Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon

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This study aimed to describe the functional organization of the ichthyofauna of forest streams from northeastern Pará State, Brazil, based on behavioral observation of species' feeding tactics. Seven streams were sampled between June and November, 2010, during snorkeling sessions, totaling 91h 51min of visual censuses at day, dusk, and night periods. Seventy three species distributed in six orders, 26 families and 63 genera were observed, with dominance of Characiformes, followed by Siluriformes. From information gathered by *ad libitum* observations, each species was included in one of 18 functional trophic groups (FTGs), according to two main characteristics: (1) its most frequently observed feeding tactic; and (2) its spatial distribution in the stream environment, considering their horizontal (margins or main channel) and vertical (water column) dimensions. The most frequent FTGs observed were Nocturnal invertebrate pickers (9 species), Diurnal channel drift feeders (8 spp.), Diurnal surface pickers (7 spp.), and Ambush and stalking predators (6 spp.). The FTGs herein defined enable a comparative analysis of the structure and composition of ichthyofauna in different basins and environmental conditions, which presents an alternative approach to the use of taxonomic structure in ecological studies. The ichthyofauna classification based in FTGs proposed in this study is compared to three other classifications, proposed by Sazima (1986), Sabino & Zuanon (1998) and Casatti *et al*. (2001).

Este estudo teve como objetivo descrever a organização funcional da fauna de peixes de riachos do nordeste do estado do Pará, Brasil, com base em observações comportamentais das táticas alimentares das espécies. Sete igarapés foram amostrados entre junho e novembro de 2010 por técnicas de observações diretas durante sessões de mergulho livre, totalizando 91h 51min de observação, nos períodos diurno, crepuscular vespertino e noturno. Foram observadas 73 espécies distribuídas em seis ordens, 26 famílias e 63 gêneros, com predomínio de Characiformes, seguidos por Siluriformes. A partir de informações coligidas por observações *ad libitum*, as espécies foram organizadas em 18 grupos tróficos funcionais (GTFs), de acordo com duas características principais: (1) a tática alimentar observada com maior frequência; e (2) sua distribuição espacial no riacho, considerando suas dimensões lateral (margens e canal central) e vertical (coluna d'água). Os GTFs mais frequentes foram Catadores noturnos de invertebrados (9 espécies), Coletores diurnos de canal (8 spp.), Catadores diurnos de superfície (7 spp.), e Predadores de tocaia e emboscada (6 spp.). Os GTFs aqui definidos possibilitam uma análise comparativa da estrutura e composição da ictiofauna, que representa uma abordagem alternativa ao uso da estrutura taxonômica em estudos ecológicos. A classificação da ictiofauna baseada em GTFs proposta neste trabalho é comparada com outras três classificações, propostas por Sazima (1986), Sabino & Zuanon (1998) e Casatti *et al*. (2001).

Key words: Feeding tactics, Natural history, Snorkeling.

Introduction

There are several factors that can contribute to determine the biological assemblages' structure and composition, including local environmental conditions and its temporal dynamics, and also intrinsic species features. However, there is no consensus about the relative importance of each of these factors on the assemblages' composition (Hérault, 2007).

Species with similar morphology, life history and autoecology can coexist in the aquatic environments (Frissell & Lonzarich, 1996) and also depend on the resources availability to survive in those environments (Peres-Neto, 1999). A set of species that subsist on the same type of resources is defined as a guild (Root, 1967). According to Odum (1986), trophic guilds are formed by groups of species with comparable roles and niche dimensions inside an assemblage. Thus, guilds can be defined

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independently of an organization based on taxonomic hierarchy, but from a common function that they play in the environment, allowing comparisons of the functional organization of different communities (Simberloff & Dayan, 1991).

Trophic guilds are defined by the diet of the species and describe "what" the fish eat. Based on this information, and combining with the species morphology, it can be inferred "where" (*e.g.*, water column, bottom) fish feeds (Matthews, 1998). The functional trophic group (FTG) concept advances by incorporating information about "how" the animal gets its food. Matthews (1998) emphasizes two important points: (1) knowing "how" fish feeds is related to the differences on the species ability to use similar food items; and (2) the way fish feeds can cause changes in the environment (*e.g.*: diggers may stir up benthic organic matter, debris and nutrients, or expose preys to other species while foraging), which could facilitate or inhibit foraging (and eventually the coexistence) of other species.

The way that fishes get their food is intimately related to their morphological and behavioral features. Food acquisition in fishes involves at least two main stages: (1) foraging (search, detection and approximation of the food item), and (2) feeding (capture and ingestion) (Keenleyside, 1979). The behavioral mechanisms used to obtain food by one species compose a feeding tactic (Alcock, 1993).

Although trophic ecology studies based on diet analysis allow the drawing of inferences about the feeding tactic(s) used by the species, direct observation of foraging behavior is usually the safest and most efficient way of obtaining this kind of information. The use of diving techniques for direct observation of the fishes is still rare as a sampling method in freshwater aquatic environments. However, this technique has been shown to be very efficient in behavioral studies, or to elucidate habitat use characteristics by the species (Uieda, 1984; Sazima, 1986; Sabino & Castro, 1990; Buck & Sazima, 1995; Sabino & Zuanon, 1998; Casatti *et al.*, 2001), generating information relevant to the natural history knowledge of freshwater fishes. This technique has the advantage of producing a low impact on the studied environment and, in addition, is considered to show low selectivity (Sabino & Zuanon, 1998). This sampling efficiency is especially relevant in environments with high richness and diversity of fish species, like in the Amazon basin, where a small stream can contain dozens of species (*e.g.*, Sabino & Zuanon, 1998; Anjos & Zuanon, 2007).

Nevertheless, the high diversity of species typical of most Amazon biological assemblages can make it hard to understand the ecological phenomena and faunal similarity patterns between study places and regions. Besides to the difficulties resulting from the selectivity of certain sampling methods, the occurrence of a significant percentage of rare species, represented by few individuals in a small fraction of the samples, can grossly underestimate the real ecological similarity between the compared assemblages. Furthermore, the use of ecological groups (replacing taxonomic groups) in comparative studies of biological assemblages can improve our ability to recognize and better understand general ecological patterns, facilitating comprehension of

ecological processes that operate at local and regional scales.

As a contribution to the understanding of functional groupings of Amazon fishes, this study aims to define and characterize the functional trophic structure of the ichthyofauna of small forest streams at eastern Brazilian Amazon, based on direct underwater observation of habit use and feeding tactics of the species in their natural environment.

Material and Methods

Study area

The study was accomplished on the northeast region of Pará State, which is one of the oldest occupation areas of eastern Amazon, where smallholder properties predominate. As a consequence of this old occupation, the original vegetation was nearly completely removed, remaining a few fragments of secondary degraded forest, frequently along the riverine network (Watrin *et al.*, 2009).

The main vegetation type in the past was Lowland Alluvial Dense Rain Forest, but nowadays it has been converted into cultivated fields and secondary vegetation of different ages (IBGE, 2004). The prevalent soil is Yellow Latosol, of medium texture and pH around 4.5, formed in Tertiary deposits of the Barreiras Group (Vieira *et al.*, 2003). According to Köppen's system, local climate is Af (Tropical rainforest climate) (Pachêco & Bastos, 2007). Total annual pluviosity varies around 2000 and 2800 mm; however, the monthly rainfall amounts are not distributed homogeneously throughout the year: higher pluviosity occurs between March and April, and lower amounts of rain in September and October. The maximum annual average air temperature is 32.2ºC, with monthly averages ranging from 30.9ºC (March) to 33.9ºC (November) (Pachêco & Bastos, 2007).

The streams that drain the region on flat terrain show sinuous unconfined channels with great structural complexity. The main channel overflows on the rainy season, flooding the forest zone adjacent for a few months. Substrate is predominantly sandy, with litter banks accumulating on the margins and depositional sections (pools); roots from riparian vegetation and submerged trunks and logs compose important habitat units, and are largely responsible for the channel structural complexity.

The studied stream reaches are located in the Maracanã and Marapanim River basins, at Igarapé-Açu, Marapanim and São Francisco do Pará counties (Fig. 1). Despite their proximity to the sea, they are not influenced by tide effects.

Study sites selection

The study was performed in small streams (orders 1 to 3 of Strahler's classification), in reaches with high structural integrity and in impoundments arising from anthropic changes. Favorable features to apply underwater observation techniques were considered, including local water horizontal transparency (at least 1 m), average channel width (minimum 2 m), and average depth (1 m). Stream reaches at places with evident signs of anthropogenic impacts (*e.g.*, presence of human habitation in
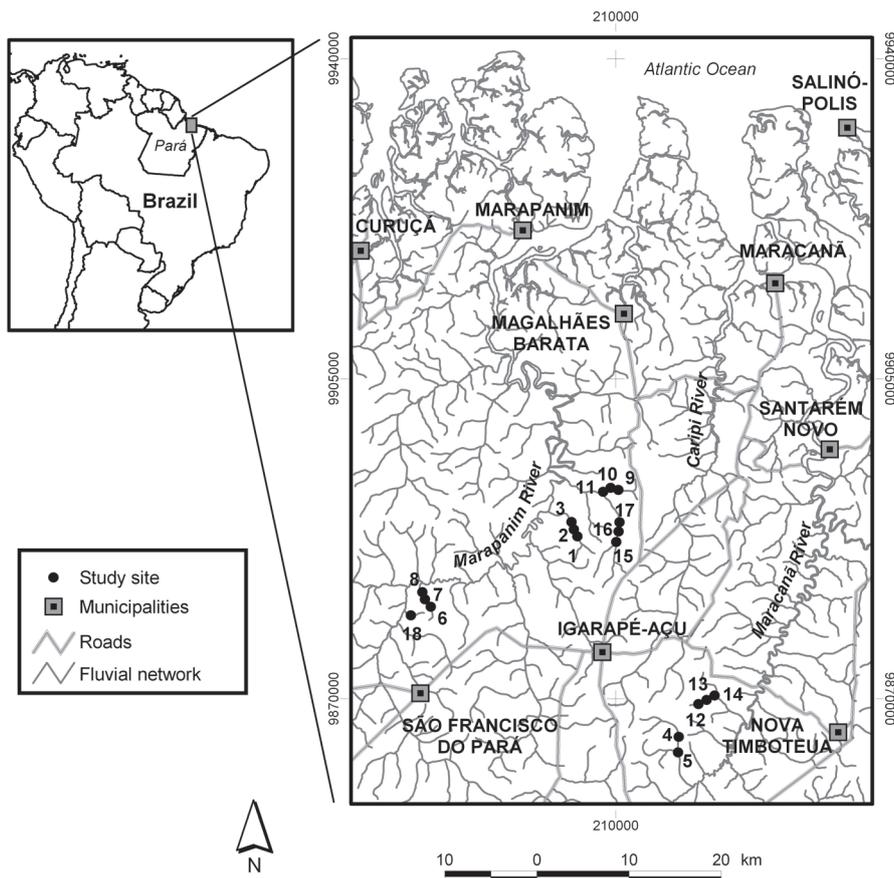
Fig. 1. Location of the 18 sampled streams reaches (enlarged detail) in the northeastern region of Pará. The road network shown on the map relates only to the main roads.

the surrounding areas, cattle presence or changes at riparian vegetation) were not included in this study.

Eighteen observation sites were installed in seven streams. Three of them are located on the Marapanim River basin (Marapanim county) and two in the Maracanã River basin (Igarapé-Açu county), all inserted in an area dominated by agricultural use. The remaining two streams also belong to the Marapanim river basin (São Francisco do Pará county), but are inserted in a forest matrix. Despite inserted in different environmental matrices, all studied streams were surrounded by riparian forest.

Sampling

Between June and November, 2010, 72 observations sessions were performed in seven streams, amounting 91h 51min of observations. The fishes were observed in 200 m long reaches of stream channel. In a previous study, it has been demonstrated that observations on a 200 m channel segment reveal between 98.1 and 100% (99.6% ±0.5, n=54) of the estimated local richness.

Behavioral observations were conducted during snorkeling sessions, through *ad libitum* and *focal animal* (Lehner, 1999)

methods. The observations in each sampled reach were performed in the downstream-upstream way, on three day periods, in order to observe the highest diversity of fish species in feeding activity: 1) diurnal (between 11:00 and 14:00); 2) dusk (between 17:00 and 18:30) and 3) nocturnal (between 19:00 and 21:00). During the nocturnal observations artificial illumination was used, provided by a diving headlamp. The observer moved upstream slowly (*ca*. 7×10^{-2} m.s^{-1}) and collected information about the observed individuals. For each individual or group of individuals observed in activity, the day period, position in the channel (margin or main channel; vertical position on water column), environment (substrate type, presence of submerged trunks, macrophytes), and behavioral characteristics, were registered. The information about the species was written with pencil on polystyrene plates of 15 x 20 cm during the snorkeling sessions.

Voucher specimens

Specimens of observed fish species were collected, preserved in 10% formalin, later washed in running water and maintained in 70% ethanol. The specimens were identified using identification keys (*e.g.*, Géry, 1977; Planquette *et al.*,

1996, Keith *et al*., 2000 a, b; Galvis *et al*., 2006, Sarmento-Soares & Martins-Ribeiro, 2008) and deposited at a reference collection maintained by one of the authors (PG). A representative set of the collected material was deposited at the Ichthyological Collection of the Museu Paraense Emilio Goeldi (MPEG 21370 to MPEG 21454, Table 1).

Functional Trophic Groups (FTGs)

The FTGs were formed according to the most frequently observed feeding tactic for each species, combined with their spatial distribution (both vertical and horizontal) in the stream reach. It were considered "where", "how" and "when" different species feed, framed in 15 predefined feeding tactics: Surface pickers, Drift feeders, Roving predators, Stalking predators, Ambush predators, Mud-eaters, Diggers, Browsers, Grubbers, Nibblers, Sit-and-wait predators, Crepuscular to nocturnal predators (*cf*. Sazima, 1986), Grazers, Parasites (*cf*. Keenleyside, 1979), and Invertebrate pickers (*cf*. Sabino & Zuanon, 1998). The terms nektonic, nektobenthic and benthic follow the definitions of Lincoln *et al*. (1995): nektonic species are organisms that swim freely in the water column, nektobenthic species are organisms typically associated with the stream bottom that swim actively in the lower portion of the water column, and benthic species are organisms living on, in, or closed associated to the stream bottom.

Results

Ichthyofauna characterization

During sessions 73 species were observed, distributed in six orders, 26 families, and 63 genera, in the seven studied streams (Table 1). Characiformes (38.4%) and Siluriformes (31.5%) were the most representative orders in number of species. Characidae, with 15 species (20.5%), and Cichlidae, with 10 (13.7%), were the most representative families.

The ichthyofauna was composed predominantly of nektonic species which occupies the shallow areas close to the stream margins. Of the 73 species, 34 (46.6%) are nektonic, 21 (28.8%) nektobenthic and 18 (24.7%) benthic (Table 1). Concerning to the lateral distribution, 44 species (60.3%) have been associated to the margins, 19 (26.0%) to the main channel and 10 (13.7%) frequently move between these two compartments. Fifteen feeding tactics were used by the species observed at the studied streams, however, the most frequent feeding tactics were Drift feeders, performed by 23 species (31.5%), and Surface pickers, by 21 species (28.8%).

Characiformes species showed the highest amount of feeding tactics and functional trophic groups, followed by Siluriformes (Table 2). Among the families, Cichlidae showed the highest amount of feeding tactics (n = 5), followed by Characidae (n = 4).

Functional Trophic Groups (FTGs).

A list of the 18 FTGs identified among the fish species of the streams of northeastern Pará State is shown below, including a short description relating to FTGs proposed by other authors, the list of species composing each group, and a brief description of each observed feeding tactic.

Diurnal channel drift feeders . Nektonic species that collect food items drifting at mid-water and at the surface, predominantly in the main channel during the day (*cf*. Sazima, 1986; Casatti *et al*., 2001).

Group composed by "lambaris" and "piabas" (tetras and characins, Characidae) that swim actively on the water column, suddenly investing on drifting particles or fallen in the water surface. *Bryconops melanurus* was observed at the main channel and in the pelagic zone of impounded stretches, swimming in schools of a least 20 individuals. *Bryconamericus* cf. *diaphanus* positions itself close to the stream bottom (5-10 cm above the substrate), between depressions of submersed sand dunes formed in high water current areas, collecting items stirred up by the water flow; they are usually observed alone and reacting aggressively to the approximation of conspecific. *Iguanodectes rachovii* and *Moenkhausia collettii* were observed very close to the margins with variable flow conditions, in groups of 3-30 individuals. *Astyanax bimaculatus*, *Jupiaba anteroides*, *Moenkhausia* cf. *comma*, and *M. oligolepis* were observed usually occupying the mid- lower strata of the water column close to the margins.

Diurnal backwater drift feeders. Nektonic species that occupy predominantly the backwaters, close to the margins and collect food items suspended in the water column or associated to the substrate (*cf*. Sazima, 1986; Casatti *et al*., 2001).

Group composed by small fish belonging to the Crenuchidae and to *incertae sedis* Characidae. *Crenuchus spilurus* remains stationary on the water column in slow flowing waters close to the margins, investing on items sinking nearby. Individuals of this species were observed occupying reentrances in the banks excavated by erosion processes. *Hemigrammus* cf. *rodwayi* and *H. heterorhabdus* form groups of 5-30 individuals and quickly invest in food particles carried by the current close to backwaters, in the upper (mid-water to surface) layers of the water column. *Hemigrammus ocellifer* was found mostly alone or in small groups of up to eight individuals, feeding on suspended particles in slow flowing water or speculating preys between branches and roots close to the margins. Groups ranging of 5- 10 individuals of *Hyphessobrycon* cf. *bentosi* were observed close to the bottom above litter banks, feeding on drifting particles and picking food deposited onto the substrate.

Diurnal surface pickers. Species occupying the uppermost layer of the water column close to the surface, predominantly at backwaters, were they pick food particles at surface or grasp small portions of periphyton during the day (*cf*. Sabino & Zuanon, 1998).

Group formed by the species of Lebiasinidae and of Cyprinodontiformes (Poeciliidae and Rivulidae). Most species were observed very close to marginal backwaters, sheltered among leaves, branches, macrophytes and roots of the banks,

Table 1. List of fish species observed in the seven streams in northeastern Pará. The taxonomic categories are arranged according Buckup *et al*. (2007). * Proposed in this study.

Order/Family/Species	Voucher (MPEG)	Vertical stratification	FTGs*	N	FO (%)
CHARACIFORMES					
Curimatidae					
Curimatopsis cf. *crypticus* Vari, 1982	21393	Nektobenthic	Mud-eater	3	42.9
Anostomidae					
Leporinus cf. *friderici* (Bloch, 1974)	-	Nektonic	Nibbler	2	28.6
Crenuchidae					
Characidium fasciatum Reinhardt, 1867	21388	Benthic	Sit-and-wait predator	6	85.6
Crenuchus spilurus Günther, 1863	21390	Nektonic	Diurnal backwater drift feeder	4	57.1
Gasteropelecidae					
Carnegiella strigata (Günther, 1864)	21394	Nektonic	Surface striker	4	57.1
Characidae					
Astyanax bimaculatus (Linnaeus, 1758)	21371	Nektonic	Diurnal channel drift feeder	4	57.1
Bryconamericus cf. *diaphanus* (Cope, 1878)	21372	Nektonic	Diurnal channel drift feeder	2	28.6
Bryconops melanurus (Bloch, 1794)	21374	Nektonic	Diurnal channel drift feeder	6	85.6
Charax cf. *metae* Eigenmann, 1922	-	Nektonic	Ambush and stalking predator	1	14.3
Gnathocharax steindachneri Fowler, 1913	21376	Nektonic	Surface striker	1	14.3
Hemigrammus cf. *rodwayi* Durbin, 1909	21399	Nektonic	Diurnal backwater drift feeder	3	42.9
Hemigrammus ocellifer (Steindachner, 1882)	21396	Nektonic	Diurnal backwater drift feeder	5	71.4
Hyphessobrycon heterorhabdus (Ulrey, 1894)	21377	Nektonic	Diurnal backwater drift feeder	7	100.0
Hyphessobrycon cf. *bentosi* Durbin, 1908	21379	Nektonic	Diurnal backwater drift feeder	4	57.1
Iguanodectes rachovii Regan, 1912	21381	Nektonic	Diurnal channel drift feeder	7	100.0
Jupiaba anteroides (Géry, 1965)	-	Nektonic	Diurnal channel drift feeder	3	42.9
Metynnis cf. *lippincottianus* (Cope, 1870)	-	Nektonic	Browser	2	28.6
Moenkhausia collettii (Steindachner, 1882)	21384	Nektonic	Diurnal channel drift feeder	5	71.4
Moenkhausia cf. *comma* Eigenmann, 1908	21385	Nektonic	Diurnal channel drift feeder	7	100.0
Moenkhausia oligolepis (Günther, 1864)	-	Nektonic	Diurnal channel drift feeder	1	14.3
Acestrorhynchidae					
Acestrorhynchus cf. *falcatus* (Bloch, 1972)	-	Nektonic	Pursuit predator	5	71.4
Erythrinidae					
Hoplerythrinus unitaeniatus (Agassiz, 1829)	-	Nektobenthic	Ambush and stalking predator	1	14.3
Hoplias cf. *malabaricus* (Bloch, 1794)	-	Nektobenthic	Ambush and stalking predator	3	42.9
Lebiasinidae					
Copella arnoldi (Regan, 1912)	21400	Nektonic	Diurnal surface picker	1	14.3
Nannostomus beckfordi Günter, 1872	21403	Nektonic	Diurnal surface picker	2	28.6
Nannostomus eques Steindachner, 1876	-	Nektonic	Diurnal surface picker	1	14.3
Nannostomus trifasciatus Steindachner, 1876	21404	Nektonic	Diurnal surface picker	3	42.9
Pyrrhulina cf. *laeta* (Cope, 1872)	21406	Nektonic	Diurnal surface picker	3	42.9
SILURIFORMES					
Cetopsidae					
Denticetopsis cf. *epa* Vari, Ferraris & de Pinna, 2005	21437	Nektonic	Crepuscular to nocturnal drift feeder	5	71.4
Helogenes marmoratus Günther, 1863	21438	Nektonic	Crepuscular to nocturnal drift feeder	3	42.9
Aspredinidae					
Bunocephalus coracoideus (Cope, 1874)	21434	Benthic	Crepuscular to nocturnal bottom predator	1	14.3
Trichomycteridae					
Paravandellia sp.	21452	Benthic	Parasites	6	85.6
Trichomycterus hasemani (Eigenmann, 1914)	21451	Benthic	Crepuscular to nocturnal bottom predator	2	28.6
Callichthyidae					
Callichthys callichthys (Linnaeus, 1758)	-	Necktobenthic	Grubber	1	14.3
Corydoras aff. *acutus* Cope, 1872	-	Necktobenthic	Grubber	2	28.6
Corydoras julii Steindachner, 1906	-	Necktobenthic	Grubber	1	14.3
Megalechis thoracata (Valenciennes, 1840)	-	Necktobenthic	Grubber	1	14.3
Loricariidae					
Ancistrus cf. *hoplogenys* (Günther, 1864)	21443	Benthic	Grazer	4	57.1
Ancistrus sp.	-	Benthic	Grazer	4	57.1
Farlowella cf. *amazona* (Günther, 1864)	-	Benthic	Grazer	4	57.1
Hemiodontichthys acipenserinus (Kner, 1853)	21444	Benthic	Digger	2	28.6
Rineloricaria cf. *hasemani* Isbrücker & Nijssen, 1979	-	Benthic	Grazer	5	71.4
Pseudopimelodidae					
Batrochoglanis cf. *raninus* (Valenciennes, 1840)	21445	Benthic	Crepuscular to nocturnal bottom predator	1	14.3

and in small reentrances in the banks in rather shallow areas (1-3 cm). When observed in stream impoundments, these species have always been associated with macrophytes stands and littoral areas, feeding at the surface or browsing periphyton-covered substrate. *Nannostomus trifasciatus* was observed always close to the surface and sheltered amid branches and roots of the riparian vegetation; differently of the rest of the group, it occupied the interface backwater/ main channel, occasionally investing on tiny food items slowly dragged by the current.

Table 1. cont. List of fish species observed in the seven streams in northeastern Pará. The taxonomic categories are arranged according Buckup *et al.* (2007). * Proposed in this study.

Order/Family/Species	Voucher (MPEG)	Vertical stratification	FTGs*	N	FO (%)
Heptapteridae					
Mastiglanis asopos Bockmann, 1994	21440	Benthic	Sit-and-wait predator	3	42.9
Pimelodella sp.	-	Benthic	Crepuscular to nocturnal bottom predator	5	71.4
Rhamdia mulleri (Günther, 1864)	21441	Benthic	Crepuscular to nocturnal bottom predator	4	57.1
Doradidae					
Acanthodoras cataphractus (Linnaeus, 1758)	-	Necktobenthic	Crepuscular to nocturnal bottom predator	1	14.3
Auchenipteridae					
Parauchenipterus galeatus (Linnaeus, 1758)	-	Nektonic	Crepuscular to nocturnal drift feeder	3	42.9
Tatia gyrina (Eigenmann & Allen, 1942)	21435	Nektonic	Crepuscular to nocturnal drift feeder	3	42.9
Tatia intermedia (Steindachner, 1876)	-	Nektonic	Crepuscular to nocturnal drift feeder	5	71.4
Tetranematichthys barthemi Peixoto & Wosiacki, 2010	21436	Nektonic	Crepuscular to nocturnal drift feeder	3	42.9
GYMNOTIFORMES					
Gymnotidae					
Gymnotus cf. *coropinae* Hoedeman, 1962	21410	Nektobenthic	Nocturnal invertebrate picker	2	28.6
Sternopygidae					
Eigenmannia cf. *trilineata* López & Castello, 1966	21411	Nektobenthic	Nocturnal invertebrate picker	6	85.6
Sternopygus macrurus (Bloch & Steindachner, 1801)	-	Nektobenthic	Nocturnal invertebrate picker	2	28.6
Rhamphichthyidae					
Gymnorhamphichthys petiti Géry & Vu, 1964	21419	Nektobenthic	Nocturnal invertebrate picker	7	100.0
Hypopomidae					
Brachyhypopomus beebei (Shultz, 1944)	21412	Nektobenthic	Nocturnal invertebrate picker	1	14.3
Hypopygus lepturus Hoedeman, 1962	21415	Nektobenthic	Nocturnal invertebrate picker	2	28.6
Microsternarchus bilineatus Fernández-Yépez, 1978	21416	Nektobenthic	Nocturnal invertebrate picker	1	14.3
Steatogenys duidae (Steindachner, 1880)	21418	Nektobenthic	Nocturnal invertebrate picker	5	71.4
Apteronotidae					
Apteronotus cf. *albifrons* (Linneaus, 1766)	-	Nektobenthic	Nocturnal invertebrate picker	1	14.3
CYPRINODONTIFORMES					
Rivulidae					
Rivulus cf. *strigatus* Regan, 1912	-	Nektonic	Diurnal surface picker	2	28.6
Poeciliidae					
Micropoecilia parae (Eigenmann, 1894)	21408	Nektonic	Diurnal surface picker	1	14.3
BELONIFORMES					
Belonidae					
Potamorrhaphis guianensis (Jardine, 1843)	21370	Nektonic	Pursuit predator	5	71.4
PERCIFORMES					
Cichlidae					
Aequidens cf. *tetramerus* (Heckel, 1840)	21421	Nektobenthic	Picker and browser	4	57.1
Apistogramma caetei Kullander, 1980	21424	Nektobenthic	Digger	6	85.6
Cichla sp.	-	Nektonic	Ambush and stalking predator	1	14.3
Crenicara punctulatum (Günther, 1863)	-	Nektobenthic	Digger	4	57.1
Crenicichla saxatilis (Linnaeus, 1758)	21429	Nektobenthic	Ambush and stalking predator	7	100.0
Crenicichla cf. *johanna* Heckel, 1840	-	Nektobenthic	Ambush and stalking predator	6	85.6
Heros cf. *efasciatus* Heckel, 1840	21430	Nektobenthic	Picker and browser	4	57.1
Krobia aff. *guianensis* (Regan, 1905)	-	Nektobenthic	Picker and browser	2	28.6
Mesonauta sp.	-	Nektobenthic	Picker and browser	1	14.3
Satanoperca jurupari (Heckel, 1840)	-	Nektobenthic	Digger	4	57.1

Surface strikers. Species that live close to the surface near to the margins, picking mainly invertebrates fallen from the riparian vegetation (*cf.* Sazima, 1986).

Carnegiella strigata and *Gnathocharax steindachneri* were observed close to the margins, between branches and hanging roots from the riparian vegetation, quickly picking up particles fallen at the water surface by fast strikes propelled by their hypertrophied pectoral fins. Both species occasionally compose mixed schools, with *G. steindachneri* occupying a slightly lower position on the water column than *C. strigata*; in such situations, *C. strigata* was the most abundant species.

Ambush and stalking predators. Nektonic or nektobenthic species that capture preys by ambush and/or stalk (*cf.* Sazima, 1986; Sabino & Zuanon, 1998).

Group composed by four families (Characidae, Erythrinidae, Gymnotidae, and Cichlidae) belonging to three orders (Characiformes, Gymnotiformes, and Perciformes). *Charax* cf. *metae* was observed stationary close to the margins during the day, near the bottom and ambushing its prey hidden among the vegetation or concealed by bank shadows. *Hoplerythrinus unitaeniatus* and *Hoplias* cf. *malabaricus* were observed hidden between branches and roots at the banks, ambushing their preys, especially at twilight and at night. *Crenicichla saxatilis* furtively approaches its prey (mostly aquatic invertebrates) concealed by the marginal vegetation, leaves or branches, from where it quickly attacks. *Crenicichla* cf.

Table 2. Number of feeding tactics, number of observed functional trophic groups (FTGs) and their respective proportions (%) within each taxonomic order

Orders	Species	Feeding tactics		FTGs	
		n	%	n	%
Characiformes	28	9	60.0	9	50.0
Siluriformes	23	7	46.7	7	38.9
Perciformes	10	5	33.3	3	16.7
Gymnotiformes	9	3	20.0	3	16.7
Cyprinodontiformes	2	2	13.3	1	5.6
Beloniformes	1	1	6.7	1	5.6

johanna was also observed near the banks in shadowed areas, approximating furtively its prey. Only one individual of *Cichla* sp. was observed foraging under a bank shadow, apparently waiting to assault a prey. These three Cichlidae species forage during the day and at dusk. *Gymnotus* cf. *coropinae* was observed foraging at night always close to the margins, swimming slowly among the submersed roots and trunks, stalking preys.

Pursuit predators. Species that capture preys by pursuiting them close to the water surface (*cf*. Goulding & Carvalho, 1984; Sazima, 1986; Sabino & Zuanon, 1998).

Acestrorhynchus cf. *falcatus*, a nektonic predator (Characiformes: Acestrorhynchidae), swims actively rovering in the stream looking for preys, both during the day and at twilight. When it localizes a potential prey, it makes a fast strike from the margin to the main channel. *Potamorrhaphis guianensis*, a surface Beloniformes, swims close to the margins amidst the marginal vegetation, where it attacks its preys (mostly invertebrates).

Mud-eaters. Nektobenthic species that scoop up and ingest substrate portions (*cf*. Sazima, 1986).

Curimatopsis cf. *crypticus* (small sized Curimatidae) swims close to the stream bottom, repeatedly scooping portions from the substrate, usually fine particulate organic matter weakly settled on the substrate, leaving digging marks. It is observed alone or in groups of up to 10 individuals, foraging during the day or at twilight.

Nibblers. Nektonic species that bites and pick food items settled on solid substrates (*cf*. Sazima, 1986).

Leporinus cf. *friderici* (a diurnal Anostomidae) occupies the lower half of the water column, searching for large food items (usually fruits) and biting them to cut small portions, which are facilitated by the incisiviform teeth; also forages picking invertebrates on the substrate.

Browsers. Nektonic species that bite off small pieces of macrophytes (*cf*. Sazima, 1986).

Metynnis cf. *lippincottianus* (diurnal and nektonic Serrasalmidae) prunes off macrophyte pieces or periphyton portions growing over trunks, branches and roots, plucking

vegetal parts or epiphytic organisms that develop over these structures.

Sit-and-wait predators. Benthic species that capture preys by stalking (*cf*. Sazima, 1986; Zuanon *et al*., 2006).

Characidium fasciatus (Crenuchidae) and *Mastiglanis asopos* (Heptapteridae) hunt by stalking their prey. The former species keeps stationary, usually sheltered behind a trunk or rock and advances suddenly toward the closer preys; the fish moves at irregular intervals of time among foraging sites, making short displacements along the stream bottom. *Mastiglanis asopos*, always observed foraging at nighttime in sand bottom reaches, keeps stationary on the channel center with its long barbels and the filamentous dorsal and pectoral-fin rays distended, waiting food items swept by the current. When a prey or a particle touches its barbels or fin rays it invests quickly towards the prey.

Grazers. Benthic species that scratch algae attached to the substrate, mainly on trunks (*cf*. Keenleyside, 1979).

Group formed exclusively by Loricariidae species, with predominantly nocturnal habits. *Ancistrus hoplogenys* and *Ancistrus* sp. have always been observed grazing on large trunks or rocky substrates, alone or in small groups. *Farlowella* cf. *amazona* was observed foraging in high current speed stream stretches, scratching algae attached to relatively thin branches (3 to 5 cm of diameter), in the long petioles of macrophytes (Nimpheaceae) and over gravel bottom. *Rineloricaria* cf. *hasemani* was also observed in high flow areas, scratching algae in thicker branches (5 - 10 cm diameter) and trunks laid down in the stream bottom and in gravel banks as well.

Grubbers. Nektobenthic species that capture preys through substrate probing (*cf*. Sazima, 1986).

Fishes of this group (representatives of the Callichthyidae) showed chiefly nocturnal habits and swim close to the stream bottom, moving the barbels through sediment particles of uppermost substrate layer; when a prey is localized, the fish quickly invests by immersing the snout into the substrate to grab it. *Callichthys callichthys* and *Megalechis thoracata* were observed close to the margins, searching the bottom mainly on patches of accumulated fine particulate organic matter. *Corydoras* aff. *acutus* and *C. julii* were observed probing the sandy substrate for preys, with little or none organic sediment deposits.

Diggers. Predominantly nektobenthic species that dig the substrate looking for food (*cf*. Sazima, 1986).

Group formed by *Hemiodontichthys acipenserinus* (Loricariidae) and *Apistogramma* cf. *caetei*, *Crenicara punctulatum* and *Satanoperca jurupari* (Cichlidae) that forage digging the substrate with their mouths, selecting edible particles inside the oral cavity and eliminating the indigestible portion through their opercular openings. Such foraging mode leaves conspicuous marks (small depressions) on the substrate. *Crenicara punctulatum* and *S. jurupari* are diurnal fishes that

swim alone or in small groups close to the bottom, plunging their protusible mouth and biting substrate portions (usually sand) near to the margins. *Apistogramma* cf. *caetei*, with diurnal habits, explores (solitary or in couples) predominantly the slow flowing stretches close to the margins, where it bites small portions of fine particulate organic matter, and shelters itself between branches and leaves deposited on the bottom. *Hemiodontichthys acipenserinus* shows a remarkable feeding tactic: foraging alone at night and supported: supported by its pectoral and pelvic fins, it projects its body forward and sinks the oral disk into the substrate (sand or organic debris); then, the fish resuspends and sucks the particles into the oral chamber (where the food is selected), expelling small clouds of sediments through the opercular openings.

Pickers and browsers. Predominantly nektobenthic species that grasps food portions adhered to the substrate and pick food items carried by the current over the substrate (*cf.* Sabino & Zuanon, 1998).

Group formed by *Aequidens* cf. *tetramerus*, *Heros* cf. *efasciatus*, *Krobia* aff. *guianensis* and *Mesonauta* sp. (Cichlidae), always observed close to the margins or in structurally complex channel places (usually with the presence of submerged trunks and roots) collecting food items dragged by the current close to the bottom. They also bite off portions of the periphyton cover.

Nocturnal invertebrate pickers. Fish of predominantly nektobenthic habits that capture preys close to the substrate during the night (*cf.* Sabino & Zuanon, 1998; Zuanon *et al.*, 2006).

Group formed exclusively by the species of Gymnotiformes of several families, which search the channel substrate and banks looking for invertebrates and small fishes, using the electrolocation ability to detect prey. *Apteronotus* cf. *albifrons* and *Sternopygus macrurus* scroll through all the channel area looking for preys, which include fish (pers. obs.). *Eigenmannia* cf. *trilineata* and *Steatogenys duidae* search the substrate close the stream margins, but while the former occupies predominantly the mid-water to the bottom layer of the water column, the second occupies the whole water column. *Brachyhypopomus beebei*, *Hypopygus lepturus* and *Microsternarchus bilineatus*, capture invertebrates inside the litter banks by inserting their heads between the leaves. *Gymnorhamphichthys petiti* swims close to the stream bottom, repeatedly digging its long snout in the substrate while hovering head-down, keeping its body inclined regarding the substrate and moving forward.

Crepuscular to nocturnal drift feeders. Crepuscular-nocturnal species that capture drifting preys at the stream surface (*cf.* Casatti *et al.*, 2001).

Group formed by Cetopsidae and Auchenipteridae species that forage alone during the twilight and at night. *Denticetopsis* cf. *epa* and *Tatia gyrina* swim actively at the main channel and close to the surface, capturing food items that fall in the water

and are drifted by the current. *Helogenes marmoratus* has a similar behavior, but explores predominantly the backwaters, capturing arthropods that fall in the water. *Tatia intermedia* also swim actively at the main channel, but collecting drifting food items at mid-water. *Parauchenipterus galeatus* and *Tetranematichthys barthemi* were observed always close to the margins, at mid-water, stationary or slowly swimming against the current, collecting food drifted by the current. All the species of this group, when observed, were alone.

Crepuscular to nocturnal bottom predators. Crepuscular-nocturnal benthic species that search the substrate looking for small preys (*cf.* Sazima, 1986).

Group of Siluriformes species that search for preys swimming close to the stream bottom. *Trichomycterus hasemani* swims fast and erratically over the bottom, searching for food and frequently burying itself into the substrate (usually sand patches). *Pimelodella* sp. swims at the main channel, in moderate current stretches, speculating the substrate with their barbels, looking for preys. *Acanthodoras cataphractus*, *Batrochoglanis* cf. *raninus*, and *Rhamdia* cf. *quelen* swim close to the margins searching for preys, mainly larger benthic macroinvertebrates and small fish, also exploring the environment with their barbels. *Bunocephalus coracoideus* swim close to the stream bottom on main channel, speculating the substrate with their small barbels.

Parasites. Parasite species that feed on blood of other fishes (*cf.* Keenleyside, 1979; Burgess, 1989).

Paravandellia sp. (small benthic Trichomycteridae) eats blood of larger fishes, attacking mainly their gills. When satisfied, it leaves the host and buries itself on the sand.

Although this feeding behavior was not observed, individuals of *Paravandellia* sp. were frequently seen in channels reaches where the main substrate was sand, actively swimming close to the bottom, mainly during the twilight. The individuals were seen moving around some dozens of centimeters during 15-30 seconds and then burying itself in the sand for some minutes. Some captured individuals showed clear signs of recently feeding, since the translucent ventral region evidenced a large portion of coagulated blood. The swimming habit resembles and may be confounded with that of *T. hasemani*.

The number of species in each FTG ranged from nine (12.0% of the observed species in this study), for the Nocturnal invertebrate pickers, to one species each (1.4%), for the mud-eaters, nibblers, grazers and parasites.

Characidae showed the highest diversity FTGs' (5), followed by Cichlidae (3); 20 families (77%) were represented by only one FTG. There was a positive correlation between species richness and the number FTGs represented in each family (Pearson's, r=0.88, p<0.01, n=26) (Table 3).

A temporal partitioning in the use of space was observed in the studied streams. Thirty-nine species (53.3%) showed diurnal habits, including all Characiformes

Table 3. Number of feeding tactics, number of observed functional trophic groups (FTGs) and their respective proportions (%) within each family.

Families	Species	Feeding tactics		FTGs	
		n	*%*	*n*	*%*
Cichlidae	10	5	33.3	3	16.7
Characidae	15	4	26.7	5	27.8
Auchenipteridae	4	2	13.3	1	5.6
Cetopsidae	2	2	13.3	1	5.6
Crenuchidae	2	2	13.3	2	11.1
Heptapteridae	3	2	13.3	2	11.1
Lebiasinidae	5	2	13.3	1	5.6
Loricariidae	5	2	13.3	2	11.1
Poeciliidae	1	2	13.3	1	5.6
Rivulidae	1	2	13.3	1	5.6
Trichomycteridae	2	2	13.3	2	11.1
Acestrorhynchidae	1	1	6.7	1	5.6
Anostomidae	1	1	6.7	1	5.6
Apteronotidae	1	1	6.7	1	5.6
Aspredinidae	1	1	6.7	1	5.6
Belonidae	1	1	6.7	1	5.6
Callichthyidae	4	1	6.7	1	5.6
Curimatidae	1	1	6.7	1	5.6
Doradidae	1	1	6.7	1	5.6
Erythrinidae	2	1	6.7	1	5.6
Gasteropelecidae	1	1	6.7	1	5.6
Gymnotidae	1	1	6.7	1	5.6
Hypopomidae	4	1	6.7	1	5.6
Pseudopimelodidae	1	1	6.7	1	5.6
Rhamphichthyidae	1	1	6.7	1	5.6
Sternopygidae	2	1	6.7	1	5.6

(except Erythrinidae), Beloniformes, Cyprindontiformes, and Perciformes. These species were almost replaced at night by Erythrinidae, and representatives of several families of Siluriformes and Gymnotiformes, totaling 34 species (46.6%). Nevertheless, such taxonomical change-over was not corresponded by a similar functional modification. Three (16.7%) of the FTGs observed during the day (Diurnal channel drift feeders, Diurnal backwater drift feeders, Diurnal surface pickers) were replaced by similar functional groups at night (Crepuscular to nocturnal drift feeders); FTGs recorded exclusively in one time period were Diurnal channel drift feeders, Diurnal backwater drift feeders, Diurnal surface pickers, Surface strikers, Nibblers, Browsers and Pickers during the day, and Crepuscular to nocturnal drift feeders, Crepuscular to nocturnal predators, Nocturnal invertebrate pickers and Parasites at night.

Discussion

Stream habitat heterogeneity

It was observed on the studied streams that the margins shows higher structural complexity provided by specific habitat subunits (*e.g.*, undercut banks, Frissell *et al.*, 1986), roots from the riparian forest, higher amount of submerged trunks and branches, macrophytes patches and recesses caused by erosion on the margins close to the surface. Most of the streams drain relatively narrow (~10^2 m) flat-bottomed valleys and show a complex morphology, with substrate

composed mostly by vegetal matter (litter, branches, trunks) from the riparian forest (in the studied areas frequently with Igapó components) and alluvial sediments (sand, silt, clay). These unconstrained streams show many secondary channels that may connect to small flooded areas; a seasonal and dynamic environment that expands and recedes following slight variations on the stream water level. This lateral complexity is largely exploited by the fishes observed in this study. The central (main) channel portion provides less shelter for smaller fishes, regarding to ambush points by bigger fishes; moreover, when using the central channel area, fishes may become vulnerable to aquatic predators attack (Power, 1984). The spatial distribution of the species indicates the occurrence lateral and vertical stratification of the stream fish assemblage, as well as the body shape may provide information about microhabitat use.

The margins were the mostly used compartment by the fish species found in this study, agreeing with the lateral distribution pattern described by Sabino & Zuanon (1998) in a Central Amazon stream, where 72.4% of the observed species occupied this local. Uieda (1984), Costa (1987), Sabino & Castro (1990) and Sabino & Silva (2004) also detected this pattern in streams of southeastern Brazil, which indicate that this form of horizontal stratification represents a common feature of Brazilian tropical stream fish assemblages.

Concerning to the vertical stratification, there was a predominance of nektonic species, counter to the pattern found by Sabino & Zuanon (1998), where 65.5% of the sampled species showed benthic habits. This difference might have occurred because these authors considered as benthic all species that have feeding activity on the bottom of the stream, including the nektobenthics.

Habitat heterogeneity is known to have strong effects on fish species distribution along streams, both in relation to longitudinal distribution and diversity of microhabitats (Angermeier & Karr, 1983; Sabino & Castro, 1990). The sampling of relatively long streams reaches, ranging from 200 to 280 m, increases the possibility of including a great variety of microhabitats, reducing the possible bias of underrepresenting the distribution patterns of rare species or habitat-specialists (Angermeier & Smogor, 1995; Anjos & Zuanon, 2007). In fact, the 200 m long reaches were adequate to sample efficiently the ichthyofauna of the selected streams and impoundments for this study by means of underwater observation, including up to 95% of the estimated local species richness.

FTGs, fish morphology and behavior

The number and variety of feeding tactics used by the species of each family (Table 3) possibly reflect the morphological diversity of the Characidae and Cichlidae. When the taxonomic level is raised to order, the FTGs show the same pattern found for the ichthyofauna composition, with Characiformes showing the greatest FTGs amount of types, followed by Siluriformes, Gymnotiformes and Perciformes. When comparing the feeding behavior similarities of marine and freshwater fish assemblages, Sazima (1986) reports that Characidae and Cichlidae showed half

of the feeding tactics exhibited by six marine fish families, suggesting that the morphological diversity of these two families is responsible for the variety of tactics and range of environments explored by them.

In this study, the group composed by the nektonic Characidae species that collect food items drifted by the current at the surface was divided in two subunits: (1) channel drift feeders and surface pickers and, (2) margin drift feeders and surface pickers. This is justified mainly by the fact that these species show differences in their horizontal distribution, which can be related to fish body size. Species belonging to the margin subunit are small, and the structurally more complex margins may provide protection against possible predators. The higher the habitat complexity, the smaller are the chances of a predator to severely impact a prey population (Power *et al.*, 1985). On the other hand, channel subunit includes medium-sized species, mostly of agile swimmers, that possibly can evade from the predators attack, allowing them to occupy the central (and more exposed) region of the stream.

Five sand-dwelling species were observed, *Bryconamericus* cf. *diaphanus* (Characidae), *Gymnorhamphichthys petiti* (Rhamphichthyidae), *Mastiglanis asopos* (Heptapteridae), *Paravandellia* sp. and *Trichomycterus hasemani* (Trichomycteridae), which shows translucent body or cryptic coloration pattern on the sand (Zuanon *et al.*, 2006). Except for *B.* cf. *diaphanus*, the other four species showed crepuscular-nocturnal activities and bury themselves in the sand during the day.

As a Loricariidae, *Hemiodontichthys acipenserinus* was expected to be a grazer, since the species of this family have the morphological features that allow them to use the abundant periphyton cover available in streams. However, *H. acipenserinus* is a digger that excavates the substrate, to feed on particulate organic matter and small organisms associated to it, similarly to species of Cichlidae, sustaining the inclusion of this species on this functional category.

Temporal organization of the fish assemblages

The studied ichthyofauna was composed by two main groups of species that alternate the use of the space and food resources. The micro-habitats where similarly explored by diurnal and nocturnal species that employ the same (or very similar) feeding tactics (*e.g.*, Surface pickers, Drift feeders Stalking predators, Ambush predators, Diggers, and Sit-and-wait predators), despite the phylogenetic and morphological differences between them.

Although not directly investigated in this study, it is probable that there are differences in the food items eaten by the Diurnal channel drift feeders (Characidae), Diurnal backwater drift feeders (Characidae and Crenuchidae), Surface strikers (Characidae and Gasteropelecidae) and Crepuscular to nocturnal drift feeders (Auchenipteridae and Cetopsidae). The species that compose all these FTGs are predominantly insectivorous, but the diurnal species mainly eat terrestrial insects, while the nocturnal species consume mostly aquatic insects (Sabino & Zuanon, 1998). The shade

produced by the riparian forest is a limiting factor to the primary productivity of aquatic systems, and fish are strongly dependent of allochthonous resources that fall in the stream during the day (Lowe-McConnell, 1999). Intentional drifting of living aquatic insects occurs mainly during the night, probably as a behavioral defense against predation by diurnal fish, which are much more abundant than nocturnal species (Flecker, 1992). In fact, the diversity of FTGs and species that feed on drifting invertebrates is considerably higher during the day (three FTGs) than in the night (just one), which is probably related to a higher effectiveness of feeding tactics that rely on visual detection of the prey.

At night, Nocturnal invertebrate pickers (Gymnotiformes), Crepuscular to nocturnal bottom predators (Siluriformes) and Grubbers (Siluriformes) use the same micro-habitats used by the Pickers and browsers (Cichlidae) and Diggers (Cichlidae) during the day, actively looking for small invertebrates and fish at the stream bed. The detection and capture of prey by species of Gymnotiformes and Siluriformes are possible by the use of electrically and chemically oriented senses, and do not depend on the presence of light. This situation seems to represent a counterpart to the predominance of the consumption of drifting invertebrates at the upper layers of the water column by visually oriented species of Characiformes during the day.

FTGs as a tool for fish assemblage comparisons

Grouping the species into functional trophic groups allows the comparison of fish assemblage structure from different environments, river basins, and even biogeographic origins. Different species that show similar morphological features tend to perform the same ecological functions and to occupy the same microhabitats, whether in tropical or temperate communities, in freshwater or marine environments (Sazima, 1986; Winemiller, 1991). Observed functional patterns may be used to infer on the nature of ecological processes, respecting the characteristics of abundance, distribution and species diversity (Cassemiro & Padial, 2008). In this study, the observed species were organized in 18 FTGs, which can be compared to the results of similar works performed in a freshwater pond and in a marine environment (Sazima, 1986); in a Central Amazon stream (Sabino & Zuanon, 1998); and in streams from the upper Paraná River basin (Casatti *et al.*, 2001). In those studies, fish species were organized according to their functional similarity, allowing to the authors to identify more than one feeding tactic being used by a species group. A comparison of the FTGs defined in the present study, with the three works above cited is depicted in Fig. 2.

Functional traits can be used to assess the convergence between communities that, due to different evolutionary histories, otherwise could not be compared. A strong functional convergence of communities in different continents could be observed regarding to the use of similar microhabitats, to the relations between assemblage patterns
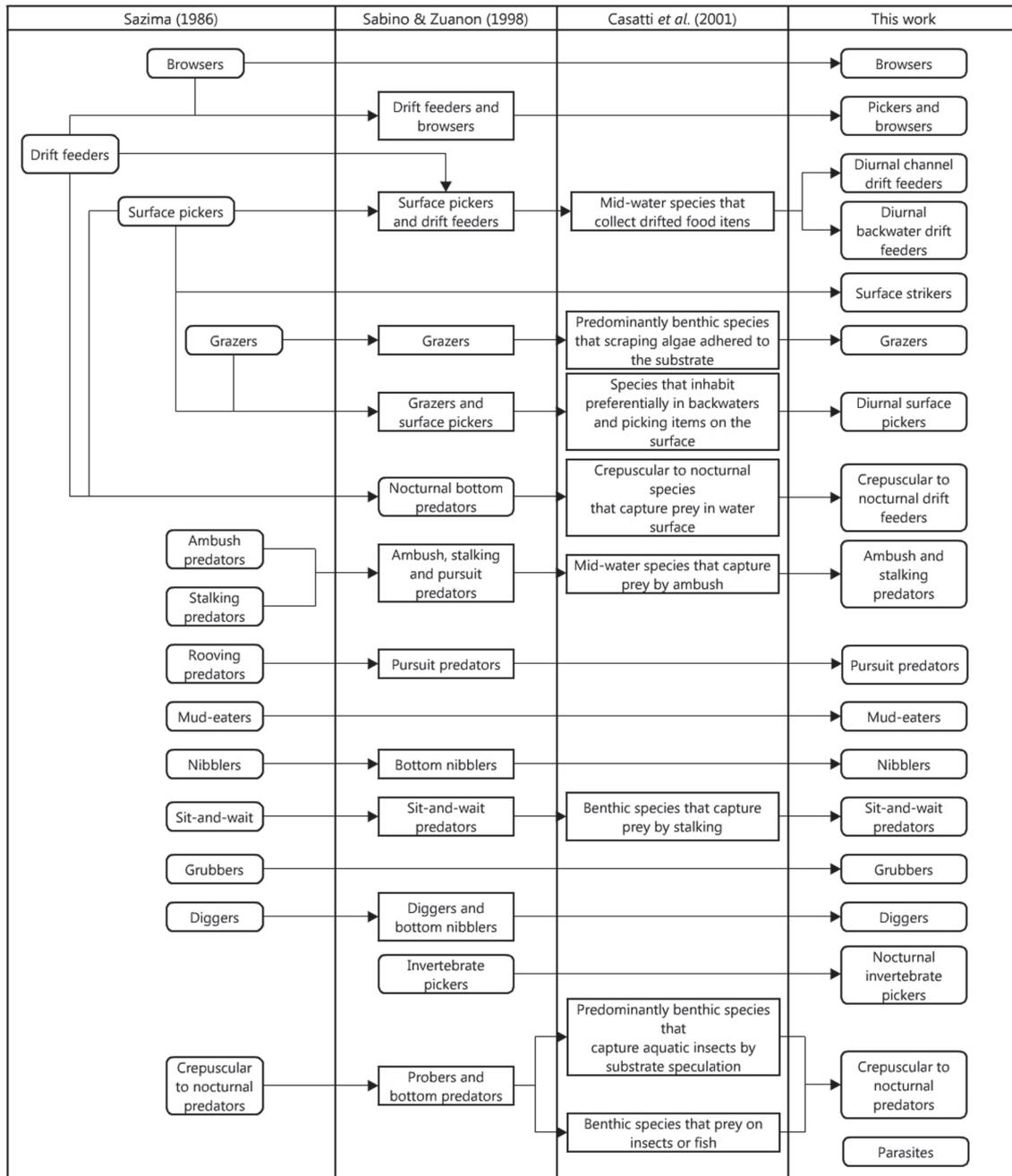
Fig. 2. Comparison between the classification of functional trophic groups proposed by this study and three other similar studies.

and environmental features, or to the longitudinal distribution of functional groups in the drainage network (Lamouroux *et al.*, 2002).

An assemblage organization in functional trophic groups is proposed in order to allow comparison among different hydrographic systems, minimizing the taxonomic particularities of their ichthyofauna (biogeographic effects). The analysis of an assemblage according to its taxonomic organization reveals the distribution patterns of the species,

but when analyzed through a functional approach, the same assemblage can be divided according to the habitat template (Southwood, 1977; Poff & Ward, 1990). Large scale processes determine the potential pool of species to occur in a specific locality, strongly influencing the local assemblage structure. However, the functional responses of an assemblage to the environmental variables occur independently of the species taxonomic history (Hoeinghaus *et al.*, 2007). This approach allows us to infer about the differences or similarities

between biological communities in distinct environments, hopefully speeding up our understanding of the ecological processes that enables the coexistence of so many species in a rapidly changing world.

Acknowledgments

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