

Influence of *Trichodactylus fluviatilis* on Leaf Breakdown in Streams: Understanding the Role of Freshwater Crabs in Detritus-based Food Webs

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Larissa Costa, Wallace Kiffer Jr., Cinthia Casotti, Juliana Rangel, and Marcelo Moretti (2016) Freshwater crabs can affect leaf breakdown by consuming leaves or invertebrate shredders. The aims of this study were to analyze the gut content of *Trichodactylus fluviatilis* and evaluate the influence of this macroconsumer on leaf breakdown. For this, we (i) performed gut analyses of 55 individuals of *T. fluviatilis* and (ii) determined leaf decay rates and FPOM production in laboratory trials containing crabs and the caddisfly shredder *Triplectides* sp., alone and together, and leaves differing in quality. We hypothesized that *T. fluviatilis* feeds both on leaves and *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together. The main food categories in *T. fluviatilis* guts were algae and FPOM, while CPOM and animal tissue were rare. Leaf decay rates and FPOM production did not differ across shredder treatments or leaf species. However, the survival of *Triplectides* sp. was higher when alone. The results support the potential for participation of *T. fluviatilis* in leaf breakdown and demonstrated that, in spite of the high abundances of algae and FPOM in the gut content, adults of this species have the potential to feed both on leaf litter and larvae of *Triplectides* sp. However, the hypothesis of this study was only partially corroborated because decay rates did not change across treatments.

Key words: Macroconsumers, Invertebrate shredders, Gut content analysis, Detritus chain, Atlantic Forest streams.

BACKGROUND

Forest headwater streams are heterotrophic ecosystems that depend on the inputs of allochthonous organic matter (Minshall 1967). In such streams, invertebrate shredders play an important role in the detritus-based food webs, converting leaf litter into fine particles of organic matter that will become available to other consumers (Graça 2001). Several studies have demonstrated that the feeding activity of shredders is affected by litter quality; *i.e.*, leaves with high nutrient content and low amounts of chemical and structural compounds are preferred (Rincón and

Martínez 2006; Bastian et al. 2007; Casotti et al. 2014).

Immature stages of some Trichoptera, Plecoptera and Diptera are usually the main shredders in streams (Webster et al. 1999; Thompson and Townsend 2000). However, in tropical streams the abundance of this functional feeding group varies in different regions (see Boyero et al. 2009; Boyero et al. 2015; Graça et al. 2015) and macroconsumers, such as crabs and shrimps, can also shred leaf litter (Moulton et al. 2010; Williner and Collins 2013). Thus, the role of macroconsumers might have been overlooked in some studies evaluating leaf breakdown in tropical

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streams (Boyero et al. 2009) because of their high mobility, nocturnal activity and large size, which restrict their access to coarse meshes in leaf litter experiments. They are also difficult to observe and sample (Baumart et al. 2015). Additionally, by consuming different food categories, the trophic level of these organisms might have been wrongly assigned (Cheshire et al. 2005).

Considering their generalist feeding behavior, macroconsumers can influence leaf breakdown both positively, shredding leaf litter (Mancinelli et al. 2013), and negatively, preying on insect shredders (Williner and Collins 2013). In some ecosystems, the shredding capacity of macroconsumers may be equivalent to that of insect shredders (March et al. 2001). Because of their high biomass and activity, it is expected that macroconsumers may play an important role in leaf breakdown (Moss 2004). In addition, the predation pressure exerted by these organisms can affect the structure of aquatic invertebrates by modifying the abundance of some taxa (Silveira and Moulton 2000; Landeiro et al. 2008). If the abundance of insect shredders is reduced by macroconsumer predation, leaf decay rates could be reduced (Obernborfer et al. 1984).

The feeding ecology of macroconsumers in streams has been evaluated elsewhere (e.g., Tomanova et al. 2006; Moulton et al. 2010; Masese et al. 2014) and different patterns have been observed. Kensely and Walker (1982) suggested that the shredding activity of shrimps of the genus *Macrobrachium* Bate, 1868 was accidental, resulting from their foraging strategy for obtaining fungal hyphae and larvae of mining chironomids. Landeiro et al. (2008) observed that the presence of these shrimps influenced the abundance of aquatic invertebrates more than leaf decay rates. On the other hand, Cowl et al. (2001) and Williner et al. (2014) observed a positive effect of shrimps and crabs on leaf breakdown; i.e., leaf mass loss was higher in the presence of these organisms.

Freshwater crabs are considered omnivores (Obernborfer et al. 1984; Tomanova et al. 2006) and are abundant in Atlantic Forest streams (Moulton et al. 2010). In those ecosystems, the caddisfly shredder *Triplectides* Kolenati, 1859 (Trichoptera, Leptoceridae) is also abundant (Casotti et al. 2014; Kiffer et al. 2016). Given these organisms are frequently found associated with leaf patches, the aims of this study were to analyze the gut content of the crab *Trichodactylus fluviatilis* Latreille, 1828 (Brachyura, Trichodactylidae) and evaluate the influence of this macroconsumer on leaf breakdown. For this, we (i) performed gut

analyses of individuals of *T. fluviatilis* sampled over one year and (ii) determined leaf decay rates and the production of fine particulate organic matter (FPOM) in laboratory trials containing individuals of *T. fluviatilis* and *Triplectides* sp., alone and together, and leaves differing in quality (*Miconia chartacea* Triana [Melastomataceae] and *Hoffmannia dusenii* Standley [Rubiaceae]). The survivorship of individuals of *Triplectides* sp. was also determined in trials where they were present. We hypothesized that *T. fluviatilis* feeds both on leaves and larvae of *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together, given the presence of crabs would decrease the activity and abundance of insect shredders.

MATERIALS AND METHODS

Study area

Leaves and specimens of *T. fluviatilis* and *Triplectides* sp. were collected from Macuco Stream (20°01'23.8"S, 40°33'00.55"W; 593 m a.s.l.), in an Atlantic Forest fragment located in the State of Espírito Santo, SE Brazil. In this reach, the riparian vegetation was well-developed, shading approximately 80% of the streambed. The substrate was heterogeneous, composed of pebbles, gravel and leaf patches in pool areas. See Casotti et al. (2014) for additional physical and chemical information.

Gut content analysis

From July 2012 to June 2013, five adult specimens of *T. fluviatilis* were sampled monthly, except in May and June when only 2 and 3 individuals were found with the same sampling effort (three person-hours). The individuals were sexed (sex ratio; 1.2: 1), measured (carapace length; males: 1.91 ± 0.10 cm, females: 2.26 ± 0.12 cm) and fixed in formalin. In the laboratory, gut content analysis was performed according to Acosta and Prat (2011). The gut of each individual was removed and the full content spread over a gridded Sedgewick-Rafter counting cell (1 mm²) containing a drop of glycerin and analyzed on a biological microscope (Opticam O400 Standard, 400x). The evaluation of the gut content was conducted by counting the occupied grids and determining the relative abundances of four pre-determined food categories: coarse particulate

organic matter (CPOM, > 1 mm, including vascular plant tissue), fine particulate organic matter (FPOM, < 1 mm), algae (including unicellular and filamentous green algae and diatoms) and animal tissue (parts of prey exoskeleton). No mineral material was found in any gut ($n = 55$).

Laboratory trials

The influence of *T. fluviatilis* on leaf breakdown was evaluated in the laboratory using leaves of *M. chartacea* and *H. dusenii*, which are among the most abundant of the vertical inputs of leaf litter measured over a year in the Macuco Stream and are palatable to insect shredders (W. Kiffer, *pers. obs.*). These leaves were chosen because they differed in the content of nutrients and toughness; the lignin: N ratio was higher in *M. chartacea* than in *H. dusenii* (see Table 1). Leaves were collected with litter traps (1 m², 10 mm mesh) that were positioned 1.5 m above the ground along both stream banks. The nets were checked regularly, and senescent leaves were taken to the laboratory where they were air-dried and stored. Before the beginning of the experiment, leaves of both species were individually enclosed in litter bags (0.5 mm mesh) and conditioned for 15 days in the studied stream.

A total of 20 adult specimens of *T. fluviatilis* and 180 larvae of *Triplectides* sp. (2nd – 3rd instars) were collected manually in the Macuco Stream. Crabs and larvae were stored separately in coolers containing stream water, and taken to the laboratory, where they were starved at 21°C for 24 h under constant aeration and a 12: 12 h photoperiod.

Leaf decay rates and FPOM production were evaluated in three treatments containing leaves of both species and (i) one *T. fluviatilis*, (ii) nine *Triplectides* sp., and (iii) one *T. fluviatilis* and nine *Triplectides* sp. The number of individuals in treatments was based on the abundance ratio

of *T. fluviatilis*: *Triplectides* sp. in the studied stream (1: 9), which was determined from monthly samplings of leaf patches over a year (4 samples per month). The initial dry mass of crabs (3.15 ± 0.25 g) and larvae (2.05 ± 0.12 mg) used in the experiment was determined from size-mass equations described for the studied populations using, respectively, the carapace length (L. Costa, unpublished data) and head capsule width (Kiffer et al. 2016) as predictors. These values did not differ between treatments (crabs: $t_{19} = -1.93$, $p = 0.069$; larvae: $t_{179} = 1.34$, $p = 0.183$).

Conditioned leaves of both species were cut into square pieces with approximately 5 cm wide. An initial wet mass of 1.00 ± 0.05 g, corresponding to 3–4 leaf pieces, of each species was placed randomly on the bottom of plastic boxes (30 × 35 × 13 cm; $n = 10$ per treatment) with 500 ml of filtered stream water. These leaves were offered together to evaluate if *T. fluviatilis* and *Triplectides* sp. would process leaves differing in quality differently. Ten additional replicates, containing leaves only, were used as controls to determine the mass loss of each leaf species in the absence of consumers. Conditioned leaves of both species were also used for the determination of correction factors dry mass/wet mass and calculate the initial dry mass of leaves. The feeding trials lasted for 10 days, under constant temperature (21°C), photoperiod (12: 12 h) and aeration. The replicates were monitored daily and the number of living larvae was recorded. At the end of the experiment, the remaining leaves of each species were removed with a pincer, dried (60°C, 72 h) and weighed (± 0.01 mg) separately. The water of each box was filtered over pre-weighed glass fiber filters (GF-3, 0.6 μ m, 47 mm, Macherey-Nagel, Germany) and the filters were dried (60°C, 72 h) and ashed (500°C, 4 h) for ash free dry mass (AFDM) determination of accumulated FPOM. In these trials, FPOM consisted of all organic particles that were produced by the shredding activity

Table 1. Nutrients, lignin and cellulose, and leaf toughness values of *M. chartacea* and *H. dusenii* leaves conditioned for 15 days. Leaf toughness was measured as the weight required to tear apart a leaf sample. Comparisons by *t*-tests (mean \pm SE, $n = 4$)

	Nitrogen (%)	Phosphorus (%)	Lignin (%)	Cellulose (%)	Toughness (g)
<i>M. chartacea</i>	1.59 \pm 0.04	0.050 \pm 0.001	24.81 \pm 4.83	21.29 \pm 6.10	142.68 \pm 21.49
<i>H. dusenii</i>	3.04 \pm 0.03	0.024 \pm 0.003	11.89 \pm 0.24	24.55 \pm 0.90	60.41 \pm 28.49
<i>t</i>	56.73	-18.12	-5.35	1.06	-4.61
<i>p</i>	< 0.001	< 0.001	0.012	0.365	0.004

of consumers, regardless of whether they had passed through the shredders guts (feces) or not. Leaf final dry mass in each replicate was corrected using the mean dry mass of each species in the control replicates. To evaluate the potential of *T. fluviatilis* to feed both on leaves and larvae of *Triplectides* sp., the guts of all specimens used in the laboratory trials were analyzed as described previously.

Leaf analysis

Some conditioned leaves of both species were dried (60°C, 72 h), ground and homogenized for analyses of total N and P, lignin and cellulose (Graça et al. 2005). Leaf toughness was estimated using a tearing device built in the laboratory with simple materials that measures the force needed to tear apart a leaf sample (see Graça and Zimmer 2005). The characteristics of the studied leaves are presented in Table 1.

Data analysis

Because the relative abundances of food categories found in the guts of *T. fluviatilis* did not differ across sampling months and sexes (Kruskal-Wallis, $p > 0.05$), data were grouped and abundances of the food categories were compared by Friedman test, a non-parametric test for equality of medians in several repeated-measures univariate groups (Hammer et al. 2001). Paired Wilcoxon tests were used for *post hoc* comparisons. Leaf decay rates (k , day⁻¹) were estimated from the exponential model $M_f/M_i = e^{-kt}$, where M_f and M_i are the final and initial dry mass and $t = 10$ days (Olson 1963). General linear models (GLMs) were used to compare the decay rates and amounts of FPOM produced across shredder treatments and leaf species. Data of FPOM production was transformed ($\ln [x + 1]$) to meet the assumptions of normality and homoscedasticity. When a model was significant, Tukey tests were used for *post hoc* comparisons. *Triplectides* sp. survival proportions in the presence and absence of crabs were compared by *t*-test. All statistical analyses were performed in PAST (version 3.8, University of Oslo) and SPSS (version 23.0 for Macintosh, SPSS, Chicago, Illinois), according to Zar (2010).

RESULTS

The main food categories in *T. fluviatilis* guts were algae and FPOM; CPOM and animal tissue were rare and together accounted for less than 2% of the content of analyzed guts (Friedman test: $\chi^2 = 145.52$, $p < 0.001$; Wilcoxon tests; Fig. 1).

In the laboratory trials, leaf decay rates ($-k$) ranged from 0.057 ± 0.008 to 0.090 ± 0.019 day⁻¹ (Fig. 2). The decay rates of leaves of *M. chartacea* were similar across shredder treatments, while the decay rates of *H. dusenii* had more variation and were lower in the treatment containing *T. fluviatilis* only. However, the observed leaf decay rates did not differ significantly across treatments or leaf species (Table 2). The amounts of FPOM produced ranged from 20.50 ± 8.42 to 28.84 ± 12.50 mg, with no differences among treatments ($F_{2,29} = 0.09$, $p = 0.905$; Fig. 3). After 10 days, the survivorship

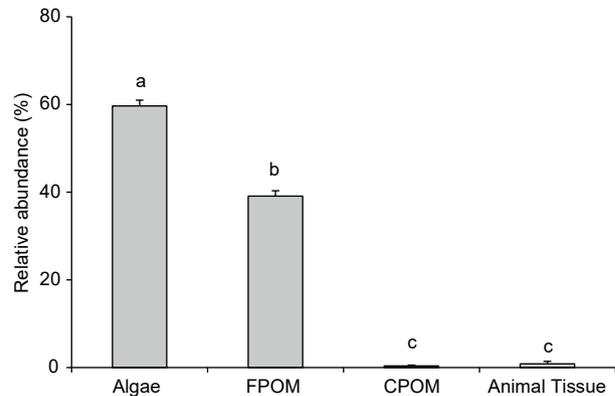


Fig. 1. Relative abundance (mean ± SE) of food categories in the gut contents of *T. fluviatilis*. Abundances with the same letter do not differ significantly (*post hoc* tests by simple pairwise Wilcoxon; $n = 55$).

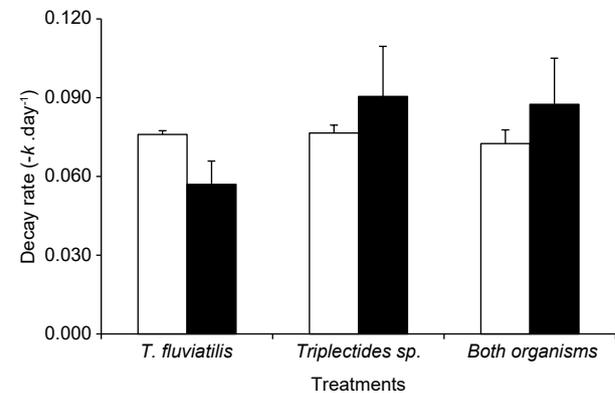


Fig. 2. Leaf decay rates (mean ± SE) of *M. chartacea* (empty bars) and *H. dusenii* (solid bars) leaves in treatments containing *T. fluviatilis* and *Triplectides* sp., alone and together.

of *Triplectides* sp. was higher when alone (84 ± 4 %) than when *T. fluviatilis* was present (46 ± 8 %; $t_{19} = 3.54$, $p < 0.001$). FPOM was the main food category in the guts of specimens of *T. fluviatilis* used in the laboratory trials; CPOM was rare and accounted for less than 0.2% (Table 3). Animal tissue was only found in trials containing both organisms, but the relative abundance of this food category did not differ from CPOM.

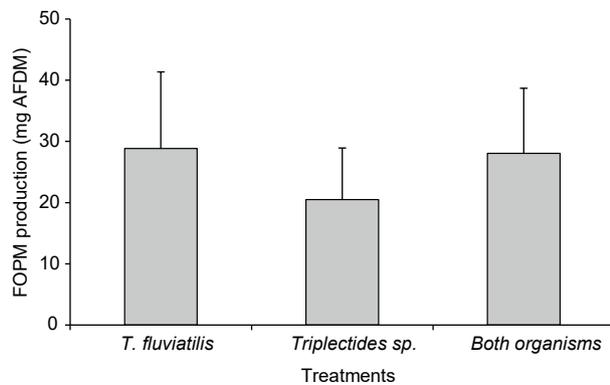


Fig. 3. Total amounts (mean \pm SE) of FPOM produced in treatments containing *T. fluviatilis* and *Triplectides* sp., alone and together. AFDM = ash free dry mass.

DISCUSSION

Algae were the most abundant food category in the guts of *T. fluviatilis*. Algae have a high nutritional value (Lieske and Zwick 2007; Deegan and Ganf 2008; Leberfinger and Bohman 2010), especially when compared to leaf litter (Cushing and Allan 2001; Yoshimura et al. 2008). A large part of algal biomass consists of carbohydrates, proteins, lipids and other compounds essential to consumers (Sterner and Hesse 1994). Cummings and Klug (1979) suggested that some taxa of aquatic invertebrates might depend on the primary production of algae and macrophytes, even in streams where light availability is limited by the riparian vegetation.

Trichodactylid crabs have a wide trophic spectrum and may consume algae, plant tissue, leaf litter, aquatic invertebrates and even small vertebrates (Collins et al. 2007; Williner et al. 2014). The low abundances of CPOM found in the gut content of *T. fluviatilis*, even in the specimens used in the laboratory trials that fed on leaves, suggest that the particles of organic matter reach the guts at small sizes; *i.e.*, in the form of FPOM. The stomach of decapods has a muscular and nervous complex in which a set of striated muscles moves the skeletal elements of

Table 2. Variation in leaf decay rates depending on shredders (*T. fluviatilis*, *Triplectides* sp. and both together) and leaf species (*M. chartacea* and *H. dusenii*) tested by general linear models

	SS	d.f.	F	p
<i>Leaf decay rates</i>				
Shredders	0.0032	2	1.229	0.301
Leaf species	0.0001	1	0.126	0.724
Interaction	0.0037	2	1.417	0.251
Error	0.0709	54		

SS: sum of squares, df: degrees of freedom.

Table 3. Relative abundance of food categories in the guts of specimens of *T. fluviatilis* used in the laboratory trials, alone and together with *Triplectides* sp. Comparisons by Friedman test. Abundances with the same letter do not differ significantly (*post hoc* tests by simple pairwise Wilcoxon; mean \pm SE, $n = 10$ per treatment)

	<i>T. fluviatilis</i>	Both organisms
FPOM	99.85 \pm 0.28 ^a	94.07 \pm 3.11 ^a
CPOM	0.15 \pm 0.10 ^b	0.10 \pm 0.07 ^b
Animal Tissue	–	5.83 \pm 3.13 ^b
χ^2	9.42	17.37
p	0.003	< 0.001

the gastric mill (Meiss and Norman 1977). Alves et al. (2010) showed the ossicles of this structure are well developed and calcified in adults of the family Trichodactylidae. Therefore, the foregut of *T. fluviatilis* can break and grind the ingested food, resulting in the low amounts of CPOM observed in the analyzed guts. On the other hand, the low abundance of animal tissue suggests that adults of *T. fluviatilis* do not exert a significant predation pressure on aquatic invertebrate communities associated with leaf patches. Normally, in the gut content of crustaceans, only the most keratinized parts of the exoskeletons of their prey are found, such as legs and head capsules (Acosta and Prat 2011). In our study, the parts of exoskeleton found in the guts were so rare and fine ground that we could not identify them taxonomically.

Given that larvae of insect shredders have a preference for feeding on high quality leaves, *i.e.*, those with low C: N and lignin: N ratios (Casotti et al. 2014; Leite-Rossi et al. 2016; Graça et al. 2016), we expected that *H. dusenni* would be more processed and, consequently, the decay rates would differ between leaf species at least in the treatment containing *Triplectides* sp. only. However, *T. fluviatilis* and *Triplectides* sp. processed similar amounts of leaves across all treatments, suggesting that differences in the characteristics of studied leaves were not sufficient to differentiate the activity of these organisms. When compared to other species from the tropical region, leaves of the Atlantic Forest are generally softer and have higher nutritional quality (see Graça and Cressa 2010; Graça et al. 2015). The high N content observed in both leaves, which is an important driver in leaf consumption by aquatic invertebrates (Leroy and Marks 2006; Graça and Cressa 2010), may have promoted the shredding activity in such way that consumers exhibited no preference for any species. Because of the mouthpart structure, which has prehensile appendages (mandibles and maxillae; Ceccaldi 1989), freshwater crabs could be more adapted to ingest tough leaves than typical aquatic insect shredders. If freshwater crabs have the ability to consume a wide range of leaf species and unconditioned leaves, as was observed for their counterparts from land and mangrove habitats (Kristensen et al. 2010; Nordhaus et al. 2011), these consumers may feed on leaves that are not preferred by shredders. In this context, leaf processing by macroconsumers may be more relevant in streams where shredders are scarce (Moulton et al. 2010). However, the ability of macroconsumers to process leaves of

poor quality, which are typically refractory to many insect shredders (Li and Dudgeon 2008; Jabiol and Chauvet 2012), should be better evaluated.

Contrasting with the abundances of food categories in the guts of *T. fluviatilis* in the wild, *Triplectides* sp. survival was lower in the presence of crabs. In trials containing both organisms, we observed that some cases of *Triplectides* sp. were drilled and found with no larva inside. In addition, a significant abundance of animal tissue was recorded in the guts of the crabs used in the mixed treatment ($5.83 \pm 3.13\%$; Table 3). Thus, our study confirmed the ability of these crabs to prey on insect shredders at least when confined together. Given larvae of *Triplectides* sp. are abundant in the studied stream (Casotti et al. 2014; Kiffer et al. 2016), the low proportion of animal tissue in the guts of *T. fluviatilis* associated with leaf patches possibly results from an efficient defensive strategy of aquatic invertebrates, such as camouflage with the substrate or different timing of activity (Williams et al. 1987; Camargos and Pes 2011), or a preference of crabs for other food categories. All of these hypotheses remain to be tested in future studies.

A reduction in the abundance of shredders caused by macroconsumer predation could alter leaf decay rates in streams (Usio 2000). Using the same abundance ratio of *T. fluviatilis*: *Triplectides* sp. observed *in situ* (1: 9), our results suggest that *T. fluviatilis* may contribute to leaf processing and its influence on leaf decay rates and FPOM production does not seem to differ from *Triplectides* sp. In addition, the high manipulation of leaves by crabs in the laboratory, *i.e.* the behavior of holding, rotating or moving leaves with the chelipeds, probably compensated for the effect of larvae that were lost in the mixed treatment. Freshwater crabs can significantly promote the decomposition of organic matter, reducing particle size during foraging (Landeiro et al. 2008) and removing the substrate (Moulton et al. 2010). However, because of the smaller size, larvae of *Triplectides* sp. process higher amounts of leaf litter per unit of biomass and may be more important to energy flow in streams where both organisms occur together (Boyero et al. 2006).

CONCLUSIONS

The obtained results support the potential for participation of *T. fluviatilis* in leaf breakdown and demonstrated that, in spite of the high abundances

of algae and FPOM in the gut content of *T. fluviatilis* in the wild, adults of this species have the potential to feed both on leaf litter and larvae of *Triplectides* sp. However, the hypothesis of this study (that *T. fluviatilis* feeds both on leaves and *Triplectides* sp. and, consequently, leaf decay rates would be lower when these organisms were together) was only partially corroborated because decay rates did not change across treatments.

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