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Neotropical freshwater crabs (Decapoda: Pseudothelphusidae) shred leaves

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ABSTRACT

Freshwater crabs are macroconsumers that are commonly found in Neotropical headwater streams that may play a key role in energy flow and nutrient cycling in detrital food webs. Although studies have examined the feeding habits of trichodactylid crabs, little is known of this behavior in pseudothelphusid species, and specifically whether they actually consume leaf material. We conducted three nine-day laboratory trials with pseudothelphusid crabs (*Ptychophallus tumimanus* (Rathbun, 1898)) and leaves (*Koanophyllon pittieri*) to investigate whether crabs shred leaves. We hypothesized that leaf mass loss would be faster with crabs present relative to control tanks with only leaves. Leaf mass loss was significantly higher ($p < 0.001$) in tanks with crabs (0.49 ± 0.07 g, mean \pm 1 SD) compared to control tanks (0.31 ± 0.05 g). We observed crabs manipulating, shredding, and consuming leaves, with leaf fragments and egesta present in tanks with crabs but not in control tanks. Their consumption and egestion activity may affect nutrient availability and transformation by stimulating microbial activity during leaf breakdown and converting coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM). Therefore, freshwater crabs need to be considered when studying energy flow and nutrient cycling in detrital food webs of Neotropical headwater streams.

KEYWORDS

Leaf breakdown, Decapod macroconsumers, Shredders, *Ptychophallus tumimanus*, Costa Rica

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INTRODUCTION

Macroinvertebrates that shred leaves play an important role in nutrient cycling in detrital food webs (Wallace and Webster, 1996; Vanni, 2002). Decapod macroconsumers, such as crabs and shrimps, increase rates of leaf breakdown in some tropical streams (Crowl *et al.*, 2001; Mancinelli *et al.*, 2013), but it is unclear whether the increased leaf breakdown rates are due to bioturbation and foraging habits or direct consumption of leaves (Landeiro *et al.*, 2008; Moulton *et al.*, 2010). Although crabs have been suggested to be important shredders in tropical streams (Hill and O'Keefe, 1992; Moss, 2005; Yang *et al.*, 2020) and plant material has been identified in gut content analyses (Pirela and Rincón, 2013; Williner *et al.*, 2014), few studies have directly examined if and how crabs shred and consume leaves. One exception is the study of Costa *et al.* (2016), which found that adult *Trichodactylus fluviatilis* Latreille, 1828 have the potential to feed on both leaf litter and caddisfly (*Triplectides* sp.) larvae during laboratory trials. If land use change or other anthropogenic activities in the tropics (see Wehrtmann *et al.*, 2016) reduce crab populations, there would be implications for the food web dynamics and ecosystem functions of these streams.

Pseudothelphusidae and Trichodactylidae are the two families of freshwater crabs found in the Neotropics (Cumberlidge *et al.*, 2014). Recent feeding ecology studies in the Neotropics have focused on trichodactylid crabs in South America and have found crab gut contents with predominantly allochthonous plant debris, as well as prey items such as macroinvertebrate larvae and fish (*e.g.*, Pirela and Rincón, 2013; Williner *et al.*, 2014). There have been fewer studies that have characterized the feeding habits of pseudothelphusid crabs; while Wehrtmann *et al.* (2019) documented the role of *Ptychophallus uncinatus* Campos and Lemaitre, 1999 as a predator of an insect larva and amphibians, to our knowledge, no studies have directly tested whether pseudothelphusid crabs shred and directly consume leaves. Here, we report on a series of three nine-day laboratory feeding trials in which we recorded the rate of leaf mass loss in treatments with and without pseudothelphusid crabs, and in which we visually documented crab feeding

behavior. We hypothesized that crabs would directly shred and consume leaves and that there would be higher loss of leaf mass in tanks with crabs present.

MATERIAL AND METHODS

We conducted this study in Monteverde, Costa Rica, where pseudothelphusid crabs are the largest invertebrate macroconsumers in streams. Located near the continental divide of the Cordillera de Tilarán, streams in the Monteverde region include first- and second-order headwater tributaries of the Guacimal River that drains into the Gulf of Nicoya in the Pacific Ocean. Mean annual precipitation is 2700 mm (Guswa *et al.*, 2007), with the majority of rainfall occurring during the wet season (May–October).

A laboratory leaf feeding experiment with crabs of the species *Ptychophallus tumimanus* (Rathbun, 1898) was carried out from 18 June to 17 July 2019 to quantify and observe effects of these decapods on leaves in a controlled environment. Crabs were manually collected from the Quebrada Máquina (10.3113818° -84.8081506°), a first-order tributary of the Guacimal River near the town of Santa Elena, province of Puntarenas. We searched for crabs by turning over rocks in riffles and runs and emergent rocks located on the stream banks. Crabs were transported to plastic aquaria tanks (27 cm x 17 cm x 18 cm) in a laboratory setting. We measured crab carapace width (CW; measured across the carapace at its widest point) and carapace length (CL; measured along the midline, from the frontal to the posterior margin) with calipers, and recorded live wet mass (\pm 0.01 g). All crabs in the experiment had a similar CW, CL, and wet mass (Tab. 1). Five crabs were males and three were females. Crabs were marked prior to the experiment to be able to quantify individual mass change over the duration of each experiment. We labeled crabs by attaching numbers written on Rite in the Rain paper (\sim 25 mm² each) to the middle of each carapace using a drop of Loctite super glue and applied quick-dry clear nail polish on top of each tag. This rapid marking method is not associated with mortality or significant stress (Yang *et al.*, 2020). Crabs from the experiment were identified to species using Magalhães *et al.* (2015). At the end of the study,

we preserved a subset of crabs in 95% ethanol and deposited voucher specimens from the experiment at the Museo de Zoología, Universidad de Costa Rica; remaining crabs were released back to the stream.

Table 1. Mean with standard deviation (\pm SD), minimum and maximum of carapace width (CW), carapace length (CL), and wet weight of crabs (*Ptychophallus tumimanus*) in the experiments.

| | Mean (\pm SD) | Minimum | Maximum | N |
|----------------|------------------|---------|---------|---|
| CW (mm) | 26 \pm 2.8 | 23 | 29 | 8 |
| CL (mm) | 19 \pm 1.2 | 17 | 20 | 8 |
| Wet weight (g) | 4.49 \pm 0.81 | 3.03 | 5.66 | 8 |

Each of eight tanks was filled with unfiltered stream water to a height of 8 cm to allow for natural microbial colonization of leaves. We added a consistent amount of cobble substrate from the stream to each tank to provide refugia for the crabs. Green leaves from the common subcanopy tree *Koanophyllon pittieri* (Asteraceae; Haber *et al.*, 2000) were picked directly from trees bordering the stream where we collected crabs. We did not use fallen leaves to minimize variability and because leaves are often displaced by wind or rain prior to natural abscission (Colón-Gaud *et al.*, 2008) and green *K. pittieri* leaves are found in leaf packs in the stream (C. Yang, pers. obs.). After drying the leaves for 72 h at 40°C, we weighed them to obtain initial dry mass before adding 1.03 \pm 0.02 g of whole leaves to each tank. Leaf incubation in stream water began after the dry leaves were added to the tanks at the start of the experiment. Four of the tanks each had two similar-sized crabs (CW 23–29 mm) and four had no crabs (control). Treatments were randomly assigned. The control tanks contained leaves but no crabs, which allowed us to estimate leaf mass loss due to leaching and microbial processing. Deploying two crabs in a tank permitted us to mimic natural densities of crabs in the Quebrada Máquina (C. Yang, unpublished data). Previous experiments confirmed that two crabs of similar sizes can use cobble for cover in the same tank and do not engage in direct aggression, but rather, passively move into different crevices or cobble surfaces (C. Yang, pers. obs.). All crabs had at least 24 h of gut clearance before the start of the experiment with the exception of one crab that molted just before the start of the

experiment and was replaced with a crab brought directly from the field.

We maintained all tanks in controlled laboratory conditions with aerated stream water and natural ambient photoperiod. Mean water temperature in the tanks was 20.48 \pm 1.64 °C and ranged between 17.76 and 25.22 °C. After nine days, the remaining leaf material was collected from each tank, dried at 40 °C for 72 h, and weighed to determine post-experiment leaf mass (Benfield *et al.*, 2017). We measured the wet mass of crabs after each experimental trial. We repeated the experiment a total of three times with the same procedures and the same crabs, allowing at least 24 h of gut clearance between each experiment, with a total of N=12 for each treatment.

The leaf mass loss for each treatment was calculated by assessing the difference between initial and post-experiment leaf dry mass. A two-sample t-test was applied to compare the mean difference in leaf mass loss between tanks with and without crabs. We calculated the amount of leaf material processed per gram of crab wet mass and the amount of leaf material consumed per crab per day. We quantified the mean mass change of crabs over each nine-day study period and the percent change in mass based on average initial wet mass. We also assessed whether the use of the same crabs in the three experimental trials affected the leaf mass loss results with a random-intercept model using the lme4 package in R. Results from the random-intercept model accounting for the non-independence of crabs between experiments were compared with t-test results. All statistical analyses were performed in R statistical software version 3.4.4 (R Core Team, 2018).

RESULTS

After nine days, the leaf mass loss was higher in the tanks with crabs (0.49 \pm 0.07 g, mean \pm 1 SD) than tanks without crabs (0.31 \pm 0.05 g), a statistically significant difference of 0.18 g (95% CI: 0.13–0.23 g), $t(26) = 7.36$, $p < 0.001$. We found identical results with the random-intercept model that accounted for repeated observations, so for simplicity we just report the t-test results. At the end of the laboratory experiments, there was 52.9% of the initial leaf mass

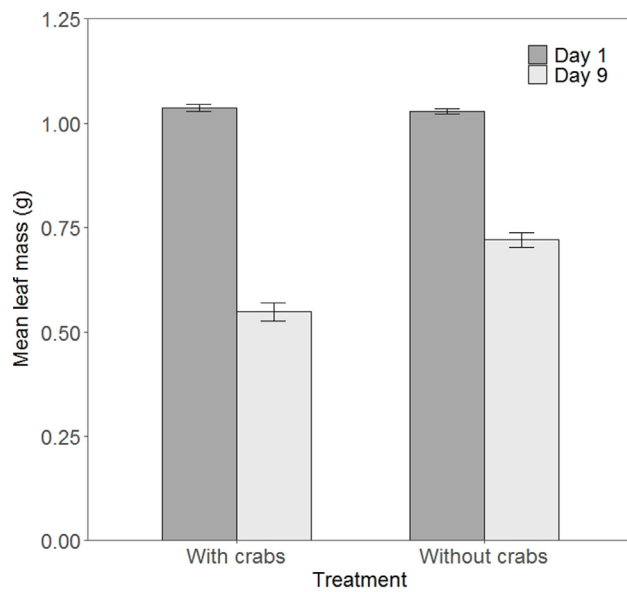


Figure 1. Mean leaf mass remaining in tanks with and without (*i.e.*, leaves only) crabs, *Ptychophallus tumimanus*, on days one and nine. Depicted are means with standard error (\pm SE). There was a statistically significant difference of 0.18 g (95% CI: 0.13–0.23 g) of leaf mass loss in tanks with and without crabs ($t(26) = 7.36, p < 0.001$).

remaining in tanks with crabs compared to 70.1% remaining in control tanks (Fig. 1). The amount of leaf material processed was equivalent to 0.02 g per gram of crab wet mass over nine days and 0.01 g of leaf consumed per crab per day.

We visually observed and video-recorded crabs actively shredding and ingesting leaves (Fig. 2, Video S1), although all such observations occurred during the latter part of each trial; no crab consumption of leaves was recorded during the first three days of any trial. In tanks with crabs, the majority of the remaining leaf mass was composed of small fragments (Figs. 3A, 4A), whereas in control tanks, the *K. pittieri* leaves were still intact after nine days (Fig. 3B). We also observed crab egesta in the tanks (Fig. 4B), providing further evidence that leaves were consumed. None of the crabs molted during these experiments, so there was no change in CW, CL, or wet mass.



Figure 2. Pseudothelphusid crab (*Ptychophallus tumimanus*) consuming leaf material in a tank.



Figure 3. *Koanophyllon pittieri* leaves in tanks after nine days of incubation: **A**, Leaves in tanks with crabs (*Ptychophallus tumimanus*); **B**, Leaves in control tank (no crabs).

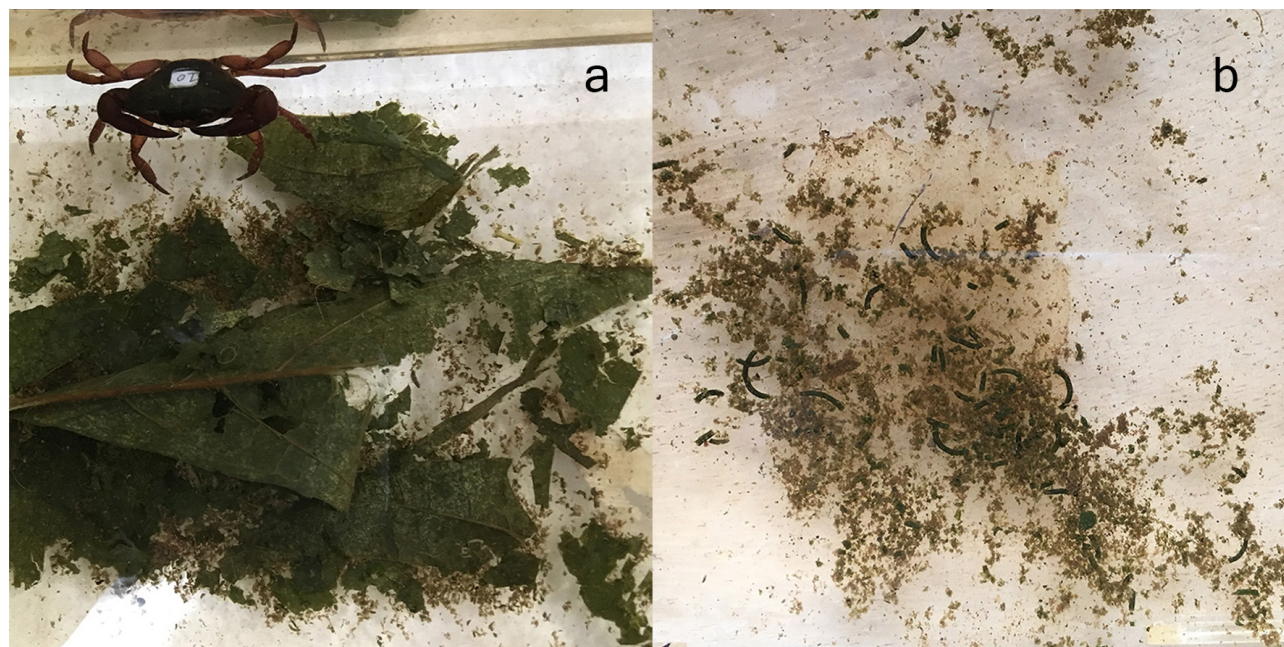


Figure 4. Tank with crabs (*Ptychophallus tumimanus*) after nine days: **A**, Crab with remaining leaf mass in tank; **B**, Crab egesta in tank.

DISCUSSION

We found clear evidence that *P. tumimanus* crabs increase leaf breakdown rates through direct consumption of leaves. We observed crabs actively

shredding pieces of leaves and tearing strands of leaf fibers for consumption in the tanks. Costa *et al.* (2016) also reported crab (*T. fluviatilis*) manipulation of leaves with chelipeds, though they did not observe

a significant difference in leaf decay rates across treatments (crabs with and without the caddisfly shredder *Triplectides* sp.). For their 10-day feeding trials, Costa *et al.* (2016) used *Miconia chartacea* and *Hoffmannia dusenii* leaves that were conditioned for 15 days prior to the experiment. In contrast, the *K. pittieri* leaves that we used were not conditioned prior to starting each experiment but were soft after nine days of incubation in the tanks.

According to Costa *et al.* (2016), fine particulate organic matter (FPOM) was the primary food category found in guts of *T. fluviatilis* that were fed leaves in laboratory trials. Crab manipulation of food particles with their chelipeds, mouthparts, and the gastric mill in their digestive structures likely results in plant matter reaching their guts in the form of FPOM (Collins *et al.*, 2007; Alves *et al.*, 2010). Pirela and Rincón (2013) conducted gut content analyses of the trichodactylid crab *Bottiella niceforei* (Schmitt and Pretzmann, 1968) and found that plant detritus was the most frequent item that occurred in crab guts. In subtropical streams, Williner *et al.* (2014) also found allochthonous plant material to be an important component of gut contents in *Trichodactylus kensleyi* Rodríguez, 1992 crabs. Our study provides evidence of the mechanisms (*e.g.*, grasping and tearing leaves with their chelipeds) that crabs use to consume leaves.

Shredding macroinvertebrates affect stream ecosystems through multiple pathways, including increased downstream transport of particulate nutrients (Wallace and Webster, 1996). As crabs consumed leaf fragments during our feeding trials, they added small pieces of leaves to the water column as coarse particulate organic matter (CPOM) and FPOM. Therefore, shredding and leaf consumption by crabs may affect the availability of CPOM and FPOM for macroinvertebrates such as filterers and collector-gatherers in Neotropical streams. In addition to leaf particles, egesta accumulated in the tanks with crabs as they consumed leaves, and we presume that crabs also excreted nitrogenous waste. Nutrient excretion and egestion by animals affect resource availability for other organisms in streams (Vanni, 2002; McManamay *et al.*, 2011; Atkinson *et al.*, 2017) and can enhance microbial activity on leaves and other detritus. However, we did not measure nutrient concentrations as part of this study.

Comparison of crab leaf consumption rates to those of other shredding organisms is challenging because of differences in methodologies employed across feeding studies (*e.g.*, leaf conditioning periods, use of leaf discs or entire leaves, varying leaf types, single- or mixed-leaf species, etc.). Leaf consumption rates from laboratory trials may also be higher than feeding rates in natural environments due to limited food resource options during experiments. We were not able to compare *P. tumimanus* leaf consumption rates to other freshwater crabs as most diet studies have focused on gut content analyses (*e.g.*, Pirela and Rincón, 2013; Costa *et al.*, 2016). However, relative to other feeding studies, the rate of leaf consumption per crab from our study – $\sim 9.99 \text{ mg crab}^{-1} \text{ d}^{-1}$ – is higher than that reported for many other aquatic invertebrates. Crowl *et al.* (2006) reported a rate of leaf consumption of $3.80 \text{ mg shrimp}^{-1} \text{ d}^{-1}$ for shrimp (*Xiphocaris elongata* (Guérin-Méneville, 1855 in Guérin-Méneville, 1855-1856)) fed *Manilkara bidentata* leaves. Herbst (1982) reported mean consumption values from 1.63 to $3.91 \text{ mg animal}^{-1} \text{ d}^{-1}$ for crane fly larvae (*Tipula abdominalis* Say, 1823) and 0.05 to $0.89 \text{ mg animal}^{-1} \text{ d}^{-1}$ for amphipods (*Gammarus pseudolimnaeus* Bousfield, 1958). The biomass and abundance of different aquatic invertebrates, however, ranges widely and the ecosystem-level effects of leaf processing by different shredder taxa depends on their population biomass and production.

Different shredder taxa have varying feeding rates and mechanisms for shredding leaves. Given their large body size and the ways in which crabs manipulate, shred, and consume leaves using their chelipeds and mouthparts, they may play an important role in converting leaf material into CPOM and FPOM. In addition, because *P. tumimanus* can reach relatively high densities (*e.g.*, ~ 4.7 crabs/m of stream length in the Quebrada Máquina; C. Yang, unpublished data), the rates of leaf consumption we measured in this experiment suggest that *P. tumimanus* are an important component of energy flow and nutrient cycling in detrital food webs in Neotropical headwater streams.

The results from our experiment contrast with studies that have suggested that invertebrates are less important than microbes in detrital processing in tropical streams (*e.g.*, Irons *et al.*, 1994; Mathuriau

and Chauvet, 2002). Tropical shredders may have been overlooked due to methodological reasons, especially because decapod macroconsumers can be difficult to sample using typical macroinvertebrate sampling techniques given their high mobility and large size (Dobson, 2004; Magana *et al.*, 2012; Masese *et al.*, 2014). Exclusion of decapods from macroinvertebrate analyses can be problematic in the tropics because they can be abundant and represent a large proportion of the macroinvertebrate biomass and production (Crowl *et al.*, 2001; Moss, 2005; Greathouse and Pringle, 2006; Pirela and Rincón, 2013). Further studies are needed to investigate whether other species of freshwater crabs, in addition to *P. tumimanus*, also consume leaves and how rates of leaf consumption may vary among crab species and of different size classes.

Leaf litter breakdown is important not only for headwater streams driven by allochthonous resources, but also for downstream transport of nutrients and energy. While our study reports a small data set, the effect of *P. tumimanus* on leaf breakdown was clear and had not been previously quantified. Our results suggest that crabs can play an important role in detrital processing and should be included in future studies that quantify tropical shredder communities and leaf breakdown processes.

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SUPPLEMENTAL MATERIAL

Video S1. Video of crabs (*Ptychophallus tumimanus*) shredding and consuming leaves. Available at <https://vimeo.com/385357347>

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