

## Downstream effects of hydropower production on aquatic macroinvertebrate assemblages in two rivers in Costa Rica

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**Abstract:** Despite the fact that little is known about the consequences of hydropower production in tropical areas, many large dams (>15m high) are currently under construction or consideration in the tropics. We researched the effects of large hydroelectric dams on aquatic macroinvertebrate assemblages in two Costa Rican rivers. We measured physicochemical characteristics and sampled aquatic macroinvertebrates from March 2003 to March 2004 in two dammed rivers, Peñas Blancas and San Lorenzo, as well as in the undammed Chachagua River. Sites above and below the dam had differences in their physicochemical variables, with wide variation and extreme values in variables measured below the dam in the San Lorenzo River. Sites below the dams had reduced water discharges, velocities, and depths when compared with sites above the dams, as well as higher temperatures and conductivity. Sites above dams were dominated by collector-gatherer-scrappers and habitat groups dominated by swimmer-clingers, while sites below dams had a more even representation of groups. In contrast, a comparison between two sites at different elevation in the undammed river maintained a similar assemblage composition. Tributaries might facilitate macroinvertebrate recovery above the turbine house, but the assemblage below the turbine house resembled the one below the dam. A massive sediment release event from the dam decreased the abundance per sample and macroinvertebrate taxa below the dam in the Peñas Blancas River. Our study illustrates the effects of hydropower production on neotropical rivers, highlighting the importance of using multiple measures of macroinvertebrate assemblage structure for assessing this type of environmental impact. *Rev. Biol. Trop.* 62 (Suppl. 2): 177-199. Epub 2014 April 01.

**Key words:** Functional feeding groups, habitat groups, hydropower, tropical river ecology, turbine house.

Due to rising energy demands, hydropower production is increasingly advocated and implemented in developing, tropical countries (Revenga, Brunner, Henninger, Kassem & Payne, 2000; Anderson, Pringle & Rojas, 2006; Finer & Jenkins, 2012). While the world-wide construction rate of large hydroelectric dams (>15m, World Commission on Dams (WCD), 2000) peaked in the 1960s, the construction rate in tropical areas is still increasing (Petts, 1990; Pringle, Freeman & Freeman, 2000; Regalado, 2011). This disparity is partially due

to the exhaustion of suitable undammed rivers for hydropower production in temperate, but not tropical, areas (Revenga et al., 2000; Finer & Jenkins, 2012). This rising development in hydropower generation comes with environmental and socio-economical costs for the countries involved (Pringle, 2000; WCD, 2000; Tollefson, 2011).

Large hydroelectric dams affect biological communities through changes in stream physicochemical characteristics. Large dams reduce river connectivity (Pringle, 2001; Finer

& Jenkins, 2012), cause habitat loss (Dudgeon et al., 2006; Freeman, Pringle & Jackson, 2007; Rodrigues & Silva, 2012), alter water temperature and oxygen (Ward & Stanford, 1983; Viana, 2002; Foto Menbohan, Koji, Ajeegah, Bilong Bilong & Njiné, 2012), and interrupt water flow, movement of sediments, nutrients and fauna (Ward & Stanford, 1983; Pringle, 1997; Bunn & Arthington, 2002; Greathouse, Pringle & Holmquist, 2006a; Williams, Armstrong, Katopodis, Lariniere & Travade, 2012). Streams affected by large dams can have decreased macrophyte total biomass, as well as macroinvertebrate abundance, richness, and biomass (Troelstrup & Hergenrader, 1990; Dejalón & Sanchez, 1994; Vinson, 2001). Additionally, due to changes in food sources and substrate, the composition of macroinvertebrate functional groups changes downstream from hydroelectric dams, favoring functional groups that can exploit plankton drifting from the reservoir, and that prefer habitats with low sediment deposition (Dejalón & Sanchez, 1994; Doi et al., 2008; Katano, Negishi, Minagawa, Doi, Kawaguchi & Kayaba, 2009). Furthermore, species assemblages of invertebrates and fish are also affected below dams, favoring organisms that are tolerant to the physicochemical characteristics imposed by hydroelectric production (Dejalón & Sanchez, 1994; Vinson, 2001; Foto Menbohan et al., 2012).

Until recently, most of our knowledge on the effects of hydroelectric dams on stream biota came from studies in temperate areas (Pringle et al., 2000). However in the last decade there has been an increased effort to understand the effects of hydroelectric dams on tropical stream biota. Most previous studies on large hydroelectric dams on tropical aquatic organisms have focused on the consequences of flow regulation on fish assemblages (e.g. Albrecht, Caramaschi & Horn, 2009; Terra, dos Santos & Araujo, 2010). Connectivity disruption along streams and changes in physicochemical characteristics associated with hydropower production alter the composition and structure of tropical fish assemblages, and lowers fish diversity downstream from dams

(Pringle et al., 2000; Agostinho, Pelicice & Gomes, 2008; Araujo, Pinto & Teixeira, 2009; Cooney & Kwak, 2013). Despite the importance of tropical aquatic macroinvertebrates as a food source for higher trophic levels (Chan, Zhang & Dudgeon, 2007; Ortaz, Martín & Lopez-Ordaz, 2011) and as a functional group in streams (Benstead, 1996; Wright & Covich, 2005), little is known about the consequences of dams on their assemblages.

The little work that has been published on the consequences of hydroelectric dams on tropical aquatic macroinvertebrates comes from particular geographic areas, limiting our general understanding of the consequences of dams on macroinvertebrates. Continental tropical rivers show a decrease in taxa richness and changes in species assemblages in rivers associated with large reservoirs (Jorcín & Nogueira, 2008; Jorcín, Nogueira & Belmont, 2009; Foto Menbohan et al., 2012). Additionally, island streams, which are shorter and have a prevalence of diadromy (March, Benstead, Pringle & Scatena, 2003; McLarney, Mafla, Arias & Bouchonnet, 2010), show negative effects of large dams on migratory tropical fauna, such as shrimps and snails, with consequences for the entire assemblage of aquatic macroinvertebrates (Greathouse et al., 2006a; Greathouse, Pringle, McDowell & Holmquist, 2006b). Little is known, however, about the effects of hydroelectric dams on rivers in isthmuses, including Central America.

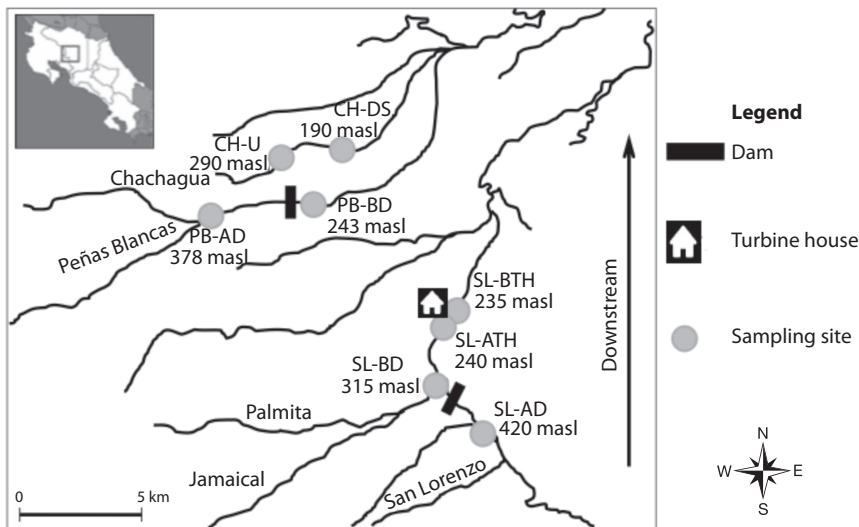
Despite the proposed expansion of hydroelectricity in Central America (Esselman & Opperman, 2010), to our knowledge there are no published studies on the effects of dams on benthic fauna in Central American rivers. Studying the consequences of hydroelectricity on aquatic macroinvertebrates in Central America can advance our understanding of the ecological effects of hydroelectricity in tropical streams as a whole. In addition, it can inform comprehensive management techniques, such as a minimal instream flow to protect aquatic biota (known as the minimum environmental flow), that can be used to mitigate the impacts of this type of energy production in Central

American rivers (Scatena, 2004; Esselman & Opperman, 2010). We studied the effects of large hydroelectric dams on aquatic macroinvertebrates in two rivers in the San Carlos River basin in Costa Rica. Our goal was to evaluate the impact of dams on physicochemical characteristics downstream the dam and the turbine house, as well as the impacts on aquatic macroinvertebrate abundance, richness and assemblages. Based on previous studies, we predicted that large hydroelectric dams in our study area will change the physicochemical characteristics of streams and decrease aquatic macroinvertebrate abundance and richness below the dam and the turbine house. Additionally, we predicted changes in the macroinvertebrate assemblages downstream from the dam. We specifically expected an increase in the relative abundance of functional groups that are favored by conditions of low sedimentation and high plankton availability, which are common downstream from dams.

## MATERIALS AND METHODS

**Study site:** This work was conducted in three rivers on the northern Caribbean

slope of Costa Rica, the dammed rivers Peñas Blancas and San Lorenzo, as well as the undammed Chachagua River (Fig. 1). The San Lorenzo, Peñas Blancas and Chachagua rivers are located in comparable life zones and have similar land use in their watersheds (Barrantes, Allan & Gallardo, 1990; Gutiérrez, 1999). The San Lorenzo River has an average annual flow of  $10.40\text{m}^3\text{s}^{-1}$  on dry years, and of  $15.50\text{m}^3\text{s}^{-1}$  on rainy years (Barrantes et al., 1990). This hydroelectric project collects water from the San Lorenzo and the Jamaical rivers in a  $63000\text{m}^3$  reservoir, behind a 21m high dam, and maintains a minimum flow of  $0.5\text{m}^3\text{s}^{-1}$  below the dam (Barrantes et al., 1990; Conelectricas, 2013; L. Torre Conelectricas, pers. comm.). The Peñas Blancas River has an average annual flow of  $35.60\text{m}^3\text{s}^{-1}$  at the Peñas Blancas gauging station, and of  $18.20\text{m}^3\text{s}^{-1}$  in the Pocosol gauging station (Gutiérrez, 1999). This hydroelectric project collects water from the Peñas Blancas River in a  $2 \times 10^6\text{m}^3$  reservoir, behind a 47m high dam, and maintains a minimum flow of  $1.0\text{m}^3\text{s}^{-1}$  below the dam (Gutiérrez, 1999). At both hydroelectric projects water is diverted and returned to the river after passing through the turbine house about



**Fig. 1.** Sampling sites: AD: above dam; BD: below dam; ATH: above turbine house; BTH: below turbine house; U: upstream; DS: downstream, in the Peñas Blancas (PB), San Lorenzo (SL) and Chachagua (CH) rivers, March 2003-March 2004.

3km downstream from the dam (Barrantes et al., 1990; Gutiérrez, 1999). Hydropower generation in San Lorenzo and Peñas Blancas occurs year-round, and at times of highest electrical demand, normally from 1000 to 1400hr. This type of electricity generation causes daily fluctuation in river flow below the turbine house. The San Lorenzo hydroelectric project receives input from two streams downstream from the dam; these streams are not used for energy production (Fig. 1).

To test for effects of hydroelectric operations on the physicochemical characteristics and aquatic macroinvertebrate assemblages, we used a paired design where each comparable site in each river was sampled seven times throughout one year. We sampled above and below the dam in the Peñas Blancas and the San Lorenzo River, and above and below the turbine house in the San Lorenzo River (Table 1, Fig. 1). Sites above the dam were free from dam effects (Fig. 1). Additionally, we chose two sampling sites in the Chachagua River for reference purposes, which were comparable in elevation to sampling sites in dammed rivers (Table 1, Fig. 1). We collected samples on five dates in 2003 –March, June, August, September and November–, and two dates in 2004 – January and March–. However, due to logistic constraints we were unable to collect data for all the study variables on every collection date (Appendix 1).

**Physicochemical sampling:** At each site we measured temperature and dissolved oxygen

(DO) using a YSI ® model 52, pH, alkalinity and hardness using Hach® test kits, and conductivity with a La Motte® conductimeter. We also collected water samples to measure total suspended solids (TSS) by weight difference of the retained material in pre-weighed glass fiber filters (GF/C) and turbidity through the determination of the absorbance at 450nm in a Shimadzu ® UV-160A spectrophotometer (Lind, 1985). Additionally, we measured mean water velocity with an electronic flow meter (Global Water (R) FP111), and depth and channel width using a tape measure. Mean water velocity and depth were measured at 1m intervals across the channel. Mean water velocity readings were taken at 60% of water depth at each measuring point. Width was measured by holding the tape measure across the channel from bank to bank on the water surface. We measured discharge using the midsection method (Hauer and Lamberti, 2007). Mean water velocity, depth, width, and water discharge were not measured upstream the dam in the Peñas Blancas River, however we obtained these measures from the hydrology department at Instituto Costarricense de Electricidad (ICE).

**Benthic macroinvertebrate sampling:**

Our sampling method for aquatic macroinvertebrates represents a capture per unit effort (CPUE). To estimate abundance per sample we performed multi-habitat collections using a 500µm mesh sized hand-net for one hour along a ~25m reach of the river at each site. We pooled samples by collection date, preserved in

TABLE 1  
Watershed area and geographic coordinates for the eight sampling sites in the Peñas Blancas, San Lorenzo and Chachagua rivers

River	Collection site	Watershed area (Ha)	Latitude	Longitude
Peñas Blancas	above dam	3 137.5	10°21'42"N	84°38'57"W
Peñas Blancas	below dam	13 792.5	10°22'02"N	84°35'91"W
San Lorenzo	above dam	15 592.5	10°16'25"N	84°32'36"W
San Lorenzo	below dam	16 087.5	10°16'90"N	84°33'46"W
San Lorenzo	above turbine house	12 225	10°18'83"N	84°33'08"W
San Lorenzo	below turbine house	15 160	10°18'91"N	84°32'91"W
Chachagua	upstream	830	10°23'66"N	84°36'32"W
Chachagua	downstream	1 057.5	10°23'52"N	84°35'28"W



70% EtOH and counted and identified all the individuals to the maximum taxonomical resolution, mostly genera, using various taxonomic keys (Merritt & Cummins, 1996; Roldán, 1996; Springer, Ramírez & Hanson, 2010). Specimens were deposited at the Museum of Zoology, University of Costa Rica. We used tropical functional feeding group (FFG) classification when available (Cummins, Merritt & Andrade, 2005; Tomanova, Goitia & Helesic, 2006; Wantzen & Wagner, 2006; Appendix 2). Groups not included in tropical studies were classified according to Merritt, Cummins & Berg (2008). Additionally, we classified the insects in habitat groups according to Merritt et al. (2008).

We collected additional aquatic macroinvertebrate samples from the Peñas Blancas River, on November 7 and December 22, 2003, in order to assess the effect of a massive sediment release event from the Peñas Blancas reservoir on October 31, 2003 (La Nación, 2003). Flushing sediments from the reservoir is a common practice in hydroelectric facilities in Costa Rica, since it prolongs the useful life of the dam.

To test for differences in physicochemical characteristics, as well as in macroinvertebrate abundance per sample between sites within each of the streams, we used paired statistical analyses. To ensure that temporal autocorrelations did not bias P-values, we confirmed that there were no significant correlations among sequential sampling dates by using the Durbin-Watson statistic test. In the case of the San Lorenzo River, we performed the paired tests for adjacent sections of the river (above dam vs. below dam, below dam vs. above turbine house, and above turbine house vs. below turbine house) and used a Bonferroni-corrected alpha of 0.017. Correlations and paired tests were performed using JMP software (SAS institute Inc., 2009).

To account for effects of differences in macroinvertebrate abundance on estimates of taxa richness, we rarified richness estimates based on the abundance of the least-abundant sample in each site per month to obtain an

unbiased expected taxa richness. Rarified taxa richness was estimated using EcoSim software version 7.0 (Gotelli & Colwell, 2001) and all randomizations were repeated 1 000 times. We also rarified estimates of total dominance (Simpson dominance index (S)). To statistically compare taxa richness and dominance between sites, we used the low and high bound for a 95% confidence interval calculated by EcoSim.

To test for effects of seasonal rainfall on the response variables collected during the study period we performed simple linear regressions between precipitation and the physicochemical variables, macroinvertebrate abundance per sample, and rarified richness measured at the different sites. The measures of precipitation for the study period were obtained from the Pocosol and the Chachagua stations (Appendix 3). Variables measured in the Peñas Blancas and the San Lorenzo rivers were regressed against precipitation data from the Pocosol station, while variables measured in the Chachagua River were regressed against precipitation data from the Chachagua station. We selected the precipitation data set used in each analysis based on distance of each station to the study sites, as well as similarities in elevation between the sites and each station. The data used in the analyses fulfilled the assumptions of regression. Regressions were performed using JMP software (SAS institute Inc., 2009).

To assess differences in macroinvertebrate assemblages among study sites, we performed a non-metric multidimensional scaling (nMDS) analysis on a Bray-Curtis dissimilarity matrix. nMDS is a distance-based approach that relies on a similarity matrix, maximizing rank-order correlation between distance measures and distance in ordination space (Clarke & Warwick, 2001). The stress value obtained from the NMDS analysis is a measure of distortion between the positions of real data points and their graphical representation (Clarke & Warwick, 2001). Thus, a low stress value is associated with a graph that more accurately represents the dissimilarities. The nMDS was performed using the vegan package (Oksanen

et al., 2010) in R statistical software (R development core team, 2009).

We used chi-square tests to test for differences in percentages of the different FFGs and habitat groups among sites within streams, using JMP software (SAS institute Inc., 2009). Only months when all compared sites were sampled were included in the nMDS, FFGs and habitat group analyses. Finally, to test the effects of the massive sediment liberation in Peñas Blancas we performed a t-test using JMP software (SAS institute Inc., 2009). We tested for a difference in the number of taxa below the dam in the Peñas Blancas River before and after the massive sediment liberation. The data used in this analysis fulfilled the assumptions of t-test.

## RESULTS

**Physicochemical characteristics:** The site below the dam in the San Lorenzo River had extreme values for several physicochemical variables. Alkalinity, hardness, and conductivity were higher immediately below the dam than in the other sites in this river, with alkalinity and hardness being >80% higher than in the other sites (Table 2). Additionally, water discharge was ~95% lower below the dam than in the other studied sites, and velocity, width, and depth were lowest below the dam (Table 2). None of these differences were statistically significant (Table 3). These physicochemical variables varied widely throughout the study period; however none of this variation had a relationship with precipitation (Appendix 4). Relative to above the turbine house, the downstream site had four times more water discharge and twice the width (Table 2), however these differences were not statistically significant (Table 3). Temperature was the only physicochemical variable that was statistically different between sites in the San Lorenzo River, with temperatures in average 1.28°C higher above the turbine house than below (Table 2 and 3). Although not statistically significant, the site below the dam had temperatures on

average 2.10°C higher than above the dam in the San Lorenzo River (Table 2 and 3).

Similar patterns as those found above vs. below the dam in the San Lorenzo River were observed for physicochemical comparisons in the Peñas Blancas River above vs. below the dam. Conductivity was 53% higher below the dam than above the dam, and temperature was 0.92°C higher below dam (Table 2). Additionally, water discharge, velocity, and depth were more than 40% lower below the dam (Table 2 and 3).

There was variation in physicochemical variables between upstream and downstream sites in the Chachagua River. Alkalinity and conductivity were 3% and 4% higher respectively downstream than upstream (Table 2). Water discharge and stream width were 76% and 165% higher upstream than downstream respectively, however only the difference in width was statistically significant (Table 3). Additionally, water velocity was 46% higher downstream than upstream (Table 2 and 3).

Most of the physicochemical variables in this study did not show a relationship with precipitation (Appendix 4). Depth decreased as precipitation increased in the site below the dam in the Peñas Blancas River and above the turbine house in the San Lorenzo River. Discharge decreased as precipitation increased in the Peñas Blancas River below the dam, while velocity increased in the site above the dam. Above the turbine house in the San Lorenzo River pH decreased with precipitation.

### **Benthic macroinvertebrate assemblage:**

A total of 5 803 individuals from 98 genera or morphogenera in 46 families from nine orders of aquatic insects were collected. At each study site the number of families ranged between 19 and 34, and between 34 and 54 genera, with the highest numbers found at the reference sites in Chachagua River and above the turbine house in San Lorenzo (Appendix 5). Few taxa contained most of the abundance (Table 4). Non-insect taxa were represented by Acari, Hirudinea and Gastropoda.

TABLE 2  
Measures of center and spread for physicochemical variables collected at the different sites in the San Lorenzo, Peñas Blancas and Chachagua rivers

	Temperature °C	Oxygen mg/L	pH	Alkalinity mg/L	Hardness mg/L	Conductivity µSi/cm	Turbidity UNT	TSS mg/L	Velocity m/s	Discharge m <sup>3</sup> /s	Width m <sup>2</sup> /s	Depth m
<b>San Lorenzo</b>												
Above dam	$\bar{X}$ =21.08 SD =1.18	$\bar{X}$ =7.98 SD =1.35	M=7.50 IQR=0.19	$\bar{X}$ =25.86 SD =7.24	$\bar{X}$ =35.37 SD =8.62	$\bar{X}$ =96.40 SD =16.70	$\bar{X}$ =57.73 SD =41.00	$\bar{X}$ =30.09 SD =34.22	$\bar{X}$ =0.91 SD =0.19	M=4.78 IQR=13.58	$\bar{X}$ =22.10 SD =14.97	$\bar{X}$ =0.53 SD =0.17
Below dam	$\bar{X}$ =23.18 SD =1.41	$\bar{X}$ =7.82 SD =1.60	M=7.50 IQR=0.38	$\bar{X}$ =52.75 SD =50.56	$\bar{X}$ =70.13 SD =68.71	$\bar{X}$ =146.67 SD =104.54	M=49.73 IQR=256.37	$\bar{X}$ =107.49 SD =111.96	$\bar{X}$ =0.60 SD =0.30	M=0.20 IQR=5.13	$\bar{X}$ =4.30 SD =3.06	$\bar{X}$ =0.38 SD =0.38
Above turbine house	$\bar{X}$ =24.27 SD =1.98	$\bar{X}$ =8.03 SD =1.36	M=7.50 IQR=0.19	$\bar{X}$ =28.71 SD =12.07	$\bar{X}$ =35.09 SD =9.00	$\bar{X}$ =90.42 SD =23.25	M=39.86 IQR=65.48	M=8.49 IQR=70.70	$\bar{X}$ =0.81 SD =0.51	M=4.25 IQR=12.24	$\bar{X}$ =10.43 SD =4.43	$\bar{X}$ =1.09 SD =0.44
Below turbine house	$\bar{X}$ =22.99 SD =1.56	$\bar{X}$ =8.70 SD =0.55	M=7.50 IQR=0.06	$\bar{X}$ =17.66 SD =6.21	M=20.54 IQR=7.73	$\bar{X}$ =76.67 SD =7.94	M=38.80 IQR=64.16	M=13.82 IQR=70.63	$\bar{X}$ =0.67 SD =0.19	$\bar{X}$ =17.34 SD =12.80	$\bar{X}$ =18.70 SD =1.84	$\bar{X}$ =1.05 SD =0.40
<b>Peñas Blancas</b>												
Above dam	M=21.85 IQR=2.75	$\bar{X}$ =8.54 SD =0.36	M=7.50 IQR=0.5	$\bar{X}$ =17.71 SD =4.14	$\bar{X}$ =23.96 SD =6.25	$\bar{X}$ =76.50 SD =10.29	$\bar{X}$ =38.41 SD =8.99	M=12.34 IQR=34.93	$\bar{X}$ =1.25 SD =0.30	$\bar{X}$ =17.23 SD =3.58	$\bar{X}$ =15.29 SD =1.47	M=1.13 IQR=0.50
Below dam	$\bar{X}$ =22.77 SD =1.78	M=8.85 IQR=1.58	M=7.50 IQR=0.25	$\bar{X}$ =20.75 SD =6.15	$\bar{X}$ =26.52 SD =5.13	$\bar{X}$ =116.67 SD =28.91	M=42.04 IQR=30.92	M=10.03 IQR=24.90	$\bar{X}$ =0.75 SD =0.25	$\bar{X}$ =8.37 SD =6.26	$\bar{X}$ =15.00 SD =6.83	$\bar{X}$ =0.68 SD =0.20
<b>Chachagua</b>												
Upstream	$\bar{X}$ =22.15 SD =0.90	$\bar{X}$ =8.22 SD =0.39	M=7.5 IQR=0.5	$\bar{X}$ =21.76 SD =7.35	M=20.54 IQR=2.55	$\bar{X}$ =58.83 SD =5.42	$\bar{X}$ =32.64 SD =1.23	M=4.09 IQR=24.49	$\bar{X}$ =0.61 SD =0.14	$\bar{X}$ =5.18 SD =2.42	M=17.60 IQR=9.50	$\bar{X}$ =0.64 SD =0.12
Downstream	$\bar{X}$ =22.86 SD =1.33	$\bar{X}$ =8.45 SD =0.80	M=7.5 IQR=0.5	M=22.5 IQR=9.17	$\bar{X}$ =19.66 SD =4.28	$\bar{X}$ =61.0 SD =4.98	$\bar{X}$ =33.03 SD =1.79	M=4.20 IQR=13.19	$\bar{X}$ =0.89 SD =0.25	$\bar{X}$ =2.94 SD =0.91	$\bar{X}$ =6.64 SD =0.68	$\bar{X}$ =0.59 SD =0.11

TSS = Total suspended solids.

$\bar{X}$  = mean, M = median, SD = standard deviation, IQR = interquartile ranges.

The median and IQR are shown in cases of skewed univariate distributions and/or outliers, ensuring the best representation of the data.

TABLE 3  
Paired t-test and Wilcoxon sign-rank test results comparing physicochemical characteristics between sites  
in the San Lorenzo, Peñas Blancas, and Chachagua rivers

Comparison	Temperature °C	Oxygen mg/L	pH	Alkalinity mg/L	Hardness mg/L	Conductivity µSi/cm	Turbidity UNT	TSS mg/L	Velocity m/s	Discharge m <sup>3</sup> /s	Width m <sup>3</sup> /s	Depth m
<b>San Lorenzo</b>												
Above vs. below dam	t <sub>3</sub> =4.70 p=0.018	t <sub>3</sub> =-1.16 p=0.33	t <sub>3</sub> =-2.45 p=0.09	t <sub>3</sub> =1.50 p=0.23	t <sub>2</sub> =1.36 p=0.31	t <sub>4</sub> =1.39 p=0.23	t <sub>4</sub> =0.97 p=0.39	t <sub>4</sub> =2.03 p=0.11	t <sub>4</sub> =-1.75 p=0.15	z <sub>5</sub> =-7.5 p=0.06	z <sub>5</sub> =-7.5 p=0.06	z <sub>5</sub> =-2.5 p=0.63
Below dam vs. above turbine house	t <sub>4</sub> =2.13 p=0.10	t <sub>4</sub> =-0.21 p=0.84	z <sub>5</sub> =0.50 p=1.00	t <sub>4</sub> =-1.26 p=0.28	z <sub>4</sub> =-3.00 p=0.38	z <sub>6</sub> =-7.50 p=0.16	z <sub>6</sub> =-6.5 p=0.22	z <sub>6</sub> =-7.50 p=0.16	t <sub>4</sub> =1.04 p=0.36	z <sub>5</sub> =7.6 p=0.06	z <sub>5</sub> =7.5 p=0.06	z <sub>5</sub> =4.5 p=0.31
Above vs. below turbine house	t <sub>6</sub> =-3.68 p=0.010*	t <sub>5</sub> =1.57 p=0.18	t <sub>5</sub> =-0.79 p=0.47	t <sub>4</sub> =-2.90 p=0.04	t <sub>3</sub> =-3.67 p=0.04	t <sub>5</sub> =-1.90 p=0.11	t <sub>5</sub> =-0.43 p=0.69	t <sub>6</sub> =0.91 p=0.40	t <sub>3</sub> =-0.63 p=0.57	t <sub>2</sub> =-0.85 p=0.50	t <sub>1</sub> =1.24 p=0.43	t <sub>5</sub> =-0.31 p=0.79
<b>Peñas Blancas</b>												
Above vs. below dam	t <sub>5</sub> =3.95 p=0.01*	t <sub>4</sub> =1.03 p=0.36	z <sub>5</sub> =3 p=0.25	t <sub>4</sub> =2.04 p=0.11	z <sub>4</sub> =3.00 p=0.25	t <sub>5</sub> =3.91 p=0.01*	t <sub>5</sub> =1.55 p=0.18	t <sub>5</sub> =1.18 p=0.29	t <sub>5</sub> =-2.75 p=0.04*	t <sub>5</sub> =-3.16 p=0.03*	t <sub>5</sub> =-0.47 p=0.66	t <sub>5</sub> =-3.90 p=0.01*
<b>Chachagua</b>												
Upstream vs. downstream	z <sub>6</sub> =7.50 p=0.06	t <sub>4</sub> =1.21 p=0.29	not enough data	t <sub>4</sub> =5.46 p=0.006*	z <sub>4</sub> =-0.5 p=1.00	t <sub>5</sub> =3.08 p=0.03*	t <sub>5</sub> =0.71 p=0.51	t <sub>5</sub> =1.62 p=0.17	t <sub>5</sub> =3.39 p=0.02*	t <sub>5</sub> =-1.81 p=0.13	z <sub>6</sub> =-9.5 p=0.06	t <sub>5</sub> =-2.24 p=0.08

TSS = Total suspended solids

Subscripts represent degrees of freedom in paired t-tests or sample size in Wilcoxon sign-rank tests. Asterisks (\*) indicate statistically significant differences. A Bonferroni corrected  $\alpha = 0.017$  was used for sites in the San Lorenzo River to compensate for multiple comparisons within this site.



TABLE 4  
Common genera –percent ( $\pm$ 1SD)—collected at each site in the San Lorenzo, Peñas Blancas and Chachagua rivers

	San Lorenzo			Peñas Blancas		Chachagua		
	above dam	below dam	above turbine house	below turbine house	above dam	below dam	upstream	downstream
Ephemeroptera								
Baetidae								
<i>Baetodes</i>	50.47 (29.29)	27.59 (25.39)	34.45 (28.06)	19.69 (19.35)	39.06 (24.43)			
<i>Camelobaetidius</i>	7.06 (7.08)	9.33 (8.03)	7.53 (6.63)	7.63 (8.91)	12.73 (8.55)	13.55 (20.48)		
Leptohyphidae								
<i>Leptohyphes</i>			9.66 (8.06)	13.45 (17.79)	11.42 (11.73)	11.57 (12.06)	28.61 (8.42)	20.69 (12.06)
Leptophlebiidae								
<i>Thraulodes</i>				5.62 (7.64)	9.82 (5.49)		6.39 (3.84)	5.08 (2.82)
Plecoptera								
Perlidae								
<i>Anacronaeria</i>					11.73 (12.79)		7.88 (2.01)	6.97 (2.88)
Trichoptera								
Hydropsychidae								
<i>Leptonema</i>						6.02 (7.04)		
<i>Smicridea</i>	7.77 (12.23)		10.85 (12.48)	6.74 (8.56)		21.20 (22.44)	6.21 (4.40)	
Coleoptera								
Elmidae								
<i>Heterelmis</i>								5.95 (3.12)
<i>Macrelmis</i>								7.12 (3.55)
Diptera								
Chironomidae								
Orthocladiinae								
Morph 1				8.54 (13.31)				
Morph 2								
Simuliidae						13.19 (15.32)		
<i>Simulium</i>							6.76 (5.55)	11.43 (11.66)

Only genera that constitute >5% of the assemblage are displayed.

The overall average abundance per sample in the San Lorenzo River was  $191 \pm 104$  individuals above the dam,  $182 \pm 69$  individuals above the turbine house,  $51 \pm 42$  individuals below the dam, and  $61 \pm 35$  individuals below the turbine house. On average the site above the dam had four times higher abundances than the site below the turbine house, however differences in abundance were only statistically significant between sites below the dam and turbine house, and above the turbine house (Table 5). In the Peñas Blancas River, the site above the dam had an average abundance per sample of  $92 \pm 35$  individuals, while the site below had  $69 \pm 66$  individuals; these differences were not statistically significant (Table 5). Both sites in the undammed river Chachagua had similar abundances per sample (Chachagua upstream= $132 \pm 46$ , Chachagua downstream= $137 \pm 50$ ; Table 5). The only collection site that had a relationship between abundance and precipitation was the site above the turbine house, with abundance decreasing as precipitation increased (Appendix 6).

Among sites in the San Lorenzo River, taxa richness was lower below the dam for all months except September 2003, and the site below the turbine house had lower observed taxa richness in all collection months except September 2003 and January 2004 (Fig. 2A). Rarefied taxa richness was significantly higher below the dam in January (72%) and March (34%) 2004 (Fig. 2B). Additionally, below the turbine house had significantly lower (19%) rarefied richness in June 2003 (Fig. 3B). In

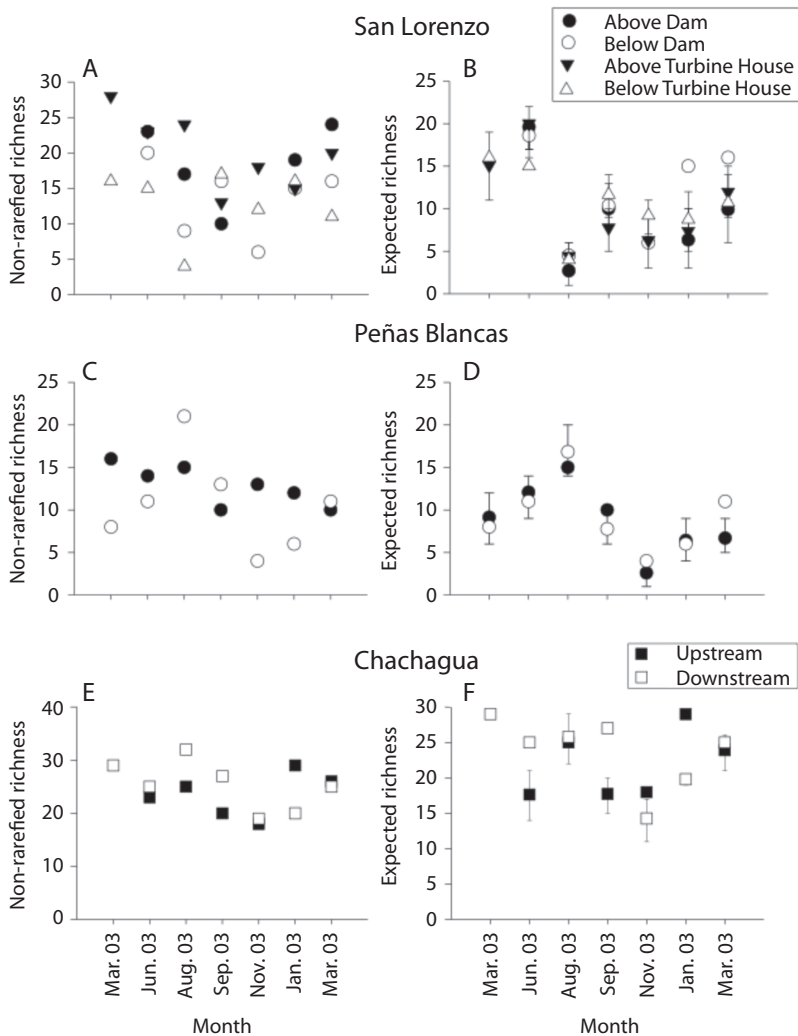
the Peñas Blancas River observed taxa richness was lower in the site below the dam than above the dam in all collection months except August and September 2003, while in March 2004 the observed richness for both sites was very similar (Fig. 2C). Rarefied richness was significantly higher (65%) for the site below the dam than above the dam in March 2004 (Fig. 2D). Observed richness in Chachagua upstream was higher than downstream only in January 2004, while November 2003 and March 2004 the observed richness was very similar (Fig. 2E). Rarefied richness was significantly higher in Chachagua downstream than upstream in June (42%) and September (52%) 2003, while it was significantly higher in Chachagua upstream in November 2003 (26%) and January 2004 (46%) (Fig. 2F). None of the collection sites had a relationship between macroinvertebrate rarefied richness and precipitation (Appendix 6).

When comparing composition among sites, the non-metric multidimensional scaling ordination (stress=0.09) separated the sites above both the dam and the turbine house from sites below both the dam and the turbine house, while both sites in the Chachagua River were closer together (Fig. 3). Sites above the dam were dominated by *Baetodes* (Ephemeroptera: Baetidae) ( $S_{\text{San Lorenzo above dam}}=0.57$ , 95% CI=0.52-0.61;  $S_{\text{Peñas Blancas above dam}}=0.45$ , 95% CI=0.42-0.47; Table 4), and above the turbine house this genus was over one-third of the taxa collected ( $S=0.33$ , 95% CI=0.29-0.38; Table 4). Sites below the dam and the turbine house in

TABLE 5  
Paired t-test results comparing relative abundance of benthic macroinvertebrates between collection sites in the San Lorenzo, Peñas Blancas, and Chachagua rivers

	Comparison	t	df	p
San Lorenzo	above vs. below dam	2.68	4	0.13
	below dam vs. above turbine house	-3.55	5	0.02*
	above vs. below turbine house	4.71	6	0.003*
Peñas Blancas	above vs. below dam	0.76	6	0.47
Chachagua	upstream vs. downstream	0.007	5	1.00

Asterisks (\*) indicate statistically significant differences. A Bonferroni corrected  $\alpha = 0.017$  was used for sites in the San Lorenzo River to compensate for multiple comparisons within this site.

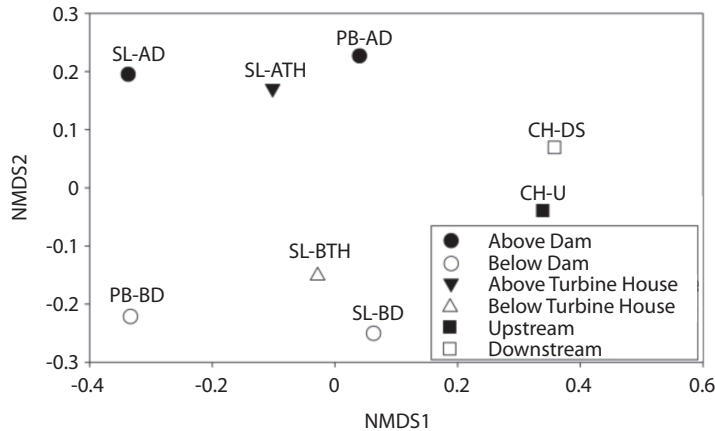


**Fig. 2.** Observed (A, C and E) and rarefied (B, D and F) taxa richness of aquatic macroinvertebrates for San Lorenzo, Peñas Blancas and Chachagua rivers. Error bars in B, D and F represent 95% CI.

the San Lorenzo River did not have a dominant taxa ( $S_{\text{San Lorenzo below dam}}=0.23$ , 95% CI=0.23 to 0.23;  $S_{\text{San Lorenzo below turbine house}}=0.18$ , 95% CI=0.16-0.20; Table 4). Below the dam in the Peñas Blancas River had high abundance per sample of *Smicridea* (Trichoptera: Hydroptychidae) ( $S=0.35$ , 95% CI=0.35 to 0.35; Table 4). Although upstream Chachagua had higher dominance than downstream ( $S_{\text{Chachagua upstream}}=0.30$ , 95% CI=0.30 to 0.30;  $S_{\text{Chachagua downstream}}=0.20$ , 95% CI=0.19-0.22), both sites

had high abundance per sample of *Leptohyphes* (Ephemeroptera: Leptohyphidae) (Table 4).

We found differences in FFG composition between sites above the dam and the turbine house in the San Lorenzo River, and the sites below these structures ( $\chi^2_{15}=342.74$ ,  $p<0.0001$ ). There was a shift from assemblages with higher relative abundance of collector-gatherer-scrappers (66%) in the site above the dam, to assemblages with high abundance of collector-gatherers (36%), collector-gatherers-scrappers



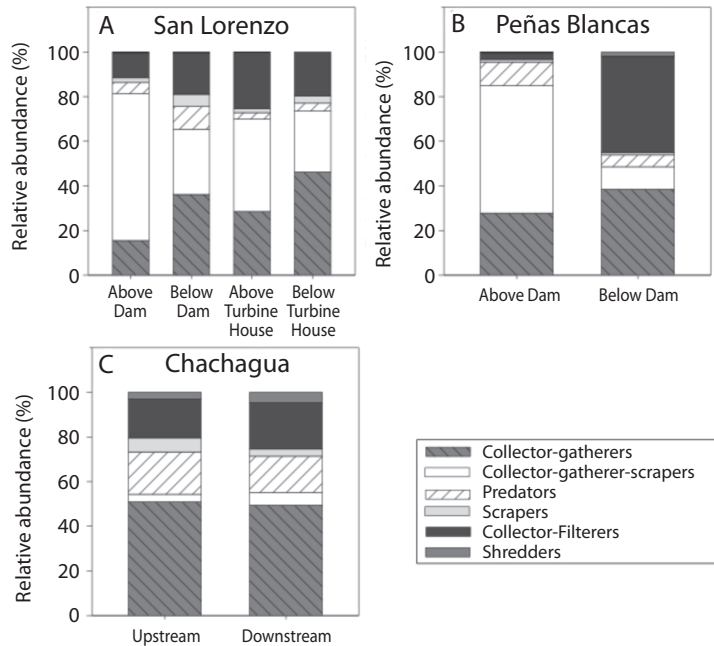
**Fig. 3.** Non-metric multidimensional scaling configuration for aquatic macroinvertebrate data (stress = 0.09) for the sampling sites (AD: above dam; BD: below dam; ATH: above turbine house; BTH: below turbine house; U: upstream; DS: downstream) in the Peñas Blancas (PB), San Lorenzo (SL) and Chachagua (CH) rivers.

(30%), and collector-filterers (19%) below the dam (Fig. 4A). The site above the turbine house had higher abundance of collector-gatherers-scrappers (41%) and collector-filterers (25%), and a lower of collector-gatherers (29%) relative to the site below the dam (Fig. 4A). The site below turbine house had fewer collector-gatherers-scrappers (27%) and collector-filterers (20%) relatively to the site above the turbine house, but more collector-gatherers (46%) (Fig. 4A). Similarly to the San Lorenzo River, the site above the dam in Peñas Blancas River had higher relative abundance of collector-gatherers-scrappers (57%), while the site below the dam had high abundances of collector-gatherers (39%) and collector-filterers (43%) ( $\chi^2_5=458.29$ ,  $p<0.0001$ ; Fig. 4B). In contrast, both sites in the undammed river had higher abundance of collector-gatherers (51% upstream and 49% downstream); Chachagua upstream had more predators and scrapers, and less collector-filterers, collector-gatherers-scrappers and shredders than downstream ( $\chi^2_5=20.15$ ,  $p=0.001$ ; Fig. 4C).

Habitat groups differed between sites above the dam and turbine house and sites below the dam and turbine house in the San Lorenzo River ( $\chi^2_{15}=301.29$ ,  $p<0.0001$ ). The

site above the dam had high relative abundance of swimmer-clingers (66%), while the site below the dam had a decrease in swimmer-clingers (32%) and an increase in clingers (50%) (Fig. 5A). Swimmer-clingers increased (44%) in the site above the turbine house in San Lorenzo relatively to the site below the dam, but decreased in the site below the turbine house (30%) (Fig. 5A). Similarly to the San Lorenzo River, above the dam in the Peñas Blancas River had high relative abundance of swimmer-clingers (59%), while the site below the dam had a decrease in swimmer-clingers (11%) and an increase in clingers (62%) ( $\chi^2_5=381.25$ ,  $p<0.0001$ ; Fig. 5B). Both sites in the reference stream were dominated by clingers (84% upstream and 86% downstream); upstream had more climbers and sprawlers, while downstream had more swimmer-clingers ( $\chi^2_5=14.52$ ,  $p=0.01$ ; Fig. 5C).

The massive sediment liberation on October 31st, 2003, in the Peñas Blancas River decreased the number of taxa below the dam from an average of 13.25 (SE=2.78) in the months previous to the sediment liberation, to 7.2 (SE=1.24) after the liberation and until the end of this study ( $t_{4,19}=1.99$ ,  $p=0.06$ ). The only specimens collected on November 7th were



**Fig. 4.** Relative abundance of aquatic macroinvertebrate functional feeding groups for the sampling sites in the San Lorenzo (A), Peñas Blancas (B) and Chachagua (C) rivers.

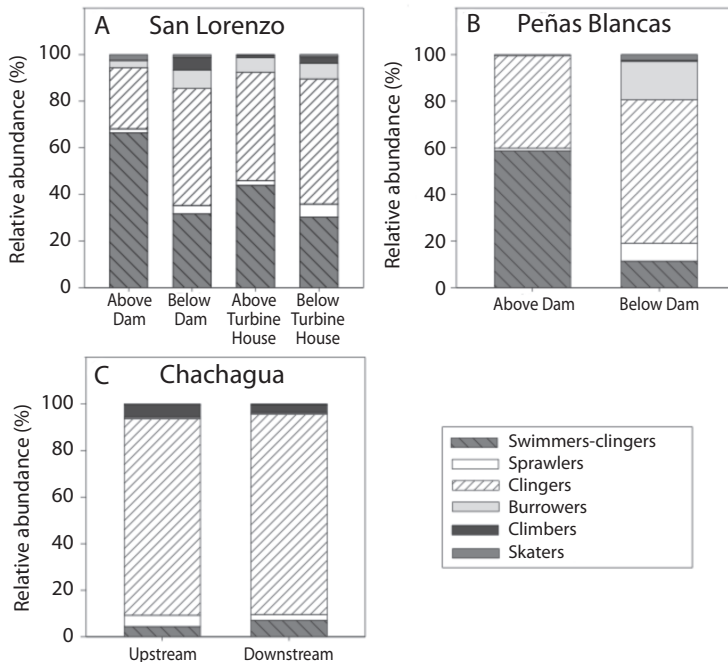
one individual from the Veliidae and four individuals in the Chironomidae.

## DISCUSSION

To the best of our knowledge this is the first published study documenting the effects of large dams on physicochemical variables and aquatic macroinvertebrates in Central America. In general, the results agree with our hypotheses on the effects of hydroelectric dams on physicochemical variables and macroinvertebrate assemblages of the studied streams. We found that sites above and below the dam had evident differences in their physicochemical variables, with wide variation and extreme values in variables measured below the dam in the San Lorenzo River. Additionally, we found changes in the assemblage structure of aquatic macroinvertebrates above and below the dams and the turbine house that were not observed in the undammed, reference river. Although sites above the dam had high dominance of a single

species, sites below the dam showed more even compositions. Composition above the turbine house resembles that of above the dam, likely due to the confluence of tributaries above the sites, but the assemblage composition below the turbine house resembles that from below the dam. Although composition was affected by damming, taxa richness and abundance were not consistently affected.

The results of our study reflect the effects of hydroelectric production on stream hydrology and further consequences on the water quality of rivers (Poff et al., 1997; Pringle et al., 2000; Bunn & Arthington, 2002). Sites below the dams had a clear trend for reduced water discharge, velocities, and depths when compared to sites above the dams. Although both of the hydroelectric plants maintained a minimum environmental flow below the dam, this flow is a reduced version of what the natural flow was before streams were dammed, and it does not necessarily reflect the habitat preferences of stream biota (Zeledón, 2001). These observed reductions in water flow below the dams could



**Fig. 5.** Relative abundance of aquatic macroinvertebrates morphological groups for the sampling sites in the San Lorenzo (A), Peñas Blancas (B) and Chachagua (C) rivers.

explain differences in water quality parameters found between above and below the dams. Increases in water temperature below dams are a known consequence of water abstraction, reducing the water's thermal capacity (Sinokrot & Gulliver, 2000). Moreover, higher conductivities below dams could be a consequence of higher temperatures in these sites (Kalf, 2002). Interestingly, there was a lack of statistical support for the observed differences in physicochemical variables between the site above and below the dam in the San Lorenzo River. This lack of statistical support is related with the wide variation in these parameters below the dam, which could be due to the nature of hydroelectric generation in this plant, where water is stored and released based on the electricity demands. Additionally, in August 2003 a flashflood blocked the minimum ecological flow, and this flow had not been re-established by the end of this study. Our results might be reflecting the importance of maintaining this minimum ecological flow.

Differences in the assemblage structure of aquatic macroinvertebrates between sites above and below the dam could be a consequence of the observed changes in hydrology and water quality. Previous studies have found that changes in hydrology and disruptions of the stream's natural connectivity affect the transportation of nutrients, energy, and sediments to sites below the dam, with effects on macroinvertebrate assemblages (Ward & Stanford, 1983; Petts, 1984; Petts, Armitage & Castella, 1993; Ligon, Dietrich & Trush, 1995; Finer & Jenkins, 2012). Increases in the abundance of collector-filterers below dams are often a consequence of increased transport of phytoplankton and zooplankton from the reservoir through the hydroelectric facility to the river downstream, creating a lake-derived subsidy for food webs below the dam (Ward & Stanford, 1983; Doi et al., 2008; Foto Menbohan et al., 2012). This increase in plankton availability could explain the observed shift from communities dominated by *Baetodes*,

a collector-gatherer-scraper, above dams in our study, to assemblages with higher relative abundance of collector-filterers in sites below the dams. Interestingly, the increase in collector-filterers was more obvious in the Peñas Blancas River, the river with the largest reservoir in our study. The lower relative abundance of swimmer-clingers downstream of the dam might be due to this group's active drifting behavior to find better sites (Merritt et al., 2008). Studies have found an increase in macroinvertebrate drifting after changes in flow discharge (Minshall & Winger, 1968; Brooker & Hemsworth, 1978; Scullion & Scintton, 1983). Furthermore, the increase of clingers downstream of the dam could be explained by the release of clear water from the reservoir, which removes fine sediment particles creating sites of low sediment deposition below the dam (Ward & Stanford, 1983; Stevens, Shannon & Blinn, 1997; Rabeni, Doisy & Zweig, 2005; Katano et al., 2009).

The resemblance in composition between the site above the turbine house and the site above the dam in the San Lorenzo River could be explained by the confluence of tributaries upstream from the turbine house. The confluence of tributaries on impounded rivers attenuates the effects of hydropower production by restoring particle size, organic debris, and increasing diversity downstream from the confluence (Petts et al., 1993; Takao, Kawaguchi, Minagawa, Kayaba & Morimoto, 2008; Katano et al., 2009; Foto Menbohan et al., 2012). The role of tributaries facilitating the recovery of the aquatic macroinvertebrate assemblages could explain the increase in the relative abundance of collector-gatherer-scrappers and swimmer-clingers above the turbine house, relative to the site below the dam in the San Lorenzo River. Below the turbine house, however, the assemblage was similar to the one below the dam. According to WCD (2000) even though water is restored after electricity production below the turbine house, the amount and periodicity of discharge is very different from the natural flow regime, affecting benthic macroinvertebrates that are adapted to natural changes in

water discharge (Cushman, 1985). This change in the natural flow regime below the turbine house was evidenced by the higher water discharges found below the turbine house. In comparison with the rest of the sites in the San Lorenzo River, these discharges were variable.

Results from the undammed Chachagua River exemplifies how longitudinal changes occur in natural rivers, but are of less magnitude than the ones measured when a dam is built. Although water discharge between Chachagua upstream and downstream did not varied significantly, width was higher upstream while water velocity was higher downstream. Additionally, the variation in other alkalinity and conductivity between these two sites was not as evident as differences found between sites above and below dams, and could be a reflection of differences in geology between the sites. Furthermore, the changes in relative abundance of FFGs and morphological groups between upstream and downstream the reference sites were less strong than the changes seen in the sites affected by hydroelectric production; both sites in the reference stream were dominated by collector-gatherers and clingers.

Despite existing monitoring efforts in dammed rivers in Central America, the studies typically remain as technical studies and there are few publications on the effects of dams on aquatic fauna. Our study highlights the importance of including community composition, especially comparisons of functional groups, in monitoring programs. We recommend future studies in tropical rivers to continue exploring the mechanisms responsible for changes in aquatic macroinvertebrates due to hydropower production. These studies should include continuous measures of physicochemical variables that allow capturing daily variation in discharge and peak flows, as well as rare, catastrophic events such as the massive sediment release that occurred in the Peñas Blancas River. These variations might be important in hydroelectric plants where water is stored and released based on electricity demands. Additionally, we recommend including measures on substrate size since this factor can be important in affecting

assemblages of aquatic macroinvertebrates. Understanding the mechanisms affecting macroinvertebrates will facilitate development of mitigation techniques in existing and future hydroelectricity projects in the tropics. Furthermore, future studies should examine the consequences of changes in community composition due to hydropower production. Changes in species composition could potentially affect aquatic and terrestrial food webs since aquatic macroinvertebrates constitute an important food source for aquatic and terrestrial predators (e.g. Nakano & Murakami, 2001). Moreover, lower abundances or shifts in dominant species, as the ones seen in this study, could influence the invasion success of non-native species (Gilbert, Turkington & Srivastava, 2009) and have implications on ecosystem function since single species can be important in maintaining ecosystem functioning in tropical ecosystems (Taylor, Flecker & Hall, 2006).

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#### RESUMEN

Existe poca información publicada sobre el efecto de grandes represas hidroeléctricas (>15m alto) en ríos tropicales. Investigamos los efectos de estas represas en las comunidades de macroinvertebrados acuáticos en dos ríos de Costa Rica. Medimos características físico-químicas y recolectamos macroinvertebrados a lo largo del año en dos ríos represados, Peñas Blancas y San Lorenzo, así como en el río Chachagua, el cual no era utilizado para la producción hidroeléctrica. Los sitios arriba y debajo de las represas presentaron diferencias físico-químicas, con amplia variación y valores extremos en las variables medidas debajo de la represa en el Río San Lorenzo. Los sitios arriba de las represas estaban dominados por colectores-recolectores-raspadores y nadadores-colgadores, mientras que debajo de las represas hubo una representación más equitativa de grupos funcionales. En contraste, las comunidades fueron semejantes en dos sitios a diferente elevación en el río sin represa. La presencia de afluentes podría haber facilitado la recuperación de macroinvertebrados arriba de la casa de máquinas, pero las comunidades fueron similares bajo la casa y abajo de la represa. Una liberación masiva de sedimentos disminuyó la abundancia y el número de táxones bajo la represa en el Río Peñas Blancas.

**Palabras clave:** grupos tróficos funcionales, grupos de hábitat, energía hidroeléctrica, ecología de ríos tropicales, casa de máquinas.

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APPENDIX 1  
Missing collection dates for particular physicochemical variables and aquatic macroinvertebrates in the San Lorenzo, Peñas Blancas and, Chachagua rivers

Variable	San Lorenzo			Peñas Blancas			Chachagua	
	Above dam	Below dam	Above turbine house	Below turbine house	Above dam	Below dam	Upstream	Downstream
Temperature	Mar-03	Mar-03 / Sep-03			Mar-03		Mar-03	
Oxygen	Mar-03 / Sep-03	Mar-03 / Sep-03	Sep-03	Sep-03	Mar-03 / Sep-03	Sep-03	Mar-03 / Sep-03	Sep-03
pH	Mar-03 / Mar-04	Mar-03 / Mar-04	Mar-04	Mar-04	Mar-03 / Mar-04	Mar-03 / Mar-04	Mar-03 / Mar-04	Mar-04
Alkalinity	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03
Hardness	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03	Mar-03 / Jun-03
Conductivity	Sep-03	Sep-03	Sep-03	Sep-03	Sep-03	Sep-03	Sep-03	Sep-03
Turbidity	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03
TSS	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03
Velocity	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03	Mar-03
Discharge	Mar-03	Mar-03	Nov-03	Aug-03 / Sep-03 / Mar-04	not collected	not collected	Mar-03	Mar-03
Width	Mar-03	Mar-03	Nov-03	Aug-03 / Sep-03 / Sep-03 / Mar-04	not collected	not collected	Mar-03	Mar-03
Depth	Mar-03	Mar-03	Nov-03	Nov-03 / Mar-04	not collected	not collected	Mar-03	Mar-03
Aquatic invertebrates	Mar-03 / Nov-03	Mar-03	Mar-03	Nov-03 / Mar-04	not collected	not collected	Mar-03	Mar-03

Collections were performed in March, June, August, September and November 2003, and January and March 2004.

APPENDIX 2  
Taxa and FFG classification used in this study

Taxa	FFG	Reference
<i>Baetis</i>	Scraper	Wantzen and Wagner, 2006
<i>Baetodes</i>	Collector-Gatherer-Scraper	Tomanova <i>et al.</i> , 2006; Wantzen & Wagner, 2006
<i>Camelobaetidius</i>	Collector-Gatherer-Scraper	Tomanova <i>et al.</i> , 2006
<i>Fallceon</i>	Collector-Gatherer-Scraper	Tomanova <i>et al.</i> , 2006
Caenidae	Collector-Gatherer	Wantzen & Wagner, 2006
<i>Leptohyphes</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Tricorythodes</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Thraulodes</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Petrophila</i>	Scraper	Tomanova <i>et al.</i> , 2006
<i>Phylloicus</i>	Shredder	Wantzen & Wagner, 2006
Hydroptilidae	Scraper	Tomanova <i>et al.</i> , 2006
<i>Oecetis</i>	Collector-Gatherer-Scraper	Wantzen & Wagner, 2006
Elmidae	Collector-Gatherer	Wantzen & Wagner, 2006
<i>Microcyloepus</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Heterelmis</i>	Collector-Gatherer-Shredder	Tomanova <i>et al.</i> , 2006
<i>Neoelmis</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Phanocerus</i>	Shredder	Tomanova <i>et al.</i> , 2006
Hydrophilidae	Collector-Gatherer	Wantzen & Wagner, 2006
Chironomidae	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Maruina</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006
<i>Limonia</i>	Collector-Gatherer	Tomanova <i>et al.</i> , 2006

FFG = functional feeding group.

Groups that are not in the table were classified using Merritt *et al.* 2008.

APPENDIX 3  
Monthly precipitation (mm) for the Pocosol and Chachagua stations, San Carlos

	2003										2004		
	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	March
Pocosol	115	115	638	617	475	476	671	639	524	678	279	330	297
Chachagua	91	33	458	493	449	423	445	380	277	459	142	257	229

Pocosol station (10°2100 N latitude, 84°4000 W longitude) Chachagua station (10°25000 N latitude, 84°35000 W longitude)  
Information provided by ICE.

APPENDIX 4

Regression results between precipitation and physicochemical variables at each site in the San Lorenzo, Peñas Blancas, and Chachagua rivers

	Temperature °C	Oxygen mg/L	pH	Alkalinity μSi/cm	Hardness UNT	Conductivity mg/L	Turbidity m/s	TSS m <sup>3</sup> /s	Velocity m <sup>3</sup> /s	Discharge m	Width	Depth
<b>San Lorenzo</b>	R <sup>2</sup> =0.27	R <sup>2</sup> =0.15	R <sup>2</sup> =0.78	R <sup>2</sup> =0.68	R <sup>2</sup> =0.90	R <sup>2</sup> =0.33	R <sup>2</sup> =0.76	R <sup>2</sup> =0.003	R <sup>2</sup> =0.09	R <sup>2</sup> =0.40	R <sup>2</sup> =0.50	R <sup>2</sup> =0.04
	F <sub>1,3</sub> =1.11	F <sub>1,2</sub> =0.36	F <sub>1,2</sub> =7.06	F <sub>1,2</sub> =4.24	F <sub>1,1</sub> =8.69	F <sub>1,3</sub> =1.49	F <sub>1,3</sub> =9.67	F <sub>1,3</sub> =0.01	F <sub>1,2</sub> =0.30	F <sub>1,3</sub> =1.99	F <sub>1,3</sub> =2.95	F <sub>1,3</sub> =0.13
	p=0.37	p=0.61	p=0.12	p=0.18	p=0.21	p=0.31	p=0.05	p=0.92	p=0.62	p=0.25	p=0.18	p=0.74
	R <sup>2</sup> =0.11	R <sup>2</sup> =0.33	R <sup>2</sup> =0.45	R <sup>2</sup> =0.38	R <sup>2</sup> =0.08	R <sup>2</sup> =0.21	R <sup>2</sup> =0.17	R <sup>2</sup> =0.15	R <sup>2</sup> =0.23	R <sup>2</sup> =0.49	R <sup>2</sup> =0.63	R <sup>2</sup> =0.70
	F <sub>1,3</sub> =0.38	F <sub>1,3</sub> =1.47	F <sub>1,3</sub> =2.47	F <sub>1,3</sub> =1.90	F <sub>1,2</sub> =0.18	F <sub>1,4</sub> =1.09	F <sub>1,4</sub> =0.84	F <sub>1,4</sub> =0.70	F <sub>1,3</sub> =0.88	F <sub>1,3</sub> =2.93	F <sub>1,3</sub> =5.17	F <sub>1,3</sub> =7.00
p=0.58	p=0.31	p=0.21	p=0.26	p=0.71	p=0.35	p=0.41	p=0.45	p=0.42	p=0.19	p=0.11	p=0.08	
Above turbine house	R <sup>2</sup> =0.27	R <sup>2</sup> =0.001	R <sup>2</sup> =0.73	R <sup>2</sup> =0.71	R <sup>2</sup> <0.001	R <sup>2</sup> =0.29	R <sup>2</sup> =0.39	R <sup>2</sup> =0.18	R <sup>2</sup> =0.29	R <sup>2</sup> =0.007	R <sup>2</sup> =0.001	R <sup>2</sup> =0.64
	F <sub>1,5</sub> =1.87	F <sub>1,4</sub> =0.005	F <sub>1,4</sub> =10.67	F <sub>1,3</sub> =7.47	F <sub>1,2</sub> =0.001	F <sub>1,4</sub> =1.61	F <sub>1,4</sub> =2.57	F <sub>1,5</sub> =1.07	F <sub>1,5</sub> =1.99	F <sub>1,5</sub> =0.03	F <sub>1,5</sub> =0.007	F <sub>1,5</sub> =8.73
	p=0.23	p=0.95	p=0.03*	p=0.07	p=0.98	p=0.27	p=0.18	p=0.35	p=0.22	p=0.86	p=0.94	p=0.03*
Below turbine house	R <sup>2</sup> =0.18	R <sup>2</sup> =0.006	R <sup>2</sup> =0.004	R <sup>2</sup> =0.50	R <sup>2</sup> =0.19	R <sup>2</sup> =0.08	R <sup>2</sup> =0.38	R <sup>2</sup> =0.16	R <sup>2</sup> =0.07	R <sup>2</sup> =0.40	No enough data	R <sup>2</sup> <0.001
	F <sub>1,5</sub> =1.13	F <sub>1,4</sub> =0.02	F <sub>1,4</sub> =0.02	F <sub>1,3</sub> =2.82	F <sub>1,2</sub> =0.47	F <sub>1,4</sub> =0.36	F <sub>1,4</sub> =2.45	F <sub>1,5</sub> =0.96	F <sub>1,2</sub> =0.15	F <sub>1,1</sub> =0.67		F <sub>1,1</sub> <0.001
	p=0.34	p=0.89	p=0.90	p=0.19	p=0.56	p=0.58	p=0.19	p=0.37	p=0.74	p=0.56		p=1.00
<b>Peñas Blancas</b>	R <sup>2</sup> =0.02	R <sup>2</sup> <0.001	R <sup>2</sup> =0.04	R <sup>2</sup> =0.21	R <sup>2</sup> =0.79	R <sup>2</sup> =0.59	R <sup>2</sup> =0.26	R <sup>2</sup> =0.24	R <sup>2</sup> =0.70	R <sup>2</sup> =0.28	R <sup>2</sup> =0.13	R <sup>2</sup> =0.08
Above dam	F <sub>1,4</sub> =0.07	F <sub>1,3</sub> =0.001	F <sub>1,3</sub> =0.12	F <sub>1,3</sub> =0.79	F <sub>1,2</sub> =7.41	F <sub>1,4</sub> =5.65	F <sub>1,4</sub> =1.40	F <sub>1,4</sub> =1.27	F <sub>1,4</sub> =9.14	F <sub>1,4</sub> =1.55	F <sub>1,4</sub> =0.58	F <sub>1,4</sub> =0.37
	p=0.80	p=0.97	p=0.75	p=0.44	p=0.11	p=0.08	p=0.30	p=0.32	p=0.04*	p=0.28	p=0.49	p=0.58
Below dam	R <sup>2</sup> =0.05	R <sup>2</sup> =0.31	R <sup>2</sup> =0.34	R <sup>2</sup> =0.19	R <sup>2</sup> =0.87	R <sup>2</sup> =0.18	R <sup>2</sup> =0.55	R <sup>2</sup> =0.01	R <sup>2</sup> =0.20	R <sup>2</sup> =0.77	R <sup>2</sup> =0.53	R <sup>2</sup> =0.67
	F <sub>1,4</sub> =0.25	F <sub>1,4</sub> =1.79	F <sub>1,3</sub> =1.53	F <sub>1,3</sub> =0.72	F <sub>1,2</sub> =13.37	F <sub>1,4</sub> =0.88	F <sub>1,4</sub> =4.95	F <sub>1,5</sub> =0.05	F <sub>1,5</sub> =1.25	F <sub>1,5</sub> =16.65	F <sub>1,5</sub> =5.69	F <sub>1,5</sub> =10.14
	p=0.63	p=0.25	p=0.30	p=0.46	p=0.07	p=0.40	p=0.09	p=0.84	p=0.31	p=0.009*	p=0.06	p=0.02*
<b>Chachagua</b>	R <sup>2</sup> =0.02	R <sup>2</sup> <0.001	R <sup>2</sup> =0.42	R <sup>2</sup> =0.65	R <sup>2</sup> =0.77	R <sup>2</sup> =0.39	R <sup>2</sup> =0.14	R <sup>2</sup> =0.11	R <sup>2</sup> =0.07	R <sup>2</sup> =0.34	R <sup>2</sup> =0.45	R <sup>2</sup> =0.08
Upstream	F <sub>1,4</sub> =0.09	F <sub>1,3</sub> <0.001	F <sub>1,3</sub> =2.14	F <sub>1,3</sub> =5.58	F <sub>1,2</sub> =6.67	F <sub>1,4</sub> =2.60	F <sub>1,4</sub> =0.63	F <sub>1,4</sub> =0.48	F <sub>1,4</sub> =0.32	F <sub>1,4</sub> =2.04	F <sub>1,4</sub> =3.21	F <sub>1,4</sub> =0.34
	p=0.78	p=0.98	p=0.24	p=0.10	p=0.12	p=0.18	p=0.47	p=0.53	p=0.60	p=0.23	p=0.15	p=0.59
Downstream	R <sup>2</sup> =0.07	R <sup>2</sup> =0.47	R <sup>2</sup> =0.45	R <sup>2</sup> =0.59	R <sup>2</sup> =0.27	R <sup>2</sup> =0.40	R <sup>2</sup> =0.33	R <sup>2</sup> =0.03	R <sup>2</sup> =0.05	R <sup>2</sup> =0.55	R <sup>2</sup> =0.04	R <sup>2</sup> =0.002
	F <sub>1,5</sub> =0.39	F <sub>1,4</sub> =3.54	F <sub>1,4</sub> =3.30	F <sub>1,3</sub> =4.24	F <sub>1,4</sub> =0.75	F <sub>1,4</sub> =2.65	F <sub>1,4</sub> =2.00	F <sub>1,5</sub> =0.15	F <sub>1,5</sub> =0.28	F <sub>1,5</sub> =6.12	F <sub>1,5</sub> =0.20	F <sub>1,5</sub> =0.009
	p=0.56	p=0.13	p=0.14	p=0.13	p=0.48	p=0.18	p=0.23	p=0.72	p=0.62	p=0.06	p=0.67	p=0.93

TSS= Total suspended solids  
 Subscripts represent degrees of freedom. Asterisks (\*) represent statistically significant relationship between the precipitation and the physicochemical variable.



APPENDIX 5

Abundance per sample of aquatic insects for each site in the San Lorenzo, Peñas Blancas and Chachagua rivers

	San Lorenzo				Peñas Blancas		Chachagua	
	above dam	below dam	above turbine house	below turbine house	above dam	below dam	upstream	downstream
Ephemeroptera	3(11)	3(8)	4(15)	4(12)	3(11)	4(11)	4(13)	5(16)
Plecoptera	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)
Odonata	1(1)	1(1)	1(2)	2(2)	1(2)	2(2)	5(5)	7(10)
Hemiptera	2(3)	3(3)	2(2)	1(1)	0	1(2)	5(6)	4(3)
Megaloptera	1(1)	2(2)	2(2)	2(2)	2(2)	1(1)	2(2)	2(2)
Lepidoptera	1(1)	0	1(1)	0	0	1(1)	0	1(1)
Trichoptera	4(6)	3(4)	5(7)	3(5)	4(7)	5(7)	6(7)	4(6)
Coleoptera	5(9)	5(9)	6(11)	3(9)	3(6)	2(2)	5(10)	5(11)
Diptera	6(9)	6(10)	9(13)	4(6)	5(5)	6(11)	6(6)	4(4)
Total	24 (42)	24 (38)	31(54)	20(38)	19(34)	23(38)	34 (50)	33(54)

The first number represents the total number of families and the number inside parenthesis the total genera collected.

APPENDIX 6

Regression results between precipitation and abundance per sample and rarified taxa richness at the San Lorenzo, Peñas Blancas, and Chachagua rivers

	Individuals per sample	Rarified taxa richness
<b>San Lorenzo</b>	$R^2=0.76$	$R^2=0.21$
Above dam	$F_{1,3}=9.35, p=0.06$	$F_{1,3}=0.81, p=0.43$
Below dam	$R^2=0.09$	$R^2=0.05$
Above turbine house	$F_{1,4}=0.40, p=0.56$	$F_{1,4}=0.19, p=0.69$
Below turbine house	$R^2=0.63$	$R^2=0.01$
	$F_{1,5}=8.41, p=0.03^*$	$F_{1,5}=0.06, p=0.82$
	$R^2<0.01$	$R^2=0.03$
	$F_{1,5}<0.01, p=0.97$	$F_{1,5}=0.13, p=0.73$
<b>Peñas Blancas</b>	$R^2=0.18$	$R^2=0.05$
Above dam	$F_{1,5}=1.11, p=0.34$	$F_{1,5}=0.29, p=0.62$
Below dam	$R^2=0.16$	$R^2<0.01$
	$F_{1,5}=0.98, p=0.37$	$F_{1,5}=0.04, p=0.84$
<b>Chachagua</b>	$R^2=0.03$	$R^2=0.44$
Upstream	$F_{1,4}=0.12, p=0.75$	$F_{1,4}=3.17, p=0.15$
Downstream	$R^2=0.18$	$R^2=0.02$
	$F_{1,5}=1.08, p=0.35$	$F_{1,5}=0.09, p=0.78$

Subscripts represent degrees of freedom. Asterisks (\*) represent statistically significant relationship between the precipitation and the biological variable.

