

Effects of litter patch area on macroinvertebrate assemblage structure and leaf breakdown in Central Amazonian streams

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Abstract Leaf breakdown in streams is affected by several factors, such as leaf characteristics, water chemistry, microbial activity, and abundance of shredders. In turn, shredders may be resource-

controlled. We hypothesized that the size of litter patches affects leaf breakdown, because large patches should be stable over time and therefore harbor high densities of shredders. We selected litter patches (area 0.25–10 m²) in 10 pools of three first-order streams (Manaus, Brazil). We installed 10 leaf packs of *Mabea speciosa* (Euphorbiaceae) in each patch, and sampled one after 1 day and three after 5, 19, and 28 days. The leaf packs were quickly colonized by the shredding caddisflies *Triplectides* and *Phylloicus*. The leaf breakdown rate (mean $k = 0.026 \pm 0.0015$ SE) was high and similar to values reported for other tropical and temperate streams, although much higher than values reported for the adjacent Cerrado biome. Assemblage composition varied over time, but was not related to the size of litter patches. Contrary to our hypothesis, litter patch area did not affect breakdown rates ($r^2 = 0.012$, $P = 0.766$) or abundance of shredders after 5, 19, and 28 days ($r^2 < 0.243$, $P > 0.147$). We found, however, a positive relationship between the abundance of tropical shredders and leaf breakdown after 19 days ($r^2 = 0.572$, $P = 0.011$), suggesting that shredders play an important role in leaf breakdown in these headwater streams. Our study indicates that leaf breakdown rates in tropical streams are variable and can be as high as those of temperate streams.

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Introduction

Studies of leaf breakdown have appeared on the literature of stream ecology for a long time (Cummins et al., 1973; Short & Maslin, 1977). Leaf breakdown is an important ecosystem process (Ruetz & Newman, 2002), acting as the main source of energy for streams with low primary production, such as headwater streams with riparian vegetation cover (Vannote et al., 1980). Tropical and temperate streams seem to differ in litter breakdown in terms of rates and in the relative importance of microbes and shredding invertebrates (Wantzen & Wagner, 2006; Jacobsen et al., 2008). The higher temperatures of tropical streams may favor microbial activity on leaf surfaces (Sioli, 1975; Covich, 1988; Irons et al., 1994), which would accelerate nutrient release. Microbial colonization of leaves enhances their quality and consumption by shredders (Benstead, 1996). Thus, high shredder density is expected in places where the microbial activity is high. However, current research has provided support for both low (Dobson et al., 2002; Wantzen et al., 2002; Gonçalves et al., 2006a, 2007) and high (Cheshire et al., 2005; Landeiro et al., 2008) densities of shredders in the tropics.

Several studies of mid-sized tropical streams have reported a lack of shredders (Rosemond et al., 1998; Gonçalves et al., 2006a, b, 2007), but these findings should be interpreted carefully and not extrapolated to pools of small streams, where shredders, especially cased caddisflies, are more likely to be found (Vannote et al., 1980; Cheshire et al., 2005; Kobayashi & Kagaya, 2005; Wantzen & Wagner, 2006). Similarly, streams differ in their retentiveness and thus stream size may not be the best surrogate for leaf-litter availability, which in turn affect shredder abundance. For instance, Li & Dudgeon (2009) studied small streams (although not first order) in Hong Kong and found few shredders. In addition, we should be cautious when allocating tropical macroinvertebrates to feeding categories, because of the lack of information on their trophic ecology (Camacho et al., 2009; see Merritt & Cummins, 1996 for details on feeding categories and trophic ecology).

Previous studies have reported wide variation in leaf decomposition rates within and among streams (Abelho, 2001). Several factors acting at different spatial scales may account for this (Royer & Minshall,

2003). Within a stream reach, the variation might be due to differences among litter patches in invertebrate density, microbial activity, streamflow (Kobayashi & Kagaya, 2005), and leaf characteristics such as toughness, nitrogen content, and chemical deterrents (Li et al., 2009). Among stream reaches or stream sites, variation might be due to stream gradient, substrate composition, water chemistry, and composition of shredder species (Camacho et al., 2009). For instance, Landeiro et al. (2008) showed that macroconsumers (shrimp, fish) had a significant effect on leaf breakdown in headwater streams in central Amazonia, although the magnitude of this effect was low when compared to the high variation observed among stream reaches (see also Moulton et al., 2010).

We studied the macroinvertebrate assemblage colonizing leaf packs and associated leaf breakdown rates in *terra-firme* streams of Central Amazonia. Landeiro et al. (2008) showed that these streams harbor high densities of caddisfly shredders of the genera *Triplectides* and *Phylloicus*. We compared the observed decomposition rates to previous studies, assessed assemblage composition during the decomposition process, and evaluated whether decomposition rates, macroinvertebrate composition, or shredder density were associated with the area of the litter patch. We hypothesized that leaf packs placed in large litter patches should be colonized quickly by shredders and decompose faster than those placed in small litter patches. This hypothesis follows the premise that the movement of shredders among leaf patches is limited, and that large litter patches are more stable and harbor high densities of shredders. We also evaluated the relationship between the number of shredders sampled in leaf packs and leaf mass loss, and predicted that high numbers of shredders would lead to increased mass loss.

Methods

Study area

This study was carried out in three first-order streams in the Amazon rainforest, located in the reserve “Km 41,” of the Biological Dynamics of Forest Fragments Project (BDFFP), approximately 100 km north of Manaus, Amazonas, Brazil (02°25'S, 59°43'W). The channel width of the streams studied were

approximately 1 m with a maximum depth of 0.4 m. The streams studied are within the Urubu River drainage basin, and are not subject to extended flood periods. The study area has low altitudinal variation (60–100 m asl), and streams has low water velocity, insufficient to move the rotor of a mechanical flowmeter (General Oceanics, model 2030R). Most small streams of central Amazonia have sandy bottoms with extensive accumulated leaf-litter patches. High precipitation events usually do not impact stream bottoms due to the low sloped relief, causing water overflows the stream bank and invade the riparian forest. Annual water temperatures average 24°C (daily values ranged 23–26°C; Santos & Ferreira, 1999) with a typical pH 3.8–4.4 (Sioli, 1984). The closed canopy of trees in the riparian zone prevents about 90% of the light incident on the canopy from reaching the ground and water surface, so that the production of aquatic macrophytes and periphyton is almost nonexistent (Walker, 1995).

Leaf pack confection

We assessed the leaf breakdown process using green leaves of *Mabea speciosa* J. Müller Argoviensis (Euphorbiaceae). In a pilot study for a previous experiment (Landeiro et al., 2008), we selected several leaf species abundant in the studied streams and that presented shredding marks. We then carried a short experiment using eight plant species and selected *M. speciosa* because it presented high densities of shredders and fast decomposition rates. Branches of *M. speciosa* were cut from trees, and the leaves were brought to the laboratory, washed in running water, and placed on a bench to drain the excess water. Air-dried leaves were arranged in packs of approximately 7 g, comprising one experimental unit.

Leaf packs were prepared using a plastic brace, a nylon cord 30-cm long, and a plastic label with an identification number of the pack. Leaf packs were constructed attaching leaves by their petiole using the plastic brace. At each site we attached three PVC pipes (2-cm diameter, 40-cm long) at the bottom of the stream and secured them in the stream bottom using two buried wooden stakes (0.3-cm diameter and 30-cm long). The nylon cord was used to tie the brace to the PVC tube. Three or four leaf packs were

anchored at each pipe. We made 110 leaf packs, of which 100 were used in the experiment and 10 were used to obtain the initial dry weight of the leaf packs, estimated by weighing after drying for 48 h in an oven at ~55°C. The dry weight of these 10 leaf packs was used to obtain a correction factor, calculated using the following formula: $CF = 1/(\sum (WW_i/DW_i))/N$, where CF is the correction factor, WW_i the wet weight of package i , DW_i the dry weight of package i , and N is the number of packages used in the estimate. To estimate the initial dry weight of a leaf pack, we multiplied its wet weight by the correction factor.

Experimental design

The study was carried out in pools, because this is the habitat where the highest density of shredders should be found, and also to avoid disturbances to the leaf packs by water flow. The experiment was conducted in 10 pools located in three first-order streams, four of them in one stream and three in each of the other two. The pools were at least 100 m apart, and the area of the litter patch ranged from 0.25 to 10 m². We placed 10 leaf packs in each pool. One leaf pack was removed from each pool after 1 day of immersion, to assess the amount of weight loss due to leaching. Subsequently, three leaf packs of each pool were removed after 5, 19, and 28 days.

Leaf breakdown

After collections, leaf packs were taken to the laboratory and washed in running water through a 250 µm sieve to retain macroinvertebrates. The remaining material was placed in an oven at ~55°C for drying for 48 h and then weighed. The breakdown rate (k) was estimated based on the negative exponential decay model: $W_t = W_0 \times e^{-kt}$, where W_t is the dry weight remaining at time t , W_0 is the initial dry weight, k is the constant of decay, and t is the period in days that the leaf pack was submersed. The k value is a measure of how fast the decomposition process occurs, and is extensively used to compare the degradation process of leaves between studies done in different locations and with different types of leaves (Abelho, 2001; Wantzen & Wagner, 2006).

Sorting and identification of aquatic insects

Insects were identified to genus or family using identification keys by Pes et al. (2005) (for Trichoptera) and Merritt & Cummins (1996) (for other orders). The assignment of functional feeding groups for neotropical stream insects is not straightforward given the scarcity of studies (Camacho et al., 2009). We opted to be conservative and consider as shredders the caddisflies *Triplectides* spp. (Trichoptera, Leptoceridae) and *Phylloicus* spp. (Trichoptera, Calamoceratidae), for which previous studies attest their feeding habit (Baptista et al., 2001; Cheshire et al., 2005; Rincon & Martinez, 2006; Camacho et al., 2009; Moretti et al., 2009). The two genera were commonly found in the leaf packs, and attained body weights, on average, greater than other insects.

Data analysis

The similarity of the macroinvertebrate assemblage among leaf packs during breakdown was evaluated using a Principal Coordinates Analysis (PCoA) to assess patterns related to the area of the litter patch and succession during the experimental period. The PCoA was performed using the Bray–Curtis dissimilarity measure of data standardized by dividing each abundance value by the species total. Leaf packs removed after 1 day of submersion contained too few individuals and were not included in the analysis.

We employed simple linear regressions to test (1) the effect of litter patch area on the abundance of shredders colonizing leaf packs, (2) the effects of litter patch area on leaf breakdown using the negative exponential rate of decay k as the response variable, and (3) the effects of the number of shredders on decomposition of the leaf packs after 5, 19, and 28 days. All analyses were run using the R software package (R Development Core Team, 2009), available at www.r-project.org.

Results

Shredder abundance and aquatic macroinvertebrate assemblage

We collected 8,365 aquatic macroinvertebrates belonging to 13 orders. A total of 35 taxa were

identified, of which nine occurred in only one or two litter patches and nine occurred in all litter patches (Fig. 1). The family with the greatest number of individuals was Chironomidae (Diptera), with 5,395 individuals. After 28 days the mean of chironomids per site (i.e., pooling of three leaf packs) was 102.23 ± 44.01 SD. Leptophlebiidae (Ephemeroptera) was the second most abundant, with 515 individuals.

Assemblage composition in leaf packs changed during the leaf breakdown (PCoA; Fig. 2). Assemblage composition after 5 days differed from the other dates on the first PCoA axis, while the difference in the assemblage composition between 19 and 28 days differed on the second axis. Some taxa colonized the leaf packs on the first day of immersion (Chironomidae, *Triplectides*, *Mortoniella* (Trichoptera, Glossosomatidae), *Helicopsyche*

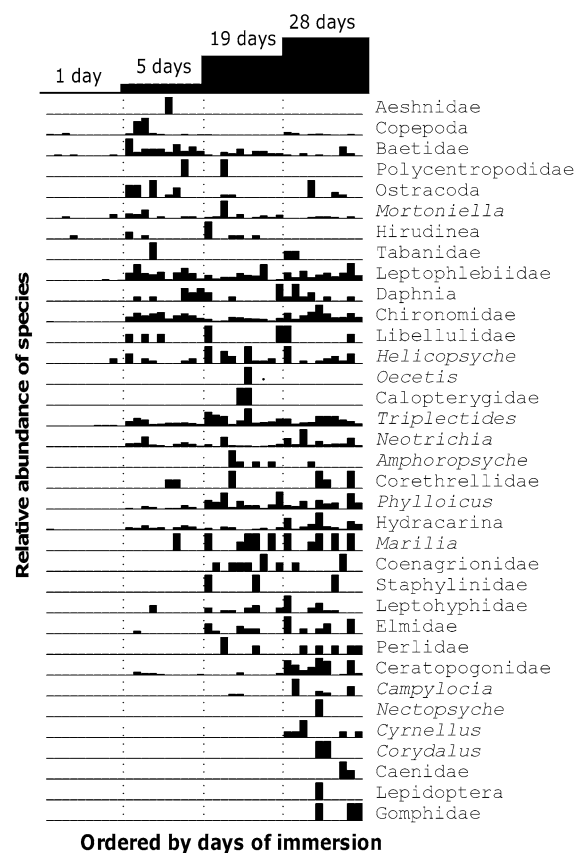


Fig. 1 Density of taxa present in leaf packs ordered by number of days after immersion. Species are ordered on the y-axis by reciprocal averaging, using time as weight. Each date is composed of 10 bars (i.e., one for each litter patch)

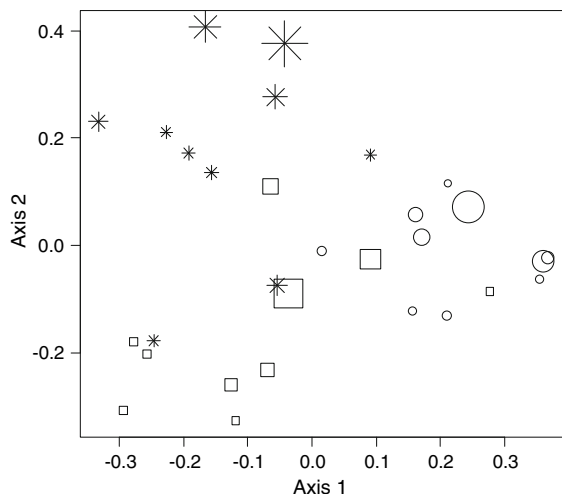


Fig. 2 Principal Coordinates Analysis of abundance data standardized by species totals (Goodness-of-fit = 0.25, eigenvalues: axis 1 = 1.301, axis 2 = 1.080). The size of the symbols is proportional to the area of the litter patch

(Trichoptera, Helicopsychidae), Leptophlebiidae and Baetidae (Ephemeroptera), Copepoda, Hirudinea, and Hydracarina (Fig. 1). Baetidae and Copepoda tended to occur in the early stages of colonization. Six taxa occurred only after 28 days of immersion (Fig. 1). Despite the changes during the experiment, assemblage composition did not appear to be affected by the area of the litter patch (Fig. 2).

The most abundant shredders were *Triplectides* spp. with 488 individuals and *Phylloicus* spp. with 161 individuals. Three leaf packs sampled after only 1 day of immersion contained one or two *Triplectides* consuming leaf tissues (revealed by chewing marks), indicating that conditioning by bacteria and fungi is not necessary for shredder activity. The abundance of shredders after 5, 19, and 28 days was not related to the area of the litter patch ($r^2 < 0.243$, $F_{1,8} < 2.570$, $P > 0.147$; Fig. 3).

Leaf breakdown

The average weight loss during the process of leaching, after 1 day of immersion, was 7.6%. After 28 days of immersion the leaf packs lost an average of $53.9\% \pm 8.5$ SD of their initial dry weight. The leaf breakdown was relatively high ($k = 0.026 \pm 0.0015$ SE). Leaf mass remaining after 28 days was mostly

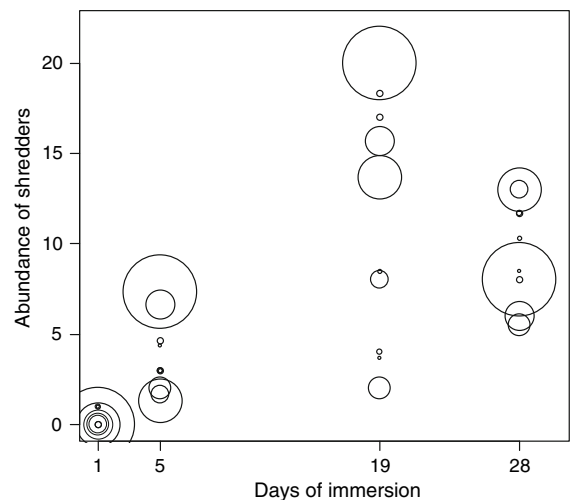


Fig. 3 Abundance of shredders (*Triplectides* spp. plus *Phylloicus* spp.) during the colonization of leaf packs. The size of the circles is proportional to the area of the litter patch (0.25–10 m²). The highest abundance was recorded in the largest litter patch; however, the second highest was in a small litter patch

restricted to conductive tissues. The number of shredders had a positive effect on leaf pack weight loss (Fig. 4); however, this effect was evident only after 19 days ($r^2 = 0.572$, $F_{1,8} = 10.709$, $P = 0.011$). After 5 ($r^2 = 0.119$, $F_{1,8} = 1.086$, $P = 0.328$) and 28 days ($r^2 = 0.003$, $F_{1,8} = 0.021$, $P = 0.888$), the weight loss was not related to the number of shredders. The area of the litter patch had no effect on the leaf breakdown process ($r^2 = 0.012$, $F_{1,8} = 0.094$, $P = 0.766$, Fig. 5).

Discussion

Assemblage structure was not apparently related to the area of the litter patch, but different taxa colonized the leaf packs during the decomposition process. The leaf breakdown was related to the number of shredders during the intermediate phase of the decomposition process (19 days), but not at the beginning (5 days) or end (28 days) phases. The density of shredders per leaf pack was not related to the area of the litter patch. In accordance with the lack of relationship between the number of shredders and the litter patch area, and contrary to our expectation, the rate of leaf breakdown was not related to the area of the litter patch.

Fig. 4 Relationship between the number of shredders and the leaf weight loss after 5, 19, and 28 days of colonization of leaf packs. The number of shredders was unrelated to leaf weight after 5 and 28 days. For day 19: $r^2 = 0.572$, $F_{1,8} = 10.709$, $P = 0.011$

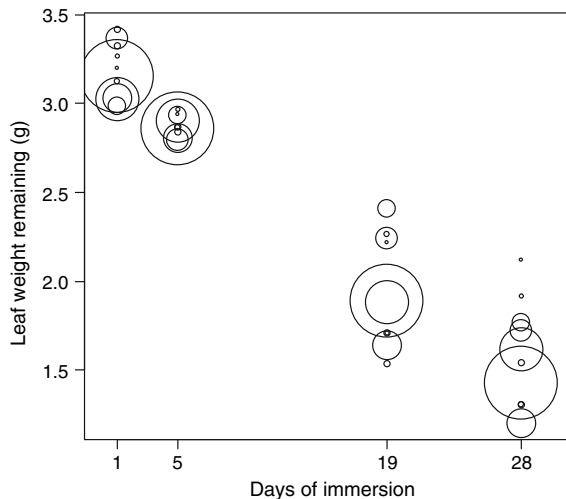
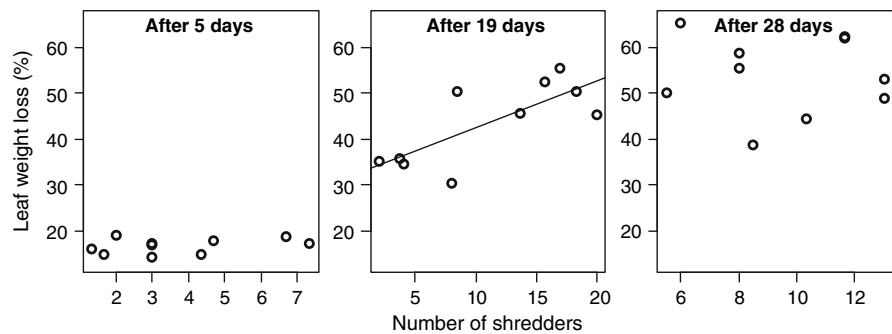


Fig. 5 Leaf breakdown during the experiment, according to the size of the litter patch where the leaf packs were installed. The size of the circles is proportional to the area of the litter patch (0.25–10 m²)

The PCoA showed that assemblage composition changed during the breakdown process. This change seems to be not only a consequence of increased species richness toward the end of the experiment, but also of reductions in the abundance of early colonizers. Change in assemblage structure during the process of colonization of leaves or rocky substrates has been reported previously (Walker, 1994; Tanaka et al., 2006). Baetidae colonized leaf packs quickly after submersion, and this is in accordance with previous studies showing that species of this family have good dispersal abilities, usually by drift, and are among the first colonizers of new substrates (Matthaei et al., 1996; Melo & Froehlich, 2004). On the other hand, assemblage structure was not affected by the size of the litter patch, indicating that movement among litter patches is common or that even the smallest litter

patches were large enough to provide colonizers for leaf packs.

Leaf breakdown is a result of leaching, physical abrasion, colonization of microorganisms, direct consumption by invertebrates, and bioturbation by large organisms (e.g., fish and shrimp) (Fazi & Rossi, 2000; Abelho, 2001). Given the many reports of low densities of shredders in different tropical ecosystems and the restrictive criterion used in this study to define shredders, only two genera of caddisflies were included in our study (Camacho et al., 2009). Accordingly, we were not surprised by the lack of a strong positive relationship between shredder density and leaf breakdown. However, our results showed a positive relationship between shredders and leaf breakdown after 19 days of colonization. The lack of relationship for samples obtained after 5 and 28 days of colonization was not unexpected, as in the first case few colonizers were present in the leaf packs, and in the second case most of the remaining material was low-quality conductive tissues. In fact, Landeiro et al. (2008) carried out a pilot experiment in which they observed that after 18 days, almost all non-conductive tissues of *M. speciosa* had been removed. It should be noted, however, that the significant positive relationship of shredder abundance and leaf breakdown was not the main objective of our experiment and resulted from a correlative analysis. An unequivocal relationship can only be established after a controlled experiment.

Several factors control shredder distribution within and among streams, such as the aggregation of resources (Abós et al., 2006), feeding preferences, the quality of leaves present in litter patches (Graça et al., 2001; Magana, 2001; Menéndez et al., 2003; Ratnarajah & Barmuta, 2009), and differences in shredder composition and abundance among litter patches (Cheshire et al., 2005; Camacho et al., 2009).

For instance, Kobayashi & Kagaya (2005) observed that litter patches located in different microhabitats within a stream reach contained distinct shredder compositions, and this resulted in a wide variation in litter breakdown. We tested whether the area of the litter patch (but not the type of litter patch) was an additional factor in the determination of shredder density and leaf breakdown rates. Our hypothesis followed two assumptions: (1) that large litter patches were stable and (2) that movement of shredders (in our study, caddisflies) among leaf patches was restricted. We found that shredder density and breakdown rates were not high in leaf packs placed in large litter patches, which was contrary to our expectations. At least two factors could account for this lack of relationship. First, the assumption of high stability of large litter patches may only be effective during the rainy season, when the superficial layers of litter patches are most likely to be moved downstream (Abelho, 2001). Second, we did not control for connectivity among leaf patches, and thus even small litter patches could receive individuals from large adjacent patches. This would be particularly relevant if mobility of *Triplectides* and *Phylloicus* is high, although no data are available to assess this hypothesis.

The presence of *Triplectides* after 1 day shows that the fragmentation by shredders begins immediately after submersion, before leaf conditioning, a process that is generally considered necessary for shredder leaf consumption (Golladay et al., 1983; Graça et al., 2001). After 5 days, most of the available taxa had colonized the leaf packs and assemblage composition was essentially the same as that observed after 19 days, the main differences were higher abundances in the latter. Following this rapid colonization, breakdown rates ($k = 0.026 \pm 0.0015$ SE) were very high when compared to previous studies, both in temperate and tropical streams (Cummins et al., 1973; Abelho, 2001). For instance, Camacho et al. (2009) studied the breakdown of leaves differing in palatability in Panama and tropical Australia, and reported k values ranging from 0.004 to 0.023, although only in a single case (combination of location and palatability) were the values above 0.020. It should be noted, however, that the *M. speciosa*, the plant species used in our experiment was selected because in a previous pilot study it was rapidly colonized by shredders and presented high rate of decomposition.

A study conducted in Amazon whitewater streams under the influence of a flash-discharge phase reported leaf breakdown rates similar to those observed in our study ($k = 0.031 \text{ day}^{-1} \pm 0.003$ SD, $k = 0.029 \text{ day}^{-1} \pm 0.006$ SD, and $k = 0.010 \text{ day}^{-1} \pm 0.003$ SD for *Cecropia latiloba*, *Tessaria integrifolia*, and *Symmeria paniculata*, respectively), despite the apparent scarcity of shredders in that study (Rueda-Delgado et al., 2006). Similarly, in a stream in Puerto Rico mostly lacking insect shredders but harboring a high density of shrimp, Wright & Covich (2005) reported k values as high as 0.039. The breakdown rates found here were similar to those found for leaves of *Alnus glutinosa* in streams of temperate regions ($k = 0.0295$ and 0.0017 day^{-1} for coarse and fine meshes, Gonçalves et al., 2006b). However, high leaf breakdown rates are far from the rule in tropical areas. Breakdown rates reported for Brazilian Cerrado streams are among the lowest rates reported ($k = 0.002 \text{ day}^{-1}$ in a third-order stream, Gonçalves et al., 2007; $k = 0.0157 \text{ day}^{-1}$ for fourth-order streams and $k = 0.0065 \text{ day}^{-1}$ for a third-order stream Gonçalves et al., 2006a; and $k = 0.014 \text{ day}^{-1}$ for a third-order stream Gonçalves et al., 2006b). The wide variation in k values among streams, riparian vegetation, and their aquatic faunas of the Amazon and Cerrado (adjacent biomes) shows that generalizations regarding the rate of decomposition in tropical areas must be made with care and should take into account particularities of streams and their faunas.

The size of streams, its retentiveness, water current and susceptibility of streams to high discharge events, and leaf characteristics should be considered in tropical streams studies. Our studied streams were first order (~ 1 -m wide), not greatly affected by high discharge events due to their low slope and presented extensive leaf-litter banks. This kind of environment is adequate for the development of *Phylloicus* (also found in lakes and small pounds) and *Triplectides* caddisflies. In addition, we selected a plant species previously known to present high decomposition rates. The stream type and the leaf plant species studied might be the main causes of the high shredder densities and fast decomposition rates observed in our study.

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