



Fish functional trophic groups in headwater karst streams from the Upper Paraguay River basin

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Data obtained by direct observation of organisms in their natural habitats can provide valuable contributions regarding intra- and inter-specific interactions, as well as spatial distribution and trophic relationships. However, relatively few such data are available for the Neotropical ichthyofauna relative to the great species diversity of this region. We present data on the ichthyofauna in karst environments of the Serra da Bodoquena, Upper Paraguay River basin regarding their categorization into functional trophic groups. We used direct observations that focused on the most frequent feeding tactics and their spatial (vertical and horizontal) distribution in the channel. We observed 83 fish species in 17 functional trophic groups. The greatest species richness was concentrated in the Characidae and Loricariidae in the categories Diurnal Backwater Drift Feeders and Grazers, respectively. Regarding horizontal depth stratification, we found a positive relationship between the association of small fish with the shallow marginal habitats. This work represents a contribution to a region known for its high tourist potential and to the important diversity of the entire ichthyofauna of the Upper Paraguay basin region that requires proper conservation strategies for sustaining these species.

Keywords: Bodoquena plateau, Freshwater fish, Habitat use, Natural history, Pantanal streams.

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Dados obtidos pela observação direta dos organismos em seus habitats naturais podem fornecer valiosas contribuições com relação a interações intra e inter-específicas, além de distribuição espacial e relações tróficas. Entretanto, relativamente poucos dados estão disponíveis no que diz respeito à ictiofauna neotropical dada à grande diversidade dessa região. Apresentamos dados sobre a ictiofauna em ambientes cársticos da Serra da Bodoquena, bacia do alto rio Paraguai e a categorização das mesmas em grupos tróficos funcionais baseada em observações diretas relacionadas às táticas alimentares mais frequentes e à sua distribuição espacial (vertical e horizontal) no canal. Assim sendo, observamos 83 espécies de peixes alocadas em 17 grupos tróficos funcionais. A maior riqueza de espécies concentrou-se nas famílias Characidae e Loricariidae, abrangendo as categorias Catadores Diurnos de Itens Arrastados pela Corrente e Pastadores, respectivamente. Com relação à estratificação horizontal, encontramos a relação positiva entre a associação de peixes de pequeno porte com relação aos habitats marginais. Esse trabalho representa uma contribuição a uma região conhecida pelo seu alto potencial turístico e à importante diversidade da ictiofauna da região da bacia do alto Paraguai que requer estratégias de conservação adequadas para sustentar essas espécies.

Palavras-chave: História natural, Peixes de água doce, Riachos do Pantanal, Serra da Bodoquena.

INTRODUCTION

Knowledge of natural history plays a key role in the protection and conservation of species (Dayton, 2003; Bury, 2006; Tewksbury *et al.*, 2014). The intrinsic relationships of the animals within their natural habitats are useful to determine demography, nature, and geography of genetic and phenotypic variations, interactions with the environment and other species, priority areas for conservation, and enhancement of the cultural value of animals to human welfare (Greene, Losos, 1988). Although natural history studies date to the 18th century (Arnold, 2003), the high diversity of organisms worldwide remains a difficult challenge especially when considering diverse tropical freshwater ecosystems. Although these habitats represent 0.01% of the world's surface, they harbor one-third of all living vertebrate species, most of it composed of Neotropical fishes (Balian *et al.*, 2007).

Overall, instream fish populations are not randomly distributed, and dimensional stratifications are expected due to differences in species morphology, behavior or natural history. Moreover, the alteration or elimination of riparian forest cover is known as a main driver of habitat homogenization (Pusey, Arthington, 2003), and consequently the depauperating and homogenization of fish communities (Casatti *et al.*, 2012; Dala-Corte *et al.*, 2020). Hence, the knowledge of how fish communities are naturally distributed can help predict the impact and consequent loss of diversity according to the habitat alteration, as well as highlighting which species are more vulnerable to the impacts of the riparian vegetation loss. This approach is especially effective for small-

bodied species, because body size is positively correlated to a high potential for species extinction (Ripple *et al.*, 2017). An order-of-magnitude decrease of body mass in small bony fish species can increase up to 148% the odds of being threatened, considering worldwide vertebrates (Ripple *et al.*, 2017). Nonetheless, smaller species tend to have restricted distribution ranges which, in turn, is a proxy for the risk of extinction due to habitat loss (Nogueira *et al.*, 2010). At the population level, chronically disturbed populations tend to have increased average body size due to the decrease or total exclusion of recruitment, especially by the loss of spawning habitats, and the predominance of persistent older individuals (Murphy *et al.*, 2013). In the Neotropics approximately 70% of the more than 4,000 species are under 15cm of standard length (Reis *et al.*, 2003; Castro, Polaz, 2020). Because of their small size, direct observations of the horizontal stratification are needed for reliable data about the species dwelling at shallow marginal areas that directly depend on the allochthonous items from the riparian forest for food and shelter (Angermeier, Karr, 1983).

Fish species have a wide range of morphological diversity that results in a wide range of habitat use and food acquisition tactics (Matthews, 1998). A usual tool to determine trophic positions consists of classifying the species based on simplifying and synthesizing dietary information to define trophic guilds. Root (1967) defined the guild as 'a group of species that exploit the same class of environmental resources in a similar way'. In this way, the clustering of species within guilds summarizes similarities, determining which species share the use of common resources regardless of their taxonomic identity. Functional relationships are the basis for the comparisons among communities (Simberloff, Dayan, 1991). Trophic guilds are useful in describing the functional roles of species within ecosystems (Franco *et al.*, 2008), as well as in identifying the species most likely to compete for food resources (Specziár, Rezsú, 2009), simplifying complex food webs (Garrison, Link, 2000), and facilitating comparison across ecosystems (Elliott *et al.*, 2007). Just as trophic guilds are useful for understanding which resources are consumed, the functional trophic group (FTG) aims to identify how the resources are obtained by the animals (Brejão *et al.*, 2013). Species classification in FTGs summarizes behavioural relationships and food acquisition that sheds light on the natural history traits represented in the community (Uieda, 1984; Sazima, 1986; Sabino, Castro, 1990; Sabino, Zuanon, 1998; Casatti *et al.*, 2001; Brejão *et al.*, 2013). In this sense, naturalistic observations are easily applied in streams where water transparency is favorable in most of the year, like in clear-water karst streams.

Our study sites in central-western Brazil are in one of the most extensive continuous karst areas in Brazil, the Serra da Bodoquena. It consists of a north-south oriented plateau of about 200 km length whose waters drains into the Pantanal floodplain, making this region one of the most unique headwaters in the Upper Paraguay River basin (UPRB). Moreover, this region has numerous species of fishes with endemic or restricted ranges, such as *Hypostomus basilisko*, *H. froehlichii*, *H. perdido* and *Oligosarcus perdido*, which points out this region as a hotspot for conservation in the UPRB. Although the region is internationally known as a tourist destination due to its clear crystalline waters, the ecology of fishes that inhabit the streams (*e.g.*, trophic, morphological and distributional attributes) is poorly known. Nonetheless, the rapid conversion in the last decade from livestock grazing pastures to monocultures, especially soybean production, caused significant environmental damage to the streams, such as siltation and the increase in the

water turbidity after rainfalls (Chiaravalloti *et al.*, 2022). The threat of increased turbidity and associated impacts of land conversion affect the region not only from the economic perspective but also as an unprecedented factor on the population dynamic of native fish.

As a contribution to the understanding of functional and trophic aspects of fishes from streams in the Bodoquena plateau, this study defines and characterizes the functional trophic structure of the stream ichthyofauna in the southern Brazilian portion of Upper Paraguay River basin. Through direct observations, our main goal was to define the spatial distribution of the fish species in their natural habitats, as well as their microhabitat use and the intra and inter-specific relationships. Also, we provide a comprehensive compilation of studies of functional trophic groups to discuss how conservative and consistent the classifications are among different biogeographical domains and taxonomical levels. FTGs are important tools to describe the foraging habits of stream fishes because they allow the comparison among different communities with distinct evolutionary histories and can provide evidence for the phylogenetic niche conservatism hypothesis. According to this hypothesis, phylogenetically related species tend to retain similar ecological niches over evolutionary time (Losos, 2008). Hence, due to the biological constraints shared among phylogenetically related species, we expect to find a consistent pattern between the FTGs classification and the fish families among Brazilian biomes. Alternatively, families that have large morphological plasticity among the species within this taxonomic level can have more representatives in a single FTG. In this sense, we aim to define how many families are clustered by a FTG and how many FTGs can be present in each family.

MATERIAL AND METHODS

Study area. The Serra da Bodoquena is situated in the southwest of the state of Mato Grosso do Sul, in the Central-Western region of Brazil. This karst formation dates to the Precambrian (Sallun Filho, Karmann, 2007). The region still contains large remnants of its native vegetative cover, especially in the highland areas, that harbors headwater streams of the Upper Paraguay River basin (ICMBIO, 2013). The Serra da Bodoquena National Park (PNSB) is located on the western border of the Serra da Bodoquena. Created in 2000, the park is the only federal fully protected conservation unit in Mato Grosso do Sul. Covering 76,000 hectares, the PNSB is divided into Northern and Southern portions, each one containing a single main drainage. At the northern portion, the PNSB is drained by Salobra River that flows into Miranda River basin, the largest river basin in the region. Altitude of Salobra River ranges from 620 to 130 m.a.s.l. The Southern portion the PNSB is drained by the Perdido River, that occurs between 560 to 390 m.a.s.l. Perdido River flows into Apa River, the main watershed, and the southern limit of Upper Paraguay River basin (Fig. 1). Although most of the rivers are within the park limits, the headwaters of both rivers are outside the PNSB boundaries, without any protection. Besides these two major rivers, in its southern portion the PNSB also includes the headwaters from Formoso and Prata rivers, both flowing into the Miranda River basin.

Underwater observations. Underwater observations of interactions were made from 2005 to 2018 during the day and night, totalizing 360 h of snorkeling (280 days and 80 nights), using *ad libitum* and *focal animal* techniques (Lehner, 1996) on 10 stream stretches ranging from 100 to 2,000 m in length (Fig. 1). Observations were done in the Miranda River basin tributaries (Salobrinha stream, Salobra River, Sucuri River, Prata River, Formoso River and Formosinho stream); and in the headwaters and main course of the Perdido River. During the nocturnal observations, waterproof flashlights with red filters were used to minimize disturbance of individuals. Information about day or night time period, behavioral characteristics, mesohabitat use, vertical (water column) and horizontal (margin or main channel) distributions were recorded for each individual or group of individuals. Due to the particular physical characteristics within and among streams, marginal habitats were considered as those shallow and near stream banks, with low current, abundant aquatic plants and deposition of allochthonous material, such as leaves, logs and branches. In contrast, the main channel category was the stretch between lateral marginal habitats, with faster current, greater depth and a more homogeneous bottom substrate. Mesohabitats were classified in three physiognomies

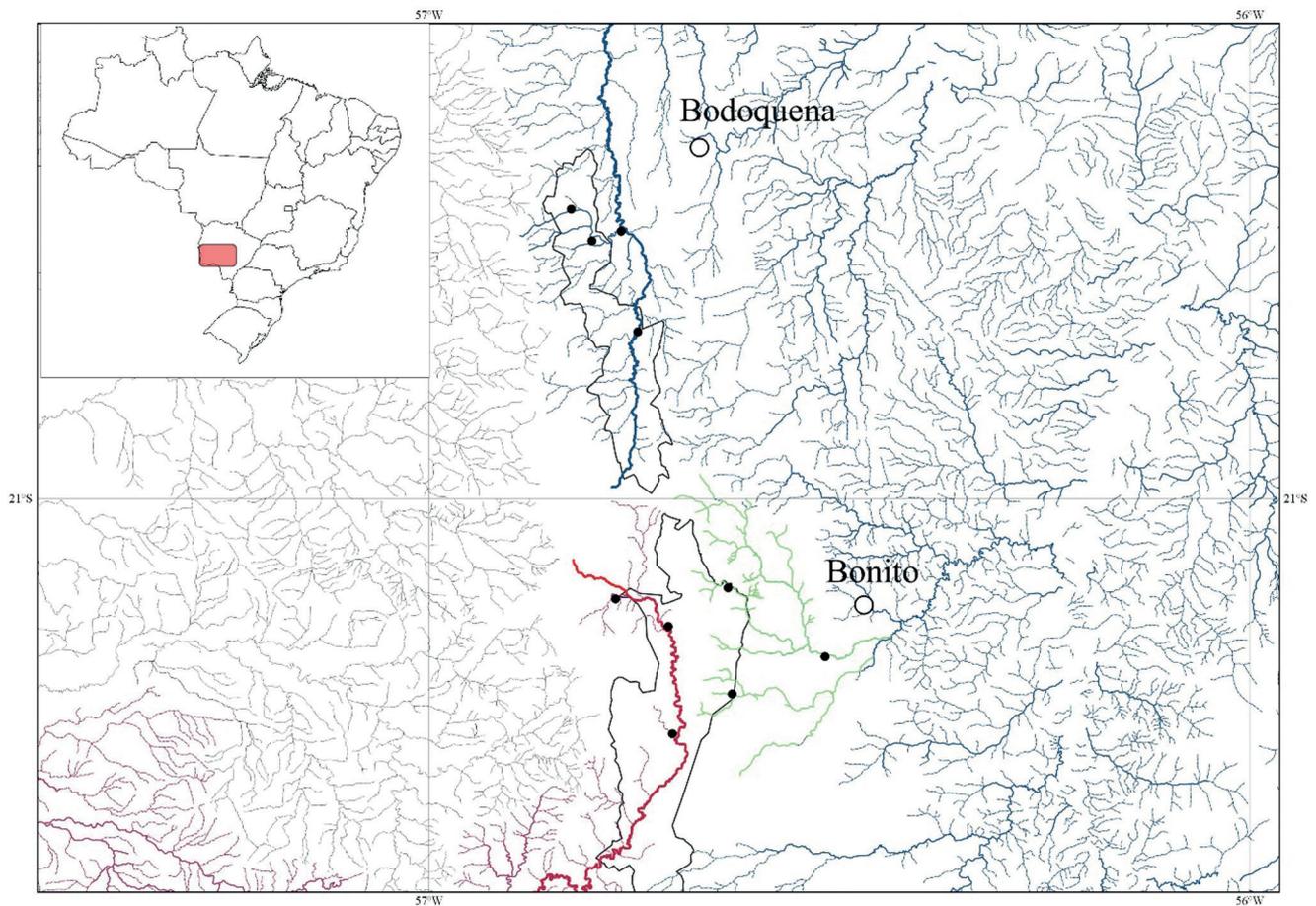


FIGURE 1 | Main drainages of Serra da Bodoquena. The Miranda River watershed (blue) and the Perdido River watershed (red). Highlighted lines represent Salobra River in the North and Perdido River in the South. In green, the Formoso River watershed, a tributary of Miranda drainage. Black dots represent the points of underwater observations of the fish species.

following Bisson *et al.* (2007): pools, to deep, low current and fine substrate (like sand, silt and clay) environments; riffles to shallow, fast current water environment, with coarse substrate and partially submerged pebbles and boulders; and runs as the intermediate environments between pools and riffles, with submerged rocks and fine to coarse substrate. Confirmation of species determination was made through the comparison among voucher specimens previously collected by other projects developed in the region and deposited at the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul (ZUFMS-PIS; Tab. S1).

To characterize the body-length distribution of the assemblages and to test the horizontal stratification of fish species according to their size, standard lengths were compiled from Britski *et al.* (2007) or from the original descriptions of the species. Body size classes followed Castro (1999) and Castro, Polaz (2020), in which small species were defined as being up to 15 cm in length, medium sized were between 15.1 and 44.9 cm, and large were those above 45 cm. To test the horizontal stratification, size classes (small, medium and large) and habitat distribution (margin or main channel) were tested through a Pearson's chi-square test performed in R software (R Development Core Team, 2020).

Functional trophic groups. Classification of functional trophic groups follows Sazima (1986), Sabino, Zuanon (1998), Casatti *et al.* (2001), and Brejão *et al.* (2013) according to foraging tactics and habitat use. The terms nektonic, nektobenthic and benthic follow the definitions of Lincoln *et al.* (1995): nektonic species swim freely in the water column, nektobenthic species are typically associated with the stream bottom and swim actively in the lower portion of the water column, and benthic species live on, in, or in close association with the stream bottom.

In order to compare our results within the Brazilian biomes context, a review of FTGs from Neotropical ichthyofauna is provided, based on the studies of Sazima (1986), Sabino, Zuanon (1998), Casatti *et al.* (2001), Brejão *et al.* (2013) and Freitas *et al.* (2021). The first study encompasses results from Pantanal, the next three from Amazon and the last from the Atlantic Forest.

RESULTS

A total of 83 species were observed and recorded, and were represented by Characiformes (with 47 species), followed by Siluriformes (23), Cichliformes (7), Gymnotiformes (3), Cyprinodontiformes (1), Beloniformes (1) and Synbranchiformes (1). The fish fauna is mostly composed of small species (N = 53, 64%), followed by medium sized (N = 20, 24%) and large species (N = 10, 12%). In terms of horizontal stratification, a significant difference was found between the richness of marginal and main channel habitats ($X^2 = 11.66$, $p < 0.05$) with small fish species predominantly occupying marginal habitats and large species associated with the main channel habitats (Fig. 2).

The ichthyofauna was composed mainly of nektonic (N = 37; 44%), followed by benthic (N = 29; 35%) and nektobenthic species (N = 17; 20%). Seventeen feeding tactics were used by the species (Tab. S1) and are described below. The most common feeding tactics were Diurnal Backwater Drift Feeder, with 18% of the species (N =

15); followed by Grazers, with 14% (N = 11) and Crepuscular to Nocturnal bottom predators with 11% (N = 9). Characiformes showed the highest number of feeding tactics (11), followed by Siluriformes (5).

Functional trophic groups. *Ambush and stalking predators:* Nektonic or nektobenthic species that ambush and/or stalk prey (Sazima, 1986; Sabino, Zuanon, 1998). This FTG included five medium-sized representatives from Characiformes and Cichliformes and three families (Erythrinidae, Serrasalminidae and Cichlidae). *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829) and *Hoplias malabaricus* (Bloch, 1794) were observed stationary on the bottom near the margins waiting to ambush prey during twilight and at night. *Serrasalmus marginatus* Valenciennes, 1837 was observed alone during the day, facing the prey while hiding its compressed body that matches submersed branches and roots. The cichlids *Crenicichla lepidota* Heckel, 1840 and *C. vittata* Heckel, 1840 usually used backwaters, transiting between the margins near the bottom and ambushing small fishes or invertebrates; *C. vittata* was more common immediately upstream and downstream of riffles.

Browsers: Nektonic fishes that bite off small pieces of plants (Sazima, 1986). This FTG was represented by two small Cheirodontinae species. Although they have not been observed eating plants, *Odontostilbe pequirá* (Steindachner, 1882) and *Serrapinnus calliurus* (Boulenger, 1900) formed large mixed shoals, foraging on filamentous algae on roots or rock surface or in high clusters of algae of about 3 m length that grow from the bottom to the surfaces in streams with small flow.

Crepuscular to nocturnal bottom predators: This group was represented by night shift species that explore the bottom of the water courses looking for small prey (Sazima, 1986). This FTG was composed of nine benthic and nektobenthic small to large specimens of catfishes from the families Heptapteridae, Pimelodidae, Pseudopimelodidae,

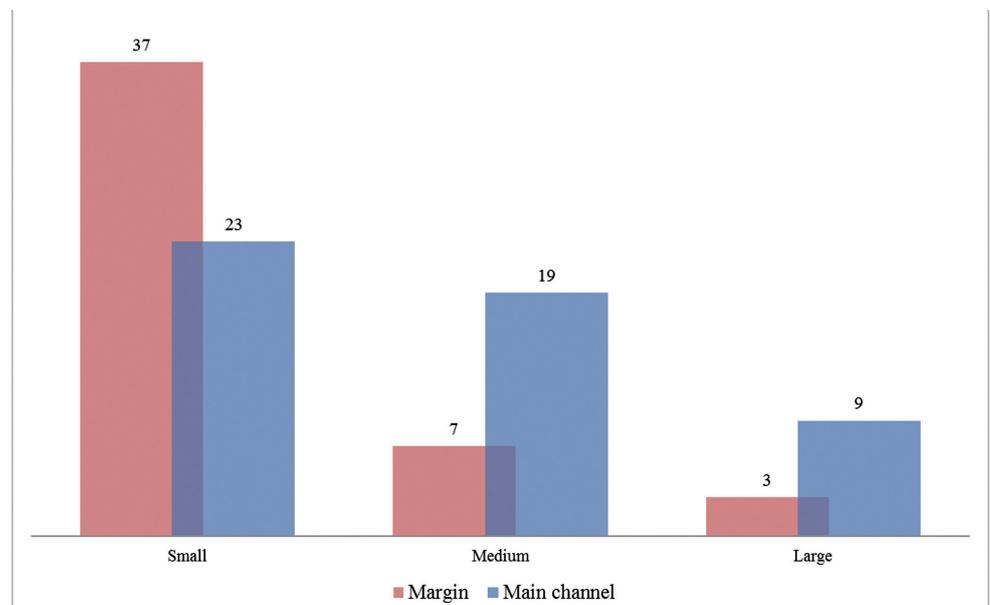


FIGURE 2 | Distribution of sizes classes of fish from Serra da Bodoquena stream according to instream horizontal occupation.

Trichomycteridae and Aspredinidae. *Pseudoplatystoma reticulatum* Eigenmann & Eigenmann, 1889, the larger representative of this FTG, remained stationary during the day under mats of floating macrophytes or inside naturally-formed holes in the margins, known as “locas”. During the night these individuals move along the bottom of the main channel exploring the environment with their barbels looking for prey, especially benthic fish species or tetras that remain stationary near the margins during the night. The same behavior and habitat use were observed for *Pseudopimelodus mangurus* (Valenciennes, 1835) that foraged exclusively alone. The other pseudopimelodid species, *Rhycoglanis paranensis* Shibatta & Vari, 2017, actively foraged together in the stream beds in shoals of up to ten individuals. *Imparfinis schubarti* (Gomes, 1956) and *Pimelodella taenioptera* Miranda Ribeiro, 1914 (Fig. 3D) move into shoals of up to 20 individuals, roving the streambed, looking for invertebrates among the pebbles by using their barbels to investigate the substrate wherever they locate prey. Although *I. schubarti* was more associated with fast-flowing waters, *P. taenioptera* used all mesohabitats, from

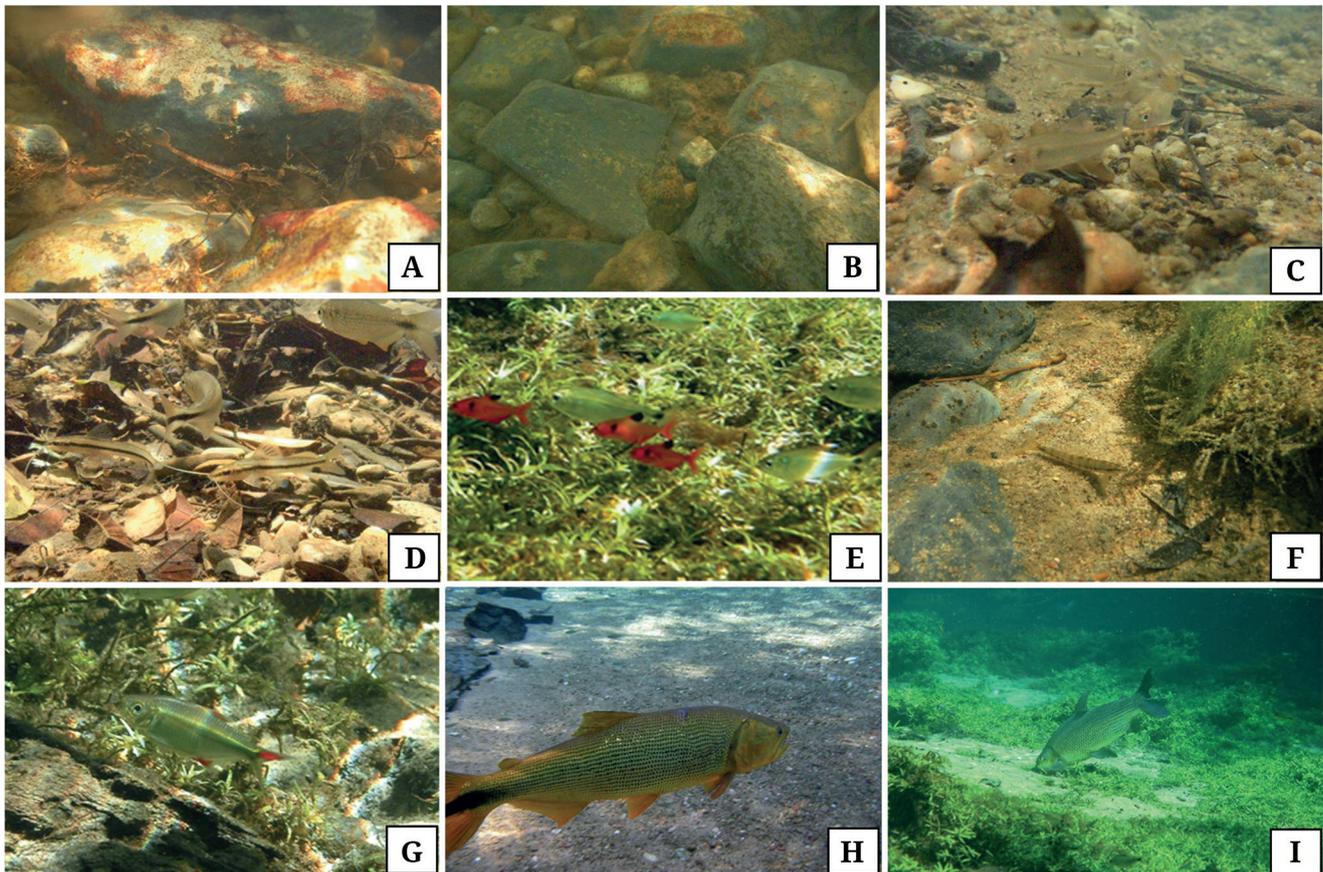


FIGURE 3 | Representative images of the fish assemblage from Serra da Bodoquena streams. **A.** *Farlowella paraguayensis* among twigs and leaf litter in the substrate; **B.** *Hypostomus froehlichii* between boulders; **C.** *Creagrutus meridionalis* foraging near a sandy substrate; **D.** *Pimelodella taenioptera* and *Astyanax lacustris* foraging among leaf litter in the substrate; **E.** *Hyphessobrycon eques* and *Jupiaba acanthogaster* using marginal vegetation; **F.** *Characidium zebra* using the sit-and-wait tactics on the sandy substrate; **G.** *Psalidodon marionae* foraging near the rocky substrate; **H.** *Salminus brasiliensis* swimming in the water column; **I.** *Prochilodus lineatus* foraging near patches of vegetation. Photos: Renato M. Romero and Fabrício B. Teresa.

riffles to pools (see Severo-Neto *et al.*, 2015b). *Rhamdia quelen* (Quoy & Gaimard, 1824) was observed alone or in small shoals of up to five individuals. In isolated pools, where it occurred alone, *R. quelen* could be observed using the whole water column, capturing moths or adults of Ephemeroptera at the water surface during the night. *Ituglanis herberti* (Miranda Ribeiro, 1940) and *Phenacorhamdia* sp. are reophilic species that occurred in the interstices of the pebbles under fast flowing mesohabitats, commonly associated with submersed or floating leaf litter. *Bunocephalus doriae* Boulenger, 1902 remained stationary during the day on soft mud substrates and leaf litter, possibly to mimic dead plant fragments with its body shape. During the night this species became active on this same substrate, probing its snout in the soft mud and litter to capture small prey.

Crepuscular to nocturnal drift feeders: Species with crepuscular to nocturnal habits that capture drifting prey in the water column and surface (Casatti *et al.*, 2001; Brejão *et al.*, 2013). *Tatia neivai* (Ihering, 1930) was the only species representing this FTG and remained stationary during the day, notably inside hollow submerged branches, and in spite of having a siluriform body pattern, usually associated with bottom activity, they were observed actively foraging throughout the water column during the night, capturing prey from the substrate to the surface.

Diggers: Species that actively dig into the substrate to feed on benthic organisms (Sazima, 1986). This FTG was only composed of the small Loricariidae species *Hemiodontichthys acipenserinus* (Kner, 1853) that occurred on sand patches in the streams bed at night, using its laterally expanded snout to dig in the substrate and to stir the sediment while looking for benthic organisms.

Diurnal backwater drift feeder: These nektonic fish species occur close to the margins in backwaters and forage on items suspended in the water column or close to the substrate (Sazima, 1986; Casatti *et al.*, 2001). This FTG contained 15 species, mainly the small Characidae fishes with laterally compressed body that occurred mainly in mixed shoals and were associated with roots or submersed macrophytes. *Hyphessobrycon eques* (Steindachner, 1882) (Fig. 3E) and *Moenkhausia bonita* Benine, Castro & Sabino, 2004 are the most conspicuous species in Salobra drainage due to their remarkable colors and were found next to the margins. *Aphyocharax anisitsi* Eigenmann & Kennedy, 1903 and *Bryconamericus exodon* Eigenmann, 1907 are active swimmers that were observed close to the margins and fed on autochthonous items. *Jupiaba acanthogaster* (Eigenmann, 1911) (Fig. 3E), *Psellogrammus kennedyi* (Eigenmann, 1903) and *Moenkhausia oligolepis* (Günther, 1864) were usually observed in shoals of about 20 individuals, using from the mid-water up to the upper surface areas for feeding. *Phenacogaster tegatus* (Eigenmann, 1911) and *Poptella paraguayensis* (Eigenmann, 1907) occurred in small shoals of conspecifics of up to six individuals and remained stationary at mid-water, investigating items that were sinking or at the surface. *Hemigrammus lunatus* Durbin, 1918 was the less common tetra species, occurring in shaded areas upstream or downstream to riffles, next to the margins. *Piabarchus analis* (Eigenmann, 1914) and *P. torrenticola* Mahnert & Géry, 1988 occurred in conspecific shoals on shallow areas, next to fallen logs or roots. *Creagrutus meridionalis* Vari & Harold, 2001 occurred in shoals of up to 30 individuals on sandy patches of low-flowing current (Fig. 3C). *Astyanax* sp. 2 and *Deuterodon luetkenii* (Boulenger, 1887) were the two tetras of this FTG found exclusively in Perdido River drainage, especially in calm water with dense vegetation near the margins.

Diurnal channel drift feeders: Nektonic species that mostly occupy the main channel during the day while foraging on food items drifting at the surface or mid-water (Sazima, 1986; Casatti *et al.*, 2001; Brejão *et al.*, 2013). This FTG was composed of 9 species, mainly of the small- to medium-sized tetra species with laterally compressed bodies and the larger “piraputangas” *Brycon hilarii* (Valenciennes, 1850). The most abundant species, *Astyanax lineatus* (Perugia, 1891), occurred in conspecific shoals up to 50 individuals. They foraged on items from the bottom to the surface of the streams, especially in shaded areas or next to fallen logs; *Astyanax abramis* (Jenyns, 1842) and *A. lacustris* (Lütken, 1875) (Fig. 3D) occurred in mixed shoals from mid water to the surface. *Psalidodon marionae* (Eigenmann, 1911) was the least common species of tetra, occurring alone or in small shoals of up to 5 individuals near the margins (Fig. 3G). *Astyanax* sp. 1 occurred in the midwater of runs. *Brachyhalcinus retrospina* Boulenger, 1892 was the only deep-bodied species of this FTG. It occurred in small conspecific groups of 5–10 individuals in small pools below waterfalls. *Brycon hilarii* was the largest species of this FTG and occurred from mid water to the surface, foraging on items that fall from the riparian forest, or jumping out of water to pick fruits from low level branches of the trees (Reys *et al.*, 2009). *Bryconops melanurus* (Bloch, 1794) occurred in shoals of up to 10 individuals roving close to the surface of the water and actively capturing insects and fruits that fell from the surrounding riparian forest.

Diurnal surface pickers: Species that swim near the surface, especially in backwaters, picking floating organisms or particles of organic debris (Sazima, 1986). This FTG was composed of one small species of Lebiasinidae, Characidae and Poeciliidae that occupy shallow densely vegetated margins and feed on invertebrates and debris. *Pyrhulina australis* Eigenmann & Kennedy, 1903 was observed usually alone, next to surface on marginal habitats, swimming among the branches or roots of aquatic plants. *Xenrobrycon macropus* Myers & Miranda Ribeiro, 1945 was observed always in conspecific shoals up to 40 individuals, swimming in mid-water to the surface, along the periphery of aquatic vegetation mats. The guppy, *Poecilia reticulata* Peters, 1859, despite being an exotic species in this region, was observed in impacted drainages, such as urban stretches of the stream, where it occupied shallow pools next to the margins, picking debris at the water surface.

Grazers: Benthic species that graze on attached algae from the substrate (Sabino, Zuanon, 1998; Brejão *et al.*, 2013). In this FTG were 11 small to large fishes, mostly represented by Loricariidae species, that have morphological adaptations such as dorso-ventrally flattened body and ventrally oriented mouth, for scraping their food from hard surfaces. *Hypostomus basilisko* Tencatt, Zawadzki & Froehlich, 2014, *H. froehlichii* Zawadzki, Nardi & Tencatt, 2021, *H. perdido* Zawadzki, Tencatt & Froehlich, 2014 and *Hypostomus* sp. 2 were the largest grazers observed. These grazers occupied the bottom of pools during the day in shaded areas or attached upside down on fallen logs. During the night they move to shallow areas to graze on algae from boulders and flat limestone rock surfaces (Fig. 3C). *Ancistrus* sp. occurred in fast-flowing habitats, such as rapids or below waterfalls, attached to the rocky substrate. Although this species could be observed during the day, larger individuals were more active during the night. *Loricaria luciae* Thomas, Rodriguez, Carvallaro, Froehlich & Castro, 2013 and *Rineloricaria lanceolata* (Günther, 1868) occurred on the bottom of pools and runs, usually on rocky substrates, matching its color pattern with the natural patches of light and shade of

the substrate. The twig catfish *Farlowella paraguayensis* Retzer & Page, 1997 (Fig. 3A), whiptail catfish *Rineloricaria parva* (Boulenger, 1895) and the Hypoptopomatinae *Otocinclus vittatus* Regan, 1904 mostly occupied soft leaf-litter substrates, where the first two species positioned their elongated stick-shaped body with submerged twigs and branches of submersed plant matter. The only non-loricariid grazer was the characiform *Parodon nasus* Kner, 1859 (Parodontidae) that occupied fast-flowing habitats, usually facing upstream while using its upper-jaw teeth to scrape algae and periphyton from flat limestone rocks.

Grubbers: Benthic species that feed on small benthic invertebrates through substrate probing while moving (Sazima, 1986). This FTG included two small Callichthyidae species that use their barbels to probe the uppermost layer of the substrate while foraging and eventually capturing prey. *Callichthys callichthys* (Linnaeus, 1758) and *Corydoras aeneus* (Gill, 1858) were observed in impacted stretches where erosive processes increased the amount of sand deposited in the bottom of the streams. *Callichthys* were observed alone during the night next to the margins and *Corydoras* occurred in shoals up to 20 individuals during the day, while exploring shallow low-flowing habitats.

Mud-eaters: Fish species that ingest soft substrate to feed on organic matter and minute organisms (Sazima, 1986). This FTG was composed of two small benthic *Steindachnerina* species and the large nektobenthic *Prochilodus lineatus* (Valenciennes, 1837), *Steindachnerina brevipinna* (Eigenmann & Eigenmann, 1889) and *S. nigrotaenia* (Boulenger, 1902). They are toothless species that occupy the bottom of the water courses in mixed shoals, picking mud using a head-standing position in pools and runs, especially over submerged leaf litter. *Prochilodus lineatus* was observed in large shoals of about 50 individuals, occupying the lower half of the water column and always foraging on rocky substrate or submerged logs, where they use the numerous small teeth implanted in their lips to scrape the surface (Fig. 3I).

Nibblers: These nektonic fishes forage by picking and biting food items on solid substrates (Sazima, 1986). In this FTG were five medium and large bodied-sized fishes, such as *Leporinus friderici* (Bloch, 1794) and *Megaleporinus obtusidens* (Valenciennes, 1837) (Anostomidae) that occupied from the midwater to the bottom of the water column, occurring with conspecifics or forming larger groups with *Piaractus mesopotamicus* (Holmberg, 1887) and *Prochilodus lineatus* shoals. They nibble fragments of fruits or invertebrates on the bottom or cut small pieces of aquatic macrophytes for food. *Leporinus striatus* Kner, 1858 and *Leporellus vittatus* (Valenciennes, 1850) moved alone exploring the bottom and the margins while picking invertebrates and fallen fruits from the streambed.

Nocturnal invertebrate pickers: Nektobenthic species that capture prey close to the substrate during the night (Brejão *et al.*, 2013). In this FTG were three medium size Gymnotiformes from the Apterotonotidae (*Apterotonotus caudimaculosus* de Santana, 2003), Gymnotidae (*Gymnotus carapo* Linnaeus, 1758) and Sternopygidae (*Sternopygus macrurus* (Bloch & Schneider, 1801)). These knifefishes move near the margin and among the boulders and logs looking for aquatic invertebrates inside litter banks, such as Odonata and Megaloptera larvae and adult shrimps.

Pickers and browsers: Nektobenthic species that pick and browse food items dispersed on the substrate or in organic debris, selecting food through their gill rakers (Sabino, Zuanon, 1998; Brejão *et al.*, 2013). In this FTG were five small and medium Cichliformes,

with daytime activity in low-current and highly heterogeneous habitats. The cichlids *Aequidens plagiozonatus* Kullander, 1984, *Australoheros* sp., *Bujurquina vittata* (Heckel, 1840) and *Cichlasoma dimerus* (Heckel, 1840) were observed usually alone or in pairs, exploring and defending areas close to the margins and chasing off other cichlids that came nearby. The non-native tilapia *Coptodon rendalli* (Boulenger, 1897) occurred in the Perdido drainage, where adult individuals occupied the water column close to the margins. Shoals of juveniles of about 10 cm total length used densely vegetated margins to pick food from the substrate and among the submersed plants.

Pursuit predators: Nektonic species that capture prey through pursuing (Brejão *et al.*, 2013). This FTG was composed of five species, from small to large Characidae and Belonidae fishes with elongated, torpedo-like bodies. *Acestrorhynchus pantaneiro* Menezes, 1992 and *Oligosarcus perdido* Ribeiro, Cavallaro & Froehlich, 2007 occurred alone or in conspecific shoals, attacking small fishes next to the surface from the margins in the direction of the main channel. *Aphyocharax dentatus* Eigenmann & Kennedy, 1903 was usually associated with runs, occurring alone or in shoals of 4 to 6 individuals and attacking fish even half their size; piscivory of this species was also demonstrated by Corrêa *et al.* (2009). *Salminus brasiliensis* (Cuvier, 1816) occurred in the main channel of the streams (Fig. 3H); adults usually alone and juveniles forming small shoals, mixed with *Brycon hilarii* adults, an example of predatory mimicry (Bessa *et al.*, 2011). *Potamorhaphis eigenmanni* Miranda Ribeiro, 1915 was observed alone or in up to five-individual shoals, hovering near the surface and striking fallen terrestrial invertebrates or small fish species, like *Xenobrycon macropus*.

Sit-and-wait predators: Benthic species that remain still while observing the surroundings and foraging on the nearby prey (Sazima, 1986; Brejão *et al.*, 2013). This FTG was composed of three species in two families (Crenuchidae and Synbranchidae) from two different orders (Characiformes and Synbranchiformes). The small *Characidium* species, *C. borellii* (Boulenger, 1895) and *Characidium* aff. *zebra*, remain stationary over a rock, faced towards the stream flow, searching the nearby substrate by moving only their head while looking for prey (Fig. 3F). *Characidium borellii* occupies the downstream stretches of shallow riffles. The second species was more often distributed over the entire stream bed. *Synbranchus marmoratus* Bloch, 1795 uses its elongated finless body to move amidst the interstices of the rocks during the day, at twilight and during the night. It puts its head or half of its body out of the rock crevices (similarly to the behavior of marine eels) and waits for preys, especially benthic invertebrates and fish.

Surface strikers: Species that occupy the uppermost layer of the water column, quickly capturing prey, such as fish or invertebrates that fall from the riparian forest (Goulding, Carvalho, 1984; Brejão *et al.*, 2013). This FTG was formed by the small nektonic Gasteropelecidae *Thoracocharax stellatus* (Kner, 1858). The species has hypertrophied pectoral fins and expansion of the coracoid bones, such as is observed in *Carnegiella* species, another Amazonian gasteropelecid species. *Thoracocharax stellatus* was observed during daylight periods, moving from the margins to the main channel and attacking invertebrates on the surface.

State-of-art of functional trophic groups among inland waters of Brazilian biomes. The compilation of FTGs defined in the available literature resulted in a total of 18 tactics represented in 31 families. Our study resulted in new data for the families Parodontidae, Pimelodidae, Prochilodontidae, Serrasalminidae; and two new FTGs to Characidae (browser and pursuit predator). The crepuscular to nocturnal bottom predator was the richest FTG with nine families (Fig. 4). Characidae was the family with more FTGs, with six tactics (Fig. 5). Nonetheless, 21 families (68%) were clustered in a single FTG regardless of biome (Fig. 4). Fourteen FTGs were shared between our results and those found for Amazonian species, and eight FTGs were shared with species from both Amazonian and Atlantic Forest streams (Fig. 4).

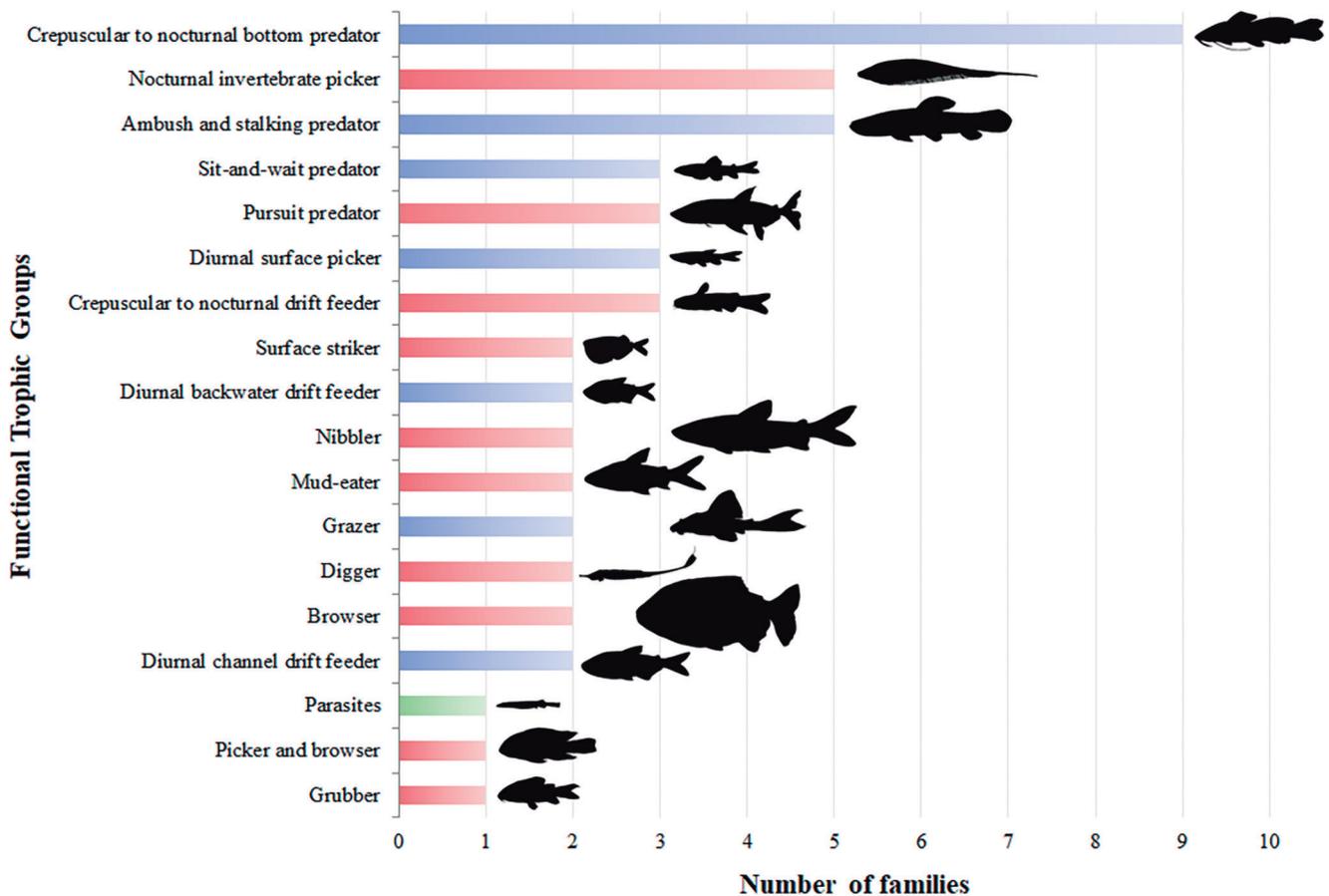


FIGURE 4 | Compilation of number of families on each Functional Trophic Group among different biomes in Brazil. Bar colors represent the shared FTGs among biomes considering Sazima (1986), Sabino, Zuanon (1998), Casatti *et al.* (2001), Brejão *et al.* (2013), Freitas *et al.* (2021), and this work. Blue bar: FTGs registered in Pantanal+Amazon+Atlantic Forest; Red bar: FTGs registered in Pantanal+Amazon; Green bar: FTG registered only in Amazon. Silhouettes represent the families with more records on each FTG.

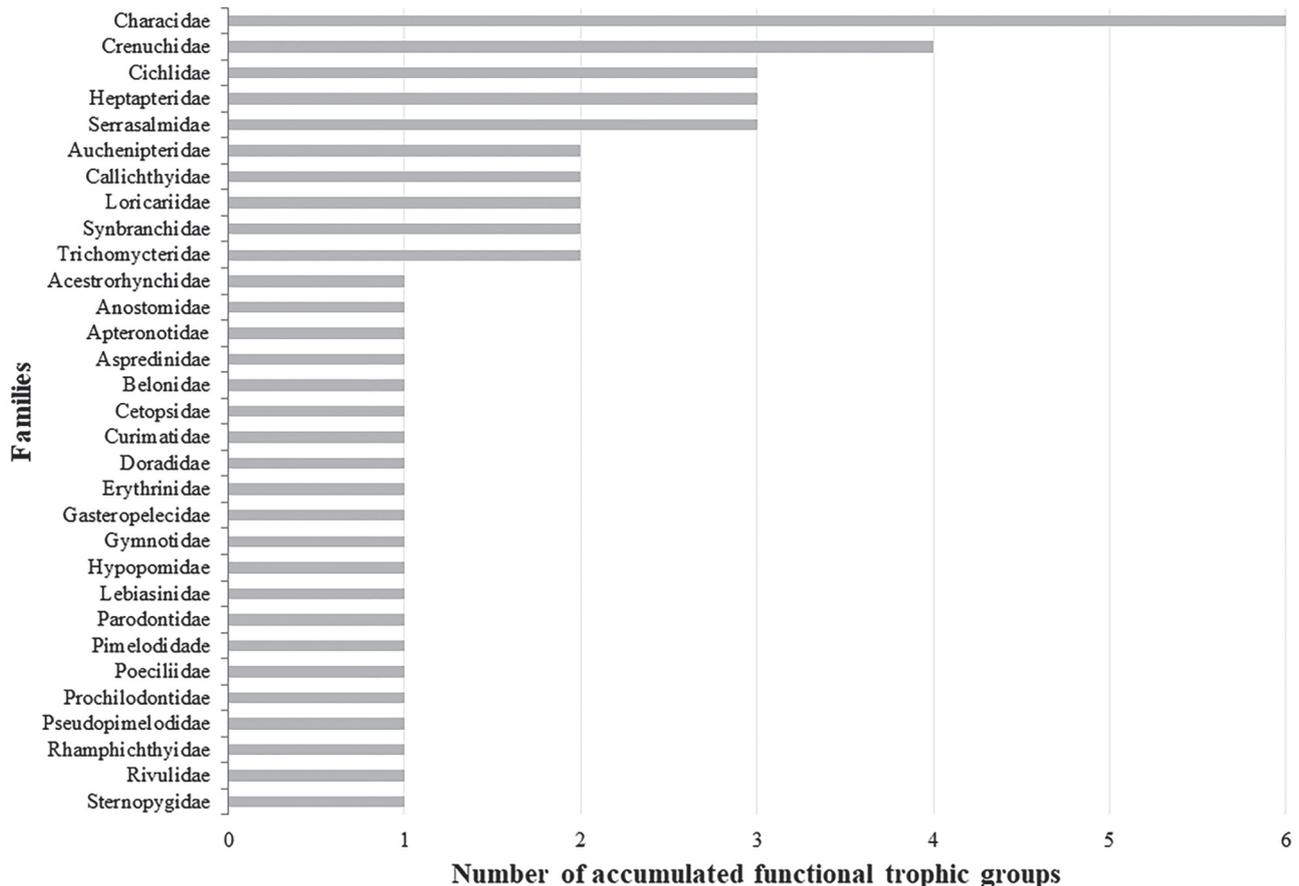


FIGURE 5 | Number of accumulated Functional Trophic Groups by fish families considering Brazilian inland freshwaters works from Sazima (1986), Sabino, Zuanon (1998), Casatti *et al.* (2001), Brejão *et al.* (2013), Freitas *et al.* (2021), and this work.

DISCUSSION

Physical habitat structure is a major factor influencing behavior and ecology of stream fish (Gorman, Karr, 1978; Smokorowski, Pratt, 2007; Dias *et al.*, 2010; Ortega *et al.*, 2021). A karst terrain such as the Serra da Bodoquena provides a distinct pattern of physical environmental heterogeneity in the southern portion of Upper Paraguay River basin (UPRB). While the Pantanal floodplain is located at an altitude of about 100 m.a.s.l. and smooth declivity, Serra da Bodoquena reaches from 200 to 800 m.a.s.l. (Sallun Filho, Karmann, 2007). This range in altitude contributes to the presence of fast flowing rivers that are less often found in the UPRB, and, consequently, contains reophilic species, as *Ancistrus*, *Phenacorhamdia* and *Parodon* which rarely occur in the floodplain. The association of some of the fish species to fast flowing habitats result in the convergence of morphological traits shared by species from different FTGs and taxonomical families, *i.e.*, expanded pectoral fins that deflects the water current and anchors the fish to the substrate. This feature has been described for the sit-and-wait predators Crenuchidae, the grazers Parodontidae (Casatti, Castro, 2006) and the crepuscular to nocturnal predators Heptapteridae. From a microhabitat perspective, the patches of sand, pebbles, boulders and limestone rocks in the substrate constitute

a diverse mosaic of foraging and refuge sites for the fish fauna that are not available in the floodplain. The large surface areas of boulders and limestone rocks are conducive to the growth of periphyton and other algae, which are fundamental for the diet of about the 15% of the studied species, especially for grazers of the families Loricariidae and Parodontidae. Furthermore, pebbles act as perches for sit-and-wait predators (such as *Characidium* species) from where they observe the surroundings while looking for invertebrates, or as foraging sites to Heptapteridae species that actively probe among the small rocks for small prey. Nonetheless, the narrow spaces available among the pebbles acts as refuges for adults of slender catfishes, such as *Trichomycterus* and *Phenacorhamdia*, and Loricariidae fry.

Sand patches develop suitable habitats to psammophilous (sand-dwelling) species that tend to have a sand-color pattern to remain cryptic relative to the substrate, performing sit-and-wait tactics, such as Heptapteridae, Crenuchidae, or buried in the sand during daytime and acting as nocturnal invertebrate pickers tactics, such as Rhamphichthyidae, families cited to Amazonian streams (Zuanon *et al.*, 2006). While sand patches are more common at higher-order streams and rivers, their presence in high the altitude streams from Serra da Bodoquena is associated with anthropogenic erosive processes, such as conversion of native vegetation to agriculture, urban influence or road construction outside the protected-conservation units. Due to the recent and unnatural sources of sand inputs to the stream beds, no true sand-dwelling species, such as those described by Zuanon *et al.* (2006) and their own tactics, were observed in Serra da Bodoquena streams. However, these patches were remarkably occupied by large shoals of *Creagrutus meridionalis* and the benthic-dwelling *Corydoras aeneus*. Indeed, the high abundance of *C. aeneus* has already been pointed out as an indicator of the loss of environmental quality in this region (Casatti *et al.*, 2010). We suggest that abundances of *C. meridionalis* should be considered as a bioindicator of recent siltation in the streambed.

Riparian forests play a key role in sustaining the aquatic diversity in the Neotropics (Dala-Corte *et al.*, 2020). Despite the anthropogenic influences in some reaches of the studied streams, riparian forests are present at different extents. Serra da Bodoquena streams have a diverse and well preserved riparian forest with high vegetation density within the conservation unit boundaries. Although we did not focus on gathering data about instream physical elements, the allochthonous input is an important factor shaping fish distribution and abundance in streams (Angermeier, Karr, 1983; Henry *et al.*, 1994; Mazzoni, Iglesias-Rios, 2002; Kawaguchi *et al.*, 2003; Perkins *et al.*, 2018). From the FTGs perspective, the riparian forest provides an input of wood and leaves that form the litter accumulations that are used by small fish seeking for refuge and food. Physical elements such as tree roots provide shelter to small backwater drift-feeder fishes, as well as cover for ambush and stalking predators. Fallen trunks become feeding sites for grazers that scrap the periphyton and the hollow logs function as day-time shelters used by crepuscular to nocturnal bottom predators, such as the driftwood catfish *Tatia neivai*. Although the habit of hiding in logs during the daytime is known for achenipterids (Rodriguez *et al.*, 1990), there is evidence that *Tatia* abundance is related to streams with more forested cover in Meridional Amazon (Casatti *et al.*, 2020). Taking one species as model, wood inputs are an essential component for *Tatia* species to persist. The environmental heterogeneity and habitats related to the presence of fallen trees and logs is critical for maintaining the diversity of species as a whole (Pusey, Arthington, 2003; Willis *et al.*, 2005; Arrington, Winemiller, 2006; Pettit *et al.*, 2013).

Along with the clear and well-recognized role of riparian forests for stream-dwelling fish communities, the instream vegetated margins are fundamental components to sustaining fish fauna diversity. Instream vegetation in Serra da Bodoquena streams is represented by a high specific richness of aquatic macrophytes with more than 40 species catalogued for the region (Scremin-Dias *et al.*, 1999). These heterogeneous, densely vegetated patches constitute the main habitat of many fish species that use them for shelter and food, especially the small bodied-sized fish. These small fish associated with the aquatic plants corresponded to 40% of the ichthyofauna richness from Serra da Bodoquena streams and were predominantly associated to the marginal habitats. We acknowledge that our study focuses on adult fishes while juveniles of larger fishes can also occupy marginal habitats. Marginal habitats can also be an integral home range of small fish (Ceneviva-Bastos *et al.*, 2010). The decrease in quality or total loss of marginal habitats can increase the extinction risk for small bodied-size fish, which already are the most threatened group of Neotropical ichthyofauna (Castro, Polaz, 2020). The streams in much of this region are a focus of ecotourism activities and tend to have protected riparian margins with strict rules about conserving vegetation. However, this riparian integrity is not typical in most of streams in the Formoso River basin, especially those historically used for livestock activities. In such areas, streams were used as source of water for cattle, that increased the trampling and siltation of the margins and totally suppressed aquatic macrophytes.

Our results reinforce the need for detailed knowledge of natural history of the tropical fish fauna to inform conservation policies and to sustain the future management and protection of stream-dwelling fishes. Also, this work provides a comprehensive comparison of functional trophic groups across Brazilian biomes. Despite the possible subjectivity associated with the categorization of species provided by different observers, the morphological constraints of the species limit the later categorization among FTGs. For example, the mouth orientation downwards of Loricariidae species is strictly associated with bottom foraging, typical for grazers. In contrast, the upwards mouth orientation in Lebiasinidae limits this family as surface pickers. Indeed, the two more consistent families regarding FTG classification across biomes were Heptapteridae and Sternopygidae (see Fig. 4), reflecting the biological features that constrains them from belonging to other groups, even among different drainages. On the other hand, the Characidae and Crenuchidae were the families with species belonging to the highest number of FTGs. The Characidae is one of the most diverse Neotropical families and has a wide range of species occupying several niches and, consequently, resulting in the highest number of functional groups. The Crenuchidae in turn have a notable differentiation between the *Crenuchus* and *Characidium* genera, in which the first is morphologically similar to midwater tetras and the second is a benthic species. In this way, the first can be considered as backwater or channel drift feeder while the second is more prone to use sit-and-wait or ambush tactics. In spite of these two cases, more than half of the Brazilian fish families belonged to only one FTG, indicating that the use of FTG can be useful tool, but also that this method of classification validates the phylogenetic niche conservatism through direct observation of the habits and foraging tactics employed by the fishes.

Data about species foraging and social behavior in their natural habitats can help elucidate distribution patterns and microhabitat preference that reinforce *a posteriori*

inference of studies using functional traits. As an example, *Rhamdia quelen* and *Tatia neivai* would parsimoniously be categorized as bottom feeders considering only their ecomorphological attributes. However, our direct observation reveals that these species are able to use the whole water column during foraging. Nonetheless, our results sheds light over the distribution of the often-neglected small fish species and their association to the margins of streams. Serra da Bodoquena has the potential to become a landmark in terms of stream's conservation and, from the ecosystem perspective, a source area to metapopulations across the entire basin, especially for small sized fish. During dry season in the Pantanal floodplain, most of the small-sized fish are retained in natural lagoons known as *baías*. In fact, a single *baía* can harbor more than a third of the amount of the species in the entire basin (Severo-Neto *et al.*, 2015a). Therefore, these habitats are important repositories of diversity and genetic pool of fishes which, in turn, play essential roles in the ecosystem dynamics. However, consecutive dry seasons in the last years have dried a large number of *baías*, consequently driving the loss of diversity and fish abundance. The Pantanal domain has lost 74% of water surface from 1985 to 2020 (Watanabe, 2021), which represents the highest water loss among all Brazilian biomes. The maintenance of small streams, which tend to be perennial, can be a key to avoid the simplification of fish communities in the Pantanal as a whole. The knowledge of natural history of the fish fauna in the Serra da Bodoquena streams makes a fundamental contribution to better understanding of how to conserve this unique set of species from Upper Paraguay River basin. Moreover, we emphasize the need for future research to further develop the Functional Trophic Groups classification based on direct observation of the fishes in their natural habitats. This technique can provide reliable and comparable information about species distribution at low cost across many streams from diverse freshwater ecosystems to provide general concepts of food-web structure and function.

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