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DOIS HOTSPOTS TROPICAIS, CAMINHOS DIFERENTES PARA A ENERGIA EM RIACHOS

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais, como parte dos requisitos para obtenção do título de Mestra em Ecologia.

ORIENTADOR: Prof. Dr. Marcos Callisto

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“Não fui eu que lhe ordenei? Seja forte e corajoso! Não se apavore, nem se desanime, pois o Senhor, o seu Deus estará com você por onde você andar”.

Josué 1:9

BOLSA:



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RESUMO

Para entender os efeitos de biomas nos ecossistemas aquáticos, nós avaliamos as hipóteses de que os riachos de cabeceira nos biomas Mata Atlântica (AF) e Cerrado (NS) apresentam padrões distintos de estruturação de (i) comunidades aquáticas e (ii) invertebrados fragmentadores. Nós utilizamos medidas de riqueza, densidade, biomassa, produção secundária instantânea, eco-exergia e eco-exergia específica como métricas de estruturação de comunidades. A composição e riqueza de comunidades de macroinvertebrados bentônicos foram significativamente diferentes entre os dois biomas, sendo o bioma AF o mais rico (média \pm erro padrão (SE), 31.3 ± 2.12). A densidade, biomassa, produção secundária instantânea, eco-exergia e eco-exergia específica não variaram entre os biomas. Os insetos fragmentadores no bioma AF apresentaram valores médios significativamente mais altos nas métricas de comprimento, densidade, biomassa, produção secundária instantânea e eco-exergia, em relação ao bioma NS. Essas diferenças podem ser atribuídas à melhor qualidade de detritos foliares disponíveis para as assembleias de invertebrados fragmentadores no bioma AF em relação ao bioma NS. Em síntese, nosso estudo evidencia que características intrínsecas dos biomas AF e NS podem atuar como fatores estruturadores de assembleias de macroinvertebrados bentônicos, influenciando a estrutura e o funcionamento de ecossistemas lóticos em região tropical.

PALAVRAS CHAVE: Eco-Exergia; Hotspots Brasileiros; Macroinvertebrados Bentônicos; Produção Secundária Instantânea.

ABSTRACT

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

Keywords: Benthic macroinvertebrates; Brazilian hotspots; Eco-exergy; Secondary production.

INTRODUÇÃO GERAL

Um dos grandes questionamentos de estudos em ecologia de comunidades é entender o porquê de nem todas as espécies estarem em todos os lugares. A ocorrência de uma espécie em um determinado local envolve uma série de requerimentos bióticos e abióticos que permitem a sua existência (Vellend, 2016). Características fisiológicas, comportamentais e morfológicas permitem que espécies ultrapassem as barreiras e contribuam para a formação de uma comunidade. Essas barreiras são, na verdade, processos ecológicos que podem atuar na estruturação e montagem de comunidades biológicas. Processos ecológicos como seleção, deriva genética, especiação e dispersão atuam em escalas regionais, enquanto que processos relacionados a fatores abióticos e bióticos atuam em escalas locais (Vellend, 2010; 2016).

Características físicas do ambiente como temperatura, umidade e geomorfologia, podem influenciar a distribuição espacial de espécies e levar à formação de comunidades distintas (Vellend, 2016). Em ecossistemas aquáticos, o conceito RIVER CONTINUUM CONCEPT sugere que os sistemas aquáticos são interligados longitudinalmente com variações de solo, formações rochosas e geomorfológicas ao longo do contínuo fluvial. Dessa forma, variações na litologia e geomorfologia de riachos podem interferir em características das comunidades presentes nesses locais (Vannote et al., 1980).

Os fatores bióticos compreendem as interações entre as espécies, como competição, predação, mutualismo e parasitismo. Essas interações levam a variações na abundância relativa das espécies dentro das comunidades, por exemplo, uma espécie afetada por um parasita pode ter diminuições em sua abundância relativa. Interações como a competição podem levar a exclusão competitiva de espécies quando um competidor é mais eficiente do que o outro, ou a coexistência de espécies

quando um dos competidores apresenta variação em seu nicho deixando de competir por um recurso limitado. As interações atuam em uma comunidade determinando a ocorrência de espécies na comunidade local (Vellend, 2010; 2016).

O interesse em conhecer as interações entre as espécies e os fatores que podem determinar a estrutura e funcionamento de comunidades me levou a trabalhar com esse tema. Dessa forma, dou início à minha contribuição para os estudos em ecologia de comunidades com um manuscrito, fruto dessa dissertação.

Nesta introdução geral apresentarei as bases conceituais que nortearam essa dissertação: o conceito de indicadores termodinâmicos e produção secundária.

INDICADORES TERMODINÂMICOS

Indicadores termodinâmicos avaliam a condição de ecossistemas de maneira integrada, baseados em propriedades e na estrutura do sistema como um todo. Assim como os indicadores ecológicos, eles auxiliam na avaliação da qualidade de ecossistemas (Jørgensen, 2007). Dois exemplos de indicadores termodinâmicos são a eco-exergia e eco-exergia específica.

A eco-exergia pode ser definida como a distância entre o estado presente do ecossistema e seu estado em caso de equilíbrio termodinâmico com o ambiente abiótico. Essa distância pode ser quantificada analisando o aumento na estrutura física do sistema na forma de biomassa e informação genética. A eco-exergia específica é mensurada pela razão entre a eco-exergia e a biomassa total (Jørgensen et al., 2005).

Os valores de eco-exergia são inversamente proporcionais à entropia, dessa forma se imaginarmos uma faixa de entropia em que temos sistemas com baixa e alta entropia, locais com alta entropia estão próximos ao equilíbrio termodinâmico e conseqüentemente apresentam valores baixos de eco-exergia. Esses valores representam áreas de menor complexidade biológica, como riachos impactados. Por

outro lado, locais com baixa entropia estão distantes do equilíbrio termodinâmico e consequentemente apresentam valores altos de eco-exergia. Esses valores representam áreas de maior complexidade biológica, como riachos de referência (Figura 1).

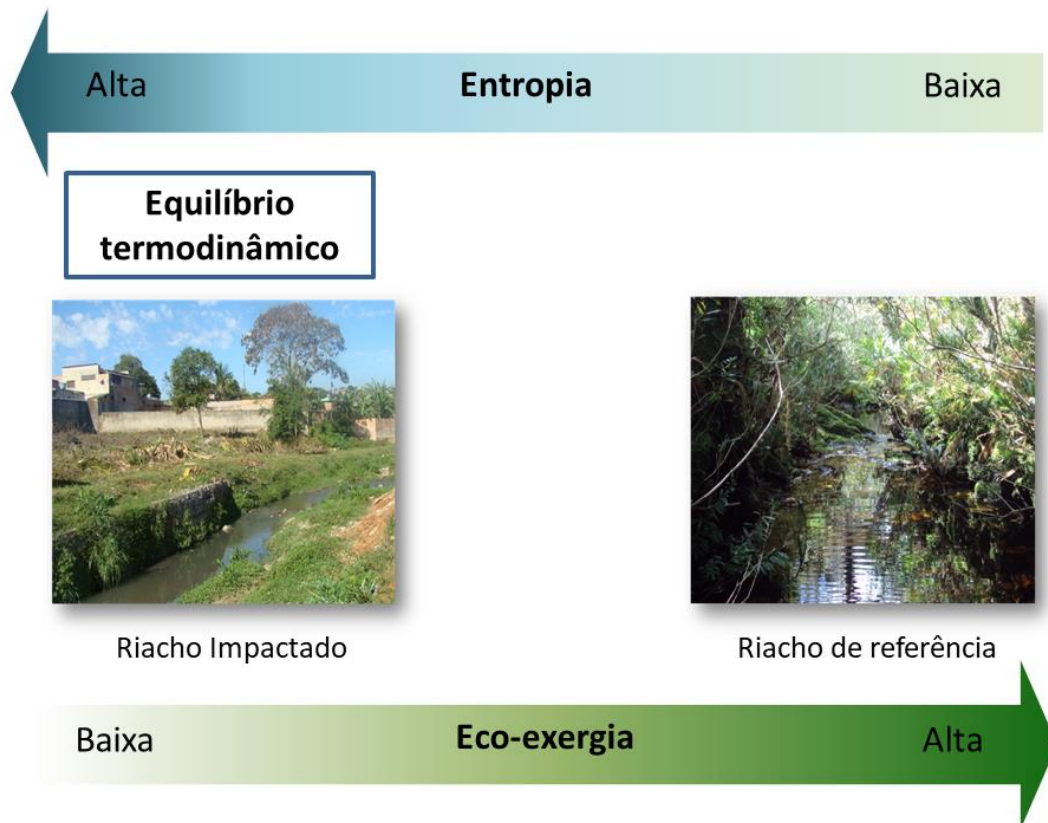


Figura 1: Representação da aplicação do conceito de eco-exergia a ecossistemas aquáticos (adaptada de Jørgensen et al., 2005; Salas et al., 2005).

Eco-exergia e eco-exergia específica são indicadores complementares, dessa forma, recomenda-se a utilização desses indicadores em conjunto (Marques et al., 2003). Esses indicadores refletem a capacidade de resiliência e diversidade de um sistema biológico. Assim, altos valores de eco-exergia e eco-exergia específica são encontrados em locais com maior diversidade de espécies, e com maior capacidade de retornar a um estado semelhante ao original após uma perturbação (Bilgen and Sarikaya, 2015).

PRODUÇÃO SECUNDÁRIA

O conceito de produção secundária está relacionado à incorporação de energia no tecido de um heterótrofo (Odum, 2007). A produtividade secundária representa a taxa de armazenamento de energia nos níveis tróficos de consumidores, e possibilita a estimativa de fluxos de energia em sistemas biológicos. Ambientes com maior produção secundária possuem altas taxas de assimilação de energia pelos heterótrofos, o que possibilita que a energia presente nesses ecossistemas flua por um maior número de níveis tróficos. No entanto nem sempre um aumento na produção secundária indica um ambiente saudável, pois algumas perturbações podem aumentar a produção dos organismos ou beneficiar espécies oportunistas (Huryñ & Wallace, 2000; Dolbeth et al., 2012).

As estimativas de produção secundária fornecem informações mais precisas sobre o funcionamento de ecossistemas quando comparadas às informações de biomassa e densidade, isoladamente. Isso ocorre porque o cálculo da produção secundária utiliza dados de biomassa, densidade e crescimento de organismos. Dessa forma, essa abordagem é uma das ferramentas utilizadas para avaliar e monitorar o fluxo de energia em comunidades aquáticas (Dolbeth et al., 2012).

DECOMPOSIÇÃO DE DETRITOS FOLIARES

A decomposição é um dos processos ecológicos que contribuem para a ciclagem de nutrientes e fluxo de energia em ecossistemas aquáticos (Graça et al., 2001; Gonçalves et al., 2013). Nestes ecossistemas a disponibilidade de energia pode ser autóctone, quando a entrada de luz solar no riacho permite que organismos realizem a fotossíntese, e alóctone com a entrada de matéria orgânica e detritos foliares da vegetação ripária (Gonçalves et al., 2013). A decomposição é um processo ecológico que pode ser dividido em três fases: lixiviação, condicionamento e fragmentação. A lixiviação caracteriza-se pela perda de compostos solúveis, seguida

pelo condicionamento quando microorganismos (bactérias, fungos e hifomicetos aquáticos) colonizam os detritos aumentando seu valor nutricional e palatabilidade para macroinvertebrados fragmentadores. A última fase é a de fragmentação, quando os detritos sofrem abrasão pelo fluxo da água ou degradação por macroinvertebrados aquáticos (Gessner et al., 1999) (Figura 2).

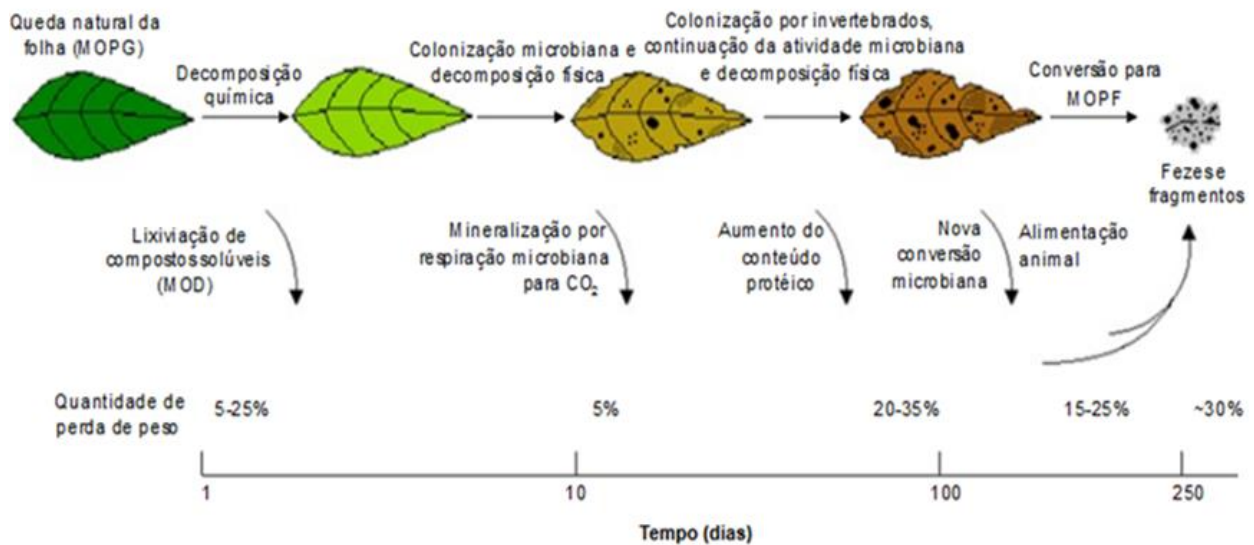


Figura 2: Representação da mudança de estado do detrito foliar, sob a influência de vários fatores bióticos e abióticos ao longo do tempo (Fonte: Gonçalves & Callisto, 2005).

A decomposição pode ser influenciada por fatores físicos e químicos na coluna d' água incluindo temperatura, velocidade de fluxo e características foliares como dureza e concentração de compostos secundários. Fatores físicos e químicos podem afetar a atividade de microorganismos e invertebrados. Diminuições nos valores de pH podem levar à diminuição da atividade microbiana, o que diminui o coeficiente de decomposição (Gonçalves et al., 2013; Mulholland et al., 1987). As concentrações de compostos secundários nas folhas (lignina, celulose, polifenóis) podem afetar a decomposição influenciando a colonização por microorganismos e invertebrados aquáticos (Graça et al., 2001).

SISTEMA DE ESTUDO E ESTRUTURA DA DISSERTAÇÃO

Nessa dissertação utilizei como modelo de estudo macroinvertebrados bentônicos. Estes são organismos, em sua grande maioria insetos aquáticos, que habitam o sedimento de fundo em lagos e riachos, sendo visíveis a olho nu. Esses organismos desempenham importante papel no funcionamento de ecossistemas aquáticos, em cadeias alimentares, contribuem no fluxo de energia e atuam como presas para peixes e outros invertebrados. Participam da ciclagem de nutrientes, sendo fundamentais na transformação da matéria orgânica. São sensíveis a perturbações ambientais, o que permite que esses organismos sejam utilizados como bioindicadores de qualidade de água. Além disso, macroinvertebrados bentônicos são abundantes e frequentes na maioria dos ecossistemas aquáticos, o que possibilita sua ampla utilização em estudos ecológicos (Esteves, 2011).

Os macroinvertebrados bentônicos podem ser classificados de acordo com suas características alimentares em 5 grupos tróficos funcionais: raspador, coletor-filtrador, coletor-catador, predador e fragmentador. Os raspadores possuem adaptações para raspar o perifíton e a microbiota associada em substratos orgânicos ou inorgânicos depositados nos rios. Os coletores filtradores possuem estruturas especializadas para filtrar partículas em suspensão. Coletores catadores alimentam-se de matéria particulada fina resultado do processamento da matéria orgânica. Predadores são organismos que se alimentam de tecido animal. Os fragmentadores retalham e consomem os detritos foliares que entram no sistema aquático transformando MOPG em MOPF, disponibilizando alimento para outros grupos tróficos funcionais como os coletores (Cummins, 1973).

Em riachos de zonas de clima temperado essa relação entre invertebrados fragmentadores e detritos foliares está bem estabelecida (Graça, 2001), no entanto, para riachos em zonas de clima tropical existem divergências quanto ao papel dos

invertebrados fragmentadores no processo de decomposição (Gonçalves et al., 2007; Wantzen & Wagner, 2006). Alguns estudos mostram que fungos e bactérias são organismos importantes no processo de decomposição em riachos tropicais, uma vez que a quantidade de invertebrados fragmentadores é muito reduzida em riachos no Cerrado (Gonçalves et al., 2007; Gonçalves et al., 2012).

Essa dissertação está em formato de manuscrito a ser submetido a uma revista científica internacional, e tem o objetivo de avaliar possíveis variações na estrutura e funcionamento de assembleias de macroinvertebrados bentônicos em riachos de cabeceira em dois biomas brasileiros.

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CAPÍTULO 1

TWO TROPICAL HOTSPOTS, TWO DIFFERENT PATHWAYS FOR ENERGY



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Abstract

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

Keywords: Benthic macroinvertebrates; Brazilian hotspots; Eco-exergy; Secondary production.

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. Because they are small order streams, they could be influenced by natural changes on a local scale such as variation in geology, edaphic, and riparian vegetation species composition (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 and at the same time allowing the entrance of allochthonous material as leaf litter (Rezende et al., 2017). The degradation of this material occurs with the transformation of fine particulate organic matter (FPOM) into coarse particulate organic matter (CPOM) through the decomposition process (Graça, 2001). This process depends on the quality of the leaf can vary according to the chemical content and physic characteristics of the leaves of different plant species (Gonçalves et al., 2006; Rezende et al., 2018).

Plants from the Neotropical Savanna (NS) usually have hard, coriaceous leaves, of poor nutritional quality and with high levels of secondary compounds (Ligeiro et al., 2010), and most show slow decomposition rates (e.g., Gonçalves et al., 2007; Gomes et al., 2018). Native riparian plant species in the Atlantic Forest (AF), on the other hand, generally have large, soft leaves with lower amounts of secondary compounds and higher nutritional contents (Tromboni et al., 2018). Therefore, native plants of the AF streams, in general, have faster decomposition rates compared to native plants of the NS (Gonçalves et al., 2012).

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 the other aquatic invertebrates (Graça, 2001). Also, shredders are sensitive to environmental changes and consequently suffer losses of biodiversity (Sanchez-Bayo and Wyckhuys, 2019).

Since the shredders activity depends on leaf litter quality (Biasi et al., 2018; Kiffer et al., 2018), they are most abundant in temperate streams than tropical streams, due to the quality of leaf litter (Boyero et al., 2015). In Brazil, the proportion of shredders in benthic macroinvertebrate assemblages varies between biomes. In the NS they are generally less abundant (~ 1%) (Gonçalves et al., 2007; Moretti et al., 2007a; 2007b), whereas in AF streams they are more common (~ 20%) (Mendes et al., 2017).

Local factors, such as characteristics of riparian vegetation and stream typology, may affect in the structure and composition of benthic macroinvertebrate assemblages (Ferreira et al., 2014). One approach to evaluate this effect is the use of thermodynamic oriented ecological indicators (Aguiar et al., 2015; Linares et al., 2018a, 2018b; Molozzi et al., 2013). Thermodynamic indicators examine the condition of ecosystems in a holistic way, based up on the properties and structure of the system as a whole (Jørgensen, 2007; Zhang et al., 2010). Two examples of thermodynamic indicators are eco-exergy and specific eco-exergy (Jørgensen and Mejer, 1977). Eco-exergy expresses the maximum quantity of work that can be obtained in a process that brings an ecosystem to thermodynamic equilibrium with its environment (Jørgensen et al., 2005). It represents the useful energy contained within an ecological system and can be quantified by analyzing the increase in the structure of the system, in the form of biomass and genetic information (Jørgensen, 2006). Specific eco-exergy, on the other hand, expresses the ecosystem's ability to use external energy flows, reflecting its complexity and stability (Silow and Mokry, 2010).

Differences in habitat may also influence 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 flow through a system (Benke and Huryn, 2010). Ecosystems with higher secondary production can change the rates of assimilation of energy by heterotrophs, which allows 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).

Secondary production is difficult to estimate for natural assemblages, as it requires data about population growth and mortality, which requires intensive field sampling (Dolbeth et al., 2012). For these reasons empirical models were developed to facilitate the estimation of secondary production, amongst them instant secondary production (Aguiar et al., 2015; Linares et al., 2018a; 2018b). These estimates allow understand how limiting factors drive community differentiation, being relevant for the conservation of biodiversity hotspots such as AF and NS.

The aim of this study was to evaluate the variation in 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 of benthic macroinvertebrate and shredders assemblages in headwater streams in the AF and NS biomes? We suggest that patterns of benthic assemblage structure and composition vary between the headwater streams of the two biomes. We expected that higher taxa richness, biomass, instant secondary production, eco-exergy and specific eco-exergy for benthic macroinvertebrate assemblages in streams in the AF biome than in the NS biome, due to the higher quality of allochthonous leaf litter in the AF biome (Gonçalves et al., 2014). Also, the patterns of structuring of the shredder functional feeding group should vary between the headwater streams of the two biomes, as length, biomass, instant secondary production, eco-exergy and specific eco-exergy should be higher for shredders in the AF biome due to the better quality of leaf litter and their higher proportion among benthic macroinvertebrates in the streams of this biome (Gonçalves et al., 2007; Mendes et al., 2017; Moretti et al., 2007).

Material and Methods

Study Area

We selected stretches of headwater streams (1st to 3rd order) in reference conditions located in the NS and AF, which are considered hotspots for biodiversity (Myers et al., 2000), but both biomes have been substantially altered by changes in land use (Strassburg et al., 2017; Joly et al., 2014). The sites were located in the Araguari (NS) and Rio das Velhas (AF) River Basins, both in Minas Gerais state, Brazil (Figure 1).

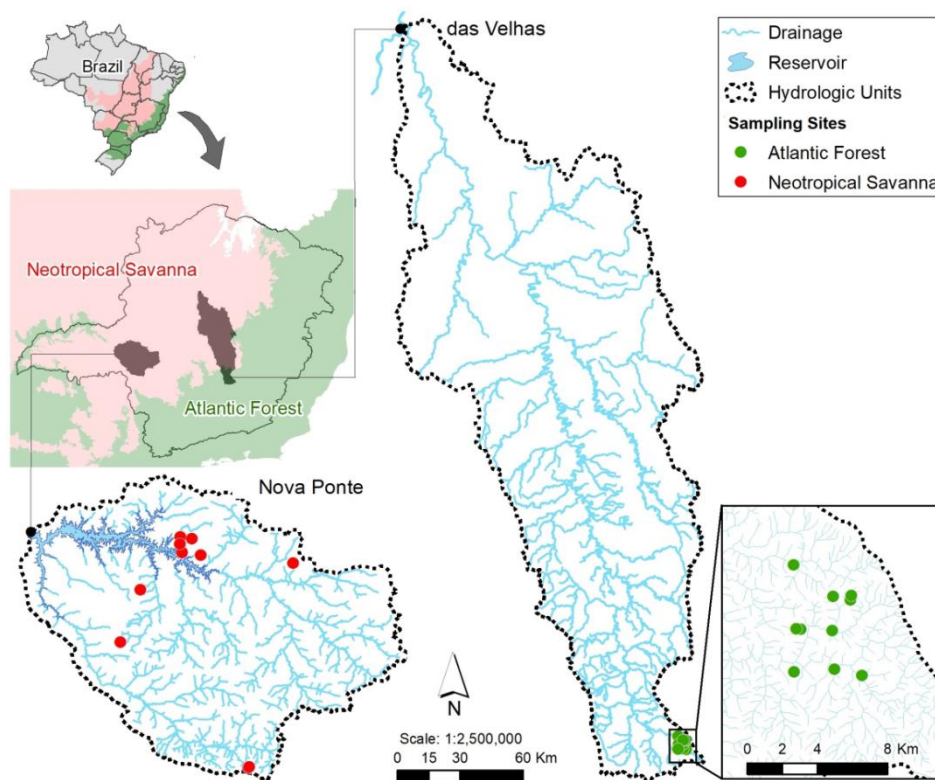


Figure 1: Location of sampling sites in the Atlantic Forest and Neotropical Savanna biomes, Minas Gerais, Brazil.

The NS biome has a dry tropical climate, with annual precipitation between 1200 and 1800 mm. The soils are old, of the red and yellow latosol type, with acidic pH between 4 and 6 and low fertility, showing high levels of iron and aluminum (Bueno et al., 2018). NS contains large numbers of springs that are part of some of the most

important hydrographic basins in South America, such as the Tocantins, São Francisco and Prata (Strassburg et al., 2017). In addition to these, the hydrographic basin of the Araguari River is home to important springs of the Paraná river basin, located on the Serra da Canastra plateau at approximately 1400 m altitude (Martins et al., 2018).

The AF is the second largest Brazilian forest and lost much of its natural cover area due to fragmentation (Joly et al., 2014; Ribeiro et al., 2009). Climate at AF 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). AF is home to the Paraná, Uruguay, Paraíba do Sul, Doce, Jequitinhonha and São Francisco hydrographic basins (Joly et al., 2014). The São Francisco hydrographic basin encompasses the Rio das Velhas basin, an important tributary which houses springs (Agra et al., 2018).

Biological data was collected in the years 2013 and 2014 at reference headwater streams in NS and AF. These streams were selected amongst potential sites based on the interpretation of a combination of fine resolution images (0.6 – 5m spatial resolution) with Landsat Thematic Mapper multispectral satellite images (Macedo et al., 2014). For the present investigation, we analyzed 10 streams from each of the two biomes, constituting a subset of 20 streams.

At each stream, measures of physical habitat were obtained following the USA Environment Protection Agency protocol (US-EPA, 2006), adapted to tropical headwater streams (Agra et al., 2018). Also, 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), mean canopy cover (%) were made with measuring tape and densiometer. In the laboratory, dissolved oxygen (mg/L) was determined by the Winkler (1888) method and total alkalinity ($\mu\text{Eq}/\text{L}$ of CO_2) was determined using Gran method (Carmouze, 1994; Table 1).

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

Biome	Stream	Water Temperature (°C)	pH	Electrical Conductivity (µS/cm)	Total Dissolved Solids (mg/L)	Turbidity (UNT)	Dissolved Oxygen (mg/L)	Alkalinity (µEq/L de CO ₂)	Mean Width (m)	Mean canopy cover (%)
Neotropical savanna	1	21.3	7.92	4.27	2.14	5.56	8.1	449.2	3.21	38.75
	2	17	7.33	0.55	0.27	3.44	8.2	34.23	7.16	7.08
	3	18.4	8.01	2.57	0.00	0.26	7.6	355.2	4.5	2.08
	4	19.2	7.12	3.47	0.00	0.27	7.6	56.14	7.16	13.12
	5	21.3	8.4	2.66	1.21	2.72	7.6	273.1	5	0
	6	20.8	7.6	4.39	2.31	1.13	8.2	552.5	6.16	9.16
	7	19.9	6.6	0.71	0.35	5.52	7.4	75.44	4.73	21.45
	8	19.8	5.34	3.27	1.43	2.37	7.8	58.33	3.58	36.25
	9	19.6	4.82	2.06	0.88	3.85	8.3	70.66	8.6	5
	10	21.2	7.94	1.77	0.94	4.08	9.1	138.9	6.5	0.41
	<i>Mean ± SE</i>	<i>19.85 ± 0.44</i>	<i>7.00 ± 0.41</i>	<i>2.46 ± 0.46</i>	<i>1.20 ± 0.23</i>	<i>3.59 ± 0.48</i>	<i>7.99 ± 0.15</i>	<i>206.37 ± 59.60</i>	<i>5.66 ± 0.54</i>	<i>13.33 ± 4.51</i>
Atlanticforest	1	16	8.51	38.2	13.04	3.97	14.2	347	1.87	21.59
	2	16.9	6.35	32.8	10.29	2.79	10.2	284.4	2.44	13.18
	3	15.7	7.57	67.9	27.6	3.35	12.3	55.94	3.08	10
	4	17.3	7.07	52.7	19.7	2.4	10.7	3.662	4.66	15.45
	5	19.1	6.37	38.9	13.74	21.7	7.9	231.1	4	26.68
	6	15.4	7.45	46.7	16.68	3.17	11.1	21.79	3.5	9.54
	7	16	6.76	40.8	13.94	1.51	12.7	26.79	2.15	23.75
	8	14	6.76	74.1	30.6	5.67	10.8	80.05	2.07	7.5
	9	16.8	6.65	20.5	4.12	40.4	10.6	14.13	2.18	20.11
	10	17.5	6.98	60.1	24.2	3.69	8.6	317.6	3.33	26.13
	<i>Mean ± SE</i>	<i>16.47 ± 0.43</i>	<i>7.04 ± 0.20</i>	<i>47.27 ± 5.22</i>	<i>17.40 ± 2.58</i>	<i>8.86 ± 3.97</i>	<i>10.91 ± 0.59</i>	<i>138.24 ± 44.14</i>	<i>2.92 ± 0.30</i>	<i>17.39 ± 2.27</i>

Benthic Macroinvertebrate Sampling

The macroinvertebrate assemblages were sampled in September of 2013 and 2014, during the dry season. In each site, a stretch was divided into six equidistant transects. In each transect, a kick-net sampler (30 cm opening, 500µm sieve) was used, resulting in six sub-samples in each site for a total area of 0.54 m² sampled (Agra et al., 2018; 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 laboratory. Individuals were identified to family level under a stereomicroscope, 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 in the following families were classified as shredders: Calamoceratidae, Leptoceridae (Trichoptera), Dryopidae (Coleoptera), Gripopterygidae (Plecoptera) and Pyralidae (Lepidoptera) (Merritt and Cummins, 1996; Tomanova et al., 2006).

Biomass Estimation

We estimated dry-mass biomass (g/m²) for each sampling site using length-mass equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). Up to 100, individuals of each taxon were 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.

Estimation of Instant Secondary Production

We estimated Instant Secondary Production (**IP**) (mg/m²/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 individual dry weight for each taxon and **GR** is the Instantaneous Growth Rate, estimated from individual equations for each taxon found in the literature (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989).

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):

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

Where **β_i** is a weighting factor based on the genetic information contained in the components (**i**) of the ecosystem, as defined by Jørgensen et al. (2005), and **c_i** is the concentration (biomass) of component **i** in the ecosystem (supplementary material Table S1 and S2).

Specific eco-exergy is given by:

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

Where **EX** is the total eco-exergy and **BM** is the total biomass.

Data analysis

To test the hypothesis that the patterns of benthic assemblage' structure and composition vary 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 the sampled biomes – AF and NS – as

independent variables and the taxa richness, density, biomass, instant secondary production, eco-exergy and specific eco-exergy as dependent variables.

For the differences in taxonomic composition between the benthic macroinvertebrate assemblages of both biomes, we ran the abundance data in a Non-Metric Dimensional Scaling (NMDS) model. A Permutational Multivariate Analysis of Variance (PERMANOVA), using Gower's coefficient as the distance metric, was used to test if the composition of the benthic macroinvertebrate assemblages differed significantly between biome streams. Multivariate homogeneity of groups dispersions (variances) PERMDISP was used to test the differences of dispersal of the taxonomic community between streams in the biomes.

To test the hypothesis that the patterns of structuring of the shredder functional feeding group vary between the headwater streams 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 the sampled biomes – AF and NS – as independent variables and the values of length, biomass, instant secondary production, eco-exergy and specific eco-exergy of shredders as dependent variables.

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

Results

Benthic Macroinvertebrate Assemblages

We sampled a total of 11,909 benthic macroinvertebrates, 7540 in the AF and 4,369 in the NS. Shredders, comprised an average of 61.8 (SE \pm 13.7) individuals (8.2%) of the AF assemblages, and 6.0 (SE \pm 2.5) individuals (1.3%) of the NS assemblages.

Taxonomic composition varied significantly between the biomes (Permanova (Gower) $F_{1,18} = 5.43$; $P < 0.001$; stress = 0.15; $R^2 = 0.23$; $n = 20$) (Figure 2). This variation was caused by the difference of taxonomic composition between biomes, and not by the dispersion of the points in the graph (Permdisp (Gower): $F_{1,18} = 0.03$; $P = 0.86$; $n = 20$).

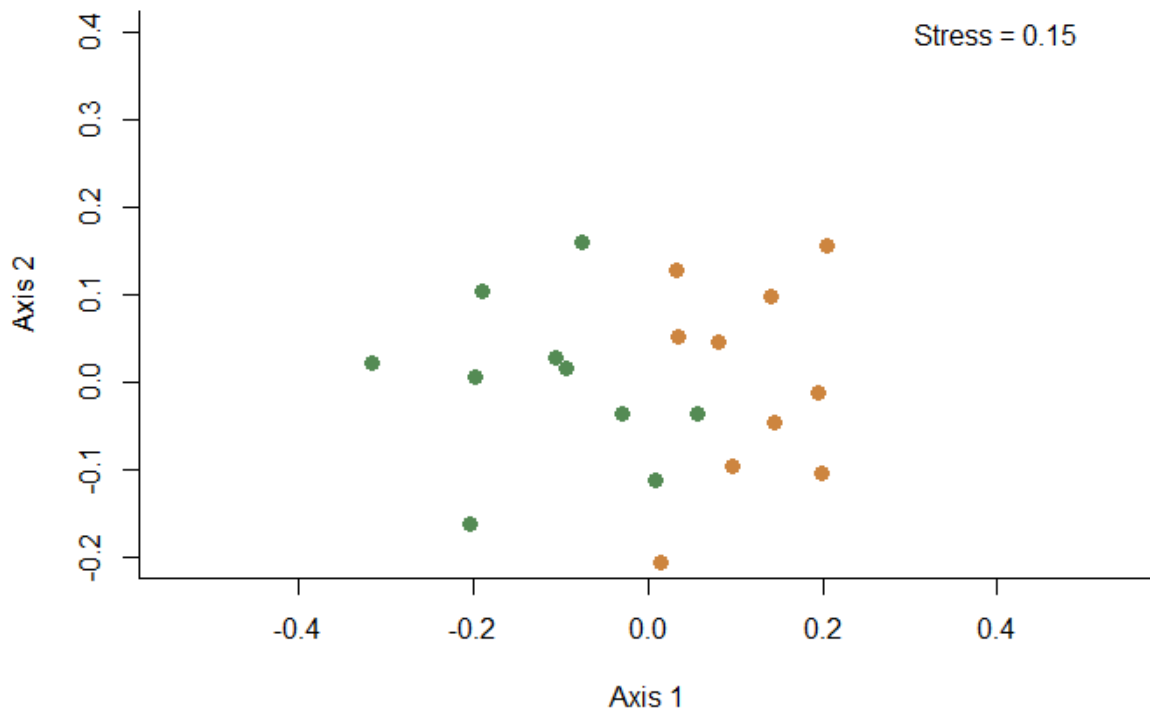


Figure 2: Non-Metric Dimensional Scaling (NMDS) results for benthic macroinvertebrate assemblage composition in the Atlantic Forest (green) and Neotropical Savanna (brown) sites.

We observed consistently higher mean values for AF in all of the measured biological metrics: taxa richness, density, instant secondary production, eco-exergy and specific eco-exergy (Table 2). Nevertheless, only taxa richness was significantly higher in AF as compared to NS ($F_{1,18} = 7.28$; $P = 0.014$; $n = 20$).

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	31.3±2.12	23.6±1.89	F _{1,18} =7.28	0.014*	20
Density (ind/m ²)	1396.29±285.21	1102.68±160.13	F _{1,18} =3.22	0.089	20
Biomass (g/m ²)	0.81±0.17	0.62±0.10	F _{1,18} =3.30	0.085	20
Instant secondary production (g/m ² /day)	146.24±52.25	121.12±38.42	F _{1,18} =0.59	0.448	20
Eco-exergy	147.39±32.16	110.14±18.38	F _{1,18} =4.04	0.059	20
Specific Eco-exergy	179.99±12.32	173.61±2.29	F _{1,18} =1.03	0.322	20

Shredders

AF streams exhibited 10 times more shredders per m² (AF - 114.44 ± 25.41; NS – 11.11 ± 4.68; F_{1,18} = 25.98; P = 0.00007527; n = 20), 16 times higher biomass (AF - 0.09 ± 0.02; NS – 0.006 ± 0.003; F_{1,18} = 19.04; P = 0.0003744; n = 20) and instant secondary production 11 times higher (AF - 1.59 ± 0.43; NS – 0.14 ± 0.08; F_{1,18} = 16.15; P = 0.0008047; n = 20) than those in NS. Shredder mean length, density, biomass, instant secondary production and eco-exergy, were significantly higher in AF sites, with the exception of specific eco-exergy. In regard to eco-exergy, the shredders in AF showed values 16 times higher than those in NS sites (AF - 16.63 ± 4.72; NS – 1.05 ± 0.65; F_{1,18} = 18.89; P = 0.0003887; n = 20). The shredders in AF also exhibited double mean length (AF – 5.11± 0.65; NS – 2.51 ± 0.53; F_{1,18}= 9.18; P = 0.007188; n = 20) than in NS sites (Figure 3).

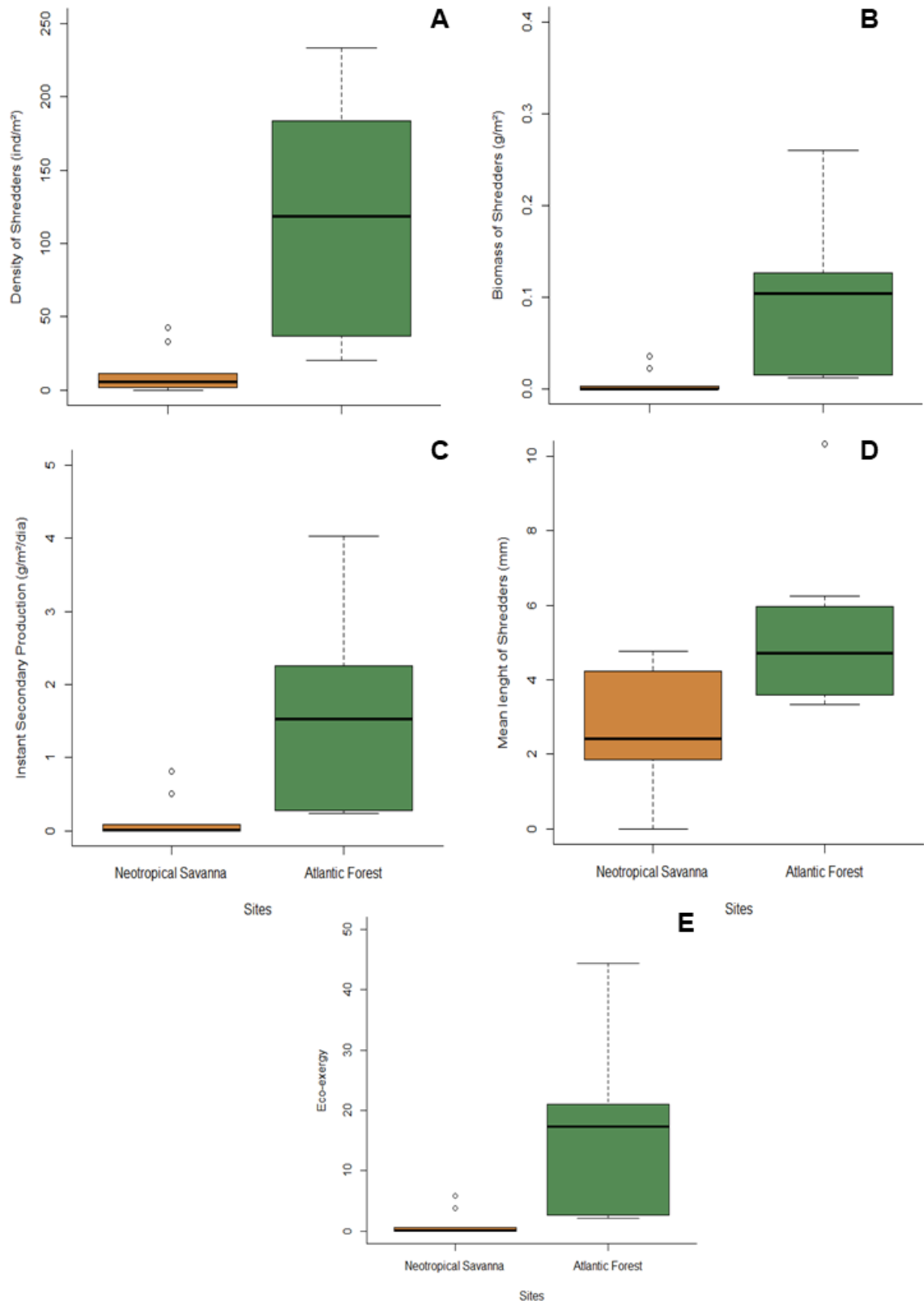


Figure 3: Biological metrics measured for shredder functional feeding group in headwater streams in Atlantic Forest and Neotropical Savanna sites (a) Density (ind/m²), (b) Biomass (g/m²), (c) Instant Secondary Production (g/m²/day), (d) Mean length (mm) and (e) Eco-exergy.

Discussion

The composition and family richness of benthic macroinvertebrate assemblages varied significantly between AF and NS sites, but this variation did not result in significant differences in eco-exergy or secondary production. On the other hand, both those indicators for shredders differed significantly between streams of the two biomes, suggesting that the structure and functioning of benthic macroinvertebrate assemblages of the AF and NS biomes vary significantly in response to the intrinsic characteristics of streams those biomes.

The biome differences in benthic macroinvertebrate assemblage composition and the higher shredder density in the AF sites suggest that allochthonous material is the main structuring factor of macroinvertebrate assemblages in the AF streams. Headwater streams in the AF biome are surrounded by dense vegetation with leaves containing lower concentrations of secondary compounds and less lignin (Gonçalves et al., 2012). This facilitates leaf litter conditioning by bacteria and fungi and greater food quality for benthic macroinvertebrates (Casotti et al., 2015; Gonçalves et al., 2014). Consequently, allochthonous organic matter is more readily available to benthic macroinvertebrate assemblages in AF streams than NS streams.

Despite the fact that the taxonomic composition of benthic macroinvertebrate assemblages differed significantly between AF and NS streams, eco-exergy, specific eco-exergy, and instant secondary production did not show significant differences between the two biomes. 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 suggests that stream types might be more important than the intrinsic energy characteristics of the two biomes in structuring benthic macroinvertebrate assemblages (Agra et al., 2018; Martins et al., 2018).

On the other hand, shredders in AF sites exhibited significantly different values of biomass and eco-exergy. This suggests that shredders may have more resilience and greater potential to

maintain the structure and composition in AF streams than in NS streams. In fact, plant species in AF riparian forests have fewer phenolic compounds than those in the NS (Gonçalves et al., 2012). Consequently, leaf litter in the AF sites is rapidly leached and conditioned, facilitating the ability of shredders to quickly and more readily use it as a food source (Gonçalves et al., 2014; Kiffer et al., 2018).

Therefore, riparian vegetation is important for aquatic communities, especially to shredders assemblages (Boyero et al., 2011; Graça et al., 2015). They process the autochthonous and allochthonous organic matter producing a good source of resources for other aquatic invertebrates (Aguiar et al., 2018). The greater proportions and lengths of shredders in the AF sites likely appear to indicate a concomitant greater availability and quality of leaf litter (Tomanova and Usseglio-Polatera, 2007; Ferreira et al., 2014) in those streams. This means that more and better food availability allow shredders to establish themselves and grow more efficiently, resulting in greater biomass values and lengths (Benke et al., 1999; Benke and Huryn, 2010; Mendes et al., 2017).

Conclusions

Our results illustrate that benthic macroinvertebrate assemblages varied between Atlantic Forest and Neotropical Savanna streams only in terms of taxonomic composition, so to say structure, exhibiting even so a similar functioning. Together with the findings of Agra et al. (2018) and Martins et al. (2018), our results suggest that benthic macroinvertebrates assemblages in headwater streams with similar typology will have similar structure and functioning, regardless of their biome. These results should be interpreted with caution, because they show patterns of assemblages structuring on a relative small scale, and while it is possible that this pattern is repeated in larger scales, we recommend increasing the sampling effort. Our results also reiterate the ecological importance of the shredders as sensitive group to environmental changes and their contribution to processing of organic matter in tropical streams. In addition, the presence of this group in headwater streams of two biodiversity hotspots accentuates the importance of conservation of these areas. For further studies, given the importance of

allochthonous organic matter to these organisms, we suggest that experiments of feeding preference should be performed using plant species with different levels of secondary compounds.

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Supplementary material

Table S1: Exergy conversion factors based on Jørgensen et al. (2005), in bold are the organisms used in this study.

Organisms	Energy Conversion Factor (β)
Virus	1.01
Bacteria	8.50
Algae	20.00
Yeast	17.40
Cnidaria	91.00
Platyhelminthes	120.00
Gastropoda	312.00
Bivalvia	297.00
Crustacea	232.00
Coleoptera	156.00
Diptera	184.00
Hymenoptera	267.00
Lepidoptera	221.00
Otherinsects	167.00
Fish	499.00

Table S2: Biological metrics of benthic macroinvertebrate and shredders assemblages in headwater streams in Atlantic Forest and Neotropical Savanna.

Assemblages	Abundance	Biomass (g/m ²)	Biome
Macroinvertebrate	234	0.2190274	Neotropical Savanna
	191	0.1394611	Neotropical Savanna
	889	0.753	Neotropical Savanna
	836	0.3483313	Neotropical Savanna
	205	0.0812499	Neotropical Savanna
	547	0.4746475	Neotropical Savanna
	315	1.1961872	Neotropical Savanna
	104	0.1169515	Neotropical Savanna
	545	0.5951189	Neotropical Savanna
	503	0.4254827	Neotropical Savanna
	176	0.1865525	Atlantic Forest
	104	0.0623645	Atlantic Forest
	852	0.8361257	Atlantic Forest
	1557	1.9095787	Atlantic Forest
	281	0.4340364	Atlantic Forest
	1040	0.8826541	Atlantic Forest
	473	1.0312573	Atlantic Forest
	726	0.5318292	Atlantic Forest
	1162	1.4023101	Atlantic Forest
	1169	0.8383161	Atlantic Forest
Shredders	5	0.000519	Neotropical Savanna
	0	0	Neotropical Savanna
	0	0	Neotropical Savanna
	18	0.035396	Neotropical Savanna
	2	0.000299	Neotropical Savanna
	1	9.87E-05	Neotropical Savanna
	6	0.00051	Neotropical Savanna
	1	0.0001	Neotropical Savanna

4	0.002773	Neotropical Savanna
23	0.022699	Neotropical Savanna
13	0.015051	Atlantic Forest
24	0.014555	Atlantic Forest
86	0.115682	Atlantic Forest
69	0.208296	Atlantic Forest
20	0.01265	Atlantic Forest
52	0.105092	Atlantic Forest
11	0.016172	Atlantic Forest
76	0.103488	Atlantic Forest
126	0.260458	Atlantic Forest
111	0.126263	Atlantic Forest

CONSIDERAÇÕES FINAIS

Essa dissertação buscou entender possíveis variações na estrutura e funcionamento de assembleias de macroinvertebrados bentônicos em riachos em condição de referência. Para tal, utilizei indicadores termodinâmicos que refletem a complexidade de ecossistemas aquáticos e medidas de produção secundária instantânea que permitem realizar estimativas de fluxos de energia em riachos. Vimos que riachos com tipologias diferentes exibem composição e riqueza de macroinvertebrados bentônicos variada. No entanto, essa variação não é suficiente para alterar o funcionamento das assembleias de invertebrados em termos de energia e produção secundária instantânea. Por outro lado, características da vegetação ripária, qualidade foliar, podem alterar o funcionamento de assembleias de fragmentadores levando a variações de biomassa, produção secundária instantânea e comprimento de indivíduos.

Dessa forma, esse trabalho contribuiu para preencher lacunas de conhecimento referentes aos padrões que levam à estruturação de assembleias de macroinvertebrados bentônicos e importância de invertebrados fragmentadores em riachos de cabeceira nos biomas Cerrado e Mata Atlântica.

Para o desenvolvimento de estudos futuros recomendo:

- Avaliar a contribuição de detritos foliares com diferentes qualidades nutricionais sobre a produção de invertebrados fragmentadores.
- Realizar experimentos que permitam verificar a assimilação de energia por macroinvertebrados bentônicos em riachos.
- Quantificar a contribuição da matéria orgânica particulada fina para comunidades aquáticas.

Tipulidae	3	0	8	45	0	4	47	10	43	36	6	5	2	2	112	10	2	2	16	37
Ephemeroptera																				
Baetidae	6	3	51	11	73	15	24	5	4	41	8	2	5	2	3	13	6	0	4	15
Caenidae	0	0	2	1	0	0	1	161	0	0	0	0	1	1	0	3	0	0	0	1
Euthyplociidae	1	0	19	0	1	0	8	0	2	0	0	1	8	0	0	0	0	0	1	0
Leptohyphidae	3	3	61	376	8	41	7	92	55	45	0	13	1	1	12	45	26	3	18	27
Leptophlebiidae	34	2	84	43	8	29	98	2	7	2	11	23	22	2	1	43	12	0	31	10
Hemiptera																				
Belostomatidae	0	0	0	0	0	0	0	0	5	2	0	0	0	0	0	0	0	0	3	0
Corixidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Helotrephidae	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Naucoridae	0	0	0	0	0	10	0	0	0	0	0	1	0	0	0	0	1	0	26	17
Notonectidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleidae	0	0	0	0	0	5	0	0	0	0	0	0	2	3	0	4	1	0	2	0
Veliidae	1	1	0	6	0	0	0	1	0	0	0	0	0	0	3	1	0	0	1	0
Lepidoptera																				
Pyralidae	0	1	0	4	0	0	0	0	2	0	1	0	0	4	0	0	2	0	3	0
Megaloptera																				
Corydalidae	3	0	8	0	5	1	0	1	4	2	0	2	0	0	0	8	13	2	5	2
Sialidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Odonata																				
Aeshnidae	0	0	1	0	0	0	0	3	2	0	3	0	0	0	0	2	0	0	0	0
Calopterygidae	1	2	0	3	0	0	0	1	0	0	2	0	0	1	0	2	10	0	0	0
Coenagrionidae	11	2	17	0	2	0	1	1	21	3	0	2	2	2	0	13	2	0	11	3
Corduliidae	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Dicteriadidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Gomphidae	1	2	12	23	0	6	5	4	4	0	3	0	0	0	8	7	2	0	2	4
Libellulidae	2	6	0	2	2	1	7	2	4	6	6	0	9	0	2	11	1	0	2	3
Megapodagrionidae	16	5	6	18	1	4	1	2	1	0	0	0	0	0	0	0	0	1	0	0
Perilestidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Plecoptera																				

Appendix A2: Biological metrics of benthic macroinvertebrates families in headwater streams in Atlantic Forest and Neotropical Savanna biomes.

Local	Richness	Abundance	Density (ind/m ²)	Biomass (g/m ²)	Eco-exergy	Specific Eco- exergy	Instant Secondary Production (g/m ² /day)
Neotropical Savanna	25	234	433.33333	0.2190274	35.3448226	161.3717133	127.5009792
Neotropical Savanna	21	191	353.7037	0.1394611	22.5256939	161.5195702	4.973888017
Neotropical Savanna	22	889	1646.2963	0.753	132.68277	176.2055271	115.9183591
Neotropical Savanna	20	836	1548.1481	0.3483313	59.1567536	169.828975	17.79871726
Neotropical Savanna	17	205	379.62963	0.0812499	14.7938472	182.0783038	9.574024942
Neotropical Savanna	34	547	1012.963	0.4746475	77.5825078	163.4529104	310.1531605
Neotropical Savanna	31	315	583.33333	1.1961872	198.251293	165.7360036	15.86065182
Neotropical Savanna	15	104	192.59259	0.1169515	18.5294457	158.4369919	311.8930317
Neotropical Savanna	28	545	1009.2593	0.5951189	98.4742523	165.4698924	30.9692477
Neotropical Savanna	23	503	931.48148	0.4254827	71.5910385	168.2584037	15.40737326
Atlantic Forest	26	176	325.92593	0.1865525	31.01047	166.2291994	4.782758249
Atlantic Forest	23	104	192.59259	0.0623645	10.5754451	169.5746831	7.608382536
Atlantic Forest	33	852	1577.7778	0.8361257	138.59936	165.7637936	420.5086746
Atlantic Forest	38	1557	2883.3333	1.9095787	323.047105	169.1719238	138.9697206
Atlantic Forest	22	281	520.37037	0.4340364	71.4659727	164.6543306	15.55993929
Atlantic Forest	29	1040	1925.9259	0.8826541	256.297506	290.3714106	41.12753716
Atlantic Forest	29	473	875.92593	1.0312573	182.969348	177.4235619	149.5900782
Atlantic Forest	36	726	1344.4444	0.5318292	87.239572	164.0368175	222.7350489

Atlantic Forest	43	1162	2151.8519	1.4023101	233.235621	166.3224249	434.4813178
Atlantic Forest	34	1169	2164.8148	0.8383161	139.47812	166.3789097	27.07356573

Appendix A3: Biological metrics of shredders invertebrate families in headwater streams in Atlantic Forest and Neotropical Savanna biomes.

Local	Abundance	Density (ind/m ²)	Biomass (g/m ²)	Eco-exergy	Specific Eco-exergy	Instant Secondary Production (g/m ² /day)	Length (mm)
Neotropical Savanna	5	9.259259259	0.000519	0.08672664	167.1033507	0.023916591	2.78
Neotropical Savanna	0	0	0	0	0	0	0
Neotropical Savanna	0	0	0	0	0	0	0
Neotropical Savanna	18	3.33E+01	0.035396	5.9111063	166.9992738	0.818238774	4.52
Neotropical Savanna	2	3.703703704	0.000299	0.04992536	166.9744582	0.007614714	2.17
Neotropical Savanna	1	1.851851852	9.8696E-05	0.01644823	166.6550337	0.00282375	1.87
Neotropical Savanna	6	11.11111111	0.00051	0.1093334	214.3792098	0.02568282	2.5
Neotropical Savanna	1	1.851851852	0.0001	0.01674115	167.41153	0.004523158	2.36
Neotropical Savanna	4	7.407407407	0.002773	0.61286355	221.0110155	0.088752192	4.23
Neotropical Savanna	23	42.59259259	0.022699	3.79068796	166.9980159	0.512901511	4.76
Atlantic Forest	13	24.07407407	0.015051	2.51346787	166.996736	0.252924275	3.34
Atlantic Forest	24	44.44444444	0.014555	2.64543532	181.7544016	0.28122657	4.75
Atlantic Forest	86	159.2592593	0.115682	19.3188893	166.9999594	1.993791306	3.4
Atlantic Forest	69	127.7777778	0.208296	35.4463372	170.1729136	2.704670193	6.22

Atlantic Forest	20	37.03703704	0.01265	2.11262871	167.0062218	0.322468807	4.12
Atlantic Forest	52	96.2962963	0.105092	17.5503134	166.9995186	1.55303715	4.67
Atlantic Forest	11	20.37037037	0.016172	2.70073163	167.0004717	0.242046434	5.17
Atlantic Forest	76	140.7407407	0.103488	17.0689944	164.9369429	1.513818773	4.75
Atlantic Forest	126	233.3333333	0.260458	44.4321955	170.5925543	4.035616989	6.24
Atlantic Forest	111	205.5555556	0.126263	21.0858814	166.9996861	2.252447135	3.6
