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Temporal leaf litter breakdown in a tropical riparian forest with an open canopy

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ABSTRACT

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In aquatic environments, especially in shaded patches (where primary production is limited by the low-light conditions), energy flow and organic-matter cycling are fundamental for maintaining a system's metabolism. The breakdown of this organic detritus is a key process for its remobilization into the trophic chains. Our objective was to describe the temporal dynamics of leaf breakdown in a tropical stream with a riparian canopy degraded by the extraction of palm trees. The vertical input of leaves was collected monthly in a natural stream and incubated for 30 days in a stream with a degraded canopy. Leaf breakdown rates (k), and leaf associated microbial biomass, fungal sporulation and invertebrate community were estimated. Higher values of k were observed in summer most likely due to high temperatures (increased metabolic activity) and rainfall (higher physical abrasion). Aquatic invertebrates (mainly shredders) and total microorganisms showed no overall influence on leaf breakdown rates. Therefore, in this large temporal sampling, water flow, temperature and precipitation were the factors controlling k in this stream. There were no observed changes in k compared to natural environments, most likely because the canopy degradation is a structural modification and does not represent a source of pollution.

Key words: Precipitation, riparian forest, microorganism, invertebrates, litter decomposition.

RESUMEN

Dinámica temporal de la descomposición de hojarasca en un arroyo tropical con cobertura arbórea abierta

En los ambientes acuáticos, especialmente en las zonas de sombra (donde la producción primaria está limitada por las condiciones de poca luz), el flujo de energía y el ciclo de materia orgánica son fundamentales para el mantenimiento del metabolismo del sistema. La descomposición de los detritos orgánicos es un proceso clave para su movilización a través de las cadenas tróficas. Nuestro objetivo fue describir la dinámica temporal de la descomposición de hojarasca en un arroyo tropical con un bosque de ribera degradado por la extracción de palmeras. Se recogió la entrada vertical de la hojarasca mensualmente en un arroyo natural y se incubaron las hojas en el arroyo afectado. Cada mes, se recogieron las muestras, y se incubaron un conjunto de nuevas muestras. Se estimaron las tasas de descomposición de la hojarasca (k)*, la biomasa microbiana, la esporulación de hongos y la comunidad de invertebrados. Se observan valores más altos de* k *en verano, muy probablemente debido a las altas temperaturas (aumento de la actividad metabólica) y precipitación (mayor abrasión física).Los invertebrados(mayoritariamente trituradores) y el número total de microorganismos no mostraron influencia en las tasas de descomposición. Por lo tanto, en este muestreo temporal, el flujo de agua, la temperatura y la precipitación fueron los factores que controlan la* k *en este arroyo. Los valores de* k *son similares con otros entornos naturales, muy probablemente debido a que la degradación del bosque de ribera es una modificación estructural y no representa una fuente de contaminación.*

Palabras clave: *Precipitaciones, bosque de ribera, microorganismo, invertebrados, descomposición.*

INTRODUCTION

Energy flow and organic-matter cycling in aquatic environments are fundamental for the maintenance of the system's metabolism and, thus, for the structure of local communities (Fisher & Likens, 1972; Tank *et al.*, 2010; Graça *et al.*, 2015), particularly in shaded patches, where 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 can be associated with hydromorphological features (control of flow between the terrestrial and stream systems; Graça *et al.*, 2015) and mainly with climatic factors, which are strongly driven by seasonal and physiological changes in riparian vegetation (plant phenology; Gonçalves Jr. *et al.*, 2006a; Li & Dudgeon, 2011). Leaf litter breakdown is a key process in the remobilization of this organic detritus into the trophic chain because it makes available the nutrients and energy retained in the dead organic matter (Petersen & Cummins, 1974; Abelho, 2001). Plant litter decomposition is biologically driven by microbial (fungi and bacteria) and invertebrate (mostly shredders) communities in a sequence of events called leaching, conditioning and fragmentation (Gessner *et al.*, 1999). However, at least to our knowledge, no information is available about leaf litter breakdown in some Brazilian savannah phytophysiognomies, such as the "veredas" systems.

The "veredas" are hydrophilous vegetation formations that are typical of the gallery forests in the Cerrado biome and are characterized by rivers with well-defined river beds during the dry winter that transform into wetland areas during the rainy season (Moreira *et al.*, 2011). The "veredas" are essentially conditioned by physical factors, such as flat surfaces or inundated bottoms that are 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 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 to the structure and composition of riparian vegetation in low-order streams by the commercial exploitation and suppression of other non-commercial vegetal species (a standard practice in the Brazilian savannah; Rezende *et al.*, 2012) may alter organic matter cycling (Tank *et al.*, 2010; Graça *et al.*, 2015). This also may lead to variations in the energy flow and threaten the availability of these environmental services and, consequently, the system's functions (e.g., leaf litter breakdown process).

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, thereby maintaining the system's integrity (Lima & Zakia, 2001; Moreira *et al.*, 2011). The consequences of its cut to the stream include modification of the streambed morphology, changes in the physical and chemical characteristics of the water, increases in sunlight exposure (affecting temperature and biological activity) and decreases in the quantity and quality of vegetation litter inputs (Lecerf & Richardson, 2010; Graça et al., 2015). Therefore, riparian vegetation can protect stream ecosystems against catastrophic events (natural and/or anthropic) that are under the control of terrestrial ecosystems (Lecerf & Richardson, 2010; Souza *et al.*, 2013). 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 & Moulton, 2011). As in other low-order streams, the allochthonous organic matter input and leaf breakdown are

important for the maintenance of the "vereda" system's metabolism. However, in the case of canopy vegetation suppression (increased of luminosity and decreased of canopy protective function), leaf breakdown process and associated communities remain poorly understood.

The effect of canopy openness on streams functioning and the leaf breakdown process is poorly documented in tropical streams, and no data for "veredas" are available, despite the economic and ecological importance of these areas. 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 be answered according to Sutherland *et al*., (2013). Therefore, our objectives were to: i) investigate the temporal dynamics (over one year) of leaf litter breakdown rates in a degraded "vereda" canopy system and ii) characterize the environmental and biological changes in leaf breakdown throughout the year. Our hypotheses are that: i) leaf litter breakdown rates will increase in the rainy season due to higher physical fragmentation and microbial activity (due to higher temperatures) and ii), the decrease in riparian canopy protective function will allow faster rates of leaf breakdown throughout the year (due to higher temperature) and alter the physical and chemical parameters of the water (mainly electrical conductivity and nutrients via decomposition).

MATERIALS AND METHODS

Study Site

This research forms part of a larger study of "veredas" and an evaluation of streams in the Pandeiros River basin, located in Minas Gerais State, southeastern Brazil. This basin has the forest types of the 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 ranging between 21 °C and 24 °C. The "vereda" used in this study had its native vegetation removed by plant-extraction activities (to facilitate

the collection of *M*. *flexuosa*) and water withdrawal for human consumption (15°34′97.33″S, 44°95′02.77″W). The canopy of this "vereda" was composed only of *M*. *flexuosa*. Therefore, to verify the impact of canopy openness on leaf litter breakdown, leaf detritus (vertical input) was collected monthly by bucket in a preserved "vereda" and transplanted to incubate in a "vereda" with an impacted canopy.

Litterfall in a preserved "vereda"

Litterfall was measured monthly from April 2009 to March 2010. Litter entering directly into the river (vertical input-VI) was measured using 30 replicate buckets (0.53 m²) that were suspended with ropes 2 m above the stream and transversely arranged in 5 rows, with 6 buckets per row and 10 m between adjacent rows. The bucket bottoms were perforated for rainwater drainage. At monthly intervals, the litter accumulated in the buckets and in the nets was retrieved and weighed in situ (wet weight), and the bucket with the highest leaf litter mass in each row was used for the leaf litter breakdown experiments (see below).

The riparian zone of the preserved "vereda" contained individual plants 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). The riparian zone of the preserved "vereda" was used only to collect the leaf litter fall (all plants described above) for incubation in a stream with a degraded canopy.

Physical and chemical parameters of the waters and stream

Conductivity, pH and dissolved oxygen levels were measured *in situ* using a multianalyzer (YSI Incorporated, model 85). The luminosity and wa-

ter temperature at the stream surface were continuously recorded using a datalogger (Onset, HOBO UA-002-08). The total alkalinity was determined by the Gram method according to Carmouze (1994) 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 canopy openness was quantified using hemispherical photographs taken with a fisheye lens throughout the year. The rainfall and air temperature were obtained from a meteorological station (number 83 386; ± 35 km from the sampling point), located at 15°26′S, 44°22′W (city of Bonito de Minas/MG) and at an altitude of 473.6 m, of the National Agency of the Waters of Brazil (available on the website hidroweb; http://hidroweb.ana.gov.br/).

Leaf litter breakdown

We used 30×30 cm litter bags (a total of 60 sampling units) with a 10 mm mesh size containing ± 3 g of leaves. We used bulk litter, which is more representative of decomposition at the site, to measure leaf breakdown instead of leaves of known species because it reflects the seasonal variation in litter quality. After 30 days, the samples were retrieved (5 replicates per month), and new samples, containing the detritus from the direct input into the stream of the preserved "vereda" over the previous 30 days, were incubated. The samples were placed at a depth of 0.2 to 0.5 m in contact with the sediment. After retrieval, litter bags were placed into plastic bags inside boxes with ice and transported to the laboratory. The remaining leaf litter was used to estimate the initial dry weight (after drying at 60 °C for 72 h).

Invertebrate community

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 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 (Cummins *et al.*, 2005; Pérez, 1988): gathering-collectors (G-C), filtering-collectors (F-C), shredders (Sh), scrapers (Sc) and predators (P).

Microbial community

In the laboratory, discs (12 mm in diameter) were cut from randomly selected leaves to analyze the ash-free dry mass (AFDM) content, microbial biomass, and aquatic hyphomycete sporulation rates (5 discs for each analysis). Total biomass of the decomposer microorganisms was determined by quantifying the ATP in the litter according to Abelho (2005; using the luciferin-luciferase reaction). Fungal biomass was estimated based on ergosterol concentration, according to Gessner (2005). Aquatic hyphomycete sporulation was assessed using discs from each litter bag (in 30 ml of filtered stream water), according to Bärlocher (2005) and Gulis *et al.* (2005), based on identification and counting under the microscope (400 ×). 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 AFDM was obtained after incinerating the discs (550 °C for 4 h) and subtracting the proportion of the remaining material, which corresponded to the inorganic fraction from the respective sample.

Statistical Analysis

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 ($\ln[W_t] = \ln[W_0 \cdot e^{-kt}] = \ln[W_0] - kt$; $W_t = W_0 e^{-kt}$; W_t = remaining weight; W_0 = 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 One way repeated-measures ANOVA (RM-ANOVA) and contrast analysis were used to test for significant differences among the months (categorical

variables) in the remaining mass, invertebrate community (richness, density and abundance of functional trophic groups) and microbial parameters (levels of ergosterol, ATP and density of spores in the detritus). The association between some variables was assessed with Spearman's correlation analysis (ρ), considering $p < 0.05$ (Zar, 1996). We also compared the structure of invertebrate (families and functional trophic groups) and fungal (species of spores) community among the studied months using a permutational multivariate analysis of variance (PerMANOVA) with the Bray-Curtis distance matrix and a permutation test (10 000) 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). All analyses were performed using the R program (R Development Core Team).

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 Decem-

ber. The water temperature was 25.9 ± 0.47 °C and the air temperature was 24.9 ± 0.57 °C, with higher values in November, December and January. The amount of precipitation during the studied period was 92.2 ± 25.0 mm, with peaks during October to April. The stream water characterics were basic pH (8.2 ± 0.12; with peaks in January and February), and high levels of oxygen (6.5 ± 0.30 mg/l and 80.6% saturation; with peaks in July), conductivity (51.0 ± 7.17 µS/cm; with peaks in April and May), and alkalinity (60.3 ± 4.73 µEq/l; with peaks in January). The ammonia (0.06 ± 0.003 mg/l), nitrate (0.1 ± 0.001 mg/l) and orthophosphate (0.02 ± 0.0001 mgl) concentrations were fairly constant throughout the year. The canopy openness of the riparian vegetation was elevated in the "vereda," with an average value of 48.5% (Table 1).

Leaf breakdown rates

The mean litter breakdown rate (k) was 0.037 day^{-1} (0.014 to 0.095 day^{-1} range), corresponding to an overall leaf litter loss of ~59% (range, 33 to 93% range) of the original mass in one month. The percentages of mass loss differed significantly among the studied months (RM-ANOVA, $F_{10,36} = 6.75$, $p < 0.01$), with higher values in November and December (contrast

Table 1. Physical and chemical characteristics of the stream water at the studied site from January to December. *Características físicas y químicas del agua del arroyo en el lugar de estudio, de Abril a Febrero.*

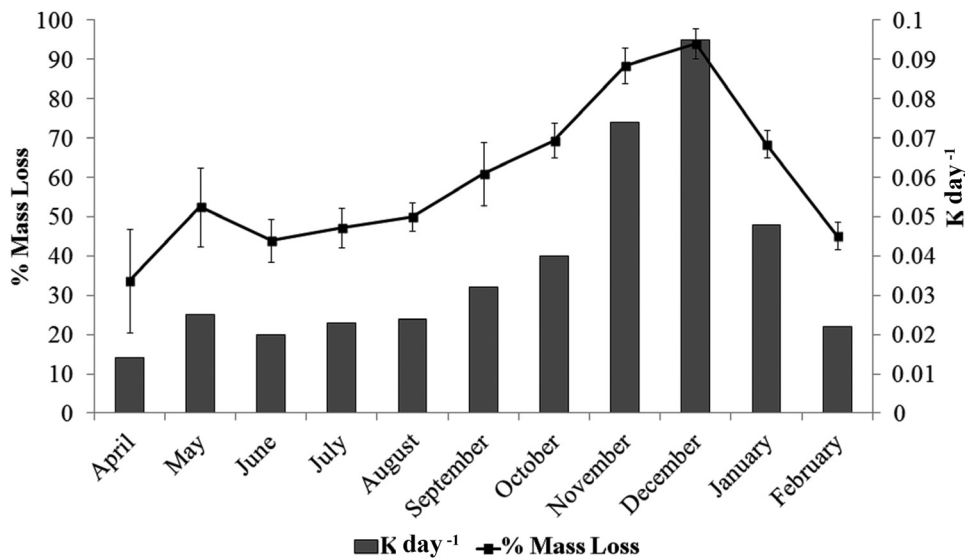|	Water Flow/m^3	pH	Oxygen (mg/l)	Conductivity uS/cm	Temp. water °C	Alkalinity MicroEq/l	Ammonia mg/l	Nitrate mg/l	Orthophosphate mg/l	Precipitation mm	Temp. air °C	Luminosity Lux
April	0.16	8.40	7.12	75.10	25.60	75.41	< 0.05	0.09	0.02	69.40	25.00	11.66
May	0.15	7.17	7.60	73.60	24.20	42.71	0.09	0.10	0.02	11.60	24.00	19.56
June	0.14	7.75	6.88	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	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	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	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	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	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	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	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	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	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	7.17	0.47	4.73	0.0038	0.0013	0.0001	7.08	0.57	6.72

Figure 1. Percentage (%) of leaf dry mass remaining (black line) and decomposition rates (gray bars-*k* day^{-1}) over the studied months (April to February). Values are means ± standard errors. *Porcentaje (%) de la masa seca de la hojarasca restante (línea de negro) y las tasas de descomposición (barras grises-*k day^{-1}*) durante los meses estudiados (de Abril a Febrero). Los valores son medias ± error estándar.*

analysis; $p < 0.05$) and lower values in May to July (Fig. 1). Litter mass loss was positively correlated with rainfall ($r = 0.44$, $p = 0.01$) and air and water temperatures ($r = 0.31$, $p = 0.02$ and $r = 0.47$, $p = 0.01$, respectively).

Biological communities

The mean (± SE) ATP content in the leaves was 475 ± 43 nmoles/g AFDM; significant differences were among the months (RM-ANOVA, $F_{10,36} = 33.06$, $p < 0.01$), with a maximum of 1021 nmoles/g AFDM and a minimum of 34 nmoles/g AFDM, in June and October, respectively. The mean ergosterol concentration (± SE) was 624 ± 52 μg/g AFDM, with significant differences found among the months (RM-ANOVA, $F_{(10,36)} = 5.33$, $p < 0.01$) and peaks of 967 and 1058 μg/g AFDM found in July and February, respectively, and a minimum value of 239 μg/g AFDM found in October. The ergosterol and ATP concentrations (Fig. 2) were positively correlated throughout the year ($r = 0.43$, $p < 0.01$), but only the ATP values were significantly correlated with litter breakdown ($r = -0.43$, $p < 0.01$).

The maximum sporulation rate (± SE) was 5 ± 1 spores/mg AFDM in July, but zero spore production was detected in November and January (Fig. 2). However, the sporulation rates (RM-ANOVA, $F_{(10,36)} = 1.07$, $p = 0.41$) did not vary significantly over the months and presented a negative relationship with temperature ($r = -0.56$, $p = 0.04$). Also, the community composition of leaf-associated fungi (PerMANOVA, $F = 1.45$, $p = 0.10$) did not vary over the months studied. The following species were recorded: *Alatospora acuminata, Anguillospora filiformis, Anguillospora longissima, Culicidospora aquatica, Goniopila monticola, Lemonniera aquatica, Lunulospora curvula, Stenocladiella neglecta* and *Tetrachaetum elegans*. A qualitative survey of the water column revealed the spores of *Anguillospora filiformis, Anguillospora longissima, Lunullospora curvula* and *Fontanospora eccentrica*.

The most abundant invertebrate *taxon* (± SE) associated with decomposing leaf litter was the Chironomidae (Diptera), which comprised 80% of the total individuals being found (mean of 293 ± 33 individuals/g AFDM). The mean (± SE) density of invertebrates ranged from 49 ± 43 in-
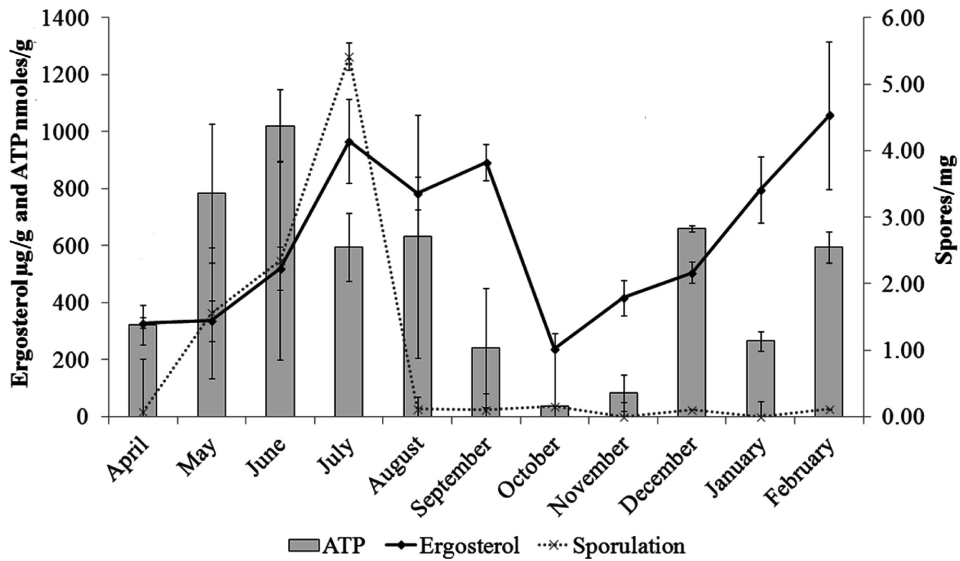
Figure 2. Fungal biomass (black continuous line-ergosterol μg/g AFDM), total microbial community biomass (gray bars-ATP nmoles/g AFDM) and abundance of fungal spores in the water (dotted line-spores/mg AFDM) over the studied months (April to February). Values are means ± standard errors. *Biomasa fúngica (línea continua-ergosterol μg/g AFDM), biomasa total de la comunidad microbiana (barras grises-ATP nmoles/g AFDM) y la abundancia de esporas de hongos (línea punteada-esporas/mg AFDM) en el período estudiado (de Abril a Febrero). Los valores son medias ± error estándar.*

dividuals/g AFDM to 590 ± 150 individuals/g AFDM, in September and July, respectively, with significant differences among the months (Fig. 3; 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 dif-
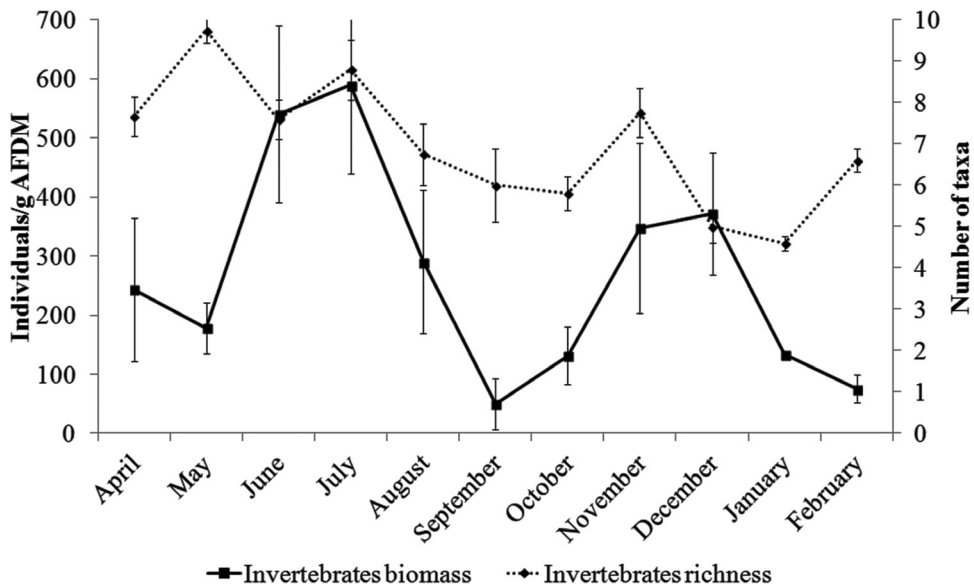

Figure 3. Density (ind/g; continuous line) and richness (dotted line) of the invertebrates that colonized the leaf litter over the studied months (April to February). Values are means ± standard errors. *Densidad (ind/g; línea continua) y riqueza (línea de puntos) de los invertebrados que colonizaron la hojarasca durante los meses estudiados (de Abril a Febrero). Los valores son medias ± error estándar.*

fered significantly among the months (Fig. 3; RM-ANOVA, $F_{(10,36)} = 4.58$, $p < 0.01$). Shredders represented only 9% of the non-chironomid 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* belonged to the 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 the functional trophic groups (PerMANOVA, $F = 2.43$, $p < 0.01$; Fig. 4) and families (PerMANOVA, $F = 2.92$, $p < 0.01$; Table S1, available at www.limnetica.net/es/limnetica/36) of the invertebrate community varied over the months studied (pairwise comparison; $p < 0.05$), mainly between winter (June and July) and summer (November, December and January).

DISCUSSION

Canopy degradation effects

We observed a strong seasonality driving the ecological processes (peaking in the summer) in this canopy degradation system that was probably helped by the loss of the protective function of the riparian zone (Lecerf & Richardson, 2010; Souza *et al.*, 2013). The loss of the protective function from canopy degradation can increase the sediment entrainment (Gardiner *et al.*, 2009; Lagrue *et al.*, 2011; de Nadaï-Monoury *et al.* 2014) and promote a greater frequency and intensity of climatic disturbances (Vannote *et al.*, 1980; Naiman & Décamps 1997; Dudgeon *et al.*, 2006), mainly in the summer season due to storm events. Therefore, the increase in sediment input can explain the low water flow (due to silting of the stream bed) in the studied stream (Lima & Zakia, 2001). Compared with a "vereda" with an intact canopy (9% canopy openness; Rezende *et al.*, 2016), the flow of the stream studied was lower, but the water had higher values of pH, alkalinity, dissolved oxygen, nutrients, and con-
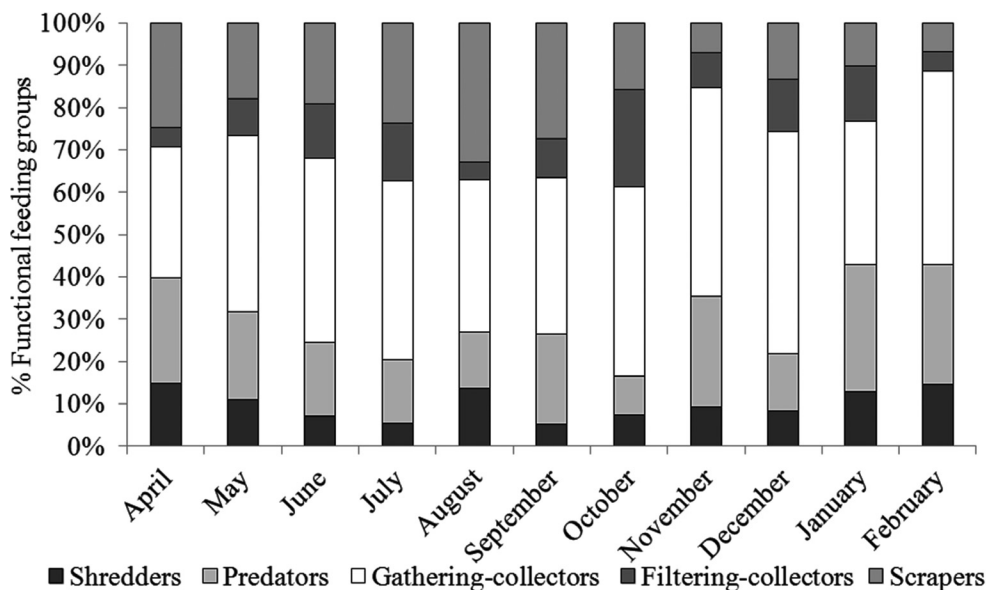

Figure 4. Relative abundance of the functional feeding groups of aquatic invertebrates that colonized the leaf litter over the studied months (April to February). *Abundancia relativa de los grupos funcionales de los invertebrados acuáticos que colonizaron la hojarasca durante los meses estudiados (de Abril a Febrero).*

ductivity. Other streams with a preserved riparian canopy of the same hydrological order in the Pandeiros watershed also showed higher water flow and low values of nutrients and conductivity (Rezende *et al*., 2012; Rezende *et al*., 2014a; Rezende *et al*., 2014b; Lidman, 2015: Table S2, available at www.limnetica.net/en/limnetica/36). This difference may indicate that environmental change caused by canopy suppression due to plant extraction may affect the ecosystem and compromise some ecological services, such as the water quality and quantity.

We also found that the partial removal of vegetation had a low effect on leaf litter breakdown ($k = -0.033$ and -0.037, intact canopy vereda in Rezende *et al*., 2016, and our study, respectively). This finding is in contrast to the hypothesis that the litter breakdown should be diminished because low detritus availability decreases the community of microbial and shredder decomposers (Suberkropp 1997); nevertheless, positive, neutral and negative effects have been reported (e.g., Lecerf *et al*. 2012, de Nadai-Monoury *et al*. 2014; Majdi *et al*., 2015). A low effect on leaf litter breakdown by plant extraction area was observed compared to that observed in areas of extensive agriculture (Feio *et al*., 2010; Griffiths *et al*., 2012) and urbanization (Paul & Meyer, 2001; Smith & Chadwick, 2014). This can most likely be explained by plant removal being a structural modification (Lecerf & Richardson, 2010) that does not represent a source of pollution (e.g., the input of chemicals as pesticides). Areas of extensive agriculture (Utz *et al*., 2009) and urbanization (Paul & Meyer, 2001) have a greater influence on biological communities, even when these land uses are present at small scales and proportions in the landscape. Thus, the negative effects of extensive agriculture and urbanization are disproportionate compared to other land uses (Johnson *et al*., 2012).

Our study indicated that macroinvertebrate community (with higher density and richness under stochastic disturbance; Benda *et al*., 2004) and microbial community (with more photosynthetic organisms after canopy degradation; Jugnia *et al*., 2000) compared to the "vereda"

with an intact canopy (Rezende *et al*., 2016) could be good biological predictors of anthropic impacts. The increase in the density of the biological communities during leaf breakdown by stochastic disturbance was also observed in other studies (Sponseller & Benfield 2001; Hagen *et al*., 2006). Therefore, we observed that leaf litter breakdown rates could be a useful indicator of impacts such as the partial removal of vegetation through plant extraction. Studies on the effects of changes in land use, such as the organic pollution of urbanized areas (Pascoal *et al*., 2001; Smith & Chadwick, 2014) and the gradient of extensive agriculture (Hagen *et al*., 2006; Feio *et al*., 2010; Griffiths *et al*., 2012), have shown the effectiveness of biological communities as a useful indicators of impacts. Therefore, we can conclude that leaf litter breakdown is also useful as a indicator of moderate impacts.

Leaf breakdown process

Leaf litter breakdown rates (k) in all months (mean of -0.037 day^{-1}) were described as fast ($k > -0.017$), except for that in April (intermediate values of $-0.004 > k < -0.017$), according to the model proposed by Gonçalves Jr *et al*. (2013). These k values are larger than those observed in other Cerrado streams (-0.0001 to -0.015 in Moretti *et al*., 2007; Gonçalves Jr *et al*., 2007; Gonçalves Jr *et al*., 2012a) but were in the lower range reported for tropical areas (-0.026 to -0.077 day^{-1}) by Abelho (2001). The high temperatures (with a minimum of 21 °C) recorded throughout the year may have had positive effects on the leaf litter breakdown rates (Suberkropp & Chauvet, 1995; Gonçalves Jr *et al*., 2012b).

The largest k was observed in the summer period, which indicates a seasonal dynamic, and explains the positive correlation with temperature and rainfall. Fungal growth and activity increase at higher water temperatures (Chauvet & Suberkropp 1998, Mas-Martí *et al*. 2015) and improve leaf litter quality and stimulate leaf mass loss (Mas-Martí *et al*. 2015). However, we found no correlation between temperature and fungal biomass. This result may indicate that

other components of the microbial community (e.g., bacteria, protozoa and/or other microorganisms) were stimulated by higher temperature and increased microbial decomposer activity (Chauvet & Suberkropp 1998, Mas-Martí *et al.* 2015), suggesting that leaf decomposition by microbes (mainly by bacteria) is more affected by temperature than fungi.

Synergistic interactions might also exist among physical abrasion (due to the higher rainfall and water flow; Santos Fonseca *et al.*, 2012), oxygen concentrations (which increase the activity of aquatic fungi; Medeiros *et al.*, 2009) and conductivity (which indicates higher nutrient inputs; Chestnut & McDowell, 2000, Medeiros *et al.*, 2015), thereby accelerating leaf litter breakdown. This indicates that higher riparian canopy openness could intensify the influence of temporal changes in the abiotic conditions and, consequently, in the biological activity and litter decomposition in this "vereda" ecosystem.

Microbial community

Fungal biomass was greater than in other Cerrado streams (50 to 420 μg ergosterol/g range for Gonçalves Jr *et al.*, 2006c; Gonçalves Jr *et al.*, 2007), and total microbial community biomass (ATP) was at the upper limit compared to tropical streams (100 to 750 nmoles/g range for Abelho, 2001; Abelho *et al.*, 2005; Gonçalves Jr *et al.*, 2006c; Gonçalves Jr *et al.*, 2007). We found greater microbial biomass in periods of low water flow due to a decrease in rain (i.e., in the winter) that was likely related to the lower physical abrasion and lower biofilm loss (Santos Fonseca *et al.*, 2012). Further, in the winter, the low cloud formation increases luminosity and stimulates photosynthetic organisms, as indicated by the ATP concentration (Vannote *et al.*, 1980; Majdi *et al.*, 2015) in low riparian canopy cover. This biofilm is composed of a higher biomass of photosynthetic organisms that use the detritus only as a substrate (we observed green macro-algae over the leaf litter) and corroborates the lower breakdown rates in periods of higher biofilm mass. However, these conclusions should be taken with caution and further

studied are needed to assess the photosynthetic activity of these organisms.

This greater microbial biomass and biofilm associated with lower leaf litter breakdown rates in the winter season may result from higher photosynthetic production (greater use of autotrophic resources; Jugnia *et al.*, 2000; Majdi *et al.*, 2015) and is synergistic with the lower metabolism of organisms due to the temperature decrease (Sridhar & Sudheep, 2010). However, higher temperatures may have a negative effect on the richness of the fungal community of the studied stream, possibly selecting only species with the ability to develop in warmer settings (Chauvet & Suberkropp, 1998). These patterns explain the hyphomycetes' tendency to sporulate more in the winter period (with the first peak of fungal density) and the negative correlation of sporulation with temperature (Mathuriau & Chauvet 2002; Gonçalves Jr *et al.*, 2007). Another important aspect is the greater number of species associated with the leaf litter compared to the water column, which can be explained by two factors: (i) the increase in diversity of the microhabitat and adhesion condition by the presence of leaf litter substrate (Rezende *et al.*, 2016) and (ii) the increase in nutrients due to litter decomposition (Chestnut & McDowell, 2000; Gonçalves Jr *et al.*, 2007), mainly because the microbial colonization in Cerrado streams is limited by the low dissolved nutrient concentration (Medeiros *et al.*, 2015). However, the community structure did not change throughout the months, possibly due to the low number of species and the dominance of *Lunulospora curvula* (42%) *Anguillospora filiformis* (35%) and *Lemonniera aquatica* (20%), totaling 97% of the density of the spores found in leaf litter.

Aquatic invertebrate community

We found higher average densities of aquatic invertebrates than in other Cerrado streams (2 to 780 ind/g range for Gonçalves Jr *et al.*, 2006b; Moretti *et al.*, 2007; Gonçalves Jr *et al.* 2012a). The higher densities and species richness, especially in winter, can be explained by the negative correlation with temperature (cool water could

increase the oxygen dilution) and indirectly indicates lower rainfall (with a lower scouring power from water; Santos Fonseca *et al.*, 2012). Chironomidae dominated the invertebrate community, as observed in other tropical streams (Moulton *et al.*, 2010; Silva-Junior & Moulton, 2011; Boyero *et al.*, 2012). The lower abundance of shredders may explain the low importance of this community in the breakdown of leaf litter, as observed in other tropical streams (0 to 11% range for Gonçalves Jr *et al.*, 2006c; Gonçalves Jr *et al.*, 2007; Moretti *et al.* 2007). Odontoceridae was the dominant shredder family, but members of this group have also been classified as scrapers and opportunistic scavengers feeding on animal and plant detritus (Cummins *et al.*, 2005; Pérez, 1988). The alternative feeding strategies of this group would help explain the low participation and importance of the invertebrate communities in the leaf litter breakdown process. The reduced litter input in the canopy openness condition can also result in a low availability of detritus and in the richness and density of invertebrate shredders (Suberkropp 1997, Majdi *et al.*, 2015).

CONCLUSION

Canopy degradation might increase the frequency and intensity of disturbances due to the loss of the riparian vegetation's capacity to stabilize ecological processes. The high biological and physical-chemical variation and the lower water flow are early indicators that the water-supply services might be impaired in the long term. This finding provides important information for the conservation of "veredas" and shows that despite the apparent process maintenance, the dynamics of such systems are being changed due to canopy degradation resulting from plant-based extraction.

A seasonal variation occurred in leaf decay (higher in summer due to an increase in water flow, temperature and precipitation) corroborating our hypothesis that leaf litter breakdown rates will increase in the rainy season. Aquatic invertebrates (mainly shredders) and total mi-

croorganisms showed no overall influence on leaf breakdown rates. These results also suggest that the temporal resolution chosen for a leaf breakdown study may affect the detection of decay patterns (the temporal macro-scale is affected by climatic factors). Despite the effect of seasonality, we also corroborate the hypothesis of faster leaf litter breakdown rates throughout the year and higher values in the physical and chemical parameters of water, probably due to a loss of the protective function of the riparian canopy. This finding also suggests the leaf litter breakdown is useful as a indicator of moderate impacts.

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REFERENCES

ABELHO, M. 2001. From litterfall to breakdown in streams: a review. *Scientific World Journal*, 1: 656–680. doi:10.1100/tsw.2001.103

ABELHO, M. 2005. Extraction and quantification of ATP as a measure of microbial biomass. In: *Methods to Study Litter Decomposition*. M.A.S. Graça, F.Bärlocher, M.O. Gessner (eds): 223–229. Springer.

ABELHO, M., C. CRESSA & M.A. S. GRAÇA. 2005. Microbial biomass, respiration, and decomposition of *Hura crepitans* L. (Euphorbiaceae) leaves in a tropical stream. *Biotropica*, 37: 397–402. doi:10.1111/j.1744-7429.2005.00052.x

APGII, APG. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: *APG II Botanical Journal of the Linnean Society*, 141: 399–436. doi:10.1046/j.1095-8339.2003.t01-1-00158.x

BÄRLOCHER, F. 2005. Sporulation of Aquatic Hyphomycetes. In: *Methods to Study Litter Decom-*

position. M.A.S. Graça, F. Bärlocher, M.O. Gessner (eds): 113–119. Springer.

BENDA, L., N.L. POFF, D. MILLER, T. DUNNE, G. REEVES, G. PESS & M. POLLOCK. 2004. The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience*, 54: 413–427. doi:10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2

BOYERO, L., L.A. BARMUTA, L. RATNARAJAH, K. SCHMIDT & R.G. PEARSON. 2012. Effects of exotic riparian vegetation on leaf breakdown by shredders: a tropical-temperate comparison. *Freshwater Science*, 31: 296–303. doi:10.1899/11-103.1

CARMOUZE, J.P. 1994. *O Metabolismo dos Ecossistemas Aquáticos. Fundamentos teóricos, métodos de estudo e análises químicas*. Edgard Blücher/FAPESP, São Paulo.

CHAUVET, E. & K. SUBERKROPP. 1998. Temperature and Sporulation of Aquatic Hyphomycetes. *Applied and Environmental Microbiology*, 64: 1522–1525.

CHESTNUT, T.J. & W.H. MCDOWELL. 2000. C and N Dynamics in the Riparian and Hyporheic Zones of a Tropical Stream, Luquillo Mountains, Puerto Rico. *Journal of the North American Benthological Society*, 19: 199–214. doi:10.2307/1468065

CLESCERI, L.S., A.E. GREENBERG & R.R. TRUSSELL. 1989. *Standards methods for the examination of water and wastewater*. vol. 17. DHAAWWAWPCK, Washington D.C.

CUMMINS, K., R. MERRITT & P. ANDRADE. 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment*, 40: 69–89. doi:10.1080/01650520400025720

DE NADAÏ-MONOURY, E., F. GILBERT & A. LECERF. 2014. Forest canopy cover determines invertebrate diversity and ecosystem process rates in depositional zones of headwater streams. *Freshwater Biology*, 59: 1532–1545. doi:10.1111/fwb.12364

DRUMMOND, G.M., C.S. MARTINS, A.B.M. MACHADO, F.A. SEBAIO & Y. ANTONINI. 2005. *Biodiversidade em Minas Gerais: Um Atlas para sua Conservação*. Biodiversidade em Minas Gerais. Fundação Biodiversitas, Belo Horizonte:

DUDGEON, D., A.H. ARTHINGTON, M. O.GESSNER, Z. KAWABATA, D.J. KNOWLER, C. LEVEQUE, R.J. NAIMAN, A.H. PRIEUR-RICHARD, D. SOTO, M.L. STIASSNY & C. A. SULLIVAN. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews of the Cambridge Philosophical Society*, 81: 163–182. doi:10.1017/S1464793105006950

FEIO, M.J., T. ALVES, M. BOAVIDA, A. MEDEIROS & M.A.S. GRAÇA. 2010. Functional indicators of stream health: a river-basin approach. *Freshwater Biology*, 55: 1050–1065. doi:10.1111/j.1365-2427.2009.02332.x

FISHER, S.G. & G.E. LIKENS. 1972. *Stream ecosystem: organic energy budget*. BioScience, 22.

GARDINER, E.P., A.B. SUTHERLAND, R.J. BIXBY, M.C. SCOTT, J.L. MEYER, G.S. HELFMAN, E.F. BENFIELD, C.M. PRINGLE, P.V. BOLSTAD & D.N. WEAR. 2009. Linking stream and landscape trajectories in the southern Appalachians. *Environmental monitoring and assessment*, 156: 17–36. doi:10.1007/s10661-008-0460-x

GESSNER, M.O. 2005. Ergosterol as a measure of fungal biomass. In: *Methods to Study Litter Decomposition*. M.A.S. Graça, F. Bärlocher, M.O. Gessner (eds): 189–195. Springer.

GESSNER, M.O., E. CHAUVET & M. DOBSON. 1999. A perspective on leaf litter breakdown in streams. *Oikos*, 85: 377–384. doi:10.2307/3546505

GONÇALVES, JR, J.F., J. FRANÇA & M. CALLISTO. 2006a. Dynamics of allochthonous organic matter in a tropical Brazilian headstream. *Brazilian Archives of Biology and Technology*, 49: 967–973. doi:10.1590/S1516-89132006000700014

GONÇALVES JR, J.F., J. FRANÇA, A.O. MEDEIROS, C.A. ROSA & M. CALLISTO. 2006b. Leaf breakdown in a tropical stream. *International Review of Hydrobiology*, 91: 164–177. doi:10.1002/iroh.200510826

GONÇALVES JR, J.F., M.A.S. GRAÇA MAS, & M. CALLISTO. 2006c. Leaf-litter breakdown in 3 streams in temperate, Mediterranean, and tropical Cerrado climates. *Journal of the North American Benthological Society*, 25: 344–355 doi:10.1899/0887-3593(2006)25[344:lbisit]2.0.co;2

GONÇALVES JR, J.F., M.A.S. GRAÇA & M. CALLISTO. 2007. Litter decomposition in a Cerrado savannah stream is retarded by leaf toughness, low dissolved nutrients and a low density of shredders. *Freshwater Biology*, 52: 1440–1451. doi:10.1111/j.1365-2427.2007.01769.x

GONÇALVES JR, J.F., R.S. REZENDE, J. FRANÇA & M. CALLISTO. 2012a. Invertebrate coloni-

sation during leaf processing of native, exotic and artificial detritus in a tropical stream. *Marine and Freshwater Research*, 63: 428–439. doi:10.1071/mf11172

GONÇALVES JR, J.F., R.S. REZENDE, N.M. MARTINS & R.S. GREGORIO. 2012b. Leaf breakdown in an Atlantic Rain Forest stream. *Austral Ecology*, 37: 807–815. doi:10.1111/j.1442-9993.2011.02341.x

GONÇALVES JR, J.F., R.T. MARTINS, B, M.P. OTTONI & S.R.M. COUCEIRO. 2013. Uma visão sobre a decomposição foliar em sistemas aquáticos brasileiros. In: *Insetos aquáticos: biologia, ecologia e taxonomia*. Hamada, N., J.L. Nessimian & R.B. Querino (eds).

GRAÇA, M.A.S. 2001. The Role of Invertebrates on Leaf Litter Decomposition in Streams – a Review. *International Review of Hydrobiology*, 86: 383–393. doi:10.1002/1522-2632(200107)86:4/5<383::aid-iroh383>3.0.co;2-d

GRAÇA, M.A.S., V. FERREIRA, C. CANHOTO, A.C. ENCALADA, F. GUERRERO-BOLAÑO, K.M. WANTZEN & L. BOYERO. 2015. A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology*, 100: 1–12. doi:10.1002/iroh.201401757

GRIFFITHS, N.A., J.L. TANK, S.S. ROLEY & M.L. STEPHEN. 2012. Decomposition of maize leaves and grasses in restored agricultural streams. *Freshwater Science*, 31: 848–864. doi:10.1899/11-095.1

GULIS, V., L. MARVANOVÁ & E. DESCALS. 2005. An Illustrated Key To The Common Temperate Species Of Aquatic Hyphomycetes. In: *Methods to Study Litter Decomposition*. M.A.S. Graça, F. Bärlocher, M.O. Gessner (eds): 153–168. Springer.

HAGEN, E.M., J.R. WEBSTER & E.F. BENFIELD. 2006. Are leaf breakdown rates a useful measure of stream integrity along an agricultural land use gradient? *Journal of the North American Benthological Society*, 25: 330–343. doi:10.1899/0887-3593(2006)25[330:ALBRAU]2.0.CO;2

JOHNSON, R.C., D.P. SMITH & C.E. MCMICHAEL. 2012. Scale Dependence in Relating Land Use/Cover to Stream Macroinvertebrate Communities in the Central Appalachian Mountains, USA GI. *Science & Remote Sensing*, 49: 53–70. doi:10.2747/1548-1603.49.1.53

JUGNIA, L.B., R.D. TADONLEKE, T. SIMENGANDO & J. DEVAUX. 2000. The Microbial Food Web in the Recently Flooded Sep Reservoir: Diel Fluctuations in Bacterial Biomass and Metabolic Activity in Relation to Phytoplankton and Flagellate Grazers. *Microbial Ecology*, 40: 317–329. doi:10.1007/s002480000056

LAGRUE, C., J.S. KOMINOSKI, M. DANGER, J.-M. BAUDOIN, S. LAMOTHE, D. LAMBRIGOT & A. LECERF. 2011. Experimental shading alters leaf litter breakdown in streams of contrasting riparian canopy cover. *Freshwater Biology*, 56: 2059–2069. doi:10.1111/j.1365-2427.2011.02637.x

LECERF, A. & J.S. RICHARDSON .2010. Litter decomposition can detect effects of high and moderate levels of forest disturbance on stream condition. *Forest Ecology and Management*, 259: 2433–2443. doi:http://dx.doi.org/10.1016/j.foreco.2010.03.022

LECERFA, A., J.-M. BAUDOINA, A.A. BESSONA, S. LAMOTHEA, & C. LAGRUE. 2012. Is smaller necessarily better? Effects of small-scale forest harvesting on stream ecosystems. *Annales de Limnologie - International Journal of Limnology*, 48: 401–409. doi:10.1051/limn/2012028

LI, A.O.Y. & D. DUDGEON. 2011. Leaf litter retention in tropical streams in Hong Kong. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 178: 159–170. doi:10.1127/1863-9135/2011/0178-0159

LIDMAN, J. 2015. *Decomposition of leaf litter in headwater streams. Effects of changes in the environment and contribution of microbial and shredder activity on litter decomposition*. Dissertation. UMEA University, Sweden.

LIMA, W.P. & M.J.B. ZAKIA. 2001. Hidrologia de Matas Ciliares. In: *Matas Ciliares: Conservação e Recuperação*. Rodrigues, R.R. & H.F. Leitão-Filho (eds) Editora de Universidade De São Paulo, Fapesp, São Paulo,

MAJDI, N., A. BOICHÉ, W. TRAUNSPURGER & A. LECERF. 2015. Community patterns and ecosystem processes in forested headwater streams along a gradient of riparian canopy openness. *Fundamental and Applied Limnology / Archiv für Hydrobiologie* 187: 63–78. doi:10.1127/fal/2015/0740

MAS-MARTÍ, E., I. MUÑOZ, F. OLIVA & C. CANHOTO. 2015. Effects of increased water temperature on leaf litter quality and detritivore performance: a whole-reach manipulative experiment. *Freshwater Biology*, 60: 184–197. doi:10.1111/fwb.12485

MATHURIAU, C. & E. CHAUVET .2002. Break-down of leaf litter in a neotropical stream. *Journal of the North American Benthological Society*, 21: 384–396. doi:10.2307/1468477

MEDEIROS, A.O., C. PASCOAL & M.A.S. GRAÇA. 2009. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshwater Biology*, 54: 142–149. doi:10.1111/j.1365-2427.2008.02101.x

MEDEIROS, A.O., CALLISTO, M., GRAÇA, M.A. S., FERREIRA, V., ROSA, C.A., FRANÇA, J., ELLER, A., REZENDE, R.S. & J.F GONÇALVES JR. 2015. Microbial colonisation and litter decomposition in a Cerrado stream are limited by low dissolved nutrient concentrations. *Limnética (Madrid)*, 34: 283–292.

MOREIRA, S.N., A. POTT, V.J. POTT & G.A. DAMASCENO-JUNIOR. 2011. Structure of pond vegetation of a vereda in the Brazilian Cerrado. *Rodriguésia*, 62: 721–729. doi:10.1590/S2175-78602011000400002

MORETTI, M., J.F. GONÇALVES JR & M. CALLISTO. 2007. Leaf breakdown in two tropical streams: Differences between single and mixed species packs. *Limnologica*, 37: 250–258. doi: 10.1016/j.limno.2007.01.003

MOULTON, T.P., S.A.P. MAGALHAES-FRAGA, E.F. BRITO & F.A. BARBOSA. 2010. Macro-consumers are more important than specialist macroinvertebrate shredders in leaf processing in urban forest streams of Rio de Janeiro, Brazil. *Hydrobiologia*, 638: 55–66. doi:10.1007/s10750-009-0009-1

NAIMAN, R.J. & H. DÉCAMPS. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology, Evolution, and Systematics*, 28: 621–658. doi:citeulike-article-id:2981131

OKSANEN, J., R. KINDT, P. LEGENDRE, B. O'HARA, G.L. SIMPSON, P. SOLYMOS, M.H.H. STEVENS & H. WAGNER. 2008. Adonis function. In: *Vegan: Community Ecology Package*. R package version 1.13-1. pp 15–10.

PASCOAL, C., F. CÁSSIO & P. GOMES. 2001. Leaf Breakdown Rates: a Measure of Water Quality? *International Review of Hydrobiology*, 86: 407–416. doi:10.1002/1522-2632(200107)86:4/5

PAUL, M.J. & J.L. MEYER. 2001. Streams in the Urban Landscape. *Annual Review of Ecology and Systematics*, 32: 333–365. doi:10.1146/annurev.ecolsys.32.081501.114040

PÉREZ, G.P. 1988. *Guía para el studio de los macro-invertebrados acuáticos del departamento de Antioquia*. Editorial Presencia Ltda, Bogotá.

PETERSEN, R.C. & K.W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwater Biology*, 4: 343–368. doi:10.1111/j.1365-2427.1974.tb00103.x

REZENDE, R.S., A.M. SANTOS & J.F.G. JUNIOR. 2012. Avaliação ambiental do rio Pandeiros utilizando macroinvertebrados como indicadores de qualidade da água. *Ecología Austral*, 22: 159–196.

REZENDE, R.S., M.M. PETRUCIO & J.F. GONÇALVES JR. 2014a. The Effects of Spatial Scale on Breakdown of Leaves in a Tropical Watershed. *Plos One*, 9: e97072. doi:10.1371/journal.pone.0097072

REZENDE, R.S., A.M. SANTOS, C. HENKE-OLIVEIRA, & J.F. GONÇALVES JR. 2014b. Effects of spatial and environmental factors on benthic a macroinvertebrate community. *Zoologia (Curitiba)*, 31: 426–434. doi:10.1590/s1984-467020140 05000001

REZENDE, R.S., M.A.S. GRACA, A.M. SANTOS, A.O. MEDEIROS, P.F. SANTOS, Y.R.P. NUNES & J. F. GONCALVES JR. 2016. Organic Matter Dynamics in a Tropical Gallery Forest in a Grassland Landscape. *Biotropica*, 48: 301–310. doi:10.1111/btp.12308

SANTOS FONSECA, A.L., I. BIANCHINI, C.M.M. PIMENTA, C.B.P. SOARES & N. MANGIAVACCHI. 2012. The flow velocity as driving force for decomposition of leaves and twigs. *Hydrobiologia*, 703: 59–67. doi:10.1007/s10750-012-1342-3

SILVA-JUNIOR, E.F. & T.P. MOULTON. 2011. Ecosystem Functioning and Community Structure as Indicators for Assessing Environmental Impacts: Leaf Processing and Macroinvertebrates in Atlantic Forest Streams. *International Review of Hydrobiology*, 96: 656–666. doi:10.1002/iroh. 201111374

SMITH, B. & M.A. CHADWICK. 2014. Litter decomposition in highly urbanized rivers: influence of restoration on ecosystem function. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, 185: 7–18. doi:10.1127/fal/2014/0581

SOUZA, A.L.T.D., D.G. FONSECA, R.A. LIBÓRIO & M.O. TANAKA. 2013. Influence of riparian vegetation and forest structure on the water quality of rural low-order streams in SE Brazil. *Forest Ecology and Management*, 298: 12–18. doi:10.1016/j.foreco.2013.02.022

SPONSELLER, R.A. & E.F. BENFIELD. 2001. Influences of Land Use on Leaf Breakdown in Southern Appalachian Headwater Streams: A Multiple-Scale Analysis. *Journal of the North American Benthological Society*, 20: 44–59. doi:10.2307/1468187

SRIDHAR, K.R. & N.M. SUDHEEP. 2010. Diurnal fluctuation of spores of freshwater hyphomycetes in two tropical streams. *Mycosphere*, 1: 89–101.

SUBERKROPP, K. & E. CHAUVET. 1995. Regulation of Leaf Breakdown by Fungi in Streams: Influences of Water Chemistry. *Ecology*, 76: 1433–1445. doi:10.2307/1938146

SUBERKROPP, K. 1997. Annual production of leaf-decaying fungi in a woodland stream. *Freshwater Biology*, 38: 169–178. Doi:10.1046/j.1365-2427.1997.00203.x

SUTHERLAND, W.J., R.P. FRECKLETON, H.C.J. GODFRAY, S.R. BEISSINGER, T. BENTON, D.D. CAMERON, Y. CARMEL, D.A. COOMES, T. COULSON, M.C. EMMERSON, R.S. HAILS, G.C. HAYS, D.J. HODGSON, M.J. HUTCHINGS, D. JOHNSON, J.P.G. JONES, M.J. KEELING, H. KOKKO, W.E. KUNIN, X. LAMBIN, O.T. LEWIS, Y. MALHI, N. MIESZKOWSKA, E.J. MILNER-GULLAND, K. NORRIS, A.B. PHILLIMORE, D.W. PURVES, J.M. REID, D.C. REUMAN, K. THOMPSON, J.M.J. TRAVIS, L.A. TURNBULL, D.A. WARDLE, T. WIEGAND & D. GIBSON. 2013. Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101: 58–67. doi:10.1111/1365-2745.12025

TANK, J.L., E.J. ROSI-MARSHALL, N.A. GRIFFITHS, S.A. ENTREKIN & M.L. STEPHEN. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, 29: 118–146. doi:10.1899/08-170.1

UTZ, R.M., R.H. HILDERBRAND & D.M. BOWARD. 2009. Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients. *Ecological Indicators*, 9: 556–567. doi:10.1016/j.ecolind.2008.08.008

VANNOTE, R.L., G.W. MINSHALL, K.W. CUMMINS, J.R. SEDELL & C.E. CUSHING. 1980. River Continuuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 130–137. doi:10.1139/f80-017

ZAR, J.H. 1996. *Bioestatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey.