Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream

James G. March, Jonathan P. Benstead, Catherine M. Pringle, and Mark W. Ruebel

Abstract: We experimentally excluded freshwater shrimp assemblages (Atyidae, Xiphocarididae, and Palaemonidae) to examine their effects on detrital processing and benthic insect biomass at three sites along an elevational gradient in a tropical stream in Puerto Rico. We also determined which shrimp taxon was responsible for leaf decay in a subsequent laboratory experiment. At the high-elevation site, the shrimp assemblage was dominated by *Atya* spp. and *Xiphocaris elongata*, and leaf decay rates were significantly faster in the presence of shrimps than in their absence. Laboratory experiments showed that this was primarily due to direct consumption of leaves by *Xiphocaris*. Shrimps had no effect on leaf decay rates at mid- and low-elevation sites where there were higher proportions of *Macrobrachium* spp. shrimps (which prey on *Xiphocaris*). Laboratory experiments showed that *Xiphocaris* consumed significantly less leaf material and experienced significantly higher mortality in the presence of *Macrobrachium*. Shrimp exclusion resulted in significantly less and significantly more insect biomass at the high- and low-elevation sites, respectively; no difference was found at the mid-elevation site. Insects played a minor role in leaf decay. Results show a strong linkage between shrimp assemblages and rates of detrital decay and illustrate the importance of conducting experiments at multiple sites.

Résumé : Nous avons artificiellement exclu les communautés de crevettes d'eau douce (Atyidae, Xiphocarididae et Palaemonidae) de trois sites le long d'un gradient altitudinal dans un cours d'eau tropical à Porto Rico dans le but de d'étudier leur effet sur la transformation du détritus et la biomasse des insectes benthiques. Dans une expérience ultérieure en laboratoire, nous avons déterminé quels taxons de crevettes étaient responsables de la décomposition des feuilles. Au site de haute altitude, le peuplement de crevettes était dominé par des *Atya* spp. et par *Xiphocaris elongata*; la décomposition des feuilles s'y opérait significativement plus vite en présence des crevettes qu'en leur absence. En laboratoire, il a été démontré que cela était dû à une consommation directe des feuilles par *Xiphocaris*. Les crevettes n'avaient pas d'effet sur le taux de décomposition des feuilles aux sites d'altitudes moyenne et basse, où il y avait une plus forte proportion de *Macrobrachium* spp., des prédateurs de *Xiphocaris*. En laboratoire, *Xiphocaris* consommait significativement moins de feuilles en présence de *Macrobrachium* et sa mortalité était significativement plus élevée. L'exclusion des crevettes a entraîné une réduction significative de la biomasse des insectes au site de haute altitude et une augmentation de cette biomasse en basse altitude; en altitude moyenne, il n'y a eu aucun changement. Les insectes ne jouaient qu'un rôle mineur dans la décomposition des feuilles. Nos résultats démontrent l'existence d'une forte relation entre les communautés de crevettes et les taux de décomposition du détritus et illustrent l'importance de mener des expériences simultanément à plusieurs sites.

[Traduit par la Rédaction]

Introduction

Understanding the roles of species in ecosystem processes such as primary production, decomposition, and nutrient cycling can provide important insights into the functioning of ecosystems as well as guide managers in designing conservation strategies (Jones and Lawton 1995). Recently, ecolo-

gists have emphasized the importance of incorporating spatial heterogeneity into experiments to explore not only whether certain species play key roles, but also under which ecological conditions they assume these roles (Hunter and Price 1992; Polis et al. 1996). Therefore, to understand species effects on ecosystem processes more fully, it is necessary to incorporate spatial heterogeneity because links between species and ecosystem function may vary with ecological conditions. In lotic ecosystems, most experimental studies are conducted at a single site and therefore are unable to address the importance of certain species beyond the context of a specific stream reach (e.g., Pringle et al. 1993). Would the role of these species change if the study was conducted a few kilometres up or downstream?

In this study, we examined the role of freshwater shrimps (Decapoda: Caridea) in determining rates of leaf litter decay

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and composition and biomass of insect assemblages at three sites along an elevational gradient in a Puerto Rican stream. Previous studies in the headwaters of this stream demonstrated that shrimps affect insect and algal community composition as well as sediment cover and the quantity and quality of fine benthic organic matter (Pringle and Blake 1994; Pringle 1996; Pringle et al. 1999). However, community composition and abiotic conditions change with elevation (Bhajan et al. 1978), and this may affect the relative roles of different macroconsumers. Understanding the role of shrimps at lower-elevation sites is important, given their migratory life cycle and the nature of recent anthropogenic disturbances. All of the shrimp species in these rivers have diadromous life cycles and migrate between upland freshwater and downstream estuaries during their lives (Covich and McDowell 1996; March et al. 1998; Benstead et al. 2000). Recent anthropogenic disturbances such as damming and water withdrawal have affected distributions of adult shrimps and larval survival rates (Holmquist et al. 1998; Benstead et al. 1999). Thus, understanding the role that shrimps play along an elevational gradient has both ecological and resource management implications.

Several studies have experimentally examined effects of large omnivorous crustaceans (shrimps and crayfishes) on insects and algae in streams (e.g., Pringle and Blake 1994; Charlebois and Lamberti 1996). These studies demonstrated that shrimps and crayfishes could have direct effects via consumption as well as indirect effects via trophic cascades and bioturbation. Considerably less is known about effects of shrimps and crayfishes in detrital food webs, specifically their effects on leaf litter and associated insects. Detrital material from terrestrial vegetation is the dominant energy source in many streams, and within-stream decay of terrestrial leaves is a well-studied process (see reviews by Webster and Benfield 1986; Boulton and Boon 1991). However, few studies have examined experimentally their contribution to leaf litter decay (but see Parkyn et al. 1997; Rosemond et al. 1998; Crowl et al. 2001) or how it varies along stream continua.

In this study, we combined the use of an in situ manipulation of shrimps at three sites along an elevational gradient in a tropical stream with a laboratory experiment to understand the role of shrimps in an ecosystem process and benthic community structure. Specifically, we addressed the following two questions. (*i*) Do different shrimp assemblages along an elevational gradient affect rate of leaf decay and insect community composition differently along this gradient? (*ii*) Which shrimp taxa are most important in determining rates of leaf decay?

Materials and methods

Study site

This study was conducted in the Río Espíritu Santo river system, which drains the northern part of the Luquillo Experimental Forest and surrounding lowlands in northeastern Puerto Rico. The physical structure of the Río Espíritu Santo changes dramatically from high-elevation headwaters to river mouth. High-elevation tributaries (>200 m above sea level) are characterized by alternating pools and cascades. Substrata are composed of large boulders with interstitial cobble and gravel. A large waterfall (>10 m), at approximately 200 m above sea level, acts as a barrier to most fishes. At

mid-elevation sites (70–200 m above sea level), small cascades are less frequent, and riffles composed of small boulders and cobble are common. Low-elevation sites (<70 m above sea level) are characterized by large deep runs and cobble–gravel riffles.

Land use also changes along this elevational gradient. Tabonuco (*Dacryodes excelsa*) forest extends from 600 m to the Luquillo Experimental Forest boundary located at 90 m. Below the boundary, land use changes to urban and pasture; however, the riparian zone is predominantly forested. Allochthonous inputs enter the river system throughout the year, although two peaks in leaf input occur in the tabonuco forest (from March to May and September to October (Covich and McDowell 1996)).

Ten species of omnivorous freshwater shrimps inhabit rivers of the Luquillo Experimental Forest. The palaemonid shrimps *Macrobrachium carcinus* (L.), *M. faustinum* (De Saussure), *M. crenulatum* Holthuis, *M. acanthurus* (Wiegmann), and *M. heterochirus* (Wiegmann) can reach sizes >230 mm in length and consume algae, macrophytes, decomposing leaf litter, insects, molluscs, small fish, and other shrimps (Covich and McDowell 1996). The atyid shrimps, represented by *Atya lanipes* Holthuis, *A. scabra* (Leach), *A. innocous* (Herbst), and *Micratya poeyi* (Guérin-Méneville), consume periphyton, small sessile insects, and leaf matter by brushing with their modified cheliped fans (Pringle et al. 1993; Pringle 1996). They use these same cheliped fans to filter feed when flow conditions are suitable (Covich 1988). *Xiphocaris elongata* (Guérin-Méneville) consumes leaf matter, insects, small flowers, and fruit using tiny pincers. No information is available on food preference for any of these shrimp species. All of these shrimp species undergo extended larval development and are amphidromous (Covich and McDowell 1996); adult females release planktonic larvae that drift downstream from freshwater habitat to the estuary (March et al. 1998). Larvae spend 50–110 days in the estuary before migrating back upstream as metamorphosed postlarvae (Hunte 1979; Benstead et al. 2000).

The remainder of the aquatic fauna consists of seven species of fishes, insects, snails, and one species of crab. Of the fishes, only the green stream goby *Sicydium plumieri* is found above the high waterfall at 200 m. The insect assemblage is depauperate when compared with continental tropical streams (Buzby 1998) and is dominated by sessile chironomids and mobile baetid and leptophlebiid mayflies (Pringle et al. 1993; Buzby 1998). Three species of freshwater snails, *Neritina punctulata*, *N. clenchi*, and *Thiara granifera*, inhabit mid- and low-elevation sites. These snails graze periphyton. The freshwater crab *Epilobocera sinuatifrons* is omnivorous and consumes insects, shrimps, fruit, and seeds (Covich and McDowell 1996).

In situ experiment

The field experiment was conducted from 18 July to 17 August 1996. The high-elevation site was at 300 m in the Sonadora, a second-order tributary of the Espíritu Santo. The mid-elevation site was located approximately 3.1 km downstream at 90 m in a third-order mainstem reach. The low-elevation site was a side channel of the fourth-order mainstem at 10 m, approximately 4.2 km downstream from the mid-elevation site. At each site, five depositional areas were chosen close to the stream bank where leaves accumulated naturally. In each depositional area, two quadrats were anchored to the stream bottom using rocks from the stream and cable ties. Quadrats were square templates (45 × 45 cm) made of 19-mm chlorinated polyvinyl chloride tubing and contained an inner and outer square of uninsulated 12-gauge copper wire. A coin flip determined which one would be electrified (shrimp exclusion) or a control (shrimp access). Each electric quadrat was connected to a solar-powered fence charger (Parker-McCrory, 12-V) by attaching 12-gauge copper wire from the inner square to the power source and from the outer square to the ground. This method excluded fishes and shrimps but not insects and snails. Leaf packs were

made from air-dried freshly fallen green leaves of *Cecropia schreberiana* cut into smaller pieces, weighed to approximately 5 g, held together with a metal binder clip, and tethered inside the quadrat. *Cecropia schreberiana* was used because it is common in the tabonuco forest, especially along stream banks (Brokaw 1998). One leaf pack was sampled randomly from each replicate treatment on days 1, 3, 6, 9, 12, 20, and 25. We sampled the remaining three leaf packs on day 30. We also sampled 30 leaf packs on day 0 to obtain an air-dried to oven-dried conversion factor, which was used to adjust the original air-dried weights of the leaf packs. After collection with a fine-mesh net, leaf packs were oven-dried at 50°C for 24 h and weighed to the nearest 0.01 g. Leaf decay rates (*k*) were calculated for each treatment replicate by regressing ln(% leaf mass remaining) against elapsed days, starting with day 1; *k* is the negative slope of the regression (Benfield 1996). We used an average percent remaining of the three leaf packs sampled from each treatment replicate for the day-30 sample. Leaf decay rates were compared between treatments and among sites using a two-way analysis of variance (ANOVA). Because we found a significant site × treatment interaction, we examined differences in leaf decay rate between treatments at each site separately using one-way ANOVAs. A one-way ANOVA was also used to compare decay rates among sites in the absence of macroconsumers. Because of a large spate on day 27, statistical analyses were conducted both with and without data from day 30.

Insects found on leaf packs on days 6, 9, and 20 were preserved in 70% ethanol, identified to family or genus, and measured to the nearest millimetre. Insect biomass per leaf pack was calculated using published family-level length–mass relationships (Benke et al. 1999). If a length–mass relationship was not available for a family, we used one from a taxon with a similar shape. Insects were assigned to a functional feeding group based on literature and mouthpart morphology (Merritt and Cummins 1984; Buzby 1998). Differences in total insect biomass, biomass of shredders, and the biomass of the two most common groups (Ephemeroptera and Chironomidae) were compared between treatments and among sites using a two-way repeated measures ANOVA on log(*x* + 1)-transformed data. If a significant site × treatment interaction was found, we examined each site individually using a one-way repeated measures ANOVA. Snails found on leaf packs were counted and compared using two-way repeated measures ANOVA.

We electroshocked a 2-m² area around each treatment replicate with a backpack electroshocker at the conclusion of the experiment. Shrimps were identified to genus (note: *M. poeyi* was lumped in with *Atya* spp.) and the carapace length of shrimps was measured to the nearest millimetre. Shrimp abundance was converted to biomass using length–mass relationships (March 2000). We also conducted 2-min observations of each quadrat on six different dates. Observations were conducted from nearby large boulders so that fish and shrimp behavior were not affected. Shrimps were identified to genus when visibility allowed.

Water depth and velocity were measured at base flow on two days at the conclusion of the experiment using a ruler and a Marsh–McBirney digital flowmeter, respectively. Water velocity was measured inside the quadrat where leaf packs were positioned. The range of water temperatures at each site was measured using submerged min–max thermometers.

Discharge values were obtained from two U.S. Geological Survey gauges in the Espíritu Santo, located just below our high-elevation site and between the mid- and low-elevation sites. Discharge at each site was then estimated using methods in March et al. (1998).

Laboratory experiment

To determine which shrimp taxa were responsible for effects on leaf decay observed in the in situ experiment, we conducted a laboratory experiment using aquaria during August 1998. Each 11.4-L

rectangular aquarium (40 × 27 × 13.5 cm) contained cleaned natural cobble–pebble substrate, a flow pump (Aquarium Systems Maxi-jet 500), and a 5.00 ± 0.37 g leaf pack of air-dried freshly fallen *C. schreberiana*. We used a factorial design with three genera of shrimp and a control. The treatments were as follows: *Atya* only (A), *Xiphocaris* only (X), *Macrobrachium* only (M), every possible combination of these genera (AX, AM, XM, and XMA), and a control with no shrimp. Each treatment was replicated three times and each aquarium contained six shrimps divided evenly among the genera. Shrimps were identified to genus, measured to the nearest millimetre (carapace length), and wet-weighed to the nearest 0.1 g (Table 1). Any dead shrimps were identified and replaced daily. Filtered stream water in each aquarium was changed at least every other day. Leaf packs were removed after 17 days, oven-dried at 50°C for 24 h, and weighed to the nearest 0.01 g. Leaf mass consumed and the number and genus of shrimp mortalities were compared among treatments using Tukey–Kramer HSD (honestly significant difference) tests with significance set at 0.05. To test for interactions among shrimp genera in aquaria, we compared predicted leaf mass consumed (based on single-taxon treatments) with actual leaf mass consumed using a *t* test. Predicted leaf mass consumed for each treatment was calculated by multiplying the leaf mass consumed per gram of shrimp of each taxon alone by the biomass (wet weight (grams)) of each shrimp taxon in each treatment.

Results

In situ experiment

Shrimp assemblages

Shrimp assemblage composition differed among sites. At the high-elevation site, *Xiphocaris* and *Atya* shrimps were observed to enter the control treatment in approximately equal numbers (Table 2). However, based on electroshocking, the shrimp assemblage was dominated by *Atya* followed by *Xiphocaris* and *Macrobrachium* in terms of both abundance and biomass (Table 3). No fishes were observed in the control treatment or sampled with electroshocking at the high-elevation site. At the mid-elevation site, shrimps observed in the control treatment were mostly *Xiphocaris*, some *Macrobrachium*, and no *Atya* (Table 2). However, *Macrobrachium* comprised the majority of the shrimp assemblage based on electroshocking, with fewer *Xiphocaris* and few small *Atya* (Table 3). Again, no fishes were observed in the controls at this site, but one fish (*Xiphophorus helleri*) was sampled with electroshocking. At the low-elevation site, *Macrobrachium* shrimps comprised the majority of the shrimp assemblage observed in controls and sampled by electroshocking (Tables 2 and 3). Again, no fishes were observed in controls; however, one individual each of three fish species (*Anguilla rostrata*, an unidentified gobiid, and *X. helleri*) and one crab (*E. sinuatifrons*) were sampled by electroshocking.

The mean size of individuals within each shrimp taxon decreased in a downstream direction (Fig. 1). Medium and large *Atya* were only found at the high-elevation site. Large *Xiphocaris* were found at the high- and mid-elevation sites, while large *Macrobrachium* were found at all sites (Fig. 1).

Leaf decay

Effects of shrimps on leaf decay varied significantly among sites ($F_{2,24}$ = 8.47, $P < 0.01$) and were therefore examined separately (Fig. 2). At the high-elevation site, leaf

Table 1. Carapace lengths and biomass of individuals of each taxon used in the laboratory experiment.

Taxon	Carapace length (mm)		Wet weight (g)	
	Range	Mean ± 1 SE	Range	Mean ± 1 SE
Atya	8–16	11.9±0.3	0.8–4.3	2.1±0.14
Macrobrachium	8–19	12.6±0.3	0.7–4.9	1.9±0.11
Xiphocaris	7–13	10.0±0.1	0.4–2.0	1.0±0.04

decay rate was significantly greater in the presence of shrimps than in their absence ($F_{1,8} = 8.23$, $P = 0.02$). In contrast, there was no significant difference in leaf decay rate between treatments at the mid-elevation ($F_{1,8} = 3.58$, $P = 0.10$) or low-elevation site ($F_{1,8} = 2.67$, $P = 0.14$). Excluding day 30 from statistical analyses did not affect significance.

Effects of shrimps on insects

The effect of shrimps on insect biomass on leaf packs also varied significantly among sites ($F_{2,24} = 6.04$, $P < 0.01$) (Fig. 3). At the high-elevation site, insect biomass was significantly greater in the control treatment ($F_{1,8} = 8.23$, $P = 0.02$). In contrast, the effect was opposite at the low-elevation site; insect biomass was significantly higher in the shrimp-exclusion treatment ($F_{1,8} = 6.75$, $P = 0.03$). The effect of shrimps on insect biomass at the mid-elevation site was not significant.

Insect shredders, ephemeropterans, and chironomids comprised 92% of the insect biomass over all sites. Insect shredders were rare and were composed of only two taxa: *Phylloicus* sp. (Trichoptera: Calamoceratidae) and *Phanocerus* sp. (Coleoptera: Elmidae). There was no effect of shrimps, site, or an interaction between the two on shredder biomass (Fig. 4).

Ephemeroptera were mostly leptophlebiids, with some baetids and caenids. The effect of shrimps on Ephemeroptera biomass in leaf packs also varied significantly among sites ($F_{2,24} = 5.70$, $P < 0.01$). When we examined each site separately, shrimp effects were significant only at the high-elevation site where mayfly biomass was greater in the presence of shrimps ($F_{1,8} = 12.40$, $P = 0.008$) (Fig. 4). Shrimps significantly reduced biomass of chironomids at all sites and there was a greater biomass of chironomids at the mid-elevation site (Fig. 4). Snails were only found at mid- and low-elevation sites and there was no shrimp effect on snail abundance ($F_{1,24} = 0.18$, $P = 0.68$).

Abiotic factors

At the high-elevation site, temperature ranged from 21 to 23°C, while water velocity averaged 0.015 m·s^{-1}. The mid-elevation site experienced temperatures of 23–28°C and higher flow velocity (0.024 m·s^{-1}). Mean flow rate at the low-elevation site was 0.043 m·s^{-1}. Temperature at this site ranged from 23 to 29°C. High-discharge events occurred during the study on days 2, 8, 17, and 27 (Fig. 2). These discharge events did not seem to have a dramatic effect on leaf decay with the exception of the storm on day 27 (Fig. 2). Despite differences in abiotic conditions, leaf decay rates were not different among sites in the shrimp-exclusion treatment ($F_{2,14} = 1.13$, $P = 0.35$).

Laboratory experiment

Leaves in the X and AX treatments lost significantly more mass than in all other treatments, except when all three genera were combined (XMA) (Fig. 5). In contrast, the amount of leaf mass lost from leaf packs in treatments A, M, AM, and XM was not significantly different from that in the control (Fig. 5).

In treatments with multiple genera of shrimp, we found differences between observed and predicted leaf mass loss based on leaf mass loss in single-taxon treatments (Fig. 6). The observed leaf mass loss was less than predicted in each treatment that contained *Macrobrachium*; however, this was only significant in treatment XM ($P = 0.04$) (Fig. 6), indicating that *Xiphocaris* breaks down less leaf mass with *Macrobrachium* present than when alone. Leaf mass loss in treatment AX was greater than predicted than when each genus was alone ($P = 0.04$) (Fig. 6), suggesting a positive interaction between *Atya* and *Xiphocaris*.

There were also differences in shrimp mortality among treatments (Fig. 7). Mortality of *Xiphocaris* was significantly higher in treatments with *Macrobrachium* (XM and XMA) than when alone (X) or with *Atya* (AX) (Tukey–Kramer, $P < 0.05$) (Fig. 7). There was also higher mortality of *Atya* with *Macrobrachium* than when alone, although not significantly higher.

Discussion

Rates of detrital processing varied along the elevational gradient as a function of the nature of the shrimp assemblage. We attribute the faster rate of leaf decay in controls at the high-elevation site primarily to shredding by *Xiphocaris* shrimp. Several lines of evidence support this. First, almost half the shrimps observed visiting leaf packs at the high-elevation site in the in situ experiment were *Xiphocaris*, and in the laboratory experiment, this species was able to break down leaves significantly faster than *Atya* or *Macrobrachium*. Furthermore, there was no difference in decay rates between laboratory treatments with *Atya* and *Macrobrachium* alone than in the no-shrimp control. Second, the only fish at this site is *S. plumieri*, which is algivorous (Erdman 1986) and was never observed entering the in situ control treatment. Third, insect shredders were rare and shredder biomass was not different between treatments. Insect biomass was significantly higher in controls at the high-elevation site; however, this was due to scraper–collector–gatherer mayflies (Ephemeroptera). Finally, a recent study conducted in a first-order stream near our high-elevation site also found that *Xiphocaris* significantly accelerated leaf litter decay (Crowl et al. 2001).

In addition to direct consumption, *Xiphocaris* may increase decay rates via facilitation of feeding by *Atya*. While atyid shrimps alone did not affect leaf decay rates in the laboratory experiment, rates were significantly faster than predicted when *Atya* and *Xiphocaris* were combined. When leaf material was partially shredded by *Xiphocaris*, the sweeping motion of atyid's chelipeds often removed pieces of leaf material from leaf packs (J.G. March, personal observation).

We attribute the lack of effect of *Xiphocaris* on leaf decay at the mid- and low-elevation sites to the greater abundance of *Macrobrachium*. Several lines of evidence from both the

Table 2. Mean (±1 SE) number of shrimps observed in the control treatment during 2-min observation periods.
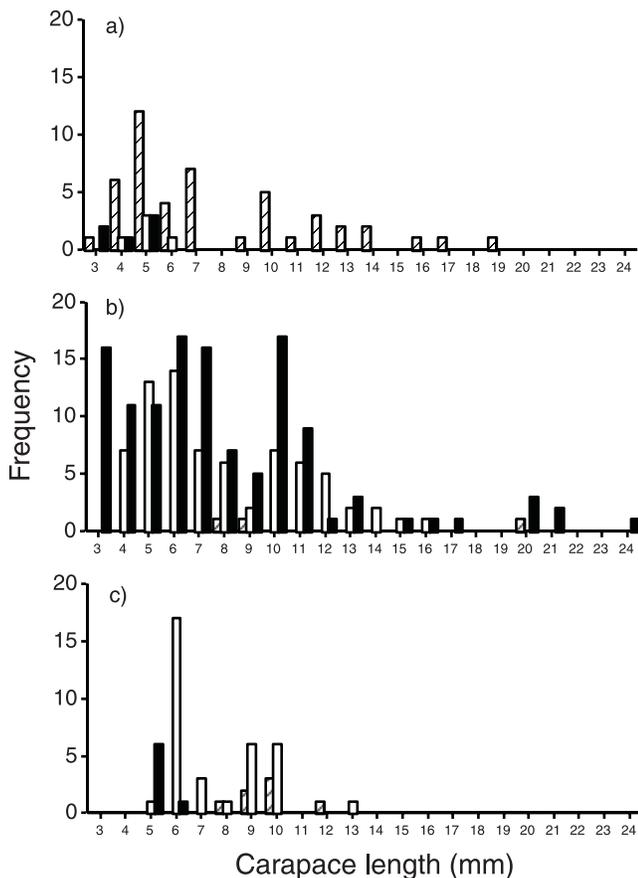
Site	Total shrimp[a]	Atya	Macrobrachium	Xiphocaris
High-elevation	0.62±0.17	0.12±0.05	0.02±0.02	0.13±0.06
Mid-elevation	0.80±0.23	0.00	0.17±0.05	0.63±0.22
Low-elevation	0.87±0.18	0.00	0.30±0.08	0.17±0.08

[a]Total shrimp observed in the control treatments includes unidentifiable shrimp.

Table 3. Mean (±1 SE) abundance (individuals·m^{-2}) and biomass (g wet weight·m^{-2}) of shrimps at each site obtained via electroshocking.

Site	Total shrimp	Atya	Macrobrachium	Xiphocaris
High-elevation				
Abundance	3.1±0.5	2.6±0.5	0.2±0.1	0.4±0.2
Biomass	3.09±1.09	2.39±1.12	0.38±0.31	0.31±0.13
Mid-elevation				
Abundance	6.1±1.0	0.3±0.2	4.1±0.9	1.8±0.7
Biomass	3.61±0.62	0.05±0.03	2.72±0.61	0.83±0.34
Low-elevation				
Abundance	6.9±0.9	0.1±0.3	6.2±0.7	0.4±0.3
Biomass	6.03±0.67	0.05±0.03	5.95±0.67	0.03±0.03

Fig. 1. Size–frequency distribution based on electroshocking of (*a*) *Atya*, (*b*) *Macrobrachium*, and (*c*) *Xiphocaris* shrimps at high- (hatched bars), mid- (open bars), and low-elevation sites (solid bars).

Fig. 2. Percentage of leaf pack mass remaining in control (squares, solid line) and shrimp-exclusion treatments (circles, broken line) and discharge (solid line, shading) at (*a*) high-, (*b*) mid-, and (*c*) low-elevation sites. Data are means ± 1 SE.
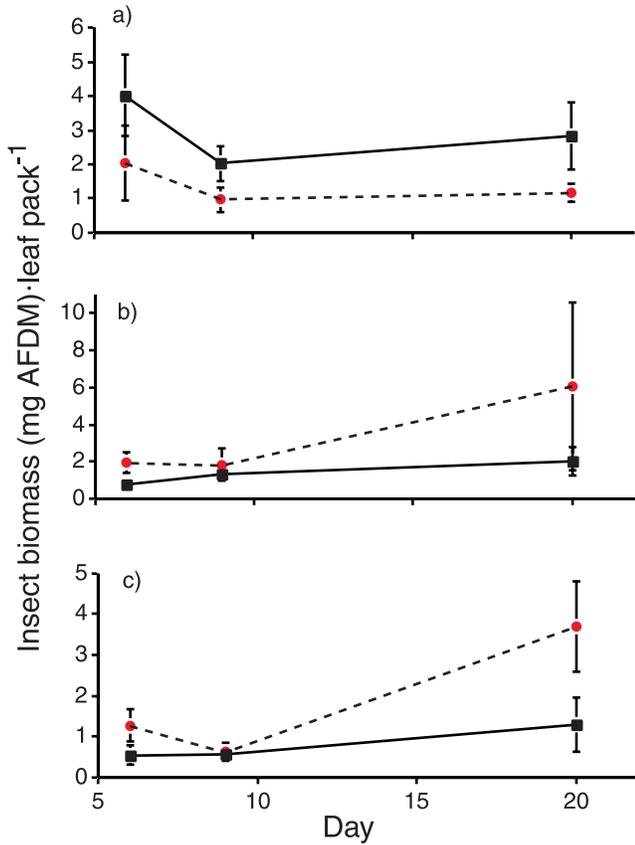

in situ and laboratory experiments support this hypothesis. First, *Macrobrachium* behaved aggressively towards other shrimp taxa in situ and in laboratory experiments. Second, in
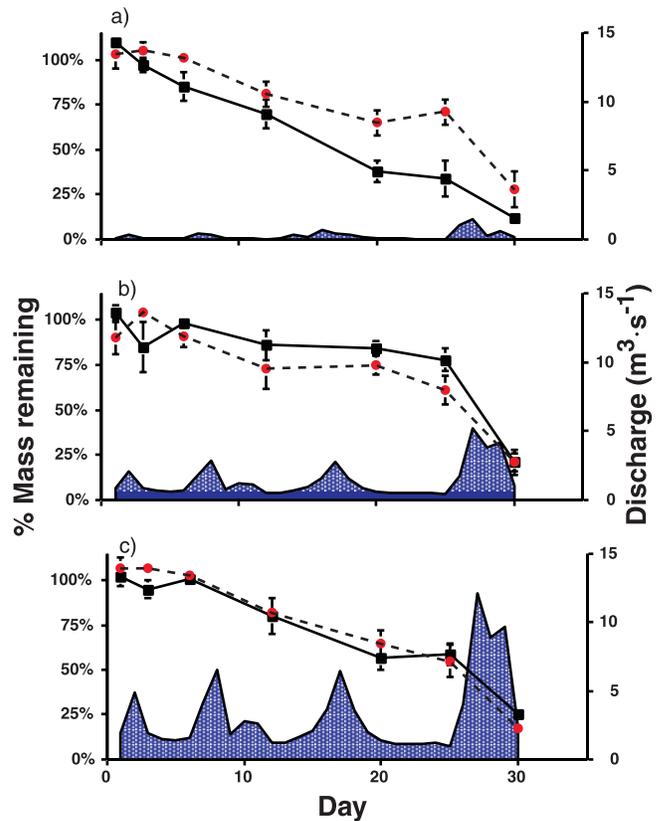
the laboratory experiment, *Xiphocaris* decomposed leaf litter faster than all other treatments. However, when *Xiphocaris* was combined with *Macrobrachium*, leaf decay rates were not different from the no-shrimp control. Third, decay in the
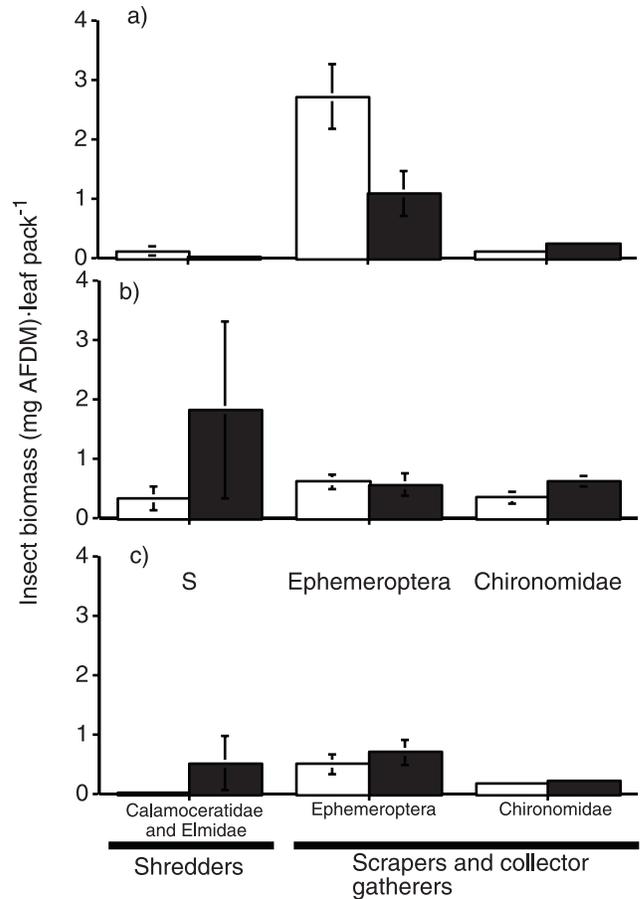
Fig. 3. Insect biomass (ash-free dry mass) in control (squares, solid line) and shrimp-exclusion treatments (circles, broken line) at (*a*) high-, (*b*) mid-, and (*c*) low-elevation sites. Data are means ± 1 SE.

Fig. 4. Biomass (ash-free dry mass) of insect shredders and the two most common taxa, ephemeropterans and chironomids, in control (open bars) and shrimp-exclusion treatments (solid bars) over all dates at (*a*) high-, (*b*) mid-, and (*c*) low-elevation sites. Data are means ± 1 SE.

Xiphocaris and *Macrobrachium* treatment was significantly less than predicted based on decay rates in treatments with each taxon alone, suggesting a negative interaction between these two taxa. Fourth, mortality of *Xiphocaris* was significantly higher in the combined *Macrobrachium* and *Xiphocaris* treatment than in treatments where each taxon was alone. Other studies have also noted the aggressive behavior of *Macrobrachium* and its ability to cause other shrimp taxa to seek shelter (e.g., Crowl and Covich 1994). Our results strongly suggest that a shrimp predator (*Macrobrachium*) affected the activity of a shrimp shredder (*Xiphocaris*), thus resulting in a slower rate of leaf decay. This relationship has also been observed between insect predators and shredders in temperate streams (e.g., Oberndorfer et al. 1984).

Alternative explanations and discrepancies between our laboratory and in situ experiments must be considered in evaluating our results. *Xiphocaris* was observed to enter control treatments in greater numbers at mid- and low-elevation sites, yet rates of leaf decay were not different between treatments. There are two possible explanations for this discrepancy and they are not mutually exclusive. First, *Xiphocaris* is omnivorous and may shift its diet among sites because of differences in relative availability of food resources. Second, although *Xiphocaris* was observed more frequently in controls at the lower sites relative to the high-

elevation site, they may have been moving out of controls as fast as they were moving in. We recorded how many shrimps were present in controls but did not measure time spent feeding. Thus, higher numbers of *Xiphocaris* at the mid- and low-elevation sites may have given rise to higher turnover of shrimps in controls, but high numbers of *Macrobrachium* disrupted their feeding, causing lower feeding pressure relative to the high-elevation site. The fact that we observed greater direct negative effects of *Macrobrachium* on *Xiphocaris* in the laboratory versus in situ experiment is not surprising. Typically, strong negative effects of predators on prey are found in cages with small mesh size or aquaria that are impermeable and allow no prey immigration and emigration (Cooper et al. 1990). However, studies that allow natural exchange of prey often find no effect of predators on prey abundance (e.g., Malmqvist 1993).

Many factors affect leaf decay, and the relative importance of each factor may change within and among streams (e.g., Minshall et al. 1983). Changes in abiotic factors among our three sites could potentially contribute to differences in leaf decay rates. Both temperature and water velocity increased in the downstream direction. However, we found no differences in leaf decay rates in shrimp-exclusion treatments

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Fig. 5. Differences in leaf decomposition among treatments in the laboratory aquarium experiment. Different lowercase letters above each treatment show statistical differences ($P < 0.05$). Taxa in each treatment: A, *Atya*; X, *Xiphocaris*; M, *Macrobrachium*. Data are means ± 1 SE.
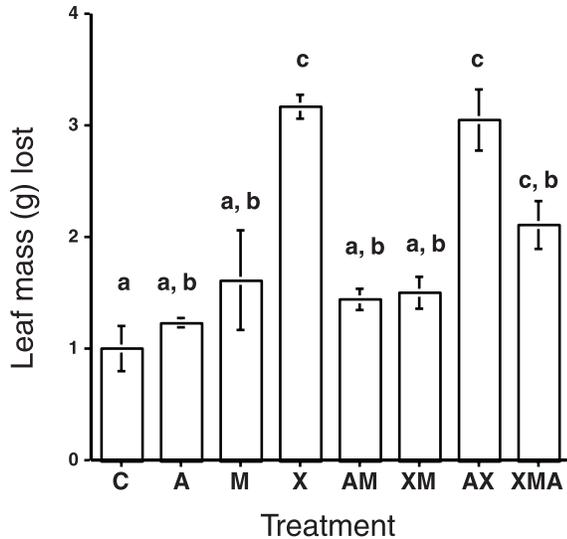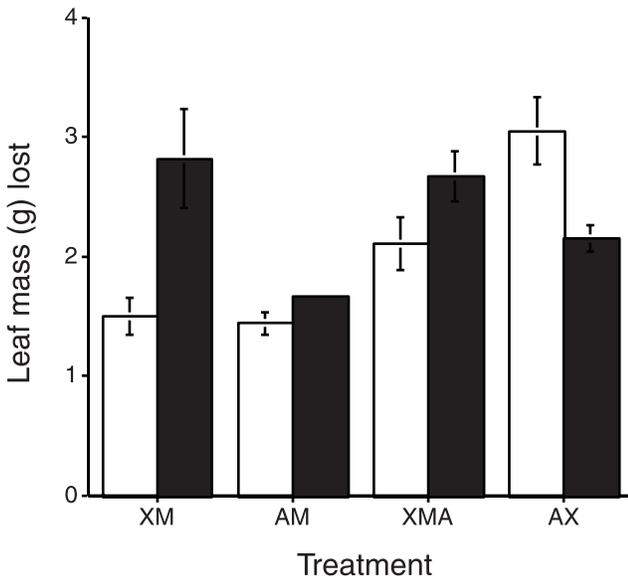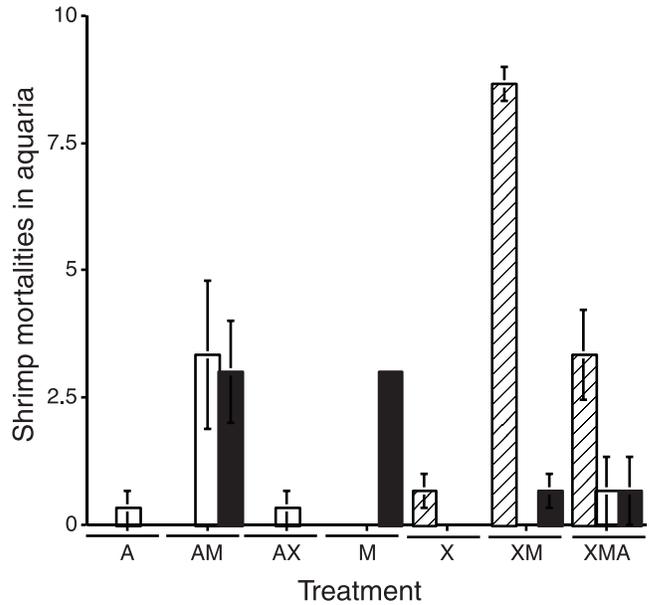

Fig. 7. Mortality of *Xiphocaris* (hatched bars), *Atya* (open bars), and *Macrobrachium* (solid bars) in different treatments. Taxa in each treatment: A, *Atya*; X, *Xiphocaris*; M, *Macrobrachium*.

Fig. 6. Differences between observed (open bars) and predicted leaf decomposition (solid bars) in multiple-taxa treatments. Predicted values greater than observed indicate a negative interaction between taxa (interference competition–predation). Predicted values less than observed indicate a positive interaction between taxa (facilitation). Taxa in each treatment: A, *Atya*; X, *Xiphocaris*; M, *Macrobrachium*.

among sites. In the absence of shrimps, therefore, differences in abiotic factors between sites had no effect on leaf decay.

In our study, insect shredders were not affected by shrimps and did not appear to play an important role in leaf decay. This finding contrasts with studies in temperate headwater streams where insect shredders play a major role in or-

ganic matter processing (Wallace and Webster 1996). However, studies in other tropical streams also suggest that insect shredders play less of a role in leaf decay compared with temperate streams (Irons et al. 1994; Ramirez and Pringle 1998; but see Benstead 1996).

Shrimps positively affected mayfly biomass. However, this effect of shrimps on mayflies was only observed at the high-elevation site. Mobile mayflies may be able to avoid predation by shrimps while benefitting from sediment removal (mostly by atyids), which increases access to underlying algae (Pringle et al. 1993) or biofilm on leaves. The absence of a positive response of ephemeropterans to shrimps at the mid- and low-elevation sites may have been due to the absence of large atyids and a consequent lack of any resource enhancement effect at these two sites.

In contrast with mobile mayflies, a greater biomass of sessile chironomids was found in the absence of shrimps at all sites. Less mobile chironomids may be more vulnerable to predation by shrimps. Two other studies conducted in tributaries near the high-elevation site have found similar results. Pringle et al. (1993) found a reduction of sessile chironomids and an increase in mobile mayflies in the presence of *Atya* and *Xiphocaris* on clay tiles at high-elevation sites. Likewise, Buzby (1998) found more mobile insect taxa in a stream dominated by shrimps and more sessile taxa in shrimp-poor streams.

Understanding effects of shrimps along stream continua is of increasing importance due to anthropogenic disturbances in rivers of Puerto Rico. Holmquist et al. (1998) demonstrated that high dams act as barriers that restrict shrimps to reaches below dams. Furthermore, Benstead et al. (1999) showed that water withdrawals from low-elevation reaches result in significant mortality of shrimp larvae during their migratory drift to estuarine larval habitat. Reduction or elimination of freshwater shrimps in headwaters could result in

dramatic changes in ecosystem processes such as leaf decay as well as changes in the quality and quantity of benthic organic matter and algal and invertebrate community composition (Pringle et al. 1999).

In summary, our in situ results showed that shrimps can significantly increase rate of leaf decay and increase or decrease insect biomass; however, these effects were dependent on location along the elevational gradient. The laboratory aquarium experiment showed that *Xiphocaris* was the most important shredder within the shrimp assemblage and suggested that interference competition and (or) predation by *Macrobrachium* can result in decreased litter processing by *Xiphocaris*. This study demonstrates that shrimp assemblages can have dramatic effects both on an important ecosystem process (leaf decay) and on community structure (benthic insect biomass). Moreover, our study illustrates the importance of examining the roles of species assemblages at multiple sites. Had we conducted our study at only one site, our interpretation of shrimp effects on leaf decay and insects would have been limited. Examining the roles of species assemblages over a variety of sites provides a more thorough understanding of their roles in ecosystems as well as insights into the potential consequences of human-induced shifts in species distributions.

Acknowledgments

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