-	-	-	N	-	-	-	N	+	N	-	LC	+	-	+	-
Chrysichthys delhezi Boulenger, 1899	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	-	-
Chrysichthys longipinnis (Boulenger, 1899)	-	-	-	N	-	-	-	-	-	-	-	-	N	-	-	LC	+	-	+	-
Chrysichthys macropterus Boulenger, 1920	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	DD	-	-	+	-
Chrysichthys sharpii Boulenger, 1901	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC	+	+	-	-
Chrysichthys thonneri Steindachner, 1912	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Parauchenoglanis punctatus (Boulenger, 1902)	-	+	-	-	-	-	-	-	+	-	-	+	-	N	+	LC	-	-	+	-
Parauchenoglanis sp. 'kalule'	-	-	-	-	-	-	-	N E	-	-	-	-	-	N	-	NE	-	-	-	-
Schilbeidae (3/5)																				
Parailia congica Boulenger, 1899	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Pareutropius debauwi (Boulenger, 1900)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	+	-
Pareutropius mandevillei Poll, 1959	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	+	-	-
Schilbe grenfelli (Boulenger, 1900)	-	N	-	-	-	-	-	-	-	N	-	N	-	-	N	LC	+	-	+	-
Schilbe intermedius Rüppell, 1832	-	N	-	+	-	N	-	N	+	N	-	N	+	N	+	LC	+	+	+	+

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park																Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Gobiiformes																				
Eleotridae (1/1)																				
Kribia nana (Boulenger, 1901)	-	-	-	-	N	+	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Synbranchiformes																				
Mastacembelidae (1/3)																				
Mastacembelus congicus Boulenger, 1896	-	+	-	N	N	N	-	N	-	-	-	+	N	N	-	LC	+	+	+	-
Mastacembelus frenatus Boulenger, 1901	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	+	+	+
Mastacembelus sp. 'lufiraensis'	-	N [E] *	-	-	-	-	-	-	+	N	-	N [E] *	-	-	+	NE	-	-	-	-
Anabantiformes																				
Anabantidae (2/4)																				
Ctenopoma multispine Peters, 1844	-	-	-	N	-	N	-	-	-	-	-	-	N	-	-	LC	+	+	+	+
Ctenopoma muriei (Boulenger, 1906)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	-	+	-	-
Microctenopoma intermedium (Pellegrin, 1920)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	-	+	+	+
Microctenopoma ocellifer (Nichols, 1928)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Channidae (1/1)																				
Parachanna obscura (Günther, 1861)	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	-	-	+	-
Carangiformes																				
Latidae (1/1)																				
Lates niloticus (Linnaeus, 1758)	-	N	-	+	-	-	-	-	-	N	-	N	+	-	N	LC	+	-	+	-
Cichliformes																				
Cichlidae (9/16)																				
Coptodon rendalli (Boulenger, 1897)	-	+	-	+	-	N	-	N	+	+	-	+	+	N	+	LC	+	+	+	+
Coptodon zillii (Gervais, 1848)	-	-	-	N	-	-	-	-	-	-	-		N	-	-	LC	+	-	-	-
Lamprologus mocquardi Pellegrin, 1903	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Lamprologus symoensi Poll, 1976	-	* E	-	* E	-	-	-	-	-	-	-	+ *	-	-	-	DD	-	-	-	-
Oreochromis macrochir (Boulenger, 1912)	-	+	-	N	-	-	-	-	+	-	-	+	N	-	+	VU	+	+	+	+
Oreochromis upembae (Thys van den Audenaerde, 1964)	-	N	-	+	-	N	-	-	-	-	-	N	+	-	-	LC	+	-	-	-
Orthochromis kimpala Schedel et al., 2018	-	-	-	-	-	-	-	N [E] *	-	-	-		-	N [E] *	-	NE	-	-	-	-
Orthochromis sp. 'lufira'	-	N	-	-	-	-	-	-	N	-	-	N	-	-	N	NE	+	-	-	-
Orthochromis torrenticola (Thys van den Audenaerde, 1963)	-	+ *	-	-	-	-	-	-	-	+	-	+ *	-	-	+	LC	+	-	-	-
Pseudocrenilabrus nicholsi (Pellegrin, 1928)	-	-	-	N	-	N	N	-	-	-	-	-	N	-	-	LC	+	-	-	-
Pseudocrenilabrus philander (Weber, 1897)	-	+	-	+	-	+	-	-	+	+	-	+	+	-	+	LC	+	+	+	+
Sargochromis sp. 'lufira'	-	-	-	-	-	-	-	-	N	-	-	-	-	-	N	NE	-	-	-	-
Serranochromis macrocephalus (Boulenger, 1899)	-	-	-	-	-	-	-	-	N	-	-	-	-	-	N	LC	+	+	+	+
Tilapia sparrmanii Smith, 1840	-	+	-	+	N	N	-	N	+	+	-	+	+	N	+	LC	+	+	+	+
Tylochromis regani Stiassny, 1989	-	N	-	N	-	+	-	-	-	N	-	N	+	-	N	NT	+	+	-	-
Tylochromis variabilis Stiassny, 1989	-	+	-	N	-	-	-	-	-	-	-	+	N	-	-	LC	+	+	-	-
Cyprinodontiformes																				
Nothobranchiidae (1/1)																				
Nothobranchius brieni Poll, 1938	-	-	-	* E	-	-	-	-	-	-	-	-	* E	-	-	LC	-	-	-	-
Procatopodidae (2/2)																				
Lacustricola lualabaensis (Poll, 1938)	-	-	-	-	-	N *	-	-	-	-	-	-	N *	-	-	LC	-	-	-	-
Micropanchax petnehazyi Nagy and Vreven, 2018	-	-	-	+	-	-	-	-	-	+	-	-	+	-	+	LC	-	+	-	-

Table 1. *Cont.*

Family (No. Genera/Species)	Upemba National Park																Neighbouring Ecoregions			
	Major (Sub) Basins											Management Area				IUCN Status				
	KM	Lu	Ng	KD	Mw	Fu	Ln	KN	Di	Lv	Ka	CZ	AZ	BM	LS		UC	BM	Kas	UZ
Tetraodontiformes																				
Tetraodontidae (1/2)																				
Tetraodon mbu Boulenger, 1899	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	+	-	+	-
Tetraodon miurus Boulenger, 1902	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	LC	-	-	+	-
Lepidosireniformes																				
Protopteridae (1/2)																				
Protopterus aethiopicus Heckel, 1851	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	LC	+	-	-	-
Protopterus annectens (Owen, 1839)	-	-	-	N	N	-	-	-	-	-	-	-	N	-	-	LC	-	+	-	+
Total number of species	10	130	9	113	24	48	5	56	40	49	9	144	135	58	74		149	82	125	43
Number of endemic species	8	15	6	3	6	5	1	13	4	3	2	29	11	12	5					

3.2. Longitudinal Distribution of Fishes in the Park: The Case of the Kalule Nord River

For this study, only the Kalule Nord River was sampled along its entire course. Five sections, separated by important falls, can be distinguished on its main course (Figure 2). A study of the ichthyofauna in these different sections shows an increase in species diversity from up- to downstream (Appendix A in Table A1).

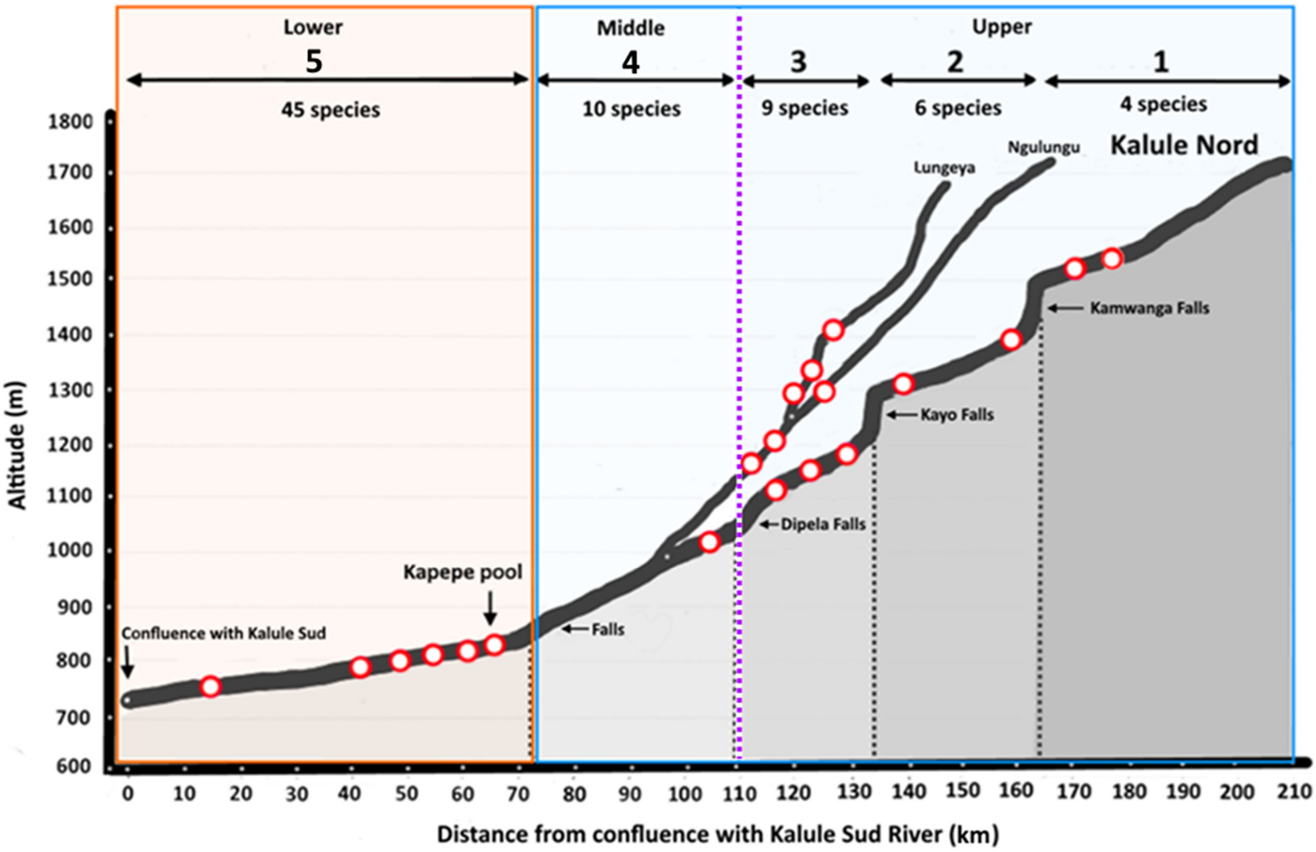

Figure 2. Longitudinal profile, subdivisions, and fish species numbers of the Kalule Nord Basin. Red dots indicate the sampling sites. Waterfalls mark the separation of the five different sections numbered 1 to 5. The blue frame represents the highland zone and the orange frame the lowland zone.

Two relatively distinct communities can be distinguished as a result of discontinuities in the river geomorphology. (i) The highland regions ($\geq$900 m a.s.l.) are characterised by a species-poor fish fauna but a high rate of endemicity. The highland community increases by the successive addition of species from the Upper (1, 2, and 3) to the Middle Kalule Nord. Further, due to the absence of waterfalls on its main course, the Ngulungu River, a right-bank tributary of Kalule Nord, enriches the fauna of the Middle Kalule Nord with high altitude species. (ii) The lowland region (<900 m a.s.l.) is characterised by a fish fauna which is very species-rich, consisting of species with a wider distribution in the Congo Basin. Here, the highland community is replaced by that of the Kamalondo Depression and other tributaries of the Upper Lualaba such as the Lubudi and Lufupa rivers further downstream (Appendix A in Table A1). These two communities are very different and are separated from each other by a small waterfall about 2 m high (name unknown).

3.3. Taxa Unidentified at Species Level

This study is the first for some of the UNP's rivers that involved intensive collection efforts. Therefore, many of the fish collected constitute new distribution records or are difficult to identify, requiring more in-depth studies. In total, 35 (14%) putative new species ('sp.') have been identified. Six taxa have uncertain taxonomic status (cf.) for which additional studies are needed to clarify their status. Only families for which taxonomic issues have been identified within the framework of the present study have been listed and discussed below according to phylogenetic order [28] (see Section 2).

3.3.1. Mormyridae

In the UNP, the family Mormyridae is the second richest fish family exceeded in number of species only by Cyprinidae (Table 1). Unfortunately, it is also the family for which the number of species has long been seriously underestimated probably due to identification problems at both the genus and the species level, as evidenced below.

One *Campylomormyrus* specimen was collected in the Kamalondo Depression at Kadia and seems to be most similar in meristics to *Campylomormyrus tamandua*, originally described from the Niger and known from the Volta, Tchad, Chari, and Congo basins [38,39]. Nevertheless, the Kadia specimen differs from *C. tamandua* in the general shape of the body and some measurements (SM: Mormyridae 1). More specimens are needed to formally describe this new species, temporarily named *Campylomormyrus* sp. 'kadia'.

Two species of the genus *Cyphomyrus* have been reported from the UNP, *Cyphomyrus discorhynchus* and *Cyphomyrus psittacus* (Boulenger, 1897) [11], described from the Lower Zambezi (Mozambique) and the Wagenia Rapids (DR Congo), respectively. However, all specimens of *Cyphomyrus* from the UNP previously attributed to *C. psittacus* were found to differ from the holotype of *C. psittacus* (SM: Mormyridae 2) and to be conspecific with *C. discorhynchus*. Thus, *C. psittacus* was removed from the list of fish species present in the UNP.

All *Gnathonemus* specimens from the UNP have previously been identified as *Gnathonemus petersii* (Günther, 1862) [8,16]. This species was described from 'Old Calabar' at the mouth of the Calabar and Cross rivers in Nigeria [40] and its reported distribution extends from the Niger Delta to all over the Congo Basin [41]. However, a detailed study of the specimens from the UNP indicated that they do not belong to *G. petersii.* Instead, they differ from it by their lower number of lateral line scales, 57–65 (vs. 67), and shorter dorsal fin length, 16.1–19.1% SL (vs. 22.0% SL), but belong to, at least, a single new species for science, here named *G.* sp. 'kamalondo', awaiting formal description.

Heteromormyrus tavernei was originally described from the Kipepe River, a right bank sub-tributary of the Middle Lufira River in the UNP [16]. In addition, within the UNP, *Heteromormyrus* specimens were also found in the Dikulwe River. These specimens are, however, morphologically distinct from *H. tavernei* (SM: Mormyridae 3), the only known species for the Upper Lualaba, and are named *H.* sp. 'dikulwe', awaiting formal description.

A few *Petrocephalus* specimens were collected in the Kamalondo Depression and seem to be similar to *Petrocephalus frieli*, described from the Luapula River Basin and known from the southern part of the Bangweulu-Mweru ecoregion [42]. This similarity is based on their general appearance and colour pattern, which is characterised by a black subdorsal spot below the anterior part of the dorsal fin only. Thus, they are here referred to as *P.* cf. *frieli*, awaiting a more in-depth study of the collected specimens.

3.3.2. Kneriidae

The rivers of the UNP harbour species of the two largest genera of the family Kneriidae, *Kneria* and *Parakneria*. The specimens of these genera have very often been misidentified in the past and species diversity is largely underestimated.

Two species of the genus *Kneria* were known from the UNP [11,16]: *Kneria wittei* Poll, 1944, described from the Lukuga, the outlet of Lake Tanganyika, and *Kneria katangae*, endemic to the Mubale River, a right-bank tributary of the Lower Lufira River in the UNP. However, according to new morphological and genetic data, *K. wittei* is absent from the UNP. Indeed, mtDNA analyses for specimens collected in the rivers from which *K. wittei* had been reported revealed the presence of four different mitochondrial lineages that were named after the corresponding four basins in which they occur, i.e., the Luena, Lusinga

(Middle Lufira), Kalule Nord, and Kalumengongo (SM: Kneriidae 1). These, four lineages are here considered as four new species for science in need of formal description (Table 1). The morphological differences between them, however, are (very) small (SM: Kneriidae 1), hence the need for a more thorough morphological study of these four species and other specimens collected from the park.

Two species of *Parakneria* were known from the UNP [16]: *P. lufirae* and *P. thysi*, described from and endemic to the Lower and the Middle as well as the Lower Lufira Basin, respectively. They are distinguished from each other by the number of lateral line scales, 97–105 for *P. lufirae* (vs. 84–94 for *P. thysi*) [14]. However, there are two groups of morphometrically well-distinct specimens within *P. lufirae*: specimens from the type locality, the Muye River, a right-bank tributary of the Lower Lufira River, and specimens from other right-bank tributaries of the Lower Lufira Basin, here named *P.* sp. 'kilwezi', pending its description as a new species for science (SM: Kneriidae 2).

In addition, a morphological study, supported by an mtDNA approach (COI and Cyt b) of newly collected *Parakneria* specimens, revealed two more distinct new species: *P.* sp. 'fungwe', including specimens from the Fungwe and Mwanza rivers, and *P.* sp. 'kalule' from the Kalule Nord River only (SM: Kneriidae 3).

3.3.3. Cyprinidae

In the UNP, the family Cyprinidae is the species-richest (Table 1) and, together with the Clariidae, one of the most widespread families, found at all sampling sites. The identification of several species has been problematic. Hence more detailed studies were undertaken as presented below.

Three species of the genus *Clypeobarbus* have been reported from the UNP [11,12,16]: *C. congicus*, *C. pleuropholis*, and *C. pseudognathodon* (Boulenger, 1915), the latter originally described from Lake Mweru within the Luapula-Mweru ecoregion [6]. However, a detailed comparison between the UNP specimens from Lake Upemba, previously identified as *C. pseudognathodon*, and other recently collected specimens for the Mwanza and Fungwe rivers within the Upper Lualaba ecoregion [6], revealed the UNP specimens to be morphologically clearly different from *C. pseudognathodon* (SM: Cyprinidae 1). Thus, the *Clypeobarbus* specimens from the UNP, here named *C.* sp. 'mwanza', belong to a new species for science awaiting formal description.

The combination of a morphological and a genetic (COI mtDNA) approach confirmed that specimens of *Enteromius janssensi* from the type locality (Fungwe Basin), and those from the Kalule Nord River are not conspecific [43]. The latter belong to a new species for science, here named *Enteromius* sp. 'ngulungu' (SM: Cyprinidae 2).

In addition, another series of *Enteromius* specimens were collected in the Kalule Nord River. These specimens are morphologically similar to *E. mocoensis* but differ in the size of both the anterior and posterior pairs of barbels (SM: Cyprinidae 3). Pending a more in-depth study, these specimens from Kalule Nord are presently identified as *E.* cf. *mocoensis*.

Another *Enteromius* species has been collected from the Kalumengongo River, a right-bank tributary of the Upper Lualaba. It generally resembles *E. neumayeri* (Fischer, 1884) as originally described [44] from the Nguruman River, Lake Natron Basin in Kenya (Southern Eastern Rift ecoregion), based on its last simple ray being strongly ossified and strongly serrated on its posterior edge, two pairs of well-developed barbels, and a dark grey lateral stripe on the body without black blotches in its course. A comparison with *E. neumayeri* and all its current junior synonyms [*Enteromius carpio* (Pfeffer, 1896), *E. luazomelae* (Lönnberg, 1911), *E. luhondo* (Pappenheim and Boulenger, 1914), *E. nairobiensis* (Boulenger, 1911), *E. percivali* (Boulenger, 1903), *E. portali* (Boulenger, 1906), and *E. serrifer* (Boulenger, 1900)] shows that the specimens from the Kalumengongo River are morphologically clearly distinct (SM: Cyprinidae 4). Thus, the specimens from the Kalumengongo River, temporarily named *E.* sp. 'kalumengongo', were found to belong to a new species for science awaiting formal description.

A series of *Enteromius* specimens were collected from the Luena River, a right-bank tributary of the Upper Lualaba. Based on some colour pattern characteristics (SM: Cyprinidae 5), these specimens do not correspond to any valid species of *Enteromius* and are thus temporarily named *E.* sp. 'luena', awaiting formal description.

Eight valid *Labeobarbus* species are currently known from the UNP [11,16], but recent sampling in the Kalumengongo, some tributaries of the Lufira River (Dikulwe, Luvilombo, and Kafwe), and the Kalule Nord revealed numerous specimens that are difficult to identify due to the high overall morphological similarity although with large morphological variability, particularly in the mouth morphology. *Labeobarbus* exhibits a large variation in mouth phenotypes which range from (i) a typical *Labeobarbus*-mouth, i.e., the rubberlip mouth phenotype with well-developed lips and an often well-developed mental lobe, to (ii) a *Varicorhinus*-mouth, i.e., the chiselmouth phenotype with a highly keratinized outer cutting edge on the anterior edge of the lower jaw, usually poorly developed lips, and without a mental lobe. In between these two extremes, there are numerous (iii) intermediate-mouth phenotypes, that have no lobe, or only a rudimentary mental lobe, and, most often, also are also without a cutting edge [45,46]. An assessment of the species diversity of *Labeobarbus* of the Kalumengongo and Kalule Nord rivers was made using a morphological and genetic (COI/Cytb mtDNA) approach.

For the Kalumengongo, morphological results enabled the identification of three species: *Labeobarbus gestetneri* (intermediate-mouth), *L. upembensis* (*Var.*-mouth), and *L.* sp. 'kalumengongo' (*Lab.*-mouth). Moreover, two groups of intermediate-mouth phenotype specimens were found, one highly similar to *L. upembensis* and the other to *L.* sp. 'kalumengongo'. By contrast, the mitochondrial data recovered only *L. gestetneri* as a separate lineage.

For the Kalule Nord, five species, all new to science, were identified morphologically, but only three distinct mitochondrial lineages could be recognised: (i) *Labeobarbus* sp. 'kapepe' (*Var.*-mouth), (ii) *L.* sp. 'thick lips' (*Lab*.-mouth), and (iii) an assemblage of the three remaining species, *L.* sp. 'ngulungu' (*Var*.-mouth), *L.* sp. 'kayo' (*Lab*.-mouth), and *L.* sp. 'nshila' (intermediate-mouth). The latter lineage also includes two groups of intermediate-mouth phenotype specimens, one highly similar to *L.* sp. 'ngulungu' and the other to *L.* sp. 'kayo'. Pending further integrative studies including nDNA data, we are tempted to conclude that the observed differences in mouth phenotypes between some of the morphotypes are due to intraspecific variation.

Labeobarbus caudovittatus (Boulenger, 1902) was described based on two small specimens from the Ubangi River, the major right-bank tributary of the Middle Congo, at Mobayi-Mbongo (formerly Banzyville) [47]. Later, several specimens from the Lower Lufira Basin were identified as *L. caudovittatus* [16]. However, examination of these specimens indicates that they belong to *Labeobarbus* sp. 'thick lips', a new species under description [48]. Thus, *L. caudovittatus* is considered to be absent from the UNP. *Labeobarbus* sp. 'thick lips' was first identified from the Epulu River Basin, in the Okapi Wildlife Reserve [48]. In addition to the mouth phenotype, *L.* sp. 'thick lips' also differs from *L. caudovittatus* by a higher number of gill rakers on the first gill arch, 19–23 (vs. 14–16), and a higher dorsal fin, 25.6–30.0% SL (vs. 19.8–20.5% SL) [48].

Labeobarbus stappersii (Boulenger, 1915) was originally described from Lake Mweru based only on the holotype [49]. Later, a second specimen was reported from the Kilwezi River, a right-bank tributary of the Lower Lufira Basin [16]. Unfortunately, this specimen, without a collection number, could not be found in the RMCA or the RBINS collections. In addition, regrettably, the Lower Lufira Basin was not further sampled within the framework of the present study due to insecurity issues resulting from the presence of armed rebel groups in the area. However, in the drawing of the lateral view of the fish, provided by Poll [16], poorly developed lips are visible, which suggests the specimen has an intermediate-mouth phenotype with small barbels, corresponding to the mouth phenotype of the holotype of *L. stappersii*. Two species with intermediate-mouth phenotype and small barbels were originally described from the same locality: *Labeobarbus altipinnis* and *L. wittei*.

The specimen from Kilwezi, attributed to *L. stappersii*, has two pairs of small barbels and a weakly ossified, flexible last unbranched dorsal-fin ray [16]. These two characteristics distinguish the Kilwezi specimen from *L. altipinnis*, which has a strong dorsal fin spine, and *L. wittei,* which has only one pair of barbels. Furthermore, the characteristics as provided in the description by Poll [16] of the specimen identified as *L. stappersii* from Kilwezi, distinguish it from *L. iphthimostoma* by the flexible last unbranched dorsal-fin ray and 10 branched dorsal-fin rays (vs. ossified and 9 branched dorsal-fin rays in *L. iphthimostoma*) and from *Labeobarbus* sp. 'thick lip' by 10 branched dorsal-fin rays and the intermediate-mouth phenotype (vs. 9 branched dorsal-fin rays and *Labeobarbus*-mouth phenotype). In addition, the caudal peduncle is clearly longer than it is deep (17.7% SL and 13.9% SL, respectively (140.0 mm SL)) on the illustrated *L. stappersii* specimen from Kilwezi [16], whereas it is about as long as it is deep on the holotype (15.4% SL and 16.3% SL, respectively (202.7 mm SL)). This is most probably not due to allometry as the caudal peduncle depth has been identified as isometric in other well-sampled species of the UNP. Due to these differences, *L. stappersii* is considered to be absent from the Lower Lufira. Thus, the specimen described by Poll [16] is regarded to belong to a new species for science, here named *L.* sp. 'lower_lufira'.

Labeobarbus trachypterus (Boulenger, 1915) was described based on the holotype from Lake Mweru [49]. Later, several specimens from the Lufira River [16] and the Kalumengongo River [11] in the UNP were also attributed to *L. trachypterus*. However, within the present study, it turned out that *L. trachypterus*, as currently conceptualised, represents a species complex. For instance, the specimens from the Kalumengongo River belong to two species: *Labeobarbus gestetneri* and *L.* sp. 'kalumengongo'. This taxonomic confusion is probably due to the small size of the specimens (maximum size: 161 mm SL) and the absence of a well-developed mental lobe. Similarly, specimens from the Lufira River that were most similar to *L. trachypterus* were found to be morphologically clearly different (SM: Cyprinidae 6). Thus, *L. trachypterus* is considered absent from the UNP. The specimens from the Lufira River are considered to belong to a new species for science, here named *L.* sp. 'middle_lufira', and also awaiting formal description.

3.3.4. Distichodontidae

A new *Nannocharax* species for science has been collected in the Lovoi River [50]. This new species, here named *N.* sp. 'lovoi', is most similar to *N. schoutedeni* Poll, 1939, by the yellow colouration with 9 to 14 oblique brownish transverse stripes, irregular and sometimes fused on the flanks, and a longitudinal black stripe on the snout. It can, however, morphologically clearly be distinguished from the latter (SM: Distichodontidae 1).

3.3.5. Clariidae

The family Clariidae is, together with the Cyprinidae, one of the most widespread families in the UNP, and found in all the sampled waterbodies. A revision of the paraphyletic genus *Clarias* [51] was undertaken at the pan-African level [20] and for the Lower Congo only [52]. However, identification problems persist mainly in the subgenus *Brevicephaloides*, especially between *Clarias dumerilii* described from Angola and reported from the Middle and the Upper Congo Basin [20], and *C. liocephalus*, described from the Lake Tanganyika Basin and widespread within central, eastern, and southern Africa [20]. Our study resulted in three diagnostic characteristics to differentiate the two species: (i) longer maxillary barbels in *C. dumerilii*, 93.3–135.5% HL (vs. 71.4–107.4% HL in *C. liocephalus*); (ii) a shallower head in *C. dumerilii*, 8.3–9.9% SL (vs. 9.4–12.3% SL); and (iii) longer pelvic fins in *C. dumerilii*, 7.4–10.1% SL (vs. 5.8–7.4% SL).

In the UNP, two different populations of *Clarias* were collected on the plateaux. The Kibara Plateau population was collected from the Lusinga and Kalumengongo rivers and was identified as *C.* cf. *liocephalus*. The other population was collected from the Biano Plateau in the Kalule Nord Basin and was identified as *C.* cf. *dumerilii*. Two characteristics distinguish these two taxa: (i) shorter mandibular barbels in *C.* cf. *liocephalus*, 81.0–94.8%

HL (vs. 78.8–162.5% HL in *C.* cf. *dumerilii*); and (ii) a longer head in *C.* cf. *liocephalus*, 22.7–23.3% SL (vs. 20.3–22.8% SL) (partial overlap due to negative allometry).

3.3.6. Amphiliidae

Amphilius is the most species-rich of the amphiliid genera occurring in the UNP (Table 1). Two species of *Amphilius* have been previously reported from the UNP [16]: *Amphilius grandis* Boulenger, 1905 and *Amphilius kivuensis* Pellegrin, 1933.

Amphilius grandis was originally described from the Chania River, a left-bank tributary of the coastal Tana Basin in Kenya [53], and further reported from several rivers in the UNP, including the Kalule Nord, and the Lower and Middle Lufira Basin [16], and was long considered a junior synonym of *A. uranoscopus* (Pfeffer, 1889) [54]. *Amphilius grandis* was revalidated and its distribution was restricted to two coastal basins in Kenya, the Ewaso Ngiro and the Tana [55]. Alfred W. Thomson re-identified the specimens preserved at the RMCA in 2010 and attributed them to two species: *Amphilius cryptobullatus* Skelton, 1986 and *A.* sp. 'lufira'. Mitochondrial DNA results for specimens from the Kalule Nord River and the Middle Lufira Basin, from which *A. grandis* has also been reported in the past [16], revealed the presence of three lineages supported by colour pattern differences representing three new species for science (SM: Amphiliidae 1).

Amphilius kivuensis has been described from Kitembo, west of Lake Kivu [56], and has previously also been reported from the UNP based on a single specimen from the Pelenge River, a right-bank tributary of the Lower Lufira. During our study, the Pelenge River was not accessible due to the presence of armed groups. An examination of the specimen (RMCA P-79001), however, confirmed the doubts previously expressed [16,57] as to its correct identification. Indeed, this specimen does not correspond to *A. kivuensis* based on the number of branched dorsal-fin rays, five (vs. six in *A. kivuensis*), and the emarginated caudal fin shape (vs. forked caudal fin shape in *A. kivuensis*). Instead, it is considered here as a new species for science, named *A.* sp. 'lufira'. Additional specimens will be instrumental to enable its formal description.

A series of *Congoglanis* specimens were collected from the Kalule Nord River. These specimens are morphologically similar to *Congoglanis alula*, originally described from Kisangani on the upper stretch of the Middle Congo Basin [58]; this is due to having shorter maxillary barbels, not extending to vertical through the anterior margin of the orbit, posterior rays of the adpressed anal fin extending to vertical through the posterior limit of the adipose fin, and anal fin origin situated approximately at the posterior tip of the adpressed pelvic fin [58]. However, the sizes of the pectoral (20–31% SL vs. 28–29% SL in *C. alula*) and pelvic fins (23–24% SL vs. 24–28% SL in *C. alula*) differ slightly. Pending a more in-depth study, these specimens from Kalule Nord are presently identified as *Congoglanis* cf. *alula*.

The genus *Zaireichthys* was known from three species from the rivers draining the UNP, i.e., *Zaireichthys brevis* (RMCA collection), *Zaireichthys heterurus* Roberts, 2003, and *Zaireichthys rotundiceps* [59]. However, four new species are recorded based on colour pattern, adipose fin size, and caudal fin shape (SM: Amphiliidae 2).

3.3.7. Mochokidae

Four *Chiloglanis* species are currently known from the UNP, including one, *Chiloglanis msirii* Kashindye et al., 2021, recently described from the Fungwe and Mwanza rivers [34]. In addition, five more new *Chiloglanis* species for science have been found (Table 1) based on their colour pattern, the number and size of the caudal fin lobes, and the size of the barbels. One of these, here named *C.* sp. 'mwanza', and only known from the Mwanza River, is currently under description and can well be distinguished morphologically from all its congeners from the Congo Basin s.l. (SM: Mochokidae 1).

We collected *Synodontis* specimens with a uniform black colouration from the Kamalondo Depression. These specimens resemble both *Synodontis unicolor* Boulenger 1915, known from the Luapula-Mweru Basin, and *S. greshoffi* Schilthuis 1891, widely distributed in the Congo Basin [18]. A morphological comparison of the specimens from the Kamalondo Depression with these two species indicates that the specimens from the Kamalondo Depression do not belong to any of them, and are therefore new to science. As such, they are here named *S.* sp. 'kifita' (SM: Mochokidae 2).

3.3.8. Claroteidae

Two populations of *Parauchenoglanis* have been collected. The first, collected from the Dikulwe River, was identified as *P. punctatus*. The second, collected from the Kalule Nord River, is similar to *P. ngamensis* (Boulenger, 1911), because of its broadly triangular humeral process generally with a slightly serrated upper edge, and a spotted pattern on the body. However, these specimens differ from the holotype of *P. ngamensis* in several morphometric measurements (SM: Claroteidae 1). Therefore, the Kalule Nord specimens are considered to belong to a new species for science, here named *P.* sp. 'kalule'.

3.3.9. Mastacembelidae

Mastacembelidae, with two species (*Mastacembelus congicus* and *M. frenatus*) [11,16], is one of the species-poorest families in the UNP (Table 1). However, a third species, *M.* sp. 'lufiraensis', has been identified based on some morphological evidence [60] (SM: Mastacembelidae 1).

3.3.10. Cichlidae

The family Cichlidae is one of the species-richest in the UNP (Table 1). The family also dominates the fishery catches in the Kamalondo Depression (B.K.M., pers. obs. 2015–2021). Two species of the genus *Orthochromis* have been reported in the UNP: *Orthochromis kimpala*, described from and endemic to Kalule Nord [61], and *Orthochromis torrenticola*, described from the Middle Lufira River, i.e., just above the Kyubo Falls [13], but also reported from the Lower Lufira, i.e., below the Kyubo Falls [16]. However, a detailed study of the meristics of the populations from the Lower Lufira revealed them to be different from those from the Middle Lufira, identified as *O. torrenticola,* and thus representing a new species for science, here temporarily identified as *O.* sp. 'lufira' (SM: Cichlidae 1).

Several specimens of *Sargochromis* were collected from the Dikulwe River, a left-bank tributary of the Middle Lufira River. These specimens seem to be similar to *Sargochromis mellandi* (Boulenger, 1905), originally described from Lake Bangweulu [62] and currently known from the Upper Lualaba [16], and which is thus the only *Sargochromis* species known from the region. However, the specimens from the Dikulwe River are morphologically distinct from *S. mellandi* and thus considered a new species for science, here temporarily named *S.* sp. 'lufira' (SM: Cichlidae 2). Additional data from radiographs and genetics are needed to complete the formal description of this new species.

4. Discussion

4.1. Contribution to the Ichthyological Knowledge of the UNP

The UNP has long been considered the best-explored area of the Upper Lualaba [63,64]. This study shows, nevertheless, that its species richness has long been underestimated. An examination of the published data and collections from the UNP housed in natural history museums illustrates that our knowledge of the ichthyofauna of the UNP has gone through three major phases. The first phase was between 1930 and 1970, when several checklists were published by Max Poll [9,10]. In the same period, new species were also described [14,65]. However, the total number of known species from the park during this period did not reach 100. The second phase was from 1971 to 2010, when several collections from the expeditions of Gaston F. de Witte (1947–1949) and the British Zaire River Expedition (1976) made by Keith E. Banister and Roland G. Bailey were studied. This resulted in the description of new species [11], taxonomic revisions such as the one on *Synodontis* [18], and species lists of the UNP [11,16]. These publications have significantly increased the number of known fish species to approximately 160. The most recent phase started with this study and brings the number of known native species for the UNP to 249 and 1 introduced species, following intensive exploration of rivers that had not yet or only poorly been explored (see Figure 1).

Moreover, the results of the present study consolidate the status of the UNP as a hotspot of fish biodiversity in the Congo Basin s.l. [66]. The current diversity of the UNP represents 19% of the total fish diversity of the Congo Basin s.l., which, with nearly 1300 valid species [28,67], is the highest on the continent. The Upper Lualaba ecoregion [6] includes 311 species, of which about 80% are found in the UNP. All the genera reported in the Upper Lualaba ecoregion are present in the UNP except for *Coptostomabarbus* David and Poll, 1937, which only occurs further upstream on the Upper Lualaba River, above the Nzilo Dam (approximately 10°29′ S, 25°27′ E). The rugged relief allows for the isolation of some river sections upstream of the falls (Figure 1) and the, at least partially, resulting habitat diversity provides favourable conditions for the occurrence of a diverse ichthyofauna in the UNP. In addition, earlier contacts between the Upper Lualaba and other neighbouring river basins [68,69] may have enriched its species diversity as illustrated for other parts of the Upper Congo Basin, such as the Luongo River [70] and the Luapula River [71] (see below).

4.2. The Endemic Fishes of the UNP

Prior to this study, 15 endemic fish species were known from the UNP [11,16]. However, three species have to be removed from this list. One is *Campylomormyrus lualabaensis*, which is currently a junior synonym of *C. rhynchophorus* [72]. This synonymisation widens the distribution area of this species beyond the borders of the UNP. Furthermore, *Enteromius janssensi* and *Synodontis dorsomaculatus* are also no longer considered endemic to the UNP as they were both also collected from the Lubudi River, a left-bank tributary of the Upper Lualaba, outside the UNP. In addition, during this study, 33 new endemic species for science were found, resulting in a total of 45 species endemic to the UNP.

The endemicity level in the UNP is higher on the plateaus (nearly 80%) than in the Kamalondo Depression (only 1%), probably due to (hydro)geographic isolation. Of the 19 species known from the plateaux, only 3 are not endemic. These are *Enteromius neefi*, which is known from the Upper Lualaba, Limpopo, and Upper Zambezi [73], and *Clarias dumerilii* and *C. liocephalus* which are both known from large parts of the Congo Basin, including the Upper Congo [20,52]. During our study, the Kalumengongo and Lusinga rivers on the Kibara Plateau and the Kalule Nord River on the Biano Plateau were sampled. Considering the high rate of endemicity in these rivers, it is expected that several other endemic species new to science remain to be discovered in the other rivers of these plateaux as well.

The Kamalondo Depression is part of a larger and interconnected system where (hydro)geographic barriers that would hinder fish dispersal are largely absent. Only two valid species are endemic to the Kamalondo Depression, *Lacustricola lualabaensis* and *Nothobranchius brieni*. The latter is an annual species living in temporary pools and marshes near Bukama City. In addition, one of the new *Gnathonemus* species currently under description, *G.* sp. 'kamalondo', is also endemic to the Kamalondo Depression.

4.3. Introduced Species

The UNP is one of the few areas in the Congo Basin where there are very few introduced species. There seem to be two reasons for this. (i) There are practically no fish farms in the Kamalondo Depression. Furthermore, few attempts to develop fish farming have been made with local species. However, the Belgian Technical Cooperation, through its PRODEPAAK project (2008–2013), has tried to develop fish farming with Nile Tilapia (*Oreochromis niloticus* (Linnaeus, 1758)) on the periphery of the UNP in the Kamalondo Depression. This attempt was not very successful, and this species was not collected during this study. (ii) In the Katanga Province, biological control of malaria using fish was favoured especially during the colonial period (1908–1960). For example, Poeciliidae were introduced in many cities to control mosquitoes (malaria vectors) [74]. Nevertheless, no biological control has been carried out in the UNP, due to the fact that the authorities, at the time, favoured the spraying of insecticides [75].

The only introduced species in the UNP collected during this study is *Heterotis niloticus*. The natural distribution of this species covers all the major basins of the Nilo-Sudanese ichthyofaunal province [76]. Its introduction in the Congo Basin is probably accidental as it escaped from fishponds in the Central African Republic in 1963 [77] and the Republic of the Congo in 1966 [78]. The first catch reports in the Congo Basin are from Pool Malebo in 1965 [79] and Lake Tumba in 1982 [80]. Locally, the species took the name '*Congo ya sika*' which means 'New Congo' and refers to the fact that the species has only recently appeared in the basin. *Heterotis niloticus* is well established in the Middle and Lower Congo but had not been reported in the Upper Congo. This led to speculation that *H. niloticus* was not able to cross the Wagenia or Boyoma Rapids near Kisangani [76]. However, according to the local fishermen, *H. niloticus* already appeared in Lake Upemba around 1980. Its commercialization began around 1997 following the heavy rains and flooding and has since become one of the most captured species in the Kamalondo Depression. Its adaptation to this region is probably linked to the presence of abundant aquatic vegetation, which is essential nesting material [80].

While the dispersal of *H. niloticus* into the Kamalondo Depression has been an economic success, as it has increased the fishers' incomes, its impact on the fish biodiversity remains undocumented, yet controversial. The species has generally been considered beneficial for fisheries where it has been introduced [81]. However, in Ogowe Basin in Gabon, where the species has been introduced as well, an increase in catches of *H. niloticus* coincided with a decrease in local cichlid species. This is due to food competition and the occupation of the habitat previously occupied by the local fish species [82]. A similar study should be carried out in the Kamalondo Depression to determine the impact of *H. niloticus* on native species such as the cichlid *Oreochromis upembae*, which is the most important species in local fisheries.

4.4. Longitudinal Patterns in Species Composition

In riverine systems, patterns of fish diversity show changes along the longitudinal profile. This pattern consists of changes in species richness, abundance, and diversity associated with changes in environmental gradients spanning from the headwaters to the river mouth. These observations are consistent with many previous works in tropical regions [70,83,84], and are explained by an increase in the size of the river, the heterogeneity of available habitats, and a decrease in environmental fluctuations from up- to downstream [85,86]. There are two relatively distinct fish communities along the longitudinal gradient in the UNP, including highland and lowland fish species. These two communities are separated by falls (see Figure A2). The role of falls and rapids as barriers to the dispersal of fish and the isolation of upstream fish leading to their high endemicity, has also been noted in the Luanza River Basin (a left-bank sub-tributary of the Middle Luapula River in the Upper Congo Basin). The Kundelungu Plateau (1310–1690 m a.s.l.) (see Figure 1) and the mountain buttress (995–1310 m a.s.l.) are colonised by a poor ichthyofauna consisting of torrenticolous species [87]. The number of species increases considerably in the lowland area (975–995 m a.s.l.). However, there is a replacement of this highland ichthyofauna by that of the lowlands, of which the latter, for the Kalule Nord at least, is richer and more abundant, with nearly 45 species (Figure 2). This species zonation is, indeed, attributed to the presence of numerous physical barriers (falls and rapids) along the river's course [88].

However, the presence of waterfalls and rapids above 900 m a.s.l. in the Kalule Nord Basin did not allow for the development of distinct faunas in between all the different elevation sections, i.e., in between the Middle section and the three sections identified within the Upper Kalula Nord (Figure 2). This may be due to the short distances between the falls (<10 km each) and the relative homogeneity of the habitats allowing fish to colonise all sections. In addition, for the Fouta Dialon (Guinea; Upper Guinea ichthyofaunal province), Daget [87] had already drawn attention to the probability of species from upstream being carried downstream of the falls without nevertheless succeeding in maintaining themselves there and thus establishing a downstream population. He justified this by either the presence of predators that can access the foot of the falls without crossing them or by competition from better-adapted vicarious forms downstream. We believe that the absence of predators above 900 m a.s.l. in the Kalule Nord Basin is one of the reasons that could explain this continuity of species from up- to downstream in the Upper and the Middle Kalule Nord. On the other hand, the presence of large predators in the lower reaches of the Kalule Nord, Lufira, and Kalumengongo rivers would be one of the reasons why the lower reaches are not colonised by highland species. Large predators include *Hydrocynus vittatus*, *Heterobranchus longifilis*, *Lates niloticus*, *Malapterurus monsembeensis*, and *Polypterus ornatipinnis*.

4.5. Ichthyofaunal Affinities with the Neighbouring Ecoregions

The distribution and composition of freshwater ichthyofaunas can shed light on their origins and relationships, through similarities between the fish fauna of certain ichthyofaunal or (hydro)geographical areas [89]. The first scientists [11,68] who analysed the ichthyofauna of the UNP differentiated between (i) endemic species, (ii) ubiquitous Congolese species, (iii) Zambezian species, and (iv) Nilotic species. The hypothesis of the presence of Nilotic species in the UNP has since been refuted [90].

Table A2 summarises the similarities of the fish of UNP with those neighbouring the Upper Lualaba ecoregion (Figure A3). First, it is observed that nearly 80% of the total fish fauna of the Upper Lualaba ecoregion is present in the UNP. However, this high value is mainly due to the lack of extensive sampling in the other parts of Upper Lualaba, such as the Lualaba upstream of Bukama City and the Upper Lufira River, Lufupa River, Musonoi River, Lubudi River, Kalule Sud River, etc. It is therefore most likely that the overall diversity of the fish fauna of the Upper Lualaba outside the UNP is largely underestimated.

Two major phenomena have been put forward to explain such ichthyofaunal similarities between (African) river basins [91]: (i) past/present (seasonal) connections across basins, which often demand active dispersal beyond the barrier, e.g., possible during high water levels in the rainy season [92,93]; and (ii) river captures [94,95], most likely a rather common phenomenon of the past, although it did not always leave identifiable traces, and which is a passive way to infuse a neighbouring basin with a set of new ichthyofaunal elements, i.e., species. As such, the role of both phenomena is not always easily discerned and although summarily documented for some parts of the Congo Basin, such as the Dja and Kasai [35,96], has remained largely un(der)reported for others, e.g., the Upper Lualaba [see 91]. On the contrary, falls have been identified as barriers to dispersal, at least to upstream migration for some fish species [91,92], thus explaining important ichthyofaunal differentiation within what is actually a single basin.

Further, a comparison of fish species in the UNP with those in neighbouring ecoregions indicates that 17 species occur in both the UNP and all neighbouring ecoregions. However, at least in some cases, these widespread species seem to represent species complexes that will require further taxonomic review. These species include *Cyphomyrus discorhynchus*, *Enteromius lineomaculatus*, *Enteromius miolepis*, *Labeo annectens*, *Clarias gariepinus*, *Schilbe intermedius*, *Ctenopoma multispine*, *Tilapia sparrmanii*, etc. (see Table 1).

In more detail, nearly 149 (60%) of the fish species reported to occur in the UNP are also present in the Upper Congo ecoregion [sensu 6]. These are the species found only in the main course of the Congo River (Table 1). This relatively high affinity seems to result from the absence of major physical and ecological barriers between the upper stretch of Upper Congo, i.e., above the Gates of Hell Rapids ("Portes de l'Enfer"), and the Upper Lualaba, in particular the Kamalondo Depression, thus allowing fish migration between parts of these two ecoregions. This might well be evidenced by, for instance, the presence of *Heterotis niloticus* in the Upper Lualaba as a result of recent upstream dispersal, although local introduction cannot be excluded. For a long time, the Gates of Hell were considered a physical barrier between the Upper Lualaba and Upper Congo ecoregions [11,69,76].

However, an analysis of the fish fauna of these two ecoregions, based on the rather limited data available at present, seems to indicate that the fish species occurring in the main course of the Congo River are the same up- and downstream of the Gates of Hell. The main difference between these two ecoregions lies in the fish fauna of the Congo River tributaries. In addition, *Chiloglanis msirii* [34] and *Nannocharax chochamandai* [50] are reported from the UNP (Upper Lualaba) and the Lukuga River basin, the outlet of Lake Tanganyika (Upper Congo), reflecting the interchange between these two ecoregions. Finally, a Cytb mtDNA genetic study between different populations of *Clarias gariepinus* from the Congo Basin and its surrounding basins revealed that the population of the Kamalondo Depression (UNP, Upper Lualaba), and those of Kisangani (Upper Congo) and Kinshasa (Pool Malebo) have a high affinity [97], thus providing the phylogenetic evidence of fish connectivity between these neighbouring ecoregions within the Congo Basin. Nevertheless, the distribution of fish species in common between the UNP and the Upper Congo is limited to the Kamalondo Depression and the lower part of its main tributaries. It is observed that families such as Citharinidae, Clupeidae, Eleotridae, Latidae, Malapteruridae, etc., do not cross physical barriers such as the Kyubo Falls delimiting the Lower from the Middle Lufira River and the rapids on the Lualaba upstream of Bukama. This confirms the first observations [16,69,90] on the existence of a fauna with Congolese affinity in the Kamalondo Depression and a fauna with Zambezi affinity on the plateaux (see below).

Similarly, 125 fish species present in the UNP (50%) are also present in the Kasai ecoregion. This similarity can be explained by the absence of real physical barriers, such as major falls, and the possibility of direct exchange between the upper reaches of the tributaries of the Upper Lualaba and the Kasai on the Kamina Plateau (1120 m a.s.l.). On this plateau, three major tributaries (Lovoi (a left-bank tributary of the Upper Lualaba in the KD), Luembe (a right-bank tributary of the Kasai/Middle Congo), and Lomami (a left-bank tributary of the upper stretch of the Middle Congo)), have their sources within a radius of less than about 10 km diameter in a flat and marshy area, thus most likely enabling ichthyofaunal exchanges between them to the present day. Previous connections between Upper Lualaba and Kasai via the Kando River, a right-bank tributary of the Upper Lualaba, have been highlighted by phylogenetic and phylogeographic studies of *Clarias gariepinus* [97]. However, details as to the nature of the connectivity are lacking at present as it might be solely due to the land-walking capacity of *C. gariepienus* [73], and/or seasonal connections during high water or even the capture of headwater streams in either direction. Nevertheless, the latter might further explain the important similarities between the ichthyofauna of these two ecoregions.

However, only 82 species of the UNP (33%) are present in the Bangweulu-Mweru ecoregion. This number of shared species is the lowest of all shared numbers with the other Congo neighbouring ecoregions. This could be explained by the presence of falls on the Luvua River in the vicinity of Kalumba that serve, at present, to isolate the Bangweulu-Mweru and (Upper) Lualaba fish faunas. The similarity between the faunas of these two ecoregions can be explained by a former connection between the Lufira and the Luapula rivers [69,77,92,94]. It is now accepted that the Luapula River (Bangweulu-Mweru), with a partially inversed flow, was connected to the Lufira River (Upper Lualaba), via the Palaeo-Kafila River, during the late Pliocene (~2.6 Ma). Later on, at the beginning of the early Pleistocene (~1.8 Ma) [69,95,98], it was separated from it and partially inversed its course, probably due to drought during this period [94].

Finally, there have also been several captures of former tributaries of, at present, the Middle Zambezi by the Upper Congo. This is true, in particular, for the Palaeo-Chambezi, with the Chambeshi becoming part of the Upper Congo and the Kafue remaining part of the Middle Zambezi [69,92–95] that could be at the origin of the strong ichthyofaunal similarity in the headwater contact zone between these two basins. This is supported by genetic evidence. Cases in point that can be cited here are the distribution and phylogeny of *C. gariepinus* [99], the monogenic parasites of Clariidae [100], and the gill parasite fauna of Cichlidae [101]. Species such as *Clarias theodorae* Weber, 1897, *Coptodon rendalli*

(Boulenger, 1897), *Ctenopoma muriei* (Boulenger, 1906), *Ctenopoma multispine*, and *Tilapia sparrmanii* can still actively move between the Kamafwafwa River (Upper Lualaba) and the Kanyita River (Upper Zambezi) during the flood period through the swamp area connecting both [69,92,93], thus further explaining the similarity between fish species in these ecoregions.

4.6. Threats and the Need for More Efficient Protection of the Ichthyofauna of the UNP

Currently, there is no national policy for the protection of aquatic biodiversity in the DR Congo. As a result, fish in the UNP are exposed to all kinds of anthropogenic threats (see examples in Figure 3), which are briefly presented below. During the spawning season, some species of the genera *Clarias* and *Labeo* migrate from the Upper Lualaba main river to the lakes of the Kamalondo Depression, hence becoming an easy fisheries' target when passing the man-made channels (Figure 3a,b) that connect the Upper Lualaba and the lakes. Traditional authorities have long taken this spawning period into account when prohibiting fishing from December to March [101]. However, with the increase in the number of (allochthonous) fishermen, this old ban on fishing in flood periods has fallen into disuse, which is one of the reasons for the depletion of the fish populations. To protect the fish fauna, the governors of the various provinces occupied by the UNP sign an annual decree closing the fishery for a period of three months, from December to the end of February. This period corresponds to the main rainy season. Unfortunately, this closing period is rarely respected.

Figure 3. Illustrations of bad practices related to fisheries and agriculture, the latter also impacting river ecosystem health. (**a**) Channel linking the Upper Lualaba and Lake Mulenda in the Kamalondo Depression (3 September 2015). (**b**) Cutting grass to facilitate seining, Lake Lukanga (10 September 2015). (**c**) Fishing dam on the Fungwe River, Kebange Village (21 August 2015). (**d**) Transport of ichthyotoxic fruits (*Amblygonocarpus andongensis*, Fabaceae) for fishing in the Mwanza River, Kabweyi Village (20 August 2016). (**e**) Transport of a seine made of mosquito nets in Lake Upemba, Misebo Village (13 October 2017). (**f**) A dry stretch of the Luvilombo River due to upstream water diversion for irrigating bean fields (25 July 2019).

Shallow rivers (<1 m), such as the Mwanza and Fungwe rivers, are mainly exploited by women and children, through subsistence fisheries. The most common fishing practice is damming the river with stones or with reeds and sticks (Figure 3c), leaving some openings where fykes are placed. Subsequently, *Amblygonocarpus andongensis* (Figure 3d) is used for its ichthyotoxin effect in these artificial pools. Although widely practised on a small scale and on a very regular or even daily basis, fishing with ichthyotoxins is forbidden by law in the DR Congo, except for scientific research (see Congo fishing rights 103/Agri. of 4 October 1937, art. 30).

The use of mosquito nets (long-lasting insecticide-treated nets, LLINs) as fishing gear (Figure 3e) causes habitat destruction and threatens fish stocks by catching large quantities of immature individuals, thus possibly compromising the reproductive capacity of certain species due to a lack of mature fish (B.K.M., pers. obs. 2015–2020). Furthermore, the LLINs are impregnated with lambda-cyhalothrin ($C_{23}H_{19}C_lF_3NO_3$) which, according to the EC Directive/2001/58, is highly toxic to plankton, the basis for the food web of the lake, but also has a high capacity for bioaccumulation in the tissues of aquatic organisms [102]. Both these issues pose a threat to aquatic wildlife in general.

Another threat that tends to become more widespread in the buffer zone of the UNP is the diversion of river water for agricultural purposes. The most flagrant case is that of the Luvilombo River (Figure 3f). Unfortunately, at the end of the dry season, this river remained completely dry, threatening the survival of nearly 45 species identified so far, including 2 endemic species.

The industrial exploitation of copper and cobalt in the Katangese copper belt area, upstream of the UNP, remains one of the greatest threats to the ichthyofauna of the UNP. This exploitation generates pollution as the effluents are discharged into the rivers without prior treatment [103–105]. The hydroelectric dam lakes, Nzilo and Nseke on the Upper Lualaba River, and Tshangalele and Koni on the Upper Lufira River serve as disposal and decanter basins. In 2005, when the floodgates of the Nseke Dam (Congo River) were opened, muddy waters, heavily contaminated with trace metal elements, killed fish in the Kamalondo Depression, the annex zone of the UNP. Unfortunately, this type of operation is likely to recur in the coming years/decades due to the high demand for electricity generated by hydroelectric dams with the recovery of the mining sector since 2006. Indeed, a more active mining sector also results in more significant siltation and deposition of sediments in these artificial lakes, which resulted in their filling up. Fully opening the floodgates of these dams is an easy way to get rid of at least part of those sediments. However, considering their heavily contaminated load, this, unfortunately, has devasting effects on the downstream aquatic fauna, etc.

Strategies for the preservation/conservation of the ichthyofauna of the UNP should be developed according to whether the hydrographic elements are situated in the core zone, i.e., the highland plateau, or the buffer zone, i.e., the Kamalondo Depression. Indeed, the fish fauna from the highland plateaux is much less species-rich and fishes are less abundant than in the Kamalondo Depression; however, the endemicity level is very high (nearly 80%). In addition, the steep slope of the terrain prevents the upstream dispersal of fishes from the Kamalondo Depression to both the highland plateaux. Thus, the establishment of artisanal miners in these regions, resulting in the establishment of several illegal villages near the rivers, threatens this largely unique ichthyofauna. Therefore, additional protection measures must be put in place quickly to protect these areas against mining exploitation.

For the annex and buffer zones, where subsistence fishing is permitted, the strategy should be oriented towards a dynamic partnership, a co-management, between local fishermen, traditional authorities, and the government. Indeed, co-management implies a sharing of responsibilities, forces, and competences in the sustainable management of these natural riches between public authorities and the users of those riches, with in particular the artisanal fishermen as the main actors. This co-management is justified in order to avoid the exorbitant resources (human, financial, and logistical) that the state, as a single authority, has to deploy to be able to regulate, control, and monitor effectively all relevant management and protection/conservation measures [106]—financial resources that the state does not possess. It is hoped that this updated checklist of the fishes of the UNP further stresses the urgent need for more efficient protection of its ichthyofauna, which is hereby confirmed as a protected area with exceptional fish biodiversity, i.e., a confirmed hotspot, for the Congo Basin as well as for the African continent as a whole.

5. Conclusions

The UNP has long been considered one of the best-explored regions of the Congo Basin with 116 fish species reported [14]. The present study, by reporting 247 native species of fish, confirms that the species diversity of the UNP was still seriously underestimated. Moreover, the results of the present study consolidate the UNP's status as a Key Biodiversity Area and one of the highest priority freshwater conservation areas of the Congo Basin [67]. Although the park provides some protection for the fish species living within its borders by prohibiting human access to the core zone, the annex and buffer zones, instead, are subject to strong anthropogenic pressures. As such, it is hoped that this study has sufficiently underscored the uniqueness and richness of the ichthyofauna of the UNP and the urgent need for its better preservation and conservation.

Author Contributions: B.K.M. and E.J.W.M.N.V. were responsible for the fieldwork, fish identification, study design, and writing the first and subsequent revised versions of the manuscript. J.S. supervised the research, as the promotor of B.K.M.'s PhD, and critically revised the final version of the manuscript. A.C.M. participated in the fish collection and was responsible for the identification of *Enteromius* specimens from Kalule Nord River. E.A. was responsible for the identification of Amphiliidae. C.M.M. was responsible for the identification of Mormyridae. M.K.I.K. was responsible for the identification of Clariidae and *Synodontis* (Mochokidae). P.K.M. was responsible for the identification of *Parakneria* (Kneriidae). L.N.K. was responsible for the identification of *Kneria* (Kneriidae). All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Distribution of the fish species in the five different sections of the Kalule Nord River (see Figure 2). Family names are followed by the number of genera/species between brackets. The light grey colour bars highlight the highland species which are morphologically similar to those of the lowland region coloured in dark grey.

Family (No. of Genera/Species)	**Kalule Nord River**				
	Upper			**Middle**	**Lower**
	1	**2**	**3**		
Polypteridae (1/1)					
Polypterus ornatipinnis					✗
Mormyridae (4/4)					
Campylomormyrus rhynchophorus					✗
Cyphomyrus discorhynchus					✗
Marcusenius macrolepidotus					✗
Mormyrops anguilloides					✗
Clupeidae (1/1)					
Microthrissa congica					✗
Kneriidae (2/2)					
Kneria sp. 'kalule'	✗ *	✗ *	✗ *	✗ *	
Parakneria sp. 'kalule'					✗ *
Cyprinidae (3/15)					
Enteromius kamolondoensis					✗
Enteromius kerstenii					✗
Enteromius cf. *mocoensis*	✗	✗	✗	✗	
Enteromius neefi	✗	✗	✗	✗	
Enteromius thespesios					✗
Enteromius sp. 'ngulungu'				✗	
Labeo cylindricus					✗
Labeo parvus					✗
Labeo simpsoni					✗
Labeo weeksii					✗
Labeobarbus sp. 'kapepe'					✗ *
Labeobarbus sp. 'kayo'		✗ *	✗ *	✗ *	
Labeobarbus sp. 'ngulungu'		✗ *	✗ *	✗ *	
Labeobarbus sp. 'nshila'					✗ *
Labeobarbus sp. 'thick lip'					✗
Danionidae (3/3)					
Chelaethiops congicus					✗
Opsaridium ubangiense					✗
Raiamas marqueti					✗
Distichodontidae (2/2)					
Nannocharax hadros					✗ *
Alestidae (4/6)					
Alestes macrophthalmus					✗
Brycinus grandisquamis					✗
Brycinus imberi					✗
Hydrocynus vittatus					✗
Micralestes acutidens					✗
Micralestes stormsi					✗
Bagridae (1/1)					
Bagrus ubangensis					✗
Clariidae (2/3)					
Clarias buthupogon					✗
Clarias cf. *liocephalus*			✗	✗	

Table A1. *Cont.*

Family (No. of Genera/Species)	Kalule Nord River				
	Upper			Middle	Lower
	1	2	3		
Heterobranchus longifilis					✗
Amphiliidae (2/4)					
Amphilius sp. 'kayo_abave'	✗ *	✗ *			
Amphilius sp. 'kayo_below'			✗ *	✗ *	
Zaireichthys brevis			✗	✗	
Zaireichthys sp. 'upemba'					✗
Malapteruridae (1/1)					
Malapterurus monsembeensis					✗
Mochokidae (3/5)					
Chiloglanis sp. 'kalule'			✗ *	✗ *	
Euchilichthys royauxi					✗
Synodontis decorus					✗
Synodontis dorsomaculatus					✗
Synodontis greshoffi					✗
Claroteidae (3/3)					
Auchenoglanis occidentalis					✗
Parauchenoglanis sp. 'kalule'					✗
Chrysichthys cranchii					✗
Schilbeidae (1/1)					
Schilbe intermedius					✗
Mastacembelidae (1/1)					
Mastacembelus congicus					✗
Cichlidae (3/3)					
Coptodon rendalli					✗
Orthochromis kimpala					✗
Tilapia sparrmanii					✗
Total	4 (7%)	6 (11%)	9 (16%)	10 (18%)	45 (80%)

* endemic species of the Kalule Nord.

Table A2. Comparison of the ichthyofauna of the UNP with that of the Upper Lualaba and its neighbouring ecoregions. UL: Upper Lualaba including UNP; BM: Bangweulu-Mweru; UC: Upper Congo; Kas: Kasai; UZ: Upper Zambezi. N is the total number of native species within an ecoregion. The number of shared species is given in absolute terms as well as in percentage. J: Jaccard similarity index.

	UNP	UL	BM	UC	Kas	UZ
N	249	311	159	284	319	158
Shared species		249	82	149	125	43
Shared species (%)		100	33	60	50	17
J		0.77	0.25	0.39	0.29	0.12

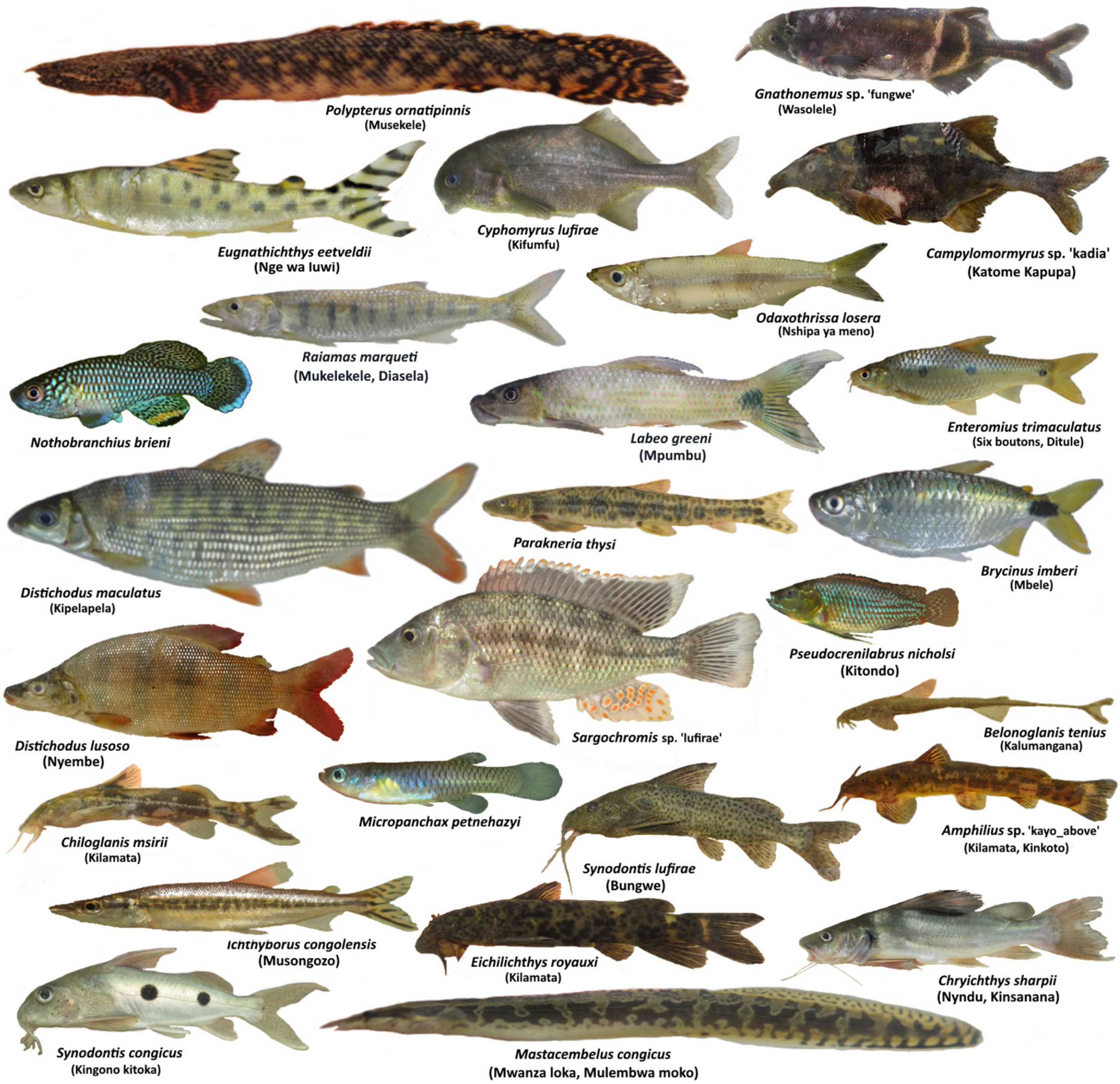

Figure A1. Representatives of the species of the Upemba National Park (UNP) caught during this study. The scientific name of each one is followed by the local name in the Luba/Sanga language (between parenthesis). All these photos of the fish were taken during sampling by the authors (B.K.M. and/or E.V.).

Figure A2. Examples illustrating the diversity of falls in Upemba National Park. **Top** two: on the Lufira River itself and one of its left-bank tributaries, the Luvilombo River. **Bottom** four: on the Kalule Nord River itself and one of its right-bank tributaries, the Lungeya River.

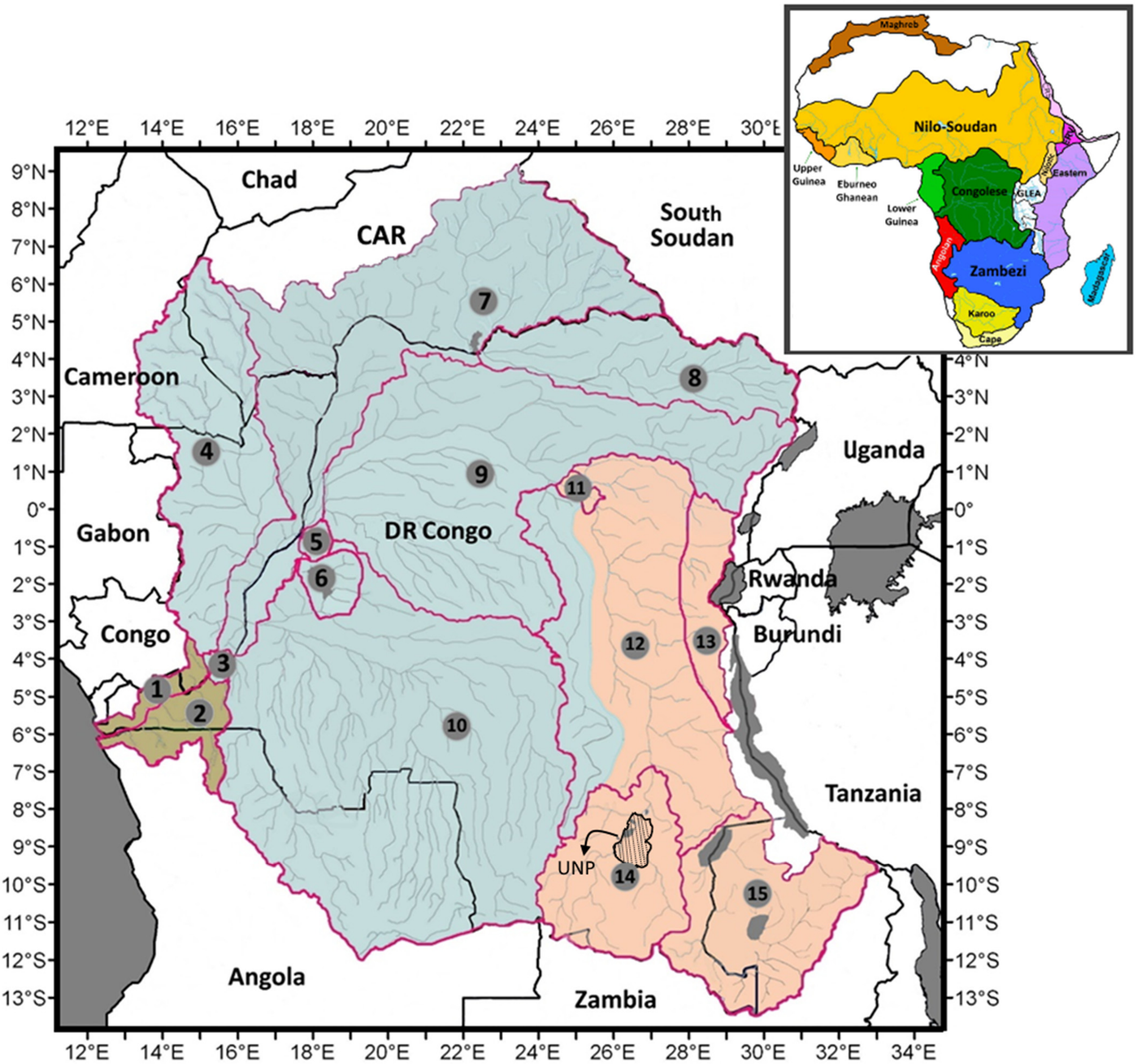

Figure A3. Ecoregions of the Congo Basin [6,92]. **Lower Congo**: (1) Lower Congo Rapids and (2) Lower Congo. **Middle Congo**: (3) Malebo Pool, (4) Sangha, (5) Tumba, (6) Mai Ndombe, (7) Sudanic Congo-Oubangi, (8) Uele, (9) Cuvette Centrale, and (10) Kasai. **Upper Congo**: (11) Upper Congo Rapids, (12) Upper Congo, (13) Albertine Highlands, (14) Upper Lualaba, and (15) Bangweulu-Mweru.

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