Resource use by two electric fishes (Gymnotiformes) of the National Forest Saracá-Taquera, Oriximiná, Pará

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Fishes of the order Gymnotiformes have high diversity of oral and head morphology, which suggests trophic specializations within each clade. The aim of this study was to describe resource use patterns by two fish species (*Gymnorhamphichthys rondoni* and *Gymnotus coropinae*) in the National Forest Saracá-Taquera, Oriximiná - Pará, analyzing microhabitat use, diet composition, feeding strategies, niche breadth and niche overlap. Stomach contents of 101 individuals (41 *G. rondoni* and 60 *G. coropinae*), sampled in 23 headwater streams were analyzed and volume of food items was quantified to characterize their feeding ecology. *Gymnorhamphichthys rondoni* was captured mainly on sandy bottoms, whereas *G. coropinae* in crevices. Both species had a zoobenthivorous diet and consumed predominantly Sediment/Detritus and Diptera larvae, but also included allochthonous prey in their diet. These species had high niche overlap, with small variations related to the higher consumption of Ceratopogonidae larvae by *G. rondoni* and of Chironomidae larvae by *G. coropinae*. Both species had a generalist feeding strategy, but *G. coropinae* had a broader niche breadth. Our results demonstrate that *G. rondoni* and *G. coropinae* occupy different microhabitats but rely on similar food resources.

Keywords: Amazon, Diet overlap, Feeding, Microhabitat, Streams.

Peixes da ordem Gymnotiformes apresentam alta diversidade morfológica, o que sugere a existência de especializações tróficas dentro dos clados. O objetivo deste estudo foi analisar o uso de recursos por duas espécies de peixes elétricos (*Gymnorhamphichthys rondoni* e *Gymnotus coropinae*) na Floresta Nacional Saracá-Taquera, Oriximiná - Pará, analisando o uso de microhabitats, composição da dieta, estratégias alimentares, amplitude de nicho e sobreposição de nicho. Conteúdos estomacais de 101 indivíduos (41 *G. rondoni* e 60 *G. coropinae*), capturados em 23 igarapés de cabeceira, foram analisados e quantificados volumetricamente para a caracterização da ecologia trófica. *Gymnorhamphichthys rondoni* foi registrada principalmente em bancos de areia, enquanto *G. coropinae* em fendas. Ambas as espécies apresentaram dieta zoobentívora e consumiram predominantemente sedimento/detritos e larvas de Diptera, mas também consumiram presas alóctones. Foi observada alta sobreposição de nicho trófico e a baixa variação encontrada foi relacionada à maior utilização de larvas de Chironomidae por *G. rondoni* e de larvas de Ceratopogonidae por *G. coropinae*. Ambas as espécies apresentaram estratégia alimentar generalista, porém *G. coropinae* apresentou maior amplitude de nicho. Nossos resultados demonstram que *G. rondoni* e *G. coropinae* ocupam microhabitats diferentes, mas dependem de recursos alimentares similares.

Palavras-chave: Alimentação, Amazônia, Microhabitat, Riachos, Sobreposição de nicho.

Introduction

The order Gymnotiformes includes electric fishes distributed in freshwaters of Central and South America, such as floodplains, coastal drainages, rivers and streams (Albert, Crampton, 2005). Gymnotiforms have an elongated body, no dorsal, pelvic or adipose fins, and possess systems for electrogenesis and electrosensory that allow communication, navigation and prey location (Albert, Crampton, 2005). In headwaters streams, gymnotiforms that have pulse-type electric organ discharge (EOD), such as those belonging to the families Gymnotidae, Rhamphichthyidae, and Hypopomidae, are the most diverse (Tagliacollo *et al.*, 2016).

This order exhibits a high functional diversity of head, mouth and nose morphology, which suggests trophic specializations (Albert, Crampton, 2005) if we consider that morphology is related to feeding mode and habitat use (Winemiller *et al.*, 1995; Oliveira *et al.*, 2010; Soares *et al.*, 2013). For example, rhamphichthyids have an elongated snout with a terminal and small oral cavity that facilitates

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the capture of insect larvae in cavities in the streambed (Albert, Crampton, 2005). Moreover, gymnotiforms that inhabit Amazonian streams are important components of the ichthyofauna because they act as linkages between detritivorous arthropods and other components of the aquatic system due to their benthivorous diet composed mainly of autochthonous prey (*e.g.* Giora *et al.*, 2014).

As gymnotiforms are generally classified as nocturnal invertebrate pickers (Brejão *et al.*, 2013) predating on autochthonous invertebrates, it could be expected that resource partitioning between syntopic species minimizes competition (Herder, Freyhof, 2006; Silva *et al.*, 2016). Resource partitioning may occur due to differential use of food and/or spatial resources (Schoener, 1974), but trophic segregation is considered as the most important type of resource partitioning in fish assemblages (Ross, 1986). Spatial segregation is often related to differences in the use of microhabitats (Casatti *et al.*, 2005; Lima *et al.*, 2008), while trophic segregation occurs due to differences in consumed prey and/or feeding strategy (Piorski *et al.*, 2005; Brazil-Sousa *et al.*, 2009).

Here, we evaluated the use of microhabitat (*e.g.* riffles, sand bottom areas) and food resources by two species of electric fish from two different Gymnotiformes families, *Gymnorhamphichthys rondoni* (Miranda Ribeiro, 1920) (Rhamphichthyidae) and *Gymnotus coropinae* Hoedeman, 1962 (Gymnotidae), in the Saracá-Taquera National Forest, Oriximiná, Pará. Fish of these genera feed predominantly on autochthonous invertebrates and display different foraging behaviors (Zuanon *et al.*, 2006; Ferriz, Iwaszkiw, 2014), but no further information about their trophic ecology in the Amazon is available due to the difficulty in sampling specimens profusely and with temporal consistency.

In order to investigate the resource use (*i.e.* space and food) by these two gymnotiforms in Amazonian headwater streams, we analyzed: (i) the proportion of microhabitat types used; (ii) diet composition; (iii) trophic niche breadth and overlap; and (iv) populational and individual strategies for the consumption of food resources. We expect that the use of different microhabitats distinguishes both species due to the known psammophilous behavior of *G. rondoni* (Zuanon *et al.*, 2006), while *G. coropinae* does not exhibit known morphological specializations to occupy sandy bottom microhabitats. Furthermore, the diet of the species are expected to differ because the use of different microhabitats would supposedly provide different potential prey and also because the morphological specialization (elongated snout) exhibited by *G. rondoni* suggests a more restricted, specialized diet.

Material and Methods

Study area. The National Forest Saracá-Taquera (1º20' to 1º55' S; 56º00' to 57º15' W) has an area of 429,600 ha and is a conservation unit for sustainable use located on the right bank of the Trombetas River, Pará State, Northern Brazil. Saracá-Taquera includes highlands areas of bauxite mining.

Samplings were carried out during an ichthyological and limnological monitoring of the streams within Saracá-Taquera due to bauxite mining activities (authorization #513/2014-Dilic/IBAMA) in May (rainy period) and September (dry period) in 2010 and 2012. We sampled in 23 streams of 1st to 3rd order belonging to five microbasins (Fig. 1): Araticum, Saracá, Urupuanã, Jamari and Moura, located in pristine forest areas.
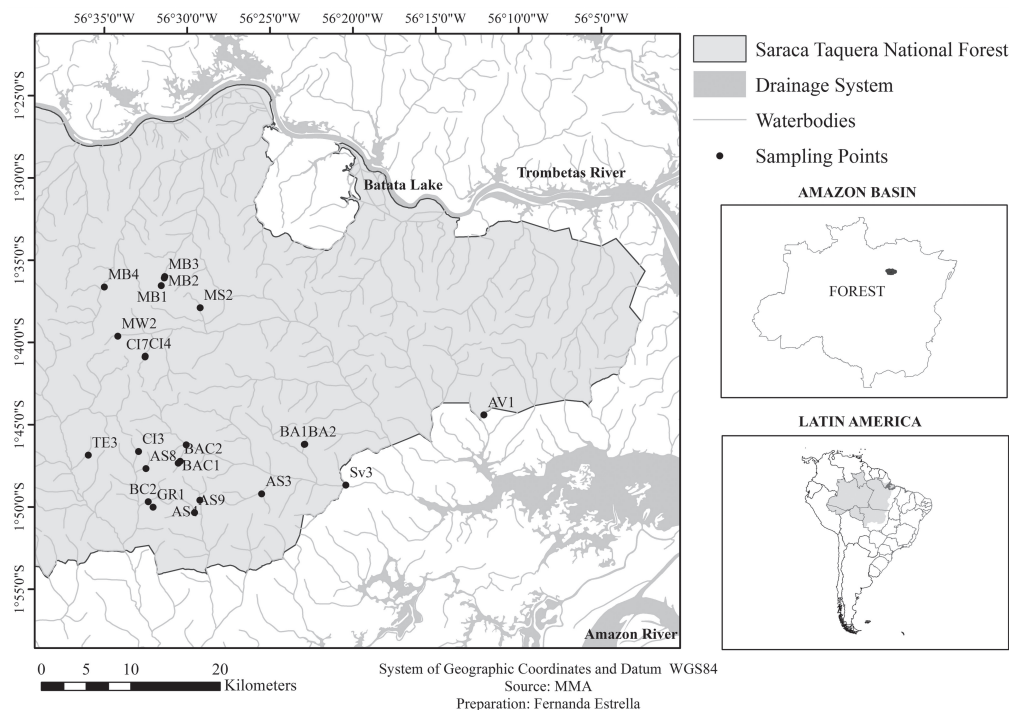

Fig. 1. Study area depicting sampled streams in the Saracá-Taquera National Forest, Pará, Brazil.

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Sampling. Sampling was carried out with manual trawl (3 mm mesh) and sieves (55 cm diameter, 0.35 mm mesh) in different microhabitats along a 50 m stretch previously blocked upstream and downstream with nets (5 mm mesh). Sampling occurred in all available microhabitats: *(i)* waterlogged fields - marginal areas inundated by rainfall and/or main channel's overflow; *(ii)* sandy bottom - occurs when sandy sediment extends from main channel to marginal areas; *(iii)* riffle - the stream's main channel; *(iv)* litter bottom - occurs in shallow portions of the stream covered by leaves; *(v)* crevices - depressions located in marginal areas that some species use as refuge or preferential habitat, and may be covered by roots or leaves. Sampling effort lasted from two to four hours depending on stream size, distributed along the different microhabitats accounting for their relative area in the stream. Sampled specimens were anesthetized with menthol, fixed in 10% formaldehyde and taken to the Laboratory of Fish Ecology (UFRJ). After that, fish were transferred to 70% ethanol to be identified, and have its digestive tract extracted for further stomach content analyses. Voucher specimens of *G. rondoni* and *G. coropinae* were deposited in the collection of the Laboratory of Fish Ecology/UFRJ, voucher numbers DEPRJ 8226 and DEPRJ 7792, respectively.

Data analysis. Stomach contents were analyzed under stereoscopic microscope and food items were identified and quantified using the methods of Frequency of Occurrence (FO%) and Volumetric (VO%). Volumes of the items were measured on a 1-mm-high transparent dish with a 1 x 1 mm grid beneath, as described by Albrecht, Caramaschi (2003). Dietary items were identified to the lowest taxonomic level with specialized bibliography (Hamada *et al.*, 2014). Sediment/Detritus was considered as a food item and it was defined as particulate matter mainly composed of organic particles, but including also mineral particles. The relative importance of the food items for each species was calculated by the Alimentary Index (IAi; Kawakami, Vazzoler 1980), according to the formula: $IAi = (Fi * Vi) / (\Sigma Fi * Vi) * 100$, where $i = 1, 2, ... n$ food items; Fi = frequency of occurrence of item i, and Vi = relative volume of item i.

We estimated the trophic niche breadth using the Levins' index, given by the formula: $BA = 1/\Sigma Pj^2$, where BA is Levins' index, Pj is the proportion of the diet consisting of prey j. BA ranges from 1 (specialist feeder) to *n* (generalist feeder), where *n* is the total number of consumed prey.

We calculated trophic niche overlap between the two species using Pianka's index. This index is given by the following formula:

$$O_{jk} = \frac{\sum_{i=1}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^{n} P_{ij}^2 \ \sum_{i=1}^{n} P_{ik}^2}},$$

where O_{jk} is the trophic niche Pianka's overlap index between species *j* and *k*, and *Pi* is the proportion of a single food item i in the diet of species *j* and *k*. The index varies from 0 (total segregation) to 1 (total overlap). We used the program EcoSim (v. 7.0) to test whether the niche overlap was higher or lower than expected in null models. We considered retained niche breadths and retained zero states (RA4 algorithm). For this analysis, we used only one stream where both species were highly abundant (a third order stream in the Araticum microbasin, code AS3). An analysis considering the whole dataset confirms a potentially high niche overlap between species, but this result is not shown because species do not co-occur in all streams.

We analyzed the potential differences in diet composition between species with an Analyses of Similarity (ANOSIM), using matrices with square-rooted proportional volumes consumed by all individuals. We used ANOSIM two-way to verify if differences among streams (stream order and microbasin) altered the pattern observed in the one-way approach. As the interaction among factors did not affect the significance and the explanation of the interspecific differences, we chose to consider only the one-way analysis further. Items that accounted for the variation were identified with a Similarity Percentage analysis (SIMPER). All tests were performed with 999 permutations and used the Bray-Curtis coefficient of similarity of squared values and were performed with the software PRIMER (version 6.1.6; PRIMER-E, Plymouth, UK).

Feeding strategies of the species population in the Saracá-Taquera National Forest were characterized using the graphical method of Amundsen *et al.* (1996) based on prey-specific abundances and frequency of occurrence of consumed items. The distribution of points (food items) along the axes indicates the importance of each prey for the population (dominant or rare), species' feeding strategy (generalist or specialist) and importance of intrapopulational variation to the niche breadth. The latter is indicated by the importance of: the between-phenotype component in the niche breadth due to dietary specialization of individuals (high prey-specific abundance and low frequency of occurrence of food items); and the within-phenotype component due to low dietary variation among individuals (low prey-specific abundance and high frequency of occurrence of food items). We also constructed bipartite webs with Pajek software (version 4.1) to analyze prey-predator interactions.

Results

A total of 101 specimens were analyzed: 41 *Gymnorhamphichthys rondoni*, with total length (TL) ranging from 80.49 to 215 mm (147.19 ± 37.11), and 60 *Gymnotus coropinae* with TL ranging from 36.56 to 108.9 mm (67.58 ± 16.96). The majority of individuals of *G. rondoni* were sampled on sandy bottoms (88%), while *G. coropinae* was more abundant in crevices (70%). Both species co-occurred in only five of the 23 sampled streams, one of first order and four of third order, and did not overlap microhabitat use in any stream (Fig. 2).
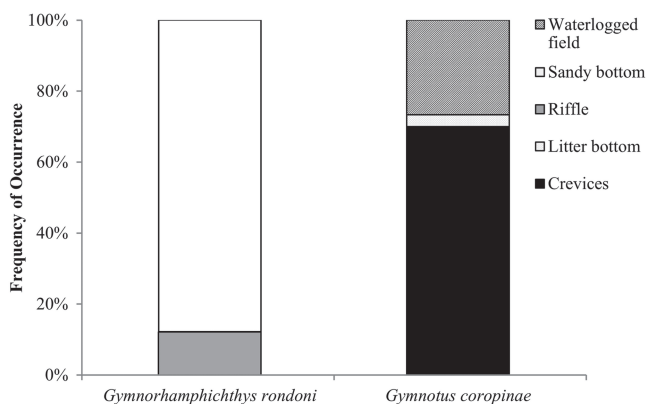
Fig. 2. Habitat use (frequency) of *Gymnorhamphichthys rondoni* and *Gymnotus coropinae* sampled in five different microhabitats in first to third order streams at the Saracá-Taquera National Forest, Oriximiná, Pará.

Gymnorhamphichthys rondoni and *Gymnotus coropinae* consumed 18 food items each, 17 of those consumed by both species, and only one was consumed exclusively by only one of the species (Tab. 1): Algae by *G. rondoni* and Decapoda by *G. coropinae*. The most important item consumed by both species was Sediment/Detritus (IAi = 41.92% and 32.72%, respectively). Other important items were Ceratopogonidae and Chironomidae larvae for *G. rondoni* (IAi = 32.99% and 18.85%, respectively), and Chironomidae and Ceratopogonidae larvae for *G. coropinae* (IAi = 21.59% and 16.81%, respectively). Plant remains were not important in the diet of *G. rondoni* (IAi = 0.09%), but slightly more consumed by *G. coropinae* (IAi = 5.52%). Both species can be classified as zoobenthivores.

Species showed high trophic niche overlap ($\theta = 0.66$; $p = 0.05$) in the stream where they co-occurred in higher abundance ($n_{G.\ coropinae} = 15$; $n_{G.\ rondoni} = 17$). *G. rondoni* exhibited a lower niche breadth ($BA_{G.\ rondoni} = 4.19$) than *G. coropinae* ($BA_{G.\ coropinae} = 8.08$). The lower occurrence of dominant items in the diet of *G. coropinae* also accounted for the larger niche breadth. Considering all individuals, the diet composition of *G. rondoni* differed slightly from the diet of *G. coropinae* (ANOSIM; R = 0.06; p = 0.02). Differences occurred by shifts in the proportion of items rather than by shifts in the type of items consumed. *G. rondoni* consumed higher proportions of Detritus and Ceratopogonidae larvae, while *G. coropinae* consumed higher proportions of Chironomidae larvae and Insect remains (Tab. 2).

Amundsen's diagram showed a generalist feeding strategy for both species (Fig. 3). Sediment/Detritus was the most frequent item and Pyralidae showed the highest prey-specific value for *Gymnorhamphichthys rondoni* (Fig. 3a). Sediment/Detritus, Ceratopogonidae and Chironomidae larvae had the highest frequencies in the diet of *G. coropinae*, while Pyralidae also had the highest prey-specific abundance (Fig. 3b). Dominant items were not identified, since no items exhibited both high prey-specific abundance and high frequency of occurrence. The high influence of the between-

phenotype component in the niche breadth was highlighted by the prevalence of rare items in the diet of *G. rondoni*, and by both the prevalence of rare items and by the consumption in large quantities of Pyralidae by *G. coropinae*. The within-phenotype component was also important, especially for *G. rondoni*, due to the consumption of items in high frequencies but with low relative abundances.

Resource use within populations can be visualized on the individual-resource networks (Fig. 4). In these graphs, a nested pattern of resource use is apparent, with preferential use of one or few items by most individuals, whereas fewer individuals consume secondary items. *Gymnorhamphichthys rondoni* exhibited three to eight trophic connections (Fig. 4a; mean = 4.6 ± 1.3), while *G. coropinae* showed one to six trophic connections (Fig. 4b; mean = 3.6 ± 1.4). Nine of the 18 dietary items of *G. rondoni* were used by three or less individuals, as complementary items that were rarely used by individuals with few trophic connections. *Gymnotus coropinae* showed a similar pattern, with 13 specialist individuals but only one used a complementary item. Despite the nested pattern, resource use by *G. coropinae* was different from *G. rondoni* due to the lower number of connections per individual and a more equitable consumption of food items with less complementary items (consumed by only one or two individuals).

Tab. 1. Alimentary Index (IAi) calculated for resources consumed by *Gymnorhamphichthys rondoni* and *Gymnotus coropinae* in first to third order streams at the Saracá-Taquera National Forest, Oriximiná, Pará. Codes: A - adult; Inv - Invertebrate; L - Larvae; P - Pupae; N - Nymphs; and T - terrestrial.

Food items	*G. rondoni*	*G. coropinae*
	IAi (%) (n = 41)	IAi (%) (n = 60)
Algae	0.01	-
Aquatic Coleoptera (A)	0.02	0.04
Aquatic Coleoptera (L)	0.30	0.52
Arthropoda (T)	0.29	1.02
Ceratopogonidae (L)	32.99	16.81
Chironomidae (L)	18.85	21.59
Decapoda	-	0.01
Diptera (L)	0.48	0.93
Eggs (Inv.)	0.06	0.38
Ephemeroptera (N)	0.03	1.25
Hydracarina	<0.01	0.01
Insect remains	1.11	14.48
Odonata (N)	<0.01	0.08
Plant Remains	0.09	5.52
Pyralidae	0.05	1.66
Scales	0.03	<0.01
Sediment/Detritus	41.92	32.72
Trichoptera (L)	3.77	2.92
Zooplankton	<0.01	0.04
Total consumed items	18	18

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Tab. 2. Food items that accounted for the differences in the diet composition of *Gymnorhamphichthys rondoni* and *Gymnotus coropinae* based on the Similarity Percentage Analysis in first to third order streams at the Saracá-Taquera National Forest, Oriximiná, Pará. Codes: Inv.- Invertebrate; L - Larvae; N - Nymphs; and T - terrestrial.

| Food Items	Average squared volume		Contribution (%)	Cumulative contribution (%)
	G. rondoni (n = 41)	*G. coropinae* (n = 60)		
Sediment/Detritus	0.64	0.41	18.07	18.07
Ceratopogonidae (L)	0.45	0.22	14.28	32.35
Chironomidae (L)	0.30	0.36	12.87	45.22
Insect remains	0.08	0.23	11.76	56.98
Trichoptera (L)	0.16	0.07	8.49	65.47
Diptera (L)	0.06	0.08	5.89	71.36
Plant Remains	0.03	0.10	5.77	77.13
Arthropoda (T)	0.05	0.07	4.59	81.72
Ephemeroptera (N)	0.01	0.08	4.30	86.01
Coleoptera (L)	0.06	0.03	3.85	89.01
Eggs (Inv.)	0.01	0.06	3.16	93.02
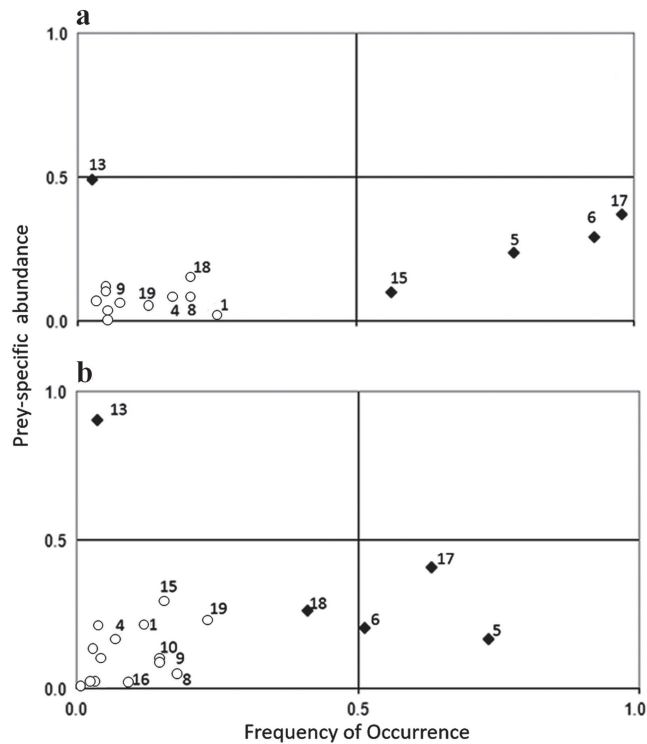
Fig. 3. Amundsen diagram for the representation of feeding strategies of *Gymnorhamphichthys rondoni* and *Gymnotus coropinae* in first to third order streams at the Saracá-Taquera National Forest, Oriximiná, Pará. Rare items are shown in empty squares. **a.** *G. rondoni*; **b.** *G. coropinae*. Codes: 1 - Arthropoda (T); 2 - Algae; 3 - Aquatic Coleoptera (A); 4 - Aquatic Coleoptera (L); 5 - Ceratopogonidae (L); 6 - Chironomidae (L); 7 - Decapoda; 8 - Diptera (L); 9 - Eggs (Inv); 10 - Ephemeroptera (N); 11 - Hydracarina; 12 - Odonata (N); 13 - Pyralidae; 14 - Scales; 15 - Trichoptera (L); 16 - Zooplankton; 17 - Sediment/Detritus; 18 - Insect remains; 19 - Plant Remains.
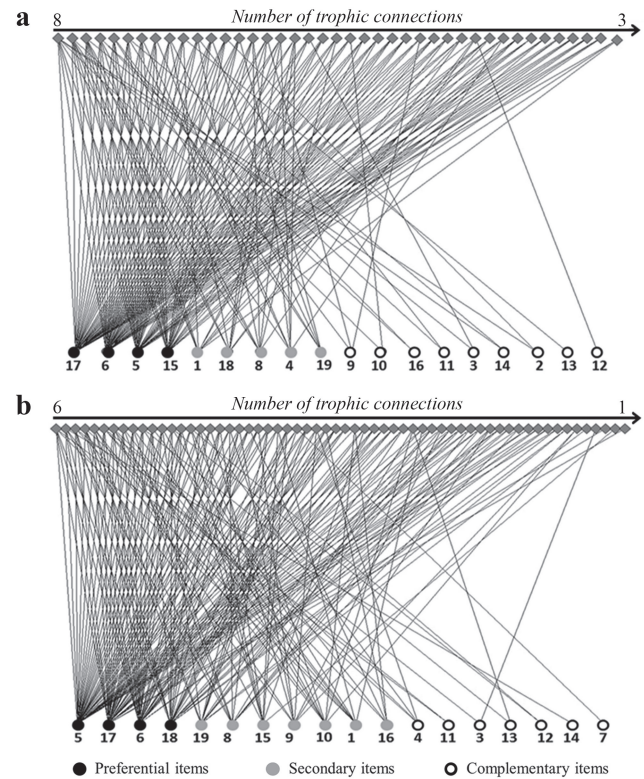
Fig. 4. Individual-resource networks of *Gymnorhamphichthys rondoni* and *Gymnotus coropinae* in first to third order streams at the Saracá-Taquera National Forest, Oriximiná, Pará. Full diamonds in the upper portion of the graphs are fish individuals. **a.** *G. rondoni*; **b.** *G. coropinae*. Codes: 1 - Arthropoda (T); 2 - Algae; 3 - Aquatic Coleoptera (A); 4 - Aquatic Coleoptera (L); 5 - Ceratopogonidae (L); 6 - Chironomidae (L); 7 - Decapoda; 8 - Diptera (L); 9 - Eggs (Inv); 10 - Ephemeroptera (N); 11 - Hydracarina; 12 - Odonata (N); 13 - Pyralidae; 14 - Scales; 15 - Trichoptera (L); 16 - Zooplankton; 17 - Sediment/Detritus; 18 - Insect remains; 19 - Plant Remains.

Discussion

Gymnotus coropinae and *Gymnorhamphichthys rondoni* occupy different microhabitats, but showed a similar diet based on benthic prey and detritus, showing a generalist feeding strategy with a potentially high trophic overlap. *Gymnotus coropinae* showed a broader diet than *G. rondoni*, but both species had a diet dominated by detritus. Differences in diet composition between the two species occurred mainly due to high intraspecific variation within the population of *G. coropinae*, whose diet is not composed of dominant items (*i.e.* items consumed by most or all individuals within a population in high quantities).

Gymnorhamphichthys rondoni inhabits sandy bottoms with high or low flow due to its psammophilous behavior (Zuanon *et al.*, 2006), which explain both its occurrence on sandy bottoms and on riffles, where individuals bury in the sand during the daytime. On the other hand, *G. coropinae* is associated with heterogeneous microhabitats with marginal vegetation, crevices or litter bottom. Feeding resources exhibit a patch-like distribution in space (Schoener, 1971), which locally affect food availability and trophic organization (Guedes *et al.*, 2015). Thus, it is commonly expected that the exploration of different microhabitats exposes fish to different food resources.

Nevertheless, both species fed predominantly on benthic invertebrates. Consumption of benthic prey was reported for several species of gymnotiforms (Winemiller, Adite, 1997; Peretti, Andrian, 1999; Giora *et al.*, 2005; Luz-Agostinho *et al.*, 2006; Rocha *et al.*, 2009; Giora *et al.*, 2012; Tesk *et al.*, 2014), suggesting it is a pattern for this fish order (Giora *et al.*, 2014). However, benthic prey was not the only food category consumed by *G. rondoni* and *G. coropinae*: both species consumed prey associated with macrophytes (*e.g.* Pyralidae larvae) and allochthonous insects that fall into the stream surface. Similar results were found for *Eigenmannia trilineata* López & Castello, 1966 in Southern Brazil, which consumed prey from several origins: nektonic, allochthonous, associated to the bottom or to macrophytes (Giora *et al.*, 2005).

Detritus was predominant in the stomach contents of both species, while plant remains were only expressive in the diet of *G. coropinae*. According to Winemiller, Adite (1997), gymnotiforms do not exhibit apparent morphological specialization for detritivory or herbivory (*e.g.* lengthening of the digestive tract), but are bottom-dwellers that feed through a suction/grasp-suction feeding modes. Thus, the dominance of detritus in the stomach contents may be due to its ingestion during the search for more nutritive prey. An alternative hypothesis is that the consumed detritus might be part of protective tunnels constructed by Chironomidae larvae of some clades (Trivino-Strixino, 2014). A similar case study identified that plant remains in the diet of numerous gymnotiforms were part of protective cases of caddisfly larvae (Trichoptera) (Winemiller, Adite, 1997).

Both dominant dietary items (except Detritus) are aquatic immature insects that are highly abundant and use a variety of habitats in aquatic systems (Pinho, Pepinelli, 2014). Some common Amazonian Chironomidae larvae build protective tunnels and use different kinds of benthic microhabitats (*e.g.* sandy bottom, mud with abundant organic matter, streambed with gravel; Butakka *et al.*, 2014) and Ceratopogonidae larvae display different behaviors like sand burying (Leptoconopinae), association to the bottom litter (Forcipomyiinae) or to the streambed (Dasyheleinae) (Ferreira-Kepler *et al.*, 2014). Therefore, even if fish prey upon dipterans of the same families, it does not mean that there is no trophic segregation among fish because they might search for dipteran species that occupy different microhabitats in these streams.

Most Chironomidae and Ceratopogonidae larvae are, at least partially, detritivores (Butakka *et al.*, 2014), thus playing an essential functional role in aquatic systems converting low quality organic matter into high-quality matter that can be assimilated by other species in the aquatic food web. Thus, the high consumption of these larvae by *G. rondoni* and *G. coropinae* includes both in the detritivory food chain. This strong linkage with the recycled organic matter highlights the importance of these electric-fishes to these streams, since a great portion of Amazonian stream fishes is known to feed predominantly on allochthonous items (Mendonça *et al.*, 2012; Gonçalves *et al.*, 2013; Silva *et al.*, 2016).

The lower niche breadth of *G. rondoni* is related to the specialized morphology of Rhamphichthyidae and to its psammophilous behavior. According to Zuanon *et al.* (2006), *G. rondoni* is dependent on prey that inhabits sandy bottom and feeds predominantly on Dipteran and Coleopteran larvae that are buried in the sand. A similar pattern was found by Tesk *et al.* (2014) for the congeneric species *G. petiti* in Amazonian streams, which feeds predominantly on aquatic immature insects and nematodes - although the latter might have been mistaken parasitic nematodes for dietary items.

Gymnotus coropinae shows a less specialized morphology and uses a greater variety of microhabitats, which influence prey diversity for consumption. Its congeneric *Gymnotus omarorum* Richer-de-Forges, Crampton & Albert, 2009 uses ambush or active hunting in marginal roots (Ferriz, Iwaszkiw, 2014), so if *G. coropinae* has a similar diverse behavior it could also explain its broader diet breadth. Even with the different morphological and behavioral adaptations, both species displayed high niche overlap. Winemiller, Adite (1997), studying gymnotiforms assemblage in Venezuelan floodplains, found the same pattern and considered that microhabitat use was an important information that was missing in their analysis. In fact, when we observe the microhabitat use and the niche overlap of *G. coropinae* and *G. rondoni*, it seems that spatial segregation is more important than trophic partitioning for gymnotiforms, contradicting the general pattern predicted for fish assemblages (Ross, 1986). Ecomorphology of the head is not uniquely associated to what can be predated, but also how efficiently species can

forage in different microhabitats (*e.g.* downturned mouth is related to detritivory, but can also be interpreted as a bottom-feeding strategy), which corroborates that microhabitat use is also related to the morphological divergence that they found, and not only dietary items.

As we did not address ecomorphological patterns, we can partially explain both our and Winemiller and Adite's pattern of high ecomorphological divergence but high trophic overlap: gymnotiforms do display different habitat use, which partially hampers the conclusion of this high trophic overlap among gymnotiforms when considering a taxonomic resolution of order/family for prey items. Marrero, Taphorn (1991) observed an extreme trophic overlap among gymnotiforms when considering only high taxonomic levels (*e.g.* aquatic insects) in Apure River basin, but Winemiller, Adite (1997) observed a broader trophic niche considering insect orders. Thus, the resolution at which we observe food items is central to understand a species' niche if we do not have information on their habitat use or feeding strategy.

Both the assessment of microhabitat use and the identification of dietary items with high resolution are not easy tasks. Many of the dietary items are often digested or torn in pieces, which hampers high-resolution identification. Assessing microhabitat use through behavioral methodologies for Amazonian species is usually a high-cost project, but less refined methodologies may be used, such as classifying the microhabitats where species were caught. The combined use of both kinds of information may reveal intriguing patterns for Amazonian stream fish species.

Gymnotus coropinae showed marked intraspecific variation. The inclusion of complementary items occurred on few individuals of *G. coropinae* and it reveals that a portion of the population used alternative items opportunistically. The presence of a single item with high prey-specific abundance and low frequency of occurrence highlights the importance of the between-phenotype component to the diet breadth and it reveals that *G. coropinae* populations may be generalists that include few specialist individuals (Smith *et al.*, 2011). Ferriz, Iwaszkiw (2014) observed a similar pattern for *G. omarorum* in Blanca Lake (Formosa, Argentina). *Gymnotus omarorum* was caught in a closed environment with low spatial variability, while our study covers higher physical variability and metapopulations, which could also explain the opportunistic consumption of these items; thus, it remains to be tested if this is an intrapopulational pattern for the *Gymnotus* genus.

The diet of *G. rondoni* was homogeneous among individuals, which could support the claim that less generalist populations support lower levels of individual specialization within it (Bolnick *et al.*, 2007) if we compare *G. rondoni* directly with *G. coropinae*. *Gymnotus coropinae* seems to display a mixed strategy among generalist/specialist individuals to compose the population niche breadth; on the contrary, the *G. rondoni* population exhibits only generalist individuals.

In this study, *G. rondoni* and *G. coropinae* were considered zoobenthivorous, but both species also consumed preys associated with other microhabitats. Both species exhibited a high trophic overlap, but *G. coropinae* had a broader niche breadth, which could be associated with its less specialized morphology and broader microhabitat use. We cannot suggest the occurrence of these patterns for these species along with their entire geographical distribution, as both have broad distributions over the Amazon and Orinoco basins, Guyana Shield or even broader (*G. rondoni* - Paraná basin; Eschmeyer *et al.*, 2016). Instead, we provide information about the ecology of these two species that can be useful to understand the ecological processes of Amazonian streams, especially from the perspective of functional diversity or trophic connections. Likewise, such information is useful for monitoring natural communities from the perspective of the modification of natural food webs by human impacts that disturb the streambed or sand patches within streams.

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