# Macroinvertebrate responses to distinct hydrological patterns in a tropical regulated river

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# ABSTRACT

Despite the fundamental importance of reservoirs and dams for socioeconomic development, their presence results in large-scale alterations to the natural flow regime of the rivers and profoundly influences aquatic processes and biodiversity. This study compared macroinvertebrate community composition and structure metrics, as well as biological and ecological traits to evaluate their dependence on inter-seasonal and intra-seasonal flows and water quality downstream of the Itutinga reservoir situated on Rio Grande in Brazil. The results demonstrated the utility of benthic macroinvertebrate abundance, density, richness, size, reproduction, locomotion and feeding modes to assess flow regime and water quality variability. Changes in the macroinvertebrate communities were closely associated with seasonal differences in parameters such as temperature, turbidity and nutrients, which were modulated by substrate particle size and heterogeneity. Modification of the flow regime, as a result of river regulation, influences the composition, structure and functioning of river ecosystems and is reflected in changes to the aquatic communities they support. The results of this study highlight the extreme complexity of the links between physicochemical, hydrological and biological processes in lotic systems and the need to better understand these links in order to develop and implement optimal environmental flow regimes in regulated rivers. Copyright © 2015 John Wiley & Sons, Ltd.

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## INTRODUCTION

Dam construction is a global phenomenon with more than half of the world's large rivers currently regulated by dams (World Commission on Dams, 2000; Richter *et al.*, 2003). Reservoir operation regimes alter the frequency, magnitude and duration of extreme flows, affecting natural seasonal and inter-seasonal flow variations (Bunn and Arthington, 2002). Such alterations in the natural hydrological regime directly affect vital support elements that shape downstream ecosystems such as organic matter and energy flow patterns and physicochemical quality of the water column and river sediments (including the availability and diversity of instream habitats) (Richter *et al.*, 2003; Chung *et al.*, 2008). These alterations influence the composition, structure and functioning of regulated aquatic ecosystems (Allan, 1995; Bunn and Arthington, 2002; Suen and Eheart, 2006).

The documented effects of river regulation on lotic ecosystems have generated considerable discussion, particularly in relation to environmental flow requirements (The Brisbane Declaration, 2007; Acreman and Ferguson, 2010; Poff *et al.*, 2010). Thus, integrated management of both existing and planned reservoirs is a major challenge to the long-term sustainability and conservation of regulated ecosystems and the services they provide (Dudgeon *et al.*, 2006; Poff, 2009; Acreman and Ferguson, 2010).

Environmental flow regimes developed for regulated rivers should reflect the natural variability that occurs in stream flow (Collischonn *et al.*, 2005; Shenton *et al.*, 2012). Ideally, they should be based on data from the historic natural flow regime in order to maintain the pre-existing ecosystems (Shenton *et al.*, 2012). However, most environmental flow methods applied downstream of dams in Brazil are based on hydrological parameters and habitat classification (Tharme, 2003; Anderson *et al.*, 2011; Shenton *et al.*, 2012) and do not consider natural temporal variation in the

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hydrological regime or the biological community responses (Acreman and Ferguson, 2010; Shenton *et al.*, 2012). As a result, most downstream flows in regulated rivers are considered insufficient to conserve aquatic biodiversity (Collischonn *et al.*, 2005). The importance of inter-seasonal and intra-seasonal flow variation is now widely recognized (Richter *et al.*, 2003; Poff, 2009; Belmar *et al.*, 2011), and the inclusion of biological community response in environmental flow requirements is the norm (Belmar *et al.*, 2011; Rolls *et al.*, 2012; Shenton *et al.*, 2012).

Benthic macroinvertebrate communities are excellent indicators of the effect of human activity on rivers (Rosenberg & Resh, 1993), including changes to the flow regime (Statzner *et al.*, 1988; Dewson *et al.*, 2007; Chessman *et al.*, 2010). The abundance, ubiquity and taxonomic and functional diversity of macroinvertebrate groups facilitate measurement of responses to changes in river flow regimes (Armitage *et al.*, 1987; Charvet *et al.*, 2000; Gore *et al.*, 2001; Wills *et al.*, 2006).

Alteration of the natural flow regime, as a result of river regulation, affects the composition and structure of macroinvertebrate communities (e.g. taxonomic diversity, relative abundance of families and orders, richness and densities), as well as their functional attributes - also known as traits (Statzner et al., 1988; Poff et al., 1997; Gore et al., 2001). Traits describe biological (e.g. body size, aquatic life stages, life cycle characteristics, dispersal mechanisms, feeding habits, reproductive characteristics, respiratory characteristics and mode of locomotion) and ecological attributes (e.g. distribution patterns, preferences for substrate type and current velocity and trophic characteristics) of the benthic macroinvertebrate community/taxa at a given location. This approach can provide important information regarding how flow regime alterations caused by river regulation can affect river ecosystem dynamics (Charvet et al., 2000; Bonada et al., 2007; Tupinambás et al., 2014).

This study assesses the responses of benthic macroinvertebrate community attributes to flow variability below a dam in a highly regulated reach of a tropical river system, over two consecutive years (2010 and 2011). Sampling was undertaken during wet and dry periods with distinct intraseasonal flows within three distinct fluvial habitats [backwater (BW), fluvial beach (FB) and running water (RN)]. We aimed to answer four ecological questions concerning macroinvertebrate response to hydrological variability: (i) Is it possible to identify metrics and traits that are sensitive to such hydrological variation? (ii) What are the main environmental parameters of water and sediment composition controlling benthic assemblages? (iii) Does habitat type (location in the channel and substrate composition) mediate these changes? and (iv) Is there a species shift but functional persistence as a result of flow variation?

Results will contribute towards more effective assessments of environmental flow requirements and monitor regulated river reaches in tropical river systems based on the use of relevant environmental parameters and benthic macroinvertebrate community data.

#### **METHODS**

## Study area

The study was undertaken in direct collaboration with the Energy Company of Minas Gerais (CEMIG) and the National Electric Energy Agency with financial support and direct implementation of flows required for the experiments. The flows/discharge regimes applied were drawn up in accordance with CEMIG energy production requirements in agreement with the National Operator of Electric System, Brazil.

Rio Grande is a highly regulated system (12 hydroelectric power plants and dams installed along the river's entire length) with a channel length of 1300 km and a catchment area of  $143\,000 \text{ km}^2$  (Santos, 2010), located in the state of Minas Gerais, Southeast Brazil (Figure 1). The Itutinga reservoir is the second reservoir located along Rio Grande



Figure 1. Location of study area on Rio Grande, part of the Paraná River basin, Southeast Brazil.

(upstream-downstream direction) and was selected for the study based on logistical criteria that guaranteed no detrimental effect on electric energy production of the CEMIG system. The Itutinga reservoir has both low height and reduced holding capacity, operating in a run-of-the-river regime. Thus, flow manipulation experiments were undertaken considering the effect of the larger Camargos reservoir, located approximately 2 km upstream of the Itutinga reservoir (Figure 1) and with around 50 times greater capacity (Table I).

The region's climate is humid subtropical (Köppen–Geiger classification: Cwb) with dry winters (April–September, mean precipitation  $107 \pm 12 \text{ mm month}^{-1}$ ) and wet summers (October–March, mean precipitation  $1410 \pm 156 \text{ mm month}^{-1}$ ) (Van Den Berg & Oliveira-Filho, 2000). The vegetation is typical of 'Cerrado' (tropical savanna) with predominating 'Campos' and 'Campos Cerrados' (Van Den Berg & Oliveira-Filho, 2000).

The sample sites were located about 5 km downstream of the Itutinga reservoir (44°39'W, 21°16'S; 850 m) (Figure 1). Flow regime dynamics, sediment characteristics and the influence of the dam have resulted in three fluvial/hydraulic habitat types: (i) BW; (ii) FB; and (iii) RN. These habitat types are mainly differentiated by their dominant substrate particle size and water current velocity (Table II), as well as other elements relevant to benthic macroinvertebrate communities.

Table I. General characteristics of Itutinga and Camargos reservoirs situated on Rio Grande, Southeast Brazil.

General characteristics	Itutinga reservoir	Camargos reservoir		
Start of operation	1955	1960		
Flooded area (km <sup>2</sup> )	2.03	50.46		
Volume (hm <sup>3</sup> )	11.4	792		
Dam height (m)	23	36		
Dam length (km)	550	608		
Installed capacity (MW)	52	45		
Generating units (turbines)	4	2		

Table II. General characteristics of the three habitat types (BW, FB and RN) sampled downstream of the Itutinga reservoir, Rio Grande, Southeast Brazil.

General characteristics	BW	FB	RN	
Depth (m)	1	1	1	
Width (m)	50	50	50	
Flow $(m^{3} s^{-1})$	0	0	0.48	
Predominant habitat type	Pools	Beach	Riffles	
Predominant substrate particle size (mm)	<0.50	0.50-1.0	>1.0	
Aquatic macrophytes	Absent	Absent	Present	
Organic matter (%)	1.62	0.52	0.7	

BW, backwaters; FB, fluvial beaches; RN, running water.

# Experimental design

We tested for the effect of flow variability on benthic macroinvertebrate communities under two distinct regime types, namely, high and low flows during relatively wet and dry periods covering two hydrological cycles (2010–2011). To determine the experimental flows, we analysed the amplitude of 25–75th percentiles of historic flow from 1931 to 1953 for the Itutinga reservoir for each season, prior to dam construction (Figure 2). We looked for patterns of natural variation in both wet and dry periods and selected the high and low flow values for each period. Final flow values selected for analyses were always made in accordance with management energy production requirements.

The experimental flow regimes (Table III) were imposed for 30 consecutive days prior to each sampling campaign. Following this period, water, sediment and benthic macroinvertebrates were collected on six consecutive days during each sampling period (wet and dry periods) over 2 years (2010 and 2011). Sediment and benthic macroinvertebrate samples were collected from all three habitat types.



Figure 2. Box whisker plots (range, median and 25–75th percentiles) of seasonal historical flows (prior to construction of the Itutinga reservoir) for the period 1931 to 1953 in the area of Rio Grande where the Itutinga reservoir is now situated.

Table III. Selected experimental flows for sampling in the wet and dry periods, based on the range (median and 25–75th percentiles) of historical flows prior to regulation).

Period/2010	Experimental flows $(m^3 s^{-1})$	Period/2011	Experimental flows $(m^3 s^{-1})$		
Wet – January	High – 327	Wet – March	High – 222		
Wet – March	Low – 96	Wet – November	Low – 110		
Dry – July	High – 108	Dry – June	High – 109		
Dry – October	Low – 76	Dry – September	Low – 65		

## Benthic macroinvertebrate communities

Benthic macroinvertebrate samples (four replicates) were collected for six consecutive days using a Petersen dredge  $(0.0375 \text{ m}^2)$  in the three habitat types – BW, FB and RN – over each of the four experimental periods for 2 years (2010 and 2011), yielding a total of 144 benthic macroinvertebrate samples and 576 replicates. Samples were washed through 1.0-, 0.5- and 0.25-mm sieves, respectively, and preserved in 70% alcohol. Material was identified to family level using specialized literature (Pérez 1988; Merritt and Cummins 1998; Mugnai *et al.*, 2010) and deposited in the reference collection of the Instituto de Ciências Biológicas of the Universidade Federal de Minas Gerais.

## Characterization of physical and chemical variables

*Water column*. Water quality samples were taken from the FB habitat type only because a priori sampling showed no significant difference in water column parameters between all three habitats, which were all situated in the same reach. Water temperature (°C), electrical conductivity ( $\mu$ S cm<sup>-1</sup>), pH, turbidity Nephelometric Turbidity Units (NTU) total dissolved solids ( $\mu$ g l<sup>-1</sup>) and water redox potential (mV) were measured daily over the 6-day period as the biological sampling programme using a YSI6600 electronic multi-parameter probe (a total of 48 water samples). Water samples were taken for laboratorial analyses of dissolved oxygen (mg l<sup>-1</sup>), total alkalinity ( $\mu$ q l<sup>-1</sup> of CO<sub>2</sub>), total phosphorous (mg l<sup>-1</sup>) and total nitrogen (mg l<sup>-1</sup>), following the Standard Methods for Examination of Water and Wastewater (APHA, 1999).

Sediment. Sediment samples (one dredge) were collected over the 6-day period from the three habitat types for subsequent granulometry and organic matter analyses using the Petersen dredge  $(0.0375 \text{ m}^2)$  in the wet and dry periods during 2010 and 2011, yielding a total of 144 sediment samples. The granulometric composition of each substrate (%) was determined using a screening method developed by Suguio (1973) and modified by Callisto and Esteves (1996). The organic content of the sediment samples was determined using the gravimetric ash-free dry-weight method. Aliquots were weighed  $(0.3 \pm 0.1 \text{ g})$  and ashed (550 °C for 4 h); the difference between the initial weight of sample and weight after ashing gave the percentage of the organic sediment content.

#### Data analysis

*Biological data*. Family level benthic richness (S), Shannon–Wiener diversity index (H') and density (ind  $m^{-2}$ ) were calculated for each habitat and experimental flow regime. Three data sets were derived as follows: (i) family level data; (ii) structural and composition metrics (standardized data); and (iii) biological and ecological traits (percentage of individuals) to test the effect of seasonality, flow regime variability and substrate composition (habitat types) on the macroinvertebrate community.

Calculation and selection of metrics and traits. Composition and structure metrics were calculated using the ASTERICS software (Version 3.3.1, http://www.aqem.de) developed as part of the EU funded AQEM project (Hering *et al.*, 2004). Biological and ecological traits were calculated based on Usseglio-Polatera *et al.* (2000), as described in Tupinambás *et al.* (2014). Redundant variables were removed using a Spearman Rank Correlation comparison method (threshold value:  $r \ge 0.6$  or  $r \le -0.6$ ), following Tupinambás *et al.* (2014).

*Statistical differences*. PERMANOVA, a permutational multivariate analysis of variance based on a (Bray–Curtis) similarity matrix (Anderson *et al.*, 2008), was used to test for differences in benthic community response (taxonomic composition, metrics and traits) in relation to season (wet vs dry), flow regime (high vs low) and habitat (BW vs FB vs RN) for each hydrological year. This analysis utilized four factors, where experimental period, flow regime and habitat types were fixed factors, while the sampling day was a random factor. A posteriori pairwise tests were performed to identify where differences occurred between habitats.

Indicator selection and flow influence. Biological data sets were assessed to identify what responded most clearly to changes in flow regime, where seasonal period was a categorical variable, and biological variables were continuous. A low number of variables were retained by general discriminant analysis for each biological data set, so they were combined for subsequent analyses. The individual characteristics for selected variables in relation to high and low flows were evaluated using box plots. Variance *t*-tests (for parametric data) and *z*-tests (for nonparametric data) were applied to identify statistically significant differences.

Environmental influences. Canonical correspondence analysis (CCA) is a direct gradient analysis technique that utilizes biotic and abiotic variables to generate linear combination of environmental parameters that maximize the dispersion of species scores obtained in an ordination (Cortes et al., 2008). A total of eight CCA were undertaken out to identify associations between the biological and environmental variables (water column physicochemical parameters and sediment composition). Four CCAs (interspecies distances in a biplot scaling, without transformation) were carried out to examine the association of benthic macroinvertebrate assemblage attributes with water column variables, and four CCAs (inter-species distances in a biplot scaling, without transformation) were undertaken to assess the association of benthic macroinvertebrate assemblages with sediment-based variables (in the wet and dry seasons of 2010 and 2011). A global Monte Carlo test, using unrestricted permutations, was undertaken to determine the statistical significance of the axes. Variables with variance inflation factors greater than 15 were rejected to avoid multicollinearity (O'Brien 2007). All analyses were carried out using PRIMER 6 software (Clarke and Gorley, 2006) PERMANOVA+ for PRIMER software (Anderson *et al.*, 2008), STATISTICA 8.0 software (StatSoft, 2007) and CANOCO 4.5 for Windows (ter Braak and Smilauer, 2002).

## RESULTS

A total of 30 726 benthic macroinvertebrates were collected from 38 taxa and composed of the following: arthropods (34 taxa), annelids (two taxa), molluscs (one taxon) and nematodes (one taxon). The BW and RN habitats had higher taxonomic richness (30 taxa), but Shannon–Wiener diversity (H') was higher in the RN habitat (RN H' = 1.09; BW H' = 0.36; FB H' = 0.29). There was higher taxonomic richness (38 taxa) and diversity (H=0.72) during the first hydrological year than for the second hydrological year (richness=25; H=0.52). The Chironomidae numerically dominated the community (>80% of identified taxa) in all periods and habitats.

Applied selection procedures resulted in subsets of nine metrics and 16 trait modalities (Table IV) for subsequent PERMANOVA analyses (Table V). PERMANOVA results indicated that macroinvertebrate abundance and selected metrics and traits were sensitive to seasonal flow modifications. These differed significantly between dry and wet periods for both years, particularly for RN habitats. Significant intra-seasonal differences among high and low flow values were observed (i) for abundance data for both sampling years; (ii) for composition and abundance metrics for 2011 samples only; and (iii) for biological and ecological traits for 2010 samples only. The three biological data matrices differed significantly between the three habitat types only during the first hydrological year (2010) (Table V).

Table IV. Non-redundant data set of benthic macroinvertebrate attributes retained for analyses following selection procedures to remove multicollinearity.

Selected metrics Selected traits			
Density (ind $m^{-2}$ )	Maximum potential size (percentage of individuals with size between 0.25 and 0.5 mm)		
Richness	Life cycle duration (percentage of individuals with life cycle less than 1 year)		
Percentage of Oligochaeta	Aquatic stages (percentage of individuals in larvae stage)		
Percentage of Ephemeroptera	Reproduction (percentage of individuals with reproduction through clutches)		
Percentage of Odonata	Dispersal (percentage of individuals with aquatic passive dispersion)		
Percentage of Trichoptera	Food (percentage of individuals that feed on detritus $- <1 \text{ mm}$ )		
Percentage of Lepidoptera	Food (percentage of individuals that feed on dead plant $- >1$ mm)		
Percentage of Coleoptera	Food (percentage of individuals that feed on live macrophytes)		
Percentage of Diptera	Food (percentage of individuals that feed on live macroinvertebrates)		
_	Feeding habits (percentage of individuals with filter-feeder habits)		
_	Feeding habits (percentage of individuals in predator habits)		
_	Respiration (percentage of individuals with spiracles)		
_	Substrate (percentage of individuals that prefer to live on macrophytes)		
_	Locomotion (percentage of crawler individuals)		
_	Locomotion (percentage of burrower individuals)		

Table V. PERMANOVA results (Pseudo-F and p) of benthic macroinvertebrate taxonomic composition (abundance), metrics and traits for wet and dry periods, flow regime and habitat type in 2010 and 2011.

2010	Abundance		Me	etrics	Traits	
	F	р	F	р	F	р
Period (wet $\times$ dry)	15.059	0.005**	23.262	0.004**	4.471	0.018*
Flow regime (high $\times$ low)	6.775	0.019*	2.872	0.082	6.282	0.006**
Habitats $(BW \times FB \times RN)$	6.608	0.001***	4.665	0.011*	3.655	0.004**
2011						
Periods (wet $\times$ dry)	11.928	0.005**	4.471	0.018*	6.497	0.028*
Flow (high $\times$ low)	15.544	0.002**	6.282	0.006**	1.867	0.157
Habitats $(BW \times FB \times RN)$	20.561	0.000***	3.655	0.004**	2.454	0.058

BW, backwater; FB, fluvial beach; RN, running water.

 $*P \le 0.05$ .  $**P \le 0.01$ .  $***P \le 0.001$ .

General discriminant analysis identified the most important variables from the macroinvertebrate data in relation to flow variability for each biological data set (Table VI). A total of 11 taxa, 6 structural metrics and 5 traits categories were retained for the 2010 analyses (4 taxa, 3 metrics and 1 trait for the wet period and 6 taxa, 3 metrics and 2 traits for the dry period), and 4 taxa, 5 metrics, 4 traits were retained from the 2011 analyses (3 taxa, 4 metrics and 3 traits in the wet period and 2 taxa, 1 metric and 1 trait in the dry period). There was considerable variability for each season and year.

Examination of box plots highlighted variability in flow and the macroinvertebrate community composition. For example, Chironomid abundance was significantly higher during low flow in the wet period of 2010 (t=-3.28; p=0.002), while there was no significant change in the total abundance of all taxa. Abundance of Baetidae (z=2.88; p=0.002), Pyralidae (z=2.63; p=0.008) and Trichoptera (z=2.50; p=0.012) decreased significantly under low flow conditions. In addition, the percentage of individuals that feed on macrophytes (z=3.03; p=0.002), Ceratopogonidae abundance (z=2.71; p=0.07) and relative abundance of Trichoptera (u=3.32; p=0.001) decreased significantly under low flow regime in the dry period of 2010. Chironomid abundance (t=-5.69; p=0.001), total abundance of taxa (t=-5.04; p=0.001), the percentage of filter feeders (t=-3.32; p=0.002) and Leptohyphidae (z=-2.31; p=0.02) increased during the low flow regime of the wet period in 2010. Only a single trait, describing the percentage of crawlers, was sensitive to low flow (z=2.33; p=0.02) during the dry period of 2011, showing a reduction in abundance.

Water column parameters explained shifts in the invertebrate assemblage composition and structure more clearly than sediment composition variables (Table VII). Axis one of the CCA was associated with water quality variables and clearly separated high and low flow regime macroinvertebrate communities (Figures 3A, 4A and 5A) except for the dry period of 2011, where no clear difference was discernible (Figure 6A). The principal water column parameters accounting for the benthic macroinvertebrate assemblage dynamics recorded were temperature, turbidity, dissolved oxygen, pH, alkalinity and nutrients. The first axis of all CCA reflected a gradient between substrate

Table VI. Results of general discriminant analyses for selecting benthic macroinvertebrate data of significant importance in relation to flow within each period in 2010 and 2011.

	2010				2011				
	Wet		]	Dry		Wet		Dry	
	F	р	F	р	F	р	F	р	
Abundance									
Chironomidae	35.004	0.000***	_	_	56.027	0.000***	_	_	
Baetidae	16.823	0.000***	_				_	_	
Pyralidae	14.226	0.000***	_	_	_	_	_	_	
Leptophlebiidae	13.691	0.000***	_	_	_	_	_	_	
Hydropsychidae	_	_	8.942	0.003**	4.677	0.032*	4.478	0.036*	
Collembola	_	_	7.691	0.006**		_			
Elmidae	_	_	6.884	0.009**		_			
Ceratopogonidae	_	_	5.774	0.017*		_			
Leptoyphidae	_	_	5.567	0.019*	25.773	0.000***			
Empididae	_	_	5.302	0.022*		_			
Simuliidae	_	_		_		_	3.967	0.048*	
Metrics									
Density (ind $m^{-2}$ )	17.053	0.000***	_	_	32.924	0.000***			
Percentage of Trichoptera	11.155	0.001***	12.967	0.000***	16.294	0.000***			
Richness	4.589	0.033*	_	_	13.308	0.000***			
Percentage of Diptera	_	_	6.473	0.012*	_	_	8.669	0.003**	
Percentage of Coleoptera	_	_	5.069	0.026*	_				
Percentage of Oligochaeta	_	_			8.542	0.004**			
Traits									
Percentage of livmacroph	18.133	0.000***	17.439	0.000***					
Percentage of filfeed	_	_	_	_	15.297	0.000***			
Percentage of 0.25–0.5		_	5.463	0.020*	6.572	0.011*		_	
Percentage of Crawl	_	_		_		_	10.454	0.002**	
Percentage of Clveg					9.007	0.003**	—	—	

 $*P \le 0.05$ .  $**P \le 0.01$ .  $***P \le 0.001$ .

	Water column $(n = 12)$				Sediment $(n = 36)$			
	2010		2011		2010		2011	
Source of variation	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Total inertia	0.575	0.872	0.472	0.777	1.189	2.027	1.316	1.252
Sum of canonical variables	0.481	0.780	0.420	0.628	0.261	0.744	0.299	0.801
Variables explication tax (%)	83.6	89.4	88.9	80.8	21.9	36.7	22.7	64.0
First axis explication (%)	63.5	51.5	71.9	70.7	44.4	39.1	72.0	70.0
Second axis explication (%)	27.1	24.9	17.2	29.2	32.5	20.7	19.0	29.0
Significance first axis (F-ratio)	0.688	2.557	7.109	4.000	3.023	4.514	5.677	21.9
Significance first axis ( <i>p</i> -values)	0.033	0.008	0.002	0.200	0.541	0.061	0.044	0.000
Significance all axis ( <i>F</i> -ratio)	2.915	3.161	4.625	1.576	1.124	1.955	1.423	5.982
Significance all axis (p-values)	0.012	0.008	0.003	0.202	0.309	0.004	0.128	0.001

Table VII. Summary of CCA analyses outputs carried out between benthic macroinvertebrate data, and water column and sediment variables in the wet and dry periods of 2010 and 2011.

CCA, canonical correspondence analysis.



Figure 3. Triplots of CCA analysis representing associations (A) between benthic macroinvertebrate abundance, traits and metrics, and water column variables and sampling period and (B) between benthic macroinvertebrate variables, and sediment composition and sampling habitats for the wet period of 2010 Brazil. DO – dissolved oxygen; TN – total nitrogen; TP – total phosphorous; Wredox – water redox; Turb – turbidity; Temp – water temperature; OM – organic content; G – gravel; VCS – very coarse sand; CS – coarse sand; MS – medium sand; FS – fine sand; S + C – silt plus clay; % livmacr – percentage of individual that feed on live macrophytes; BW – backwater; FB – fluvial beach; and RN – running water.

characteristics and granulometry (in particular, the proportion of gravel and fine sand) and macroinvertebrate community structure (Figures 3B, 4B, 5B and 6B).

#### DISCUSSION

Impacts on biological communities from the construction of dams and resulting hydrological modifications (Poff and Zimmerman, 2010) result in a simplification of biodiversity downstream, thereby providing opportunities for the establishment of more tolerant organisms such as Chironomidae and Oligochaeta (Rosenberg and Resh, 1993). Despite the predominance of Chironomidae during all hydrological conditions and in all habitats, significant seasonal differences in benthic macroinvertebrate community attributes were detected and indicate temporal shifts in macroinvertebrate community composition, structure and function. Other studies have also detected seasonal differences in the macroinvertebrate community attributes associated with flow regime variability in both unregulated (Tupinambás *et al.*, 2007; Ríos-Touma *et al.*, 2011) and regulated south American river reaches (Tomanova *et al.*, 2008; Rosin *et al.*, 2009; Maroneze *et al.*, 2011; Castro *et al.*, 2013).

Changes in benthic macroinvertebrate attributes in relation to high and low flows within both sampling periods were also observed. This temporal pattern has also been reported by Lajoie *et al.* (2007) and Mori (2011). However, only shifts in taxonomic composition were detected in relation to intra-seasonal flow regime variability in this study. The lack of response by some metrics and traits demonstrates structural and functional persistence of the benthic macroinvertebrate communities in relation to



Figure 4. Triplots of CCA analyses illustrating associations (A) between benthic macroinvertebrate abundance, traits and metrics, and water column variables and sampling periods and (B) relative abundance of benthic macroinvertebrate families sediment composition and sampling habitats for the dry period of 2010, downstream Itutinga reservoir, Brazil. Alcal – total alkalinity; Cond – electrical conductivity; TDS – total dissolved solids; and % > 0.25-0.5 – percentage of individuals with size between 0.25 and 0.5 mm.



Figure 5. Triplots of CCA analyses illustrating associations (A) between benthic macroinvertebrate abundance, traits and metrics, and water column variables and sampling periods, and (B) between benthic macroinvertebrate abundance, traits and metrics, and sediment composition and sampling habitats for the wet period of 2011, downstream Itutinga reservoir, Brazil. % Clveg – percentage of individuals with reproduction through clutches (in vegetation); % filfeed – percentage of filter-feeder individuals; BW – backwater; FB – fluvial beach; and RN – running water.



Figure 6. Triplot of CCA analysis representing the correlations (A) between benthic macroinvertebrate abundance, traits and metrics, and water column variables and sampling periods, and (B) between benthic macroinvertebrate abundance, traits and metrics, and sediment composition and sampling habitats, in the dry period of 2011, downstream Itutinga reservoir, Brazil. % Crawler – percentage of crawler individuals.

flow regime variability (Arthington *et al.*, 2006). This is possibly a result of adaptive evolution (Statzner *et al.*, 1988, 2001; Mori, 2011) and successful exploitation of available habitats (Southwood, 1977). Thus, species cohorts change in relation to intra-seasonal flow fluctuations simulating the natural flow variability (Shenton *et al.*, 2012), while community function was more resistant to such fluctuations, probably as a consequence of taxon replacement preserving the same functions.

The results of variance analysis allowed us to identify potential indicators of changes in flow regime character for different seasons across composition, structural metrics and faunal trait data sets. Variables such as Chironomid abundance, total abundance and traits describing food preferences, feeding habitats and locomotion modes responded to variations in flow. The documented resistance of Chironomid subfamilies and tribes to flow impacts allows them to increase their density under low flow regime (Armitage et al., 1987). Their resulting dominance strongly influences the total abundance of taxa. The food preference trait describing the percentage of individuals that feed on macrophytes increased under high flow regime tested. The increase of the percentage of macrophytes recorded in fish stomach has also been reported for the same reach of Rio Grande (Gandini et al., 2012). It is possible that under higher flow regime conditions, flow expanding onto the adjacent floodplain results in increased access to macrophytes by benthic macroinvertebrates (Poff et al., 1997) and fishes (Gandini et al., 2012).

Testing on the influence of substrate composition on the benthic macroinvertebrate communities illustrated that habitat structure (primarily substrate composition) was a vital parameter for assessing the effect of flow modifications within regulated river systems (Usseglio-Polatera & Biesel, 1994; Statzner *et al.*, 2001; Takeda *et al.*, 2001; Cortes *et al.*, 2008; Blettler *et al.*, 2012). The results clearly showed how the benthic macroinvertebrate assemblages were influenced by differences in the substrate composition among habitats. This is due to the direct and indirect effects of flow, acting as an environmental filter that shapes morphological and physiological adaptations of the invertebrates within each habitat type (Southwood, 1977; Brown & Brussock, 1991; Townsend & Hildrew, 1994; Beisel *et al.*, 1998; Gallo *et al.*, 2010; Blettler *et al.*, 2014).

The substrate composition of the RN habitat differed markedly from the BW and FB habitats, due to the greater heterogeneity and instability that is common within RN habitats (Statzner *et al.*, 2008; Gallo *et al.*, 2010). The greater complexity and dynamics of RN habitats are well-known (Brown and Brussock, 1991; Brooks *et al.*, 2005; Gallo *et al.*, 2010). Development of taxonomically, functionally and structurally diverse macroinvertebrate communities (Gallo *et al.*, 2010). Reportedly, seasonal and inter-seasonal variations in flow are less marked in

downstream reaches of regulated rivers, due to flow stabilization resulting from retention of water behind dams (Agostinho *et al.*, 2007). Thus, when considering the most appropriate macroinvertebrate attributes to examine flow variability based on historic baseline data (prior to dam construction), we agree with Collischonn *et al.* (2005) and Shenton *et al.* (2012) regarding the importance of intraseasonal variation for the maintenance of downstream ecosystems dynamics. However, the results of this study (PERMANOVA and general discriminant analysis) also demonstrate that macroinvertebrate community structure and function display higher persistence when compared with community composition.

The CCA results revealed key associations between benthic macroinvertebrate communities, and water column and sediment variables. The retained subset of benthic macroinvertebrate abundance, metrics and traits exhibited was strongly influenced by alterations to the flow regime, water quality (turbidity, dissolved oxygen, nutrients and temperature) and substrate composition. All of these factors are directly or indirectly influenced by flow releases from the reservoir. Taxonomic responses (Hydropsychidae, Leptohyphidae, Leptophlebiidae and Simuliidae) as well as selected metrics and traits (percentage of Trichoptera, percentage of individuals producing clutches of eggs and percentage of individuals that deposit their eggs on macrophytes) showed a close association with coarser, more heterogeneous sediment fractions, typical of rheophilic reaches (RN habitat) and similar to patterns reported by Jackson et al. (2010). Taxa such as Chironomidae and Elmidae and metrics/traits (percentage of Coleoptera and percentage of organisms with size >0.25-0.5) were more closely associated with fine sediment fractions and were more frequently recorded in FB and RN habitats. These results are similar to previous studies on macroinvertebrate preferences in lentic and lotic reaches described by Mérigoux and Dolédec (2004) and reinforce the importance of habitat quality and heterogeneity for maintaining ecological structural and functional diversity and for mitigating the effect of extreme flow regime variability associated with hydropeaking.

## CONCLUSIONS

River regulation by dams causes profound changes in the complex and interrelated physicochemical, hydromorphological and biological processes that characterize lotic systems. These alterations affect the composition, structure and function of the biological communities inhabiting regulated river systems. This can be carried out by evaluating aquatic community indicator responses that should cover measurable change in community structure and function as a result of imposed flow regimes. The

results of this study, based on findings that compared distinct flow regimes over different years, seasons and habitat types in highly regulated rivers, highlight the complex, dynamic and often indirect nature of the benthic macroinvertebrate response to pressures. Responses of macroinvertebrate community data differed both temporally (between years and season) and spatially (between habitats and habitat descriptors), and no single biological data type exhibited a markedly stronger response than the other types. This indicates that, at least in this study area when considering the macroinvertebrate community as an indicator of environmental flow efficacy, a combined approach is necessary. In fact, even if it was detected a shift in composition related to hydrological changes, descriptors of structure and function exhibit a lower variability, probably because of taxa replacement. These results clearly show that there is a need to better understand and identify the links between the physicochemical, hydromorphological and biological dynamics of regulated rivers, namely, the factors that influence biodiversity, through continued longer term studies.

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