

Diversity and conservation of fishes from karstic areas of the Jandaíra Formation in the Brazilian semiarid

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Abstract. Few studies have focused on non-troglophic fishes occurring in Brazilian caves, especially those in the Caatinga region. The present study is the first survey of fishes from karstic areas of the Jandaíra Formation in Rio Grande do Norte State, northeastern Brazil. This region is characterized by a high concentration of caves and a rich subterranean biodiversity, especially of troglitic invertebrates, but remains considered a gap on the knowledge of the subterranean ichthyofauna in Brazil. Four field expeditions were carried out covering two dry and two rainy seasons, in 2018 and 2019, in 23 localities in small river basins along the western part of the Jandaíra Formation. A total of 829 fish specimens, none of them troglitic, was captured and identified as belonging to 25 species of 12 families and five orders. Amongst them, four species are endemic of the Mid-Northeastern Caatinga ecoregion, and two non-native species were recorded. Habitats were classified into three categories: superficial, associated to cave, and cave. Although no troglitic fish species was found in this study, we recorded 64.1% of the Apodi-Mossoró river ichthyofauna occurring in caves or associated to caves, corroborating the hypothesis that part of the ichthyofauna exploits these environments as a refuge during the dry season. In addition, we suggest conservation policies for the maintenance of subterranean and aquatic semiarid ecosystems in the Jandaíra formation, which is currently under threat due to anthropogenic activities, such as mining and deforestation.

Keywords. Caatinga; Subterranean fauna; Neotropical fish; Mid-Northeastern Caatinga ecoregion; Furna Feia National Park.

INTRODUCTION

One among the diverse types of landscapes of the semiarid Caatinga in Brazil, the karstic areas constitute sets of carbonate rocks (mainly limestones) that can be subject to dissolution during long geological periods, resulting in the formation of caves and other subterranean environments (Ford & Williams, 1989). Although

somehow neglected in the past, caves are currently known for their capacity to shelter a rich fauna of invertebrates and vertebrates, with high endemism and evolutionary importance (Gibert & Deharveng, 2002; Culver & Pipan, 2009).

Fishes are considered top predators in subterranean environments, therefore are fundamental elements in subterranean communities (Bichuette & Trajano, 2003). In Brazil, the subterranean fish

Pap. Avulsos Zool., 2023; v.63: e202363011

<https://doi.org/10.11606/1807-0205/2023.63.011>

<https://www.revistas.usp.br/paz>

<https://www.scielo.br/paz>

Edited by: Murilo Nogueira de Lima Pastana

Received: 13/06/2022

Accepted: 06/02/2023

Published: 06/03/2023

ISSN On-Line: [1807-0205](https://doi.org/10.11606/1807-0205)

ISSN Printed: [0031-1049](https://doi.org/10.11606/0031-1049)

ISNI: [0000-0004-0384-1825](https://orcid.org/0000-0004-0384-1825)



fauna stands out for its high species richness and ecological diversity, represented by 36 troglobitic species, 22 of which were formally described, distributed among 12 genera, seven families, and three orders (Trajano, 2021). There are also several troglophilic fish species in Brazil (Bichuette & Gallão, 2021 and references therein). Such fish diversity is recorded in the Amazon, Atlantic Forest, Cerrado, and Caatinga, where subterranean fishes occupy niches in streams close to flooded caves, phreatic lakes and in aquifers of karstic formations. These environments are fragile, unique, and among the most threatened in the world (Mammola *et al.*, 2019, Bichuette, 2021; Bichuette & Gallão, 2021).

Most aquatic subterranean studies in the Caatinga focused on the karst areas of the São Francisco river basin, where 11 troglobitic species (*i.e.*, species restricted to subterranean habitats, usually exhibiting the so-called troglomorphisms such as loss or reduction of eyes and pigmentation; Sket, 2008; Culver & Pipan, 2009) are found. However, in other karstic outcrops in the Brazilian semiarid, gaps of knowledge regarding the subterranean ichthyofauna remain. Among these, the Jandaíra Formation, located in Rio Grande do Norte (RN) and Ceará (CE) states, is one of the most conspicuous carbonate ranges of the Phanerozoic in Brazil (Bezerra *et al.*, 2007). This region concentrates about 90% of the caves currently registered in RN (CANIE/CECAV, 2022). The Jandaíra Formation has a rich subterranean biodiversity, particularly of troglobitic invertebrates, including aquatic organisms such as crustaceans and planarians (Bento *et al.*, 2021). However, this region was not included in the most recent national surveys that compiled occurrences of subterranean fishes in the main Brazilian karst areas (Trajano, 2021; Bichuette & Gallão, 2021). Furthermore, many studies focused only on species restricted to caves (*i.e.*, troglobitic), especially those exhibiting troglomorphisms that are usually regarded as evidences of medium- to long-term isolation in the subterranean environment. The paucity of ichthyological surveys highlights the lack of scientific guidance for non-troglobitic fishes that, nevertheless, can spend a significant part of their life in caves and play important ecological roles in these environments (Mattox *et al.*, 2008; Ratton *et al.*, 2018).

The semiarid climate influences the small and medium-sized drainages of the Caatinga, the main hydrological effect is the intermittent regime (Lima *et al.*, 2017). Although threatened by human activities, such as the introduction of exotic species and modifications in the water flow (*e.g.*, the São Francisco interbasin water transfer project, SFRIWT) (Berbel-Filho *et al.*, 2016), little is known about the ecological and demographic dynamics of the Caatinga's fishes, as well as their potential use of subterranean habitats as refuge areas in the dry season (Silva *et al.*, 2020).

During the last century, the ichthyofauna of the RN has been investigated using different approaches, such as inventories and ecological studies (Starks, 1913; Nascimento *et al.*, 2014; Paiva *et al.*, 2014; Costa *et al.*, 2017; Medeiros *et al.*, 2019). However, only two studies recorded fishes in caves (Ferreira *et al.*, 2010; Abrantes *et al.*,

2020). In order to identify potential temporary refuges for fishes in the dry season or even potentially troglobitic fishes, we surveyed the ichthyofauna of surface and subterranean springs in karstic landscapes of the Jandaíra Formation in the Caatinga's drainages. We evaluate the geographic distribution of the species recorded, discuss species richness patterns, and describe the water regime of the sampling sites. In addition, we suggest conservation policies for the maintenance of subterranean aquatic semiarid ecosystems in the Jandaíra Formation area, which is currently threatened due to anthropogenic activities, especially mining and deforestation.

MATERIALS AND METHODS

Study area

The study area comprised 23 sampling sites distributed among the municipalities of Mossoró, Baraúna, Felipe Guerra, Governador Dix-Sept Rosado, Upanema, Caraúbas and Apodi, located in the western RN (Fig. 1). This region has a high biospeleological potential, with a rich fauna of troglomorphic and troglobitic invertebrate species, and concentrates about 90% of the caves currently registered in RN (Bento *et al.*, 2021; CANIE/CECAV, 2022).

This area is included in the semiarid Caatinga, characterized by deciduous hyperxerophilic vegetation, with formation of the shrub-tree Caatinga. The predominant climate is the semiarid type BSh (Alvares *et al.*, 2013), whose influence makes rivers and streams in the region seasonal. Prolonged periods of drought are common in the region with the rainy season extending from October to April, and the annual rainfall varying between 500 mm and 800 mm on average (Silva *et al.*, 2017).

Some of the localities (sampling sites 3, 4, 5, 6 and 7 in Fig. 1) are in the limits of the Furna Feia National Park (FFNP), created in 2012 with the aim of protecting and preserving the speleological heritage and biodiversity of the Caatinga (Brasil, 2012). The topographic boundary of the FFNP area is the Serra de Mossoró mountain range, which is the divisor between the coastal micro-basins (Virgínio and Mata streams) to the west, the Onça stream to the north and the Apodi-Mossoró river basin to the south. The Bom Sucesso and Carmo tributary rivers compose the Apodi-Mossoró river basin (Fig. 1), which is one of the main basins of the Mid-Northeastern Caatinga freshwater ecoregion (MNCE) and receiver of the SFRIWT (Silva *et al.*, 2020). The Apodi-Mossoró river basin is characterized by an intermittent hydrological regime, and an area of 14,278 km². Its headwaters and estuary are in the RN, crossing the state from south to north, including most of the limestone outcrops of the Jandaíra Formation (Silva *et al.*, 2020).

Sampling

Four field expeditions were carried out covering two dry (October and November) and two rainy seasons

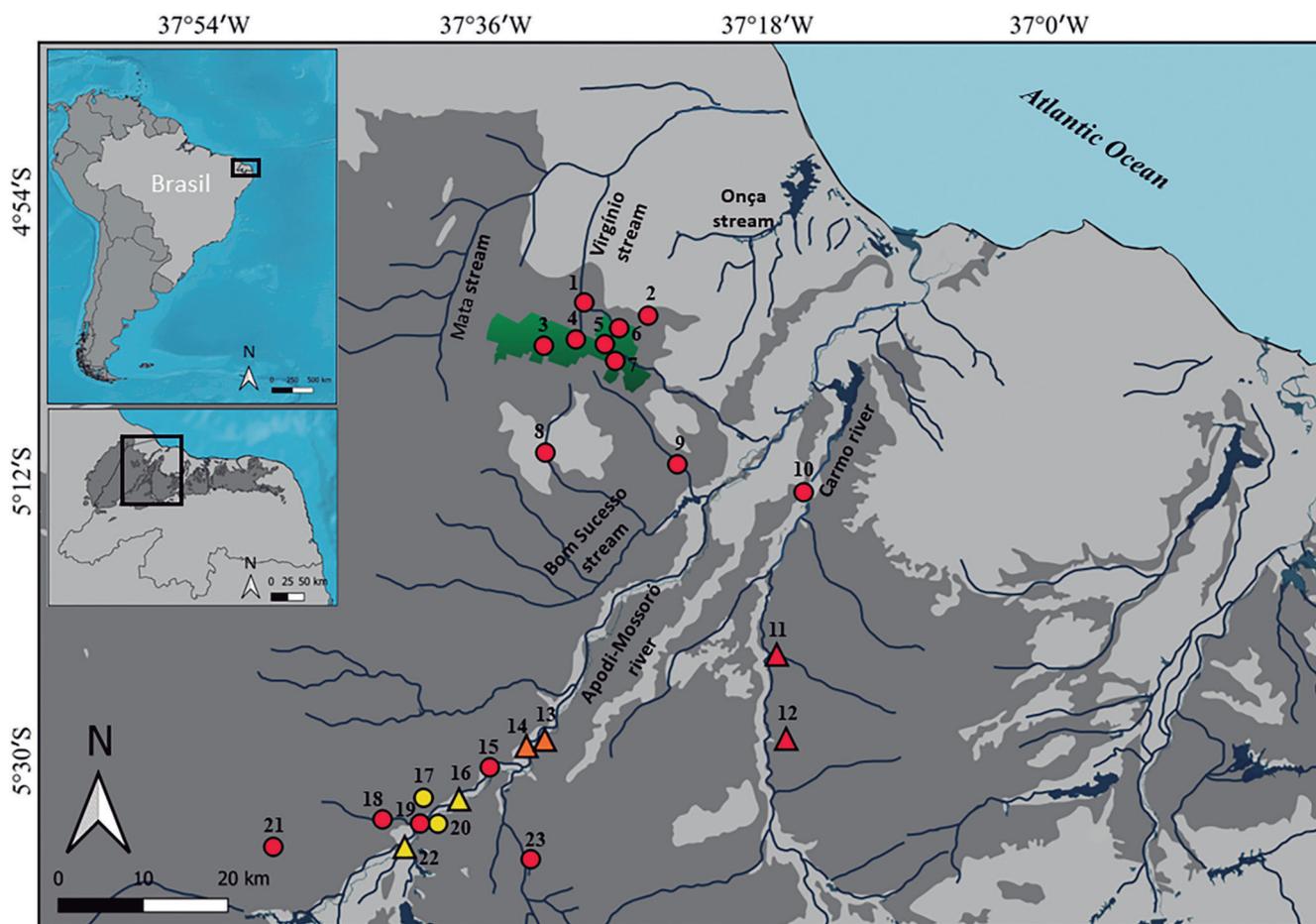


Figure 1. Map of the sampling sites in the karstic Jandaíra Formation (dark gray areas), Rio Grande do Norte State, Northeast Brazil. Dark blue lines indicate hydrography. Green shape shows the limits of the Furna Feia National Park. Circles represent temporary water bodies and triangles represent perennial localities. Surface sites are show in red, those associated to caves in orange, and caves in yellow.

(June) in 2018 and 2019. Each campaign included seven days of samplings. In the surface water bodies, fishes were collected using sieves (40 × 30 cm, mesh size 5 mm), hand nets (45 cm of diameter, mesh size 8 mm) and trawl nets (5 m length, mesh size 25 mm). The sampling effort in subterranean localities or associated to them consisted of visual observations through snorkeling, followed by active capture whenever possible, given the difficulties imposed by subterranean habitats.

The 23 sampling sites were classified as “surface”, “associated to caves”, and “caves”, according to the physical and ecological attributes indicated by Culver & Pipan (2009) (Table 1, Figs. 1 and 2). The hydrological regime of each site was also classified as perennial or temporary (Table 1, Fig. 3). For this characterization, we observed the localities in each season, in addition to investigating them temporally through the Google Earth Pro software (version 7.3.2.5776).

The specimens were anesthetized with eugenol solution (10 mL of eugenol diluted in 90 mL of ethanol), following Lucena *et al.*, (2013). They were subsequently preserved in 4% formaldehyde solution and then preserved in 70% ethanol, except for some fin-clip samples or small specimens preserved directly in ethanol P.A. 99% for molecular studies. In the laboratory, the specimens were identified according to available specialized

literature and taxonomic keys (Buckup *et al.*, 2007; Costa, 2001, 2007; Jerep & Malabarba, 2014; Ramos *et al.*, 2018). Vouchers are deposited in the ichthyological collection of the Universidade Federal do Rio Grande do Norte (Table 2). Due to the lack of information necessary for an ecological-evolutionary categorization, we were not able to identify if there are troglomorphic fish species among those we collected in the present study. However, we tried to identify evidences of troglomorphisms (traits related to live in caves), such as loss or reduction of eyes or loss of pigmentation, in the specimens collected (Sket, 2008; Culver & Pipan, 2009; Trajano, 2021).

The taxonomic nomenclature and classification followed Eschmeyer’s Catalog of Fishes (Van der Laan *et al.*, 2022). The conservation status of each species is indicated according to the Brazilian list of threatened fish species (MMA, 2022). Species endemism in the MNCE was defined by Berbel-Filho *et al.* (2018). Google Earth Pro (version 7.3.2.5776) and QGIS (version 3.20) softwares were used to georeference the study area. Collections were carried out under permits 30532-1/2011 and 54274-2/2018, issued by the Instituto Chico Mendes de Conservação da Biodiversidade/Sistema de Autorização e Informação em Biodiversidade (ICMBio/SISBIO).

Table 1. Sampled sites of fish survey in the basins of the Jandaíra Formation karstic area in the Rio Grande do Norte State, Brazil. Abbreviations: A = Associated to cave, C = Cave, P = Perennial, S = Surface, T = Temporary. * Sampling sites in the Furna Feia National Park.

Locality	Microbasin	Geographic coordinates	Altitude	Habitat			Hydrology	
				S	A	C	T	P
1	Virginio stream	05°01'20"S 37°25'38"W	68 m	X			X	
2	Onça stream	05°00'29"S 37°29'43"W	58 m	X			X	
3*	Mata stream	05°02'52"S 37°30'15"W	107 m	X			X	
4*	Virginio stream	05°03'16"S 37°32'18"W	148 m	X			X	
5*	Virginio stream	05°03'10"S 37°28'24"W	138 m	X			X	
6*	Virginio stream	05°02'43"S 37°28'00"W	117 m	X			X	
7*	Virginio stream	05°04'15"S 37°27'44"W	139 m	X			X	
8	Bom Sucesso stream	05°10'09"S 37°32'12"W	97 m	X			X	
9	Bom Sucesso stream	05°10'54"S 37°23'46"W	29 m	X			X	
10	Carmo river	05°12'42"S 37°15'42"W	19 m	X			X	
11	Carmo river	05°23'09"S 37°17'25"W	35 m	X				X
12	Carmo river	05°28'34"S 37°16'49"W	64 m	X				X
13	Apodi-Mossoró river	05°28'49"S 37°32'28"W	39 m		X			X
14	Apodi-Mossoró river	05°29'14"S 37°33'30"W	42 m		X			X
15	Apodi-Mossoró river	05°30'24"S 37°35'45"W	40 m	X			X	
16	Apodi-Mossoró river	05°32'28"S 37°37'43"W	48 m			X		X
17	Apodi-Mossoró river	05°32'47"S 37°39'59"W	81 m			X	X	
18	Apodi-Mossoró river	05°33'45"S 37°42'36"W	89 m	X			X	
19	Apodi-Mossoró river	05°34'01"S 37°40'12"W	57 m	X			X	
20	Apodi-Mossoró river	05°33'46"S 37°39'54"W	70 m			X	X	
21	Apodi-Mossoró river	05°35'31"S 37°49'35"W	120 m	X			X	
22	Apodi-Mossoró river	05°35'32"S 37°41'11"W	52 m			X		X
23	Apodi-Mossoró river	05°36'19"S 37°33'08"W	74 m	X			X	



Figure 2. Examples of sampling sites in karstic areas of the Jandaíra Formation in Rio Grande do Norte State, Brazil. Surface habitats of sites 5, 11 and 18 (A, B and C), habitats associated to caves of sites 13 (D and E) and 14 (F), cave habitats of sites 16, 17 and 22 (G, H and I).

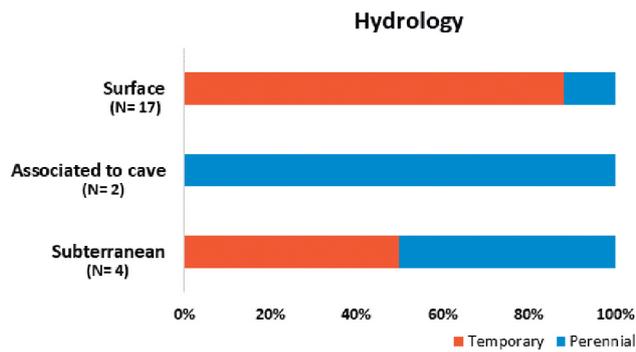


Figure 3. Hydrology regime in habitats (surface, cave associated, and cave). Abbreviation: N = number of sites sampled.

RESULTS

Among the 23 sampling sites, 17 were classified as surface areas, two as associated to caves, and four as caves (Table 1). According to the hydrology regime, we classified 17 sites as temporary, since the water levels drastically declined during the dry periods, while six localities were classified as perennial, with low water level fluctuations between seasons.

In total, 829 specimens were captured and identified as belonging to 21 species and genera, distributed in nine families and five orders (Table 2, Fig. 4A). Four additional species (*Steindachnerina notonota*, *Leporinus piau*,

Table 2. Taxonomic list of fish species in the karst areas of the semiarid Jandaíra Formation. Abbreviations: A = cave associated, C = cave, DD = data deficient, END = endemic, LC = least concern, NE = not evaluated, NNA = non-native, UFRN = Universidade Federal do Rio Grande do Norte, S = surface. — = Visually recorded only, * Recorded in the Furna Feia National Park.

Taxon	Habitat	Site	Voucher	Status
CHARACIFORMES (14)				
Curimatidae (1)				
<i>Steindachnerina notonota</i> (Miranda Ribeiro, 1937)	A	13,14	—	LC
Prochilodontidae (1)				
<i>Prochilodus brevis</i> Steindachner, 1875	S,A,C	10,13,14,16	UFRN 5112	LC
Anastomidae (1)				
<i>Leporinus piau</i> Fowler, 1941	A,C	13,14	—	LC
Erythrinidae (2)				
<i>Hoplerethrinus unitaeniatus</i> (Spix & Agassiz, 1829)	S	12	UFRN 5739	LC
<i>Hoplias malabaricus</i> (Bloch, 1794)	S,A,C	12,13,14,15,16	UFRN 5737	LC
Characidae (8)				
<i>Cheirodon jaguaribensis</i> Fowler, 1941	S	10	UFRN 5749	DD,END
<i>Moenkhausia costae</i> (Steindachner, 1907)	S	11	UFRN 5753	LC
<i>Psalidodon fasciatus</i> (Cuvier, 1819)	S	9	UFRN 5716	LC
<i>Astyanax bimaculatus</i> (Linnaeus, 1758)*	S,A,C	6,9,10,11,12,13, 14,15,18,19	UFRN 5999	LC
<i>Compsura heterura</i> Eigenmann, 1915	C	16	UFRN 5069	LC
<i>Hemigrammus marginatus</i> Ellis, 1911	S,C	10,11,16	UFRN 5094	LC
<i>Pselogrammus kennedyi</i> (Eigenmann, 1903)	C	11,15,16	UFRN 5093	LC
<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	C	9,10,16	UFRN 5091	LC
Crenuchidae (1)				
<i>Characidium bimaculatum</i> Fowler, 1941	S	12	UFRN 5746	LC,END
SILURIFORMES (3)				
Auchenipteridae (1)				
<i>Trachelyopterus galeatus</i> (Linnaeus, 1766)	A, C	13,14,16	UFRN 5103	LC
Loricariidae (2)				
<i>Hypostomus puarum</i> (Starks, 1913)	S,A,C	10,11,14,16	UFRN 5096	LC,END
<i>Loricariichthys derbyi</i> (Fowler, 1915)	S,A	11,14	UFRN 5737	LC
CYPRINODONTIFORMES (3)				
Rivulidae (2)				
<i>Cynolebias micropthalmus</i> Costa & Brasil, 1995	S	8,9	UFRN 5623	LC,END
<i>Hypsolebias antenori</i> (Tulipano, 1973)*	S,C	3,7,8,9,17,18,20,21	UFRN 5624	LC,END
Poeciliidae (1)				
<i>Poecilia vivipara</i> Bloch & Schneider, 1801	S,C	10,11,12,13	UFRN 5099	LC
SYNBRANCHIFORMES (1)				
Synbranchidae (1)				
<i>Synbranchus marmoratus</i> Bloch, 1785	C	22	—	NE
CICHLIFORMES (4)				
Cichlidae (4)				
<i>Cichla</i> sp.	A	13	—	NNA
<i>Cichlasoma orientalis</i> Kullander, 1983	S,A	10,11,13,14,19	UFRN 5738	LC
<i>Crenicichla brasiliensis</i> (Bloch, 1792)	S,A	11,13,14,19	UFRN 5702	LC
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	S,A	13	UFRN 5101	NNA
Total = 25				

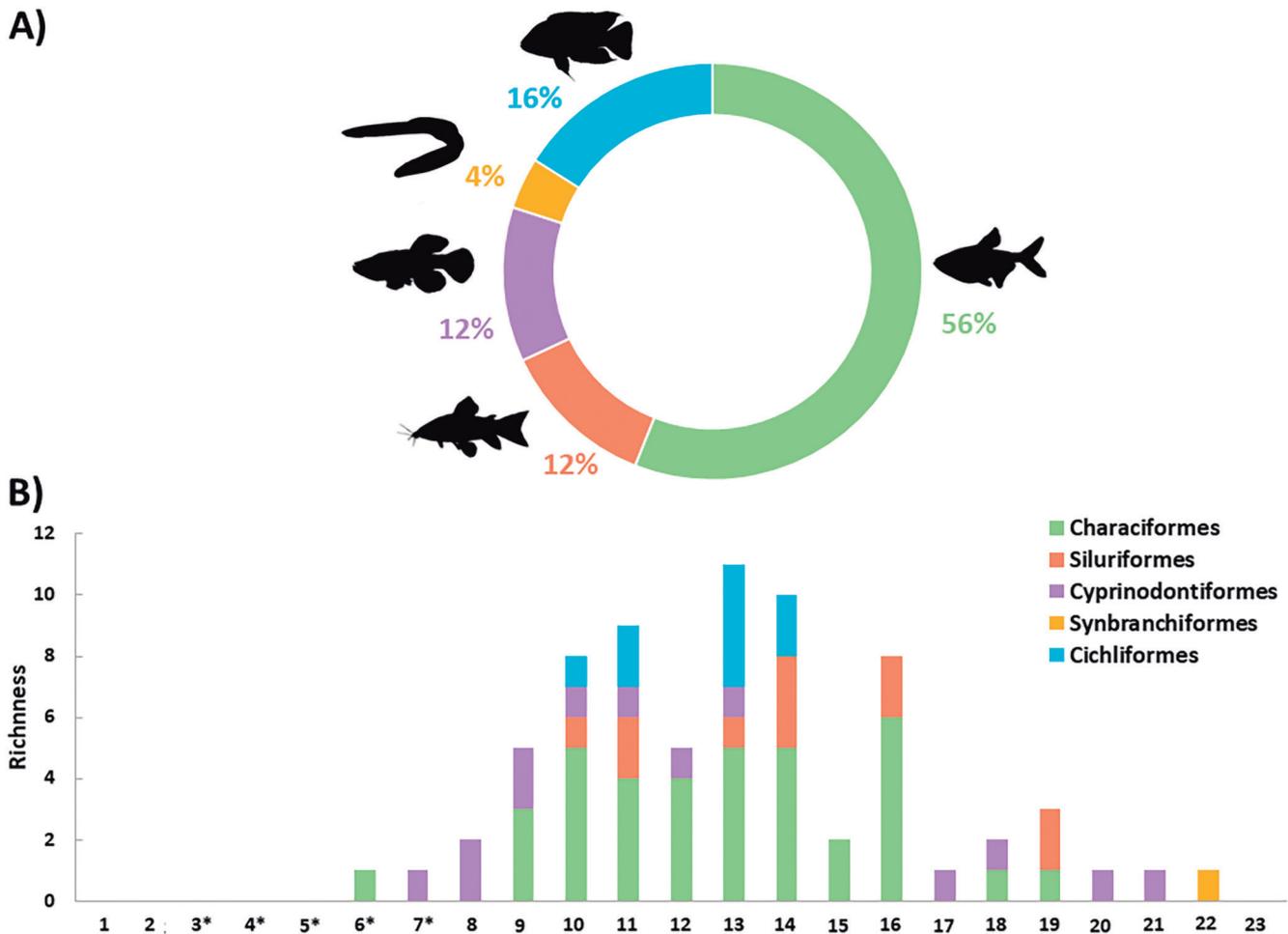


Figure 4. Graphic representation of fish by orders (A), and fish richness in each sampling site (B). * Located in the Furna Feia National Park.

Synbranchus marmoratus and *Cichla* sp.) were only visually recorded through snorkelling in surface (11) and subterranean (13, 14 and 22) localities of the Apodi-Mossoró river basin (Fig. 2). In this study, we did not find evidences of troglomorphy in any fish specimen, therefore, all species recorded in the subterranean environments were considered as non-troglomorphic (Trajano, 2012). However, we recorded 64.1% of the ichthyofauna of the Apodi-Mossoró river occurring in habitats associated with caves or in caves (Silva et al., 2020).

The most representative order was Characiformes, with six families, 14 genera and species (56% of the total), followed by Cichliformes with one family, four genera and species (16% of the total). Siluriformes and Cyprinodontiformes were both represented by two families, three genera and species each (summing up 24% of the total) (Table 2, Fig. 4A). Synbranchiformes was represented by a single species (*Synbranchus marmoratus*), visually recorded at the Três Lagos cave (22).

The predominant orders in terms of number of species in the three types of habitats were Characiformes and Cyprinodontiformes, distributed in 11 sites, followed by Siluriformes occurring in six (Table 2, Fig. 4B). The most commonly observed species by habitat were *Astyanax bimaculatus* in the surface sites, *Cichlasoma orientale* and *Trachelyopterus galeatus* in cave associated sites (Figs. 5C, D and F), and *Hypsolebias antenori* in caves.

Our results showed that sites associated to caves (13 and 14) harbor more species (n = 11) in comparison to the surface (n = 9) and subterranean ones (n = 8) (Fig. 4B).

Of the 25 species recorded, two were introduced in the Caatinga's rivers (*Oreochromis niloticus* and *Cichla* sp. (Figs. 5C and I). Four species are endemic of the MNCE (*Cheirodon jaguaribensis*, *Characidium bimaculatum*, *Cynolebias microphthalmus*, and *Hypsolebias antenori*). None of the species recorded is currently included in the Brazilian endangered fish fauna lists (MMA, 2022).

The sites visited in or near the Furna Feia National Park are all shallow temporary (from site 1 to 7), where only the piaba *A. bimaculatus* (6) and the seasonal killifish *Hypsolebias antenori* (3 and 7) were recorded. *Hypsolebias antenori* also occur in sympatry with another seasonal killifish species, *C. microphthalmus*, in two temporary pools (8 and 9) located 12 km south of the conservation unit.

Besides exhibiting the higher richness in the study, the cave associated sites (13 and 14) are also the most affected by anthropogenic action. While the first site (13, Fig. 2E) is visited in a disorderly manner generating plastic waste pollution, the second (14, Fig. 2F) faces the impacts of limestone and native-wood extraction, the latter is used as burning fuel in the production of lime. This implies in deforestation, silting and even toxic residues flowing into the headwaters and streams.

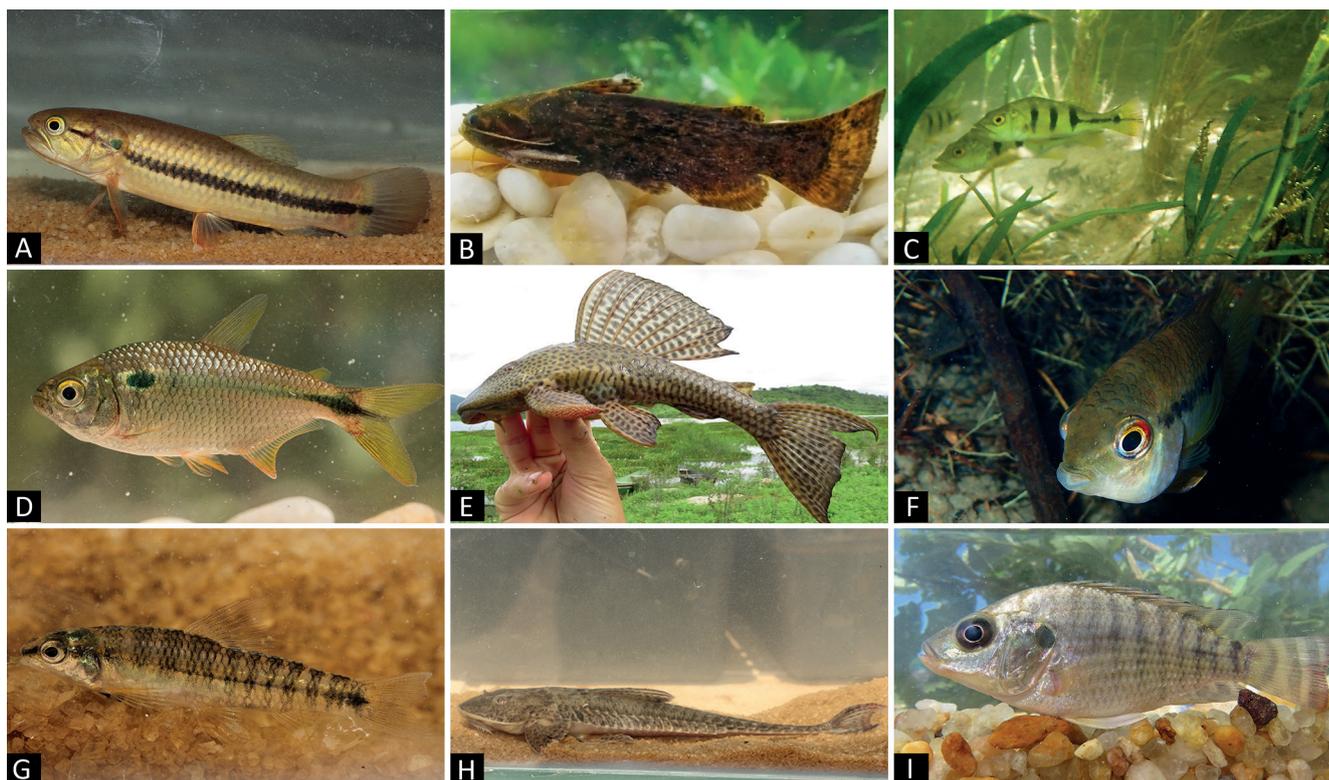


Figure 5. Examples of fishes recorded in the Apodi-Mossoró river basin, Jandaíra formation karst, Rio Grande do Norte State, Brazil. (A) *Hoplerythrinus unitaeniatus*, (B) *Trachelyopterus galeatus*, (C) *Cichla* sp., (D) *Astyanax bimaculatus*, (E) *Hypostomus pusalum*, (F) *Cichlasoma orientale*, (G) *Characidium bimaculatum*, (H) *Loricariichthys derbyi* and (I) *Oreochromis niloticus*.

Regarding the subterranean habitats, fishes were recorded in four flooded caves (16, 17, 20 and 22), of which only site 16 has a community composed of eight species. In the other caves (17 and 20), the seasonal killifish *H. antenori* was recorded in the Toco and Rosario outcrops, respectively (Fig. 2H). In the cave at site 22 only *S. marmoratus* was observed and was the only fish recorded in this cave, even though it has connections with superficial headwaters (Fig. 2I).

DISCUSSION

In the last decade, the knowledge of the fish fauna in Rio Grande do Norte (RN) State basins has increased drastically (Nascimento *et al.*, 2014; Paiva *et al.*, 2014; Costa *et al.*, 2017; Medeiros *et al.*, 2019). However, none of these studies has focused on fishes occurring in subterranean habitats. This can be explained in part by the difficulty of accessing and collecting in subterranean and karstic environments, and by the fact that many fish studies in the Caatinga restricted their investigations to the main courses of the drainages (Rosa & Groth, 2004). The first occurrences of fishes in RN's caves were reported by Ferreira *et al.* (2010), who highlighted the diversity of invertebrates and vertebrates in the subterranean ecosystems of RN. Among fish species, *Astyanax bimaculatus*, *Hoplias malabaricus*, and *Synbranchus marmoratus* were recorded in a cave in the municipality of Felipe Guerra. Herein, we expand the number of species that occur in the karst environments of the Jandaíra Formation

to 22 fish species, 16 of which were recorded in caves. These species have already been recorded in the Apodi-Mossoró river basin (Silva *et al.*, 2020), but 10 of those species represent new records in caves in the RN.

The two seasonal killifishes species sampled, *C. microphthalmus* and *H. antenori* (in the sites 3, 7, 8 and 9), have been previously recorded by Abrantes *et al.* (2020), which also pointed out the anthropogenic pressures affecting the temporary pools in the region. Abrantes *et al.* (2020) suggested an expansion of the current area of the FFNP as the main protection measure for the conservation of these two species. An alternative approach for the conservation of *C. microphthalmus* would be the introduction of some specimens in the FFNP sites 4 and 5 (temporary pools currently without fish). However, this would require *a priori* studies about the temporal and ecological dynamics of *C. microphthalmus*, as well as on the biotic and abiotic characteristics of the receiving sites.

The richness of fish species in the surface is considerably higher in the Carmo and Apodi-Mossoró rivers (Fig. 1 and 3B). Among the 17 surface sites sampled, sites 10, 11 and 12 (Fig. 3B) presented more species. The sites 10 and 12 (Fig. 6) stand out due to the record of *Cheirodon jaguaribensis* and *Characidium bimaculatum*, both endemic species to the MNCE drainages (Berbel-Filho *et al.*, 2018).

Through snorkeling, we observed that the environments associated to caves are the deepest (about 2 m depth) (Fig. 2F). It is possible that the diversity of fish communities in these environments is related to water depth, as suggested by significant correlations between depth and species richness (Taylor *et al.*, 1993; Rattou



Figure 6. *Hoplias malabaricus* (bottom right), shoal of *Astyanax bimaculatus*, and *Poecilia vivipara* in a shallow waterhole at site 12 in the Carmo river.

et al., 2018; Souza-Silva et al., 2021). In addition, the proximity to the Apodi-Mossoró main river, the perennial hydrology of some springs, and the partial illumination in the two sites associated to caves (13 and 14) can turn these habitats into refuges when the rivers start running low on water during the dry season.

Most of the surface habitats (90%) dry out completely in the dry season. In addition to the seasonal killifishes, other species found in our study have adaptations to poorly oxygenated environments that may facilitate their survival during the dry season. For instance, some specimens of *Poecilia vivipara* captured at site 10 had swollen lips, a trait usually associated to enhanced surface respiration in hypoxic conditions (Barros-Neto et al., 2020).

In addition to exhibiting the highest species richness, sites 13 and 14 are also the most negatively affected by anthropic activities and the presence of two introduced cichlid. Invasive species are a threat to the native fish fauna and the aquatic troglobitic invertebrates that occur at these sites (Bellard et al., 2016; Bento et al., 2021). The anthropic impacts identified in both sites were also reported by Cruz et al., (2010) as one of the main speleological impacts in RN, responsible for negative effects on the local flora and fauna. In this scenario, we consider surveillance and management actions by the competent environmental agencies as necessary in order to reduce habitat loss and to provide orientation and regulation toward sustainable tourism and exploration.

The region comprising the sampling sites 13 to 23 (Fig. 1), located mainly in Felipe Guerra and Governador Dix-Sept Rosado municipalities, was identified as of very high biological importance and as a priority area for the

Caatinga conservation (MMA, 2018). In this area, 40 species of woody trees and more than 200 species of amphibians, reptiles, birds and mammals were recorded (Marinho et al., 2018; Vargas-Mena et al., 2018; Sagot-Martin et al., 2020; Marques et al., 2021). In addition, the record of more than 700 caves in this region and the higher concentration of troglobitic invertebrate species in the RN complement this scenario of extreme biological relevance (CANIE/CECAV 2022, Bento et al., 2021). The human impacts in this region are mainly related to oil and natural gas production, as well as mining activities. We reinforce the proposal to create the Pedra de Abelha Environmental Protection Area, presented by Bento et al. (2015), aiming the protection of the surface and subterranean diversity, regulating spatial occupation, and ensuring the sustainable use of the natural resources.

The fish inventory of the karstic Jandaíra Formation area presented here represents an important advance in the knowledge on the diversity and distribution of Caatinga fish species, proposing cave associated habitats as putative refuges for the ichthyofauna during the dry period. Furthermore, this study does not exhaust the possibilities for potential troglobitic fishes inhabiting the Jandaíra Formation, considering that only a portion of the aquatic caves in the region have been sampled here and that we did not assess the populations dynamics in order to properly assess the ecological-evolutionary category to which the species found in the region belong. Finally, this study provides an updated list of the local ichthyofauna, and contributes to the characterization of habitats and anthropogenic impacts on the limestone outcrops of the Jandaíra Formation.

AUTHOR CONTRIBUTIONS: SMQL, DBM, YGA: Conceptualization; YGA, ABAB, SYLC: Methodology, Software Data curation, Formal analysis, Writing – original draft, Visualization, Investigation; YGA, SMQL, DBM, TPRA: Writing – review & editing; DBM: Funding acquisition; SMQL, DBM: Supervision. All authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

CONFLICTS OF INTEREST: Authors declare there are no conflicts of interest.

FUNDING INFORMATION: This study was supported with funds from the Chico Mendes Institute for Biodiversity Conservation (ICMBio)/National Center for Cave Research and Conservation (CECAV), as part of the project “Annual inventory of the national speleological heritage”. SMQL receives a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) productivity research grant (Nº Proc 312066/2021-0), SLYC (Nº Proc 152423/2022-2) and TPRA (Nº Proc 102460/2022-1) a CNPq post-doctoral scholarship, and YGA a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) master’s scholarship (Nº Proc 88887.684319/2022-00).

ACKNOWLEDGMENTS: The authors are grateful to the Centro Nacional de Pesquisa e Conservação de Cavernas (CECAV/ICMBio), especially to Iatagan Freitas and Uilson Paulo for their support in fish collections. To Dona Rita and Geilson Goes for their hospitality and field support in Felipe Guerra, and to the staff of the Laboratory of Ichthyology and Evolutionary Systematics (LISE) at UFRN who contributed to the field activities: Mateus Arthur, Mateus Germano, Lucas Paiva, Luciano Barros-Neto, Origilene Dantas and Salu Coelho.

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