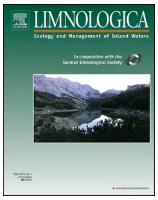
Limnologica 92 (2022) 125945

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno



Habitat heterogeneity increases leaf litter retention and fragmentation in a Cerrado savanna stream

Dianne M.A.S. Nuven[a,*], Alan M. Tonin[a], Renan de Souza Rezende[b], Raiane S. Rabelo[a], Guilherme Sena[a], Paulino Bambi[a], José F. Gonçalves Jr[a]

[a] *Department of Ecology, Institute of Biological Sciences, University of Brasília, 70910-900, Brasília, DF, Brazil*
[b] *Communitarian University of Chapecó Region – Unochapecó, 89809-000, Chapecó, Santa Catarina, Brazil*

ARTICLE INFO

Keywords:
Leaf litter fragmentation
Leaf processing
Pool
Riffle
Retention capacity
Roughness
Trunks

ABSTRACT

Leaf litter fragmentation is one of the main determinants of the availability of food resources for aquatic biota, and this process is strongly influenced by the retention capacity of streams. Retention capacity depends on habitat heterogeneity, as well as on other factors such as leaf litter characteristics and microhabitat diversity. However, the effects of these factors have not yet been clearly understood. In this study, our hypotheses were as follows: (i) habitat heterogeneity increases leaf litter retention, particularly of larger leaves, and (ii) water flow enhances leaf litter fragmentation by promoting physical abrasion of leaf litter, particularly of softer leaves. We tested these hypotheses using (i) the proportion of leaves in transport and the variation of retentive structures such as rock, pebbles, trunks, and roots for habitat heterogeneity in three reaches and (ii) litterbags of two mesh sizes (fine and coarse) incubated in riffle and pool habitats in three reaches of a headwater stream of the Cerrado biome. Our results demonstrated that habitat heterogeneity and leaf litter size increased leaf litter retention rates, and that water flow is an important factor for leaf litter fragmentation in tropical streams. Large leaves interacted with local conditions of streambed heterogeneity (trunks and roots) to reduce transport distances, and hydrology (water flow) accelerated the fragmentation of soft leaves. Our findings suggest that management strategies promoting the accumulation of woody leaf litter in the streambed (trunks and roots) can be valuable to increase the retention capacity of streams, on the other hand the water flow increases the processing of allochthonous organic matter.

1. Introduction

Headwater streams are important connections between terrestrial vegetation and large rivers because they receive and transform large amounts of organic matter (mostly litter) from the riparian forest into smaller particles through abrasion and through consumption by various organisms, including microbes and invertebrates (Rezende et al., 2017; Tonin et al., 2017). They are capable of retaining and incorporating a significant fraction of this leaf litter into their food webs (Entrekin et al., 2020). Consequently, streams contribute to leaf litter processing due to substrate heterogeneity (retentive structures) and water flow. The substrate heterogeneity increases leaf litter residence time, while variable water flow in space (e.g., pool-riffle configuration) or time (e.g., low-high water flow conditions) increases leaf litter physical abrasion (Bastias et al., 2018; Lamberti et al., 2017). Headwater stream food webs rely on the terrestrial sources of leaf litter, given that the canopy cover above the streambed limits the available sunlight and subsequently the in-stream primary production (Neres-Lima et al., 2017). Once in the stream, litter can be (i) immediately retained by structures present in the stream that act as obstacles to leaves (e.g., rocks, roots or trunks), (ii) decomposed by microorganisms and detritivores, or (iii) transported downstream and eventually decomposed (Bastias et al., 2019; Gonçalves et al., 2017).

Leaf litter retention and transport are contrasting processes that are influenced by stream morphology (e.g., width, depth, sinuosity, and slope of stream channel), water flow variability (e.g., riffle and pool distribution within the stream), and streambed heterogeneity (Bastias et al., 2019; Hoover et al., 2006; Lamberti et al., 2017). Stream heterogeneity is characterized by substrates of different sizes (e.g., pebbles, stones, gravel, and sand) and by structures derived from riparian plants (e.g., living tree roots and dead trunks) where leaf litter may be retained, decreasing the downstream leaf litter transport (Frainer et al., 2018).

---

* Corresponding author.
E-mail address: diannenuven@gmail.com (D.M.A.S. Nuven).

https://doi.org/10.1016/j.limno.2021.125945
Received 16 June 2021; Received in revised form 18 December 2021; Accepted 20 December 2021

Retention occurs when leaf litter encounters streambed substrates or other retentive structures, such as living tree roots, large pieces of deadwood, and trunks (see Webster et al., 1994). However, there are many other variables that vary systematically with leaf litter transport distances and are more likely to be directly related to leaf litter retention. For example, larger leaves are more likely to be trapped by substrates (Brouwer et al., 2017), and thus have higher retention rates (Kobayashi and Kagaya, 2008). Although it is evident that leaves must come into contact with the roughness elements before being retained, it is not known how leaf morphology influences the likelihood of contact with retentive structures such as rocks, pebbles, roots, and trunks.

Once retained, the residence time of coarse particulate organic matter in streams is affected by (i) the action of water flow, which dissolves soluble compounds (i.e., leaching), (ii) water abrasion on leaf litter tissues (i.e., physical fragmentation), and (iii) biological action (i.e., microorganisms and detritivores). These processes lead to the conversion of leaf litter into fine particulate organic matter and dissolved organic matter, that is suspended and transported downstream and eventually decomposed into inorganic nutrients (Graça et al., 2005). Invertebrates are important for the processing of organic matter in tropical streams (Boyero et al., 2021; Rezende et al., 2020; Salomão et al., 2019). Nonetheless, in Cerrado streams, the contribution of shredders invertebrate to litter fragmentation is less compared to microorganisms, given the low biomass of shredders (Alvim et al., 2015b; Boyero et al., 2012, 2011; Bruder et al., 2014; Ferreira et al., 2012; Fonseca et al., 2013; Gonçalves et al., 2017; Graça et al., 2015) and the low quality of the litter (i.e., lower phosphorus content and higher toughness; Ardón et al., 2009; Ramos et al., 2021).

Differences in the environmental conditions of streams, such as increased water flow, can play a determining role in the processing of organic matter (Bastias et al., 2019). For example, in two tropical rivers in Australia, Pettit et al. (2012) found that water velocity had a greater impact on leaf mass loss than aquatic macroinvertebrates and leaf-associated microbial communities. Water flow can increase leaf litter physical abrasion, thereby stimulating fungal activity (Ferreira and Graça, 2006; Ferreira et al., 2012; Fonseca et al., 2013), particularly in the final stages of the decomposition process (Abril et al., 2021; Bastias et al., 2019), when leaves are more fragile due to microbial-mediated enzymatic maceration. Physical fragmentation can be expected in softer leaves (which are more susceptible to physical abrasion) and in riffles (where physical abrasion is higher). Initially, the chemical quality of the leaf litter can affect leaching by determining the amount of water-soluble compounds (such as certain micro- and macro-nutrients, low-molecular-weight molecules, and certain secondary compounds) and their resistance to dissolution (Schreeg et al., 2013). On the other hand, slower water flow in pools can decrease fungal activity and development through reduced fluxes of dissolved oxygen and nutrients (Bruder et al., 2016) and increased fine sediment deposition (Marjakangas et al., 2019). The deposited inorganic fine sediment is accompanied to a varying degree by particulate nutrients and organic matter (Parkyn, 2004), and the proportion of mineral particles to organic matter is crucial for decomposition processes and for the quality and availability of food for aquatic macroinvertebrates. In pools, the leaf litter patches can act as microhabitats for shredders, leading to higher fragmentation rates by shredders than that in riffles (Gonçalves et al., 2012; Kobayashi and Kagaya, 2002; Moretti et al., 2007a,b; Rezende et al., 2016). Given the tight connections between habitat heterogeneity, leaf litter retention, and fragmentation (Frainer et al., 2018; Muotka and Laasonen, 2002), an integrated assessment of these processes is important to understand the effects of the stream-riparian forest link for the functioning of aquatic ecosystems (e.g., Bastias et al., 2019; Lamberti et al., 2017).

In tropical streams, many studies have considered the effects of characteristics of leaf litter, such as leaf quality, on the functioning of aquatic ecosystems (Navarro and Júnior, 2020; Sena et al., 2020; Tonin et al., 2014). However, there is little evidence on how the diversity in leaf litter morphology and tenacity together affect leaf litter retention and processing. Therefore, our aims were to: (i) quantify leaf litter retention rates by releasing and estimating the proportion of marked leaves retained, (ii) compare leaf litter fragmentation by incubating leaf litter in riffle and pool areas using litterbags. The study premise was that the stream physical characteristics (e.g., habitat heterogeneity and water flow) influenced the two key related processes of leaf litter dynamics of leaf litter retention and fragmentation. We hypothesized that (i) in-stream heterogeneity enhances leaf litter retention (particularly of larger leaves), and that (ii) water flow increases leaf litter fragmentation by water abrasion (particularly of softer leaves).

2. Materials and methods

2.1. Study site and experimental design

The study was carried out in a headwater stream (Cabeça-de-Veado) (15°53′11.74″ S; 47°50′33.27″ W), located at the Ecological Station of Botanical Garden of Brasilia in Federal District, Brazil, during the rainy season, from November to December of 2016. The climate is tropical savanna (Aw), with a dry season from May to September (mean temperature of 18 °C), and a rainy season from October to April (mean temperature of 29 °C). The average annual precipitation is 1500 mm, which ranges from 750 mm to 2000 mm (Silva et al., 2008). During the experimental period, water pH was 6.6 ± 0.1 (mean and standard deviation), temperature 20.0 ± 0.2 °C, water flow 0.99 ± 0.10 m s^{-1}, conductivity 6.3 ± 1.6 µS cm^{-1}, nitrate (0.13 mg L^{-1}), and turbidity (1.8 ± 0.2 NTU).

The study consisted of two independent experiments on leaf litter retention and fragmentation, which were conducted on three adjacent and 50-m long stream reaches (Fig. 1). This extension of the stream reach was important for assessing environmental heterogeneity based on data on productivity, habitat diversity, and organic matter dynamics observed in other studies carried out in the same stream (Bambi et al., 2017; Tonin et al., 2019). We calculated the coefficient of variation (CV) to estimate the spatial heterogeneity between the reaches, considering the sediment data (percentage of silt, clay, sand, gravel, pebbles, and stones), benthic stock of organic matter (% of reach), root density, density of branches (apparent range %), and stream channel morphology (bank height, stream width, and angle of inclination of the curves or sinuosity). The coefficient of variation (CV) is the relationship between the standard deviation and the mean of the environmental variables measured in situ. The CV has been provided as a percentage; a CV close to 100 % indicates high heterogeneity of the reach. We selected leaves from four plant species: *Protium spruceanum* (Benth.) Engl., *Richeria grandis* Vahl., *Calophyllum brasiliense* Cambess., and *Maprounea guianensis* Aubl. All plant species are native and commonly found in the Cerrado riparian zone, as well as in our study stream (Bambi et al., 2017). Fresh leaf litter from the four plant species was collected in the study area during the period of greatest leaf litter production, air-dried, and stored until the beginning of the experiments.

2.2. Leaf litter retention experiment

Leaves of *Protium spruceanum*, *Calophyllum brasiliense*, and *Richeria grandis* (n = 100 of each species) were marked with colored ink, soaked in water to confer neutral buoyancy (Speaker et al., 1984), and released uniformly across the width of the channel upstream of each stream reach. We determined 10 subsections of 5 m for the retention experiment in each of the stream reach. We counted the number of leaves of each species retained after one hour in each 5 m subsection (Fig. 1a). We measured the length and width of all retained leaf litter using calipers. The leaf litter average proportional size was calculated by adding its width and length for each species and in each reach (Fig. 2). The values (mean ± SE) for *P. spruceanum*, *R. grandis*, and *C. brasiliense* were 14.41 ± 0.30, 17.98 ± 0.42, and 11.49 ± 0.27. The calculation of the

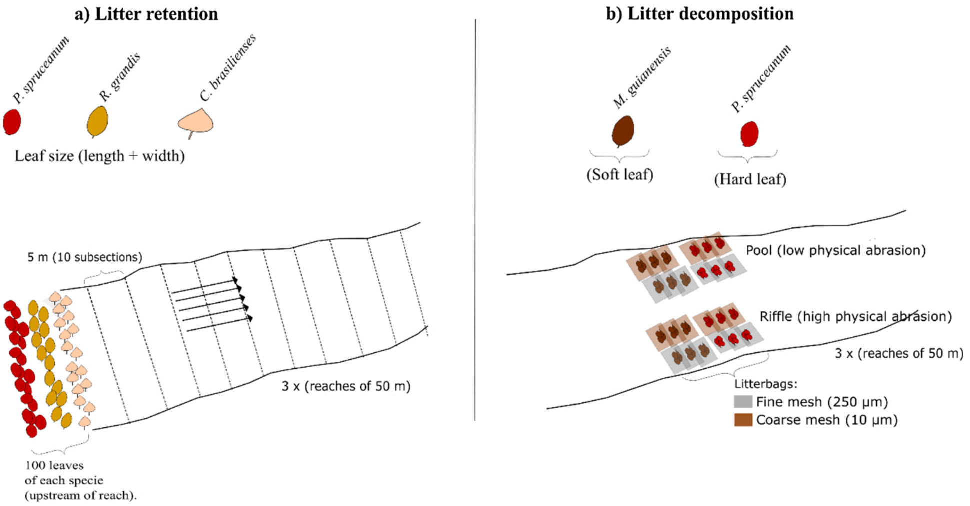


Fig. 1. A schematic representation of the study design. (a) Leaf litter retention experiment, in which three types of leaf litter with different sizes and morphology were deployed in the upstream part of each reach; (b) Leaf litter fragmentation experiment, in which different leaf litter species (hard and soft) were deposited in litterbags in two micro-habitats (riffles and pools). Species used in the study: *Calophyllum brasiliense*, *Maprounea guianensis*, *Protium spruceanum*, and *Richeria grandis*.

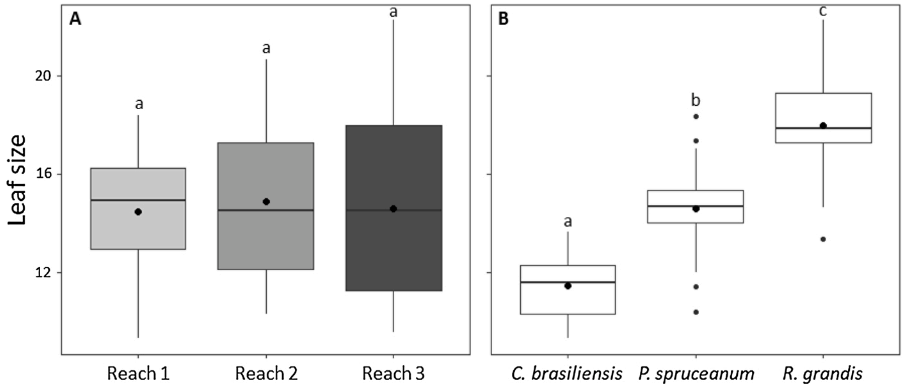


Fig. 2. Boxplots representing leaf litter size for the three plant species (*Calophyllum brasiliense*, *Protium spruceanum*, and *Richeria grandis*) retained in each stream reach (A) and for each species (B). Different letters (a, b, and c) indicate significant differences (Tukey's Multiple Comparison test, $p < 0.05$).

area (length × width) was not used, as the lanceolate and spatulate shape of the Cerrado leaves does not allow exact measurements of the area. Thus, when we added the width and length, we estimated the proportional leaf litter size in relation to its length and width. We measured leaf litter size only of the leaves that were retained in the streambed in the retention experiment. Thus, from a total of 300 leaves that were released in each reach, we measured only 139 for reach 1, 259 for reach 2, and 281 for reach 3. At each stream reach, we determined the substrate composition through a visual estimate of the proportion of each substrate type in all 10 subsections of 5 m (Cummins, 1962). For each subsection, we evaluated the visual percentages of clay, sand, gravel, silt, pebbles, stones, and leaf litter bank on the streambed. We also evaluated the proportion (0–10) of internal habitat structures, such as roots and trunks in the channel and in-stream reach margins.

We calculated the average leaf litter path distance from the release point in each study reach. Therefore, we plotted the proportion of leaves transported at a given displacement distance (Speaker et al., 1984). Thus, the number of released leaves transported was plotted against the drift distance (subsection). We fitted the retention dynamics to a negative exponential model (Young et al., 1978):

$$L_d = L_0 e^{-kd} \tag{1}$$

where, L_0 is the number of leaves (i.e., 100 leaves for each species) released into the reach during each sampling occasion, L_d is the number of leaves transported to a downstream distance d (meters) from the release point, and $-k$ is the retention coefficient (m^{-1}), which is related to the proportion of leaves settling per meter (Larrañaga et al., 2003; Webster et al., 1999). Larger values of k indicate higher retention rates. From the calculations, the average leaf litter drift distance, $1/k$, can be determined. The slope $-k$, is the instantaneous leaf litter retention rate, and $1/k$ is the average distance traveled by a leaf in the stream before its retention (Speaker et al., 1984).

2.3. *Leaf litter fragmentation experiment*

The plant species used for this experiment were *Maprounea guianensis* and *Protium spruceanum*. *M. guianensis* (considered here as softer leaves), and *P. spruceanum* (harder leaves) (Navarro and Júnior, 2020; Rezende et al., 2019, 2020). Leaf litter fragmentation was evaluated using fine (0.25 mm mesh size, which allows for colonization only by microorganisms) and coarse mesh (10 mm mesh size, which allows for colonization by microorganisms and invertebrates) litterbags. We prepared 48 litterbags of fine and coarse mesh, totaling 72 litterbags. Litterbags were filled with 2 g (±0.2 g) of *M. guianensis* (n = 18 each in coarse and fine mesh) or *P. spruceanum* (n = 18 each in coarse and fine mesh). Litterbags were incubated in riffles (high physical abrasion) or pools (low physical abrasion) in all three stream reaches. Thus, each stream reach had 24 litterbags, 12 for each microhabitat (riffle and pool) of two leaf litter species (soft or hard) in coarse or fine mesh bags (Fig. 1b).

The litterbags were recovered after 45 days, placed in plastic bags, and transported to a laboratory in a thermal container with ice. The leaves from the litterbags were carefully washed with distilled water to remove sediments and invertebrates. From each litterbag, we chose five leaf litter samples and then removed five discs (12 mm; one disc from each leaf litter), totaling five discs for each litterbag. This disc set was used to estimate the dry mass (DM) of the removed discs and to obtain the ash-free dry mass (AFDM). The discs were dried at 60 °C for 72 h, weighed, incinerated at 550 °C for 4 h, and weighed again (with an accuracy of 0.01 mg).

The remaining leaf litter was dried at 60 °C for 72 h, weighed, and added to removed discs DM: Final DM = litter DM + (discs DM). We quantified leaf litter fragmentation in each litterbag as the proportion of litter mass loss (LML) (after 45 days of incubation): LML = [initial AFDM (g) – final AFDM (g)] / initial AFDM (g), with initial AFDM corrected by drying, and ash content (i.e., after multiplying discs AFDM by dry mass; (Bärlocher, 2005); Webster et al., 1999). We calculated the contribution of invertebrates to leaf litter fragmentation as the difference in LML between paired coarse- and fine-mesh litterbags for each block (n = 3).

2.4. Statistical analyses

We tested separate models for overall fragmentation in coarse mesh litterbags, microbial fragmentation in fine-mesh bags, and detritivore-mediated fragmentation. We used linear models with the gls (generalized least squares) function of the ‘nlme’ package (Pinheiro et al., 2018) to test the effect of the microhabitats (pool and riffle) and leaf litter species (soft or hard) (predictor variables) and all interactions on leaf litter fragmentation (response variable).

A principal component analysis (PCA; cmdscale function of the vegan package) was used to encapsulate a set of environmental information of in-stream heterogeneity. We first selected the retentive structures relevant to leaf litter retention (percentage of pebbles, stones, roots, and trunks). We then retained the first axis (hereafter PCA1), which summarized 60 % of the total variation in PCA and was mostly related to stones and pebbles ($r = -0.90$), and tree roots ($r = 0.92$). This provided a single variable that represented stream heterogeneity to be used in further analyses. We examined the individual and interactive effects of habitat heterogeneity (PCA1), leaf litter size, and plant species (*P. spruceanum*, *C. brasiliense*, and *R. grandis*) on leaf litter retention (of transported leaves) using linear mixed-effect models. The models were first defined in terms of a random structure, and a model selection procedure was used to identify the interactions between the predictors. The random structure of the fitted models included reach as a random term and a constant variance function structure (VarIdent) to allow different variances among reaches. Individual and interactive effects were explored through seven models, all containing at least one predictor, but varying in the number of interactions. The null model (model 7) assumed no interactions between predictors (i.e., intercept only), two models (models 1 and 2) included interactions between habitat heterogeneity and species type, or habitat heterogeneity and leaf litter size, and one model (model 1) included all interactions, including the three-way interaction. The seven models were compared using an Akaike’s information criterion corrected for sample size (AICc)-based model selection approach, with the most plausible models being selected based on delta AICc (Δi; i.e., difference in AICc value relative to the best model) and Akaike weights (*wi*; i.e., the probability that a model is the best among the whole set of models). Residuals from each model were inspected to ensure that the parametric assumptions for the linear models were not violated. Models were constructed and selected using nlme (“gls”, “lme” and “VarIdent” functions; (Pinheiro et al., 2021) and MuMIn packages (“model. Sel”; (Bartoń, 2019). To test whether leaf litter retention depended on features of reaches, species, or both, we used linear models (gls function of the nmle package; (Pinheiro et al., 2021). Models were first defined in terms of the best random structure, which were attained with the presence of a constant variance function structure (VarIdent) in relation to species and reach, and a temporal correlation component (corAR1) that considered the dependence of adjacent subsections within each reach (Zuur et al., 2009). When a statistically significant interaction between reach and species was detected, we refitted the model using only reach as a predictor and data for each species separately. Pairwise comparisons among reaches were performed with Tukey tests using the glht function of the multcomp package, with adjusted p-values (Hothorn et al., 2008). The analyses were performed using the software R version 4.0.4 (R Development Core Team, 2020).

3. Results

3.1. Leaf litter retention

The reaches 2 and 3 presented a higher spatial heterogeneity than reach 1 (Tukey test; $p < 0.001$, Fig. 3). We found significant differences in the retention of leaves downstream between the leaf litter species (*P. spruceanum*, *C. brasiliense*, and *R. grandis*) and the type of reach (Tables 1 and 2). The retention rates were higher in reaches 2 and 3 (mean k ± SE, 0.032 ± 0.009; 0.038 ± 0.007, n = 3, respectively) than in reach 1 (0.01 ± 0.002, n = 3; Fig. 4, Table 1S). In our study, we observed instantaneous retention rates ranging from 0.006 $k.\ m^{-1}$ (*C. brasiliense* in reach 1) to 0.052 $k.\ m^{-1}$ (*R. grandis* in reach 3). These retention rates represent ranges that require 166 m to 20 m to retain 31 % and 98 % of leaves inserted, respectively (Table 1S).

Habitat heterogeneity (in terms of pebbles, stones, and roots) was more correlated with axis 1 of the PCA. The percentage pebbles and stones were negatively related to axis 1, whereas the percentage of root structures was positively related to axis 1 (Fig. 1S, Table 2S). The percentage of trunk structures was more closely related to PCA axis 2 (Table 2S). The model selection procedure revealed one model that best explained the observed patterns (90 % probability based on Akaike weights). This model included habitat heterogeneity and leaf litter size, which are important for leaf litter retention (Table 3). In addition, leaf litter retention depends on the interaction between the type of reach and the leaf litter species. Only *P. spruceanum* showed a difference in retention between reaches, with higher values for reach 3 ($p < 0.001$).

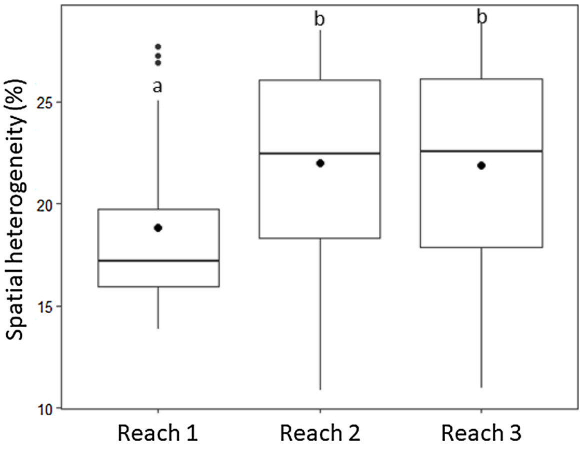


Fig. 3. Environmental coefficient of variation (%) by sediment (percent of silt, clay, sand, gravel, pebbles, and stones), benthic stock of organic matter (% in reach), root density, branches density (% apparent in reach), and morphology of the stream channel (height of the margins, stream width, and angle of inclination of curves or sinuosity) in three savanna streams. First (lower line) and third (higher line) quartiles, the median (bold line), and outliers (circles) are shown. Different letters (a and b) indicate significant differences between reaches (Tukey’s Multiple Comparison test, $p < 0.05$).

Table 1
Results of linear models testing the effects of the leaf litter species (*P. spruceanum, C. brasiliensis* and *R. grandis*) in three different reaches (1, 2 and 3) on the leaf litter retention.

	DF	F-value	*P*-value
Intercept	1	25.11	<0.001
Reach	2	18.39	<0.001*
Species	2	67.87	<0.001*
Reach x Species	4	3.90	0.006*

* Statistically significant differences.

Table 2
Results of linear models and contrast analyses (AC; $P < 0.05$) testing the differences in leaf litter retention for the three plant species (*Protium spruceanum*, *Calophyllum brasiliense* and *Richeria grandis*) in each stream reach.

	DF	F-value	*P*-value	Contrast analysis
Protium spruceanum				
Intercept	1	65.97	<0.001	
Reach	2	10.27	<0.001*	T3 > T1 = T2
Calophyllum brasiliense				
Intercept	1	132.87	<0.001	
Reach	2	2.32	0.11	
Richeria grandis				
Intercept	1	142.12	<0.001	
Reach	2	0.71	0.49	

* Statistically significant differences.

3.2. *Leaf litter fragmentation*

Soft and hard leaves incubated in pool and riffle habitats lost 18.1 % ± 0.1 % (mean and standard deviation) of their initial mass at the end of the experiment. We observed consistent responses of leaf litter species in both habitats (pools and riffles) for both mesh sizes, as indicated by the non-significant interactions between leaf litter species and habitats (fine mesh bags: $F_{1,30} = 2.10, p = 0.158$; coarse mesh bags: $F_{1,30} = 0.19, p = 0.662$). For instance, leaf litter incubated in riffles lost 33–50 % more mass than those in pools, irrespective of litterbag mesh size (i.e., coarse or fine). Soft leaves showed 2.5- and 3.0-fold higher fragmentation than hard leaves in coarse and fine-mesh bags, respectively (Fig. 5, Table 4). Finally, the model that explained detritivore-mediated leaf litter fragmentation showed that the interactions between leaf litter species and microhabitat were significant (Table 4). We explored the interactions with a second type of model by evaluating the micro-habitat effect (predictive variable) for the detritivore-mediated fragmentation (response variable) for each leaf litter species (soft and hard). These models revealed that the contribution of invertebrates was similar between habitats (riffle vs. pool) for soft leaves ($p = 0.30$), while for hard leaves it was greater in pools than in riffles ($p = 0.01$; Table 3S).

4. Discussion

The findings of our study showed that both habitat heterogeneity and water flow can be important drivers of leaf litter dynamics in streams, as they control retention patterns and can influence leaf litter fragmentation (Bastias et al., 2019; Lamberti et al., 2017). Since leaf litter inputs are temporarily retained in retentive structures on the reach, the leaf litter is susceptible to the action of local hydrological conditions, which through the abrasion of water contribute to the physical fragmentation of leaf litter. Therefore, our results suggest that the interactions between habitat heterogeneity and physical abrasion in the reaches of streams generate certain patterns consistent with the formation of leaf litter patches that provide resources and habitats for aquatic communities. The efficiency of leaf litter retention in streams is ecologically relevant, as it determines the fraction of these inputs that will be available to be processed later, contributing to the water flow of nutrients and

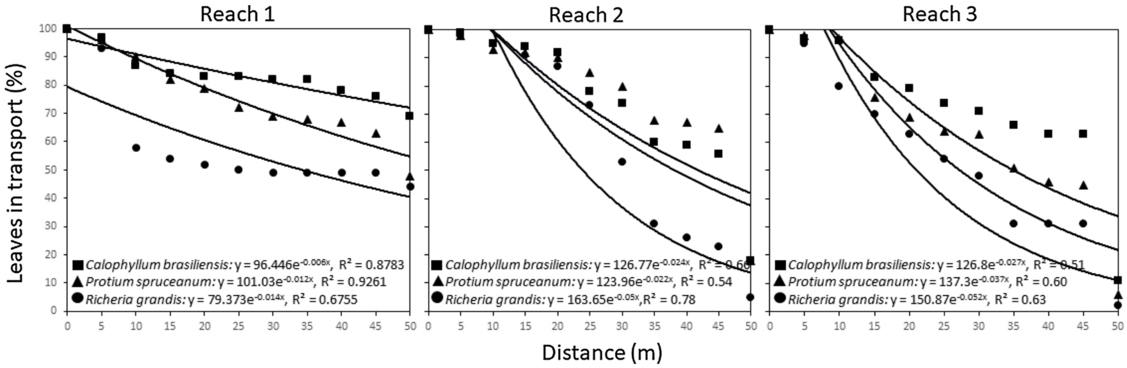


Fig. 4. Relationship between leaf litter retention (percentage of leaves in transport) and distance traveled from the release point in each study stream reach. The regression line represents fit to the negative exponential model. Squares represents *Calophyllum brasiliense*; triangles: *Protium spruceanum* and circles: *Richeria grandis*.

Table 3
Summary of model selection procedure for the set of models used to test the effects of habitat heterogeneity (PC1), leaf litter size (size), leaf litter species (species) on leaf litter retention based on the Akaike weights (*wi* is the probability that a model is the best among the whole set of models). Models are ordered from the best to the poorest fit according to Akaike weights. df, number of estimated parameters for each model; AICc, Akaike information criterion corrected for sample size; Δi (delta AICc), difference in AICc value relative to the best model.

Model	Intercept	PC1	size	species	PC1:size	PC1:species	df	AICc	Δ_i	w_i
M4	0.069	0.050*	0.004*				7	−71.6	0.00	0.908
M3	0.066	0.050*	0.004*	+			9	−65.0	6.56	0.034
M6	0.131	0.057					6	−64.9	6.66	0.032
M2	0.049	0.038*	0.005*	+		+	11	−64.2	7.40	0.022
M1	0.053	0.014*	0.005*	+	0.002*	+	12	−59.7	11.91	0.002
M5	0.023		0.007*				6	−56.8	14.80	0.001
M7	0.132						5	−52.4	19.24	0

* Statistically significant differences.

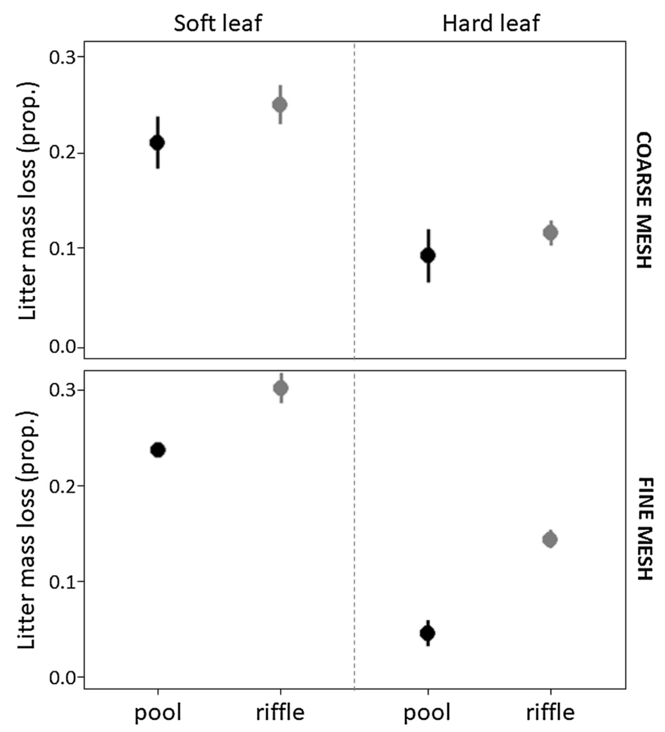


Fig. 5. Proportion of litter mass loss for each leaf litter species (soft and hard) incubated in riffle and pool habitats in coarse- and fine-mesh litterbags.

Table 4

Results of linear models testing for the effects of leaf litter species (soft or hard), micro-habitat (pool or riffle) and their interaction on the proportion of leaf litter fragmentation in fine and coarse mesh bags. Denominator degrees of freedom is 31 for the first two models and 12 for the last model.

	DF	F-value	*P*-value	Details
Fine mesh bags				
Leaf litter species	1	239.38	<0.001 *	Soft leaves > Hard leaves
Micro-habitat	1	52.14	<0.001 *	Riffle > Pool
Leaf litter x micro-habitat	1	2.09	0.15	
Coarse mesh bags				
Leaf litter species	1	175.25	<0.001 *	Soft leaves > Hard leaves
Micro-habitat	1	5.52	0.02*	Riffle > Pool
Litter x micro-habitat	1	0.19	0.66	
Detritivore-mediated fragmentation				
Leaf litter species	1	0.18	0.66	
Micro-habitat	1	2.71	0.11	
Leaf litter x micro-habitat	1	6.57	0.01*	

[*] Statistically significant differences.

secondary production (Bastias et al., 2019; Brouwer et al., 2017). Leaf litter retention in the study sections followed a negative exponential decay model. In addition, the number of drifting leaves decreased with increasing distance downstream from the input point, due to increased heterogeneity. This result corroborates our hypothesis that in-stream heterogeneity increases leaf litter retention capacity (e.g., Bastias et al., 2019; Brouwer et al., 2017; Kobayashi and Kagaya, 2008). However, our results differ from those of previous studies, as we consider both the intrinsic characteristics of leaf litter and the importance of the water flow for the leaf litter retention and fragmentation processes in Cerrado streams.

Riparian vegetation plays an important role in leaf litter retention through the supply of trunks and roots (Brouwer et al., 2017) and contributes to the storage of plant organic matter (Brouwer et al., 2017; Hoover et al., 2010; Koljonen et al., 2012). The high quantity of trunks and rooting by riverside vegetation may stabilize the stream banks and may act as an obstacle for the leaves, creating local retention zones (Lamberti et al., 2017). Previous studies have shown that trunks can be used in stream restoration. The addition of whole logs with branches that fill the water column, often extending to the water surface, leads to increased water flow resistance (and corresponding changes in depth and water flow), which often initiates the formation of debris dams that contribute significantly to the long-term retention capacity of a stream (Elosegi et al., 2016). For example, Flores et al. (2011) observed an up to 70-fold increase in organic matter storage after large trunks and branches were introduced in mountain streams in the Basque country (Spain). In our study, the complexity of trunks and roots may have increased over time, which intensified the blockages of woody materials and increased leaf litter retention. Therefore, any disturbance in the riparian zone (i.e., removal of riparian vegetation) has direct effects on nutrient dynamics in streams, affecting the efficiency of retention and the flow of terrestrial nutrients to streams. Thus, the addition of riparian forest structures such as roots and trunks in the streambed can contribute to the dynamics of organic matter in streams and is important for restoring forested streams (Brouwer et al., 2017; Koljonen et al., 2012).

Leaf litter size was also a key variable for retention rates during its drift downstream (Inoue et al., 2012; Kobayashi and Kagaya, 2008). We found that the retention coefficients were higher in *R. grandis* than in the other three leaf species, which can be explained by leaf litter size (Fig. 2B). Previous studies have also shown that large leaves may increase the probability of contact with roughness elements (Inoue et al., 2012; Kobayashi and Kagaya, 2008). The leaves are generally flat and flexible, which allows them to be 'wrapped' by the water flow force around obstacles, such as protruding stones and woody debris (Kobayashi and Kagaya, 2008). In addition, smaller leaves tend to travel longer distances (Cordova et al., 2008). In our study, leaf litter drift distances were also different in the three study reaches, with shorter drift distances (20-m path) in reaches with greater spatial heterogeneity (reach 3), mainly for larger leaves such as *R. grandis*. In addition, the retention efficiency of larger leaves can be related to the degree of leaf litter flexibility (Kobayashi and Kagaya, 2008; Steart et al., 2002). Leaves with high flexibility may be more easily retained by retentive structures (e.g., trunks and roots) as the flexibility increases the possibility of adhering to or contacting these structures (Steart et al., 2002). We did not measure flexibility, but according to previous studies, the larger leaves in our study, such as those of *R. grandis*, are the most flexible (Navarro and Júnior, 2020; Rezende et al., 2019), which may have contributed to higher retention coefficients. Therefore, changes in leaf litter size in the riparian zone of streams, such as phenological processes that change leaf litter size during periods of drought, can alter leaf litter retention rates and potentially fragmentation, thereby influencing the availability of organic matter and nutrients in headwater streams.

As expected, the increased fragmentation in riffles and the low effect of detritivores suggest that physical abrasion caused by water flow has direct implications for leaf litter fragmentation in tropical ecosystems (Bastias et al., 2019; Colas et al., 2017). However, the higher leaf litter fragmentation in the riffle in the fine mesh for the soft leaves suggests that water flow can stimulate the activity of microbial decomposers (Ferreira and Graça, 2006), as well as the physical fragmentation of leaf litter (Heard et al., 1999). The positive effect of microbial activity on physical fragmentation is in line with the descriptions in previous studies in tropical streams that leaf litter decomposition is a sequential process that begins with leaf litter leaching, followed by microbial colonization and continues with the mechanical effects of physical abrasion and macroinvertebrate activity (Alvim et al., 2015a; Cid et al., 2019; Rezende et al., 2020, 2018; Sena et al., 2020). Furthermore, other studies in the same stream have shown that microorganisms may be more important than shredders for leaf litter fragmentation (Rezende et al., 2014). These results can be expected in tropical systems (Graça and Cressa, 2010), considering the lower leaf litter processing effects by shredders and the high litter tenacity observed in these environments (Gonçalves et al., 2007). Our results differ from the findings of other studies in which the presence of shredders in the riffles increased the rate of litter mass loss (Abril et al., 2021; Ferreira et al., 2006; Ferreira and Graça, 2006). According to a study carried out in the same stream, Leite et al. (2016) found a low density of shredders throughout the year. Particularly in the Cerrado, shredders have little influence on leaf litter fragmentation (Gonçalves et al., 2012; Moretti et al., 2007b; Rezende et al., 2016), possibly because of the low abundance of these organisms (Boyero et al., 2012; Gonçalves et al., 2007; Moretti et al., 2007a,b; Moulton et al., 2010; Rezende et al., 2016).

In summary, our results suggest that physical abrasion through the effect of water flow is important for leaf litter fragmentation, especially for softer leaves. Harder leaves are more resistant to physical abrasion and fragmentation (Fonseca et al., 2013). During physical fragmentation, many water-soluble compounds, such as proteins, amino acids, carbohydrates, and lipids, are leached. This process is important for the subsequent stages of fragmentation that are affected by microorganisms and invertebrates in aquatic systems (Bastias et al., 2019; Fonseca et al., 2013; Graça et al., 2015). The higher detritivore-mediated fragmentation in pools, especially for hard leaves, suggests that water flow is the main driver of leaf litter fragmentation in riffles. Furthermore, leaf litter patches can be more heterogeneous in pools than in riffles and act as microhabitats for detritivores (Kobayashi and Kagaya, 2002; Mendes et al., 2017). Therefore, we found considerable evidence that changes in leaf litter size in the riparian zone of streams (e.g., phenological processes that alter leaf litter size after drought) can alter leaf litter retention rates, and potentially decrease the transfer of resources for stream aquatic communities. Furthermore, changes in the vegetation composition that influence leaf litter resistance, can be determining factors for the processing of allochthonous organic matter.

5. Conclusions

In summary, our results suggest that leaf litter can be retained spatially, depending on the presence of trunks and roots, especially for larger leaves. The interaction between habitat heterogeneity and leaf litter size is necessary to create leaf litter patches that provide resources and habitats for aquatic communities. In addition, since leaf litter inputs are temporarily retained within the stream reach, hydrological conditions on a local scale can influence leaf litter fragmentation rates through physical abrasion. Therefore, an assessment of the retention is necessary to understand the role of leaf litter inputs as subsidies for organic matter in streams. Management policies that increase the capacity of streams to retain leaf litter should be encouraged. In addition, it is important to preserve riparian forests in less retentive reaches and within areas with anthropogenic influence, since riparian forests are primary sources of woody debris such as trunks and roots; structures whose effect on leaf litter retention seems significant. Detailed studies should preferably be carried out throughout the year in a large number of streams and ideally using a diverse pool of species to test the consistency of our findings. Furthermore, studies should be carried out to explore the different effects of seasonal changes in the leaf litter phenology of riparian vegetation and water flow regimes on retention, transport, and fragmentation of leaf litter.

Authorship statement

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the Limnologica Journal.

Authorship contributions

A. Tonin, R. Rezende and J. F. Gonçalves Jr. conceived the study. A. Tonin, R. Rezende, J. F. Gonçalves Jr. and P. Bambi performed the experiments. G. Sena performed the limnological analysis. D. Nuven, A. Tonin D. Nuven and R. Rezende performed statistical analysis. D. Nuven wrote the article, with contributions from R. Rabelo, A. Tonin, R. Rezende, J. F. Gonçalves Jr., P. Bambi and G. Sena.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

DN, GS and RSR acknowledges the financial support provided by Coordination for the Improvement of Higher Education Personnel (CAPES) for the granting of a PhD scholarship. JFG had had financial support from National Council for Scientific and Technological Development (CNPq; project number 310641/2017-9). Finally, we would like to thank all students who participated in the field and laboratory work, and the AquaRiparia group for their support throughout the study.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2021.125945.

References

Abril, M., Menéndez, M., Ferreira, V., 2021. Decomposition of leaf litter mixtures in streams: effects of component litter species and current velocity. Aquat. Sci. 83 https://doi.org/10.1007/s00027-021-00810-x.

Alvim, E.A.C.C., Medeiros, A.O., Rezende, R.S., Gonçalves, J.F., 2015a. Small leaf breakdown in a Savannah headwater stream. Limnologica 51, 131–138. https://doi.org/10.1016/j.limno.2014.10.005.

Alvim, E.A.C.C., Medeiros, A.O., Rezende, R.S., Gonçalves Jr, J.F., 2015b. Leaf breakdown in a natural open tropical stream. J. Limnol. 74, 248–260. https://doi.org/10.4081/jlimnol.2014.982.

Ardón, M., Pringle, C.M., Eggert, S.L., 2009. Does leaf chemistry differentially affect breakdown in tropical vs temperate streams? Importance of standardized analytical techniques to measure leaf chemistry. J. North Am. Benthol. Soc. 28, 440–453. https://doi.org/10.1899/07-083.1.

Bambi, P., Rezende, R.S., Feio, M.J., Leite, G.F.M., Alvin, E., Quintão, J.M.B., Araújo, F., Gonçalves Júnior, J.F., 2017. Temporal and spatial patterns in inputs and stock of organic matter in Savannah streams of Central Brazil. Ecosystems 20, 757–768. https://doi.org/10.1007/s10021-016-0058-z.

Bastias, E., Ribot, M., Romaní, A.M., Mora-Gómez, J., Sabater, F., López, P., Martí, E., 2018. Responses of microbially driven leaf litter decomposition to stream nutrients depend on litter quality. Hydrobiologia 806, 333–346. https://doi.org/10.1007/s10750-017-3372-3.

Bärlocher, F., 2005. Sporulation by aquatic hyphomycetes. *Methods to study litter decomposition*. Springer, Dordrecht., pp. 185–188

Bartoń, K., 2019. MuMIn: Multi-Model Inference. R package version 4.0.4. https://CRAN.R-project.org/package=MuMIn.

Bastias, E., Bolivar, M., Ribot, M., Peipoch, M., Thomas, S.A., Sabater, F., Martí, E., 2019. Spatial heterogeneity in water velocity drives leaf litter dynamics in streams. Freshw. Biol. 65, 435–445. https://doi.org/10.1111/fwb.13436.

Boyero, L., Pearson, R.G., Gessner, M.O., Barmuta, L.A., Ferreira, V., Graça, M.A.S., Dudgeon, D., Boulton, A.J., Callisto, M., Chauvet, E., Helson, J.E., Bruder, A., Albariño, R.J., Yule, C.M., Arunachalam, M., Davies, J.N., Figueroa, R., Flecker, A.S., Ramírez, A., Death, R.G., Iwata, T., Mathooko, J.M., Mathuriau, C., Gonçalves, J.F., Moretti, M.S., Jinggut, T., Lamothe, S., M'Erimba, C., Ratnarajah, L., Schindler, M.H., Castela, J., Buria, L.M., Cornejo, A., Villanueva, V.D., West, D.C., 2011. A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration. Ecol. Lett. 14, 289–294. https://doi.org/10.1111/j.1461-0248.2010.01578.x.

Boyero, L., Pearson, R.G., Dudgeon, D., Ferreira, V., Graça, M.A.S., Gessner, M.O., Boulton, A.J., Chauvet, E., Yule, C.M., Albariño, R.J., Ramírez, A., Helson, J.E., Callisto, M., Arunachalam, M., Chará, J., Figueroa, R., Mathooko, J.M., Gonçalves, J.

F., Moretti, M.S., Chará-Serna, A.M., Davies, J.N., Encalada, A., Lamothe, S., Buria, L.M., Castela, J., Cornejo, A., Li, A.O.Y., M'Erimba, C., Villanueva, V.D., Del Carmen Zúñiga, M., Swan, C.M., Barmuta, L.A., 2012. Global patterns of stream detritivore distribution: implications for biodiversity loss in changing climates. Glob. Ecol. Biogeogr. 21, 134–141. https://doi.org/10.1111/j.1466-8238.2011.00673.x.

Boyero, L., Gessner, M.O., Pearson, R.G., Chauvet, E., Pérez, J., Tiegs, S.D., Tonin, A.M., Correa-araneda, F., López-rojo, N., Graça, M.A.S., 2021. The Ecology of Plant Litter Decomposition in Stream Ecosystems. Springer International Publishing. https://doi.org/10.1007/978-3-030-72854-0.

Brouwer, J.H.F., Eekhout, J.P.C., Besse-Lototskaya, A.A., Hoitink, A.J.F., Ter Braak, C.J.F., Verdonschot, P.F.M., 2017. Flow thresholds for leaf retention in hydrodynamic wakes downstream of obstacles. Ecohydrology 10, 1–10. https://doi.org/10.1002/eco.1883.

Bruder, A., Schindler, M.H., Moretti, M.S., Gessner, M.O., 2014. Litter decomposition in a temperate and a tropical stream: the effects of species mixing, litter quality and shredders. Freshw. Biol. 59, 438–449. https://doi.org/10.1111/fwb.12276.

Bruder, A., Salis, R.K., McHugh, N.J., Matthaei, C.D., 2016. Multiple-stressor effects on leaf litter decomposition and fungal decomposers in agricultural streams contrast between litter species. Funct. Ecol. 30, 1257–1266. https://doi.org/10.1111/1365-2435.12598.

Cid, C.Cdel, Rezende, R.S., Calor, A.R., Dahora, J.S., de Aragão, L.N., Guedes, M.L., Caiafa, A.N., Medeiros, A.O., 2019. Temporal dynamics of organic matter, hyphomycetes and invertebrate communities in a Brazilian savanna stream. Community Ecol. 20, 301–313. https://doi.org/10.1556/168.2019.20.3.10.

Colas, F., Baudoin, J.M., Gob, F., Tamisier, V., Valette, L., Kreutzenberger, K., Lambrigot, D., Chauvet, E., 2017. Scale dependency in the hydromorphological control of a stream ecosystem functioning. Water Res. 115, 60–73. https://doi.org/10.1016/j.watres.2017.01.061.

Cordova, J.M., Rosi-Marshall, E.J., Tank, J.L., Lamberti, G.A., 2008. Coarse particulate organic matter transport in low-gradient streams of the Upper Peninsula of Michigan. J. North Am. Benthol. Soc. 27, 760–771. https://doi.org/10.1899/06-119.1.

Elosegi, A., Elorriaga, C., Flores, L., Martí, E., Díez, J., 2016. Restoration of wood loading has mixed effects on water nutrient, and leaf retention in Basque mountain streams. Freshw. Sci. 35, 41–54. https://doi.org/10.1086/684051.

Entrekin, S.A., Rosi, E.J., Tank, J.L., Hoellein, T.J., Lamberti, G.A., 2020. Quantitative food webs indicate modest increases in the transfer of allochthonous and autochthonous C to macroinvertebrates following a large wood addition to a temperate headwater stream. Front. Ecol. Evol. 8. https://doi.org/10.3389/fevo.2020.00114.

Ferreira, V., Graça, M.A.S., 2006. Do invertebrate activity and current velocity affect fungal assemblage structure in leaves? Int. Rev. Hydrobiol. 91, 1–14. https://doi.org/10.1002/iroh.200510833.

Ferreira, V., Graça, M.A.S., Lima, J.L.M.P., Gomes, R., 2006. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. Archiv Fur Hydrobiologie 165, 493–513. https://doi.org/10.1127/0003-9136/2006/0165-0493.

Ferreira, V., Encalada, A.C., Graça, M.A.S., 2012. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshw. Sci. 31, 945–962. https://doi.org/10.1899/11-062.1.

Flores, L., Larrañaga, A., Díez, J., Elosegi, A., 2011. Experimental wood addition in streams: effects on organic matter storage and breakdown. Freshw. Biol. 56, 2156–2167. https://doi.org/10.1111/j.1365-2427.2011.02643.x.

Fonseca, A.L.S., Bianchini, I., Pimenta, C.M.M., Soares, C.B.P., Mangiavacchi, N., 2013. The flow velocity as driving force for decomposition of leaves and twigs. Hydrobiologia 703, 59–67. https://doi.org/10.1007/s10750-012-1342-3.

Frainer, A., Polvi, L.E., Jansson, R., McKie, B.G., 2018. Enhanced ecosystem functioning following stream restoration: the roles of habitat heterogeneity and invertebrate species traits. J. Appl. Ecol. 55, 377–385. https://doi.org/10.1111/1365-2664.12932.

Gonçalves, J.F., Graça, M.A.S., Callisto, M., 2007. Litter decomposition in a Cerrado savannah stream is retarded by leaf toughness, low dissolved nutrients and a low density of shredders. Freshw. Biol. 52, 1440–1451. https://doi.org/10.1111/j.1365-2427.2007.01769.x.

Gonçalves, J.F., Rezende, R.S., Martins, N.M., Gregório, R.S., 2012. Leaf breakdown in an Atlantic Rain Forest stream. Austral Ecol. 37, 807–815. https://doi.org/10.1111/j.1442-9993.2011.02341.x.

Gonçalves, J.F., Couceiro, S.R.M., Rezende, R.S., Martins, R.T., Ottoni-Boldrini, B.M.P., Campos, C.M., Silva, J.O., Hamada, N., 2017. Factors controlling leaf litter breakdown in Amazonian streams. Hydrobiologia 792, 195–207. https://doi.org/10.1007/s10750-016-3056-4.

Graça, M.A.S., Cressa, C., 2010. Leaf quality of some tropical and temperate tree species as food resource for stream shredders. Int. Rev. Hydrobiol. 95, 27–41. https://doi.org/10.1002/iroh.200911173.

Graça, M.A.S., BäRlocher, F., Gessner, M.O., 2005. Methods to study litter decomposition: a practical guide. Methods to Study Litter Decompos. Clin. Pract. Guidel. Quick Ref. Guide Clin. 1–329. https://doi.org/10.1007/1-4020-3466-0.

Graça, M.A.S., Ferreira, V., Canhoto, C., Encalada, A.C., Guerrero-Bolaño, F., Wantzen, K.M., Boyero, L., 2015. A conceptual model of litter breakdown in low order streams. Int. Rev. Hydrobiol. 100, 1–12. https://doi.org/10.1002/iroh.201401757.

Heard, S.B., Schultz, G.A., Ogden, C.B., Griesel, T.C., 1999. Mechanical abrasion and organic matter processing in an Iowa stream. Hydrobiologia 400, 179–186. https://doi.org/10.1023/A:1003713307849.

Hoover, T.M., Richardson, J.S., Yonemitsu, N., 2006. Flow-substrate interactions create and mediate leaf litter resource patches in streams. Freshw. Biol. 51, 435–447. https://doi.org/10.1111/j.1365-2427.2005.01499.x.

Hoover, T.M., Marczak, L.B., Richardson, J.S., Yonemitsu, N., 2010. Transport and settlement of organic matter in small streams. Freshw. Biol. 55, 436–449. https://doi.org/10.1111/j.1365-2427.2009.02292.x.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Inoue, M., Shinotou, Sichi, Maruo, Y., Miyake, Y., 2012. Input, retention, and invertebrate colonization of allochthonous litter in streams bordered by deciduous broadleaved forest, a conifer plantation, and a clear-cut site in southwestern Japan. Limnology 13, 207–219. https://doi.org/10.1007/s10201-011-0369-x.

Kobayashi, S., Kagaya, T., 2002. Differences in litter characteristics and macroinvertebrate assemblages between litter patches in pools and riffles in a headwater stream. Limnology 1, 37–42. https://doi.org/10.1007/s102010200004.

Kobayashi, S., Kagaya, T., 2008. Differences in patches of retention among leaves, woods and small litter particles in a headwater stream: the importance of particle morphology. Limnology 9, 47–55. https://doi.org/10.1007/s10201-007-0235-z.

Koljonen, S., Louhi, P., Mäki-Petäys, A., Huusko, A., Muotka, T., 2012. Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. Freshw. Sci. 31, 1121–1130. https://doi.org/10.1899/11-173.1.

Lamberti, G.A., Entrekin, S.A., Griffiths, N.A., Tiegs, S.D., 2017. Coarse particulate organic matter: storage, transport, and retention. Methods Stream Ecol. 2, 55–69. https://doi.org/10.1016/B978-0-12-813047-6.00004-8. Third Ed.

Larrañaga, S., Díez, J.R., Elosegi, A., Pozo, J., 2003. Leaf retention in streams of the Agüera basin (northern Spain). Aquat. Sci. 65, 158–166. https://doi.org/10.1007/s00027-003-0623-3.

Leite, G.F., Silva, F.T.C., Keley, F., Navarro, F.K.S., Rezende, R.S., Gonçalves, J.J., 2016. Leaf litter input and electrical conductivity may change density of Phylloicus sp. (Trichoptera: calamoceratidae) in a Brazilian savannah stream. Acta Limnol. Bras. 28 https://doi.org/10.1590/S2179-975X1516.

Marjakangas, E.L., Abrego, N., Grøtan, V., Lima, R.A.F., Bello, C., Bovendorp, R.S., Culot, L., Hasui, É., Lima, F., Muylaert, R.L., Niebuhr, B.B., Oliveira, A.A., Pereira, L.A., Prado, P.I., Stevens, R.D., Vancine, M.H., Ribeiro, M.C., Galetti, M., Ovaskainen, O., 2019. Fragmented tropical forests lose mutualistic plant–animal interactions. Divers. Distrib. 154–168. https://doi.org/10.1111/ddi.13010.

Mendes, F., Kiffer, W.P., Moretti, M.S., 2017. Structural and functional composition of invertebrate communities associated with leaf patches in forest streams: a comparison between mesohabitats and catchments. Hydrobiologia 800, 115–127. https://doi.org/10.1007/s10750-017-3249-5.

Moretti, M., Gonçalves, J.F., Callisto, M., 2007a. Leaf breakdown in two tropical streams: differences between single and mixed species packs. Limnologica 37, 250–258. https://doi.org/10.1016/j.limno.2007.01.003.

Moretti, M.S., Gonçalves, J.F., Ligeiro, R., Callisto, M., 2007b. Invertebrates colonization on native tree leaves in a neotropical stream (Brazil). Int. Rev. Hydrobiol. 92, 199–210. https://doi.org/10.1002/iroh.200510957.

Moulton, T.P., Magalhães-Fraga, S.A.P., Brito, E.F., Barbosa, F.A., 2010. Macroconsumers are more important than specialist macroinvertebrate shredders in leaf processing in urban forest streams of Rio de Janeiro. Brazil. Hydrobiologia 638, 55–66. https://doi.org/10.1007/s10750-009-0009-1.

Muotka, T., Laasonen, P., 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. J. Appl. Ecol. 39, 145–156. https://doi.org/10.1046/j.1365-2664.2002.00698.x.

Navarro, F.K.S.P., Júnior, J.F.G., 2020. Effects of microbial conditioning and temperature on the leaf-litter shredding activity of phylloicus sp. Acta Sci. - Biol. Sci. 42, 1–9. https://doi.org/10.4025/actascibiolsci.v42i1.52919.

Neres-Lima, V., Machado-Silva, F., Baptista, D.F., Oliveira, R.B.S., Andrade, P.M., Oliveira, A.F., Sasada-Sato, C.Y., Silva-Junior, E.F., Feijó-Lima, R., Angelini, R., Camargo, P.B., Moulton, T.P., 2017. Allochthonous and autochthonous carbon flows in food webs of tropical forest streams. Freshw. Biol. 62, 1012–1023. https://doi.org/10.1111/fwb.12921.

Parkyn, S., 2004. Review of riparian buffer zone effectiveness. Ministry of Agriculture and Forestry Policy MAF Techni. ISBN No: 0-478-07823-4, ISSN No: 1171-4662.

Pettit, N.E., Davies, T., Fellman, J.B., Grierson, P.F., Warfe, D.M., Davies, P.M., 2012. Leaf litter chemistry, decomposition and assimilation by macroinvertebrates in two tropical streams. Hydrobiologia 680, 63–77. https://doi.org/10.1007/s10750-011-0903-1.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2021. Nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 4.0.4 152. https://CRAN.R-project.org/package=nlme.

R Development Core Team, 2020. R: A language and environment for statistical computing. R Pachage Version 4.0.4. http://www.R-project.org.

Ramos, S.M., Graça, M.A.S., Ferreira, V., 2021. A comparison of decomposition rates and biological colonization of leaf litter from tropical and temperate origins. Aquat. Microb. Ecol. 55, 925–940. https://doi.org/10.1007/s10452-021-09872-3.

Rezende, R.S., Petrucio, M.M., Goņcalves, J.F., 2014. The effects of spatial scale on breakdown of leaves in a tropical watershed. PLoS One 9, 1–11. https://doi.org/10.1371/journal.pone.0097072.

Rezende, R.S., Graça, M.A.S., Santos, A.M., Medeiros, A.O., Santos, P.F., Nunes, Y.R., Gonçalves, J.F.J., 2016. Organic matter dynamics in a Tropical Gallery Forest in a grassland landscape. Biotropica 48, 1–10. https://doi.org/10.1111/btp.12308.

Rezende, R.S., Santos, A.M., Medeiros, A.O., Gonçalves, J.F., 2017. Temporal leaf litter breakdown in a tropical riparian forest with an open canopy. Limnetica 36, 445–459. https://doi.org/10.23818/limn.36.14.

Rezende, R.S., Leite, G.F.M., Ramos, K., Torres, I., Tonin, A.M., Gonçalves, J.F., 2018. Effects of litter size and quality on processing by decomposers in a tropical savannah stream. Biotropica 50, 578–585. https://doi.org/10.1111/btp.12547.

Rezende, R., de, S., de Albuquerque, C.Q., Hirota, A.S.V., Silva, P.F.R.S., Umetsu, R.K., Cabette, H.S.R., Bambi, P., Guedes, N., Lima-Rezende, C.A., Gonçalves-Júnior, J.F.,

2019. Post-fire consequences for leaf breakdown in a tropical stream. Acta Limnol. Bras. 31 https://doi.org/10.1590/s2179-975x4118.

Rezende, R.S., Bernardi, J.P., Gomes, E.S., Martins, R.T., Hamada, N., Gonçalves, J.F., 2020. Effects of Phylloicus case removal on consumption of leaf litter from two Neotropical biomes (Amazon rainforest and Cerrado savanna). Limnology 22, 35–42. https://doi.org/10.1007/s10201-020-00628-w.

Salomão, V.P., Tonin, A.M., Rezende, R.S., Leite, G.F.M., Alvim, E.A.C.C., Quintão, J.M. B., Gonçalves, J.F., 2019. Small dam impairs invertebrate and microbial assemblages as well as leaf breakdown: a study case from a tropical savanna stream. Limnologica 77, 1–6. https://doi.org/10.1016/j.limno.2019.125685.

Schreeg, L.A., Mack, M.C., Turner, B.L., 2013. Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species. Ecology 94, 94–105. https://doi.org/10.1890/11-1958.1.

Sena, G., Francisco Gonçalves Júnior, J., Tavares Martins, R., Hamada, N., de Souza Rezende, R., 2020. Leaf litter quality drives the feeding by invertebrate shredders in tropical streams. Ecol. Evol. 10, 8563–8570. https://doi.org/10.1002/ece3.6169.

Silva, H.G., Figueiredo, N., Andrade, G.V., 2008. Estrutura da vegetação de um cerradão e a heterogeneidade regional do Cerrado no Maranhão, Brasil. Rev. Árvore 32, 921–930. https://doi.org/10.1590/S0100-67622008000500017.

Speaker, R., Moore, K., Gregory, S., 1984. Analysis of the process of retention of organic matter in stream ecosystems. Sil Proc. 1922-2010 (22), 1835–1841. https://doi.org/10.1080/03680770.1983.11897582.

Steart, D.C., Boon, P.I., Greenwood, D.R., Diamond, N.T., 2002. Transport of leaf litter in upland streams of Eucalyptus and Nothofagus forests in southeastern Australia. Arch. fur Hydrobiol. 156, 43–61. https://doi.org/10.1127/0003-9136/2002/0156-0043.

Tonin, A.M., Hepp, L.U., Restello, R.M., Gon??alves, J.F., 2014. Understanding of colonization and breakdown of leaves by invertebrates in a tropical stream is enhanced by using biomass as well as count data. Hydrobiologia 740, 79–88. https://doi.org/10.1007/s10750-014-1939-9.

Tonin, A.M., Hepp, L.U., Gonçalves, J.F., 2017. Spatial variability of plant litter decomposition in stream networks: from litter bags to watersheds. Ecosystems. https://doi.org/10.1007/s10021-017-0169-1.

Tonin, A.M., Boyero, L., Bambi, P., Pearson, R.G., Correa-Araneda, F., Gonçalves, J.F., 2019. High within-stream replication is needed to predict litter fluxes in wet–dry tropical streams. Freshw. Biol. 1–10. https://doi.org/10.1111/fwb.13459.

Webster, J.R., Covich, A.P., Tank, J.L., Crockett, T.V., 1994. Retention of coarse organic particles in streams in the southern Appalachian Mountains. J. North Am. Benthol. Soc. 13, 140–150. https://doi.org/10.2307/1467233.

Webster, J.R., Benfield, E.F., Ehrman, T.P., Schaeffer, M.A., Tank, J.E., Hutchens, J.J., D'Angelo, D.J., 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshw. Biol. 41, 687–705. https://doi.org/10.1046/j.1365-2427.1999.00409.x.

Young, S.A., Kovalak, W.P., Del Signore, K.A., 1978. Distances travelled by autumn-shed leaves introduced into a woodland stream. Amer. Midi. Nat 100, 217–222. https://doi.org/10.2307/2424792.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer Science & Business Media.