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PRIMARY RESEARCH PAPER

Factors controlling leaf litter breakdown in Amazonian streams

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Abstract Our objective was to assess the relative importance of leaf litter quality, and the microbial and aquatic invertebrate communities involved in leaf litter breakdown in Amazonian streams. We test the hypothesis that leaf litter quality is the driving force of leaf breakdown rates, rather than the microbial or invertebrate community, independent of stream characteristics. We incubated 3 g of *Eucalyptus camaldulensis* (EC), *Baccharis platypoda*, *Symphonia globulifera*, *Mabea speciosa* (MS), and *Eperua duckeana* (ED) leaves in five streams for 75, 56, 46, 26, 14, or 7 days. In all of the streams, leaf litter breakdown was higher for EC and lower in ED. This result may be related to different chemical characteristics among the five studied species. We observed higher frequency of shredders in MS and stream 4, and scrapers in streams 1 and 2. The concentration of ergosterol was higher in MS and lower in EC when adenosine triphosphate differed significantly among streams. Our data indicated that leaf litter quality (chemical and structural components) is a main factor affecting leaf breakdown in Amazonian streams.

Keywords Chemical composition · Decomposition · Riparian vegetation · Microbial biomass · Invertebrates

Introduction

Modification of the plant species composition could alter the availability of organic matter and, consequently, the cycling of nutrients (Wallace et al., 1997; Lecerf & Richardson, 2010). Another aspect is that the

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quantity and quality of allochthonous organic matter is important for aquatic systems, especially in low-order streams where the closed canopy limits primary production (Webster & Meyer, 1997). In low-order streams, decomposition is a key process in the remobilization (cycling) of organic matter into the food web and makes the nutrients retained in dead matter available (Gessner et al., 1999).

Leaves are readily used by aquatic decomposers in litter breakdown (Abelho, 2001; Tank et al., 2010; Gonçalves et al., 2012a, 2014; Rezende et al., 2014), particularly by bacteria, fungi and shredder invertebrates (Rezende et al., 2016). However, these organisms have different influences on leaf breakdown. For example, due to the higher concentrations of structural compounds (e.g., lignin and cellulose) in leaf litter in Brazilian Savannah stream systems, microbes (mainly fungi, due to their greater ability to degrade structural compounds) are more important for leaf breakdown in relation to the invertebrate community (Abelho, 2001; Gonçalves et al., 2014). Leaf quality is another important factor that influences the use of leaf litter by aquatic decomposers (Graça et al., 2001; Bruder et al., 2014), because it controls the activity and frequency of decomposers and, consequently, the decay rate (Tank et al., 2010; Bruder et al., 2014). In tropical stream systems, leaf litter with high concentrations of labile compounds (e.g., polyphenols and tannins) and nutrients (e.g., nitrogen and phosphorus) generally exhibits a higher leaf breakdown rate than leaf litter with a high percentage of structural compounds (e.g., lignin and cellulose) and high degree of leaf hardness (Tank et al., 2010; Gonçalves et al., 2012a, b; Rezende et al., 2014).

The Amazonian forest has the most diverse flora in the world, including many species with different chemical compounds in their leaves. Martins et al. (2015) found that leaf litter quality influenced decomposition along an urbanization gradient in Manaus, as was also observed by Irons et al. (1994), suggesting that the microbial community has a strong influence on this process. According to a conceptual model of litter breakdown in low-order streams (Graça et al., 2015), the chemical components of leaf litter quality will control the decomposer community at a local scale. We test the hypothesis that leaf litter quality is the driving force of leaf breakdown rates, rather than the microbial or invertebrate community, independent of stream characteristics. Our objective was to assess the relative importance of leaf litter quality, stream characteristics, and the microbial and aquatic invertebrate communities in leaf litter breakdown in Amazonian streams.

Materials and methods

Study area

We studied leaf litter breakdown in five streams located in the “Reserva Florestal Ducke” (RFD) in Manaus–Amazon State (Fig. 1), an area of 10,000 ha of preserved tropical upland forest (02°55′03°01′S and 59°53′59°59′W). The climate is tropical equatorial humid with rainy (November–May) and dry (June–October) seasons. The mean annual temperature is 27°C, and the altitude varies between 40 and 120 m above s.l. (sea level). The soil is formed in plateaus of yellow oxisol and shoals of podzols and quartz sands (Ribeiro et al., 1999). The streams are shaded by riparian vegetation, and the beds are mainly covered by sand and leaf litter (Mendonça et al., 2005). We used streams of the second hydrological order, which according to Mendonça et al. (2005), exhibit pH values near 4.0 (±0.2 SE; the acidic character of the streams occurs because the Negro River draining basin is a sedimentary region with a high content of organic matter and sandy soil that allows leaching of most humic and fulvic acids into streams). The electrical conductivity and water velocity ranged from 3 to 5 μS/cm and from 14 to 21 cm/s, respectively, highlighting the differences among the streams (Table 1). The dissolved oxygen concentration (7.0 ± 0.6 SE mg/l) and the water temperature (24.0 ± 0.8°C) were similar in all of the streams.

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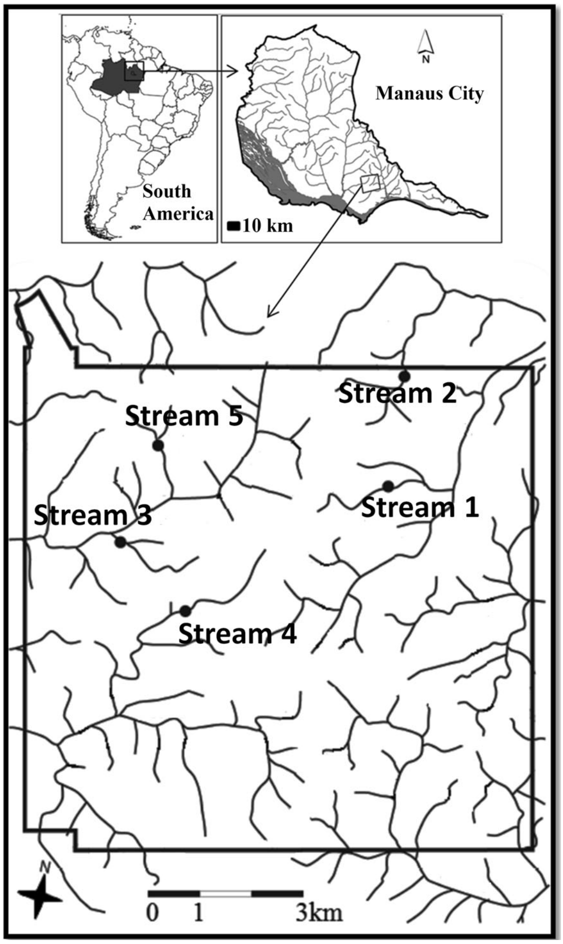

Fig. 1 Geographical location of the sampling points in the study area, Reserva Florestal Ducke, Manaus, Amazonas State, Brazil

Procedures

In the present study, we used senescent leaves of *Eucalyptus camaldulensis* Dehn (exotic species) and *Baccharis platypoda* DC (Cerrado species) and green leaves of *Symphonia globulifera* L. (Amazonian species), *Mabea speciosa* Müll.Arg. (Amazonian species), and *Eperua duckeana* Cowan (Amazonian species). These Amazonian leaf species are frequently recorded in the riparian vegetation of this region. Moreover, green leaves are an important resource of allochthonous organic matter in Amazonian streams and have been used previously in studies of leaf litter breakdown in this region (Landeiro et al., 2008; Martins et al., 2015). Exotic species were particularly selected to simulate the possible effects of changes in the *Eucalyptus* forest or savanization (with increasing colonization of Cerrado trees) on Amazon streams. Leaves were dried at room temperature until a constant weight was achieved. For each species, 90 litter bags (10 × 20 cm and 10 mm^2 mesh) were prepared, each of which contained 3.00 g (±0.05) of leaves. In each stream, three litter bags (sub-samples) containing each species were incubated (March 2010) for 75, 56, 46, 26, 14, or 7 days; all of the samples were removed on the same day (June 2010). The samples were removed and placed individually into insulated plastic bags and transported in thermal containers to the laboratory, where they were transferred to a refrigerator (4°C) until the time of processing.

In the laboratory, the leaves were washed with tap water in a 120-mm-mesh sieve. The invertebrates retained on the sieve were preserved in 70% alcohol for later identification and enumeration (Hamada and Ferreira-Keppler, 2012; Hamada et al., 2014). The numbers of *taxa* and individuals were calculated for the aquatic invertebrate community. The invertebrates were classified into five feeding categories (Pérez, 1988; Cummins et al., 2005; Merritt et al., 2008): gathering-collectors, filtering-collectors, shredders, scrapers, and predators. Among these categories, only the frequencies of shredders and scrapers were used to determine the direct effects on leaf litter.

Table 1 Mean values and standard errors of pH, electrical conductivity (μS/cm), dissolved oxygen (mg/l), and the water current (cm/s) at the five sampling sites (Streams 1, 2, 3, 4, and 5) in four sub-basins (Acará, Tinga, Aguá Branca, and Bolívia streams) of the Reserva Florestal Ducke, according to Mendonça et al. (2005)

Sub-basin	Points	pH	Conductivity	Oxygen	Water current
Tinga	Stream 1	4.5 ± 0.1	3 ± 1	7 ± 1	19 ± 15
Aguá Branca	Stream 2	4.0 ± 0.1	3 ± 1	8 ± 1	21 ± 15
Acará	Stream 3	4.2 ± 0.3	4 ± 2	7 ± 2	16 ± 9
Bolívia	Stream 4	4.3 ± 0.2	5 ± 2	6 ± 1	18 ± 11
Acará	Stream 5	4.4 ± 0.3	4 ± 1	7 ± 1	14 ± 9

Five leaves from each litter bag were randomly collected, and three disks (1.2 cm in diameter) were extracted from each leaf litter. One set was used to determine the remaining ash-free dry mass (AFDM; calculated after incineration in a muffle furnace at 550°C for 4 h), and the other sets were used to assess ergosterol and adenosine triphosphate (ATP) concentrations. The remaining material was oven-dried at 60°C for 72 h to determine its dry weight, and the material was later ground for analysis of the quality of leaf litter based on total polyphenol and tannic acid concentrations (Bärlocher and Graça, 2005) as well as lignin and cellulose contents (Gessner, 2005a).

The microbial total biomass was estimated through ATP quantification (Abelho, 2005). The biomass of aquatic hyphomycetes was estimated through the quantification of ergosterol, which is a lipid exclusive to fungal membranes (Gessner, 2005b).

Data analyses

Leaf litter breakdown rates (k) were calculated using a negative exponential model of the percent of mass lost over time ($W_t = W_0 e^{-kt}$; W_t = remaining weight; W_0 = initial weight; $-k$ = decay rate; t = time). We used repeated measures analysis of variance (RM-ANCOVA) to analyze the remaining leaf litter mass, invertebrate communities (number of *taxa* and density), frequency (relative abundance) of functional trophic groups of invertebrates (shredders and scrapers), fungal biomass (ergosterol), and microbial biomass (ATP) as dependent variables against the studied leaf litters as well as the interaction between the two factors (categorical factors). RM-ANCOVA was used to avoid pseudoreplication, not only temporally but also spatially. Time (days) was used in the repeated measures analysis as a fixed factor (continuous variable) for the correction of temporal pseudoreplicates. The litter bags collected at each time point were transformed into replicates (the sample number in the analysis corresponds to 5 leaf species $\times 5$ streams $\times 6$ times = 150 samples in total). Contrast analysis was used to discriminate among statistically significant categorical variables. We assessed the association between some variables (mean values for leaf litter at the sampling sites) using Spearman correlation (Crawley, 2007). In this contrast analysis (orthogonal), the months were ordered (increasingly) and tested in pairwise (with the closest values). Then monthly values with no differences were sequentially added to the model, and testing was performed with the next values in a simplified step-wise model (for more see also Chap. 9 of Crawley, 2007). We tested the normality of the data and the homogeneity of variances using the Kolmogorov–Smirnov and Levene tests, respectively. The data were transformed whenever necessary using the neperian logarithm (ln) to obtain the best fit (Crawley, 2007).

We employed Spearman's correlation to verify the relationship between leaf litter breakdown rates and leaf chemical compounds (lignin, cellulose, total polyphenols, and tannins). This analysis was also used to verify the relationship between leaf litter breakdown rates and decomposer communities (aquatic invertebrates and microbial community). All analyses were conducted in R (The R Core Team, 2013).

Results

Leaf litter breakdown

Leaf species quality (44.7% of the sum square) was a more important factor in leaf litter breakdown in comparison with the stream (1.1% of the sum square). The post hoc test (contrast analyses) highlighted stream 2 with high decay values. In all streams, the leaf litter of the exotic *E. camaldulensis* ($k = -0.034$ day^{-1}) showed the highest leaf litter breakdown rates, followed by the leaf litter of also the exotic *B. platypoda* ($k = -0.018$ day^{-1}), *M. speciosa* ($k = -0.016$ day^{-1}), *S. globulifera* ($k = -0.013$ day^{-1}), and *E. duckeana* ($k = -0.007$ day^{-1}). A significant difference in the percent of mass remaining at the end of the experiment (75 days) was recorded between species (Table 2). The lowest remaining masses were observed for the exotic *E. camaldulensis* (mean and SE 11 ± 1%), followed by the exotic *B. platypoda* (31 ± 1%) and *M. speciosa* (32 ± 1%), which were similar to each another, then *S. globulifera* (38 ± 2%) and, lastly, *E. duckeana* (64 ± 1%; Table 2; Fig. 2A). The most rapid mass loss was observed in the first 7 days in all of the studied leaf species, and the highest values of biomass loss were observed in the exotic *E. camaldulensis* (36 ± 4%), followed by the exotic *B. platypoda* (25 ± 3%), *M. speciosa* (24 ± 3%), *S. globulifera* (19 ± 3%), and *E. duckeana* (9 ± 1%). After the first several days, we

Table 2 Repeated measures analysis of variance (RM ANOVA in stream factor = Error: stream) and contrasts for the remaining leaf litter biomass (%), shredder and scraper frequency (%), invertebrate abundance (individuals g^{-1} AFDM) and number of taxa (*taxa* number), hyphomycete biomass (μg ergosterol g^{-1} AFDM leaf litter), and microbial biomass (mmoles ATP g^{-1}AFDM leaf litter) in the leaf litter of *Eucalyptus camaldulensis* (EC), *Eperua duckeana* (ED), *Symphonia globulifera* (SG), *Baccharis platypoda* (BP), and *Mabea speciosa* (MS) in five Amazon streams and the interaction between the two factors

RM-ANCOVA	Df	Sum Sq (%)	*F* value	*P*	Analysis of contrasts
Remaining mass					
Erro:days	1	45.21			
Streams	4	1.06	4.20	0.003	Stream 4 = stream 1 = stream 3 = stream 5 < stream 2
Leaf litter	4	44.77	177.74	0.000	*E. camaldulensis* = *B. platypoda* = *M. speciosa* < *S. globulifera* < *E. duckeana*
Leaf litter*streams	16	1.16	1.15	0.314	
Residuals	124	7.81			
Shredders					
Erro:days	1	0.81			
Streams	4	5.93	6.71	0.000	Stream 5 = stream 3 = stream 2 = stream 1 < stream 4
Leaf litter	4	3.50	3.96	0.004	*B. platypoda* = *E. camaldulensis* = *S. globulifera* = *E. duckeana* < *M. speciosa*
Leaf litter*Streams	16	4.72	1.34	0.171	
Residuals	124	85.03			
Scraper					
Erro:days	1	2.70			
Streams	4	4.62	5.07	0.001	Stream 4 = stream 5 = stream 3 < stream 1 = stream 2
Leaf litter	4	0.76	0.84	0.502	
Leaf litter*Streams	16	4.37	1.20	0.265	
Residuals	124	87.56			
Shredders + Scraper					
Erro:days	1	3.51			
Streams	4	3.00	3.47	0.008	Stream 5 = stream 3 = stream 1 < stream 4 = stream 2
Leaf litter	4	4.06	4.70	0.001	*S. globulifera* = *B. platypoda* = *E. camaldulensis* = *E. duckeana* < *M. speciosa*
Leaf litter*Streams	16	6.32	1.83	0.026	
Residuals	124	83.12			
Density of invertebrates					
Erro:days	1	0.32			
Streams	4	0.61	0.65	0.624	
Leaf litter	4	3.53	3.76	0.005	*E. duckeana* = *S. globulifera* = *M. speciosa* = *B. platypoda* < *E. camaldulensis*
Leaf litter*Streams	16	5.07	1.35	0.164	
Residuals	124	90.46			
Richness of invertebrates					
Erro:days	1	2.04			
Streams	4	22.70	33.40	0.000	Stream 4 = stream 3 = stream 5 < stream 1 < stream 2
Leaf litter	4	3.51	5.16	0.000	*E. duckeana* = *S. globulifera* = *B. platypoda* = *E. camaldulensis* < *M. speciosa*
Leaf litter*Streams	16	1.43	0.53	0.932	
Residuals	124	70.32			
Ergosterol					

Table 2 continued

RM-ANCOVA	Df	Sum Sq (%)	*F* value	*P*	Analysis of contrasts
Erro:days	1	1.35			
Streams	4	3.65	1.74	0.147	
Leaf litter	4	33.70	16.04	0.000	*E. duckeana* < *B. platypoda* = *E. camaldulensis* = *S. globulifera* < *M. speciosa*
Leaf litter*Streams	16	5.11	0.61	0.871	
Residuals	124	56.19			
ATP					
Erro:days	1	6.84			
Streams	4	8.78	3.66	0.008	Stream 5 = stream 2 = stream 3 = stream 4 < stream 1
Leaf litter	4	3.79	1.58	0.186	
Leaf litter*Streams	16	19.39	2.02	0.018	
Residuals	124	61.21			

observed faster mass loss, followed by stabilization, especially at the end of the experiment (Fig. S1A). Leaf litter breakdown rates were negatively correlated with lignin ($r = -0.79$, $P = 0.02$) and cellulose ($r = -0.91, P = 0.02$), and positively correlated with the invertebrate density ($r = 0.72$, $P = 0.01$) and scraper density ($r = 0.84$, $P = 0.04$). The other variables were not related to leaf litter decomposition rates.

Invertebrate communities

Regarding leaf colonization by shredders and scrapers, the stream (5.9 and 4.6% of the sum square, respectively) was a more important factor compared with leaf quality (3.5 and 0.7% of the sum square, respectively), with low mean abundance values being observed in all experiments (3.9 and 6.6% of the invertebrate frequency, respectively). We found the highest frequency of shredders (mean and SE = 3.9 ± 0.6%) in the *M. speciosa* leaf litter, mainly in stream 4. However, we observed a significant difference in the frequency of scrapers only between streams (higher values in streams 1 and 2) and not between leaf species (6.7 ± 1%; Fig. 2B, C; Table 2). The highest frequency of shredders and scrapers was recorded in the leaf litter of *M. speciosa* (7.7 ± 0.4 and 7.8 ± 0.5%, respectively). The frequency of shredders and scrapers increased from the beginning to the end of the experiment, with higher values being observed in later stages in most of the leaf litter (Figs. 2B, C, S1B, C).

Fig. 2 Mean values (*columns*) and standard errors (*vertical bars*) of the remaining mass (**A**; in %/AFDM), shredder frequency (**B**; in %), scraper frequency (**C**; in %), density of invertebrates (**D**; individuals g^{-1} AFDM), leaf litter, number of invertebrate *taxa* (**E**; *taxa* number), biomass of fungal hyphomycetes (**F**; µg ergosterol g^{-1} AFDM leaf litter), and total microbial biomass (**G**; mmoles ATP g^{-1}AFDM leaf litter) over time in leaf litter from *Eucalyptus camaldulensis, Eperua duckeana, Symphonia globulifera, Baccharis platypoda,* and *Mabea speciosa* in five Amazon streams. The *dashed line* is the total mean value in each stream ▶

The density of invertebrates in the leaf litter differed significantly only between the species (Fig. 2D; Table 2), and the highest value was observed in the exotic *E. camaldulensis* (120 ± 53 individuals g^{-1} AFDM). Leaf quality (3.5% of the sum square) was a more important factor in leaf colonization compared with the stream (0.6% of the sum square). The number of taxa also differed between the species (Fig. 2E; Table 2), with the highest values being observed in *M. speciosa* (total mean and SE = 3 ± 0.2 *taxa*). However, the stream (22.7% of the sum square) was a more important factor (mainly in streams 1 and 2) in leaf colonization compared with leaf quality (3.5% of the sum square). In the exotic *E. camaldulensis* and *E. duckeana*, we observed a clear peak of the invertebrate density at 46 days of incubation (Fig. S1D). In all of the leaf litters from the different species, the number of *taxa* increased from the beginning to the end of the experiment, with higher values being observed in later stages (Fig. S1E).

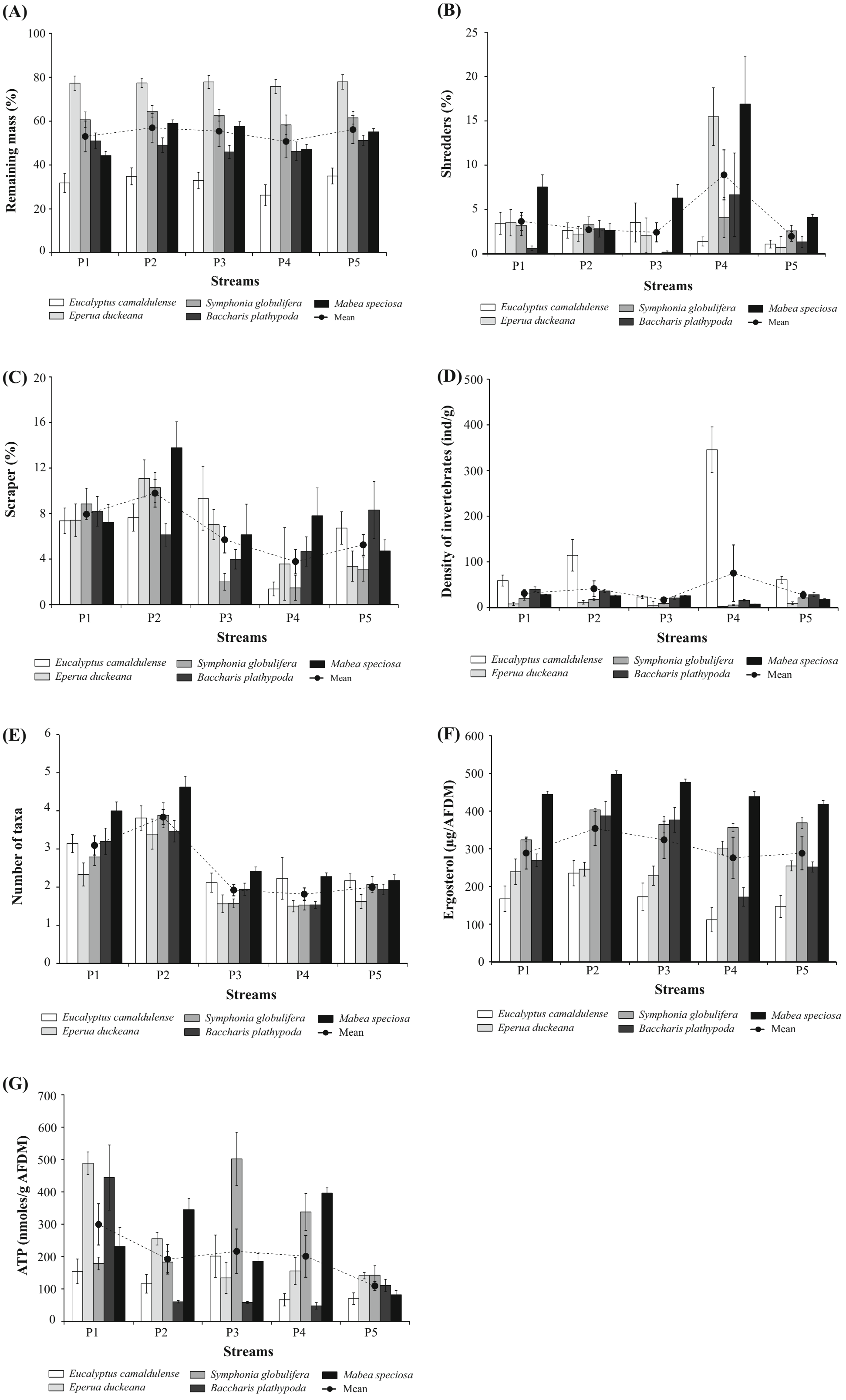
(A)
Remaining mass (%)
0
20
40
60
80
100
P1
P2
P3
P4
P5
Streams
(B)
Shredders (%)
0
5
10
15
20
25
P1
P2
P3
P4
P5
Streams
(C)
Scraper (%)
0
4
8
12
16
20
P1
P2
P3
P4
P5
Streams
(D)
Density of invertebrates (ind/g)
0
100
200
300
400
500
P1
P2
P3
P4
P5
Streams
(E)
Number of taxa
0
1
2
3
4
5
6
P1
P2
P3
P4
P5
Streams
(F)
Ergosterol (µg/AFDM)
0
100
200
300
400
500
600
P1
P2
P3
P4
P5
Streams
(G)
ATP (nmoles/g AFDM)
0
100
200
300
400
500
600
700
P1
P2
P3
P4
P5
Streams
Eucalyptus camaldulense
Eperua duckeana
Symphonia globulifera
Baccharis plathypoda
Mabea speciosa
Mean

Table 3 Analysis of variance (one-way ANOVA) and comparisons of the percentages of cellulose, lignin, total polyphenols, and tannins in the leaf litter of *Eucalyptus camaldulensis* (EC), *Eperua duckeana* (ED), *Symphonia globulifera* (SG), *Baccharis platypoda* (BP), and *Mabea speciosa* (MS) in five Amazon streams. Degrees of freedom (DF), residuals, sum of squares (%), *F* test values, significance values for analyses of variance (*Pr*)

One-way ANOVA	Df	Sum Sq %	*F* value	*P*	Analysis of contrasts
Cellulose	4	69.0	13.4	<0.001	*E. camaldulensis* < *B. platypoda* = *M. speciosa* < *S. globulifera* = *E. duckeana*
Residuals	24	31.0			
Lignin	4	13.8	1.0	0.445	
Residuals	24	86.2			
Total Polyphenols	4	46.7	29.6	<0.001	*M. speciosa* = *E. duckeana* = *E. camaldulensis* < *S. globulifera* = *B. platypoda*
Residuals	135	53.3			
Tannins	4	30.2	5.0	0.002	*E. duckeana* = *B. platypoda* = *M. speciosa* = *E. camaldulensis* < *S. globulifera*
Residuals	46	69.8			

Microbial biomass

The fungal biomass (stream mean and SE of ergosterol = 306 ± 14 µg g^{-1} AFDM) in the leaf litter differed significantly only between the species (Fig. 2F; Table 2). Leaf quality (33.7% of the sum square) was a more important factor in fungal biomass colonization compared with the stream (3.6% of the sum square). We found the highest values in *M. speciosa*, which were 536 and 473 µg g^{-1} AFDM at 56 days and 72 days, respectively. The lowest fungal biomass was observed in the exotic *E. camaldulensis* (Fig. S1F) at 46 days (72 µg g^{-1} AFDM).

The microbial biomass in the leaf litter estimated based on ATP (Adenosine triphosphate) concentrations (stream mean and SE = 203 ± 30 nmol g^{-1} AFDM) did not differ significantly between the species but did differ significantly between streams (higher values in stream 1; Fig. 2G; Table 2). The stream (8.7% of the sum square) was a more important factor in microbial biomass colonization compared with leaf quality (3.7% of the sum square). Higher values of microbial biomass were observed at 7 days of incubation (395 ± 37 nmol g^{-1} AFDM) in the leaf litter of most of species, except for *E. duckeana*, which exhibited a high value at 14 days of incubation (499 nmol g^{-1} AFDM; Fig. S1G). The lowest microbial biomass was observed at 75 days in the exotic *B. platypoda* (50 nmol g^{-1} AFDM; Fig. S1G).

Quality of leaf litter

The five leaf species studied were significantly different in their chemical characteristics (Table 3). The lowest concentration of cellulose was found in the exotic *E. camaldulensis* (mean and SE = 13 ± 1%), and the highest concentrations were observed in *S. globulifera* (22 ± 1%) and *E. duckeana* (25 ± 1%). The content of lignin did not differ between the leaf litter species (44 ± 3%). The concentration of total polyphenols was highest in *S. globulifera* (10 ± 0.005%), followed by the exotic *B. platypoda* (9 ± 0.001%) and *E. duckeana* (6 ± 0.001%), and all these species presented higher concentrations than the exotic *E. camaldulensis* (6 ± 0.001%) and *M. speciosa* (5 ± 0.001%). The tannin content was highest in *S. globulifera* (0.04 ± 0.005%), followed by the exotic *E. camaldulensis* (0.02 ± 0.004%), *M. speciosa* (0.02 ± 0.004%), the exotic *B. platypoda* (0.01 ± 0.002%), and *E. duckeana* (0.01 ± 0.003%).

Discussion

We observed that leaf litter quality (chemical and structural components) can be the main factor affecting leaf breakdown in the studied streams. Besides, we did not find effects if the detritus were of the origin exotic or natural. However, we observed that biological communities were influenced by quality of detritus and water characteristics.

Leaf litter breakdown

Leaf litter quality was found to be the main driving force of leaf litter breakdown compared with biological decompositors. This result corroborates the hierarchical conceptual model proposed by Graça et al. (2015), indicating that the litter chemical characteristics is important in the watershed scale. There are several studies that have indicated higher importance of the microbial community compared with leaf litter quality in low latitudes (Abelho, 2001; Tank et al., 2010; Boyero et al., 2012). However, we highlight the lack of studies in Amazonia (despite being the largest biome of Brazil), compared with other biomes in South America (see also the revision proposed by Gonçalves et al., 2014). The present study indicated that leaf litter breakdown rates (*k*) are strongly dependent on the composition of riparian vegetation due to changes in leaf litter quality (Petersen and Cummins, 1974; Cummins et al., 1983). Moreover, our data indicated that the *k* values for leaf litters of similar quality were homogeneous. Therefore, chemical characterization of the riparian vegetation will help to understand the functioning of large areas in this ecosystem (organic matter cycle and energy flow), and we would like to highlight the need for further studies on Amazonian riparian vegetation. The findings of the present study are also important evidence that the recovery of vegetation which differs from the original vegetation will change the energy flow and the cycling of organic matter (Gonçalves et al., 2012b). Therefore, our findings may guide the recovery of degraded areas and the implementation of preservation and restoration management (e.g., which species to use in reforestation) in Amazonian streams.

The finding that the lowest remaining mass occurred in *E. camaldulensis* was related to its low content of cellulose and high contents of polyphenols and tannins. A synergistic effect in leaf litter with low contents of structural compounds (e.g., lignin and cellulose; Meentemeyer, 1978) facilitates the release of other chemical compounds through leaching of compounds that are highly hydrophilic (e.g., polyphenols, tannins and nutrients; Ardón et al., 2006; Gonçalves et al., 2012b). Therefore, the *E. camaldulensis* leaf litter exhibited greater chemical decomposition and palatability compared with the other leaf litters, indicating that litter quality may determine the rate of mass loss (Gessner et al., 1999; Graça et al., 2001). This phenomenon also explains the higher remaining mass in *E. duckeana*, whose leaves are harder compared with the leaves of *E. camaldulensis* (Gonçalves et al., 2012a, b; Rezende et al., 2014). The large amount of leaf litter breakdown in the exotic species (*E. camaldulensis*) also corroborates the idea that compared with tropical species, native species present low palatability and nutritional quality, larger quantities of secondary metabolites, and larger recalcitrant compounds due to the higher pressure from herbivores suffered by native species during the evolutionary process (Gimenes et al., 2010; Gonçalves et al., 2014). The leaching process may also explain the rapid loss of mass in the first days of the experiment (Gessner et al., 1999). Leaching occurs throughout the leaf litter breakdown process; however, it occurs more intensively in the first days of incubation, which may explain why the most rapid mass loss occurred in the first seven days (Gessner et al., 1999).

The average *k* values determined in our experiment were within the upper range of the values obtained in other tropical streams (Abelho, 2001; Gonçalves et al., 2014). The *k* values recorded for *E. camaldulensis* and *B. platypoda* can be classified as high ($k > -0.017$ day^{-1}) according to Gonçalves et al. (2014), who developed an index for tropical systems. However, the *k* values for *M. speciosa*, *S. globulifera*, and *E. duckeana* can be classified as intermediate ($-0.004 > k < -0.017$ day^{-1}). According to the index proposed by Petersen and Cummins (1974) for temperate systems, the *k* values for all of the species may be classified as high ($k > -0.010$ day^{-1}), except for *E. duckeana*, which would be classified as intermediate ($-0.005 > k < -0.010$ day^{-1}). A fast decay rate of *E. camaldulensis* has been observed in other studies in non-Amazonian streams (Abelho et al., 2010; Gonçalves et al., 2012b; Rezende et al., 2014). These results reinforce the finding that *Eucalyptus* exhibits faster decay rates than native species. Another plant species that showed an increase in the leaf litter breakdown rate in Amazonian streams was *B. platypoda* ($k = -0.018$ day^{-1} in our study, but $k = -0.0019$ day^{-1} in a Cerrado stream according to Alvim et al., 2015), indicating that leaf litter responds in different ways depending on the biome. Thus, the preservation of native vegetation is important mainly because exotic species can alter ecosystem functioning through increase in nutrient and FPOM in food webs of Amazonian streams, and endangering biodiversity (Gonçalves et al., 2012b; Rezende et al., 2014).

Biological community

The frequency of shredders and scrapers observed in our study was low compared with that observed in other Amazonian streams (ranging from 7 to 15%, excluding chironomids, as reported by Landeiro et al., 2008, 2010) and tropical streams (ranging from 7 to 30%, excluding chironomids, as reported by Moretti et al., 2007; Rezende et al., 2014). Despite these low densities, the highest density of shredders and scrapers was observed in the stream showing the highest leaf litter breakdown rates (stream 2). The importance of the density of invertebrates in leaf litter decomposition is rarely reported in tropical studies (Rezende et al., 2014), indicating that invertebrate biomass could be an important factor to be considered in relation to mass loss (Tonin et al., 2014). Due to the ability of shredders to feed directly on leaf litter tissue, they are the most important functional trophic group in the leaf litter breakdown process (Graça, 2001; Tank et al., 2010), although they are scarce in some tropical regions (Boyero et al., 2011a, b). However, studies have demonstrated that scrapers (with a scraping apparatus such as a radula) accelerate leaf litter fragmentation through their feeding activity (Casas and Gessner, 1999; Rezende et al., 2010), explaining the higher decay rates observed in stream 2. The frequency of shredders and scrapers was higher in *M. speciosa* (intermediate *k* rate) compared with the other leaf litters studied. This result may indicate that these functional feeding groups could be using this resource mainly as a substrate (Moulton et al., 2010; Boyero et al., 2012; Gonçalves et al., 2012b), and not as a food source because of the low quality of the leaf litter.

Local conditions in streams were found to be important only for shredders, scrapers, and the richness of invertebrates, while leaf litter quality was important for the invertebrate density, indicating that different factors are related to the structure of the invertebrate community (Rezende et al., 2014). In contrast to the findings of the present study, a direct influence of shredders on leaf litter breakdown has been observed in some tropical systems (Landeiro et al., 2010; Rezende et al., 2014); however, we must consider the possibility of indirect effects of this community. The effects of shredders on leaf litter breakdown can be observed in our study in that the highest decay rates and shredder density were found in stream 4. The higher richness of aquatic invertebrates in *M. speciosa* may be explained by intermediate leaf litter breakdown rates, which allow larger amounts of leaf litter (as a substrate) to accumulate in the environment, allowing more time for invertebrate colonization (Ligeiro et al., 2010). In contrast, rapid leaf litter breakdown results in little time for invertebrate colonization, a high proportion of structural compounds (decrease in litter quality), and uniformity of leaf litter (decrease in litter substrate), resulting in low invertebrate diversity (Capello et al., 2004).

The density (overall mean of 35 ind/g) and richness (overall mean of 2.5 number of *taxa*) of invertebrates associated with leaf litter in the studied streams were quite low compared with other tropical streams (Moretti et al., 2007; Gonçalves et al., 2012a, b; Rezende et al., 2014). In our study, the highest values of invertebrate density were recorded in *E. camaldulensis*, possibly due to higher litter palatability, as described in other tropical studies (see also Rezende et al., 2014), helping to explain the faster leaf litter breakdown rates of this species due to higher decomposer activity. These results could indicate if we had have a replacement of native trees by exotic species in riparian zones can affect the ecological functioning of aquatic amazon ecosystems (e.g., increasing the nutrients). The temporal variation of particular parameters of the invertebrate community (shredder and scraper frequency, density, and richness) increased from the beginning to the end of the experiment, which also illustrates the natural effect of the ecological succession process that litter undergoes over time (Landeiro et al., 2010; Ligeiro et al., 2010; Martins et al., 2011; Gonçalves et al., 2012a). Results showing the importance of invertebrates in the process of leaf litter breakdown in tropical systems are rare and contradict the hypothesis that fungi are the most important players in the tropical systems (Landeiro et al., 2010; Gonçalves et al., 2012a; Rezende et al., 2014).

The fungal biomass (determined from the ergosterol concentration) recorded in the present study was in the upper range compared with other tropical streams (ranging from 150 to 550 $\mu g\ g^{-1}$, as reported by Gonçalves et al., 2006b; Gonçalves et al., 2007; Gonçalves et al., 2012b; Rezende et al., 2014), which indicates high leaf litter breakdown rates. The lower values of ergosterol observed in *E. camaldulensis* (due to fast chemical decomposition) and the higher values found in *M. speciosa* (a less water reactive and more resistant substrate) corroborate the idea that leaf litter quality may drive increases in fungal biomass, as observed by Gonçalves et al. (2012b, 2014). However, microbial biomass (determined from the ATP concentration—Adenosine triphosphate) showed lower values in the present work compared with other tropical streams (ranging from 50 to 3000 nmol g^{-1}, as reported by Abelho, 2001; Abelho et al., 2005; Gonçalves et al., 2006b, 2007; Rezende et al., 2014), probably due to the acidic water in the streams. Acidity can have a greater negative effect on the bacterial community compared with the fungal community (Rousk et al., 2010). The microbial community may be composed of fungi, bacteria, algae, and other microorganisms that modify their relative biomass according to environmental characteristics or the stage of the leaf litter breakdown process (Gessner et al., 1999; Abelho, 2001; Tank et al., 2010). The highest ATP values occurred in the initial stages, probably due to the capacity of bacteria to metabolize molecules that are easy to assimilate from litter. However, the ergosterol content (fungi) was higher in more advanced stages due to the capacity of the fungal community to degrade more complex compounds (Gonçalves et al., 2006a). Therefore, fungi can also be considered as a successional state in the chain of higher order leaf litter breakdown in streams and are not necessarily of lesser importance, as observed in other tropical streams (Gonçalves et al., 2006b; Gonçalves et al., 2007; Gonçalves et al., 2012b; Rezende et al., 2014).

Conclusion

In general, our data indicated that leaf litter quality does drive mass loss. The greater importance of leaf litter quality indicates strong dependence of leaf litter breakdown rates on the composition of riparian vegetation. Therefore, changes in the composition of vegetation can modify feed litter quality in Amazonian stream systems. Thus, the preservation of native vegetation is important because higher quality exotic species can increase the nutrient availability in food webs of Amazonian streams, alter ecosystem functioning, and endanger the aquatic biodiversity.

The greater importance of leaf litter quality also indicates that the chemical characterization of riparian vegetation will help to understand the functioning of large areas in this ecosystem (organic matter cycle and energy flow), demonstrating the need to study the composition of Amazonian riparian vegetation. These findings are also important evidence that the recovery of vegetation which differs from the original vegetation will change energy flows and the cycling of organic matter.

Moreover, stream characteristics mainly drive the structure of invertebrate communities, which can lead to increased leaf litter breakdown rates at these sites. We observed a low influence of shredders and stream characteristics, partially confirming our hypothesis. Biological decomposition and high fungal biomass were of secondary importance for leaf litter breakdown rates, together with chemical decomposition. This result shows the complexity of ecological processes and the connectivity of the various aspects (chemical, physical, and biological) involved in these processes.

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