

## Original Articles

## Two tropical biodiversity hotspots, two different pathways for energy

Gisele Moreira dos Santos<sup>a,\*</sup>, Marden Seabra Linares<sup>a</sup>, Marcos Callisto<sup>a</sup>, João Carlos Marques<sup>b</sup>

<sup>a</sup> Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Genética Ecologia e Evolução, Laboratório de Ecologia de Bentos, Av. Antônio Carlos n° 6627, CP. 486, CEP 30161-970 Belo Horizonte, MG, Brazil

<sup>b</sup> MARE, Marine and Environment Sciences Centre, DCV, Faculty of Sciences and Technology, University of Coimbra, Portugal

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## ABSTRACT

Local factors, such as riparian vegetation and stream type, affect the structure and composition of benthic macroinvertebrate assemblages in streams. To better understand the effects of biomes on lotic ecosystems, we evaluated whether Atlantic Forest (AF) and Neotropical Savanna (NS) biomes showed distinct patterns in (i) benthic macroinvertebrate assemblage structure and (ii) the shredder functional feeding group. We predicted that (i) richness, density, biomass, instant secondary production, eco-exergy, and specific eco-exergy would be higher for benthic macroinvertebrate assemblages in AF stream sites than in NS sites. We also predicted that (ii) length, density, biomass, instant secondary production, eco-exergy, and specific eco-exergy would be higher for shredders in AF stream sites. We found that benthic macroinvertebrate assemblage composition and taxa richness were significantly different between stream sites in the two biomes, with the AF biome being the richest. But we found no differences in density, biomass, instant secondary production, eco-exergy, or specific eco-exergy between AF and NS stream sites. For AF shredders, the mean length, density, biomass, secondary production and eco-exergy were significantly higher than for NS stream sites. These differences were attributed to the quality of leaf litter, which was generally higher in AF than in NS stream sites. This indicates that the intrinsic characteristics of the AF and NS biomes act as structuring factors for benthic macroinvertebrate assemblages, influencing the structure and functioning of tropical lotic ecosystems.

## 1. Introduction

Headwater streams (1st to 3rd order; Strahler, 1957) are ecosystems with high biotic diversity and species richness (Meyer et al., 2007). These ecosystems represent ~80% of the channel length in a hydrographic basin (Datry et al., 2014). Because they are small, they are easily influenced by local variation in geomorphology, lithology, soil, and the species composition of riparian vegetation (Vannote et al., 1980).

In general, the riparian vegetation of headwater streams acts as a buffer between terrestrial and aquatic ecosystems (Naiman and Decamps, 1997; Tonkin et al., 2018). The vegetation stabilizes river banks and increases shading (Kaylor and Warren, 2017), limiting the entrance of radiant energy into the ecosystem while introducing allochthonous material as leaf litter (Rezende et al., 2017). The degradation of this material occurs with the transformation of coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM) through decomposition (Graça, 2001). The rate of this process depends on the chemical content and physical characteristics of the leaves of different plant species (Gonçalves et al., 2006; Rezende et al.,

2018).

Allochthonous organic matter is considered the main energy source for heterotrophic organisms in shaded headwater streams (Kiffer et al., 2018; Vannote et al., 1980). Aquatic organisms, such as shredder macroinvertebrates, feed on leaf litter by breaking it into smaller particles and making it available to other aquatic invertebrates (Graça, 2001). Also, shredders are sensitive to environmental changes because they are reduced in abundance or may disappear in heavily disturbed streams (Sánchez-Bayo and Wyckhuys, 2019).

Shredder activity depends on leaf litter quality and tropical plant species have highly lignified leaves that are low in nutrients (Biasi et al., 2019; Boyero et al., 2016; Kiffer et al., 2018). In Brazil, the proportion of shredders in benthic macroinvertebrate assemblages varies between biomes. In the Neotropical Savanna (NS) they are generally less abundant (~1%) (Gonçalves et al., 2007; Moretti et al., 2007a,b), whereas in Atlantic Forest (AF) streams they are more common (~20%) (Mendes et al., 2017). Presumably, this is because of the differing quality of the leaf litter available in these biomes. Plants from the NS usually have hard, coriaceous leaves of poor nutritional quality with high levels of secondary compounds (Ligeiro et al., 2010)

\* Corresponding author at: Universidade Federal de Goiás, Departamento de Ecologia, Av. Esperança s/n, CP 131, CEP 74001-970 Goiânia, GO, Brazil.

E-mail addresses: [santos.giselem@gmail.com](mailto:santos.giselem@gmail.com) (G.M.d. Santos), [callistom@ufmg.br](mailto:callistom@ufmg.br) (M. Callisto), [jemimar@ci.uc.pt](mailto:jemimar@ci.uc.pt) (J.C. Marques).

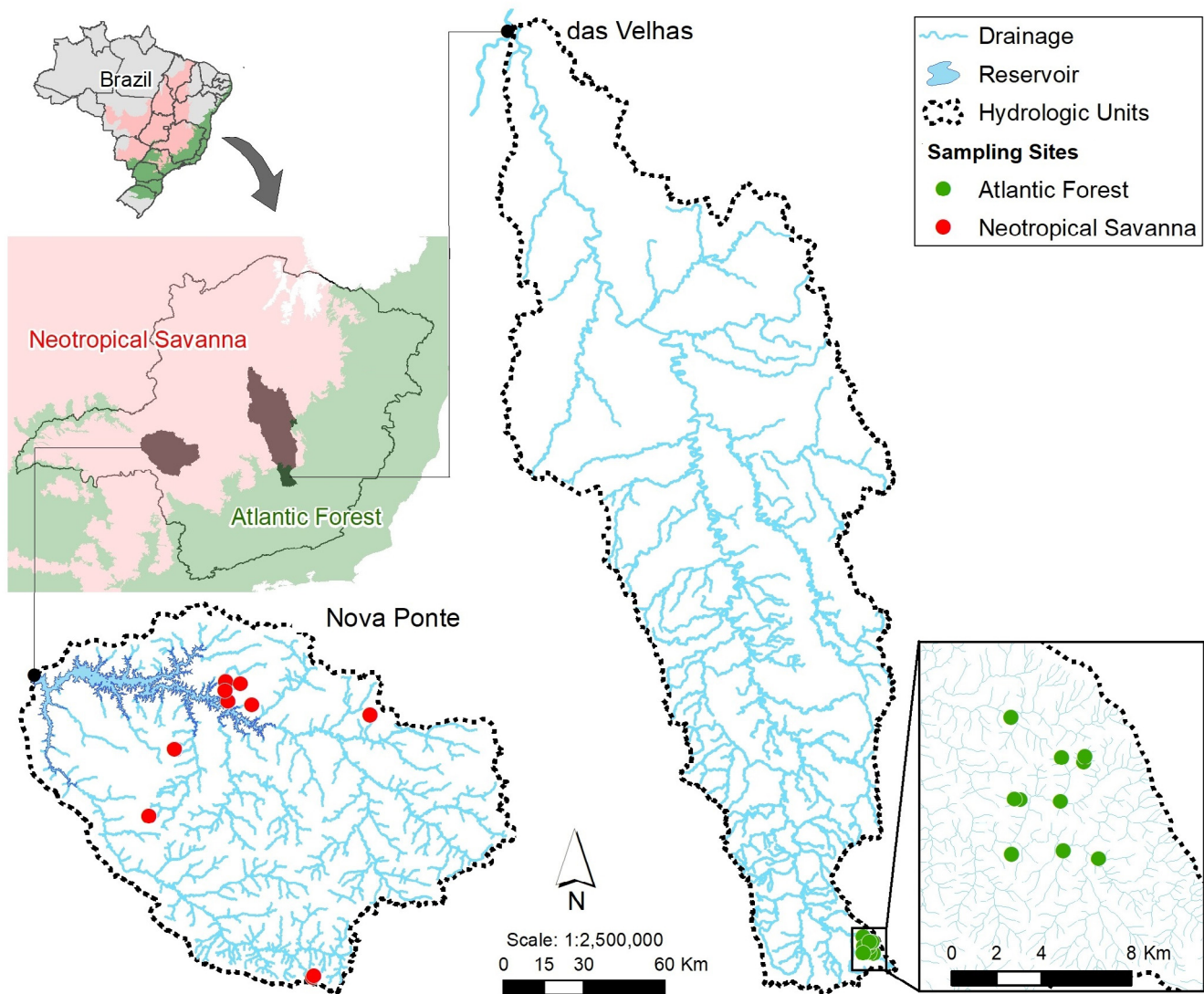


Fig. 1. Location of sampling sites in the Atlantic Forest and Neotropical Savanna biomes, Minas Gerais, Brazil.

and slow decomposition rates (e.g., Gomes et al., 2018; Gonçalves et al., 2007). Native riparian plant species in the Atlantic Forest (AF), on the other hand, often have larger, softer leaves with lower amounts of secondary compounds, higher nutritional content (Tromboni et al., 2018), and faster decomposition rates than those of the NS (Gonçalves et al., 2012).

Local differences in riparian vegetation composition and stream type affect the structure and composition of benthic macroinvertebrate assemblages (Ferreira et al., 2014). For example, dense riparian vegetation limits light entry to streams and limits local primary production and grazing macroinvertebrates (Neres-Lima et al., 2017; Vannote et al., 1980), but facilitates shredder diversity and abundance (Sánchez-Bayo and Wyckhuys, 2019). Stream size, substrate type, and water quality also affect the composition, richness, and abundance of aquatic macroinvertebrate assemblages (Agra et al., 2019; Silva et al., 2014).

In addition to assessing assemblage structure and composition it is useful to assess local effects on ecosystem functioning. One way to do so is by measuring secondary production, which is the rate of formation of heterotrophic biomass in a population or community and provides an estimation of the energy flow through a system (Benke and Huryn, 2010). Ecosystems with higher secondary production rates allow the energy present in the ecosystems to flow through a greater number of trophic levels and to support a greater diversity of organisms (Benke,

1993; Dolbeth et al., 2012). However, higher secondary production does not always indicate a healthy ecosystem, because some disturbances simply increase production of opportunistic species (Dolbeth et al., 2012; Huryn and Wallace, 2000).

Secondary production is difficult to estimate for natural assemblages, because it requires data about population growth and mortality, which requires intensive field sampling (Dolbeth et al., 2012). Because secondary production is such an energy-demanding variable to measure, models were created to estimate it (Aguiar et al., 2015; Linares et al., 2018a,b). Instant secondary production is of such estimates of secondary production. This approach evaluates secondary production from the biomass, density, and estimates of the growth of organisms at a single time in an ecosystem (Aguiar et al., 2015).

An alternative approach for evaluating local effects on ecosystem processes is the use of thermodynamic oriented ecological indicators (Linares et al., 2018a,b; Molozzi et al., 2013). Thermodynamic indicators also indicate ecosystem condition in a holistic way (Jørgensen, 2006; Zhang et al., 2010). Two examples of thermodynamic indicators are eco-exergy and specific eco-exergy (Jørgensen and Mejer, 1977). Eco-exergy is the energy of all living things present in an ecosystem that is available to do useful work (Jørgensen et al., 2005; Lu et al., 2015). This energy is quantified by measuring the biomass and genetic information of the system (Jørgensen, 2006; Linares et al., 2018a;

Molozzi et al., 2013; Silow and Mokry, 2010). Specific eco-exergy is a measure of the genetic information present in living things. Thus specific eco-exergy reflects the complexity and stability of living things in the ecosystem (Lu et al., 2015; Silow and Mokry, 2010).

Therefore, the aim of this study was to quantify the difference in function, structure and composition between headwater streams in two major Brazilian biomes: AF and NS. We sought to answer this question: What are the differences in the structure and function of benthic macroinvertebrate and shredder assemblages in headwater streams in the AF and NS biomes? We expected higher taxa richness, biomass, instant secondary production, eco-exergy and specific eco-exergy in benthic macroinvertebrate assemblages in AF biome sites than in NS biome sites because of the higher quality of leaf litter in the AF (Gonçalves et al., 2014). Also, we expected that the length, biomass, instant secondary production, eco-exergy and specific eco-exergy would be higher for shredders in the AF because of the better quality leaves and the greater abundance of shredders in AF streams (Gonçalves et al., 2007; Mendes et al., 2017; Moretti et al., 2007a).

## 2. Material and methods

### 2.1. Study area

In each biome, we selected 10 headwater stream sites (1st to 3rd order) in reference condition, constituting a subset of 20 streams. Reference conditions were defined as being in least-disturbed condition (LDC) for streams across the landscape (Stoddard et al., 2008), including the absence of anthropogenic alterations and the presence of dense riparian vegetation (Bailey et al., 2014; Hughes et al., 1986). The sites were selected amongst potential sites to be least-disturbed based on the interpretation of a combination of fine resolution images (0.6–5 m spatial resolution) and Landsat Thematic Mapper multi-spectral satellite images (Macedo et al., 2014).

The sites were located in the Araguari (NS) and Rio das Velhas (AF) River Basins, both in Minas Gerais state, Brazil (Fig. 1). Both the NS and AF are considered biodiversity hotspots (Myers et al., 2000), but both biomes have been substantially altered by changes in land use (Joly et al., 2014; Strassburg et al., 2017). The NS biome has a dry tropical climate, with annual precipitation between 1200 and 1800 mm. The soils are old red and yellow latosols, acidic (pH 4–6) with low fertility, and have high levels of iron and aluminum (Bueno et al., 2018). The AF is the second largest Brazilian forest and has lost much of its natural cover area (Joly et al., 2014; Ribeiro et al., 2009). The AF climate is humid tropical, with annual rainfall between 1000 and 4200 mm. The soils are shallow with acidic pH and low fertility (Ribeiro et al., 2009).

At each site, measures of physical habitat were obtained following the USA Environment Protection Agency protocol (US-EPA; Lazorchak et al., 1998), adapted to tropical headwater streams (Agra et al., 2019). Measures of electrical conductivity ( $\mu\text{S}/\text{cm}$ ), pH, total dissolved solids (mg/L), turbidity (nephelometric turbidity units, NTU) and water temperature ( $^{\circ}\text{C}$ ) were carried out *in situ* with a portable multiprobe (YSI 6600). Mean width (m) and mean canopy cover (%) were obtained with a measuring tape and a densiometer, respectively. In the laboratory, dissolved oxygen (mg/L) was determined by the Winkler (1888) method and total alkalinity ( $\mu\text{Eq}/\text{L}$  of  $\text{CO}_2$ ) was determined using the Gran method (Carmouze, 1994; Table 1).

### 2.2. Benthic macroinvertebrate sampling

The macroinvertebrate assemblages were sampled in September of 2013 and 2014, during the dry season. Each site was divided into six equidistant transects. In each transect, a kick-net sampler (30 cm opening, 500  $\mu\text{m}$  sieve) was used, resulting in six sub-samples in each site for a total area of 0.54  $\text{m}^2$  sampled (Agra et al., 2019; Martins et al., 2018). 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 the

**Table 1**  
Physical habitat characteristics and water quality metrics of sampling sites (data from Agra et al., 2019; Martins et al., 2018).

Biome	Stream	Water Temperature ( $^{\circ}\text{C}$ )	pH	Electrical Conductivity ( $\mu\text{S}/\text{cm}$ )	Total Dissolved Solids (mg/L)	Turbidity (UNT)	Dissolved Oxygen (mg/L)	Alkalinity ( $\mu\text{Eq}/\text{L}$ de $\text{CO}_2$ )	Mean Width (m)	Mean canopy cover (%)
Neotropical Savanna	1	21.30	7.92	4.27	2.14	5.56	8.10	449.20	3.21	38.75
	2	17.00	7.33	0.55	0.27	3.44	8.20	34.23	7.16	7.08
	3	18.40	8.01	2.57	0.00	0.26	7.60	355.20	4.50	2.08
	4	19.20	7.12	3.47	0.00	0.27	7.60	56.14	7.16	13.12
	5	21.30	8.40	2.66	1.21	2.72	7.60	273.10	5.00	0.00
	6	20.80	6.60	4.39	2.31	1.13	8.20	552.50	6.16	9.16
	7	19.90	6.60	0.71	0.35	5.52	7.40	75.44	4.73	21.45
	8	19.80	5.34	3.27	1.43	2.37	7.80	58.33	3.58	36.25
	9	19.60	4.82	2.06	0.88	3.85	8.30	70.66	8.60	5.00
	10	21.20	7.94	1.77	0.94	4.08	9.10	138.90	6.50	0.41
	Mean $\pm$ SE	19.85 $\pm$ 0.44	7.00 $\pm$ 0.41	2.46 $\pm$ 0.46	1.20 $\pm$ 0.23	3.59 $\pm$ 0.48	7.99 $\pm$ 0.15	206.37 $\pm$ 59.60	5.66 $\pm$ 0.54	13.33 $\pm$ 4.51
Atlantic Forest	1	16.00	8.51	38.20	13.04	3.97	14.20	347.00	1.87	21.59
	2	16.90	6.35	32.80	10.29	2.79	10.20	284.40	2.44	13.18
	3	15.70	7.57	67.90	27.60	3.35	12.30	55.94	3.08	10.00
	4	17.30	7.07	52.70	19.70	2.40	10.70	3.66	4.66	15.45
	5	19.10	6.37	38.90	13.74	21.70	7.90	231.10	4.00	26.68
	6	15.40	7.45	46.70	16.68	3.17	11.10	21.79	4.00	9.54
	7	16.00	6.76	40.80	13.94	1.51	12.70	26.79	2.15	23.75
	8	14.00	6.76	74.10	30.60	5.67	10.80	80.05	2.07	7.50
	9	16.80	6.65	20.50	4.12	40.40	10.60	14.13	2.18	20.11
	10	17.50	6.98	60.10	24.20	3.69	8.60	317.60	3.33	26.13
	Mean $\pm$ SE	16.47 $\pm$ 0.43	7.04 $\pm$ 0.20	47.27 $\pm$ 5.22	17.40 $\pm$ 2.58	8.86 $\pm$ 3.97	10.91 $\pm$ 0.59	138.24 $\pm$ 44.14	2.92 $\pm$ 0.30	17.39 $\pm$ 2.27

laboratory. Individuals were identified to family level under a stereomicroscope and by using specialized literature (Hamada et al., 2014; Merritt and Cummins, 1996; Mugnai et al., 2010). 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. Individuals belonging to the following families were classified as shredders: Calamoceratidae and Leptoceridae (Trichoptera), Dryopidae (Coleoptera), Gripopterygidae (Plecoptera) and Pyralidae (Lepidoptera) (Merritt and Cummins, 1996; Tomanova et al., 2006).

### 2.3. Biomass estimation

Up to 100 individuals of each taxon were randomly selected and photographed in a stereomicroscope (Leica M80) equipped with a digital camera (Leica IC 80 HD). The length of each individual was measured using Motic Image Plus 2.0 software. We estimated dry biomass ( $\text{g}/\text{m}^2$ ) for each site by using length-mass equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). Based on those measurements we estimated the mean dry-biomass for each taxon in each site as well as the total dry-biomass for each sampling site.

### 2.4. Estimation of instant secondary production

We estimated instant secondary production (**IP**) ( $\text{mg}/\text{m}^2/\text{day}$ ) for each site, following the equation of Morin (1997):

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

where **D** is the density of each taxon, **W** is the mean dry weight for each taxon and **GR** is the instant growth rate (Supplementary Material Table S1), estimated from individual equations for each taxon found in the literature (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989). The empirical models used to estimate **GR** were:

$$\text{Log}_{10}(\text{GR}) = a + b \text{Log}_{10}(\text{IW}) + c (\text{T}) \quad (1)$$

$$\text{Log}_{10}(\text{GR}) = 0.06 + 0.79 \text{Log}_{10}(\text{IW}) - 0.16 \text{Log}_{10}(\text{IW}) + 0.05 (\text{T}) \quad (2)$$

$$\text{Log}_{10}(\text{GR}) = a + b \text{Log}_{10}(\text{IW}) + c \text{Log}_{10}(\text{T}) \quad (3)$$

where **a**, **b** and **c** correspond to specific coefficients, **T** corresponds to the water temperature and **IW** corresponds to the individual dry weight. Eq. (1) was used for insect taxa (Morin and Dumont, 1994), Eq. (2) for Annelida (Plante and Downing, 1989) and Eq. (3) for Mollusks and Platyhelminthes (Edgar, 1990).

### 2.5. Calculation of exergy indicators

We calculated eco-exergy and specific eco-exergy for each site. Eco-exergy was calculated using the following equation (Jørgensen et al., 2010):

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

where  $\beta_i$  is a weighting factor based on the genetic information contained in the components (i) of the ecosystem, based on the number of codifying genes as defined by Jørgensen et al. (2005), and  $c_i$  is the biomass of component i in the ecosystem (Supplementary Material Tables S2 and S3).

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. Data analysis

To test the hypothesis that benthic assemblage composition, structure, and function differ between the headwater sites of the two biomes we used a generalized linear model (GLM) with Poisson distribution corrected for overdispersion (quasipoisson). Model significance was tested by an F test (Kaur et al., 1996). We used AF and NS as independent variables and the total taxa richness, density, biomass, instant secondary production, eco-exergy and specific eco-exergy as dependent variables.

For the differences in family composition between the benthic macroinvertebrate assemblages of both biomes, we ran their abundance data ( $\log(x + 1)$ ) in a Permutational Multivariate Analysis of Variance (PERMANOVA), using Gower's (taxa relative abundance; as modified by Anderson et al. (2006)) coefficient as the distance metric. We used Non-Metric Dimensional Scaling (NMDS) model to plot the variability in macroinvertebrate family composition among the sites in each biome. To test the hypothesis that shredders differed between sites of the two biomes we also used a generalized linear model (GLM) with Poisson distribution corrected for overdispersion (quasipoisson). Model significance was tested by an F test (Kaur et al., 1996). We again used the AF and NS as independent variables and length, density, biomass, instant secondary production, eco-exergy and specific eco-exergy of shredders as dependent variables. We used length instead of taxa richness because we had previously determined shredder taxa richness.

All calculations were performed through use of R software, version 3.2.3 (R Core Team, 2017) and the vegan package (Oksanen, 2018).

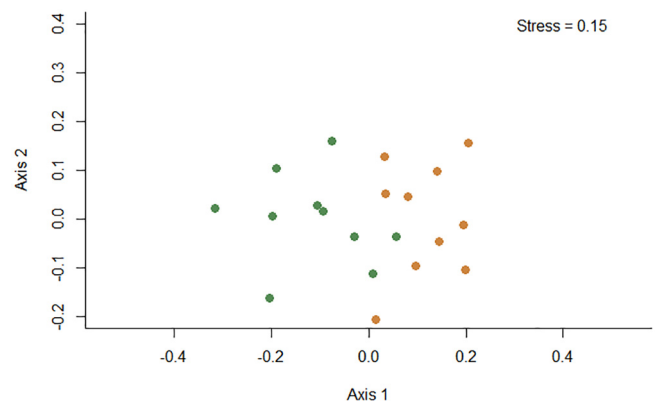
## 3. Results

### 3.1. Benthic macroinvertebrate assemblages

We sampled a total of 11,909 benthic macroinvertebrates, 7540 in the AF and 4369 in the NS. Family richness was significantly higher in AF sites compared to NS sites ( $F_{1,18} = 7.28$ ;  $P = 0.014$ ;  $n = 20$ ). Family composition varied significantly between the biomes (Permanova (Gower)  $F_{1,18} = 5.43$ ;  $P < 0.001$ ; stress = 0.15;  $R^2 = 0.23$ ;  $n = 20$ ) (Fig. 2). We did not observe significant differences in assemblage density, instant secondary production, eco-exergy, or specific eco-exergy (Table 2).

### 3.2. Shredders

Shredders averaged 61.8 (SE  $\pm$  13.7) individuals (8.2%) in the AF assemblages, and 6.0 (SE  $\pm$  2.5) individuals (1.3%) in the NS



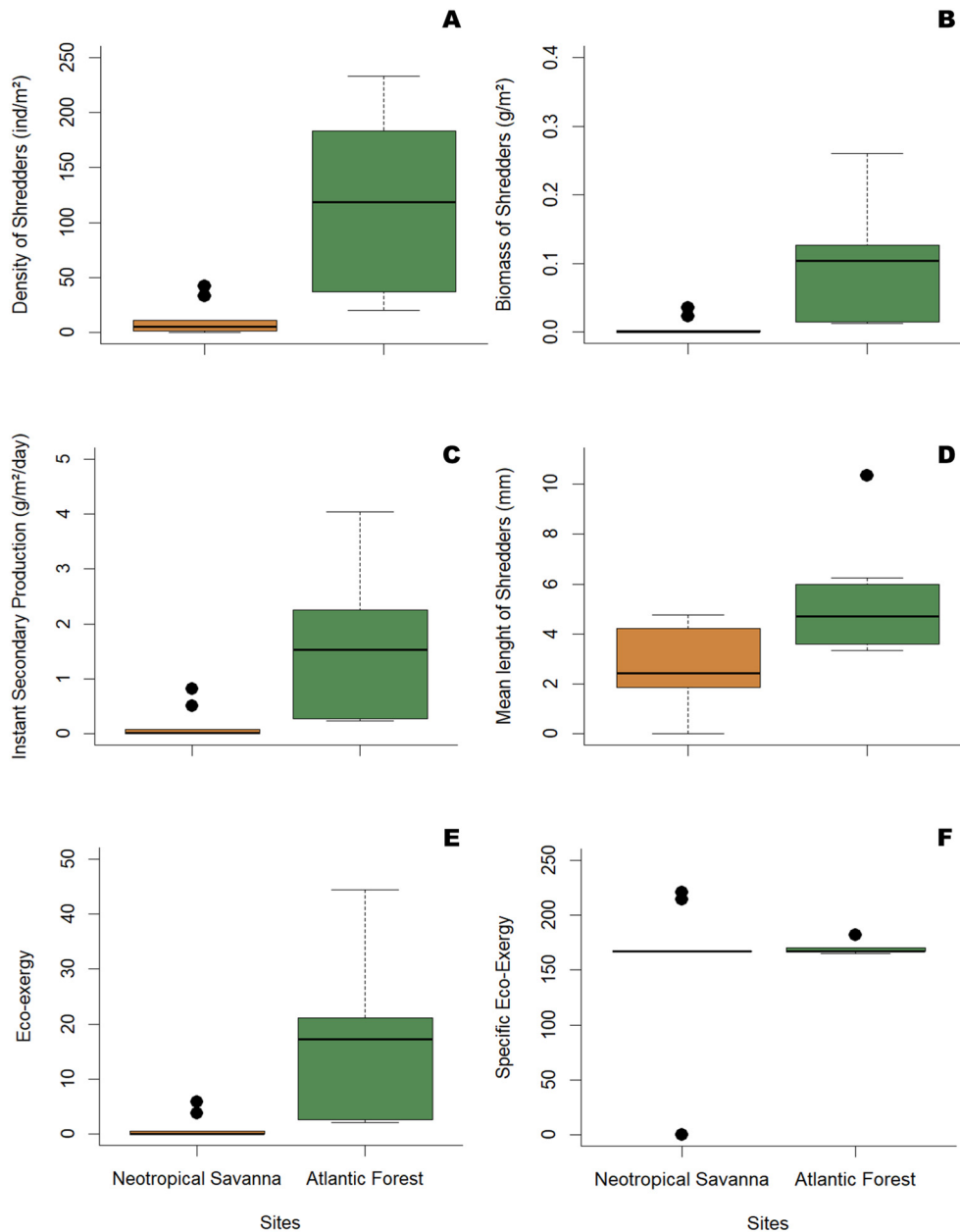
**Fig. 2.** Non-Metric Dimensional Scaling (NMDS) results for benthic macroinvertebrate assemblage composition in the Atlantic Forest (green) and Neotropical Savanna (brown) sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

Mean values and standard error for the measured biological metrics for benthic macroinvertebrate assemblages in the Atlantic Forest and Neotropical Savanna sites.

Metrics	Biome		$F_{df}$	p value	n
	Atlantic Forest	Neotropical Savanna			
Taxa richness	31.30 ± 2.12	23.60 ± 1.89	$F_{1,18} = 7.28$	0.01*	20
Density (ind/m <sup>2</sup> )	1396.29 ± 285.21	1102.68 ± 160.13	$F_{1,18} = 3.22$	0.08	20
Biomass (g/m <sup>2</sup> )	0.81 ± 0.17	0.62 ± 0.10	$F_{1,18} = 3.30$	0.08	20
Instant secondary production (g/m <sup>2</sup> /day)	146.24 ± 52.25	121.12 ± 38.42	$F_{1,18} = 0.59$	0.44	20
Eco-exergy	147.39 ± 32.16	110.14 ± 18.38	$F_{1,18} = 4.04$	0.05	20
Specific Eco-exergy	179.99 ± 12.32	173.61 ± 2.29	$F_{1,18} = 1.03$	0.32	20

\* Statistically significant results.

**Fig. 3.** Biological metrics measured for shredder functional feeding group in headwater streams in Atlantic Forest and Neotropical Savanna sites (A) Density (ind/m<sup>2</sup>), (B) Biomass (g/m<sup>2</sup>), (C) Instant Secondary Production (g/m<sup>2</sup>/day), (D) Mean length (mm), (E) Eco-exergy and (F) Specific Eco-exergy.

assemblages. AF sites exhibited significantly greater shredder numbers m<sup>-2</sup> than NS sites (AF - 114.44 ± 25.41; NS - 11.11 ± 4.68;  $F_{1,18} = 25.98$ ;  $p = 0.00007527$ ;  $n = 20$ ) (Fig. 3). The shredders in AF also exhibited significantly greater mean lengths (AF - 5.11 ± 0.65; NS

- 2.51 ± 0.53;  $F_{1,18} = 9.18$ ;  $p = 0.007188$ ;  $n = 20$ ) than in NS sites. Shredder biomass was significantly greater in the AF than in the NS (AF - 0.09 g m<sup>-2</sup> ± 0.02; NS - 0.006 g m<sup>-2</sup> ± 0.003;  $F_{1,18} = 19.04$ ;  $p = 0.0003744$ ;  $n = 20$ ). Likewise, instant secondary production in AF

sites was significantly higher than in NS sites (AF =  $1.59 \text{ g m}^{-2} \text{ day}^{-1} \pm 0.43$ ; NS =  $0.14 \text{ g m}^{-2} \text{ day}^{-1} \pm 0.08$ ;  $F_{1,18} = 16.15$ ;  $p = 0.0008047$ ;  $n = 20$ ). Regarding eco-exergy, the AF shredders had significantly higher values than those in NS sites (AF =  $16.63 \pm 4.72$ ; NS =  $1.05 \pm 0.65$ ;  $F_{1,18} = 18.89$ ;  $p = 0.0003887$ ;  $n = 20$ ). There was no significant biome difference in specific eco-exergy (AF =  $168.99 \pm 1.52$ ; NS =  $143.73 \pm 24.83$ ;  $F_{1,18} = 0.94$ ;  $p = 0.3429$ ;  $n = 20$ ).

#### 4. Discussion

Family composition and richness of benthic macroinvertebrate assemblages differed significantly between AF and NS sites, but did not result in significant differences in eco-exergy or secondary production at the assemblage level. On the other hand, both indicators differed significantly between the two biomes for shredders, suggesting that the functioning of benthic macroinvertebrate assemblages of the AF and NS biomes differs significantly in response to the intrinsic characteristics of streams in those biomes. This is further supported by significant differences in shredder lengths, abundances, densities, and biomasses between AF and NS sites.

The biome differences in benthic macroinvertebrate assemblage composition and the higher shredder density in AF sites suggest that allochthonous material is the main structuring factor of macroinvertebrate assemblages in AF streams. Headwater streams in the AF biome are surrounded by dense vegetation with leaves containing fewer phenolic compounds than those in surrounding NS sites (Gonçalves et al., 2012). Consequently, leaf litter in AF sites is rapidly leached and conditioned by bacteria and fungi, facilitating the ability of shredders to use it as a food source compared with NS sites (Casotti et al., 2015; Gonçalves et al., 2014; Kiffer et al., 2018). This also suggests that shredders may have more resilience and greater potential to maintain their structure and composition in AF streams than in NS streams. Therefore, riparian vegetation is important for aquatic communities, especially shredder assemblages (Boyer et al., 2011; Graça et al., 2015), which also produce fine particulate organic matter for other aquatic invertebrates (Graça, 2001; Aguiar et al., 2018). The greater densities, lengths, and biomasses of shredders in the AF sites also indicate greater availability and quality of leaf litter (Ferreira et al., 2014; Tomanova and Usseglio-Polatera, 2007) leading to more efficient growth (Benke et al., 1999; Benke and Huryn, 2010; Mendes et al., 2017).

Although family composition of benthic macroinvertebrate assemblages differed significantly between AF and NS streams, eco-exergy, specific eco-exergy, and instant secondary production did not. Eco-exergy allows evaluating the distance between an ecosystem's present state and its potential state at thermodynamic equilibrium, representing the useful energy in the form of biomass and genetic information (Zhang et al., 2010). This constitutes to some degree the resilience potential of an ecosystem. Our results suggest that stream macroinvertebrate assemblages in the two biomes may have similar efficiencies in maintaining their biological complexities. This further suggests that stream types or habitat types may be more important than the intrinsic energy characteristics of the two biomes in structuring benthic macroinvertebrate assemblages (Agra et al., 2019; Martins et al., 2018).

#### 5. Conclusions

Our results demonstrate that benthic macroinvertebrate assemblages differ between Atlantic Forest and Neotropical Savanna streams in assemblage composition as well as shredder biomass and function because of differences in riparian vegetation. These results should be interpreted with caution, because they show patterns of assemblage structuring at relatively small spatial extents and few sites; therefore, we recommend greater numbers of sites throughout both biomes. Future studies should also include thermodynamic indicators to clarify

ecosystem processes and resilience. Our results also show the importance of shredders as sensitive indicators of environmental conditions and trends in tropical streams. Given the importance of allochthonous organic matter to these organisms, we suggest that experiments of feeding preference should be conducted using plant species with different levels of secondary compounds.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105495>.

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