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ORIGINAL ARTICLE

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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INTRODUCTION

About 90% of terrestrial primary production falls directly into the dead organic matter pool (Cebrian, 1999; Abelho, 2001), becoming available to the so-called "brown food webs" (Kaspari, 2004). Especially in low-order streams covered by dense riparian vegetation, allochthonous organic matter represents the main resource for aquatic fauna (Wallace *et al.*, 1997). Leaves compose the major fraction of allochthonous organic matter entering in streams (França *et al.*, 2009; Gonçalves *et al.*, 2014; Bambi *et al.*, 2017) and once in the lotic environment, fauna colonize and start the process of leaf breakdown (Gessner *et al.*, 1999; Graça, 2001; Tank *et al.*, 2010).

Benthic macroinvertebrates have been found to be positively related to the availability of allochthonous organic matter in lotic ecosystems (Egglishaw, 1964; González and Graça, 2005; Mbaka *et al.*, 2015). Leaves and other categories of allochthonous organic matter can provide food and additional resources such as substrate and refuge from predators and water currents (Inoue and Nakano, 1998; Braccia and Batzer, 2001). Also, terrestrial material can accumulate fine particulate organic matter and nutritious biofilms formed by microorganisms which represent food resources for benthic macroinvertebrates (Hax and Golladay, 1993; Crook and Robertson, 1999; Dudgeon and Wu, 1999; Eggert and Wallace, 2007).

Leaves are broken down by physical abrasion, leaching of soluble compounds and through micro and macrofauna consumption (Gessner *et al.*, 1999; Jugnia *et al.*, 2000; Graça, 2001). Macroinvertebrate shredders, organisms that feed directly on leaf tissues while converting coarse matter into small particles, are important in litter breakdown in many systems (Webster and Benfield, 1986; Wallace and Webster, 1996; Graça *et al.*, 2015).

Due to the quantitative dominance of allochthonous matter over autochthonous production in small low-order

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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; Li and Dudgeon, 2008; 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 μScm^{-1} in Córrego da Andorinha and 33 μScm^{-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 Densiometers, 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

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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

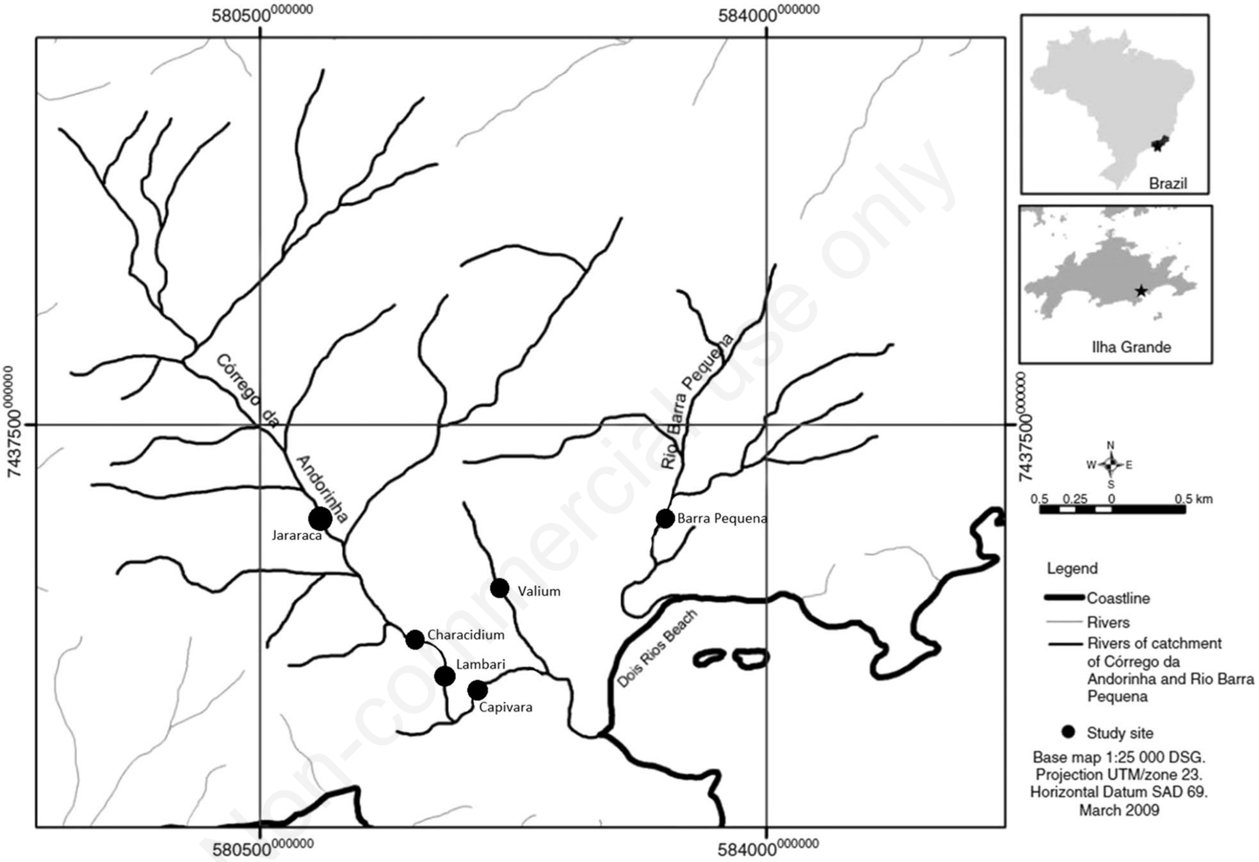

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Fig. 1. Map of the study site at Ilha Grande, Rio de Janeiro.

Tab. 1. Characteristics of the sites.

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

**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; Ramírez 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_{5,42=}$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 *Triplectides* Kolenati, 1859 (Trichoptera, Leptoceridae), and *Phylloicus* Mueller, 1880 (Trichoptera, Calamoceratidae), the leaf miner *Stenochironomus*

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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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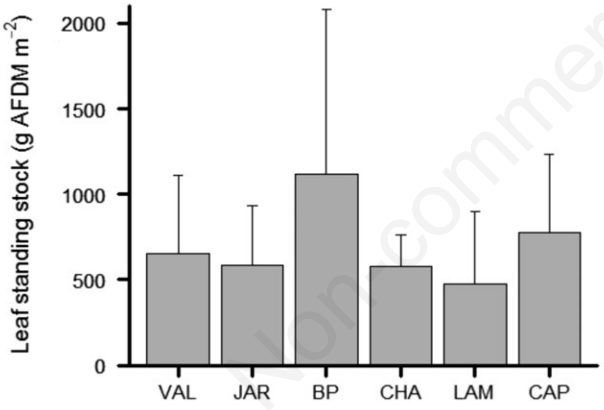

Fig. 2. Leaf standing stock in litter-banks (error bars=SD, n=8). Sites are ordered in increasing stream size.

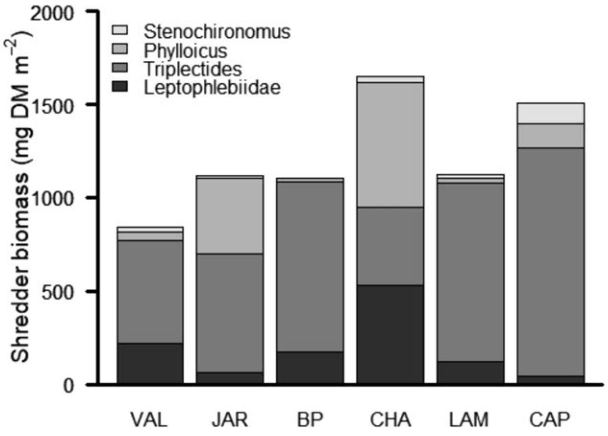

Fig. 3. Biomass of main shredder taxa in studied sites (mean, n=8).

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

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

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 exclosure 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).

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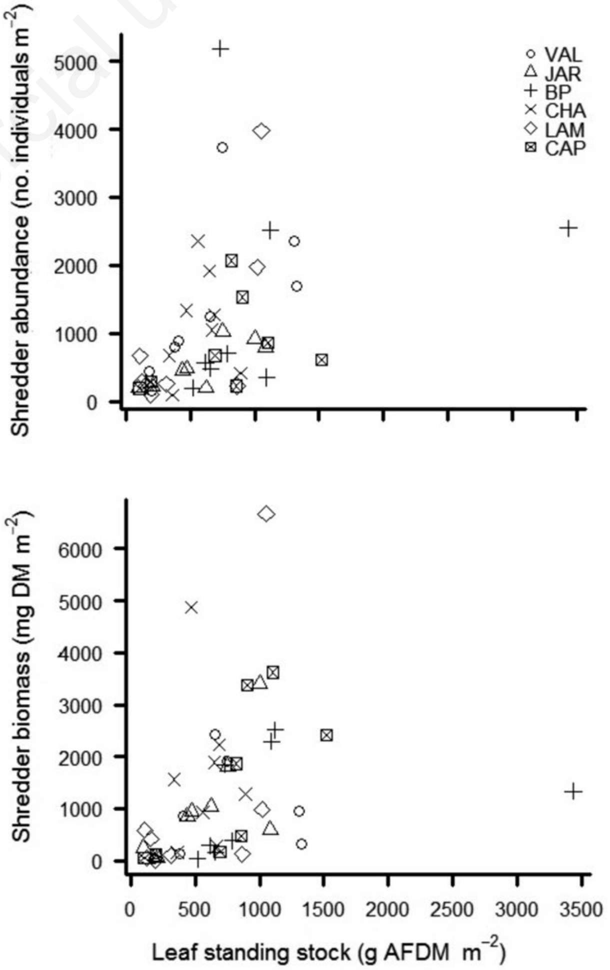

Fig. 4. Relationships among shredder abundance, biomass and leaf standing stock in studied sites.

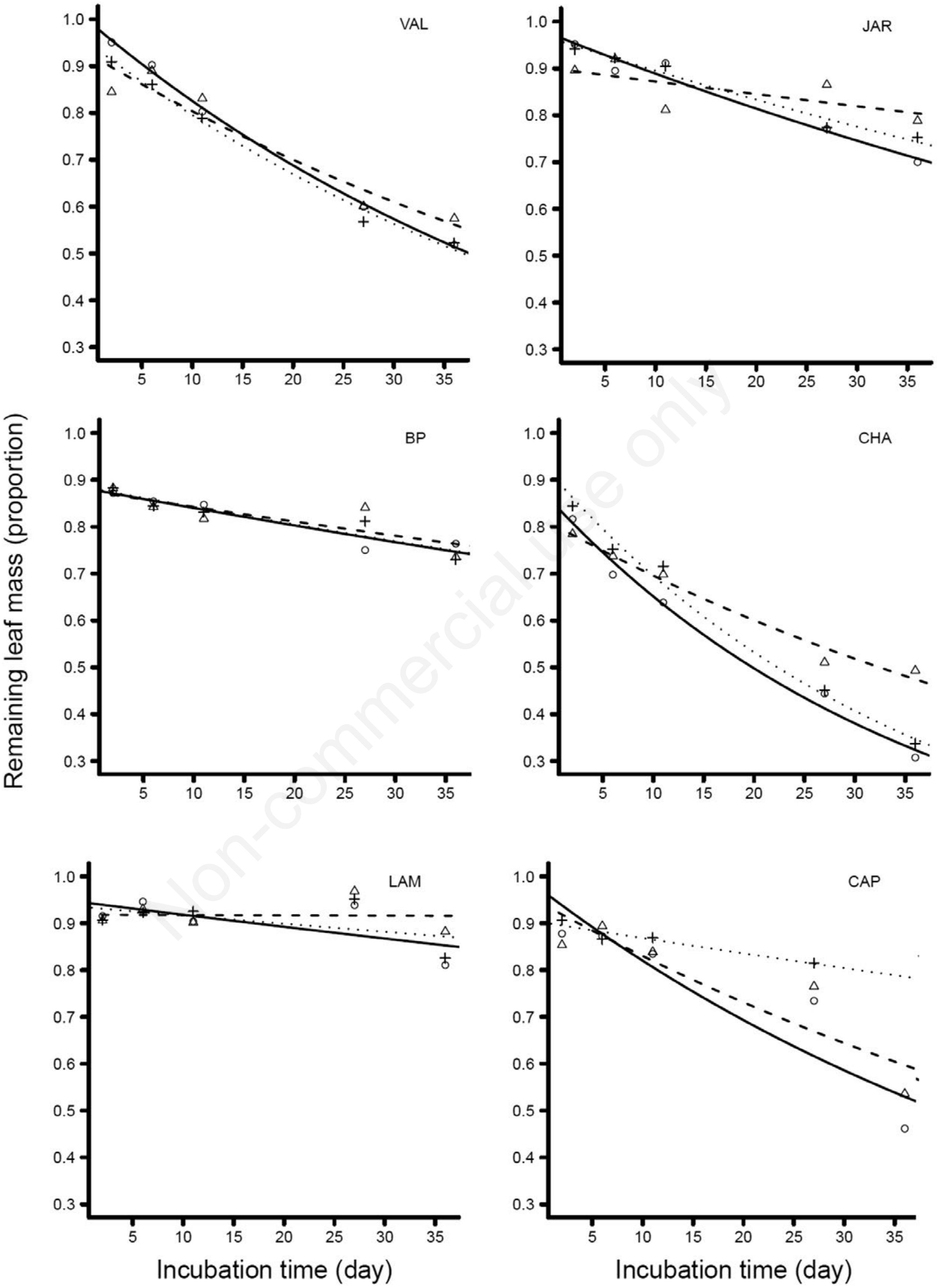

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Fig. 5. Proportion of remaining leaf mass for three cords (blocks) over time (days) for leaf packs in all studied sites. Curve fits were to the exponential model.

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 Santelloco, 2009). Leaves of *F. insipida* are characterized by low lignin and polyphenol content (Ardón *et al*., 2006; Rincón and Santelloco, 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, $k > 0.01\ d^{-1}$; intermediate, $0.005\ d^{-1} < k < 0.01\ d^{-1}$; and slow, $k < 0.005\ d^{-1}$), we observed association between shredders and accumulated leaves (Fig. 4). In these sites, it was previously observed that *Triplectides* 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-

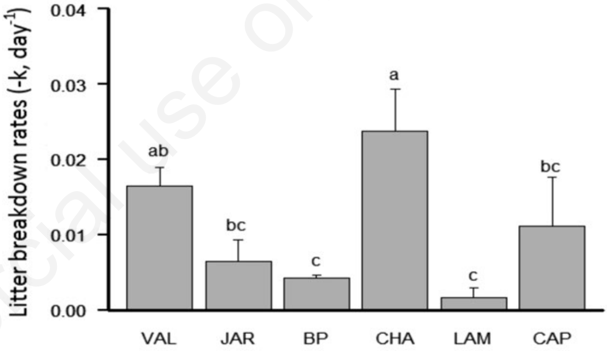

Fig. 6. Breakdown rates (*k*) of leaf packs in studied sites. Different letters indicate significant differences among sites (Tukey's test, P<0.01). Error bars are one SE of the mean (n=3).

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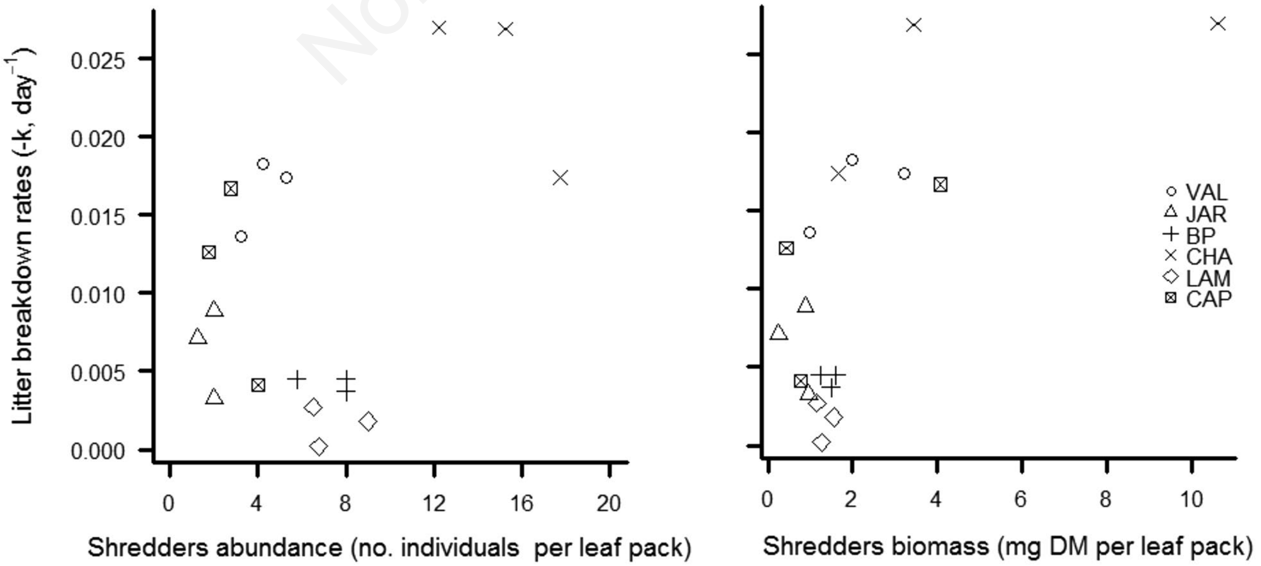

Fig. 7. Relationships between shredder abundance and biomass in leaf packs and litter breakdown rates (n=3).

tion (Bunn *et al.*, 1999a, 1999b; Lau *et al.*, 2009). In this manner, we speculate that shredders may be consuming some autochthonous carbon along with their predominant diet of leaves and that they might benefit from algae attached to leaves (Guo *et al.*, 2016).

In BP and LAM, where leaf mass loss was almost absent, shredder biomass per leaf pack seems weakly related to breakdown rates (Fig. 7). This observation could indicate that shredders rejected the most abundant local leaves, consuming preferentially other leaves due to their food selection behavior (Casotti *et al.*, 2015). The lack of relationship between shredder biomass and leaf breakdown suggests that shredders were exploiting other food categories. Laboratory experiments indicated that four of five studied species, usually classified as shredders, exhibited generalist behavior, whereas only one species grew up consuming exclusively coarse organic matter (Mihuc and Mihuc, 1995). Additionally, stable isotopes and gut content analyses revealed that organisms classified as shredders can behave as generalists, consuming coarse and fine organic matter and periphyton (Tomanova *et al*., 2006; Leberfinger and Bohman 2010; Leberfinger *et al*., 2011; Callisto and Graça, 2013; Ferreira *et al.*, 2015), including in a study conducted in Córrego da Andorinha (Neres-Lima *et al*., 2016). In this manner, the interaction of shredders and leaves as food resource could be mainly related to litter and algal resources quality than to leaf quantity or canopy cover shading.

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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