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Longitudinal and altitudinal changes of macroinvertebrate functional feeding groups in neotropical streams: a test of the River Continuum Concept

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With 3 figures, 2 tables and 1 appendix

Abstract: The River Continuum Concept (RCC) explains the structural and functional characteristics of stream communities focusing on the gradually changing physical components from headwaters to downstream habitats of streams and rivers. The global value of the RCC is still uncertain, possibly because physical factors (e.g., altitude and then temperature, stream order, channel width) can vary differently in longitudinal river axes across the world. Moreover, RCC predictions in relation to different physical factors have not been tested adequately in different biomes, especially biomes outside of temperate North America. Here, we report on the functional structure of macroinvertebrate communities in neotropical streams from Bolivia along a broad altitudinal gradient (from 1120 to 4300 m a.s.l.), aiming to understand how altitude can affect the longitudinal changes in functional feeding groups (FFG) and richness predicted by the RCC. The RCC predictions for functional structure were not completely matched when analyzing FFGs in relation to an index of longitudinal stream gradient. However, after removing the effect of altitude by using residuals from regressions between FFGs and altitude, FFG patterns matched RCC predictions more closely. We detected significant relationships between altitude and the relative abundance of collector-gatherers, shredders and scrapers which may be related to changes in temperature, UV radiation and canopy cover along the altitudinal gradient. Our results indicate that altitude combined with position along the longitudinal gradient is an important factor governing the FFG structure of macroinvertebrate communities in neotropical streams.

Key words: organism distribution, distance from source, width, slope, altitude, Amazon sub-basin, Bolivia.

Introduction

Identifying the environmental factors driving macroinvertebrate community structure is an important area of study in freshwater ecology. The influence of various abiotic factors has been highlighted by relating them to taxonomic and functional community metrics (see for review Power et al. 1988). As an integrating framework, the River Continuum Concept (RCC) (Vannote et al. 1980) is a widely used model for the

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interpretation of the structural and functional characteristics of stream communities focusing on the gradually changing physical components from upstream to downstream habitats of streams and rivers. The RCC predicts that this continuous gradient of physical conditions, mainly related to stream size (e.g., stream width, stream discharge), affects types and availability of food resources, which in turn, drive the shift in the functional feeding groups (FFG) of macroinvertebrate communities.

Studies from temperate streams and rivers have often observed the FFG shifts predicted by the RCC (e.g., Hawkins & Sedell 1981, Minshall et al. 1983, Grubaugh et al. 1997, Rosi-Marshall & Wallace 2002). However, various studies from other climatic zones have found that the longitudinal distribution of FFG fitted, at best, only partially to the RCC (e.g., Dudgeon 1984 for Asia, Marchant et al. 1985 for Australia, Miserendino 2004 for South America, Greathouse & Pringle 2006 for Central America). Therefore, the global value of the RCC is still uncertain and the factors potentially responsible for the observed discrepancies have not been explicitly identified.

Studies have generally attempted to explain the FFG variability using factors reflecting the position of sites along the longitudinal gradient (e.g., stream width, stream order, and distance from source) or sites' food availability (e.g., fine and coarse organic matter), also reflecting longitudinal position (Naiman et al. 1987). However, the RCC predictions for FFGs could also be affected by stream specific ecological processes like leaf litter inputs and decomposition rates or periphyton production, themselves influenced by various environmental factors. For instance, leaf litter inputs depend on the density and type of vegetation which are mainly determined by temperature and precipitation regimes (Kharkwal et al. 2005). Leaf litter palatability for shredders depends, among other factors (e.g., leaf hardness), on microbial colonization of leaves, i.e., conditioning of leaves (Gessner et al. 1999, Graça et al. 2001), which may increase with water temperature (Irons et al. 1994, Fabre & Chauvet 1998) and eutrophication (Gulis & Suberkropp 2003). Finally, periphyton growth, influencing the density of scrapers, depends on nutrients (e.g., Kim & Richardson 2000, Larned & Santos 2000), light (e.g., Vinebrooke & Leavitt 1999, Kim & Richardson 2000, Larned & Santos 2000) and water temperature (e.g., Phinney & McIntire 1965, Kishi et al. 2005). All these factors can vary differently along longitudinal axes of rivers across the world and may be responsible for the observed discrepancies with the RCC predictions.

Altitude is usually related to several environmental factors such as temperature, land cover or oxygen availability (Finn & Poff 2005). Altitude has been widely linked to macroinvertebrate taxonomic variability in the tropical zone (e.g., Suren 1994, Jacobsen et al. 1997, Sites et al. 2003), however, functional approaches are rare (e.g., Greathouse & Pringle 2006). Since altitude is strongly related to temperature, light (UV radiation) and canopy cover, variations in ecological processes such as leaf litter inputs, decomposition rates and periphyton production can be expected across a large altitudinal gradient. Then, if the RCC predictions for FFGs are influenced by the leaf litter inputs, decomposition rates and periphyton production (see above) varying along the altitudinal gradient, removing the influence of altitude could eventually reveal the expected RCC patterns.

This study aims to (1) test if the RCC can be observed in neotropical zone and (2) to test if altitude can mask the predicted functional variability along the longitudinal river gradient. We tested this hypothesis by analyzing the relationship between macroinvertebrate FFGs and the longitudinal gradient in thirty sites (altitude ranging from 1120 to 4300 m a.s.l.) in several pristine streams and rivers of Bolivia. The RCC predictions were evaluated, before and after removing the effect of altitude, using a synthetic factor (the first axis of Principal Component Analysis of distance from source, slope and river width) as an index of position along the longitudinal gradient

Material and methods

Study sites and data collection

Four previous studies of the same study scheme (Campero 1998, Claros 1999, Arévalo 2000, Tomanova & Usseglio-Polatera 2007) provided the macroinvertebrate assemblages data

Table 1. Mean, minimum and maximum environmental parameters of study sites; n (number of sites with available information) is indicated only if different from 30.

	Mean	Min – Max
Altitude (m a.s.l.)	2519	1120 – 4300
Slope (%)	4.24	0.028 – 14.4
Distance from source (km)	38.5	0.05 – 254
River width (m)	16.2	6 – 27.3
Temperature (°C)	13.8	6.4 – 21
Conductivity (µS cm^{-1})	211.6	7.7 – 1305.2
pH	7.7	6.9 – 8.5
Mean flow velocity (m s^{-1}) ($n = 28$)	0.48	0.008 – 1.59
Mean depth (cm) (n = 28)	22.1	10.8 – 36

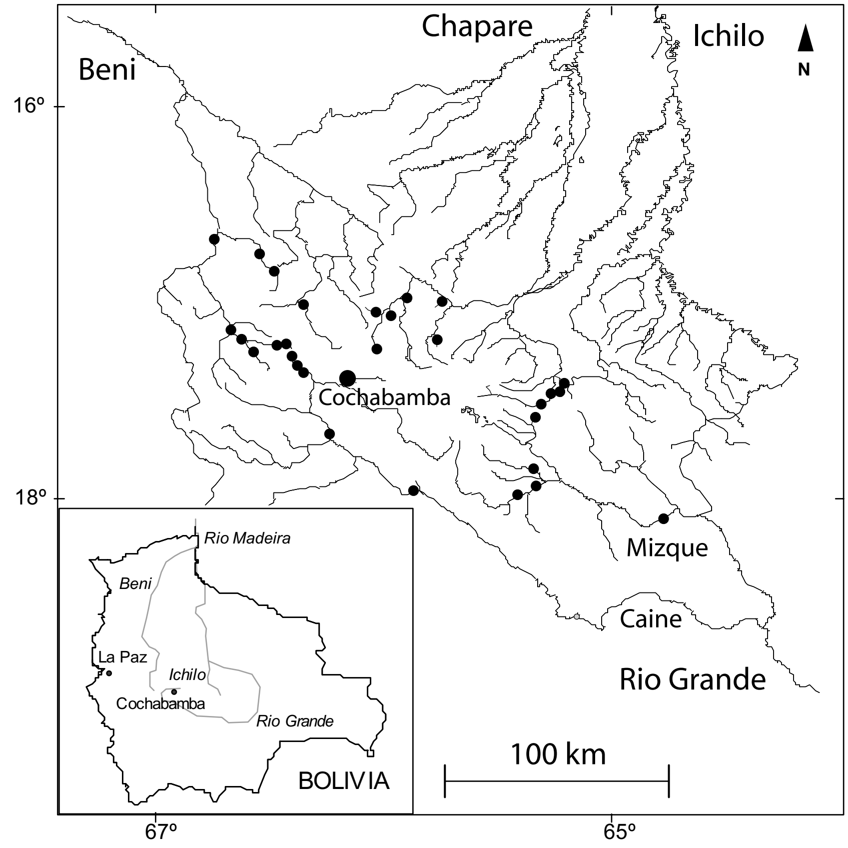

Fig. 1. Location of study sites in the department of Cochabamba, Bolivia (small black dots, not all tributaries are represented).

for 30 sites from the Upper Madeira sub-basin of the Bolivian Amazon (Fig. 1). These sites ranged from headwaters (order 1) to medium-sized rivers (order 5) and from high- to low-elevation in mountainous terrain (see Table 1 for more detail). All sites were pristine, with abundant riparian vegetation below approximately 3000 m a.s.l. and an obvious decrease at higher elevation.

Tropical aquatic environments are characterized by alternating dry and wet seasons. Unpredictable (mainly in streams and medium-sized rivers) and frequent hydraulic disturbances occurring during the wet season strongly affect aquatic communities (Flecker & Feifarek 1994) and could produce instability in the dynamic equilibrium (*sensu* Vannote et al. 1980). Consequently, our results are based only on samples from the more ecologically stable dry season. The benthic macroinvertebrate fauna was sampled on a single occasion during the dry season. Depending on the studies, four to six Surber samples (0.09 m^2, net mesh size 250 µm) were taken at each site from all present habitats (runs, riffles, pools) as a function of their proportional occurrence to assess macroinvertebrate assemblage richness and composition. Macroinvertebrates were sorted in the laboratory and identified to the family level using the keys of Merritt & Cummins (1996), Roldán (1996), and Fernández & Domínguez (2001). Mean stream width, pH, conductivity and temperature were measured at each site (Table 1). Water depth and near bottom current velocity were measured at each sample in 28 sites. The estimates of each variable were subsequently averaged to give a mean value per site. The geographical position and altitude of each site were measured using a GPS. Stream slope and distance from sources were estimated from 1 : 50,000-scale maps (see Campero et al. 2003 for further details about study sites).

FFG and data analysis

Data on macroinvertebrate functional feeding groups (FFG) were gathered mainly from Tomanova et al. (2006) who studied Bolivian taxa, and occasionally completed with information from Poi de Neiff (1990), Merritt & Cummins (1996), Bello & Cabrera (2001), Graça et al. (2001), Miserendino & Pizzolón (2000), Polegatto & Froehlich (2003), and Molina (2004). As the assignment of a taxon to a single FFG category can lead to inaccurate characterization of biological/ecological taxa profiles (Chevenet et al. 1994), family FFG affinity was transcribed into fuzzy codes (*sensu* Chevenet et al. 1994, Usseglio-Polatera 1994), scaling from 0 (no taxon affinity to a particular FFG) to 3 (strong affinity) (Appendix 1). The fuzzy coding technique has been widely applied to aquatic communities (e.g., Usseglio-Polatera 1994, Gayraud et al. 2003, Lamouroux et al. 2004) and helps to compensate for different types and levels of information available for different species (Chevenet et al. 1994). This functional approach is less sensitive to sampling methodology (Charvet et al. 1998, Bady et al. 2005) and taxonomic resolution (Dolédec et al. 2000, Gayraud et al. 2003).

The FFG coding of the 54 taxa was first multiplied by taxon abundance per m^2, and then transformed to relative abundance of FFGs for each site. The environmental variables and taxonomic richness were log-transformed. We used the first axis

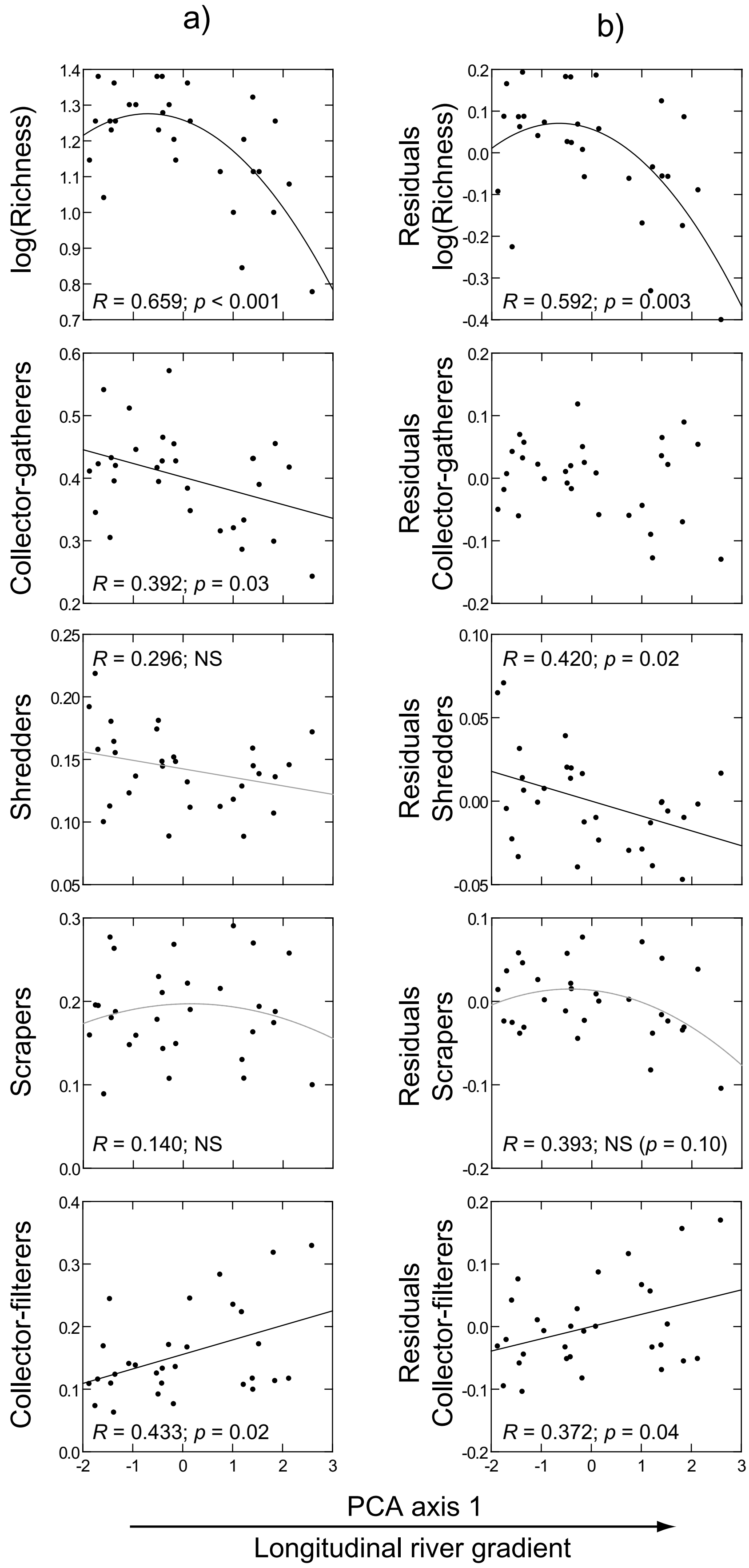

Fig. 2. **(a)** Family richness and relative abundance of functional feeding groups in relation to the longitudinal river gradient (coordinates of PC1) and **(b)** the same relationships after removing the altitudinal effect (i.e., residuals of models accounting for altitude) (*R* – correlation coefficient, NS – non significant, black lines – significant relationships, grey lines – non significant relationships). Linear or quadratic models corresponding to the RCC predictions are only shown.

(PC1) of a Principal Component Analysis (PCA) of distance from source, river slope and mean river width as a synthetic environmental factor reflecting the stream longitudinal gradient. We did not use stream order for this analysis because geomorphological variability influences the density of the hydrographical network implying sites with the same order to be situated differently along the longitudinal river gradient. We examined the relations of the PC1 and environmental parameters using simple correlation test. The coordinates of sites on PC1 were further used to study the taxonomic richness and FFG shifts predicted by the RCC (Vannote et al. 1980). Only linear (decreasing relationship for shredders and increasing relationship for collector-filterers) or quadratic (unimodal relationship for richness and scrapers) models predicted by the RCC were explored. No relationship for collector-gatherers was expected. These predictions were also assessed after removing the effect of altitude by using the residual values from the regression models relating biological variables to altitude. Finally, we investigated the altitudinal patterns of FFG for which the RCC observations seemed to be affected by altitude. This was done after removing the effect of longitudinal position of the sites within the catchment (i.e., by using the residual values from the regression models relating biological variables to longitudinal river gradient). Statistical analyses were performed using the Systat 10 software package.

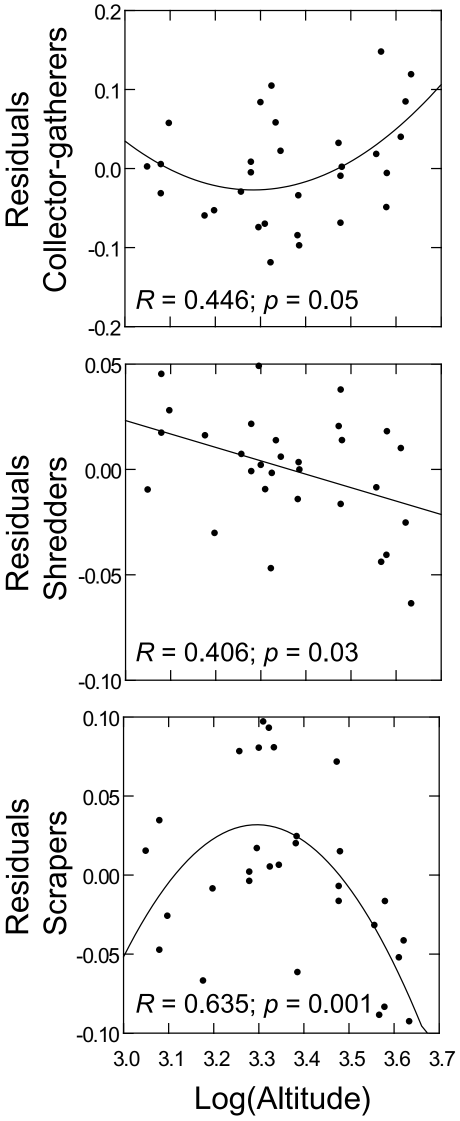

Fig. 3. Relative abundances of collector-gatherers, shredders and scrapers along the altitudinal gradient after removing the effect of longitudinal river position (using residual values of models accounting for longitudinal river position). Correlation coefficients (R) and the corresponding p-values are given.

Results

Together, the first two principal components (PC) of the PCA performed on the sites-by-environmental variables (distance from source, slope and width) explained 89.8 % of the overall variability. PC1 (57.4 % of the variability) reflected the longitudinal gradient with high correlations of distance from source and stream slope (Table 2). The PC1 score was positively related to water temperature, pH and conductivity. Altitude, the second studied driving factor, was negatively related to water temperature and depth but not to sites position along the longitudinal gradient (Table 2).

Taxonomic richness showed a unimodal relationship with PC1 ($R = 0.659$, $p < 0.001$) (Fig. 2a). Rela-

Table 2. Correlation matrix of first PCA axis (PC1) representing longitudinal river gradient and environmental parameters of sites; *n* (number of sites with available information) is indicated only if different from 30; bolded values for $p < 0.05$.

	PC1	Altitude	Slope	Source	Width	Temperature	Conductivity	pH	Flow (n = 28)
Altitude	–0.221	1							
Slope	**–0.871**	0.194	1						
Source	**0.915**	–0.194	**–0.692**	1					
Width	0.270	–0.211	–0.063	0.148	1				
Temperature	**0.550**	**–0.776**	**–0.450**	**0.544**	0.120	1			
Conductivity	**0.722**	–0.182	**–0.447**	**0.752**	0.219	**0.483**	1		
pH	**0.433**	–0.020	–0.284	**0.496**	0.182	0.161	**0.388**	1	
Flow (*n*=28)	0.090	–0.245	–0.032	–0.015	0.143	0.346	0.349	–0.104	1
Depth (*n*=28)	–0.180	**–0.466**	0.296	–0.097	0.280	0.247	–0.024	–0.055	**0.427**

tive abundance of collector-gatherers significantly decreased ($R = 0.392$, $p = 0.03$) while relative abundance of collector-filterers significantly increased ($R = 0.433$, $p = 0.02$) with PC1. Although negative linear and unimodal trends were observed along the PC1 for relative abundance of shredders and scrapers, respectively; these relationships were not statistically significant.

After removing the altitudinal effect on these assemblage variables (Fig. 2b), only taxonomic richness and relative abundance of collector-filterers showed the same patterns with PC1 (compare Fig. 2a and 2b). The decreasing pattern in relative abundance of collector-gatherers changed to a non-significant relationship ($R = 0.223$, $p = 0.24$), while the decreasing pattern in relative abundance of shredders was strengthened ($R = 0.420$, $p = 0.02$). Finally, the unimodal relationship found between relative abundance of scrapers and PC1 was also strengthened but still not significant ($R = 0.393$, $p = 0.10$).

After removing the effect of longitudinal site position on the functional groups whose longitudinal patterns were affected by altitude (Fig. 2a, b), we observed that relative abundance of collector-gatherers was significantly related to altitude ($R = 0.446$, $p = 0.05$), shredders significantly decreased along the altitudinal gradient ($R = 0.406$, $p = 0.03$) and scrapers peaked in middle altitudes ($R = 0.635$, $p = 0.001$) (Fig. 3).

Discussion

Taxonomic richness and FFG patterns along the longitudinal gradient

According to the RCC (Vannote et al. 1980), the highest taxonomic richness should be observed in middle-sized streams and our results corroborate this prediction (Fig. 2a, b). Nevertheless, this conclusion is somewhat limited because the prediction was made for species richness and our results are only based on number of families.

Without removing the altitudinal effect, the RCC predictions concerning FFGs were not confirmed since functional groups as shredders and scrapers did not fit the expected predictions (Fig. 2a). Primarily, the RCC addressed changes in biomass of functional feeding groups (Vannote et al. 1980) and it is possible that working on relative abundances might have influenced our results. However, even comparison of densities should to some extent reflect the capacity of a stream section to produce individuals. For instance, Hawkins & Sedell (1981) and Minshall et al. (1983) have shown that shift in FFG structure is also visible when considering relative abundance and densities of functional groups.

When removing the altitudinal effect, the RCC predictions of FFG variability along the longitudinal gradient became more visible (Fig. 2b). Collector-gatherers (no specific prediction for this FFG by the RCC) did not present any significant trend along the longitudinal gradient. Shredders decreased and collector-filterers increased significantly, as predicted by the RCC. Even if the predicted unimodal relationship of scrapers along the longitudinal gradient was not statistically significant, the pattern was nevertheless stronger after removing the altitudinal effect (Fig. 2a, b). Moreover, if applying the same relationship but considering only the distance from source (i.e., the parameter best related to the PC1; Table 2), the predicted unimodal relationship of scrapers become significant after removing the altitudinal effect ($R = 0.503$; $p = 0.02$). These results clearly confirm our working hypothesis that altitude can mask the FFG variability along the longitudinal river gradient predicted by the RCC.

FFG patterns along the altitudinal gradient

Independently of river size, our results revealed changes in some FFG relative abundances along the altitudinal gradient (Fig. 3) which can be associated to temperature and vegetation changes affecting leaf litter inputs, leaf palatability and periphyton development. In cold streams, running in highlands with stronger UV radiation and less-developed vegetation, shredders and scrapers were scarce probably because leaf litter quantity (Ward 1994) and palatability (i.e., conditioning by microorganisms), and periphyton development (Vinebrooke & Leavitt 1999) should be lower in these areas. Scrapers increased in intermediate altitudes where warmer, less UV-radiated zones and medium-developed riparian vegetation should allow the development of periphyton. This group decreased in importance in lowland warm streams where periphyton development should be limited by well-developed canopy cover. Shredders increased in these rivers certainly because the high rate of litter input (i.e., increasing canopy cover) and microbial activity (Mathuriau & Chauvet 2002, Dobson et al. 2003) may increase the availability and conditioning of this food type. The increase of collector-gatherers in highland sites seems to be in accordance with Winterbourn & Ryan (1994) who suggested that in many mountain streams and rivers, invertebrate populations are usually dominated by insect larvae that feed primarily on fine organic matter because periphyton standing crop and biomass of coarse detritus are often low.

Conclusions

Previous studies have stated that lateral interactions between riparian zone, floodplain and river channel may be central features of tropical river ecosystems (Junk et al. 1989, Lorenz et al. 1997). Our study suggests that longitudinal transport and processing of energy (i.e., organic matter) (Naiman et al., 1987) can also influence trophic structure of macroinvertebrate communities in neotropical streams in a similar manner as in temperate running waters (Vannote et al. 1980, Hawkins & Sedell 1981, Minshall et al. 1983, Grubaugh et al. 1997, Rosi-Marshall & Wallace 2002). Nevertheless, altitude appears as an important factor affecting the FFG structure of macroinvertebrate communities in neotropical streams. We state that the use of stream width or distance from source (i.e., parameters describing usually the longitudinal river gradient) is not sufficient to accurately predict the FFG structure in different regions, and that the influence of other environmental factors, such as altitude or latitude (related to the temperature and hence to vegetation changes, leaf litter decomposition or periphyton production), should be accounted for.

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Appendix 1. Coding of functional feeding groups (FFG) for neotropical taxa (CG – collector-gatherer; SH – shredder; SC – scraper; CF – collector-filterer; PR – predator; 0 – no affinity of taxon to FFG; 3 – strong affinity of taxon to FFG).

		CG	SH	SC	CF	PR
Ephemeroptera	Baetidae	3	1	2	0	0
	Caenidae	3	0	1	1	0
	Euthyplociidae	1	3	0	0	0
	Leptohyphidae	3	1	1	0	0
	Leptophlebiidae	3	1	3	1	0
Plecoptera	Perlidae	1	1	0	0	3
Trichoptera	Calamoceratidae	1	3	1	0	0
	Glossosomatidae	1	0	3	0	0
	Helicopsychidae	2	0	3	0	0
	Hydrobiosidae	1	0	0	0	3
	Hydropsychidae	0	1	0	3	1
	Hydroptilidae	1	0	3	0	0
	Leptoceridae	3	3	1	0	1
	Limnephilidae	2	3	1	0	0
	Odontoceridae	3	1	3	0	1
	Philopotamidae	0	1	0	3	0
	Polycentropodidae	0	0	0	2	3
	Xiphocentronidae	3	0	0	0	0
Coleoptera	Curculionidae	0	3	0	0	0
	Dytiscidae	0	0	0	0	3
	Elmidae	3	3	2	0	0
	Hydrophilidae	2	2	0	0	3
	Psephenidae	1	0	3	0	0
	Staphylinidae	2	2	0	0	1
Diptera	Anthomyidae	0	0	0	0	3
	Athericidae	0	0	0	0	3
	Blephariceridae	0	0	3	0	0
	Ceratopogonidae	1	0	1	0	2
	Chironomidae	3	1	1	1	1
	Culicidae	3	0	0	2	0
	Dixidae	3	0	1	1	1
	Empididae	1	0	0	0	3
	Ephydridae	3	2	1	0	1
	Psychodidae	3	1	1	0	1
	Raghionidae	0	0	0	0	3
	Simuliidae	0	0	1	3	0
	Stratiomyidae	2	3	1	0	1
	Tabanidae	0	0	0	0	3
	Tipulidae	2	2	0	0	3
Odonata	Coenagrionidae	0	0	0	0	3
	Gomphidae	0	0	0	0	3
	Odonata Indet.	0	0	0	0	3
Hemiptera	Gerridae	0	0	0	0	3
	Hydrometridae	0	0	0	0	3
	Naucoridae	0	0	0	0	3
Lepidoptera	Pyralidae	0	2	1	0	0
Megaloptera	Corydalidae	1	1	0	0	3
Annelida	Hirudinea	0	0	0	0	3
	Oligochaeta	3	0	0	1	0
Acari		0	0	0	0	3
Hydrozoa		0	0	0	0	3
Mollusca		3	0	3	3	0
Nematoda		0	0	0	1	1
Turbelaria		1	0	0	0	3