Relationships of shredders, leaf processing and organic matter along a canopy cover gradient in tropical streams

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ABSTRACT
Terrestrial allochthonous organic matter represents a structuring element and an important source of energy and carbon to fauna in small forested streams. However, the role of this matter as a food resource for benthic macroinvertebrates, and consequently, for shredders and their performance in riverine processes, is not clear in low-order tropical streams. Aiming to investigate the relationship between shredders and leaves, we analyzed along a gradient of 8-93% canopy cover biomass and abundance of shredders, accumulated leaves and breakdown rates of local leaves to verify if these parameters were related to shade conditions and to each other. Three hypotheses were tested: i) shredder biomass, accumulated leaves and breakdown rates are related to canopy cover and exhibit higher values in shaded sites; ii) shredder biomass is positively related to accumulated leaves and breakdown rates; and iii) due to the relatively large body size of the important shredders, the association of shredders with leaves and importance to leaf processing should be better expressed in terms of guild biomass than abundance. Shredder biomass varied between 846 and 1506 mg dry mass (DM) m$^{-2}$ and accumulated leaves varied between 479 and 1120 g ash free dry mass (AFDM) m$^{-2}$ across sites. Leaf breakdown rate ($k$), the only measured variable that varied significantly among sites, varied between -0.0015 and -0.0238 day$^{-1}$. Neither shredder biomass nor leaf biomass were associated with the shading gradient. On the other hand, shredder abundance and biomass, mainly represented by Triplectides (Trichoptera, Leptoceridae), was positively related to accumulated leaves within sites and to breakdown rates assessed by leaf packs. Leaf breakdown, as assessed by the experimental leaf packs, was associated with shredder biomass, but not with shredder abundance. This result suggests that macroinvertebrates are important for leaf detritus processing and that their biomass reflects their activity, presumably because it is related to their secondary production and perhaps non-consumptive action. Their activity was observed at the scale of leaf packs and not at the scale of variation in canopy cover because apparently canopy did not modulate availability of leaves, which were apparently not limiting to the shredders.

Key words: Headwater; body size; biomass; benthic macroinvertebrate; leaf breakdown.

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streams, one of the principal tenets of the River Continuum Concept (RCC; Vannote et al., 1980) is that fauna in these parts of the streams rely mainly on terrestrial resources. However, despite the applicability to temperate forested headwaters (Fisher and Likens, 1973; Wallace et al., 1999), RCC is a controversial model in tropical running waters. Evidence from global studies indicates high variability in shredder occurrence and in breakdown rates across tropical sites (Boyero et al., 2012, 2015), which corroborates contrasting results obtained in tropical regions. A growing body of evidence emphasizes the importance of algal carbon in tropical food webs of forested small streams (Salas and Dudgeon, 2001; Mantel et al., 2004; Brito et al., 2006; Lau et al., 2009; Neres-Lima et al., 2016; Brett et al., 2017) and it has been claimed that the contribution of macroinvertebrate shredders to leaf breakdown is small in certain tropical running waters due their scarcity (Dudgeon and Wu, 1999; Dobson et al., 2002; Gonçalves et al., 2006b, 2007; Ardón and Pringle, 2008; Alvim et al., 2015). On the other hand, there is contrary evidence of high diversity and abundance of macroinvertebrate shredders, high secondary production and importance on leaf breakdown (Cheshire et al., 2005; Camacho et al., 2009; Yule et al., 2009; Encalada et al., 2010; Masese et al., 2014; Tonin et al., 2014; Andrade et al., 2017, Neres-Lima et al., 2017).

Independently of the source of carbon supporting fauna, we propose that, in part, shredders and their role have been overlooked in the tropics. Methodological factors could underestimate shredder importance in tropical running waters: benthic macroinvertebrates are frequently assigned to functional feeding groups according to classifications proposed for temperate organisms (Camacho et al., 2009). Thus, certain organisms, abundant in tropical running waters and not usually classified as shredders, like Leptophlebiidae, could be involved in leaf processing (Bello and Cabrera, 2001; Andrade et al., 2017). Also, the scarcity of data based on biomass could hinder the investigation of the role of shredders in tropical streams since common tropical shredders, like caddisflies, have large bodies and data based on abundance can underestimate their importance (Tonin et al., 2014).

Therefore, this study examined benthic macroinvertebrate biomass, leaf standing stock and breakdown rates of the most abundant riparian species along a canopy cover gradient. Our objectives were i) analyze patterns in shredder biomass, accumulated leaves and leaf breakdown rates along a canopy cover gradient; ii) investigate the association of macroinvertebrate shredders with leaf standing stock and leaf breakdown; and iii) verify if shredder association with leaves and contribution to leaf breakdown is more evident in terms of number of individuals or biomass. We hypothesized that shredder biomass, accumulated leaves and leaf breakdown rates follow a gradient in canopy cover, and that shredders are positively related to leaf quantity and to leaf breakdown. We also hypothesized that association between shredders and leaves will be clearer in terms of biomass than in terms of abundance.

**METHODS**

**Study site**

The study was conducted in Córrego da Andorinha and Rio Barra Pequena, small third-order streams located in a well-preserved dense Atlantic rainforest within the State Park of Ilha Grande Island in Rio de Janeiro State, Brazil (23°04’ to 23°14’S and 44°05’ to 44°23’W; Fig. 1). Average annual temperature is 23.2°C and average annual precipitation, 2071 mm, according to the nearest meteorological station situated in Angra dos Reis municipality (data from December/2015 - November/2016). Total catchment of Córrego da Andorinha is ~1260 ha and the highest point is 1030 m above sea level. Rio Barra Pequena has a catchment area of ~566 ha. Both streams have a steep bed slope for most their courses, discharging into small tidal estuaries without meanders or transition zones. Substrate is generally well embedded, with large boulders and some sandy stretches. The geology is principally Pre-Cambrian granite; the water chemistry is oligotrophic (total-N=180 μg L⁻¹, total-P=10 μg L⁻¹, pH=6.6) and did not change along the stream. Conductivity is 27 μSm⁻¹ in Córrego da Andorinha and 33 μSm⁻¹ in Rio Barra Pequena.

We selected six sites - one in Rio Barra Pequena, BP, four in Córrego da Andorinha - JAR (Jararaca), CHA (Characidium), LAM (Lambari) and CAP (Capivara) - and VAL (Valium), a first order tributary of Córrego da Andorinha (Fig. 1 and Tab. 1). Sites were selected following a canopy cover gradient that varied between 8% and 93%. VAL, BP and JAR showed higher canopy cover mean values (93, 83 and 73%) and LAM and CAP, the lower mean values (12% and 8%) and CHA was intermediate (55%). Canopy cover was measured using a spherical densitometer Model-C (Forest Densimeters, Bartlesville, OK, USA). Along 10 equally-spaced transect transects distributed in a 10-m reach, we averaged four readings facing north, south, east and west. Discharge was estimated on two occasions during the leaf breakdown experiment (except in JAR). In each site, we conducted a leaf breakdown experiment over 36 days during January and February/2016. At the same six sites, we sampled benthic macroinvertebrates and leaf standing stock in two campaigns during the leaf breakdown experiment.

**Shredder biomass and leaf standing stock**

We collected eight samples of benthic organic matter and associated macroinvertebrate where leaves had accumulated naturally (“litter-banks”) - most of them were in...
pools of slow-moving water - using a stovepipe corer (314 cm²). We inserted the corer into the substrate and manually collected all leaves, debris and coarse material from the corer and placing them in a bucket. We bailed approximately 20L of water from the corer to the bucket to collect suspended organic matter and macroinvertebrates.

The material inside the bucket was elutriated and poured through a sieve (250 μm mesh). The procedure of elutriation was repeated several times using fresh stream water until rinse water was clear. The material was stored in a plastic bag filled with fresh stream water to maintain organisms alive. We washed organic matter samples through

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**Fig. 1.** Map of the study site at Ilha Grande, Rio de Janeiro.

**Tab. 1.** Characteristics of the sites.

<table>
<thead>
<tr>
<th>Site code</th>
<th>Site name</th>
<th>Distance from mouth (m)</th>
<th>Altitude (m asl)</th>
<th>Discharge (Ls⁻¹) Mean SD</th>
<th>Canopy cove r(%) Mean</th>
<th>Leaf input* (AFDM g m⁻² month⁻¹) Mean SD</th>
<th>Presence of macro-fauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>VAL</td>
<td>Valium</td>
<td>-</td>
<td>53</td>
<td>9.97±3.19</td>
<td>93</td>
<td>129.46±10.45</td>
<td>M, P, T</td>
</tr>
<tr>
<td>JAR</td>
<td>Jararaca</td>
<td>2231</td>
<td>254</td>
<td>91.10</td>
<td>73</td>
<td>86.19±31.76</td>
<td>T</td>
</tr>
<tr>
<td>BP</td>
<td>Barra Pequena</td>
<td>236</td>
<td>34</td>
<td>135.50±3.53</td>
<td>83</td>
<td>-</td>
<td>M, P</td>
</tr>
<tr>
<td>CHA</td>
<td>Characidium</td>
<td>1240</td>
<td>83</td>
<td>432.80±42.56</td>
<td>55</td>
<td>22.38±4.64</td>
<td>M, P, F, T</td>
</tr>
<tr>
<td>LAM</td>
<td>Lambari</td>
<td>913</td>
<td>43</td>
<td>531.55±177.04</td>
<td>12</td>
<td>44.78±0.05</td>
<td>M, F</td>
</tr>
<tr>
<td>CAP</td>
<td>Capivara</td>
<td>497</td>
<td>36</td>
<td>565.61±190.04</td>
<td>8</td>
<td>14.15±1.30</td>
<td>M, F</td>
</tr>
</tbody>
</table>

*Data from January and February/2014 (Lisboa, 2017); F, fishes; M, Macrobrachium (shrimp); P, Potimirim (shrimp); T, Trichodactylus (crab).
sieves to separate macroinvertebrates and organic matter into coarse (>1000 µm) and fine (>250 µm) fractions. After removing macroinvertebrates (picked alive and fixed in ethanol 70%), leaves were separated for leaf standing stock estimate. The leaves were dried at 55°C for 48 h, weighed and then combusted in a muffle furnace at 500°C for 4 h to obtain ash free dry mass (AFDM).

To separate small macroinvertebrates, the fine organic matter fraction was subsampled to a maximum of 1/8 of the sample, depending on the amount of material. We sorted the preserved macroinvertebrates under a stereomicroscope at 40x magnification. All the organisms were identified to the lowest possible taxonomic level with a local key (Mugnai et al., 2009) and classified as shredders or non-shredders according to previous classifications and evidence of food consumption obtained in tropical streams (Cheshire et al., 2005; Rueda-Delgado et al., 2006; Tomanova et al., 2006; Chará-Serna, 2010; Ramirez and Gutiérrez-Fonseca, 2014). Leptophlebiidae was assigned as shredder due to its terrestrial carbon assimilation in Córrego da Andorinha (Neres-Lima et al., 2016) and role in leaf breakdown (Andrade et al., 2017). All organisms were measured (body length) to obtain biomass estimates in mg dry mass (DM) m⁻², using taxon-specific length-mass relationships (Benke et al., 1999). Abundance of each taxon was estimated to number of individuals m⁻² and biomass was calculated as a product of abundance and average individual body mass, for each taxon and sample. The estimated biomasses of different taxa were then used to estimate total macroinvertebrate and shredder biomasses.

**Leaf breakdown experiment**

At each site, we collected fallen leaves on rocks and boulders following two separate transects of ~5 m on both margins. Leaves were taken to the laboratory and separated to identify the three most abundant local species in each site (Supplementary Tab. 1). After air-dried and weighed, ~3 g of leaves were fastened together using paper clips to form bagless packs. Each pack comprised the three most abundant species of each site (Supplementary Tab. 1). Leaf species 1, most abundant, corresponded to 50% of packs (~1.5 g) and the same weight of leaf species 2 and 3 (~0.7 g) completed the mixed packs. Three groups, here referred to as blocks, of five packs attached to a cord were then incubated in litter-banks placed ~1 m apart in all sites.

After 2, 6, 11, 27 and 36 days of incubation, three packs, one of each block were randomly retrieved from all sites. The material was stored in plastic bags and taken to the laboratory for analysis of leaf mass loss and biomass of associated shredders. Leaves were gently washed under running water over a 250-µm mesh sieve to remove detritus and retain associated benthic fauna (preserved in ethanol 70%). Leaf material was oven-dried (72 h, 55°C) and ashed (4 h, 500°C) to estimate the remaining AFDM and breakdown rates (k) of leaf packs.

Shredder macroinvertebrates associated with leaf packs were identified and measured for biomass estimates as previously detailed for organisms sampled with stovepipe.

**Statistical analyses**

We calculated breakdown rate using the model $M_t = M_0 e^{-kt}$, where $M_t$ represents mass (g, AFDM) after time t (days), $M_0$ represents initial mass and k is the rate of leaf breakdown (per day; Olson, 1973). $M_0$ was calculated as AFDM using DM:AFDM relationship established for each different combination of leaves used in the experiment after combustion of retrieved packs. For each site and cord, k was calculated by linear regression of the natural log of proportion of remaining mass by time (Benfield, 2007). We included the constant of regression and did not include time zero data, which implies excluding the initial time interval (the initial phase of processing can be faster due physical process of leaching, whereas we aimed to measure leaf processing).

Overall variation in leaf standing stock and breakdown rates among sites were analyzed by one-way ANOVA. To analyse differences in shredder abundance and biomass among sites and the association between shredders and leaf standing stock, we performed an ANCOVA using shredder abundance or biomass as dependent variable, leaf AFDM as continuous variable and site as fixed factor. To analyse the relationship between breakdown rates and biomass of shredders associated with experimental leaf packs, we regressed breakdown rates against shredder biomass (means per block). All statistical analyses were conducted using Systat 12.

**RESULTS**

**Leaves and shredder biomass along a canopy cover gradient**

The standing stock of leaves varied between 479±422 and 1120±960 g AFDM m⁻² (mean ±SD, n=8), but quantity of material did not differ significantly among sites (ANOVA, $F_{3,37} = 1.49$, P=0.20), nor was it associated with canopy cover (Fig. 2).

Shredder biomass represented ~45% of total benthic macroinvertebrate biomass in accumulated litter and ranged from 846±891 to 1506±775 mg DM m⁻² in the different sites but showed no apparent relationship with stream size or canopy. Shredder taxa found were the caddisflies *Tripletodes* Kolenati, 1859 (Trichoptera, Leptoceridae), and *Phylloicus* Mueller, 1880 (Trichoptera, Calamoceratidae), the leaf miner *Stenochironomus.*
Kieffer 1919 (Diptera, Chironomidae), and leptophlebiids, mainly *Farrodes* Peter, 1971 (Ephemeroptera). In all sites, except CHA, *Triplectides* responded for more than half of shredder biomass (Fig. 3).

The abundance and biomass of shredders were positively related to leaf standing stock within sites (Tab. 2 and Fig. 4), but there were no significant differences between sites (Tab. 2).

**Leaf breakdown**

Breakdown rates of experimental leaf packs revealed different patterns across sites, but did not exhibit any tendency related to riparian cover (Figs. 5 and 6). In CHA, leaves lost ~30% of mass by day 11 of the experiment, when, in most other sites, leaf mass loss was less than 20% (Fig. 5). JAR and BP exhibited slow mass loss, ~25% until day 36, and in LAM, leaf mass loss was less than 20% at the end of experiment (Fig. 5). Breakdown rates showed variation ranging from -0.0015±0.0013 to -0.0238±0.0055 d⁻¹ (Fig. 6), with significant difference among sites (ANOVA, $F_{5,10}=14.09, P<0.001$). The fastest rate was observed in CHA ($k=-0.0238±0.0055$ d⁻¹), significantly different to breakdown rates observed in JAR, BP, LAM and CAP (Fig. 6).

VAL also showed high breakdown rate (-0.0164±0.0025 d⁻¹), significantly higher than observed in BP and LAM, where we observed the slowest rates (Fig. 6). A total of 534 shredders were found associated with leaves in retrieved packs. The biomass of these organisms exhibited significant relation with leaf breakdown ($F_{1,13}=13.4, P=0.002$; Fig. 7), but this correlation was more evident in VAL, CHA and CAP. Oppositely, shredder abundance was not significantly related to breakdown rates ($F_{1,16}=3.34, P=0.086$).

**DISCUSSION**

**Longitudinal patterns in shredders and leaves**

Contrary to some studies conducted in tropical ecosystems, we did not detect a pattern of decrease in shredder biomass along a longitudinal gradient (Greathouse and

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**Fig. 2.** Leaf standing stock in litter-banks (error bars=SD, n=8). Sites are ordered in increasing stream size.

**Fig. 3.** Biomass of main shredder taxa in studied sites (mean, n=8).

**Tab. 2.** Analysis of covariance of shredder abundance and biomass with leaf biomass and sites.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shredder abundance</td>
<td>Leaves</td>
<td>5048</td>
<td>1</td>
<td>5048</td>
<td>4.69</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td>Sites</td>
<td>2656</td>
<td>5</td>
<td>531</td>
<td>0.49</td>
<td>0.779</td>
</tr>
<tr>
<td></td>
<td>Leaves*sites</td>
<td>4865</td>
<td>5</td>
<td>973</td>
<td>0.90</td>
<td>0.489</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>38,735</td>
<td>36</td>
<td>1075</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shredder biomass</td>
<td>Leaves</td>
<td>7692</td>
<td>1</td>
<td>7692</td>
<td>4.39</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td>Sites</td>
<td>5206</td>
<td>5</td>
<td>1041</td>
<td>0.59</td>
<td>0.705</td>
</tr>
<tr>
<td></td>
<td>Leaves*sites</td>
<td>13,690</td>
<td>5</td>
<td>2738</td>
<td>1.56</td>
<td>0.196</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>63,110</td>
<td>36</td>
<td>1753</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*df*, degrees of freedom.
Pringle, 2006; Jiang et al., 2011). We also did not observe a positive relationship between canopy cover, accumulated leaves and breakdown, as had been expected. The stock of litter in streams can often reflect the organic matter input from adjacent vegetation (Bilby and Likens, 1980; Swanson et al., 1982), and exhibit similar patterns (Bambi et al., 2017). However, the presence and persistence of terrestrial material in the streambed is also related to several factors including composition, organization and densities of trees, seasonality and channel morphology (Fleituch, 2001; Gonçalves et al., 2006a; França et al., 2009; Tank et al., 2010; Flores et al., 2013; Lisboa et al., 2015; Bambi et al., 2017). Therefore, even with variation among sites in the degree of canopy cover and leaf input (Tab. 1), the lack of substantial differences in leaf standing stock indicates that canopy cover did not determine patterns in organic matter distribution in stream channel. In Córrego da Andorinha and Barra Pequena, channel morphology is possibly a more important factor governing the accumulation of litter.

In an Atlantic Forest environmental quality assessment, Baptista et al. (2007) concluded that shredder abundance was related to reference sites. In general, reference sites exhibit features that match with shredders demands, like litter accumulation and lower temperatures due riparian vegetation presence. Accumulated allochthonous organic matter can provide food for shredders and the positive correlation between these elements is well-established in temperate ecosystems (Richardson, 1992; Wallace et al., 1999; Rowe and Richardson, 2001; González and Graça, 2005; Flores et al., 2013). In this manner, as our studied sites are in the same well-preserved rainforest and accumulated leaves were not restricted to dense riparian covered sites, shredder biomass and abundance seem not restricted as well.

We can also observe that litter was abundant at all sites relative to the biomass of shredders, and was probably not limiting for their growth and population density. Thus, shredders and other macroinvertebrates may be limited by predators, as has been observed in enclosure experiments in these streams (Moulton et al., 2004; Andrade et al., 2017). If this were the case, we could expect that shredders would seek out the most nutritious and easily assimilated leaves, and thus their action would be observed at the level of leaf packs (see below).

**Shredders, accumulated leaves and breakdown rates**

We observed that shredder biomass and abundance were related to quantity of leaves of samples within sites (Tab. 2, Fig. 4). We expected this relationship based on the simple assumption that leaves provide substrate and that number of organisms would increase as substrate availability increased. Only if substrate were limited and the pool of potential shredders constant might we expect that shredder abundance would not increase with substrate availability.

On the other hand, shredder biomass per leaf pack was positively associated with leaf processing (Fig. 7). This association was evident in VAL, CHA and CAP, where leaf breakdown rates were higher. Interestingly, shredder abundance per leaf pack did not show a significant relationship with leaf breakdown rate, which implies the importance of measuring biomass as an indicator of shredder activity. Biomass, as a variable directly associated with secondary production, can potentially better illustrate the role of organisms in processes because secondary production integrates, among other factors, resource consumption and growth rate (Benke, 2010; Benke and Huryn, 2010).

Although the macrofauna of crustaceans and fish could potentially affect leaf breakdown, the pattern of leaf breakdown we observed did not correspond to presence or absence of the different macrofauna (cf. Tab. 1 and Fig. 6).
Fig. 5. Proportion of remaining leaf mass for three cords (blocks) over time (days) for leaf packs in all studied sites. Curve fits were to the exponential model.
Previous research in these streams showed a strong indirect relationship of sites with fish and the density of periphyton (Moulton et al., 2010). Apparently, the presence of fish had an inhibiting effect on grazing shrimp (Potimirim), such that sites with fish had greater density of periphyton. In the current case, however, the sites with fish (LAM and CAP) showed no reduction of leaf processing that could be attributed to an inhibition of shredders. Other possible direct or indirect interactions might have involved Macrobrachium shrimps which were shown to reduce leaf processing presumably by inhibiting shredding insects (Andrade et al., 2017). Again, the site without Macrobrachium, JAR, did not show increased leaf processing.

The leaf packs of the leaf breakdown experiment were made from the three most abundant species of each site. Thus, part of the variation among sites could have come from differences in rates of breakdown of the different species. At site CHA, which showed the fastest breakdown of leaf packs, the most abundant tree species was Ficus insipida Willd. (Moraceae), which exhibited fast breakdown rates in other studies (Rosemond et al., 1998; Ardón et al., 2009; Rincón and Santolloco, 2009). Leaves of F. insipida are characterized by low lignin and polyphenol content (Ardón et al., 2006; Rincón and Santolloco, 2009), and are thus a potential high-quality detritus for consumers. In VAL and CHA, where we observed faster leaf breakdown rates, Leptophlebiidae contributed an important fraction of shredder biomass. This observation supports previous local findings that leptophlebiid ephemeropterans are associated with leaf mass loss (Andrade et al., 2017). In JAR and CAP, where breakdown rates can be classified as intermediate and fast, according classifications of Petersen and Cummins (1974) (rapid, \( k >0.01 \, \text{d}^{-1} \); intermediate, \( 0.005 \, \text{d}^{-1} < k <0.01 \, \text{d}^{-1} \); and slow, \( k <0.005 \, \text{d}^{-1} \)), we observed association between shredders and accumulated leaves (Fig. 4). In these sites, it was previously observed that Tripletides and Phylloicus diet is not restricted to allochthonous resources, and further, autochthonous resources can correspond to a third (JAR) to a half (CAP) of the food assimilated by these caddisflies in Córrego da Andorinha (Neres-Lima et al., 2016). In JAR, despite high canopy cover, local fauna is highly supported by autochthonous carbon (Neres-Lima et al., 2016). These observations match with the prediction that even highly covered tropical streams have enough light incidence to sustain a reasonable level of primary produc-

Fig. 6. Breakdown rates \((k)\) of leaf packs in studied sites. Different letters indicate significant differences among sites (Tukey's test, \( P<0.01 \)). Error bars are one SE of the mean \((n=3)\).

Fig. 7. Relationships between shredder abundance and biomass in leaf packs and litter breakdown rates \((n=3)\).
CONCLUSIONS

We conclude that despite the absence of a linkage between canopy cover and shredder abundance and biomass, shredders were associated with leaf quantity within sites and with processing of leaf packs, and thus they appear important for leaf processing. However, this linkage between shredders and accumulated leaves and breakdown was not evident in all sites, which indicates that other factors (e.g., litter and algal resource quality and availability) can be more relevant and determinant in this interaction. Also, shredder biomass rather than abundance was related to leaf breakdown, suggesting that analyses based on biomass may reveal their importance in this ecosystem process. Leptophlebiid ephemeropterans are not generally classified as shredders, but evidence from other studies and their distribution here indicate them as shredders, emphasizing the importance of accurate classifications into functional feeding groups based on regional studies.

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