Assigning functional feeding groups to aquatic arthropods in a Neotropical mountain river

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ABSTRACT: The importance of aquatic arthropods in the processing of organic matter in fluvial systems is well known, but this topic has been poorly studied in Neotropical rivers. In this research, we studied the composition of functional feeding groups (FFGs) associated with differences in elevation in a tropical river in northern Colombia during the wet and dry seasons. Between 2008 and 2013, we collected benthic arthropods at 3 sites located in the upper (San Lorenzo), intermediate (La Victoria) and lower (Puerto Mosquito) sections of the Gaira River. We found some differences in the gut contents and FFGs of the animals from different sites and between the climatic seasons. The dominant food source at all the sites and during both seasons was fine particulate organic matter (FPOM). At La Victoria, the genera *Leptonema*, *Smicridea* and *Phylloicus* (all belonging to Trichoptera) presented significant differences in the consumption of coarse particulate organic matter (CPOM) between the rainy and dry seasons (p < 0.05). At San Lorenzo, *Leptonema* had the highest animal tissue consumption value (p < 0.05). A discriminant function analysis based on gut contents suggested that some taxa may have been assigned to the wrong FFGs. We concluded that the diets of the aquatic arthropods in our study tended to present high trophic plasticity. Consequently, our results suggest that Neotropical rivers need to be re-evaluated in terms of traditionally established FFGs, which heretofore have been based on information from other regions of the world, producing incorrect assessments of aquatic systems.

KEY WORDS: Aquatic insects · Feeding ecology · Gaira River · Gut contents · Trophic groups

1. INTRODUCTION

The degree of allochthonous contributions to organic material, principally coarse particulate organic matter (CPOM) from the leaf litter of riparian vegetation to mountain rivers, varies along elevation gradients. Geomorphological changes that occur along altitudinal gradients are evident, with a differential contribution of CPOM that is higher at higher elevations and gradually decreases with decreases in elevation (Webster et al. 1999, Gonçalves et al. 2006).

This pattern is directly related to the canopy cover of waterways, since canopies are generally denser in upper and intermediate areas (with the exception of some alpine and paramo rivers), resulting in decreased light penetration. In the lower sections of rivers, current velocities are reduced, widths are broader and canopies are more open, meaning the river receives greater light energy input, thus favoring autochthonous production by periphytic algae and aquatic plants (Dobson & Frid 1998, Webster et al. 1999).

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Elevation differences in the contributions of autochthonous or allochthonous organic materials are associated with differences in the relative abundances of macroinvertebrate taxa with specific modes of feeding (called functional feeding groups, FFGs). The greatest abundance of shredder-detritivores (Sh-Dt; organisms that cut or chew pieces of dead plant material) is expected at higher elevations, scrapers (Sc; organisms that scrape biofilm and algae from the surface of rocks and vegetation) are mainly found in intermediate sections and collector-gatherers (CG; organisms with modified mouthparts that collect particles, <1 mm, that have accumulated at the bottom of rivers) dominate lower river basins (García et al. 2016). This supposition is supported by the idea that the contribution of organic matter is different along the gradient, with CPOM being more significant in narrower channels with arboreal riparian vegetation and fine particulate organic matter (FPOM) being more significant in broader waterways with open riparian vegetation in the lower parts of river basins; moreover, the contributions of these different fractions of organic matter are modified by seasonal changes in rainfall (Boyero et al. 2012, Giraldo et al. 2014, García et al. 2016).

Precipitation is the main factor associated with seasonality in tropical aquatic systems, affecting water quantity and quality (Boulton et al. 2008, Gonçalves et al. 2014). The rainy season provides a large amount of water which influences the quantity of organic matter available, while the dry period affords greater hydrological stability; both periods result in changes to the flow and characteristics of the basin in freshwater systems (Power et al. 1995).

Placing invertebrates in FFGs indirectly characterizes the available food sources in streams and is a functional measurement that provides an idea of the benthic trophic structure of a river. However, the categorization of Neotropical invertebrates into FFGs has low taxonomic resolution (mostly at the family level; Tomanova et al. 2006, Ramírez & Gutiérrez-Fonseca 2014) and might be a deficiency that limits the functional analysis of communities. More research is required, especially at the genus and species levels, to show how the role of invertebrates change along a latitudinal gradient and with geographic conditions. Other traits that are used in trophic ecology to assign individual taxa to FFGs include behavioral characteristics (especially those related to food acquisition) and analysis of stomach contents and feeding structures (Ramírez & Gutiérrez-Fonseca 2014). Many studies on FFGs have been conducted in temperate zones (Cummins 1973, Merritt et al. 1996, 2008, Merritt & Cummins 1996), but even in these better-studied regions, many species living in mountain streams have not yet been assigned to FFGs (for example, Niedrist & Füreder 2017 in the Alps).

For Neotropical rivers, there are some studies on trophic characterizations based on gut content examination (e.g. Cummins et al. 2005, Tomanova et al. 2006, Chará-Serna et al. 2012, Frauendorf et al. 2013) or biological traits (Tomanova & Usseglio-Polatera 2007), but as mentioned, more research is required, especially at finer taxonomic levels. It is necessary to evaluate the trophic relationships and feeding habits of invertebrate species in Neotropical rivers to identify their trophic role, trophic position in the food web and importance as key organisms to the functional integrity of streams (Tomanova et al. 2006).

The function of aquatic macroinvertebrates varies according to their geographical location (Webster et al. 1999, Motta & Uieda 2004, Chará-Serna et al. 2012, Reynaga & Rueda 2014), making it impossible to always assign the same FFG to a particular taxon (especially at gross taxonomic levels, such as families) even when they are common in the tropics or other regions (Tomanova et al. 2006, 2007, Frauendorf et al. 2013, Guzmán-Soto & Tamaris-Turizo 2014, Ramírez & Gutiérrez-Fonseca 2014). The presence of the Sc FFG is frequent in the intermediate zones of temperate rivers (Cummins 2002, Paunovi et al. 2006), but this pattern has not been sufficiently confirmed in Neotropical lotic environments; shedders and predators might be in high abundance in the upper section (Vannote et al. 1980); however, the intermediate zones are the most abundant areas in tropical rivers (Motta & Uieda 2004, Chará-Serna et al. 2012), and more studies are necessary to confirm these patterns. Therefore, it is necessary to conduct studies that include the spatial and temporal dynamics of tropical systems. Analyses from different environments in Colombia, namely Gorgona Island (Longo & Blanco 2014a,b), the Risaralda region streams (Chará-Serna et al. 2012) and the rivers in the Sierra Nevada de Santa Marta (Tamaris-Turizo et al. 2007, Guzmán-Soto & Tamaris-Turizo 2014, Granados-Martínez et al. 2016), have shown that trophic groups or FFGs for the same taxa that have been collected in different geographic regions are not consistent with the available literature (Torres-Zambrano & Torres-Zambrano 2016). In these studies, changes in diets along elevation gradients have not been evaluated and neither has the trophic variation resulting from differences in climatic periods.

In the present study, we assessed the feeding of arthropod communities in a Neotropical mountain river at different taxonomic levels during 2 climatic periods (dry and rainy seasons) and at 3 locations (San Lorenzo, La Victoria and Puerto Mosquito) along the downstream progression of the river. The feeding habits of the most abundant aquatic arthropod genera were defined in sections of the river at different elevations. We hypothesized that as the elevation decreased, the contribution of CPOM to the diets would decrease along with a reduction in the dominance of CG and Sh-Dt FFGs in comparison with the prevalence of those groups of aquatic arthropods at intermediate and low elevations. We presumed that with an increase in the FPOM contribution in the intermediate and lower sections, there would be an increase in the relative abundance of filterers (Ft; organisms with adaptations for capturing particles directly from the water column) as the elevation decreased, given that at lower altitude there is a greater availability of finer particles that could favor this feeding group. Additionally, we hypothesized that during the rainy season, FOPM would make up a major portion of the gut content, while the proportion of COPM would increase during the dry season because in this period of less rainfall the contribution of allochthonous organic matter is greater (Rodríguez-Barrios et al. 2011). We compared the spatial (elevation) and temporal (dry and rainy seasons) variations in trophic characteristics of the aquatic arthropods and determined whether the FFGs that were defined for the same taxa in other regions were consistent with those observed in the studied Neotropical river.

2. MATERIALS AND METHODS

2.1. Study sites

The Gaira River is located in the Sierra Nevada de Santa Marta in northern Colombia; the main channel is 32 km long and its catchment area encompasses 105 km^2. We collected data in 3 sections of the Gaira River: the upper section (San Lorenzo) at 1700 m above sea level (m a.s.l.), the intermediate section (La Victoria) at 900 m a.s.l. and the lower section (Puerto Mosquito) at 80 m a.s.l. At San Lorenzo, riparian vegetation was well-conserved and dominated by large trees that provided abundant and permanent shade over the river. The following riparian vegetation dominated: *Chamaedorea linearis* Ruiz & Pav 1823, *Geonoma interrupta*

Ruiz & Pav 1823, *Ceroxylon ceriferum* Pittier 1926, *Perrottetia multiflora* Lundell 1985 and *Tovomita weddelliana* Planch & Triana 1860. At La Victoria (the intermediate section), many coffee plantations as well as transitional plantations such as corn and fruit farms were located near the stream, which at times comprised more than 300 ha. Despite these anthropogenic activities, the riverbanks were well-conserved. The riverbed maintained heterogeneous microhabitats, and the water exhibited good physico-chemical conditions. Riparian vegetation included large trees (canopy greater than 15 m); the most common taxa were *Ficus* spp., *Guarea guidonia* Sleumer 1956, *Zygia longifolia* Britton & Rose, 1928, *Myrsine costaricensis* Lundell, 1985, *Clusia* sp., *Trichospermum mexicanum* Baillon, 1872 and *Vismia baccifera* Triana & Planch, 1862, which all provided ample shade over the river. In Puerto Mosquito (lower section), average rainfall was 448 mm, discharge was 0.69 m^3 s^{-1} and the channel width was 7.14 m; arboreal plants such as *Cavanillesia platanifolia* Kunth 1821, *Pseudobombax septenatum* Dugand 1943, *Anacardium excelsum* Bertero & Balb 1912 and *Pradosia colombiana* Pennington & Humboldt 1988 were predominant. This section had high anthropogenic influences from farms near the river and from tourist and recreational activities; these human activities tended to modify the abiotic and biotic fluvial characteristics at this site.

2.2. Sample collection and lab analysis

At each site, 5 samples were collected during the dry and rainy seasons between February 2010 and December 2013, in 100 m long sections that were heterogeneous in their aquatic habitats and included rapids and pools. The samples encompassed the rainy periods (October to November 2010, 2011 and 2013) and dry periods (February to April 2010 and 2011, plus December 2013). We sampled gravel, submerged leaf litter and stone microhabitats. Samples in the gravel areas were collected with a Surber net (area: 0.09 m^2; mesh: 250 µm). Approximately 500 g of wet leaf litter material was collected and weighed with a dynamometer. These samples were processed directly in the field to extract the arthropods. Rocks with different diameters (18 to 23 cm) were selected, and the organisms were manually extracted for 30 min. The microhabitat samples were grouped into integrated samples (bulk samples). The arthropods were preserved in 96% ethanol and analyzed at the ecology laboratory of the University of Magdalena.

We did not observe mollusks or annelids in our samples, possibly because the capture methods were not optimal for these groups. Arthropods were identified at the most detailed taxonomic level (genus for most families and subfamily for the Chironomidae) using taxonomic keys such as Posada-García & Roldán-Pérez (2003), Domínguez et al. (2006), Merritt et al. (2008), Domínguez & Fernández (2009) and Stark et al. (2009). The length of each individual was measured with a caliper and the average total length of each taxon was calculated.

We analyzed gut contents according to a technique proposed by Tomanova et al. (2006). This method is advantageous because it quantifies the area occupied by all food elements. For each integrated sample, we extracted the digestive tracts of up to 5 individuals from each taxon, combined the contents and homogenized them with glycerin on a slide. For taxa with fewer than 5 specimens, gut content analysis was performed separately for each individual. We randomly examined 20 microscopic fields with magnifications of 10 and 40× and determined the average area occupied by each item using an AxioCam ERc5s camera placed on a Carl Zeiss Primo Star microscope. Last, we identified and quantified the area occupied by each food item that was found in the gut contents; the area of each item was calculated with respect to the total area occupied by all items. The data are reported as percentages.

Food items in the gut contents were categorized according to the size of the materials and their origins; i.e. animal tissue, vegetal tissue, microalgae, fungi, CPOM (≥1 mm) or fine particulate organic matter (FPOM, <1 mm). The CPOM and FPOM categories were based on Vannote et al. (1980). Initially, taxa were assigned to FFGs according to the categorization recommended by Ramírez & Gutiérrez-Fonseca (2014); we then tested these categories with a statistical analysis as explained below. We assessed the composition of diets from the 3 sample sites during each season.

2.3. Data analysis

Gut contents were initially compared graphically using the proportionate occurrence of food items in all arthropods' gut contents at each site. To determine whether the relative number of ingested items was significantly different between the 2 seasons (rainy and dry), we applied a Mann-Whitney U-test for each taxon after checking for data normality using a Shapiro-Wilks test. To classify the feeding type

(Sneath & Sokal 1973, Wantzen & Rueda-Delgado 2009), we conducted an analysis of cluster conglomerates based on the proportions of the food items and applied Bray-Curtis dissimilarity (Clarke & Gorley 2001). To verify significant differences between cluster branches, we used ANOSIM at an $\alpha = 0.05$ level of significance (Anderson 2001). We carried out discriminant functional analysis to verify whether the proportions of diets correctly conformed with the FFGs, using the categories proposed in the literature for aquatic insects (Ramírez & Gutiérrez-Fonseca 2014) and for decapods (Cummins et al. 2005). For this analysis, the discriminant variables were the proportions of the food items, and the grouping variable was the respective FFG, with previous transformation of the data with the root of arcsine function. We compared the groups with a cross-validation of the test. FFGs were defined as CG, Ft, predators (Pr; organisms that consume other organisms), Sh-Dt and Sc. To understand the functional ecology of the arthropod FFGs in the 3 sections of the river, a principal component analysis (PCA) was employed, in which the food items of the invertebrate orders were used as variables to explain the organization of the sizes (lengths) of the arthropods. All analyses were performed in R v.3.1.3 (R Development Core Team 2018) using the following packages: 'ANOSIM' and 'PAR' for the discriminant analysis and 'prcomp' for the PCA.

3. RESULTS

3.1. Variation in diets mediated by changes in elevation

In total, we dissected 698 intestines from 48 arthropod taxa; 31 taxa were collected in San Lorenzo, 31 in La Victoria and 29 in Puerto Mosquito (Table S1 in the Supplement at www.int-res.com/articles/suppl/b029p045_supp.pdf). Generally, all of the food items available for gut analysis showed little variation between sites, with FPOM as the dominant item (62.8% in Puerto Mosquito and 70.8% in La Victoria). CPOM and animal tissue showed similar percentages at all sites, varying between 8.9 and 14.3%, with the highest value in Puerto Mosquito (lower section), followed by San Lorenzo (upper section) and La Victoria (intermediate section). A similar tendency was recorded for vegetal tissue, with values ranging from 5.0 to 6.8%. Microalgae and fungi contributed less than 2% to the diet compositions (Fig. 1).

Coleoptera presented a similar diet composition at the 3 collection sites, with a predominance of FPOM.
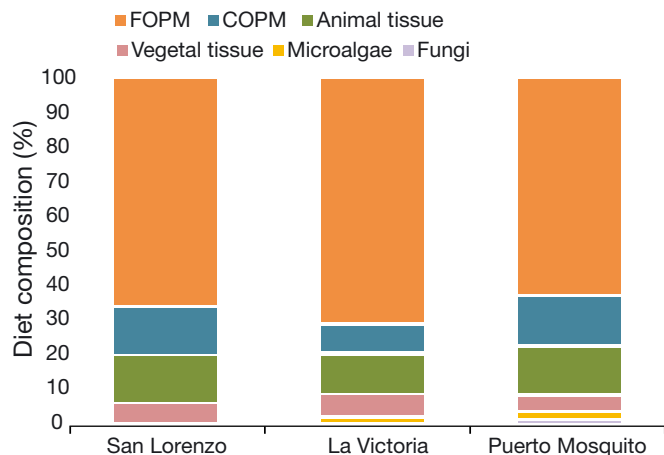
Fig. 1. Diet composition of aquatic arthropods at the 3 sampling sites. FPOM: fine particulate organic matter; CPOM: coarse particulate organic matter. Similar contributions of feeding items were observed at all 3 sites, where FOPM and COPM were the principal components of the diet in all taxa

The percentage of this resource increased as elevation decreased. The proportion of FPOM in the diet varied from 57.6% in San Lorenzo to 86.9% in Puerto Mosquito. Diptera (Chironomidae) and Ephemeroptera (i.e. *Baetodes*, *Leptohyphes* and *Tricorythodes*) showed similar tendencies in terms of FPOM; in San Lorenzo and La Victoria there were greater percentages of this item, while the percentages decreased in both insect orders in Puerto Mosquito. For the predator orders, such as Megaloptera (*Corydalus*), Odonata (principally *Progomphus*) and Plecoptera (*Anacroneuria*), animal tissue was quantified at approximately 100% of diet composition in San Lorenzo and La Victoria, while at Puerto Mosquito the proportions were 83.8, 88.9 and 75.0%, respectively, for each order. The Trichoptera food spectrum was principally composed of CPOM and animal tissue at San Lorenzo (36.0 and 27.7%) in genera such as *Phylloicus* and *Leptonema*. Additionally, at La Victoria and Puerto Mosquito, the most important item for these caddisflies was FPOM (56.2 and 40.7%, respectively at each site); CPOM and animal tissue all had similar values to each other. Lepidoptera and Decapoda were found in Puerto Mosquito, and their gut contents contained mostly FPOM (41.6 and 70.8%, respectively). For example, the proportion of FPOM was 39.8% for the larvae of Lepidoptera of the genus *Petrophila*; 20.5% animal tissue was found in the gut contents of the genera *Atya* and *Macrobrachium* of the order Decapoda (Fig. 2).

The relationships between arthropod length and consumed items (Fig. 3) showed that many large organisms (total length > 20 mm), such as Megaloptera, Odonata and Plecoptera (located towards the right of the PCA figure), mainly consumed animal tissue (i.e. as Pr FFG). In the opposite sector there were 2 groups: one in the upper quadrant of the figure that corresponded to small taxa (total length < 10 mm), such as Diptera, Coleoptera and Ephemeroptera, and another in the lower part of the graph (Trichoptera, Lepidoptera and Coleoptera) which were intermediate sizes (between 10 and 20 mm total length). The smallest arthropods were Sc that consume microalgae and FPOM. The medium-sized arthropods were made up of a group of Sh-Dt that consumed vegetal tissue and CPOM.

3.2. Temporal variation in the diets

When comparing the percentages of each food item between the seasons, the genera *Leptonema*, *Smicridea* and *Phylloicus* (all caddisflies) showed significant differences for at least one of the items. At San Lorenzo, the gut contents of *Leptonema* showed differences in the relative content of animal tissue ($W = 0$, n = 10, p < 0.05), with a lower proportion during the rainy seasons. At La Victoria, this genus consumed smaller proportions of CPOM ($W = 0$, n = 8, p < 0.05), a greater proportion of FPOM ($W = 16$, n = 8, p < 0.05) during the rainy seasons and an absence of animal tissue during the rainy seasons ($W = 20$, n = 8, p < 0.05). *Smicridea* consumed mostly CPOM during the dry periods ($W = 16$, n = 17, p < 0.05) and, in the *Phylloicus* genus, the highest proportions of CPOM ($W = 25$, n = 10, p < 0.05) and FPOM ($W = 5.5$, n = 8, p < 0.05) consumption occurred during the dry periods (Table 1).

Cluster analyses of the taxa clearly reflected the formation of 4 significantly different dietary groups (ANOSIM; R = 0.91, p < 0.01) (Fig. 4), suggesting the following groupings: Group 1, organisms with a diet dominated by animal tissue that represented more than 70% of the overall gut contents (90% Odonata and Magaloptera); Group 2, in which significant amounts of CPOM (30 to 78%) and vegetal tissue (20 to 42%) were found in the gut contents (one representative genus was *Phylloicus*); Group 3, in which the diets contained more than 90% FPOM for organisms comprised of subgroup 'C', which included the taxa Diptera, Coleoptera and Ephemeroptera, and where the gut contents of subgroup 'D' (mainly the genera *Dixella* [Diptera: Dixidae], *Heterelmis*, *Microcylloepus* and *Cylloepus* [Coleoptera: Elmidae], *Protroptila* [Trichoptera: Glossosomatidae] and *Americabaetis*, *Baetodes, Camelobaetidius* [Ephemeroptera: Baetidae] and *Thraulores* [Ephemeroptera: Leptophlebiidae])
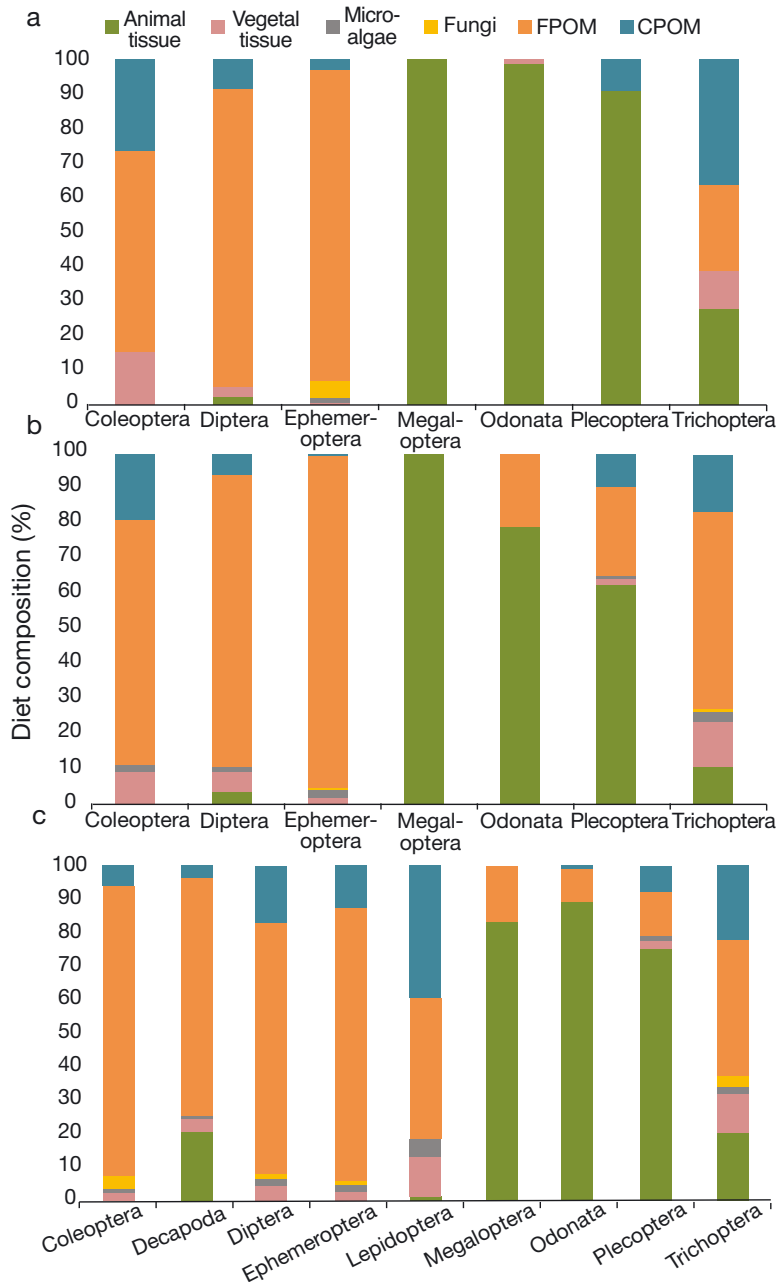
Fig. 2. Diet composition by aquatic arthropod orders in the Gaira River: (a) San Lorenzo, (b) La Victoria, (c) Puerto Mosquito. FPOM: fine particulate organic matter; CPOM: coarse particulate organic matter. In addition to the high representation of FPOM and CPOM, the importance of animal tissue is denoted for some typically predatory orders

amounts of FPOM (48 to 63%), CPOM (10 to 50%) and animal tissue (39 to 43%) in their gut contents and 'F', which included a mixture of organisms that obtain their food by filtering water that is passed through structures (typical of caddisfly larvae of *Leptonema* and *Smicridea* [Hydropsychidae]). Other taxa of this group, such as *Tipula* (Diptera: Tipulidae), *Petrophila* (Lepidoptera: Crambidae) and *Hemerodromia* (Diptera: Empididae), had the greatest proportions of FPOM (42 to 53%), CPOM (30 to 42%) and vegetal tissue (12 to 13%) in their gut contents, except for *Hemerodromia*, which contained no vegetal tissue in its intestines.

When assessing the composition of the FFGs in the different seasons at San Lorenzo, CG and Ft showed the same number of taxa, while the diversity of Pr increased from 1 taxon during the rainy seasons to 8 taxa during the dry seasons. The Sh-Dt increased from 2 to 5 taxa, and the Sc decreased from 2 to 0 taxa. At La Victoria, the CG doubled the number of taxa in the dry seasons (10) from the number seen in the rainy seasons (5), while the Ft and Pr had similar number of species. Fewer Sc were present during the rainy season compared to the dry season. At Puerto Mosquito, richness was similar to that recorded at the other 2 sites (5 taxa during the rainy seasons and 8 during the dry seasons), but Ft, Pr and Sc were greater during the dry seasons (Fig. 5).

The discriminant analyses of the FFGs assigned to the taxa showed an accumulation of 87.6% for the variance of the 2 first axes (Fig. 6), which highlights an association between the variables, meaning that the separation of the FFGs was reliable. Upon review of the cross-validation for each case (observed vs. expected), the model reassigned some taxa to different FFGs (Table 2), which corresponded to 18.8% error. Within the FFGs assigned by the cross-validation, some did not correspond to the habit of the organisms or to the morphology of their mouthparts. For example, *Leptonema*, which was initially assigned Ft, was considered Pr by this model.

There was a configuration in the relationship between the functional groups and the items consumed (Fig. 7) independent of seasonality and altitude. Each functional group corresponded to all organisms sampled.

showed CPOM at between 8 and 23%, notable proportions of vegetal tissue (7%) and the greatest amounts of microalgae (2%) and fungi (2.3%) because these arthropods consume food items by scraping substrates; and Group 4, consisting of 2 subgroups, 'E' (with *Macrobrachium* [Palaemonidae] and the Tanypodinae subfamily), which showed significant
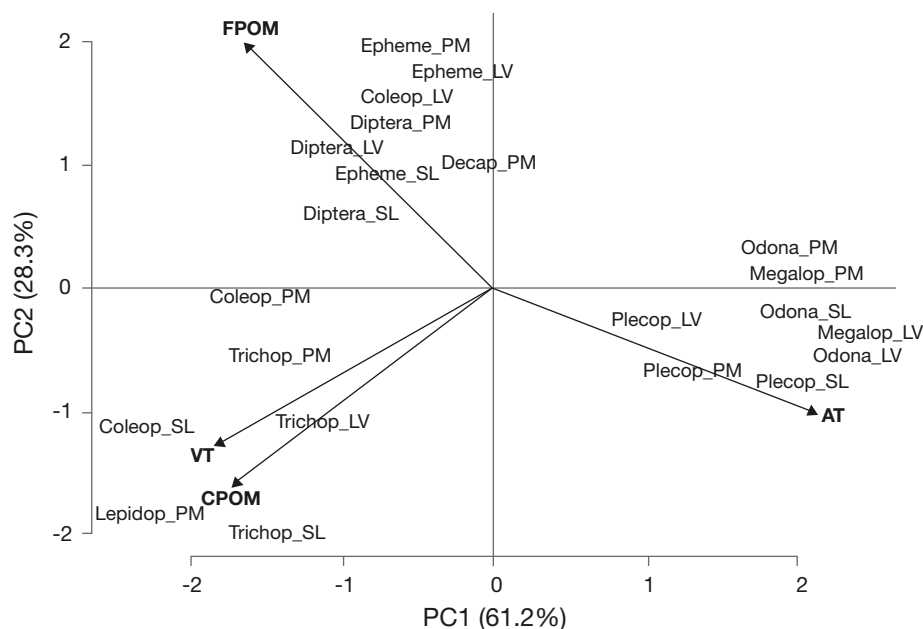
Fig. 3. Principal component analysis (PCA) of the food types and arthropod size in the 3 sections of the Gaira River: SL: San Lorenzo (upper section); LV: La Victoria (middle section); PM: Puerto Mosquito (lower section). FPOM: fine particulate organic matter; CPOM: coarse particulate organic matter; AT: animal tissue; VT: vegetal tissue. Megalop: Megaloptera; Odona: Odonata; Plecop: Plecoptera; Coleop: Coleoptera; Lepidop: Lepidoptera; Trichop: Trichoptera; Epheme: Ephemeroptera; Decap: Decapoda. The separation of arthropod orders according to the sizes of individuals is notable, such that larger animals are related to predatory habits, while smaller and medium-sized organisms correspond to scraper and shredder-detritivore taxa

Table 1. Percentages of ingested food items that were significantly different (Mann-Whitney *U*-test: p < 0.05) between the rainy and dry seasons. CPOM: coarse particulate organic matter; FPOM: fine particulate organic matter; NP: not present

Site	Taxon	CPOM		FPOM		Animal tissue	
		Dry	Rainy	Dry	Rainy	Dry	Rainy
San Lorenzo	*Leptonema*	NP	NP	NP	NP	24.1	12.3
La Victoria	*Leptonema*	58.8	1.72	15.1	79.7	8.5	0
	Smicridea	49.1	3.1	NP	NP	NP	NP
	Phylloicus	87.6	63.3	17.5	0.9	NP	NP

4. DISCUSSION

4.1. Spatial and seasonal variations in the diets

Our results partially supported our hypothesis. In fact, the diet of some taxa did change according to season. This effect was observed in the shredder caddisflies *Leptonema*, *Smicridea* and *Phylloicus* at San Lorenzo (upper section) and at La Victoria (intermediate section), indicating the greater importance of CPOM and FPOM resources as supplies of energy. However, differences in elevation did not significantly influence the dietary composition of the invertebrate communities in the analysis, except for the absence of Sc at high elevations during the dry seasons and the lack of Sh-Dt in the lower basin during the rainy seasons. However, we did not evaluate some variables that affected the structure and composition of the communities in the rivers, such as the composition of the riparian vegetation (quality and input), vegetative cover and anthropic activities. Greathouse & Pringle (2006) pointed out that the composition of FFGs is mainly structured on the availability of baseline resources, such as CPOM and FPOM, which do not necessarily change with elevation. However, Hyslop & Hunte-Brown (2012) found that Sh-Dt and Pr declined and Sc increased with decreasing elevations in a Jamaican river. Our hypothesis was partially proven, since with a decrease in elevation the abundance of Sh-Dt decreased and the abundance of collectors increased; however, the abundance of Pr did not follow this pattern.

The importance of FPOM in trophic networks has been frequently reviewed for North American rivers (Cummins 1973, Merritt et al. 2008) and for some tropical rivers (Motta & Uieda 2004, Tomanova et al. 2006, Chará-Serna et al. 2012). In this study, FPOM was found in the greatest percentage in organism intestines at all sites and during both seasons, which was contrary to our hypothesis, as we expected the highest contribution during the rainy season. FPOM could be a product of arthropod shredding activity on CPOM (Cummins 1973, Boyero et al. 2011) or could result from the mechanical and abiotic shredding of CPOM (Allan & Castillo 2007), although complex microbial interactions are known to influence the FPOM pool (Boyero et al. 2016). The results from our study partially agree with those reported by Rodríguez-Barrios et al. (2011), who quantified the CPOM and FPOM stored
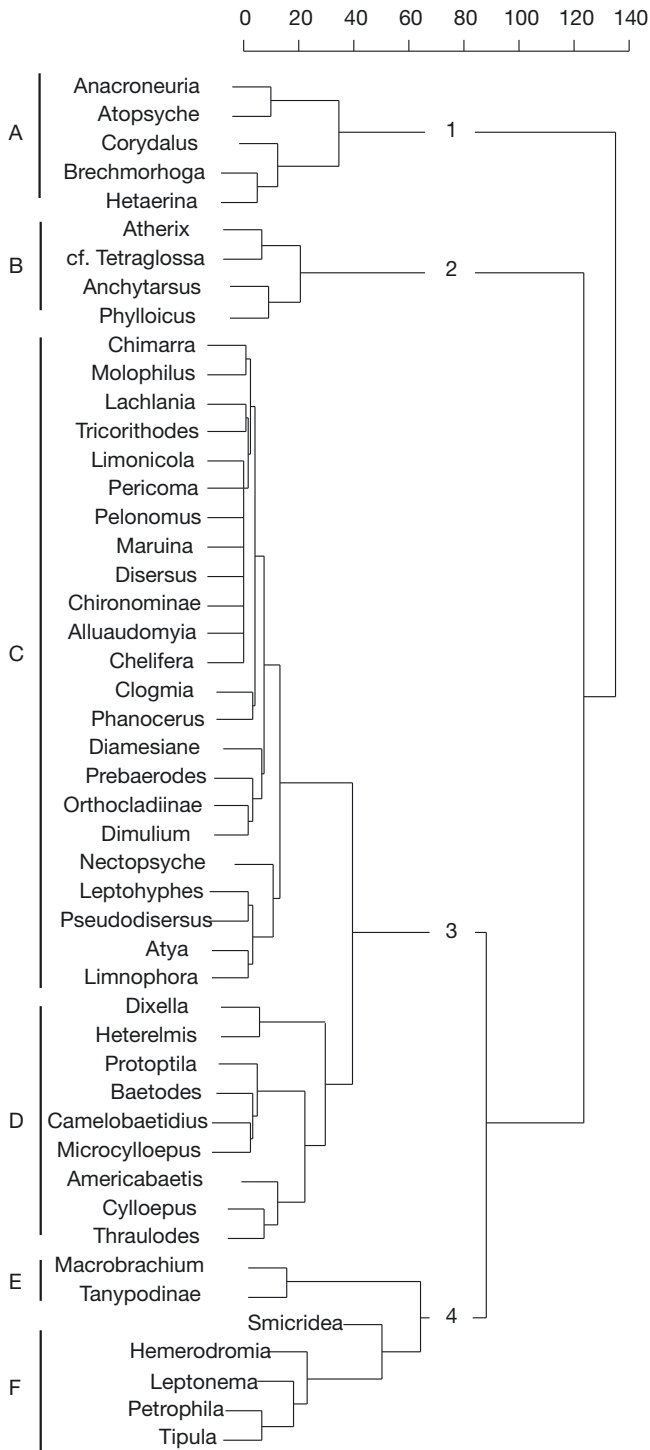
Fig. 4. Cluster analysis based on the percentage of the arthropod diets in the sampled sites. Numbers and capital letters indicate the trophic groups established. Each group formed in the dendrogram corresponds to taxa with certain food preferences: 1A: predators; 2B: consumers of coarse particulate organic matter (CPOM); 3C: mainly consumers of fine particulate organic matter; 3D: consumers of CPOM and plant tissue; 4E and 4F: mixture of different types of consumers
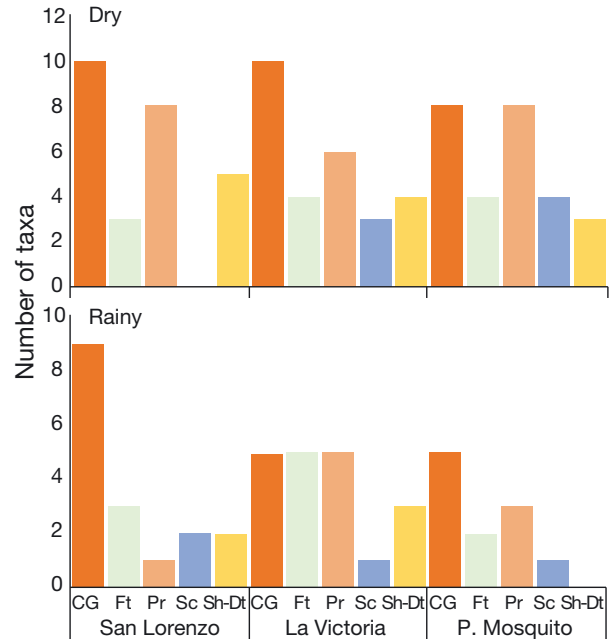

Fig. 5. Number of taxa by functional feeding groups found at the sample sites during the 2 seasons. GC: collector-gatherers; Ft: filterers; Pr: predators; Sc: scrapers; Sh-Dt: shredder-detritivores. The richness of CG taxa stands out especially in the upper basin of the river in both climate periods

in the Gaira riverbed in the same sections of the river. These authors found that the FPOM availability increased from the upper part (San Lorenzo) towards the downstream sections of the river (Puerto Mosquito). In comparison with FPOM, CPOM was higher in the upper section of the river; in the intermediate section they had similar values; and in the lower section the 2 fractions increased greatly, although CPOM continued to be higher.

In our research, the caddisflies *Leptonema*, *Smicridea* and *Phylloicus* showed significant temporal differences for at least one food item. Motta & Uieda (2004) found similar tendencies in a subtropical river in Brazil, where temporal variations were observed in the caddisflies *Oxyethira* and *Leptonema*, which they classified as Sh-Dt and omnivores during the rainy season and as herbivores and carnivores during the dry season. *Leptonema* is probably not a permanent predator, meaning that the high proportion of animal tissue found in their gut contents during the dry seasons could be the result of restrictions resulting from reduction of the river's flow. Such situations would increase the possibility that *Leptonema* would ingest the remains of other organisms that can fall into the webs that they construct to catch food (Wiggins 2004, Ramírez & Gutiérrez-Fonseca 2014), but they can also consume other organisms. On the other
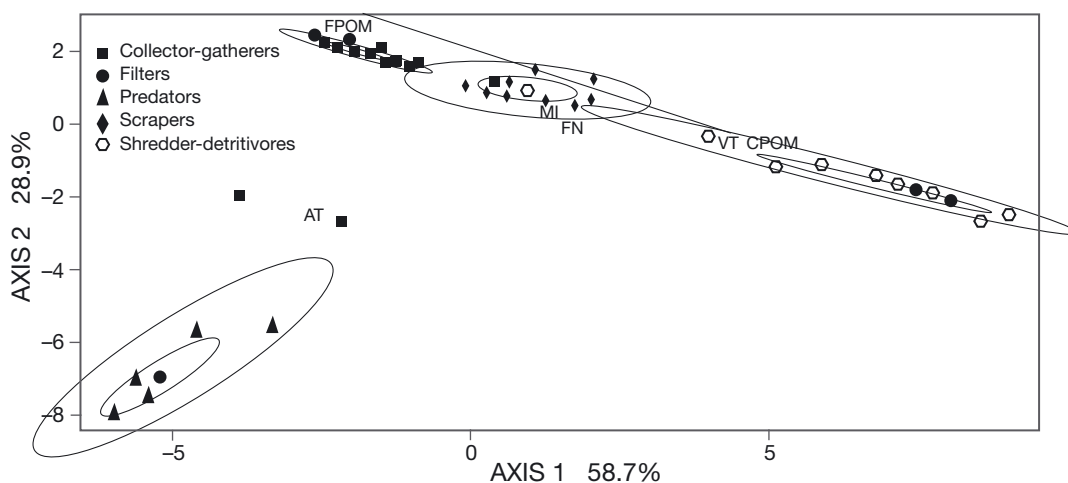
Fig. 6. Discriminant analysis of the functional feeding groups assigned to arthropod taxa according to the proportions of stomach contents. AT: animal tissue; VT: vegetal tissue; MI: microalgae; FN: fungi; CPOM: coarse organic particulate matter; FPOM: fine organic particulate matter. The 2 axes explain 87.6% of the variance, with which the separation of the trophic groups is reliable

hand, *Phylloicus*, which is typically a Sh-Dt, mostly included CPOM in its diet during the dry seasons. Ferreira et al. (2015) stated that *Phylloicus* larvae mainly consume FPOM, and that the presence of other items, such as CPOM and animal tissue, is accidental. The predominance of CPOM in the diet of this caddisfly may indicate that this item is important in the diet of this trichopteran in the Gaira River, given the great abundance of CPOM in the stream during the 2 climatic periods, even though both fractions were available in significant amounts during the entire year (Rodríguez-Barrios et al. 2011). The perpetual contribution of leaves in the upper and intermediate sections of the river could favor a constant availability of both forms of organic matter

Table 2. Differences in functional feeding groups (FFG) assigned *a priori* and the FFG proposed by cross-validation of the discriminant analysis. Sh-Dt: shredder-detritivores; Ft: filterers; CG: collector-gatherers; Sc: scrapers; Pr: predators. Only the cases that did not show coincidences in the discriminant analysis are presented

Order	Taxon	FFG assigned	FFG proposed
Trichoptera	*Leptonema*	Ft	Pr
	Smicridea	Ft	Sc
	Nectopsyche	CG	Sc
Coleoptera	*Microcylloepus*	Sc	CG
	Cylloepus	Sc	Ft
Lepidoptera	*Petrophila*	Sc	Ft
Diptera	*Tipula*	Sh-Dt	Sh
	Hemerodromia	Sh-Dt	Sc
Ephemeroptera	*Camelobaetidius*	Sc	CG

(Tomanova et al. 2006). Similar trends were found for other arthropods in the Gaira River, which may be evidence of feeding plasticity and the dominance of generalist organisms (Tomanova et al. 2006). The feeding plasticity observed in these Trichoptera has been previously documented for various groups of aquatic insects (Merritt et al. 2008, Ferreira et al. 2015, Niedrist & Füreder 2017), especially for the order Plecoptera (Stewart & Stark 2002, Stark et al. 2009) and for the Chironomidae (subfamily Tanypodinae) (Armintage 1968, Baker & McLachlan 1979). Niedrist & Füreder (2018) found that feeding plasticity has an important role for chironomids living in glacier-fed streams. In this context, Frauendorf et al. (2013) determined that omnivory was common in all FFGs and particularly in predators in a Panamanian stream. This means that functional assignments developed in temperate regions may not be appropriate for tropical rivers, and it confirms that few taxa have a differentiation of this diet during the seasonal variation (as Trichoptera) and that diet composition was similar in the 3 localities. Therefore, we propose that the assignment of organisms to the FFGs should be related to the genus taxonomic level.

As expected, the composition of diets at the arthropod order level showed little variability among the 3 sites, even though their altitudes differed by up to 1000 m. These results, which are based on low taxonomic resolution, show high community similarity along an elevational gradient and are similar to those recorded by Tomanova et al. (2007) and by Hyslop & Hunte-Brown (2012) for tropical rivers in Bolivia and Jamaica. With regard to community composition, it
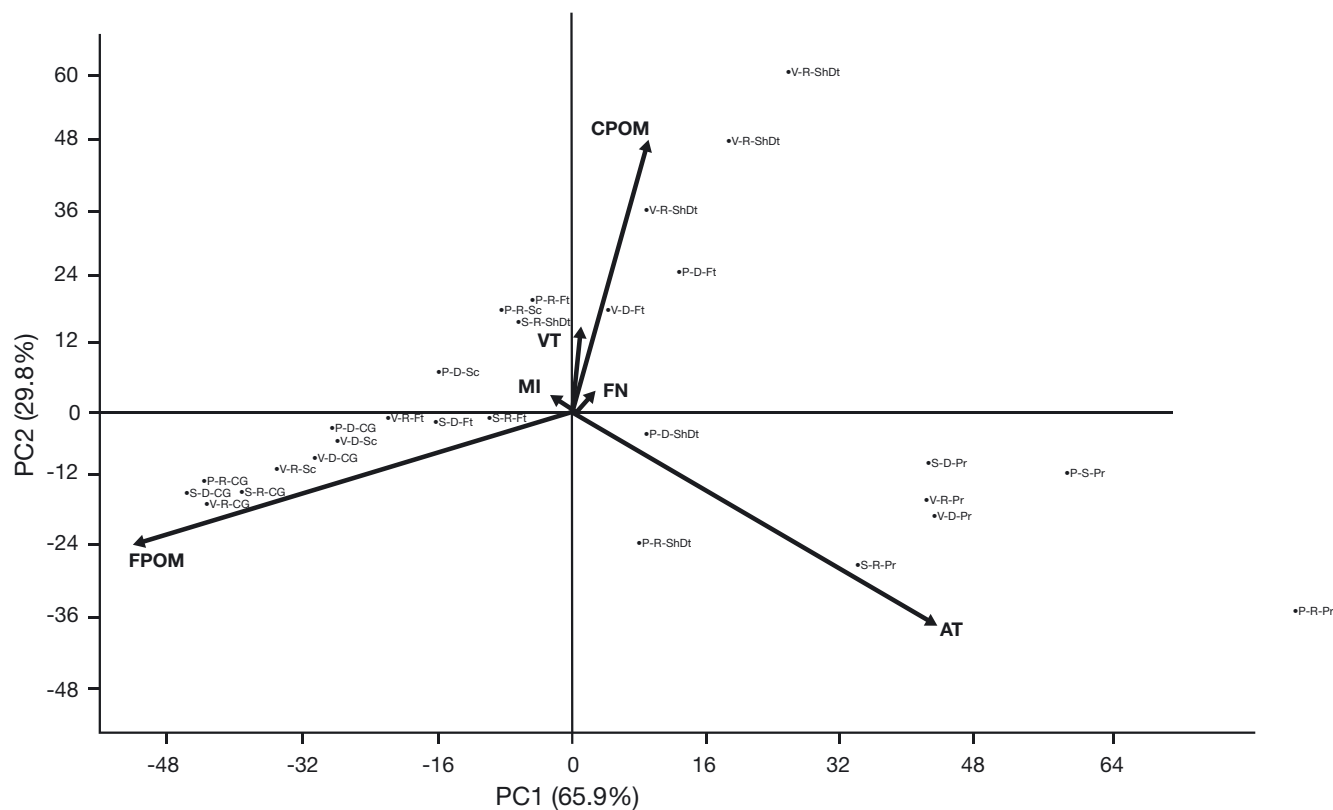
Fig. 7. Principal components analysis (PCA) showing the relationships between the functional feeding groups and seasonal and altitudinal variations. FPOM: fine particulate organic matter; CPOM: coarse particulate organic matter; AT: animal tissue; VT: vegetal tissue; MI: microalgae; FN: fungi. R: rainy; D: dry. S: San Lorenzo; V: La Victoria; P: Puerto Mosquito. GC: collector-gatherers; Ft: filterers; Pr: predators; Sc: scrapers; ShDt: shredder-detritivores. Regardless of the weather or sampling station, trophic groups tend to be associated with the type of food they consume

was notable that Lepidoptera and Decapoda were recorded at Puerto Mosquito but did not appear at other sites. A previous study recorded low abundances of lepidopterans in the intermediate sections of the Gaira River (Guerrero-Bolaño et al. 2003). Decapods have been found at the Minca site of the river (at 630 m elevation), but were apparently not found at La Victoria. This part of the river has high waterfalls (approximately 20 m) that make upstream movements impossible for these freshwater shrimps.

Some groups (e.g. Trichoptera) have genera with different feeding habits (Wiggins 2004, Merritt et al. 2008, Domínguez & Fernández 2009). In the rivers of the Sierra Nevada de Santa Marta, Trichoptera are represented by one Sh-Dt genus (*Phylloicus*), 2 genera cataloged as Ft (*Leptonema* and *Smicridea*) and a Pr (*Atopsyche*). The orders Plecoptera and Megaloptera are each represented by just one genus of Pr (Tamaris-Turizo et al. 2007, Rodríguez-Barrios et al. 2011, Guzmán-Soto & Tamaris-Turizo 2014, Granados-Martínez et al. 2016). Additionally, some groups (e.g. Plecoptera) are known to change their diets throughout nymphal development (Bottová et al.

2013), but we could not verify this aspect since we did not discriminate diets by size given that, in many cases, the number of individuals was very small. Reynaga & Rueda (2014) studied the trophic role of 3 *Marilia* species (Trichoptera: Odontoceridae) based on analyses of diets and mouthpart morphology. However, they did not assign a FFG at the genus level because of (according to these authors) a need for more research to make adequate trophic categorizations.

In the Gaira River, the CG taxa had the highest richness at all sites and during both seasons. These results concur with those found by Chará-Serna et al. (2012) in 3 mountain streams of the Otún River (Risaralda, Colombia) and by Granados-Martínez et al. (2016) in the El Molino River on the lower sections of the Rancheria River (La Guajira, Colombia), where CG dominated the invertebrate communities. The greater activity of decomposer microorganisms in tropical waters is driven by water temperatures (Gessner et al. 1999, Carvalho et al. 2005). This could explain the great abundance of FPOM, which further explains the predominance of CG and Ft. The influence of microbes on the structure of invertebrate

FFGs should be specifically tested. Our results differ from those recorded by Rodríguez-Barrios et al. (2011) because Sh-Dt was the principal FFG in the Gaira River. Long-term monitoring is needed to elucidate the shifts in dominance of invertebrate FFGs. Our result that Sh-Dt diversity decreases with decreasing elevation coincides with records for other Neotropical rivers (Greathouse & Pringle 2006, Dudgeon 2008, Masese et al. 2014). However, our study further shows that it is necessary to review the dynamics of the composition of functional groups not only at the scale of river stretches but also at multiple spatial and temporal scales (Boyero 2005).

4.2. Observations for assigning FFGs

According to the analysis of the crustacean diets, these arthropods can be assigned to the FFGs Sh-Dt and Pr. Some authors think it is questionable to consider crustaceans as predators (Cummins et al. 2005) because they are usually considered detritivores within the shredder FFG. However, the high proportions of animal tissue found in *Macrobrachium* showed a clear nonselective predator habit; this behavior was observed during field visits.

The groups defined through cluster analysis and by cross-validation using discriminant analysis illustrated that the information from gut contents provides partial evidence for assigning FFGs (Mihuc 1997, Ferreira et al. 2015). Consequently, the filterer *Simulium* was grouped with the CG according to the analysis of conglomerates. However, the particles filtered by *Simulium* are usually transported by stream drift, and the main component of their diet is FPOM and, to a lesser extent, microalgae and fungi, which is why the classification technique does not assign it to the Ft organisms. Similarly, the mayfly *Lachlania* and the caddisflies *Leptonema*, *Nectopsyche* and *Chimarra* are filter feeders, but were grouped with the CG or Sh-Dt. The other mayfly taxa (*Leptohyphes*, *Baetodes* and *Prebaetodes*) showed a dietary composition similar to that of *Simulium*. These Ephemeroptera acquire food by scraping the biofilm from different substrates (Baptista et al. 2006) and they do not filter the suspended particles like blackflies. *Americabaetis* (Baetidae) are classified as CG (Merritt et al. 2008) but, in the Gaira River, they live on rocks in the splash zone (outside the water column), and they have been observed to eat the biofilm of this substrate. Therefore, they would be classified into the Sc functional group.

4.3. Body size and feeding

Analyses of the relationship between food items and the length of the arthropods revealed the importance of an organism's body size as a variable that explains the trophic groupings in the river. At the watershed scale, body sizes did not seem to differ between high, intermediate and low elevation sections of the Gaira River, but arthropods performing different feeding habits were of different sizes. Most of the taxa evaluated in this study (except Decapoda) showed a relationship between size and eating habit, which was reflected in the fact that those animals of greater average sizes had predatory habits, while the smaller organisms predominately relied on FPOM as a food source. Although FFGs are not necessarily associated with a certain body size, the organisms with higher trophic positions in the Gaira River tended to be larger than the basal taxa.

It is already known that, to adequately assign an FFG, the morphology of the mouthparts and attributes of behaviors must be considered in addition to what the organism ingests (Merritt et al. 2008, Ramírez & Gutiérrez-Fonseca 2014). Such attributes would allow adequate assessments of the trophic strategies in Neotropical rivers. Additionally, the size of organisms could aid in identifying or assigning FFGs within the invertebrate communities. Although the assignment of an FFG in the family hierarchy has been shown to be useful, there are disparities and inconsistencies in this method. Therefore, trophic characterizations must be carried out at a generic level. In the case of Neotropical rivers, aquatic arthropods tend to have diverse and changing diets, meaning that they tend towards omnivory and trophic plasticity, which is also known from other regions (Niedrist & Füreder 2018). These characteristics reaffirm the need to review trophic assignments based on information from other regions, even within a tropical zone. For these reasons, we propose that distinct FFGs could be assigned for arthropods from different biomes (e.g. tropical zone, arid areas, temperate regions).

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