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Tese de Doutorado

Eco-exergia como indicador de condição ambiental em bacias hidrográficas na savana neotropical

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Orientador: Prof. Dr. Marcos Callisto (UFMG)

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Belo Horizonte, Agosto de 2017

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Tese de Doutorado apresentada ao Programa de Pós Graduação em Ecologia, Conservação e Manejo de Vida Silvestre da Universidade Federal de Minas Gerais como parte dos requisitos necessários à obtenção do título de Doutor em Ecologia.

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Resumo

Os ecossistemas lóticos estão entre os mais ameaçados por atividades antrópicas em escala global. Para proteger e conservar a qualidade ambiental destes ecossistemas são necessárias medidas precisas de como eles respondem a alterações naturais e antropogênicas, tornando a utilização de indicadores ecológicos imprescindível. Dentre uma ampla gama de indicadores ecológicos, os indicadores baseados em exergia (eco-exergia e eco-exergia específica) destacam-se por prover uma linguagem universal para comparar diferentes organismos e sistemas, baseados em conceitos da física. Apesar de estarem bem estabelecidos como indicadores ecológicos em regiões temperadas, existe pouca informação sobre o uso de eco-exergia e eco-exergia específica em ecossistemas tropicais. O objetivo desta tese foi testar a capacidade de indicadores ecológicos baseados em exergia para avaliar as condições ambientais em diferentes ecossistemas em bacias hidrográficas de empreendimentos hidrelétricos na savana neotropical (bioma cerrado). Para tanto esta tese é dividida em três capítulos onde (1) buscou-se caracterizar os efeitos da presença de bivalves invasores sobre a estrutura de comunidades de macroinvertebrados bentônicos em reservatórios neotropicais; (2) determinou-se a influência da cobertura de dossel de mata ripária sobre a estrutura e funcionamento de comunidades de macroinvertebrados bentônicos em riachos de cabeceira em condições de referência; (3) determinou-se a influência de uma pequena central hidrelétrica sobre a estrutura de comunidades de macroinvertebrados bentônicos na calha de um rio. No primeiro capítulo foi observado que a presença de bivalves invasores aumenta a complexidade de comunidades de macroinvertebrados bentônicos em reservatórios neotropicais, representada por valores significativamente maiores de eco-exergia e eco-exergia específica. Isto sugere que os bivalves invasores integram-se às comunidades invadidas, provendo maior integração da comunidade bentônica com a produção na coluna d’água. No entanto, foi também verificado que a presença das espécies invasoras diminui a riqueza e biomassa de espécies nativas enquanto aumenta a biomassa do gastrópode invasor *Melanoides tubertulata*, o que sugere um cenário de *Invasion Meltdown*. No segundo capítulo os resultados mostram que a abertura do dossel de mata ripária tem efeito significativo na produção secundária e complexidade de comunidades de macroinvertebrados bentônicos, o que implica em uma dependência destas comunidades da produção autóctone em riachos neotropicais em condições de referência. No terceiro capítulo as seções fluviais diretamente afetadas pela Pequena Central Hidrelétrica (PCH) no rio Pandeiros possuem eco-exergia e eco-exergia específica significativamente diferentes daquelas sob regime hidrológico não regulado, a montante da PCH. Em conjunto com a dominância de espécies invasoras este resultado evidencia que a presença da barragem da PCH afeta significativamente a estrutura de comunidades de macroinvertebrados bentônicos em um rio com barramento hidrelétrico. Estes resultados mostram que eco-exergia e eco-exergia específica são bons indicadores em uma ampla variedade de ecossistemas aquáticos neotropicais, capazes de responder a diferentes alterações naturais ou antrópicas.

Palavras-chave: Áreas de referência; empreendimentos hidrelétricos; espécies invasoras; indicadores termodinâmicos.

Abstract

Lotic ecosystems are among the most threatened ones by human activities on a global scale. To protect and conserve the environmental quality of these ecosystems, accurate measurements of how they respond to natural and anthropogenic changes are necessary, making the use of ecological indicators essential. Among a wide range of ecological indicators, indicators based on exergy (eco-exergy and specific eco-exergy) stand out for providing a universal language to compare different organisms and systems, based on concepts of physics. Although well-established as ecological indicators in temperate regions, little information exists on the use of eco-exergy and specific eco-exergy in tropical ecosystems. The objective of this thesis was to test the ability of ecological indicators based on exergy to evaluate the environmental conditions of different ecosystems in hydropower basins in neotropical savannah (Cerrado biome). For this purpose, this thesis is divided into three chapters where the aims were to characterize (1) the ecological effects of the presence of invading bivalves on the structure of benthic macroinvertebrate communities in neotropical reservoirs; (2) the influence of riparian forest canopy cover on the structure and functioning of benthic macroinvertebrate communities in reference condition headwater streams; (3) the influence of a small hydropower dam on the structure of benthic macroinvertebrate communities in the main channel of a high-order river. In the first chapter it was observed that the presence of invasive bivalves significantly increases the complexity of communities of benthic macroinvertebrates in neotropical reservoirs, represented by significantly higher values of eco-exergy and specific eco-exergy. This suggests that the invasive bivalves are integrated to the native communities, providing greater integration of the benthic community with the water column production. However, it was also verified that the presence of the invaders decreases the richness and biomass of the native species while increasing the biomass of the invading gastropod *Melanoides tubertulata*, which suggests an *Invasion Meltdown* scenario. In the second chapter the results show that the riparian canopy cover has an ecological significant effect on the secondary production and complexity of the benthic communities, which implies a dependence of these communities on autochtonous production in neotropical streams under reference conditions. In the third chapter, the sampling sites directly affected by the small hydroelectric dam in the Pandeiros river have eco-exergy and specific eco-exergy significantly different from the areas under the river's non-regulated hydrological regime. In conjunction with the dominance of invasive species, these results show that the presence of the dam significantly affects the structure of the benthic macroinvertebrate communities. These results show that eco-exergy and specific eco-exergy are good indicators for a wide range of neotropical aquatic environments capable of responding to various types of natural or atrophic alterations.

Keywords: Reference sites; hydroelectric dams; invasive species; thermodynamic indicators

Sumário

Introdução

Sociedades humanas beneficiam-se imensamente de ecossistemas aquáticos continentais como rios e riachos como fonte de água para múltiplas funções, incluindo geração de energia elétrica, abastecimento doméstico e industrial, transporte, irrigação, piscicultura e recreação (Karr, 1999; Tundisi & Matsumura-Tundisi, 2008). No entanto, os ecossistemas lóticos estão entre os mais ameaçados por atividades antrópicas em escala global devido à urbanização, agricultura e atividades industriais, que têm como resultado a deterioração de qualidade de água, perda de habitat e perda de biodiversidade (Friberg, 2014). Para proteger e melhorar a qualidade ambiental destes ecossistemas são necessárias medidas precisas de como eles respondem a alterações naturais e antropogênicas (Silveira, 2004). Assim, a utilização de indicadores ecológicos é imprescindível, pois estes ilustram as respostas dos ecossistemas frente a modificações naturais ou antrópicas (Jørgensen, 2006).

Indicadores Ecológicos

Indicadores ecológicos são definidos como características mesuráveis de estrutura, composição ou função de sistemas ecológicos que podem ser utilizadas para avaliar a saúde ambiental ou para diagnosticar as causas de alterações ambientais (Jørgensen, 2007c). Estes indicadores sintetizam uma ampla gama de respostas dos ecossistemas em um valor numérico que pode ser relacionado a várias características físicas, químicas, morfológicas e biológicas (Jørgensen & Nielsen, 2007). Ao combinar vários atributos do ecossistema em um único valor, os indicadores também fornecem uma medida da qualidade ambiental de uma forma potencialmente acessível ao público leigo (Friberg, 2014). Desta forma, indicadores ecológicos podem subsidiar a proposição de medidas de manejo e fornecer subsídios para tomadores de decisões e gestores implementarem medidas que protejam os ecossistemas lóticos e os bens e serviços que estes proporcionam às sociedades humanas (Karr, 1999).

No Brasil indicadores biológicos são pouco utilizados por órgãos de gestão, pois a legislação ambiental que classifica a qualidade de água (CONAMA 357, 2005) determina apenas a utilização de parâmetros físicos, químicos e bacteriológicos como indicadores ecológicos de qualidade da água para a avaliação da qualidade ambiental de ecossistemas aquáticos. Em geral, as avaliações de qualidade de água através destes parâmetros atendem aos usos para consumo doméstico e industrial e agricultura, mas não fornecem respostas claras sobre a condição de qualidade ecológica (Silveira, 2004). Indicadores biológicos apresentam uma clara vantagem por medirem diretamente respostas ecologicamente relevantes a perturbações, serem capazes de integrar os efeitos sinergéticos de várias perturbações e as respostas dos ecossistemas ao longo do tempo (Friberg, 2014).

Dentre as várias categorias de indicadores biológicos, os indicadores termodinâmicos destacam-se por serem baseados em conceitos da física necessários para descrever o estado de um ecossistema (Ludovisi & Jørgensen, 2009). Os indicadores termodinâmicos não estão sujeitos às limitações dos indicadores taxonômicos, por proverem uma linguagem universal para comparar diferentes organismos e ecossistemas. Em outras palavras, há dificuldade para generalização e comparação entre diferentes ecossistemas ao se utilizar indicadores taxonômicos, pois a composição taxonômica varia geograficamente de acordo com a história evolutiva e os limites ambientais locais (Karr, 1999).

Termodinâmica e Ecologia

Termodinâmica é a ciência que estuda os processos de troca e conversão de energia e sua relação com trabalho (Stremke et al., 2011). As leis da termodinâmica regem estes processos, sendo invioláveis por quaisquer meios naturais ou tecnológicos (Pulselli et al., 2011). A primeira lei da termodinâmica, também chamada de Lei da Conservação de Energia, afirma que a energia pode ser transformada de uma forma em outra, mas não pode ser criada ou destruída (Svirezhev, 2000). A segunda lei, também conhecida como Lei da Entropia, afirma que nenhum processo de transformação energética ocorrerá espontaneamente a menos que haja degradação da energia de uma forma mais concentrada em outra mais dispersa (Svirezhev, 2000). A terceira lei, conhecida como Teorema de Nernst, afirma que quando a temperatura de um sistema se aproxima do zero absoluto seu grau de desordem aproxima-se ao seu valor mínimo (Svirezhev, 2000).

Processos de transformação de energia não possuem 100% de eficiência e parte da energia é perdida em uma forma incapaz de realizar trabalho útil, geralmente como energia térmica na forma de calor. Como resultado, a quantidade total de energia permanece a mesma (obedecendo à primeira lei), mas a sua qualidade é diminuída (conforme a segunda lei). Esta forma de energia incapaz de realizar trabalho útil é chamada de entropia, termo que também denota o grau de desordem de um sistema (Svirezhev, 2000). Com o tempo, em um sistema fechado, a tendência é que a entropia aumente até atingir um ponto máximo onde não haja mais gradientes energéticos e cessem os fluxos de energia. Este estado é chamado de equilíbrio termodinâmico (Jørgensen, 2007a).

Para que um sistema possa continuar indefinidamente com processos de transformação de energia é preciso que se mantenha distante do equilíbrio termodinâmico (Jørgensen, 2007b). Para tanto, o sistema necessita absorver um fluxo contínuo de energia de alta qualidade (ou baixa entropia) e expelir continuamente energia de baixa qualidade (ou alta entropia). Assim, para se manter distante do equilíbrio termodinâmico um sistema precisa ser termodinamicamente aberto, capaz de realizar trocas de energia com o ambiente externo.

Nos sistemas ecológicos o distanciamento do equilíbrio termodinâmico é alcançado através da produção primária e da respiração, respectivamente (Jørgensen, 2007a). Na produção primária o ecossistema absorve energia de alta qualidade, geralmente na forma de energia radiante proveniente do Sol, e transforma parte dela em energia potencial química que é armazenada na biomassa dos seres autotróficos (Jørgensen, 2009). Na respiração esta energia armazenada é utilizada para alimentar diversos processos metabólicos e então eliminada do ambiente sob na de energia térmica (Svirezhev, 2000).

A aplicação dos conceitos de termodinâmica na ecologia teve início nos primórdios da ecologia moderna, com a síntese de Lindemann (1942) que descreveu a estrutura do ecossistema como uma pirâmide trófica. Influenciado pelos trabalhos de Elton, que em 1927 desenvolveu o conceito de nicho e publicou os primeiros estudos sobre teias tróficas e fluxo de energia, e Hutchinson, que em 1940 publicou trabalhos sobre transferência de energia, processos tróficos e sucessão, Lindemann conseguiu descrever importantes padrões para comunidades com base em relações nutricionais e tróficas regidas pela segunda lei da termodinâmica (Rezende et al., 2008). No entanto, a difusão da ecologia termodinâmica foi impulsionada após a publicação em 1953 do livro “Fundamentos de Ecologia” pelos irmãos Howard e Eugene Odum, onde é descrito um modelo termodinâmico para a sucessão e o desenvolvimento de ecossistemas. Durante as décadas seguintes a essa publicação seminal surgiram várias abordagens ecossistêmicas com ênfase na relação entre a termodinâmica e a teoria da informação (p.ex. Fisher & Likens, 1973; Golley, 1961; Odum, 1956).

Indicadores Termodinâmicos

A partir deste desenvolvimento e popularização do uso de conceitos da termodinâmica na ecologia foram desenvolvidos indicadores termodinâmicos que buscam avaliar a condição de um sistema ecológico de forma holística, baseada nas propriedades e na estrutura do sistema como um todo (Jørgensen, 2007b). Dentre os vários indicadores termodinâmicos destacam-se os baseados em exergia, como a eco-exergia e eco-exergia específica (Jørgensen & Mejer, 1977).

Exergia é definida como a quantidade máxima de trabalho em um sistema que pode ser obtida em um processo que o leve ao equilíbrio termodinâmico com um estado de referência, ou seja, representa a distância do sistema em seu presente estado em relação ao equilíbrio termodinâmico (Silow & Mokry, 2010). No entanto, uma vez que um estado de referência externo seria apenas outro ecossistema, a eco-exergia utiliza como estado de referência o próprio ecossistema em um estado teórico de degradação máxima, sendo formado apenas por seus elementos químicos básicos. Outra importante diferença é que o cálculo para a exergia mecânica leva em conta primariamente diferenças de temperatura e pressão entre o sistema e o estado de referência (Susani et al., 2006). Como o estado de referência utilizado na eco-exergia é o próprio ecossistema em um diferente estado de desenvolvimento, diferenças de pressão e temperatura são pouco relevantes (Susani et al., 2006).

Eco-exergia é definida por Jørgensen et al. (2005) como a medida da distância entre o estado presente do ecossistema e como este seria caso estivesse em equilíbrio termodinâmico com o ambiente abiótico (Figura 1). Em outras palavras, é a medida da quantidade de trabalho necessária para criar um determinado sistema biológico a partir de seus compostos químicos primários (Susani et al., 2006). Tomada por si só, a eco-exergia de um ecossistema é a diferença entre o conteúdo de entropia de um sistema e o de sua referência (Svirezhev, 2000) e representa a medida estrutural da biomassa e a informação nela embutida (Jørgensen et al., 1995). Eco-exergia específica é definida como a eco-exergia total dividida pela biomassa total, medindo a capacidade do ecossistema de utilizar fluxos externos de energia, refletindo o grau de complexidade ou desenvolvimento do sistema (Silow & Mokry, 2010). O distanciamento do sistema em relação ao equilíbrio termodinâmico ocorre de três formas: (1) aumento na estrutura física do sistema na forma de biomassa; (2) aumento do número de ligações entre os componentes do sistema aumentando o fluxo interno de energia; (3) aumento da informação embutida no sistema, aumentando sua complexidade (Jørgensen, 2006).

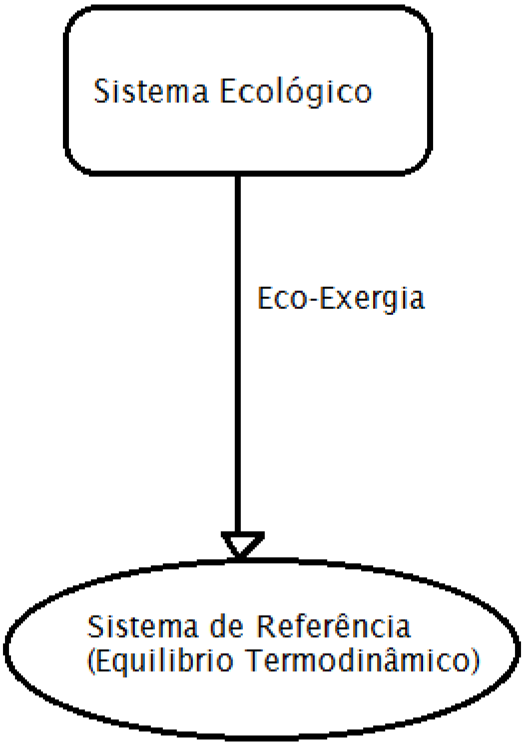

Figura 1 – Representação gráfica do conceito da eco-exergia, representando a medida da diferença de energia entre um sistema ecológico e um sistema de referência com a mesma composição química, mas em equilíbrio termodinâmico (adaptado de Jørgensen, 2007b).

Buscando explicar a complexidade de sistemas ecológicos através do arcabouço teórico da eco-exergia, Jørgensen (2007b) desenvolveu a Teoria Integrada dos Ecossistemas baseada em dez princípios observacionais:

1- *Todos os ecossistemas são sistemas abertos localizados em um ambiente no qual recebem inputs de matéria e energia e no qual descarregam um output de matéria e energia.*
2- *Ecossistemas possuem vários níveis de organização e operam hierarquicamente.*
3- *Termodinamicamente, a vida baseada em carbono é viável entre 250 e 350 Kelvin.*
4- *Massa, incluindo biomassa, e energia são conservadas.*
5- *A vida baseada em carbono na Terra possui uma bioquímica básica característica, que todos os organismos compartilham.*
6- *Nenhum sistema ecológico existe em isolamento, mas sim conectado a outros.*
7- *Todos os processos ecossistêmicos são irreversíveis.*
8- *Processos biológicos utilizam energia capturada (input) para se colocarem distantes do equilíbrio termodinâmico e se manterem em um estado de baixa entropia em relação ao ambiente.*
9- *Após a absorção inicial de energia, o crescimento e desenvolvimento de um ecossistema é possível por: (i) aumento em sua estrutura física (biomassa); (ii) aumento nas ligações entre suas partes constituintes (maior ciclagem); (iii) aumento na informação embutida no sistema.*
10- *Um ecossistema recebendo energia tentará maximizar sua capacidade de armazenamento de energia útil se mais de uma possibilidade lhe for apresentada, de modo que em longo prazo aquela que mova o sistema mais distante do equilíbrio termodinâmico será a selecionada.*

Eco-exergia e eco-exergia específica podem ser usadas como indicadores ambientais e devem ser utilizadas complementarmente (Marques et al., 2003). Valores mais altos destes parâmetros são indicativos de maior diversidade, maior redundância funcional e maior resiliência de sistemas mais complexos (Salas et al., 2005). Isto pode ser interpretado como uma consequência do principio 10 da Teoria Integrada dos Ecossistemas (Jørgensen, 2007b), onde o ecossistema tende a maximizar a sua capacidade de armazenamento de eco-exergia, tendendo a se estabilizar na condição que deixe o sistema mais distante do equilíbrio termodinâmico. Desta forma, é esperado que um ecossistema perturbado apresente menor eco-exergia e eco-exergia específica quando comparado a um ambiente pouco perturbado, uma vez que distúrbios aumentariam a entropia do ecossistema (Jørgensen, 2007c). Neste contexto teório, a utilização da eco-exergia como indicador ecológico propõe uma relação inversa da eco-exergia de um sistema ecológico em um gradiente de distúrbios ambientais.

Apesar de sua publicação inicial ter acontecido no final dos anos 70 (Jørgensen & Mejer, 1977), as primeiras utilizações práticas da eco-exergia como indicador ambiental foram publicadas no final dos anos 90. Marques et al. (1997) testaram as respostas de eco-exergia e eco-exergia específica em um gradiente de eutrofização no estuário do rio Mondego, Portugal, comparando-as com as respostas de indicadores de biodiversidade. Xu (1997) utilizou eco-exergia e eco-exergia específica como indicadores no lago Chaolu, China, determinando suas relações com diversos parâmetros ambientais, como eutrofização e biodiversidade. Estes trabalhos pioneiros detectaram uma forte correlação da eco-exergia com biodiversidade, bem como forte correlação negativa com eutrofização, demonstrando que eco-exergia é um bom indicador da qualidade ambiental de ecossistemas aquáticos.

Na China os estudos com eco-exergia continuaram focados no desenvolvimento de indicadores ecológicos em ambientes lênticos. Inicialmente foi desenvolvido um modelo para os sintomas estruturais e funcionais ao nível de ecossistema para a contaminação por acidificação, cobre, petróleo e pesticidas (Xu et al., 1999).

Posteriormente este modelo foi expandido para o desenvolvimento de um índice de integridade ecológica (Xu et al., 2001, 2005) e criação de um modelo preditivo para a restauração de lagos (Kong et al., 2013). Através destes estudos foi possível comprovar a robustez da eco-exergia como indicador ecológico, demonstrando que este indicador responde bem aos vários tipos de impactos aos quais os ecossistemas aquáticos estão sujeitos.

Em Portugal os estudos subsequentes no estuário do rio Mondego testaram o desempenho de eco-exergia e eco-exergia específica em conjunto com outros indicadores em experimentos de colonização (Patrício et al., 2006) e testaram o efeito da distinção taxonômica em sua avaliação ambiental (Salas et al., 2006). Posteriormente estes índices foram utilizados para detectar mudanças após restauração da conexão entre os braços norte e sul do estuário do rio Mondego (Veríssimo et al., 2012) e em um estudo de longo prazo das consequências desta ação de manejo em larga escala (Veríssimo et al., 2016). Nestes estudos, além de demonstrar a efetividade da eco-exergia como indicador e sua capacidade de responder a impactos antrópicos, foi demonstrada a sua conformidade com os resultados de outros indicadores ecológicos, como índices de diversidade taxonômica e de diversidade funcional.

Eco-exergia e eco-exergia específica vêm sendo utilizados como indicadores na Europa e Ásia nos últimos 20 anos (p.ex. Ludovisi, 2014; Nguyen et al., 2014; Silow et al., 2011). Dentre estes, destacam-se os estudos no lago Chozas (Espanha) que utilizaram a eco-exergia como indicador para os efeitos do lagostim invasor *Procambarus clarkii* (Cambaridae) no ecossistema. Inicialmente foram comparados dados antes e após o estabelecimento da espécie invasora (Bastianoni et al., 2010), que demonstraram o grande impacto deste invasor sobre o ecossistema. Posteriormente foi desenvolvido um modelo preditivo para os efeitos do invasor utilizando eco-exergia

(Marchi et al., 2011), que foi utilizado para testar a resistência e capacidade de recuperação do sistema (Marchi et al., 2012). Estes estudos detalham as conseqüências de uma invasão biológica sobre um ecossistema aquático e interações da espécie invasora com diversos componentes do ecossistema.

Apesar de estarem bem estabelecidos como indicadores ecológicos em ambientes temperados, existe pouca informação sobre seu uso em ecossistemas tropicais. Molozzi et al. (2013) testaram a eficiência da eco-exergia e eco-exergia específica como indicadores ambientais em reservatórios neotropicais. Ainda existe uma lacuna no conhecimento sobre a aplicação da eco-exergia como indicador em ambientes lóticos neotropicais. Outra lacuna no conhecimento são os resultados da interação de espécies exóticas com função de espécies engenheiras de ecossistema, espécies que causam alterações na estrutura física onde se instalam (Jones et al., 1994), na estrutura e composição de comunidades de macroinvertebrados bentônicos.

Assim o objetivo desta tese foi testar a capacidade de indicadores biológicos baseados em exergia (eco-exergia e eco-exergia específica) para avaliar as condições ambientais de diferentes ecossistemas (riachos, rio, reservatórios) em bacias hidrográficas na savana neotropical (bioma cerrado).

No primeiro capítulo buscou-se caracterizar os efeitos da presença de bivalves invasores sobre a estrutura de comunidades de macroinvertebrados bentônicos em reservatórios neotropicais. No segundo capítulo o objetivo foi determinar a influência da cobertura de dossel de mata ciliar sobre a estrutura e funcionamento de comunidades de macroinvertebrados bentônicos em riachos de cabeceira em condições de referência. No terceiro capítulo objetivou-se determinar a influência de uma pequena central hidrelétrica sobre a estrutura de comunidades de macroinvertebrados bentônicos na calha de um rio de alta ordem.

Esta tese de doutorado foi desenvolvida como parte dos projetos P&D ANEEL/CEMIG GT 487 ("*Desenvolvimento de Índices de Integridade Biótica: macroinvertebrados bentônicos como indicadores de qualidade de água em bacias hidrográficas de empreendimentos hidrelétricos da CEMIG em Minas Gerais*") e P&D ANEEL/CEMIG GT 550 ("*Desenvolvimento de metodologia para avaliação da viabilidade de descomissionamento de uma Pequena Central Hidrelétrica (PCH)*"). Com isto esta tese teve acesso a um amplo banco de dados que possibilitou expandir a abordagem da eco-exergia em diferentes ecossistemas lóticos na savana neotropical.

Metodologia

Áreas de estudo

Reservatórios

Para a coleta em reservatórios foram estabelecidos pontos de coletas em quatro reservatórios de empreendimentos hidrelétricos no cerrado – Nova Ponte, São Simão, Três Marias e Volta Grande - localizados no estado de Minas Gerais (Figura 3). A rede amostral estabelecida nas margens de cada reservatório foi definida conforme descrito em Macedo et al. (2014). A partir de um ponto sorteado aleatoriamente, o perímetro total do reservatório foi dividido em 40 trechos equivalentes e no início de cada trecho foi estabelecido um ponto de coleta. As coletas foram realizadas no período seco nos anos de 2009 (Nova Ponte), 2010 (São Simão), 2011 (Três Marias) e 2012 (Volta Grande), totalizando 160 pontos de coleta.

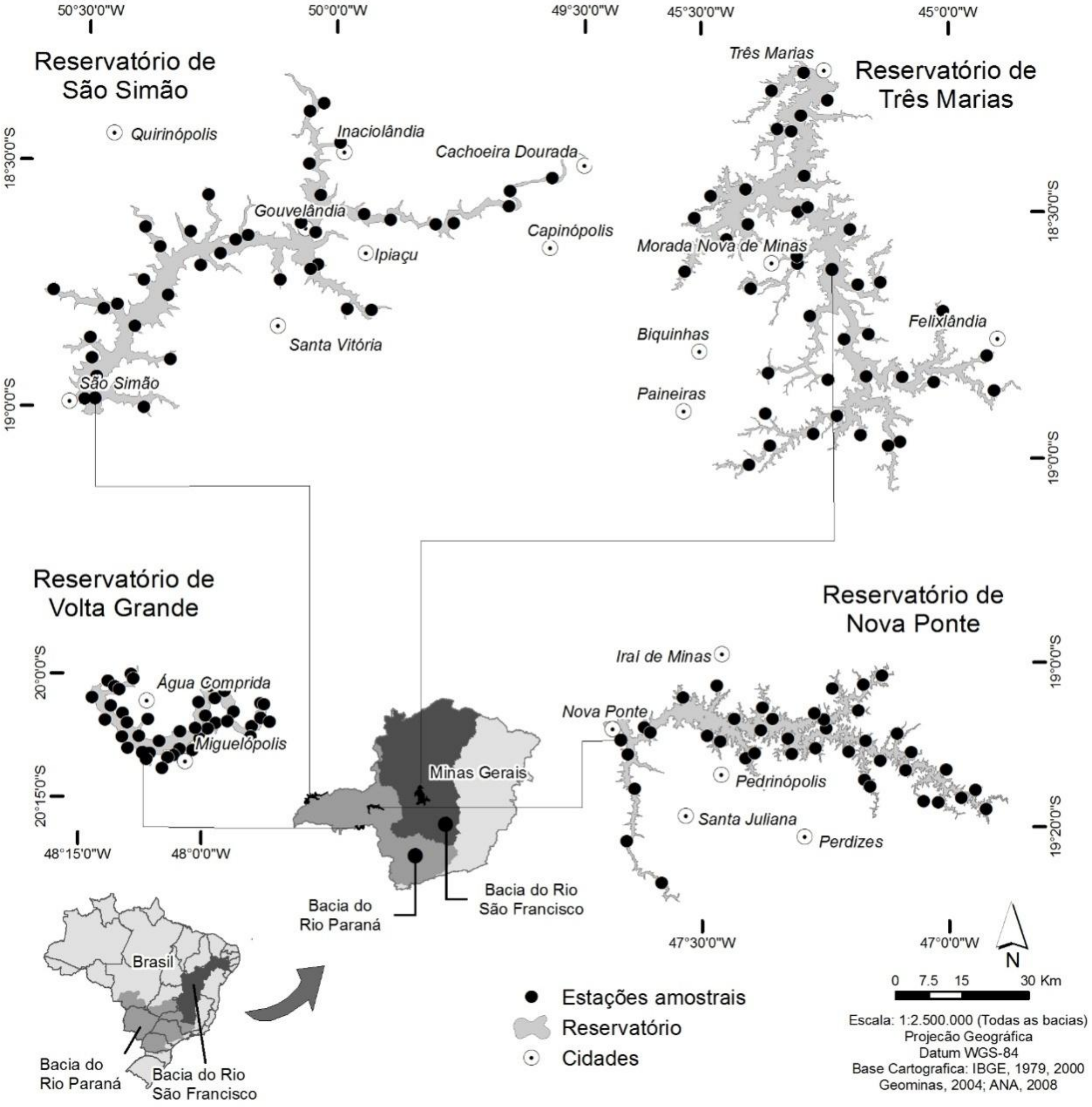

Figura 3 – Localização dos reservatórios de Nova Ponte, São Simão, Volta Grande e Três Marias e distribuição dos pontos de coleta.

O reservatório de Nova Ponte está localizado nos rios Araguari e Quebra-Anzol, construído para geração de energia hidrelétrica. Este reservatório é o maior de uma série de reservatórios no rio Araguari, com profundidade de 120 m próxima à barragem, comprimento de 115 km e volume de 12,8 bilhões m³. Suas comportas foram fechadas em 1993 e as operações iniciaram-se em 1994 (CEMIG, 2014).

O reservatório de São Simão é também um reservatório de grande porte, com área de superfície de 722 km², volume total de 11 bilhões de m³ e profundidade máxima de 126,45 m. Ele é formado pela regulação do rio Parnaíba e seus tributários: os rios Alegre, Preto, São Francisco, Rio dos Bois, Meia Ponte, Tijuco e Prata (Pinto-Coelho, 2013). Sua operação começou em 1978, visando a geração de energia hidrelétrica (Souza & Souza, 2009).

O reservatório de Volta Grande situa-se na porção baixa da bacia hidrográfica do rio Grande entre os estados de Minas Gerais e São Paulo. Abrange os municípios de Conceição das Alagoas, Água Comprida e Uberaba (MG), Miguelópolis, Aramina e Igarapava (SP). Trata-se de um reservatório de médio porte, com área inundada de aproximadamente 222 km, perímetro de 80 km (Rolla et al., 1990) e volume de 2,3 bilhões m³ construído para geração de energia elétrica (Braga & Gomieiro, 1997). Tendo iniciado sua operação em 1974, possui capacidade instalada para a geração de 380 MW (Campos, 2003).

O reservatório de Três Marias está localizado no trecho alto da bacia do rio São Francisco. É um dos maiores reservatórios do país, com uma área de superfície de 1040 km², volume total de 21 bilhões m³ e profundidade máxima de 58,5 m (CEMIG, 2014). Suas águas vem primariamente do rio São Francisco e tributários, como os rios São Vicente, Paraopeba, Sucuriú, Indaiá, Ribeirão do Boi, Ribeirão da Extrema e Borrachudo (Esteves et al., 1985). Ele começou a operar em 1962 para controle de enchentes, melhorar navegação, encorajar desenvolvimento e irrigação e gerar energia hidrelétrica (Freitas & Filho, 2004).

Riachos de Cabeceira

Os riachos de cabeceira estudados localizam-se na bacia hidrográfica do rio Araguari, no estado de Minas Gerais, sudeste do Brasil. Os riachos de cabeceira desta bacia encontram-se no platô da Serra da Canastra, a uma altitude de aproximadamente

1440 metros acima do nível do mar (Rodrigues & Souza, 2013). Os riachos foram selecionados entre áreas de estudo potenciais baseadas na interpretação de uma combinação de imagens de alta resolução (resolução especial de 0.6-5 m; imagens do Google Earth) com imagens multiespectrais de satélite Landsat Thematic Mapper (Macedo et al. 2014). As áreas de estudo em potencial foram então classificadas durante campanha de reconhecimento como de dossel aberto ou fechado através de um densiômetro (Kaufmann et al., 1999). Dentre estas, oito riachos foram selecionados (Figura 4) seguindo os critérios: mínimo de distúrbios antropogênicos na área de drenagem, ausência de influencia antropogênica direta e presença de vegetação ripária nativa. Todos os riachos selecionados foram classificados como áreas de referência para a bacia hidrográfica do rio Araguari por Martins et al. (2017). Baseado nos dados de cobertura do dossel, quarto dos riachos selecionados foram classificados como de dossel aberto e quatro como de dossel fechado (Tabela 1).

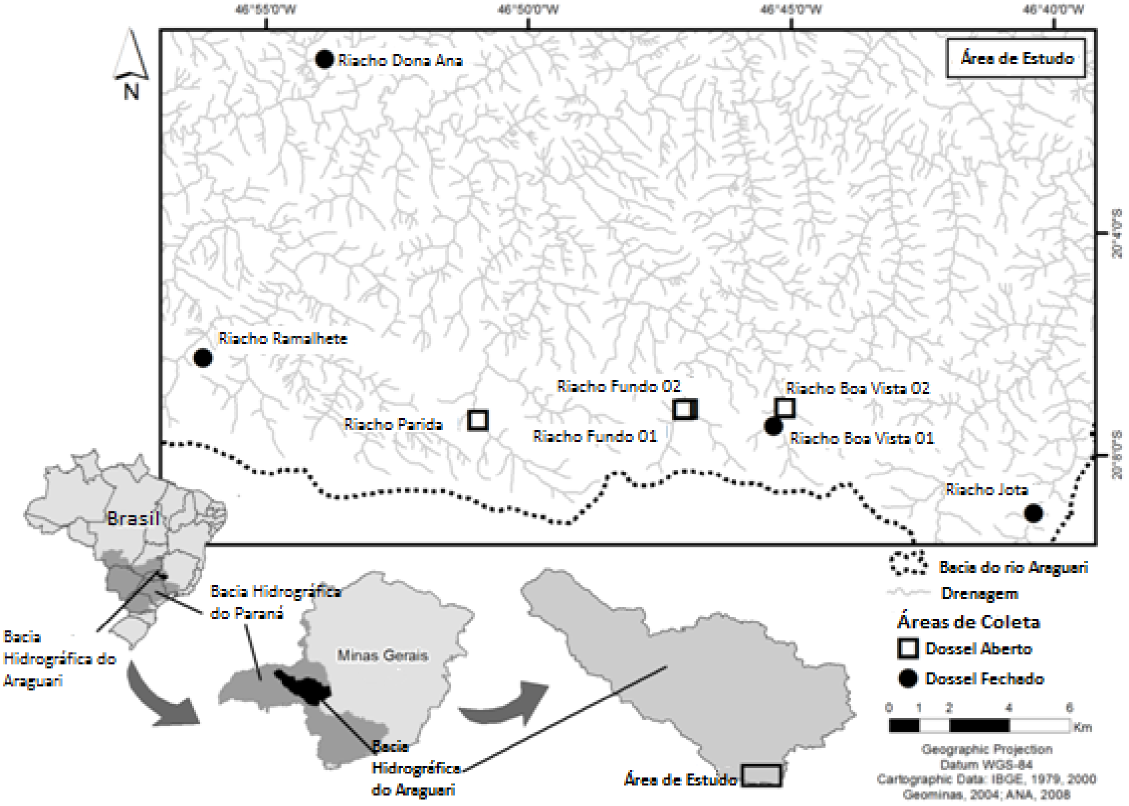

Figura 4 – Localização das áreas de estudo na bacia hidrográfica do rio Araguari.

Tabela 1 – Áreas de estudo na bacia do rio Araguari caracterizadas pela cobertura de dossel da mata ciliar.

Riacho	Cobertura de dossel média (±DP)	Categoria
Parida	3.21(±7.60)	Aberto
Fundo I	6.55(±14.50)	Aberto
Fundo II	8.42(±10.44)	Aberto
Boa Vista II	0(±0)	Aberto
Jota	50.80(±44.95)	Fechado
Ramalhete	37.30(±37.12)	Fechado
Boa Vista I	39.57(±38.64)	Fechado
Dona Ana	46.66(±45.44)	Fechado

Rio Pandeiros

A amstragem de rios ocorre no rio Pandeiros foram determinados quatro sítios amostrais: um em trecho de curso livre a montante do reservatório, dois em trechos afetados diretamente pela barragem da PCH e um na planície de inundação a jusante da barragem (Figura 5). O rio Pandeiros é um importante afluente da margem esquerda do rio São Francisco, com extensão aproximada de 145 km. A região alagada e as veredas no rio Pandeiros estão entre as áreas prioritárias para conservação do bioma cerrado, sendo também considerada de Importância Biológica Especial, por constituírem-se em ambientes únicos no estado e possuírem alta riqueza de espécies (Drummond et al., 2005).

A PCH Pandeiros foi instalada no rio de mesmo nome em 1957 e encontra-se desativada. Seu reservatório apresenta área de 280 hectares e sua barragem, de crista livre, altura máxima de 10,30 metros. Sua casa de força localiza-se a cerca de 400 metros a jusante da barragem e, quando em operação, o aproveitamento, a fio d'água, turbinava até 35 m^3/s, com potência de 4,2 MW (Fonseca et al., 2008).

Por sua potencial importância para o recrutamento das espécies de peixes na bacia do São Francisco, em 1992 foi promulgada a Lei Estadual 10.629 que estabeleceu o conceito de rio de preservação permanente e declarou o rio Pandeiros enquadrado nesta categoria. Em janeiro de 1995 foi criada a Área de Proteção Ambiental do rio Pandeiros - APA Pandeiros, com 380.000 hectares, englobando a área da PCH, com o objetivo de proteger o Pântano de Pandeiros (Lei Estadual nº 11.901). Em 2004, por meio do Decreto Estadual 43.910, foi criado o Refúgio Estadual de Vida Silvestre do rio Pandeiros, unidade de conservação de proteção integral.

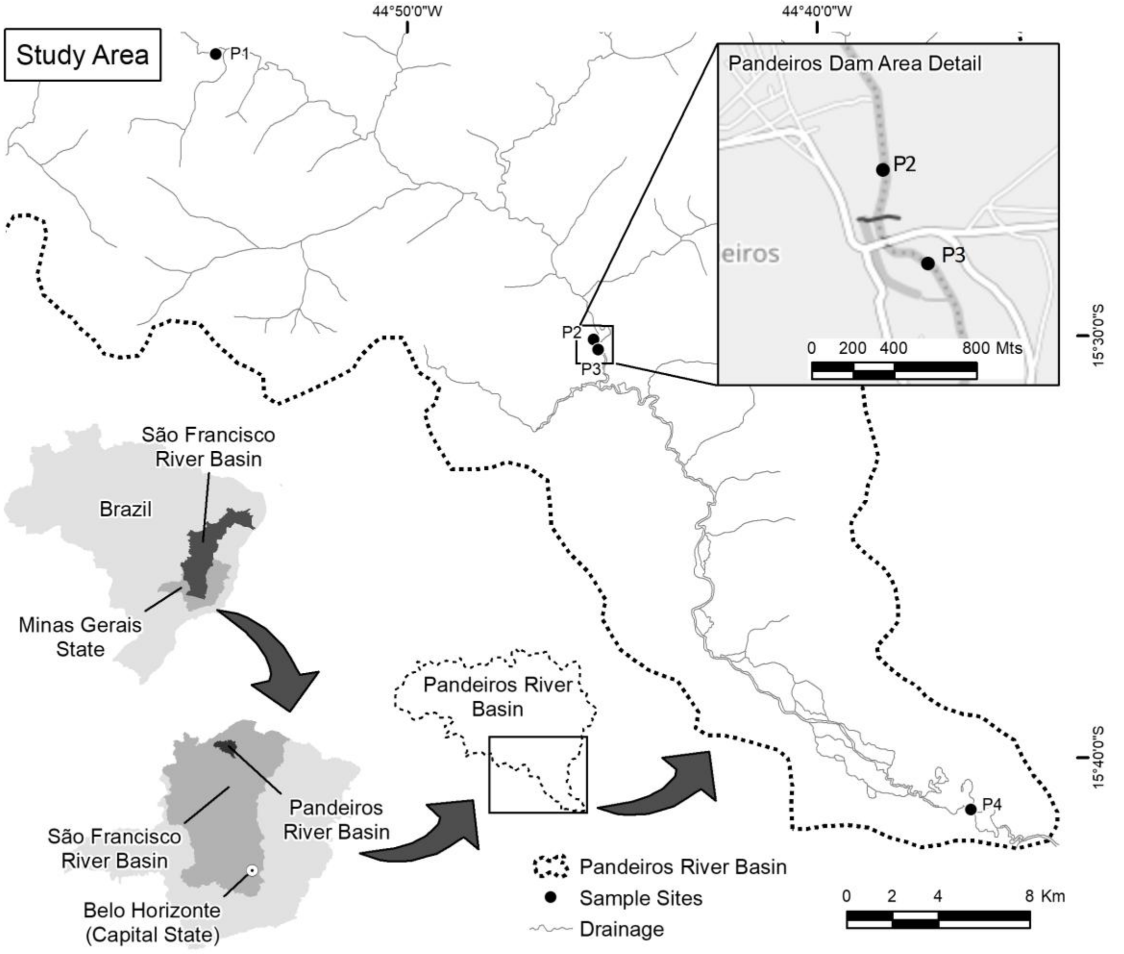

Figura 5 – Localização das áreas de estudo no rio Pandeiros.

Amostragens de organismos bentônicos

Nos reservatórios, os macroinvertebrados bentônicos foram coletados em cada ponto de amostragem dos reservatórios utilizando uma draga de Eckman-Birge (área de 15 cm²) lançada a cerca de 5-10 metros da margem. As campanhas amostrais foram realizadas nos anos de 2009 a 2012 (Figura 6 a).

Nos riachos de cabeceira foi utilizado um amostrador do tipo “kick-net” (30cm de abertura, 500µm de malha, área de 0,09 m²) (Figura 6 b). Em cada um dos riachos selecionados foi determinado um trecho amostral de 25m de comprimento, dividido em seis transectos equidistantes. Os macroinvertebrados foram coletados em todos os seis transectos com um coletor do tipo “kick-net”, totalizando seis sub-amostras em cada sítio amostral. As campanhas amostrais foram realizadas em abril e maio de 2014.

No rio Pandeiros, em cada ponto amostral foram coletadas (Figura 6 c) quatro sub-amostras de um amostrador do tipo “kick-net” (30cm de abertura, 500µm de malha, área de 0,09 m²). Foram realizadas seis campanhas amostrais, três no período chuvoso (dez/14, jan/15 e fev/15) e três no período seco (set/14, abr/15 e jun/15).

Figura 6 – Amostragem de organismos bentônicos em reservatórios (a), riachos de referência (b) e no rio Pandeiros (c).

Atividades em Laboratório

Em laboratório as amostras foram lavadas, triadas (Figura 7 a) e os macroinvertebrados bentônicos foram identificados em estereomicroscópio (Figura 7 b) com o apoio de literatura específica (Merritt and Cummins 1996; Mugnai et al. 2010; Hamada et al. 2014). Os espécimes foram identificados até o nível taxonômico mais preciso o possivel, geralmente até o nível de gênero ou família. Os espécimes foram então fixados em álcool 70% e depositados na Coleção de Referência de Macroinvertebrados Bentôncos, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

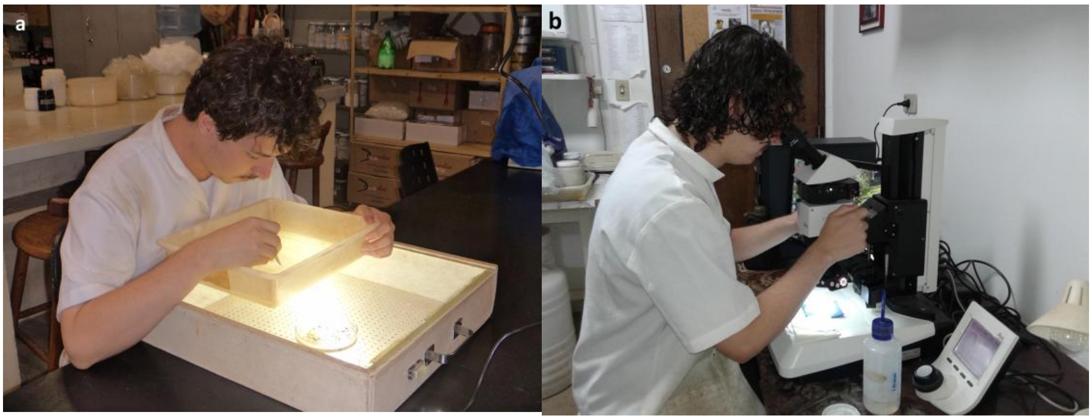

Figura 7 – Triagem (a) e identificação (b) em laboratório de amostras de macroinvertebrados bentônicos.

Utilizando equações de comprimento-massa foi estimada a biomassa seca (g/m²) de cada táxon coletado. A biomassa seca (g/m²) foi estimada utilizando equações de comprimento-massa (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). Cada espécime coletado, até 100 por táxon em cada área de coleta, foi fotografado em um estereomicroscópio (modelo Leica M80) equipado com uma câmera digital (modelo Leica IC 80 HD). O comprimento de cada espécime fotografado foi medido (Figura 8) utilizando o software Motic Image Plus 2.0.

Figura 8 – Medida do comprimento de um macroinvertebrado bentônico (Belostomatidae – Hemiptera) através do software Motic Image Plus 2.0.

Eco-Exergia

Para calcular a eco-exergia foi utilizada a seguinte equação (Jørgensen, 2006):

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

Onde ***βi*** é uma constante baseada na informação genética contida no componente (**i**) do ecossistema, definidas por Jørgensen et al. (2005) e **ci** é a concentração (biomassa) do componente **i** do ecossistema.

Eco-exergia específica foi calculada pela seguinte formula:

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

Onde ***EX*** é a eco-exergia total e ***BM*** é a biomassa total.

Capítulo 1

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Invasive bivalves increase benthic communities complexity in neotropical reservoirs

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Highlights

1 – Invasive bivalves do not act as facilitators for benthic macroinvertebrate communities.

2 – Benthic macroinvertebrate communities become more complex with the presence of invasive bivalves.

3 – Eco-exergy and specific eco-exergy are able to capture the effects of biological invasion over the complexity of benthic macroinvertebrate communities.

4 – Results suggest an invasion meltdown scenario with the invasive bivalves being followed by the invasive gastropod *Melanoides tuberculata*.

Abstract

Invasive bivalves often act as ecosystem engineers, generally causing physical alterations in the ecosystems in which they establish themselves. However, the effects of these physical alterations over benthic macroinvertebrate communities' structure are less clear. The objective of this study was to characterize the ecological effects of the invasive bivalves *Corbicula fluminea* and *Limnoperna fortunei* on the structure of benthic macroinvertebrate communities in neo-tropical reservoirs. Three hypotheses were tested: (1) invasive bivalves act as facilitator species to other benthic macroinvertebrates, resulting in communities with higher number of species, abundance and diversity; (2) invasive bivalves change the taxonomic composition of benthic macroinvertebrate communities; (3) invasive bivalves increase the complexity of benthic macroinvertebrate communities. For that it was used data from 160 sampling sites from four reservoirs. We sampled sites once in each area, during the dry season in 2009 to 2012. The first hypothesis was rejected, as the presence of invasive bivalves significantly decreased the host benthic communities' number of species and abundance. The second hypothesis was corroborated, as the composition of other benthic macroinvertebrates was shown to be significantly different between sites with and without invasive bivalves. We observed a shift from communities dominated by common soft substrate taxa, such as Chironomidae and Oligochaeta, to communities dominated by the invasive Gastropoda *Melanoides tuberculata*. The biomass data corroborated that, showing significantly higher biomass of *M. tuberculata* in sites with invasive bivalves, but significantly lower biomass of native species. Benthic macroinvertebrate communities presenting invasive bivalves showed significantly higher eco-exergy and specific eco-exergy, which corroborate the third hypothesis. These results suggest that while the presence of invasive bivalves limits the abundance of soft bottom taxa such as Chironomidae and Oligochaeta, it enhances benthic communities’ complexity and provide new energetic pathways to benthic communities in reservoirs. This study also suggests a scenario of invasion meltdown, as *M. tuberculata* was facilitated by the invasive bivalves.

Key-words: Eco-exergy, ecosystem engineers, invasive species, thermodynamic ecological indicators

Introduction

Invasive species are considered the second highest cause of biodiversity loss at a global scale (Ricciardi, 2007; Thomaz et al., 2015; Vitousek, 1997). Freshwater ecosystems are especially vulnerable, due to widespread human disturbance, such as channelization, pollution and dam and reservoir construction (Havel et al., 2005; Turak et al., 2016).

Invasive bivalves are among the most successful invasive species in freshwater ecosystems (Oliveira et al., 2011; Paschoal et al., 2015; Ricciardi, 2007). As most successful invasive species, invasive bivalves are typically r-selected species, adapted to colonize a wide range of aquatic environments and exhibiting high fecundity, rapid growth and broad physiological tolerance to several abiotic factors (Nakano et al., 2015). Such characteristics allow them to become dominant species, exhibiting high densities and constituting a major fraction of the benthic macroinvertebrates community biomass (Karatayev et al., 2007b).

Most of the impacts on benthic communities caused by invasive bivalves are a direct result on their function as ecosystem engineers, which cause environmental physical modifications (Jones et al., 1994; Sousa et al., 2009; Zaiko and Daunys, 2015). Actually, bivalve shell production, filter feeding and bioturbation, result in new interactions or process pathways, markedly affecting ecosystem structure and functioning (Sylvester et al., 2007).

While some studies show negative impacts over benthic macroinvertebrate communities (eg.,Nalepa et al. 1998; Lozano et al. 2001), invasive bivalves generally act as facilitators for benthic macroinvertebrates, increasing their abundance, biomass and number of species, as their shells usually form a complex hard substrate that would be otherwise rare in most aquatic ecosystems (Mathers et al., 2016; Norkko et al., 2006;

Sardiña et al., 2011). However, different benthic macroinvertebrate taxa do not benefit equally of this facilitation process (Boltovskoy and Correa, 2015). Scrapers, deposit feeders and their predators benefit the most from the physical modifications caused by invasive bivalves, while burrowers and other taxa adapted to soft bottom habitats, may thrive better in bare sediment habitats (Karatayev et al., 2007a). This often results in significant changes in benthic macroinvertebrate communities composition, namely in soft bottom ecosystems, such as reservoirs (Burlakova et al., 2012).

Changes in community taxonomic structure may result in changes in communities' capacity for self-organization, which represents the entropy within a community's boundaries (Jørgensen, 2007). Since entropy is difficult to quantify directly in ecosystems, thermodynamic indicators, such as eco-exergy, may be used to capture ecosystem's self-organization capacity (Marchi et al., 2010). Exergy can be defined as the difference between the system's entropy content and the one from its reference system (Svirezhev, 2000). Eco-exergy constitutes a static structural estimation resulting from dynamic qualities of the communities, which may be seen as biomass with a built in measure of quality, so to say encompassing the biomass in a system and the information embedded in it. Eco-exergy is assumed to express the complexity of the system and providing information about its stability (Li et al., 2016; Marques et al., 2003, 1997; 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 (Jørgensen, 2007; Jørgensen et al., 1995; Jørgensen and Nielsen, 2007; Silow and Mokry, 2010; Susani et al., 2006). Eco-exergy and specific eco-exergy may be used complementary as ecological indicators to capture the complexity and state of the system, expressing shifts in species composition and trophic structure, as for instance in shallow lakes ecosystems and reservoirs (Marques et al. 2003; Molozzi et al., 2013).

According to Marchi et al. (2010), the establishment of invasive species can result in three outcomes for invaded communities: (1) a gradual decrease of eco-exergy, as the invasive species reduce the community abundance and number of species; (2) no significant changes in eco-exergy in the invaded communities, as the invasive species are integrated into the community without significant effect over other taxa; (3) increase in eco-exergy in the invaded communities, as the invasive species create new interactions and energetic pathways within the community. Previous studies have focused in the outcome from the invasion of north American crayfish species *Procambarus clarkii* in lake Chozas, Spain, showing that it is an example of the first predicted scenario, reducing the communities eco-exergy (Bastianoni et al., 2010; Marchi et al., 2012, 2011).

The objective of this study was to characterize the effects of the presence of invasive bivalves on the structure of benthic macroinvertebrate communities. For that, three hypotheses were tested: (1) invasive bivalves act as facilitator species to other benthic macroinvertebrates, resulting in communities' higher number of species, abundance and diversity in sites where invasive bivalves are present; (2) the presence of invasive bivalves causes changes in the taxonomic composition of benthic macroinvertebrate communities, reflected in a shift from a community dominated by soft bottom collectors to a new one dominated by scrapers; (3) invasive bivalves cause an increase in benthic macroinvertebrate communities complexity, reflected in significantly higher eco-exergy and specific eco-exergy.

Materials and methods

Study Sites

Study sites were four hydropower reservoirs located in neotropical savannah habitats (Brazilian cerrado biome), respectively Nova Ponte, São Simão, Três Marias and Volta Grande, in the states of Goiás, Minas Gerais, and São Paulo, in southeastern region of Brazil (Figure 1).

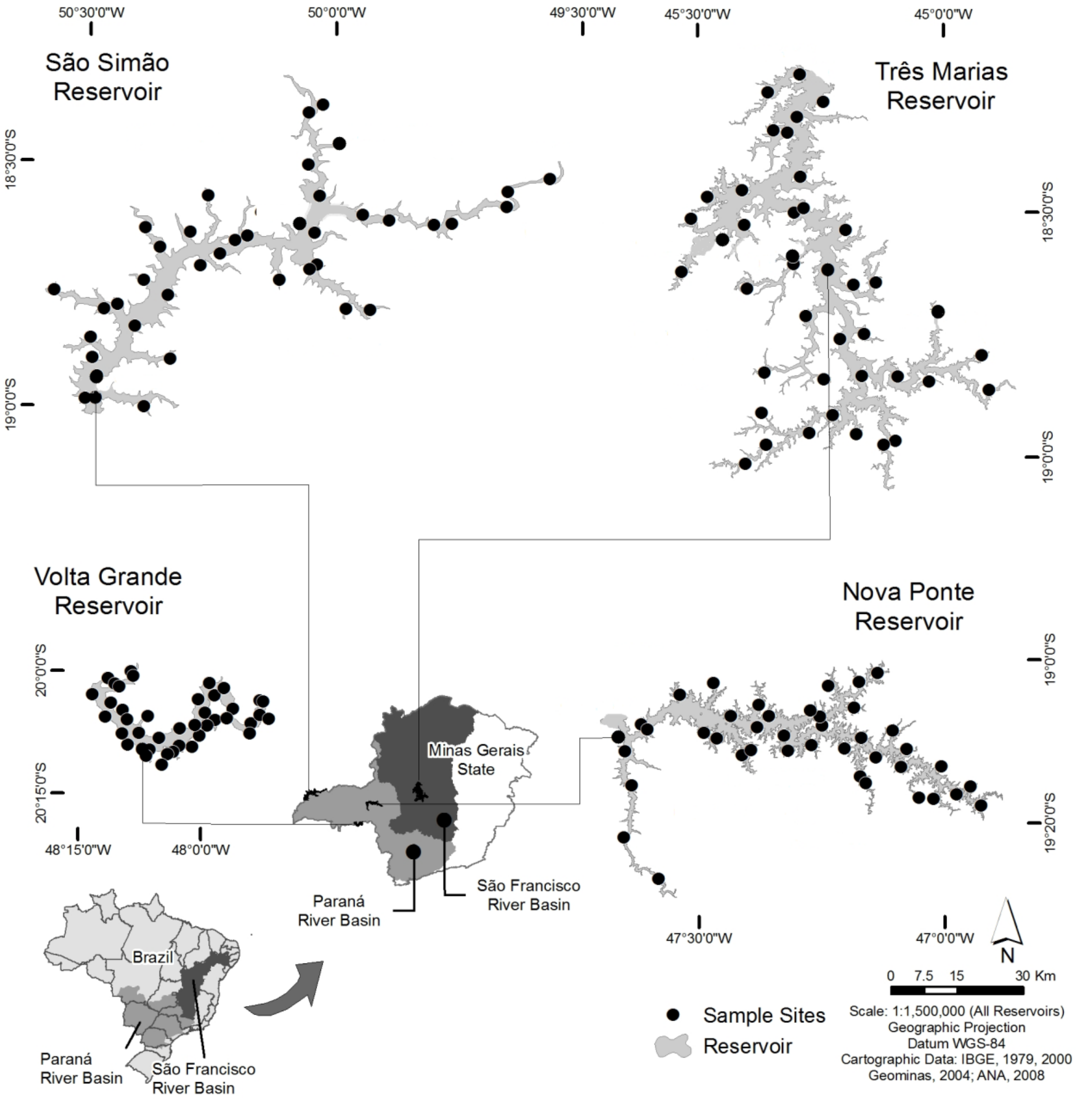

Figure 1 - Location of Nova Ponte, São Simão, Volta Grande, and Três Marias reservoirs and distribution of sampling sites.

The Nova Ponte reservoir is located in the rivers Araguari and Quebra-Anzol, built for hydropower generation. This reservoir is the largest of a series of reservoirs on the river Araguari, with a depth of 120 m near the dam, length of 115 km and volume of 12.8 billion m³. Its floodgates were closed in 1993 and operations began in 1994 (CEMIG 2014).

The São Simão reservoir is also a large reservoir, with a surface area of 722 km², a total volume of 11 billion m³ and a maximum depth of 126.45 m. It is formed by the regulation of the Parnaíba river and its tributaries: the Alegre, Preto, São Francisco, Rio dos Bois, Meia Ponte, Tijuco and Prata rivers (Pinto-Coelho et al., 2010). It started its operation in 1978 for the production of hydroelectric power (Souza & Souza, 2009).

The Volta Grande reservoir is located in the lower Rio Grande basin, between the states of Minas Gerais and São Paulo. It covers the municipalities of Conceição das Alagoas, Água Comprida and Uberaba (MG), Miguelópolis, Aramina and Igarapava (SP). It is a medium-sized reservoir, with a flooded area of approximately 222 km, perimeter of 80 km (Rolla et al., 1990) and a volume of 2.3 billion m³ built for electricity generation, Having started its operation in 1974 (Braga & Gomieiro, 1997; Campos 2003).

The Três Marias Reservoir is located on the upper reaches of the São Francisco river basin. It is one of the largest reservoirs in Brazil, with a surface area of 1040 km², a total volume of 21 billion m³ and a maximum depth of 58.5 m (CEMIG, 2014). Its waters come primarily from the São Francisco river and tributaries, such as the rivers São Vicente, Paraopeba, Sucuriú, Indaiá, Ribeirão do Boi, Ribeirão da Extrema and Borrachudo (Esteves et al., 1985). It began operating in 1962 to control flooding, improve navigation, encourage development and irrigation, and generate hydroelectric power (Freitas & Filho, 2004).

Sampling sites were defined according to the concept of spatially balanced sampling (Stevens and Olsen, 2004) adapted to large reservoirs (Macedo et al. 2014).

From a point randomly selected, each reservoir's perimeter was divided into 40 sections with the same size. Sampling stations were located at the beginning of each section and at equidistant distances from each other.

Samples were collected at 160 sampling sites during the dry season, respectively in 2009 (Nova Ponte), 2010 (São Simão), 2011 (Três Marias), and 2012 (Volta Grande). Water quality was estimated in each sampling site using the Throphic State Index (CETESB, 2010). All the sampling sites were classified as Ultra Oligothrophic, therefore showing similar water quality. In consequence of that we treated the 160 sampling sites as a single data set.

Benthic Sampling

Benthic macroinvertebrates were collected at the littoral zone of each sampling site using an Eckman-Birge grab (0.0225 cm² area). A single sample was collected at each site and stored in plastic bags, fixed in 10% formalin, and subsequently washed through a sieve (0.5 mm mesh) in the laboratory.

Macroinvertebrates were identified under a stereo-microscope using specialized literature (Merritt and Cummins, 1996; Mugnai et al., 2010; Trivinho-Strixino, 2011): Specimens from the invasive bivalve species *Limnoperna fortunei* (Mytilidae) and *Corbicula fluminea* (Corbiculidae) were identified to species level, while the specimens from the Chironomidae family (Diptera) were identified to genus level. Other taxa were identified to family (Insecta) or subclass (Anellida) levels. All specimens collected were fixed in 70% alcohol and deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

Due to their capacity to cause physical alteration in the sediment, their sessile nature and aggregate distribution (Sousa et al., 2009), the absence or presence of individuals of invasive bivalve species was used to classify the sampling sites in two groups: **Absent** and **Present**. Of the 160 sites, 118 were categorized as Absent and 38 as Present. 4 sites did not show any individuals and were excluded from the analysis.

To test if invasive bivalves act as facilitators to other benthic macroinvertebrates originating communities with higher abundances and diversity, the Simpson (dominance) and Margalef (taxa richness) indices, as well as total abundance (excluding the invasive bivalves),were calculated for each sampling site.

Biomass calculation

Biomass (dry weight) was estimated using length-mass equations (Benke et al., 1999; Johnston and Cunjak, 1999; Miserendino, 2001; Smock, 1980; Stoffels et al., 2003). The specimens were photographed in a stereomicroscope (model Leica M80) equipped with a digital camera (model Leica IC 80 HD). Each specimen's length was measured using the software Motic Image Plus 2.0. Using the length-mass equations the dry biomass (g/m^2) of each sampled taxon was estimated.

For each site we estimated total biomass, biomass of native species and the biomass of *Melanoides tuberculata*.

Exergy Based Indicators Computation

Eco-exergy and specific eco-exergy indices were calculated for each sampling site.

Eco-exergywas computed as follows(Jørgensen et al., 2010):

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

Where $\boldsymbol{\beta i}$ is a weighting factor (Table 1) based on the information contained in the components (**i**) of the ecosystem, defined by Jørgensen et al. (2005) and **ci** is the concentration (biomass) of component **i** of the ecosystem.

Table 1 – Exergy conversion factors for benthic communities, based on Jørgensen et al. (2005). The values in bold were used in this study.

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

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 assess if invasive bivalves act as facilitators originating more diverse associated benthic communities, a Generalized Linear Model (GLM) with a Quasipoisson error structure for the number of species, abundance and a Gaussian error structure for the Simpson and Margalef indices based on the benthic macroinvertebrate taxa found at each site, were used to test for possible differences between sites categorized as Absent and Present. The model's significance was tested by an Analysis of Deviance (F test). The calculations were performed on R software, version 3.2.3, (R Core Team, 2015).

To verify if the presence of invasive bivalves changes the taxonomic composition of associated benthic communities, data on abundance (excluding the invasive bivalves) underwent a square root transformation, then we used the Bray-Curtis distance to build the similarity matrix. PERMANOVA (1000 permutations) was used to test if the benthic macroinvertebrate communities in Absent and Present sites were significantly different from each other. We also used a Generalized Linear Model (GLM) with a Gaussian error structure was used to test the values of biomass for native species and for *Melanoides tuberculata* calculated at each site, testing for possible differences between sites categorized as Absent and Present. The calculations were performed on R software, version 3.2.3, (R Core Team, 2015) and the vegan package (Oksanen et al., 2016).

To check if invasive bivalves increase benthic macroinvertebrate communities complexity, a Generalized Linear Model (GLM) with a Gaussian error structure was used to test the values of eco-exergy and specific eco-exergy calculated for the benthic macroinvertebrate communities at each site, testing possible differences between sites categorized as Absent and Present. The model's significance was tested by an Analysis of Deviance (F test). The calculations were performed on R software, version 3.2.3, (R Core Team, 2015).

Results

The number of species, abundance, and the Simpson and Margalef indices were consistently lower in Present sites. Nevertheless, we only observed statistically significant differences for the number of species and abundance (Table 2). Results of PERMANOVA analysis showed that taxonomic composition was significantly different between Absent and Present sites (F1.155 = 14.685, p = 0.000999). Regarding abundances (Figure 2) benthic communities at Absent sites were dominated by Chironomids and Oligochaeta, while at Present sites were dominated by the invasive Gastropoda *Melanoides tuberculata* (Thairidae).

Table 2 – Mean (±SE) and GLM results of Richness, Abundance, Simpson diversity index and Margalef diversity index for sites with invasive bivalves Absent and Present.

	Mean (±SE)		GLM	
	Absent	Present	F	P
Abundance	43.44 (±6.16)	23.84 (±3.34)	5.3726	0.021
Richness	7.00 (±0.37)	5.36 (±0.43)	5.4721	0.020
Margalef	1.81 (±0.08)	1.50 (±0.11)	3.7484	0.054
Simpson	0.63 (±0.01)	0.58 (±0.03)	1.6643	0.199

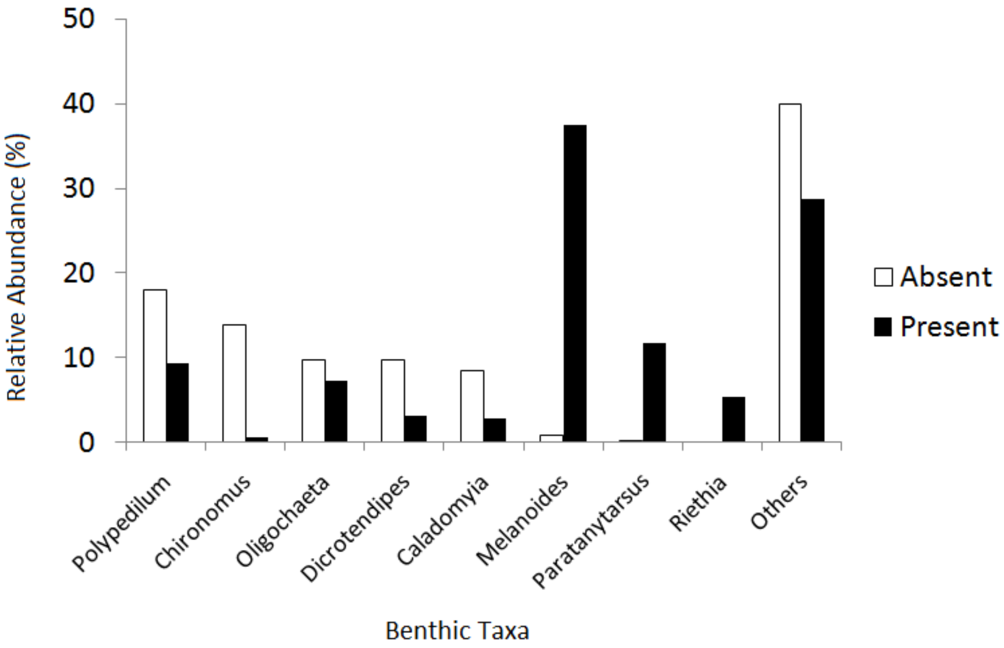

Figure 2 –Relative abundance of associated benthic macroinvertebrate communities for sites with invasive bivalves Absent and Present.

Total biomass was significantly higher in Present sites (Table 3), as was *Melanoides tuberculata* biomass. However, native species biomass was not significantly different between Absent and Present sites.

Table 3 – Mean (±SE) and GLM results of Total Dry-Weight Biomass (g/m²), *Melanoides tuberculata* Dry-Weight Biomass (g/m²) and Native Species Dry-Weight (g/m²) Biomass for sites with invasive bivalves Absent and Present.

	Mean (±SE)		GLM	
	Absent	Present	F	P
Total Biomass	0.33(±0.05)	1.09(±0.37)	11.031	0.00119
M. tuberculata Biomass	0.002 (±0.001)	0.04(±0.008)	63.148	<0.001
Native Biomass	0.32(±0.05)	0.18(±0.06)	2.4686	0.1182

Eco-exergy and specific eco-exergy showed statistically significant higher average values in Present sites (Table 4).

Table 4 – Mean (±SE) and GLM results of Eco-exergy and Specific Eco-exergy for sites with invasive bivalves Absent and Present.

	Mean (±SE)		GLM	
	Absent	Present	F	P
Eco-exergy	56.44 (±8.44)	301.26 (±110.95)	14.504	0.0002
Specific Eco-exergy	173.93 (±1.96)	298.28 (±6.51)	279.18	<0.001

Discussion

The results show that the presence of invasive bivalves causes a significant decrease in the benthic macroinvertebrate communities' number of species and abundance. Although this was not captured by diversity measures like the Simpson and Margalef indices, in general we could not confirm the first hypothesis. However, the communities' composition with regard to the other benthic macroinvertebrates, taxa was significantly different between Absent and Present sites, corroborating the second hypothesis. Finally, assuming that eco-exergy and specific eco-exergy are able to express the communities' complexity, given that the values of these two indicators were significantly higher in sites with invasive bivalves, our results appear to corroborate the third hypothesis.

First hypothesis

Present sites show benthic communities with a significantly lower number of species and abundance in comparison with those found in Absent sites, and therefore invasive bivalves did not act as facilitators to new benthic macroinvertebrate taxa. Physical changes caused by invasive bivalves as ecosystem engineers may eventually explain results observed, in the sense that their aggregations formed a kind of biological modified hard substrate that that otherwise would be rare in reservoirs, which are typically characterized by soft sediment (Johnson et al., 2008; Sousa et al., 2009; White, 2014). As a consequence, soft bottom taxa, such as the Chironomids *Polypedilum* and *Chironomus* (Corbi and Trivinho-Strixino, 2017) and Oligochaeta, normally dominant in benthic macroinvertebrate communities in reservoirs (Havel et al., 2005; Horsák et al., 2009; Martins et al., 2015), have most probably been negatively influenced by this biological modified substrate, exhibiting relatively lower abundances in Present sites. However, as both Margalef and Simpson indices failed to show significant difference between Absent and Present sites, suggesting that the benthic communities show similar structure of dominance (Simpson index) and taxa diversity (Margalef index) (Gamito, 2010; Peet, 1974).

Studies in Brazil highlight the wide distribution and the dominant status of the invasive bivalves in reservoirs, but do not present a clear pattern of their effects over benthic macroinvertebrate communities (e.g., Martins et al., 2015; Morais et al., 2016; Suriani et al., 2007). Most studies in reservoirs in South America (e.g., Boltovskoy et al., 2009; Burlakova et al., 2012; Karatayev et al., 2003) showed contrary results, highlighting the capability of invasive bivalves to act as facilitators to other benthic macroinvertebrates.

Second hypothesis

Lower number of species and abundances, as well as the shift in communities' taxonomic composition observed in Present sites may be explained by the dominance of *Melanoides tuberculata*. This invasive Asian Gastropoda species occurs presently in most Brazilian river ecosystems (Fernandez et al., 2003), namely in reservoirs where it usually exhibits high densities. This usually results in a decrease in the number of native taxa, as well as a decrease in their populations' densities (Lima et al., 2013; Santos and Eskinazi-Sant'Anna, 2010; Souto et al., 2011).

Since *Melanoides tuberculata* only were dominant and showed higher biomass than the native species in sites with invasive bivalves, our results also suggest an invasion meltdown scenario, where positive interspecific relationships between two or more invasive species occur, leading to an acceleration of the impacts of these species on the ecosystem and an increased rate of establishment of introduced species (Simberloff, 2006; Simberloff and Von Holle, 1999). Johnson et al. (2008) found a similar pattern in reservoirs located in northern USA, where the establishment of invasive species increased the chances of subsequent invasions and determined cumulative impacts and associated effects on the native benthic macroinvertebrate communities. However, the invasion meltdown scenario should be considered carefully, as with our results it is not possible to discern if the negative impacts over the native benthic macroinvertebrates number of taxa, abundance and biomass were directly resultant from the increased *Melanoides tuberculata* abundance or the physical habitat alterations caused by the invasive bivalves.

Third hypothesis

Higher eco-exergy values found in the presence of invasive bivalve species, however, suggest that invaders became integrated with their host benthic macroinvertebrate communities, contributing afterwards to increase the overall communities' complexity. Actually, introduced ecosystem engineers, such as invasive bivalves, generally tend to increase their host communities complexity (Burlakova et al., 2012; Crooks, 2002). Such increased complexity should result in new energetic pathways and interactions in the invaded communities (Bastianoni et al., 2010). Our results show that this stem from the dominance of the invasive species, as reservoirs are highly altered ecosystems in which such generalist species probably have competitive advantage (Havel et al., 2005; Johnson et al., 2008; Thomaz et al., 2015). In this context higher eco-exergy is reflecting communities dominated by species with higher fitness to their environment (Jørgensen, 2007).

Increased specific eco-exergy values also suggest a more efficient use of ecosystems' resources. For instance, South American freshwaters lacked powerful benthic suspension feeders able to provide a direct link between benthic and water column components of the ecosystem (Karatayev et al., 2007b), role eventually undertaken by invasive bivalve species. Resources produced in the water column captured by invasive bivalves may then become available to the benthic communities as feces and pseudo-feces, constituting an important food source for benthic collectors (Sardiña et al., 2008). Therefore, invasive bivalves may open new energetic pathways for benthic macroinvertebrate communities, making accessible resources that otherwise would not be so available (Boltovskoy and Correa, 2015).

Conclusions

The present study in neo-tropical reservoirs illustrates that the presence of invasive bivalves does not forcibly act as facilitator to benthic macroinvertebrate communities, and may instead have a negative impact over the most common taxa, which contradicts most previous studies.

However, we also observed that the presence of bivalve invasive species caused a significant taxonomic shift, from communities dominated by soft sediment reservoir taxa to those dominated by *M. tuberculatus*, and results in their increased overall complexity.

Eco-exergy and specific eco-exergy, used complementary, were able to capture the effects of invasive bivalve species on the benthic macroinvertebrate communities.

Finally, our results appear to illustrate an invasion meltdown scenario between *Corbicula fluminea* and *Limnoperna fortunei*, invasive bivalves and the invasive gastropod *Melanoides tuberculata*.

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Capítulo 2

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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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Highlights

1. The diversity of benthic macroinvertebrate assemblages and their efficiency in using food resources available in the system are not affected by canopy cover.
2. Benthic macroinvertebrate assemblages in open canopy streams are able to use available resources to build a more complex structure.
3. Autochthonous production is implied to constitute the main energy source in Neotropical headwater streams.

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 macroinvertebrateassemblages in tropical headwater streams. Four hypothesis 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 exhibitmore 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 maysupport 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 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 toplay 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.

Key-words: Diversity; Exergy based indicators; Headwater streams; Instant secondary production; Neotropical savannah.

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 trough taxonomic based indicators, such as richness and diversity indices. Likewise, thermodynamic oriented indicators may provide additional informationon 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., 2003, 1997; 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, amongst them Instant Secondary Production (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989).

Our objective was to asses show 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.

Material and Methods

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^2, 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 1,440 meters 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; 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 (Figure 1) to minimize the natural variability among then. 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).

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

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

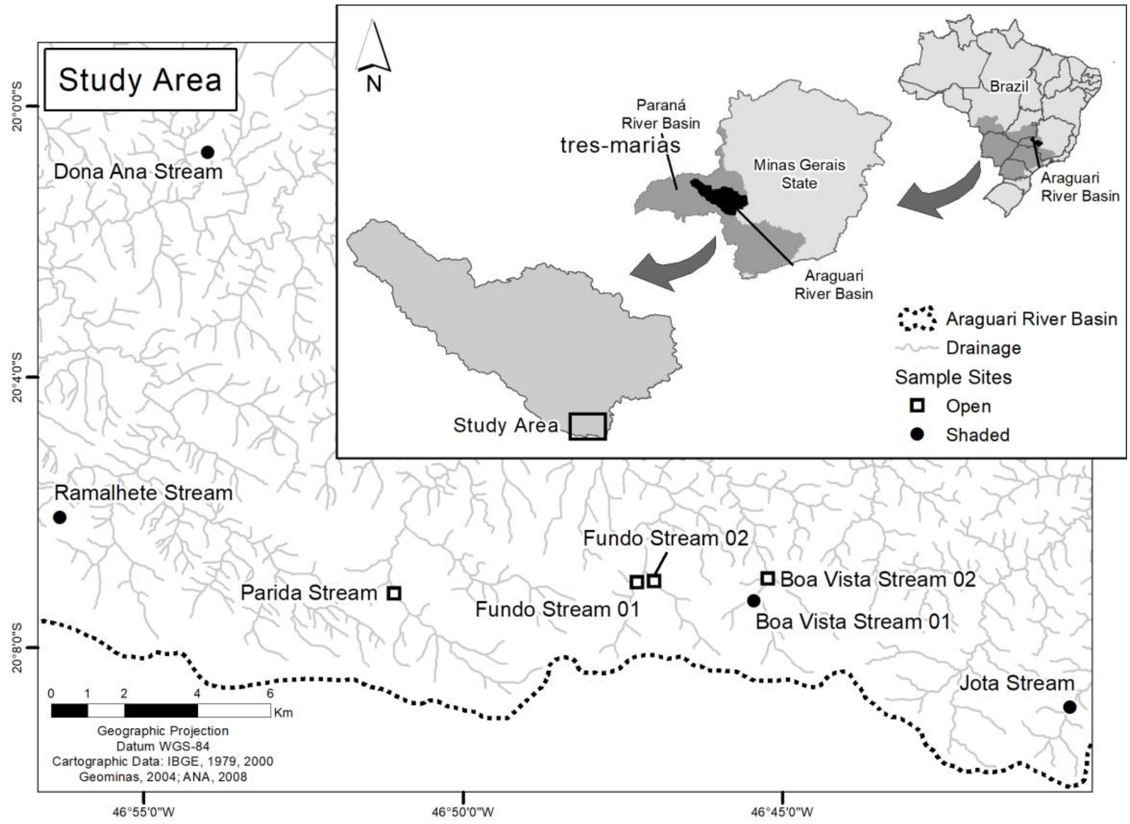

Figure 1 - Location of sampling sites in the Araguari river basin.

Benthic Macroinvertebrate Sampling

The macroinvertebrate communities were sampled in April and May of 2015, during the dry season. In each stream a 25m stretch was divided into six equidistant transects. In each transect a kick-net sampler (30cm opening, 500μm sieve) was used, resulting in six sub-samples in each stream for a total area of 0.54m² 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.

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-Wienner (Shannon, 1948) and the Simpson (Simpson, 1949) diversity indices were calculated for each stream.

Shannon-Wienner diversity index was computed as follows:

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

Where ***pi*** is the proportion of the total of individuals belonging to the taxon ***i***.

Simpson diversity index was computed as follows:

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

Where ***pi*** is the proportion of the total of individuals belonging to the taxon ***i***.

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 the dry-mass biomass (g/m²) of each sampled taxon was estimated.

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):

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

Where ***βi*** is a weighting factor based on the information contained in the components (**i**) of the ecosystem, defined by Jørgensen et al. (2005) and **ci** 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.

Calculation of Instant Secondary Production

To test if benthic assemblages in open canopy streams support higher secondary production, Instant Secondary Production (mg/m²/day) was calculated for each stream.

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

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

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 based on individual equations for each taxon found in the literature (Edgar, 1990; Morin and Dumont, 1994; Plante and Downing, 1989).

Data Analysis

A Generalized Linear Model (GLM) with a Gaussian error structure was used to test ifthetotal number of taxa and the number of EPT at each site, as well as the values of the Shannon-Wienner and Simpson diversity indices (see hypothesis 1), eco-exergy and specific eco-exergy (see hypotheses 2 and 3), and instant secondary production (see 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 (Oskanen et al., 2016).

Results

A total of 13,633 benthic macroinvertebrate specimens belonging to 72 taxa were sampled, of which 11,448 in open canopy streams and 2,185 in shaded streams. The total number of taxa, the number of EPT taxa, as well as the values of the Shannon-

Wienner 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%) (Figure 2).

Table 2 – Mean (±SE) and GLM results of Number of Taxa, Number of EPT Taxa, Simpson diversity index and Shannon-Wienner diversity index for streams with Open and Shaded canopy.

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

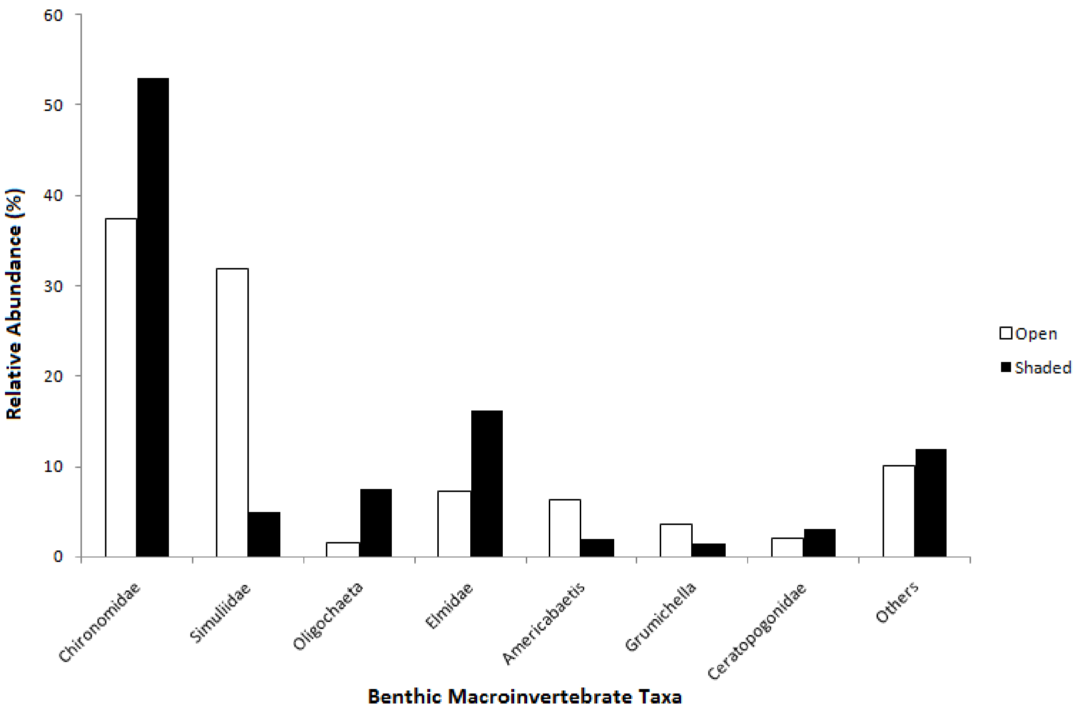

Figure 2 – Relative abundance of benthic macroinvertebrateassemblages for streams with Open and Shaded canopy.

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 difference in the two situations (GLM; $F_{1.7}$ = 5.9423, p = 0.5063) (Figure 3). Finally, instant secondary production was also significantly higher in streams with open canopy (GLM; $F_{1.7}$ = 9.8751, p = 0.02001) (Figure 4).

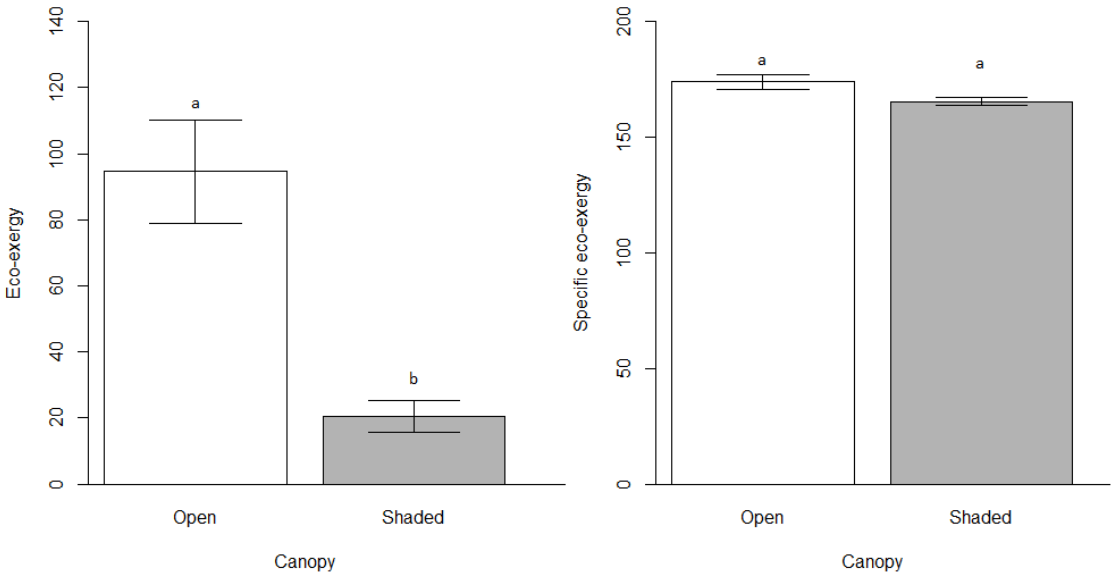

Figure 3 – Mean and standard error of Eco-exergy and Specific Eco-exergy for streams with Open and Shaded canopy. “a” and “b” mark significantly different plots.

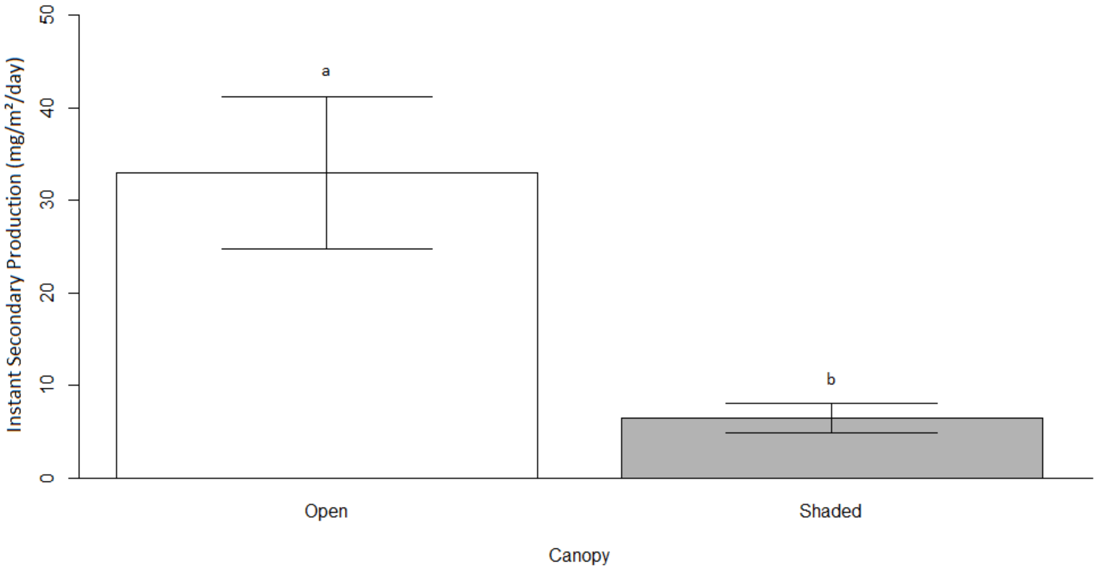

Figure 4 – Mean and standard error of Instant Secondary Production (g/m²/day) for streams with Open and Shaded canopy. “a” and “b” mark significantly different plots.

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 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 differencesregarding 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; Datry et al., 2016; Tonkin et al., 2013). The fact is that studies that reported higher diversity in open canopy streams were in generalcarried 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, b; 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 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 autochthonousproduction 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 autochthonousorganic matter is more easily absorbed by benthic macroinvertebrates (Pearson et al., 2015).

Conclusions

The present study illustrates the importance of canopy cover in the structure and functioning of benthic macroinvertebrate assemblages, as our results imply thatstreams with open canopyshow benthic assemblages withmore complex dissipativeand higher secondary production. Additionally, our results illustrate how autochthonousproduction 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 implyingthat these aspects might be controlledand 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 supportenvironmental decisionswith regard to protection and restoration measures.

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Thermodynamic based indicators illustrate how run-of-river impoundment in a neotropical savanna attracts invasive species and alters the benthic macroinvertebrate assemblages' complexity

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Highlights

1 Areas directly affected by the dam support high density of invasive species.

2 When compared to non-regulated stretches of the river, diversity is lower in the reservoir stretch, but increased downstream of the dam.

3 The ecological impacts of the dam are localized, not affecting the river further downstream.

Abstract

Hydropower dams are widespread sources of anthropogenic alteration on lotic ecosystems, found in most hydrological basins system in the world. Our objective was to assess how such a run-of-river dam influences benthic macroinvertebrate assemblages in a neotropical river under a deactivated run of river dam. For that we tested four hypotheses: (1) a run-of-river dam diminishes the local diversity of the benthic macroinvertebrate assemblages; (2) the presence of the dam results in a more propitious habitat to the establishment of invasive species; (3) the presence of the dam results in a lower complexity of local benthic macroinvertebrate assemblages; (4) the ecological impacts are restricted to the sites directly affected by the dam. While the presence of the dam lowers the benthic macroinvertebrate assemblages' diversity in its reservoir, the diversity downstream next to the dam actually increases. The habitats directly affected by the dam also supported much higher biomass proportion of invasive species. By using eco-exergy and specific eco-exergy indicators, we were able to assess the complexity of benthic macroinvertebrate assemblages and the assemblages in the reservoir appeared to be enhanced by the presence of invasive species. These results illustrate that deactivated run-of-river dams still alter significantly the physical habitat for lotic benthic macroinvertebrate assemblages, which turns advisable a management intervention decommissioning of the dam. Finally, our results show that exergy based indicators may improve our comprehension of systems functioning regarding ecological impacts of dams, supporting environmental sustainable practices.

Keywords: *Corbicula fluminea*; Dams impact; Invasive species; *Limnoperna fortunei*; Thermodynamics based indicators.

Introduction

Hydropower dams are widespread sources of anthropogenic alteration on lotic ecosystems, found in almost every river system in the planet (Bednarek, 2001). Hydropower is the most common renewable energy source in the world, accounting for 16% of worldwide total electricity generation (Anderson et al., 2015) and for more than 64% of Brazilian electricity production (EPE, 2016).

Due to a crescent demand for renewable energy sources and to most of the areas suitable for large scale hydropower dams already occupied by existing dams, construction of small run-of-river hydroelectric dams have increased globally in the last decades (Abbasi and Abbasi, 2011; Fearnside, 2014). Brazil has followed this trend, installing many small run-of-river dams through its river systems in the last decades, due to lower costs and easier licensing (Almeida et al., 2009), for a total of 431 installed small hydropower dams which respond for 3.21% of the national power generation, plus 27 small hydropower dams in construction (ANEEL, 2017).

Run-of-river hydropower dams are those that use in-stream flow to operate and therefore need little or no water storage (Wang et al., 2016). Despite small run-of-river dams being common in most river systems around the world, most studies focus on large dams (e.g. Agostinho et al., 2008; Horsák et al., 2009; Martins et al., 2015), there is little information about the ecological impacts of run-of-river dams (Anderson et al., 2017; Mbaka and Wanjiru Mwaniki, 2015; Wang et al., 2016).

Due to their smaller size, many of these small dams end up outliving their economic usefulness, ending their operations (Hastings et al., 2016). Dam removal have been used in the last decades as a tool to reestablish natural hydrological conditions in Europe and North America (Bednarek, 2001). Characterizing the effects of run-of-river dams over lotic ecosystems is essential in terms of their management, to predict and mitigate potential ecological impacts, and for future dam removal initiatives (Hastings et al., 2016).

While many taxa are used as bioindicators to assess ecological impacts, benthic macroinvertebrates are among the most ubiquitous and widely used, due to their ability to respond predicatively to modifications in lotic environments (Bonada et al., 2006; Castro et al., 2017; Klemm et al., 2003; Macedo et al., 2016). Usually the structure of benthic macroinvertebrate assemblages is assessed trough taxonomic based indicators, such as richness and diversity indices (Friberg, 2014). However, the taxonomic structure may vary geographically due to differences in the evolutive history of the local environment, thus limiting taxonomic indicators' capacity for generalization (Karr, 1999). Thermodynamic oriented indicators are not subjected to these limitations, as they are rooted in universal concepts, thus providing an unified language to compare different organisms and systems (Ludovisi et al., 2005). Among thermodynamic oriented indicators, eco-exergy and specific eco-exergy have been successfully used in different ecosystems in the last decades, namely in estuaries (Marques et al., 2003, 1997; Veríssimo et al., 2016), lakes (Silow et al., 2011; Xu, 1997; Xu et al., 2001), streams (Linares et al., 2017a) and reservoirs (Linares et al., 2017b; Molozzi et al., 2013).

Eco-exergy and specific eco-exergy were adapted from exergy, a concept originated in physics, that represents the useful energy contained within a system (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., 2003, 1997; 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).

Eco-exergy and specific eco-exergy can be used as environmental indicators and should be used in combination (Marques et al., 2003). Higher values of these parameters are indicative of greater diversity, greater functional redundancy and greater resilience, characteristics of more complex systems (Salas et al., 2005). This can be interpreted as a consequence of the tendency of the ecosystem to maximize its eco-exergy storage capacity, stabilizing in the condition that leaves the system farther from the thermodynamic equilibrium (Jørgensen, 2007b). Thus, a perturbed ecosystem is expected to exhibit lower eco-exergy and specific eco-exergy when compared to a poorly disturbed environment, since disturbances would increase ecosystem entropy (Jørgensen, 2007c). In this theoretical context, the use of exergy based indicators represents a good holistic tool to assess the ecological impacts of run-of-river dams, the first of its kind to be realized in the neotropical savanna.

Our objective was to assess how a run-of-river dam influences benthic macroinvertebrate assemblages in a large river in the Neotropical savanna. For that we tested four hypotheses: (1) the presence of the dam diminishes local diversity of the benthic macroinvertebrate assemblages compared to the free-flowing stretch of the river, which will result in lower values of diversity indices; (2) the presence of the dam result in a more propitious habitat to the establishment of invasive species, which will result in a dominance of these species in the benthic macroinvertebrate assemblages; (3) the presence of the dam lowers the local benthic macroinvertebrate assemblages complexity (in terms of information embedded in the organisms’ biomass), which will be expressed by lower eco-exergy and specific eco-exergy values; (4) the ecological impacts will be restricted to the river stretches directly affected by the dam, meaning that the downstream floodplain stretch will show for all tested indicators values not significantly from those of the free-flowing stretch.

This study is part of a larger project aiming to evaluate the ecological impacts of the dam over the Pandeiros river and to provide a baseline for a future decommission of the dam, which is the first in South America. As far as we know, this study presents a unique opportunity to assess the ecological impacts of a small run-of-river hydropower dam in Brazil using thermodynamic ecological indicators, providing useful data for its ecological management and for the possible dam removal.

Material and Methods

Study Area

This study was conducted in the Pandeiros river, located in Minas Gerais state, Brazil. The Pandeiros river is an important tributary of the left bank of the São Francisco river, with an approximate extension of 145 km. The floodplains of the Pandeiros river are among the top priority areas for conservation in the neotropical savannah, considered by state law to be of "Special Biological Importance", due to their unique nature and high diversity (Drummond et al., 2005). This Area of Environmental Protection encompasses almost 400000 ha, the largest unit for sustainable use in Minas Gerais state, and covers the entire basin of the Pandeiros River in the municipalities of Januária, Bonito de Minas, and Cônego Marinho (Lopes et al., 2010). The objective of the AEP-Pandeiros is to protect the Pandeiros Wetland and the biological diversity in the surrounding area for development and reproduction of native fish species, as the

Pandeiros Wetland is considered to be the nursery of most migratory fishes of the São Francisco river Basin (Santos et al., 2015).

The small hydropower dam Pandeiros was installed in 1957. Its reservoir presents an area of 280 hectares and its dam, with free crest, and possesses a maximum height of 10.30m. Its powerhouse is located about 400 meters downstream from the dam and, when operational, had a power output of 4.2 MW (Fonseca et al., 2008). The powerhouse was deactivated in 2007 and since then all economical activities in the dam have ceased, allowing the reservoir to be filled by sediment.

For this study four sampling sites were chosen in the main channel of the Pandeiros river (Figure 1) aiming to represent the diversity of environmental conditions in the Pandeiros river main channel related to the presence of the dam. P1 is a free-flowing stretch 12 km upstream of the dam, characterized by soft bottom sandy sediment, wide channel, shallow water column (less than 1 m) and natural riparian vegetation. P2 is a stretch in the mouth of the reservoir circa 500 m from the dam, characterized by soft bottom sandy sediment, shallow water column (less than 2m) wider channel and no riparian vegetation in one of its margins, as it is next to a human settlement. P3 is a stretch localized downstream/next to the dam circa 50 m to the dam, characterized by sandy sediment in a rocky matrix, deeper water column (more than 3 m), narrower channel and natural riparian vegetation on its margins. P4 is a stretch located 30 km downstream, in the Pandeiros river floodplains, characterized by soft bottom sandy sediment, deeper water column (more than 2m), wide channel and a mix of natural riparian vegetation and pasture on its margins. To further characterize the physical habitat of the chosen sampling sites, physical and chemical variables of the water column and sediment of each site were measured. At each site temperature, turbidity, pH, conductivity and total dissolved solids (TDS) were measured in situ by a portable multiprobe model YSI 6600. Water samples were taken to measure in laboratory the water contents of phosphate, total nitrogen, nitrate and nitrites. Substrate samples were taken to estimate granulomentry of the sediment.

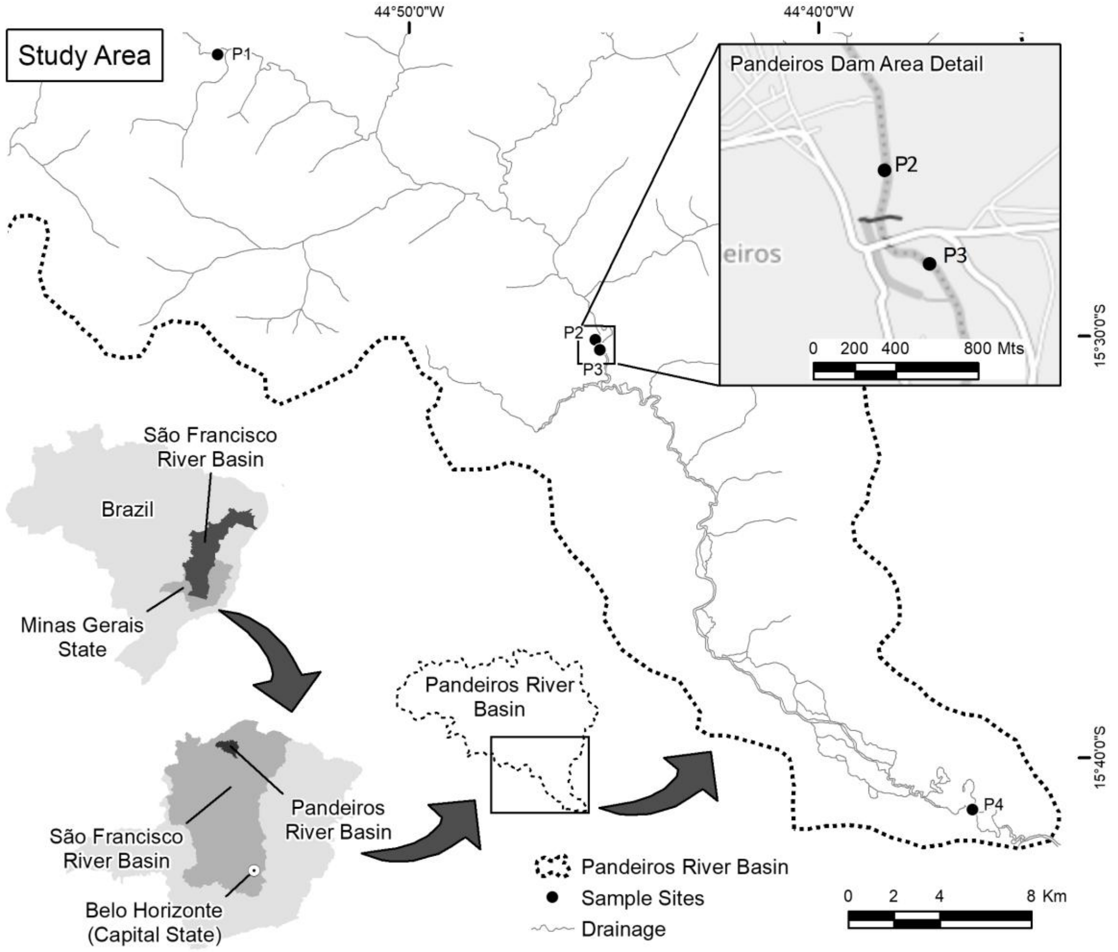

Figure 1 – Location of the sampling sites in the Pandeiros river basin.

Benthic Macroinvertebrate Sampling

The macroinvertebrate communities were sampled in a total of six sampling campaigns. These campaigns were chosen to contemplate both the dry and rainy seasons of the region, resulting in three samplings in dry season (September/15, April and June/16) and three samplings in rainy season (December/15, January and

February/16). Our preliminary tests failed to detect any significant difference for any of the tested indicators between seasons in any site, and therefore we pooled all of them as temporal replicates for each site.

At each sampling site, a kick-net sampler (30cm opening, 500µm sieve) was used, resulting in four sub-samples in each sampling sites for a total area of 0.36m² sampled per site per field campaign. 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 invasive species *Corbicula fluminea* (Corbiculidae) and *Melanoides tuberculata* (Thiaridae) were identified to species 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.

Diversity Measures Calculation

To test if the presence of the dam lower the local diversity of the benthic macroinvertebrate assemblages compared to the free-flowing segments of the river, the Shannon-Wienner (Shannon, 1948) and the Simpson (Simpson, 1949) diversity indices were calculated for each sampling site.

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 the dry-mass biomass (g/m^2) of each sampled taxon was estimated.

To test if the presence of the dam results in a more propitious habitat to the establishment of invasive species, the proportion of the biomass of the invasive species to the total biomass of each sampling site was calculated.

Calculation of Exergy Based Indicators

To test if the presence of the dam lowers the local benthic macroinvertebrate assemblages' complexity, eco-exergy and specific eco-exergy values were calculated for each stream. Eco-exergy was computed as follows (Jørgensen et al., 2010):

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

Where ***βi*** is a weighting factor based on the information contained in the components (**i**) of the ecosystem, defined by Jørgensen et al. (2005) and **ci** 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.

Data Analysis

A Generalized Linear Model (GLM) with a Gaussian error structure was used to test if the Shannon-Wienner and Simpson diversity indices (hypothesis 1) and eco-exergy and specific eco-exergy (hypothesis 3) were significantly different between the free-flowing stretch (P1) and the other sampling sites. The model's significance was tested by an Analysis of Deviance (F test) (Kaur et al., 1996).

A Generalized Linear Model (GLM) with a Quasibinomial error structure was used to test if the proportion of the biomass of the invasive species to the total biomass (hypothesis 2) was significantly different between the free-flowing stretch (P1) and the other sampling sites. The model's significance was tested by an Analysis of Deviance (F test) (Kaur et al., 1996).

Results

The water physical and chemical variables for the sampling sites were characterized (Table 1). Temperature, pH, dissolved oxygen, alkalinity and nutrient content were similar among the sites. Only conductivity, TDS and turbidity showed significant variation among the sampling sites. P1 was characterized by relatively the lowest conductivity (73.9 µS/cm), relatively low TDS and relatively high turbidity. Compared to this, P2 showed higher conductivity, the highest TDS (40.6 mg/L) and the lowest turbidity (6.7 UNT) while P3 showed higher the highest turbidity (91.6 µS/cm), higher TDS and lower turbidity. P4 was characterized as having higher conductivity, the lowest TDS (31.6 mg/L) and the highest turbidity (18.2 UNT). Considering the sediment granulometry (Table 2), all sampling sites showed sandy sediments. P2 granulometry was mostly fine sand (64.1%), while P1, P3 and P4 were mostly composed of very fine sediment (respectively 67.4, 59.3 and 89.5).

Table 1 – Water column physical and chemical variables for the selected sampling sites.

Sampling Sites	Temperature (°C)	pH	Condutivity (µS/cm)	TDS (mg/L)	Turbidity (UNT)	DO (mg/L)	Alcalinity (mEq/L CO_2)	Total N (mg/L)	Tota
1	24,9 ± 2,6	7,3 ± 0,3	73,9 ± 4,0	35,1 ± 18,5	9,4 ± 9,5	7,2 ± 1,4	524,7 ± 62,6	0,06 ± 0,03	9,9
2	23,3 ± 2,2	7,3 ± 0,7	82,7 ± 9,8	40,6 ± 18,7	6,7 ± 5,6	7,2 ± 1,6	572,1 ± 56,6	0,05 ± 0,02	9,4
3	25,1 ± 1,3	7,4 ± 0,3	91,6 ± 31,7	38,4 ± 14,9	7,0 ± 6,3	6,8 ± 1,6	566,2 ± 87,7	0,07 ± 0,02	10,2
4	25,4 ± 2,2	7,3 ± 0,2	83,6 ± 3,8	31,6 ± 4,6	18,2 ± 23,9	6,5 ± 0,9	602,8 ± 45,2	0,06 ± 0,02	13,8

Table 2 – Granulometry variables for the selected sampling sites.Table 2

Site	Gravel	Very Coarse Sand	Coarse Sand	Medium Sand	Fine Sand	Very Fine Sand
1	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	31,8 ± 19,7	67,4 ± 19,2
2	0,0 ± 0,0	0,0 ± 0,0	0,2 ± 0,1	1,1 ± 0,6	64,1 ± 28,6	34,1 ± 28,5
3	0,0 ± 0,0	0,0 ± 0,0	0,1 ± 0,1	0,2 ± 0,1	39,8 ± 15,8	59,3 ± 15,3
4	0,0 ± 0,1	0,2 ± 0,2	1,0 ± 0,4	1,8 ± 0,5	2,1 ± 0,6	89,5 ± 2,6

A total of 30,094 benthic macroinvertebrate specimens belonging to 61 taxa were sampled, 37 taxa were sampled in P1, 47 in P2, 41 in P3 and 35 in P4. The Shannon-Wienner and Simpson diversity indices showed significant differences between P1 and the sampling sites directly affected by the dam (Figure 2). P2 showed significantly lower values, while P3 showed significantly higher values for both indices. Only P4 showed no significant differences in relation to P1.

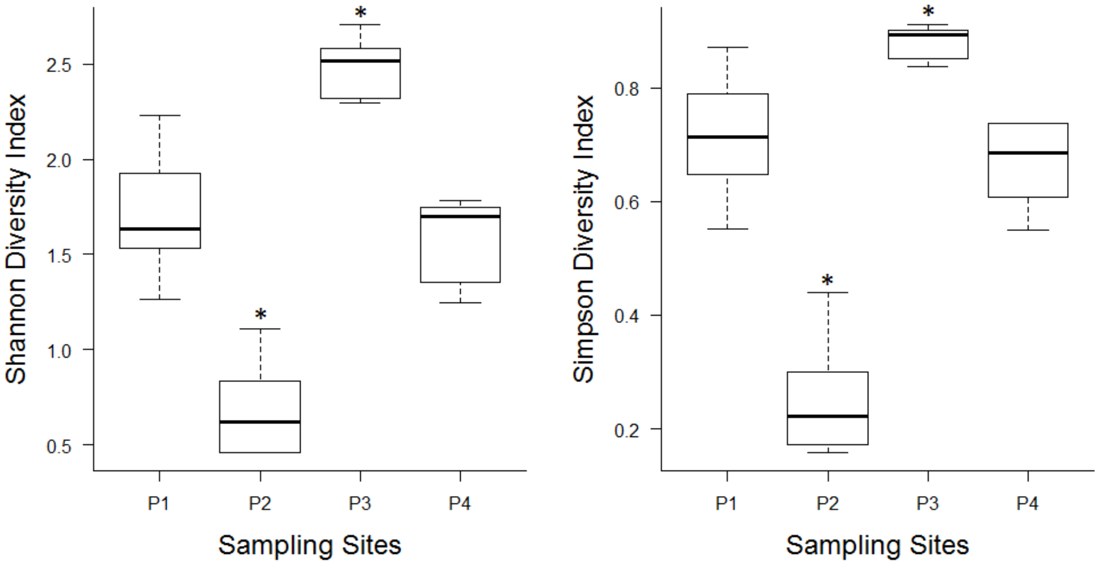

Figure 2 – Shannon-Wienner and Simpson diversity indices for the different sampling sites. “*” mark significantly different values from P1.

On the other hand, both P2 and P3 showed significantly higher proportion of invasive species biomass than P1, while P4 showed no significant differences as compared to P1 (Figure 3).

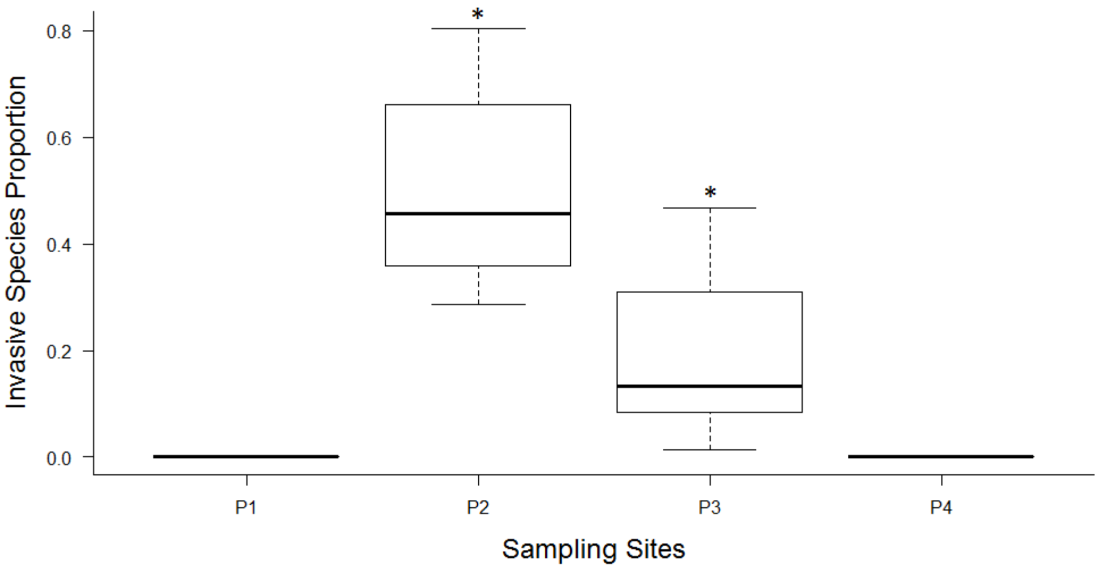

Figure 3 – Proportion of the invasive species biomass for the different habitats. “*” mark significantly different values from P1.

Eco-exergy and specific eco-exergy exhibited significant higher values in P2, as compared to P1 (Figure 4), but no significant differences were observed in relation to P3 and P4.

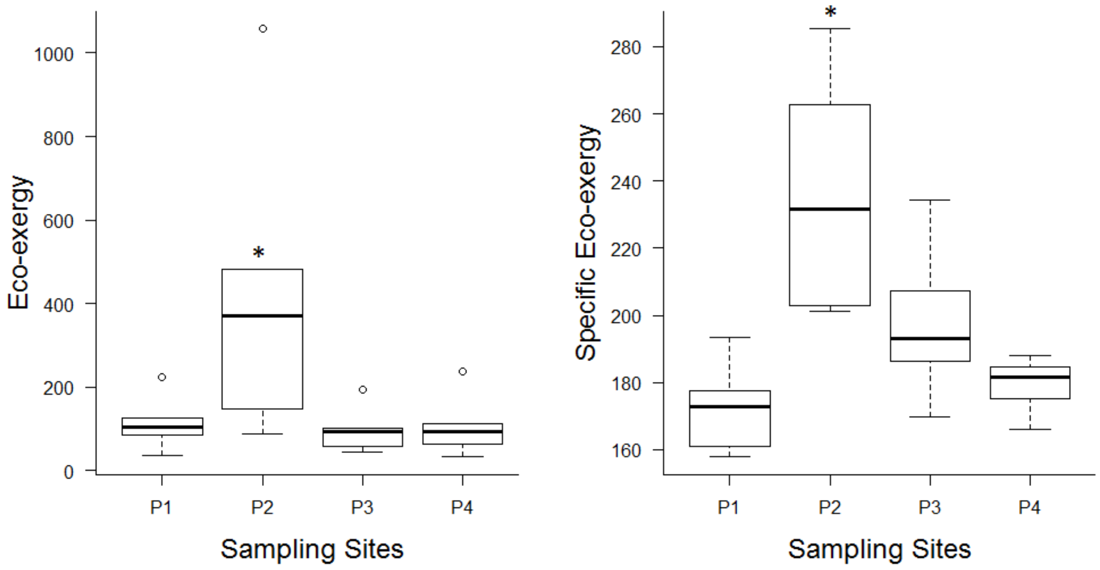

Figure 4 – Eco-exergy and specific eco-exergy for the different habitats. “*” mark significantly different values from P1.

Discussion

Our first hypothesis, that the presence of the dam would diminish local diversity of the benthic macroinvertebrate assemblages compared to the free-flowing stretch of the river was only partially corroborated by the results. In fact, while the Shannon-Wienner and Simpson diversity indices were significantly lower in the reservoir stretch (P2) as compared to the upstream free-flowing stretch (P1), they were significantly higher in the next to the dam stretch (P3). The hypothesis that the presence of the dam would result in a more propitious habitat to the establishment of invasive species was corroborated, as the proportion of biomass belonging to invasive species was higher in both P2 and P3. The hypothesis that the presence of the dam would result in a lower complexity of local benthic macroinvertebrate assemblages was not corroborated, as eco-exergy and specific eco-exergy exhibited significantly higher values in P2 as compared to P1, while no significant differences were found in P3. Finally, the hypothesis that the ecological impacts would be restricted to the sites directly affected by the dam was corroborated, as no significant differences were found between P1 and P4 for all the tested indicators.

For the reservoir stretch (P2), the differences in diversity can be explained by the alterations of the physical habitat caused by the dam itself such as the (Chester and Norris, 2006; Kloehn et al., 2008; Van Looy et al., 2014). These changes away from the natural physical environment of the Pandeiros river may be the cause of shifts in the benthic macroinvertebrate assemblages taxonomic composition, which may explain the lower diversity of its benthic macroinvertebrate assemblages. For the downstream stretch next to the dam (P3), the presence of rock outcroppings provide hard substrate for the benthic macroinvertebrate assemblages, which may explain the observed higher diversity. This allowed the establishment of taxa that otherwise would be rarer or not present under in the Pandeiros river, which is largely characterized sandy bottoms (Fonseca et al., 2008). This, however, cannot be reliably linked to the presence of the dam and may be a natural occurrence of this stretch of the Pandeiros river.

The dominance of invasive species populations is likely another consequence of the probable physical alterations caused by the dam. Anthropogenically altered habitats, such as impoundments, often support larger populations of invasive species, facilitating their introduction and acting as refuges for them (Johnson et al., 2008; Oliveira et al., 2011). This is supported by the observation that while both invasive species are commonly found in large densities throughout the São Francisco basin (Fernandez et al., 2003; Rodrigues et al., 2007), in the Pandeiros river main channel they are only found in large densities in the sites directly affected by the dam.

The fact that eco-exergy and specific eco-exergy exhibited higher values in the dam reservoir suggests that the occurrence of high densities and biomass of *C. fluminea* and *M. tubertulata* without visible negative impacts on the native species, therefore adds to the overall structure of the benthic macroinvertebrate assemblage (Hall et al., 2001; Strayer et al., 1999). This result suggests the opening a new energetic pathway, as the invasive species access resources that were not previously available for the assemblage (Marchi et al., 2010). Similar results were found in reservoirs invaded by two species of invasive bivalves (Linares et al., 2017b).

Our results also suggest that while changes in the physical habitat downstream from the dam allowed taxa that otherwise would be rarer or not present to establish, which was captured by diversity indices, it did not affect too much the benthic assemblage taxonomic structure in terms of its complexity. In general, this suggests that changes occurred did not change the energy flows and the available energy for the benthic macroinvertebrate assemblages, thus not altering the complexity of their dissipative structure (Jørgensen, 2007b; Marchi et al., 2011; Rezende et al., 2008).

Conclusions

Ecological impacts occurred essentially in the dam reservoir and in the downstream river stretches next to the dam, but the fact that conditions in the reservoir allowed invasive species to become dominant constitute a risk for other habitats in the Pandeiros river basin. In fact, although the capacity of *Corbicula fluminea* and *Melanoides tuberculate,* invasive species, to establish themselves in non-altered stretches of the Pandeiros river appears to be very limited, reservoirs may be used as stepping stones for these species to spread further in the region (Johnson et al., 2008), and thus our results suggest that a future dam decommissioning is advisable.

Our results also highlight the necessity to understand physical habitat changes caused by the presence and management of run-of-river dams. Deactivated dams in particular are increasingly common and a clear understanding of their impact over benthic macroinvertebrate assemblages is key for future dam removal projects. For further studies, we suggest a greater emphasis on the effects of sediment quality over benthic macroinvertebrate assemblages' structure, namely focusing on the metacommunity and on the dynamics of *C. fluminea* and *M. tuberculata* populations in the Pandeiros river basin.

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Conclusões Gerais da Tese

Os resultados desta tese evidenciam que eco-exergia e eco-exergia específica são bons indicadores ecológicos em ecossistemas aquáticos neotropicais. Os resultados destes indicadores mostraram-se consistentes em uma ampla gama de condições ambientais, sendo capazes de oferecer respostas significativas a alterações tanto naturais quanto antropogênicas.

A presença de bivalves invasores altera significativamente a estrutura de comunidades bentônicas em reservatórios neotropicais, uma consequência direta de sua natureza como engenheiros de ecossistemas.

Comunidades de macroinvertebrados bentônicos apresentam maior complexidade e produção secundária em riachos de cabeceira com vegetação ripária naturalmente de dossel aberto, o que implica em que os ecossistemas de riachos de cabeceira neotropicais são dependentes da produção primária autóctone.

Os efeitos significativos da barragem da pequena central hidrelétrica no rio Pandeiros sobre as comunidades bentônicas evidenciam que mesmo barragens de pequeno porte alteram a estrutura de comunidades de macroinvertebrados bentônicos.

Perspectivas Futuras

Os resultados obtidos nesta tese evidenciam os indicadores de exergia como ferramentas promissoras para avaliação ambiental no Brasil e em regiões tropicais em geral. Para seu futuro desenvolvimento recomendo:

- Testar as respostas de eco-exergia e eco-exergia específica a um gradiente de condições ambientais.
- Caracterizar os efeitos da presença de espécies invasoras sobre a estrutura de comunidades de macroinvertebrados bentônicos em ecossistemas naturais.
- Aumentar a resolução taxonômica dos valores do coeficiente de infomação genética (**β**) da equação de cálculo da eco-exergia, de modo a tornar os indicadores de exergia mais precisos.

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Anexos

Anexo 1 – Indicadores testados no Capítulo 1

Biomassa Total (g/m^2)	Biomassa Bivalves Invasores (g/m^2)	Biomassa *Melanoides* (g/m^2)	Biomassa Nativos (g/m^2)	Eco-exergia	Eco-exergia Específica	Bivalves Invasores
0.926418	0.911379	0.009716	0.005323	274.6709	296.4871	Presente
0.079865	0.039082	0.004858	0.035925	19.63234	245.8198	Presente
0.473856	0.357985	0	0.11587	131.7483	278.0347	Presente
0.485006	0.286072	0.194318	0.004615	145.9781	300.9821	Presente
0.078292	0.039082	0.029148	0.010063	22.62152	288.9367	Presente
0.777275	0.742552	0.014574	0.020149	228.5846	294.0848	Presente
0.917046	0	0.019432	0.897614	125.4066	136.7506	Ausente
0.719052	0.312653	0.029148	0.377251	167.7718	233.3235	Presente
0.924478	0.787884	0.019432	0.117163	261.3237	282.6715	Presente
1.189538	0.301662	0	0.887876	238.2761	200.3098	Presente
0.15513	0	0	0.15513	28.53305	183.9303	Ausente
0.367636	0.273572	0.058296	0.035769	105.9038	288.0672	Presente
0.121022	0	0	0.121022	21.30022	176.0032	Ausente
1.787827	0	0	1.787827	241.5726	135.1208	Ausente
0.532269	0.46898	0.009716	0.053573	151.8189	285.2298	Presente
1.592482	1.446022	0.102017	0.044443	469.2713	294.6792	Presente
0.396936	0.312653	0.014574	0.069709	109.5641	276.0245	Presente
0.231399	0.039082	0.04858	0.143738	49.67933	214.6912	Presente
0.829155	0	0.014574	0.814582	134.5301	162.2495	Ausente
0.014908	0	0	0.014908	2.214153	148.5173	Ausente
0.23971	0.039082	0.116591	0.084038	60.12073	250.8058	Presente
0.108242	0	0.106875	0.001367	33.3828	308.4089	Ausente
0.409287	0.351735	0.04858	0.008972	121.1758	296.0659	Presente
0.688899	0.156327	0.02429	0.508282	133.0603	193.1493	Presente
0.162215	0.039082	0.004858	0.118276	33.42295	206.0407	Presente
0.166107	0.117245	0	0.048862	43.81244	263.7598	Presente
14.06859	13.94424	0.04858	0.075767	4170.012	296.406	Presente
0.50277	0.461149	0.034006	0.007615	148.7749	295.9103	Presente
0.16634	0.156327	0	0.010013	48.25401	290.0926	Presente
0.235823	0.123495	0.019432	0.092896	59.31752	251.534	Presente
1.562935	1.250613	0.165171	0.147151	447.7821	286.5007	Presente
1.028284	0.772222	0.019432	0.23663	278.4277	270.7693	Presente
0.094817	0	0.063153	0.031663	25.40363	267.9233	Ausente
1.167655	1.055205	0.004858	0.107592	334.6988	286.6418	Presente
1.608892	1.224032	0.121449	0.263411	449.0446	279.1018	Presente
0.74936	0.46898	0.087443	0.192937	198.9804	265.5337	Presente
2.906835	0.429898	0.165171	2.311766	571.5142	196.6105	Presente
0.94937	0.748802	0.04858	0.151989	265.0182	279.1515	Presente
1.322849	1.016123	0.126307	0.180418	371.4054	280.7618	Presente

Biomassa Total (g/m²)	Biomassa Bivalves Invasores (g/m²)	Biomassa *Melanoides* (g/m²)	Biomassa Nativos (g/m²)	Eco-exergia	Eco-exergia Específica	Bivalves Invasores
0.059125	0	0	0.059125	10.52473	178.0084	Ausente
0.017903	0	0	0.017903	3.217449	179.717	Ausente
0.076329	0	0	0.076329	14.04446	184	Ausente
0.017419	0	0	0.017419	3.192454	183.2701	Ausente
0.012038	0	0	0.012038	2.214932	184	Ausente
2.03286	0	0	2.03286	373.8696	183.9131	Ausente
1.08373	0	0	1.08373	199.4064	184	Ausente
0.607921	0	0	0.607921	106.7636	175.6208	Ausente
0.171228	0	0	0.171228	31.20233	182.2268	Ausente
1.332905	0	0	1.332905	230.523	172.9478	Ausente
0.184999	0	0	0.184999	33.87518	183.1105	Ausente
0.584451	0	0	0.584451	107.3799	183.7279	Ausente
0.057274	0	0	0.057274	10.51066	183.515	Ausente
0.048357	0	0	0.048357	8.29445	171.5246	Ausente
0.259276	0	0	0.259276	45.7373	176.4036	Ausente
0.069492	0	0	0.069492	12.34596	177.6591	Ausente
0.789128	0	0	0.789128	144.9642	183.7017	Ausente
2.297391	0	0	2.297391	420.5587	183.0592	Ausente
0.330717	0	0	0.330717	60.11294	181.7657	Ausente
0.216523	0	0	0.216523	39.20469	181.0652	Ausente
0.068898	0	0	0.068898	12.11547	175.8471	Ausente
0.077877	0	0	0.077877	14.32938	184	Ausente
0.023414	0	0	0.023414	3.965208	169.3511	Ausente
0.146919	0	0	0.146919	27.00752	183.8256	Ausente
0.134566	0	0	0.134566	23.25166	172.7905	Ausente
0.744202	0	0	0.744202	134.3616	180.5444	Ausente
0.325481	0	0	0.325481	59.67256	183.3367	Ausente
3.642514	0	0	3.642514	670.2226	184	Ausente
0.359569	0	0	0.359569	66.13514	183.9287	Ausente
0.652162	0	0	0.652162	119.8376	183.7542	Ausente
0.718864	0	0	0.718864	132.1065	183.7711	Ausente
0.146127	0	0	0.146127	22.81395	156.1238	Ausente
0.246559	0	0	0.246559	45.33044	183.8525	Ausente
0.192226	0	0	0.192226	34.85501	181.3235	Ausente
0.043838	0	0	0.043838	7.530942	171.7907	Ausente
0.458265	0	0	0.458265	84.29441	183.9423	Ausente
0.017841	0	0	0.017841	3.208105	179.812	Ausente
0.069059	0	0	0.069059	12.70683	184	Ausente
0.01634	0	0	0.01634	2.94885	180.4673	Ausente
0.205199	0	0	0.205199	37.38414	182.1851	Ausente
0.067685	0	0	0.067685	12.19861	180.2263	Ausente
1.009652	0	0	1.009652	183.5986	181.8436	Ausente

Biomassa Total (g/m²)	Biomassa Bivalves Invasores (g/m²)	Biomassa *Melanoides* (g/m²)	Biomassa Nativos (g/m²)	Eco-exergia	Eco-exergia Específica	Bivalves Invasores
0.485327	0	0	0.485327	88.27203	181.8815	Ausente
0.749033	0	0	0.749033	124.8882	166.7325	Ausente
0.059897	0	0	0.059897	9.895077	165.201	Ausente
0.257227	0	0	0.257227	44.61497	173.4458	Ausente
0.328629	0	0	0.328629	58.25295	177.2605	Ausente
0.031371	0	0	0.031371	5.772183	184	Ausente
0.155705	0	0	0.155705	29.33223	188.3834	Ausente
0.09697	0	0	0.09697	17.83818	183.9555	Ausente
0.06335	0	0	0.06335	11.59	182.9516	Ausente
0.240579	0	0	0.240579	43.39112	180.3609	Ausente
0.053447	0	0	0.053447	9.760739	182.6249	Ausente
0.015812	0	0	0.015812	2.656613	168.0173	Ausente
0.481999	0	0	0.481999	80.64111	167.3056	Ausente
0.06233	0	0	0.06233	10.64639	170.808	Ausente
0.042745	0	0	0.042745	7.865114	184	Ausente
0.113113	0	0	0.113113	20.88028	184.5959	Ausente
0.067064	0	0	0.067064	12.33976	184	Ausente
0.016714	0	0	0.016714	3.075301	184	Ausente
0.066218	0	0	0.066218	11.77466	177.8166	Ausente
0.049263	0	0.001155	0.048107	9.157399	185.8886	Ausente
0.270941	0	0	0.270941	49.55897	182.9142	Ausente
4.218211	4.110532	0.001733	0.105946	1242.053	294.4502	Presente
0.375388	0	0	0.375388	66.5572	177.3027	Ausente
0.080392	0	0	0.080392	14.6947	182.7884	Ausente
0.198085	0	0	0.198085	36.43533	183.9378	Ausente
0.013248	0	0	0.013248	2.297241	173.4025	Ausente
0.087243	0	0	0.087243	15.34567	175.8956	Ausente
0.378526	0	0	0.378526	69.69533	184.1228	Ausente
0.102156	0	0	0.102156	17.80034	174.247	Ausente
0.04669	0	0	0.04669	8.48936	181.825	Ausente
0.204321	0	0	0.204321	37.52724	183.6681	Ausente
0.188642	0	0	0.188642	33.44126	177.274	Ausente
0.756081	0	0	0.756081	128.1973	169.555	Ausente
0.418895	0	0	0.418895	73.91178	176.4448	Ausente
0.313914	0	0	0.313914	55.93639	178.1902	Ausente
0.056203	0	0.000578	0.055625	10.27216	182.7704	Ausente
0.022098	0	0	0.022098	4.066046	184	Ausente
0.291264	0.018751	0.034006	0.238507	49.65073	170.4666	Presente
0.053793	0.025001	0	0.028792	12.0048	223.1677	Presente
0.13717	0	0	0.13717	19.49398	142.1155	Ausente
0.069528	0	0	0.069528	10.99773	158.1772	Ausente
0.034324	0	0	0.034324	6.315597	184	Ausente

Biomassa Total (g/m^2)	Biomassa Bivalves Invasores (g/m^2)	Biomassa *Melanoides* (g/m^2)	Biomassa Nativos (g/m^2)	Eco-exergia	Eco-exergia Específica	Bivalves Invasores
0.028163	0	0	0.028163	3.74571	133	Ausente
0.021751	0	0	0.021751	3.643112	167.4913	Ausente
0.011944	0	0	0.011944	1.838656	153.9368	Ausente
0.021751	0	0	0.021751	3.643112	167.4913	Ausente
0.258919	0	0	0.258919	36.4517	140.784	Ausente
0.093145	0	0	0.093145	15.7023	168.5796	Ausente
0.136169	0	0	0.136169	19.61089	144.019	Ausente
0.122889	0	0	0.122889	18.09478	147.2447	Ausente
0.034865	0	0	0.034865	5.906206	169.4013	Ausente
0.016848	0	0	0.016848	2.740884	162.6865	Ausente
0.653915	0	0	0.653915	102.7253	157.0928	Ausente
0.477002	0	0	0.477002	67.56422	141.6434	Ausente
0.761596	0	0	0.761596	105.0434	137.9253	Ausente
0.105989	0	0	0.105989	17.34753	163.6726	Ausente
0.024517	0	0	0.024517	4.51114	184	Ausente
0.374748	0	0	0.374748	54.57993	145.6444	Ausente
0.144839	0	0	0.144839	21.26424	146.8125	Ausente
0.363124	0	0	0.363124	59.8588	164.8437	Ausente
0.026654	0	0	0.026654	4.54534	170.5283	Ausente
0.925611	0	0	0.925611	124.35	134.3437	Ausente
0.161545	0	0	0.161545	22.90173	141.7669	Ausente
0.690118	0	0	0.690118	114.7083	166.2155	Ausente
2.142613	0	0	2.142613	313.9761	146.5389	Ausente
0.154143	0	0	0.154143	28.00327	181.6705	Ausente
0.108755	0	0	0.108755	18.21556	167.4913	Ausente
0.024517	0	0	0.024517	4.51114	184	Ausente
0.049914	0	0	0.049914	7.388822	148.0302	Ausente
0.007041	0	0	0.007041	0.936428	133	Ausente
0.222342	0	0	0.222342	32.293	145.2401	Ausente
0.013291	0.00625	0	0.007041	2.792743	210.1224	Presente
0.050063	0.00625	0.034006	0.009807	14.27056	285.0533	Presente
0.045567	0.0125	0	0.033067	8.360569	183.4782	Presente
0.039945	0.00625	0	0.033695	7.338083	183.7024	Presente

Anexo 2- Indicadores testados no Capítulo 2

Abertura de Dossel	Produção Secundária Instantânea (g/m²/dia)	Eco-Exergia	Eco-Exergia Específica	Biomassa (g/m²)	Deinsidade (Ind/m²)	Temperatura (ºC)
Open	53.20532	103.6662	180.6789	0.573759	6785.185	19.3
Open	12.88455	68.39271	169.8008	0.402782	3635.185	19.2
Open	30.94431	135.1034	167.6058	0.806078	5357.407	19.2
Open	34.79792	71.01435	178.1048	0.398722	5422.222	18.2
Shaded	6.951554	23.45391	169.1336	0.138671	829.6296	16.7
Shaded	8.250475	24.27409	161.7343	0.150086	1364.815	20.3
Shaded	8.928955	27.61622	164.2049	0.168181	1590.741	18.4
Shaded	1.826057	6.333297	166.6152	0.038012	261.1111	19.4

Anexo 3 – Indicadores testados no Capítulo 3

Estação de Coleta	Biomassa (g/m^2)	Biomassa Invasores (g/m^2)	Eco-exergia	Eco-exergia Específica	% de Biomassa de Invasores	Riqueza	Shannon	Simpson
P1	0.225113	0	36.24118	160.9908	0	10	1.534763	0.717637
P1	0.79758	0	125.8438	157.7821	0	20	2.226627	0.87078
P1	0.630839	0	108.3107	171.6931	0	18	1.26189	0.552633
P1	0.563009	0	99.98931	177.5982	0	24	1.703356	0.710129
P1	0.442821	0	85.5964	193.2978	0	21	1.56572	0.648436
P1	1.292764	0	224.8128	173.9009	0	23	1.925075	0.789655
P2	0.375258	0.174239	87.86863	234.1551	0.464318	18	1.108929	0.440676
P2	2.376255	0.852701	482.0527	202.8624	0.358842	16	0.594492	0.227013
P2	0.64033	0.286976	146.5435	228.8563	0.448169	20	0.457603	0.157065
P2	3.706562	2.976577	1057.343	285.2625	0.803056	28	0.463294	0.171447
P2	1.726862	0.494398	347.5699	201.2725	0.286298	32	0.83629	0.29926
P2	1.504722	0.995153	395.3117	262.7141	0.661353	21	0.650483	0.21506
P3	0.281819	0.087317	58.38764	207.1811	0.309833	18	2.498784	0.890376
P3	0.26327	0.003409	44.71066	169.8283	0.012949	24	2.583164	0.902264
P3	0.831467	0.387948	194.9741	234.494	0.466583	28	2.70402	0.911107
P3	0.498114	0.068346	97.30275	195.3424	0.13721	29	2.294082	0.850783
P3	0.494391	0.041689	92.20684	186.506	0.084323	29	2.317869	0.838739
P3	0.533505	0.069461	101.7767	190.7698	0.130197	26	2.529808	0.895232
P4	0.194576	0	32.28036	165.9012	0	13	1.784923	0.737532
P4	0.452222	0	79.24171	175.2273	0	17	1.747054	0.738054
P4	0.589279	0	107.4709	182.377	0	15	1.356716	0.608249
P4	0.627	0	113.3174	180.7297	0	20	1.656082	0.645622
P4	0.339837	0	62.70947	184.528	0	20	1.748809	0.72672
P4	1.256733	0	236.2311	187.9724	0	18	1.246533	0.550765