Hydrobiologia
https://doi.org/10.1007/s10750-023-05458-2

PRIMARY RESEARCH PAPER

Decomposition rates appear stable despite elevated shrimp abundances following hurricanes in montane streams, Puerto Rico

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Received: 1 August 2023 / Revised: 7 December 2023 / Accepted: 12 December 2023
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Abstract Leaf litter decomposition is a key ecosystem process in headwater streams, influenced by physical fragmentation, microbial degradation and feeding activity by stream biota. In some tropical streams, feeding by freshwater shrimps can exert strong top-down control on leaf litter decomposition, however, variation in shrimp macroconsumer effects across small spatial scales or among years is not well-known. We ran 50-day macroconsumer exclusion experiments to measure shrimp effects on leaf decomposition in two adjacent headwater streams in Puerto Rico, in 2017 (immediately prior to two Category 4 and 5 hurricanes) and again in 2018 and 2019, to assess shrimp effects in the context of post-hurricane conditions that included reduced canopy cover and higher shrimp (*Atya* and *Xiphocaris*) counts. Leaf decomposition was faster when shrimp had access to leaf packs, but only in the study stream with larger pools, which also had higher overall shrimp counts. However, increased shrimp abundances following the hurricanes did not result in faster decomposition, potentially because shrimp diets shifted toward algae post-hurricanes when canopies were more open. We conclude that shrimp effects on leaf litter breakdown may vary between adjacent streams that differ in habitat conditions and that increasing local shrimp abundances may fail to accelerate decomposition.

Handling editor: Verónica Ferreira

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05458-2.

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Published online: 29 January 2024

Keywords Leaf decomposition · Headwater streams · Hurricane · Macroconsumers · Puerto Rico · Top-down effects

Introduction

Decomposition of allochthonous leaf material (i.e., leaf litter) is a well-studied (Tank et al., 2010) ecosystem-level process in streams, where physical fragmentation by flow, microbial degradation, and direct ingestion by biota all contribute to the mass loss of leaves (Gessner et al., 1999). Leaf litter is an important energy source for stream consumers (Vannote et al., 1980; Wallace et al., 1997; Benfield et al., 2017), and the relative effects of consumers on leaf breakdown are likely to vary depending in part on consumer abundances.

Decapod crustacean macroconsumers can accelerate leaf litter breakdown through both direct (consumptive) and indirect (non-consumptive) effects according to a meta-analysis from 17 sites across a latitudinal gradient (Mancinelli et al., 2013). Research in Africa and Costa Rica indicates that freshwater crabs can increase leaf breakdown through direct and indirect actions (Dobson et al., 2004; Yang et al., 2020). Conversely, research from Brazil shows that electrical-exclusion of shrimp can actually increase leaf breakdown in the presence of insect consumers (Moulton et al., 2019). Freshwater crabs and shrimp can thus cause trophic cascades by preying on or inhibiting feeding by smaller detritivores that contribute to decomposition (Ho & Dudgeon, 2016; Andrade et al., 2017; Moulton et al. 2019). In tropical streams of Puerto Rico, shrimp macroconsumers contribute to loss in leaf mass directly through ingestion and indirectly through bioturbation (Pringle et al., 1993; Crowl et al., 2001). These effects can be quite substantial. For example, in high-elevation streams located above waterfalls within the El Yunque National Forest (EYNF), Puerto Rico, shrimps in the genera *Atya* and *Xiphocaris* dominate macroconsumer assemblages, and *Xiphocaris* in particular accelerates leaf litter decomposition (Crowl et al., 2001; March et al., 2001; Torres, 2020). However, because leaf breakdown may be driven by physical (e.g., storm runoff) as well as biotic processes (including microbial activity), it is not clear how strongly variation in local abundances of particular stream consumers, such as shrimp, is likely to affect decomposition rates.

Macroconsumer effects on stream ecosystem processes are of particular interest in the context of extreme events that physically alter stream habitats. Climate change models predict an increase in frequency and severity of hurricanes and droughts worldwide (IPCC, 2022), including in Puerto Rico where predictions are for more intense hurricanes in the wet season and longer drought periods in the dry season (Jennings et al., 2014). High winds and intense rainfall associated with hurricanes can have immediate effects on stream ecosystems. Hurricane-force winds can destroy forest canopies, initially depositing large amounts of leaf material into stream channels (Scatena et al., 2012), followed by a period of reduced leaf-fall (Gutiérrez-Fonseca et al., 2023) and potentially enhanced growth by stream algae, until canopies recover (Zimmerman et al., 2021). Rainfall associated with hurricanes can increase discharge, scour benthic material (Hudson, 2021) and alter the geomorphology of stream habitats (Covich et al., 1991). Drought effects on streams may evolve more slowly (Lake, 2003; Gutiérrez-Fonseca et al., 2020), however, previous studies in streams draining the EYNF have shown that droughts can reduce pool volume and result in reductions in shrimp abundances (Covich et al., 2003; Gutiérrez-Fonseca et al., 2020). Conversely, shrimp abundances increased in response to Hurricane Hugo (in 1989; Covich et al., 1991), but it is unknown if this increase in shrimp led to increased top-down pressure on basal resources.

The initial motivation for this study was to provide baseline data on shrimp (primarily *Xiphocaris* and *Atya* species) macroconsumer effects on *in-situ* leaf litter decomposition rates in two adjacent montane streams in Puerto Rico prior to a future planned flow-reduction experiment, where one of the study stream reaches would be de-watered to simulate drought conditions. After running an in-situ leaf decomposition experiment (in both the presence and absence of shrimp) in 2017, two large hurricanes struck Puerto Rico with extensive effects on the forest canopy at our experimental site. Our 2017 experiment thus provided a pre-hurricane measurement of decomposition rates in the presence and absence of shrimp. We then repeated macroconsumer exclusion experiments in 2018 and 2019 in post-hurricane conditions. Here we ask three questions using data for leaf litter mass loss in macroconsumer exclusion experiments conducted in 2017 (pre-hurricane), 2018 (5 months post-hurricanes Irma and Maria) and 2019 (21-months post-hurricanes): (Q1) Did shrimp effects on leaf litter decomposition differ between two adjacent streams that also differed in size and presumably shrimp abundances? (Q2) Were shrimp effects and decomposition rates altered following the hurricanes? and (Q3) Did higher shrimp abundances in individual pools correlate with faster decomposition rates? Combining multi-year data collected in replicated experiments and at fixed sites thus allowed us to test for temporal and between-stream variation in shrimp effects on leaf litter decomposition.

Methods

Study design

To assess differences in shrimp macroconsumer effects on leaf litter breakdown (Q1), we experimentally estimated decomposition rates in the presence compared with absence of shrimp macroconsumers in each of two study streams before and after two back-to-back hurricanes. We measured mass loss of leaf packs over seven weeks in 2017, 2018, and 2019. We refer to mass loss through time via various factors (physical abrasion, ingestion, bioturbation, and microbial decomposition) as decomposition. We used linear, mixed effects regressions to compare the rate of mass loss (decomposition rate; *k*) between streams and among years and with shrimp present or excluded. Additionally, we interpreted decomposition rates within the larger context of abiotic (canopy cover, leaf litter input, pool volume) and biotic (shrimp abundance) factors that were altered following hurricanes (Q2). To assess pool-specific effects of shrimp on decomposition rate (Q3), we regressed 2019 decomposition rates against visual counts of shrimp abundance in pools where experimental units were placed. We interpreted these data in the context of differences in pool volume, as habitat for shrimp.

Study site description

This study was conducted at the Luquillo Long-Term Ecological Research (LTER) site in the El Yunque National Forest (EYNF; ~ 11,300 ha) in northeastern Puerto Rico (18° 18′ N, 65° 47′ W, Fig. 1). The EYNF, also known as the Luquillo Experimental Forest, is the most biologically diverse forest in the U.S National Forest System (Quiñones et al., 2018). The EYNF is located within the Luquillo mountains, with peaks that rise over 1000 m a.s.l. Mountain peaks are frequently under cloud cover and the forest has a high frequency of low-intensity rainfall (Brokaw et al., 2012). Migratory amphidromous fish and shrimp, and non-migratory aquatic insects inhabit the streams, and invertebrate biomass is dominated by shrimp macroconsumers above waterfalls which exclude fish predators from upstream passage (Covich, 1988).

Research described here is focused on two adjacent headwater streams (inset, Fig. 1) within the Espiritu Santo watershed which is one of the nine major watersheds within the EYNF. A 150 m reach in each of two first-order streams, Prieta A (PA) and Prieta B (PB), were used as focal study reaches (inset, Fig. 1). The stream channel for both PA and PB is approximately 2 m wide and 0.75 m deep, with primarily pebble- to boulder-sized sediment and sand and silt deposits in pools. PA drains a watershed area of 0.17 km^2 and PB drains a watershed area of 0.24 km^2. PA and PB join to form the Prieta mainstem tributary of the Sonadora River which is part of the larger Espiritu Santo drainage. None of the rivers within this watershed have dams over 5 m tall, but water withdrawals for municipal water supplies can be relatively high (Crook et al., 2007; Chappell et al., 2019).

The upper Sonadora and Prieta tributaries lack predaceous fishes, due to large waterfalls in the lower drainage, but harbor diverse macroinvertebrates. The only fish species that occur in EYNF headwater streams are the sirajo *Sicydium* spp. (Gobiidae), which are algivorous. While ten species of freshwater shrimp occur in streams draining the EYNF (Pérez-Reyes et al., 2013), *Xiphocaris elongata* (Guérin-Méneville) and *Atya lanipes* Holthuis dominate shrimp assemblages (> 90% of individuals) in our study stream reaches. The family Atyidae is represented by four species including *Atya lanipes, A. innocous* (Herbst)*, A. scabra* (Leach)*,* and *Micratya poeyi* (Guérin-Méneville). Five species are represented by the family Palaemonidae including *Macrobrachium acanthurus* (Wiegmann), *M. carcinus* (Linnaeus), *M. faustinum* (de Saussure), *M. crenulatum* Holthuis, and *M. heterochirus* (Wiegmann). Finally, the family Xiphocarididae is represented by

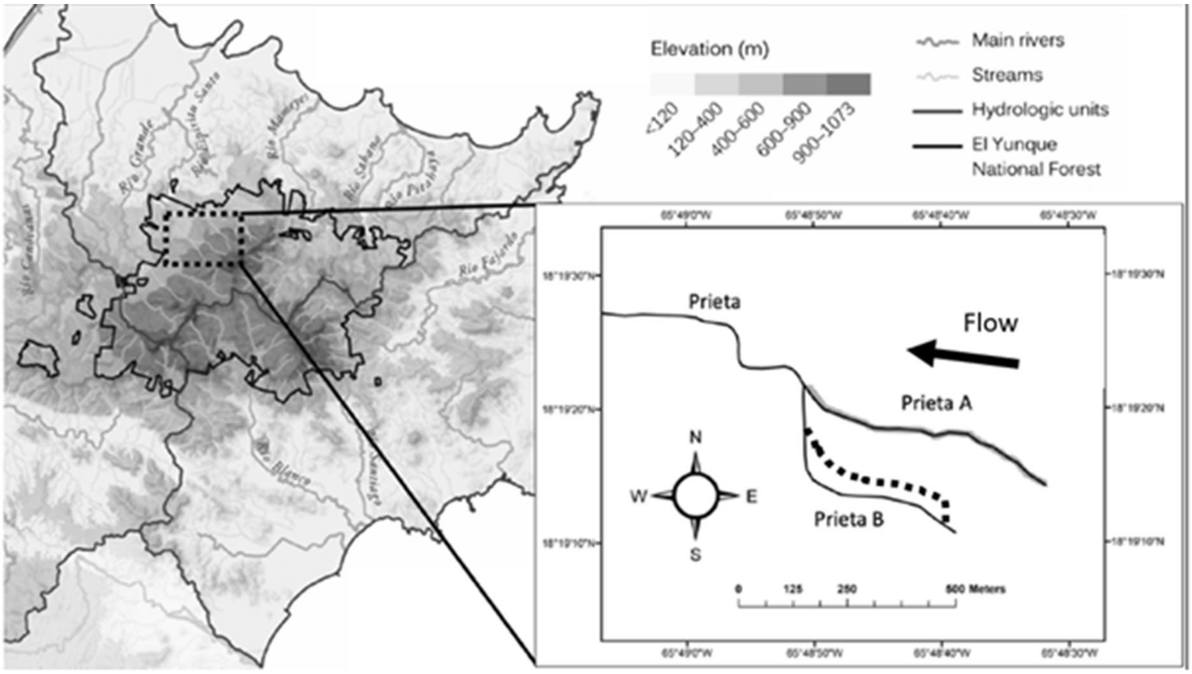


Fig. 1 Location of study site in the El Yunque National Forest in Puerto Rico. Inset shows location of two study stream reaches, Prieta A and Prieta B, in the upper Espiritu Santo watershed. Dashed line shows location of future flow diversion (Modified from Hudson 2021)

only one species, *Xiphocaris elongata*. An endemic crab species in the family Epiloboceridae, *Epilobocera sinuatifrons* (Milne-Edwards), is also present but less common in these streams. Aquatic insects are abundant and dominated by mayflies (Ephemeroptera), mostly in the family Leptophlebiidae and midge (Diptera) larvae in the family Chironomidae. Notably, case-building caddisfly (Trichoptera) larvae in the family Calamoceratidae are one of the few obligate insect shredders (Rincón & Covich, 2014).

Leaf litter decomposition experiments

We ran a leaf litter decomposition experiment over a seven-week period in each of three years: 2017, 2018, and 2019 (Experiments I, II, and III; Fig. 2). Two large hurricanes struck Puerto Rico in 2017 after the conclusion of Experiment I, which represented pre-hurricane conditions, thus becoming a de-facto pre-hurricane experiment (Fig. 2). We then repeated this initial experiment in 2018 (Experiment II) and 2019 (Experiment III) in post-hurricane conditions. Post-hurricane conditions can consist of decreased leaf litter inputs, increased stream nutrients, and decreased canopy cover (Covich et al., 1991; Brokaw et al., 2012; present study). Accordingly, experimental findings presented here are interpreted in the context of pre- and post-hurricane conditions and they also provide additional baseline information on leaf litter decomposition rates in years preceding a flow-reduction experiment that began in 2022.

For each experiment, we assessed decomposition rates in the presence and absence of shrimp macroconsumers in each of our two study streams (PA and PB). Experiment I (2017) and Experiment II (2018) included $n=3$ replicate pools in study reaches of both PA and PB. In Experiment III (2019), we included two additional replicate pools ($n=5$) within each study reach (PA, PB). We installed paired rectangular quadrats (20.32 cm × 20.32 cm) in each pool in locations that typically maintained adequate stream flow to keep leaf packs submerged (Fig. 3). One quadrat within each pair was randomly selected to be electrified using copper wire attached to 12-V batteries connected to solar-powered chargers (Parmak Magnum Solar-Pak 12) located on nearby stream banks,

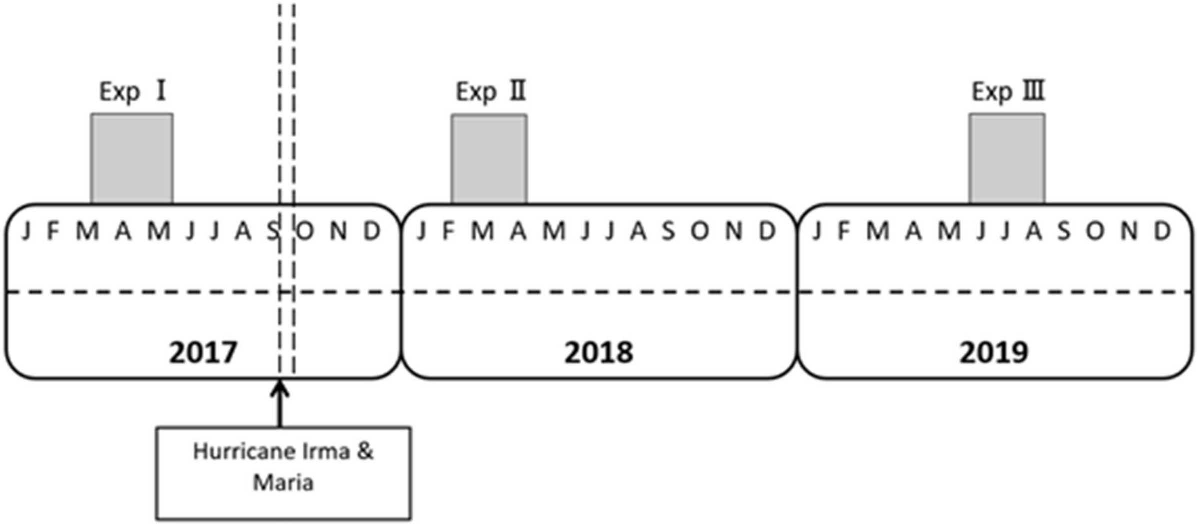


Fig. 2 Timeline for three stream decomposition experiments: Exp I (March 16–May 5, 2017), Exp II (February 23–April 15 2018), and Exp III (July 1–August 20 2019). The occurrence of Hurricanes Irma and Maria in September 2017 is indicated by parallel vertical dashed lines, with the 2017 experiment occurring prior to the hurricanes and the 2018 and 2019 experiments occurring five- and 21-months post-hurricane, respectively

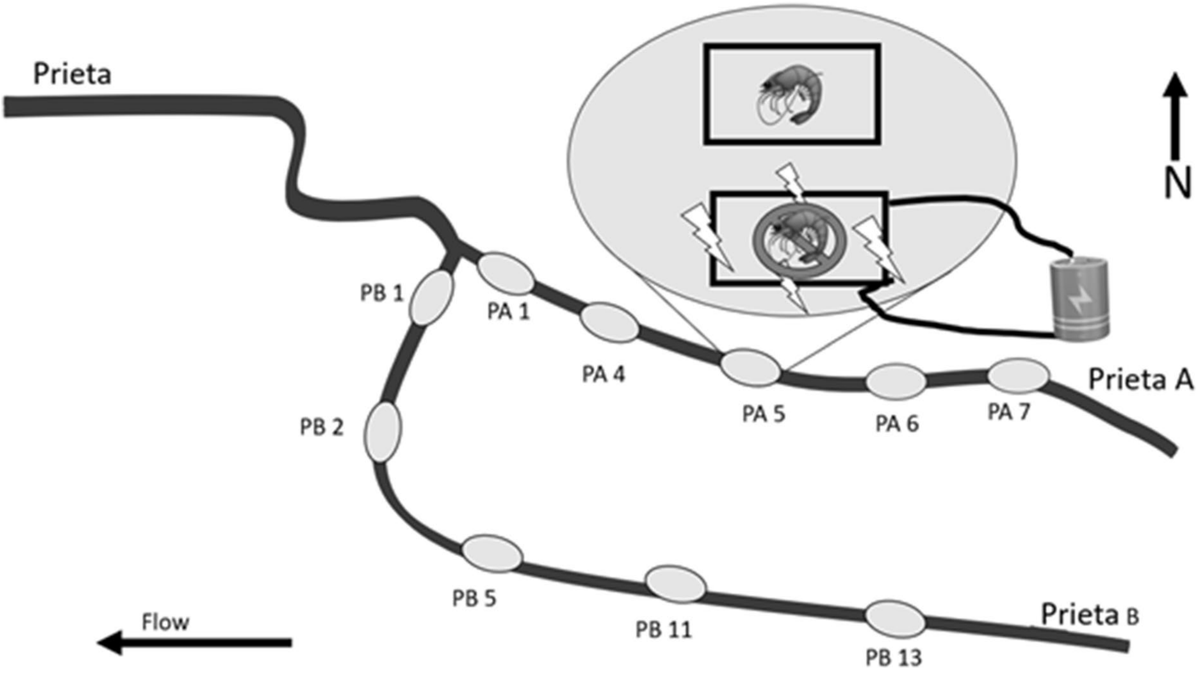


Fig. 3 Schematic drawing showing location of experimental pools in study stream reaches of Prieta A (PA) and Prieta B (PB) for Experiment III (2019). Inset shows experimental set-up nested within each pool which includes two quadrats: one shrimp access (unelectrified control, no lightning strikes or charger) and one shrimp exclusion (electric, lightning strikes reflecting hook up to battery powered fence charger on stream bank)

a technique modified from Pringle and Blake (1994). The location of electrified quadrats was randomly assigned for each pool. The electrified quadrat served as a macroconsumer exclusion treatment. Electric exclosures have been shown to effectively exclude shrimp and fish macroconsumers in previous experiments conducted in headwater streams of the Espiritu Santo, Puerto Rico (Pringle et al., 1993, 1999; March et al., 2001), and did not affect insect shredder biomass at high-elevation sites (March et al., 2001). The unelectrified quadrat (macroconsumer access control) within each pair was lined with copper wire of the same size and shape (Fig. 3). The batteries powering the exclosures were replaced every two days to ensure consistent electric charge to exclude shrimp macroconsumers. On each leaf pack collection date, a random leaf pack was removed from both access control and exclusion quadrats and processed as indicated below. Our experimental setup remained operational through high discharge events that occurred during Experiments I and III.

To assess leaf decomposition rates, we incubated leaf packs of freshly abscised Tabonuco (*Dacryodes excelsa* Vahl) leaves in pools in each of our two study stream reaches, and retrieved them at intervals over a seven-week period. We chose to use leaves of Tabonuco for experimental leaf packs because it is a dominant riparian tree species along both of our study reaches (Weaver 1997; Heartsill Scalley 2017). Leaf litter input in headwater streams of ENYF varies little throughout the year and is considered to be aseasonal (Gutiérrez-Fonseca et al., 2020). We attempted to run experiments before the onset of heavy rains which often occur in September-December (Brokaw et al., 2012).

Prior to each experiment, leaves were air-dried at room temperature for 5–7 days, with leaves rotated at least twice a day to promote equal drying. Leaves were then grouped into packs of 5.0 ± 0.6 g and clipped together at the petiole using a binder clip. Each leaf pack was attached to a wire frame with plastic zip ties and secured by steel rebars hammered into the stream substrate. To determine how much mass was lost in handling between the lab and the stream, five leaf packs were submerged for five minutes in each study stream on the first day of the experiment. Upon retrieval, they were oven-dried in the laboratory at 70 °C for 72 h. The amount of mass lost via handling was then applied as a correction to all further leaf packs deployed (see: Benfield et al., 2017). Experimentally, we have added a similar leaf volume to each pool in each year, and asked whether differences in our measure of shrimp abundance in the same pools across years (or among pools in Experiment III) correspond to differences in rate of leaf mass loss. Conceptually, differences in shrimp abundance (as we have measured it) correspond to differences in density of shrimp per gram of leaf in experimental leaf packs.

In Experiments I (2017) and II (2018), leaf packs were collected on days 3, 7, 14, 21, 28, 35, 42, and 49. In Experiment III (2019), packs were collected on days, 3, 7, 14, 22, 29, 36, 43, and 50. Leaf packs were collected by placing a small net downstream of the pack as it was removed from the frame to avoid loss of invertebrates or leaf material. The pack and any invertebrates collected in the net were then placed in a plastic bag and transported to the lab on ice. Once the leaf pack was retrieved, each leaf was gently rinsed over a 250 µm sieve, and any insects dislodged were placed in ethanol vials and labeled for future identification. Leaf packs were placed in tinfoil envelopes and dried at 70 °C for 24 h and then weighed to the nearest 0.0001 g. Once dry, the leaves were placed in a muffle furnace for 1 h at 500 °C and then re-weighed to calculate Ash Free Dry Mass (AFDM).

During Experiment III (2019), we conducted visual shrimp observations during both day ($n = 6$ dates: July 1, 11, 16, 22; August 7, 12) and night ($n = 5$, July 2, 11, 22; August 7, 12) in all study pools in PA ($n = 5$) and PB ($n = 5$). Mean shrimp abundance was estimated over a two-minute observation period for the control and electric treatment nested within each pool. Observed shrimp were identified as one of three taxa (i.e., *Xiphocaris*, *Atya*, or *Macrobrachium*). Shrimp were observed from a distance, so as to not disturb shrimp activity. When two observers were present, they would simultaneously count the shrimp for one minute per person. To avoid counting the same shrimp twice, observers would select a marker in the pool, with one observer counting clockwise while the other counted counterclockwise. The same protocol was used for nocturnal observations, except that we used red headlamps in order to not disturb shrimp. If shrimp were disturbed upon arrival, observers would turn off their headlamps until shrimp activity resumed. In total, we made 60 daytime observations (6 dates × 10 pools) and 50 nighttime observations

(5 dates × 10 pools), totaling over 220 min of observation within all study pools.

Statistical analysis

To assess differences in decomposition rates and shrimp effects between our study streams (Q1), we initially fit a mixed-effects linear regression model to the leaf litter mass data from all three experiments, allowing decomposition rate (k) to differ between control and shrimp exclusion treatments, separately in each of the two study streams (Model 1). For this model, we assumed that shrimp and stream-identity effects on decomposition rate were constant across the three experiments, and included a random effect of pool-year combination to account for unmodeled differences in decomposition of leaf packs grouped together in pools in each year. We then fit a second model (Model 2) that relaxed the assumption of constant rates across years. This model allowed us to quantify the strength of top-down control by shrimp macroconsumers in differing conditions (streams and years), and particularly to assess evidence that shrimp effects differed between pre- and post- hurricane disturbance (Q2). Finally, we fit a third model (Model 3) to the leaf mass data from Experiment III to evaluate effects of shrimp abundance (based on visual estimates made in Experiment III only) on decomposition rate (Q3).

The response variable for each model was the observed percent AFDM remaining (%AFDM) for a leaf pack collected on a specific day, from one of the treatments (i.e., control or shrimp exclusion), and in a given pool and year. We assumed that decomposition was exponential beginning on the first collection date (i.e., day 3), and constant for each treatment within a pool and year. We thus estimated decomposition rate (k) by fitting the following model to the %AFDM remaining measurements:

$$\mathrm{naturallog}\left(\%AFDM_{i,t}\right) \sim N\left(\mu_{i,t}, \tau\right)$$

$$\mu_{i,t} = a + k_{i,t} * day_{i,t}$$

and

$$k_{i,t} \sim N\left(\mu k_{i,t}, \tau k\right)$$

$$\mu k_{i,t} = \beta * predictors_i + e_i,$$

where % AFDM$_{i,t}$ = % AFDM remaining in leaf pack i collected on day t; a is the intercept (allowed to differ from ln(100) to account for initial mass loss by leaching; held constant in Models 1 and 3, but allowed to vary among years in Model 2); $k_{i,t}$ represents decomposition rate for leaf pack i collected on day t; B represents effects of *predictors* on decomposition k; and k represents normally distributed residuals for ln(% AFDM remaining) and decomposition rate k of each leaf pack, respectively; and e_i represents a normally distributed random effect for the pool and year where leaf pack i was collected. The *predictors* on decomposition rate for Model 1 were treatment (control or shrimp exclusion) and, within each treatment, stream-identity (PA or PB). Model 2 relaxed this model to allow each treatment, stream, and year to differ in decomposition rate. Finally, Model 3 (fit to 2019 data only) estimated k separately for control and shrimp exclusion, with a covariate of pool-specific shrimp abundance (mean of visual counts) on k in control treatments. In Model 3, we fit separate models for daytime and nighttime counts.

We fit models to the data using Markov chain Monte Carlo software [JAGS, (Plummer, 2017) implemented with R packages rjags (Plummer, 2016), runjags (Denwood, 2016) and coda (Plummer et al., 2006)]. Model simulations ran three chains with 30,000 sampling iterations and a burn-in period of 5000 iterations. Parameters had diffuse prior distributions; the prior for model intercepts was set as uniform between 4 and 5 on a natural log scale (i.e., 55–148% AFDM), and priors for beta values were normal with mean 0 and precision 0.001. Models with an Rhat value of less than 1.1 for all parameters were considered to have converged successfully (Gelman & Hill, 2007). We evaluated evidence for each hypothesized effect ($\beta * predictor$) based on the posterior parameter means and 95% credible intervals. Code available at https://github.com/Max-Kelly/LLDecomp_17-19.

Background environmental data (2017–2019)

We examined differences in leaf litter decomposition among the experiments in the context of variation in stream gage height, water temperature, canopy cover, leaf-litter input, pool volume, and shrimp collected in traps in Prieta A and B from 2017 to 2019. These data were provided by the Luquillo LTER (https://

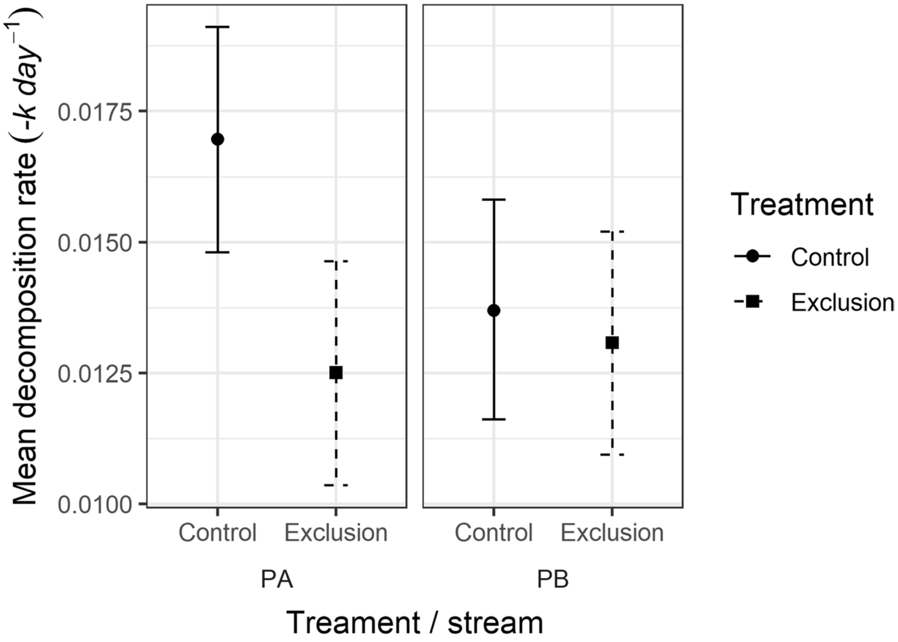
luquillo.lter.network/data-catalog/, Luquillo LTER Network, 2022). Water level (cm) and temperature (°C) were measured at the downstream ends of PA and PB (just upstream of their confluence) at 15-min intervals with pressure transducers that also recorded water temperature (Ramírez 2021). Variation in gage height through time is used as a proxy for increases or decreases in stream flow. We use the coefficient of variation (CV) of mean daily gage height to measure temporal variation in flow regimes during experiments. Canopy openness was measured monthly using a spherical densiometer in all pools (Ramírez et al., 2021a) and leaf litter input was measured biweekly from baskets hanging above the channels of PA and PB (Ramírez et al., 2021b).

Pool volume (m^3) was measured monthly in all pools within PA and PB and was calculated as pool surface area (m^2) multiplied by mean depth (m), the latter obtained through five random measurements per pool. To obtain pool area, a photo image of the pool was processed in ImageJ (Schneider et al., 2012) with a reference 1 m stick (Ramírez et al., 2021c). The volume of *experimental* pools (those with nested electric exclusions and controls within the pools for this study) was measured 2–3 times over the duration of each experiment. Shrimp abundance was estimated monthly from January 2017–December 2019 using baited minnow traps (galvanized minnow traps: 43-cm long, 19-cm diameter, 0.5-cm mesh) placed in $n = 9$ *trapping* pools of each of the two study stream reaches for 24 h. The number of traps in each pool was adjusted to correspond to a constant traps/m^2 of pool surface area, adapted from Covich et al. (2006; Ramírez et al., 2021d). We extracted shrimp trapping data collected in our experimental pools during each experiment (three pools sampled twice during the Experiments I and II in each stream, and five pools sampled twice in each stream in Experiment III). We used these trapping data to estimate differences in shrimp abundance among experiments.

Results

Decomposition rate was faster with shrimp present (control treatment) than when excluded (exclosure treatment) in PA but not PB (Fig. 4), based on data combined across the three experiments (Model 1). Shrimp access to leaf packs in PA accelerated decomposition by 36% compared to the exclusion treatment (Table S1). Decomposition, averaged over all experiments with shrimp present, was also faster in PA (− 0.0170 day^{-1}; Table S1) than in PB (− 0.0137 day^{-1}, difference in k $day^{-1} = 0.0033$, 95% Credible Intervals (CI) 0.0004 to 0.0062, Fig. 4, Table S1). There was no evident effect of shrimp

Fig. 4 Mean decomposition rates (− k $day^{-1} \pm 95\%$ credible intervals) generated by Model 1, using combined data for all three experiments in PA (left) and PB (right), in the shrimp access (solid line, circle) and the shrimp exclusion treatment (dotted line, square)



exclusion on decomposition rate in PB (Fig. 4). Notably, in the absence of shrimp, decomposition rates were similar in PA and PB (Fig. 4, Table S1).

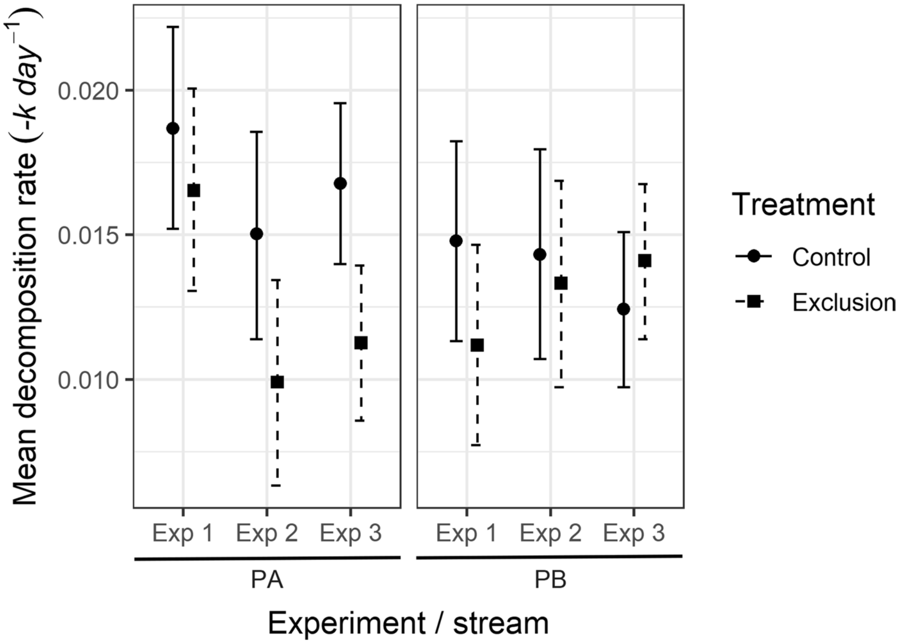
Allowing for year- as well as stream-specific effects on decomposition rates (Model 2) provides evidence for stronger shrimp effects in the second two experiments compared with the first, but only in PA (Fig. 5). Excluding shrimp slowed decomposition in PA by 11% in 2017 compared with 34% and 33% in 2018 and 2019, respectively (Fig. 5, Table S2). Effects of excluding shrimp on rates of decomposition in PB varied from 24% slower in 2017, to an unexpected 14% faster in 2019 (Fig. 5). In the absence of shrimp, PA had lower estimated rates of decomposition than PB except in 2017, when PA had the fastest rates observed for either treatment (Fig. 5).

Higher shrimp abundance in individual pools, measured by daytime visual observations, corresponded with faster decomposition in Experiment III (Model 3). Estimated decomposition rate increased by 13% as shrimp abundance increased by one standard deviation (~ 13 shrimp) above the mean (Fig. 6, Table S3; effect on k day^{-1} = – 0.0017, 95% CI – 0.0036 to – 0.0001). This effect of increased decomposition rate was driven by data for PA, which had higher shrimp counts in daytime and nighttime visual observations (Table S4). Only two pools in PB had a mean shrimp abundance greater than the combined daytime mean of PA and PB (15.5 ± 13.2 SD). Models with nighttime counts, which were approximately 6 × higher than daytime counts (Table S4), did not show an effect of shrimp abundance on decomposition (effect on k day^{-1} = – 0.0004, 95% CI – 0.0023 to 0.0015).

Between-stream and among-year variation in canopy cover, streamflow, and shrimp abundances

Faster decomposition in the presence of shrimp in PA, compared with PB (Model 1, Fig. 4), corresponded to differences in pool volume and shrimp abundances. PA has larger pools (mean pool volume: 0.72 m^3 ± 0.68 SD) than PB (mean pool volume: 0.47 m^3 ± 0.34 SD). The mean number of shrimp sampled monthly from 2017 to 2019 averaged 1.8X higher in PA (26.0 ± 26.93 SD) than in PB (14.57 ± 12.97, Fig. S1; data based on 9 *trapping* pools in each stream). Other measured environmental variables averaged across years showed smaller differences between the study streams. Canopy was on average 34.1% open in PA and 31.9% open in PB (Figure S2). Leaf litter input rates were slightly higher in PB (0.94 g m^{-2} day^{-1} ± 1.09 SD) than PA (0.82 g m^{-2} day^{-1} ± 0.95 SD) but followed similar trends through time (Fig. S3). Mean daily stream water level (gage height) for our three experiments

Fig. 5 Mean decomposition rates (– k day^{-1} ± 95% credible intervals) generated by Model 2, for Experiments (Exp) I–III in PA (left) and PB (right), in the shrimp access control (solid line, circle) and the shrimp exclusion treatment (dotted line, square)



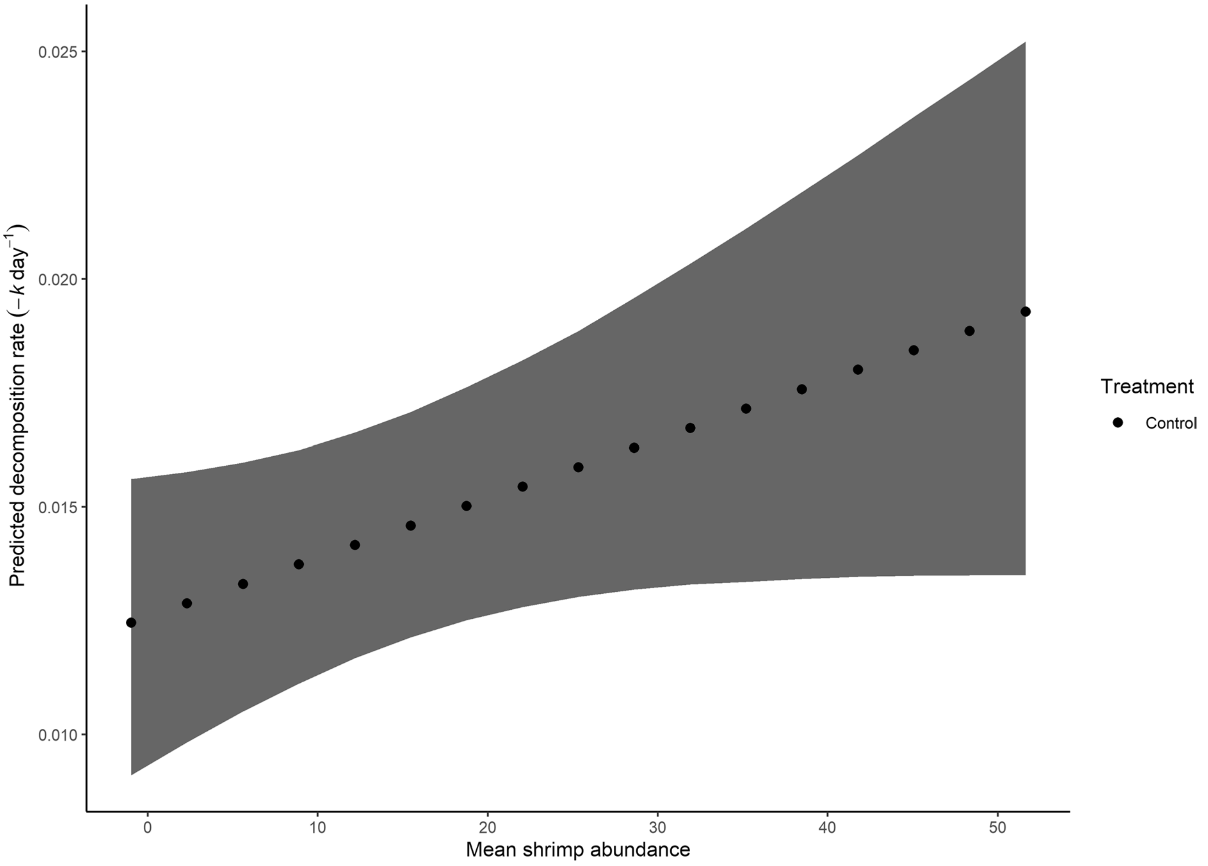


Fig. 6 Predicted decomposition rate ($-$ k day^{-1} ± 95% credible intervals) generated by Model 3 (Table S3) for Experiment III based on shrimp abundance for the shrimp access control. Shading around points depicts the 95% credible interval. The mean shrimp abundance (15.5 ± 13.2) is from all combined daytime observations in both PA and PB ($n = 60$) over the experimental period (July 1–Aug 20, 2019)

showed similar patterns between our two study reaches, with gage height generally 1.2X higher in PA than in PB (Fig. S4).

The small estimated differences in decomposition rates among years (Model 2) occurred despite large hurricane effects on canopy cover and leaf input. Canopy openness was the lowest for Experiment I (2017), which was completed four months prior to Hurricanes Irma and Maria, with canopy openness at 9.5% and 11.9% in PA and PB, respectively (Fig. S2). Defoliation by Hurricane Irma and Maria increased canopy openness by > 80% in both streams (Fig. S2). Experiment II (2018) was conducted five months post-hurricanes, with canopy openness at 59.2% and 43.8% in PA and PB, respectively. In Experiment III (2019), 21 months post-hurricanes, canopy openness was still above pre-hurricane levels, at 32.2% and 43.4% in PA and PB, respectively (Fig S2). Experiment I had the highest leaf litter input rate of all three experiments (1.8 g m^{-2} day^{-1} ± 1.2 SD in PA and 1.4 g m^{-2} day^{-1} ± 0.5 in PB), because it was conducted prior to Hurricanes Irma and Maria and the canopy was still intact. This input rate was over 1.5X greater than the mean across the 2017–2019 experiments. The pulsed leaf litter input rate from Hurricane Irma was over seven-fold greater than the long-term mean (Fig. S3). In contrast, we were unable to measure the effects of Hurricane Maria as litter baskets were damaged by the storm. In Experiments II and III, leaf litter input rate was well below the long-term mean in PA (Exp II: 0.24 g m^{-2} day^{-1} ± 0.1 SD, Exp III: 0.65 g m^{-2} day^{-1} ± 0.2 SD) and PB (Exp II: 0.58 g m^{-2} day^{-1} ± 0.2 SD, Exp III: 0.79 g m^{-2} day^{-1} ± 0.2 SD, Fig. S3).

Mean daily water temperatures were similar between the two streams and among the three experiments in PA (Exp I: 21.12 °C ± 0.31 SD, Exp II: 22.10 °C ± 0.84 SD. Exp III: 23.70 °C ± 0.28 SD) and PB (Exp I: 21.12 °C ± 0.25 SD, Exp II: 21.70 °C ± 0.54 SD. Exp III: 23.53 °C ± 0.22 SD).

Streamflow regimes differed among experiments (based upon mean gage height and coefficient of variation; Fig. S4) but showed similar patterns in the two streams. In Experiment I, the mean daily gage height varied in response to several high discharge events (CVs: PA: 16.9, PB: 31.2). In contrast, Experiment II had a relatively stable flow regime with no large discharge events (CVs: PA: 15.3, PB: 17.0). In Experiment III, most variability occurred due to a single large discharge event in the second half of the experiment (CVs: PA: 19.0, PB: 26.8).

Shrimp abundance increased post-hurricanes in the experimental pools (Table 1). *Atya* had the most dramatic increase, with a mean abundance 3 × higher in Experiment III than in Experiment I, in PA. *Xiphocaris* and *Macrobrachium* abundance increased in the year directly following the hurricane (2018), with mean abundances about 2 × that of Experiment I. In Experiment III, *Xiphocaris* and *Macrobrachium* abundances decreased compared with Experiment II, but remained higher than Experiment I (Table 1). In PB, *Xiphocaris* abundance remained relatively stable across the three experiments. *Atya* and *Macrobrachium* abundances followed a similar trend as those in PA, except with smaller increases.

Data from trapping and visual observations provided strong evidence that shrimp abundances correlated with pool volume. Mean pool volume (m^3) and mean shrimp abundance based on trapping data were strongly correlated in each year (2017: $R^2 = 0.72$, $n = 18$, 2018: $R^2 = 0.68$, $n = 18$, 2019: $R^2 = 0.72$, $n = 18$, Fig. S5). Daytime visual observations of shrimp in Experiment III also showed a strong correlation ($R^2 = 0.91$, $n = 9$) between pool volume and shrimp abundance (Fig. 7). The majority of the shrimp observed in Experiment III (Table S4) were either *Xiphocaris* or *Atya*, with very few *Macrobrachium*.

Discussion

Our three macroconsumer exclusion experiments showed spatial (between streams) and temporal (pre- and post-hurricane) variation in the role of shrimp macroconsumers on leaf litter decomposition (Figs. 4, 5). In response to our research questions 1–3, we found that: (1) shrimp accelerated decomposition rate by 36% in stream with larger pools (PA) which had a 1.8X greater shrimp abundance than PB. There was no top-down effect in stream with smaller pools. (2) The top-down effect of shrimp on decomposition rate in PA was stronger following two major hurricanes (34% and 33% faster in the presence of shrimp versus absence of shrimp in 2018 and 2019, respectively) than pre-hurricane (11% faster in the presence versus

Table 1 Mean shrimp abundance (+ SD) for Experiments (Exp) I-III, estimated using baited traps placed within trapping pools that overlapped with our experimental pools for the *Xiphocaris* (xipho), *Atya*, and *Macrobrachium* (mac)

Experiment (year) Stream	Mean xipho. abundance	± SD	Mean atya abundance	± SD	Mean mac. abundance	± SD	Total n
Exp I (2017)							
PA	16.50	10.89	10.00	5.33	0.83	0.98	6
PB	11.67	9.85	5.83	3.43	0.00	0.00	6
Exp II (2018)							
PA	30.67	17.74	19.50	6.80	2.67	2.42	6
PB	9.67	1.97	8.00	4.98	1.33	1.75	6
Exp III (2019)							
PA	19.90	15.16	30.20	16.78	1.80	1.62	10
PB	8.90	9.70	9.70	10.06	0.40	0.52	10

For Exp I and II, three experimental pools were sampled twice during the experimental period for a total of $n = 6$ for each study stream. For Exp III, five experimental pools were sampled twice during the experimental period in each stream for a total of $n = 10$ per study stream (please note that these data are a subset of data in Fig. S4)

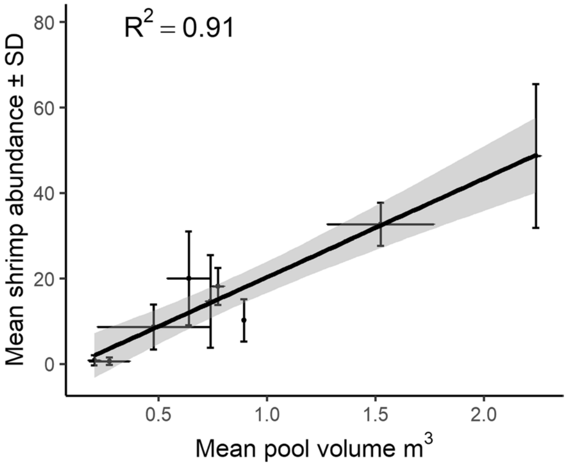


Fig. 7 Mean shrimp abundance and mean pool volume (m^3) as measured by daytime visual shrimp observations on six dates during Experiment III from *experimental* pools in PA ($n=5$) and PB ($n=4$). One pool in PB is not included as pool volume was not measured until 2020. Solid diagonal line indicates the slope (slope $= 23 \pm 2.5$ SE, $R^2 = 0.91$). Visual shrimp observations were not recorded on the same days that experimental pool volumes were estimated. To address this, visual shrimp observations are paired with the pool volume measurement closest to the shrimp observation date

absence of shrimp). However, decomposition rates did not increase in post-hurricane experiments despite a two-fold increase of shrimp in PA. (3) Finally, there was a strong correlation between pool volume and shrimp abundance, and higher daytime shrimp abundance in larger pools correlated with faster decomposition rates in Experiment III. Taken together, these findings suggest that the strength of a top-down effect of shrimp macroconsumers on the ecosystem process of leaf litter breakdown only partly depends on local shrimp abundances.

The magnitude of shrimp effects reported in our study are similar to those from other macroconsumer exclusion experiments conducted globally. We found that decomposition rates were 1.36 × faster in the presence versus absence of shrimp in PA. Leaf litter bag decomposition studies conducted in the larger Prieta mainstem found decomposition rates of Tabonuco leaves in mesh bags to be 1.48 × and 2.07 × faster in the presence versus absence of shrimp (Wright & Covich, 2005; Rincón & Covich, 2014). It is interesting to note that an electric exclusion experiment at a high-elevation site in the Sonadora River (most analogous to our headwater study streams) found that decomposition rates were approximately 1.8 × faster in the presence versus absence of shrimp (March et al., 2001). That study used *Cecropia schreberiana* Miq. leaves which represent another dominant riparian species in EYNF. In headwater streams in Costa Rica, leaves decayed 1.25 × faster in enclosures that had freshwater crabs compared to enclosures without crabs (Yang et al., 2020). Electric exclusion experiments in Brazil found that shrimp exclusion led to faster leaf processing, and the authors attribute this contrasting result to *Macrobrachium* (a dominant predator) in unelectrified quadrats inhibiting insect mediated leaf breakdown (Moulton et al., 2019).

Stream geomorphology may explain some of the spatial variation in shrimp effects on decomposition in our study. The approximately 1.5 × larger pools (by area) in PA may accommodate higher shrimp numbers and this may partially explain the more evident shrimp effect. Large pools tend to have undercut banks and rock crevices where *Xiphocaris* and *Atya* shrimp can hide from predatory *Macrobrachium* shrimp (Covich et al., 2003, 2006). *Macrobrachium* haven been shown to inhibit feeding by *Xiphocaris* (March et al., 2001) and inhibit feeding by insects as well (Moulton et al., 2019). Large pools also often provide a greater retention of debris dams (Covich et al., 1991; Pyron et al., 1999; Wohl et al., 2019). Therefore, it is logical that large pools are advantageous for shrimp because debris dams provide a concentrated source of microbially conditioned leaves along with diverse habitat to escape predation. Channel shape may also influence the role of high flow events and scour on leaf breakdown. The more incised channel of PA might be expected to lead to more scouring during high flows relative to PB. This may explain overall faster decomposition rates in 2017 in PA, when high flows occurred early and repeatedly in the experiment.

Stream flow and microbial breakdown likely drive decomposition in the absence of shrimp. Insect shredders are in low abundances and have a minor role in decomposition in the Espiritu Santo Drainage (March et al., 2001; Bobeldyk & Ramírez, 2007). As mentioned above, stream flow can result in leaf mass loss through abrasion and physical fragmentation of leaf litter (Gessner et al., 1999). The effects of stream flow are likely more significant in high flows when fine sediment and rocks are transported downstream (Heard et al., 1999; Ferreira, 2006). Microbes (bacteria, fungi, and protists) contribute to breakdown through colonization and consumption of dissolved organic matter and fine particulate organic matter (Marks, 2019). In the tropics, microbial breakdown can be a large portion of leaf mass loss, partially attributed to warmer water temperatures that enhance microbial activity (Irons et al., 1994; Boyero et al., 2016; Marks, 2019; Tiegs et al., 2019). When light enters a stream channel, algae can grow on leaves and stimulate growth of microbial communities (Kuehn et al., 2014). Microbial breakdown may have had a greater importance in post-hurricane experiments due to an increased algal priming effect facilitated by hurricanes which resulted in a more open canopy.

Although previous studies have demonstrated top-down effects of freshwater shrimp on leaf litter decomposition, high shrimp abundances do not always result in faster breakdown. March et al. (2001) conducted shrimp exclosure studies at three sites along a 4.2 km elevation gradient in EYNF. The highest elevation site in the March et al. (2001) study is most analogous to PA in terms of biotic composition, with *Xiphocaris* and *Atya* exerting strong top-down control on decomposition rates. In contrast, at mid and low-elevation sites, *Xiphocaris* and *Atya* were considerably less effective in consuming leaf material, as predatory *Macrobrachium* were fourfold and sixfold more abundant relative to the high-elevation site. Notably, at the mid and low-elevation sites, shrimp abundance was twofold higher than at the high-elevation site, yet, only at the high-elevation site did shrimp have top-down effects on leaf litter breakdown. Studies in Brazil showed that decomposition rates were faster in the exclusion of *Potimirim brasiliana* Villalobos and *Macrobrachium olfersii* (Wiegmann) because these shrimp were preying on insects that contributed to breakdown (Andrade et al., 2017). Subsequent experiments reinforced this finding and inferred that the presence of predatory *Macrobrachium* in unelectrified quadrats inhibited insect mediated leaf breakdown (Moulton et al., 2019). In a tropical stream in Hong Kong, decomposition rates were similar in the presence and exclusion of *Macrobrachium hainanense* (Parisi), as shrimp mainly functioned as predators on insects that contributed more substantially to breakdown (Ho & Dudgeon, 2016).

In our study, we observed that a 2- to 3-fold increase in shrimp abundance following hurricane disturbance did not increase leaf litter breakdown rates. This may be due in part to a saturation effect of shrimp numbers on leaf decomposition rate, where shrimp were consuming almost all available resources. That is, it is possible decomposition did not increase despite increased numbers of shrimp because pre-hurricane abundances were already effectively consuming all leaf material except the most nutrient poor and recalcitrant litter within pools. In addition, algal availability increased in response to a more open canopy after the hurricanes defoliated riparian vegetation. While algal standing stocks remained low due to intense grazing by shrimp (Hudson 2021), food web studies using stable-isotope analysis in Quebrada Prieta found that shrimp shifts their diet from mostly leaf litter before the hurricanes to mostly algae after (Gutiérrez-Fonseca et al., 2023). Even in heavily forested streams, it is often algae that is being assimilated into the biomass of stream organisms (March & Pringle, 2003; Lau et al., 2009; Dudgeon et al., 2010; Neres-Lima et al., 2016). Thus, we suggest that Hurricanes Irma and Maria may not have resulted in increased decomposition rates despite increased shrimp abundance because the shrimp were already consuming most available detrital resources, and also shifted their diet to more nutritious algae (Guo et al., 2016) as opposed to the less nutritional leaf litter.

One explanation for the increased abundance of shrimp post-hurricane is increased survival and higher growth rates of small shrimp after the hurricanes in response to more nutritious algal resources. A line of evidence supporting this increased survival and higher growth rate hypothesis is the observed dietary shift of *Xiphocaris* and *Atya* from detritus to algae following hurricanes Irma and Maria (Gutiérrez-Fonseca et al., 2023). We suggest that increased survival and growth rate of small shrimp allowed them to become large enough to be retained in shrimp traps. Although *Xiphocaris* are primarily shredders and *Atya* primarily scrapers and collectors, both species benefited from the increase in algal resources post-hurricane (Gutiérrez-Fonseca et al., 2023). Similarly, March and Pringle (2003) found that 9 months after hurricane George impacted Puerto Rico and left the Sonadora heavily defoliated, the resultant pulse of algae was assimilated into the biomass of *Xiphocaris* (selective feeding with pincers) and *Atya* (indiscriminate feeding with cheliped fans). The conditions of March & Pringle (2003) are similar to our post-hurricane experiment and suggest that *Xiphocaris* and *Atya* opportunistically fed on the pulse of algae.

The visual estimation of shrimp numbers in the third experiment (i.e., Table S4) enhanced our ability to relate macroconsumer abundances to top-down effects on leaf decomposition. This method could be helpful for future studies considering it is time and cost effective relative to shrimp trapping (i.e., Table 1, Fig. S1). Shrimp abundance can be estimated within short timed intervals (e.g., 2 min) for individual pools throughout the duration of an experiment. In contrast, shrimp trapping is a two-day process where baited minnow traps are placed in the stream over-night and trapped shrimp are not counted until the next day. In this study, visual observations were helpful as further evidence of spatial variability in decomposition rates at the pool level. Our model found evidence that increased shrimp abundance corresponded with faster decomposition rates, but only using daytime abundances. Although shrimp are more active during the night (Johnson & Covich, 2000), one explanation for why nighttime observations did not correspond to faster decomposition rates would be a potential saturation effect as described above. Possibly, variation in nighttime abundances that already exceed a threshold for overall consumption rate do not further affect decomposition. In contrast, variation in lower daytime abundances may in fact relate to overall consumption (and thus measured rates of decomposition). Overall, visual observation of shrimp in our study provided another line of evidence that habitat size influences shrimp abundance and, in-turn, decomposition rates.

In summary, our three experiments can be viewed as snapshots in time (one before hurricanes and two after) measuring among-year and between-stream variation in shrimp macroconsumer effects on decomposition rate, which is a key ecosystem process. Despite an increase in shrimp abundance following the hurricanes our study did not find evidence that decomposition rates were altered. It is a challenge to infer direct hurricane effects due to variation in other factors like flow regimes that contribute uniquely to decomposition in individual experiments. Nonetheless, our study provides substantial baseline information, from separate experiments run in each of three years, on decomposition rates in headwater streams dominated by shrimp. These data will be used for comparative purposes as baseline data on decomposition rates, and the effects of shrimp, to ongoing flow-reduction experiments in this study system.

Acknowledgements We thank Dr. Alan Covich (University of Georgia) who provided key insights into the field site and comments on Kelly's masters thesis. Any use of trade, product, or firm names does not imply endorsement by the U.S. Government.

Author contributions M-K wrote the master's thesis from which he adapted this manuscript. Kelly also analyzed data, ran statistical analysis and made figures. MF provided leadership on the statistical analysis and provided comments on versions of the thesis and manuscript. PG-F, JEG, RP, and LL were responsible for running experiments reported in this manuscript, collected essential data, and provided background knowledge on study site and methods. AR provided editorial comments on early versions of the thesis. CP played a role in experimental design of experiments and provided comments throughout the thesis and manuscript. All authors contributed to editing the final manuscript.

Funding This work was partially funded by the Luquillo Long-Term Ecological Research Program funded by the US National Science Foundation (NSF Award: DEB-1831952).

Data availability https://github.com/Max-Kelly/LLDecomp_17-19

Declarations

Competing interests The authors have no financial, non-financial or competing interests to declare.

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