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# TÍTULO:
# DECOMPOSIÇÃO DE DETRITOS FOLIARES EM SISTEMAS RIPÁRIOS TROPICAIS: EFEITOS DAS ESCALAS ESPACIAL E TEMPORAL.

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia.

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**"Decomposição de detritos foliares em sistemas ripários tropicais: efeitos das escalas espacial e temporal".**

por

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Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (Port. no. 20/PPGECO/ 2014) do Programa de Pós-Graduação em Ecologia - UFSC, composta pelos Professores Doutores:

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**Florianópolis, 27 de junho de 2014.**

*Dedico...*

*A Deus, único senhor da minha vida, que desde o meu nascimento tem sido misericordioso, me protegendo e guiando...*

*A Cássia... Pois seu companheirismo em todas as situações me fez chegar até aqui, principalmente nos momentos difíceis, de angústia e tristeza...*

*Aos meus pais Pedro e Lúcia, por todo afeto, compreensão e força dadas a mim, mesmo na distância, no decorrer desta jornada.*

“O único lugar onde o êxito chega
antes do trabalho é no dicionário”.

*Vidal Sassoon*

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## SUMÁRIO

# RESUMO

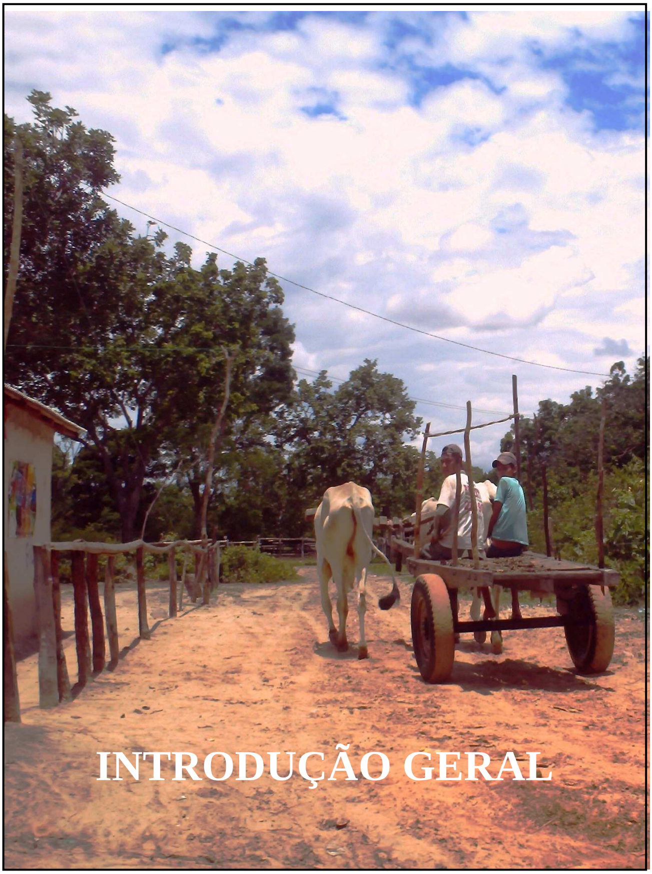
A avaliação da decomposição em diferentes níveis e escalas (espacial e temporal) possibilita o desenvolvimento de uma visão integrada sobre a ótica deste importante processo ecológico. O objetivo deste estudo foi avaliar a influência de diferentes escalas espaciais e temporais na decomposição de detritos foliares e os efeitos da composição química, invertebrados e micro-organismos em riachos de região tropical (Brasil). Foram estudados rios do Norte de Minas Gerais (Capitulo 1 e 2) e do planalto central em Brasília (Capitulo 3). Assim, esta tese é composta por 3 capítulos e os seus principais resultados foram: 1- **"Coarse Particulate Organic Matter Dynamics in a Tropical Vereda System"**, onde a produção de serapilheira em área de veredas foi baixa (365g $m^{-2}$ $ano^{-1}$ de entrada terrestre e 181 g $m^{-2}$ $ano^{-1}$ vertical sobre o rio). A decomposição foliar foi elevada quando comparada com outros sistemas tropicais, com valores máximos coincidindo com o período chuvoso. O conteúdo de ergosterol das folhas foi elevado, mas as densidades de esporos na água foram baixas. Menos de 10% dos invertebrados foram fragmentadores, sugerindo pouca participação desta comunidade no processo de decomposição. Apesar da baixa produtividade e rápida decomposição, a matéria orgânica acumulada no leito é alta. Isso pode estar relacionado com ciclos de inundação e a dinâmica de secas sazonais, permitindo o transporte de detritos foliares das áreas terrestre através da corrente da água. 2**- "Canopy degradation effects on temporal leaf breakdown rates in a tropical stream",** os maiores valores na taxa de decomposição foram observados no período chuvoso, provavelmente devido às altas temperaturas (aumento da atividade metabólica) e chuvas (maior abrasão física). Encontramos maior biomassa microbiana (aumento de organismos fotossintéticos) e maiores densidades e riqueza de invertebrados (menor

lavagem da comunidade pela água) no período de seca. O fluxo de água, temperatura e precipitação foram os fatores que controlam a decomposição neste sistema. A degradação do dossel modificou o *k* e pode altera o metabolismo do ecossistema (heterotróficas para autotróficas), apesar da grande resistência ecológica das "veredas". A degradação do dossel também deixou o sistema mais suscetíveis a alterações sazonais. Este impacto ambiental modificou também as comunidades de micro-organismos e invertebrados, indicando que este processo é um útil bioindicador. 3**- "The effects of spatial scale on breakdown of leaves in a tropical watershed"**, onde as comunidades microbiana e de fragmentadores foram mais influenciadas pela escala local (ordem de rio), conduzindo a decomposição foliar nesta escala. Entretanto, as maiores influencias sobre o processo de decomposição foram observadas em escala regional (sub-bacia), mostrando que a escala de estudo altera a resposta do processo estudado. As maiores taxas de decomposição (independente da qualidade do detrito) ocorreram em ambientes com elevados valores de velocidade da água, oxigênio dissolvido e temperatura, os quais aceleram o metabolismo biológico. Assim, bacias com microclimas mais quentes e córregos com níveis mais elevados de nutrientes e oxigênio poderiam estar acelerando o metabolismo do ecossistema, independente da qualidade detritos.

# ABSTRACT

The evaluation of the leaf breakdown at different levels and scales (spatial and temporal) enables the development of integrated view of this important ecological process. The aim of this study was to evaluate the influence of different spatial and temporal scales in the evaluation and the effects of chemical composition, invertebrates and micro-organisms in streams of tropical region (Brazil). Rivers in northern of Minas Gerais State (Chapter 1 and 2) and the central plateau in Brasília City (Chapter 3) were studied. Thus, this thesis consists of three chapters and the main results were: 1- **"Coarse Particulate Organic Matter Dynamics in a Tropical Vereda System"**; Litter production in the riparian area was low (365g $m^{-2}$ $year^{-1}$ falling on the forest soil and 181 g $m^{-2}$ $year^{-1}$ fallen directly into the stream). The litter breakdown was high when compared with other South American systems, with maximum values coinciding with the rainy season. Ergosterol content in decomposing leaves was high, but spore densities in the water were low. Nearly 10% of invertebrates were shredders suggesting a low role in litter decomposition. Despite the low litterfall and fast decomposition, accumulated organic matter in the bed is high. This could be related to seasonal flood/dry dynamics allowing the transportation of terrestrial litter into the stream. 2- **"Canopy degradation effects on temporal leaf breakdown rates in a tropical stream"**; Higher values of leaf breakdown rates ($k$) were observed in rainy season, most likely due to high temperatures (increasing metabolic activity) and rainfall (higher physical abrasion). However, we found higher microbial biomass (increase of photosynthetic organisms) and greater densities and richness of invertebrates (lower washing power by water) in dry season. Therefore, on the large temporal sampling, water flow, temperature and precipitation were the factors controlling the $k$ in this stream system. The canopy

degradation modify the *k* and can change the metabolism of the ecosystem (from heterotrophic to autotrophic), despite the great ecological resistance of “veredas”. The canopy degradation left the system higher susceptible to seasonal changes. This environmental impact modified also the communities of micro-organisms and invertebrates indicate that this process is useful as bioindicators. 3- **“The effects of spatial scale on breakdown of leaves in a tropical watershed”**; The microbial and shredder were most influenced at the local scale (stream order), leading to leaf breakdown in this scale. Moreover, differences in the overall *k* and abiotic variables were more strongly influenced at the regional scale (sub-basin), showing that the study scale alters the response of the studied variables. We found higher *k* values (independent of the detritus quality) at higher values of water velocity, dissolved oxygen and temperature, all of which accelerate biological metabolism in response to variations on the regional scale. Watersheds with warmer microclimates and streams with higher nutrient levels and oxygen could be accelerating the ecosystem metabolism, independent of the detritus quality.



# INTRODUÇÃO GERAL

# INTRODUÇÃO GERAL

A origem da limnologia moderna geralmente é reportada para o final do século XIX, quando o médico suíço François Alphonse Forel iniciou os seus estudos no lago Léman, publicando três volumes entre 1892 e 1904. Entretanto, duas figuras assumem grande relevância na consolidação da limnologia como uma importante área do conhecimento, são eles o entomólogo alemão August Friedrich Thienemann e o botânico sueco Einar Christian Leonard Naumann. Thienemann e Naumann foram os fundadores da Sociedade Internacional de Limnologia - SIL (1922) que proporcionou grande impulso à Limnologia, onde em seu primeiro congresso na cidade de Kiel (Alemanha), foi redefinida como sendo "a ciência que estuda os corpos d’água continentais do ponto de vista ecológico, independentemente do seu tamanho, origem e concentração de sais". Após estes eventos, as mais diversas vertentes ligadas à limnologia se desenvolveram e se consolidaram ao passar dos anos. Uma destas vertentes que se consolidaram ao longo dos anos foi a relacionada à ciclagem de nutrientes e do fluxo de energia.

Stephen Alfred Forbes trouxe o prenuncio do conceito de ecossistema, com ideias sobre dinâmica de nutrientes e fluxo de energia na cadeia alimentar (Forbes, 1887; Croker, 2001). Esta visão influenciou Charles Elton na década de 1920, que traçou importantes relações entre a forma de alimentação dos seres vivos, concluindo que estas interações tróficas ligam os organismos através da comunidade biológica. Tansley na década de 1930, preferiu discutir o sistema como uma associação de animais e plantas juntamente com os fatores físicos, denominada ecossistema. Nesta mesma época Alfred J. Lotka, discorreu sobre as taxas de transformação de energia e matéria dentro dos sistemas ecológicos através dos princípios termodinâmicos. Assim, todas estas questões culminaram em Raymond Lindeman, que foi responsável por introduzir a ideia do ecossistema como um sistema transformador de energia, fornecendo uma notação formal para o fluxo energético nos diferentes níveis tróficos (Lindeman, 1942). A partir das ideias propostas por Elton (teia alimentar), Lotka (transformação de energia) e Tansley (ecossistema) brilhantemente agrupadas ao conceito de ecossistema por Lindeman, surgiu uma nova proposta de compreensão dos sistemas ecológicos (Lindeman, 1942; Ricklefs, 2003). Desta fusão de conceitos, novos elementos foram propostos para melhorar o entendimento dos sistemas ecológicos, que foram: *cadeia alimentar, níveis tróficos e pirâmide de energia*. Na década de 1950, por intermédio de Eugene Odum ganha força a *ecologia ecossistêmica*, fundamentada nestes novos conceitos, tratando principalmente do fluxo de energia e reciclagem de matéria em diversos ecossistemas e condições.

Os enfoques dos estudos referentes ao fluxo de energia e ciclagem de matéria orgânica em ecossistemas aquáticos sofreram mudança ao longo do tempo, caminhando para uma visão mais abrangente dos ecossistemas, integrando padrões e processos em vários níveis de organização (Hynes 1970; Allan 1995, Cummins et al., 1995, Wallace et al., 1997). Uma consequência importante foram as primeiras pesquisas sobre decomposição de tecido vegetal de origem alóctone realizadas por Kaushik & Hynes (1971) e Petersen & Cummins (1974), impulsionando os estudos para outros processos e sistemas (Cummins 1974, Minshall 1988, Cummins et al. 1995). Tank et al. (2010), em um trabalho de revisão construiram uma linha do tempo (Figura 1), ilustrando as principais contribuições para a compreensão do processamento da matéria orgânica em ecossistemas lóticos a partir de Lindeman (1942).

O avanço dos estudos limnológicos sobre o processamento da matéria orgânica foi importante principalmente para as regiões de cabeceira dos rios.

Normalmente estes ambientes são compostos por rios de primeira ordem que apresentam vegetação ciliar sombreando o leito do riacho, formando matas de galerias. Nestes ambientes a matéria orgânica alóctone proveniente da vegetação ripária é uma fonte de energia fundamental para as comunidades aquáticas, pela baixa luminosidade que limita a produção primária (Mosisch et al., 2001). Fica evidente que a decomposição de detritos vegetais é um processo ecológico chave para o funcionamento dos ecossistemas lóticos (Gessner et al., 1999), pois é por ela que os nutrientes são mineralizados e disponibilizados para os produtores primários, permitindo sua remobilização para a cadeia trófica (Allan, 1997; Cleveland et al., 2004).

Gessner et al. (1999) propôs um modelo tradicional de decomposição de detritos vegetais que separa este processo em 3 fases: A **lixiviação** é a rápida perda de componentes químicos solúveis presentes no detrito após a imersão em água (horas). O **condicionamento** (semanas) corresponde à modificação da matriz do detrito por incremento da biomassa de micro-organismos, acarretando em um enriquecimento nutricional e melhorando sua palatabilidade para os macroinvertebrados detritívoros chamados **fragmentadores.** Os fragmentadores colonizam o detrito (meses), e conseguem fazer uso direto do tecido foliar. Ocorre também a **fragmentação física** por abrasão decorrente das condições do meio, que assim como a fragmentação biológica, seria a redução do detrito em partículas menores. Entretanto, esta sequência de eventos ocorre simultaneamente e interagem durante toda o processo de decomposição dos detritos.

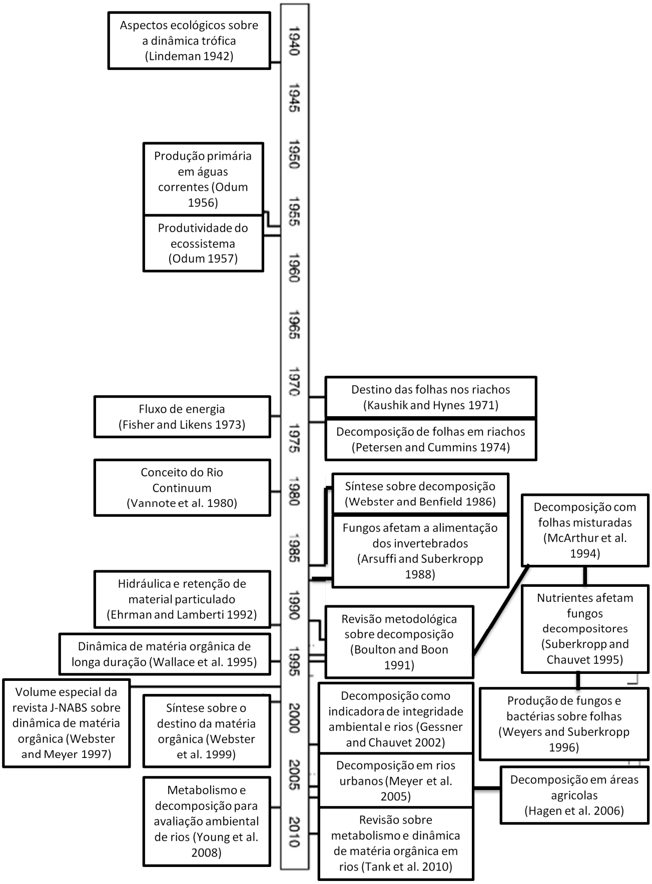


**Figura 1.** Linha do tempo ilustrando as principais contribuições para a compreensão da dinâmica de matéria orgânica, decomposição e metabolismo em ecossistemas lóticos. Adaptado de Tank et al., (2010).

Os invertebrados aquáticos são importantes no processo de decomposição, principalmente os pertencentes ao grupo trófico funcional dos fragmentadores, que se alimentam diretamente do tecido foliar e são mais abundantes em trechos de cabeceira (Wallace et al., 1982; Cummins et al. 1989; Graça 2001). Porém, a relevância deste grupo trófico funcional tem sido questionada no processamento de matéria orgânica de origem vegetal nos ecossistemas tropicais (Dobson et al. 2002), ao menos no bioma Cerrado. Em rios de regiões tropicais a presença de fragmentadores tem se mostrado muitas vezes rara (Yule et al., 2009), permitindo que outros grupos tróficos funcionais (p.ex. raspadores) preencham este papel funcional (Covich, 1988, Rezende et al., 2010) e também conferindo aos micro-organismos decompositores maior importância neste processo (Gonçalves et al., 2005; Moretti et al., 2007).

A colonização bacteriana em folhas tem uma importância relativa menor em termos de biomassa (Gaudes et al. 2009; Rincón & Santelloco 2009). Normalmente, participam ativamente da colonização nos estágios iniciais da decomposição e atuam sobre moléculas de fácil assimilação (Petersen et al., 1989; Tanaka, 1991). Diante desse fato, especial atenção tem sido dada ao estudo dos fungos avaliando seu papel na decomposição e no incremento nutricional do substrato (qualidade do detrito), devido à sua capacidade de metabolizar moléculas de difícil decomposição como celulose e lignina (Canhoto & Graça, 1996; Gessner et al., 1999; Graça, 2001). Além desta variação, a comunidade biótica pode ser influenciada pelos parâmetros abióticos locais, como: a elevação das concentrações de nutrientes (da água e do detrito), temperatura e vazão da água (Gulis & Suberkropp, 2004; Ardón & Pringle, 2007; Cornelissen et al. 2007). Estes fatores podem promover o aumento da diversidade das comunidades decompositoras e de suas atividades, acelerando a decomposição foliar (Gulis & Petersen et al. 1989; Suberkropp, 1998; Cornelissen et al. 2007).

Entretanto, apesar de alguns padrões observados sobre a decomposição, existem incertezas principalmente sobre os ambientes tropicais, onde encontramos um menor número de estudos quando comparados aos sistemas temperados. Perguntas como a variação na importância dos fatores bióticos e abióticos ao longo de uma escala espacial (ponto amostral, ordem de rio e sub-bacia) e temporal (horas, dias, semanas, meses e anos) ainda não estão definidas em sistemas tropicais. Estas questões se agravam à medida que colocamos a influencia antrópica (ex. degradação ambiental, perda de serviços ambientais, emissão de carbono e etc.) e suas implicações para o funcionamento do ecossistema. Assim, nota-se que devido ao pouco tempo existente desde os primeiros estudos ainda há um longo caminho nesta área do conhecimento.

Ao considerar o estudo da decomposição foliar em maiores escalas, é possível o reconhecimento de padrões emergentes e a identificação dos fatores que estruturam os ecossistemas em diferentes escalas (Wiens 1989; Tiegs et al. 2009). Segundo Schneider (2001), estudos que abordem apenas uma única escala podem estar sujeito a problemas, como: (i) a maioria das variáveis só podem ser medidas diretamente em pequenas áreas ou ao longo de períodos de tempo curto; (ii) relativamente poucas variáveis, podem ser medidas em resolução fina em grandes escalas; (iii) mudanças em pequenas escalas não se mantém em grandes escalas.

Espacialmente, a escala pode ser percebida como áreas de rápido e remanso, que estão dentro dos trechos, e estes estão aninhados em rios extensos, que compõem uma bacia hidrográfica, enquanto que temporalmente, temos processos que ocorrem em horas, outros levam dias, meses ou anos (Wiens 2002; Tiegs et al. 2009). Assim, fica evidente uma série de unidades geomórficas e temporais sucessivamente menores aninhadas (Wiens 2002; Lowe et al. 2006) podem apresentar diferentes padrões e estruturas e temporais a medida que mudamos a escala (Frissell et al. 1986; Allan 2004). Através desta perspectiva, a avaliação da decomposição em diferentes níveis possibilita o desenvolvimento de uma visão integrada sobre a ótica deste importante processo ecológico (Del Arco et al. 2012).

Porém, a maior parte dos trabalhos que avaliam a decomposição de detrito alóctone usando a bacia hidrográfica como unidade de estudo ou longos períodos temporais foram realizadas em sistemas temperados (Tank et al. 2010; Del Arco et al. 2012). Assim, esta tese aborda aspectos relacionados decomposição de detritos foliares em sistemas ripários tropicais, avaliando os efeitos das escalas espacial e temporal em ambientes tropicais. Este documento foi subdividido em Introdução Geral, Áreas de Estudo, Capítulos 1, 2 e 3 Considerações finais, Perspectivas Futuras. O primeiro capítulo, intitulado **“Coarse Particulate Organic Matter Dynamics in a Tropical Vereda System”,** o segundo capítulo que tem por nome **“Canopy degradation effects on temporal leaf breakdown rates in a tropical stream”**, e o terceiro e ultimo capítulo, encontra-se publicado na revista PlosOne (doi:10.1899/08-170.1), é intitulado **“The effects of spatial scale on breakdown of leaves in a tropical watershed”**.

## Objetivo Geral da Tese:

Avaliar a influência de diferentes escalas espaciais e temporais na decomposição de detritos foliares. Além disso, foram avaliados os efeitos da composição química, invertebrados e micro-organismos neste processo em riachos de região tropical (Brasil).

## Objetivos dos Capítulos:

### Capítulo 1

1. Avaliar a contribuição das espécies vegetais na entrada de matéria orgânica no aporte vertical e terrestre durante 12 meses em uma vereda preservada.
2. Mensurar a contribuição dos tipos de matéria orgânica (folhas, galhos, flores e frutos,) no aporte vertical e terrestre durante 12 meses em uma vereda preservada.
3. Estudar a taxa de decomposição foliar da mistura de folhas que entra pelo aporte vertical, além da densidade e biomassa de invertebrados, biomassa microbiana e esporulação de hifomicetos aquáticos associados a esta matéria orgânica vegetal alóctone durante 12 meses em um sistema lótico de vereda preservada.

### Capítulo 2

4. Descrever a dinâmica temporal (um ano) das taxas de decomposição de folhas em uma vereda com dossel degradado.
5. Caracterizar as mudanças físicas, químicas e biológicas do processo de decomposição foliar ao longo do ano em uma vereda com dossel degradado.
6. Identificar possíveis indicadores ambientais da degradação do dossel no processo de decomposição foliar.

**Capítulo 3**

7. Avaliar o efeito da variabilidade natural de algumas estruturas físicas do meio sobre as comunidades e o coeficiente de decomposição de *Eucalyptus cloeziana* F. Muell e *Inga laurina* Sw. Willd.
8. Identificar o fator controlador em diferentes gradientes e escalas de estudo (ordem de rio e sub-bacias).

## ÁREA DE ESTUDO

Os experimento que compõe esta tese ocorreram em zonas de vegetação riparia do Bioma Cerrado. A vegetação riparia é um dos principais sistemas responsáveis pela conservação dos processos ecológicos nos sistemas aquáticos dos quais estão associados (Naiman & Decamps 1997; Wantzen et al., 2008). Este ambiente que naturalmente margeia os corpos aquáticos possui várias funções como a filtragem do escoamento superficial, controle de aporte e erosão pelo bloqueio das chuvas pela copa das árvores, aumento da capacidade de armazenamento de água e o equilíbrio térmico, que mantêm a integridade da microbacia sobre sua influência (Naiman & Decamps 1997; Lima & Zakia, 2001).

A vegetação riparia também serve como importante corredor longitudinal e transversal para a troca de material e dispersão da biota (Naiman et al., 2005), e portanto, é muito mais que uma faixa-tampão (Naiman & Decamps 1997; Wantzen et al., 2008). Este é um ecótono com característica peculiares em relação à composição florística, biodiversidade e processos ecológicos, exercendo grande controle no balanço energético dos sistemas lóticos (Naiman & Decamps 1997; Lima & Zakia, 2001; Wantzen et al., 2008).

A vegetação ripária pode ser subdividida em duas categoria, mata ciliar e mata de galeria. A mata ciliar é definida como a vegetação florestal que acompanha os rios de médio e grande porte, onde o dossel da vegetação não forma galerias. A mata de galeria corresponde a vegetação que acompanha os rios de pequeno porte e córregos, formando corredores fechados (galerias) sobre o curso de água. A altura média do estrato arbóreo varia entre 20 e 30 metros, apresentando uma superposição das copas que fornecem cobertura arbórea de 70% a 95%, onde no seu interior a umidade relativa é alta.

Dentre os diferentes tipos de vegetação ripária, o Bioma Cerrado apresenta uma peculiaridade, que são os ambientes de vereda, uma importante fitofisionomia deste bioma estudadas nos **Capítulos 1 e 2** (Figuras 2 e 3). As veredas são formações vegetais hidrófilas, típicas das matas de galeria no Cerrado, e possuem como características rios com leitos bem definidos no período de seca seco, que se transformam em áreas pantanosas durante o verão chuvoso, condicionada, basicamente, por fatores físicos, como superfícies planas ou fundos planos alagados, associado a um camada superficial superposta acima de outra impermeável (Drummond et al. 2005; Moreira et al., 2011).

As veredas além de possuírem importância ecológica, também possuem importância socioeconômica para a comunidade local que explora comercialmente frutos e folhas do buriti (Mauritia flexuosa L.) e fazem a captação de água para abastecimento. M flexuosa é uma palmeira de folhas grandes que pode chegar a até 35 metros, nativa das regiões Central e Norte da América do Sul (Moreira et al., 2011). As veredas figuram também entre as áreas prioritárias para conservação do Cerrado (refúgios fauno-florísticos), pois representam um “berçário” para diversas espécies de peixes de importância econômica para a região e constituem fontes hídricas (nascentes), que alimentam os cursos d’água (Drummond et al. 2005; Moreira et al., 2011).

O local de estudo do **Capítulo 1 e 2** (Figuras 2 e 3) corresponde a veredas pertencentes a bacia do Rio Pandeiros, localizada nos Municípios de Januária, Bonito de Minas e Cônego Marinho, todos pertencentes ao estado de Minas Gerais. Estes municípios estão situados na região do Médio São Francisco, no lado esquerdo do Rio São Francisco da Microrregião de Januária e Macrorregião Norte de Minas. Bonito de Minas possui área de 3.911,42 km$^2$, altitude média de 600 metros, com uma população de 3.902 habitantes. Cônego Marinho possui área de 1.640,20

$km^2$, altitude média de 640 metros, com uma população de 6.279 habitantes. O município de Januária possui área de 6.670,41 $km^2$, altitude média de 455,59 metros, com uma população de 64.985 habitantes. Nestes municípios localiza-se a Área de Proteção Ambiental do Rio Pandeiros (APA-Pandeiros). Esta possui uma área de 380.000 ha., com as tipologias florestais predominantes de Cerrado, Floresta Estacional Decidual e Semi-decidual e Veredas.

O local de estudo do **Capítulo 3** (Figuras 4 e 5), corresponde a matas de galeria da Área de Proteção Ambiental (APA) Gama e Cabeça do Veado, pertencente ao Distrito Federal. A APA Gama e Cabeça do Veado foi criada pelo Decreto nº 9417 de 21 de abril de 1986 pelo Governo do Distrito Federal, tendo como um dos principais objetivos a proteção das cabeceiras dos cursos d'água que integram a bacia do Paranoá (Figura 4). Esta área possui cerca de 25.000 hectares compreendendo os mais diversos usos (urbano, rural, preservação e experimentação), com destaques para as áreas: Reserva Ecológica do IBGE (RESEC do IBGE); Estação Ecológica UnB (ESEC da Universidade de Brasília); Estação Ecológica do Jardim Botânico de Brasília (ESEC do Jardim Botânico), como as maiores áreas de preservação.

A ESEC da Universidade de Brasília é uma fazenda experimental e de ensino da Universidade de Brasília com 4.500 hectares, onde cerca de 1.200 hectares estão destinados à experimentos e produção agro-florestal, 2.340 hectares para preservação e o restante da área (cerca de 950 ha) mantidos em bom estado de conservação. A Reserva Ecológica do IBGE com 1.360 hectares é uma unidade de conservação permanente criada pela presidência do IBGE, em 1975 que inclui nascentes de importantes cursos d'água que formam a Bacia do Paranoá. A Estação Ecológica do Jardim Botânico de Brasília com 5.000 hectares tem como objetivo proteger as mais diversas fisionomias de Cerrado, bem como proteger as cabeceiras do Córrego Cabeça de Veado.

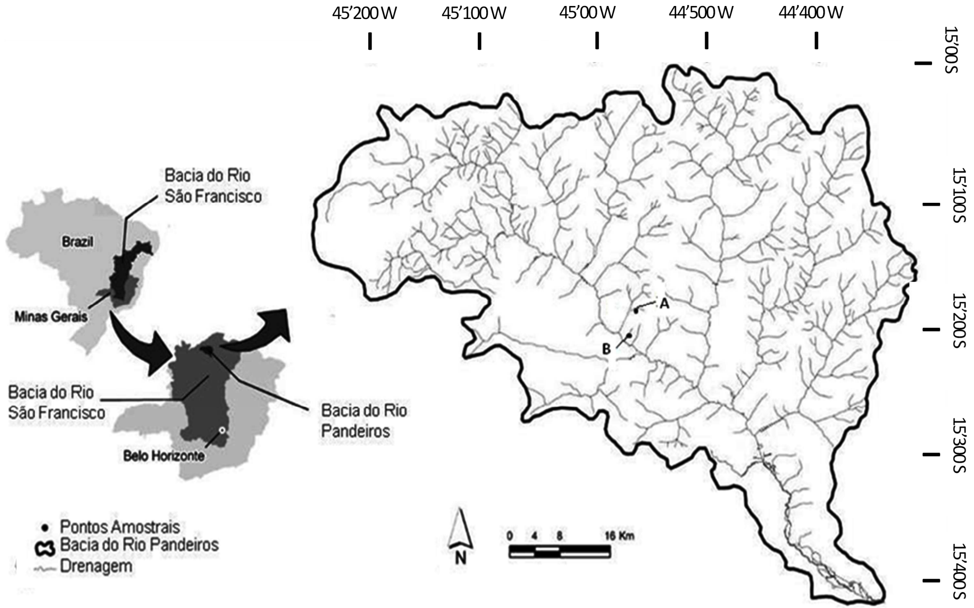


**Figura 2.** Pontos amostrais nas veredas utilizada no Capitulo 1 (A) e Capitulo 2 (B), localizadas na Bacia do Rio Pandeiros em relação ao Brasil e Estado de Minas Gerais.

**Figura 2**. Imagem dos pontos amostrais nas veredas utilizada no Capitulo 1 (A) e Capitulo 2 (B), localizadas na Bacia do Rio Pandeiros (Fotos: Renan Rezende).

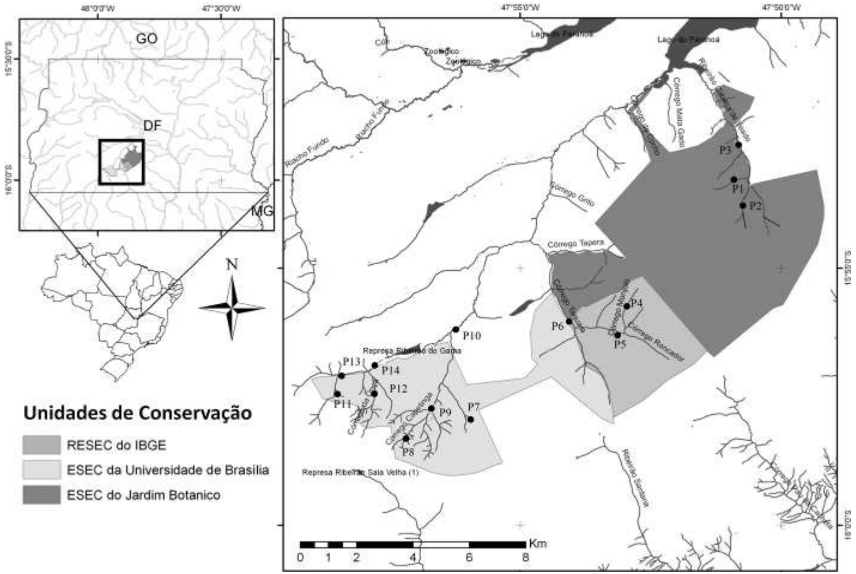


**Figura 4**: Pontos amostrais na drenagem da Bacia do Rio Gama e Cabeça de Veado e sua localização em relação ao Brasil e Distrito Federal. Os pontos amostrais estão distribuídos em 3 unidades de conservação, que são: Reserva Ecológica do IBGE (RESEC do IBGE); Estação Ecológica UnB (ESEC da Universidade de Brasília); Estação Ecológica do Jardim Botânico de Brasília (ESEC do Jardim Botânico)

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**Figura 5:** Fotos dos pontos de coleta na Bacia do Rio Gama e Cabeça de Veado - DF. (Fotos: Renan Rezende).

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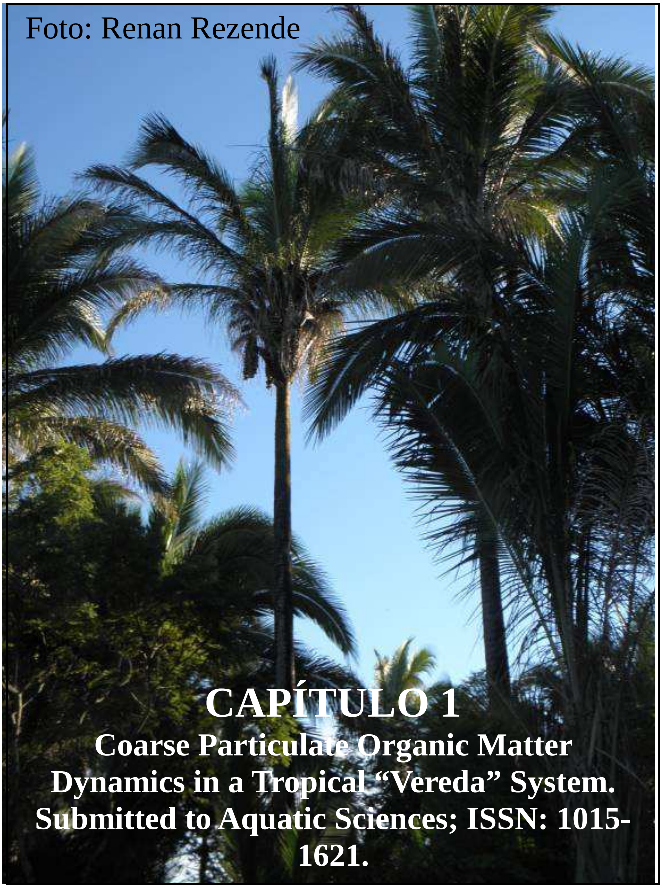

Foto: Renan Rezende

# CAPÍTULO 1

## Coarse Particulate Organic Matter Dynamics in a Tropical "Vereda" System.

Submitted to Aquatic Sciences; ISSN: 1015-1621.

# Coarse Particulate Organic Matter Dynamics in a Tropical "Vereda" System
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## ABSTRACT

We assessed litterfall, breakdown rate, density and biomass of invertebrates, and microbial biomass and sporulation of aquatic hyphomycetes during one year in a South American vereda / morichal stream. Litter production in the riparian area was low (365g $m^{-2}$ $year^{-1}$ falling on the forest soil and 181 g $m^{-2}$ $year^{-1}$ fallen directly into the stream), but litter breakdown was high when compared with other South American systems (k =0.033; range 0.013 – 0.084) with maximum values coinciding with the rainy season. Ergosterol content in decomposing leaves was high when compared with other South American studies (mean 549 µg $g^{-1}$; range 290 – 1,183), but spore densities in the water were low. Chironomids in the benthos accounted for ~ 70% of all invertebrates; nearly 10% of non Chironomidae invertebrates were shredders. Invertebrates were not abundant in litter bags (X specimens / g of litter) suggesting a low role in litter decomposition. Therefore, fungi are the drivers of litter decomposition in the "Vereda". Despite the low litterfall (productivity) and fast decomposition, organic matter accumulated in the stream bed (> 1 m thick of litter). This could be related to seasonal flood/dry dynamics allowing the transportation of terrestrial litter into the stream.

**Key words:** decomposition, breakdown, litter fall, microbial communities, sporulation, shredders.

## INTRODUCTION

Allochthonous organic matter, particularly leaf litter, is an important energy source for low order streams especially where canopy shade stream beds limiting primary production (Tank et al. 2010; Webster and Meyer

1997). Studies on the dynamics of allochthonous organic matter and leaf decomposition in streams are concentrated mainly in temperate deciduous forests (Abelho 2001; Webster and Meyer 1997) and, in a lesser extent in the tropical (but see Boulton et al. 2008; Wantzen et al. 2008). “Tropical stream” is a designation for water bodies running through very heterogeneous environments, including rainforests, mountains, savannas dry forests, and others (Boulton et al. 2008). Among those environments, grasslands or savanna occupy large areas of South America and are locally known as “Llanos”, “Pampas” and “Cerrados”, the later can have a larger number of trees.

In some grasslands groundwater outcrops along streams promote the formation of swampy gallery forests locally known as “veredas” in Portuguese and “morichales” in several Spanish speaking countries (Moreira et al. 2011; San-Jose et al. 2010). The veredas are characterized by *Mauritia* spp. palm trees (Moreira et al. 2011) and subject to seasonal inundations pulse (see also the flood pulse concept by Junk et al. 1989). Veredas are priority areas for the Cerrado conservation because they are biological refuges, nursery areas for many fish with economic local value and source of water for local populations (Drummond et al. 2005; Moreira et al. 2011; San-Jose et al. 2010). Veredas are also threatened by pollution and habitat modification for food production.

Given the high tree and shrub density of some veredas, it is likely that organic matter in these systems could be an important energy source for their streams. As far as we know, there is no baseline information about organic matter input and nutrient cycling / litter decomposition and therefore it is difficult to measure deviations from the reference conditions in these systems subjected to strong human pressure including agriculture, livestock production and wood harvesting (Boaventura 2007; Moreira et al. 2011).

We made four predictions regarding the organic matter dynamics in a vereda. Firstly, we predicted that because of elevated temperatures and non-limiting water availability, primary production in a veredas is high, resulting in large production of litter. We also predicted seasonality in litterfall, with peaks coinciding with the dry season (water stress) and with the onset of rainy season (by mechanically leaf removal). Because "tropical" streams have often been referred in the literature as poor in shredders (Abelho 2001; Gonçalves et al. 2007; Moulton et al. 2010; Wantzen and Wagner 2006) and poor in aquatic hyphomycetes (Schoenlein-Crusius and Grandi 2003), our third prediction is that shredders and aquatic hyphomycetes will not be abundant and, consequently, decomposition will be slow.

Finally, as physical abrasion is an important process in leaf breakdown (particularly when there is low microbial and shredder activity), then we predicted that decomposition would be faster during the rainy season. To address the above predictions we assessed litterfall, litter breakdown, density and biomass of invertebrates, and microbial biomass and sporulation of aquatic hyphomycetes of detritus during one year in a Southeastern Brazil vereda.

## MATERIALS AND METHODS

### Study Site

The study was carried out in the Pandeiros River basin, in Brazil, a sub-arid region with 900 – 1,200 mm rainfall and 24 °C mean temperature (Fig. 1). Litterfall was measured monthly from April 2009 to March 2010 along a 50-m-long strip in the vereda.

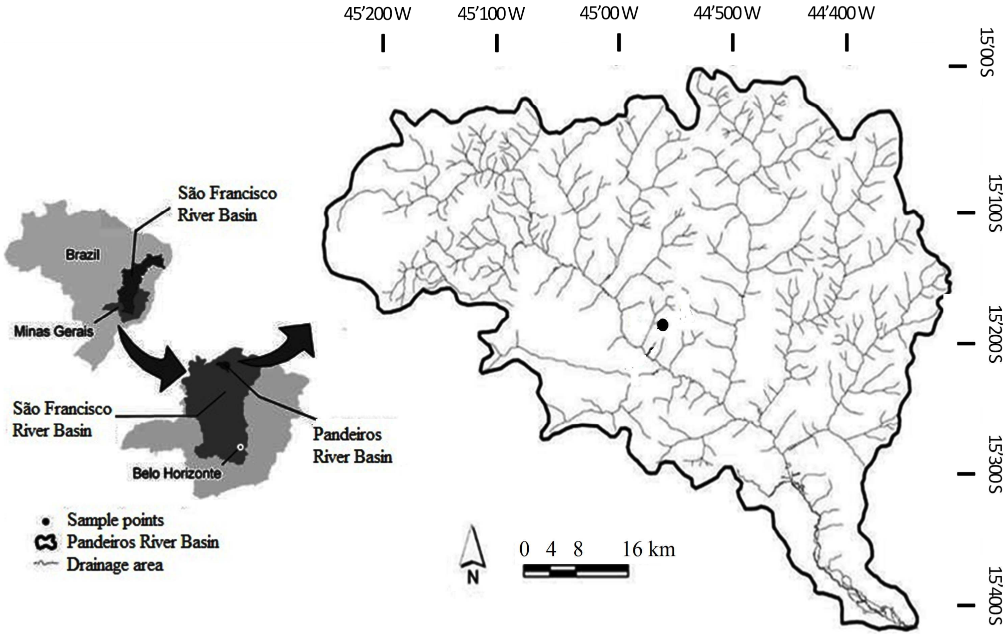

**Fig. 1** Sampling site in Pandeiros River Basin in Minas Gerais, Brazil.

## Physical and Chemical parameters of the stream waters

A multianalyzer (YSI Incorporated, model 85) was used to measure the *in situ* temperature, electrical conductivity, pH, and dissolved oxygen. Luminosity at the stream surface was continuously recorded with a datalogger (Onset, HOBO UA-002-08). We estimated water current velocity with a flow meter (Global Water; model Sigma Sports FP101) depth and width with measuring tapes. Water samples were collected (sterile vials) placed into ice boxes and transported to the laboratory to measure total alkalinity (Gram method; Carmouze 1994), nitrate (cadmium reduction method; detection limit: 0.05), ammonia (Nesslerization method; detection limit: 0.05) and orthophosphate (vanadomolybdophosphoric acid method; detection limit: 0.015; Bartram and Ballance 1996 ; Clesceri et al. 1989). The canopy openness was quantified using hemispherical photographs taken with a fisheye lens. Data of rainfall and air temperature were obtained from the meteorological station (number 83386), located 15º 26’ S, 44º22’ W, and 473.6 m altitude of National Agency of Waters of Brazil available on the website hidroweb (http://hidroweb.ana.gov.br/).

## Litterfall

The organic matter falling directly to the ground (terrestrial input - TI) was estimated using 6 nets (1 $m^2$, 1-mm mesh; 3 in each side of the stream; 10 m apart). Litter entering directly in the river (vertical input - VI) was measured using 30 buckets (0.53 $m^2$) suspended with ropes 2 m above the stream, transversely displayed in 5 rows, 6 buckets each, with 10 m between adjacent rows. The bucket bottoms were perforated for rain water evacuation. At monthly intervals the litter accumulated in the buckets was retrieved, weighed (wet weight) *in situ*, and the bucket with the highest (wet) leaf mass in each row was used for the leaf breakdown experiments (see below).

The contents of the remaining five buckets of each row were oven dried to constant mass (60 ºC, 72 h); the resulting weight was used to estimate the moisture of the litter used in the leaf breakdown experiment as a correction factor. The dry material was separated into categories leaves, branches), reproductive material (flowers and fruits) and “miscellaneous”. Leaves were identified according to the *Angiosperm Phylogeny Group* II system (APGII 2003).

### Leaf litter breakdown and aquatics invertebrates

Leaf breakdown is traditionally measured by immersing known amounts of monospecific litter in streams and samples recovered at time intervals to determine mass loss through time, frequently fitting the mass loss values in an exponential regression (mass over time; see Bärlocher 2005). This process demands frequent visits to the experimental site, which is not practical if seasonal variation is investigated in remote areas. Moreover, litter used in these experiments may not reflect the real quality of the litter reaching streams during the experiments. As an alternative, the material collected in five of the buckets above the stream was weighed (see above), and placed in 30 × 30 cm litter bags, 10 mm mesh size and submerged in the stream until the next sampling period (30 days). The amount of material placed in bags ranged from 1 to 3 g. After one month, litter samples were removed and replaced by new ones. After removal, litter bags were placed into boxes with ice and transported to the laboratory.

In the laboratory, litter remains were washed with distilled water over a 250-µm sieve. The retained invertebrates were fixed in 70% ethanol and later identified to the family level according to Pérez (1988); Merritt and Cummins (1996) and classified into five functional trophic groups (Pérez 1988; Merritt and Cummins 1996): gathering-collectors, filtering-collectors, shredders, scrapers, and predators.

Leaf discs (12-mm diameter) were removed from randomly selected leaves for ash-free dry mass (AFDM) calculations, ergosterol, ATP and sporulation (5 discs for each analysis; see below). The remaining litter was placed in aluminum trays and dried in an oven at 60°C for 72 h to determine the dry weight.

### Microbial biomass

The biomass of the fungi associated with the decomposing leaf litter was assessed by ergosterol content according to Gessner (2005). The lipid was extracted by boiling the samples in KOH/methanol, and the obtained extract was filtered. The ergosterol was then eluted in isopropanol and analyzed by high-performance liquid chromatography (HPLC). The total biomass of the decomposer microorganisms (aquatic hyphomycetes and others) was measured by quantifying the ATP in the leaves as described in Abelho (2005): leaf discs were homogenized (Polytron, 1 min, position 30) and the resulting material centrifuged (Eppendorf 5430R, 20 min, 4° C and 10,000 g), filtered (Sterile Millipore, 0.2 µm) at 10º C and the samples were placed in a reaction vessel (Eppendorf, 2 ml) with the Firelight enzyme (50 µm), and the bioluminescence (proportional to the ATP level) was measured in a luminometer (Luciferin-Luciferase reaction).

### Aquatic hyphomycetes

To assess the sporulation of the hyphomycetes in the decomposing litter, five discs from each litter bag were incubated separately in an orbital shaker (100 rpm) in Erlenmeyer flasks with 50 ml of filtered (Sterile Millipore 5mwp, 0.25 mm) river water at 25 º C in the laboratory. After 48 h, the suspension containing the spores was fixed with formaldehyde for counting and identification under the microscope according with Bärlocher (2005) and Gulis et al. (2005). In addition, to determine the richness and density of the hyphomycete spores in the water column, 5 L of water were filtered and stained with lactophenol cotton blue (0.1%) for later counting and identification under the microscope (400 X).

**Statistical Analysis**

Data normality was assessed with the Kolmogorov-Smirnov test, the homogeneity of variances was assessed with Levene's test, and values were Ln (+1) transformed if needed. For litter fall, differences between the terrestrial and vertical inputs were analyzed by repeated-measures ANOVA (RM-ANOVA). The RM-ANOVA can be used in nested sampling, as when repeated measurements are taken from the same individual (in our case, buckets and nets), or observational studies are conducted at several different spatial scales (mostly random effects), for more information see also the chapter 11 of Crawley (2007). Contrasts analysis was used to assess differences between the categorical variables (Crawley 2007). Leaf litter breakdown rates ("k") at monthly intervals were obtained assuming a negative exponential model of percent mass loss during the 30 days of incubation ($W_t=W_0e^{-kt}$; Wt=remaining weight; $W_0$=initial weight; -k=decay rate; t=time). RM-ANOVAs and contrasts analyses were used to test for significant differences between months (categorical variables) in the remaining mass, invertebrate and shredders abundances, microbial (ATP) and fungal biomass (ergosterol), sporulation rates and spore densities in the water. The association between some variables was assessed with Spearman's correlation (Crawley 2007).

## RESULTS

### Physical and Chemical Parameters of Stream Waters

Precipitation during the studied period was low (92.2 ±25.0 mm, mean ± SE; Fig. 2) with peaks in October to April. The average stream flow was 0.4 (±0.1) $m^3$/s and water temperature ranged from 21 to 28 ºC (mean 24.4 ±0.4 ºC). Stream water was circumneutral (pH = 7.3 ±0.1), with low levels of oxygen (4.4 ±0.3 mg/l), electrical conductivity (19.5 ±2.2 µS/cm), alkalinity (49.8 ±4.3 mEq/l), ammonia (<0.05 mg/l), nitrate (0.1 mg/l) and orthophosphate (<0.015 mg/l; Table 1).

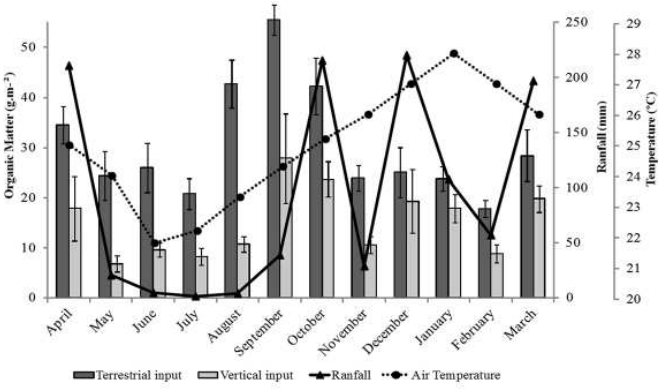

**Fig. 2** Litterfall in the riparian area (dark gray), and in direct inputs in the river (light gray) and rainfall (black triangle) and air temperature (black square), over time (Mean and standard error).

**Table 1** Flow ($m^3$.s), pH, dissolved oxygen (mg.$L^{-1}$), electrical conductivity (condut., µS.$cm^{-1}$), water temperature (T. water in ºC), alkalinity (Alkal., mEq.$L^{-1}$), ammonia, nitrate and orthophosphate (OrthoP) concentrations (mg.$L^{-1}$) in the stream water and total rainfall (Precipitation.mm), air temperature (T. air in ºC) and luminosity (lux) from April to March in the vereda. No average was calculated when values were below the detection limit. NA = not applied

| | April | May | June | July | August | September | October | November | December | January | February | March | Mean | Std. Error |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Flow | 0.37 | 0.35 | 0.19 | 0.15 | 0.15 | 0.15 | 0.25 | 0.25 | 0.42 | 0.88 | 0.98 | 0.59 | 0.39 | 0.08 |
| pH | 7.7 | 7.1 | 7.1 | 7.6 | 7.2 | 7.1 | 6.7 | 6.7 | 7.6 | 7.9 | 7.2 | 7.6 | 7.3 | 0.1 |
| Oxygen | 6.8 | 4.8 | 3.8 | 3.0 | 3.2 | 5.5 | 4.2 | 5.3 | 4.5 | 4.1 | 3.7 | 4.4 | 4.4 | 0.3 |
| Condut. | 13.7 | 22.3 | 26.7 | 22.71 | 15.7 | 25.0 | 25.5 | 28.0 | 15.9 | 22.1 | 15.0 | 1.4 | 19.5 | 2.2 |
| T. water | 25.1 | 21.9 | 25.1 | 24.5 | 24.2 | 22.5 | 22.8 | 24.7 | 25.9 | 25.2 | 26.2 | 25.4 | 24.4 | 0.4 |
| Alkal. | 69.12 | 36.51 | 37.72 | 37.54 | 38.62 | 54.12 | 33.01 | 60.82 | 41.41 | 47.33 | 78.43 | 63.11 | 49.79 | 4.32 |
| Ammonia | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | <0.05 | 0.12 | <0.05 | <0.05 | <0.05 | <0.05 | NA |
| Nitrate | 0.1 | 0. 1 | 0. 1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.0 |
| OrthoP. | <0.015 | <0.015 | <0.015 | <0.015 | <0.015 | 0.016 | <0.015 | <0.015 | 0.016 | <0.015 | <0.015 | <0.015 | <0.015 | NA |
| Precipitation | 210.9 | 20.5 | 4.6 | 1.5 | 4.0 | 38.8 | 215.5 | 28.8 | 220.3 | 107.7 | 57.0 | 197.0 | 92.2 | 26.7 |
| T. air | 25.1 | 24.2 | 21.8 | 22.2 | 23.3 | 24.3 | 25.2 | 26.1 | 27.2 | 28.2 | 27.1 | 26.1 | 24.9 | 0.5 |
| Luminosity | 11.6 | 19.6 | 86.1 | 42.3 | 23.6 | 19.6 | 11.7 | 10.0 | 9.0 | 8.0 | 9.0 | 10.0 | 21.7 | 6.7 |

## Organic Matter Inputs

Annual organic matter input (Terrestrial input-TI) in the riparian area was two-fold higher (365 g $m^{-2}$ $year^{-1}$, or 31 g $m^{-2}$ $month^{-1}$), than over the stream bed (Vertical input-VI; 181 g $m^{-2}$ $year^{-1}$, or 15 g $m^{-2}$ $month^{-1}$; $F_{(1, 430)} = 34.2$, $p < 0.001$; Fig. 2). Litterfall was seasonal - bimodal with two input peaks, one in March - April and a second (larger) in September and October ($F_{(11, 347)} = 3.2$, $p < 0.001$); minimum values were recorded between May and August. Litter inputs were correlated with rainfall ($r = 0.67$, $p = 0.01$) i.e. maximum litterfall coincided with rainy events, but not with maximum air temperature ($r = 0.33$, $p = 0.31$).

Overall, the major components of TI and VI were virtually identical and composed mainly by leaves (68% TI, 63% VI) followed by branches (20% TI, 15% VI), miscellaneous (8% TI, 15% VI) and reproductive material (4% TI, 7% VI; Table A1 and Fig. A1A and A1B). Among the plant species, an unidentified liana (Indeterminate sp. 2) was the largest contributor to leaf litter fall (especially between August and October), followed *Cecropia pachystachya* Trécul (August to October), *Zygia latifolia* (L.) Fawc. and Rendle (October, December, and January) and a minor contribution by a second unidentified liana species (Indeterminate sp. 1), *Croton urucurana* Baill., *Mauritia flexuosa* L.f., *Simarouba versicolor* A.St.-Hil., *Styrax camporum* Pohl and *Xylopia emarginata* Mart. in both compartments (Fig. A2).

## Leaf Breakdown Rates

Overall leaf litter lost on average 53% of its mass (range: 33-86%) in one month; that corresponds to a mean k value of 0.033 (0.013-0.084 range). Litter breakdown was seasonal ($F_{(1,50)} = 7.4$, $p = 0.02$), with maximum values in April, September and December (rainy season; $r = 0.44$, $p = 0.01$) and minimum in May to August (dry season; Fig. 2 and 3). Highest leaf litter breakdown rates were also correlated with *C. urucurana* (r = 0.72, p = 0.01) and *M. flexuosa* (r = 0.59, p = 0.04) were more abundant in the litter.

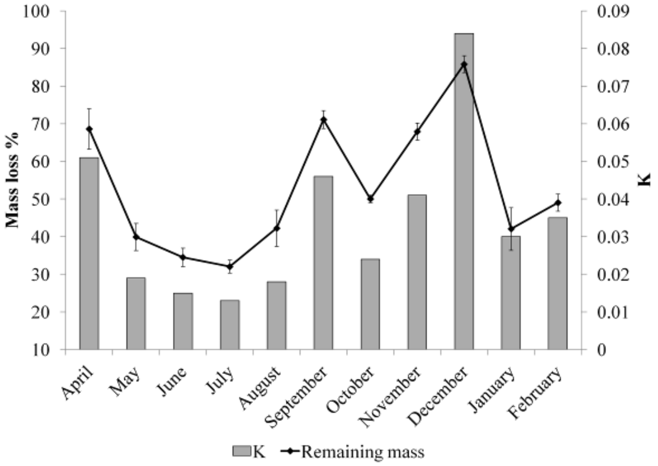

**Fig. 3** Remaining mass (black line - %) and decomposition rates (gray bars - k) along one year (means and standard error).

## Microbial Assemblages

The mean (± SE) ATP was 456 ± 57 nmoles $g^{-1}$ AFDM, with a maximum of 1327 nmoles $g^{-1}$ in February and a minimum of 17 nmoles $g^{-1}$ in December. The difference was significant ($F_{(1,50)}$ = 49.15, $p < 0.01$) across months (Fig. 4A). The ergosterol mean (±SE) content in leaves was 549 ± 88 µg $g^{-1}$ AFDM, with a maximum of 1183.3 µg $g^{-1}$ in August and a minimum of 289.8 µg $g^{-1}$ in April (Fig. 4B) but no differences across months ($F_{(1,50)}$ = 0.23, p = 0.64). Ergosterol and ATP concentrations were positively correlated throughout the year (r = 0.56, p = 0.01). The lowest Ergosterol (r = -0. 51, p = 0.01) and ATP

($r = -0.34$, $p = 0.01$) values were obtained during high flow.

Sporulation rates were highly variable with no apparent relationship with other variables. Maximum sporulation rates in leaf litter reached 6.42 (spores/mg AFDM) in June, but zero spore production was found in January, February, July and December (Fig. 4C) and no differences were observed across months ($F_{(1,50)} = 0.01$, $p = 0.92$; mean 1.48 spores/mg$^{-1}$ AFDM). In the same way, spore richness in the water was very low (mean of 2 fungal species, range of 0 to 6 spores mg$^{-1}$ AFDM) with no monthly variations ($F_{(1,50)} = 1.02$, $p = 0.43$). The spores in the water included *Anguillospora filiformis*, *Anguillospora longíssima*, *Anguillospora furtive*, *Lunullospora curvula*, *Lemoniera pseudofoscula*, *Tricelophorus acuminatus*, and *Ypsilina gramínea*.

### Aquatic invertebrates

The number of invertebrates colonizing leaves ranged from 197 (July) to 12 individuals g$^{-1}$ AFDM (February), with an average of 84 individuals g$^{-1}$ AFDM and no differences across months ($F_{(1,50)} < 0.7$, $p > 0.41$; Fig. 4D; Fig. A3). Neither total invertebrate nor shredder densities were correlated with mass loss ($r < -0.08$, $p > 0.54$). The most abundant *taxon* in leaves was the Chironomidae (Diptera), with 68% of total individuals (mean of 58 individuals g$^{-1}$ AFDM). Nearly 10% of non Chironomidae invertebrates were shredders and the most important *taxon* being the Odontoceridae (Trichoptera; Fig. 4E; Fig. A4).

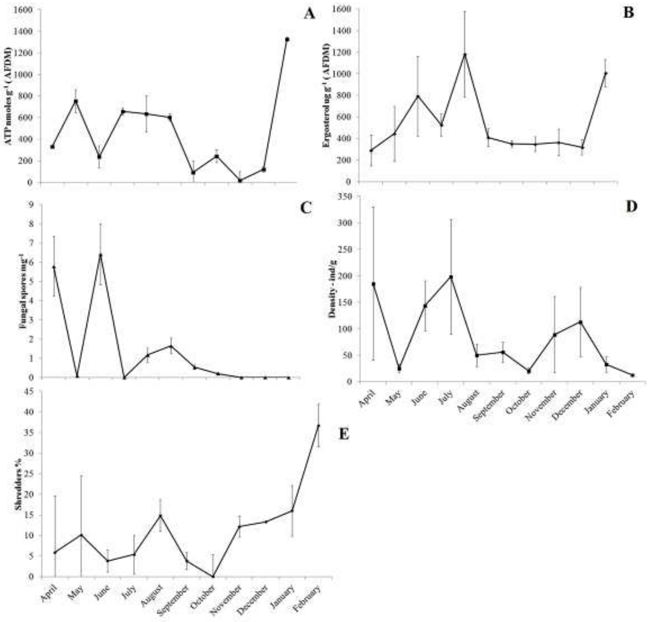

**Fig. 4** Total microbial biomass (ATP nmoles /g AFDM; A), fungal biomass (ergosterol µg / g AFDM; B), fungal spores (numbers / mg AFDM; C), invertebrates density (ind/g, D) and percentage of shredders (E) in leaves after one month in stream water (means and standard error).

# DISCUSSION

## Organic Matter Dynamics

Our first prediction that litter production would be high in the vereda was not supported. Our estimation of direct litter input to the stream of 365 g $m^{-2}$ $year^{-1}$, was in the lower range of the reported values for other tropical forests (113 – 1445 $g.m^{-2}$ $year^{-1}$; reviewed by Abelho 2001), but close to the 288 – 336 g $m^{-2}$ $year^{-1}$ reported for other Cerrado streams (França et al. 2009; Gonçalves et al. 2006a; Gonçalves and Callisto 2013). The real value of organic matter available for decomposers could be even lower since the direct input into the rivers was nearly half of the input measured as litterfall in the riparian area, a tendency also observed in other studies in the Cerrado (e.g. França et al. 2009; Gonçalves and Callisto 2013) and in the Atlantic rain forest (697 in VI – 856 in TI g $m^{-2}$ $year^{-1}$ by Gonçalves et al. 2014).

However, the material falling in the riparian area can potentially be accessed by aquatic decomposers. The veredas are subject to seasonal inundations pulse as described by Junk et al. (1989) for flood pulse concept in aquatic/terrestrial transition zone (ATTZ), and high waters can take litter from the stream into the banks, but the reverse can also be true. It is therefore not clear how the availability of litter inputs to the aquatic system can be related with flood-dry seasonal dynamics. Since during high waters litter in the riparian zone is submerged, we propose a mean value of direct and riparian zones inputs, which in our case would be 273 g $m^{-2}$ $year^{-1}$. This low litter productivity can be the result of Cerrado nutrient-poor soils (Drummond et al. 2005; Moreira et al. 2011) and the stress imposed by the flood and dry cycles.

Litterfall was markedly seasonal as reported for other tropical systems (e.g. Abelho 2001; Wantzen et al. 2008; Zhang et al. 2014) corroborating our second prediction. It was more intense at the end dry season and the start of the rainy season (August, September, and October) suggesting that two types of leaves may be arriving in the streams: (1) senescent leaves in the dry season and (2) green leaves mechanically removed by the rain. If this is the case, leaf litter stock may be composed by leaves of contrasting quality, resulting in seasonal differences in decomposition rates.

Litterfall seasonality was driven mainly by the input of the four dominant species in the litter: *Cecropia pachystachya* and *Zygia latifolia* and the two lianas. This contrasts with less species richness and evenness when compared as other tropical streams (França et al. 2009; Gonçalves and Callisto 2013; Gonçalves et al. 2006a).

### Leaf Breakdown Rates

Litter breakdown rates in this study (k~0.033) were faster according to the classification of Webster and Benfield (1986) and the model proposed by Gonçalves et al. (2013; k > 0.017) for tropical systems. It was also faster than values reported for Cerrado streams (0.0001 – 0.015 in Gonçalves et al. 2007; Gonçalves et al. 2012a; Gonçalves et al. 2006b; Moretti et al. 2007b). These results do not support our third prediction, although comparisons should be done with caution since in the literature most values are obtained for leaves of single species. Our study has used the mixture of available leaves in each season, which more closely represents natural conditions.

Biologically-driven leaf breakdown could be aided by physical abrasion since higher rates of breakdown occurred in the rainy period which is when the current increased and physical fragmentation is expected to be more intense (Rueda-Delgado et al. 2006; Santos Fonseca et al. 2012), supporting our fourth prediction. Additionally, high waters may carry nutrients from the riparian zone (Naiman and Décamps 1997), which even at low levels, they could stimulate microbial activity. Indeed, decomposition seems to increase rapidly with nutrient concentration in a Michaelis–Menten type relationship (Ferreira et al. 2006) suggesting that at low ranges of decomposition, small increases in nutrients can have a very important stimulatory effect on decomposition (Rosa et al. 2013; Woodward et al. 2012). It is also possible that leaves falling during the rainy season could be of better quality than the senescent leaves of the dry season, due to the reduction of water stress and increased nutrient availability (higher decomposition). These results are different to those found by Ferreira et al. (2014), who in their meta-analysis suggests that the effect of nutrient enrichment might be strongest in cold oligotrophic streams that depend on low-quality plant litter inputs.

Litter breakdown is influenced by litter traits (Gonçalves et al. 2012b; Meentemeyer 1978; Rueda-Delgado et al. 2006); it is therefore expectable that, besides physical abrasion and fungal activity, seasonal variation in litter breakdown could reflect changes in the dominance of species in the litter. Indeed, faster decomposition rates were observed when litter from *Croton urucurana* and *Mauritia flexuosa* were more abundant. It would be interesting to investigate the quality of leaves of the dominant species to determine whether seasonal differences in litter decomposition are controlled by the leaf quality.

## Biological assemblages

Fungal biomass in decomposing litter in the vereda (549 ±88 µg ergosterol $g^{-1}$ AFDM ±SE) was higher than the values reported for other South American savanna streams (50 – 420 µg $g^{-1}$ range for Gonçalves et al. 2007; Gonçalves et al. 2006c), forest tropical streams (4 – 180 µg $g^{-1}$ range for Capps et al. 2011; Foucreau et al. 2013; MacKenzie et al. 2013), and in the range of temperate streams (200 – 1200 µg $g^{-1}$ range for Danger et al. 2013; Feio et al. 2010; Lecerf et al. 2007). This suggests that fungi are important decomposers in veredas in contrast with other South American studies. This importance was reinforced by the significant correlation between ergosterol and ATP. We also observed ATP values were high compared to most temperate streams systems (0.13 – 200 nmoles $g^{-1}$ range for review of Abelho 2001) and similar to other tropical streams (100 – 750 nmoles $g^{-1}$ range for Abelho et al. 2005; Gonçalves et al. 2007; Gonçalves et al. 2006c).

The high fungal biomass (especially in January and August) does not support our third prediction of low fungal biomass, but contrasted with the low and irregular sporulation rates in detritus and spore richness in the water with zero spores in some months. It is possible that sporulation rates are naturally low in these systems or we may be losing key undescribed spores, highlighting the need for further research in this system. It is also possible that low sporulation rates were a methodological artifact since intense sporulation frequently occurs in less than one month after the leaves fall in the water (Ferreira et al. 2012). If this is also the case in the vereda, we missed the important reproductive period. The most abundant spores in the sporulation experiments in all periods were from cf. *A. filiformis*, cf. *A. longissima*, and *L. curvula* which are normally associated with warm waters (Chauvet and Suberkropp 1998). Low diversity of spores were also reported by Sridhar and Sudheep (2010) in southwest India and Ferreira et al. (2012; k range of 0.001 – 0.034) in Ecuadorian Amazon forest.

Invertebrates are crucial to litter decomposition in most temperate streams (Abelho 2001; Gessner et al. 1999), but, in many tropical streams, they are less important (Boyero et al. 2012; Moulton et al. 2010). In the vereda, we also found a yearly mean lower (84 individuals $g^{-1}$) than the referred for other savanna streams (2 – 780 individuals $g^{-1}$ range for Gonçalves et al. 2012a; Gonçalves et al. 2012b; Ligeiro et al. 2010; Moretti et al. 2007b), with the highest values in the dry season (June and July). Chironomids were dominant as in many others tropical streams (Gonçalves et al. 2012a; Moretti et al. 2007a; Wantzen and Wagner 2006). The proportion of shredders (10%) was similar than other Cerrado streams (0 – 11% range for Gonçalves et al. 2007; Gonçalves et al. 2006c; Moretti et al. 2007b), supports our prediction, that shredders are not abundant and important in litter breakdown.

## Conclusion: Litter Dynamics in Veredas

Besides the low productivity of the vereda, and the high litter breakdown rates, organic matter accumulation is high in these systems. The entire riparian area and stream bed was composed by > 1 m think pure organic substrate. This can only happen if litter retention is high in relation to litter decomposition at the (or below) the stream bed. A raise in litter productivity can be expected if seasonal flood/dry dynamics allows terrestrial input being transported to the permanently wet channel. This subject needs further investigation. The drivers of litter decomposition in the "Vereda" seem to be fungi, but their identity and reproductive biology still needs to be investigated. As in many other tropical systems invertebrates had little importance to litter decomposition

## ACKNOWLEDGMENTS

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## APPENDICES

**Table A1** Analysis of variance (RM-ANOVA) and contrast (AC) for leaves, branches, reproductive and miscellaneous material, collected from the terrestrial (TI) and stream vertical (AV) inputs over one year. F values, degrees of freedom and significance P

| Material | Type of input | RM-ANOVA | AC |
|---|---|---|---|
| Leaves | TI | $F_{(11, 59)} = 10.2, p < 0.001$ | August, September and October |
| | VI | $F_{(11, 347)} = 3.2, p < 0.001$ | September and October |
| Branches | TI | $F_{(11, 59)} = 0.9, p = 0.50$ | |
| | VI | $F_{(11, 347)} = 3.5, p < 0.001$ | December and January |
| Reproductive Material | TI | $F_{(11, 59)} = 0.7, p = 0.68$ | |
| | VI | $F_{(11, 347)} = 0.9, p = 0.46$ | |
| Miscellaneous Material | TI | $F_{(11, 59)} = 2.2, p = 0.02$ | April and March |
| | VI | $F_{(11, 347)} = 2.9, p < 0.001$ | January |

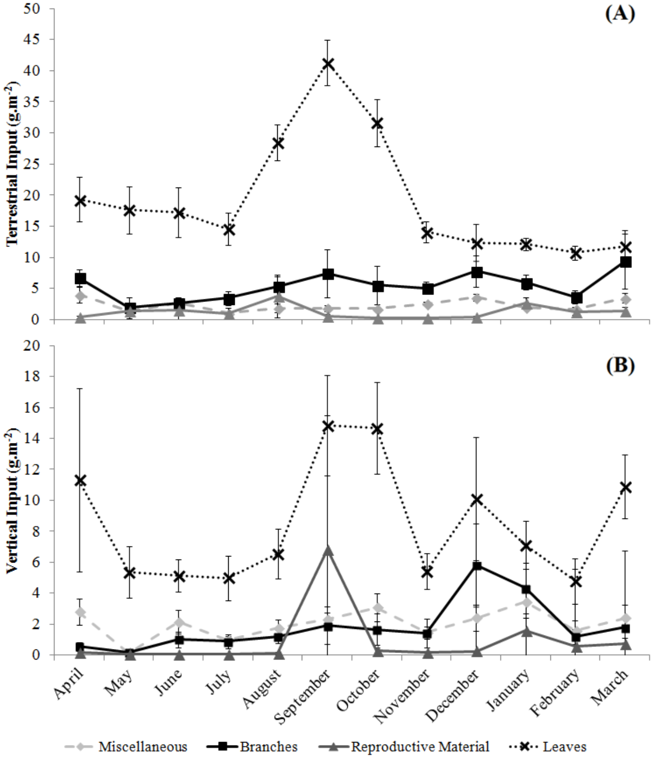

**Fig. A1** Organic matter inputs from the riparian zone to the forest soil (terrestrial input) and directly into the stream (vertical input). Means and standard errors. Leaves, branches, miscellaneous and reproductive material.

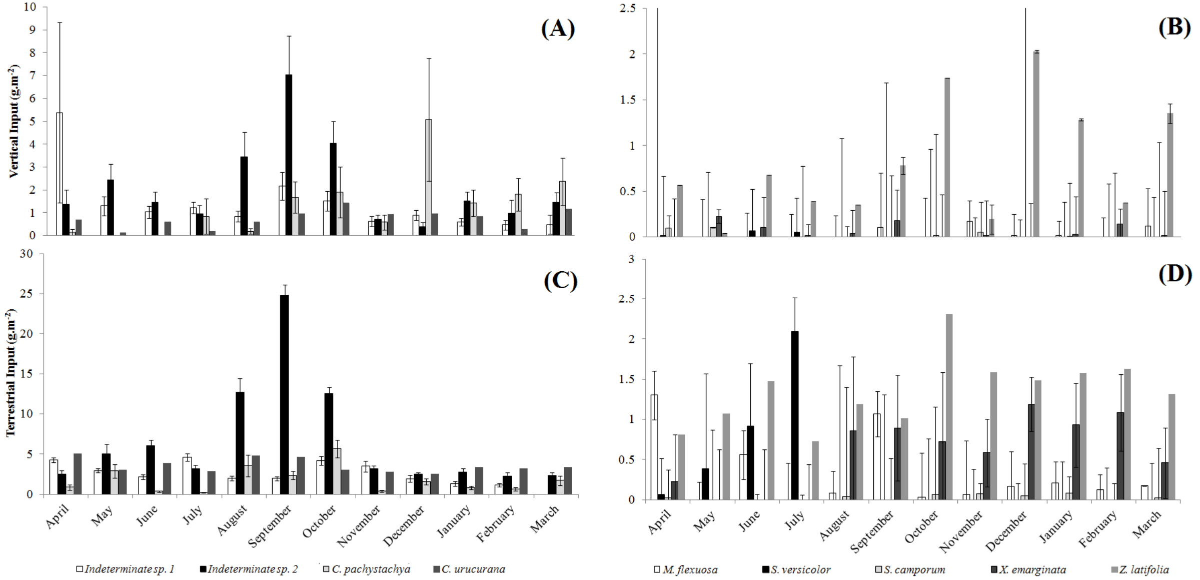

**Fig. A2** Larger (A and C) and smaller (B and D) contributions of species of plants to the leaf litter input to the forest soil (top) and directly to the river (below). Mean and standard error.

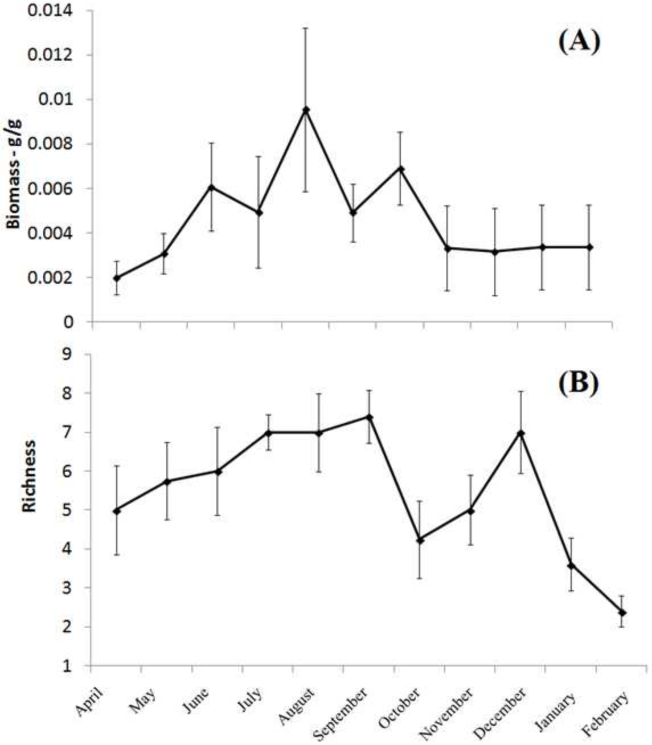

**Fig. A3** Invertebrates biomass (g/g$^{-1}$; A) and richness (B) in decomposing leaves incubated in the stream bed for one year (means and standard error).

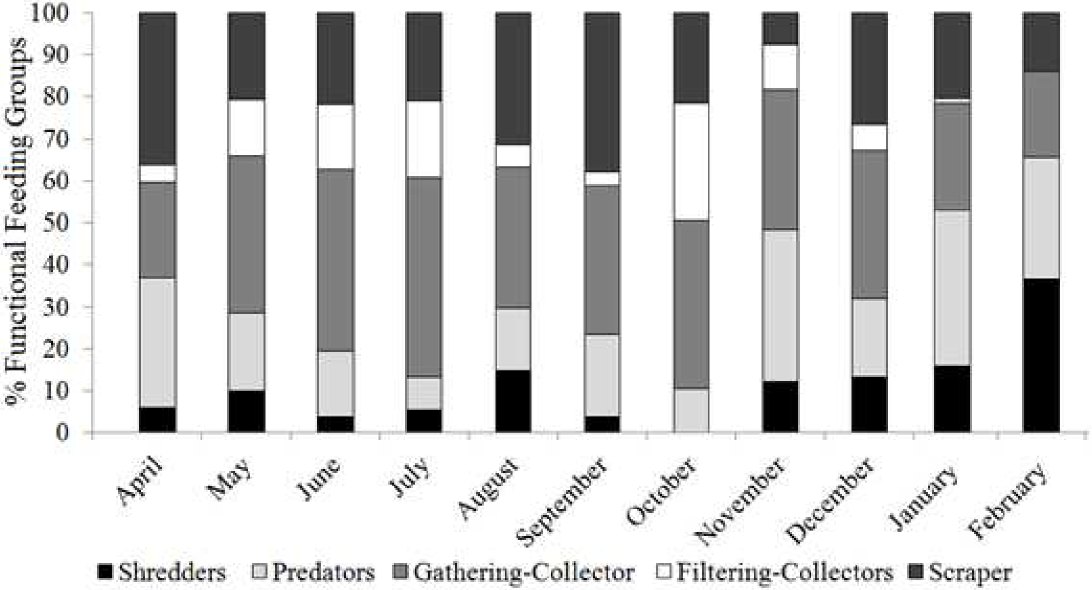

**Fig. A4** Percentage of relative abundance of the functional feeding groups of the aquatic invertebrates that colonized the leaf litter over one year.

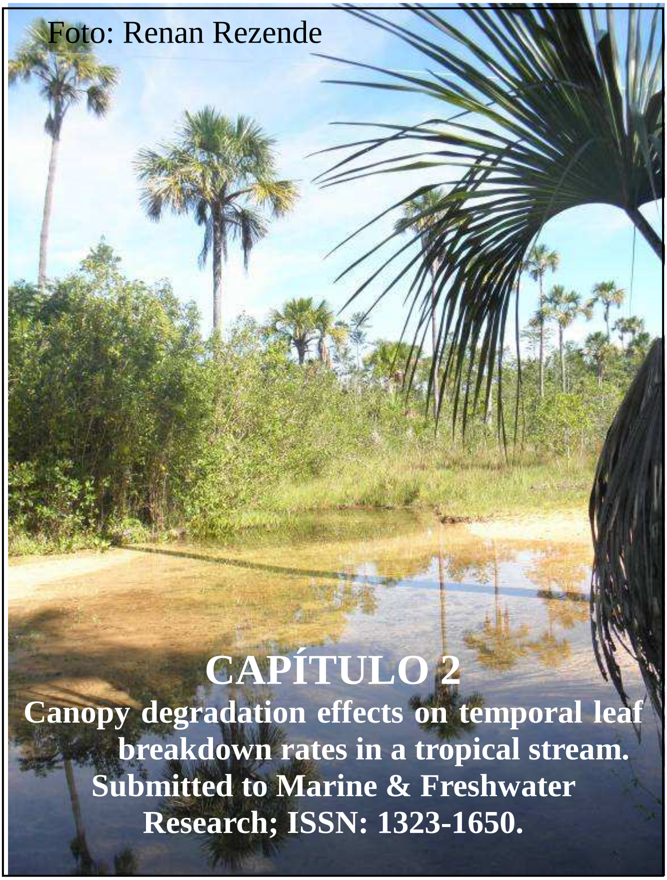

Foto: Renan Rezende

# CAPÍTULO 2

## Canopy degradation effects on temporal leaf breakdown rates in a tropical stream.

Submitted to Marine & Freshwater Research; ISSN: 1323-1650.

# Canopy degradation effects on temporal leaf breakdown rates in a tropical stream.

**Submitted to Marine & Freshwater Research; ISSN: 1323-1650.**

## ABSTRACT:

Our objectives were to describe the temporal dynamics of leaf breakdown rates (*k*) and to identify possible indicators (physical, chemical and biological characteristics) from a stream with a degraded riparian canopy. The vertical input of leaves was collected monthly in a natural stream and incubated in a stream with a degraded canopy. In each month, the samples were collected, and other new samples were incubated. The *k*, microbial biomass (ergosterol and ATP), fungal sporulation and invertebrate community characteristics (biomass density, richness and trophic functional groups) were estimated in the detritus leaves. Higher values of *k* were observed in rainy season, most likely due to high temperatures (increasing metabolic activity) and rainfall (higher physical abrasion). However, we found higher microbial biomass (increase of photosynthetic organisms) and greater densities and richness of invertebrates (lower washing power by water) in dry season. Therefore, on the large temporal sampling, water flow, temperature and precipitation were the factors controlling the *k* in this stream system. The canopy degradation modify the *k* and can change the metabolism of the ecosystem (from heterotrophic to autotrophic), despite the great ecological resistance of “veredas”. The canopy degradation left the system higher susceptible to seasonal changes. This environmental impact modified also the communities of micro-organisms and invertebrates indicate that this process is useful as bioindicators.

**Keywords:** Precipitation Effects; Veredas; decomposition community.

# INTRODUCTION

Energy flow and organic-matter cycling in aquatic environments are fundamental for the maintenance of the system's metabolism and, therefore, for the structuring of the local communities (Fisher and Likens 1972; Tank et al. 2010), especially in shaded patches, where the primary production is limited by the low-light conditions (Gessner et al. 1999; Graça 2001). The quantity, quality, processing and retention of allochthonous organic matter in streams are associated mostly with climatic factors, being strongly directed by seasonal and physiological changes in the vegetation (plant phenology; Gonçalves et al. 2006a; Li and Dudgeon 2011). Decomposition is a key process in the remobilization of this organic detritus into the trophic chain because decomposition makes available the nutrients and energy retained in the dead organic matter (Abelho 2001; Petersen and Cummins 1974). According to Gessner et al. (1999), decomposition is biologically driven by the microorganism (fungi and bacteria) and invertebrate (mostly the shredders) communities in a sequence of events named leaching, conditioning and fragmentation. However, we have no found information about this process in "veredas" systems that are common in the Brazilian Savannah.

The "veredas" are hydrophilous vegetation formations typical of the gallery forests in the Cerrado biome and are characterized by rivers with well-defined river beds during the dry season that transform into wetland areas during the rainy season (Moreira et al. 2011). The "veredas" are conditioned essentially by physical factors, such as flat surfaces or inundated bottoms associated with a surface layer above a second, impermeable layer (Drummond et al. 2005). In addition to their ecological importance, "veredas" are socioeconomically important for the local communities, which sell the fruits and leaves of the Buriti palm (*Mauritia flexuosa* L.) and also use the systems for water supply. The “veredas” are among the priority areas for the conservation of the Cerrado (faunal and floral refuges) because they act as nursery areas for many fish species (e.g., *Hoplias malabaricus* and *Lophiosilurus alexandri*) of economic importance in the region and serve as water sources (springs) that feed the watercourses (Drummond et al. 2005; Moreira et al. 2011). Modifications of the structure and composition of vegetation by commercial exploitation (a standard regional practice; Rezende et al. 2012) may alter the organic matter cycling, which may lead to variations in the energy flow and threaten the availability of all these environmental services and, consequently, the system’s function.

Riparian vegetation provides services such as filtering the surface runoff, controlling the precipitation input and soil erosion through tree canopies that block the rain, increasing the water-storage capacity and maintaining the heat balance, thus maintaining the system integrity (Lima and Zakia 2001; Moreira et al. 2011). Clearcutting to stream edges changes streambed morphology, alters the physical and chemical characteristics of the water, increases sunlight exposure (affecting temperature and biological activity) and decreases vegetation litter (quantity and quality) inputs (Lecerf and Richardson 2010). Therefore, riparian vegetation can protect stream ecosystems against catastrophic events (natural and/or anthropic) that are under the control of terrestrial ecosystems (Lecerf and Richardson 2010). This buffering includes protection against abrupt temporal/annual changes in water flux and, consequently, in ecological processes (e.g., leaf breakdown) and ecosystem functioning due to seasonal dynamics (Benda et al. 2004; Silva-Junior and Moulton 2011). This relation shows that ecological processes, such as leaf breakdown, can be used to detect environmental changes due to anthropic impacts (Pascoal et al. 2001).

The use of leaf breakdown to detect anthropogenic environmental changes was developed mainly in the last decade (Gessner and Chauvet 2002; Tank et al. 2010). However, few studies have been conducted in tropical streams (Silva-Junior and Moulton 2011; Silva-Junior et al. 2014). The data available in the literature concerning the effects of anthropic impacts (e.g., pollution) on leaf breakdown are contradictory (Pascoal et al. 2001). Leaf breakdown is faster with higher nutrient levels, but when this enrichment is accompanied by another pollutant, we can observe a negative effect and slower breakdown (Gessner and Chauvet 2002; Pascoal et al. 2001; Silva-Junior and Moulton 2011). The possible losses of environmental functions and services due to the degradation of ecological processes in tropical regions are among the 100 fundamental ecological questions to answer, according to Sutherland et al. (2013).

If environmental and temporal/annual changes (due to anthropic and/or natural factors) occurring in riparian systems modify the leaf breakdown rates, our hypothesis is that: i) greater canopy openness will increase the leaf breakdown rates in the rainy season due to higher physical fragmentation (by rain) and microbial activity (due to higher temperatures); and ii) canopy degradation increases the range of variation in the leaf breakdown process throughout the year due to the loss of the protective function of the canopy. Our objectives were: i) to describe the temporal dynamics (over one year) of leaf breakdown rates in a degraded “veredas” canopy (based on changes in autotrophic metabolism due to the low contribution of allochthonous organic matter); ii) to characterize the physical, chemical and biological changes in the leaf breakdown process throughout the year; and iii) to identify possible environmental indicators of riparian degradation in the leaf breakdown process. We address the following questions: i) What are the peaks and most important variables (abiotic and/or biotic) for leaf breakdown rates throughout the year? ii) How does canopy degradation affect stream functioning and the leaf breakdown process? The research forms part of a larger study of “veredas” and an evaluation of streams in the Pandeiros Basin, Minas Gerais/Brazil.

## MATERIALS AND METHODS

### Study Site

The study was conducted in the Pandeiros River basin, located in Minas Gerais State, southeastern Brazil. This basin has the forest types of Cerrado, deciduous seasonal forest, semi-deciduous forest and “vereda” within a sub-arid climate. The average rainfall varies from 900 to 1,200 mm, with temperatures between 21°C and 24°C. The “vereda” used in this study was impacted by the removal of native vegetation, plant-extraction activities (*M. flexuosa*) and water withdrawal for human consumption (Fig. 1). The leaf detritus (vertical input) was collected monthly by bucket in a preserved “vereda” and transplanted to incubate in a “vereda” with an impacted canopy. The riparian zone of the preserved “vereda” contained plant individuals belonging to the following groups: Indeterminate sp. 1 (Liana group), Indeterminate sp. 2 (Liana group), *Cecropia pachystachya Trécul*, *Croton urucurana Baill.*, *Mauritia flexuosa* L.f., *Simarouba versicolor* A.St.-Hil., *Styrax camporum* Pohl, *Xylopia emarginata* Mart. and *Zygia latifolia* (L.) Fawc. and Rendle. The collected material was used to identify plant families according to the *Angiosperm Phylogeny Group* II system (APGII 2003).

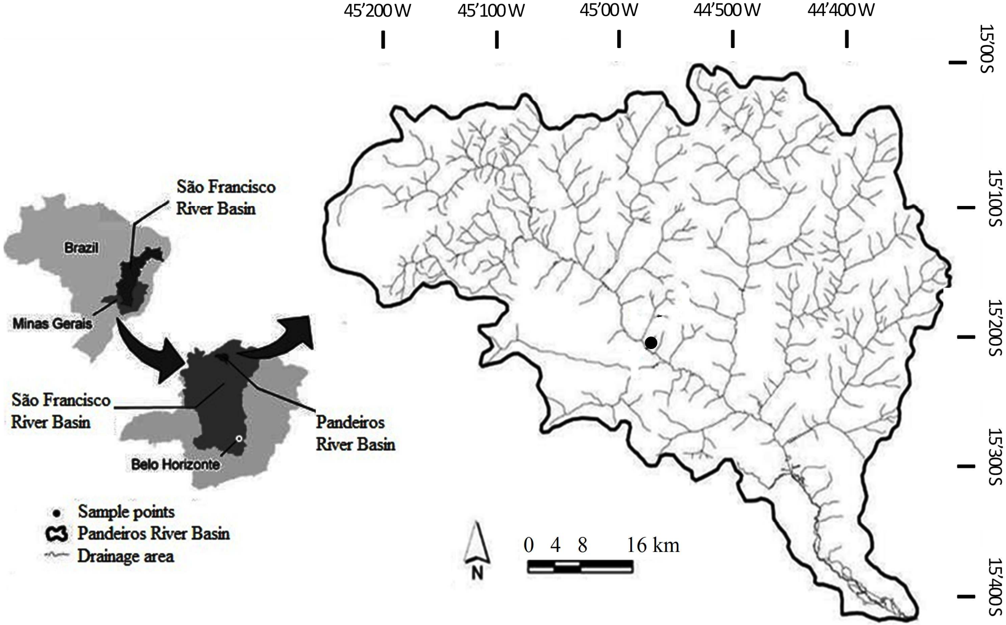

**Fig. 1.** Sampling site in the Pandeiros River Basin and its location with regard to Minas Gerais State in Brazil.

### Procedure

The electrical conductivity, pH and dissolved oxygen levels were measured *in situ* using a multianalyzer (YSI Incorporated, model 85). The luminosity and water temperature at the stream surface were continuously recorded with a datalogger (Onset, HOBO UA-002-08). The total alkalinity was determined by the Gran method according to Carmouze (1994), and in the water, the N (nitrate and ammonia; detection limit: 0.05) and P (orthophosphate; detection limit: 0.015) concentrations were analyzed according to Clesceri et al. (1989). The rainfall and air temperature were obtained from a meteorological station (number 83386), located at 15º 26' S, 44º22' W and 473.6 m altitude, of the National Agency of Waters of Brazil (available on the website hidroweb; http://hidroweb.ana.gov.br/), and the canopy openness was quantified using hemispherical photographs.

The experiment used litter bags (10 mm open mesh, 30 x 30 cm), with a sample (± 3 g of leaves) incubation period of 30 days. After this period, the samples were removed, and new samples were incubated, containing the detritus from the direct input into the stream of the preserved "vereda" during the previous 30 days. The samples were incubated at a depth of 0.2 to 0.5 m in contact with the sediment. After removal, the litter bags were placed into plastic bags inside of boxes with ice and transported to the laboratory. The remaining leaf litter used in this study was used to estimate the initial dry weight (after being dried at 60 ºC for 72 h). In the laboratory, the leaves were washed with distilled water over a 180-µm sieve. The retained material was fixed (70% ethanol), and the invertebrates were later identified to the family level according to (Pérez 1988) and (Cummins et al. 2005). The taxonomic richness and density were calculated for invertebrates based on the community survey. The invertebrates were classified into five functional trophic groups (Pérez 1988; Cummins et al. 2005): gathering-collectors (G-C), filtering-collectors (F-C), shredders (Sh), scrapers (Sc) and predators (P).

Afterward, discs (12 mm in diameter) were removed from randomly selected leaves to analyze the ash-free dry mass (AFDM), the microbial biomass measured based on ergosterol and ATP concentrations and the aquatic hyphomycete sporulation (5 discs for each analysis). The total biomass of the decomposer microorganisms was determined by quantifying the ATP in the litter fall according to Abelho (2005; using the luciferin-luciferase reaction). The fungal biomass was assessed by quantifying ergosterol concentrations according to Gessner (2005; using a lipid exclusive to fungal membranes). Aquatic hyphomycete sporulation was assessed using discs from each litter bag according to Bärlocher (2005) and Gulis et al. (2005) based on posterior counting and identification under the microscope (400 X). The remaining litter fall was placed in trays and dried in an oven at 60°C for 72 h to determine the dry weight. The initial AFDM was obtained after incinerating the discs (550 º C for 4 h) and subtracting the proportion of the remaining material, which corresponded to the inorganic fraction, from the respective sample.

## Statistical Analysis

The leaf breakdown rates (*k*) at the sampling points in the sampling months were obtained assuming a linear model (log transformed) of the percentage of mass lost during the 30 days of incubation ($W_t = W_0 e^{-kt}$; Wt = remaining weight; W0 = initial weight; -k = decay rate; t = time). Data normality was assessed with the Kolmogorov-Smirnov test, the homogeneity of variance was assessed with Levene’s test, and the data were log transformed when needed (Zar 1996). A repeated-measures ANOVA (RM-ANOVA) and contrast analysis were used to test for significant differences among months (categorical variables) in the remaining mass, invertebrate community (richness, density and abundance of functional trophic groups) and biomass of microorganisms (levels of ergosterol, ATP and density of spores in the detritus-dependent variables). The association between some variables was assessed with Spearman's correlation analysis (ρ) considering $p < 0.05$ (Zar 1996). We also compared invertebrate community structure among the studied months with a permutational multivariate analysis of variance (PerMANOVA) based on the species and functional trophic groups using the Bray-Curtis distance matrix and a permutation test (10000) with pseudo-F and discriminating months through a Bonferroni-corrected pairwise comparison (using the Adonis function of the vegan package in R; Oksanen et al. 2008).

## RESULTS

### Physical and chemical parameters of the stream waters

The mean discharge of the stream was 0.18 ± 0.02 $m^3$, with peaks in November and December. The water temperature was 25.9 ± 0.47 ºC, and the air temperature was 24.9 ± 0.57 ºC, with higher values in November, December and January. Precipitation during the studied period was 92.2 ± 25.0 mm, with peaks in October to April. The stream waters were basic (8.2 ± 0.12; with peaks in January and February), with high levels of oxygen (6.5 ±0.30 mg $L^{-1}$ and 80.6% saturation; with peaks in July), electrical conductivity (51.0 ± 7.17 µS $cm^{-1}$; with peaks in April and May) and alkalinity (60.3 ± 4.73 µEq $L^{-1}$; with peaks in January). The ammonia (0.06 ± 0.003 mg.$L^{-1}$), nitrate (0.1 ± 0.001 mg.$L^{-1}$) and orthophosphate (0.02 ± 0.0001 mg.$L^{-1}$) concentrations were fairly constant throughout the year. The canopy openness of the riparian vegetation was elevated in the "vereda," with average values of 48.5% (Table 1).

**Table 1.** Water flow ($m^3$), pH, dissolved oxygen ($mg.l^{-1}$ and saturation %), electrical conductivity (uS $cm^{-1}$), water temperature (T.water, ºC), alkalinity (MicroEq $L^{-1}$) and ammonia, nitrate and orthophosphate concentrations ($mg.l^{-1}$) in the water as well as the total precipitation (mm), air temperature (T.air. in ºC) and luminosity from January to December.

| | Flow | pH | Ox (mg) | Ox (%) | Conduct. | T.water | Alkal. | Ammonia | Nitrate | Orthop. | Precipitation | T.air | Luminosity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| April | 0.16 | 8.40 | 7.12 | 86.60 | 75.10 | 25.60 | 75.41 | <0.05 | 0.09 | 0.02 | 69.40 | 25.00 | 11.66 |
| May | 0.15 | 7.17 | 7.60 | 90.01 | 73.60 | 24.20 | 42.71 | 0.09 | 0.10 | 0.02 | 11.60 | 24.00 | 19.56 |
| June | 0.14 | 7.75 | 6.88 | 82.66 | 64.94 | 24.32 | 52.72 | 0.07 | 0.10 | 0.02 | 4.60 | 21.96 | 86.11 |
| July | 0.10 | 8.11 | 7.84 | 93.60 | 72.80 | 24.70 | 52.72 | <0.05 | 0.10 | 0.02 | 0.00 | 22.21 | 42.33 |
| August | 0.12 | 8.42 | 7.05 | 82.50 | 70.10 | 23.80 | 41.03 | <0.05 | 0.10 | 0.02 | 2.00 | 23.34 | 23.60 |
| September | 0.12 | 8.15 | 6.18 | 75.30 | 3.40 | 26.10 | 84.54 | 0.06 | 0.09 | 0.02 | 35.60 | 24.36 | 19.56 |
| October | 0.10 | 8.20 | 4.70 | 70.20 | 20.00 | 28.00 | 54.45 | <0.05 | 0.10 | 0.02 | 68.40 | 25.29 | 11.66 |
| November | 0.31 | 8.30 | 6.95 | 88.40 | 35.30 | 27.00 | 53.36 | <0.05 | 0.10 | 0.02 | 16.00 | 26.00 | 10.00 |
| December | 0.30 | 8.11 | 6.42 | 82.30 | 42.30 | 26.00 | 51.23 | <0.05 | 0.10 | 0.02 | 41.80 | 27.00 | 9.00 |
| January | 0.16 | 8.51 | 5.23 | 66.80 | 67.20 | 28.90 | 90.02 | 0.07 | 0.10 | 0.02 | 29.70 | 28.00 | 8.00 |
| February | 0.27 | 8.65 | 5.12 | 68.50 | 35.70 | 26.50 | 65.59 | 0.06 | 0.09 | 0.02 | 28.50 | 27.00 | 9.00 |
| Mean | 0.18 | 8.16 | 6.46 | 80.62 | 50.95 | 25.92 | 60.34 | 0.06 | 0.10 | 0.02 | 27.96 | 24.92 | 22.77 |
| Std. Error | 0.02 | 0.12 | 0.30 | 2.64 | 7.17 | 0.47 | 4.73 | 0.0038 | 0.0013 | 0.0001 | 7.08 | 0.57 | 6.72 |

## Leaf breakdown rates

The mean litter breakdown rate (*k*) was 0.037 (0.014 to 0.095 range), corresponding to an overall leaf litter loss of ~59% (33 to 93% range) of the original mass in one month. The percentages of mass loss significantly differed among the studied months (ANOVA, $F_{10, 36} = 6.75$, $p < 0.01$), with higher values in November and December (contrast analysis; $p < 0.05$) and lower values in May to July (Fig. 2). The litter mass loss was positively correlated with rainfall ($r = 0.44$, $p = 0.01$) and the air and water temperatures ($r = 0.31$, $p = 0.02$ and $r = 0.47$, $p = 0.01$, respectively).

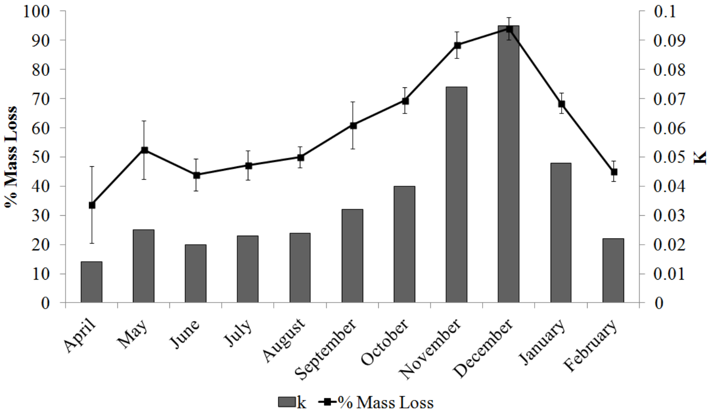

**Fig. 2.** Mean values and standard errors of the remaining mass (black line - %) and decomposition rates (gray bars - k) over the studied months (April to February).

## Biological communities

The mean (± SE) value of ATP content in the leaves was 475 ± 43 nmoles.g$^{-1}$ AFDM, with significant differences among the months (RM-ANOVA, $F_{10, 36} = 33.06$, $p < 0.01$), with a maximum of 1021 nmoles.g$^{-1}$ AFDM (June) and a minimum of 34 nmoles.g$^{-1}$ AFDM (October). The ergosterol mean (± SE) was 624 ± 52 µg.g$^{-1}$ AFDM, with significant differences among months (RM-ANOVA, $F_{(10, 36)} = 5.33$, $p < 0.01$), with peaks of

967 and 1058 µg.g$^{-1}$ AFDM (in July and February, respectively) and a lowest value of 239 µg.g$^{-1}$ AFDM (October). The ergosterol and ATP concentrations (Fig. 3) were positively correlated throughout the year ($r = 0.43$, $p < 0.01$), but only the ATP values were related to the litter breakdown ($r = -0.43$, $p < 0.01$).

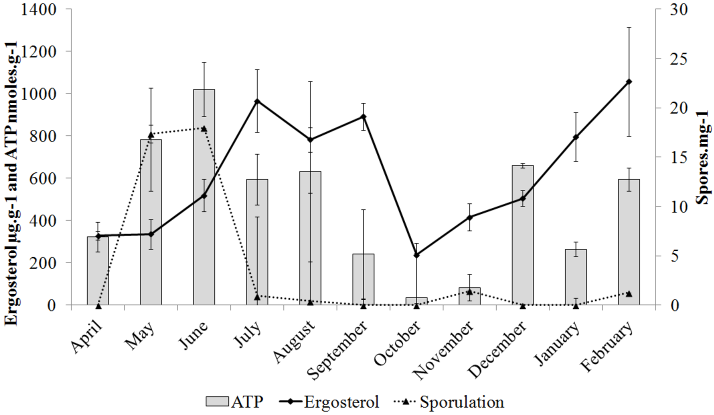

**Fig. 3.** Mean values and standard errors of fungal biomass (continuous line - ergosterol µg g$^{-1}$ AFDM), total microbial community activity (gray bars - nmoles ATP g$^{-1}$ AFDM) and abundance of fungal spores (dotted line - spores.mg AFDM$^{-1}$) over the studied months (April to February).

The maximum sporulation rate (± SE) was 18 ± 1 spores.mg$^{-1}$ AFDM (May and June), but zero spore production was detected in January, April, September, October and December (Fig. 3). Sporulation rates were highly variable (RM-ANOVA, $F_{(10,\ 36\ )} = 2.29$, $p = 0.03$) and presented a negative relationship with temperature ($r = -0.33$, $p = 0.02$). A qualitative survey in the water column contained spores of the species *Anguillospora filiformis*, *Anguillospora longíssima*, *Lunullospora curvula* and *Fontanospora eccentrica*.

The most abundant *taxon* of invertebrates (± SE) associated with the litter breakdown was Chironomidae (Diptera), with 80% of the total individuals (mean of 293 ± 33 individuals.$g^{-1}$ AFDM). The mean (± SE) density of invertebrates ranged from 49 ± 43 individuals.$g^{-1}$ AFDM (September) to 590 ± 150 individuals.$g^{-1}$ AFDM (July), and there were significant differences among months (Fig. 4; RM-ANOVA, $F_{(10, 36)} = 5.21$, $p < 0.01$). The richness (± SE) of invertebrates ranged from 4 ±0.4 (January) to 10 ± 0.5 (May) *taxa* and significantly differed among months (Fig. 4; RM-ANOVA, $F_{(10, 36)} = 4.58$, $p < 0.01$). Shredders represented only 9% of non-Chironomidae invertebrates, with the highest values (RM-ANOVA, $F_{(10, 36)} = 3.41$, $p < 0.01$) in January (13%), April (13%) and August (12%) and lower values in September (3%) when the main *taxa* was Odontoceridae (Trichoptera). The invertebrate densities ($r = 0.15$, $p = 0.29$) and shredder ($r = -0.11$, $p = 0.44$) abundances were not correlated with mass loss. However, the invertebrate and shredder densities were positively correlated with dissolved oxygen ($r = 0.54$, $p < 0.01$ and $r = 0.35$, $p = 0.02$, respectively) and negatively correlated with temperature ($r = -0.45$, $p < 0.01$ and $r = -0.36$, $p = 0.01$, respectively). The composition of functional trophic groups (PerMANOVA, $F = 2.43$, $p < 0.01$; Fig. 5) and *taxa* (PerMANOVA, $F = 2.92$, $p < 0.01$; Table 2) of the invertebrate community varied over the months studied (pairwise comparison; $p < 0.05$), mainly between the months of dry (June and July) and rain (November, December and January).

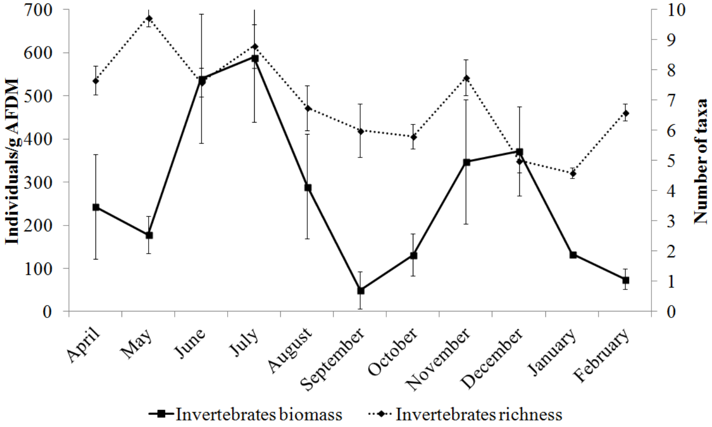

**Fig. 4.** Mean values and standard errors of the density (ind/g; continuous line) and richness (dotted line) of the invertebrates that colonized the leaf litter over the studied months (April to February).

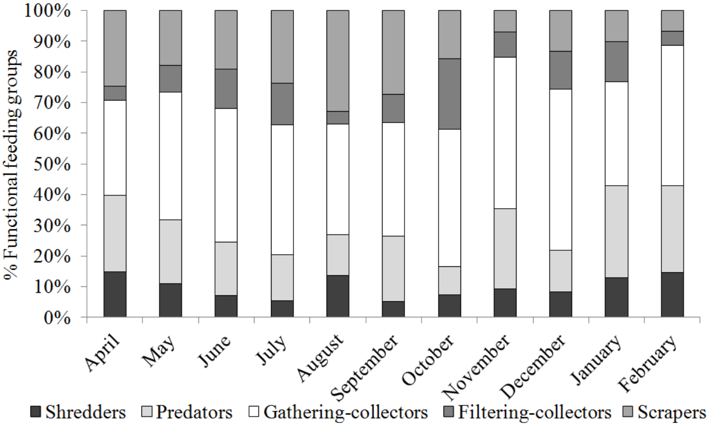

**Fig. 5.** Relative abundance of the considered functional feeding groups of the aquatic invertebrates that colonized the leaf litter over the studied months (April to February).

**Table 2.** Means and standard error (s.e.) of the densities of invertebrates colonizing (ind. $g^{-1}$) leaves during breakdown in the months studied. Functional feeding groups (FFG): P, predators; Ga-Co, gathering-collectors; Fil-Co, filtering-collectors; Shr, shredders; Scr, scrapers; * not classified.

| Taxa | FFG | January | February | April | May | June | July | August | September | October | November | December |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Annelida** | | | | | | | | | | | | |
| Oligochaeta | Ga-Co | 26 ± # | 2.8 ± 1.5 | 21 ± 17 | 3.3 ± 1.9 | 2.4 ± 1.5 | 8.2 ± 6.2 | 2.3 ± 1.3 | 16 ± 7.8 | 6.2 ± 2.6 | 2.3 ± 1.4 | 23 ± 12 |
| Hyrundinae | | 11 ± 6 | 1.6 ± 0.6 | 7.7 ± 5 | 6 ± 2.5 | 16.4 ± 14.6 | 17 ± 10.4 | 0.5 ± 0.5 | 4.5 ± 2 | 0.4 ± 0.3 | 1.8 ± 1 | 3 ± 2.8 |
| **Arthropoda** | | | | | | | | | | | | |
| Amphipoda | | | | | | | | | | | | |
| Hyalidae | Shr | 0 ± 0 | 0 ± 0 | 0 ± 0 | 1.8 ± 1 | 1.8 ± 2 | 0 ± 0 | 0 ± 0 | 2 ± 1.2 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Insecta | | | | | | | | | | | | |
| Coleoptera | | | | | | | | | | | | |
| Elmidae | Ga-Co/Scr/Shr | 0 ± 0 | 0.4 ± 0.4 | 0 ± 0 | 2.8 ± 2.4 | 1 ± 0.9 | 7.4 ± 6.4 | 1 ± 0.6 | 1 ± 0.6 | 0.2 ± 0.2 | 1 ± 0.7 | 0 ± 0 |
| Lampyridae | P | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.3 ± 0.3 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.6 ± 0.7 | 0.5 ± 0.5 | 0 ± 0.2 |
| Diptera | | | | | | | | | | | | |
| Chironomidae | * | 86 ± # | 52 ± 20 | 114 ± 47 | 127 ± 31 | 534 ± 385 | 1092 ± 348 | 328 ± 111 | 91 ± 40 | 111 ± 47 | 375 ± 138 | ## ± 92 |
| Ceratopogonidae | Ga-Co/P | 0.8 ± 1 | 0.6 ± 0.4 | 0 ± 0 | 0.8 ± 0.5 | 0 ± 0 | 0.6 ± 0.7 | 0 ± 0 | 0.5 ± 0.3 | 0 ± 0 | 0.3 ± 0.3 | 0 ± 0 |
| Simuliidae | Fil-Co | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.3 ± 0.3 | 0 ± 0 | 0.6 ± 0.7 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.8 ± 0.5 | 0 ± 0 |
| Empididae | Ga-Co/P | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.5 ± 0.5 | 0.8 ± 0.9 | 0.6 ± 0.7 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Tabanidae | P | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.8 ± 0.8 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Psychodidae | Ga-Co | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 2 ± 1.2 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Ephemeroptera | | | | | | | | | | | | |
| Leptophlebiidae | Ga-Co/Scr | 1.4 ± 2 | 0.6 ± 0.4 | 0.7 ± 1 | 2.3 ± 1.7 | 3.6 ± 3.8 | 6.2 ± 4.5 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 4.5 ± 3.3 | 1 ± 1.1 |
| Leptohyphidae | Ga-Co/Scr | 4.2 ± 2 | 12 ± 5 | 36.7 ± 27 | 9 ± 3.7 | 17.6 ± 10.7 | 15.2 ± 6.3 | 3.3 ± 2.1 | 4 ± 2.3 | 4.4 ± 2.4 | 35 ± 16.5 | 27 ± 11 |
| Baetidae | Ga-Co/Scr | 0 ± 0 | 0.4 ± 0.4 | 13.3 ± 7 | 13.5 ± 7.6 | 3.4 ± 2.3 | 15.4 ± 9.1 | 8.3 ± 4.2 | 0 ± 0 | 0 ± 0 | 5.3 ± 1.3 | 0 ± 0 |
| Caenidae | Ga-Co/Fil-Co | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 6.6 ± 7.4 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Trichoptera | | | | | | | | | | | | |
| Hydropsychidae | Fil-Co/P | 0 ± 0 | 1 ± 0.5 | 0.7 ± 1 | 0 ± 0 | 1.2 ± 1.3 | 5 ± 3.1 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 4.8 ± 2.6 | 1 ± 0.9 |
| Leptoceridae | Ga-Co/P/Shr | 0 ± 0 | 0.2 ± 0.2 | 0 ± 0 | 1.3 ± 0.8 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 2.4 ± 2.4 | 0 ± 0 | 0 ± 0 |
| Philopotamidae | Fil-Co | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.5 ± 0.5 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Calamoceratidae | Shr | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.8 ± 0.9 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Odontoceridae | Ga-Co/Shr | 4.2 ± 2 | 0.4 ± 0.4 | 32 ± 21 | 4 ± 3 | 5.2 ± 3.5 | 9.4 ± 6.1 | 1.3 ± 0.5 | 3 ± 1.7 | 3.2 ± 2.3 | 3.5 ± 1.4 | 1 ± 1 |
| Hydroptilidae | Ga-Co/Fil-Co/Scr | 0 ± 0 | 0 ± 0 | 0 ± 0 | 1.3 ± 1.3 | 3.4 ± 3.8 | 1 ± 1.1 | 2.5 ± 1.3 | 0 ± 0 | 1.6 ± 1.5 | 0 ± 0 | 0 ± 0 |
| Polycentropodidae | Fil-Co/P | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0.6 ± 0.4 | 0 ± 0 | 0.8 ± 0.8 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Hemiptera | | | | | | | | | | | | |
| Nepidae | P | 0 ± 0 | 0 ± 0 | 0.7 ± 1 | 0 ± 0 | 0.4 ± 0.4 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Odonata | | | | | | | | | | | | |
| Libellulidae | P | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 1 ± 0.9 |
| Gomphidae | P | 0 ± 0 | 0 ± 0 | 6.7 ± 6 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Coenagrionidae | P | 0 ± 0 | 3.6 ± 1.6 | 0 ± 0 | 3.5 ± 2.4 | 2 ± 2 | 0.4 ± 0.4 | 0.8 ± 0.8 | 0 ± 0 | 0 ± 0 | 0.5 ± 0.5 | 1 ± 0.7 |
| Calopterygidae | P | 0 ± 0 | 0 ± 0 | 11 ± 8 | 0.5 ± 0.5 | 0 ± 0 | 5.2 ± 5 | 0.8 ± 0.5 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Gastropoda | | | | | | | | | | | | |
| Lymnaeidae | Scr | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 15 ± 13 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 |
| Thiaridae | Scr | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 27.2 ± 30.4 | 41.2 ± 32.5 | 0 ± 0 | 0 ± 0 | 1.6 ± 1.8 | 0 ± 0 | 0 ± 0 |

## DISCUSSION

### Canopy degradation effects

The canopy degradation in our study site can allow higher sediment entrainment (Gardiner et al. 2009) and promote a greater frequency and intensity of climatic disturbances (Dudgeon et al. 2006; Naiman and Décamps 1997; Vannote et al. 1980), and a consequence could be a decreasing flow of the water. This may explain the lower flow of the present studied stream, due to decrease of water-storage capacity and maintaining the system integrity by riparian vegetation (Lima and Zakia 2001). The loss of the hydrological functions by riparian vegetation, may be responsible for the water contained higher values of pH, alkalinity, dissolved oxygen, nutrients and conductivity other stream in the Pandeiros basin (Rezende et al. 2012). This may indicate that environmental change caused by canopy degradation due to plant-based extractivism may affect the ecosystem, compromising some ecological services.

Compared with a stream system with an intact canopy (±9% canopy openness), we can expect a change in the metabolism of canopy degradation system, increasing their source of autotrophic resource for the higher incidence of light (Vannote et al. 1980). The canopy degradation to allow more light incidence can also lead to an increase in temperature of the water. This can be an important factor explaining the higher leaf breakdown rates (k= -0.037), mainly in December (rainy season). Therefore, with the loss of the services by riparian vegetation as controlling the precipitation input (Lima and Zakia 2001; Moreira et al. 2011), we found higher water velocity (mechanical fragmentation and leaching), dissolved oxygen and temperatures, which accelerate biological metabolism (Gulis and Suberkropp 2003; Medeiros et al. 2009), explaining the high rates of decomposition.

This pattern indicates that canopy degradation modify the ecological process studied and can change the metabolism of the ecosystem (from heterotrophic to autotrophic), despite the great ecological resistance of “veredas” (Benda et al. 2004). This environmental impact also modified the communities of fungi and invertebrates, confirming our second hypothesis and indicating that the leaf breakdown process was useful as a bioindicator. The leaf breakdown rates were a useful indicator of impacts, such as the organic pollution of urbanization areas (Pascoal et al. 2001) and the gradient of extensive agricultural changes in the land use of the landscape (Hagen et al. 2006). Our study indicated that the macroinvertebrate community (with higher density and richness under stochastic disturbance; Benda et al. 2004) and total microbial community (with more photosynthetic organisms after canopy degradation; Jugnia et al. 2000) could be biological predictors. The increase in the density of biological communities during the leaf breakdown process by stochastic disturbance was also observed in other studies (Hagen et al. 2006; Sponseller and Benfield 2001) and indicates that this variable can be a useful indicator. Therefore, as also observed by Schwarz and Schwoerbel (1997), our data regarding the leaf breakdown were dependent on the chemical and physical properties of the leaves, the abundance of the decomposing community and the climatic pattern.

However the partial removal of vegetation for plant-based extractivism can be considered a slight impact, most likely because plant removal is a structural modification and does not represent a source of pollution (e.g., the input of chemicals as pesticides). The practices of agriculture-forestry, such as plant extractivism, cause smaller environmental changes than extensive agriculture and urbanization (Daniel et al. 2002; Gardiner et al. 2009; Sponseller and Benfield 2001). Areas of extensive agriculture (Utz et al. 2009) and urbanization (Paul and Meyer 2001) have greater influence on biological communities, even when these land uses are present in small sizes and proportions on the landscape. Thus, the negative effects of extensive agriculture and urbanization are disproportionate compared to other land uses (Johnson et al. 2012).

## Leaf breakdown process

The leaf breakdown rates (*k*) in all the months (mean of -0.037) were described as fast (k > -0.017) except for April (intermediate values of -0.004 > k < -0.017) according to the model proposed by Gonçalves et al. (2013). These *k* values are superior to those observed in other Cerrado streams (-0.0001 to -0.015 in Gonçalves et al. 2007; Gonçalves et al. 2012a; Moretti et al. 2007) but were in the lower range reported for tropical areas (-0.026 to -0.077) by Abelho (2001). We believe that the high temperatures recorded throughout the entire year (with a minimum of 21°C) had positive effects on the leaf breakdown rates (Suberkropp and Chauvet 1995; Gonçalves et al. 2012b). The largest *k* was observed in the rainy season, evidencing a seasonal dynamic, and explains the positive correlation with temperature and rainfall, confirming our first hypothesis. There might also be synergistic interactions between higher physical abrasion (due to the higher rainfall and water flow; Santos Fonseca et al. 2012), oxygen concentrations (which increases the activity of aquatic fungi; Medeiros et al. 2009) and electrical conductivity (which indicates higher nutrient inputs; Chestnut and McDowell 2000) accelerating the leaf breakdown rates. This result indicates that litter decomposition could be influenced by temporal changes in abiotic conditions and, consequently, by changes in the biological activity in this ecosystem.

The fungal biomass (ergosterol) was greater than in other Cerrado streams (50 to 420 µg.g-1 range for Gonçalves et al. 2007; Gonçalves et al. 2006c), and the total microbial community activity (ATP) was at the upper limit compared to tropical streams (100 to 750 nmoles.g-1 range for Abelho 2001; Abelho et al. 2005; Gonçalves et al. 2007; Gonçalves et al. 2006c). We found greater microbial biomass in periods of low water flow due to a decrease of rain (i.e., in the dry season) that was likely related to a decrease of lower physical abrasion and lower biofilm loss (Santos Fonseca et al. 2012). Another aspect is that in the dry season, the low cloud formation enables a luminosity increase and stimulates photosynthetic organisms, represented by ATP concentration (Vannote et al. 1980), that use the detritus only as a substrate, increasing the biofilm mass.

Higher photosynthetic production (greater autotrophic resource; Jugnia et al. 2000) was associated with lower metabolisms of organisms due to the temperature decrease in dry season (Sridhar and Sudheep 2010). This change might decrease the use of heterotrophic resources and explains the lower breakdown despite the higher microbial biomass. Higher temperatures can have a negative effect on fungal diversity, selecting only species with the ability to develop in warmer settings (Chauvet and Suberkropp 1998), as observed in the fungal community of the studied stream. These patterns explain the hyphomycetes' tendency to sporulate more in the dry season and the negative correlation of sporulation with temperature (Mathuriau and Chauvet 2002; Gonçalves et al. 2007). Therefore, our results show that the increase of luminosity (corresponding to fewer clouds) and lower temperatures in dry season can lead to a higher use of the autotrophic resource and a decrease of microbial activity, thus slowing the leaf breakdown rates.

We found higher average densities of aquatic invertebrate community than in other Cerrado streams (2 to 780 ind/g range for Gonçalves et al. 2012a; Gonçalves et al. 2006b; Moretti et al. 2007). The higher densities and richness, especially in dry season, can be explained by the negative correlation with temperature (cool water could increase the oxygen dilution) and indirectly indicates lower rainfall (with a lower washing power by water; Santos Fonseca et al. 2012). The invertebrate community was dominated by Chironomidae, as observed in other tropical streams (Boyero et al. 2012; Moulton et al. 2010; Silva-Junior and Moulton 2011). The lower abundance of shredders may explain the low importance of this community in the leaf breakdown, as observed in other tropical streams (0 to 11% range for Gonçalves et al. 2006c; Gonçalves et al. 2007; Moretti et al. 2007). Odontoceridae was the most important shredder, but members of this group have also been classified as scrapers and as opportunistic scavengers feeding on animal and plant detritus (Pérez 1988; Cummins et al. 2005). The alternate feeding strategies of this group would help explain the low participation and importance of the invertebrate community in the leaf breakdown process.

## Conclusion

In general, the data indicate that the partial removal of native vegetation due to plant-based extractivism affect the functioning of this ecosystem. The leaf breakdown rates were fast throughout all the studied years, and the more openness left the system higher susceptible to seasonal changes (Dudgeon et al. 2006; Naiman and Décamps 1997; Vannote et al. 1980). Canopy degradation might increase the frequency and intensity of disturbances (Benda et al. 2004) due to the loss of the capacity of riparian vegetation to stabilize ecological processes (Naiman and Décamps 1997). The high biological and physical-chemical variation and the lower water flow are also initial indications that the water-supply services might be impaired in the long term. This finding is important information for "veredas" conservation and shows that despite the apparent process maintenance, the dynamics of such systems are being changed due to canopy degradation by plant-based extractivism.

There was a clear seasonal variation in leaf decay, suggesting that the temporal resolution chosen for a leaf breakdown study may affect the detection of decay patterns. Rainy season had a higher leaf breakdown rate due to higher water flow, temperature and precipitation (Santos Fonseca et al. 2012; Sridhar and Sudheep 2010). In the rainy season, higher leaf breakdown was observed despite the lower biomass of decomposers due to lower dissolved oxygen, alkalinity and electrical conductivity (Pérez 1988; Cummins et al. 2005). The aquatic invertebrates (mainly shredders) and total microorganisms showed no overall influence on the leaf breakdown. These results for a temporal macro-scale (month and year) are similar to the results for a spatial macro-scale proposed by Wiens (1989). On a micro-scale (hours and days), the phenomenon can induce an increase in the heterogeneity of the detected signal, but the macro-scale is affected by climatic factors (Schwarz and Schwoerbel 1997; Wiens 1989). Thus, these results indicated that on a temporal macro-scale (months and the average annual), the water flow, temperature and precipitation are the factors that control the leaf breakdown rates.

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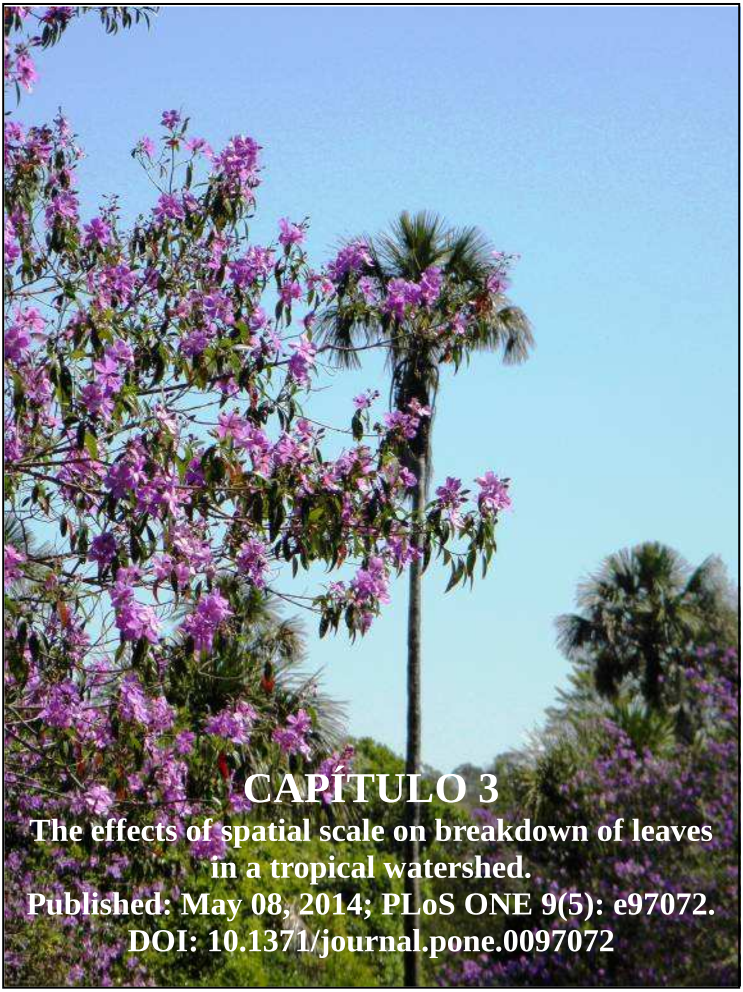

# CAPÍTULO 3

## The effects of spatial scale on breakdown of leaves in a tropical watershed.

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# The effects of spatial scale on breakdown of leaves in a tropical watershed

**Published: May 08, 2014; PLoS ONE 9(5): e97072. DOI: 10.1371/journal.pone.0097072**

## ABSTRACT

The objective was to assess the effects of natural variation in the physical structure of the environment on biological communities and on the processing of *Eucalyptus cloeziana* and *Inga laurina* and to identify the controlling factors at different scales along stream order gradients. The study area consisted of 14 sampling sites distributed within a tropical watershed (1st, 2nd, 3rd and 4th order streams replicated in 4 sub-basins). Our samples consisted of 3 g of leaves of *E. cloeziana* (high-quality) and *I. laurina* (low-quality) placed in 252 bags with 10mm mesh (measured by the chemical composition of the detritus). Four samples of each leaf type were collected periodically (three times) over a period of 75-125 days and washed on a sieve to separate the invertebrates. A series of leaf disks were cut to determine ash-free dry mass, polyphenol, lignin, cellulose, total microbial biomass and fungal biomass, and the remaining material was oven-dried to determine the dry weight. We performed analyses within and between spatial scales (regional and local) to assess which watershed scale was the more import determinant of the leaf breakdown rate (*k*). The microbial and shredder were most influenced at the local scale (stream order). Shredders were influenced by microorganisms, with stronger interactions between them than were found to drive the *k* at the local scale. Moreover, differences in the overall *k* and abiotic variables were more strongly influenced at the regional scale (sub-basin), showing that the study scale alters the response of the studied variables. We found higher *k* values at higher values of water velocity, dissolved oxygen and temperature, all of which accelerate biological metabolism in response to variations on the regional scale. Watersheds with warmer microclimates and streams with higher nutrient levels and oxygen could be accelerating the ecosystem metabolism, independent of the detritus quality.

**Keywords:** Decomposition; sub-basin; stream order; microorganisms; shredders; detritus quality; abiotic variables.

## INTRODUCTION

The characteristics of lotic ecosystems show natural patterns along an upstream-downstream gradient due to variations in geomorphology and topography in the watershed (Fabre and Chauvet 1998; Vannote et al. 1980). Natural changes along this gradient (upstream to downstream) include an increase in the dimensions of the stream (width), changes (increases or decreases) in the velocity of the water, and openings in the riparian canopy that allow greater light penetration (Benda et al. 2004; Statzner and Higler 1985). Greater luminosity increases the temperature and accelerates photosynthetic production and autotrophic metabolism (Statzner and Higler 1985). Along this gradient, therefore, the relative abundance of micro-organisms increases but that of invertebrates decreases (primarily shredders of organic matter), decreases from the headwaters to the downstream sections (Vannote et al. 1980). These natural changes also modify the energy input and cycling of organic matter in space and time (Larned et al. 2010; Vannote et al. 1980). Senescent leaves are an important source of nutrients and food resources in heterotrophic metabolic environments, primarily in headwaters and small streams (Gessner et al. 1999; Graça et al. 2001). However, this material is mineralized and available for use by primary producers and other trophic levels after its decomposition. As a result, leaf breakdown is a key process in lotic ecosystems (Gessner et al. 1999; Mathuriau and Chauvet 2002). Leaf breakdown can be influenced by many factors, such as physical and chemical variables (associated with water and detritus) and the activities of communities of decomposers (micro-organisms and aquatic invertebrates)

(Abelho 2001; Gessner et al. 1999; Gonçalves et al. 2013; Graça et al. 2001; Mathuriau and Chauvet 2002; Moulton et al. 2010; Suberkropp and Chauvet 1995; Wantzen and Wagner 2006).

The study of leaf breakdown at the scale of a watershed allows us to observe emerging patterns and identify certain factors that structure the ecosystems at different scales (Tiegs et al. 2009; Wiens 1989). It is evident that a series of successively smaller and nested geomorphologic units can have various patterns and structures depending on the scale that is being analyzed (Lowe et al. 2006; Wiens 1989). These patterns and structures can be observed in riffles and pools within continuous stretches, which are nested within large rivers that make up a watershed (Schneider 2001; Tiegs et al. 2009; Wiens 2002). Studies that address only one scale are subject to problems because certain variables are measured directly in small areas or across short time intervals, whereas few can be measured at fine resolution over large areas (Schneider 2001; Wiens 2002). In addition, changes at smaller scales are not maintained at larger scales (Wiens 1989). Therefore, the issue is that unless patterns are consistent at all scales, the findings at one scale cannot be extrapolated to yield accurate predictions at other scales. Accordingly, tests at multiple scales are needed for confident extrapolation. From this perspective, the evaluation of leaf breakdown at different scales enables the development of an integrated vision of the landscape during this important ecological process (Allen and Starr 1982; Del Arco et al. 2012).

The streams in a watershed can be considered within a hierarchical framework that presents organized view of spatial and temporal variations among and within stream systems along the “riverscapes” (Allan 2004; Frissell et al. 1986; Royer and Minshall 2003). Therefore, several studies have examined leaf processing at large spatial scales across biomes (Irons et al. 1994; Minshall et al. 1983), latitudinal gradients (Irons et al. 1994), and altitudinal gradients (Fabre and Chauvet 1998) and influences of land use (Hagen et al. 2006; Sponseller and Benfield 2001). Moreover, several recurrent topics emerge from considerations of several spatial scales. These topics include the relative importance of fungi and invertebrates (Hieber and Gessner 2002), the use of bioindicators (Del Arco et al. 2012) and the hierarchical nature of lotic ecosystems (Tiegs et al. 2009). Studies assessing allochthonous leaf breakdown at a watershed scale are rare worldwide, but they have been performed in temperate systems (Del Arco et al. 2012; Royer and Minshall 2003; Tiegs et al. 2009; Young and Collier 2009) .

In tropical streams, individual riffles or short stream reaches continue to be the most frequent sites for studies of leaf processing based on the traditional conceptual model (Cummins 1974; Petersen and Cummins 1974). Several factors are known to cause variation in the rates of processing within and among tropical stream reaches (Bianchini_Jr. 1999; Gonçalves et al. 2013). These factors include the effects of species mixing (Bruder et al. 2013; Moretti et al. 2007), litter quality (Gonçalves et al. 2007; Gonçalves et al. 2012b), micro-organism communities (Medeiros et al. 2009; Wright and Covich 2005), invertebrate communities (Gonçalves et al. 2012a; Li et al. 2009; Ligeiro et al. 2010), detritivores and shredders (Boyero et al. 2012; Wantzen and Wagner 2006) and seasonal effects (Larned 2000; Mathuriau and Chauvet 2002; Rueda-Delgado et al. 2006). However, systematic assessments of variability in allochthonous leaf breakdown rates across multiple spatial scales using the watershed as the sampling unit have not been performed in tropical stream systems. This study could help to answer important questions, such as “how does spatial structure influence ecosystem function and how do we integrate within and between spatial scales to assess function”, suggested by Sutherland et al. (Sutherland et al. 2013) as one of 100 fundamental ecological questions.

Based on the premise that leaf breakdown is the result of the activity of decomposer organisms and the physical and chemical processes occurring in the stream water, which vary along the scale investigated in the study scale (Abelho 2001; Gessner et al. 1999; Gonçalves et al. 2013), the following hypotheses were tested in this study: (i) natural differences in the physical nature of the stream (increasing canopy opening, water velocity, temperature and nutrient concentrations) accelerate biological metabolism and leaf breakdown from upstream to downstream; (ii) shredders decrease and micro-organisms increase in importance from upstream to downstream; and (iii) differences in the overall *k* values will be more clearly understandable (strongly explained) at an increased spatial scale. The objective of the study was to assess the natural effects of variation in the physical environment on biological communities and the leaf breakdown rates of *Eucalyptus cloeziana F. Muell* and *Inga laurina Sw. Willd* and to identify the controlling factors at different scales along the stream order gradient.

## METHODS

### The Study System

The study area consisted of 14 sampling sites distributed along the Gama-Cabeça do Veado watershed, a part of the Federal District in west central Brazil, comprising 1st, 2nd, 3rd and 4th order streams replicated in 4 sub-basins (Figure 1). The area includes important waterways that form the Paraná basin, a part of the Cerrado biome (Brazilian Savannah). The climate is tropical and has distinct rainy-hot (October to April) and cold-dry seasons (May to September). The mean annual temperature is 20°C, and the altitude varies between 1025 and 1150 m above sea level. The study area included three conservation units protecting the entire watershed and all sampling sites studied (Ecological Station of the University of Brasília, Ecological Reserve of IBGE and Ecological Station of the Botanical Gardens of Brasília). The study was approved by Ministry of Environment of Brazil through the System of Information and Authorization on Biodiversity (SISBIO) for activities with scientific purpose (code: 39629-1), and also was approved by the Scientific and Technical Council of the Ecological Station of the University of Brasília (code: 05-12), IBGE Ecological Reserve (code: 54 PC - PAD 1) and Botanical Gardens of Brasília (code: 13/2011).

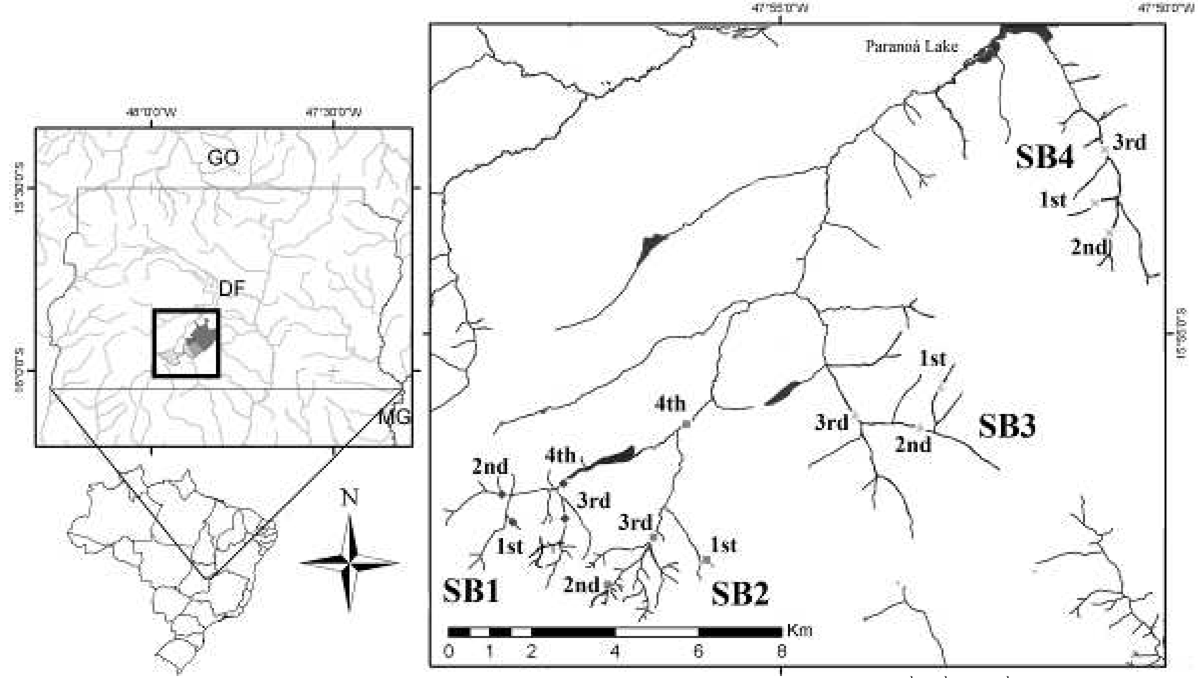


**Figure 1. Sampling sites.** Geographic location of the sampling sites consisting of streams of the 1st, 2nd, 3rd and 4th orders replicated in 4 sub-basins in the Gama-Cabeça de Veado watershed, Federal District (Brazil).

## Procedures

The experiment was conducted from June through October 2011 (the dry season), a period of zero rainfall, resulting in a high level of homogeneity in the physical and chemical features of the environment. Based on their chemical composition, we selected leaves from two species for use as detritus. The leaves of an exotic species (*Eucalyptus cloeziana F. Muell*) were used to represent high-quality detritus. The planting of *Eucalyptus* monocultures in place of the native vegetation has potential repercussions for stream basins. The area in which the study was conducted does not contain *Eucalyptus* plantations. However, the substitution of this monoculture for native vegetation has occurred in neighboring basins, where this monoculture has expanded, as it has throughout Brazil, e.g., to supply charcoal for steelmaking and pulp for papermaking (Gonçalves et al. 2012b). The low-quality detritus from a native species (abundant in riparian vegetation; *Inga laurina Sw. Willd*) was also used in the study, as this species best represents the plants of the Cerrado.

The leave The two types of leaves were chemically characterized by the mean values of total polyphenols (22.80 ± 2.5; 18.29 ± 1.8 mg/g$^{-1}$), total tannic acids (0.003 ± 0.0002; 0.002 ± 0.0004 mg/g$^{-1}$), lignin (42.61 ± 0.7; 45.94 ± 0.5%), cellulose (24.69 ± 1.5; 37.39 ± 1.2%), hardness (0.17 ± 0.1; 0.6 ± 0.3 cm/g$^{-1}$), nitrogen (13.16 ± 1.3; 16.41 ± 1.0 g/kg$^{-1}$) and phosphorus (0.46 ± 0.05; 0.53 ± 0.07 g/kg$^{-1}$) in *E. cloeziana* and *I. laurina*, respectively. The breakdown rates for these two leaf types (collected in nets 1 m$^2$ in area placed 1.5 m from the ground) were measured individually by the loss of weight of 3 g (± 0.1 g dry weight) of leaves, correcting for the initial humidity and transport loss (Graça et al. 2005), incubated in litter bags (15 x 15 cm, 10 mm mesh size).

In total, 252 litter bags were placed at a depth of 0.3 m in pool areas at the 14 sampling sites in 1st, 2nd, 3rd and 4th order streams (Strahler 1952) in the 4 sub-basins (Gama – SB1, Capetinga – SB2, Taquaras – SB3 and Cabeça de Veado – SB4 sub-basins). The removal of the *E. cloeziana* and *I. laurina* leaves occurred initially after 10 days of incubation, which corresponds to the expected time required for leaching and initiating microbial colonization (Graça et al. 2005). After this sampling, the principal leaf breakdown rate (*k*) was used to estimate the next sampling time for each detritus type (at approximately 75% of the remaining mass), which was determined to be 40 days for *E. cloeziana* and 85 days for *I. laurina.* This stage of decomposition occurs when microbial activity is high and the invertebrate community is already established. Subsequently, the *k* value was used a second time to perform corrections and acquire new values to obtain approximately 50% of the remaining mass for each detritus type. This sampling time was determined to be 75 days for *E. cloeziana* and 125 days for *I. laurina*. After this period, the community established during the ecological process of degradative succession is affected by the reduction in the available detritus (additional information about k, see also Chapter 6 of (Graça et al. 2005)).

The sampling times were calculated by dividing the initial weight (W0) by the estimated value of *k*. This calculation yields the time for the total course of leaf processing (TLP, days). From the equation *W0 / k = TLP*, we can calculate how many days will be required to reach a desired percentage of the initial weight (Wt). The first sample was collected after 10 days of incubation for both species, so that TLP for 10 days / 0.25 = day on which Wt = 75%. The next sample was collected after 40 days for *E. cloeziana* and after 75 days for *I. laurina*, so that TLP 40/75 days / 0.5 = day by which Wt = 50%. The above procedure was performed for each sample site (based on the mean value) and type of detritus. However, it was not possible to determine the final value for *I. laurina* because the dry season ended after 120 days, before 50% of the mass had been lost. Measurements after the end of the dry season would not have been meaningful because variations in rainfall and associated variations in other physical and chemical conditions would have influenced the results.

On removal from the streams, the litter bags were placed individually into insulated plastic bags and transported in thermal containers (± 4°C) to the laboratory. Temperature, electrical conductivity, pH, dissolved oxygen and water turbidity were obtained *in situ* with a multi-analyzer measured each time leaf bags were removed. The depth and average speed of the right, left and central portions of the watercourse were measured with a flow-meter, and the instantaneous discharge of water was then calculated. We collected 1 L of water to determine the nitrate (Golterman et al. 1978), ammonia (Koroleff 1976) and orthophosphate (Strickland and Parsons 1960) concentrations. The canopy openings were quantified using hemispherical photographs taken with a digital camera equipped with a fish-eye lens. These photographs were later analyzed using Gap Light Analyzer software (2.0). The leaves were washed with tap water in a 120 µm mesh sieve. The invertebrates retained on the sieve were preserved in 70% alcohol for later identification and counting (Pérez 1988; Merritt and Cummins 1996). The numbers of *taxa* and individuals were calculated for the aquatic invertebrate community, and biomass was obtained by desiccation at 60°C for 72 h. The invertebrates were classified into five feeding categories (Pérez 1988; Cummins et al. 2005; Merritt and Cummins 1996): gathering-collectors (G-C), filtering-collectors (F-C), shredders (Sh), scrapers (Sc) and predators (P).

Five leaves from each sample were randomly collected, and three disks (1.2 cm diameter) were extracted from each leaf, resulting in three five-disk sets. One set was used to determine the remaining ash-free dry mass (AFDM; calculated after incineration in a muffle furnace at 550°C for 4 h), and the other sets were used to assess the ergosterol and ATP concentrations. The remaining material was oven-dried at 60°C for 72 h to determine its dry weight. The leaf breakdown rates (*k*) were calculated using the negative exponential model of percent mass lost over time ($W_t = W_0 e^{-kt}$; Wt = remaining weight; W0 = initial weight; -k = decay rate; t = time). After the leaves had been dried and weighed, they were pulverized for further analysis of the total polyphenol and tannic acid concentration (Bärlocher and Graça 2005), lignin and cellulose contents (Gessner 2005b) and the resistance of leaves to rupture (hardness of intact leaves (Graça et al. 2005)). Values for total nitrogen were obtained using a CHN basic analyzer (Carlo Erba 1500 for WI; Thermo Electron Corp. Milan, Italy), and values for total phosphorus were obtained using the ascorbic acid method after acid digestion. The total micro-organism biomass was measured by quantifying ATP (Abelho 2005). The biomass of aquatic Hyphomycetes was evaluated by quantifying ergosterol, a lipid exclusive to fungal membranes in this community (Gessner 2005a).

**Data Analysis**

An analysis of variance (function lm, package stats for R version 2.12.1; (Crawley 2007)) was used to analyze the physical and chemical parameters of the water (temperature, electrical conductivity, pH, dissolved oxygen, turbidity, nitrites, nitrates, orthophosphates and mean velocity) and the structure of stream stretches (instantaneous discharge of the stream and canopy openings in riparian vegetation) as dependent variables, using two categorical factors, namely, sub-basins and stream order . Stream order was also used as a co-variate (continuous variable). We also used the leaf mass remaining, invertebrate communities (number of *taxa*, density and biomass), the relative abundance of functional trophic groups of invertebrates (gathering-collectors, filtering-collectors, shredders, scrapers and predators) and microbial biomass (ATP and ergosterol) as dependent variables against the same two categorical factors. Stream order was also used as a co-variate (continuous variable). This procedure was performed similarly for both types of detritus. All models used a Gaussian distribution (link = log; test = F). We used an analysis of contrasts to discriminate among categorical variables. The normality of the data was tested using a Kolmogorov-Smirnov test, the homogeneity of variance was determined with a Levene test, and the data were transformed whenever necessary with the Naperian logarithm (ln) to obtain the best fit (Crawley 2007).

## RESULTS

### Abiotic Variables

The values of instantaneous discharge, electrical conductivity and nitrates were the highest in the 3rd and 4th order streams. In contrast, the 1st order streams had the highest values for temperature, canopy opening and nitrite concentrations in the water, and the water velocity was the lowest. Dissolved oxygen, pH, turbidity and orthophosphates did not differ among the stream orders (analysis of contrasts, $p < 0.05$; Table S1, Table 1, Figure 2). In sub-basin 2 (SB2), we observed high electrical conductivity, high nitrite and nitrate concentrations and low water temperatures. The values for canopy opening and water velocity were highest in sub-basins 1 (SB1) and 4 (SB4), respectively. Dissolved oxygen and orthophosphates were highest in sub-basin 3 (SB3). Instantaneous discharge, pH and turbidity did not differ among the sub-basins (analysis of contrasts, $p < 0.05$; Table S1, Figure 2). We observed that the higher percentages of sums of squares and variance in instantaneous discharge and water velocity could be explained by differences in the stream order. However, dissolved oxygen, electrical conductivity, temperature, pH, turbidity, canopy opening, nitrates, nitrites and orthophosphates exhibited a high level of variance among the sub-basins (Table 1).

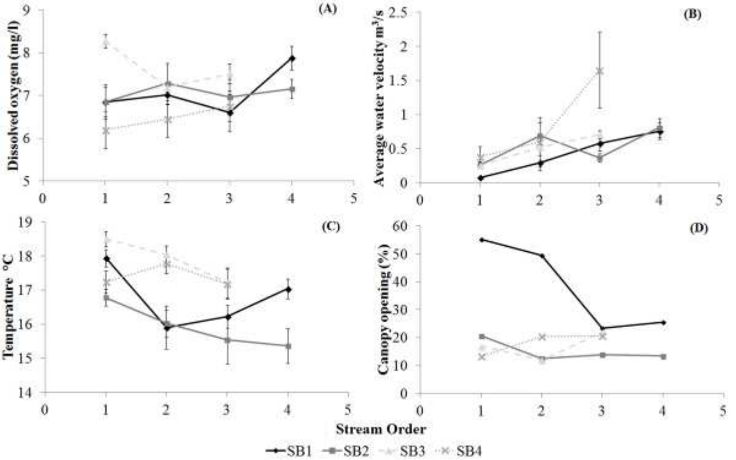


**Figure 2. Abiotic variables.** Mean values and standard errors for dissolved oxygen (A), water velocity (B), water temperature (C) and canopy opening (D) for the stream orders and among sub-basins.

## Leaf Breakdown Rates

The leaf breakdown rates (*k*) were the highest in the 2nd order streams, with values of -0.0083 and -0.0022 for *E. cloeziana* and *I. laurina*, respectively, followed by the 3rd order stream sections, with values of -0.0071 and -0.0022. We also observed higher *k* values in 1st order streams (-0.0053 and -0.0015) than in 4th order streams (-0.0051 and -0.0018) for *E. cloeziana* and *I. laurina*, respectively. However, the remaining mass did not differ among stream orders for either of the detritus types (Figure S2, Table 2, Figure 3A and 4A). The highest *k* values were observed in SB4 (-0.0105 and -0.0030), followed by SB3 (-0.0088 and -0.0022 for *E. cloeziana* and *I. laurina*, respectively). For *E. cloeziana*, the values were -0.0062 and -0.0049, whereas *I. laurina* exhibited values of -0.0018 and -0.0016 (for SB1 and SB2, respectively). The remaining mass showed the lowest values in SB4 and SB3 among the sub-basins studied. The variance in the remaining mass was higher (by sums of squares) and also explained the variations in the sub-basins (Figure S2, Table 2, Figure 3A and 4A).

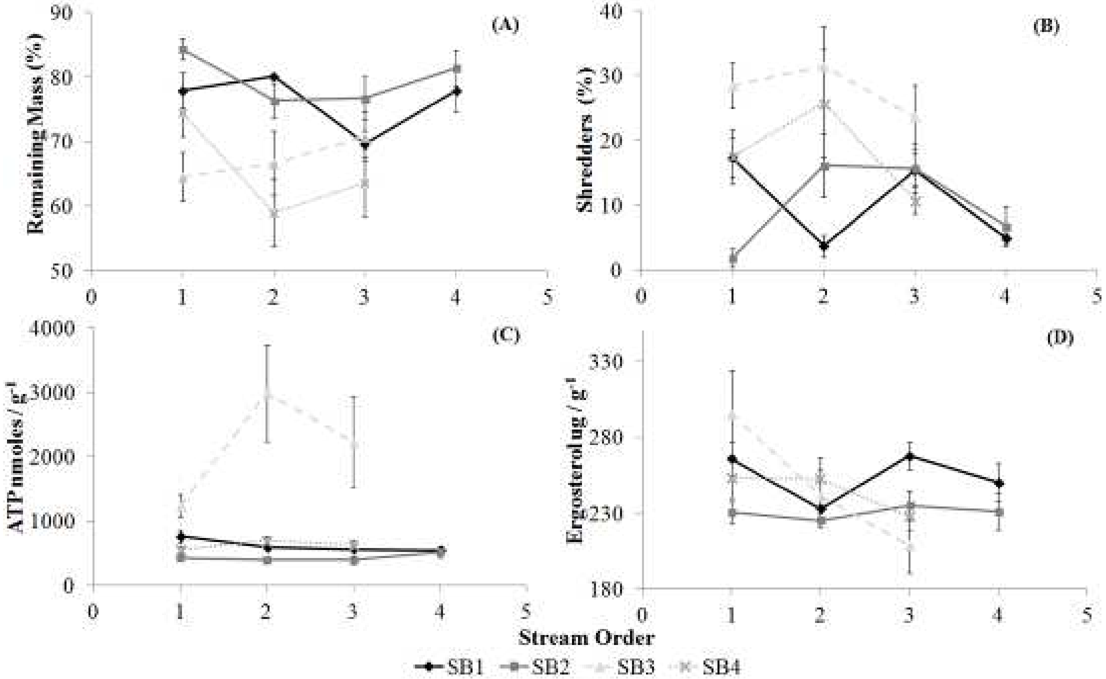


**Figure 3. Leaf breakdown process in *E. cloeziana*.** Mean values and standard errors for the remaining mass (A), shredder abundance (B), total microbial biomass (ATP; C) and fungal hyphomycetal biomass (Ergosterol; D) for the stream orders and sub-basins for *E. cloeziana*.

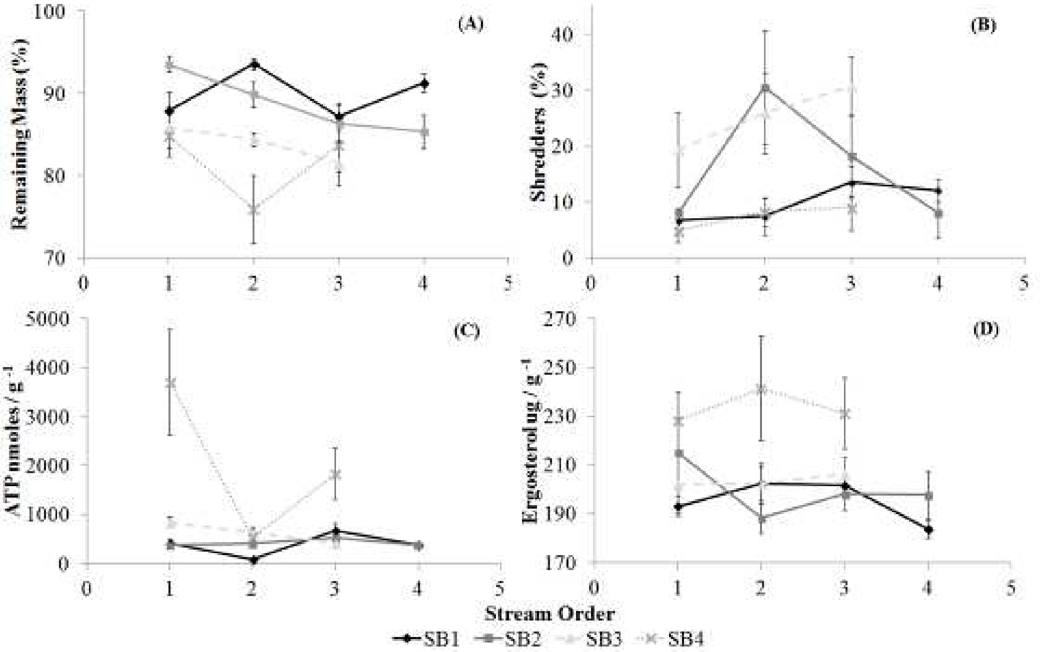


**Figure 4. Leaf breakdown process in *I. laurina*.** Mean values and standard errors for the remaining mass (A), shredder abundance (B), total microbial biomass (ATP; C) and fungal hyphomycetal biomass (Ergosterol; D) for the stream orders and sub-basins for *I. laurina*.

**Table 2.** Degrees of freedom (DF), residuals, sums of squares (%), F test and analyses of variance and contrasts (AC) for the remaining mass, density, richness and biomass of invertebrates, functional trophic groups of invertebrates (predators, shredders, gatherer-collectors, filtering-collectors and scrapers), ATP and ergosterol in sub-basins and along the stream orders in the Gama-Cabeça de Veado Basin for *E. cloeziana* and *I. laurina*.

|  |  | *E. cloeziana* |  |  |  |  | *I. laurina* |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | Df | Sum Sq (%) | F value | Pr(>F) | AC | Df | Sum Sq (%) | F value | Pr(>F) | AC |
| Remaining mass | Sub-Basin | 3 | 15.05 | 6.51 | <**0.001** | SB4 = SB3 < SB1 = SB2 | 3 | 11.01 | 4.72 | **0.004** | SB4 = SB3 < SB2 = SB1 |
|  | Order | 1 | 0.18 | 0.24 | 0.628 |  | 1 | 1.95 | 2.51 | 0.116 |  |
|  | Residuals | 110 | 84.76 |  |  |  | 112 | 87.04 |  |  |  |
| Invertebrate Density | Sub-Basin | 3 | 0.63 | 0.25 | 0.864 |  | 3 | 9.29 | 4.14 | **0.008** | SB2 = SB1 < SB3 = SB4 |
|  | Order | 1 | 5.49 | 6.43 | **0.013** | 2nd = 1st = 3rd < 4th | 1 | 6.88 | 9.19 | **0.003** | 2nd = 1st = 3rd < 4th |
|  | Residuals | 110 | 93.88 |  |  |  | 112 | 83.83 |  |  |  |
| Invertebrate Richness | Sub-Basin | 3 | 12.42 | 5.65 | **0.001** | SB2 = SB1 < SB4 = SB3 | 3 | 25.53 | 15.24 | <**0.001** | SB2 < SB1 = SB3 = SB4 |
|  | Order | 1 | 7 | 9.55 | **0.003** | 1st = 4th = 2nd < 3rd | 1 | 11.92 | 21.33 | <**0.001** | 1st = 2nd < 4th = 3rd |
|  | Residuals | 110 | 80.58 |  |  |  | 112 | 62.56 |  |  |  |
| Invertebrate Biomass | Sub-Basin | 3 | 1.29 | 0.48 | 0.697 |  | 3 | 4.1 | 1.62 | 0.189 |  |
|  | Order | 1 | 0.18 | 0.2 | 0.652 |  | 1 | 1.47 | 1.74 | 0.19 |  |
|  | Residuals | 110 | 98.53 |  |  |  | 112 | 94.43 |  |  |  |
| Predators | Sub-Basin | 3 | 9.44 | 3.84 | **0.012** | SB1 = SB2 = SB3 < SB4 | 3 | 11.87 | 5.09 | **0.002** | SB1 = SB2 < SB3 = SB4 |
|  | Order | 1 | 0.45 | 0.55 | 0.461 |  | 1 | 1.12 | 1.45 | 0.232 |  |
|  | Residuals | 110 | 90.11 |  |  |  | 112 | 87.01 |  |  |  |
| Shredders | Sub-Basin | 3 | 13.89 | 5.99 | **0.001** | SB2 = SB1 = SB4 < SB3 | 3 | 9.76 | 4.09 | **0.008** | SB4 = SB1 = SB2 < SB3 |
|  | Order | 1 | 1.12 | 1.45 | 0.232 |  | 1 | 1.26 | 1.58 | 0.211 |  |
|  | Residuals | 110 | 84.99 |  |  |  | 112 | 88.99 |  |  |  |
| Gatherer-Collectors | Sub-Basin | 3 | 22.51 | 10.68 | <**0.001** | SB4 = SB3 < SB2 = SB1 | 3 | 27.15 | 14.29 | <**0.001** | SB3 = SB2 = SB4 < SB1 |
|  | Order | 1 | 0.23 | 0.33 | 0.565 |  | 1 | 1.91 | 3.02 | 0.085 |  |
|  | Residuals | 110 | 77.26 |  |  |  | 112 | 70.93 |  |  |  |
| Filtering-Collectors | Sub-Basin | 3 | 11.14 | 4.89 | **0.003** | SB1 < SB3 = SB4 = SB2 | 3 | 10.61 | 4.75 | **0.004** | SB1 = SB2 = SB3 < SB4 |
|  | Order | 1 | 5.23 | 6.88 | **0.01** | 1st = 2nd = 4th < 3rd | 1 | 5.98 | 8.03 | **0.005** | 1st < 4th = 2nd = 3rd |
|  | Residuals | 110 | 83.63 |  |  |  | 112 | 83.41 |  |  |  |
| Scrapers | Sub-Basin | 3 | 21.7 | 10.21 | <**0.001** | SB3 = SB4 = SB2 < SB1 | 3 | 11.79 | 5.07 | **0.002** | SB3 = SB4 = SB2 < SB1 |
|  | Order | 1 | 0.34 | 0.47 | 0.493 |  | 1 | 1.5 | 1.94 | 0.166 |  |
|  | Residuals | 110 | 77.96 |  |  |  | 112 | 86.71 |  |  |  |
| ATP | Sub-Basin | 3 | 26.4 | 13.19 | <**0.001** | SB2 = SB1 = SB4 < SB3 | 3 | 17.59 | 8.07 | <**0.001** | SB2 = SB1 = SB3 < SB4 |
|  | Order | 1 | 0.2 | 0.31 | 0.581 |  | 1 | 1.06 | 1.46 | 0.23 |  |
|  | Residuals | 110 | 73.4 |  |  |  | 112 | 81.35 |  |  |  |
| Ergosterol | Sub-Basin | 3 | 2.25 | 0.87 | 0.457 |  | 3 | 9.82 | 4.07 | **0.009** | SB1 = SB2 = SB3 < SB4 |
|  | Order | 1 | 3.27 | 3.81 | 0.053 |  | 1 | 0.1 | 0.13 | 0.72 |  |
|  | Residuals | 110 | 94.47 |  |  |  | 112 | 90.08 |  |  |  |

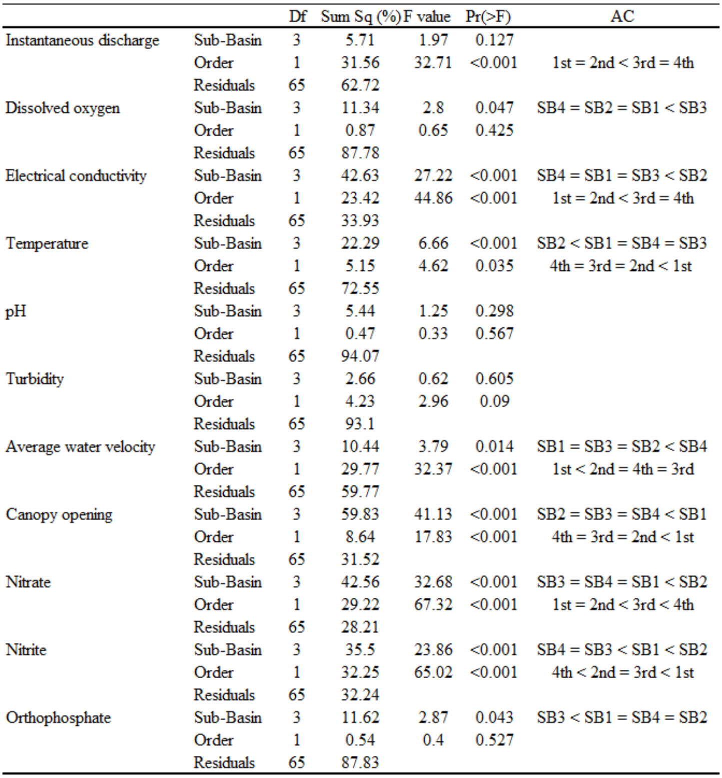
## Biotic Community

The density of invertebrates was higher in 4th order streams for both detritus types (means of 27 and 21 ind/g for *E. cloeziana* and *I. laurina*, respectively). Differences for *I. laurina* were observed among sub-basins, with high values in SB3 (mean 24 ind/g) and SB4 (mean 26 ind/g). The number of *taxa* was significantly different among the stream orders and sub-basins, with the highest values in SB3 (mean of 7 and 6 *taxa* for *E. cloeziana* and *I. laurina*, respectively) and SB4 (mean of 6 *taxa* for *E. cloeziana* and *I. laurina*), primarily in 3rd order streams for both detritus types (mean of 7 and 6 *taxa* for *E. cloeziana* and *I. laurina*, respectively). However, the biomass (total mean 0.003 and 0.002 ind/g for *E. cloeziana* and *I. laurina*, respectively) did not differ among the stream orders or sub-basins for either of the detritus types. The high variances in density, richness and biomass (in terms of the percentage of the sums of squares) were explained by differences in the sub-basins for both detritus types, except for the density of invertebrates in *I. laurina* (Figure S3 and S4, Table 2).

The functional trophic groups differed significantly among stream orders only for the filtering-collectors, with the highest values in the 3rd order streams (mean 20% for *E. cloeziana* and *I. laurina*) and the lowest in the 1st order streams (mean of 10% for *E. cloeziana* and *I. laurina*) for both detritus types. The relative abundance of predators was higher in SB3 (mean 24 and 25% for *E. cloeziana* and *I. laurina*, respectively) and SB4 (mean of 32 and 34% for *E. cloeziana* and *I. laurina*, respectively), whereas the values for shredders were higher in SB3 (mean of 27 and 25% for *E. cloeziana* and *I. laurina*, respectively) for both detritus types. However, SB1 exhibited high abundances of gathering-collectors (mean of 41 and 50% for *E. cloeziana* and *I. laurina*, respectively) and scrapers (mean of 18 and 16% for *E. cloeziana* and *I. laurina*, respectively) but a low abundance of filtering-collectors (mean of 6 and 8% for *E. cloeziana* and *I. laurina*, respectively) for both detritus types. The high variance in the relative abundance for all functional trophic groups (by the sums of squares) was also explained by changes in sub-basins for both detritus types (Figure S3 and S4, Table 2, Figure 3B and 4B).

The ATP values differed only among sub-basins for both detritus types, with the highest values in SB3 (mean of 2155.8 nmoles/g AFDM) for *E. cloeziana* (total mean 991.8 nmoles/g AFDM) and in SB3 (mean 633.3 nmoles/g AFDM) and SB4 (mean 2023.9 nmoles/g AFDM) for *I. laurina* (total mean 847.8 nmoles/g AFDM) (Table 2; Fig. 2C and 3C). There were no differences in the ergosterol concentrations among the hydrological stream orders and sub-basins for *E. cloeziana* (total mean 541.2 ug/g). However, we found higher ergosterol concentrations for *I. laurina* (total mean 382.9 ug/g) in SB3 (mean 392.6 ug/g) and SB4 (mean 464.1 ug/g), although they did not differ among the hydrological stream orders. The variances in ATP and ergosterol concentrations were also explained by changes in sub-basins for both detritus types, except for ergosterol in *E. cloeziana*, which showed a high level of variation with stream order (Figure S3 and S4, Table 2, Figure 3D and 4D).

**Table 1.** Degrees of freedom (DF), residuals, sums of squares (%), F tests and analyses of variance and contrasts (AC) for dissolved oxygen, electrical conductivity, water temperature, pH, turbidity, water velocity, canopy openness and nitrites, nitrates and orthophosphates in sub-basins and along the stream orders in the Gama-Cabeça de Veado Basin.



| | | Df | Sum Sq (%) | F value | Pr(>F) | AC |
|---|---|---|---|---|---|---|
| Instantaneous discharge | Sub-Basin | 3 | 5.71 | 1.97 | 0.127 | |
| | Order | 1 | 31.56 | 32.71 | <0.001 | 1st = 2nd < 3rd = 4th |
| | Residuals | 65 | 62.72 | | | |
| Dissolved oxygen | Sub-Basin | 3 | 11.34 | 2.8 | 0.047 | SB4 = SB2 = SB1 < SB3 |
| | Order | 1 | 0.87 | 0.65 | 0.425 | |
| | Residuals | 65 | 87.78 | | | |
| Electrical conductivity | Sub-Basin | 3 | 42.63 | 27.22 | <0.001 | SB4 = SB1 = SB3 < SB2 |
| | Order | 1 | 23.42 | 44.86 | <0.001 | 1st = 2nd < 3rd = 4th |
| | Residuals | 65 | 33.93 | | | |
| Temperature | Sub-Basin | 3 | 22.29 | 6.66 | <0.001 | SB2 < SB1 = SB4 = SB3 |
| | Order | 1 | 5.15 | 4.62 | 0.035 | 4th = 3rd = 2nd < 1st |
| | Residuals | 65 | 72.55 | | | |
| pH | Sub-Basin | 3 | 5.44 | 1.25 | 0.298 | |
| | Order | 1 | 0.47 | 0.33 | 0.567 | |
| | Residuals | 65 | 94.07 | | | |
| Turbidity | Sub-Basin | 3 | 2.66 | 0.62 | 0.605 | |
| | Order | 1 | 4.23 | 2.96 | 0.09 | |
| | Residuals | 65 | 93.1 | | | |
| Average water velocity | Sub-Basin | 3 | 10.44 | 3.79 | 0.014 | SB1 = SB3 = SB2 < SB4 |
| | Order | 1 | 29.77 | 32.37 | <0.001 | 1st < 2nd = 4th = 3rd |
| | Residuals | 65 | 59.77 | | | |
| Canopy opening | Sub-Basin | 3 | 59.83 | 41.13 | <0.001 | SB2 = SB3 = SB4 < SB1 |
| | Order | 1 | 8.64 | 17.83 | <0.001 | 4th = 3rd = 2nd < 1st |
| | Residuals | 65 | 31.52 | | | |
| Nitrate | Sub-Basin | 3 | 42.56 | 32.68 | <0.001 | SB3 = SB4 = SB1 < SB2 |
| | Order | 1 | 29.22 | 67.32 | <0.001 | 1st = 2nd < 3rd < 4th |
| | Residuals | 65 | 28.21 | | | |
| Nitrite | Sub-Basin | 3 | 35.5 | 23.86 | <0.001 | SB4 = SB3 < SB1 < SB2 |
| | Order | 1 | 32.25 | 65.02 | <0.001 | 4th < 2nd = 3rd < 1st |
| | Residuals | 65 | 32.24 | | | |
| Orthophosphate | Sub-Basin | 3 | 11.62 | 2.87 | 0.043 | SB3 < SB1 = SB4 = SB2 |
| | Order | 1 | 0.54 | 0.4 | 0.527 | |
| | Residuals | 65 | 87.83 | | | |

## DISCUSSION

### Scale Analysis

The instantaneous discharge, water velocity, turbidity and nitrogen series (nitrate and nitrite) were more influenced by changes in stream order (high heterogeneity), with higher values downstream (increasing from 1st to 4th order), as expected according to Vannote et al. (Vannote et al. 1980), except that nitrites exhibited the inverse pattern. The finding of relatively few influences at local scales can be explained by the large discontinuities inherent in smaller geomorphological units (habitat patches create discontinuities in space) that increase the potential influence from the local characteristics of the environment (Benda et al. 2004; Larned et al. 2010; Wiens 1989; Wiens 2002). Flow changes, for example, create hydrological discontinuities along stream corridors and isolate habitats. However, the other abiotic variables were influenced by changes in sub-basins (high homogeneity) that correspond to regional scales (Allen and Starr 1982; Frissell et al. 1986). These factors worked at the watershed level and may increase its fragility in the face of intense climatic changes because the climate is the primary controlling factor at large scales (Allan 2004). The basins are influenced by environmental factors that systematically change across longitudinal (upstream/downstream), vertical (sediment/water) and lateral (terrestrial/aquatic) gradients, forming different spatial and temporal patterns at regional and local scales (Larned et al. 2010; Schneider 2001; Wiens 2002).

As expected, the high-quality detritus (*E. cloeziana*) showed more rapid leaf breakdown rates ($k$) than the low-quality (*I. laurina*) detritus, indicating that the rate could be driven by micro-scale processes (Wiens 1989). These findings represent important evidence that the riparian vegetation could be responsible for determining the ecosystem characteristics (Cummins 1974; Naiman and Décamps 1997; Petersen and

Cummins 1974), as also proposed by Gonçalves et al. (Gonçalves et al. 2012b) for tropical systems, highlighting the need to study this vegetation. For example, if riparian vegetation is composed of plant species that have a higher stoichiometric ratio (higher quality), we expect more rapid response for organic matter cycling (higher decomposition). This direct relationship between terrestrial and aquatic ecosystems demonstrates that any modification in a riparian ecosystem would affect the function, primarily in areas composed of palatable plants (high quality and decomposition), corroborating the work of Frauendorf et al. (Frauendorf et al. 2013). Thus, lower quality vegetation (slower decomposition) will be less sensitive to other factors, and this may explain the resistance of the Brazilian savanna in comparison with other Brazilian tropical systems (Carvalho et al. 2009). Moreover, the leaf breakdown at the macro-scale was more influenced by the regional scale (sub-basin) than by the local scale (stream order) (Wiens 1989), confirming our hypothesis. This result indicates that the patterns observed in studies covering a given time period (timely studies), common in tropical literature (for more see also (Bianchini_Jr. 1999; Gonçalves et al. 2013)), cannot be generalized from local to regional scales (Bae et al. 2011; Schneider 2001; Young and Collier 2009) or to whole watersheds (Lowe et al. 2006; Tiegs et al. 2009; Wiens 1989; Wiens 2002). In addition, this finding may indicate fragility in the upstream basins due to the slower leaf breakdown rates. However, the upstream area is a source of nutrients and organisms for the downstream basins (Vannote et al. 1980). The upstream basins can give support productivity and may be responsible for extending the depuration capability of the system (as represented by the microbial pools) and maintaining functionality downstream (Frauendorf et al. 2013). Therefore, we believe that the association between detritus quality (important at the micro-scale) and the environmental features of the watershed (important at the macro-scale) is responsible for shaping organic matter cycling in the watershed and should be further investigated in future studies.

Previous studies indicating that the microbial community is the principal decomposer (Cummins 1974; Gessner et al. 1999; Gonçalves et al. 2012b), are confirmed by our results, as we found that the high-quality leaf species was also more susceptible to leaching and microbial action, whereas the low-quality leaf species was influenced primarily by fungal colonization. Both leaf samples were consumed by shredders, but a higher abundance of shredders was observed in the *E. cloeziana* detritus. We also found a higher loss of mass due to the high water velocity (mechanical fragmentation and leaching), dissolved oxygen and temperatures, which accelerate biological metabolism (Gulis and Suberkropp 2003; Medeiros et al. 2009). The detritus quality is important only for defining the local rates and their pathways for leaf breakdown (Ardon and Pringle 2008; Gessner et al. 1999; Gonçalves et al. 2012b). However, the detritus quality has little influence on the general pattern along the "riverscape" and at any specific scale (Tiegs et al. 2009). Therefore, based on an analysis of the samples after a certain percentage of mass has been lost (25, 75 and 50%) and not simply at predefined time points (e.g., 7, 15, 30 days), it is possible to show a clear colonization effect independent of quality. To be sure, detritus quality is a highly important determinant of the abundance of shredders and explains the importance of shredders for both detritus types (Gonçalves et al. 2012a). We cannot study the variations associated with spatial scale in terms only of the local context because there are many factors in the ecological levels (community and ecosystem) that are responsible for variability found in the large scale (Wiens 2002; Young and Collier 2009). However, the local approach has been used in all previous tropical studies of leaf breakdown (Abelho 2001; Gonçalves et al. 2013).

## Leaf Breakdown Rates

In agreement with the proposal of Gonçalves et al. (Gonçalves et al. 2013) for tropical systems, the *k* values of *E. cloeziana* were classified as intermediate (-0.0173 > k > -0.0041), and those of *I. laurina* were classified as slow (k < -

0.0041) for all sampling sites, indicating a strong influence of detritus quality. The high leaching due to the high solubility of polyphenols and tannins (secondary compounds) in *E. cloeziana* can accelerate the decay rate (Ardon and Pringle 2008; Ardon et al. 2006). Therefore, the rapid leaching of these secondary compounds, which has an inhibitory effect on detritivores, as well as the lower hardness of *E. cloeziana,* did not limit biotic colonization due to the low residence time in this type of detritus (Ardon and Pringle 2008; Gonçalves et al. 2012b). Additionally, *Eucalyptus* sp. (an exotic species) is rapidly colonized and decomposed in the Brazilian savannah. It is possible that this pattern is due to the high quality of *Eucalyptus* relative to native species (Gonçalves et al. 2012a; Gonçalves et al. 2012b; Oliveira-Filho and Ratter 1994).

In contrast, we found lower breakdown rates for *I. laurina* which were most likely a consequence of a high content of structural compounds (lignin and cellulose) and relative hardness (cuticle thickness), hindering the release of other chemical compounds (e.g., polyphenols, nitrogen and phosphorus (Ardon et al. 2006; Gonçalves et al. 2012b; Oliveira-Filho and Ratter 1994)). Therefore, the chemical characteristics of detritus determine the speed of processing (primarily at local scales), showing that leaf breakdown rates increase with quality and palatability (Gessner et al. 1999; Gonçalves et al. 2012a; Gonçalves et al. 2012b; Graça et al. 2001). Detritus quality is of lower importance when if it is observed at different scales. In the study area, we observed that the regional scale is decisive for driving the general pattern of this important ecological process along the "riverscapes" (Allan 2004; Frissell et al. 1986).

## Abiotic and Biotic Variables in Leaf Breakdown

The natural environmental changes that occur across stream orders (Benda et al. 2004) were not sufficient to modify the remaining mass, and the local scale could not affect the decomposer communities (shredders and microorganisms) for either of the detritus types. Decomposer communities are the driving factors for leaf breakdown, and their absence leads to similar breakdown patterns along the stream order gradient (Gessner et al. 1999). This finding might indicate that ecological functioning in headwater streams (1st to 3rd order) was similar within the same sub-basin (Vannote et al. 1980) . However, this process might change over a large spatial gradient, as represented by the sub-basin scale (Allan 2004). Nevertheless, increases in richness and the density of invertebrates and a decrease in the abundance of filtering-collectors for both detritus types were observed across this large spatial gradient. These results demonstrate that these variables had no effect on leaf breakdown (Cummins et al. 2005; Merritt and Cummins 1996).

The values of the remaining mass for both detritus types were lower in SB4 and SB3 (high decomposition) than in the other sub-basins. It is probable that the reason for this difference was the higher temperatures, dissolved oxygen concentrations and water velocities resulting from the microclimate of the geographic location (within a valley). Therefore, the higher temperatures (Gulis and Suberkropp 2003) and oxygen concentrations (Medeiros et al. 2009) observed in SB4 and SB3 may elevate the metabolic activity of the decomposer community (Suberkropp and Chauvet 1995), especially microorganisms. The higher metabolic activity of the decomposer community, associated with high water velocity (mechanical fragmentation and leaching), which increased the degree of physical abrasion (Santos Fonseca et al. 2012), accelerated the leaf breakdown rates. In SB4 and SB3, higher density and richness of invertebrates and higher shredder abundance, with the greatest densities in *E. cloeziana,* were also observed. The shredders directly utilize leaf tissues for feeding, and increasing biological fragmentation (Boyero et al. 2012; Graça et al. 2001) can also accelerate the leaf breakdown rates (Sponseller and Benfield 2001). Certain shredders in these locations (genus *Phylloicus*) can build their capsules from leaf tissue, and this use of leaf material also contributes to fragmentation (Cummins et al. 2005; Merritt and Cummins 1996).

The relative abundance of shredders was influenced by variation, primarily among the sub-basins. A greater relative abundance of shredders in comparison with other tropical systems was observed in SB3 for both detritus types (Boyero et al. 2012; Gonçalves et al. 2012a; Wantzen and Wagner 2006). A low relative abundance of shredders was found in the other sub-basins. This result is consistent with the findings of previous studies in the Cerrado (Gonçalves et al. 2007; Gonçalves et al. 2012a; Gonçalves et al. 2013). The importance of shredders for leaf breakdown is unclear in the tropics due to their low abundance or absence in these streams (Boyero et al. 2012; Gonçalves et al. 2012a; Wantzen and Wagner 2006), but studies have shown little effect in tropical streams (Moretti et al. 2007; Moulton et al. 2010). From a global perspective, the strong effects observed in the current study were most likely due to the preference of shredders (primarily Trichoptera and Plecoptera) for high altitudes (due to the lower temperatures) in tropical regions (Boyero et al. 2012). The preference of this group for *E. cloeziana* indicates that detritus quality is also important (Wantzen and Wagner 2006) and that the composition of the vegetation influences the functioning of aquatic systems. Therefore, higher altitudes (low temperature (Boyero et al. 2012)), high dissolved oxygen, the composition of the flora (ideally including *E. cloeziana* (Wantzen and Wagner 2006)) and moderate values of nutrient concentrations in the water (Bae et al. 2011) favor a high abundance of shredders. The predominance in the Cerrado of leaves that are low in nutrients (Oliveira-Filho and Ratter 1994), is associated with hydric and thermic stress and could be responsible for the absence or low abundance of shredders found in most tropical streams (Boyero et al. 2012; Wantzen and Wagner 2006).

The high-quality detritus (*E. cloeziana*) was shown to be most influenced by the total microbial community and the low-quality detritus (*I. laurina*) by the fungal community in SB4 and SB3 (high decomposition). *E. cloeziana* has elevated amounts of labile compounds, facilitating the activity of bacteria (rapid life cycles) that use compounds derived from the leaching of the leaves of labile detritus as their preferred resource (Weyers and Suberkropp 1996). These bacteria could be important during leaf breakdown and not only, as observed by several authors, at the early stages of the process (Gessner et al. 1999; Gonçalves et al. 2012b; Gonçalves et al. 2013). However, this pattern is rarely observed in tropical streams. In lower-quality detritus (*I. laurina*), we observed an interaction between the biomass of the two microbial communities, highlighting fungi as the principal component (Gulis and Suberkropp 2003). Due to its high capacity to metabolize refractory molecules (e.g., cellulose and lignin) and to decompose them, the fungal community is the primary decomposer in tropical streams, and this principle explains the great significance of fungi in *I. laurina* decomposition (Gessner et al. 1999; Gonçalves et al. 2012b; Weyers and Suberkropp 1996). Fungal action can increase the palatability of detritus, as well as its nutritional quality, for other decomposers, and the high biomass of fungi might be another factor responsible for the higher abundance of shredders in these sub-basins (Gonçalves et al. 2012b; Graça et al. 2001).

In general, we conclude that variations in scale contribute to the variation in the leaf breakdown rate, highlighting the importance of similar studies of this type that determine effects at different scales. The variability of the physical structure of streams (primarily temperature, dissolved oxygen and nutrients) accelerates leaf breakdown from upstream to downstream, but this process was only demonstrated at the sub-basin scale in the location studied, partially corroborating the initial hypothesis. The replacement of shredder invertebrates by microorganisms was observed but was contrary to the prediction of our hypothesis. Shredders were favored by microorganisms (primarily in *E. cloeziana*), with stronger interactions between them than those previously found to drive leaf breakdown rates. Based on our interest in the influence of spatial structure on ecosystem functions, we observed that watersheds with warmer microclimates and streams with higher nutrient levels and oxygen in the water could be accelerating the metabolism of the ecosystem in the watershed, with increased negative effects downstream. For the management of tropical watersheds, we noted that the upstream areas are more fragile and sensitive to environmental impacts but show greater importance in the cycling of nutrients. We performed analyses within and between spatial scales to assess the relative importance of various watershed scales in determining the local breakdown rate for leaves. Local characteristics are responsible for the diversification of this process across the “riverscape”, and high heterogeneity underscores the difficulty of making predictions based on local studies.

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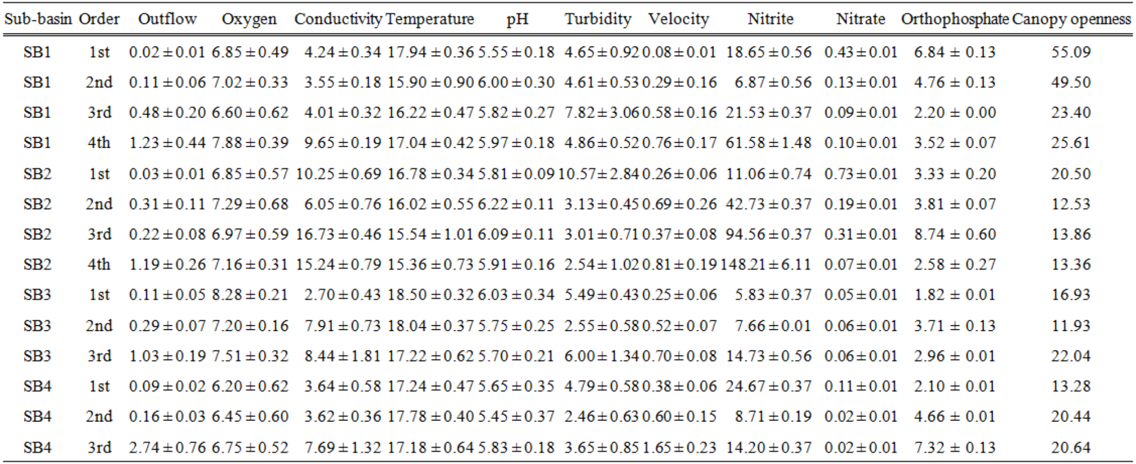
# APPENDICES

**Table S1.** Average values and the standard deviation of outflow, dissolved oxygen in the water (mg l$^{-1}$), electrical conductivity (μS-cm$^{2}$), water temperature (Temp. °C), pH, turbidity (NTU), water velocity (m-s), nitrite, nitrate, orthophosphate (mg l$^{-1}$) and the percentage of canopy openness (%) in sub-basin and stream order along the Gama-Cabeça de Veado Basin.



| Sub-basin | Order | Outflow | Oxygen | Conductivity | Temperature | pH | Turbidity | Velocity | Nitrite | Nitrate | Orthophosphate | Canopy openness |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SB1 | 1st | 0.02 ± 0.01 | 6.85 ± 0.49 | 4.24 ± 0.34 | 17.94 ± 0.36 | 5.55 ± 0.18 | 4.65 ± 0.92 | 0.08 ± 0.01 | 18.65 ± 0.56 | 0.43 ± 0.01 | 6.84 ± 0.13 | 55.09 |
| SB1 | 2nd | 0.11 ± 0.06 | 7.02 ± 0.33 | 3.55 ± 0.18 | 15.90 ± 0.90 | 6.00 ± 0.30 | 4.61 ± 0.53 | 0.29 ± 0.16 | 6.87 ± 0.56 | 0.13 ± 0.01 | 4.76 ± 0.13 | 49.50 |
| SB1 | 3rd | 0.48 ± 0.20 | 6.60 ± 0.62 | 4.01 ± 0.32 | 16.22 ± 0.47 | 5.82 ± 0.27 | 7.82 ± 3.06 | 0.58 ± 0.16 | 21.53 ± 0.37 | 0.09 ± 0.01 | 2.20 ± 0.00 | 23.40 |
| SB1 | 4th | 1.23 ± 0.44 | 7.88 ± 0.39 | 9.65 ± 0.19 | 17.04 ± 0.42 | 5.97 ± 0.18 | 4.86 ± 0.52 | 0.76 ± 0.17 | 61.58 ± 1.48 | 0.10 ± 0.01 | 3.52 ± 0.07 | 25.61 |
| SB2 | 1st | 0.03 ± 0.01 | 6.85 ± 0.57 | 10.25 ± 0.69 | 16.78 ± 0.34 | 5.81 ± 0.09 | 10.57 ± 2.84 | 0.26 ± 0.06 | 11.06 ± 0.74 | 0.73 ± 0.01 | 3.33 ± 0.20 | 20.50 |
| SB2 | 2nd | 0.31 ± 0.11 | 7.29 ± 0.68 | 6.05 ± 0.76 | 16.02 ± 0.55 | 6.22 ± 0.11 | 3.13 ± 0.45 | 0.69 ± 0.26 | 42.73 ± 0.37 | 0.19 ± 0.01 | 3.81 ± 0.07 | 12.53 |
| SB2 | 3rd | 0.22 ± 0.08 | 6.97 ± 0.59 | 16.73 ± 0.46 | 15.54 ± 1.01 | 6.09 ± 0.11 | 3.01 ± 0.71 | 0.37 ± 0.08 | 94.56 ± 0.37 | 0.31 ± 0.01 | 8.74 ± 0.60 | 13.86 |
| SB2 | 4th | 1.19 ± 0.26 | 7.16 ± 0.31 | 15.24 ± 0.79 | 15.36 ± 0.73 | 5.91 ± 0.16 | 2.54 ± 1.02 | 0.81 ± 0.19 | 148.21 ± 6.11 | 0.07 ± 0.01 | 2.58 ± 0.27 | 13.36 |
| SB3 | 1st | 0.11 ± 0.05 | 8.28 ± 0.21 | 2.70 ± 0.43 | 18.50 ± 0.32 | 6.03 ± 0.34 | 5.49 ± 0.43 | 0.25 ± 0.06 | 5.83 ± 0.37 | 0.05 ± 0.01 | 1.82 ± 0.01 | 16.93 |
| SB3 | 2nd | 0.29 ± 0.07 | 7.20 ± 0.16 | 7.91 ± 0.73 | 18.04 ± 0.37 | 5.75 ± 0.25 | 2.55 ± 0.58 | 0.52 ± 0.07 | 7.66 ± 0.01 | 0.06 ± 0.01 | 3.71 ± 0.13 | 11.93 |
| SB3 | 3rd | 1.03 ± 0.19 | 7.51 ± 0.32 | 8.44 ± 1.81 | 17.22 ± 0.62 | 5.70 ± 0.21 | 6.00 ± 1.34 | 0.70 ± 0.08 | 14.73 ± 0.56 | 0.06 ± 0.01 | 2.96 ± 0.01 | 22.04 |
| SB4 | 1st | 0.09 ± 0.02 | 6.20 ± 0.62 | 3.64 ± 0.58 | 17.24 ± 0.47 | 5.65 ± 0.35 | 4.79 ± 0.58 | 0.38 ± 0.06 | 24.67 ± 0.37 | 0.11 ± 0.01 | 2.10 ± 0.01 | 13.28 |
| SB4 | 2nd | 0.16 ± 0.03 | 6.45 ± 0.60 | 3.62 ± 0.36 | 17.78 ± 0.40 | 5.45 ± 0.37 | 2.46 ± 0.63 | 0.60 ± 0.15 | 8.71 ± 0.19 | 0.02 ± 0.01 | 4.66 ± 0.01 | 20.44 |
| SB4 | 3rd | 2.74 ± 0.76 | 6.75 ± 0.52 | 7.69 ± 1.32 | 17.18 ± 0.64 | 5.83 ± 0.18 | 3.65 ± 0.85 | 1.65 ± 0.23 | 14.20 ± 0.37 | 0.02 ± 0.01 | 7.32 ± 0.13 | 20.64 |

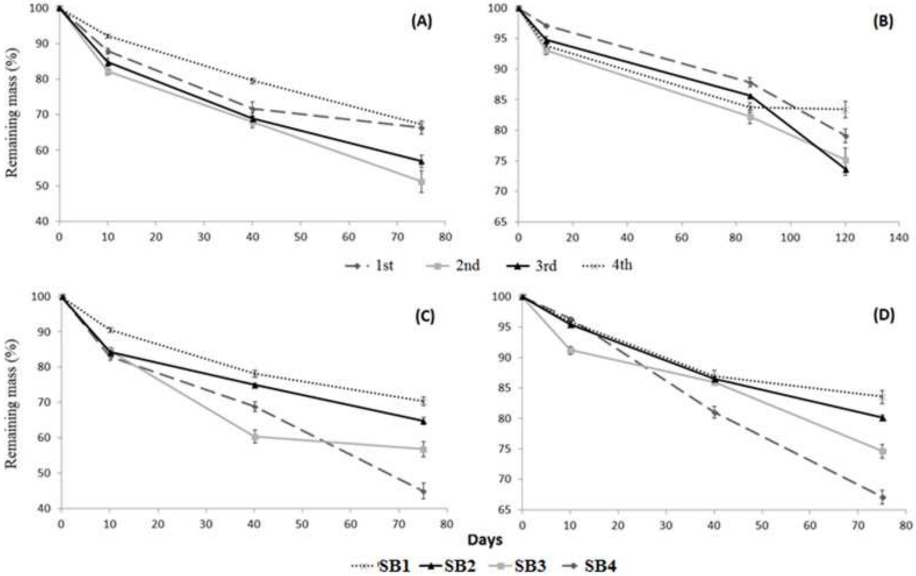


**Figure S2.** Percentages of remaining mass along of the day in *E. cloeziana* (A and C) and *I. laurina* (B and D), between stream order (A e B) and sub-basin (C and D).

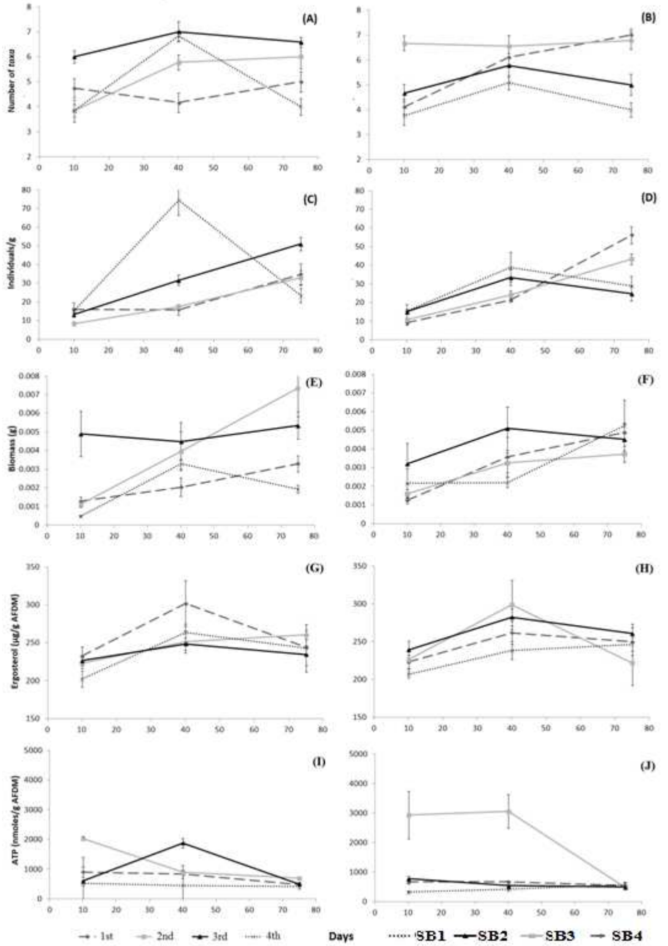


**Figure S3.** Average values and standard error of density (A and B), richness (C and D), biomass (E and F) of aquatic invertebrates, total microbial biomass (ATP; G and H) and fungal hyphomicetos biomass (I and J) along of the days in *E. cloeziana*, among stream order (A, C, E, G and I) and sub-basin (B, D, F, H and J).

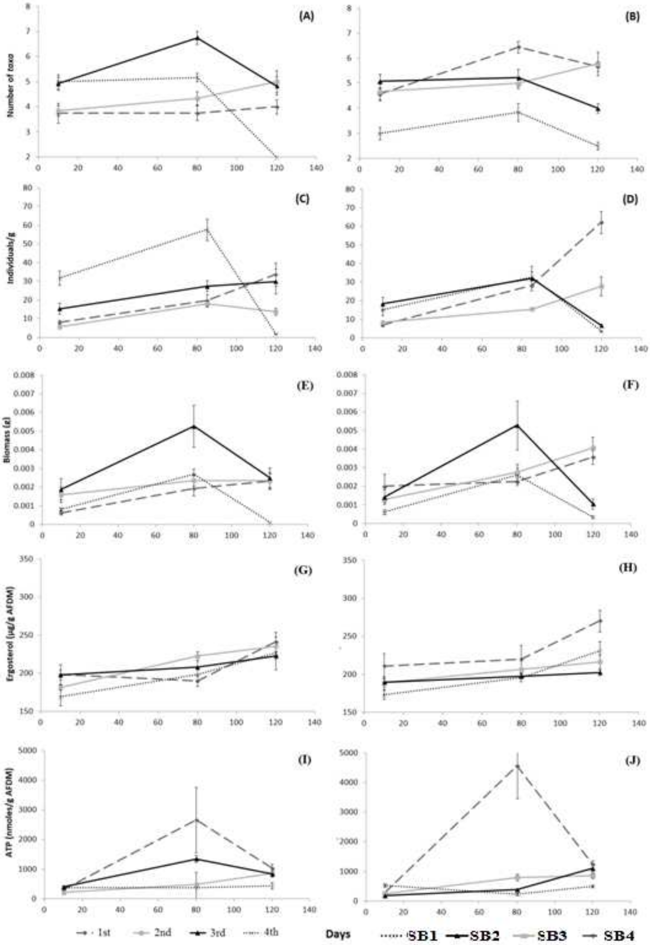


**Figure S4.** Average values and standard error of density (A and B), richness (C and D), biomass (E and F) of aquatic invertebrates, total microbial biomass (ATP; G and H) and fungal hyphomicetos biomass (I and J) along of the days in *I. laurina*, among stream order (A, C, E, G and I) and sub-basin (B, D, F, H and J).

# CONCLUSÕES FINAIS

A temperatura e a biomassa de micro-organismos (principalmente fungos, que apresentou espécies adaptadas a locais de maior temperatura) foram os fatores mais importantes para a decomposição em sistemas ripários tropicais/Cerrado, em ambas as escalas avaliadas (espacial e temporal). Isso pode ser um passo importante para produzir modelos matemáticos capazes de prever as taxas de decomposição a partir de características ambientais simples.

A variação temporal modifica a resposta da decomposição foliar em sistemas lóticos, com menores taxas na seca e maiores no início das chuvas. Assim, como a maioria dos trabalhos realizados em região tropical/Cerrado ocorreram na seca, tornando as tentativas de traçar padrões gerais pouco realistas e subestimadas. A variação temporal permite maiores picos de entrada de matéria orgânica (setembro e outubro) no final do período da seca. Entretanto, observou-se a existência de um "time lag" com o pico de decomposição (dezembro), indicando a possibilidade de prever ambos os picos através do regime climático (temperatura e pluviosidade). Outro aspecto é que temporalmente os sistemas ripários estudados apresentaram uma maior instabilidade no processo de decomposição e parâmetros físicos e químicos da água nos meses de transição, entre os períodos de seca e chuva. No período de seca foi observado maiores densidade e riqueza de invertebrados, biomassa de micro-organismo. Entretanto, no período chuvoso foi observado maiores taxas de decomposição, possivelmente em função das elevadas temperaturas, que pode acelerar o metabolismo das comunidades decompositoras.

Sobre o funcionamento de veredas, verificamos que apesar de apresentar um solo muito orgânico, este sistema apresenta baixa produtividade, possivelmente, em função de elevada capacidade de retenção de matéria orgânica associado a baixa capacidade de transporte destas áreas. Outro aspecto é que em função dos pulsos de inundação (seca e chuva), o rápido acumulo e empilhamento de matéria orgânica, pode gerar um ambiente com baixa concentração de oxigênio, e assim desacelerar a decomposição nestas camadas mais profundas, comparadas as superficiais (alta decomposição no extrato mais superficial da serapilheira). Isso pode explicar o solo rico em humos nos extratos mais profundos do solo das veredas.

O impacto sobre a remoção parcial do dossel da vegetação nativa (extrativismo vegetal) afetou parâmetros bióticos (invertebrados e micro-organismos) e abióticos (parâmetros físicos e químicos da água) associados a decomposição indicando que este processo é útil na avaliação de impactos ambientais. Estudos mostram que a vegetação nativa pode funcionar como uma zona de proteção, mantendo constante o micro clima em áreas riparias (menor variação na luminosidade, temperatura e umidade), e sua remoção interrompe essa proteção natural deixando o sistema mais suscetíveis as mudanças sazonais. Este fato pode explicar o aumentando a frequência e intensidade das mudanças ambientais com retirada da vegetação nativa, consequentemente, elevando a amplitude sobre os parâmetros bióticos e abióticos observados no nosso estudo.

Quando avaliado as diferentes escalas, se observou maior explicação da variância das taxas de decomposição foliar, variáveis bióticas e abióticas relacionadas a este processo pela escala regional, independente do tipo de detrito. A variabilidade da estrutura física nos sistemas lóticos (principalmente temperatura, oxigênio e nutrientes dissolvidos) podem atuar diretamente acelerando o metabolismo das comunidades decompositoras e, consequentemente a decomposição. Assim, os resultados obtidos a partir de um ponto amostral não permitem generalizações para toda a bacia. Para estudos de ordem hidrológica a nível de bacia hidrográfica é necessário réplicas de rios em diferentes sub-bacias de mesma ordem, em função do gradiente crescente na taxa de decomposição de montante para jusante na bacia hidrográfica. Isso pode ser explicado pelo aumento da temperatura e biomassa de micro-organismos e abundancia de invertebrados fragmentadores ao longo deste gradiente.

## PESPECTIVAS FUTURAS

Os seguintes tópicos são recomendados para serem avaliados em experimentos futuros:

1. Buscar padrões de produtividade dos ecossistemas aquáticos e zonas ripárias tropicais e verificar como os gradientes (longitudinais e latitudinais) de produtividade podem influenciar a decomposição foliar em sistemas lóticos tropicais.
2. Estimar as taxas de retenção e transporte de matéria orgânica ao longo da dinâmica sazonal em ambientes tropicais e sua influencia sobre a decomposição.
3. Avaliar como outras formas de impacto ou alteração ambiental modificam o processo de decomposição foliar em sistemas lóticos tropicais.
4. Produzir mecanismos de valoração do processo de decomposição, considerando os serviços e prejuízos em função de atividade antrópica.
5. Investir na decomposição como uma ferramenta de biomonitoramento, ajudando a determinar fatores e mecanismos responsáveis pela resistência dos ecossistemas aquáticos às perturbações externas.
6. Ampliar estudos que abordem como a estrutura espacial dos ecossistemas aquáticos tropicais pode influenciar os processos ecológicos, como a decomposição foliar.
7. Verificar a importância dos fatores ambientais e / ou espaciais sobre a biodiversidade (alfa e beta) da comunidade decompositora e, consequentemente, como esta variação pode alterar as taxas de decomposição foliar em sistemas lóticos.
8. Entender o padrão de distribuição dos fragmentadores em sistemas tropicais e explicar sua baixa participação na decomposição quando comparado a sistemas temperados.

9. Produzir modelos matemáticos a partir da distribuição de características simples, como por exemplo, composição da vegetação ripária, temperatura e precipitação que sejam capazes de prever taxas de decomposição.