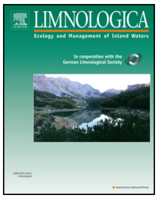
Limnologica 77 (2019) 125685

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno



Small dam impairs invertebrate and microbial assemblages as well as leaf breakdown: a study case from a tropical savanna stream

Valéria Prota Salomão[a,1], Alan M. Tonin[a,1], Renan de Souza Rezende[a,b], Gustavo Figueiredo Marques Leite[a], Elisa Araújo Cunha Carvalho Alvim[a], José Maurício Brandão Quintão[a], José Francisco Gonçalves Júnior[a,*]

[a] AquaRiparia / Laboratory of the Limnology, Ecology Department, Institute of Biological Sciences, University of Brasilia, CEP 70910-900, Asa Norte, Brasilia, Distrito Federal, Brazil

[b] Programa de Pós graduação em Ciências Ambientais, Universidade Comunitária Regional de Chapecó - Unochapecó, CEP 89809-000, Santa Catarina, Brazil

ARTICLE INFO

Keywords:
Cerrado
litter decomposition
reservoir
water quality
microorganisms
invertebrates

ABSTRACT

Globally, dams severely affect the hydrology of lotic ecosystems, impacting biotic assemblages and ecological processes. Although their consequences are not fully explored, especially in the tropics, hundreds of small dams have been constructed worldwide in the last decade for hydropower development and water supply. Here, we assessed the effects of a small dam (ca. 0.14 km^2) on water quality, leaf breakdown and the associated assemblages (microbes and invertebrates) in three reaches of a tropical savanna stream (upstream and downstream and in the reservoir). Water quality measured as pH, dissolved oxygen, and electrical conductivity were similar in all reaches, but turbidity and temperature were higher and water velocity lower in the downstream reach and in the reservoir. The upstream reach had higher leaf breakdown (as leaf mass loss, 72, 41 and 53%), microbial biomass (98, 74 and 73 nmol ATP g^{-1} AFDM), fungal biomass (347, 240 and 260 μg ergosterol g^{-1} AFDM) and invertebrate richness (4, 2 and 3 taxa $sample^{-1}$) than the reservoir and downstream reach. These results suggest that damming a stream can reduce water quality, impoverish invertebrate assemblages, and reduce microbial biomass and carbon processing.

1. Introduction

Hundreds of small dams have been constructed globally in the last decades, especially in tropical areas, for hydropower development and water supply. A global synthesis estimated that there are more than 82,800 small hydropower plants in operation or under construction (Couto & Olden, 2018). Despite their widespread dissemination and potential negative consequences to biodiversity and river habitats, there is still insufficient scientific information to support their construction and maintenance (e.g., Poff et al., 2007). For instance, in the Brazilian tropical savanna – which is a strategic biome of South America in terms of water resources – the abundant fresh waters have promoted population growth, energy development, industrialization and urbanization in such an extent that numerous reservoirs have been constructed in the area (Couto & Olden, 2018).

Small hydropower plants greatly vary in size and operational mode, and can be classified according their flow control and the presence of diversion structures (McManamay et al., 2016). In general, hydropower plants vary from those that store water in the reservoir to plants that do not retain much water or intermediate classes that control flow during some periods of the year. In this sense, reservoirs are created to reduce variability in water supply, also for human use such as irrigation, livestock farming and urban consumption (Lehner et al., 2011). As a consequence of reservoir creation, this type of operational mode cause major alterations to natural flow of rivers and has greater potential to alter the surrounding environment through flooding natural riparian vegetation. Alteration in natural flow of streams and rivers has multiple correlated consequences for the physical structure of habitats, which resulted from alterations in sediment transport dynamics, wetted width, water depth, water turbidity, and riverbed substrate type and composition (Poff & Hart, 2002). In the reservoir area, it is also expected an increase of tree mortality due to the presence of flood-intolerant plant species in the inundated riparian vegetation (Nilsson & Berggren, 2000). Additionally, dam construction also restricts the movement of organisms from downstream to upstream segments, consequently affecting the diversity and composition of aquatic assemblages (Pringle

---

* Corresponding author.
E-mail address: jfjunior@unb.br (J.F. Gonçalves Júnior).

[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.limno.2019.125685
Received 18 May 2018; Received in revised form 4 April 2019; Accepted 7 April 2019

et al., 2000). Finally, in addition to the effect on biological communities, dams also limit carbon and nutrient transport to downstream segments via physical retention (Poff & Hart, 2002). Thus, several key ecosystem processes are impaired by stream damming and reservoir creation, such as leaf breakdown (e.g., González et al., 2013; Martinez et al., 2013), which is the centerpiece of carbon processing and nutrient recycling.

Plant litter inputs is especially important for forested headwater streams as leaf litter is the main energy source to stream food webs and its breakdown is a first step to organic carbon processing (Neres-Lima et al., 2017, Tonin et al., 2017). Leaf breakdown is driven by physical, chemical and biological agents, and then, tend to respond to changes in water characteristics (i.e., water temperature, pH, dissolved nutrients, current velocity) and biological communities, mainly to invertebrate shredders and microbial decomposers (Tonin et al., 2018). For instance, flow reduction due to dam construction is expected to slow physical abrasion of leaf litter (at least in comparison to stream riffle conditions; Fonseca et al., 2013) – which is especially relevant as biological fragmentation are of low relevance in such systems (Gonçalves et al., 2007) –, decrease sporulation activity of fungal decomposers (which are intensified in more turbulent water; Bärlocher, 2005), while temperature increases stimulate microbial activity upon a certain threshold (Brown et al., 2004). Invertebrate shredders and other functional groups also tend to be affected by flow modification, mainly in the reservoir area, where a lotic ecosystem is converted to a lentic one, and then habitat homogenization occurs (e.g., loss of rifle-pool configuration, litter pools and habitats as refuge against predators; Poff et al., 2007).

Although studies on the effect of dams based on leaf breakdown are infrequent when compared to those assessing impacts on the ecosystem physical structure and biological communities, they suggested potential alterations on stream functioning. Most studies evidenced a decrease in leaf breakdown (González et al., 2013, Mendoza-Lera et al., 2012, Muehlbauer et al., 2009, Nelson & Roline, 2000), whereas others a potential increase (Short & Ward 1980) or no change in response to stream dams (Casas et al. 2000). The scarcity of information about functional consequences of stream dams is even more evident considering tropical streams as study models, as very few studies on this topic were performed in the tropics (but see Abril et al., 2013, Quintão et al., 2013). Here we tested whether a small dam decreases leaf breakdown (both in the reservoir area – where flow reduction and a physical barrier promote a greater leaf accumulation – and downstream) as would be expected based on previous studies on temperate and Mediterranean climatic regions. We expected potential negative effects on leaf breakdown to be driven by changes in water characteristics – such as an increase in turbidity and temperature that may influence negatively invertebrates and microbial assemblages – and stream hydrodynamics – i.e., flow reduction that slow physical abrasion of leaves and may alter biological communities (e.g., lower microbial biomass in less turbulent waters and lower proportion of shredders in simplified habitats that lack riffle-pool configuration and litter availability is reduced) – that directly regulate the presence, biomass and/or activity of decomposer assemblages.

2. Materials and Methods

2.1. Study area

The study was conducted in a fourth-order segment of the Ribeirão do Gama stream located in the Gama Cabeça-de-Veado Environmental Protection Area in Distrito Federal, Brazil. A small dam was constructed in 1970s for water supply of local population in this stream, which caused an increase in riparian plant mortality (due to inundation), bank erosion and sedimentation both in the reservoir and below the dam. In the upstream part of reservoir, natural conditions were generally conserved, mainly riparian vegetation, bank stability and water flow. The reservoir has an area of 0.14 km^2 and a maximum depth of 5 m, while upstream and downstream of the reservoir the maximum depth was 0.40 m.

We, thus, selected three stream reaches to assess the impact of damming on water parameters, leaf breakdown and associated assemblages: a natural stream reach (to be used as a control) located approximately 2 km upstream of the dam (hereafter upstream); the reservoir area, which comprised the inundated area after dam construction (hereafter reservoir) and where a great amount of organic material (most leaves) are accumulated due to lentic conditions and the physical barrier imposed by the dam; and a downstream reach of the reservoir, which was approximately 2 km downstream of the dam (hereafter downstream).

2.2. Experimental design

We collected senescent leaf litter during natural abscission with suspended nets between July and September 2011. Four common native riparian tree species of the Brazilian savanna were selected based on their frequency in riparian vegetation of streams – to represent a natural mixture of leaf litter entering most streams – and on a gradient of leaf litter hardness (*Maprounea guianensis,* 146 g; *Protium heptaphyllum,* 260 g; *Copaifera langsdorffii,* 294 g; and *Calophyllum brasiliensis,* 765 g). Leaf litter hardness was estimated as the mass necessary to puncture the leaf tissue (Graça & Zimmer, 2005).

Air-dried leaves of each species were weighed into 3.0 g ± 0.2 g portions and placed in coarse-mesh bags (10 cm x 10 cm, 10-mm mesh size) to allow the access of microbes and invertebrates to leaf litter. In total, there were 72 litter bags of each species for the experiment. Litter bags were arranged in four blocks with six bags per species and incubated in stream reaches. The experiment was performed during the rainy season (November 2011 to March 2012), and samples were recovered after 7, 14, 30, 60, 90, and 120 days (4 litter bags per sampling per species). Four additional litter bag of each species were set up to control for the mass loss due to handling and field transport.

We measured *in situ* at each reach and sampling time several water parameters such as pH (JENWAY 3510), electrical conductivity (Quimis Q405 M), temperature (Quimis Q405 M), dissolved oxygen (Digimed – DM-4 P), turbidity (Quimis – Q279 P) and current velocity (GLOBAL WATER - FP101 & 201). Additionally, one water sample was collected in each reach and sampling time, filtered (through 0.45 μm pore size cellulose filter) and analyzed in TOC-VCSH (Shimadzu®) for total dissolved carbon and total dissolved nitrogen. Four sediment samples were collected at each reach (using a core of 7.5 cm diameter), placed into individual plastic bags, transported to the lab and analyzed (following Suguio, 1973). Sediment samples were first incinerated (550 °C, 4 h) to remove organic particles, passed through five sieves and classified into five categories according its size: pebbles and gravel ($\geq$ 2 mm), coarse sand (1 mm), medium sand (0.50 mm), fine sand (0.25 - 0.125 mm), and clay and silt ($\leq$ 0.063 mm).

2.3. Experimental procedures

In the laboratory, leaves were cleaned with distilled water over a sieve (120 μm) to collect associated invertebrates and remove inorganic sediments. Invertebrates were stored in 70% alcohol, sorted, identified using Neotropical taxonomic keys (Mugnai et al., 2010, Pes et al., 2005), and classified into five main functional feeding groups (gathering-collectors, filtering-collectors, shredders, scrapers, and predators; Merrit & Cummins, 1996, Cummins et al., 2005). In the case a taxon belonged to more than one functional feeding group, its abundance was divided into them. Fifteen discs (12 mm diameter) were cut from each litter bag sample and separated in three subsamples for subsequent analyses. One subsample of five discs was oven dried (60 °C, 72 h), weighed (0.01 mg), incinerated (550 °C, 4 h) and reweighed to estimate dry mass (DM) and ash-free dry mass (AFDM). The last two subsamples were first frozen (at -20 °C) and used to estimate total microbial biomass (ATP content; Abelho, 2005) and fungal biomass (ergosterol content; Gessner, 2005a). The remaining leaves (including those from which the discs were cut) were oven dried (60 °C for 72 h) to determine the final DM, ground and stored for chemical analyses. Leaf breakdown was expressed as the proportion of leaf mass loss (after 7, 14, 30, 60, 90 or 120 days of incubation), which was calculated through the difference from the initial and the final AFDM (after multiplying discs AFDM by dry mass) divided by initial AFDM (but in the text, leaf mass loss was presented as percentage to facilitate interpretation). Litter breakdown rates (k day^{-1} and degree-day^{-1}) were estimated for the upstream, reservoir and downstream reaches separately, independently of plant species (as explained below in the *Data analysis* section). The natural logarithm was applied to the quotient of initial mass by final mass (%) and by elapsed time (in days, for k day^{-1}) or thermal sum (in degree-days, for k degree-days^{-1}).

The chemical composition of leaves over the incubation period was determined by the concentration of total polyphenols, lignin and cellulose. Polyphenols were extracted in 70% acetone at 4 °C and quantified using a spectrophotometer (at 760 nm) (Bärlocher & Graça, 2005). Lignin and cellulose were estimated gravimetrically by successive removals of each constituent from leaf litter with a detergent acidic solution followed by a 72% sulfuric acid solution (Gessner, 2005b). The chemical composition of leaves (initial and after the incubation period) is available in the Supplementary Material 1 (SM 1).

2.4. Data analysis

We tested damming effects on water characteristics (pH, dissolved oxygen, conductivity, turbidity, temperature and water velocity), total microbial and fungal biomass (as ATP and ergosterol content on decomposing leaves, respectively), richness (as the number of taxa) and each functional feeding group (as the relative proportion) of invertebrates by comparing each response variable among the three stream reaches (upstream, reservoir and downstream). To perform such comparisons, we fit linear models using the gls function (generalized least squares) and restricted maximum likelihood (REML) method in the nlme R package (Pinheiro et al., 2017; R Core Team, 2017, version 3.4.2). Initial data exploration for each response variable revealed that (for some response variables) there was a violation of homogeneity of variances assumption for linear models; for such cases, we took it into account using specific variance structures from nlme package (Zuur et al. 2009). The optimal variance structure was defined by comparing AIC from models with different variance structures (using VarIdent). The optimal models allowed residual spread to vary in relation to reach type only, reach type and plant species or plant species only. Temporal autocorrelation, which occurred among samples collected on different sampling times, were considered in all models using the corAR1 correlation structure (Zuur et al. 2009; also using the nlme R package). When significant damming effect was observed for one response variable, the pairwise multiple comparisons from the linear models were obtained using the summary function.

We first tested whether the influence of dam on leaf breakdown (as the proportion of leaf mass loss on each sampling time) depend on plant species through the interaction between reach type (upstream, reservoir or downstream reach) and plant species (*Calophyllum*, *Protium*, *Maprounea* or *Copaifera*). We fit a linear model using the gls function and REML method as explained above. We also detected different variances among reaches and plant species, which required the use of variance structures (VarIdent); temporal autocorrelation was considered using the corAR1 correlation structure. We did not find an interaction between reach type and plant species ($F_{6,\ 268} = 1.32$, $P = 0.245$), which indicated that there is no need to analyse how each plant species respond to damming effects. Thus, all subsequent analyses were performed independently of plant species.

We used a backward model selection procedure to explore which environmental and biological variables best predict leaf breakdown. We first defined the most relevant and non-correlated variables (through pair plots) to leaf breakdown such as water temperature (which affect decomposer metabolism), water current (which enhance physical abrasion of leaf litter), microbial and fungal biomass (which accelerate decomposition), total water nitrogen (which can intensify microbial C acquisition from leaf litter and thus, decomposition) and shredder and scraper abundance (which both have the potential to promote leaf breakdown through fragmenting and/or scraping leaf litter surface). All predictors were standardized using z-scores before fitting the models. We follow the same steps as above to define the optimal random structure (VarIdent structure, which for this model allowed residual spread to vary in relation to reach type and plant species) and temporal autocorrelation (corAR1 correlation structure). However, visual exploration of residuals showed a much higher variability in leaf mass loss for one species in particular (i.e., *Maprounea*), we thus decided to perform the multiple regression model using a dataset containing the other three species only.

3. Results

3.1. Dam effects on physic-chemical water characteristics

Water was circumneutral (6.98 ± 0.06) with a high level of dissolved oxygen (6.92 ± 0.07 mg L^{-1}, > 75% of saturation) and low

Table 1
Mean ± SD values (over sampling times) of water environmental parameters (a) and granulometric fractions of the streambed substrate (b) in the upstream, reservoir, and downstream sites. Summary of linear model results for the comparison of each environmental parameter among reaches (degrees of freedom: 2, numerator; 18, total). Statistical significant P-values ($P < 0.05$) are in bold; different superscript letters indicate statistically significant differences (at $P < 0.05$) among reaches for turbidity, temperature and water current.

	Upstream	Reservoir	Downstream	Statistics
(a) Environmental parameters				
pH	6.9 ± 0.4	6.8 ± 0.4	7.0 ± 0.4	$F = 0.47$, $P = 0.636$
Dissolved oxygen (mg L^{-1})	6.2 ± 0.3	7.5 ± 0.4	7.6 ± 0.8	$F = 0.96$, $P = 0.403$
Electrical conductivity (µS cm^{-1})	11.6 ± 4.2	11.6 ± 1.2	16.8 ± 2.6	$F = 3.05$, $P = 0.077$
Turbidity (NTU)	9.4 ± 1.9^{a}	59.2 ± 16.0^{b}	67.0 ± 16.8^{b}	$F = 4.69$, $\mathbf{P = 0.026}$
Temperature (°C)	18.4 ± 0.3^{a}	23.1 ± 0.4^{b}	23.6 ± 0.3^{b}	$F = 42.93$, $\mathbf{P < 0.001}$
Water current (m s^{-1})	1.3 ± 0.1^{a}	0.0 ± 0.0^{b}	0.7 ± 0.1^{c}	$F = 13.49$, $\mathbf{P < 0.001}$
Dissolved nitrogen (µg L^{-1})	157 ± 7	155 ± 15	157 ± 13	$F = 0.01$, $P = 0.994$
Dissolved carbon (mg L^{-1})	12.2 ± 8.6	16.6 ± 21.1	6.1 ± 3.5	$F = 1.95$, $P = 0.176$
(b) - Granulometric fractions (%)				
Pebbles and gravel	98.5	39.5	7.0	-
Coarse sand	1.2	10.0	12.1	-
Medium sand	0.3	9.5	18.0	-
Fine sand	0.0	32.0	32.9	-
Silt + Clay	0.0	9.0	30.0	-

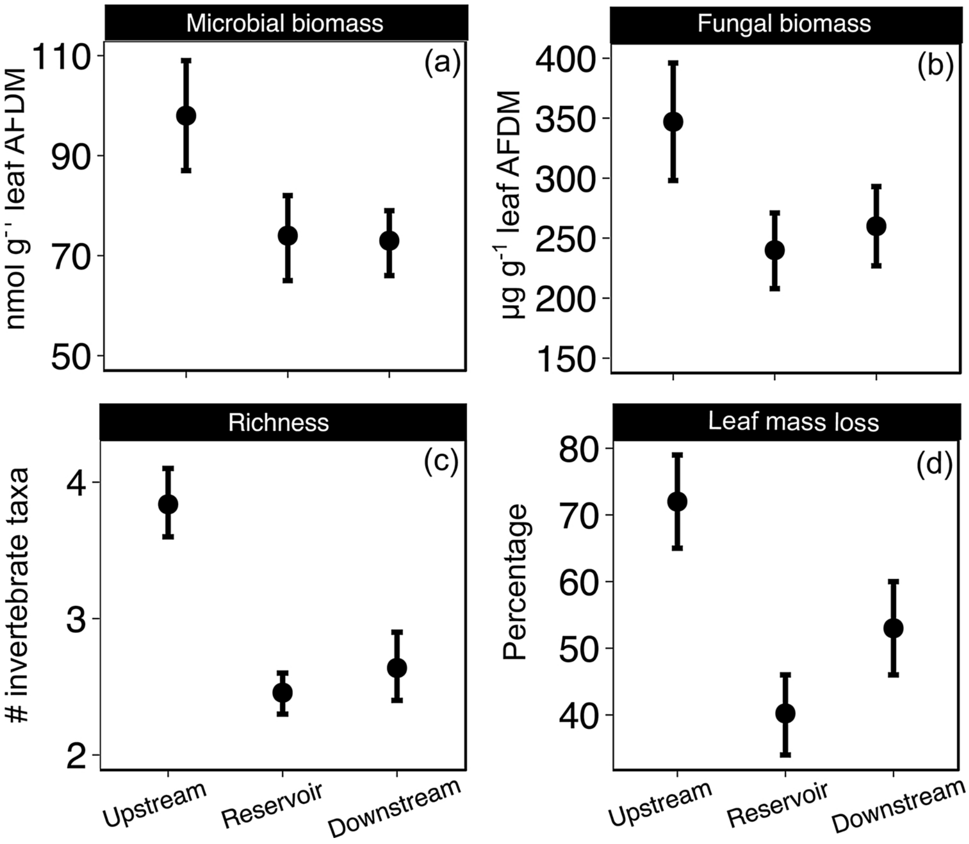


Fig. 1. Microbial biomass (a; as ATP content), fungal biomass (b; as ergosterol content) and invertebrate richness (c; as number of taxa) on decomposing leaf litter and leaf breakdown (d; as percentage of leaf mass loss) in the upstream, reservoir and downstream reaches. Circles are means and upper and lower vertical lines the standard error.

electrical conductivity (13.89 ± 0.14 µS cm^{-1}; Table 1a) in all stream reaches. However, water turbidity was five times higher and temperature five degrees higher in the reservoir and downstream than in the upstream reach (Table 1a). Also, water velocity was 80% higher in the upstream than in the downstream reach, and virtually zero in the reservoir (Table 1a). In general, the granulometric composition of the substrate in the reservoir and downstream differed from the upstream reach ($\chi = 36.9$, df = 4, $P < 0.001$): the percentage of pebbles and gravel was higher in the upstream reach, while fine sand and silt/clay predominated in the reservoir and downstream reaches (Table 1b).

3.2. Dam effects on microbial and invertebrate assemblages

Total microbial biomass, measured as ATP content on decomposing leaves, was on average 33% higher in upstream than in the reservoir and downstream reaches (98 vs. 74 vs. 73 nmol ATP g leaf AFDM^{-1}, respectively; $F_{2,265} = 7.59$, $P < 0.001$; Fig. 1b). Consistently, total microbial biomass was higher after 120 days of leaf incubation (135 ± 17 nmol ATP g leaf AFDM^{-1}). Fungal biomass, measured as ergosterol content on decomposing leaves, was on averaged 39% higher in upstream than in the reservoir and downstream reaches (347, 240 and 260 µg ergosterol g leaf AFDM^{-1}; $F_{2,199} = 7.59$, $P < 0.001$; Fig. 1c). In contrast to microbial biomass, the highest fungal biomass occurred after 60 days of leaf incubation (453 ± 52 µg ergosterol g leaf AFDM^{-1}).

Invertebrate taxa richness was also reduced due to dam effects ($F_{2,164} = 10.96$, $P < 0.001$; Fig. 1d). Reservoir and downstream reaches recorded, approximately, one invertebrate taxa less than the upstream reach (2, 3 and 4 invertebrate taxa, on average, respectively). Invertebrate assemblage composition also showed relevant differences among reaches; in the upstream reach, six invertebrate taxa represent more than 96% of total abundance (Chironomidae [80.6%], Oligochaeta [7.5%], Simuliidae [2.5%], Leptohyphidae [2.1%], Hydropsychidae [2.0%] and Elmidae [1.7%]), while in the reservoir and downstream reaches the same proportion was comprised by 2 (Chironomidae [84.2%], Oligochaeta [14.1%]) and 4 taxa (Chironomidae [46.2%], Oligochaeta [22.3%], Hydropsychidae [14.7%] and Simuliidae [13.7%]), respectively. In general, the proportion of invertebrate's functional feeding groups was also affected by dam (Fig. 2): the proportion of filtering-collectors were, respectively, 8% and 19% higher in the reservoir and downstream reaches than in the upstream reach ($F_{2,139} = 8.13$, $P < 0.001$); gathering-collector proportion was similar between upstream and reservoir-downstream reaches, but was

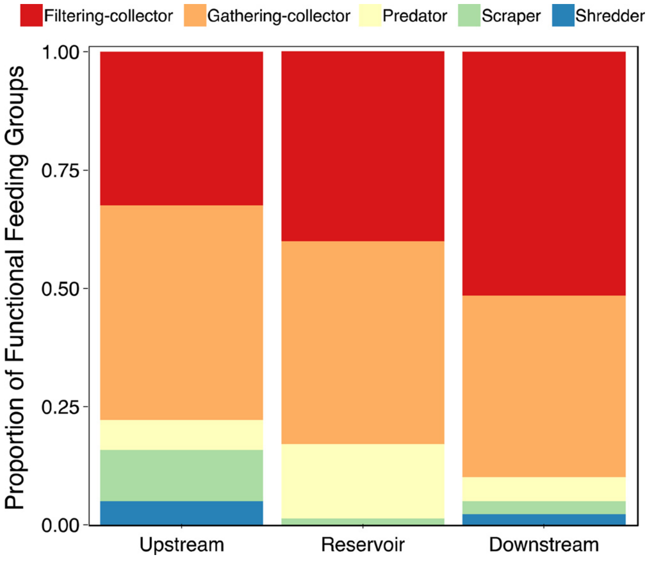


Fig. 2. Proportion of each functional feeding group (filtering-collector, gathering-collector, predator, scraper and shredder) on decomposing leaf litter incubated in the upstream, reservoir and downstream reaches.

6% higher in reservoir than downstream reach ($F_{2,136}$ = 3.20, P = 0.044); predator proportion was 10% higher in the dam, but similar between downstream and upstream reaches ($F_{2,136}$ = 4.89, P = 0.009); scraper proportion was on average 9% lower in reservoir and downstream than in upstream reach ($F_{2,136}$ = 7.92, $P <$ 0.001); finally, shredder proportion was similar among reaches ($F_{2,136}$ = 1.92, P = 0.151), but shredder invertebrates only occurred in upstream and downstream reaches being absent in the reservoir reach (mean = 5, 2 and 0% of total invertebrate abundance, respectively).

3.3. Dam effects on stream functioning

Damming effects consistently reduced leaf breakdown of the four plant species by ca. 53% ($F_{2,277}$ = 5.62, P = 0.004). In the upstream reach, leaves loss on average 72% of its initial mass (k = - 0.0119 ± 0.0016 day^{-1}), while in reservoir and downstream reaches leaf mass loss was 41 and 53%, respectively (k = - 0.0032 ± 0.0008 and 0.0057 ± 0.0006 day^{-1}; Fig. 1a; Table S2). The model selection procedure showed that leaf breakdown was reduced by damming due to lower microbial biomass (slope ± SE = 1.73 ± 0.52, t-value = 3.36), lower water current (slope ± SE = 1.00 ± 0.54, t-value = 1.84) and higher water temperature (slope ± SE = - 0.80 ± 0.41, t-value = - 1.94; Table 2; Table S3; SM 3).

4. Discussion

Our results provided evidence of how damming a stream can alter system morphology and water characteristics (mainly water temperature, flow and turbidity). Damming a stream limits sediment transport and increases the sediment retention capacity along its fluvial gradient, increasing the deposition of fine particles. According to Poff & Hart (2002), water retention and the subsequent reduction in current caused by damming directly influences other abiotic factors, such as water temperature and sediment transport, both in the reservoir and downstream reaches. Also, a recent review consistently showed that a reduction in water current, and an increase in water temperature and turbidity are typical consequences of damming effects, which corroborate our findings (Mbaka & Mwaniki, 2016). Additionally, the increase in sediment deposition in reservoir and downstream reaches (as shown by altered proportions of sediment type and size among reaches), as a result of intensification of stream bank erosion and inundation, may led to lower richness of aquatic invertebrates due to habitat homogenization consequences (Molozzi et al., 2011).

The greater abundance of scrapers in the upstream reach may be due to higher overall microbial (but also fungal) biomass on decomposing leaves. Microbes are key components of stream biofilms, which are an important energy source for scrapers and shredders that are capable of scraping or shredding leaf tissues, respectively (Graça, 2001). Also, the greater proportion of scrapers in the upstream reach suggests that they can make an important contribution to leaf breakdown by scraping the leaf surface. In general, scrapers (such as Gastropoda) may be indicative of advanced stages of leaf breakdown to be associated with a higher quality leaf litter (i.e., better colonized by microbes), as observed elsewhere (Quintão et al., 2013). The greater proportion of filtering-collectors, commonly represented by Bivalvia and Oligochaeta, in the reservoir and downstream reaches may be attributed to invertebrate taxa that are tolerant to environmental alterations such as increase in water temperature, turbidity and fine sediment transport or deposition, and alteration in natural water flow. In fact, Oligochaeta occurrence is associated to lentic conditions (no water flow) and higher abundance is observed in silt, clay and fine sand sediments (Verdonschot, 2001). This functional feeding group is capable of filtering fine organic particles from the water using the leaf litter as a substrate, and thus play a small role in leaf breakdown (Moulton & Magalhães, 2003). The increased proportion of predators in the reservoir reach could be explained by a large availability of food resources, such as small larvae (e.g., Chironomidae), supported by the 2-4 times greater abundance of invertebrates observed in the reservoir reach. Finally, although we found similar proportions of shredder invertebrates among reaches, shredders were not observed in the reservoir area. The absence of damming effect in this case could be attributed to a lower frequency of this functional group in natural streams of Cerrado savanna (e.g., Gonçalves et al., 2007), although they have a prominent role in leaf breakdown when they are present (Tonin et al., 2014).

Table 2
Results of the model that best predicted leaf mass loss (coefficients ± standard error, t- and P-values) after a backward model selection procedure. Residual SE = 26.6, degrees of freedom = 50, residual; 54, total.

	Coefficient	SE	t value	P-value
Intercept	11.01	1.56	7.06	< 0.001
Water current	1.00	0.54	1.84	0.071
Microbial biomass	1.73	0.52	3.36	0.001
Water temperature	−0.81	0.41	−1.94	0.057

We observed negative effects of damming on microbial decomposers (especially fungi that are key organisms to decomposition), which were supported by Mbaka & Mwaniki (2016) findings. Microbes are generally sensitive to even slightly physic-chemical water alterations and are thus good indicators of stream health and water quality (Solé et al., 2008). Increases in water temperature (due to reductions in riparian canopy cover (higher deforestation in our study by dam construction that led to an increase of solar radiation) and reduced flow were also previously reported to negatively affect fungal biomass, fungal sporulation activity and, thus species composition and diversity (Fernandes et al., 2009). Lower total microbial biomass (as ATP content) in the reservoir and downstream reaches may be a consequence of higher water turbidity and fine sediment deposition (also on decomposing leaves), which reduced the transparency of water to algae or other primary producers (which growth on stream surfaces including decomposing leaves) and difficult the establishment of microbes on leaf litter (Pascoal et al., 2005).

Leaf breakdown was reduced by stream damming through a reduction in microbial biomass (which were responsible to metabolize leaf organic carbon) and in leaf physical fragmentation (which was decreased by lower water current in the reservoir and downstream reaches). Leaf physical fragmentation is especially important considering the lower representativeness of shredder invertebrates observed in such systems (Gonçalves et al., 2007), as fragmentation is responsible to produce smaller leaf particles that are consumed by many other aquatic organisms. Also, leaf breakdown was reduced by an increase in water temperature – that was on average of 5 °C –, which could have altered the metabolic activity of organisms (including decomposers; supported by lower microbial and fungal biomass on reservoir and downstream reaches) or even exclude some intolerant organism from the system (e.g., some caddisfly shredder such as the genus *Phylloicus*). Negative effects of damming on leaf breakdown were previously reported for small and large reservoirs and are generally associated to reduction in flow and of decomposer activity (e.g., Mendoza-Lera et al., 2012, González et al., 2013, Mbaka and Mwaniki, 2016). In this context, although our experimental design was restricted to a single stream (and one dam), we were able to demonstrate that a more general prediction about damming effects on stream functioning (i.e., stream dam slow leaf breakdown) may also be valid for tropical streams (but see Colegrave & Ruxton, 2018 for a discussion of the relevance of a sample size of one).

Our study provided evidence of multiple environmental alterations of stream damming, which have repercussions to physical structure of habitats, stream assemblages (both microbial and invertebrates), but also to ecosystem functioning. Such repercussions were mainly due to modifications in stream physic-chemical parameters (e.g., water temperature, water turbidity and water current) that may have reduced invertebrate taxa richness and impaired stream food webs (at least of invertebrate assemblages, i.e., proportion of each functional feeding group), and reduced carbon processing and the generation of smaller leaf particles. Although the ecological significance of our results, they should be considered with caution until a greater replication and broader-context studies are performed. Despite this limitation, this study provide an useful example of how a small dam could affect stream functioning, and it can be useful for future studies (i.e., identification of most relevant and sensible parameters) to identify spatial patterns of damming effects on lotic systems. Finally, our findings supported the use of microbial estimates (such as ATP and ergosterol content on decomposing material) and leaf breakdown (using the widely applied litter bag method) as useful tools and ecological indicators to inform or monitor stream health, especially by water public agencies and water managers in much less studied areas such as developing countries at the tropics.

Acknowledgments

We thank Limnology/Aquariparia lab team for fieldwork support and University of Brasília and Decanato de Pesquisa e Pós-Graduação (DPG) for financial grant to English review (Edital 01/2014). The study was supported by several national grants (CNPq / Chamada Pública MCTI / CNPq Nº 14 / 2013 – Universal Proc.: 471767 / 2013-1; CNPq / INPA – Proc. 480298 / 2008-4, CT-Hidro / Climatic Changes / Water Resources / CNPq Proc.403949 / 2013-0).

References

Abelho, M., 2005. Extraction and quantification of ATP as a measure of microbial biomass. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 223–229.

Abril, G., Parize, M., Pérez, M.A., Filizola, N., 2013. Wood decomposition in Amazonian hydropower reservoirs: An additional source of greenhouse gases. Journal of South American Earth Sciences 44, 104–107.

Bärlocher, F., 2005. Sporulation by aquatic hyphomycetes. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 185–188.

Bärlocher, F., Graça, M.A.S., 2005. Total Phenolics. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 97–100.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85 (7), 1771–1789.

Casas, J.J., Zamora-Muñoz, C., Archila, F., Alba-Tercedor, J., 2000. The effect of a headwater dam on the use of leaf bags by invertebrate communities. Regulated Rivers: Research & Management 16 (6), 577–591. https://doi.org/10.1002/1099-1646(200011/12)16:6<577::aid-rrr587>3.0.co;2-p.

Colegrave, N., Ruxton, G.D., 2018. Using Biological Insight and Pragmatism When Thinking about Pseudoreplication. Trends in Ecology & Evolution 33 (1), 28–35.

Couto, T.B., Olden, J., 2018. Global proliferation of small hydropower plants - science and policy. Frontiers in Ecology 16, 91–100.

Cummins, K.W., Merritt, R.W., Andrade, P.C.N., 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Studies on Neotropical Fauna and Environment 40 (1), 69–89. https://doi.org/10.1080/01650520400025720.

Fernandes, I., Uzun, B., Pascoal, C., Cássio, F., 2009. Responses of Aquatic Fungal Communities on Leaf Litter to Temperature-Change Events. International Review of Hydrobiology 94 (4), 410–418.

Fonseca, S.A., Bianchini Jr, J., Pimenta, C., Soares, C., Mangiavacchi, N., 2013. The flow velocity as driving force for decomposition of leaves and twigs. Hydrobiologia 703 (1), 59–67. https://doi.org/10.1007/s10750-012-1342-3.

Gessner, M.O., 2005a. Ergosterol as a measure of fungal biomass. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 189–195.

Gessner, M.O., 2005b. Proximate lignin and cellulose. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 115–120.

Gonçalves Jr, J.F., Graça, M.A.S., Callisto, M., 2007. Litter decomposition in a Cerrado savannah stream is retarded by leaf toughness, low dissolved nutrients and a low density of shredders. Freshwater Biology 52 (8), 1440–1451. https://doi.org/10.1111/j.1365-2427.2007.01769.x.

González, J.M., Mollá, S., Roblas, N., Descals, E., Moya, O., Casado, C., 2013. Small dams decrease leaf litter breakdown rates in Mediterranean mountain streams. Hydrobiologia 712 (1), 117–128.

Graça, M.A.S., 2001. The Role of Invertebrates on Leaf Litter Decomposition in Streams – a Review. International Review of Hydrobiology 86 (4-5), 383–393.

Graça, M.A.S., Zimmer, M., 2005. Leaf toughness. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition: A Practical Guide. Springer, Netherlands, pp. 121–125.

Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., Nilsson, C., Robertson, J.C., Rödel, R., Sindorf, N., Wisseret, D., 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. Frontier in Ecology and Environment 9, 494–502.

Martinez, A., Larranaga, A., Basaguren, A., Perez, J., Mendoza-Lera, C., Pozo, J., 2013. Stream regulation by small dams affects benthic macroinvertebrate communities: from structural changes to functional implications. Hydrobiologia 711 (1), 31–42. https://doi.org/10.1007/s10750-013-1459-z.

Mbaka, J.G., Mwaniki, M.W., 2016. A critical review of the effect of water storage reservoirs on organic matter decomposition in rivers. Environmental Reviews 1–6. https://doi.org/10.1139/er-2016-0041.

McManamay, R.A., Oigbokie, C.O., Kao, S.-C., Bevelhimer, M.S., 2016. Classification of US hydropower dams by their modes of operation. River Research and Applications 22, 1–19.

Mendoza-Lera, C., Larrañaga, A., Pérez, J., Descals, E., Martínez, A., Moya, O., Arostegui, I., Pozo, J., 2012. Headwater reservoirs weaken terrestrialñaquatic linkage by slowing leafñlitter processing in downstream. regulated reaches River Research and Applications 28 (1), 13–22.

Merrit, R.W., Cummins, K.W., 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque.

Molozzi, J., França, J.S., Araujo, T.L., Viana, T.H., Hughes, R., Callisto, M., 2011. Diversidade de habitats físicos e sua relação com macroinvertebrados bentônicos em reservatórios urbanos em Minas Gerais. Iheringia Série Zoologia 101, 191–199.

Moulton, T., Magalhães, S., 2003. Responses of leaf processing to impacts in streams in Atlantic rain Forest, Rio de Janeiro, Brazil-a test of the biodiversity-ecosystem functioning relationship? Brazilian Journal of Biology 63 (1), 87–95.

Muehlbauer, J.D., LeRoy, C.J., Lovett, J.M., Flaccus, K.K., Vlieg, J.K., Marks, J.C., 2009. Short-term responses of decomposers to flow restoration in Fossil Creek, Arizona, USA. Hydrobiologia 618 (1), 35–45.

Mugnai, R., Nessimian, J.L., Baptista, D.F., 2010. Manual de identificação de Macroinvertebrados aquáticos do Estado do Rio de Janeiro. Techinal Books, Rio de Janeiro.

Nelson, S.M., Roline, R.A., 2000. Leaf litter breakdown in a mountain stream impacted by a hypolimnetic release reservoir. Journal of Freshwater Ecology 15 (4), 479–490.

Neres-Lima, V., Machado-Silva, F., Baptista, D.F., Oliveira, R., Andrade, P.M., Oliveira, A.F., Sasada-Sato, C.Y., Silva-Junior, E.F., Feijó-Lima, R., Angelini, R., Camargo, P.B., Moulton, T., 2017. Allochthonous and autochthonous carbon flows in food webs of tropical forest streams. Freshwater Biology 62 (6), 1012–1023.

Nilsson, C., Berggren, K., 2000. Alterations of Riparian Ecosystems Caused by River Regulation: Dam operations have caused global-scale ecological changes in riparian ecosystems. AIBS Bulletin 50 (9), 783–792.

Pascoal, C., Cássio, F., Marcotegui, A., Sanz, B., Gomes, P., 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. Journal of the North American Benthological Society 24 (4), 784–797. https://doi.org/10.1899/05-010.1.

Pes, A.M.O., Hamada, N., Nessimian, J.L., 2005. Chaves de identificação de larvas para famílias e gêneros de Trichoptera (Insecta) da Amazônia Central. Brasil. Revista Brasileira de Entomologia 49, 181–204.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., Maintainer, R., 2017. Package 'nlme'. Linear and nonlinear mixed effects models. 3-1. .

Poff, N.L., Hart, D.D., 2002. How Dams Vary and Why It Matters for the Emerging Science of Dam Removal. BioScience 52 (8), 659–668.

Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences 104 (14), 5732–5737.

Pringle, C.M., Freeman, M.C., Freeman, B.J., 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical–temperate comparisons. BioScience 50 (9), 807–823.

Quintão, J.M.B., Rezende, R.S., Gonçalves, J.F.Jr, 2013. Microbial effects in leaf breakdown in tropical reservoirs of different trophic status. Freshwater Science 32 (3), 933–950.

R Core Team, 2017. R: A language and Environment for Statistical Computing. version 3.4.2 URL. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Short, R.A., Ward, J.V., 1980. Leaf litter processing in a regulated Rocky Mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 37 (1), 123–127.

Solé, M., Fetzer, I., Wennrich, R., Sridhar, K., Harms, H., Krauss, G., 2008. Aquatic hyphomycete communities as potential bioindicators for assessing anthropogenic stress. Science of the Total Environment 389 (2), 557–565.

Suguio, K., 1973. Introdução à sedimentologia.

Tonin, A.M., Hepp, L.U., Restello, R.M., Gonçalves Jr, J.F., 2014. Understanding of colonization and brekdown of leaves by invertebrates in a tropical stream is enhanced by using biomass as weel as count data. Hydrobiologia 740 (1), 79–88. https://doi.org/10.1007/s10750-014-1939-9.

Tonin, A.M., Gonçalves, J.F., Bambi, P., Couceiro, S.R., Feitoza, L.A., Fontana, L.E., et al., 2017. Plant litter dynamics in the forest-stream interface: precipitation is a major control across tropical biomes. Scientific Reports 7 (1), 10799.

Tonin, A.M., Hepp, L.U., Gonçalves, J.F.Jr., 2018. Spatial variability of plant litter decomposition in stream networks: from litter bags to watersheds. Ecosystems 21 (3), 567–581.

Verdonschot, P.F., 2001. Hydrology and substrates: determinants of oligochaete distribution in lowland streams. Hydrobiologia 463 (1-3), 249–262.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effect Models and Extensions in Ecology With R. Springer-Verlag, New York, NY, USA.