



# Compliance of secondary production and eco-exergy as indicators of benthic macroinvertebrates assemblages' response to canopy cover conditions in Neotropical headwater streams



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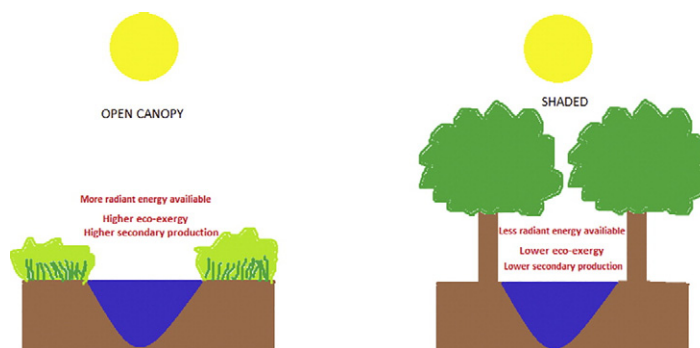
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## HIGHLIGHTS

- Benthic macroinvertebrate assemblages' diversity is not affected by canopy cover.
- Benthic macroinvertebrate assemblages to build a more complex structure in open canopy streams.
- Autochthonous production is the main energy source in Neotropical headwater streams.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Riparian vegetation cover influences benthic assemblages structure and functioning in headwater streams, as it regulates light availability and autochthonous primary production in these ecosystems. Secondary production, diversity, and exergy-based indicators were applied in capturing how riparian cover influences the structure and functioning of benthic macroinvertebrate assemblages in tropical headwater streams. Four hypotheses were tested: (1) open canopy will determine the occurrence of higher diversity in benthic macroinvertebrate assemblages; (2) streams with open canopy will exhibit more complex benthic macroinvertebrate communities (in terms of information embedded in the organisms' biomass); (3) in streams with open canopy benthic macroinvertebrate assemblages will be more efficient in using the available resources to build structure, which will be reflected by higher eco-exergy values; (4) benthic assemblages in streams with open canopy will exhibit more secondary productivity. We selected eight non-impacted headwater streams, four shaded and four with open canopy, all located in the Neotropical savannah (Cerrado) of southeastern Brazil. Open canopy streams consistently exhibited significantly higher eco-exergy and instant secondary production values, exemplifying that these streams may support more complex and productive benthic macroinvertebrate assemblages. Nevertheless, diversity indices and specific eco-exergy were not significantly different in shaded and open canopy streams. Since all the studied streams were selected for being considered as non-impacted, this suggests that the potential represented by more available food resources was not used to build a more complex dissipative structure. These

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results illustrate the role and importance of the canopy cover characteristics on the structure and functioning of benthic macroinvertebrate assemblages in tropical headwater streams, while autochthonous production appears to play a crucial role as food source for benthic macroinvertebrates. This study also highlights the possible application of thermodynamic based indicators as tools to guide environmental managers in developing and implementing policies in the neotropical savannah.

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## 1. Introduction

Riparian vegetation is considered one of the main factors influencing ecosystem structure and functioning in headwater streams (Clarke et al., 2008; Rezende et al., 2008, 2016). It controls radiant energy availability to stream ecosystems, thus limiting local primary production, while providing allochthonous detritus as an alternative energy source (Carroll et al., 2016; Death and Collier, 2009; Vannote et al., 1980).

Tropical streams, due to higher radiant energy availability and typically higher temperatures, usually possess lower dependence to allochthonous production as compared to the temperate climate ones (e.g., Boyero et al., 2016; Brito et al., 2006; Ferreira et al., 2014). However, most studies regarding the effects of light availability (e.g., Aguiar et al., 2015; Che Salmah et al., 2014; Masese et al., 2014) in tropical streams have focused on the impacts of anthropogenic land use, such as agriculture, pasture and deforestation, which are concomitant to the occurrence of more open canopies. Nevertheless, what is the structural and functional response of tropical headwater streams' communities under the influence of naturally open canopies is largely unknown.

To understand the structure and functioning of biological communities in natural headwater streams is essential, as these ecosystems may represent 80% of the channel length in a hydrographic basin, and are critical sites for organic matter processing, nutrient cycling and biodiversity (Clarke et al., 2008; Dodds and Oakes, 2008). While many taxa contribute to biodiversity in headwater streams, benthic macroinvertebrates are among the most ubiquitous and diverse and are widely used as bioindicators due to their ability to respond to changes in lotic environments (Bonada et al., 2006; Klemm et al., 2003; Macedo et al., 2016). Assessments of both structural characteristics and ecological processes of benthic macroinvertebrate assemblages are important to provide a better understanding on how the riparian vegetation can influence tropical headwater stream ecosystems' dynamics (Aguiar et al., 2015; Boyero et al., 2016; Clarke et al., 2008).

The structure of benthic macroinvertebrate assemblages is generally assessed through taxonomic based indicators, such as richness and diversity indices. Likewise, thermodynamic oriented indicators may provide additional information on ecosystems' self-organization capacity (Silow and Mokry, 2010). These indicators are rooted in physical concepts, providing an universal language to compare different organisms and systems (Ludovisi et al., 2005). Among thermodynamic oriented indicators, the exergy based have been widely and successfully used in different types of ecosystems in the last decades (e.g., Linares et al., 2017; Marques et al., 1997; Xu et al., 2001).

Exergy is a concept originated in physics, defined as the maximum quantity of work that can be obtained in a process that brings a system to thermodynamic equilibrium with its environment (Silow and Mokry, 2010). It represents the useful energy contained within a system and was adapted to ecology under the form of two indicators: eco-exergy and specific eco-exergy (Jørgensen, 2007a; Jørgensen and Fath, 2004; Jørgensen and Mejer, 1977). Eco-exergy is assumed to express the complexity of an ecological system and provide information about its stability (Li et al., 2016; Marques et al., 1997, 2003; Xu et al., 1999). Specific eco-exergy is defined as the total eco-exergy divided by the total biomass, which is assumed to take into account how well it uses the available resources, independently from the amount of resources, measuring the ability of the ecosystem to use external energy flows and

reflecting the degree of complexity and development of the system (Molozzi et al., 2013; Patrício et al., 2009; Patrício and Marques, 2006; Silow and Mokry, 2010).

Structural variable assessments, however, may not always properly indicate changes in ecosystem functioning (Benke, 1993; Benke et al., 2001). Differences in habitat are often reflected in important ecosystem processes, such as organic matter composition, ecosystem metabolism and secondary production (Rezende et al., 2016). Secondary production is the rate of formation of heterotrophic biomass in a population or community, representing an estimative of the energy flows through these systems (Dolbeth et al., 2012; Frauendorf et al., 2013). Assessments of secondary production can provide important information about the energy flow through the ecosystem (Benke and Wallace, 2015). As it combines compositional information with process information, secondary production is a measure of the overall evolutive success of a biological assemblage (Aguiar et al., 2015). It also indicates changes in ecosystem carbon and energy fluxes and nutrient cycling (Benke, 2010; Brabender et al., 2016; Woodcock and Huryn, 2007). However, secondary production is difficult to estimate for natural assemblages, as it requires data about population growth and mortality, which means an intense effort of field sampling (Dolbeth et al., 2012). For these reasons empirical models were developed in order to facilitate the estimation of secondary production, among them Instant Secondary Production (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989).

Our objective was to assess how riparian shading influences benthic macroinvertebrate assemblages' structure and functioning in Neotropical savannah headwater streams. For that we tested four hypotheses: (1) Open canopy will determine the occurrence of higher diversity in benthic macroinvertebrate assemblages, which will be expressed by higher values of diversity indices; (2) Streams with open canopy will exhibit more complex (in terms of the information embedded in the organisms biomass) benthic macroinvertebrate communities, which will be expressed by higher eco-exergy and specific eco-exergy values; (3) In streams with open canopy benthic macroinvertebrate assemblages will be more efficient in using the available resources to build structure, which will be reflected by higher eco-exergy values; (4) Benthic assemblages in streams with open canopy will exhibit more secondary productivity, which will be expressed by higher instant secondary production values. Regarding exergy based ecological indicators, it was intended to assess their performance in capturing natural ecologic conditions for environmental quality assessments in Neotropical streams.

## 2. Material and methods

### 2.1. Study area

Samples were taken in streams located along the Araguari river basin, located in the Neotropical savannah (Cerrado) in the Minas Gerais state, southeastern Brazil. The Araguari River Basin has an area of 21,856 km<sup>2</sup>, most of the regional geology is composed of shales and quartzites, and the headwaters are located in the plateaus of the Canastra Range, at an altitude of approximately 1440 m above sea level (Rodrigues and Souza, 2013). In this area three distinct geological regions are defined (Baptista et al., 2010): Phyllite region, dominated by the phyllite metamorphic type of the Rio Verde geological formation;

**Table 1**  
Study sites characterized by canopy cover (%).

Stream	Mean canopy cover ( $\pm$ SD)	Category
Parida	3.21 ( $\pm$ 7.60)	Open
Fundo I	6.55 ( $\pm$ 14.50)	Open
Fundo II	8.42 ( $\pm$ 10.44)	Open
Boa Vista II	0 ( $\pm$ 0)	Open
Jota	50.80 ( $\pm$ 44.95)	Shaded
Ramalhete	37.30 ( $\pm$ 37.12)	Shaded
Boa Vista I	39.57 ( $\pm$ 38.64)	Shaded
Dona Ana	46.66 ( $\pm$ 45.44)	Shaded

Shale region, dominated by micaschists, amphibolite, quartzite, gneiss, and banded iron formations; and the Canastra Group region, composed mostly of quartzites, as well as some phyllites and shales.

The streams were selected among potential sites based on the interpretation of a combination of fine resolution images (0.6–5 m spatial resolution; Google Earth images) with Landsat Thematic Mapper multispectral satellite images (Macedo et al., 2014), resulting in a total of 60 potential sites. Among these locations, eight streams were selected (Table 1) after reconnaissance verification of the following criteria: a) minimal anthropogenic disturbance at catchment scale; b) absence of direct influence of anthropogenic alterations at the sampling sites and c) presence of native riparian vegetation at the sampling sites. The eight selected sites were all located in the Canastra Group region (Fig. 1) to minimize the natural variability among them. Based on the canopy cover data, four streams were classified as open canopy and four classified as shaded (Table 1). In this methodology the percentage of canopy cover of each stream was estimated by six measurements using a densiometer (following Kaufmann et al., 1999 and Martins et al., 2017), two in each margin and two in the middle of

the stream, which explains the high standard deviations found (Table 1).

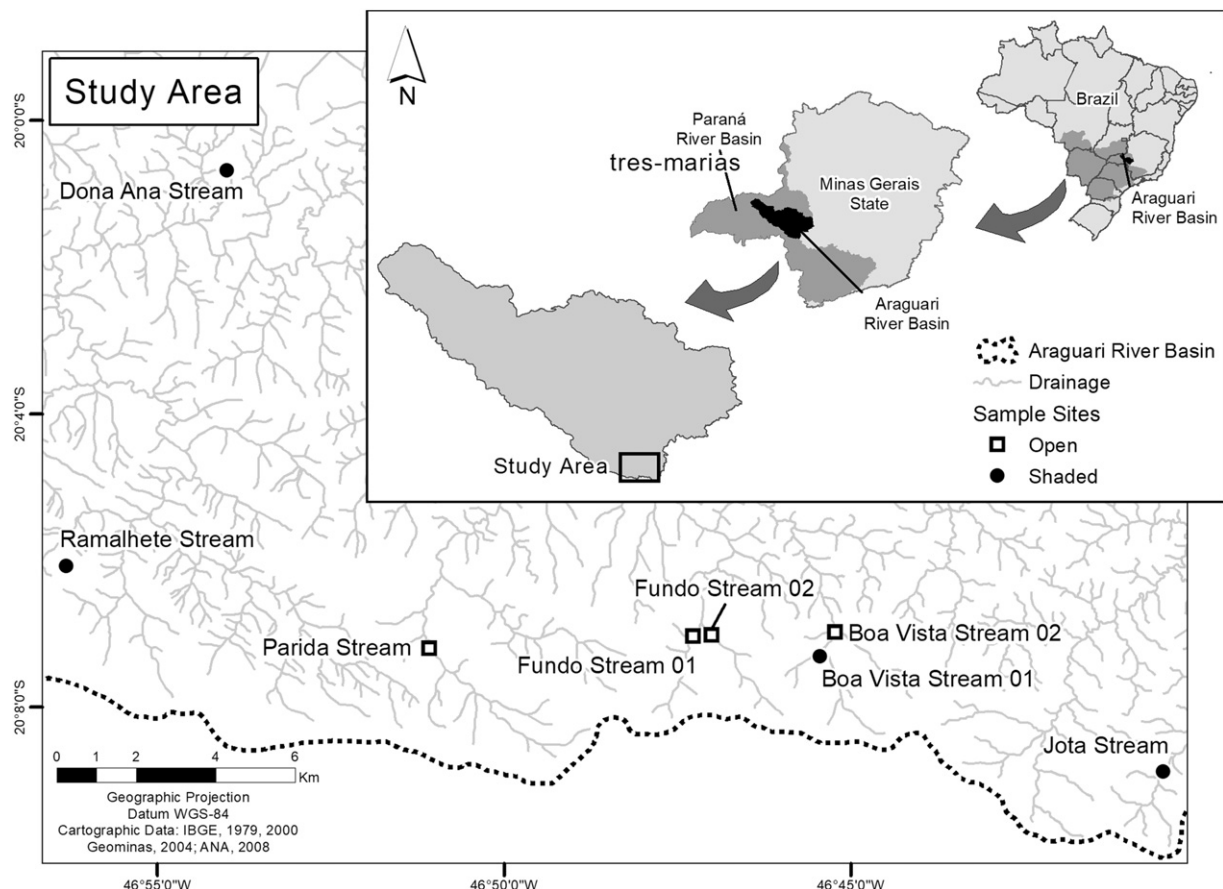
## 2.2. Benthic macroinvertebrate sampling

The macroinvertebrate communities were sampled in April and May of 2015, during the dry season. In each stream a 25 m stretch was divided into six equidistant transects. In each transect a kick-net sampler (30 cm opening, 500  $\mu$ m sieve) was used, resulting in six sub-samples in each stream for a total area of 0.54m<sup>2</sup> sampled. Organisms from each sub-sample were stored in plastic bags, fixed in 10% formalin, and then washed in a sieve (0.5 mm mesh) in laboratory.

Macroinvertebrates were identified under a stereomicroscope, using specialized literature (Hamada et al., 2014; Merritt and Cummins, 1996; Mugnai et al., 2010). The individuals of the insect orders Ephemeroptera, Plecoptera and Trichoptera (EPT) were identified to genus level. Other taxa were identified to family (other Insecta) or subclass (Anellida). The specimens were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

## 2.3. Diversity measures calculation

To test whether benthic macroinvertebrate assemblages present higher diversity in open canopy streams, the total number of taxa and the number of EPT genera were counted for each stream. Additionally, the Shannon-Wiener (Shannon, 1948) and the Simpson (Simpson, 1949) diversity indices were calculated for each stream.



**Fig. 1.** Location of sampling sites in the Araguari river basin.

Shannon–Wiener diversity index was computed as follows:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

where  $p_i$  is the proportion of the total of individuals belonging to the taxon  $i$ .

Simpson diversity index was computed as follows:

$$\lambda = \sum_{i=1}^R p_i^2$$

where  $p_i$  is the proportion of the total of individuals belonging to the taxon  $i$ .

#### 2.4. Biomass estimation

Dry-mass biomass was estimated for each sampling site. Biomass was estimated using length-mass equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). Each individual of each taxon, up to 100, were 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 the software Motic Image Plus 2.0. Using the length-mass equations (Supplementary Material 1) the dry-mass biomass ( $g/m^2$ ) of each sampled taxon was estimated.

#### 2.5. Calculation of exergy based indicators

To test if open canopy streams exhibit more complex benthic macroinvertebrate communities and more efficient in using the available resources to build structure, eco-exergy and specific eco-exergy values were calculated for each stream. Eco-exergy was computed as follows (Jørgensen et al., 2010):

$$EX = \sum_i^{i=0} \beta_i c_i$$

where  $\beta_i$  is a weighting factor based on the information contained in the components  $i$  of the ecosystem, defined by Jørgensen et al. (2005) and  $c_i$  is the concentration (biomass) of component  $i$  in the ecosystem.

Specific eco-exergy is given by:

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

where  $EX$  is the total eco-exergy and  $BM$  is the total biomass.

#### 2.6. Calculation of instant secondary production

To test if benthic assemblages in open canopy streams support higher secondary production, Instant Secondary Production ( $mg/m^2/day$ ) was calculated for each stream.

Instant Secondary Production (Morin, 1997) was calculated as follows:

$$IP = \sum D \cdot W \cdot GR$$

where  $D$  is the density of each taxon,  $W$  is the mean individual dry weight for each taxon and  $GR$  is the Instantaneous Growth Rate, estimated based on individual equations for each taxon found in the literature (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989).

#### 2.7. Data analysis

A Generalized Linear Model (GLM) with a Gaussian error structure was used to test if the total number of taxa and the number of EPT at each site, as well as the values of the Shannon–Wiener and Simpson diversity indices (hypothesis 1), eco-exergy and specific eco-exergy (hypotheses 2 and 3), and instant secondary production (hypothesis 4) were significantly different between open and shaded canopies. The model's significance was tested by an Analysis of Deviance (F test) (Kaur et al., 1996).

To verify if the canopy cover changes the taxonomic composition of associated benthic communities, data on abundance underwent a square root transformation, and then we used the Bray–Curtis distance to build the similarity matrix (Bray and Curtis, 1957). PERMANOVA (1000 permutations) was used to test if the benthic macroinvertebrate communities were significantly different under open canopy and shaded canopies.

All calculations were performed using R software, version 3.2.3 (R Core Team, 2015) and the vegan package (Oksanen et al., 2016).

### 3. Results

A total of 13,633 benthic macroinvertebrate specimens belonging to 72 taxa were sampled, of which 11,448 in open canopy streams and 2185 in shaded streams. The total number of taxa, the number of EPT taxa, as well as the values of the Shannon–Wiener and Simpson diversity indices were not significantly different between streams with open canopy and the shaded ones (Table 2). Nevertheless, results of PERMANOVA illustrated that the taxonomic composition was significantly different in the two situations ( $F_{1,7} = 3.8826$ ,  $p = 0.02398$ ), since although Chironomidae was the dominant taxon in both cases, its relative abundance was significantly higher (53.09%) in shaded streams, while under open canopies Simuliidae did also show high relative abundance (31.87%) (Fig. 2).

Eco-exergy was significantly higher in open canopy streams (GLM;  $F_{1,7} = 20.349$ ,  $p = 0.004056$ ), but specific eco-exergy values were not significantly different in the two situations (GLM;  $F_{1,7} = 5.9423$ ,  $p = 0.5063$ ) (Fig. 3). Finally, instant secondary production was also significantly higher in streams with open canopy (GLM;  $F_{1,7} = 9.8751$ ,  $p = 0.02001$ ) (Fig. 4).

### 4. Discussion

Our results illustrate that we could not sanction our first hypothesis, that open canopy streams would have higher diversity, since all the diversity measures tested failed in showing significant differences between open canopy and shaded streams. On the other hand, the second hypothesis, that streams with open canopy would have more complex macroinvertebrate assemblages, was only partially confirmed, since eco-exergy values were significantly higher in open canopy sites, but specific eco-exergy did not show significant differences. The third hypothesis, that macroinvertebrate assemblages would be more efficient in using the available resources to build structure in open canopy streams, was confirmed, since eco-exergy values were significantly higher in open canopy sites. Finally, the fourth hypothesis, that the

**Table 2**  
Mean ( $\pm$ SE) and GLM results of Number of Taxa, Number of EPT Taxa, Simpson diversity index and Shannon–Wiener diversity index for streams with Open and Shaded canopy.

	Mean ( $\pm$ SE)		GLM	
	Shaded	Open	F	p
Number of Taxa	22.5 ( $\pm$ 2.60)	29.0 ( $\pm$ 4.26)	1.6957	0.2406
Number of EPT Taxa	10.75 ( $\pm$ 2.95)	17.25 ( $\pm$ 2.01)	3.3029	0.119
Shannon–Wiener Index	1.590 ( $\pm$ 0.19)	1.558 ( $\pm$ 0.27)	0.0091	0.9273
Simpson Index	0.634 ( $\pm$ 0.07)	0.631 ( $\pm$ 0.09)	0.00004	0.9845

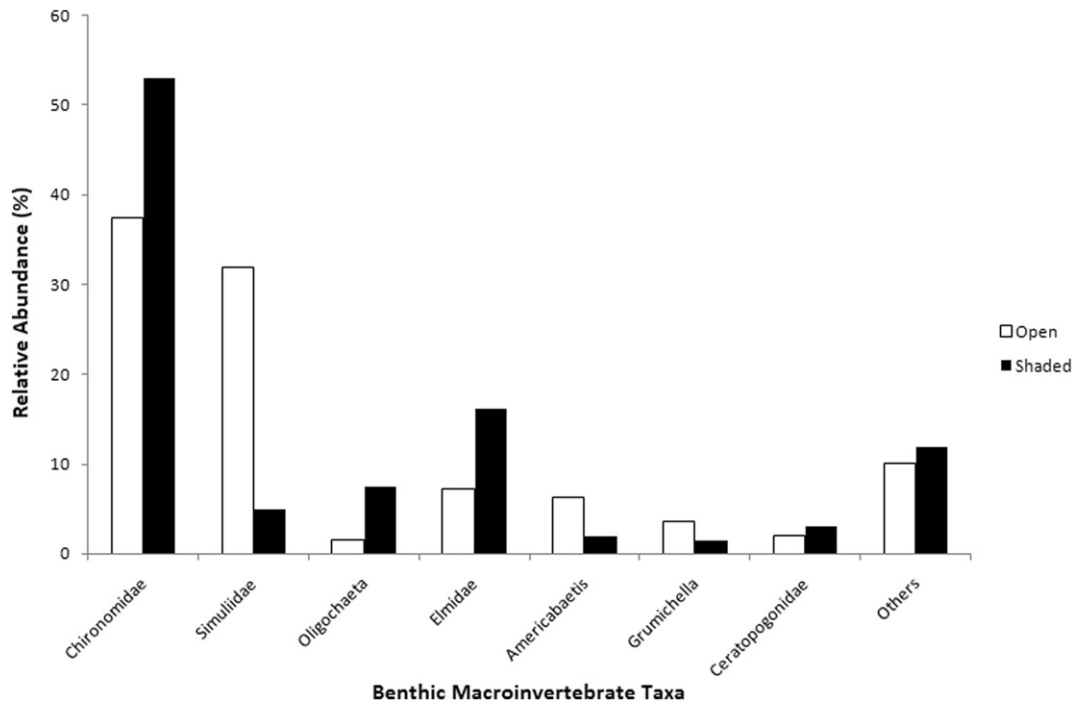


Fig. 2. Relative abundance of benthic macroinvertebrate assemblages for streams with Open and Shaded canopy.

secondary productivity of open macroinvertebrate assemblages would be higher in open canopy streams, was confirmed since the values of instant secondary production estimated were higher in open canopy sites.

The absence of significant differences regarding diversity measures between open and shaded streams can eventually be understood based on the fact that the sites selected were non-disturbed. In fact, although many studies in tropical streams reported higher benthic macroinvertebrate diversity in open canopy streams (e.g., Che Salmah et al., 2014; Masese et al., 2014; Md Rawi et al., 2013), which has driven to the establishment of our working hypothesis. Several other studies claim that in non-disturbed headwater streams the macroinvertebrate assemblages tend to exhibit similar biodiversity patterns, independently from the shading effects of the canopy (Ceneviva-Bastos and Casatti, 2014; Detry et al., 2016; Tonkin et al., 2013). The fact is that studies

that reported higher diversity in open canopy streams were in general carried out in streams where the canopy riparian vegetation was already anthropogenically altered, such as pastures and agriculture crops (Death and Zimmermann, 2005; Johnson et al., 2013; Zimmermann and Death, 2002), which explain differences in assemblages' diversity.

Higher eco-exergy values found in open canopy streams can be explained by the higher amount of radiant energy input available (Marchi et al., 2011; Rezende et al., 2008), resulting in an increased use of the available resources to build a more complex dissipative structure (Jørgensen, 2007a, 2007b; Jørgensen et al., 2007), corresponding to growth in the network and information (growth forms II and III – see Jørgensen et al., 2016), but most probably principally to biomass storage (growth form I – see Jørgensen et al., 2016). A similar response may, for

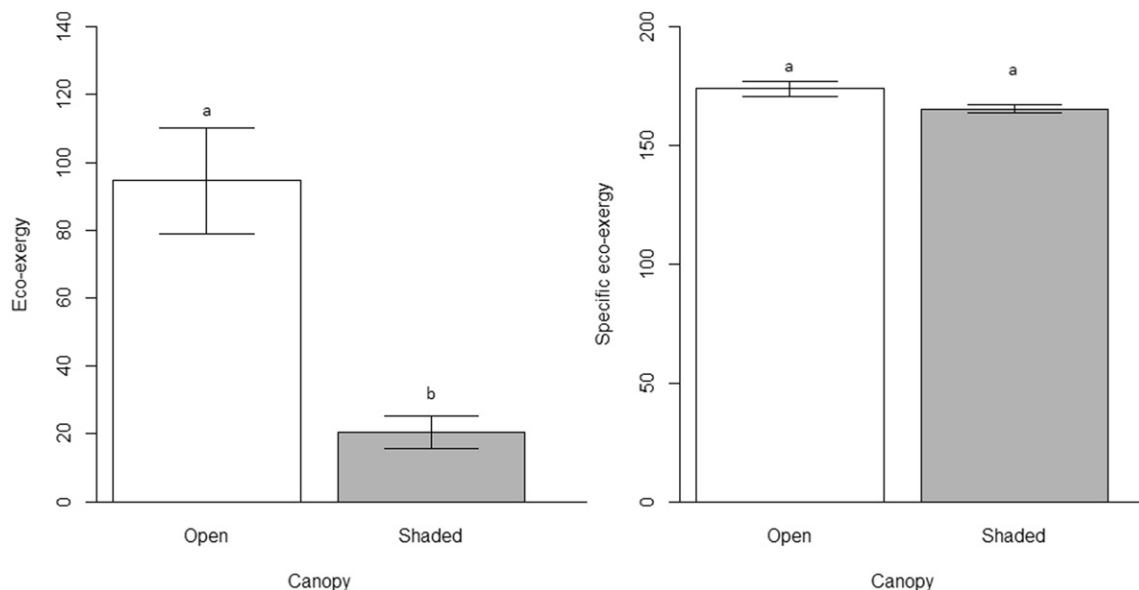
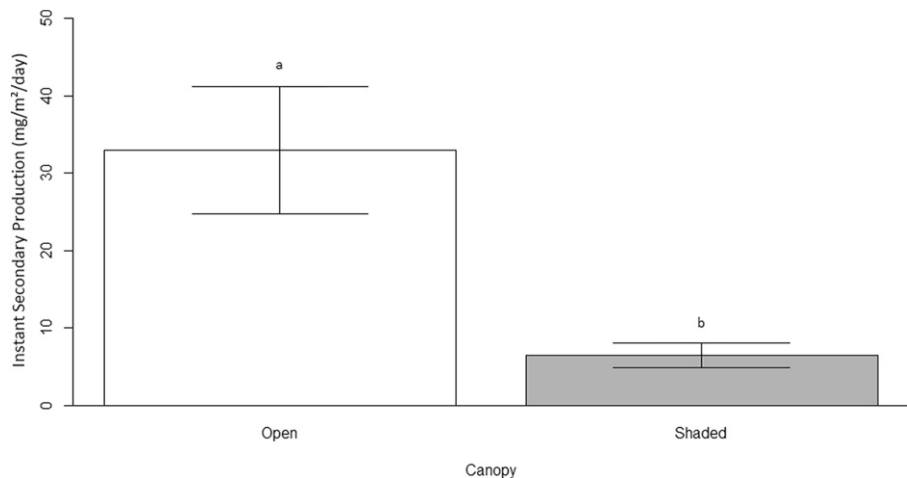


Fig. 3. Mean and standard error of Eco-exergy and Specific Eco-exergy for streams with Open and Shaded canopy. "a" and "b" mark significantly different plots.



**Fig. 4.** Mean and standard error of Instant Secondary Production ( $\text{g}/\text{m}^2/\text{day}$ ) for streams with Open and Shaded canopy. "a" and "b" mark significantly different plots.

instance, take place in systems where a non-excessive nutrient input enrichment occurs, resulting in more energy available to benthic assemblages and a consequent increase in eco-exergy (Marques et al., 1997; Molozzi et al., 2013). Regarding specific eco-exergy, which is assumed to express the overall degree of complexity and development of a biological system (Jørgensen, 2007a, 2007b; Jørgensen and Fath, 2004), the fact that values did not show significant differences in open canopy and shaded streams may be interpreted as indicating that macroinvertebrate assemblages are similarly fitted in both environments.

Higher instant secondary production in open canopy streams is straight interpretable as a result of higher instream energy availability of energy, in compliance with the higher eco-exergy values also observed, exemplifying that these streams may, to a certain extent, as hypothesized, support more complex and productive benthic macroinvertebrate assemblages. Additionally, this may also imply the conclusion that both in open canopy and shaded streams benthic macroinvertebrate assemblages mainly depend on autochthonous resources, eventually more available in open canopy streams (Fuß et al., 2017; Guo et al., 2016; Rezende et al., 2008). These results are in concordance with the Riverine Productive Model Theory (Thorp and Delong, 1994), which assumes that autochthonous production is the most important source of energy to lotic ecosystems, especially in the tropics. This also maintained in other studies (e.g., Carroll et al., 2016; Ferreira et al., 2014; Ivković et al., 2015), which argue that autochthonous organic matter is more easily absorbed by benthic macroinvertebrates (Pearson et al., 2015).

## 5. Conclusions

The present study illustrates the importance of canopy cover in the structure and functioning of benthic macroinvertebrate assemblages, as our results imply that streams with open canopy show benthic assemblages with more complex dissipative structure and higher secondary production. Additionally, our results illustrate how autochthonous production play a crucial role in tropical headwater streams, and so we suggest that future studies should focus in the relative importance of the various food sources available to benthic macroinvertebrate assemblages in Neotropical headwater streams. Stable isotope analysis is a very promising methodology to this end, being already successfully used in the Neotropical savannah with benthic macroinvertebrates (Castro et al., 2016) and fishes (Carvalho et al., 2015, 2017). Canopy cover, however, did not show any correlation to the benthic macroinvertebrate assemblages' diversity and specific eco-exergy, eventually implying that these aspects might be controlled and explained by other factors, such as the level of disturbance (see for instance Ferreira et al., 2014; Junqueira et al., 2016; Ligeiro et al.,

2013), namely at the light of the intermediate disturbance hypothesis (Connell, 1978).

Our results highlight the need of understanding the ecological structure and dynamics of headwater streams in the Neotropical savannah, which constitute global diversity hotspots (Fernandes et al., 2012). These ecosystems are highly threatened by human land use and climate change (Callisto et al., 2012), and a sound base information on their natural functioning and variations is indispensable. The dependence of headstreams macroinvertebrate communities on autochthonous food sources implied by our results is specially relevant, as autotrophic lotic ecosystems are less stable and thus more susceptible to disturbances (Benke, 2010; Death and Zimmermann, 2005; Tonkin et al., 2013). Eco-exergy and specific eco-exergy, as holistic ecosystem health indicators based on a universal thermodynamic language, stand out as useful biomonitoring tools, potentially helpful as indicators to support environmental decisions with regard to protection and restoration measures.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2017.08.282>.

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