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Effects of litter size and quality on processing by decomposers in a tropical savannah stream

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ABSTRACT

Litter fragment size and quality can have profound effects on ecosystem functioning and global biogeochemical cycling due to differential utilization by decomposers. Here we study the influence of these factors on decomposers from two guilds found in a tropical savannah stream: invertebrate shredders of the genus *Phylloicus* and microorganisms. Containers (16 × 16 × 12 cm, ~ 3L) with either *Phylloicus* (cases removed; $N = 16$) or stream water containing microorganisms ($N = 16$) were supplied with litter from the species *Inga laurina, Maprounea guianensis,* and *Richeria grandis*, and cut into disks of 18.7, 13.2, and 8.1 mm in diameter (3 sizes × 3 species = 9 disks per container). Relative decomposition was greater for smaller leaf disks and disks of higher quality in microbial-only cultures. *Phylloicus* preferentially harvested large fragments for case building, also preferring the leaves of *M. guianensis* and *R. grandis*, likely due increased robustness for case formation. Microbial decomposition resulted in ~20% litter mass loss compared to 30% in *Phylloicus* (of which 8% was used for case building and 24% for food). Thus, changes to input litter size, such as a decrease in leaf size after drought, may alter microbial decomposition and potentially affect shredder populations by limiting the availability of casing material.

Abstract in Portuguese is available with online material.

Key words: invertebrates; leaf decomposition; microbial communities; shredders.

Decomposition of litter is a key aspect of system metabolism that affects ecosystem functioning (Tank *et al.* 2010, Graça *et al.* 2015). In the tropics, understanding the factors that control litter decomposition has implications for global biogeochemical cycling (Webster & Meyer 1997, Tank *et al.* 2010, Rinkes *et al.* 2014). The rate at which litter is recycled can be influenced by both biotic and physical factors (Gessner *et al.* 1999, Ferreira *et al.* 2014). For instance, invertebrates (*e.g.*, the shredder functional guild) and microorganisms (*e.g.*, fungi and bacteria) degrade coarse particulate organic matter into fine particles and mineralize organic matter (Graça *et al.* 2015, 2016).

Most research on decomposition has been conducted in terrestrial systems (Tank *et al.* 2010). However, litter decomposition is also a critical process in aquatic systems (Gessner *et al.* 1999, Graça *et al.* 2015), although the sequence of decomposition is different. In streams, bacteria play an important role early in decomposition by assimilating labile molecules, while fungi become gradually more important through processing of structural compounds (Gonçalves *et al.* 2006, Mora-Gómez *et al.* 2016). Microorganisms condition the litter (*i.e.*, via nutritional enrichment), thereby increasing resource quality for subsequent consumption by invertebrates (Gessner *et al.* 1999, Foucreau *et al.* 2013). In terrestrial systems, this sequence is inverted, with the invertebrates conditioning the leaf litter for microorganisms via bioturbation (Rinkes *et al.* 2014). Invertebrate bioturbation increases nutrient availability at the leaf surface by introducing fresh organic matter (Rinkes *et al.* 2014).

Factors that are known to influence the rate of litter decomposition in streams include the chemical characteristics of litter and the amount of canopy cover (Graça *et al.* 2015). Leaves with low concentrations of nitrogen and phosphorus (Tank *et al.* 2010, Ferreira *et al.* 2014) typically have increased lignin, cellulose, tannins, and polyphenols and are thus considered poor-quality resources for decomposers. Consequently, these leaves have low breakdown rates by invertebrates and microorganisms as food resources (Graça *et al.* 2015, Sales *et al.* 2015). However, some studies have suggested that some shredder invertebrates (including genera of *Phylloicus*) prefer higher phenolic, lignin, and cellulose concentrations in the litter used for case construction

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(Rincón & Martínez 2006, Moretti *et al.* 2009). High concentrations of structural compounds make the case more robust and provide greater protection against predators (Rezende *et al.* 2015). In this way, litter quality can potentially influence organic matter processing by organisms (Tank *et al.* 2010, Navarro *et al.* 2013, Cornut *et al.* 2015, Graça *et al.* 2015).

Organic matter processing dynamics may also be influenced by leaf litter size. Size may vary based on spatial or temporal gradients in plant species and productivity (Meier & Leuschner 2008) or due to leaf litter fragmentation from physical degradation (Cummins & Klug 1979, Cornejo *et al.* 1994). Litter size can potentially influence the decomposer community by altering the litter surface area available for colonization (for more see also Rinkes *et al.* 2014, Alvim *et al.* 2015). Fragmented leaves also release more soluble compounds (as phenols) than not fragmented leaves, mainly due to leaching (Gessner *et al.* 1999, Graça *et al.* 2015). Smaller leaf litter sizes (fragmented or not) increase some nutrients (e.g., nitrogen) by microbial bioaccumulation and/or invertebrate bioturbation due to a higher surface-area-to-volume ratio (Cornejo *et al.* 1994, Rinkes *et al.* 2014, Alvim *et al.* 2015). Understanding the influence of litter size may contribute to our general understanding of processes that have previously been observed in savannahs, including: i) a decrease in leaf size resulting from global warming (see also Silverio *et al.* 2013) and ii) the increase in biological leaf fragmentation due to higher activity of shredder invertebrates also in response to global warming (see also Navarro *et al.* 2013, Navarro & Gonçalves-Jr 2017).

Shredder invertebrates are specialized to process allochthonous detritus in tropical streams, and several experimental studies have investigated the influence of shredders on litter breakdown (Nolen & Pearson 1993, Cheshire *et al.* 2005, Boyero & Pearson 2006, Casotti *et al.* 2014, Kiffer *et al.* 2016), particularly in caddisflies of the genus *Phylloicus* (Muller, 1880; Rincón & Martínez 2006, Moretti *et al.* 2009, Navarro *et al.* 2013, Vidovix *et al.* 2013, Casotti *et al.* 2014, Rezende *et al.* 2015, Leite *et al.* 2016, Martins *et al.* 2016, Navarro & Gonçalves-Jr 2017). *Phylloicus* (Calamoceratidae: Trichoptera) is a caddisfly genus with daytime and crepuscular activity of which there are 17 known species in Brazil (Paprocki & França 2014). While adult *Phylloicus* spp. live in riparian zones near their streams of origin (Paprocki & França 2014), larvae occupy areas with accumulated leaf litter in stream pools, where leaf tissue is used as food and to construct protective cases (Paprocki & França 2014, Leite *et al.* 2016, Martins *et al.* 2016). *Phylloicus* spp. are reported to exhibit foraging preference for leaves of higher abundance and/or nutritional quality (Moretti *et al.* 2009, Leite *et al.* 2016).

Smaller leaf or litter fragments of the same species may alter litter quality and, consequently, the rate of decomposition by invertebrate feeding and microorganisms (Rinkes *et al.* 2014, Alvim *et al.* 2015, Gomes *et al.* 2016). In streams, litter size (Alvim *et al.* 2015) and quality (Gomes *et al.* 2016) have variously been shown to be important for microbial decomposer activity. However, it is unknown how leaf size and quality affect invertebrate shredders relative to microbial decomposer communities in tropical or savannah stream ecosystems. In this study, we evaluated the importance of leaf litter fragment size and quality on decomposition by microorganisms and consumption by invertebrate shredders in savannah streams. We tested the following hypotheses: (1) *Phylloicus* larvae prefer smaller leaf fragments for consumption, and larger leaf fragments for case construction due to the foraging efficiency and better protection from larger fragments; (2) *Phylloicus* larvae prefer higher quality litter (lower lignin and polyphenol content), and lower quality litter are preferred for case construction (higher structural compounds provide better protection); (3) microorganisms decompose smaller fragments faster due to positive surface area effects (Alvim *et al.* 2015) compared to larger fragments with higher organic matter content; and (4) litter of higher quality is decomposed faster by microorganisms than is lower quality litter.

METHODS

Field procedures.—We collected *Phylloicus sp.* (Calamoceratidae, Trichoptera) specimens by kicknet in the Capetinga Stream (15°57′40.75″S – 47°56′38.04″W) located in the Gama-Cabeça de Veado catchment of the Federal District, Brazil. The site is in the Brazilian savannah region (also called Cerrado), with two distinct climate periods: dry winter and rainy summer. The mean annual temperature of the site is 20°C, and the altitude varies between 1025 and 1150 m above sea level. We measured the length of the stream channel (about 2 m), channel depth (0.20 m), water velocity (0.37 ± 0.08 m/s), dissolved oxygen concentration (6.97 ± 0.59 mg/l), electrical conductivity (16.73 ± 0.46 μS cm^2), temperature (19.54 ± 1.01°C), pH (6.09 ± 0.11), and turbidity (3.01 ± 0.71 NTU).

Laboratory procedures.—We took invertebrates to the laboratory in cool boxes and placed them in containers (15.5 × 15.5 × 12 cm, 2883 cm^3 volume) with water from the stream. We placed gravel that was previously sterilized in an oven for 4 h at 550°C in the bottom of the containers. We kept containers with invertebrates in a room with continuous aeration at a temperature of 18°C, and a light/dark cycle of 12 h/12 h. We measured dissolved oxygen concentration and pH daily using a Jenway 970 DO_2 meter and Jenway 430 pH/cond. meter, respectively. In both experiments, the water was circumneutral (mean of 6.5; range of 6.2–6.8) with high levels of oxygen (mean of 7.5; range of 7.2 to 8.4 mg/l). We kept the temperature of water in containers constant at 20°C for the duration of the experiments. Cases were removed from invertebrates prior to the start of experiments.

We conditioned and leached leaf litter from *Inga laurina* (Sw.) Willd., *Maprounea guianensis* Aubl., and *Richeria grandis* Vahl. in litter bags (0.5 mm mesh) for seven days at the Capetinga Stream. The effects of conditioning and leaching processes on leaf chemical compounds (which helped to determine this period) are described in Gomes *et al.* (2016), who used the same litter pool as in this work. Following Gomes *et al.* (2016), we classified the litter according to decomposer preference with respect to leaf toughness and lignin and cellulose concentration as low, intermediate, and high for *I. laurina*, *R. grandis,* and *M. guianensis*, respectively. We cut the conditioned leaves into disks of three sizes: (1) large (18.7 mm diameter); (2) medium (13.2 mm diameter); and (3) small (8.1 mm diameter). We freeze-dried the disks (Terroni, LT-AISI 304 model) and weighed them on a precision balance (0.01 mg; Shimadzu, AUW220D model) to determine the initial dry mass. Leaf freeze-drying killed the microbial community but preserved the nutritional enrichment by this community for the start of the experiments. At the end of the experiments, we oven-dried the remaining leaf disk material at 60°C for 48 h and obtained the final dry weight. We calculated the loss in mass between treatments by determining the difference between the initial and final dry weights.

EXPERIMENTAL DESIGN.—We tested the effect of fragment size on leaf processing by decomposers in container mesocosms filled with unfiltered stream water and gravel bottoms. Disks of three fragment sizes (large, medium, and small; 3 disks of each size) for each of three species of leaf detritus (*I. laurina*, *M. guianensis,* and *R. grandis*; 1 disk of each species) were added to each container. Each container contained disks of similar weights for each species (3 disk sizes × 3 species = 9 disks per container total). A total of 32 containers were tested.

The processing of leaf detritus by microorganisms was tested in an experiment using 16 containers for 14 days (Experiment 1; absence of *Phylloicus* sp. in container). The effects of leaf fragment size on use (case building and food resource) by *Phylloicus* sp. was tested using 16 containers (Experiment 2). However, in contrast to experiment 1 (one sampling at the end of 14 days), four replicates were taken on the 1, 3, 7, and 14 days (one per day) in Experiment 2.

STATISTICAL ANALYSIS.—We used percentage litter mass loss from different fragment sizes (large, medium, and small) and species (*I. laurina*, *M. guianensis,* and *R. grandis*) as the dependent variable in analyses. We tested differences between treatment groups with a factorial two-way repeated measures ANOVA (RM-ANOVA). In RM-ANOVA, we used the containers (Experiment 1) or time (Experiment 2) as the repeated measurements (Crawley 2007). The RM-MANOVA is a common procedure for experiments with different error variances (for more see also chapter 11 of Crawley 2007). We used contrast analysis to assess differences among the categorical variables (Crawley 2007). In this contrast analysis (orthogonal), we ordered the mass percentage loss of leaf litter of different sizes (large, medium, and small) and detritus species (*I. laurina*, *M. guianensis,* and *R. grandis*) by increasing magnitude and performed pairwise tests with the closest values. We then added to the model groups with no differences for testing in subsequent model simplification steps by forward selection (Crawley 2007). We tested the data for normality with a Kolmogorov–Smirnov test, and log-transformed percentages as necessary.

RESULTS

LEAF DECOMPOSITION BY MICROORGANISMS IN EXPERIMENT 1.—Leaf mass loss (%) due to microbial activity in containers without invertebrates differed significantly among leaf sizes and plant species (Table 1; Fig. 1, Figs. S1 & S2). The smallest leaf size of the

TABLE 1. *Results of comparisons among leaf fragment size, leaf species and the interaction (factorial two-way RM-ANOVA), and the contrast analysis (*P *< 0.05) for microbial consumption, use for food resource, and case building by invertebrates.*

RM-ANOVA	Df	Sum Sq	F	Pr(>F)	Contrast analysis
Mass loss (A)					
Error:Sampling	1	0.07			
Size	2	1.91	4.50	0.014	Medium = large < small
Species	2	74.57	176.05	<0.001	*I. laurina* < *R. grandis* < *M. guianensis*
Size:Species	4	2.69	3.18	0.017	
Residuals	98	20.76			
Food resource (B)					
Error:Time	1	10.66			
Size	2	0.03	0.03	0.970	
Species	2	49.63	61.72	<0.001	*I. laurina* < *R. grandis* < *M. guianensis*
Size:Species	4	0.28	0.17	0.952	
Residuals	98	39.40			
Case building (C)					
Error:Time	1	0.05			
Size	2	12.64	8.32	<0.001	Small < medium = large
Species	2	6.77	4.45	0.014	*I. laurina* < *M. guianensis* = *R. grandis*
Size:Species	4	6.04	1.99	0.102	
Residuals	98	74.50			

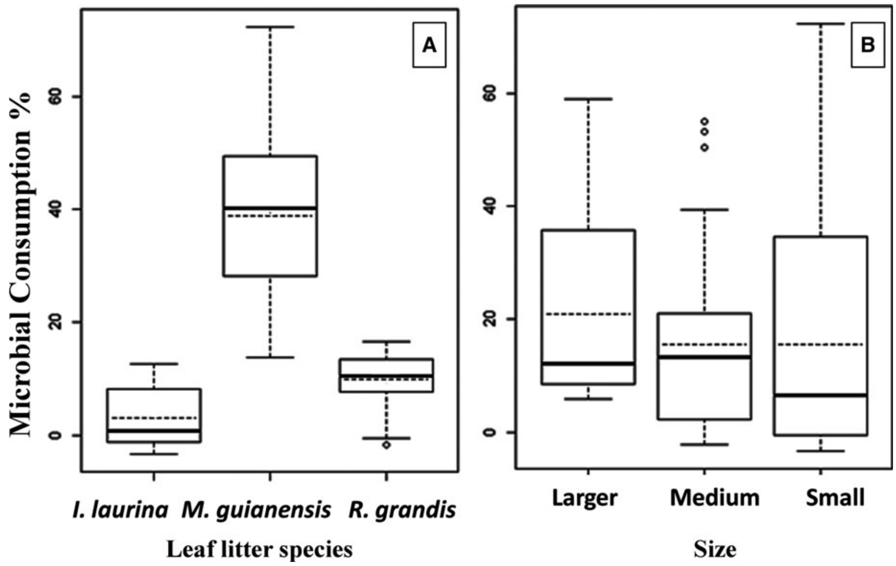

FIGURE 1. Leaf litter consumption by microorganisms from different leaf species (A) and size (B). Boxes represent the quartiles, the bold line represents the median, the horizontal dashed line the mean, and the vertical dashed line represents the upper and lower limits and circles the outliers.

highest quality leaf species was associated with the highest relative litter mass loss. Smaller leaf fragments had higher mass loss rates (mean of 24.5 ± 4.1% standard error—SE) in comparison with medium (19.5 ± 3.6%) and large (18.5 ± 5.1%) leaf fragments. Higher mass loss was observed for *M. guianensis* (39.8 ± 3.9%), followed by *R. grandis* (14.7 ± 1.1%) and *I. laurina* (7.9 ± 1.2%). The mass loss of *I. laurina* was 13.1% (±0.3) for the small leaf fragment treatment, and 6.9% (±0.7) and 3.6% (±0.2) for medium and large fragment size treatments, respectively. The mass loss of *M. guianensis* was also higher in the small fragment size treatment (44.9 ± 1.8%), followed by large (40.4 ± 2.9%) and medium (34.1 ± 2.2%) treatments. *R. grandis* displayed a mass loss of 17.1% (±0.4) for medium-sized leaves, followed by 15.5% (±0.4) for small leaves and 11.5% (±0.8) for large leaves (Table 1A).

LEAF UTILIZATION BY PHYLLOICUS IN EXPERIMENT 2.—The mass loss in leaf detritus due to *Phylloicus* did not differ significantly among small (mean of 25.3 ± 3.7% SE), medium (24.8 ± 5.3%), and large (24.3 ± 3.1%) leaf litter fragments (24.8 ± 4.4% SE) (Fig. 2; Figs. S1 & S3; Table 1B). There was a significant difference in mass loss among leaf species, with the highest losses recorded for *M. guianensis* leaf litter (37.3 ± 4.7%) followed by *R. grandis* (27.4 ± 2.3%) and *I. laurina* (8.3 ± 0.7%). The interaction between factors (size and species) was not significant (Table 1B). Leaf litter mass loss of *I. laurina* was 9.9% (±0.9) for medium leaf fragments, 8.2% (±0.6) for small fragments, and 7.8% (±0.6) for large fragments. *M. guianensis* had a 38.4% (±2.4) mass loss for small, 37.1% (±7.1) for medium, and 36.4% (±3.7) for large leaf fragments. Mass loss for *R. grandis* was 28.5% (±2.7) for large-, 28.3% (±1.7) for small-, and 25.2% (±2.5) for medium-sized fragments. There was no mortality of *Phylloicus* sp. in Experiment 2.

The mass loss due to case building (mean of 8.2 ± 2.7% SE) by *Phylloicus* was higher for large (12.4 ± 3.2%) and medium (8.8 ± 2.4%) fragment sizes, and lower for small fragment sizes (3.3 ± 1.7%) (Fig. 2; Figs. S1 & S3; Table 1C). There were significant differences among leaf species, with the highest losses in *R. grandis* (10.6 ± 2.9%) and *M. guianensis* (9.8 ± 2.8%) and the lowest in *I. laurina* (4.2 ± 2.1%). The interaction between size and species was not significant (Table 1C). Mass loss for case construction per leaf species and fragment size category was as follows: *I. laurina*, 4.9% (±2.2) large, 4.6% (±2.1) medium, 3.2% (±2.1) small; *M. guianensis*, 13.8% (±3.2) large, 10.3% (±2.9) medium, and 5.3% (±1.9) small; *R. grandis,* 18.5% (±3.4) large, 11.3% (±3.1) medium, 1.1% (±0.9) small.

DISCUSSION

EFFECT OF LITTER SIZE AND QUALITY.—Smaller leaf fragments from species thought to have higher litter quality experienced the greatest proportional decomposition, mainly due to higher microbial activity. The same pattern of preferential degradation of small, high-quality litter is observed in terrestrial systems and is explained by mechanisms such as bioaccumulation and bioturbation (Rinkes *et al.* 2014). In this experiment, small leaf disks had proportionally more damaged tissue, which may leach herbivory and fungicide defense compounds. These compounds may have catalyzed microbial colonization and litter mass loss (Alvim *et al.* 2015, Sales *et al.* 2015). Smaller litter fragments in plants of the same species experience higher rates of mass loss by biological activity (mainly by microbial) (Cummins & Klug 1979, Cornejo *et al.* 1994). Gonçalves *et al.* (2016) in a study of native and exotic leaf litter in Amazonian streams observed a preference for native and higher quality litter (*Mabea speciosa*) by shredders and microbial decomposers compared to leaf litter from the exotic

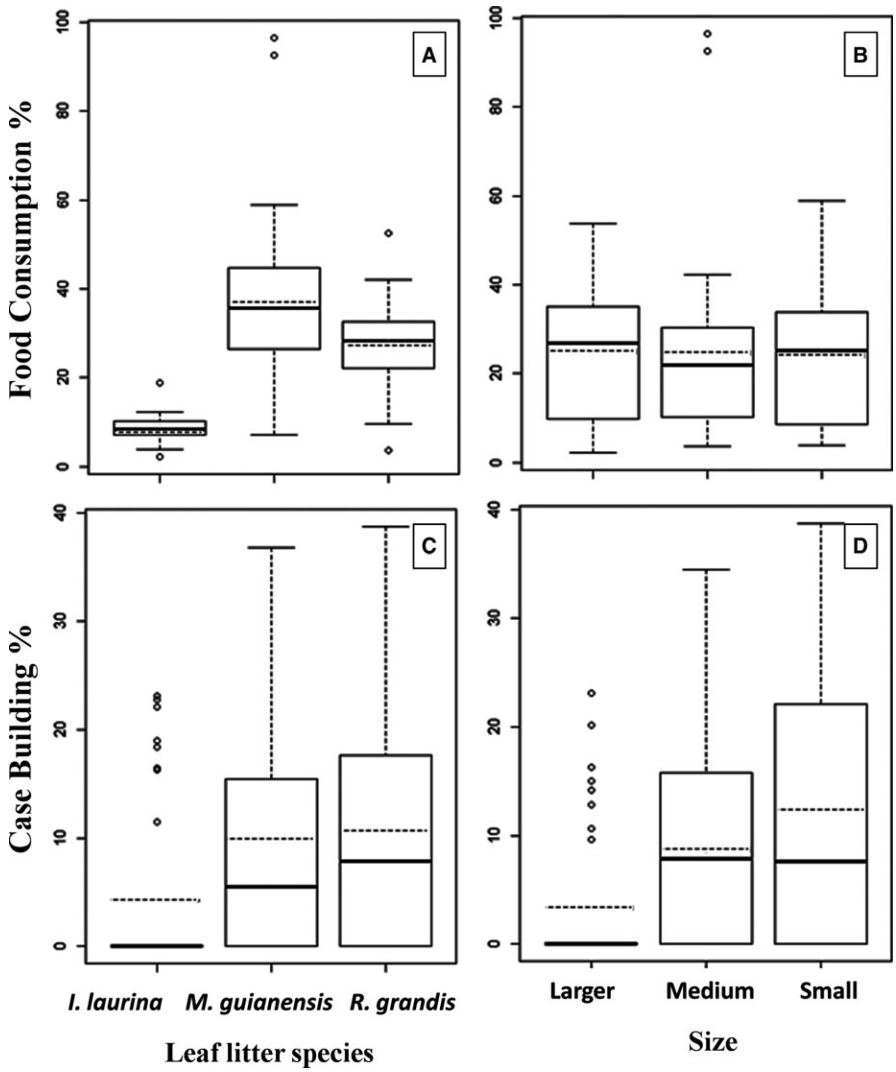

FIGURE 2. Leaf litter used for food resources (A and B) and case building (C and D) by *Phylloicus* spp from different species (A and C) and size (C and D). Boxes represent the quartiles, the bold line represents the median, the horizontal dashed line the mean, and the vertical dashed line represents the upper and lower limits and circles the outliers.

Eucalyptus camaldulensis. These results imply that decomposer communities may be influenced by changes in riparian vegetation composition (see also Sales *et al.* 2015, Leite *et al.* 2016). Our study supports the idea that the size and structural characteristics (quality) of litter are important factors that affect decomposer communities and litter breakdown rates in savannah streams.

We found that leaf litter size influenced the degradation rates of litter by the microbial community, as well as harvesting by *Phylloicus* larvae for case building, but not feeding. The highest microbial decomposition rates were found for small litter fragments, mainly *M. guianensis*. By contrast, *Phylloicus* preferred larger fragments for case building. *M. guianensis* litter is characterized by a low concentration of lignin and cellulose and intermediate values of nitrogen and phosphorus compared to many other species of plants in savannah riparian zones (for more see also Gomes *et al.* 2016). The smaller sized, higher quality litter has an increased surface-area-to-volume ratio, which facilitates colonization of organic matter by microorganisms and results in faster degradation (Alvim *et al.* 2015). It is possible that invertebrates choose larger leaf fragments for optimal case formation (Navarro *et al.* 2013, Martins *et al.* 2016, Navarro & Gonçalves-Jr 2017), supporting our hypothesis that invertebrates prefer larger fragments for case building. Our hypothesis that *Phylloicus* prefer higher quality litter was also supported, but we did not observe a preference for lower quality litter for case construction. Our hypotheses that microorganisms would degrade smaller and higher quality leaf litter fragments faster was also supported.

Our study suggests that microorganisms and invertebrate shredders have similar potential decomposition rates for litter in this study system. This differs from terrestrial systems where invertebrates contribute more to breakdown via bioturbation (Rinkes *et al.* 2014). Mean microbial breakdown for all fragment sizes and litter types was around 20 percent, while the use of leaf litter by *Phylloicus* larvae was around 30 percent. Eight percent of the biomass harvested by invertebrates was used for case building. Material used for case building remains in a disaggregated state, in contrast to the 24 percent used as a food resource. Low shredder density is commonly observed in tropical streams (Boyero *et al.* 2011, 2012), although this group can be abundant in some places (Cheshire *et al.* 2005, Allan *et al.* 2009). Despite the low density used in the experiment (=1 individual per container), the processing rates (mean of 0.04 g m^2 in total use by *Phylloicus*) were still high for *Phylloicus* larvae. In the same stream, Leite *et al.* (2016) observed a leaf input of 24 g m^2 monthly and density of *Phylloicus* ranging from 2.4 to 13.7 ind/m^2 monthly. Extrapolating our results, the monthly leaf processing rates by *Phylloicus* would be 0.2–1.2 g m^2, depending on density. It is important to note that this is only one genus within the trophic group of shredders. The presence of shredders can influence leaf processing (Tonin *et al.* 2014). Also, despite having low density and diversity in tropical streams (Leite *et al.* 2016), they nonetheless play key roles in maintaining energy flow and processing of organic matter in the study system (Tonin *et al.* 2014, Leite *et al.* 2016).

Leaf mass loss by microorganisms.—Mass loss due to microorganism activity was highest in small leaf fragments, especially of the species *M. guianensis*. Similar results were found in an investigation of the composition of different small leaves during the breakdown process in savannah headwater streams (Alvim *et al.* 2015). These authors show empirically that litter decomposition is faster in smaller leaf fragments due to fast leaching of secondary compounds (as *M. guianensis*) and a subsequent increase in fungal colonization (Barlocher & Schweizer 1983, Rezende *et al.* 2014, Graça *et al.* 2016).

Greater mass loss occurred in higher quality leaves. In terms of decreasing litter quality and decreasing relative biomass loss, species were as follows: *Maprounea guianensis*, followed by *Richeria grandis*, and *Inga laurina*, indicating a gradient of litter quality (Gomes *et al.* 2016). The quality of litter (*i.e.*, species effect) was an important factor driving microbial decomposition rates among the different fragment sizes in savannah streams. One potential explanation is that the high content of structural compounds (*e.g.*, lignin and cellulose) in some leaves hinders the release of other secondary chemical compounds (Gonçalves *et al.* 2012, Rezende *et al.* 2014). A study of the hyphomycete community (Gomes *et al.* 2016) found higher sporulation rates on *M. guianensis* (268 conidia/mg AFDM/day) compared to *I. laurina* (>25 conidia/mg AFDM/day) and *Richeria grandis* (>10 conidia/mg AFDM/day).

In addition to the importance of litter quality for processing rates by microorganisms (Rezende *et al.* 2014, Graça *et al.* 2016), we found significant effects due to litter fragment size. Higher relative mass loss was observed in small fragments than in large and medium fragments, especially for *M. guianensis*. Regardless of the litter quality, decomposition rates were lower for larger fragments. This was particularly evident for *I. laurina*. Other studies found a strong effect of substrate size and no significant effect of substrate quality on the decomposer bacterial community (Walpola *et al.* 2009, Wurzbacher *et al.* 2016). The results of this study highlight the role of biological fragmentation in accelerating decomposition in savannah streams (Tank *et al.* 2010, Rezende *et al.* 2014, 2015, Graça *et al.* 2015, Leite *et al.* 2016, Martins *et al.* 2016). However, physical fragmentation was not measured. Given this dynamic, changes in the composition of riparian vegetation resulting in changes to the chemical composition (for more see also Gomes *et al.* 2016, Sales *et al.* 2015, Top *et al.* 2017) or litter size can modify rates of microbial decomposition and ecosystem functioning in savannah streams.

Leaf consumption and use by Phylloicus.—*Phylloicus* did not exhibit a preference for leaf fragment size, but did exhibit a preference based on quality of leaf material (Navarro *et al.* 2013, Leite *et al.* 2016). The pattern in degradation rates for species was the same as that observed for microbial decomposition, with *M. guianensis* preferentially consumed over *R. grandis* and then *I. laurina*. This reinforces the importance of detritus quality for *Phylloicus,* including for case building (Moretti *et al.* 2009, Casotti *et al.* 2014, Gonçalves *et al.* 2016, Kiffer *et al.* 2016, Leite *et al.* 2016, Rezende *et al.* 2016). The observed preference for higher quality detritus for case building was contrary to our expectations that were based on the use of low-quality litter for case building to avoid the consumption of its case by other shredders (Moretti *et al.* 2009, Vidovix *et al.* 2013). According to Moretti *et al.* (2009), *Phylloicus* show a preference for high leaf phenolic concentrations in savannah streams, which may explain this result. These results also indicate that *Phylloicus* is a species that can act not only on large particles but also on leaf particles in advanced stages of decomposition.

Leaf fragment size explained most of the variance (in sums of squares from Table 1) in relative leaf mass loss allocated to case building. Most litter used for case building was from large- and medium-sized fragments. Case building by *Phylloicus* can be energetically expensive (Moretti *et al.* 2009), but compensatory due to protection against predators, mainly fish (Rezende *et al.* 2015). The costs of case building using larger organic matter fragments are reduced relative to small particles, which may explain *Phylloicus'* preference for larger leaf fragments. Despite the observed preference for large particles, our results also indicate high plasticity in the use of the leaf litter resources by *Phylloicus*, showing that the invertebrates do use litter fragments of other sizes and quality.

CONCLUSION

Changes in savannah riparian vegetation composition may lead to variation in litter chemical composition and size (Rezende *et al.* 2015, Sales *et al.* 2015, Gomes *et al.* 2016, Leite *et al.* 2016). We have demonstrated that these differences can affect leaf decomposition rates and, consequently, ecosystem functioning of savannah streams. In this study, the microbial community showed higher sensitivity to changes in litter size and quality compared to *Phylloicus* larvae. Our results aid our understanding of detritus decomposition in complex savannah streams, as there are few shredder species that play key roles in energy flow chains and processing of organic matter.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rj79251 (Rezende *et al.* 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Leaf litter consumption by microorganisms and used for food resource and case building by *Phylloicus* spp. among leaf species and sizes.

FIGURE S2. Percentage and standard error of microbial consumption of leaf litter among leaf sizes and species.

FIGURE S3. Percentage and standard error of leaf litter used for case building and food resource by *Phylloicus* spp. among leaf sizes and species.

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