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Trophic network of aquatic macroinvertebrates along an altitudinal gradient in a Neotropical mountain river



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ABSTRACT

Studies of trophic networks and the evaluation of processes that occur along altitudinal gradients in river systems are of great importance because they allow an understanding of energy flow dynamics and provide scientific tools for the planning and management of river ecosystems. This research describes the trophic network of aquatic macroinvertebrates along an altitudinal gradient of the Gaira River, a mountain Neotropical watercourse located in the Sierra Nevada de Santa Marta in northern Colombia. The organisms were collected in the upper, middle and lower reaches of the river during the rainy and dry seasons (between 2010 and 2013). Trophic relationships were evaluated through gut content analysis. The contents were determined and quantified using photographs and expert review, and a binary consumption matrix was used to determine the characteristics of the trophic network. We characterized the diet composition at each site for each season using discriminant analysis. Trophic networks during the dry seasons showed higher trophic species richness and linkage density, and the predominance of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) in the high and medium sections of the river. During the dry seasons the diets had a lower number of basal species, but in the low river section there was a high percentage of fungi and microalgae. During the rainy seasons, no patterns were observed for the percentage of resources. Results indicated a direct relation between periods of hydrologic stability and an increase of CPOM during dry seasons and an increase of resource diversity consumed by macroinvertebrates at all sites during the rainy season, showing that changes in trophic networks of the Gaira River were more important during seasonal periods than along the altitudinal gradient.

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Introduction

Macroinvertebrates constitute an abundant group in freshwater ecosystems. They play a fundamental role in the transfer of energy through trophic networks (Allan and Castillo, 2007). Energy transfer depends mainly on the diversity, quality and quantity of resources available in the system, as well as on the number of consumers and their trophic relationships (Merritt et al., 2008; Cummins et al., 2005). Energy transfer is evaluated mainly through the attributes of trophic networks (Vander Zanden and Rasmussen, 1999), which help to understand changes in trophic relationships that occur during variations in climatic periods or at sites with different environmental conditions (Ruhí et al., 2016). Many

macroinvertebrates incorporate principally allochthonous organic matter (e.g. energy that is not produced locally) that come from the riparian forest or is transported from upstream and from tributaries (Jackson and Fisher, 1986). This source of allochthonous energy includes different types of plant remains (e.g. leaf and flowers fractions, wood), animal tissues (carrion and terrestrial invertebrates), dead microbes, extracellular polymers, root exudates and mucilage (Moore et al., 2004). In addition, macroinvertebrates have considerable influence on the processing of autochthonous organic matter that comes from the production of microalgae, macroalgae and macrophytes (Anderson and Sedell, 1979; Vannote et al., 1980; Minshall et al., 1985; Martínez-Silva, 2015).

Many of the physical and biotic variables of rivers show changes along their altitudinal and longitudinal gradients (Allan and Castillo, 2007). Theories such as the River Continuum Concept (Vannote et al., 1980) emphasize the importance of longitudinal hydrological connectivity as a key role in the structure of the communities, because the unidirectional flow of water relates the

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processes that occur in the downstream sections to those that take place upstream. Thus, changes in biotic composition and in loading, transport, use and storage of organic matter (OM) along the continuum will be relatively predictable. In temperate latitude rivers, for example, the recurrent seasonal dynamics marked by temperature variations have been extensively studied (Dallas, 2008; Boyero et al., 2011; Orr et al., 2015; Wagner et al., 2017). In those ecosystems, temperature is an important factor regulating input and transport of allochthonous OM; it also affects the dispersion of organisms and influences the availability and quality of energy sources. In tropical aquatic systems seasonality is determined mostly by precipitation (Boulton et al., 2008; Gonçalves et al., 2014), which directly affects the water amount and quality. The rainy season means an important input of water that can condition the amount of OM available in the riverbed, and in contrast, the dry period can imply a greater hydrological stability (Brendonck et al., 2015). Changes in water flow are considered a “master variable” in the functioning of fluvial systems, due to its influence on the river’s physical, chemical, and biological features (Powers et al., 1995). Hydrological dynamics and availability of OM have a great influence on the trophic relationships that are established between aquatic invertebrates and their food sources, aspects that have not been studied in detail in tropical rivers (Ramírez et al., 2008; Gonçalves et al., 2014).

Studies of trophic networks are important because they allow us to understand the relationships of food dependence between organisms and, therefore, the connections between biotic elements of the system. This information can be very useful for the conservation and proper management of Neotropical rivers. So strong seasonality and changes in temperature lead to highly predictable inputs and dynamics of OM in temperate streams. This causes modifications in the biological assemblages according to the temporary changes in OM. In Neotropical streams thermal seasonality is much less marked and changes in OM are driven mainly by hydrology (Gonçalves et al., 2014). Neotropical rivers have not been studied enough to be able to evaluate trophic networks throughout the hydrological cycle; however, important research has been done by Motta and Uieda (2005), Uieda and Motta (2007) and Ceneviva-Bastos et al. (2012) in some Brazilian rivers. The goal of the present research was to describe the structure of the macroinvertebrate trophic network through an analysis of gut contents during two contrasting hydroclimatic periods (rainy and dry seasons) at three sites along an altitudinal gradient (60–1700 m) of the Gaira River (a Colombian Neotropical river). Spatial and seasonal variations in the food web structure of the community were evaluated to determine if differences in flow and altitude caused changes in the trophic network of the invertebrates.

According to Vannote et al. (1980), the quantity and origin of the OM in the river change along the longitudinal gradient, then we expect similar pattern that would affect the network structure. Low flows favor OM accumulation (Schmid-Araya and Schmid, 2000) that could be a more available resource for invertebrates. The higher availability in the dry season in our river could determine some changes in basal resources and in network properties. Seasonal differences would not be so obvious in the lower part of the river, where the role of autochthonous OM should be greater and more constant due to the dominance of FPOM, a product of the physical and biological processing of the CPOM.

Material and methods

Study site

The Sierra Nevada de Santa Marta (SNSM) is a coastal mountain massif isolated from the Andes and characterized by high

biodiversity and endemism. It is located in northern Colombia and has the appearance of a triangular-based pyramid. Its northern flank borders one of the most arid parts of the country (La Guajira) and the Caribbean Sea, the east flank faces a valley that separates the massif from the Serranía de Perijá, the northernmost extension of the Andes Eastern Cordillera, while the western flank faces the Caribbean Sea, the Ciénaga Grande de Santa Marta and a part of the Magdalena River valley. SNSM is subject to anthropic disturbances like deforestation, the establishment of unsuitable crops on inappropriate and deficient soils and extensive cattle ranching. These activities have exerted significant pressure on watersheds causing alterations in local aquatic ecosystems. The impact of these activities is reflected in alterations in the hydrological, physical and chemical variables of the rivers, such as increased runoff, flow and temperature, and the increase of nutrients from soil leaching in the rainy seasons (Prosierra, 1998).

The Gaira River is located on the western side of the SNSM and has a length of 32.5 km from its headwaters at the mouth of the river where it empties into the Caribbean Sea. Samples were collected in three sections, the first one in the upper part (San Lorenzo) of the river at 1700 m altitude, the second in the middle section at intermediate altitude (La Victoria, 900 m), and the third at the lowest part (Puerto Mosquito, 60 m). At the upper section, the riparian vegetation is well-preserved and dominated by large trees that provide shade over the river. The site, located very close to the source of the Gaira River, is steep ($>70^\circ$) with no anthropic activities. In the middle section, there are many coffee plantations and other crops such as corn and fruit trees. The coffee plantations in the middle zone can exceed 300 ha. The riparian vegetation at this site corresponds to trees of considerable size (greater than 15 m) that offer an extensive canopy that shades the river similarly to the upper section. In the lowest sector shrub vegetation dominates with the presence of some trees that provide little shading over the river. This zone has extensive anthropic influence due to land holdings near the river that are used as spas by tourists and residents. The geographic coordinates of each site, as well as some environmental conditions and physicochemical water characteristics are presented in Table 1. A more detailed description of these sampling sites can be found in Tamaris-Turizo et al. (2013).

Sampling

Six intensive sampling regimens were conducted at each site on the Gaira River. The whole region has a rainy season from April to November, and a dry season from December to March, which in turn causes increases and reductions in river flow (Tamaris-Turizo et al., 2007). Collections were done during the rainy seasons (October–November 2010, 2011 and 2013) and dry seasons (February–March 2010 and 2011, and December 2013). The samples collected during the three years were grouped by seasons, taking into account the coincidence in the months of rainfall or drought. During all the samplings, the following physical and chemical variables were measured *in situ* with a WTW multiparameter portable meter (Xylem, Germany): water temperature ($^\circ\text{C}$), pH (units), conductivity ($\mu\text{S cm}^{-1}$) and dissolved oxygen (mg L^{-1}). In addition, the average flow velocity (m s^{-1}) was recorded with a flow meter (Global Water – FP 211, Xylem, USA). The discharge was calculated by multiplying the cross-sectional area by the velocity (m s^{-1}). Simultaneously, water samples were taken from the river with 500 mL plastic bottles, that were kept refrigerated and transferred to the Water Quality Laboratory of the University of Magdalena to perform nutrient analyses (nitrates, nitrites and orthophosphates) according to standard methodologies (APHA, 1998). Organisms were collected in three types of substrate: gravel, pebbles and leaf litter. A Surber net (mesh: 250 μm , area: 0.09 m^2 , five minutes sampling) was used for the gravel sampling; manual

Table 1
Mean and standard deviation of the environmental, physical and chemical variables in the study sites. Number of samples per site: 6, D, dry; LI, rainy; ND, no determined. Nitrite, nitrate and phosphate information was taken from Rodríguez-Barrios et al. (2011).

Variable	San Lorenzo (Upper)		La Victoria (Middle)		Puerto Mosquito (Lower)	
	D	LI	D	LI	D	LI
Altitude (m)	1700		900		60	
Coordinates	N 11°07'39"	W 74°03'14"	N 11°07'44.2"	W 74°05'35.8"	N 11°10'26"	W 74°10'37"
Average rainfall (mm)	2683		2249		448	
Flow velocity (m s ⁻¹)	0.40 ± 0.08	0.73 ± 0.06	0.56 ± 0.45	0.62 ± 0.01	0.21 ± 0.03	0.56 ± 0.10
Discharge (m ³ s ⁻¹)	0.20 ± 0.12	0.39 ± 0.09	0.36 ± 0.17	0.58 ± 0.18	0.36 ± 0.21	0.42 ± 0.02
River channel depth (m)	0.20 ± 0.01	0.33 ± 0.03	0.29 ± 0.01	0.42 ± 0.12	0.47 ± 0.50	0.73 ± 0.01
River channel width (m)	4.3 ± 0.5	4.8 ± 1.2	5.0 ± 1.2	5.8 ± 1.4	7.14 ± 0.11	12.00 ± 0.31
Water temperature (°C)	14.10 ± 0.01	15.82 ± 0.02	17.98 ± 0.69	19.10 ± 0.36	24.85 ± 0.39	25.14 ± 0.66
pH	6.68 ± 0.37	7.88 ± 1.16	7.60 ± 0.97	7.02 ± 1.10	7.33 ± 0.16	7.39 ± 0.13
Conductivity (μS cm ⁻¹)	39.17 ± 13.76	60.90 ± 3.76	53.29 ± 28.61	76.33 ± 0.52	116.58 ± 14.45	114.83 ± 11.99
Dissolved oxygen (mg L ⁻¹)	8.56 ± 0.99	8.70 ± 1.30	7.82 ± 0.73	8.52 ± 0.64	7.14 ± 0.68	8.48 ± 0.54
Nitrates (μg L ⁻¹ NO ₃)	0.18 ± 0.09	ND	0.22 ± 0.10	ND	0.24 ± 0.12	ND
Nitrites (μg L ⁻¹ NO ₂)	0.79 ± 0.26	ND	0.79 ± 0.40	ND	1.42 ± 1.11	ND
Orthophosphates (μg L ⁻¹ PO ₄)	4.41 ± 2.48	ND	4.77 ± 3.31	ND	4.62 ± 3.16	ND

extraction was done for the pebbles with diameters between 18 and 23 cm in which a total of 0.25 m² of substrata were analyzed; in the litter 500 g of wet weight were collected and specimens were extracted manually. In all cases the organism extraction was done in the field. We performed sampling to assure maximum organism representation at each habitat and the same effort in all sites. We grouped all organisms at each substrate into an integrated sample by site and season. The invertebrates were preserved in 96% ethanol and transferred to the laboratory for further analysis. We identified the animals to the most detailed taxonomic level possible using taxonomic (genus level in most cases) keys such as those of Wiggins (1996), Posada-García and Roldán-Pérez (2003), Domínguez et al. (2006), Merritt et al. (2008), Domínguez and Fernández (2009) and Ramírez (2010).

Trophic analysis

Gut contents were analyzed using a technique proposed by Tomanova et al. (2006), with some modifications. For this, the anterior part of the digestive tracts of five individuals of each taxon were extracted; taxa represented by less than five individuals were analyzed individually. When analyzed the five gut contents were combined and homogenized with glycerin on a microscope slide. We took photomicrographs of 20 random fields with an AxioCam ERc5s camera fitted to a CARL ZEISS Primo Star microscope (Zeiss, Germany) using 10× and 40× magnification. When the guts had little content, the entire sheet was photographed. From these images, the percentage of each food item in the stomach contents was identified and quantified. The food categories were animal tissue (AT, insects were identified to genus whenever possible); plant tissue (PT); microalgae (MI) and fungi (FUN) whose cells could be identified under microscope; coarse particulate organic matter >1 mm (CPOM, amorphous material that could not be identified under microscope); and fine particulate organic matter (FPOM, organic particles between 50 μm and 1 mm). In order to confirm the relations of consumption and to assign a trophic category to the organisms, we referred to the studies of Motta and Uieda (2004), Tomanova et al. (2006), Chará et al. (2012) and Reynaga and Rueda-Martín (2014).

Data analysis

We analyzed consumer relations using a binary matrix of predator vs. prey. This matrix was based on an analysis of the gut contents and these data were used to visualize the models of trophic networks. At each site and season we estimated the following attributes of the trophic networks according to Dunne et al.

(2002): the number of trophic species or the number of taxa (S); the number of links (L, each pairwise interactions in the network, establishing the predator-prey interactions through the identification at the genus level of the organisms in the gut contents); the link density (L/S, average number of feeding links per species); and the connectance ($C = L/S^2$, the proportion of possible links that occur between species). Standard deviations of both generality (SD-G) and vulnerability (SD-V) were the normalized mean number of prey per consumer and the normalized mean number of consumers per prey, respectively (Bersier et al., 2002), thus, SD-V of a node is the number of species that is consumed, normalized by L/S. Other variables that were calculated from the trophic network were mean chain length (mCL), maximum chain length (maxCL) and fractions of basal resources (b) intermediate taxa (i) and top taxa (t) (top if the taxon has prey but no consumers, intermediate if it has prey and consumers, and basal if it only has consumers, Bersier et al., 2002). All trophic analyses and trophic models were performed in the Network3D program (Yoon et al., 2004; Williams, 2010). A discriminant analysis was carried out using the mean values of gut content area to evaluate the variation in the composition of the food resources consumed at the different sites and seasons. This analysis was performed with the RWizard 2.3 program (Guisande et al., 2016).

Results

A total of 698 guts belonging to 48 taxa of aquatic macroinvertebrates were dissected. At all sites the trophic species richness was higher during the dry seasons (from 31 to 33 species). The highest number of trophic species was found in the upper part during periods of drought (33). At this same site, the lowest number of trophic species was found during the rainy seasons (17). The composition of the communities was similar between the climatic periods (Supplement 1). When comparing sites, the lowest section showed the lowest value and the upper section showed the highest value. The number of trophic levels and the maximum food chain length were similar between sites (about three in all cases) (Fig. 1 and Table 2). The proportions of top taxa (t) showed an important seasonal variation in the highest section of the river from 0.58 during the dry seasons to 0.29 during the rainy seasons. However, the middle and lower sections showed values of 0.53 and 0.58 during the dry periods and 0.41 and 0.29 during the rainy phases respectively. The opposite occurred with the fraction of the intermediate taxa (i) on the lowest section, which was reduced during the dry seasons compared to the rainy seasons. Fractions of basal species (b) were low at all sites during the dry seasons with slightly higher records during the rainy seasons. Connectance (C) was low at all sites and during

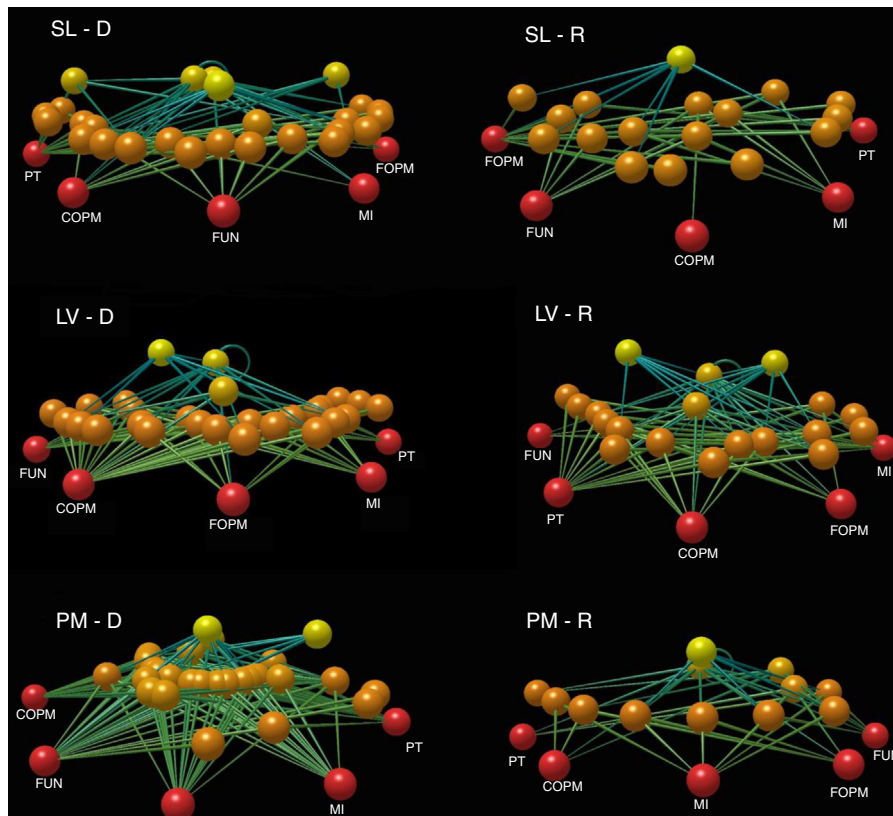


Fig. 1. Static models of trophic networks at three sites in the Gaira River representing basal resources (red), intermediate consumer (orange) and top predators (yellow) and the interactions among them. SL, San Lorenzo, upper sector; LV, La Victoria, middle sector; PM, Puerto Mosquito, lower sector; D, dry season; R, rainy season.

Table 2

Attributes of the models of trophic networks at the three study sites. SD, standard deviation; Fr, fraction.

Site	San Lorenzo (Upper)		La Victoria (Middle)		Puerto Mosquito (Lower)	
	Dry	Wet	Dry	Wet	Dry	Wet
Trophic species richness (S)	31	17	32	24	33	22
Number of trophic level	2.87	2.83	3.12	3.10	2.87	3.12
Number of trophic links (L)	77	39	87	75	123	42
Linkage density (L/S)	2.48	1.77	2.71	3.12	4.33	2.47
Connectance (C)	0.08	0.08	0.08	0.13	0.13	0.14
SD generality (SD-G)	1.15	0.93	0.82	0.84	0.60	1.13
SD vulnerability (SD-V)	1.90	2.13	1.99	1.49	1.87	0.98
Mean chain length (mFCL)	1.95	1.81	1.93	1.92	2.03	1.84
Max chain length (maxFCL)	3.00	2.83	3.13	3.10	3.00	3.12
Fr. Number of basal taxa (b)	0.15	0.23	0.16	0.21	0.15	0.29
Fr. Number of intermediate taxa (i)	0.27	0.23	0.31	0.37	0.27	0.41
Fr. Number of top taxa (t)	0.58	0.54	0.53	0.41	0.58	0.29

the two sets of climatic periods, although it was slightly higher in the upper section of the river (Table 2).

In the highest section, the standard deviation of the generalists (SD-G) during the rainy months almost doubled from that of the dry seasons. The standard deviation of vulnerability (SD-V) was lower in the rainy seasons in the middle and upper sections of the river but increased as the elevation increased (Table 2). The SD-V values of the main food resources increased downstream (Fig. 2). These items were COPM, FPOM and plant tissues, which constitutes the basal sources with the highest proportion in the guts of the consumers in the three trophic networks. The FPOM was the most important item at the three sites, but its SD-V values decreased downstream, independently of the hydrological period. During the dry seasons the COPM had an inverse behavior, with the SD-V increasing at the lowest site, whereas during the rainy season it was slightly higher in the middle sections of the river. The plant tissues showed little

altitudinal variation in the dry seasons and clearly increased in its SD-V values as the elevation increased in the rainy season. Results showed the great importance of FPOM along the altitudinal gradient in this tropical river, especially at the upper and middle parts of the river, even greater than that of COPM and plant tissues. The FPOM was the most common food item for consumers in all sections. In the most elevated part of the river, although the FPOM showed the highest SD-V, its value decreased during the rainy seasons. In the middle section FPOM and COPM were important items, particularly during the dry seasons. During the dry seasons the SD-V of the COPM was notable in the lowest section of the river (Fig. 2).

As observed in the discriminant analysis (Fig. 3), during dry periods FPOM, COPM, animal tissues and plant tissues were the most consumed resources in upper and middle sections. In the lower parts, an important contribution of the FPOM, microalgae and fungi were observed. The last two food items contributed to the definition

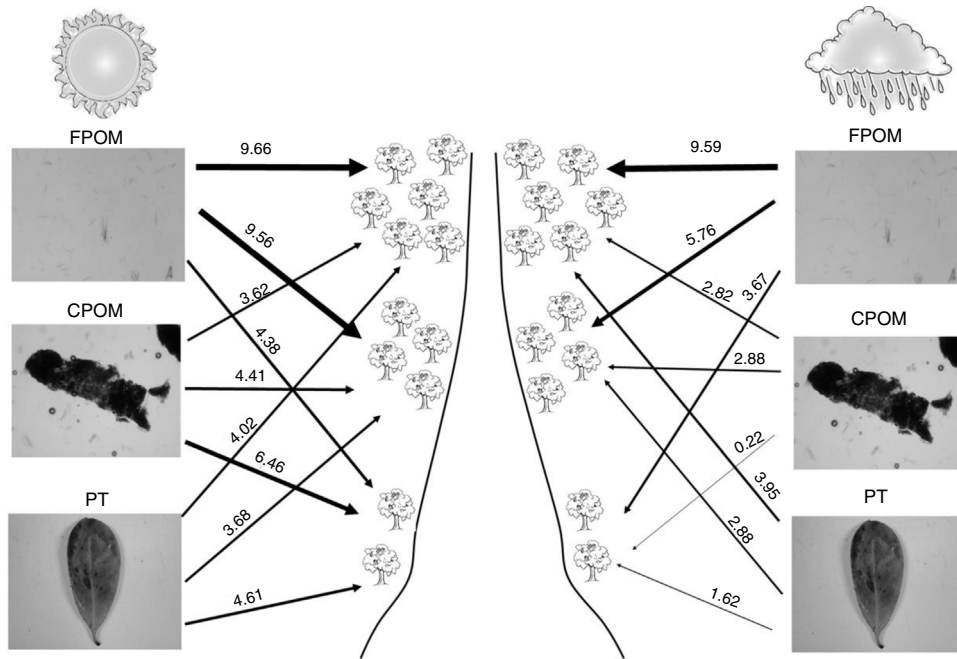


Fig. 2. Representation of the standard deviation of vulnerability (SD-V) of the main food sources (FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter; PT, plant tissue) calculated from the ratios recorded in the guts of the macroinvertebrates sampled in the elevational gradient of Gaira River during the dry and rainy seasons. Arrow thickness indicates the vulnerability importance.

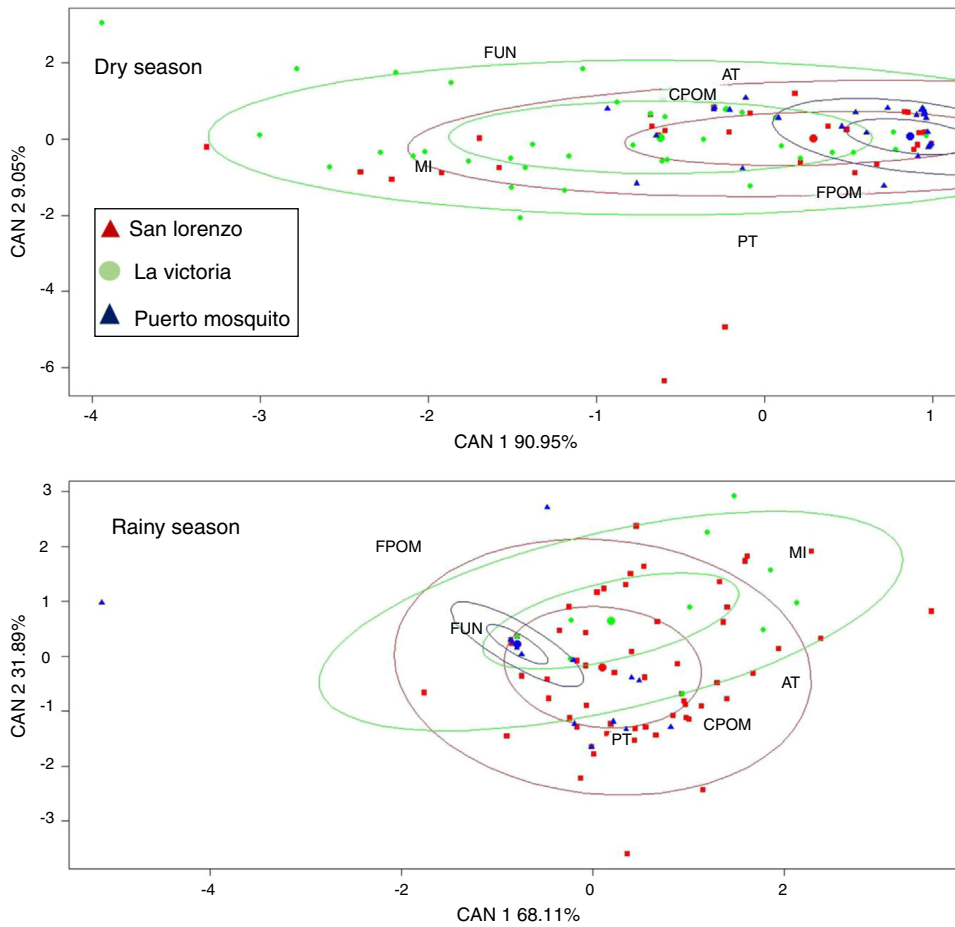


Fig. 3. Discriminant analysis of percentages of gut contents for macroinvertebrates analyzed at the three sampling sites. FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter; FUN, fungi; AT, animal tissue; PT, plant tissue; MI, microalgae.

of the groups seen on the middle and lowest reaches of the river. In contrast, during the rainy seasons the consumption of resources was more heterogeneous at each of the three sites. The fractions of CPOM and FPOM were elevated in middle and lowest sections, whereas fungi showed higher contributions on the uppermost and middle parts of the river (Fig. 3) and this was not seen during the dry seasons.

Discussion

Our assumption of a higher accumulation of CPOM during dry period was not possible to verify, because, it was the most important resource during dry and wet seasons. Although CPOM contribution in the food web was higher during the dry seasons, this only occurred in the middle and lowest sections of the river. There seems to be less retention of CPOM during the rainy seasons (Rodríguez-Barríos et al., 2011) and, therefore, there is a tendency for a lower contribution of this item to the food chains as expected but this occurred mainly in the lowest river section. During the dry periods, the lowest river flows increase retention of organic matter such as leaves and small fragments of wood. This is because the low flows are not capable of suspending the bottom material and move it with the river current (Rolls et al., 2012). Considering the contribution of FPOM during the dry seasons, higher values of SD-V were confirmed for this period of greater water stability when compared to the rainy seasons (Cheshire et al., 2005; Boulton et al., 2008). However, unlike what was expected, in the lowest section of the river there were marked seasonal differences in the two OM fractions and in the vegetal tissues contained in the stomachs of the invertebrates.

Results indicate that the trophic networks varied between the two seasons. During the dry seasons the food web attributes were similar at all sites, a fact that is related to the stability of the system and an increase in the retention of the CPOM. During the rainy seasons the food webs had lower numbers of trophic species and link density, but more basal species that could be associated with a lower contribution of CPOM to the trophic network and in general with a smaller amount of resources through a food web that has a lower density of organisms in these wet periods. Although we expected great contrasts along the altitudinal gradient, the differences in the attributes of the networks were not very drastic. This may be due to some aspects of the river's geomorphology, such as the short length of the main channel and the strong slopes of the river basin (Webster and Meyer, 1997; Prosierra, 1998).

The number of top species, the increase of basal species, and the connectance showed variations, especially in the altitudinal gradient. This coincides with other research done in tropical streams of Australia and Venezuela (Cheshire et al., 2005; Layman et al., 2005). However, in our study the values of these trophic network properties were lower, which might be due to the taxonomic resolution used in our work (Supplement 1). Specifically for the case of plant tissue and microalgae, it is possible that the number of basal species is undervalued, because these items could only be categorized by large groups, without being able to arrive at more precise taxonomic detail. The increase in the fraction of basal species and the corresponding reduction in the fraction of intermediate species observed during the rainy seasons at all sites are related to the disturbance effect generated by the runoff during these periods (Cheshire et al., 2005; Motta and Uieda, 2005; Pedroza-Ramos et al., 2016). Further, the increase of top species during the dry seasons could be associated with (1) the greater stability of the river current and consequently to a generally less variable system and (2) with the capacity of organisms such as the Plecoptera and Megaloptera to attach themselves to substrates where they live. In Brazil, Krawczyk et al. (2013) also found a higher number of predators dur-

ing the dry season and this result might be related to the reduced volume of water favoring the colonization of many prey taxa along the river so that top species have a greater number of resources. It is possible that a more restricted wet zone constrains aquatic organisms to a smaller surface area, which would favor predators (described for temporary rivers during the dry phase) (Gasith and Resh, 1999).

The altitudinal gradient affected to some extent the number of links in the trophic network, since this attribute increased with a decrease in the elevation, but this was not evident in other characteristics of the trophic network. It is possible that the lowest sector of this river has the high heterogeneity of microhabitats (Tamaris-Turizo et al., 2013), due to the decreased slope that does not favor the creation of different substrata, which in turn generates low species diversity, specially during rainy season (Ceneviva-Bastos et al., 2012). Also, human impacts in the region are likely to contribute to fewer links in the lowest section of the river. In effect, the altitudinal gradient also corresponds to an impact gradient. Other research has shown that the properties of trophic networks vary with elevation; Romanuk et al. (2006) have documented the variation in the structure of the trophic network in temperate rivers of Canada. These authors compared the networks in three rivers along an altitudinal gradient (mountainous zone, piedmont and plains) and found that the percentage of intermediate species and the percentage of herbivory were higher in the middle sections, while connectance and cannibalism had the greatest impact on the upper sections.

Maximum food chain length was not affected by altitudinal or seasonal changes. It remained the same in both types of hydrological periods and had similar magnitudes to those recorded in other tropical rivers (Layman et al., 2005; Motta and Uieda, 2005). The decrease in the number of links caused a greater connectance upstream, but mainly during the rainy season, probably due to a decrease in the average species richness of the trophic network. However, these analyses were based only on macroinvertebrate communities and did not include groups such as fish and amphibians, which are very important in the transfer of energy in these systems (Ranvestel et al., 2004; Barros-Maestre and Granados-Martínez, 2016). We, therefore, expected that the food chain length in the Gaira River would be longer if these higher consumers are taken into account.

The trophic networks drawn with the results of the gut content analysis highlights the importance of FPOM as a food item that dominates most aquatic invertebrates (Covich et al., 1999; Moore et al., 2004; Amadeu-Santana et al., 2015; Ferreira et al., 2015). This fact was evident in the present study because it was the resource with greater vulnerability (SD-V) during the two seasons at the upper and middle sites. However, stable isotope analysis is required to check for the extent to which FPOM is actually assimilated. Otherwise, CPOM seemed to be an important resource, especially during the dry season, when the retention of leaves is high (Rodríguez-Barríos et al., 2011) and the macroinvertebrates are concentrating because of the reduction in flow. On the middle part of the Gaira River, where 65% of plant matter belongs to leaves from the riparian forest (Collantes et al., 2014), the processing of litterfall increased during the dry season.

The observed differences in the conformation of the food web in the discriminant analyses during wet and dry seasons also confirms the changes in the supply and availability of resources in the river. During the dry season the system is more stable, which might allow the CPOM to be retained by the rocks and the trunks that are in the channel. The rainy seasons favor the trawling of nutrients from the riverside (Ramírez et al., 2007), a fact that seems to stimulate the growth of fungi and microalgae on different substrates (leaves, logs, rocks), especially in the middle and lowest sections. The lower availability of CPOM during the rainy seasons forced the

invertebrates to feed on alternative resources, as observed with the greater abundance of algae in the gut contents. As expected, in the lower sections of the Gaira River there will be a greater tendency for autochthonous organic matter to contribute to the trophic network of the invertebrate community, as has been reported for a Brazilian river (Neres-Lima et al., 2016).

In summary, the variability of the high and low water periods in the river caused remarkable seasonal changes in the structure of the food web in the Gaira River. Changes in the food web attributes were more relevant contrasting both seasons than contrasting the longitudinal gradient. Fine and coarse organic matter are the most abundant resources in the guts of the invertebrates, which is in accordance with most of the fluvial food webs around the world. However, in this Neotropical river the availability of the organic matter, and consequently the food web structure, were more determined by seasonal changes in hydrology than by a longitudinal continuum.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.rbe.2018.07.003](https://doi.org/10.1016/j.rbe.2018.07.003).

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