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Tese de Doutorado

Dinâmica do carbono alóctone, fluxo de energia e produção secundária de macroinvertebrados detritívoros

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Resumo

O material alóctone oriundo da vegetação terrestre pode representar uma importante fonte de carbono e energia para fauna local, além de configurar um elemento estruturador em riachos florestados de baixas ordens. Entretanto, o papel deste material enquanto fonte de carbono e energia para comunidades de macroinvertebrados bentônicos em ambientes lóticos tropicais não é claro. Assim como a importância da matéria alóctone na manutenção da biota riverina, o papel dos fragmentadores na decomposição foliar permanece como questão em aberto. Ainda, estudos abordando a produção secundária da comunidade de macroinvertebrados, necessários para estimativas relacionadas ao consumo e assimilação de recursos e fluxo de energia, são escassos em rios tropicais. No intuito de compreender a relação entre macroinvertebrados consumidores, dinâmica do material terrestre no meio aquático e cobertura vegetal, analisamos ao longo de um gradiente 8-93% de cobertura ripária a relação entre biomassa, produção de macroinvertebrados consumidores, disponibilidade e decomposição da matéria orgânica terrestre. Assim, esta tese foi dividida em dois capítulos, onde (1) buscou-se avaliar, ao longo de um gradiente de cobertura vegetal, a relação entre biomassa de macroinvertebrados fragmentadores, disponibilidade e taxas de decomposição foliar; e (2) estimar o processamento de folhas via fragmentadores e verificar a relação entre a biomassa e produção secundária de consumidores e a disponibilidade de diferentes categorias de matéria orgânica potencialmente utilizadas como recurso alimentar. No primeiro capítulo foi observado que apesar da ausência de um padrão relacionado à cobertura vegetal na biomassa de fragmentadores, disponibilidade de folhas e taxas de decomposição, a biomassa de fragmentadores, representada principalmente por *Triplectides spp.* (Trichoptera, Leptoceridae), foi positivamente relacionada à disponibilidade e taxas de decomposição de material foliar.

Além disso, apesar da baixa diversidade de macroinvertebrados fragmentadores, a biomassa do grupo foi superior a 40% da biomassa bentônica na maior parte dos depósitos foliares. Os resultados indicam ainda que o emprego da biomassa de macroinvertebrados pode representar uma ferramenta útil em análises relacionadas a grupos tróficos e processos ecossistêmicos. Assim, apesar da ausência de um padrão relacionado ao sombreamento, os resultados indicam a importância de macroinvertebrados fragmentadores no processo de decomposição foliar e elevada representatividade do grupo em termos de biomassa em depósitos foliares. No segundo capítulo observamos grande importância do material terrestre na manutenção dos organismos bentônicos e correlação positiva entre os grupos tróficos e a disponibilidade de seus potenciais recursos alimentares. Entretanto, apesar da correlação positiva entre a produção secundária de fragmentadores e quantidade de material foliar, a participação desses organismos no processo de decomposição é pequena, correspondendo a menos de 15% do desaparecimento total de material na maioria dos sites. Ainda, os valores de produção secundária bentônica estimados são superiores aos encontrados em pequenos rios preservados de regiões tropicais e podem ser considerados intermediários em relação às estimativas obtidas em regiões temperadas.

Palavras-chaves: produção de biomassa; matéria orgânica alóctone; fragmentadores; processos ecossistêmicos.

Abstract

Allochthonous organic matter can represent an important source of energy and carbon to local fauna and a structuring element in low order streams covered by riparian vegetation. However, the role of organic matter as carbon source for benthic macroinvertebrates is not yet clear. Likewise, the role of shredders in litter breakdown is still an open question. Estimates of secondary production, which are necessary for approaches related to consumption and assimilation of resources and energy flux, are scarce in tropical lotic ecosystems. Aiming to understand the relationship among macroinvertebrate consumers, allochthonous organic matter dynamics and riparian vegetation, we analyzed along an 8-93% canopy cover gradient macroinvertebrate biomass and secondary production, organic matter availability and litter breakdown. This thesis was divided in two chapters, where the aims were (1) to analyze along an 8-93% canopy cover gradient the relationship among shredders biomass, leaf availability and breakdown rates; and (2) estimate litter consumption by shredders and analyze the relationship between potential consumer biomass and secondary production and availability of organic matter fractions. In chapter one we observed that despite the absence of pattern in shredder biomass, litter availability and breakdown related to canopy cover, shredders biomass, mainly represented by *Triplectides* (Trichoptera, Leptoceridae), was positively related to litter availability and breakdown rates. Additionally, despite low shredder diversity, the biomass of this group responded for up 40% of total macroinvertebrate biomass in most litter-banks. Our results suggest that biomass estimates represent a useful tool for analyzing functional feeding groups and ecosystem processes. To conclude, despite the lack of a pattern related to riparian vegetation, results indicate high biomass and importance of shredders macroinvertebrates on litter breakdown. In chapter two we observed the importance of allochthonous organic matter for the maintenance of benthic macroinvertebrates and positive relationship between functional feeding groups (FFG) and the availability of their potential resource. However, despite positive relationship between shredder secondary production and leaf availability, the ingestion of leaf material by this group corresponded to <15% of estimated leaf breakdown in most sites. Additionally, our secondary production estimates were higher than observations from tropical headwaters, but intermediate compared to temperate streams.

Key-words: biomass production; allochthonous organic matter; shredders; ecosystem processes

Sumário

Introdução

Riachos de cabeceira, margeados por vegetação ripária, são fortemente influenciados pelo ambiente terrestre adjacente. A interface entre o ambiente terrestre e aquático afeta muitas taxas ecossistêmicas (McClain et al., 2003) em especial, pelo controle sobre a energia disponibilizada para manutenção da cadeia trófica aquática (Vörösmarty et al., 2010). Além do aporte de material, em especial folhas (França et al., 2009; Gonçalves et al., 2014; Bambi et al., 2016), o sombreamento promovido pela vegetação previne o aquecimento excessivo da água e, concomitantemente, limita a produção primária aquática (Vannote et al., 1980; Allan & Castillo, 2007).

O material de origem terrestre que alcança o meio aquático contribui para diversidade de substratos (Allan & Castillo, 2007) e favorece a colonização de diversos organismos (Lautenschläger & Kiel, 2005). Em decorrência da diversidade de habitats e alta complexidade, ecossistemas aquáticos naturais podem suportar diversas comunidades, de micro a macrorganismos, dentre estas, as comunidades bentônicas, que habitam o sedimento destes ecossistemas (Wetzel, 2001).

A matéria terrestre pode representar a principal fonte de energia para macroinvertebrados fragmentadores, i.e. organismos que obtêm recursos alimentares via fragmentação de folhas (*sensu* Cummins, 1973), sustentando cadeias marrons (*brown food webs*; Kaspari 2004), que são redes tróficas mantidas por detritos. De acordo com estimativas obtidas em rios temperados, macroinvertebrados fragmentadores podem processar mais de 60% do material foliar (Webster & Benfield, 1986; Wallace & Webster, 1996; Heiber & Gessner, 2002; Graça et al., 2015).

Através da fragmentação, esses organismos promovem a ciclagem de matéria e nutrientes, incorporando carbono oriundo do ambiente terrestre na cadeia trófica riverina (Wallace et al., 1999). Ainda, o processamento da matéria, por micro e macrorganismos, culmina com a diversificação de frações da matéria orgânica no meio uma vez que durante o processo de conversão de matéria orgânica particulada grossa (CPOM) em partículas menores, há continua liberação de matéria orgânica particulada fina (FPOM), matéria orgânica particulada ultrafina (UFPOM) e matéria orgânica dissolvida (DOM; Cummins & Klug, 1979). Essas frações representam recursos alimentares para microrganismos e outros macroinvertebrados, como coletores, que obtêm recursos alimentares através do consumo de FPOM (Cummins & Klug, 1979).

Em decorrência da dominância do material de origem terrestre em relação à produção primária produzida *in situ* em pequenos riachos, margeados por densa vegetação, um dos pontos centrais do *River Continuum Concept* (RCC; Vannote et al., 1980) é o papel central do carbono alóctone na manutenção da fauna de riachos de cabeceira. Em ecossistemas lóticos de regiões temperadas, onde foi desenvolvido, o RCC é bem-ajustado, refletindo bem as alterações ao longo de ecossistemas lóticos (Fisher & Likens, 1973; Wallace et al., 1999; mas veja Thorp & Delong, 1994, 2002). Entretanto, em ecossistemas tropicais, o RCC é considerado uma teoria controversa.

De acordo com Bunn (1999a, b), em ambientes tropicais, mesmo em pequenos riachos de cabeceira, densamente cobertos por vegetação ripária, há luminosidade suficiente para sustentar considerável produção primária. Ainda, folhas de muitas espécies vegetais tropicais tendem a exibir elevadas concentrações de compostos secundários e recalcitrantes em relação às espécies de regiões temperadas (Coley & Aide, 1991; Coley & Barone, 1996), o que poderia prevenir o consumo por fragmentadores e reduzir a colonização de macroinvertebrados em depósitos foliares à busca por substrato (Li et al., 2009).

Em regiões tropicais, estudos indicando ausência de relação entre decomposição foliar e macroinvertebrados colonizadores (Ardón & Pringle, 2008; Silva-Jr & Moulton, 2011), bem como escassez e baixa participação de fragmentadores na decomposição (Dudgeon & Wu, 1999; Dobson et al., 2002; Gonçalves et al., 2006, 2007; Ardón and Pringle, 2008; Alvim et al., 2015) colocam a importância do carbono terrestre e dos fragmentadores em questão. Ainda outros estudos, através do emprego de isótopos estáveis, apontam as algas como principal fonte de energia em córregos tropicais (Salas & Dudgeon, 2001a; Mantel et al., 2004; March & Pringle, 2003; Brito et al., 2006; Li & Dudgeon, 2008; Neres-Lima et al., 2016; Brett et al., 2017).

Por outro lado, evidências contrárias, indicando alta diversidade, abundância, produção de biomassa e importância de macroinvertebrados fragmentadores no processo de decomposição foram observadas na Austrália, Brasil, Equador, Malásia, Panamá e Quênia (Cheshire et al., 2005; Camacho et al., 2009; Yule et al., 2009; Encalada et al., 2010; Masese et al., 2014; Tonin et al., 2014; Andrade et al., 2017; Neres-Lima et al., 2017; Aguiar et al., 2017). Estudos recentes realizados na Mata Atlântica indicam que o principal recurso consumido por macroinvertebrados, ingerido e assimilado, é oriundo do ambiente terrestre (Neres-Lima et al., 2017). No referido estudo foi constatado que poucos *taxa* - fragmentadores e filtradores - dominam o fluxo de energia, e assimilam majoritariamente carbono alóctone (Neres-Lima et al., 2017). Ainda, na mesma localidade, um experimento de decomposição foliar revelou importante participação de macroinvertebrados fragmentadores no processo (Andrade et al., 2017). O estudo também indicou os efemerópteros Leptophlebiidae, não usualmente classificados como fragmentadores, como principais insetos atuantes no processo de decomposição (Andrade et al., 2017).

Evidências obtidas a partir de estudos globais, indicam grande variabilidade na ocorrência de macroinvertebrados fragmentadores e na decomposição foliar em ambientes tropicais (Boyero et al., 2012, 2015), corroborando resultados contraditórios obtidos nessas regiões. Por outro lado, independente da fonte de carbono majoritariamente utilizada por macroinvertebrados, fatores metodológicos podem estar subestimando os fragmentadores em ambientes tropicais.

Macroinvertebrados tropicais são frequentemente classificados em grupos funcionais de alimentação (FFG) de acordo com classificações propostas para ambientes temperados (Camacho et al., 2009). Porém, organismos não usualmente classificados como fragmentadores, podem estar atuando na decomposição. O gênero *Farrodes* (Leptophlebiidae) por exemplo, foi classificado como fragmentador por Bello e Cabrera (2001). Adicionalmente, a participação dos fragmentadores pode estar sendo subestimada pelas classificações embasadas em números de indivíduos. Uma vez que típicos fragmentadores, como os Trichoptera *Triplectides* e *Phylloicus*, apresentam dimensões corporais bem maiores que os usuais organismos abundantes (ex: Chironomidae). Assim, estimativas relacionadas à biomassa e/ou produção secundária podem ser mais adequadas para elucidar a importância e papel do grupo no processamento de material terrestre.

Macroinvertebrados bentônicos são componentes fundamentais em ecossistemas lóticos e estão associados à diversos processos. Através da formação de biomassa, via consumo de material alóctone e autóctone, esses organismos atuam reciclando e disponibilizando energia basal a níveis tróficos superiores (Allan & Castillo, 2007). A produção secundária, processo decorrente do fluxo de energia e matéria via ingestão e assimilação de recursos, implica em formação de tecido vivo. Individualmente, o processo implica em crescimento do organismo e coletivamente, quando se trata da formação de biomassa de uma população. No âmbito individual, as perdas ocorrem através das fezes, excreção e respiração e sob a perspectiva populacional, as perdas ocorrem através da emigração e morte (Figura 1; Benke, 2010). A produção secundária é determinada por variáveis como biomassa, taxa de crescimento, dimensões corporais, densidade, fecundidade, sobrevivência e longevidade, e assim é também considerada uma medida de *fitness* ou 'sucesso' de uma população (Benke, 2010).

A biomassa de uma população é produto da biomassa individual média e densidade, variáveis que podem também ser afetadas por diversas características ambientais como estabilidade e os tipos de substrato, temperatura, química da água, vazão, qualidade e quantidade de recursos alimentares, que atuarão sinergicamente determinando a produção da população (Benke et al., 1988; Dudgeon, 1999; Rosi-Marshall & Wallace, 2002; Cross et al., 2005; Cross et al., 2006).

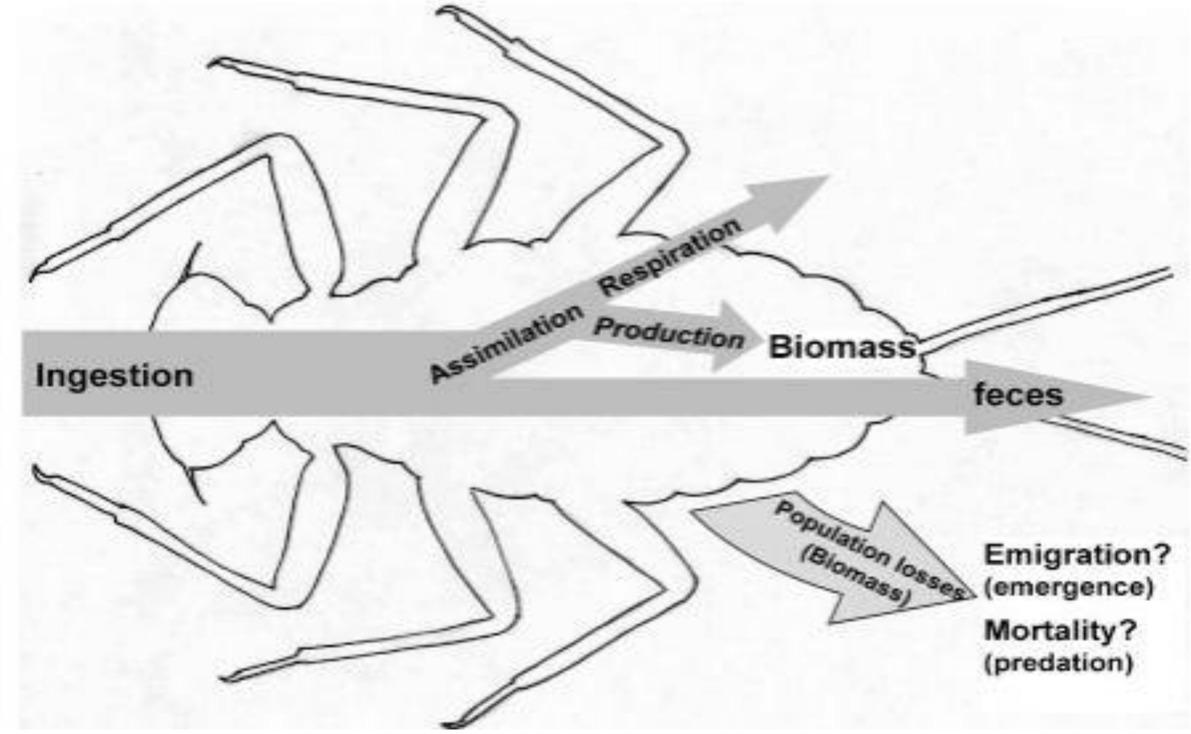

Figura 1. A produção secundária como um fluxo de formação de biomassa através do crescimento de um indivíduo ou coletivamente, através do crescimento da população e suas respectivas perdas (Benke, 2010).

A interação entre recurso e consumidor rege os fluxos de energia e matéria nas comunidades (Schindler & Lubetkin, 2004) e a participação de uma determinada população no fluxo de energia só pode ser compreendida via estimativas de produção secundária (Benke & Wallace, 1980; Benke & Huryn, 2010). Como a produção é um processo associado a diversas variáveis, portanto suscetível às alterações destas, o emprego desta ferramenta pode ser útil para analisar questões de variadas naturezas, como relações tróficas (Huryn, 1998), relações interespecíficas (Johnson et al., 1992; Lamberti et al., 1995; Huryn, 1998), estimativas de contribuição de diferentes fontes de carbono na manutenção de teias tróficas (Linares et al., 2017; Neres-Lima et al., 2017), estimativas de fluxo de energia entre ecossistemas (Henschel et al., 2001; Sabo & Power, 2002; Cratton & Zanden, 2009) e avaliação de impactos e alterações ambientais

(Whiles & Wallace, 1995; Shieh et al., 2002, 2003; Gücker et al., 2011; Aguiar et al., 2015).

Entretanto, estudos quantificando a produção de biomassa de macroinvertebrados e a relação destes organismos e suas fontes alimentares são inconclusivos, não permitindo inferências a respeito de padrões em ambientes lóticos tropicais (Ramírez & Pringle, 1998; Dudgeon, 1999; Salas & Dudgeon, 2001b; Yam & Dudgeon, 2006; Aguiar et al., 2015; Linares et al., 2017; Neres-Lima et al., 2017). E trabalhos que estimaram a produção de comunidades bentônicas, ou de parte delas (de insetos aquáticos), em ecossistemas preservados são raros (Ramírez & Pringle, 1998; Dudgeon, 1999; Linares et al., 2017; Neres-Lima et al., 2017).

Algumas barreiras dificultam a abordagem da produção secundária bentônica de macroinvertebrados bentônicos em ambientes tropicais, a começar pelo fato que a identificação desses organismos pode ser difícil pela carência de estudos (Boyero, 2002). Talvez a maior parte dos organismos que compõem a fauna bentônica em países tropicais seja desconhecida ou ainda não tenha sido descrita (Cressa & Holzental, 2003). A ausência de um padrão no tempo de desenvolvimento, gerando desenvolvimento assíncrono e o multivoltinismo, dificultam estimativas de produção de populações, uma vez que o desenvolvimento de espécies bem como o número de coortes pode variar de acordo com habitat ou região (Jacobsen et al., 2008).

Modelos baseados em medidas de biomassa e temperatura (Morin & Bourassa, 1992; Morin & Dumont, 1994; Morin, 1997, Jacobsen et al., 2008) podem representar uma alternativa para realização de pesquisas relacionadas à produção secundária em ambientes tropicais (Aguiar et al., 2015; Linares et al., 2017; Neres-Lima et al., 2017).

Embora não sejam perfeitos substitutos de medidas reais, modelos podem fornecer estimativas da magnitude da produção secundária (Benke, 1996).

Para contornar problemas relacionados a dificuldades taxonômicas e de discernimento de coortes, o modelo *Size Frequency* foi desenvolvido (Hynes & Coleman, 1968). O método original envolve estimativas baseadas em classes de tamanho, sem identificação taxonômica e nem considerar sobrevivência e crescimento. Este modelo foi posteriormente modificado para ser aplicado para táxon individualmente (Hamilton, 1969; Benke et al., 1984), sendo o emprego do método recomendável em conjunto a estimativas de tempo de geração (Benke et al., 1984).

Apesar do amplo emprego de macroinvertebrados bentônicos em estudos relacionados à ecologia de ecossistemas aquáticos, a abordagem dessa comunidade da perspectiva funcional é escassa em ambientes terrestres. A carência de estudos relacionando organismos bentônicos e questões relativas aos métodos frequentemente empregados dificultam a compreensão do funcionamento de rios. Ainda, lacunas a respeito de estimativas de produção secundária e de outras taxas ecológicas impedem estimativas de fluxo energético e abordagens relacionando estrutura e processos.

Assim, o objetivo desta tese foi analisar, ao longo de um gradiente de cobertura vegetal, a relação entre a biomassa e produção secundária de FFG de macroinvertebrados bentônicos em bancos de folhas e diferentes frações de matéria orgânica alóctone para analisar a importância do carbono alóctone para metazoários de ecossistemas lóticos. Ainda, com este trabalho pretendeu-se avaliar a importância de macroinvertebrados fragmentadores nas taxas de decomposição foliar, através de estimativas de ingestão e assimilação e desaparecimento de massa total e classificados em FFG, em bancos de folhiço

No primeiro capítulo, o objetivo foi analisar a influência da cobertura da vegetação ripária sobre a relação entre biomassa de macroinvertebrados fragmentadores e disponibilidade e decomposição do material foliar. No segundo capítulo buscou-se, além de estimar a magnitude da participação dos fragmentadores no processamento de folhas, analisar a relação entre as diferentes frações da matéria orgânica e biomassa e produção secundária de consumidores de detritos.

Métodos

Área de estudo

O estudo foi conduzido no Rio Barra Pequena e Córrego da Andorinha, situados na Vila Dois Rios em Ilha Grande, Estado do Rio de Janeiro, Brasil (23°04′ a 23°14′S e 44°05′ a 44°23′W; Figura 2). Ilha Grande é a maior ilha do estado do Rio de Janeiro. Situada na Reserva da Biosfera da Mata Atlântica, é reconhecida pelo seu relevante papel ecológico, apresentando um conjunto diversificado de habitats associados inseridos na Floresta Pluvial Tropical Atlântica.

Os dois sistemas lóticos estudados - Córrego da Andorinha e o Rio Barra Pequena - estão situados em uma região preservada de Floresta Ombrófila Densa. O Córrego da Andorinha é caracterizado como um sistema lótico de 3ª ordem e possui uma área de bacia ~1260 ha. O Rio Barra Pequena, também de 3ª ordem, possui uma área de bacia ~566 ha. A formação geológica local é de gnaisse do Pré-Cambriano. As baixas concentrações de nutrientes dissolvidos na água caracterizam condições oligotróficas (total-N = 180 μg L^{-1}, total-P = 10 μg L^{-1}, pH = 6.6) e não mudam ao longo do percurso do rio. A condutividade é 27 μScm^{-1} no Córrego da Andorinha e 33 μScm^{-1} no Rio Barra Pequena.

Seis locais foram selecionados para a amostragem de matéria orgânica, macroinvertebrados bentônicos e realização do experimento de decomposição foliar. Os locais foram escolhidos seguindo um gradiente de cobertura da vegetação ripária, com sombreamento variando entre 8 e 93%. No Córrego da Andorinha foram selecionados quatro pontos – Jararaca (JAR), Characidium (CHA), Lambari (LAM) e Capivara

(CAP) – e um tributário de primeira ordem, Valium (VAL). No Barra Pequena (BP), um local de amostragem (Figura 2). A cobertura vegetal foi estimada usando um densiômetro esférico (Model-C, Forest Densiometers, Oklahoma, USA). Ao longo de transectos de 10 metros, a cada metro, foram tomadas medidas sentido norte, sul, leste e oeste para estimativa de cobertura vegetal média (Tabela 1). A vazão foi estimada em duas ocasiões (janeiro e fevereiro/2016; Tabela 1).

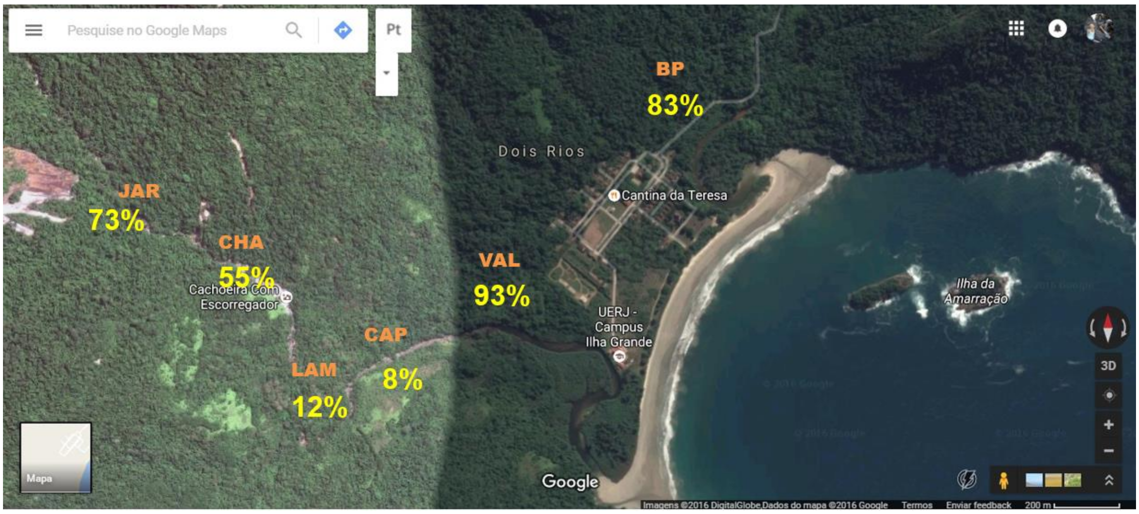

Figura 2. Locais de amostragem no Córrego da Andorinha e Rio Barra Pequena e respectivos valores de cobertura vegetal.

Tabela 1. Locais de amostragem e características

Sigla	Nome do local	Distância da foz (m)	Altitude (m asl)	Vazão (Ls^{-1})	Cobertura da vegetação(%)	Presença de macrofauna
				Média SD	Média	
VAL	Valium	-	53	9.97 ± 3.19	93	M, Po
JAR	Jararaca	2231	254	91.10	73	T
BP	Barra Pequena	236	34	135.50 ± 3.53	83	M, Po
CHA	Characidium	1240	83	432.80 ± 42.56	55	M, Po, P
LAM	Lambari	913	43	531.55 ± 177.04	12	M, P
CAP	Capivara	497	36	565.61 ± 190.04	8	M, P

P = peixes, **M** = *Macrobrachium* (camarão), **Po** = *Potimirim* (camarão), **T** = *Trichodactylus* (caranguejo)

Amostragem de matéria orgânica e macroinvertebrados bentônicos

A matéria orgânica e macroinvertebrados associados foram amostrados em bancos de folhiço em trechos de fluxo lento, favoráveis ao acúmulo de material vegetal. Foram realizadas oito campanhas de coleta mensais, de dezembro/2015 a julho/16, onde em cada local e cada campanha foram realizadas quatro amostragens.

Para amostragem, utilizamos um *stovepipe*, que consiste em um amostrador cilíndrico, com 20 cm de diâmetro, inserindo-o no substrato e removendo manualmente folhas, galhos e todo material aprisionado. Para retirar a matéria orgânica e macroinvertebrados suspensos e separar a matéria orgânica da inorgânica, aproximadamente 20 L de água foram transferidas de dentro do amostrador para um balde com um copo plástico e posteriormente, toda água foi passada por uma peneira (250 µm; Figura 3). O material restante no balde foi lavado repetidas vezes até que toda matéria orgânica fosse retida na peneira. Todo o material coletado foi armazenado em saco plástico e adicionada água do rio para manter os organismos bentônicos vivos.

A matéria orgânica bentônica ultrafina (UFBOM) foi coletada através da amostragem de ~300 ml de água de dentro do *stovepipe* passada por uma peneira (250 µm). A água foi armazenada em saco plástico apropriado (Whril-Pak, Nasco, Fort Atkinson, USA), vedado e devidamente identificado. O volume total de água aprisionado no *stovepipe* foi calculado através da mensuração da altura da coluna d’água para o cálculo do volume do cilindro. Após a amostragem, o material foi imediatamente levado para o laboratório do CEADS/UERJ – Ilha Grande para processamento.

Figura 3. Procedimento de amostragem da matéria orgânica e fauna bentônica associada – transferência da água aprisionada e todo material suspenso para o balde (à esquerda) e retenção do material coletado na peneira (à direita).

Processamento da matéria orgânica

No laboratório, as amostras foram cuidadosamente lavadas em peneiras de diferentes malhas (1000 µm e 250 µm) para separação da matéria orgânica em matéria orgânica particulada grossa (CPOM) e matéria orgânica em matéria orgânica particulada fina (FPOM). A CPOM foi posteriormente separada em folhas, galhos, partes reprodutivas e “outros” (material constituído majoritariamente por folhas processadas). O material categorizado foi seco em estufa a 55°C por 48 horas, pesado para estimar a massa seca (DM), e posteriormente incinerado em mufla a 500°C por 4 horas para obtenção da massa seca livre de cinzas (AFDM). Amostras de grande volume foram homogeneizadas, subamostradas antes da combustão posteriormente o percentual foi corrigido para a amostra total.

Volumes conhecidos de amostras de água foram filtrados em filtros de microfibra de vidro pré-incinerados (GFF, 0.7 µm Whatman) para estimativas de UFBOM. Após a filtragem, os filtros foram secos em estufa a 55°C por 24 horas para estimar a DMe incinerados em mufla a 500°C por 1 hora para obtenção da AFDM. Os valores totais de UFBOM das amostras foram estimados para o volume total de água aprisionado no *stovepipe*.

Macroinvertebrados bentônicos

Os macroinvertebrados bentônicos associados à CPOM foram triados vivos, concomitantemente à separação da matéria orgânica (Figura 4). Os organismos foram fixados em álcool 70% para posterior identificação e mensuração do comprimento corporal (mm). Os macroinvertebrados associados à FPOM foram triados com o auxílio de uma lupa eletrônica (40x). Amostras foram subdividas (no máximo 1/8 da amostra) para separação de macroinvertebrados, dependendo da quantidade de material.

Figura 4. *Triplectides* (Leptoceridae, Trichoptera) encontrados nas amostras de matéria orgânica.

Todos os macroinvertebrados bentônicos foram identificados até o menor nível taxonômico possível usando chaves de identificação (Mugnai et al., 2010). Os dípteros Chironomidae foram classificados em Tanypodinae (predadores) e não-Tanypodinae (coletores). Os efemerópteros Leptophlebiidae foram classificados como fragmentadores em virtude das evidências locais indicando elevada assimilação de carbono alóctone (Neres-Lima et al., 2017) e participação na decomposição foliar (Andrade et al., 2017). Os organismos foram classificados em grupos funcionais de alimentação (FFG) de acordo com as classificações de Baptista et al. (2006), Henriques-Oliveira e Nessimian (2010), e Ramírez e Gutiérrez-Fonseca (2014).

Estimativas de biomassa, produção secundária de macroinvertebrados bentônicos e de consumo de folhas

Através das medidas de tamanho corporal foi possível estabelecer relações entre comprimento (mm) e biomassa (mg DM m^{-2}) utilizando coeficientes táxon-específicos (Benke et al., 1999). A biomassa individual foi calculada através da equação:

$$B = a.L^{b}$$

Onde: **B** é biomassa individual, **L** comprimento, e ***a*** e ***b*** coeficientes táxon-específicos.

A biomassa total da população foi obtida através do produto da biomassa individual média e densidade (indivíduos m^{-2}) para cada local e mês.

Para o cálculo da produção secundária dos macroinvertebrados, foram utilizados diferentes métodos. Para os taxa mais abundantes, a produção foi obtida através do método *Size-Frequency* (Hynes & Coleman, 1968; Hamilton, 1969; Benke et al., 1984). O método não exige acompanhamento de coorte e a produção é estimada através da média da distribuição das classes de tamanho e de como se aproximam da curva de mortalidade de uma coorte média (Benke & Huryn, 2006). A diferença entre as densidades das categorias de tamanho (ΔN) foi multiplicada pela biomassa média entre tais categorias (W média). A soma dos produtos de W média e ΔN foi então multiplicada pelo número de classes de tamanho (Benke & Huryn, 2006). No presente trabalho foram estipulados, para todos os taxa, dez classes de tamanho. As estimativas de produção anual (mg DM m^{-2} ano^{-1}) foram obtidas através do produto da produção pelo intervalo de produção de coorte (CPI). A correção da produção e o emprego do CPI são necessários quando o intervalo de produção é diferente de um ano, como o multivoltinismo. Neste estudo utilizamos CPI obtidos por Jackson & Sweeney (1995), Barros & Fontoura (1996) e Jacobsen et al., (2008).

A produção dos taxa menos abundantes foi estimada através do modelo de crescimento instantâneo (mg DM m^{-2} dia^{-1}), convertida para produção anual. O modelo empírico é baseado na biomassa média da população (i.e. produto da biomassa individual média e densidade), temperatura da água e coeficientes específicos (Morin & Bourassa, 1992; Morin & Dumont, 1994):

$$\mathrm{log10(gr)} = a + b\,\mathrm{log10(B)} + c\,\mathrm{(T)}$$

Onde: **gr** é crescimento instantâneo, **B** é biomassa individual, **T** temperatura da água, e ***a***, ***b*** e ***c*** coeficientes específicos.

A produção de biomassa de cada população, amostragem e data foi então obtida como produto da taxa de crescimento instantânea média e biomassa total.

A produção de camarões e caranguejos foi obtida através das razões Produção/Biomassa obtidas por Neres-Lima (dados não publicados).

As estimativas de processamento foliar (ingestão anual de folhas) por fragmentadores foram estimadas dividindo-se a produção secundária do grupo por valores de eficiência, ou seja, pelo produto da eficiência de assimilação (Perry et al., 1987; Eggert & Wallace, 2007) e eficiência de produção (Benke & Wallace, 1980) de consumidores de matéria alóctone.

Experimento de decomposição foliar

Em cada local de estudo, em agosto/2015, foram coletadas folhas senescentes em seixos margeando o canal. Em cada margem, foram demarcados transectos ~5 metros, onde as folhas foram coletadas. As folhas foram levadas para o laboratório para serem separadas e identificadas as três espécies mais abundantes de cada local. As folhas foram identificadas e sua ocorrência confirmada em cada local por especialistas em Botânica.

As folhas foram secas e as três espécies mais abundantes foram unidas com clipes de papel para compor os pacotes foliares (~3g). As espécies mais abundantes representaram metade dos pacotes (~1,5g) e as duas compuseram a outra metade (~0,7g de cada). Os pacotes foram amarrados em cordas, presas ao substrato com pedras e/ou vergalhões (Figura 5a, b). Em cada local foram incubadas três cordas com cinco pacotes foliares amarrados em cada. As folhas foram incubadas em bancos de folhiço acumulado (Figura 5c).

Após 2, 6, 11, 27 e 36 dias foram retirados, aleatoriamente, em cada local, três pacotes, um de cada bloco. O material foi armazenado em sacos plásticos e conduzido para o laboratório, onde foi cuidadosamente lavado sobre peneira (250 µm) para remoção de detritos e retenção da fauna bentônica associada. Os organismos foram identificados, medidos e contados para estimativas de biomassa. As folhas foram secas em estufa a 55°C por 72 horas para determinar o peso seco (Figura 5d) e incineradas em mulfa a 500°C por 4 horas para obtenção da massa seca livre de cinzas (AFDM) para os cálculos de taxas de decomposição (*k*) dos pacotes foliares, como mostra o modelo:

$$M_t = M_0 \, e^{-kt}$$

Onde $\mathbf{M_t}$ é massa no tempo (dias), $\mathbf{M_0}$ massa inicial, e $\boldsymbol{k}$ é o coeficiente de decomposição (Olson,1973)

Figura 5. Folhas incubadas e amarradas (a), folha incubada apresentando sinais de consumo e, aparentemente, um *Triplectides* dentro do casulo aderido (b), corda com folhas incubadas em banco de folhiço (c), folhas recuperadas e secas (d).

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Capítulo 1

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Relationships of shredders, leaf processing and organic matter along a canopy cover gradient in tropical streams

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Highlights

1 Canopy cover is not associated with the availability of terrestrial matter and shredder biomass.

2 Shredders are not scarce in litter-banks and their biomass is positively related to litter abundance and breakdown rates.

3 Estimates of biomass reflects better the role of shredders than analysis based on numbers of individuals.

Abstract

Terrestrial allochthonous organic matter represents a structuring element and an important source of energy and carbon to fauna in small forested streams. However, the role of this matter as food resource for benthic macroinvertebrates, and consequently, for shredders and their performance in riverine process, is not clear in low-order tropical streams. Aiming to investigate the relationship between shredders and leaves, we analyzed along a gradient of 8 - 93% canopy cover biomass and abundance of shredders, accumulated leaves and breakdown rates of local leaves to verify if these parameters were related to shade conditions and to each other. Three hypotheses were tested: a) shredder biomass, accumulated leaves and breakdown rates are related to canopy cover and exhibit higher values in shaded sites; b) shredder biomass is positively related to accumulated leaves and breakdown rates; and c) due to the relatively large body size of the important shredders, the association of shredders with leaves and importance to leaf processing should be better expressed in terms of guild biomass than abundance. Shredder biomass varied between 846 and 1506 mg DM m^{-2} and accumulated leaves varied between 479 and 1120 g AFDM m^{-2} across sites. Leaf breakdown rate (*k*), the only measured variable that varied significantly among sites, varied between -0.0015 and -0.0238 day^{-1}. Neither shredder biomass nor leaf biomass were associated with the shading gradient. On the other hand, shredder abundance and biomass, mainly represented by *Triplectides* (Trichoptera, Leptoceridae), was positively related to accumulated leaves within sites and to breakdown rates assessed by leaf packs. Leaf breakdown, as assessed by the experimental leaf packs, was associated with shredder biomass, but not with shredder abundance. This result suggests that macroinvertebrates are important for leaf detritus processing and that their biomass reflects their activity, presumably because it is related to their secondary production and perhaps non-consumptive action. Their activity was observed at the scale of leaf packs and not at the scale of variation in canopy cover because apparently canopy did not modulate availability of leaves, which were apparently not limiting to the shredders.

Key-words: headwater, body size; biomass; benthic macroinvertebrate; leaf breakdown.

Introduction

About 90% of terrestrial primary production falls directly into the dead organic matter pool (Cebrian, 1999; Abelho, 2001), becoming available to the so-called “brown food webs” (Kaspari, 2004). Especially in low-order streams covered by dense riparian vegetation, allochthonous organic matter represents the main resource for aquatic fauna (Wallace *et al.*, 1997). Leaves compose the major fraction of allochthonous organic matter entering in streams (França *et al.*, 2009; Gonçalves *et al.*, 2014; Bambi *et al.*, 2016) and once in the lotic environment, fauna colonize and start the process of leaf breakdown (Gessner *et al.*, 1999; Graça, 2001; Tank *et al.*, 2010).

Benthic macroinvertebrates have been found to be positively related to the availability of allochthonous organic matter in lotic ecosystems (Egglishaw, 1964; González and Graça, 2005; Mbaka *et al.*, 2014). Leaves and other categories of allochthonous organic matter can provide food and additional resources such as substrate and refuge from predators and water currents (Inoue and Nakano, 1998; Braccia and Batzer, 2001). Also, terrestrial material can accumulate fine particulate organic matter and nutritious biofilms formed by microorganisms which represent food resources for benthic macroinvertebrates (Hax and Golladay, 1993; Crook and Robertson, 1999; Dudgeon and Wu, 1999; Eggert and Wallace, 2007).

Leaves are broken down by physical abrasion, leaching of soluble compounds and through micro and macrofauna consumption (Gessner *et al.*, 1999; Jugnia *et al.*, 2000; Graça, 2001). Macroinvertebrate shredders, organisms that feed directly on leaf tissues while converting coarse matter into small particles, are important in litter breakdown in many systems (Webster and Benfield, 1986; Wallace and Webster, 1996;

Graça *et al.*, 2015). Macroconsumers, such as fishes and large decapod crustaceans, are also recognized as being involved in leaf breakdown (Petersen and Cummins, 1974; March *et al.*, 2001; Cogo and Santos, 2013; Mancinelli *et al.*, 2013; Masese *et al.*, 2014). These organisms can act on leaf breakdown through direct consumption and bioturbation (Crowl *et al.*, 2001; Landeiro *et al.*, 2008), which contribute positively to breakdown. On the other hand, in some circumstances they can act negatively, by reducing the activity of insect shredders (Andrade *et al.*, 2017).

Due to the quantitative dominance of allochthonous matter over autochthonous production in small low-order streams, one of the principal tenets of the *River Continuum Concept* (RCC; Vannote *et al.*, 1980) is that fauna in these parts of the streams rely mainly on terrestrial resources. However, despite the applicability to temperate forested headwaters (Fisher and Likens, 1973; Wallace *et al.*, 1999), RCC is a controversial model in tropical running waters. Evidence from global studies indicates high variability in shredder occurrence and in breakdown rates across tropical sites (Boyero *et al.*, 2012, 2015), which corroborates contrasting results obtained in tropical regions. A growing body of evidence emphasizes the importance of algal carbon in tropical food webs of forested small streams (Salas and Dudgeon, 2001; Mantel *et al.*, 2004; Brito *et al.*, 2006; Li and Dudgeon, 2008; Lau *et al*., 2009; Neres-Lima *et al.*, 2016; Brett *et al*., 2017) and it has been claimed that the contribution of macroinvertebrate shredders to leaf breakdown is small in certain tropical running waters due their scarcity (Dudgeon and Wu, 1999; Dobson *et al.*, 2002; Gonçalves *et al*., 2006b, 2007; Ardón and Pringle, 2008; Alvim *et al.*, 2015). On the other hand, there is contrary evidence showing high diversity and abundance of macroinvertebrate shredders, high secondary production and importance on leaf breakdown (Cheshire *et* *al*., 2005; Camacho *et al*., 2009; Yule *et al*., 2009; Encalada *et al*., 2010; Masese *et al*., 2014; Tonin *et al*., 2014; Andrade *et al*., 2017; Neres-Lima *et al*., 2017).

Independently of the source of carbon supporting fauna, we propose that, at least, shredders and their role have been overlooked in the tropics. Methodological factors could underestimate shredder importance in tropical running waters: benthic macroinvertebrates are frequently assigned to functional feeding groups according to classifications proposed for temperate organisms (Camacho *et al*., 2009). Thus, certain organisms, abundant in tropical running waters and not usually classified as shredders, like Leptophlebiidae (Ephemeroptera), could be involved in leaf processing (Bello and Cabrera, 2001; Andrade *et al*., 2017). Also, the scarcity of data based on biomass could hinder the investigation of the role of shredders in tropical streams since common tropical shredders, like caddisflies, exhibit large bodies and data based on abundance can underestimate their importance (Tonin *et al*., 2014).

Therefore, this study examined benthic macroinvertebrate biomass, leaf standing stock and breakdown rates of the most abundant riparian species along a canopy cover gradient. Our objectives were (a) analyze patterns in shredder biomass, accumulated leaves and leaf breakdown rates along a canopy cover gradient; (b) investigate the association of macroinvertebrate shredders with leaf standing stock and leaf breakdown; and (c) examine whether shredder association with leaves and contribution to leaf breakdown is more evident in terms of number of individuals or biomass. We hypothesized that shredder biomass, accumulated leaves and leaf breakdown rates follow a gradient in canopy cover, and that shredders are positively related to leaf quantity and to leaf breakdown. We also hypothesized that association between shredders and leaves will be clearer in terms of biomass than in terms of abundance.

Methods

Study site

The study was conducted in Córrego da Andorinha and Rio Barra Pequena, small third-order streams located in a well-preserved dense Atlantic rainforest within the State Park of Ilha Grande Island in Rio de Janeiro State, Brazil (23º04’ to 23º14’S and 44º05’ to 44º23’W; Fig. 1). Average annual temperature is 23.2 ºC and average annual precipitation, 2071 mm, according to the nearest meteorological station situated in Angra dos Reis municipality (data from December/2015 – November/2016). Total catchment of Córrego da Andorinha is ~1260 ha and the highest point is 1030 m above sea level. Rio Barra Pequena has a catchment area of ~566 ha. Both streams have a steep bed slope for most their courses, discharging into small tidal estuaries without meanders or transition zones. Substrate is generally well embedded, with large boulders and some sandy stretches. The geology is principally Pre-Cambrian granite; the water chemistry is oligotrophic (total-N = 180 $\mu g\ L^{-1}$, total-P = 10 $\mu g\ L^{-1}$, pH = 6.6) and did not change along the stream. Conductivity is 27 μScm^{-1} in Córrego da Andorinha and 33 μScm^{-1} in Rio Barra Pequena.

We selected six sites – one in Rio Barra Pequena, BP, four in Córrego da Andorinha – JAR (Jararaca), CHA (Characidium), LAM (Lambari) and CAP (Capivara) - and VAL (Valium), a first order tributary of Córrego da Andorinha (Fig. 1 and Tab. 1). Sites were selected following a canopy cover gradient that varied between 8% and 93%. VAL, BP and JAR showed higher canopy cover mean values (93, 83 and 73%) and LAM and CAP, the lower mean values (8% and 12%) and CHA was intermediate (55%). Canopy cover was measured using a spherical densitometer Model-C (Forest

Densiometers, Oklahoma, USA). Along 10 equally-spaced transects distributed in a 10 m reach, we averaged four readings facing north, south, east and west. Discharge was estimated on two occasions during the leaf breakdown experiment (except in JAR). In each site, we conducted a leaf breakdown experiment over 36 days during January and February/2016. At the same six sites, we sampled benthic macroinvertebrates and leaf standing stock in two campaigns during the leaf breakdown experiment.

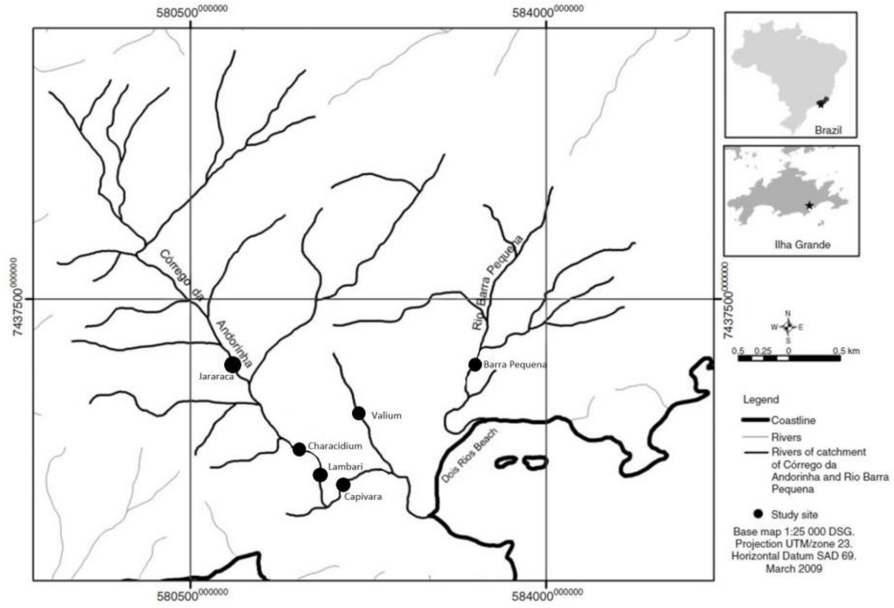

Figure 1. Map of the study site at Ilha Grande, Rio de Janeiro.

Table 1. Characteristics of the sites.

Site code	Site Name	Distance from mouth (m)	Altitude (m asl)	Discharge (Ls^{-1})	Canopy cover (%)	*Leaf input (AFDM g m^{-2} $month^{-1}$)	Presence of macro-fauna
				Mean SD	Mean	Mean SD	
VAL	Valium	-	53	9.97 ± 3.19	93	129.46 ± 10.45	M, P
JAR	Jararaca	2231	254	91.10	73	86.19 ± 31.76	T
BP	Barra Pequena	236	34	135.50 ± 3.53	83	-	M, P
CHA	Characidium	1240	83	432.80 ± 42.56	55	22.38 ± 4.64	M, P, F
LAM	Lambari	913	43	531.55 ± 177.04	12	44.78 ± 0.05	M, F
CAP	Capivara	497	36	565.61 ± 190.04	8	14.15 ± 1.30	M, F

*Data from January and February/2014 (Lisboa, 2017). **F** = fishes, **M** = *Macrobrachium* (shrimp), **P** = *Potimirim* (shrimp), **T** = *Trichodactylus* (crab)

Shredder biomass and leaf standing stock

We collected eight benthic macroinvertebrate and leaf samples at points where leaves had accumulated naturally (“litter-banks”) - most of them were in pools of slow-moving water. We used a 314 cm² stovepipe corer to collect the material, inserting the sampler into the substrate and manually removing all leaves, debris and coarse material from the corer and placing them in a bucket. We bailed approximately 20L of water from the corer to the bucket to collect suspended organic matter and macroinvertebrates. The material inside the bucket was elutriated and poured through a sieve (250 µm mesh). The procedure of elutriation was repeated several times using fresh stream water until rinse water was clear. The material was stored in a plastic bag filled with fresh stream water to maintain organisms alive.

We washed organic matter samples through sieves to separate macroinvertebrates and organic matter into coarse (>1000 µm) and fine (>250 µm) fractions. After removing macroinvertebrates (picked alive and fixed in ethanol 70%), leaves were separated for leaf standing stock estimate. The leaves were dried at 55ºC for 48h, weighed and then combusted in a muffle furnace at 500ºC for 4h to obtain ash free dry mass (AFDM).

To separate small macroinvertebrates, the fine organic matter fraction was subsampled to a maximum of 1/8 of the sample, depending on the amount of material. We sorted the preserved macroinvertebrates under a stereomicroscope at 40x magnification. All the organisms were identified to the lowest possible taxonomic level with a local key (Mugnai *et al.*, 2009) and classified as shredders or non-shredders. Leptophlebiidae was assigned as shredder due to its terrestrial carbon assimilation in

Córrego da Andorinha (Neres-Lima *et al*., 2016) and role in leaf breakdown (Andrade *et al*., 2017). All organisms were measured (body length) to obtain biomass estimates (mg) dry mass (DM) m^{-2}, using taxon-specific length-mass relationships (Benke *et al*. 1999). Abundance of each taxon was estimated to number of individuals m^{-2} and biomass was calculated as a product of abundance and average individual body mass, for each taxon and sample. The estimated biomasses of different taxa were then used to estimate total macroinvertebrate and shredder biomasses.

Leaf breakdown experiment

At each site, we collected fallen leaves on rocks and boulders following two separate transects of ~5 m on both margins. Leaves were taken to the laboratory and separated to identify the three most abundant local species in each site (supplementary material, Tab. S1).

After air-dried and weighed, ~3 g of leaves was fastened together using paper clips to form packs. Each pack comprised the three most abundant species of each site (Tab. S1). Leaf species 1, most abundant, corresponded to 50% of packs (~1.5 g) and the same weight of leaf species 2 and 3 (~0.7 g) completed the mixed packs. Three groups, here referred to as blocks, of five packs attached to a cord were then incubated in litter-banks in all sites.

We retrieved three packs of each combination of leaves before incubating to estimate mass loss caused by handling. After 2, 6, 11, 27 and 36 days, three leaf packs, one of each block, were randomly collected from all sites. The material was stored in plastic bags and taken to the laboratory where it was gently washed under running water over a 250-µm mesh sieve to remove detritus and retain associated benthic fauna. The organisms were identified and measured for biomass estimates. Leaf material was oven-dried (72 h, 55 ºC) and ashed (4 h, 500ºC) to estimate the remaining AFDM and breakdown rates (k) of leaf packs.

Statistical analyses

We calculated breakdown rate using the model $M_t = M_0 e^{-kt}$, where M_t represents mass (g, AFDM) after time t (days), M_0 represents initial mass and k is the rate of leaf breakdown per day (Olson, 1973). M_0 was calculated as AFDM using DM:AFDM relationship established for each different combination of leaves used in the experiment after combustion of retrieved packs. For each site and cord, k was calculated by linear regression of the natural log of proportion of remaining mass by time (Benfield, 2007). We included the constant of regression and did not include time zero data, which implies excluding the initial time interval (the initial phase of processing can be faster due physical process of leaching, whereas we aimed to measure leaf processing).

Overall variation in leaf standing stock and breakdown rates among sites were analyzed by one-way ANOVA. To analyse differences in shredder abundance and biomass among sites and the association between shredders and leaf standing stock, we performed an ANCOVA using shredder abundance or biomass as dependent variable, leaf AFDM as continuous variable and site as fixed factor. To analyse the relationship between breakdown rates and biomass of shredders associated with experimental leaf packs, we regressed breakdown rates against shredder biomass (means per block). All statistical analyses were conducted using Systat 12.

Results

Leaves and shredder biomass along a canopy cover gradient

The standing stock of leaves varied between 479 ± 422 and 1120 ± 960 g AFDM m^{-2} (mean ± SD, n = 8), but quantity of material did not differ significantly among sites (ANOVA, $F_{5,42} = 1.49$, $P = 0.20$), nor was it associated with canopy cover (Fig. 2).

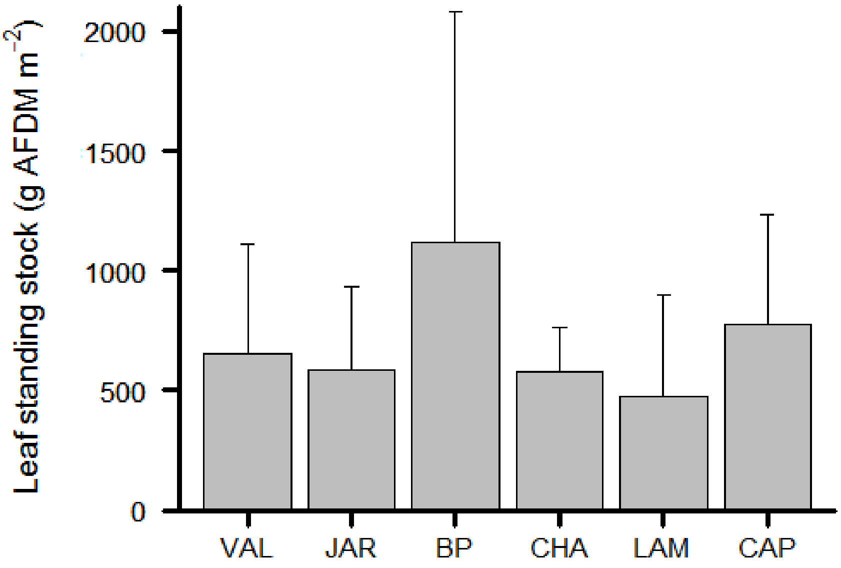

Figure 2. Leaf standing stock in litter-banks (error bars = SD, n = 8). Sites are ordered in increasing stream size.

Shredder biomass represented ~45% of total benthic macroinvertebrate biomass in accumulated litter and ranged from 846 ± 891 to 1506 ± 775 mg DM m^{-2} in the different sites but showed no apparent relationship with stream size or canopy. Shredder taxa found were the caddisflies *Triplectides* Kolenati, 1859 (Trichoptera, Leptoceridae), and *Phylloicus* Mueller, 1880 (Trichoptera, Calamoceratidae), the leaf miner *Stenochironomus* Kieffer 1919 (Diptera, Chironomidae), and leptophlebiids, mainly

Farrodes Peter, 1971 (Ephemeroptera). In all sites, except CHA, *Triplectides* responded for more than half of shredder biomass (Fig. 3).

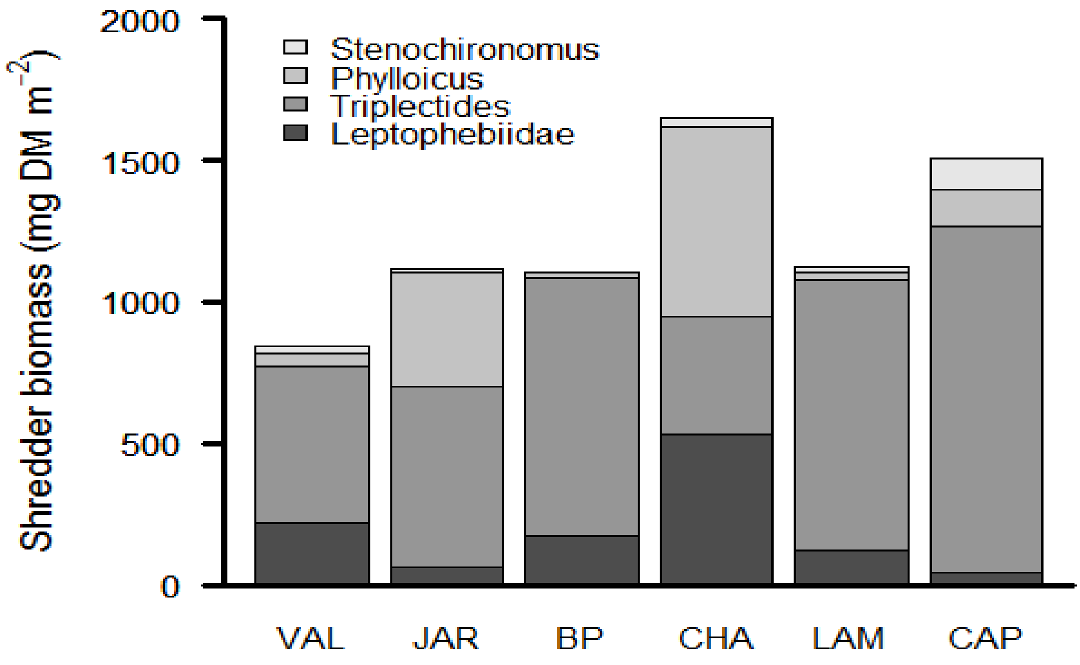

Figure 3. Biomass of main shredder taxa in studied sites (mean, n = 8).

The abundance and biomass of shredders were positively related to leaf standing stock within sites (Tab. 2 and Fig. 4), but there were no significant differences among sites (Tab. 2).

Table 2. Analysis of covariance of shredder abundance and biomass with leaf biomass and sites

Dependent variable	Source of variation	Sum of squares	df	Mean square	*F*-ratio	*P*
Shredder abundance	Leaves	5048662	1	5048662	4,69	0,037
	Sites	2656628	5	531326	0,49	0,779
	Leaves*Sites	4865894	5	973179	0,90	0,489
	Error	38735750	36	1075993		

Shredder biomass	Leaves	7692842	1	7692842	4,39	0,043
	Sites	5206251	5	1041250	0,59	0,705
	Leaves*Sites	13690910	5	2738182	1,56	0,196
	Error	63110910	36	1753081		

df, degrees of freedom

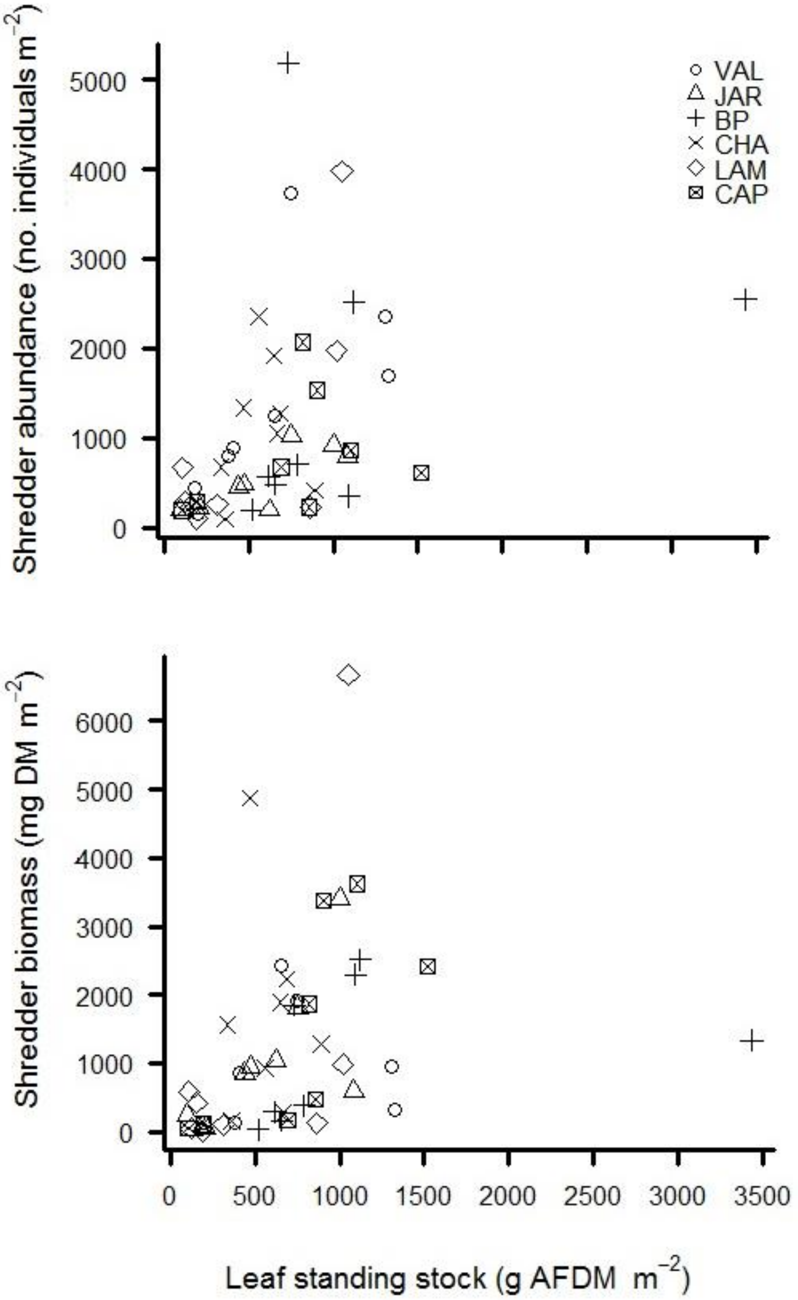

Figure 4. Relationships between shredder abundance, biomass and leaf standing stock in studied sites.

Leaf breakdown

Breakdown rates of experimental leaf packs revealed different patterns across sites, but did not exhibit any relationship to riparian cover (Figs. 5 and 6). In CHA, leaves lost ~30% of mass by day 11 of the experiment, when, in most other sites, leaf mass loss was less than 20% (Fig. 5). JAR and BP exhibited slow mass loss, ~25% until day 36, and in LAM, leaf mass loss was less than 20% at the end of experiment (Fig. 5).

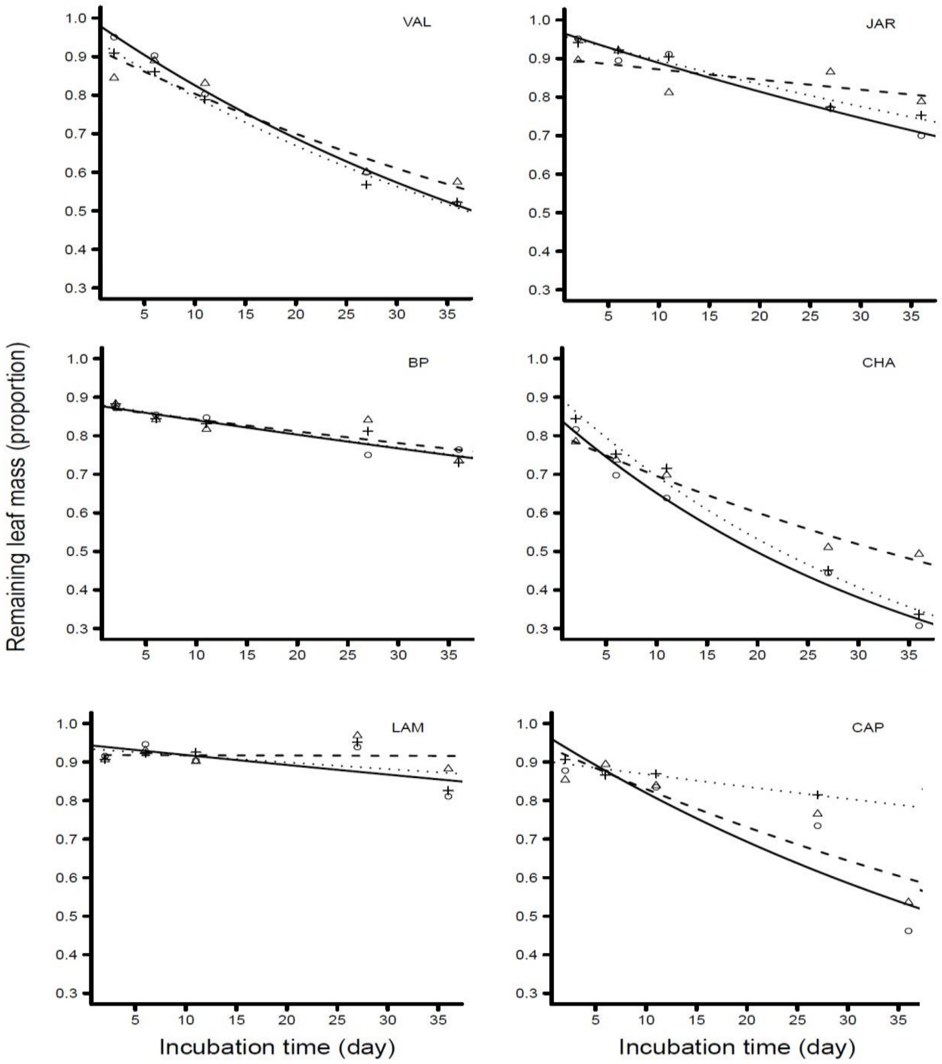

Figure 5. Proportion of remaining leaf mass for three cords (blocks) over time (days) for leaf packs in all studied sites. Curve fits were to the exponential model.

Breakdown rates showed variation ranging from -0.0015 ± 0.0013 to -0.0238 ± 0.0055 d^{-1} (Fig. 6), with significant difference between sites (ANOVA, $F_{5,10} = 14.09$, $P < 0.001$). The fastest rate was observed in CHA ($k = -0.0238 \pm 0.0055$ d^{-1}), significantly different to breakdown rates observed in JAR, BP, LAM and CAP (Fig. 6). VAL also showed high breakdown rate (-0.0164 ± 0.0025 d^{-1}), significantly higher than observed in BP and LAM, where we observed the slowest rates (Fig. 6).

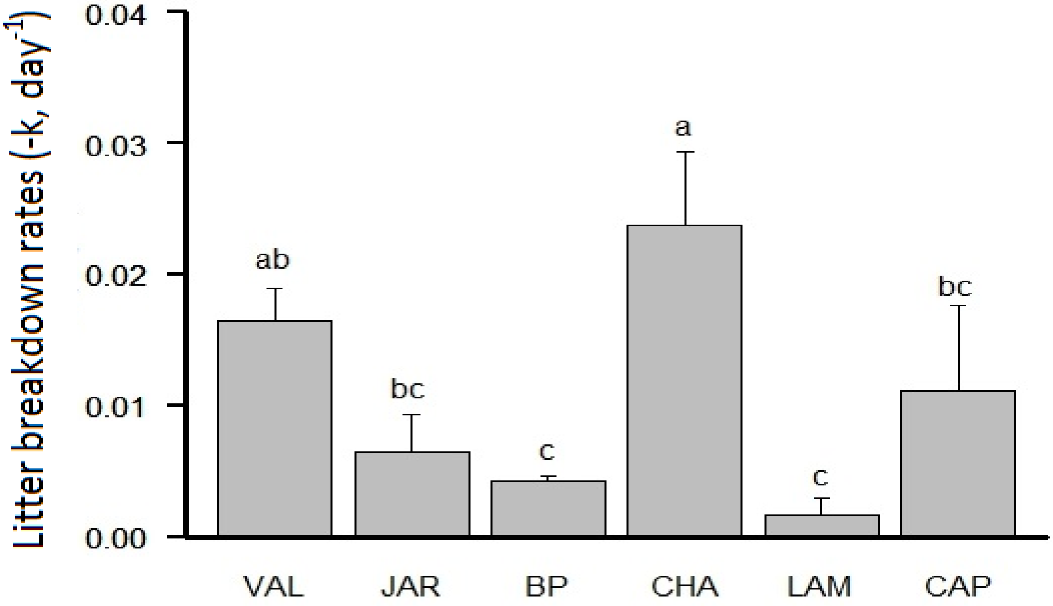

Figure 6. Breakdown rates (*k*) of leaf packs in studied sites. Letters indicate groups that did not differ significantly (Tukey's test, $P < 0.01$). Error bars are one S.E. of the mean (n = 3).

A total of 534 shredders were found associated with leaves in retrieved packs. The biomass of these organisms exhibited significant relation with leaf breakdown ($F_{1,13} = 13.4$, $P = 0.002$; Fig. 7), but this correlation was more evident in VAL, CHA and CAP. Oppositely, shredder abundance was not significantly related to breakdown rates ($F_{1,16} = 3.34$, $P = 0.086$).

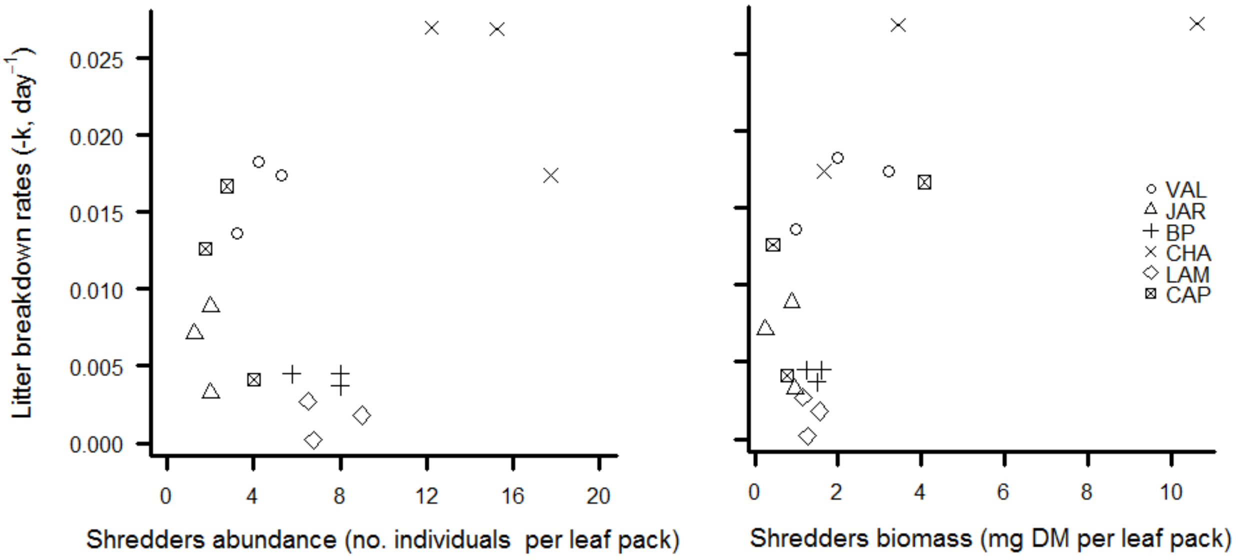

Figure 7. Relationships between **s**hredder abundance and biomass in leaf packs and litter breakdown rates (n= 3).

Discussion

Longitudinal patterns in shredders and leaves

Contrary to some studies conducted in tropical ecosystems, we could not detect a pattern of decrease in shredder biomass along a longitudinal gradient (Greathouse and Pringle, 2006; Jiang *et al.*, 2011). We also could not relate canopy cover to accumulated leaves and breakdown, as had been expected.

The stock of litter in streams can often reflect the organic matter input from adjacent vegetation (Bilby and Likens, 1980; Swanson *et al.*, 1982), and exhibit similar patterns (Bambi *et al.*, 2016). However, the presence and persistence of terrestrial material in the streambed is also related to several factors including composition, organization and densities of trees, seasonality and channel morphology (Fleituch, 2001; Gonçalves *et al.*, 2006a; França *et al.*, 2009; Tank *et al.*, 2010; Flores *et al.*, 2013;

Lisboa *et al.*, 2015; Bambi *et al.*, 2016). Therefore, even with variation among sites in the degree of canopy cover and leaf input (Tab. 1), the lack of substantial differences in leaf standing stock indicates that canopy cover did not determine patterns in organic matter distribution in stream channel. In Córrego da Andorinha and Barra Pequena, channel morphology is possibly a more important factor governing the accumulation of litter.

In an Atlantic Forest environmental quality assessment, Baptista *et al*. (2007) concluded that shredder abundance was related to reference sites. In general, reference sites exhibit features that match with shredders demands, like litter accumulation and lower temperatures due riparian vegetation presence. Accumulated allochthonous organic matter can provide food for shredders and the positive correlation between these elements is well-established in temperate ecosystems (Richardson, 1992; Wallace *et al*., 1999; Rowe and Richardson, 2001; González and Graça, 2005; Flores *et al*., 2013). In this manner, as our studied sites are in the same well-preserved rainforest and accumulated leaves were not restricted to dense riparian covered sites, shredder biomass and abundance seem not restricted as well.

We can also observe that litter was abundant at all sites relative to the biomass of shredders, and was probably not limiting for their growth and population density. Thus, shredders and other macroinvertebrates may be limited by predators, as has been observed in exclosure experiments in these streams (Moulton *et al.*, 2004; Andrade *et al.*, 2017). If this were the case, we could expect that shredders would seek out the most nutritious and easily assimilated leaves, and thus their action would be observed at the level of leaf packs.

Shredders, accumulated leaves and breakdown rates

We observed that shredder biomass and abundance were related to quantity of leaves of samples within sites (Tab.2, Fig. 4). We expected this relationship based on the simple assumption that leaves provide substrate and that number of organisms would increase as substrate availability increased. Only if substrate were limited and the pool of potential shredders constant might we expect that shredder abundance would not increase with substrate availability.

On the other hand, shredder biomass per leaf pack was positively associated with leaf processing (Fig. 7). This association was evident in VAL, CHA and CAP, where leaf breakdown rates were higher. Interestingly, shredder abundance per leaf pack did not show a significant relationship with leaf breakdown rate, which implies the importance of measuring biomass as an indicator of shredder activity (see Tonin *et al.*, 2014).

Although the macrofauna of crustaceans and fish could potentially affect leaf breakdown, the pattern of leaf breakdown we observed did not correspond to presence or absence of the different macrofauna (cf Tab. 1 and Fig. 6). Previous research in these streams showed a strong indirect relationship of sites with fish and the density of periphyton (Moulton *et al.,* 2010). Apparently, the presence of fish had an inhibiting effect on grazing shrimp (*Potimirim*), such that sites with fish had greater density of periphyton. In the current case, however, the sites with fish (LAM and CAP) showed no reduction of leaf processing that could be attributed to an inhibition of shredders. Other possible direct or indirect interactions might have involved *Macrobrachium* shrimps which were shown to reduce leaf processing presumably by inhibiting shredding insects

(Andrade *et al*. 2017). Again, the site without *Macrobrachium*, JAR, did not show increased leaf processing.

The leaf packs of the leaf breakdown experiment were made from the three most abundant species of each site. Thus, part of the variation among sites could have come from differences in rates of breakdown of the different species. At site CHA, which showed the fastest breakdown of leaf packs, the most abundant tree species was *Ficus insipida* Willd. (Moraceae), which exhibited fastest breakdown rates in other studies (Rosemond *et al.*, 1998; Ardón *et al.*, 2009; Rincón and Santelloco 2009). Leaves of *F. insipida* are characterized by low lignin and polyphenol content (Ardón *et al.*, 2006; Rincón and Santelloco 2009), and are thus a potential high-quality detritus for consumers. In VAL and CHA, where we observed faster leaf breakdown rates, Leptophlebiidae contributed with an important fraction of shredder biomass. This observation supports previous local findings that leptophlebiid ephemeropterans are associated with leaf mass loss (Andrade *et al.*, 2017).

In JAR and CAP, where we observed intermediate-fast breakdown rates (k = -0.0064 and -0.011 d^{-1}, respectively; Petersen and Cummins, 1974), we observed association between shredders and accumulated leaves (Fig. 4). In these sites, it was previously observed that *Triplectides* and *Phylloicus* diet is not restricted to allochthonous resources, and further, autochthonous resources can correspond to a third (JAR) to a half (CAP) of the food ingested by these caddisflies in Córrego da Andorinha (Neres-Lima *et al.*, 2016). In JAR, despite high canopy cover, local fauna is highly supported by autochthonous carbon (Neres-Lima *et al.*, 2016). These observations match with the prediction that even highly covered tropical streams have enough light incidence to sustain a reasonable level of primary production (Bunn *et al.*, 1999a, b; Lau *et al.*, 2009). In this manner, we speculate that shredders may be consuming some autochthonous carbon along with their predominant diet of leaves and that they might benefit from algae attached to leaves (Guo *et al.*, 2016).

In BP and LAM, where leaf mass loss was almost absent, shredder biomass per leaf pack seems weakly related to breakdown rates (Fig. 7). This observation could indicate that shredders rejected the most abundant local leaves, consuming preferentially other leaves due to their food selection behaviour (Casotti *et al.*, 2015). The lack of relationship between shredder biomass and leaf breakdown can also suggests that shredders are exploiting other food categories. Stable isotopes and gut content analyses revealed that organisms classified as shredders can behave as generalists, consuming coarse and fine organic matter and periphyton (Tomanova *et al.*, 2006; Leberfinger and Bohman 2010; Leberfinger *et al.*, 2011; Callisto and Graça, 2013; Ferreira *et al.*, 2015; Neres-Lima *et al.*, 2016). In this manner, the interaction of shredders and leaves as food resource could be mainly related to litter and algal resources quality than to leaf quantity or canopy cover shading.

Conclusions

We conclude that despite the absence of a linkage between canopy cover and shredder abundance and biomass, shredders were associated with leaf quantity within sites and with processing of leaf packs, and thus they appear important for leaf processing. However, this linkage between shredders and accumulated leaves and breakdown was not evident in all sites, which indicates that other factors (*e.g.* litter and algal resource quality and availability) can be more relevant and determinant in this interaction. Also, shredder biomass rather than abundance was related to leaf breakdown, suggesting that analyses based on biomass may reveal their importance in this ecosystem process. Leptophlebiid ephemeropterans are not generally classified as shredders, but evidence from other studies and their distribution here indicate them as shredders, emphasizing the importance of accurate classifications into functional feeding groups based on regional studies.

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Supplementary material

Tab. S1. Leaf species utilized in leaf breakdown experiment. Leaf species 1, the most abundant, and 2 and 3, less abundant in studied sites.

Site		Leaf species 1	Leaf species 2	Leaf species 3
VAL	Species	*Hyeronima alchorneoides*	*Coussapoa microcarpa*	*Alseis floribunda*
		Allemão	(Schott) Rizzini	Schott
	Family	Euphorbiaceae	Urticaceae	Rubiaceae
JAR	Species	*Coussapoa microcarpa*	*Hyeronima alchorneoides*	*Protium heptaphyllum*
		(Schott) Rizzini	Allemão	(Aubl.) March
	Family	Urticaceae	Euphorbiaceae	Burseaceae
BP	Species	*Clitoria fairchildiana*	*Inga edulis*	*Pithecoctenium crucigerum*
		R.A. Howard	Martius	(L.) A.H. Gentry
	Family	Fabaceae	Leguminosae	Bignoniaceae
CHA	Species	*Ficus insipida*	*Hyeronima alchorneoides*	*Protium heptaphyllum*
		Willd	Allemão	(Aubl.) March
	Family	Moraceae	Euphorbiaceae	Burseaceae
LAM	Species	*Guarea guidonia*	*Erythroxylum pulchrum*	*Inga edulis*
		(L.) Sleumer	A.St.-Hil	Martius
	Family	Meliaceae	Erythroxylaceae	Fabaceae
CAP	Species	*Erythroxylum pulchrum*	*Coussapoa microcarpa*	*Mucuna urens*
		A.St.-Hil	(Schott) Rizzini	(L.) Medik
	Family	Erythroxylaceae	Urticaceae	Fabaceae

Capítulo 2

Energy flux, organic matter distribution and secondary production of detritus-based macroinvertebrates and in tropical streams

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Highlights

1 Allochthonous organic matter is important for maintenance of macroinvertebrates in tropical headwaters.

2 The ingestion of leaves by shredders corresponds to a small fraction of total leaf mass loss.

3 Shredder secondary production corresponded to the largest part of total macroinvertebrate production in litter banks.

Abstract

The interaction between consumers and resources determines the flux of matter and energy in communities, and linking species to ecological processes is necessary to comprehend the ecosystem functioning. We estimated secondary production of benthic macroinvertebrates and terrestrially-derived organic matter fractions to examine the role of shredders, through ingestion estimates, in leaf breakdown process. Biomass production of macroinvertebrates, classified in functional feeding groups (FFG), was estimated through size-frequency and instantaneous growth methods. The accumulated allochthonous matter was estimated for eight months, and using breakdown rates and the leaf substrate coverage, we modeled the breakdown to compare the fraction of the total ingested by shredders. Despite the importance of terrestrial organic matter in maintaining macroinvertebrates, since FFG exhibited positive relationships with their potential resources, the amount of leaf matter ingested by shredders varied from <0.1 to 1.51 g AFDM m^{-2} $month^{-1}$ and was small compared to total leaf breakdown, which corresponded to <15% in most sites. Shredder secondary production varied between 10.20 and 17.03 g AFDM m^{-2} $year^{-1}$ and corresponded to the largest part of total macroinvertebrate production. We conclude that despite shredder dominance in litter-banks and the importance of allochthonous resources to macroinvertebrates, the role of these organisms in litter processing is small.

Key-words: biomass production, leaf ingestion, net production efficiency, allochthonous organic matter, ecosystem processes

Introduction

With Lindeman's model (1942) introducing the concept of trophic levels, the perspective of benthic habitat was expanded. The association of model and the concept of an ecosystem partitioned by trophic levels into stages of energy processing (Odum, 1971), lead to the concept that trophic levels are not reduced to a group of species, but rather, it represents an ecosystem function (Levine, 1980). From this perspective, studies progressed from description of diversity, distribution and life history to a systemic view, increasing attention on *ecological processes* and in *system functioning* through energy flux, primary and secondary production, organic matter dynamics and breakdown approaches (Benke et al., 1988; Benke & Huryn, 2010; Tank et al., 2010; Neres-Lima et al., 2016, 2017).

Secondary production, or the formation of heterotrophic biomass through time, represents a linkage between consumers and ecosystem processes. Through consumption of autochthonous and/or allochthonous matter, benthic macroinvertebrates promote a link between basal resources and higher trophic levels (Benke, 2010). Thus, estimates of secondary production are crucial for understanding the role of a population in energy flow (Benke & Wallace, 1980; Benke & Huryn, 2010). Despite its ecological importance, this approach has been little employed in tropical studies and estimates of assemblage production are rare (Benke, 1993, 2010; Jacobsen et al., 2008). This lack of information represents an additional obstacle towards the comprehension of the functioning of tropical running waters, where the origin of carbon that mainly maintain trophic webs remains as a controversial subject (Brito et al., 2006; Li & Dudgeon, 2008; Brett et al., 2017; Neres-Lima et al., 2017).

In the tropics, forests can reach an annual primary production of 1800 g dry mass m^{-2} $year^{-1}$, whereas less than 5% of this production is lost to herbivory (Ricklefs, 2000). An amount of this organic matter will end up in streams, especially in headwaters and heavy shaded streams, whereas leaves comprise the largest fraction of this coarse material (França et al., 2009; Gonçalves et al., 2014; Bambi et al., 2016). Despite the high availability of terrestrial organic matter in tropical streams (Aguiar et al., 2017), the fate of this matter is yet not clear (Neres-Lima et al., 2017).

Allochthonous organic matter, especially leaves, can represent the main energy source for macroinvertebrates and its importance in litter breakdown has been widely explored in temperate lotic ecosystems (Webster & Benfield, 1986; Wallace et al., 1999; Hieber & Gessner, 2002; González & Graça, 2003). In tropical streams, however, neither the importance of allochthonous as food resources on trophic webs maintenance (Brito et al., 2006; Li & Dudgeon, 2008; Brett et al., 2017; Neres-Lima et al., 2017) nor the activity of shredders on leaf breakdown (Cheshire et al., 2005; Gonçalves et al., 2006; Camacho et al., 2009; Yule et al., 2009; Encalada et al., 2010; Longo & Blanco et al., 2013; Masese et al., 2014; Alvim et al., 2015; Aguiar et al., 2017; Andrade et al., 2017) are clear, and the contrasting results have indicated that stream ecologists are not close to establish a model for tropical ecosystems.

Aggravating the lack of agreement about the importance of terrestrial carbon and shredder activity, data obtained in tropical streams are not often comparable, which makes understanding of the ecosystem difficult. The scarcity of analyses based on appropriated approaches possibly hinder the investigation of the importance of allochthonous carbon to tropical food webs and the role of macroinvertebrates in terrestrial matter processing. A recent study conducted in the Brazilian Atlantic Forest, through primary and secondary production estimates and energy flow models, indicated that the principal resource for macroinvertebrates, both ingested and assimilated, comes from the terrestrial environment (Neres-Lima et al., 2017). This somewhat contradicted earlier works using a more simplistic analysis which showed a preponderance of autochthonous material in the food webs (Brito et al. 2006; Neres-Lima et al. 2016). Another study, also conducted in the Brazilian rainforest, indicated participation of Leptophlebiidae, not usually classified as shredder, in litter breakdown (Andrade et al., 2017). Tonin et al. (2014) and Aguiar et al. (2017) indicated that shredder biomass, and not abundance, as a better approach to infer the importance of this group in litter breakdown. As such, the role of terrestrial carbon and shredders requires more investigation, but especially, approaches based on local classifications into functional feeding groups (FFG) and biomass and/or secondary production estimates. FFG distribution in the environment reflects the availability of resources and approaches based on number of individuals could not properly reveal the importance of some taxa (Tonin et al., 2014; Aguiar et al., 2017).

The aim of the present study was, through estimates of biomass and secondary production, analyse the importance of macroinvertebrates in leaf mass loss and the relationships between production of FFG and availability of potential resources. The main objectives of this study were (a) to estimate the amount of leaf ingested by shredders; (b) to analyze the relationship among organic matter categories and secondary production of FFG; and (c) to provide estimates of biomass and secondary production of tropical macroinvertebrates. Considering that allochthonous organic matter represents the main carbon source to macroinvertebrates (Neres-Lima et al., 2017) and that shredders have a significant role in leaf breakdown (Aguiar et al., 2017;

Andrade et al., 2017), we predicted that i. shredders ingest the largest fraction of the total leaf mass loss estimates, and ii. that secondary production of the different FFG and quantity of respective potential resources belonging to different organic matter categories are related.

Methods

Study site

The study was carried out in Córrego da Andorinha and Rio Barra Pequena, small third-order streams located in a well-preserved dense Atlantic rainforest within the State Park of Ilha Grande Island in Rio de Janeiro State, Brazil (23°04’ to 23°14’S and 44°05’ to 44°23’W; Fig. 1). Total catchment of Córrego da Andorinha is ~1260 ha and the highest point is 1030 m above sea level. Rio Barra Pequena has a catchment area of ~566 ha. Both streams have a steep bed slope for most their courses, discharging into small tidal estuaries without meanders or transition zones. Water chemistry is oligotrophic (total-N = 180 $\mu g\ L^{-1}$, total-P = 10 $\mu g\ L^{-1}$, pH = 6.6) and did not change along the stream. Conductivity is 27 μScm^{-1} in Córrego da Andorinha and 33 μScm^{-1} in Rio Barra Pequena. Substrate is generally well embedded, with large boulders and some sandy stretches. Average annual temperature was 23.2 °C and annual precipitation, 2071 mm, (meteorological station situated in Angra dos Reis municipality; data from December/2015 – November/2016).

Six sites were selected for benthic stock and associated fauna samples, one site was in Rio Barra Pequena (BP), four in Córrego da Andorinha – Jararaca (JAR), Characidium (CHA), Lambari (LAM), Capivara (CAP), and one in a first order tributary of Córrego da Andorinha, Valium (VAL; Tab. 1; Fig.1). Canopy cover was measured using a spherical densitometer Model-C (Forest Densiometers, Oklahoma, USA): along 10 equally-spaced transects distributed in a 10 m reach, we averaged four readings facing north, south, east and west. In each site, we sampled benthic macroinvertebrates and benthic stocks monthly in eight campaigns.

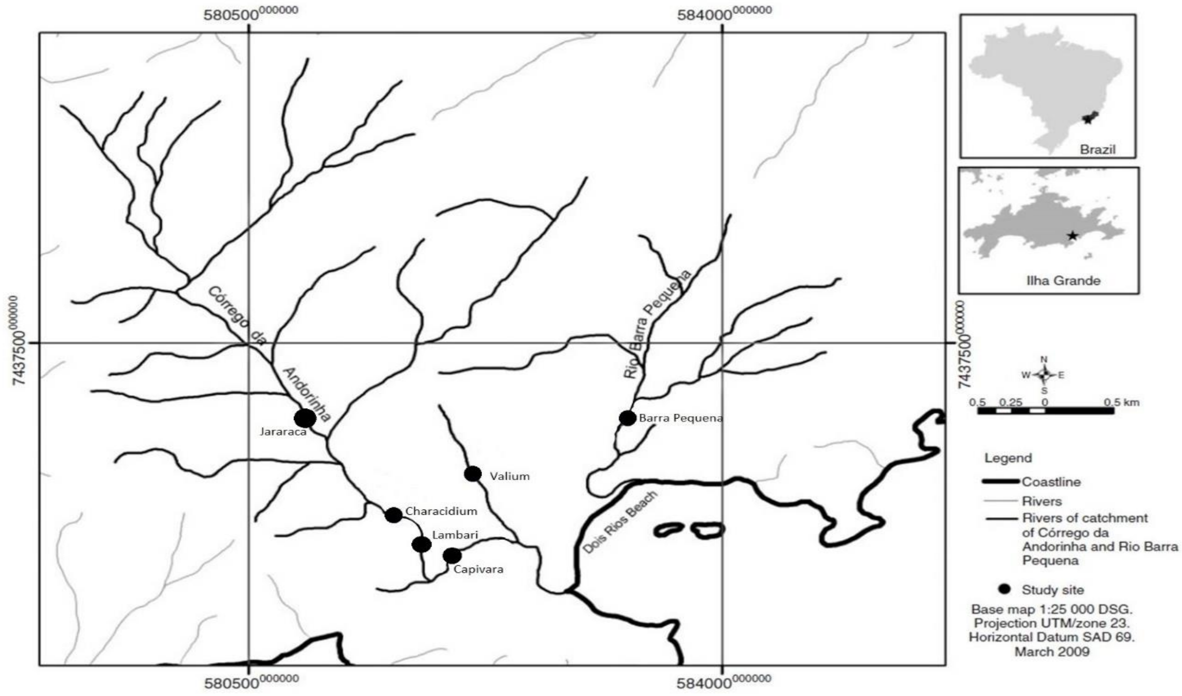

Figure 1. Map of the study site at Ilha Grande, Rio de Janeiro and studied sites.

Table 1. Description of site characteristics sampled in this study.

Site code	Site Name	Distance from mouth (m)	Altitude (m asl)	Leaf breakdown rate (k, day^{-1})*	Canopy cover (%)	Leaf substratum coverage (%)
VAL	Valium	-	53	-0.01644	93	3.0
JAR	Jararaca	2231	254	-0.00642	73	1.5
BP	Barra Pequena	236	34	-0.00424	83	2.5
CHA	Characidium	1240	83	-0.02377	55	3.0
LAM	Lambari	913	43	-0.00159	12	2.6
CAP	Capivara	497	36	-0.01113	8	2.0

*Jan/Feb 2016 (Aguiar et al., 2017)

Organic matter

Organic matter standing stocks (coarse particulate organic matter [CPOM] >1000 µm; fine particulate organic matter [FPOM] <1000 µm and >250 µm; ultrafine benthic organic matter [UFBOM] <250 µm) were collected monthly, from December 2015 to July 2016. In each site and month, organic matter was estimated from depositional habitats using a 314 cm^{-2} stovepipe corer (total n = 4).

The stovepipe was pushed into the substrate to enclose all material. Leaves, debris and all coarse material were manually removed from the corer and placed into a bucket. To separate organic matter from mineral sediments we bailed approximately 20 L of water from the corer to the bucket and collected suspended organic matter and macroinvertebrates. The material inside the bucket was elutriated repeated times and poured through a sieve (250 µm mesh). The collected material was stored in a plastic bag filled with fresh stream water to maintain associated macroinvertebrates alive. Before we manually removed benthic organic matter, the water enclosed in the stovepipe was agitated and samples of UFBOM were taken with ~300 ml of water. Samples were passed through a sieve and stored into labeled Whirl-Pak bags (Nasco, Fort Atkinson, USA).

In the laboratory, samples were rinsed through sieves (1000 µm and 250 µm) to separate CPOM and FPOM categories. CPOM was then classified into leaves, wood, reproductive parts and roots. All material was dried in an oven at 55 °C for 48h, weighed and then combusted in a muffle furnace at 500 °C for 4h to obtain ash-free dry mass (AFDM). Large samples were homogenized and subsampled before combustion and then, the percentage of organic matter was estimated for the entire sample. Samples of UFBOM were homogenized and a subsample was placed in a graduated bucket and the volume was recorded. The water was filtered through a pre-combusted glass microfiber filter (GFF, 0.7 µm Whatman) and the estimates of AFDM were taken after filters were dried and combusted, as was done with CPOM and FPOM.

Macroinvertebrate biomass and secondary production

Macroinvertebrates associated with organic matter were monthly collected (December 2015 – July 2016) in four depositional habitats all sites using a 314 cm² stovepipe corer (total n = 4) to estimate biomass and secondary production. The procedures for macroinvertebrate sampling was the same as previously detailed for organic matter standing stocks. In laboratory, samples were washed through sieves to separate large categories of organic matter (>1000 µm) and fine matter (<1000 µm and >250 µm). The large fraction was entirely processed and macroinvertebrates, picked alive, were fixed in ethanol 70% for identification and body length measures. The fine organic matter fraction was often subsampled to a maximum of 1/8 of the sample, depending on the amount of material, for macroinvertebrate removal.

Preserved macroinvertebrates were sorted under a stereomicroscope at 40x magnification. All the organisms were identified to the lowest possible taxonomic level using a local key (Mugnai *et al*., 2009), counted and measured (mm; body length or carapace length for shrimps) and counted. Organisms were classified into FFG according to studies of tropical taxa (Baptista et al., 2006; Henriques-Oliveira & Nessimian, 2010; Ramírez & Gutiérrez-Fonseca, 2014). Chironomids were classified as *Stenochironomus*, Tanypodinae or (other) Chironomidae. Leptophlebiidae was assigned to the FFG shredder due to its terrestrial carbon assimilation in Córrego da Andorinha (Neres-Lima *et al.*, 2016) and role in leaf breakdown (Andrade *et al.*, 2017).

Taxon-specific length-mass relationships were used to obtain biomass estimates, mg AFDM m^{-2}, of all organisms (Benke et al. 1999). Secondary production was obtained using different methods. For the most abundant taxa, production was calculated through the size-frequency method (Hynes & Coleman, 1968; Hamilton 1969; Benke, 1994). The estimate was corrected for cohort production interval (CPI; Benke, 1979; Jackson & Sweeney, 1995, Barros & Fontoura, 1996; Johnson et al., 2000; Jacobsen et al., 2008).

For less abundant insect taxa, or when it was not possible to apply the size-frequency method, production was calculated using the instantaneous growth method (IG, g AFDM m^{-2} day^{-1}). This method is based on population biomass (i.e. the product of the mean individual biomass and individuals per m^2), water temperature (°C) and specific coefficients of empirical models (Morin & Bourassa, 1992; Morin & Dumont, 1994). Instantaneous growth rate (GR) was estimated for each taxon and sample based on individual biomass (B), water temperature (T, °C), and taxon-specific coefficients (a, b and c; see equation 1 below). Tipulidae, *Leptohyphes*, shrimps and crabs secondary production were estimated using local production:biomass ratios (P/B ratio; Waters, 1977; Cressa, 2003; Neres-Lima, unpublished data). Results were corrected to year estimates.

$$\log_{10}(GR) = a + b \log_{10}(B) + c(T) \qquad \text{equation 1}$$

Overall leaf processing and shredders consumption

We used monthly litter standing stock estimates and percentage of local leaf substratum coverage (values between 1.5 and 3.0%; Tab. 1) to predict overall leaf density and then, with breakdown rates per day (see Aguiar et al., 2017), estimated for each site, we could estimate overall leaf processing (g AFDM m^{-2} day^{-1}). We estimated overall shredder secondary production and through division of production by gross production efficiency (i.e. product of assimilation efficiency and net production efficiency), we could estimate the amount of consumed leaves (Benke, 2011; Neres-Lima et al., 2017). We assumed an assimilation efficiency of 13% for allochthonous consumption (Perry et al., 1987; Eggert & Wallace, 1997) and net production efficiency of 50% (Benke & Wallace, 1980; Fig. 2).

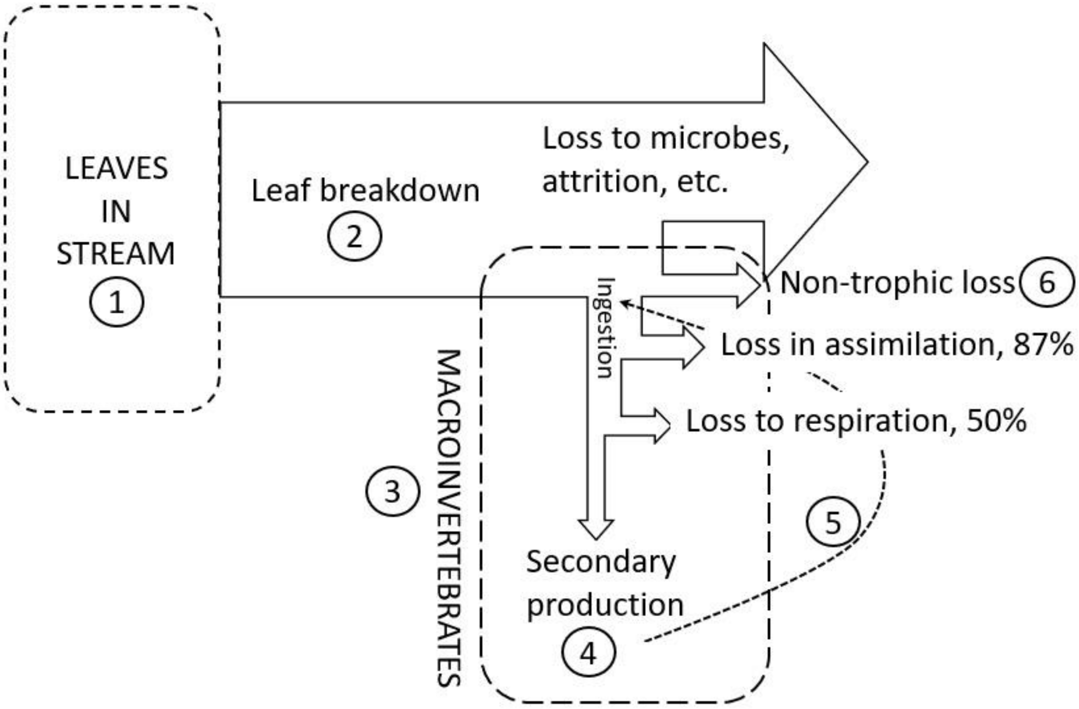

Figure 2. Modeling leaf ingestion from litter stocks to macroinvertebrate secondary production – 1. Biomass of leaves from monthly benthic sampling and % of substratum coverage used to calculate overall leaf density; 2- Rate of leaf breakdown determined in

separate experiment (Aguiar et al., 2017) and multiplied by leaf biomass to give leaf breakdown; 3. Biomass of macroinvertebrates collected with monthly samples of leaves; 4. Secondary production of macroinvertebrates transformed to overall secondary production; 5. Ingestion estimated by including assumed losses to assimilation and respiration; and 6. Non-trophic loss to bioturbation - not calculated.

Statistical analysis

Overall variation in organic matter, macroinvertebrate biomass and secondary production among sites were analyzed by one-way ANOVA. Differences in consumer macroinvertebrate biomass and secondary production among sites and the association with organic matter fractions (potential resources) were analyzed through ANCOVA using consumer biomass and production (separately) as dependent variable, organic matter fractions as continuous variable and site as fixed factor.

Results

Macroinvertebrates biomass and secondary production

A total of 24667 organisms belonging to approximately 50 taxa found in association with organic matter were identified and measured for abundance (n. individuals per m^2), biomass and secondary production estimates. Most abundant shredder taxa found were the caddisflies *Triplectides* Kolenati, 1859 (Trichoptera, Leptoceridae), and *Phylloicus* Mueller, 1880 (Trichoptera, Calamoceratidae), the leaf miner *Stenochironomus* Kieffer 1919 (Diptera, Chironomidae), and leptophlebiids, mainly *Farrodes* Peter, 1971 (Ephemeroptera). Chironomidae and Elmidae (larvae) were the main collectors; Tanypodinae and dragonflies were the main predators;

Macronema Guerin, 1843 (Trichoptera, Hydropsychidae) was the principal filterer and *Americabaetis* Lugo-Ortiz & McCaffery, 1996 (Ephemeroptera, Baetidae) represented the scrapers.

In all sites, except VAL, secondary production of shredders responded for the largest part of macroinvertebrate production, varying between 10.20 ± 4.62 and 17.03 ± 7.22 g AFDM m^{-2} y^{-1} and not differing significantly among sites (ANOVA, $F_{5,39}$ = 0.940, P = 0.46). Shredder biomass varied between 0.85 ± 0.40 and 1.75 ± 1.48 g AFDM m^{-2} and did not differ significantly among sites (ANOVA, $F_{5,\ 39}$ = 0.896, P = 0.49). Macrofauna biomass (crustaceans) responded for the largest part of macroinvertebrates biomass in VAL and BP (Fig. 3). In terms of secondary production, macrofauna responded for the largest part of macroinvertebrates production only in VAL (Fig.4). Secondary production of crustaceans showed high variation (from 0.04 ± 0.09 to 11.17 ± 15.62 g AFDM m^{-2} y^{-1}), and was not significantly difference among sites (ANOVA, $F_{5,\ 39}$ = 1.997, P = 0.10).

Collectors exhibited an increase in secondary production along the gradient of shading (ANOVA, $F_{5,39}$ = 3.275, P = 0.015) and varied between and 1.01 ± 0.63 and 10.67 ± 10.33 g AFDM m^{-2} y^{-1}. The multiple-range test (Tukey) showed that the difference was between LAM and most shaded sites, VAL (Difference = 9.366, P = 0.022) and BP. Collector biomass varied between 0.03 ± 0.02 and 0.21 ± 0.20 g AFDM m^{-2}) and varied significantly (ANOVA, $F_{5,\ 39}$ = 2.43, P = 0.05) but Tukey-test did not detect any difference among sites.

Filterer biomass and secondary production varied among sites (ANOVA, $F_{5,39}$ = 15.427, $P < 0.001$ and $F_{5,45}$ = 8.077, $P < 0.001$, respectively), showing higher values in

CAP (2.31 ± 0.96 g AFDM m^{-2} and 6.94 ± 4.47 g AFDM m^{-2} y^{-1}, respectively) and CHA (0.86 ± 0.88 g AFDM m^{-2} and 4.50 ± 4.05 g AFDM m^{-2} y^{-1}). Biomass and production of scrapers varied among sites (ANOVA, $F_{5,\ 39} = 3.238$, $P = 0.015$ and $F_{5,\ 39} = 3.072$, $P = 0.02$, respectively). Biomass means were low (less than 0.05 g AFDM m^{-2} in all sites) and secondary production varied between 0.03 ± 0.05 and 0.66 ± 0.68 g AFDM m^{-2} y^{-1}, respectively) and higher values were observed in LAM and CAP (0.66 and 0.21 g AFDM m^{-2} y^{-1}, respectively). Secondary production of predators varied among sites (ANOVA, $F_{5,\ 39} = 2.577$, $P = 0.04$) but Tukey-test did not detect any difference among sites.

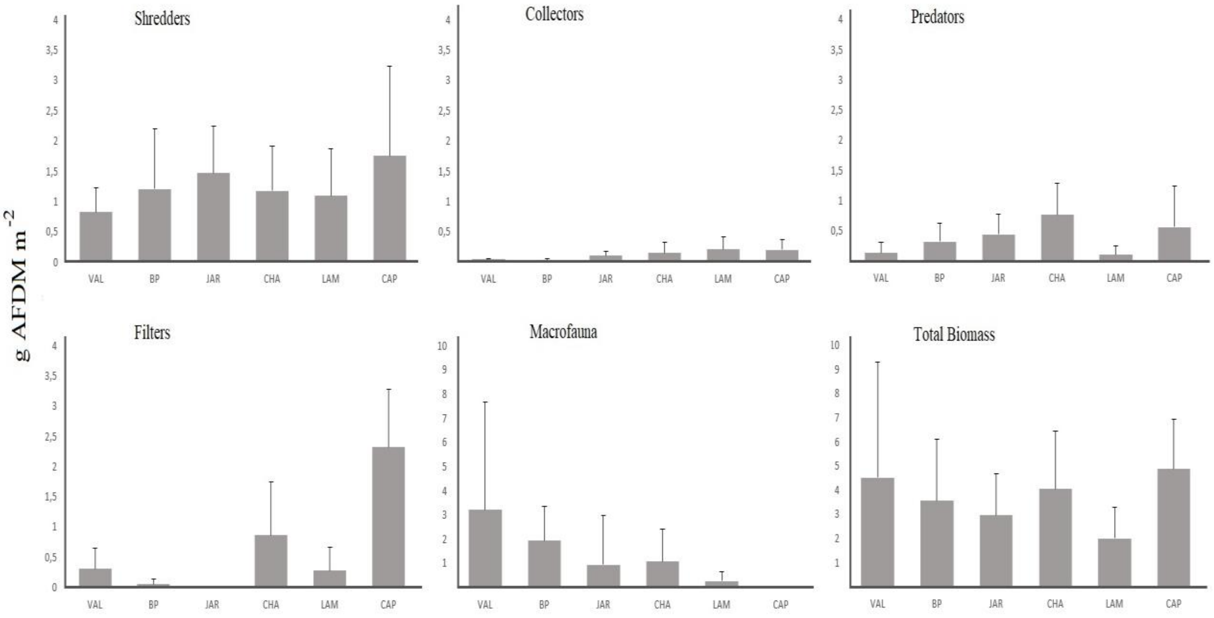

Figure 3. Biomass of FFG – shredders, predators, collectors, filterers, macrofauna (shrimps and crabs) and total macroinvertebrates in studied sites. Sites are ordered with respect to canopy cover. Bars are means of four samples per site over eight months, error bars are SD. (n=39).

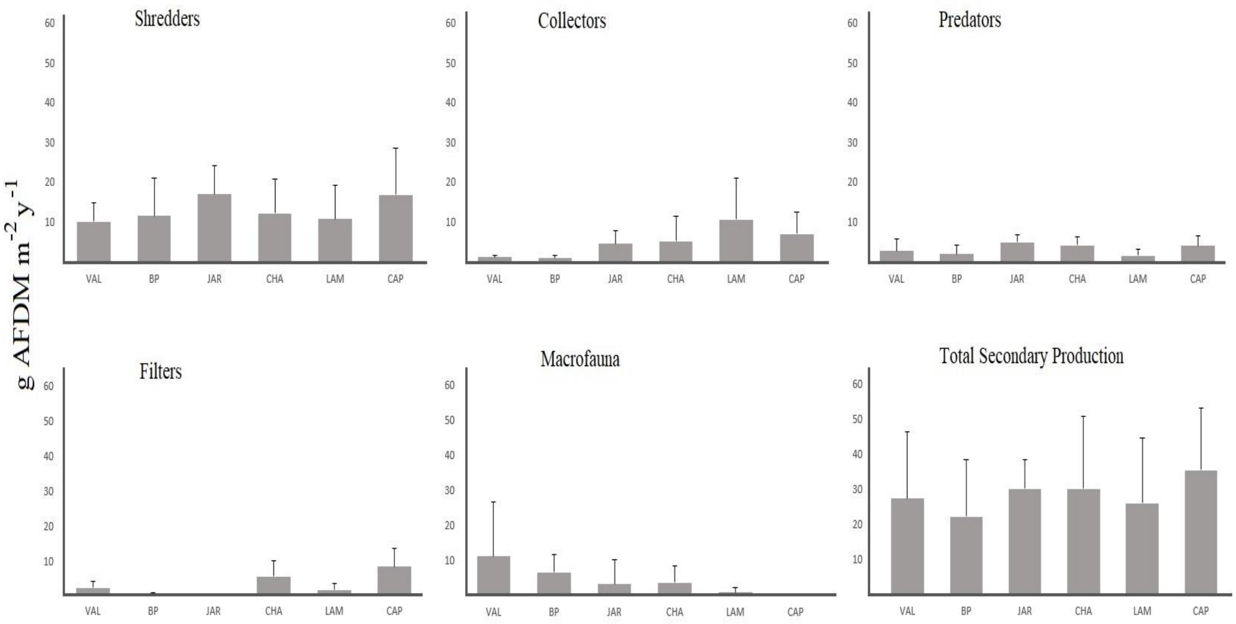

Figure 4. Secondary production of FFG – shredders, predators, collectors, filterers - macrofauna (shrimps and crabs) and total macroinvertebrates in studied sites. Sites are ordered with respect to canopy cover. Bars are means of four samples per site over eight months, error bars are SD. (n=39).

Organic matter

Benthic leaf density in litter banks varied significantly among sites (ANOVA, $F_{5,39}$ = 3.490, P = 0.005), but Tukey-test revealed differences just between VAL (383.8 ± 243.5 g AFDM m^{-2}) and JAR (178.9 ± 72.4 g AFDM m^{-2}; P = 0.009; Fig. 4). Density of ‘others’ also did vary among sites (ANOVA, $F_{5,39}$ =6.103, $P < 0.001$), whereas JAR (630.4 ± 221.0 g AFDM m^{-2}) and CHA (526.4 ± 175.9 g AFDM m^{-2}) exhibited higher mean values than LAM (232.2 ± 124.2 g AFDM m^{-2}; Tukey-test, $P < 0.001$ and P = 0.019) and CAP (197.4 ± 141.8 g AFDM m^{-2}; Tukey-test, $P < 0.001$ and P = 0.016 Fig. 5). The sum of leaves and ‘others’, which was mainly composed of processed leaves, also varied among sites (ANOVA, $F_{5,39}$ = 2.921, P = 0.015), where VAL and JAR showed higher mean values than LAM (P = 0.043 and P = 0.035).

Benthic FPOM varied significantly among sites (ANOVA, $F_{5,39} = 2.453$, $P = 0.036$ Fig. 5), but Tukey-test revealed differences just between BP (268.1 ± 373.0 g AFDM m^{-2}) and CAP (29.2 ± 29.7 g AFDM m^{-2}; $P = 0.026$). UFBOM also varied significantly among sites (ANOVA, $F_{5,39} = 14.8$, $P < 0.000$), where the highest mean was observed in CHA (except than VAL Fig. 5).

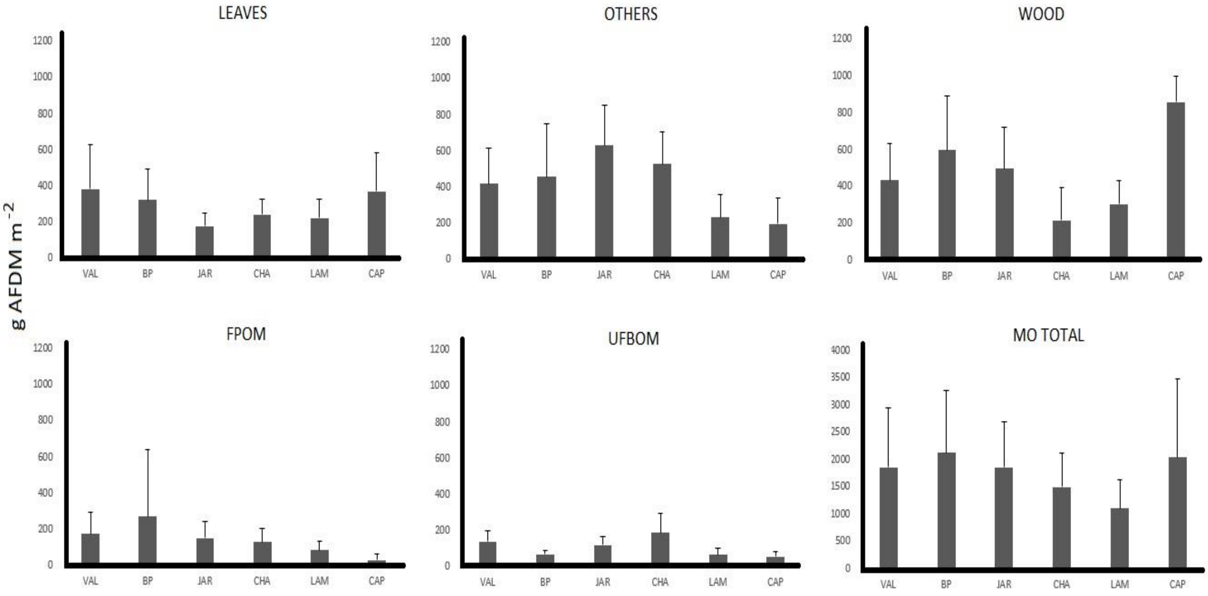

Figure 5. Organic matter fractions and total in studied sites (means of four samples per site over eight months, error bars are SD, n=39.

Our analysis indicated that FFG and organic matter categories were related: secondary production of shredders was related to leaf density; collectors exhibited strong relationship with FPOM and interaction between FPOM and site; and filterer secondary production was not significantly related to UFBOM, but exhibited a strong interaction between UFBOM and site (Tab. 2).

Table 2. Analysis of covariance of FFG secondary production with organic matter and sites. Leaves, FPOM and UFBOM are covariates

Dependent variable	Source of variation	Sum of squares	df	Mean square	*F*-ratio	*P*
Shredder production	Leaves	579.764	1	579.764	0.782	0.003*
	Sites	228.329	5	45.666	9.931	0.570
	Leaves*Sites	436.648	5	87.330	1.496	0.218
	Error	1926.424	33	58.376		
Collector production	FPOM	177.502	1	177.502	19.183	<0.001**
	Sites	242.892	5	48.578	5.250	0.001**
	FPOM *Sites	853.190	5	170.638	18.441	<0.001**
	Error	305.352	33	9.253		
Filter production	UFBOM	3.765	1	3.765	0.946	0.338
	Sites	125.077	5	25.015	6.287	<0.001**
	UFBOM *Sites	62.765	5	12.553	3.155	0.020*
	Error	131.303	33	3.979		

df, degrees of freedom

Leaf ingestion and processing

Through leaf breakdown estimates, monthly leaves in litter stock data and estimates of leaf substratum coverage, we predicted the rate of leaf processing (AFDM m^{-2} $month^{-1}$) for each site (Fig. 6). VAL and CHA exhibited faster rates, mean 11.89 and 16.44 AFDM m^{-2} m^{-1}; respectively and LAM exhibited the slowest rate, 0.57 AFDM m^{-2} m^{-1}. The rate of leaf ingestion was estimated by combining secondary production with efficiency of assimilation (Fig 2). Mean values of macroinvertebrates leaf ingestion varied between 0.32 and 0.50 AFDM m^{-2} m^{-1} of leaf ingested. These values corresponded to less than 5% of leaf processing in VAL and CHA, and less than 15% in JAR and CAP and indicates that leaf ingestion corresponded to a small proportion of mass loss.

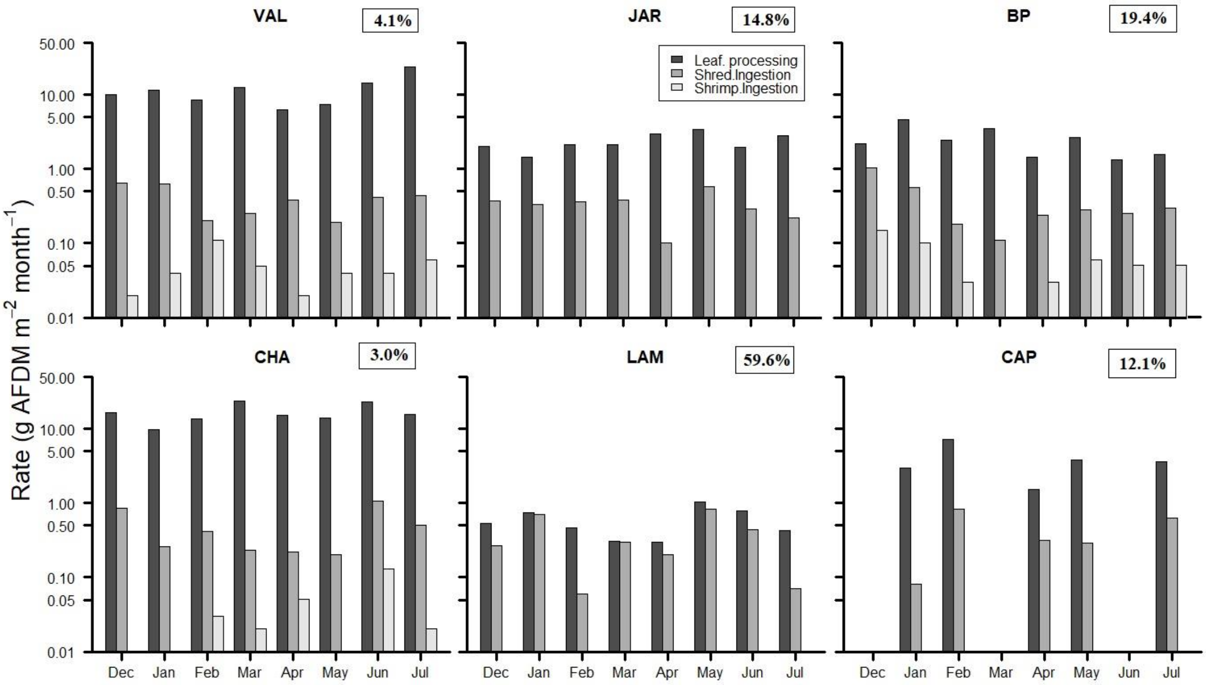

Figure 6. Rates of leaf processing and leaf ingestion by shredders (insects) and by shrimps (*Potimirim brasiliana*) per site over eight months. In boxes, summed up contribution of insects and shrimps to leaf processing.

Discussion

Our first hypothesis was not corroborated since estimated leaf ingested by invertebrates represented a small fraction of leaf processed. Our second hypothesis, however, was corroborated and consumers – shredders, collectors and filterers – exhibited positive relationships with the availability of their potential resources.

Despite our data indicating that terrestrial detritus represents the main energy source for macroinvertebrates in litter banks, rates of leaf ingestion shows that ingestion by shredders is not the main pathway for leaf mass loss. Results indicate a contribution of < 5% of leaf processing in VAL and CHA and < 15% in JAR and CAP. Although in BP and LAM leaf ingestion corresponded to 19% and 60%, respectively, of leaf processing, this supposed consumption is just reflection of a slow rate of leaf processing as these sites exhibited the slowest breakdown rates (Aguiar et al., 2017).

Assessment found in literature indicates varied contribution of shredders in litter mass loss. Oertli (1993) observed that shredders processed 11.2% of leaf litter and estimated that microorganisms responded for the largest part of matter disappearance. Likewise, Petersen et al., (1989) indicate leading role of microorganisms on the breakdown process, estimating that microbial detritus consumption was 13x higher than animal assimilation for macroinvertebrates. According to this study, macroinvertebrates removed 11.6% of terrestrial detritus, where shredders assimilated 20% of total animal assimilation. On the other side, Petersen & Cummins (1974) indicated 56% of animal assimilation against 44% microbial consumption. There are estimates indicating that shredders respond for 51-64% of leaf breakdown (Heiber & Gessner, 2002).

The excess of allochthonous organic matter in all sites indicates that this material availability is not limiting for the detritivores, conversely it is not feasible that these organisms would consume all the matter, or a great part of it, due to its high availability. A recent study conducted in Atlantic Forest showed high reliance of macroinvertebrates on allochthonous resources, however annual ingestion of all basal resources did not exceed 26.57 g DM m^{-2} (Neres-Lima et al., 2017). According to this study, more than 90% of net primary production is not consumed by macroinvertebrates, but is processed by microorganisms or transported downstream, and probably, the fate of terrestrially derived organic matter could also be microbes, burial and downstream transport (Neres-Lima et al., 2017).

Total macroinvertebrate production of this study varied between 22.03 and 35.27 g AFDM m^{-2} y^{-1} and was higher than that reported in other preserved tropical streams. Limited available information obtained from macroinvertebrate assemblages in tropical ecosystems indicate low secondary production (Jacobsen et al., 2008). A recent study conducted in Brazilian savannah indicated biomass production varying from ~2.37 to ~11.20 g AFDM m^{-2} y^{-1}, in shaded and open sites, respectively (converted from daily estimates that varied from ~7 to 33 mg DM m^{-2} d^{-1}; Linares et al., 2017). Data obtained in Hong Kong indicate that macroinvertebrate secondary production varied between 5.24 and 7.10 g AFDM m^{-2} y^{-1} (original data in DM, Dudgeon, 1999), which are 10 times higher than estimates obtained in Costa Rica, that did not exceed 0.5 g AFDM m^{-2} y^{-1} (Ramírez & Pringle, 1998).

Despite the scant observations that indicate low macroinvertebrate secondary production in tropical streams and higher values obtained in the present study, it is important to observe that neither Ramírez and Pringle (1998) nor Dudgeon (1999) quantified the entire macroinvertebrate assemblage, and did not consider crustaceans. The production of abundant shrimps was not included in invertebrate secondary production in Costa Rica (Ramírez & Pringle, 1998) and the study conducted in Hong Kong investigate production of 19 insect taxa. Linares et al. (2017) did not select a substrate type or investigated variation among microhabitat, which can be relevant, as different compartments exhibit differences in activity and metabolism (Tromboni et al., 2017). Despite leaf substrate representing less than 3% of substrate in all studied sites, this compartment contributes disproportionally to ecosystem respiration (Tromboni et al., 2017), indicating leaves as a productive substrate in streams.

Comparing our data with values obtained in temperate small streams, with detritus-based assemblages, our values can be considered intermediate (Benke, 1993; Huryn & Wallace, 2000). Results obtained in headwater streams at Coweeta Creek exhibited community production varying from ~6 to ~10 g AFDM m^{-2} y^{-1} and shredder production varying from ~2 to ~4 g AFDM m^{-2} y^{-1} (Cross et al., 2006). Griffith et al. (1994) reported similar values of annual shredder secondary production, varying between 1.9 and 3.7 g AFDM m^{-2}. Huryn & Wallace (1987) showed shredder production varying between 0.6 and 2.6 g AFDM m^{-2} y^{-1} across microhabitats and total community production values <10 g AFDM m^{-2} y^{-1}. Lower macroinvertebrate secondary production results were reported in three forested streams by Entrekin et al., (2007), whereas values did not exceed 3.5 g AFDM m^{-2} y^{-1}. Otherwise, there are also studies that reported higher invertebrate secondary production. Krueger and Waters (1983) reported annual productions of 27.0, 36.9 and 119.6 g AFDM m^{-2} in headwater streams of different geologic origin and alkalinity. Benke and Wallace (2015) reported invertebrate production varying between 148 and 203 g AFDM m^{-2} y^{-1} in snags.

Shredder secondary production corresponded to more than 40% (10.20–17.03 g AFDM m^{-2} y^{-1}; Fig. 4) of total production, comprising the dominant functional feeding group, except in VAL. Despite variation in leaf stock among sites, and relationship between leaves and shredder secondary production, this variable showed similar values, which indicate that shredders did not appear to be resource limited. In VAL and BP crustaceans, specifically *Potimirim brasiliana*, dominated total benthic biomass (3.19 and 1.92 g AFDM m^{-2}, respectively; Fig. 3) and secondary production in VAL (11.17 g AFDM m^{-2} y^{-1}; Fig. 4).

In CHA, *P. brasiliana* also contributed to the major fraction of macrofauna production (3.74 g AFDM m^{-2} y^{-1}) and in JAR, LAM and CAP these shrimps were absent (Fig. 4). Atyid shrimps usually occur in higher densities and dominate benthic communities in headwater streams (Pringle, 1996; Greathouse & Pringle, 2006), whereas, bellow waterfalls, in intermediate reaches, these organisms exhibit low densities (Covich & McDowell, 1996; Moulton et al., 2010).

The opposite trend was observed for collectors, that increased in biomass and secondary production along the river. Despite the low biomass (less than 200 mg AFDM m^{-2}), secondary production varied between 1.01 and 10.67 g AFDM m^{-2} y^{-1}, whereas in LAM, collectors and shredders production showed the same value (10.67 and 10.80 g AFDM m^{-2} y^{-1} respectively; Fig.3). Oppositely, FPOM accumulation decreased along the gradient (Fig. 4), indicating linkage between collector's biomass production and FPOM availability, confirmed by analysis of covariance. Despite the low contribution of scrapers, the increase in biomass and, especially in secondary production downstream suggests a possible increase in algal resource availability in litter banks in less shaded sites. Filterer biomass and secondary production exhibited higher values in CAP and CHA.

We conclude that despite the dominance of shredders on litter-banks in terms of biomass and secondary production and results indicating high dependence of macroinvertebrates on terrestrial organic matter, the role of metazoans on litter mass loss seems small. Despite the high availability of terrestrial organic matter and importance on macroinvertebrates maintenance, most part of this material does not seem to be incorporated into the riverine food web, instead it probably is exported and/or processed by microbes.

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Appendix 1. Density (individuals per m^{-2}), biomass (mg AFDM m^{-2}), secondary production (mg AFDM m^{-2} year^{-1}) and P/B (production/biomass) of main macroinvertebrate taxa of each FFG founded. Methods used to calculate secondary production – Size-frequency (SF), P/B ratio and Instantaneous growth rate (IG).

Site	Taxon	Density	Biomass	Production	P/B	Method
	Shredders					
	Triplectides					SF
VAL		387 ± 287	491.46 ± 398.04	5203.32 ± 43012.93	10.6	
BP		304 ± 248	1077.92 ± 920.78	9242.87 ± 8012.64	8.6	
JAR		438 ± 345	842.15 ± 522.41	8751.12 ± 4264.26	10.4	
CHA		498 ± 398	500.76 ± 233.81	6030.27 ± 3867.65	12.0	
LAM		304 ± 174	833.47 ± 550,98	7049.35 ± 5815.65	8.5	
CAP		226 ± 142	1387.09 ± 1129.70	12370.12 ± 8552.59	8.9	
	Phylloicus					SF
VAL		103 ± 72	125.92 ± 116.59	2119.73 ± 2059.42	16.8	
BP		7 ± 8	37.77 ± 50.28	453.95 ± 528.18	12.0	
JAR		51 ± 26	533.66 ± 454.12	6092.71 ± 4327.75	11.4	
CHA		26 ± 24	450.37 ± 682.29	1497.16 ± 1658.68	3.32	
LAM		8 ± 9	26.72 ± 42.07	417.87 ± 489.78	15.6	
CAP		11 ± 20	209.40 ± 288.50	868.72 ± 1940.04	4.1	
	Leptophlebiidae					SF
VAL		835 ± 497	120.99 ± 81.69	1844.34 ± 1279.11	15.2	
BP		675 ± 710	86.12 ± 76.48	1794.66 ± 1890.22	20.8	
JAR		379 ± 337	75.70 ± 45.44	1975.66 ± 1302.17	26,1	
CHA		1,257 ± 930	203.19 ± 182.79	4219.45 ± 3573.75	20.7	
LAM		1,569 ± 1676	208.26 ± 252.78	2736.94 ± 3286.58	13.1	
CAP		645 ± 651	90.67 ± 76.57	996.44 ± 879.22	11.0	
	Stenochironomus					SF
VAL		75 ± 67	12.35 ± 11.12	264.41 ± 238.20	21.4	
BP		14 ± 17	1.99 ± 2.55	53.64 ± 61.06	26.9	
JAR		27 ± 34	3.86 ± 7.03	84.70 ± 129.04	21.9	
CHA		82 ± 77	23.62 ± 19.94	480.30 ± 367.70	20.3	
LAM		60 ± 44	16.59 ± 17.11	510.89 ± 468.21	30.8	
CAP		339 ± 200	62.67 ± 70.12	2604.02 ± 1963.75	41.5	
	Tipulidae					P/B ratio
VAL		56 ± 67	67.78 ± 73.73	677.80 ± 737.27	10	
BP		5 ± 7	1.29 ± 2.43	12.86 ± 24.30	10	
JAR		17 ± 32	11.07 ± 17.12	110.74 ± 171.20	10	
CHA		1 ± 2	0.97 ± 2.75	9.73 ± 27.53	10	
LAM		5 ± 9	8.73 ± 23.73	87.31 ± 237.27	10	
CAP		8 ± 13	3.73 ± 6.30	37.33 ± 62.98	10	

- **continued**

Site	Taxon	Density	Biomass	Production	P/B	Method
	Collectors					
	Chironomidae					SF
VAL		340 ± 193	17.27 ± 10.96	836.35 ± 468.62	48.4	
BP		365 ± 253	30.88 ± 22.41	982.07 ± 633.96	31.8	
JAR		2274 ± 1540	65.67 ± 57.33	3771.02 ± 2891.82	57.4	
CHA		1485 ± 1908	144.83 ± 169.68	5112 ± 6252.14	35.3	
LAM		5098 ± 5065	205.48 ± 202.66	10595.54 ±10340.60	51.6	
CAP		4014 ± 2925	190.26 ± 166.32	7023.78 ± 5449.7	36.9	
	Elmidae					IG
VAL		105 ± 106	29.73 ± 21.11	469.67 ± 311.48	15.8	
BP		28 ± 18	1.86 ± 1.21	33.34 ± 15.48	17.9	
JAR		409 ± 422	39.75 ± 39.02	886.79 ± 876.66	22.3	
CHA		54 ± 43	7.81 ± 12.66	121.52 ± 166.28	15.5	
LAM		48 ± 51	2.82 ± 3.84	65.51 ± 79.39	22.1	
CAP		11 ± 17	0.71 ± 0.98	14.34 ± 20.47	20.1	
	Predators					
	Tanypodinae					SF
VAL		374 ± 306	18.50 ± 16.63	1047.52 ± 910.48	56.6	
BP		105 ± 81	5.39 ± 3.87	255.07 ± 174.75	47.3	
JAR		587 ± 346	45.87 ± 19.42	1778.19 ± 968.98	38.8	
CHA		435 ± 418	34.79 ± 25.06	1345.60 ± 1253.07	38.7	
LAM		593 ± 415	35.94 ± 29.54	1342.46 ± 1314.10	37.4	
CAP		640 ± 505	43.19 ± 32.31	1754.65 ± 1124.62	40.6	
	Ceratopogonidae					IG
VAL		50 ± 69	5.31 ± 8.03	240.72 ± 367.46	45.3	
BP		47 ± 87	3.66 ± 7.57	166.67 ± 343.02	45.6	
JAR		84 ± 110	11.30 ± 14.10	500.23 ± 629.32	44.3	
CHA		11 ± 25	2.00 ± 4.40	86.54 ± 191.59	43.3	
LAM		4 ± 11	1.00 ± 2.83	42.61 ± 120.53	42.6	
CAP		19 ± 38	1.34 ± 2.14	62.10 ± 102.37	46.5	
	Other taxa					IG
VAL	(mainly Odonata)	59 ± 67	104.88 ± 175.47	1500.84 ± 2060.50	14.3	
BP		26 ± 15	309.99 ± 308.25	1667.47 ± 2319.28	5.4	
JAR		51 ± 46	379.33 ± 352.26	2716.95 ± 2211.64	7.1	
CHA		53 ± 45	725.78 ± 523.46	2743.98 ± 1623.52	3.8	
LAM		13 ± 28	64.21 ± 133.99	303.37 ± 618.61	4.7	
CAP		56 ± 45	513.06 ± 677.60	2249.10 ± 1538.20	4.4	

- continued

Site	Taxon	Density	Biomass	Production	P/B	Method
	Filterers					
	Macronema					SF
VAL		45 ± 34	302.35 ± 336.69	1385.45 ± 1325.36	4.6	
BP		9 ± 11	44.34 ± 73.66	168.11 ± 221.04	3.8	
JAR		0	0	0	-	
CHA		80 ± 68	859.11 ± 877.45	4496.37 ± 4044.58	5.2	
LAM		42 ± 42	274.51 ± 387.69	1138.57 ± 1463.09	4.1	
CAP		229 ± 155	2,309.79 ± 954.81	6917.25 ± 4443.87	3.0	
	Scrapers					
	Americabaetis					IG
VAL		87 ± 116	7.72 ± 8.17	87.06 ± 112.96	11.3	
BP		269 ± 320	26.41 ± 33.16	424.2 ± 636.64	16.1	
JAR		57 ± 73	3.23 ± 4.31	39.84 ± 50.84	12.3	
CHA		14 ± 23	2.09 ± 4.26	16.72 ± 28.41	8.0	
LAM		445 ± 509	43.48 ± 47.58	631.8 ± 670.2	14.5	
CAP		139 ± 180	10.17 ± 11.20	141.28 ± 176.81	13.9	
	Macrofauna					
	P. brasiliana					P/B ratio
VAL		96 ± 60	1250.19 ± 732.32	4357.65 ± 2563.11	3.5	
BP		112 ± 73	1755.42 ± 1407.97	6143.98 ± 4927.91	3.5	
JAR		0	0	0	-	
CHA		31 ± 39	851.92 ± 1089.55	2981.71 ± 3813.44	3.5	
LAM		0	0	0	-	
CAP		0	0	0	-	
	Trichodactylus					P/B ratio
VAL		6 ± 8	1923.07 ± 4385.06	6730.75 ± 15347.73	3.5	
BP		0	0	0	-	
JAR		18 ± 20	932.55 ± 2019.58	3263.93 ± 7068.52	3.5	
CHA		3 ± 6	218.20 ± 604.21	736.70 ± 2114.72	3.5	
LAM		0	0	0	-	
CAP		2 ± 4	12.49 ± 27.92	43.70 ± 97.72	3.5	

Conclusões Gerais da Tese

Com os resultados obtidos nesta tese, conclui-se que apesar da importância do material terrestre na manutenção dos macroinvertebrados bentônicos e do papel dos decompositor desses organismos, a efetiva participação de fragmentadores no desaparecimento de matéria é pequena.

A biomassa e produção secundária dos fragmentadores representaram melhor a importância desses organismos na decomposição que a abundância, uma consequência da baixa representatividade em termos de números de indivíduos (em relação a organismos abundantes como Chironomidae) compensada pela elevada biomassa individual.

A produção secundária de macroinvertebrados bentônicos não foi especialmente alta, mas nem tão baixa como mostram os trabalhos que utilizaram tal abordagem em ecossistemas tropicais. Porém, tais dados devem ser analisados com cautela, uma vez que apesar dos bancos de folhas serem componentes extremamente ativos no ambiente lótico, a cobertura de substrato foliar em todos os locais de amostragem foi inferior a 3%.

Perspectivas Futuras

Os resultados obtidos nessa tese evidenciam que o papel do carbono alóctone no meio aquático deve ser analisando em conjunto com outras variáveis, especialmente processos ecossistêmicos. Para o desenvolvimento das pesquisas nesse sentido, recomenda-se:

- Avaliar a taxa de ingestão de fragmentadores de detritos foliares de qualidades contrastantes;
- Avaliar outros parâmetros associados ao crescimento e demandas nutricionais como excreção de nutrientes e composição elementar do consumidro e de recursos;
- Estimar as perdas de massa foliar na decomposição física e microbiológica no intuito de compreender o processo de maneira mais ampla e identificar se maior processamento ocorre via abrasão ou consumo microbiológico;
- Pesquisas direcionadas a gerar informações relacionados à fauna bentônica tropical, incluindo classificações em grupos funcionais de alimentação e ciclo de vida.

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