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Patterns of litter inputs, hyphomycetes and invertebrates in a Brazilian savanna stream: a process of degradative succession

Research Article

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Abstract

Litter breakdown is an important ecological process at the bottom of food webs in streams. Previous studies have been based only on a temporal interval of a single season, thus ignoring seasonal variation in litter input and community structure. We investigated organic matter input in a Brazilian savanna stream and the influence of its associated hyphomycetes on the invertebrate community. Organic matter input was sampled monthly and the leaves submitted to decomposition experiments. There were lower breakdown rates and higher invertebrate species richness and abundance during the dry season, which reached their maximum in July due to low stream discharge. Invertebrate composition was best explained by hyphomycetes (mainly by *Flagellospora curvula* and *Anguillospora filiformis*). Hyphomycetes have the capacity to degrade complex compounds of litter and to rapidly absorb nutrients by growing branched filaments, thus making the leaves more favourable for consumption by invertebrates. Shredder abundance was negatively related to litter richness, indicating possible species-specific relationships. We observed a sequential process with increased leaf litter input promoting an increase in hyphomycetes biomass, which in turn favoured invertebrate density.

Introduction

Litterfall in temperate streams is regulated by reduced temperature and daylength during autumn (Abelho 2001), while litterfall in tropical streams is related to hydric stress during the dry season (Rezende *et al.* 2016, 2017b). Allochthonous organic matter's (AOM) biomass and plant species composition change throughout the year (Bambi *et al.* 2016), being strongly linked to temperature and rainfall (Tonin *et al.* 2017), and influence ecological processes and biological communities in streams (Rezende *et al.* 2016, Sales *et al.* 2015, Tank *et al.* 2010). Therefore, climatic alterations (e.g. temperature and rainfall) drive food resources by litter input (quality and quantity) and decomposition in low order streams (Graça *et al.* 2015, Tonin *et al.* 2017).

Climatic conditions also drive the functional role of invertebrates by determining growth rate and seasonal timing of egg and nymph development, and limiting their distribution in stream systems (Brittain & Sartori 2009, Hauer & Benke 1987). The functional role of invertebrates in tropical streams is favoured by reduced rainfall during the dry season (Rezende *et al.* 2014a, 2016), while in temperate systems it is favoured by temperature in the summer (Graça *et al.* 2015, Tank *et al.* 2010). The efficiency of trophic pathways (e.g. litter breakdown rates) controls the availability of particulate and dissolved AOM for consumers and producers in streams (Graça *et al.* 2015, Tank *et al.* 2010). The dynamics of AOM also drive the availability of limiting nutrients in streams, particularly phosphorus (Ferreira V *et al.* 2014).

Changes in the litter chemistry of AOMs affect colonization by aquatic invertebrates (Gonçalves *et al.* 2016, Leite *et al.* 2016) and micro-organisms, mainly hypomycetes, which are the main fungi in aquatic systems (Graça *et al.* 2016, Sales *et al.* 2015). High concentrations of lignin and cellulose increase litter toughness (protection from herbivory), and thus decrease detritivore biomass and the rate of litter decomposition (Gonçalves *et al.* 2016, Rezende *et al.* 2014a). Therefore, the conditioning level (by fungi) of litter is fundamental to leaf quality and may determine invertebrate food preferences (Gonçalves *et al.* 2016, Graça *et al.* 2015).

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Aquatic hyphomycetes are the dominant group of the conditioning process in streams of Brazilian savannas (Graça *et al.* 2016). Furthermore, invertebrates may regulate fungal assemblages by selecting leaves rich in fungal biomass (Ferreira *et al.* 2016, Graça *et al.* 2016). The interaction between hyphomycetes and invertebrates has a significant influence on food webs and nutrient cycling in streams (Graça *et al.* 2015, Sales *et al.* 2015). Colonization of leaves by hyphomycetes may range from a few days to months, depending on leaf quality, resulting in a time-lag effect for invertebrate use (Gonçalves *et al.* 2016, Rezende *et al.* 2016, 2017c). This process of degradative succession, however, remains poorly known for tropical freshwater systems (Rezende *et al.* 2016, Sales *et al.* 2015, Tank *et al.* 2010).

Assuming that leaf litter, fungi and aquatic invertebrates have a high degree of interaction during the ecological processes of leaf breakdown and degradative succession, and that there is intra-annual variation in these processes, we hypothesized that: (1) increased organic matter (OM) input (more resources) over time will positively affect the abundance and richness of fungal and, consequently, invertebrate communities; (2) due to the conditioning process, fungi biomass will be more important than litter amount (OM input) in predicting invertebrate abundance and richness; and (3) the peak of these communities (OM input, fungal and invertebrate in this sequence) on the degradative succession process will happen with a time-lag of a few months.

Materials and methods

Study area

An experiment to test the proposed hypotheses was carried out from January to December 2011 in a second-order stream (12°59′45.5′′S, 41°19′37.2′′W) located in Mucugê municipal park (Chapada Diamantina, Bahia, Brazil). The stream studied is ~2 m in width and 50 cm in depth. The region possesses characteristics of different biomes, with the area of the study site being classified as a phytophysiognomy of the Cerrado. The climate is mesothermal, with the temperatures ranging from 15–30ºC between dry (May to August) and summer/rainy (November and February) seasons, which are separated by transition seasons: rainy to dry season (March–April), and dry to rainy season (September–October; Sales *et al.* 2015).

Experimental design

The following water parameters were measured during the study period: conductivity (Handylab LF1, Shott – Duran), pH (ML 1010, Misura Line), temperature (Politerm) and dissolved oxygen (Oximeter, Politerm). Rainfall data were obtained from the Mucugê meteorological station (Appendix 2; number 1241033; located at 13°1′37.1994′′S, 41°13′16.32′′W) of the National Water Agency (ANA) of Brazil (http://hidroweb.ana.gov.br/).

Litterfall was measured monthly from January to December 2011. Organic matter from riparian vegetation was collected from vertical inputs at five points spaced at 10-m intervals along the river. Sampling occurred every 30 ± 2 days over the course of the 12 months of the study (for more information see Sales *et al.* 2015 and Rezende *et al.* 2016). Litter was accumulated in buckets during each sampling period, retrieved and weighed *in situ* (wet weight), after which the bucket with the greatest mass in each row was selected for experimental analysis of leaf litter breakdown. Sampled leaves (1–3 g) were placed in 30 × 30-cm mesh (10 cm) litter-bags (n = 5 sampling sites × 3 replicates × 12 mo = 180 total samplings), and submerged in the stream until the next monthly sampling period. The plant species with potential for comprising the leaf mixture used in the experiment are described in Sales *et al.* (2015). The remaining content of the buckets was dried in an oven at 60°C for 72 h, identified, weighed and described (Sales *et al.* 2015). The dried material was used to create a conversion factor for estimating the initial dry mass of the leaves incubated in the litter-bags and the ash-free dry mass (AFDM) for final mass. The total amount of phosphorus in the leaf mixture of each bucket was obtained using the ascorbic acid method after acid digestion following Flindt & Lillebø (2005).

After the incubation period, the litter-bags were removed from the stream, placed in individual plastic bags, stored cold and transported to the laboratory. In the laboratory, the litter was washed with distilled water over a 180-μm sieve and the invertebrates present were fixed in 70% ethanol. All invertebrates were identified to the family level according to Cummins *et al.* (2005) and Hamada *et al.* (2014). Taxonomic richness and density of the invertebrate assemblages were calculated for each litter-bag and the invertebrates were classified into the following five functional feeding groups (FFGs) according to Cummins *et al.* (2005) and Hamada *et al.* (2014): gathering-collectors (GC), filtering-collectors (FC), shredders (Sh), scrapers (Sc) and predators (Pr). To analyse AFDM and fungi (hyphomycetes) parameters, ten 12-mm diameter discs were removed from randomly selected leaves (five discs for each analysis; for more details see Sales *et al.* 2015). For fungi analysis, the discs were allocated to 100-ml Erlenmeyer flasks containing 25 ml of filtered stream water and shaken (100 rpm) for 48 h at 19 ± 1°C to induce spore formation. Suspensions of released spores (10 ml) were then filtered through a 25-μm diameter Millipore membrane filter, and the retained spores stained with 0.1% cotton blue in lactophenol for subsequent counting and identification using an optical microscope (×400) (Bärlocher 2005).

Statistical analysis

The importance of geographic location (spatial position of sampling points), fungal community and leaf litter input on the structure of the invertebrate community were assessed by a partial Redundancy Analysis (pRDA). The geographic coordinates (latitude and longitude in UTM) of each sampling point were subjected to a Principal Coordinates of Neighbour Matrices (PCNM) analysis as described by Borcard & Legendre (2002) and Dray *et al.* (2006). A Redundancy Analysis (RDA) was then used to remove the effect of non-important variables from the spatial and environmental data matrix with one forward selection being made for each set of predictor variables (geographic location, fungal community and leaf litter input variables) among explanatory variables (invertebrate community). A global test was also performed including all explanatory variables with their R^2_{adj} (according to Ezekiel's correction) serving as a second criterion (in addition to an alpha-value of 0.05) for the selection of variables to retain in subsequent analyses (Peres-Neto *et al.* 2006). The selected explanatory variables that maximized the fit of the model were used in the RDA, with the F-ratio and P-value being computed by permuting the residuals under the full-model approach (Blanchet *et al.* 2008). Whenever $P \leq 0.05$ was obtained, R^2_{adj} was computed for the forward-selection model. If R^2_{adj} was smaller for the forward-selection model than for the global test, another environmental variable was added to the analysis, and the permutation test repeated (Blanchet *et al.* 2008). All analyses were performed using the average values of the environmental and biological variables measured during all sampling periods at each site.

To determine if invertebrate community structure (abundance and richness), FFGs, fungal community and leaf litter input differed significantly among seasons and months, a PerMANOVA and pairwise-contrast analyses (Bonferroni correction) were performed. An indicator species analysis was undertaken to determine which taxa were the most important to community structure over seasons and months during the processes of leaf litter colonization by invertebrates, fungal community establishment and leaf litter input. This method combines the abundance and frequency of each group (seasons and months) from the study and the fidelity of the occurrence of a taxon in a particular group to yield indicator values (IV) for each species in each group (Dufrêne & Legendre 1997).

Temporal variation in richness and abundance of leaf litter input and invertebrate and fungal communities (using the Poisson distribution) and the relative abundances of FFGs (GC, FC, Sh, Sc and Pr using the Binomial distribution) were determined using Generalized Linear Models (GLM; one model per response variable). We adjusted for under- or overdispersion using quasi-Poisson (link = log, test = chi-square) and quasi-binomial distributions (link = logit, test = chi-square) for the Poisson and binomial distributions, respectively. Richness and abundance of invertebrate communities and relative abundance of FFGs (response variables) were analysed in terms of season (dry, rainy and transition) and month (January–December). Contrast analysis was used to discriminate among seasons and months (Crawley 2007). In the contrast analysis (orthogonal), season and month were ordered (increasingly) and tested pairwise with the closest values and sequentially, adding to the model month values with no differences and testing again in a stepwise model simplification (Crawley 2007). A multiple linear regression was used to evaluate the richness and abundance of the invertebrate community and relative abundance of FFGs against richness and abundance of leaf litter input and fungal community (Crawley 2007).

The time-lag between the richness and abundance of the three matrices, leaf litter input, the establishment of fungal community and after colonization by the invertebrate community was assessed by Mantel correlogram/periodogram with 1000 permutations (Legendre & Legendre 1998). Mantel correlogram/periodogram analysis is a multivariate extension of autocorrelation and can be based on any similarity or distance measure (in our case Bray–Curtis distance). The Mantel periodogram shows the average similarity between the time series and time-lag copies of different lag times with high values (in case 1) in the similarity matrix indicating matrix connection. Since a Bray–Curtis distance matrix was used, high values indicate a high difference between matrices (for more see Borcard & Legendre 2012). All analyses were done in R environment using the vegan package (Oksanen *et al.* 2013).

We used GLMs to evaluate the peaks of the communities over time and linear regressions to evaluate the positive/negative effects among communities to test the first hypothesis. For the second hypothesis we used partial redundancy analysis to determine the relative importance of fungi and OM input to aquatic invertebrates. We also used the indicator species analysis to determine the most important taxa in the community in each sample period. Finally, to test the third hypothesis we used a Mantel periodogram to evaluate the time-lag in positive/negative effects among plant, fungi and invertebrate communities.

Results

Abiotic matrix

Rainfall averaged along the study period was 81.1 mm y^{-1} (± 17.9 mm y^{-1}, standard error – SE) throughout the study period, while water temperature ranged between 18–22°C (19.9 ± 0.3°C SE). The water of the stream was slightly acidic, with high levels of oxygen (6.2 ± 0.4 mg l^{-1} SE) and electrical conductivity (38.9 ± 2.5 uS cm^{-1} SE; Appendix 1). The phosphorus content from leaf litter input during the study period was 0.23 mg g^{-1} (± 0.08 mg g^{-1} SE) ranging from 0.16 mg g^{-1} to 0.29 mg g^{-1}.

Variation of the biological matrix

Based on the pRDA (adjusted R^2) analysis, 7% of the variation in the structure of invertebrate community (Appendix 2) was explained by the fungal community (adjusted $R^2 = 4.4\%$; $P < 0.01$) and geographic location (spatial matrix; adjusted $R^2 = 2.6\%$; $P < 0.01$). Variation shared between leaf litter input and geographic location was near zero, indicating that their effects were independent and low. Leaf litter composition did not explain the variation in the structure of the invertebrate community and its shared explanation with fungal community (adjusted $R^2 = 0.05\%$) was low. The shared explanation among all three matrices was 0.21% (adjusted R^2). A single spatial explanatory variable was selected (PCNM 1: adjusted $R^2 = 0.019$, $F = 2.08$, $P = 0.03$). From the seven species of aquatic hyphomycetes identified, only one species was selected as an explanatory variable throughout the year (*Flagellospora curvula*: adjusted $R^2 = 0.049$, $F = 3.57$, $P = 0.04$). The Mantel correlogram/periodogram revealed dissimilarity between invertebrate and fungi communities over time, as well as between invertebrates and litter. Indices near 1 indicate low correlation between the communities over time. The time-lags identified were on the order of 4–5 months (Figure 1). For instance, after 4–5 months the dissimilarity between communities (invertebrates and fungi; invertebrates and litter) was lower than in the other months (after and before 4–5 months).

Invertebrate community

A total of 22 families of invertebrates belonging to six different orders were found associated with leaves in the litter bags, with the maximum average family richness and abundance of individuals being during the dry season (3.85 ± 0.51 and 36.76 ± 6.01, respectively), mainly in July (3.61 ± 0.53 and 39.56 ± 6.11, respectively). The minimum average richness and abundance was during the rainy season (2.15 ± 0.56 and 18.96 ± 8.03, respectively), mainly in February (1.41 ± 0.43 and 4.93 ± 0.72, respectively). The most common invertebrates belonged to the family Chironomidae (Appendix 2). Richness (average: 3 ± 0.2 taxa SE; range: 1–5) and abundance (average: 26 ± 3 ind g^{-1} SE; range: 5–47) of invertebrates varied among seasons (GLM; $\chi^2 = 33.4_{\ (2,177)}$, $P < 0.01$ and $\chi^2 = 373.2_{\ (2,177)}$, $P < 0.01$, respectively), being higher in the dry season (Contrast Analysis, $P > 0.05$; Figure 2). Richness and abundance also varied among months (GLM; $\chi^2 = 145.2_{\ (11,168)}$, $P < 0.01$ and $\chi^2 = 235.3_{\ (11,168)}$, $P < 0.01$, respectively), with May, June and August having the highest richness, and April to August having the highest abundances (Contrast Analysis, $P > 0.05$).

The structure of the invertebrate community (Appendix 2) differed among seasons (PerMANOVA, $F_{(2,53)} = 2.64$; $P = 0.01$), with the dry season differing from rainy and transition seasons (pairwise comparisons, Bonferroni; $P < 0.05$). Still, the structure of the invertebrate community varied among months (PerMANOVA, $F_{(11,44)} = 2.44$; $P < 0.01$), especially between February and March (pairwise comparisons, Bonferroni; $P < 0.05$). Only four months had an indicator taxa: Baetidae was an indicator for August (IV = 0.36; P = 0.02), Coenagrionidae

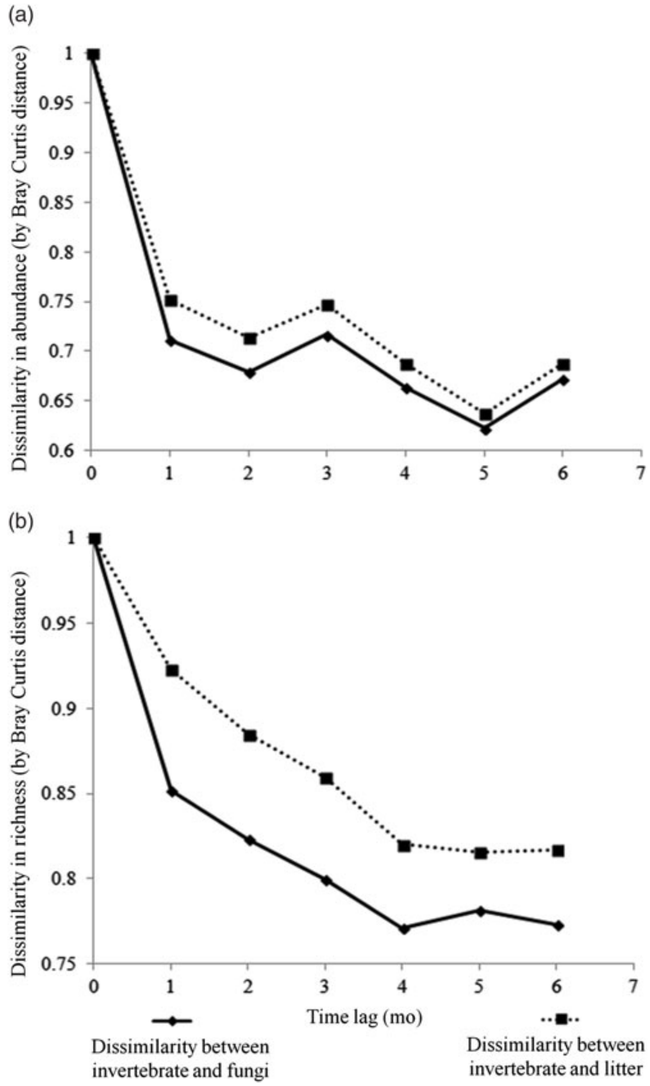

Figure 1. Time lags between invertebrate community against abundance (A) and richness (B) of leaf litter input (dissimilarity between invertebrate and litter; dotted line) and fungal (dissimilarity between invertebrate and fungi; continuous line) communities by Mantel periodogram.

for September (IV = 0.68; $P < 0.01$), Simuliidae for November (IV = 0.45; P = 0.01), and Perilestidae (IV = 0.51; P = 0.02) and Protoneuridae (IV = 0.27; P = 0.02) for December. The composition of invertebrate FFGs also differed among seasons (PerMANOVA, $F_{(2,177)} = 5.24$; $P < 0.01$), with the rainy season differing from the dry season, while the transition seasons were not significantly different from either (pairwise comparisons, Bonferroni; $P < 0.05$). The relative abundance of shredders (Sh, average = 25% ± 10%; range = 5–45%) varied among seasons ($F = 3.24_{(2,177)}$, P = 0.04) and months ($F = 2.81_{(11,168)}$, P = 0.01) and was higher in the dry season (June and July; Contrast Analysis, $P > 0.05$; Figure 2) but also in March. The relative abundance of scrapers (Sc – average: 6% ± 3%; range = 1–10%) did not vary among seasons ($F = 0.34_{(2,177)}$, P = 0.71) or months ($F = 1.56_{(11,168)}$, P = 0.11; Figure 2). The relative abundance of Sh (adjusted R^2; = 0.73, $F_{(4,175)} = 5.97$; P = 0.04) was not related to fungi richness (Beta = 0.02) or abundance (Beta = −0.03) or leaf litter abundance (Beta = 0.01); however, leaf litter richness was negatively related to Sh abundance (Beta = −0.27). The relative abundance of Sc (adjusted R^2; = 0.45, $F_{(4,175)} = 1.41$; P = 0.19) was also not related to richness (Beta = −0.06 and 0.11) or abundance (Beta = −0.07 and 0.17) of fungi and leaf litter, respectively.

Fungal community

Seven species of hyphomycetes were identified in the leaf discs throughout the year: *Anguillospora filiformis* (20.72 ± 6 mean spore mg^{-1} AFDM d^{-1}), *Anguillospora furtiva* (0.01 ± 0.007 mean spore mg^{-1} d^{-1}), *Anguillospora longissima* (0.71 ± 0.26 spore mg^{-1} AFDM d^{-1}), *Flagellospora curvula* (0.03 ± 0.01 mean spore mg^{-1} d^{-1}), *Lunulospora curvula* (0.58 ± 0.36 mean spore mg^{-1} d^{-1}), *Mycocentrospora acerina* (0.0008 ± 0.0008 mean spore mg^{-1} d^{-1}) and *Mycofalcella calcarata* (0.003 ± 0.003 mean spore mg^{-1} d^{-1}). The maximum average richness of hyphomycetes was for leaves in the dry season (1.1 ± 0.25), with the highest value in July (1.4 ± 0.25). High richness of hyphomycetes was also found in the transition season (6.39 ± 2.16) with the highest in October (9.71 ± 2.03). The minimum value of richness of hyphomycetes was during the rainy season (0.74 ± 0.52), mainly in January (0.7 ± 0.25).

The richness of the fungal community did not differ significantly among seasons (average: 1 ± 0.1; range: 0.5 to 2; GLM; $\chi^2 = 2.1_{(2,177)}$, P = 0.33) or months (average: 3 ± 1.1; range: 0.5 to 5; GLM; $\chi^2 = 13.9_{(11,168)}$, P = 0.23). However, fungal spore abundance (Figure 3) was higher (GLM; $\chi^2 = 984.1_{(2,177)}$, $P < 0.01$) in the transition compared to the other seasons (Contrast Analysis, $P > 0.05$). A higher (GLM; $\chi^2 = 1817_{(11,168)}$, $P > 0.05$) abundance of fungi was observed in October compared with the other months (Contrast Analysis, $P > 0.05$; Figure 3). Richness (average: 6 ± 0.2 SE; range: 4 to 8; GLM; $\chi^2 = 7.8_{(2,177)}$, $P < 0.01$) and abundance (average: 0.18 ± 0.02 SE; range: 0.8 to 0.5; GLM; $\chi^2 = 3.3_{(2,177)}$, $P < 0.01$) of leaf litter input were higher in the rainy and transition seasons than in the dry season (Contrast Analysis, $P > 0.05$). The richness of leaf litter input ($\chi^2 = 38.5_{(11,168)}$, $P < 0.01$), was higher in August to December than during the other months (Contrast Analysis, $P > 0.05$), while the abundance of leaf litter input ($\chi^2 = 12.3_{(11,168)}$, $P < 0.01$) was highest in October and November (Contrast Analysis, $P > 0.05$; Figure 3).

Leaf litter input

The vertical input (VI) of leaf litter was higher in the rainy season (2461 ± 566 g m^{-2} SE) than in the dry season (1261 ± 157 g m^{-2} SE). Higher leaf litter input peaks were found in October (187 ± 50 g m^{-2} SE) and November (212 ± 60 g m^{-2} SE; Sales *et al.* 2015). A total of 27 plant species contributed to the VI of leaves, with seven species contributing 85% of the total VI: *Bonnetia stricta* (Nees) Nees & Mart., *Doliocarpus elegans* Nees & Mart., *Laplacea fruticosa* (Schrad.) Kobuski *Tapirira obtusa* (Benth.) J.D. Mitch., *Tibouchina barnebyana* Wurdack, *Richeria grandis* Vahl and *Vochysia acuminata* Bong (Sales *et al.* 2015).

The maximum average richness and abundance of plant species being during the rainy season (6.1 ± 0.56 and 0.23 ± 0.06, respectively), especially in November (7.6 ± 0.63 and 0.51 ± 0.08, respectively). The minimum average richness and abundance were during the dry season (4.9 ± 0.39 and 0.11 ± 0.02, respectively), with the lowest values in May (4.4 ± 0.35 and 0.09 ± 0.01, respectively). The most abundant plant species was *Laplacea fruticosa* (6.12 ± 0.53 g m^{-2} y^{-1}; described in Sales *et al.* 2015).

The structure of leaf litter input did not differ among seasons (PerMANOVA, $F_{(2,52)} = 0.81$; P = 0.63) or months (PerMANOVA,

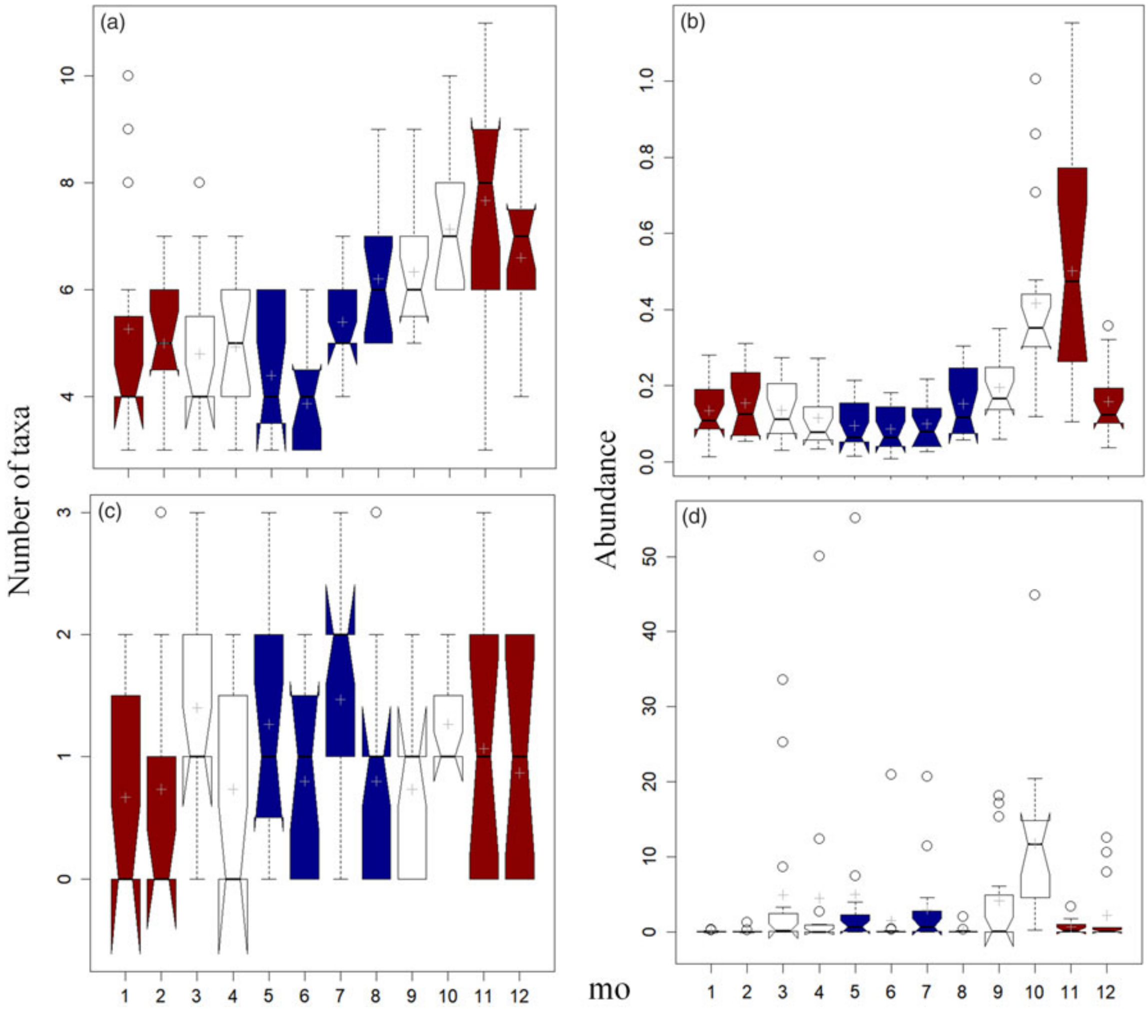

Figure 2. Richness (a; number of taxa) and abundance (b; individuals g^{-1}) of the aquatic invertebrate community and the relative abundance of shredders (c; %) and scrapers (d; %) over months (1 January–12 December). Months are coloured according to season: dry (blue), rainy (red) and transition (white). First (lower line) and third (higher line) quartile, median (bold line), mean (cross), upper and lower limits (dashed lines) and outliers (circles).

$F_{(11,44)} = 0.61$; $P = 0.98$). The structure of the fungal community, however, did differ among seasons (PerMANOVA, $F_{(2,52)} = 2.56$; $P = 0.02$) and months (PerMANOVA, $F_{(11,44)} = 1.73$; $P = 0.01$). The transition season differed from the rainy season, but neither differed from the dry season (pairwise comparisons, Bonferroni; $P < 0.05$). November had the most different aquatic hyphomycets community structure (pairwise comparisons, Bonferroni; $P < 0.05$). A single taxon, *A. filiformis*, was the indicator species for season and months: $IV = 0.64$ ($P < 0.01$) for the rainy season and $IV = 0.33$ ($P = 0.01$) in November.

Discussion

Variation of the biological matrix

We hypothesized that interactions among invertebrates, fungi and litter would be sequential, due to changes throughout the year in litter quality (due to variation in plant species input), breakdown processes and biological interactions. The microbial community, mainly hyphomycetes in Brazilian savanna streams, are early colonizers of AOM, while only later (some months) do invertebrates colonize leaf litter when they are facilitated by fungal conditioning in the process of leaf degradative succession. Contrary to our expectations, leaf litter had a small influence (and only when associated with fungi) on the invertebrate community, possibly due to limited variation in the amount of litter input throughout the course of the year. The fungal community had high importance in structuring the invertebrate community (mainly spore abundance), in accordance with our hypothesis. Our results (by Mantel correlogram/periodogram) indicate that the interaction between fungi and leaf litter had a positive effect on the richness and abundance of the invertebrate community, which was observed after a time-lag of four to five months (Appendix 3).

The fungal community has the most important role in the degradation of the more complex compounds present in leaf litter (e.g. lignin and celullose). Fungi can quickly absorb nutrients by the rapid growth of branched filaments, which facilitates the translocation of organic substances and nutrients by its decomposition activity (Alvim *et al.* 2015, Graça *et al.* 2016). Increased leaf litter decomposition by fungi may increase the resource availability and thus contribute positively to the invertebrate community of tropical streams (Ferreira *et al.* 2016, Rezende *et al.* 2016, 2017c). Our results revealed *Flagellospora curvula* to be the most important fungal species, probably due to its great ability to increase litter

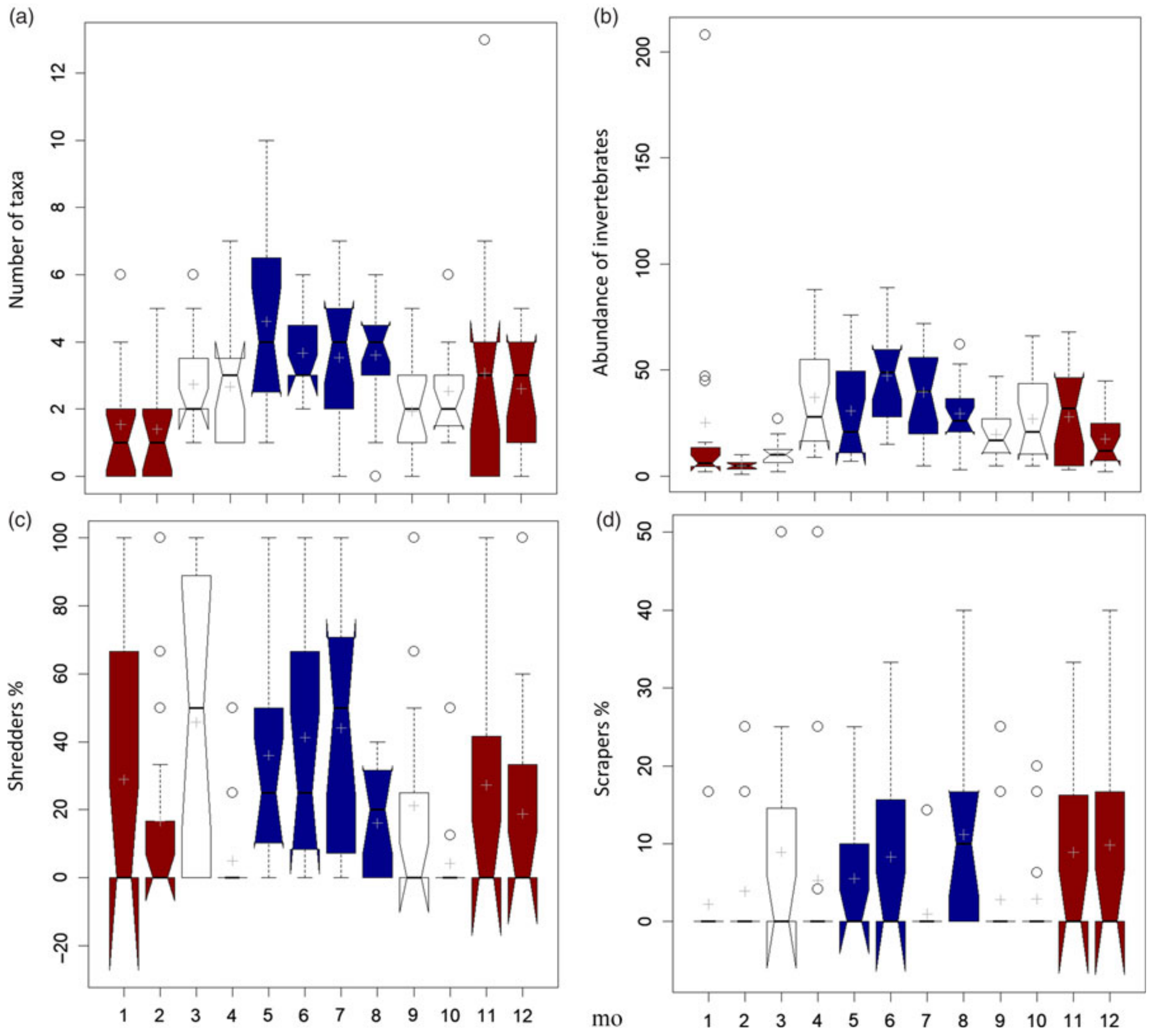

Figure 3. Richness (a and c; number of taxa) and abundance (b and d) for leaf litter input (a and b – ind m^{-2}) and fungal communities (c and d – ind g^{-1}) over months (January 1 to December 12). Months are coloured according to season: dry (blue), rainy (red) and transition (white). First (lower line) and third (higher line) quartile, median (bold line), mean (cross), upper and lower limits (dashed lines) and outliers (circles).

palatability (for more details see Sales *et al.* 2015). The high importance of *F. curvula* highlights the need to investigate the role of individual fungal species in the process of leaf degradative succession, particularly their capability to degrade leaf litter in tropical systems.

Habitat connectivity and the dispersal capacity of species (Durães *et al.* 2016, Hepp & Melo 2013) can contribute to explain the spatial structure of invertebrate communities. A spatial explanation is somewhat surprising given the short distance among sampling points (Hepp *et al.* 2012, Hepp & Melo 2013, Siqueira *et al.* 2012). However, microhabitats present at different sampling points may differ even over short distances (Rezende *et al.* 2014b). For instance, sampling points along a stream can vary in hydraulic conditions (water velocity and depth), substrate size and diversity or deposits of organic matter (Feio *et al.* 2007, Lamouroux *et al.* 2004). These three factors are relevant environmental aspects that structure invertebrate communities (Feio *et al.* 2007, Lamouroux *et al.* 2004). Additionally, variation in fungal (by biological interaction) and plant (used as substrate and food resource) communities among different sampling points were previously reported for the same stream system (Sales *et al.* 2015). Therefore, abiotic factors (e.g. hydraulic and substrate) are not the only relevant aspects driving the invertebrate community, since fungal community and leaf litter quality also help to explain the structure of invertebrate communities in tropical streams.

Invertebrate community structure

The structure of the invertebrate community during the dry season (higher richness and abundance) differed from the structure observed in the other seasons, especially from rainy to dry transition season (February to March). Seasonal differences in invertebrate communities can be explained by the profound changes in environmental conditions that such tropical streams experience: in the dry season there is a narrow channel (increased limnetic zone; Hatje *et al.* 2017, Tonin *et al.* 2017), low stream discharge (and less displacement force; Niu & Dudgeon 2011, Rezende *et al.* 2017c) and high nutrient concentrations (Tonin *et al.* 2017). Along with the low water level of the dry season comes increased alternation between pools and riffles, which are associated with higher resource availability (nutrients). High nutrients availability leads to greater species richness (Ferreira WR *et al.* 2014, Rezende *et al.* 2014a), due to the need for a broader spectrum of traits needed to confer adaptability to species in varied environmental conditions (Lamouroux *et al.* 2004). During the rainy season, increased water flow and velocity washes away litter (and other substrates), hindering the fixation of invertebrates on the substrate, thus decreasing invertebrate abundance in tropical streams (Rueda-Delgado *et al.* 2006, Santos Fonseca *et al.* 2012).

Lower stream discharge (Niu & Dudgeon 2011, Rezende *et al.* 2017c) and higher nutrient concentrations (Tonin *et al.* 2017) also may explain the elevated abundance of Calamoceratidae, Megapodagrionidae, Calopterygidae and Elmidae during the dry season, and the indicator taxon Baetidae during the driest months (i.e. August). Calamoceratidae are shredders that are usually found in leaf litter deposits in pools of tropical streams (Martins *et al.* 2016, Navarro and Gonçalves 2017, Rezende *et al.* 2015), and increase in abundance during the dry season (Leite *et al.* 2016). Baetidae and Elmidae are gathering-collectors or scrapers, which may benefit from an increased abundance of shredders, which convert coarse organic matter into fine particulate matter by fragmentation (Cummins *et al.* 2005, Hamada *et al.* 2014). Lower stream discharge and higher nutrient concentrations (resources) can also increase periphyton biomass among organic and inorganic stream substrates (Rosa *et al.* 2013), which consequently explains the increased density of scrapers during the dry season (Alvim *et al.* 2015, Gonçalves *et al.* 2016). Coenagrionidae are predators and were positively associated with the dry to rainy transition season (September), after an increase in prey density during the dry months (Cummins *et al.* 2005, Hamada *et al.* 2014). Finally, Simuliidae (November), Perilestidae (December) and Protoneuridae (December) were typical of rainy months, probably because these families have a high capacity to adhere to the substrate and resist impacts of increased water flow during the rainy season (Cummins *et al.* 2005, Hamada *et al.* 2014).

In accordance, the abundance of FFGs differed only between the rainy and dry seasons, mainly due to variation in the months of August and October. Shredders (Martins *et al.* 2016, Rezende *et al.* 2015) and scrapers (Rezende *et al.* 2010) have been considered highly important for the production of allochthonous detritus for invertebrate communities in tropical streams. Our results indicated a relative high abundance of shredders (~25%) compared with other tropical streams (about 15%), but still low values compared with temperate streams (about 39%; Boyero *et al.* 2011, 2015; Rezende *et al.* 2015). Furthermore, the ecological niche usually occupied by shredders can be filled by scrapers, which indirectly promote the fragmentation of leaves by scraping the substrate (such as gastropods that use their radulae to obtain food; Rezende *et al.* 2010). Nonetheless, the present study found no clear temporal trends in the variation of shredders and scrapers.

Fungal community structure and leaf litter input

The richness and abundance of leaf litter input in the present study was higher in the rainy and transition seasons than during the dry season, as has been observed for other tropical riparian zones (Rezende *et al.* 2016, 2017a), confirming the marked seasonality of litterfall in tropical systems (França *et al.* 2009, Gregório *et al.* 2007, Wantzen & Mathooko 2008). Based on other studies of tropical streams in Brazil, leaf litterfall occurs mainly from August to October (França *et al.* 2009, Gonçalves & Callisto 2013, Rezende *et al.* 2016, 2017a), but our results identified input peaks occurred in October to December. This finding can be explained by two different mechanisms: the lateral input of the litter from the dry season by increased rainfall in the beginning of the rainy season; and the mechanical removal of green leaves from trees by the increased rainfall in October to December (late rainfall; Rezende *et al.* 2016, 2017a). The time-lag for the peak of leaf litter input (by one or two months) in the present study may indicate the need for increased rainfall to start leaf senescence or to make the leaves more susceptible to mechanical removal by rainfall, in comparison to other tropical systems.

Low fungal (seven species) in leaf richness helps to explain the lack of variation in richness among seasons and months. Sridhar & Sudheep (2010) in southwest India, and Ferreira *et al.* (2012) in an Amazon forest of Ecuador, found similar results. Low species richness can be explained by low nutrient concentrations, acidic pH and low dissolved oxygen due to warm water temperatures (Graça *et al.* 2016, Medeiros *et al.* 2009). However, fungal communities differed between the transition and rainy season (mainly in November). The beginning of the rainy season (September and October) can stimulate fungal spore production by increasing water flow and storm events (increased water turbulence), as has been observed in other tropical streams (Graça *et al.* 2016, Sales *et al.* 2015). According to Bärlocher (1992) and Ferreira & Graça (2006), high water-flow increases water velocity and turbulence, stimulating sporulation by (1) decreasing spore development time and increasing conidiophore density, and by (2) stimulating conidia detachment or (3) facilitating nutrient acquisition. Another important aspect was that *Anguillospora filiformis* (the most abundant fungal species in the present study) is the single indicator species for the rainy season (mainly November). This species is normally associated with warm water (Chauvet & Suberkropp 1998, Rezende *et al.* 2016), which explains its high abundance in the present study and confirming the positive effect of water turbulence on fungi abundance.

Therefore, the present study highlights the fungal community as the most important factor in temporal changes to the invertebrate community. We focused on the analysis of biological components, and so other factors that were not explored, such as organic matter input due to tropical phenology, could contribute to explaining the patterns observed for the invertebrate community. The time-lag presence may be responsible for the weak direct relationship observed between leaf litter and invertebrates. The time-lag may be obscuring any direct importance of litterfall throughout the year, suggesting an indirect effect on the invertebrate community. The temporal scale is the main factor influencing the leaf litter input, the aquatic invertebrate community and the fungal community. Therefore, temporal differences may be responsible for the minimal direct relationship between these biological components.

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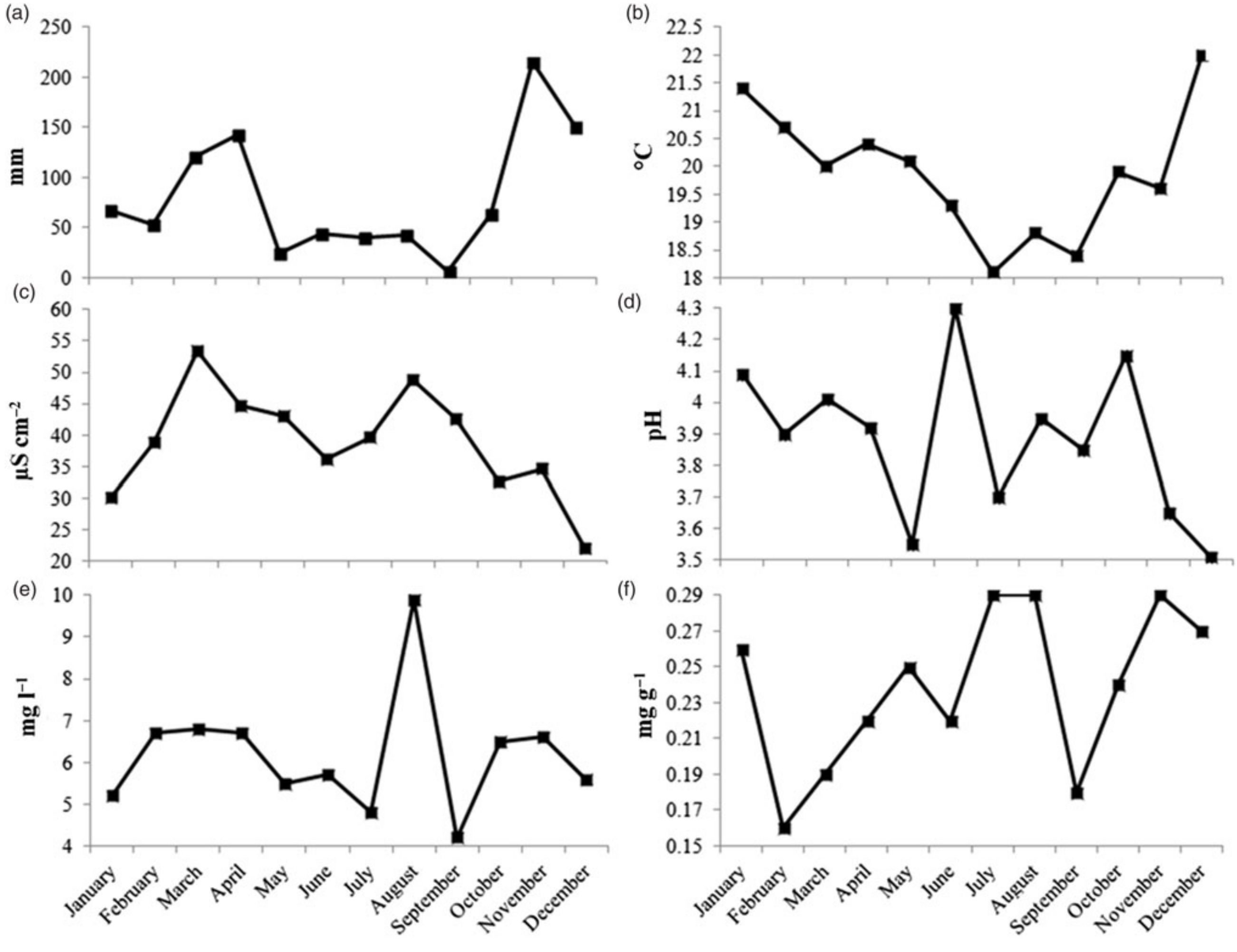
Appendix 1

Monthly values of rainfall (a; mm), water temperature (b; °C), electrical conductivity (c; μs cm^{-2}), pH (d), dissolved oxygen in the water (e; mg l^{-1}) and phosphorus in leaf litter (f; mg g^{-1}) during the study period in a Brazilian savanna stream.



Appendix 2

Monthly mean (and standard deviation) taxon density of invertebrates (individuals g^{-1}) of leaf litter in a Brazilian savanna stream.

Taxa	January	February	March	April	May	June	July	August	September	October	November	December
Arthropoda												
Insecta												
Megaloptera												
Corydalidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Ephemeroptera												
Baetidae	0.07 ± 0.26	0.07 ± 0.26	0.6 ± 1.24	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0.13 ± 0.52
Leptophlebiidae	0 ± 0	0.13 ± 0.35	0.2 ± 0.41	0.2 ± 0.41	0.4 ± 0.83	0.8 ± 1.32	0.13 ± 0.52	1.13 ± 1.46	0.07 ± 0.26	0.13 ± 0.52	1 ± 1.41	0.73 ± 1.58
Trichoptera												
Leptoceridae	0.27 ± 0.59	0.4 ± 0.74	1.27 ± 1.91	0.2 ± 0.56	1.47 ± 1.25	0.87 ± 1.13	0.93 ± 1.03	0.53 ± 0.74	0.67 ± 1.18	0.07 ± 0.26	0.73 ± 0.96	0.93 ± 1.39
Calamoceratidae	0.13 ± 0.35	0 ± 0	0.2 ± 0.41	0 ± 0	0.27 ± 0.46	0.6 ± 1.12	0.67 ± 0.98	0.27 ± 0.59	0.07 ± 0.26	0.07 ± 0.26	0.33 ± 0.72	0 ± 0
Hydroptilidae	0.2 ± 0.56	0 ± 0	0.07 ± 0.26	0 ± 0	0.6 ± 1.18	0.07 ± 0.26	0 ± 0	0 ± 0	0.07 ± 0.26	0.13 ± 0.35	0 ± 0	0.2 ± 0.41
Polycentropodidae	0.13 ± 0.35	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Hydropsychidae	0 ± 0	0.07 ± 0.26	0.27 ± 0.8	0.53 ± 1.13	0.8 ± 1.7	0.13 ± 0.35	0.07 ± 0.26	0.07 ± 0.26	0	0.47 ± 0.83	0.07 ± 0.26	0.07 ± 0.26
Philopotamidae	0 ± 0	0 ± 0	0.33 ± 1.29	0 ± 0	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26
Odonata												
Protoneuridae	0.27 ± 0.59	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0.07 ± 0.26	0.13 ± 0.35	0.4 ± 0.63	0.4 ± 0.63	0 ± 0	0.07 ± 0.26	0.2 ± 0.56
Megapodagrionidae	0 ± 0	0.13 ± 0.52	0.07 ± 0.26	0.13 ± 0.35	0.53 ± 0.64	0.53 ± 1.06	0.07 ± 0.26	0.53 ± 0.83	0 ± 0	0 ± 0	0.13 ± 0.35	0 ± 0
Calopterygidae	0 ± 0	0 ± 0	0.13 ± 0.35	0.2 ± 0.56	0.6 ± 1.12	0.330.62	0.27 ± 0.46	0.27 ± 0.59	0.07 ± 0.26	0 ± 0	0.47 ± 0.92	0.27 ± 0.46
Coenagrionidae	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0.4 ± 0.83	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Lestidae	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.52	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Perilestidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.35	0 ± 0	0 ± 0	0 ± 0
Coleoptera												
Staphylinidae	0 ± 0	0.07 ± 0.26	0 ± 0	0.4 ± 1.55	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.56	0.27 ± 0.7	0 ± 0
Elmidae	0 ± 0	0.07 ± 0.26	0 ± 0	0.2 ± 0.56	0.4 ± 0.74	0.2 ± 0.41	0.33 ± 0.72	0.2 ± 0.41	0 ± 0	0.27 ± 0.59	0 ± 0	0 ± 0
Dytiscidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Diptera												
Chironomidae	21.1 ± 52.1	0.67 ± 1.23	4.8 ± 4.28	31.1 ± 23.8	21.1 ± 19.8	39.9 ± 21	32.9 ± 19.9	22.4 ± 14.3	15.1 ± 11.3	21.4 ± 19.2	21.8 ± 19.6	11.5 ± 10.8
Ceratopogonidae	0 ± 0	0.07 ± 0.26	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.35	0.27 ± 0.59	0 ± 0	0.2 ± 0.77	0.13 ± 0.35	0 ± 0	0 ± 0
Empididae	0 ± 0	0 ± 0	0.07 ± 0.26	0.53 ± 1.55	0.33 ± 1.29	0 ± 0	0.33 ± 0.62	0.27 ± 0.7	0 ± 0	0.27 ± 0.59	0 ± 0	0.13 ± 0.35
Simuliidae	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.26	0.2 ± 0.56	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.8 ± 1.32	0 ± 0	0 ± 0

Appendix 3

Graphical representation of the interaction among the decomposer community (fungi and invertebrates) and leaf litter over time: (a) the high fungal biomass observed in the end of rainy season due to the increase of water turbulence may decrease the litter (by decomposition) and invertebrate density (by low litter resource and high water washing); (b) an increase (over time) on fresh litter input (more leaching of secondary compounds) decreases the fungal biomass, but increases the substrate use by invertebrate communities in the transition period (rainy to dry season); (c and d) a decrease of secondary compounds by leaching process increases the fungi biomass and litter conditioning, and consequently, increases the use of litter as substrate and resource by invertebrate communities during the dry period; (e) the beginning of the fresh litter input (more leaching of secondary compounds) decreases the fungal biomass and the first rains (high water washing) decrease the invertebrate density in the transition period (dry to rainy season); (f) finally, at the beginning of the rainy season an increase in the litter input and rain is observed, decreasing fungi and invertebrate communities. Afterwards, the seasonal cycle restarts in typical years.