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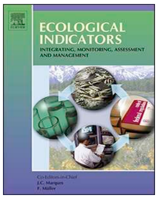

Assessing biological diversity and thermodynamic indicators in the dam decommissioning process

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ABSTRACT

Water level regulation is one of the most common anthropogenic disturbances of lentic ecosystems, which is especially evident in shallow lakes. The objective of this study was to assess the ecological effects of water level regulation in a shallow lake using thermodynamic indicators to support decision makers in a dam decommissioning process. For that we tested three hypotheses: 1) the regulated lake supports lower taxonomic diversity than the naturally fluctuating lake; 2) the structure of the benthic macroinvertebrate assemblage is different in the regulated lake than in the naturally fluctuating lake; 3) the regulated lake supports less complex benthic macroinvertebrate assemblages than the naturally fluctuating lake. Our results show that the first hypothesis, tested using taxa richness, Shannon-Wiener and Simpson diversity indices, was not validated. The second hypothesis was tested using taxonomic composition and was validated, with the two types of lakes exhibiting dissimilar macroinvertebrate assemblages. The third hypothesis, tested using two thermodynamic based indicators, eco-exergy and specific eco-exergy, was partially supported, which was illustrated, overall, by higher eco-exergy (degree of complexity) of the benthic assemblages in the naturally fluctuating lake, although the specific eco-exergies (capacities to use external energy resources) were similar. As a whole, our results endorse the importance of natural water level fluctuations as a driving force in shallow lake ecosystems and reinforced the idea that dam decommissioning is a good option for restoring natural conditions in this type of ecosystem.

1. Introduction

Water level fluctuation is an essential factor in structuring lentic ecosystems (Wantzen et al., 2008). This process can enhance the production of a lake, carrying nutrients from rivers or surrounding terrestrial ecosystems, leading to accumulation and resuspension of nutrient-rich organic matter (Gownaris et al., 2018). This is especially true for floodplain lakes, the smaller ones of which are often called lagoons or alcoves. Lake water level fluctuation patterns depend on many natural factors, such as frequency and intensity of precipitation, floodplain topography, and evaporation rates (Kutyła, 2015), as well as human uses.

Water level regulation, typically involving the construction of dams, is one of the most common anthropogenic disturbances of lentic and lotic ecosystems (e.g., Bednarek, 2001; Poff et al., 1997; Stanford and Ward, 2001). Extreme drawdowns of reservoirs and lakes, including those from climate change, may be indicators of anthropogenic disturbance (USEPA, 2016). The impacts of water level regulation are especially evident in shallow lakes, in which even small variations in the water level can cause significant shifts in nutrient loads, water quality and physical habitat condition (Terborgh et al., 2018). Such changes often result in altered species composition, community structure, and energy flow, which are highly complex and difficult to predict (Cott et al., 2008). Most studies focusing on the effects of changes in patterns of water level fluctuation focus on aquatic macrophytes (e.g., Agostinho et al., 2004; Brundu, 2015; dos Santos and Thomaz, 2007; Fleming and Dibble, 2015) and plankton assemblages (e.g., Agostinho et al., 2009; da Motta Marques et al., 2019; Fantin-Cruz et al., 2011), while the effects on other taxa, such as benthic macroinvertebrates, have been relatively unexplored, particularly in tropical lakes (but see Ruocco et al., 2018; Klein et al., 2018).

Benthic macroinvertebrates are among the most ubiquitous and diverse taxa in freshwater ecosystems and are widely used as bioindicators because of their ability to rapidly respond to changes in their environments (Cummins et al., 2005; Macedo et al., 2016; Merritt et al.,

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2008; Morais et al., 2016). Assessments of structural characteristics of benthic macroinvertebrate assemblages can provide insights into ecosystem functioning (Azevêdo et al., 2015; Linares et al., 2018a).

Both eco-exergy and specific eco-exergy have been used as ecological indicators in recent decades (Marques et al., 2003; Veríssimo et al., 2016; Xu et al., 1999). Eco-exergy has been widely and successfully used in assessments of estuaries (Marques et al., 1997; Veríssimo et al., 2016), rivers (Linares et al., 2018a), streams (Linares et al., 2018b; Nguyen et al., 2014), lakes (Marchi et al., 2012; Zhang et al., 2003) and reservoirs (Linares et al., 2017; Molozzi et al., 2013).

Eco-exergy is an estimation of both the assemblage biomass in an ecosystem and the genetic information embedded in that biomass (Jørgensen and Marques, 2001). Thus, it constitutes a proxy of ecosystem complexity and stability (Li et al., 2016; Linares et al., 2017; Xu et al., 1999). On the other hand, specific eco-exergy is defined as the total eco-exergy divided by the total assemblage biomass, which is an estimate of the potential of an assemblage to use the energy and materials available to it, independently of its biomass (Jørgensen, 2007; Jørgensen et al., 1995; Susani et al., 2006). Eco-exergy and specific eco-exergy have been used as complementary ecological indicators to assess ecosystem state and complexity, expressing shifts in species composition and trophic structure (Linares et al., 2018a; Marques et al., 2003; Molozzi et al., 2013). Assemblages with high values of both indicators are presumed to have greater biological diversity, functional redundancy, stability and resilience, which are characteristics of more complex ecosystems (Salas et al., 2005). Thus, a disturbed ecosystem is expected to exhibit lower eco-exergy and specific eco-exergy when compared to an undisturbed ecosystem (Jørgensen, 2007).

This study is part of a large joint scientific assessment of the ecological effects of a run-of-river dam in the Pandeiros River Basin, in Brazil. That assessment aims to develop ecological assessment methodologies to support decision making regarding a possible decommissioning of the Pandeiros Dam, which if realized will be the first in South America. Previous results (e.g. Linares et al., 2018a, 2019) are being discussed with members of the local community, state agencies, public prosecutor's office, river basin committee and Brazil's national hydropower regulation agency (ANEEL). These environmental stakeholders are defining the best sustainable options for decommissioning the Pandeiros Dam. This study will help close the gap of this management decision about rehabilitation of river natural flow using benthic thermodynamic indicators.

In this context, our objective was to provide additional ecological information to decision makers by assessing the ecological condition of a regulated lake using thermodynamic oriented indicators applied to the benthic assemblages. We compared the structure and composition of the benthic macroinvertebrate assemblages from a regulated lake and a naturally fluctuating one, downstream of the run-of-river hydropower reservoir. Three hypotheses were tested. 1) The regulated lake supports lower assemblage diversity than the naturally fluctuating lake, thus predicting that the regulated lake would display lower taxa richness and lower Shannon-Wiener and Simpson index scores than the naturally fluctuating lake. 2) The structure of benthic macroinvertebrate assemblages is different in the regulated lake than in the naturally fluctuating lake, thus predicting that benthic macroinvertebrate assemblages in the two lakes would differ in taxonomic composition and functional feeding group abundances. 3) The regulated lake supports less complex benthic macroinvertebrate assemblages than the naturally fluctuating lake, thus predicting that the eco-exergy and specific eco-exergy of the benthic macroinvertebrate assemblage would be lower in the regulated lake than in the naturally fluctuating lake.

2. Material and methods

2.1. Study area

This study was conducted in marginal lakes of the Pandeiros River Basin, Minas Gerais state, Brazil. The Pandeiros River is an important left bank tributary of the São Francisco River, with an approximate length of 145 km. An Area of Environmental Protection (AEP) with almost 4000 km^2, the largest unit for sustainable use in Minas Gerais state, covers the entire Pandeiros River Basin in the municipalities of Januária, Bonito de Minas, and Cônego Marinho (Lopes et al., 2010). The Pandeiros River Basin floodplains are among the top priority areas for conservation in the neotropical savanna, considered by Minas Gerais state law to be of "Special Biological Importance" because of their unique nature regarding its state and high biodiversity (Drummond et al., 2005). The AEP-Pandeiros was created to protect the Pandeiros wetlands and the biological diversity in the surrounding area, which are considered the nursery of most migratory fish species of the São Francisco River Basin (Santos et al., 2015). The Pandeiros hydropower dam was installed in 1957, and its reservoir covers 280 ha, with a free-crest dam height of 10.3 m (Fonseca et al., 2008). The powerhouse was deactivated in 2007 and since then, all economic activities of the dam and reservoir have ceased.

Multidisciplinary teams have been studying the Pandeiros River Basin, with a special focus on the prospect of a future dam decommissioning project (Linares et al., 2018a, 2019). A strategic site for the decommissioning process is a single marginal shallow lake (P1; Fig. 1) linked to the reservoir by a series of channels. This lake has an area of 14.93 ha and a maximum depth of 2 m. Because of the presence of the reservoir, its water level fluctuation is regulated, varying less than 30 cm between dry and wet seasons and constituting a unique environment in the Pandeiros River Basin. Recovery of its natural fluctuation regime and its proximity to human populations make this lake a strategic target for ecological assessment prior to dam decommissioning.

To assess the effects of water level regulation on benthic macroinvertebrate assemblages we compared the unique regulated lake with another marginal lake in the Pandeiros River floodplain (P2; Fig. 1), located 35 km downriver and not influenced by the dam (Linares et al., 2018a,b; Linares et al., 2019). This other lake has natural water level fluctuations typical of non-regulated shallow lakes in the region, with a variation of more than 1 m between dry and wet seasons (Drummond et al., 2005). This lake has an area of 13.25 ha and a maximum depth of 2 m. Due to the constrains of the Pandeiros dam project, our team was only able to sample one naturally fluctuating lake, which therefore limits our capacity for generalization based on these results.

In order to characterize the habitat of the sampled lakes, physical and chemical variables of the water column were measured (Table 1). At each lake water temperature, turbidity, pH, conductivity and total dissolved solids (TDS) were measured in situ by a portable multiprobe model YSI 6600. Water samples were taken to measure in laboratory the water contents of phosphate, total nitrogen, nitrate and nitrites.

2.2. Benthic macroinvertebrate sampling and processing

We sampled the macroinvertebrate assemblages in both lakes six times, covering both the dry (September 2015, April 2016, June 2016) and the rainy (December 2015, January 2016, February 2016) seasons. Each time, at each lake, we sampled a single 15 m transect, randomly selected along the margin, with the point of entrance randomly selected through satellite images. The transects were oriented from the margin to the center of the lakes, and we sampled the same transects each visit. Four kick net sub-samples, 5 m apart from each other, were collected along the transect through use of a D-net (30 cm opening, 500 µm mesh) in an area of 0.09 m^2. The sub-samples were combined into a single sample in the data analysis, representing a total area of 0.36 m^2 per site visit. Organisms collected from each sub-sample were stored in plastic bags, fixed in 10% formalin, and later washed in the laboratory, through a sieve with 500 µm mesh size.

We sorted and identified all macroinvertebrates specimens under a stereomicroscope using appropriate taxonomic keys (Hamada et al., 2014; Merritt and Cummins, 1996; Mugnai et al., 2010). Non-native

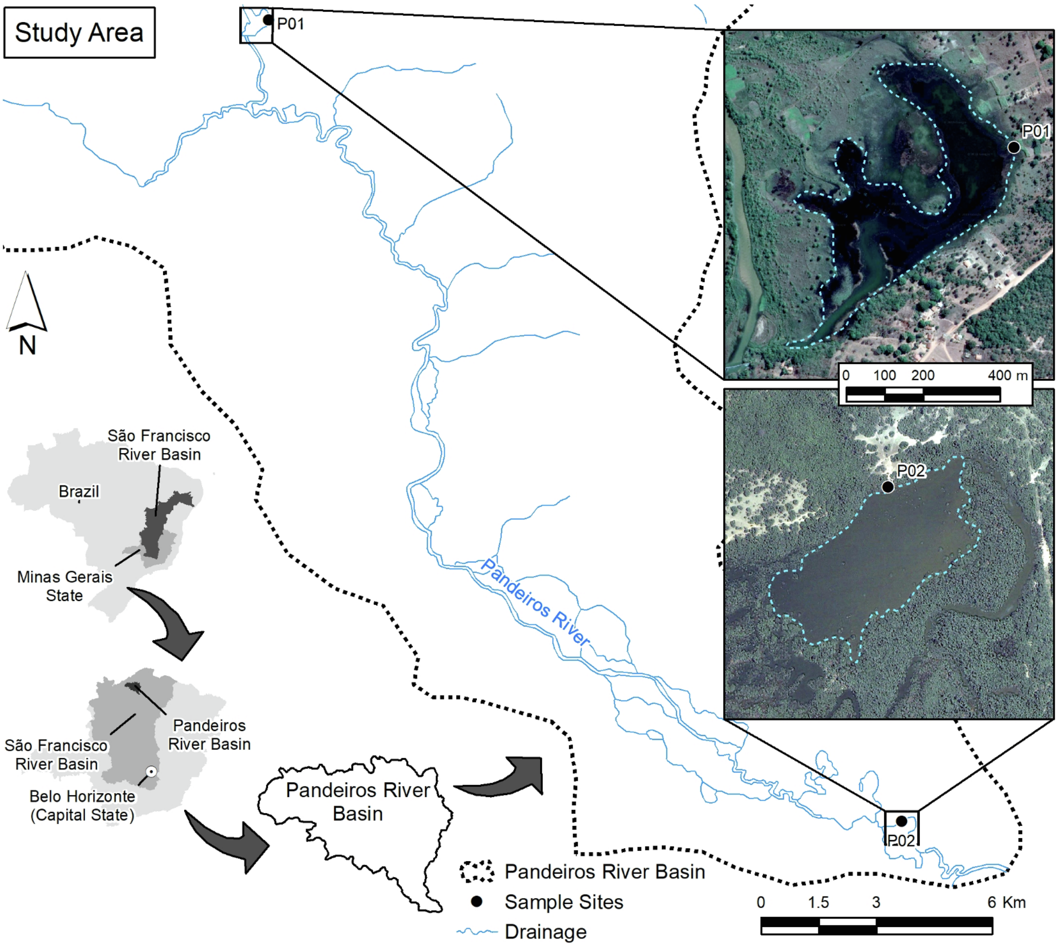

Fig. 1. Locations of the Pandeiros River Basin, Pandeiros PCH and the sampling sites, the regulated lake (P1) and the non-regulated lake (P2).

Table 1
Physio-chemical variables of the studied lakes.

Variable	P1		P2	
	Mean	Standard Deviation	Mean	Standard Deviation
Water Temperature	25.83	4.06	25.29	2.45
pH	7.32	0.36	6.85	0.32
Conductivity	71.15	6.03	94.05	14.93
Total Dissolved Solids	35.47	22.14	34.55	4.97
Turbidity	2.34	1.35	15.05	21.99
Dissolved Oxygen	5.65	1.37	5.70	2.25
Alcalinity	588.68	164.36	615.62	50.82
Total Nitrogen	0.07	0.02	0.07	0.02
Total Phosphorus	9.12	5.13	12.99	5.58
Orthophosphate	4.97	2.30	6.04	3.08
Nitrates	0.01	0.01	0.01	0.01
Nitrites	0.06	0.02	0.07	0.04

invasive *Melanoides tuberculata* (Thiaridae, Gastropoda) individuals were identified to species level. The other taxa were identified to family (Insecta), class (Bivalvia) or subclass (Annelida), a taxonomic resolution that saves labour time without compromising the performance of the indices used (Silva et al., 2017; Whittier and Van Sickle, 2010). Additionally, the macroinvertebrate taxa were classified into functional feeding groups (gathering-collectors, filtering-collectors, shredders, scrapers, or predators) following specialized literature (Cummins et al., 2005; Ramirez and Guitiérrez, 2014; Tomanova et al., 2006). Specimens were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil.

2.3. *Biomass estimation*

Dry-mass biomass (g/m^2) was estimated for each sampling site visit through use of length-weight equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). Each specimen of each taxon, up to 100, was photographed in a stereomicroscope (model Leica M80) equipped with a digital camera (model Leica IC 80 HD). Each photographed specimen's length was measured using Motic Image Plus 2.0 software.

2.4. *Eco-exergy calculation*

Eco-exergy was calculated using the following equation (Jørgensen et al., 2010):

$$EX = \sum_{i}^{i=0} \beta i c i$$

where $\boldsymbol{\beta i}$ is a weighting factor based on the genetic information contained in the macroinvertebrate taxa (i). It was defined by Jørgensen et al. (2005) based on the number of codifying genes of each taxon (Table 2). The factor **ci** is biomass of each macroinvertebrate taxon.

Specific eco-exergy is given by the following equation:

$$SpEX = \frac{EX}{BM}$$

where ***EX*** was the assemblage total eco-exergy and ***BM*** was the assemblage total biomass.

Table 2
Exergy weighting factors for benthic macroinvertebrate assemblages, based on Jørgensen et al. (2005).

Organisms	Energy Conversion Factor (β)
Virus	1.01
Bacteria	8.5
Algae	20
Yeast	17.4
Cnidaria	91
Platyhelminthes	120
Gastropoda	312
Bivalvia	297
Crustacea	232
Coleoptera	156
Diptera	184
Hymenoptera	267
Lepidoptera	221
Other Insecta	167
Fish	499

2.5. *Data analysis*

To test for temporal differences in macroinvertebrate structure and composition among sites, we ran a preliminary test using a Generalized Linear Model (GLM) for all tested indices (taxa richness, Shannon-Wiener, Simpson diversity, eco-exergy and specific eco-exergy), and then tested model significance with an analysis of deviance. Because these tests failed to detect significant temporal differences, we pooled all six samples for each lake in our subsequent procedures.

To test if the regulated lake supported lower diversity than the naturally fluctuating one, we estimated taxa richness, Shannon-Wiener and Simpson diversity indices for both lakes. We then tested the difference between the values of these indices calculated for both lakes, using a Generalized Linear Model (GLM) with a Poisson error structure for richness and a Gaussian error structure for the other indices. The model significance was tested by an Analysis of Deviance (chi-squared and F test, respectively).

PERMANOVA (1000 permutations) was used to test if differences in the structure of benthic macroinvertebrate assemblages between the two lakes were significant. Moreover, differences in proportion of the five functional feeding groups (gathering-collectors, filtering-collectors, shredders, scrapers, and predators) between the two lakes were tested using a General Linear Model (GLM) with a quasibinomial error structure. The model's significance was tested by an Analysis of Deviance (F test).

Finally, to evaluate if macroinvertebrate assemblages are less complex in the regulated lake than in the naturally fluctuating one, we used a Generalized Linear Model (GLM) with a Gaussian error structure to test the significance of differences in the values of eco-exergy and specific eco-exergy calculated for each lake. Model significance was tested by an Analysis of Deviance (F test).

3. Results

We collected a total of 3460 benthic macroinvertebrates and 44 taxa. Regarding diversity, none of the indices tested (taxa richness, Shannon-Wiener diversity index or Simpson diversity index) showed significant differences between the two lakes, however richness was consistently higher in the unregulated lake. (Fig. 2). Regarding assemblage structure, PERMANOVA results ($F_{11} = 3.6986$, $p = 0.01898$) indicated that taxonomic composition was significantly different between the two lakes, as were the proportions of gathering-collectors, filtering-collectors and scrapers (Fig. 3). In fact, gathering-collectors were significantly more abundant ($F_{11} = 14.683$, $p = 0.003309$) in the regulated lake, whereas filtering-collectors ($F_{11} = 6.1654$, $p = 0.03237$) and scrapers ($F_{11} = 32.173$, $p = 0.0002061$) were predominant in the naturally fluctuating one. Shredders ($F_{11} = 0.17669$, $p = 0.1541$) and predators ($F_{11} = 0.2914$, $p = 0.6012$) did not exhibit significant differences in abundance between the two lakes. Regarding thermodynamic indicators, the benthic macroinvertebrate assemblages had significantly higher eco-exergy values in the naturally fluctuating lake ($F_{11} = 7.0621$, $p = 0.024$) (Fig. 4), but we found no significant difference in specific eco-exergy ($F_{11} = 0.3606$, $p = 0.5619$).

4. Discussion

Our three hypotheses were only partially supported. Our first hypothesis, that regulated lakes support lower diversity than fluctuating lakes, was not supported. Our second hypothesis, that assemblage structure would differ between the two lakes, was confirmed. Finally, our third hypothesis that regulated lakes support less complex benthic

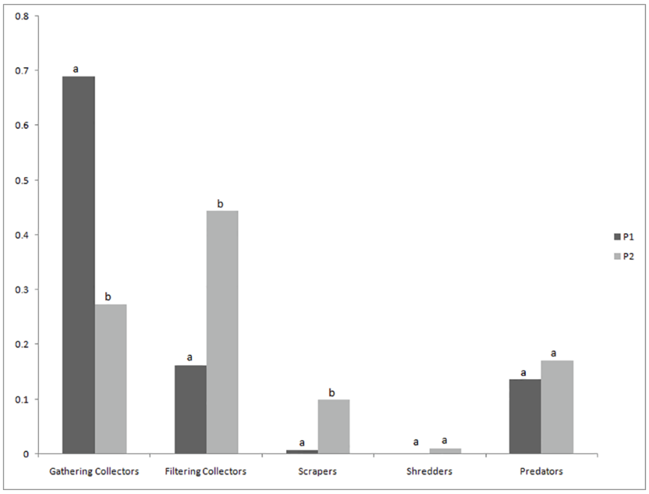

Fig. 3. Functional feeding group relative abundance at the sampled marginal lakes, the regulated lake (P1) and the non-regulated lake (P2). Same letters indicate lack of significant difference.

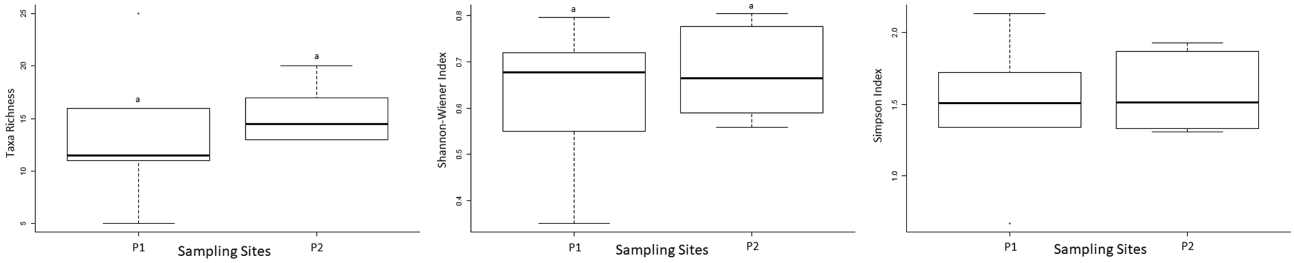

Fig. 2. Taxonomic richness, Shannon-Wiener diversity index and Simpson diversity index at the sampled marginal lakes, the regulated lake (P1) and the non-regulated lake (P2). Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; circles = outliers calculated from six site visits. Same letters indicate lack of significant difference.

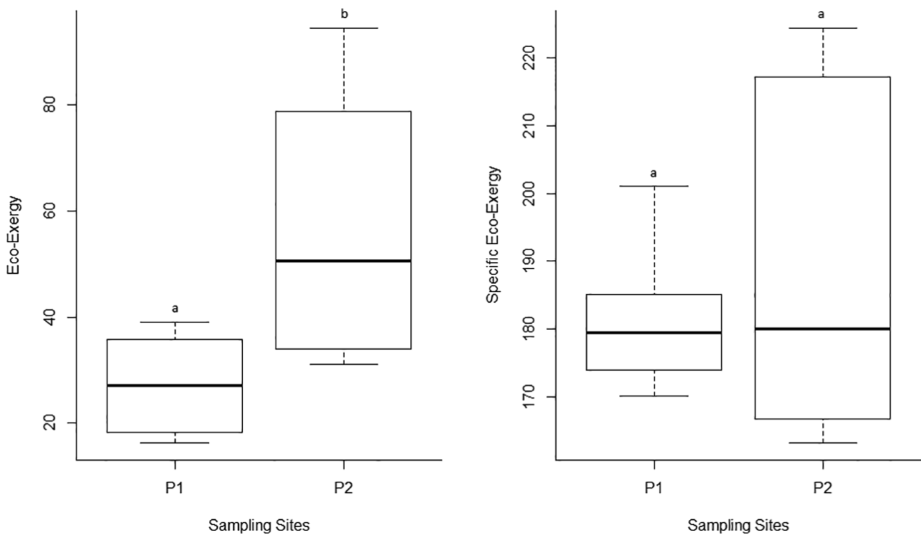

Fig. 4. Eco-exergy and specific eco-exergy at the sampled marginal lakes, the regulated lake (P1) and the non-regulated lake (P2). Bold horizontal lines = medians; boxes = 25th and 75th percentiles; vertical lines = ranges; circles = outliers calculated from six site visits. Same letters indicate lack of significant difference.

macroinvertebrate assemblages than naturally fluctuating ones, was supported by eco-exergy, but not specific eco-exergy.

Differences in taxonomic composition illustrate the ecological conditions to which the lakes are exposed. Gathering-collector taxa, such as oligochaetes and chironomid larvae, were the dominant group in the regulated lake, suggesting that the benthic macroinvertebrate assemblages depend largely on organic matter deposited in the sediment. This can be explained by the lack of natural disturbances resulting from water level fluctuations, which much more likely allows the accumulation of fine particulate organic matter in the sediment, leaving it available to burrowing benthic taxa (White et al., 2010). In the naturally fluctuating lake, on the other hand, benthic macroinvertebrate assemblages were dominated by filtering-collectors and also included a significantly higher abundance of scrapers, which suggests that water level fluctuations play an important role in the organic matter re-suspension and resultant availability for consumers (Cott et al., 2008; Gownaris et al., 2018; Magbanua et al., 2015).

The fact that benthic macroinvertebrate assemblages had higher eco-exergy in the naturally fluctuating lake can also be explained by the higher level of available energetic resources represented by re-suspended organic matter, resulting in a higher overall degree of complexity, stability and development of the macroinvertebrate assemblage (Jørgensen, 2007; Jørgensen and Fath, 2004; Ludovisi and Jørgensen, 2009). Comparable situations have been observed in systems with non-excessive nutrient enrichment and other forms of higher energy input, including headwater streams (Linares et al., 2018b), estuaries (Marques et al., 1997) and hydropower reservoirs (Molozzi et al., 2013).

The fact that the benthic macroinvertebrate assemblages did not show significant differences in specific eco-exergy can be explained by the predominance, in both lakes, of predator taxa such as Odonata nymphs and Belostomatidae (Heteroptera), typical in lentic ecosystems (Benke et al., 2001; Benke and Huryn, 2010; Cummins et al., 2005). The high relative abundance of predator taxa in both lakes smoothed the differences in the overall specific eco-exergy calculated, expressing therefore, in average, relatively alike capacities to use external energy resources and more or less similar complexities of the benthic macroinvertebrate assemblages in the two types of lakes.

As a whole, our results illustrate the importance of natural water level fluctuations as a driving force in shallow lake ecosystems, as previously observed (Agostinho et al., 2004; Thomaz et al., 2015; Wantzen et al., 2008). Regarding the perspective of a future dam decommissioning, we have shown that fluctuating water levels affect the structure and function of benthic macroinvertebrates in shallow lakes. In regulated lakes, benthic assemblages are dominated by taxa resistant to anthropogenic disturbances (*sensu* Macedo et al., 2016; Silva et al., 2017), exhibiting lower complexity and resilience (Liao et al., 2012; Zhang et al., 2010). It is assumed that dam decommissioning and subsequent return to natural water level fluctuations will shift macroinvertebrate assemblages, structurally and functionally, to characteristics similar to those occurring in a non-regulated lake in the same basin. Therefore, this reinforces the idea that dam decommissioning can probably be considered as a good option for restoring natural conditions in this type of basin, as has been argued by others (Bednarek, 2001; Dynesius and Nilsson, 1994; Van Looy et al., 2014).

Our results should be analyzed carefully. Due to the limitations of a two-site study, their capacity for inferences in larger scales is compromised. It does fit our objectives, however, by focusing in the regulated lake and the effects caused by the dam in this unique ecosystem.

5. Conclusions

Eco-exergy and functional groups were more sensitive to differences in lake-level fluctuation than taxonomic richness, diversity, or specific eco-exergy; therefore, we recommend their use in other bioassessments employing macroinvertebrates as lentic ecological indicators.

We recommend the elimination of Pandeiros dam, which will allow restoring natural water movements, organic matter dynamics, and energy flows in this ecosystem of special biological importance and unique for the conservation of freshwater biodiversity in the neotropics. If the Pandeiros Dam is removed, our study will be part of the first comprehensive BACI (before-after-control-impact) study of dam removal in South America; therefore, it will be important to track the multiple ecological changes after removal.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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