Trophic guilds of EPT (Ephemeroptera, Plecoptera, and Trichoptera) in three basins of the Brazilian Savanna

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ABSTRACT

Insects of the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) are prominent among stream biota and are associated with many ecological processes in these environments, meaning that a proper definition of their habits is essential. We studied EPT from three watersheds in Brazil (Paraguai, Paraná, and São Francisco) in order to (i) determine the trophic guilds of EPT genera sampled; (ii) determine whether trophic guilds reflect EPT phylogenetic component (taxonomic distance); (iii) compare trophic guild composition among watersheds; and (iv) verify the effect of environmental components in trophic guild composition. Eight trophic guilds were determined based on gut content analysis: detritivores, fine-detritivores, fine-detritivores/algivores, coarse-detritivores, coarse-detritivore/algivores, periphytivores, carnivores, and omnivores. Caddisflies presented the most variable diet and many genera belonged to different trophic guilds in different basins. Overall trophic guild composition did not reflect the taxonomic distance among taxa and it did not differ among the three basins. Instead, EPT guilds were related to local environmental variables, evidencing that their diet probably varies according to local resource availability, highlighting the importance of empirical assessments of diet for ecological studies.

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1. Introduction

Recently, there has been a growing interest in unraveling the diversity of Neotropical streams, as well as their functioning and dynamics. Streams and rivers are the most impacted aquatic ecosystems worldwide (Lake et al., 2007) and measuring these impacts requires the application of multimetric indices that encompass biological and ecological characteristics of the aquatic biota, notably that of macroinvertebrates (Hering et al., 2006; Bonada et al., 2006; Baptista et al., 2007; Oliveira et al., 2008; Buss and Vitorino, 2010). However, both conceptual and practical applications of such indices in the tropics are limited by a vast knowledge gap regarding basic aspects of the biology of aquatic organisms. For instance, essential ecological aspects as properly determining aquatic macroinvertebrates functional feeding groups (FFG) remain poorly understood. This characterization is fundamental to access the functional aspect of stream ecosystems and the lack of it is one of the major obstacles to a broader understanding of Neotropical streams.

The fact that there is still no robust literature available on macroinvertebrate FFGs of the Neotropics has forced several researches to use literature data from North America (e.g. Merritt and Cummins, 1996) to characterize FFGs of macroinvertebrates from tropical regions. However, this strategy can lead to cumulative miscategorizations, since there is no straightforward correspondence of FFG in the two regions (temperate *vs.* tropical). In general, FFGs of Nearctic insects seem to be less generalist than those from the Neotropics (Covich, 1988). In this scenario, studies that focus on macroinvertebrates functional feeding group characterization in Neotropical streams should be prioritized and put together with former datasets (e.g. Tomanova et al., 2006) to allow for generalizations about the functioning of these systems.

Several functional generalizations regarding tropical freshwaters are based on data from temperate regions. Regardless of some exceptions, tropical insect fauna has predominantly multivoltine life histories, with semi-continuous or continuous reproduction with asynchronous emergence, whereas most insects from temper-

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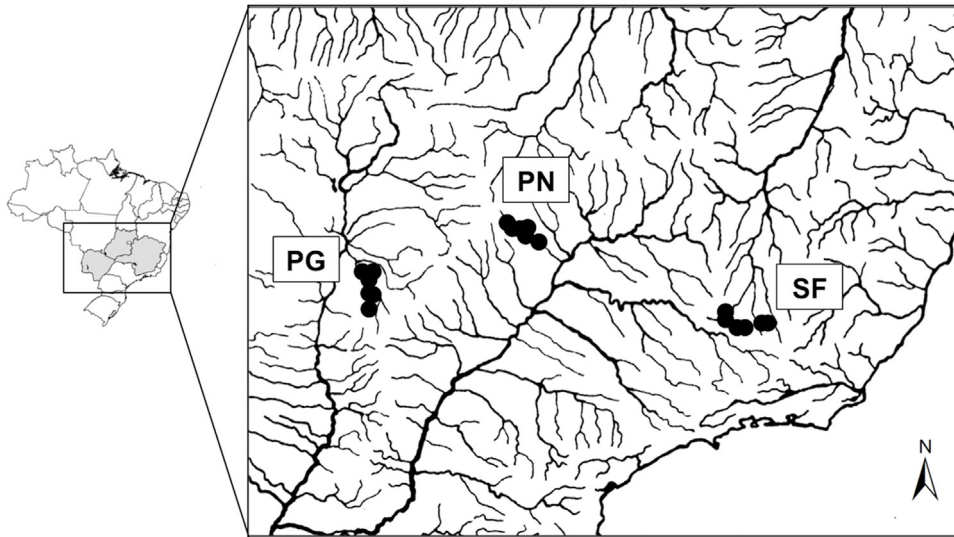 *E-mail address:* mcbastos@gmail.com (M. Ceneviva-Bastos).

Fig. 1. Location of the sampled streams in the Paraguay (PG), Paraná (PN), and São Francisco (SF) river basins, Brazil.

ate streams are univoltine (Jacobsen et al., 2008). With regards to feeding habits, Neotropical species have been reported to present a higher degree of omnivory than their temperate counterparts, being able to explore at least two trophic levels (Tomanova et al., 2006; Uieda and Motta, 2007; Ceneviva-Bastos et al., 2012; Ceneviva-Bastos and Casatti, 2014). Although ecological processes that occur in tropical and temperate streams can be fundamentally different (see Boyero et al., 2009 for further discussion), they are generally driven by the same factors (e.g. similar biotic responses to climate events as droughts and spates; instream primary productivity limited by nutrients and shading), which can vary at a regional and/or local scale, since both sets of streams present an array of climatic and hydrological conditions (Boulton et al., 2008).

Insects that belong to the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) are prominent among stream biota in terms of abundance, taxonomical and functional diversity (Rosenberg and Resh, 1993). The greatest diversity of these insects occurs in clear and well-oxygenated waters. They are very sensitive to environmental disturbances and thus are considered good indicators of habitat quality and integrity, being used as a metric in many indices of environmental assessment (Baptista et al., 2007). Moreover, an EPT trophic guild approach can be useful because it consists of a set of species that use certain resources in a similar way (Root, 1967), encompassing the trophic function of the community instead of single species (Jaksić, 1981). Hence, improving the existing knowledge about Neotropical fauna under a functional point of view can contribute to the proposition of more robust hypotheses regarding stream functioning, which in turn can help predict the consequences of anthropic activities and global warming on the functioning of these systems.

Current research has been focusing on the search for metrics and traits to access functional diversity (Colzani et al., 2013) and compare communities with distinct taxonomic composition (Wooster et al., 2012). Thus, a proper definition of insect functional feeding groups is essential to an adequate application of these approaches. In this context, the present study was conducted as an effort to highlight and discuss a complementary approach to defining functional feeding groups of EPT. Our aim was to (i) determine the trophic guilds of EPT genera sampled in three different watersheds; (ii) determine whether trophic guilds reflect EPT taxonomic distance; (iii) compare the trophic guild composition among watersheds; and (iv) verify the effect of environmental components in trophic guild composition.

2. Methods

2.1. Study area

The Brazilian Savannah biome (known as *Cerrado*) formerly covered 23% of the country's surface, occupying more than 2,000,000 km2 (Ratter et al., 1997). It is an assortment of different vegetation types (Sano and Almeida, 1998) and it harbors springs and drainage divisions of the major watersheds in Brazil (Padovesi-Fonseca, 2006). We sampled 19 headwater streams located near or within the National Parks of Serra da Bodoquena, Emas, and Serra da Canastra (*Cerrado* protected areas), which belong to the upper portions of Paraguay (PG), Paraná (PN), and São Francisco (SF) river basins, respectively (Fig. 1). For more details see Romero et al. (2013).

2.2. Samplings and diet analysis

Physical and chemical parameters (temperature, dissolved oxygen, pH, turbidity, and conductivity) were measured at each site with Horiba® U-10 equipment. Stream reaches (100 m long) were divided in ten equidistant transects and stream width, depth (seven measurements), and current velocity (with three replicates) were measured at each transect. The percentage of runs, riffles, and pools was estimated along the entire stream reach. We also evaluated environmental descriptors related to instream structural diversity, as substrate composition (proportion of bottom occupied by silt/clay; sand, gravel, cobble, boulder, rock, bedrock), stream internal habitat (proportion of logs and branches, leaf litter, submerged network roots, rooted submerged macrophytes, fluctuant macrophytes, adhered algae/vegetation), and ecotone structure (proportion of stream banks occupied by bryophytes, ferns, trees, shrubs, grasses, exposed soil, exposed roots, rocks, trunks). These physical, chemical, and structural attributes comprised the original pool of environmental variables.

At each site, six samples of macroinvertebrates from each main substrate type were collected with a 250 μm-mesh Surber net by washing the substrate within Surber delimited area (0.09 m^2) for one minute. The insects retained in the net were fixed in 10% formalin and preserved in ethanol 70%. The EPT specimens were identified to genus level using specific keys for each group (Fernández and Domingues, 2001; Costa et al., 2006; Mugnai et al., 2010) and specialists confirmed the identifications made.

Diet analysis was conducted in up to ten specimens of each EPT genus sampled at each stream, totalizing 428 analyzed guts; it was performed by removing the digestive tubes through a ventral incision, under a stereomicroscope, and then by setting them on slides to identify the gut contents under the microscope. We visually estimated the percentage that each food item occupied of the total gut content using a graded microscope eyepiece (40X objective). The food items were identified to the lowest taxonomic resolution possible.

2.3. Analysis

The quantitative diet data (% of gut occupied by each food item) was square root transformed to stabilize variance (Clarke and Gorley, 2006). Trophic guild determination was based on the Distance-Based Redundancy Analyses (dbRDA) (Legendre and Anderson, 1999) and on the 60% similarity cut of dendrograms, constructed using the Bray-Curtis coefficient (though the 18 dendrograms, six for each basin, were not presented herein). Both analyses used the quantitative diet data as variables. We conducted a Relate routine to evaluate the contribution of the phylogenetic component to macroinvertebrates' diet through the comparison between the trophic guild similarity matrix and taxonomic distance matrix. The taxonomic matrix was manually constructed to indicate the distances between genus pairs according to their classification: each genus pair was scored as '1′ for genera within the same family, '2′ for genera of different families, and '3′ for genera of different orders (Somerfield and Clarke, 1995). In the Relate procedure, a Spearman correlation was calculated to verify the significance of the relationship between matrices (Somerfield and Clarke, 1995), resulting in an R-value that ranges from 0 to 1. All analyses were conducted in the software Primer 6.0 (Clarke and Gorley, 2006).

To evaluate the similarity of trophic guild composition among basins we conducted a similarity analysis (ANOSIM), using the Bray-Curtis similarity coefficient in the software Primer 6.0 (Clarke and Gorley, 2006), with the trophic guilds of all samples and considered the basins as factors. Finally, the influence of environmental variables on trophic guild composition was evaluated through a Canonical Correspondent Analyses (CCA) in the Canoco 5 software (Ter Braak and Smilauer, 2012), using macroinvertebrate trophic guild abundance and local environmental variables from the three studied basins. We performed the CCA using the dissolved oxygen, conductivity, current velocity, stream width, depth, channel internal structure and percentage of runs, riffles and pools as environmental variables. These nine variables were selected ($r = 0.8$; $P < 0.05$) from a larger variable pool based on a Pearson correlation matrix, constructed using the STATISTICA 7 software (Statsoft, 2007).

3. Results

3.1. Trophic guilds

The orders Ephemeroptera, Plecoptera, and Trichoptera were represented by 2,728 specimens, distributed in 44 genera and 17 families (for more information on overall EPT assemblage structure, see Romero et al., 2013). The feeding items registered in the 428 analyzed guts were grouped into seven categories: fine particulate organic matter (FPOM); coarse particulate organic matter and plant material (CPOM); fungi (FUN); diatoms (DIA); algae and cyanobacteria (ALG); aquatic insects (AI), and undetermined items (UND) (Table 1). Of these, FPOM was the most consumed food resource, representing 78% of the diet of all analyzed specimens, followed by
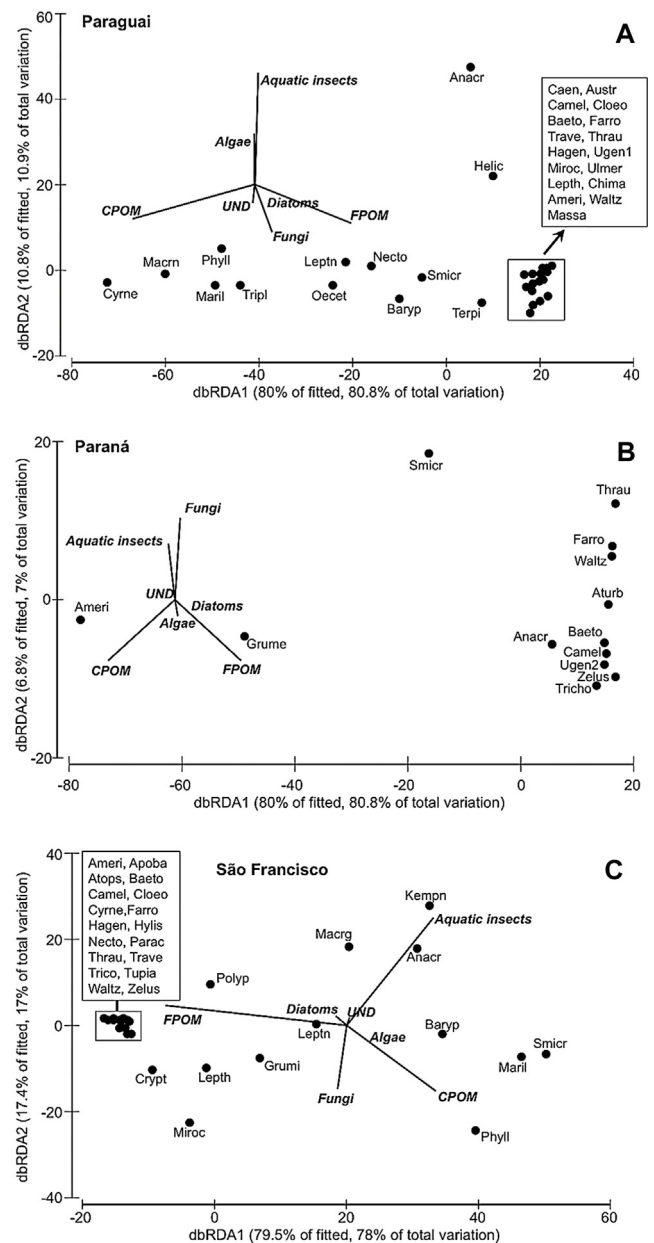

Fig. 2. Biplot resulting from the Distance-Based Redundancy Analysis (dbRDA) showing the effect of each diet component on EPT genera sampled in the Paraguay (A), Paraná (B), and São Francisco (C) river basins and the relationship among them. The vector overlap indicates a correlation higher than 90%. See Table 1 for genera codes.

coarse particulate organic matter (14%), aquatic insects (4.7%) and fungi (2%).

Eight trophic guilds were determined based on the similarity analysis and dbRDA results (Table 1, Fig. 2): detritivores, fine detritivores, fine detritivores/algivores, coarse detritivores, coarse detritivores/algivores, periphytivores, carnivores, and omnivores. The fine detritivores group was represented by more than 55% of all analyzed genera. Stoneflies were carnivores and mayflies were predominantly fine detritivores. Caddisflies presented the most flexible trophic guilds, being classified into different guilds depending on the site (Table 1), although they were most frequently classified as omnivores.

The trophic guilds were not related with taxonomic distance, both when considering the data of all basins (RELATE: R = 0.5,

Table 1
Trophic guilds of Ephemeroptera, Plecoptera, and Trichoptera genera sampled in the Paraguai, Paraná, and São Francisco river basins. Main food items consumed: FPOM = fine particulate organic matter; CPOM = coarse particulate organic matter; periphyton = clumped combination of FPOM + fungi + diatoms. Genera that belong to different trophic guilds in distinct basins are marked with (*).

Trophic guild	Main food items	Paraguai	Paraná	São Francisco
Detritivores	FPOM and CPOM	–	–	Phyll*
Fine detritivores	FPOM	Ameri, Baeto, Camel, Cloeo, Waltz, Lepth*, Trave, Caeni, Farro, Ugen1, Hagen, Massar, Miroc*, Terpi, Thrau, Ulmer, Chima, Austr	Ameri, Aturb, Baeto, Camel, Ugen2, Waltz, Zelus, Trico, Farro, Thrau, Anacr*	Ameri, Apoba, Baeto, Camel, Cloeo, Crypt, Parac, Tupia, Waltz, Zelus, Trave, Trico, Farro, Hagen, Hylis, Thrau, Necto*, Atops, Cyrne*
Fine detritivores/algivores	FPOM and filamentous algae	Helic	–	–
Coarse detritivores	CPOM and plant material	Leptn*, Smicr*, Baryp*, Necto*, Oecet	Grume	–
Coarse detritivores/algivores	CPOM, plant, and algae	Macro, Cyrne*, Maril*, Tripl, Phyll*	–	–
Periphytivores	Periphyton	–	–	Lepth*, Miroc*, Grumi
Carnivores	Aquatic insects	Anacr*	–	Anacr*, Macrg, Kempn, Polyp
Omnivores	Detritus and/or algae and aquatic insects	–	Smicr*	Leptn*, Smicr*, Maril*, Baryp*

Genera abbreviations. Ephemeroptera: Ameri = *Americabaetis*, Apoba = *Apobaetis*, Aturb = *Aturbina*, Baeto = *Baetodes*, Camel = *Camelobaetidius*, Cloeo = *Cloeodes*, Crypt = *Cryptonympha*, Parac = *Paracloeodes*, Tupia = *Tupiara*, Waltz = *Waltzohyphius*, Zelus = *Zelusia*, Lepth = *Leptohyphes*, Trave = *Traverhyphes*, Trico = *Tricorythopsis*, Caeni = *Caenis*, Farro = *Farrodes*, Hagen = *Hagenulopsis*, Hylis = *Hylister*, Massar = *Massartella*, Miroc = *Miroculis*, Terpi = *Terpides*, Thrau = *Thraulodes*, Ulmer = *Ulmeritoides*, Ugen = undetermined genus. Plecoptera: Anacr = *Anacroneuria*, Kempn = *Kempnyia*, Macrg = *Macrogynoplax*. Trichoptera: Atops = *Atopsyche*, Austr = *Austrotinodes*, Baryp = *Barypenthus*, Chima = *Chimarra*, Cyrne = *Cyrnellus*, Grume = *Grumichella*, Grumi = *Grumicha*, Helic = *Helicopsyche*, Leptn = *Leptonema*, Macro = *Macronema*, Maril = *Marilia*, Necto = *Nectopsyche*, Oecet = *Oecetis*, Phyll = *Phylloicus*, Polyp = *Polyplectropus*, Smicr = *Smicridea*, Tripl = *Triplectides*.
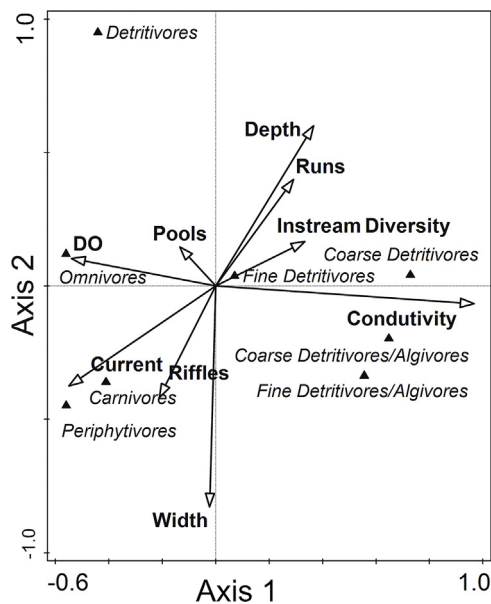

Fig. 3. Projection of the first two axes of the Canonical Correspondence Analysis conducted using macroinvertebrate trophic guilds and local variables of the three studied basins. Both axes were significant ($P = 0.002$) and the local variables explained 74% of the variation in trophic guild abundance.

$P < 0.05$) as when considering each basin separately (RELATE: PG: R = 0.518, $P = 0.01$; PN: R = 0.446, $P = 0.037$; SF: R = 0.51, $P = 0.01$).

3.2. Spatial variation of trophic guilds

Trophic guild composition was not significantly different among the three basins (ANOSIM: R = 0.012, $P = 0.305$). Instead, EPT guilds were related to local environmental variables: depth, percentage of runs, and instream structural diversity were positively correlated with CCA axis 1 (Fig. 3), while current, percentage of riffles, percentage of pools and dissolved oxygen were negatively correlated with the axis 2. Variables as conductivity, instream structural diversity,

and the percentage of runs were related to coarse and fine detritivores, whereas current velocity and the percentage of riffles were more related to carnivores and periphytivores (Fig. 3).

4. Discussion

Although Neotropical stream biota is still largely unknown, most studies conducted so far have found that omnivory is common and that consumers tend to be generalist feeders (Covich, 1988; Jepsen and Winemiller, 2002; Tomanova et al., 2006; Wantzen and Wagner, 2006; Uieda and Motta, 2007; Ceneviva-Bastos et al., 2012; Frauendorf et al., 2013; Ceneviva-Bastos and Casatti, 2014). Such dietary flexibility was illustrated herein by the fact that some taxa changed their diet according to habitat features and thus belonged to different guilds in distinct basins. The mayflies *Leptohyphes* and *Miroculis*, for example, were periphytivorous in the SF basin and fine-detritivores in the PG basin; the caddis *Phylloicus* and *Nectopsyche* fed mostly on coarse detritus in the PG basin, and predominantly on fine detritus in the SF; changes in the diet of caddis *Leptonema*, *Smicridea*, *Barypenthus* and *Marilia* (which belong to different families) were even more drastic, since they fed mostly on CPOM at the PG basin (coarse detritivores) and also fed on aquatic insects at the SF (all four) and PN (*Smicridea*); *Cyrnellus* was coarse-detritivore at the PG, fine-detritivore at the SF and was not sampled at the PN, though a previous study found it to be an omnivorous predator as well (taxon number 100 in Fig. 4 in the paper of Ceneviva-Bastos and Casatti, 2014). However, the stonefly *Anacroneuria*, which is a known predator, does not fit these diet-shift examples because their classification as fine-detritivore at the PN basin is more likely an artifact of finding only remains of their prey's digestive tubes in analyzed specimens guts.

In summary, all coarse-detritivore genera of the PG basin that were also sampled in the other basins belonged to different trophic guilds in the last, either to the fine-detritivores or omnivores. Except for *Grumichella*, which was the only coarse detritivore in the PN basin, no other genera from this guild were found at both PN and SF, indicating that genera classified as coarse detritivores in the PG basin are likely generalist feeders that are able to explore other food resources (as FPOM and aquatic insects) in the absence of a prefer-

able one (which could be CPOM and plant material). Despite these particularities, the diet of EPT, in general, did not differ among river basins and it did not mirror the taxonomic distance among taxa.

The composition of EPT trophic guilds was influenced by local environmental variables and, therefore, to local resource availability. The carnivores and periphytivores were more abundant in streams with a higher percentage of riffles and current velocity, which can strongly act as a selective pressure for the distribution of stream organisms (Bispo et al., 2006). Because fine sediment is often washed out in streams with high current velocity, the substrate of riffles is mainly composed of rocks and cobbles, which are usually colonized by periphyton (Cattaneo et al., 1997). Periphyton is a biofilm composed of algae and diatoms, bacteria, fungi and fine sediment (Burns and Ryder, 2001) and it is considered the main autochthonous basal source that supports food webs in shaded streams (Lau et al., 2009). This biofilm is widely consumed by periphytivores, which can be highly abundant in fast-flowing waters and attract their predators, the carnivores (Feltmate et al., 1986). In our study, this classical relationship was exemplified by the presence of the mayfly *Leptohyphes* in most Plecoptera guts.

The detritivores were widespread throughout the studied streams, following the wide distribution of detritus in stream environments, which is a ubiquitous food resource (Closs and Lake, 1994). In fact, if we consider coarse and fine detritus altogether, they comprised 92% of EPT diet. Detritus can be defined as any form of non-living organic matter, which includes plant tissues—such as leaf litter—animal tissues, feces, and dead microorganisms (Moore et al., 2004). Detritus dynamics is considered an important component of ecosystem structure and functioning (Wallace et al., 1997) and aquatic insects play a key role in such dynamics (Rich and Wetzel, 1978).

Coarse-detritivores and detritivores are the consumers that link terrestrial primary producers to aquatic food chains (Wallace et al., 1997). The allochthonous leaf litter that enters the streams, for instance, is broken by the joint action of physical fragmentation, microorganisms, and aquatic insects (Ruetz et al., 2002). In this process, the largest particles used by coarse detritivores are fragmented into smaller particles available for fine-detritivores (Graça and Canhoto, 2006), thus assembling detritus-based food webs. Fine particulate organic matter is considered a basal resource of primal importance in Neotropical streams (Boulton et al., 2008). Accordingly, our results indicate the same for the Brazilian savanna, since FPOM was the most consumed food item in the three studied basins, representing over 70% of all gut contents. Such high consumption and the high percentage of fine-detritivores (represented mostly by mayflies) can be related to the great availability of FPOM mentioned above, since most aquatic insects present great trophic plasticity and opportunistic feeding habits (Mihuc and Minshall, 1995; Ceneviva-Bastos and Casatti, 2014).

The feeding plasticity of caddisflies was the most expressive, being their genera classified into all trophic guilds identified in this study. The mayflies were mostly fine-detritivores and the stoneflies were mostly carnivores. These particular differences in the diet of each order illustrate the importance of the choice of specific taxonomic groups to be used in biomonitoring protocols, for they can act in distinct environmental niches. The use of the classification in functional feeding groups (FFG), proposed by Merritt et al. (1996), is very common in the scientific literature. However, this approach was mostly based on insect morphological and behavioral mechanisms used to acquire food. Also, it was originally proposed for temperate stream ecosystems, though it is vastly used throughout the world (Palmer et al., 1993; Heino, 2009; Silva et al., 2009). In some cases, adaptations for Brazilian streams were made (Cummins et al., 2005), but diet analysis was not performed and overall FFG characterization was based on Merritt and Cummins' 1996 book of Aquatic Insects of North America (Cummins et al.,

2005). Hence, the use of these literature-based data should be done carefully and generalizations should be limited to its unspecific applications instead of using this classification under a trophic ecology approach.

The main importance of conducting empirical diet analysis is the ecosystem function perspective it provides, since predators likely control their prey populations and vice-versa, while primary consumers can influence the availability of their resources to other consumers. Even when a broad resolution is used (i.e. trophic group), it can still depict species trophic niches. In this context, a trait-based approach is useful for data comparisons across systems, linking community and ecosystem ecology (Webb et al., 2010). The importance of incorporating trophic data in stream ecology studies is commonly acknowledged in studies of Neotropical fish assemblages, in which the evaluation of community attributes, biotic integrity and/or functional diversity frequently include the analysis of species diets or their trophic guilds (e.g. Casatti et al., 2009; Barletta et al., 2010; McIntyre and Flecker, 2010; Braga et al., 2012; Pease et al., 2012; Montaña and Winemiller, 2013; Casatti et al., 2015; Ferreira et al., 2015). When it comes to Neotropical macroinvertebrates this practice is extremely rare as a consequence of (i) knowledge gap regarding invertebrate diet and local FFG classification and (ii) widespread use of literature-based FFG as a surrogate for diet analysis, even though the inaccuracy of doing so has already been pointed (Tomanova et al., 2006; Oliveira and Nessimian, 2010).

In the present study, we conducted a thorough gut content analysis and classified EPT genera into trophic guilds, which takes into consideration the resource sharing among species (Blondel, 2003). Given that functional groups are suits of species that play equivalent roles in the ecosystem, the applicability of 'trophic groups' (or 'trophic guilds') and 'functional feeding groups' is the same and these definitions can be regarded as synonyms (Blondel, 2003). Following this reasoning, main items consumed by taxa that belong to a given FFG should also be the main items used to define its trophic group. For example, if the dominant food resource of 'shredders' is CPOM and plant detritus, that of 'filtering-collectors' is FPOM, and that of 'predators' are other animals (Cummins et al., 2005), these FFG would correspond to the 'coarse detritivores', 'fine detritivores' and 'carnivores' trophic groups, respectively. Omnivores would not have a direct FFG correspondent. However, *Leptonema* and *Smicridea*, which are 'filtering collectors' (Cummins et al., 2005) and thus should belong to the 'fine detritivores' trophic group, were actually coarse detritivores at the PG basin and 'omnivores' at the SF basin (19% and 33% of their diet were aquatic animals). Thus, using a FFG classification of EPT taxa sampled herein could lead to mismatches between FFG and diet, especially regarding caddisflies.

Hence, we believe that stream ecologists should join their efforts in producing a large dataset on macroinvertebrate dietary data for the Neotropical region to fulfill this great knowledge gap. By doing so, these basic studies (as Tomanova et al., 2006 and this one) can lead to a more accurate understanding of the functioning of lotic ecosystems. Information from different regions and biomes could then be compiled to create results that can be generalized and accurately applied in further studies of functional diversity, biomonitoring and conservation of Neotropical streams.

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