



## Fish fauna of the São Francisco River Interbasin Water Transfer reservoirs

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**Abstract:** Artificial impoundments are frequently built to mitigate the water scarcity in the drylands such as the Caatinga region in Brazil. The São Francisco Interbasin Water Transfer (SF-IWT) megaproject implemented many artificial reservoirs for that purpose. A checklist of fish species from the SF-IWT reservoirs is provided based on samples from eight years of monitoring. The collections were conducted semiannually at 28 reservoirs divided into three groups: the East Axis, North Axis, and Agreste Branch. The SF-IWT reservoirs presented a total of 47 species, 46 were recorded in the North Axis, 27 in the East Axis, and only seven in the Agreste Branch. Characids and cichlids represented most of the species. The three analyzed groups of reservoirs presented distinct communities and the reservoirs' age, richness and abundance were relevant variables responsible for fish composition. The SF-IWT reservoirs present a diverse and heterogeneous ichthyofauna, typical of lentic environments. The main colonizers of the SF-IWT reservoirs were fish from the São Francisco donor basin, invasive species anthropically released in those sites, and eventual species from the surrounding receiving basins. As the accumulation curves suggested, a continuous effort could reveal additional species, patterns in long-term colonization, and contribute to data on the reservoirs' future stabilization phase. Since invasive species were present in most reservoirs, along with donor-basin native species with potential to disperse to the receiving basins, a continuous and detailed monitoring is key for management planning and possible impacts assessment.

**Keywords:** *Artificial reservoirs; Brazilian Semiarid; non-native fish; water diversion.*

## Ictiofauna dos reservatórios do Projeto de Integração do Rio São Francisco

**Resumo:** Barramentos artificiais são comumente construídos para mitigar a escassez hídrica em áreas semiáridas como a região da Caatinga brasileira. O Projeto de Integração do Rio São Francisco (PISF) com Bacias Hidrográficas do Nordeste Setentrional implementou muitos reservatórios artificiais com este propósito. Uma lista de espécies de peixes dos reservatórios do PISF foi obtida após amostragens realizadas em oito anos de monitoramento. As campanhas foram realizadas semestralmente em 28 reservatórios divididos em três grupos: Eixo Leste, Eixo Norte e Ramal do Agreste. Os reservatórios amostrados apresentaram um total de 47 espécies, 46 delas foram registradas no Eixo Norte, 27 no Eixo Leste e apenas sete no Ramal do Agreste. Characidae e Cichlidae foram as famílias mais representativas. Os três grupos de reservatórios analisados apresentaram comunidades distintas e a idade, a riqueza e a abundância de cada reservatório foram as variáveis que mais influenciaram a composição das espécies de peixes. Os reservatórios do PISF apresentaram uma ictiofauna diversa e heterogênea, característica de ambientes lênticos. Os principais colonizadores dos reservatórios do PISF foram peixes da bacia doadora do São Francisco, espécies invasoras antropicamente liberadas nesses locais e eventuais espécies das bacias receptoras do entorno. De acordo com o resultado das curvas de acúmulo, um esforço contínuo poderia revelar espécies adicionais, padrões na colonização em longo prazo e contribuir com dados para a fase futura de estabilização dos reservatórios. Visto que espécies invasoras estiveram presentes em quase todos os reservatórios, juntamente com espécies nativas da bacia doadora com potencial de dispersão para as bacias receptoras, um monitoramento contínuo e detalhado é essencial para o planejamento de manejo e avaliação de impactos.

**Palavras-chave:** *Desvio de águas; Peixes não-nativos; Reservatórios artificiais; Semiárido brasileiro.*

## Introduction

The Semi-arid Northeast region of Brazil, dominated by the Caatinga biome, has very low precipitation ranging from 200 mm to 800 mm annually, with short rainy periods of two to four months (January to April), and a long dry period (generally from May to December) (Maltchik 1999). The average annual temperature ranges from 25 to 30° C, with the maximum reaching almost 40° C in hotter months (September to November). These two distinct seasons in the Caatinga, wet and dry with extremely low precipitation, are responsible for the great number of intermittent rivers (Maltchik & Florín 2002). The deficit in the hydric balance has a major socioeconomic impact in semi-arid regions, leaning policymakers to focus on solutions that minimize social issues and meet economic needs. The implementation of artificial man-made reservoirs is reported as a commonly used way to mitigate the water scarcity in dry regions, supplying water for both economic (e.g., irrigation, agriculture, industry) and domestic use (Thornton & Rast 1993).

In the Brazilian semi-arid, the São Francisco Interbasin Water Transfer (SF-IWT) project was the governmental solution to mitigate centuries of water scarcity (Andrade et al. 2011). The São Francisco River, the largest exclusively Brazilian river, is the main naturally perennial water resource in the Semi-arid Caatinga domain (Andrade et al. 2011, Roman 2017) and, therefore, the groundwork for the SF-IWT. The SF-IWT megaproject consists of 477 km of canals, pipes, aqueducts, pump stations, and reservoirs divided into two main axes: East (EA) and North (NA) (Andrade et al. 2011), diverting water from the donor basin (São Francisco) to eight different receiving basins. By August 2022, 12 of the SF-IWT artificial reservoirs along the EA and 14 along the NA were fully operational. Moreover, the EA sub-division, the Agreste branch (AB), possesses two more fully operational reservoirs. The EA axis provides water to the receiving basins of the

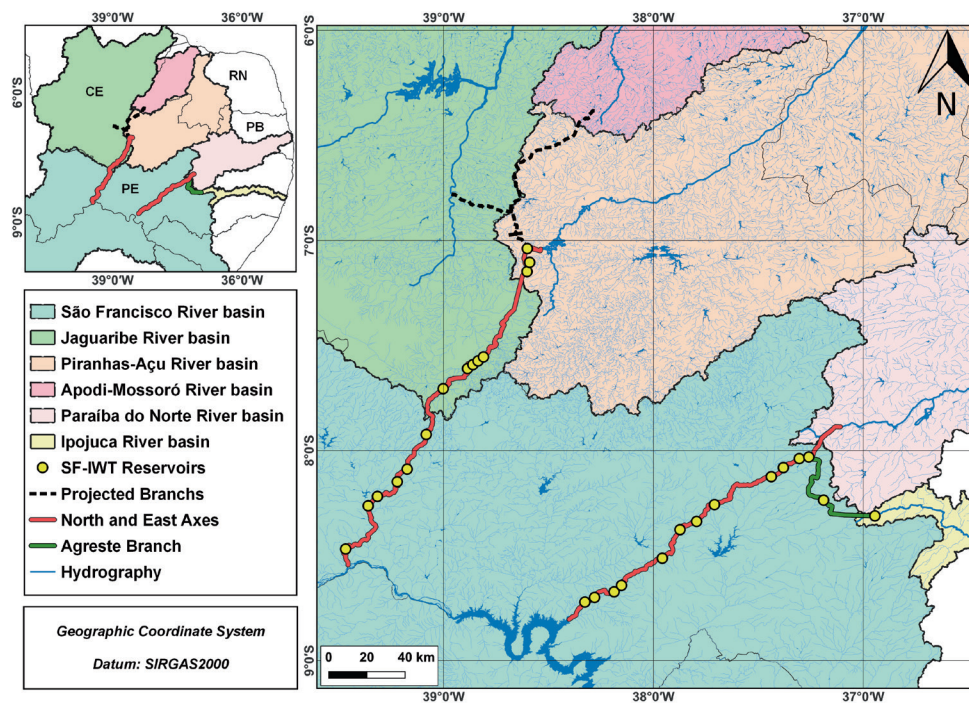
Paraíba do Norte, Moxotó, and Pajeú rivers, and its AB to the Ipojuca River basin, located in a region known as “Agreste”. Meanwhile, the NA axis supplies water to receiving basins of the Jaguaribe, Apodi-Mossoró, Piranhas-Açu, and Brígida rivers (Andrade et al. 2011).

The SF-IWT reservoirs are artificially regulated, receiving water from the perennial São Francisco River according to management demands, not following the natural seasonal variation affected by the longer dry and shorter rainy periods. Furthermore, due to these man-regulated dynamics, the SF-IWT reservoirs present distinctive features from other semi-arid reservoirs (Barbosa et al. 2012, Barbosa et al. 2021). For the same reason, the fish fauna in the SF-IWT reservoirs is directly affected by the water management dynamics. Silva et al. (2020) compiled information on the ichthyofauna of five basins surrounding the SF-IWT, generating a comprehensive baseline of that Semi-arid region previous to the project’s full implementation. Meanwhile, Silva et al. (2023) analyzed the fish fauna that is dispersing through the SF-IWT East Axis reaching the Paraíba do Norte River receiving basin after ten years of water diversion. Nonetheless, previous studies did not discuss the fish taxonomic composition of artificially created SF-IWT reservoirs. Thus, this work aimed to provide a list of fish species recorded in the 28 SF-IWT artificial reservoirs, and the results represent important insights on the changes in the fish community composition that occurred over the eight years of monitoring.

## Material and Methods

### 1. Sampling area

Field campaigns were conducted twice a year, from 2015 to 2022, in 12 reservoirs of the SF-IWT East Axis (EA), 14 reservoirs in the North Axis (NA), and two reservoirs in its Agreste branch (AB) (Figure 1). All the reservoirs on the East Axis and the Agreste Branch, in addition to



**Figure 1.** Study area showing the 28 São Francisco Interbasin Water Transfer reservoirs, the São Francisco River, and the basins surrounding the transposition project.

six reservoirs on the North Axis are located in the state of Pernambuco, Brazil; five reservoirs of the North Axis are located in the state of Ceará, and three in the state of Paraíba, Brazil. Despite being a sub-section of the EA, the AB was separately considered since it diverts the SF-IWT waters to the Ipojuca River basin, while EA diverts to the Paraíba do Norte River basin. The branch is also located in a unique region of the Caatinga, the Agreste, a transition area between the forest (humid sub-region with tropical vegetation) and the semi-arid (a dry sub-region with semi-arid vegetation) (CONDEPE 2005).

## 2. Sampling effort

A three-days-sampling effort was conducted for each analyzed reservoir. Each three-days-sampling corresponded to one campaign. Campaign numbers varied for each sampling site since the reservoirs presented different filling dates (Table 1), according to the SF-IWT construction progress. Fish were caught using trawls (10 m long, 5 mm mesh), sieves (50 cm diameter, 5 mm mesh), cast nets (mesh sizes of 15 and 30 mm between opposite knots), and hand nets (40 cm/side rectangular base, 5 mm mesh), with at least three attempts per sampling-day for each of those methods. Gill nets (10 or 50 m long with mesh sizes of 20, 30, 40, 50, 60, and 80 mm between adjacent knots) were kept for one sampling-night (12–14 hours) at each site. In eventual encounters with fisherman during sampling, we registered the species collected by them and added to our data as one record (one specimen per species).

## 3. Processing of collected specimens

Captured fish were promptly identified and released. When identification was not possible in the field, specimens were euthanized by overexposure to 1 g/mL clove oil (based on MCTI – CONCEA 2018), fixed in a 10% formaldehyde solution, preserved in 70° GL alcohol, and transported to be identified in the Laboratório de Ictiologia (CEMAFAUNA, Universidade Federal do Vale do São Francisco – UNIVASF). Voucher specimens were deposited in the Ichthyological Collection of the Museu de Fauna da Caatinga (MFCI), UNIVASF, Petrolina, Brazil. The material was registered in the SisGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado) system, under the license number A8EC2B0. Fish species were identified according to identification keys provided by Britski et al. (1988) and Ramos et al. (2018), original species descriptions, and complemented by reviews of some taxonomic groups. The nomenclature and systematic classification of species were based on Betancur-R et al. (2017) and Fricke et al. (2023).

## 4. Data analysis

The richness extrapolation estimator (Chao, 2005) was calculated and the generated accumulation curve (EstimateS v9.1.0) was used to demonstrate the fish sampling efficiency. We used Chao1 and Chao2 estimators combined to verify whether the estimates were dependent on sample size or stabilized towards the full sampling. The reservoirs' age (months since filling date), each axis or branch (East, North, Agreste), fish abundance, and richness were used as explanatory variables to assess the relevance of the independent variables (reservoirs). The most suitable model was generated using an ordistep information criterion. The ordistep builds a forward model so that it maximizes the adjusted R2 at every step, and stops when the adjusted R2 starts to decrease, the scope is exceeded, or the selected permutation P-value is exceeded

(Blanchet et al. 2008). The model analysis is used to identify predictor variables that significantly explain the patterns observed in the fish assemblage. Furthermore, a db-RDA (Distance-based Redundancy Analysis) was performed to visualize dbLM data, and a PERMANOVA based on the similarity matrix obtained by Euclidean distance, with 999 permutations, helped determine the significance of explanatory variables. Statistical analysis, other than richness estimators, was

**Table 1.** A detailed list of names and locations of the 28 artificial reservoirs of São Francisco Interbasin Water Transfer Project. Reservoirs are ordered according to the Axis (North, East, or Agreste Branch), and distance from the São Francisco River (closer to farthest). Each reservoir was filled on different dates, according to the construction progress, and the number of campaigns (one campaign = 3-day-sampling, bi-annual) was counted after filling date.

Reservoir	Latitude	Longitude	Filling Date	Campaigns
<b>North Axis (NA)</b>				
Tucutu	08°28'09"S	39°27'57"W	Jul-2015	14
Terra Nova	08°15'49"S	39°21'18"W	Dec-2015	12
Serra do Livramento	08°13'09"S	39°18'59"W	Dec-2017	7
Mangueira	08°08'41"S	39°13'08"W	Apr-2018	8
Negreiros	08°05'25"S	39°10'48"W	Aug-2018	3
Milagres	07°55'02"S	39°04'40"W	Jan-2020	4
Jati	07°42'33"S	39°00'21"W	Jun-2020	4
Porcos	07°37'43"S	38°53'19"W	Jan-2021	2
Cana Brava	07°35'18"S	38°51'18"W	Jul-2022	1
Cipó	07°34'29"S	38°50'36"W	Aug-2022	1
Boi	07°33'40"S	38°49'09"W	Sep-2022	1
Morros	07°09'07"S	38°36'21"W	Oct-2021	1
Boa Vista	07°06'09"S	38°35'35"W	Oct-2021	1
Caiçara	07°02'04"S	38°36'09"W	Jan-2022	2
<b>East Axis (EA)</b>				
Areias	08°43'13"S	38°19'17"W	Oct-2014	16
Braúnas	08°41'43"S	38°16'44"W	Oct-2015	8
Mandantes	08°40'18"S	38°11'13"W	Jan-2017	5
Salgueiro	08°38'39"S	38°09'08"W	Jan-2017	5
Muquem	08°30'54"S	37°57'24"W	Feb-2017	11
Cacimba Nova	08°21'43"S	37°51'53"W	Feb-2017	5
Bagres	08°20'07"S	37°47'35"W	Feb-2017	5
Copiti	08°15'26"S	37°42'31"W	Feb-2017	11
Moxotó	08°07'26"S	37°26'14"W	Feb-2017	4
Barreiro	08°04'43"S	37°22'33"W	Feb-2017	4
Campos	08°02'10"S	37°18'26"W	Mar-2017	4
Barro Branco	08°01'52"S	37°15'38"W	Mar-2017	11
<b>Agreste Branch (AB)</b>				
dos Góis	08°13'40"S	37°10'48"W	Feb-2021	6
Ipojuca	08°18'41"S	36°56'40"W	Dec-2021	6

performed using R software (R Core Team, 2020). The functions used were from package Vegan (Oksanen et al. 2013). Plots were made using the package ggplot2 (Wickham, 2006).

## Results

A total of 70,522 individuals representing 47 fish species (Figures 2 and 3) from 18 families, and seven orders were registered (Table 2). The North Axis (NA) presented 46 species, 27 species were registered in the East Axis (EA), and seven in the Agreste Branch (AB). There was one exclusive species from the AB reservoirs (*Parotocinclus*

*jumbo* Britski & Garavello, 2002), and 20 species were only registered in the NA reservoirs (see Table 2). *Anchoviella vaillanti* (Steindachner, 1908), *Astyanax lacustris* (Lütken, 1875), *Oreochromis niloticus* (Linnaeus, 1758), and *Poecilia reticulata* Peters, 1859 were the only common species to all three analyzed groups of reservoirs (Figures 2 and 3). The richest order was Characiformes (59.5%; n = 28), followed by Cichliformes (14.9%; n = 7), and Siluriformes (10.6%; n = 5). The fish families with greater species richness were Characidae (25.5%; n = 12), and Cichlidae (14.8%; n = 7). Eight fish were considered non-native to the Caatinga domain, while eight are endemic in the region (Table 2).

**Table 2.** Fish species collected in the East and North Axis and the Agreste Branch reservoirs of the São Francisco Interbasin Water Transfer Project. Status: N = Native to the Caatinga domain, NN = Non-Native to the Caatinga domain, E = Endemic to the Caatinga domain. Origin: DB = Donor Basin (São Francisco River basin), WS = Wide Spread in the Caatinga and other Brazilian regions, AM = Amazon River basin, AF = Africa, CA = Central America.

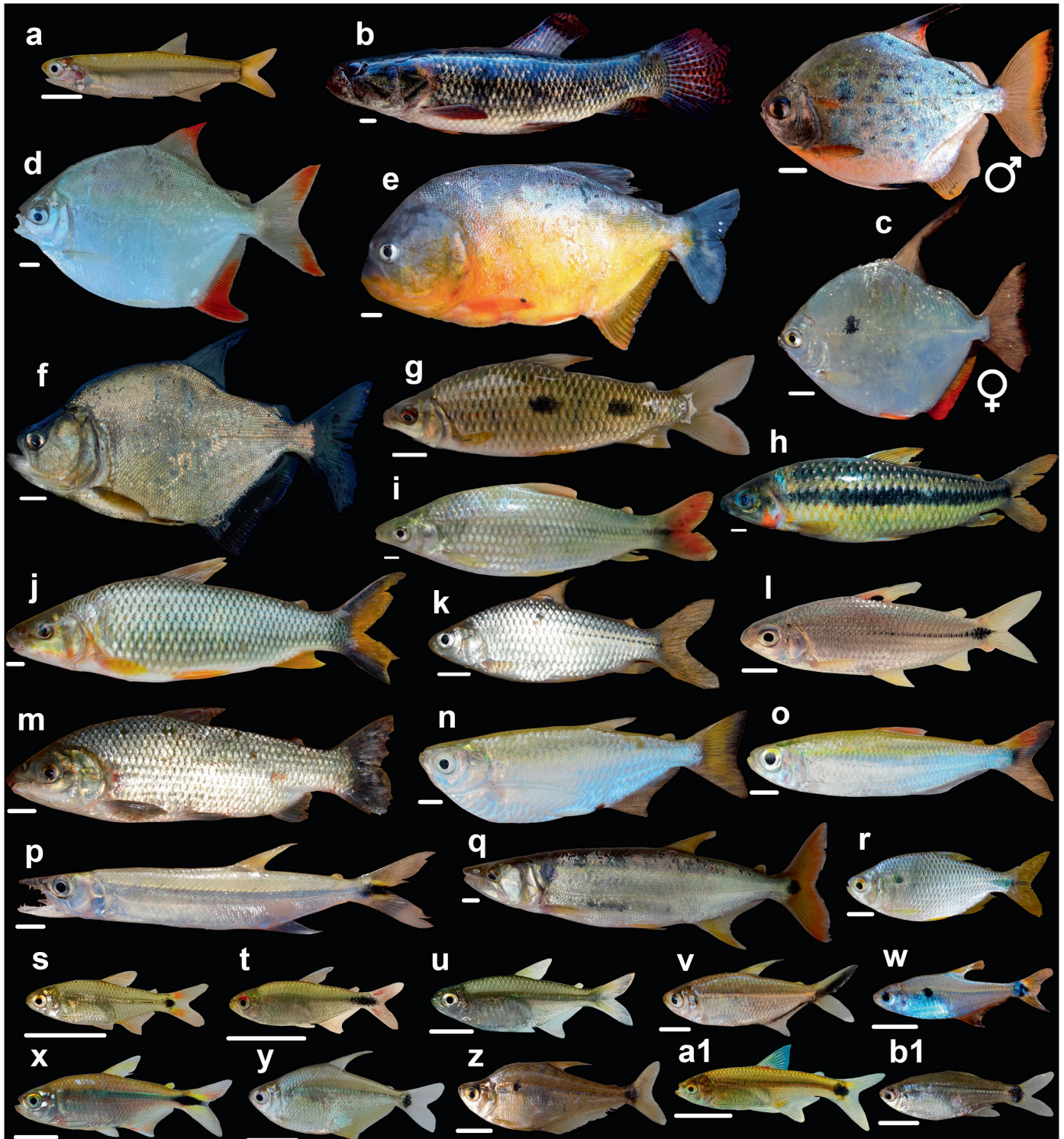
Taxa	Abundance			Status	Origin	Voucher
	EA	NA	AB			
<b>CLUPEIFORMES</b>						
<b>Engraulidae</b>						
<i>Anchoviella vaillanti</i> (Steindachner, 1908)	9303	8220	303	N	DB*	MFCI009548
<b>CHARACIFORMES</b>						
<b>Erythrinidae</b>						
<i>Hoplias gr. malabaricus</i> (Bloch, 1794)	166	218	0	N	WS	MFCI009030
<b>Serrasalminidae</b>						
<i>Metynnis lippincottianus</i> (Cope, 1870)	361	645	0	NN	AM	MFCI007745
<i>Myleus micans</i> (Lütken, 1875)	1	115	0	N	DB	MFCI006078
<i>Pygocentrus piraya</i> (Cuvier, 1819)	0	4	0	N	DB	MFCI007335
<i>Serrasalmus brandtii</i> Lütken, 1875	809	801	0	N	WS	MFCI006616
<b>Anostomidae</b>						
<i>Leporinus piau</i> Fowler, 1941	0	84	0	N	WS	MFCI009274
<i>Leporinus taeniatus</i> Lütken, 1875	1	2	0	E	WS	MFCI006142
<i>Megaleporinus obtusidens</i> (Valenciennes, 1836)	0	1	0	N	DB**	MFCI009276
<i>Schizodon knerii</i> (Steindachner, 1875)	0	3	0	E	DB	Not Deposited
<b>Curimatidae</b>						
<i>Steindachnerina elegans</i> (Steindachner, 1875)	0	70	0	N	DB	MFCI008967
<i>Steindachnerina notonota</i> (Miranda Ribeiro, 1937)	0	9	0	E	WS	Not Deposited
<b>Prochilodontidae</b>						
<i>Prochilodus brevis</i> Steindachner, 1875	0	5	0	E	WS	Not Deposited
<b>Triporthidae</b>						
<i>Triporthus guentheri</i> (Garman, 1890)	5	11	0	E	DB	MFCI006639
<b>Iguanodectidae</b>						
<i>Bryconops aff. affinis</i> (Günther, 1864)	248	1018	0	N	DB	MFCI007135
<b>Acestrorhynchidae</b>						
<i>Acestrorhynchus britskii</i> Menezes, 1969	0	3	0	N	DB	MFCI008954
<i>Acestrorhynchus lacustris</i> (Lütken, 1875)	4	20	0	N	DB	MFCI008600
<b>Characidae</b>						
<i>Astyanax lacustris</i> (Lütken, 1875)	10355	11411	496	N	WS	MFCI006038
<i>Compsura heterura</i> Eigenmann, 1915	0	9	0	N	WS	Not Deposited

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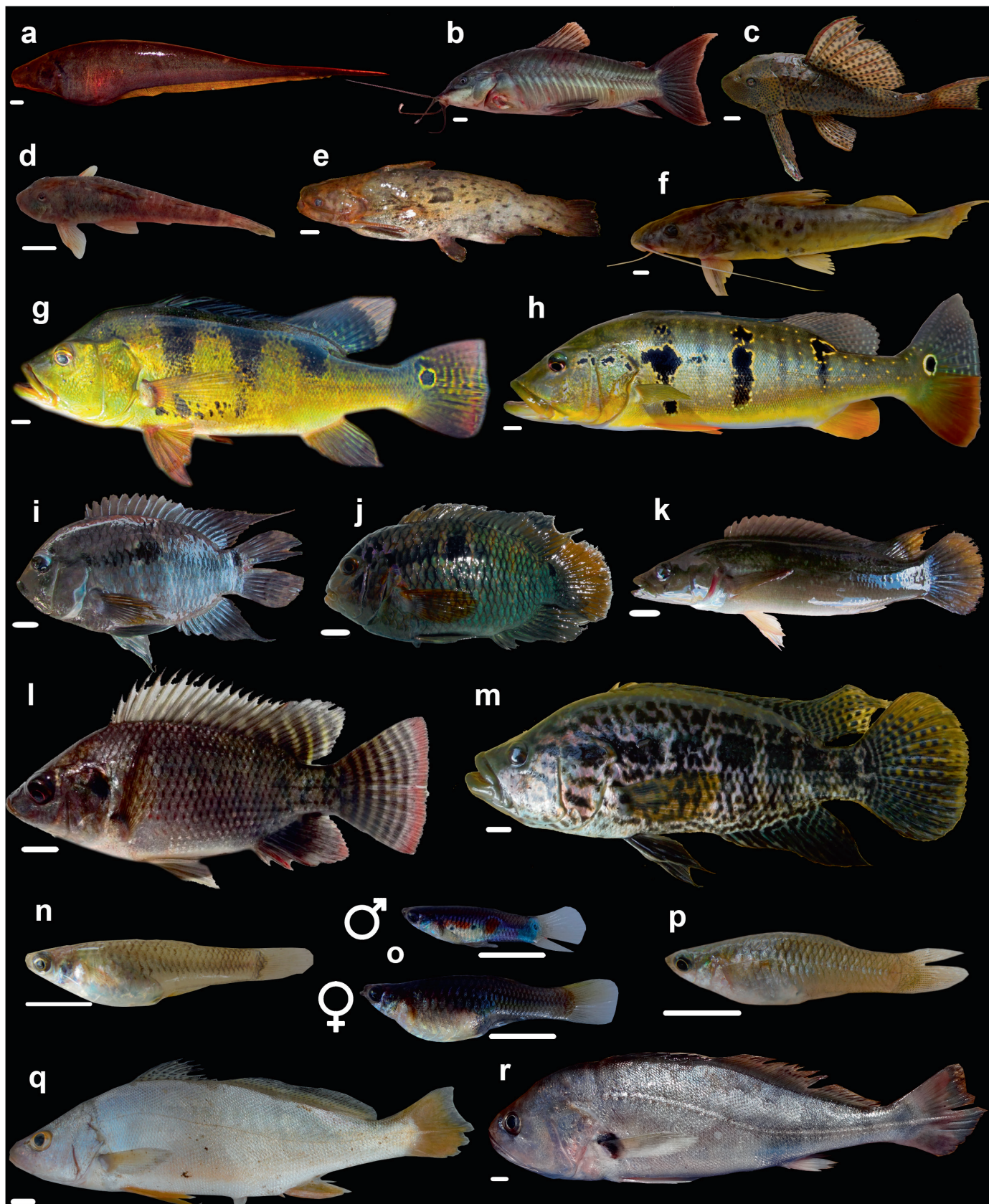
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Taxa	Abundance			Status	Origin	Voucher
	EA	NA	AB			
<i>Hemigrammus brevis</i> Ellis, 1911	1033	1319	0	N	DB	MFCI009773
<i>Hemigrammus gracilis</i> (Lütken, 1875)	59	2026	0	N	DB	MFCI005989
<i>Hemigrammus marginatus</i> Ellis, 1911	1200	3236	0	N	WS	MFCI007328
<i>Moenkhausia costae</i> (Steindachner, 1907)	4732	515	0	E	WS*	MFCI006632
<i>Phenacogaster franciscoensis</i> Eigenmann, 1911	0	53	0	N	DB	MFCI007724
<i>Psalidodon fasciatus</i> (Cuvier, 1819)	0	670	0	N	WS	MFCI009546
<i>Psellogrammus kennedyi</i> (Eigenmann, 1903)	0	84	0	N	WS	MFCI008975
<i>Roeboides xenodon</i> (Reinhardt, 1851)	238	373	0	N	DB	MFCI006104
<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	0	183	0	N	WS	MFCI007800
<i>Serrapinnus piaba</i> (Lütken, 1875)	0	15	0	N	WS	MFCI006614
<b>GYMNOTIFORMES</b>						
<b>Sternopygidae</b>						
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	3	10	0	N	DB	MFCI007342
<b>SILURIFORMES</b>						
<b>Callichthyidae</b>						
<i>Hoplosternum littorale</i> (Hancock, 1828)	1	39	0	NN	WS	MFCI008654
<b>Loricariidae</b>						
<i>Hypostomus pusarum</i> (Starks, 1913)	24	24	0	E	WS	MFCI006141
<i>Parotocinclus jumbo</i> Britski & Garavello, 2002	0	0	10	E	WS	MFCI008769
<b>Auchenipteridae</b>						
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	379	159	0	N	WS	MFCI006178
<b>Pimelodidae</b>						
<i>Pimelodus maculatus</i> Lacepède, 1803	0	2	0	N	DB	Not Deposited
<b>CICHLIFORMES</b>						
<b>Cichlidae</b>						
<i>Cichla monoculus</i> Spix & Agassiz, 1831	970	1217	3	NN	AM	MFCI006070
<i>Cichla temensis</i> Humboldt, 1821	0	143	0	NN	AM	Not Deposited
<i>Cichlasoma orientale</i> Kullander, 1983	2	21	0	N	WS	MFCI008668
<i>Cichlasoma sanctifranciscense</i> Kullander, 1983	452	160	0	N	DB**	MFCI007165
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	2866	1245	872	NN	AF	MFCI009495
<i>Parachromis managuensis</i> (Günther, 1867)	0	2	373	NN	CA	MFCI008759
<i>Saxatilia brasiliensis</i> (Bloch, 1792)	1	124	0	N	WS	MFCI009495
<b>CYPRINODONTIFORMES</b>						
<b>Poeciliidae</b>						
<i>Poecilia hollandi</i> (Henn, 1916)	338	190	0	N	DB	MFCI009035
<i>Poecilia reticulata</i> Peters, 1859	95	14	183	NN	AM	MFCI007303
<i>Poecilia vivipara</i> Bloch & Schneider, 1801	1441	522	0	N	WS	MFCI006752
<b>ACANTHURIFORMES</b>						
<b>Sciaenidae</b>						
<i>Pachyurus francisci</i> (Cuvier, 1830)	0	67	0	N	DB	MFCI006591
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	2	362	0	NN	AM	MFCI006081

\* Introduced in the East Axis receiving basin, Paraíba do Norte (Ramos et al. 2021; Silva et al. 2023). \*\* Reports in the receiving basins, Paraíba do Norte and Jaguaribe (in prep.)

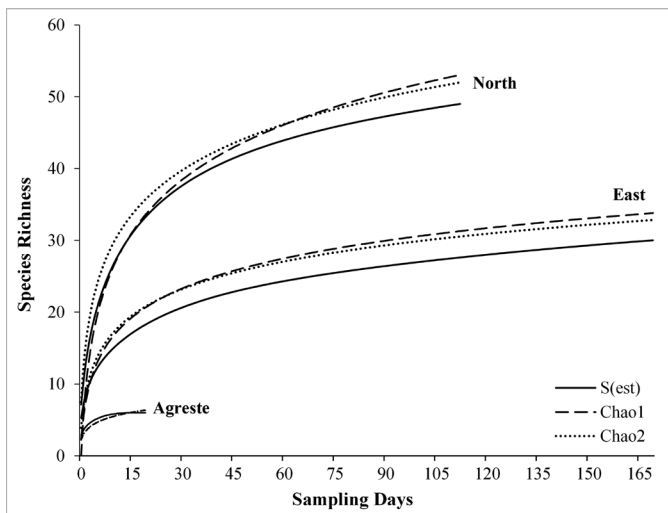


**Figure 2.** Clupeiformes and Characiformes collected in in the São Francisco Interbasin Water Transfer reservoirs: a. *Anchoviella vaillanti*, b. *Hoplias* gr. *malabaricus*, c. *Metynnis lippincottianus*, d. *Myleus micans*, e. *Pygocentrus piraya*, f. *Serrasalmus brandtii*, g. *Leporinus piau*, h. *Leporinus taeniatus*, i. *Megaleporinus obtusidens*, j. *Schizodon knerii*, k. *Steindachnerina elegans*, l. *Steindachnerina notonota*, m. *Prochilodus brevis*, n. *Triportheus guentheri*, o. *Bryconops* aff. *affinis*, p. *Acestrorhynchus britskii*, q. *Acestrorhynchus lacustris*, r. *Astyanax lacustris*, s. *Compsura heterura*, t. *Hemigrammus brevis*, u. *Hemigrammus marginatus*, v. *Moenkhausia costae*, w. *Phenacogaster franciscoensis*, x. *Psalidodon fasciatus*, y. *Psellogrammus kennedyi*, z. *Roeboides xenodon*, a1. *Serrapinnus heterodon*, and b1. *Serrapinnus piaba*. Scale bar = 1 cm.



**Figure 3.** Gymnotiformes, Siluriformes, Cichliformes, Cyprinodontiformes, and Acanthuriformes collected in the São Francisco Interbasin Water Transfer reservoirs: a. *Sternopygus macrurus*, b. *Hoplosternum littorale*, c. *Hypostomus pusarum*, d. *Parotocinclus jumbo*, e. *Trachelyopterus galeatus*, f. *Pimelodus maculatus*, g. *Cichla monoculus*, h. *Cichla temensis*, i. *Cichlasoma orientale*, j. *Cichlasoma sanctifranciscense*, k. *Saxatilia brasiliensis*, l. *Oreochromis niloticus*, m. *Parachromis managuensis*, n. *Poecilia hollandi*, o. *Poecilia reticulata*, p. *Poecilia vivipara*, q. *Pachyurus francisci*, and r. *Plagioscion squamosissimus*. Scale bar = 1 cm.

The most abundant species in the EA reservoirs were *As. lacustris* (30%), *A. vaillanti* (27%), *M. costae* (14%), and *O. niloticus* (8%). In NA reservoirs, the predominant species were *As. lacustris* (34%), *A. vaillanti* (22%), and *Hemigrammus marginatus* (9%). Meanwhile, in AB the species with the largest number of individuals were *O. niloticus* (47%), *As. lacustris* (22%), and *Parachromis managuensis* (17%). In general, the most predominant species were *As. lacustris* (32%), *A. vaillanti* (24%), and *M. costae* (8%) (Figures 2 and Figure 3).



**Figure 4.** Species accumulation curve with expected number of species –  $S(\text{est})$  – and the richness extrapolation estimators Chao 1 (abundance-based data) and Chao 2 (incidence-based data). Sample collections made in the three group of reservoirs from the São Francisco Interbasin Water Transfer project: East Axis, North Axis, Agreste Branch.

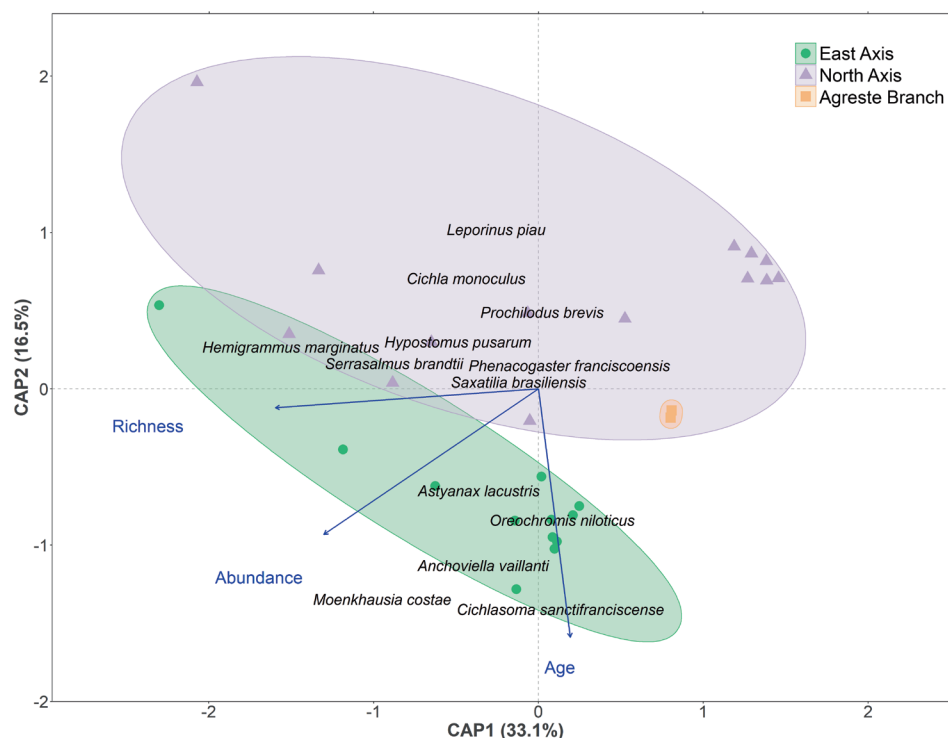
**Table 3.** Forward selection model ANOVA with adjusted p-testing for significant variables between fish assemblage (abundance, richness) and reservoir characteristics (age, axis). \* Significance at  $p < 0.05$ ; Df = degrees of freedom; AIC = Akaike Information Criterion.

ANOVA	Df	Adjusted R2	AIC	F	Pr(>F)
Abundance	1	0.282	148.36	11.630	<b>0.002*</b>
Age	1	0.273	141.79	1.547	<b>0.042*</b>
Axis	2	0.145	143.73	4.330	<b>0.002*</b>
Richness	1	0.269	141.43	3.819	<b>0.002*</b>

During the first years of sampling in the reservoirs, the same species were recurrent recorded in most of them: *A. vaillanti*, *As. lacustris*, *H. malabaricus*, *M. costae*, and *O. niloticus* (Supplementary File S1).

Data suggests that increasing the sampling effort would result in collecting additional species since the species accumulation curves did not present a tendency to stabilize, except for the Agreste Branch (Figure 4). The richness estimators indicated that the East Axis would present additional six species (observed  $n = 27$ ), and seven in the North Axis (observed  $n = 46$ ).

The forward selection model applied to fish assemblage (abundance, richness) and reservoir (age, location) characteristics (Figure 1, Table 1) identified richness, abundance, age, and location (Axis) as good predictors (Table 3). The first db-RDA axis (CAP 33.1%) distinguished reservoirs location and age (Figure 5). The second db-RDA axis was related to reservoir richness and abundance, explaining 16.5% of the variation in fish composition. Areias (EA) and Tucutu (NA) reservoirs are represented in the farther left of CAP1 since those were the reservoirs most influenced by richness and abundance.



**Figure 5.** Ordination of 28 reservoirs in the São Francisco Interbasin Water Transfer project according to the distance-based redundancy analysis (db-RDA), with the effect of reservoir age on fish assemblages. Represented species are the most strongly related to the ordination axes:  $R^2 > 0.5$ .



## Discussion

The São Francisco Interbasin Water Transfer artificial reservoirs presented 47 fish species, the great majority represented in the North Axis, about half of them were presented in the East Axis, and only seven were found in the Agreste Branch. Characids and cichlids represented most of the reported species. The three analyzed groups of reservoirs presented distinct fish compositions, however, AB shared most species with both axes. The reservoirs' richness, abundance, and age were relevant variables responsible for fish composition, separating axes and species groups. The species that first colonized the reservoirs and recurrently occurred in first years of sampling, considered as pioneer species, were: *A. vaillanti*, *As. lacustris*, *O. niloticus*, *M. costae*, and *H. malabaricus*.

All the SF-IWT reservoirs are less than ten years old, still in the colonization formation stage (Agostinho et al. 1999). The instability of reservoir conditions can last 5 to 30 years after its formation, with fish community stabilization estimated to happen between 15 and 40 years (Agostinho et al. 1999, Agostinho et al. 2016). The richness observed in each SF-IWT reservoirs was at maximum of 29 species, which is close to the average richness of  $n = 30$  found in most Neotropical reservoirs (Agostinho et al. 2007). In general, small diversity and richness are expected for Neotropical impounded areas (Agostinho et al. 2007, Agostinho et al. 2016), especially new ones such as SF-IWT reservoirs. We observed a positive correlation between age and richness. Reservoirs were as richer as they were older. However, despite those observed peaks of richness in the colonization phase of the reservoirs, it is expected that after reaching the stabilization phase, reservoirs older than 20 years present lower richness than the younger ones (Agostinho et al. 2007). Those richness variations are the consequence of several variables such as the reservoir location, distance from the species matrix (rivers), impoundment area, and anthropogenic activities in and around the reservoirs.

Besides age, the reservoirs' location has influenced the fish composition in SF-IWT reservoirs. The main species matrix (São Francisco River), has its water pumped through all SF-IWT canals and reservoirs, serving as a major species pool. However, the East and North Axes reservoirs are surrounded by other basins along their path: the Moxotó, and Pajeú (São Francisco) sub-basins surrounding EA, Ipojuca basin surrounding AB, and the Brígida (São Francisco) sub-basin, Jaguaribe, Apodi-Mossoró, and Piranhas-Açu basins surrounding the NA. The EA had all of its native species originating from the São Francisco River (Silva et al. 2023) since its surrounding basins are mainly subsections of the São Francisco and not independent basins, as seen for the NA. Meanwhile, the four different basins surrounding the NA together with the São Francisco basin, supplied the NA reservoirs with a larger number of species, many exclusive, when compared to the EA. Moreover, the NA catchment is located in a lotic portion of the São Francisco River, which is naturally richer compared to the lentic reservoir catchment of EA. These watershed species matrixes helped determine the distinction in fish assemblage between regions.

The most abundant species were *As. lacustris*, *A. vaillanti*, *C. monoculus*, *H. marginatus*, *H. brevis*, *H. gracilis*, *M. costae*, *O. niloticus*, and *P. vivipara*. Following a pattern described in the literature for the Neotropical region, there was a prevalence of specimens from the Characidae family (*As. lacustris*, *M. costae* and *Hemigrammus* spp.),

characterized by small-sized sedentary species, with generalist habit, high tolerance, and efficient reproductive strategies (opportunistic *sensu* Winemiller 1989, Agostinho et al. 1999, Agostinho et al. 2007, Dagosta & De Pinna 2019). The second most abundant species was the anchovy *A. vaillanti*. The species demonstrated a great colonization capacity, with fast establishment and spread through all reservoirs. *Anchoviella vaillanti* successful residence in SF-IWT reservoirs can be explained by the species efficient trophic and reproductive strategies (Silva et al. 2023). The other prevalent group, Cichlidae was represented by the non-natives: *O. niloticus* and *Cichla* spp. Cichlids in general present great reproductive, feeding, and abiotic plasticity, as well as high adaptability to lentic environments (Agostinho et al. 2021), being already widely dispersed in many Caatinga-region reservoirs (Costa et al. 2017, Silva et al. 2020, Silva et al. 2023).

Reservoirs assemblages are supposed to be similar to the surrounding basins (Rahel 2007). However, constant man-mediated non-native fish releases in reservoirs cause biotic differentiations (Daga et al. 2015). The ichthyofauna of the SF-IWT reservoirs was composed mainly by species native to the Caatinga domain, except for the non-natives: *O. niloticus*, *P. managuensis*, *C. monoculus*, *C. temensis*, *H. littorale*, *P. reticulata*, *M. lippincottianus*, and *P. squamosissimus*. This is a small but yet very common group of species, constantly released in the Northeast Brazilian reservoirs (for commercial or recreative purposes), that are widely spread in most of the Caatinga domain basins, considered well-established invasive species in the region (Leão et al. 2011, Brito et al. 2020, Silva et al. 2020, D'Avilla et al. 2021). These invasives represented more than 12% of the total abundance in our study, compared to endemics that represented just 9%. As pointed by Agostinho et al. (2007), non-native species are usually more successful in recent reservoirs, such as the SF-IWT reservoirs, mainly due to their resistance and opportunism during environmental disturbances (e.g., reservoir formation), the abundant presence of small preys (e.g., *As. lacustris*, *M. costae*, and *A. vaillanti*), absence of natural predators, and few large competitors present (for Semiarid reservoirs also discussed by Brito et al. 2020). Moreover, the parental care and fractionated-type spawning strategies seen in most of the presented invasives (equilibrium *sensu* Winemiller 1989, Assis et al. 2017, Brito et al. 2020), associated with generalist diet, represent major advantages to establishment in reservoirs (Agostinho et al. 2007). For example, *Oreochromis niloticus* is well known in the literature for dominating reservoirs, being highly prolific, having high resistance to environmental variations (Canónico et al. 2005, Attayde et al. 2011), and contributing to the homogenization of species in invaded sites (Canónico et al. 2005, Leão et al. 2011, Vitule & Prodócimo 2012, Daga et al. 2015). Moreover, the dominance of *Parachromis managuensis* and *Cichla* spp. in some reservoirs may explain the reduced richness and low abundance of native predators (Pelicice & Agostinho 2009), since the invasive predators can inhibit the natives' growth and compete for food resources (Carvalho et al. 2014, França et al. 2017, Resende et al. 2020, Sastraprawira et al. 2020). *Cichla* spp. are also known to succeed in reservoirs due to reproductive strategies, opportunistic feeding behavior, cannibalism of young, and resistance to environmental changes (Gomiero & Braga 2004, Carvalho et al. 2014, D'Avilla et al. 2021).

Although crucial on the socioeconomic perspective, the construction of interconnected artificial reservoirs by SF-IWT project

raised a major environmental concern: the dispersal of fish species between historically separated basins (Silva et al. 2020). Some recorded species, despite considered native to the Caatinga domain, are exclusively native or endemic to the donor basin, the São Francisco. Therefore, those São Francisco River species were geographically isolated from the receiving basins before the SF-IWT implementation. The spread and introduction of *M. costae* e *A. vaillanti* thought EA reaching the Paraíba do Norte receiving basin was discussed by Ramos et al. (2021) and Silva et al. (2023), however no impact by these species was yet detected. Remarkably, *A. vaillanti* is also spreading through NA and has already been detected in the Jaguaribe basin (in prep.). We also observed the spread of *Cichlasoma sanctifranciscense* through all the EA reservoirs and canals over time, and this species was already registered in the Paraíba do Norte basin in April 2023 (in prep.). Meanwhile, reports of *Megaleporinus obtusidens* in the Paraíba do Norte and Jaguaribe basins are speculated to be accidental, non-related to the SF-IWT, since just one specimen was captured in one reservoir (Tucutu) during all monitoring time, and none along the reservoirs SF-IWT (as seem for *C. sanctifranciscense*). Other São Francisco basin species that did not reach the receiving basins yet but we detected spreading through NA reservoirs are: *Steindachnerina elegans*, *Bryconops* aff. *affinis*, *H. brevis*, and *Roebooides xenodon*. All of those species present efficient life strategies that allow successful spread and colonization in reservoirs (Winemiller 1989, Agostinho et al. 1999, Agostinho et al. 2007). The constant influx of donor-basin-fish-propagules into the SF-IWT reservoirs seems to guarantee a viable propagule number, supporting these opportunistic species to overcome demographic and ecological barriers, determining a successful establishment and spread (Simberloff 2009).

The balance between socioeconomic and environmental benefits/impacts should be extensively discussed prior to implementation of megaprojects such as the SF-IWT. The SF-IWT reservoirs are artificial impoundments especially built to mitigate the shortage of water in the driest region of Brazil and represented a great change in the Caatinga region, bringing water and species to places that were previously dominated by dry lands and intermittent rivers. Those reservoirs constantly undergo several anthropogenic actions, mainly related to water fluctuation and species introduction. The human-induced changes are dramatic in fish colonization and establishment success (Jia et al. 2020). This reinforces the importance of monitoring the reservoirs over time and registering the ichthyofauna development over the years. As the accumulation curves suggested, a continuous effort could reveal additional species, patterns in long-term colonization, and serve as base-data on the reservoirs' future stabilization phase. Our data indicate that the fish fauna from the São Francisco donor basin are the main colonizers of the SF-IWT-created new environments, along with invasive species deliberately released in those sites, and eventual species from the surrounding receiving basins. Considering the presented potential of SF-IWT system to serve as dispersal bridge from donor to receiving basins, prevention measures are key points to minimize introduction risks. To avoid the translocation of species, we reinforce that the physical and electrical barriers described by Silva et al. (2023) should be implemented to mitigate the introduction of new species in the receiving basins. As for species that already reached the previous isolated basins, a continuous and detailed monitoring is essential for management planning and possible impacts assessment.

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## Conflicts of Interest

The authors declares that they have no conflict of interest related to the publication of this manuscript.

## Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

## Data availability

The datasets generated during and/or analyzed during the current study are available at: <https://doi.org/10.48331/scielodata.ELHXGF> and <https://sisgen.gov.br/paginas/pubpesqatividade.aspx> (Código de Cadastro: A8EC2B0)

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