Landscape patterns in top-down control of decomposition: omnivory disrupts a tropical detrital-based trophic cascade

Troy N. Simon,[1,2,8] Andrew J. Binderup,[1] Alex S. Flecker,[3] James F. Gilliam,[4] Michael C. Marshall,[1] Steven A. Thomas,[5] Joseph Travis,[6] David N. Reznick,[7] and Catherine M. Pringle[1]

[1]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*
[2]*Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602 USA*
[3]*Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*
[4]*Department of Biology, North Carolina State University, Raleigh, North Carolina 27695 USA*
[5]*School of Natural Resources, University of Nebraska–Lincoln, Lincoln, Nebraska 68583 USA*
[6]*Department of Biological Science, Florida State University, Tallahassee, Florida 32306 USA*
[7]*Department of Biology, University of California-Riverside, Riverside, California 92521 USA*

Abstract. Detrital-based trophic cascades are often considered weak or absent in tropical stream ecosystems because of the prevalence of omnivorous macroconsumers and the dearth of leaf-shredding insects. In this study, we isolate top-down effects of three macroconsumer species on detrital processing in headwater streams draining Trinidad's northern mountains. We separated effects of different macroconsumers by experimentally manipulating their temporal access to isolated benthic habitat over the diel cycle. We found no evidence that omnivorous macroconsumers, including a freshwater crab (*Eudaniela garmani*) and guppy (*Poecilia reticulata*), increased leaf decomposition via consumption. By contrast, above a waterfall excluding guppies, the insectivorous killifish, *Anablepsoides hartii*, reduced the biomass of the leaf-shredding insect *Phylloicus hansoni* 4-fold, which consequently reduced leaf decomposition rates 1.6-fold. This detrital cascade did not occur below the barrier waterfall, where omnivorous guppies join the assemblage and reduce killifish densities; here killifish had no significant effects on *Phylloicus* or decomposition rates. These patterns of detrital processing were also observed in upstream–downstream comparisons in a landscape study across paired reaches of six streams. Above waterfalls, where killifish were present, but guppies absent, leaf decomposition rates and *Phylloicus* biomass were 2.5- and ~35-fold lower, respectively, compared to measurements below waterfalls. Moreover, the strength of top-down control by killifish is reflected by the 20- and 5-fold reductions in variability (±SE) surrounding mean *Phylloicus* biomass and leaf decomposition rates in upstream relative to downstream reaches where no top-down control was detected. Findings show a clear, detrital-based trophic cascade among killifish, a leaf-shredding insect, and leaf decomposition rates. Results also show how omnivorous guppies disrupt this cascade by depressing killifish densities, thereby releasing invertebrate shredders from predation, and significantly increasing decomposition rates. Moreover, this combination of direct and indirect trophic interactions drives patterns in decomposition rates in stream networks at a landscape scale, resulting in significantly lower rates of decomposition above vs. below barrier waterfalls. Our findings reveal that omnivory can result in significant indirect effects on a key ecosystem process, illustrating the importance of these hidden trophic pathways in detrital-based systems and suggesting that resource control in tropical systems may be even more complex than previously envisioned.

Key words: Anablepsoides hartii; *detrital processing; detrital-based trophic cascade; killifish; leaf decomposition; leaf-shredding insects; macroconsumers; omnivory;* Phylloicus hansoni; Poecilia reticulata; *Trinidadian guppy; trophic cascade; tropical streams.*

INTRODUCTION

Although direct, top-down control of basal resources has been shown across many systems, much less is known about how basal resources are controlled indirectly through the interactions between predatory and omnivorous consumers. Omnivores feed across multiple trophic levels, making accurate prediction of top-down effects difficult (Pace et al. 1999). In the presence of omnivores, the indirect effects of predation on basal resources have been shown to weaken (Finke and Denno 2004) or disappear completely (Pringle and Hamazaki 1998, Bruno and O'Connor 2005). Although these studies have investigated the interactive effects of predatory and omnivorous macroconsumer species on primary production, few studies have attempted to understand these interactive effects in detrital-based food webs.

Top-down effects of macroconsumers in detrital-based "brown" food webs have received considerably less attention that those in "green" food webs. Nonetheless, strong top-down effects on detrital processing via trophic cascades have been reported in multiple habitats, including forests (O'Dowd et al. 2003), fields (Wu et al. 2011), ponds (Srivastava and Bell 2009), streams (Konishi et al. 2001), and artificial environments (Sitvarin and Rypstra 2014). In streams, the relative importance of direct and indirect top-down effects on detrital processing appear to change between temperate and tropical environments (Irons et al. 1994). Detrital-based trophic cascades are thought to be more prevalent in temperate streams in which large insectivorous fish and leaf-shredding insects are abundant (Ruetz et al. 2002). In contrast, in tropical streams, leaf-shredding insects are often less abundant and large omnivorous decapods and even fish can directly consume detritus (Rosemond et al. 1998, March et al. 2001). Despite several studies that make this point, to our knowledge, no studies have attempted to isolate the top-down effects of both predators and omnivores on detrital resources in macroconsumer communities in either temperate or tropical streams.

Measuring the interactive effects of macroconsumer species is challenging in natural communities, because species-specific effects are difficult to isolate experimentally in situ. In stream ecosystems, there is a general pattern of a decrease in numbers of macroconsumer species as elevation increases (Gilliam et al. 1993, Grossman et al. 2010). This gradient provides an opportunity to isolate the top-down effects of adding or subtracting macroconsumer species without the need to conduct logistically difficult and costly large-scale addition or removal experiments (sensu Carpenter et al. 1985).

In the headwater streams of Trinidad's Northern Range mountains, different macroconsumer assemblages occur above and below barrier waterfalls (Fig. 1). In headwater streams above barrier waterfalls, the dominant macroconsumers are predaceous (mostly insectivorous) killifish, *Anablepsoides hartii*, and the omnivorous freshwater crab, *Eudaniela garmani*. Below barrier waterfalls, the omnivorous guppy, *Poecilia reticulata*, joins these two taxa (Fig. 1). Guppies and killifish strongly interact in this system, such that killifish density (Fraser and Lamphere 2013) and growth (Walsh et al. 2011) are reduced when guppies are present, although exact mechanisms behind these effects remain unknown. Here we combine in situ experiments that manipulate macroconsumer access to the stream bed in a single focal stream, with a landscape-scale study across six streams to determine how species-specific effects interact to alter leaf litter decomposition.

Given that large omnivorous decapods and fish often directly consume detritus (Pringle and Hamazaki 1998), and given the general lack of specialist leaf-shredding insect taxa in tropical streams and rivers (March et al. 2001, Boyero et al. 2015), we predicted that (1) macroconsumers both above and below barrier waterfalls would directly enhance rates of leaf litter decomposition via consumption relative to rates measured in macroconsumer exclusion areas; (2) leaf decomposition rates would be highest below barrier waterfalls because of the additive effects of omnivorous guppies and crabs; (3) leaf-shredding invertebrate taxa (shredders) would play a minor role in leaf decomposition, rendering trophic cascades unlikely; (4) omnivorous crabs would have the strongest positive direct effects on leaf decomposition of all consumers present; and finally (5) the aforementioned longitudinal patterns in rates of leaf decomposition would be statistically detectable at the landscape scale (>420 ha) across paired upstream–downstream reaches of six streams.

METHODS

Study site

Our studies were carried out within the Caroni drainage on the southwestern slope of the Northern Range Mountains in Trinidad (10°39′ N, 61°18′ W). The Caroni is the largest drainage in Trinidad ($\approx$60,000 ha; Fig. 2). Low-order rivers within the Caroni are characterized by decreases in fish diversity with increasing elevation (Gilliam et al. 1993). High-elevation reaches above barrier waterfalls are characterized by killifish and crabs, with guppies joining this assemblage below barriers (Fig. 1). Additionally, whereas predatory killifish are primarily insectivorous (Fraser et al. 1999), guppies and crabs are omnivorous, feeding broadly on both animal and plant prey, as well as on fine detritus. Gut contents of guppies include benthic macroinvertebrates (predominantly midges from the family Chironomidae followed by caddisflies), algae (both filamentous and diatoms), as well as a high proportion of fine detritus (Zandona et al. 2011). Guppies also consume larval killifish (Fraser and Lamphere 2013). Less is known about the diet of freshwater crabs in Trinidad; however, crabs have been directly observed consuming leaf litter (Marshall et al. 2012) and studies have reported predatory behavior on both aquatic and terrestrial prey (Maitland 2003).
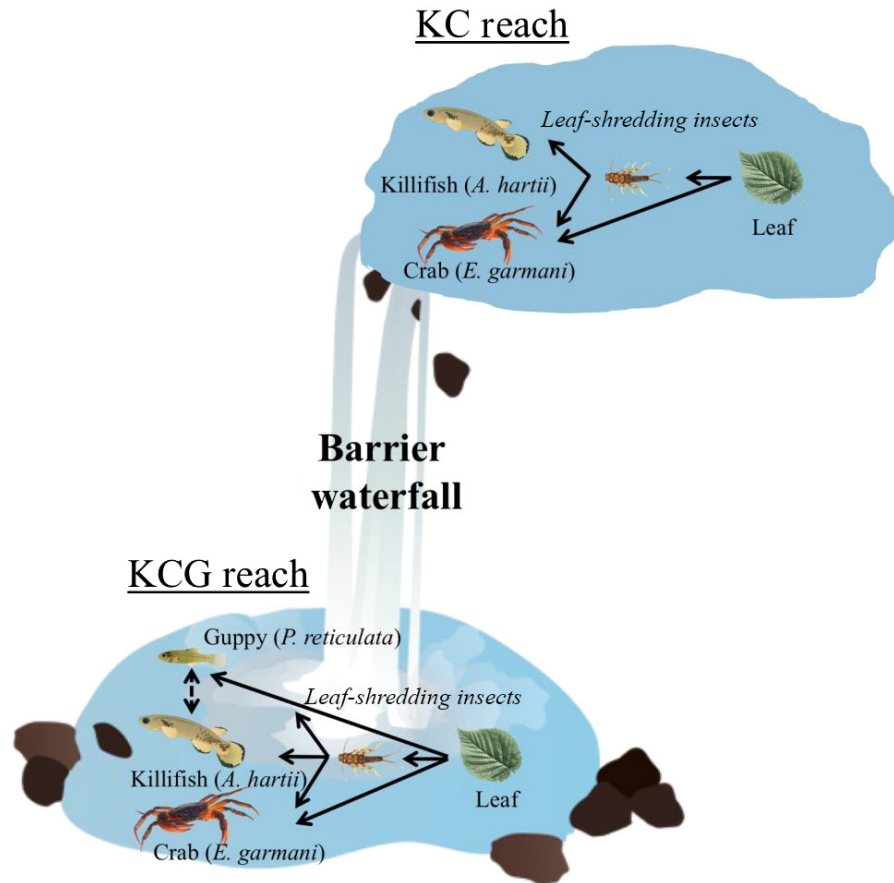
Fɪɢ. 1.   Conceptual diagram illustrating two detrital-based food webs in reaches separated by barrier waterfalls in the headwater streams of Trinidad's Northern Range mountains. KC reaches, located upstream of barrier waterfalls, contain killifish and crabs, whereas KCG reaches, located downstream of barrier waterfalls, contain killifish, crabs, and guppies. Guppies are unable to migrate up barrier waterfalls, so they are constrained to downstream reaches. Solid arrows indicate hypothesized energy movement up trophic levels; dashed arrows represent movement within a trophic level. [Color figure can be viewed at wileyonlinelibrary.com]

Killifish and crabs can disperse over land and bypass barrier waterfalls during wet periods and are commonly the only macroconsumer species present in the uppermost stream reaches (Gilliam et al. 1993). Stream reaches with killifish, crabs, and guppies (downstream KCG reaches) and those with only killifish and crabs (upstream KC reaches) are typically isolated by a single barrier waterfall (Fig. 1) and are often separated by <200 m. Consequently, stream reaches located immediately above and below barrier waterfalls have similar physical habitat and environmental characteristics, while maintaining distinct consumer assemblages (Walsh and Reznick 2009, Simon et al. 2017).

Experimental macroconsumer exclusion in focal stream

Experimental design.—We conducted experiments in two reaches of a focal study stream, the Caigual River, a third-order tributary of the Guanapo River within the Caroni drainage (Fig. 2). Experiments were run during the dry season when stream discharge was consistently low [upstream KC (22 February 22–23 March 2009) and downstream KCG (16 April–13 May 2009)] to reduce the confounding effects of seasonal variation in stream discharge between experiments. Temporal separation of experiments within the dry season was necessary because of logistical constraints. We assumed stable populations of macroconsumers between reaches because of stable base flow with no storm events, which can "reset" the benthic environment between experimental periods. The Caigual drains a heavily forested watershed (≈170 ha) that provides abundant canopy cover in KCG (25% canopy openness) and KC (11.3% canopy openness) reaches. The two study reaches (200 m long) of our focal experiment were isolated by a barrier waterfall and separated by ~200 m (located at elevations from ≈195 to 210 m above sea level [a.s.l.]). Reaches were characterized by a distinct pool and riffle structure, where stream benthic substrate was dominated by gravel and cobble, with some boulders and large woody debris at the edges of pools. Pools in the KCG reach were
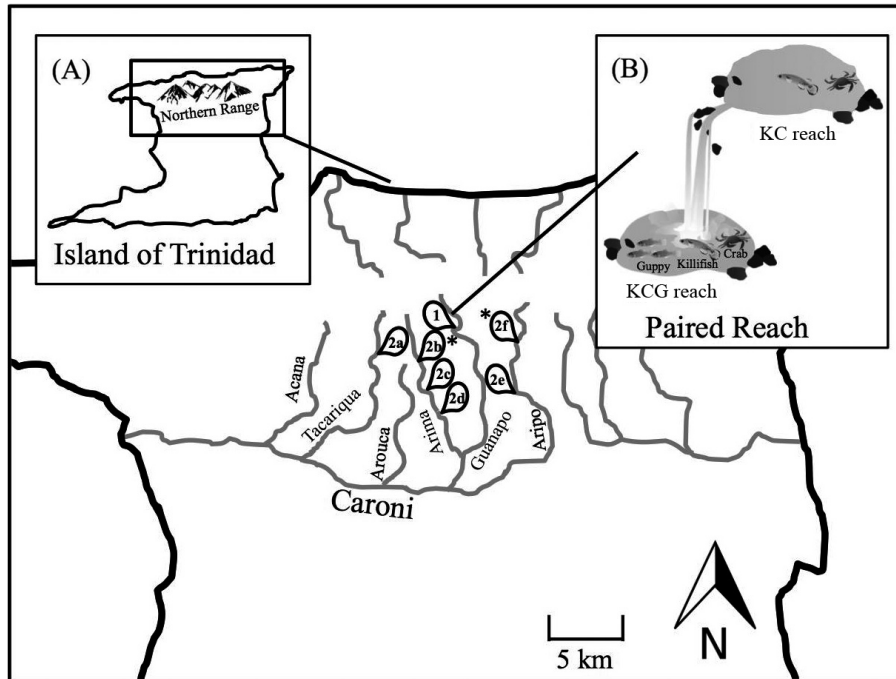
FIG. 2. Location of study sites in the Caroni drainage of Trinidad's Northern Range (A) for focal stream experiment (1) and landscape study (2a–2f). Each study site consists of paired reaches (B) containing killifish, crabs, and guppies (KCG) downstream, and killifish and crabs (KC) upstream. Guppies are naturally excluded from upstream KC reaches by barrier waterfalls. The asterisks denote study sites with "tufa" limestone complexes.

similar in depth, with slightly slower water velocity than pools in the upstream KC reach (22.9- vs. 25.5-cm depth and 0.23 vs. 0.33 m/s).

To isolate the top-down effects of macroconsumers (guppies, killifish, and crabs) on leaf decomposition rates, we used an underwater electric exclosure technique (modified from Pringle and Blake 1994), where macroconsumers are either allowed access (nonelectrified control) or excluded (electrified exclusion treatment). Electric exclosures excluded all macroconsumers and were accessible to aquatic invertebrates in the study streams (Simon et al. 2017). Underwater electric exclosures have been used to manipulate the presence and absence of aquatic consumers from localized areas of the stream bottom, in situ, across a range of taxa and geographic locations without introducing experimental artifacts associated with cages (Pringle and Hamazaki 1997, Greathouse et al. 2006, Connelly et al. 2008, Moulton et al. 2012).

In order to test the effectiveness of exclosures in our focal stream, macroconsumers (crabs, guppies, and killifish) were placed inside electrified quadrats and observed. Fishes exited quadrats immediately (2–4 s) after exposure to electric fields, while crabs generally exited within 30 s (Binderup, *unpublished data*). Macroinvertebrate taxa (e.g., odonates, trichopterans >5 mm) placed inside the electrified area were unaffected by the electric field and did not migrate out.

We separated the top-down effects of the three macroconsumer species by manipulating their temporal access to localized benthic patches over a diel cycle based on species-specific diel patterns of activity, using methods developed by Pringle and Hamazaki (1998) in a lowland Costa Rican stream. A study by Marshall et al. (2012), in the same focal study stream as our current study, found that killifish were active both day and night (cathemerally active), whereas guppies were diurnal and crabs nocturnal. Thus, we deployed four exclosure treatments: 24-h total exclusion, 12-h daytime exclusion, 12-h nighttime exclusion, and a 24-h access control treatment. Replicate sets of macroconsumer manipulation treatments (24-h access, 24-h exclusion, 12-h daytime exclusion, 12-h nighttime exclusion) were deployed in five separate pools across each of the two 200-m study reaches of the Caigual, resulting in 20 total treatment frames per reach. Electric frames excluded macroconsumers from small (0.125 m^2) benthic patches within each pool. Pools were located ≈40 m apart within each study reach.

Exclusion treatment frames were constructed of two concentric rectangles of 8-gauge solid copper wire, connected by plastic cable ties (outer rectangle 25 × 50 cm, inner 8 × 30 cm) (following Simon et al. 2017) We used Speedrite®1000 fence chargers (Tru-Test Limited, Auckland, New Zealand) set on the low power and slow pulse settings. These settings result in energy output of about 1

joule at ≈2-s intervals to power each exclusion frame. Control treatment frames were identically constructed but not electrified.

Macroconsumer visitation.— To confirm observations of diel macroconsumer activity patterns as reported in previous studies (Marshall et al. 2012), we estimated the density of macroconsumers over timed observation periods during both day and night. We made observations of each macroconsumer access treatment (control and nonelectrified 12-h treatment) for 1 h, spread across four 15-min observation periods per experiment: two diurnal and two nocturnal (totaling 10 h of observation per reach). Nocturnal observations were made on relatively clear nights with the moon in either first or last quarter phase. We recorded the number of each macroconsumer species present using visual point counts, made once per minute, over a 15-min period ($n = 15$ point counts) for each treatment. Before making observations, we waited 5 min to allow macroconsumers to resume normal activity. Visitation of each species was estimated as the average number of individuals observed across point counts, divided by the frame area (0.125 m^2) and number of minutes observed and converted to an hourly rate, resulting in units of individuals·m^{-2}·h^{-1} (following Marshall et al. 2012).

Leaf decomposition.— In order to assess macroconsumer effects on leaf decomposition rates, we used bagless packs of recently fallen leaves from the Guarumo tree, *Cecropia peltata* (hereafter referred to as *Cecropia*). *Cecropia* is a common Neotropical tree genus found in riparian areas across Central and South America and throughout many of the islands of the Caribbean Basin (Rickson 1977), including Trinidad. We chose *Cecropia* because it is a common riparian tree, and because its leaves tend to be high in nutrients and low in secondary compounds (Zou et al. 1995), allowing for significant decomposition to occur during our 29-d experiment. Leaves were oven dried at 40°C for at least 3 d and then grouped in batches of 5 g, weighed to the nearest 0.01 g, and clipped together at the petiole using a binder clip (following Marshall et al. 2012) to allow access by larger leaf-shredding consumers (e.g., crabs and guppies). Leaf packs were attached to copper wire frames using plastic zip ties, and one pack from each frame was collected after 4, 8, 15, 22, and 29 d by placing a 63-μm mesh net downstream of the pack while removing it from the frame to avoid loss of invertebrates or leaf material. Retrieved leaf packs were rinsed over a 250-μm sieve, and all remaining leaf material was placed in preweighed paper bags. Bags were dried at 40°C for at least 3 d and weighed to the nearest 0.01 g. The average dry mass lost in handling packs was subtracted from the initial dry mass of leaf packs. We calculated the percent of leaf dry mass remaining at each collection date using initial and final dry mass measurements.

Leaf invertebrates.— We collected macroinvertebrates from each leaf pack to assess the overall invertebrate community present, and, in particular, to determine how experimental treatments impacted the biomass of leaf-shredding insects associated with leaf packs. Invertebrate samples were dyed with Rose Bengal stain for 24 h and sorted; all invertebrates >1 mm were identified to the lowest taxonomic resolution possible (usually genus) using taxonomic keys by Merritt et al. (2008) and Perez (1988). All invertebrates >1 mm were also assigned to functional feeding groups, as described by Merritt et al. (2008). We used length–mass regressions (Benke et al. 1999, Becker et al. 2009) to estimate invertebrate biomass in each leaf pack, which was then divided by the final leaf mass of the pack on the corresponding sample date to estimate resource-specific biomass (RSB).

Landscape scale study

Study design.— We expanded our studies to six additional streams draining subwatersheds within the larger Caroni drainage (≈14,053 ha; Fig. 2) to determine if longitudinal patterns in rates of leaf decomposition observed in the focal stream would be statistically detectable at a larger landscape scale. We measured leaf decomposition rates and the abundance of macroconsumers in paired upstream KC and downstream KCG reaches (Fig. 2) of the six study streams. Our original focal stream was not included in this study because guppies were introduced soon after the completion of our experiment as part of a larger guppy evolution project (Simon et al. 2017).

Leaf packs were deployed and collected after 4, 8, 15, 22, and 29 d in all six streams simultaneously under base-flow conditions toward the end of the dry season (23 April–21 May 2014). *Cecropia* leaf packs were placed in three replicate pools of each stream reach (separated by >50 m) both up- and downstream of waterfalls ($n = 6$ replicate pools per stream). Paired reaches within streams were separated by no more than 200 m, and elevation was similar among subwatersheds, ranging from 180 to 240 m a.s.l.

All sites contained heavily forested subwatersheds that ranged from ≈53 to 105 ha in drainage area. Similar to the Caigual subwatershed where we conducted our exclosure experiments, all study reaches were characterized by a distinct pool and riffle structure, with stream benthic substrate dominated by gravel and cobble, and some boulders and large woody debris at the edges of pools. Two of our six streams (Fig. 2, 2b, 2f) were characterized by distinct visually striking bedrock geology consisting of limestone complexes termed "tufa" associated with alkaline water (Wetzel 2001). These systems have very low phosphorous concentrations in the water column because of coprecipitation with calcium carbonate, which may exaggerate P limitation in these stream communities (Day and Chenoweth 2004). For each pool,

we estimated percent canopy openness, percent leaf cover (visually estimated for entire pool), and areal biomass of leaf litter from randomized transects (0.125 m wide) across pools. We also measured discharge (m^3/s) at the downstream end of each reach, percent saturation of dissolved oxygen, and water temperature using a YSI Pro2030 (Yellow Springs, Ohio) at the downstream end of each pool, and depth and current velocity near leaf packs using a Marsh McBirney Flo-Mate 2000 (Loveland, Colorado).

Macroconsumer abundance/density and leaf invertebrate biomass.—Fish abundance (killifish and guppies) was estimated by placing two baited minnow traps in each pool ($n = 6$ per stream) for 10 min. All captured fish were counted and promptly returned to a pool, yielding a catch per unit effort (CPUE; Seber 1982). Total catch in each of the two traps in a pool was combined for CPUE calculation. Crabs are primarily nocturnal and often too large to be captured in minnow traps, and thus, their density was estimated using nocturnal transect counts across a 100-m stream reach. One transect count was conducted in each of the two reaches per stream ($n = 12$ total transects), yielding number of crabs per meter of stream length.

Following the rationale of our focal stream experiment, leaf invertebrates were also collected from each leaf pack. Identification and enumeration of invertebrates also followed methods used in the focal stream experiment.

Statistical analysis

Experimental macroconsumer exclusion in focal stream.—Because experiments in downstream KCG and upstream KC reaches were spatially and temporally isolated from each other, we compared relative treatment effects within reaches only and did not make statistical comparisons between KCG and KC manipulations. Macroconsumer visitation data from diurnal and nocturnal observations within each reach were compared using paired *t*-tests to investigate the effects of diurnal vs. nocturnal activity (i.e., full access and daytime access observed during diurnal periods, and full access and nighttime access during nocturnal periods) and data was paired by replicate pool. The rate of leaf decomposition (percentage of mass lost per day) was determined using a linear fit because mass loss through time was not strongly exponential. Differences in leaf decomposition rate among all macroconsumer access treatments were first examined with the use of a one-way ANOVA where treatment was a fixed effect and pool was a random block effect. Significant treatment effects led to examination of pairwise differences in decay rates using Tukey–Kramer honestly significant difference (HSD) post hoc tests. To test our prediction that trophic cascades were unlikely in this system, we compared the biomass of any specialist leaf-shredding insects (milligrams invertebrate dry mass/milligrams leaf material remaining) among treatments using one-way analysis of variance (ANOVA) and Tukey–Kramer HSDs. Leaf decomposition rate and leaf-shredding invertebrate biomass data were natural log transformed to meet the assumptions of normality.

Landscape scale study.—Macroconsumer CPUE abundance data between reaches were compared using one-way ANOVA, where reach was the fixed effect and stream was the random block effect. The rate of decomposition (% mass lost per day) was determined using a linear fit because mass loss through time was not strongly exponential. Leaf decomposition rates between reaches were compared using one-way ANOVA where reach was the fixed effect and stream was the random block effect. Following the rational from our focal stream experiment, we also compared the biomass of any specialist leaf-shredding insects between reaches using the same methods described above for leaf decomposition rates. Leaf decomposition rate and leaf-shredding invertebrate biomass data were natural log transformed to meet the assumptions of normality. All statistical analyses were conducted using R (R Version 3.0.1).

RESULTS

Experimental macroconsumer exclusion in focal stream

Macroconsumer visitation.—No fish or crabs were observed in either the 24-h or 12-h exclusion treatments. Additionally, treatment visits within the same diel period were similar, such that during the day macroconsumers visited control frames and daytime access at a similar rate and at night macroconsumers visited control frames and nighttime access frames similarly. Although previous studies in the Caigual River (Gilliam et al. 1993) recorded very low numbers of the Pimelodid catfish, *Rhamdia quelen*, no individuals were observed in experimental pools of our focal study stream during the study.

In the downstream KCG reach, guppies were predominantly diurnally active ($t_4 = 4.20$, $P = 0.01$; daytime 29.23 ± 6.90 [mean $\pm$ SE] individuals$\cdot m^{-2}\cdot h^{-1}$; nighttime 0.11 ± 0.11). Only one individual guppy was observed active at night during our study. Killifish were active both day and night, and we found no significant differences in their diel activity in both KCG ($t_4 = 1.95$, $P > 0.05$; daytime 1.39 ± 0.49 individuals$\cdot m^{-2}\cdot h^{-1}$; nighttime 4.69 ± 1.37 individuals$\cdot m^{-2}\cdot h^{-1}$) and KC reaches ($t_4 = 1.70$, $P > 0.05$; daytime 2.24 ± 1.31 individuals$\cdot m^{-2}\cdot h^{-1}$; nighttime 5.44 ± 2.08 individuals$\cdot m^{-2}\cdot h^{-1}$). Counter to previous studies, in the KCG reach, crabs were observed at similar rates during day and night ($t_4 = 0.13$, $P > 0.05$; daytime 0.64 ± 0.26 individuals$\cdot m^{-2}\cdot h^{-1}$; nighttime 0.59 ± 0.46 individuals$\cdot m^{-2}\cdot h^{-1}$) but, in the KC reach crabs were

significantly more active at night ($t_4 = 3.65$, $P = 0.02$; daytime 0.64 ± 0.52 individuals·m^{-2}·h^{-1}; nighttime 7.57 ± 2.20 individuals·m^{-2}·h^{-1}). We should note, however, that during the day crabs in the KCG reach were typically hiding around leaf packs within control frames rather than actively foraging.

Leaf decomposition rates.—In the downstream KCG reach we found no evidence of our original prediction that macroconsumers would increase leaf decomposition rates where they had access via direct consumption, relative to areas where macroconsumers were experimentally excluded. Decomposition rates of *Cecropia* in control treatments (full access) were similar to those in all exclusion treatments ($F_{3,16} = 0.023$, $P = 0.85$; Fig. 3a).

In contrast to our original prediction, decomposition rates of *Cecropia* leaf packs were reduced in the upstream KC reach in the presence of killifish and crabs ($F_{3,16} = 6.67$, $P = 0.004$; Fig. 3b). Tukey HSD post hoc tests showed that decomposition rates were reduced by 40% in controls relative to the three exclusion treatments ($P < 0.03$; Fig. 3b). Additionally, results suggest that killifish rather than crabs reduced decomposition rates, because rates were similar in diurnal (excluding killifish)

and nocturnal (excluding crabs and killifish) treatments ($P > 0.1$).

Invertebrate community composition.—Invertebrate communities in both reaches were similar in terms of invertebrate diversity but differed in abundance and biomass (Table 1). In the upstream KC reach we identified 3,458 individuals from 15 distinct taxa with an average total resource specific biomass (RSB) of 59.65 ± 9.07 (SE; milligrams of dry mass per gram of *Cecropia* $\pm$ SE). In the downstream KCG reach we identified 1,364 individuals from 18 distinct taxa with an average total biomass of 86.90 ± 31.57 (SE; milligrams of dry mass per gram of *Cecropia* $\pm$ SE).

After assigning functional feeding groups we identified a single species of leaf-shredding insect, the caddisfly, *Phylloicus hansoni* (hereafter *Phylloicus*), as the single greatest contributor to insect biomass in both reaches (Table 1). In the downstream KCG reach *Phylloicus* made up 70.9% of the total biomass and the next greatest contributor had an eightfold lower percentage of biomass (Trichopteran from the genus *Chimarra*; Table 1). Upstream in the KC reach *Phylloicus* made up 41.6% of the total biomass and the next greatest
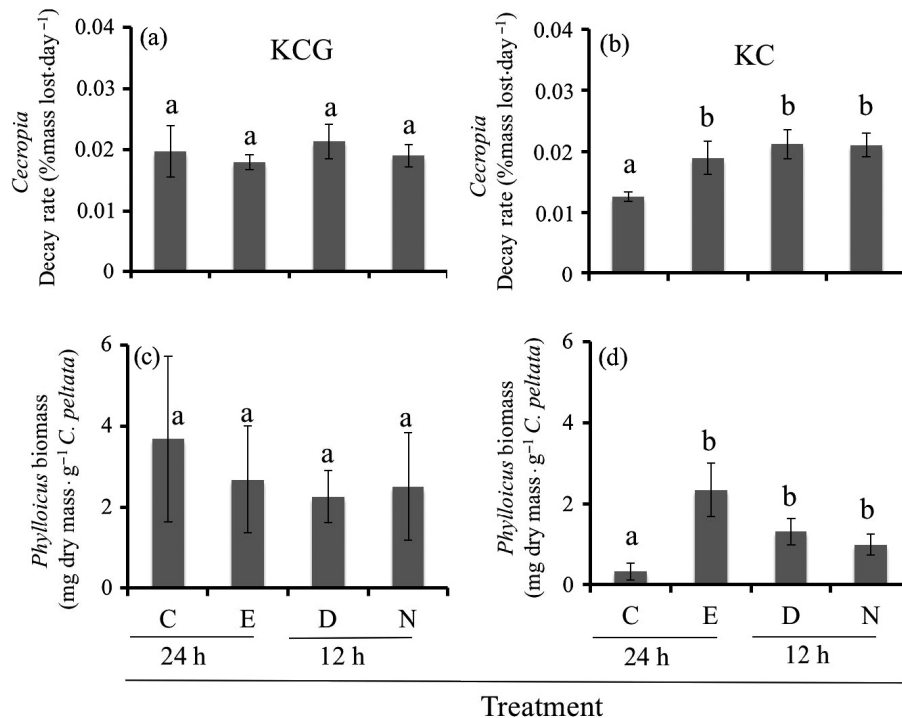

FIG. 3. Mean ($\pm$SE) for (a,b) decay rate of *Cecropia peltata* leaves (percentage of mass lost per day) and (c,d) resource-specific biomass of *Phylloicus hansoni* (milligrams of dry mass per gram of *Cecropia*) for the focal stream experiment, where 24-h treatments allow full macroconsumer access [control (C)] or completely exclude macroconsumers [electric (E)]. Twelve-hour treatments exclude access to either diurnally active [day (D)] or nocturnally active [night (N)] macroconsumers. Results from the downstream reach (a,c) containing killifish, crabs, and guppies (KCG) and the upstream reach (b,d) containing killifish and crabs (KC) across replicate pools ($n = 5$). Letters between bars indicate results of post hoc Tukey–Kramer honestly significant difference tests, with different letters indicating significant within-reach differences in pairs of means between treatments.

TABLE 1. Invertebrate community composition on *Cecropia peltata* leaves in the exclosure experiment. Table shows functional feeding group (FFG), order, and lowest taxonomic grouping for both KCG (killifish, crabs, and guppies) and KC (killifish and crabs) reaches. Mean biomass (±SE) of each taxon were collected from each replicate pool ($n = 5$). For each pool biomass was summed across experimental treatments ($n = 4$) and sampling periods ($n = 5$) for the 4-week experiment. Percent (%) biomass indicate contributions of each taxon to the overall biomass and abundance of the entire community. *Phylloicus hansoni* was the only specialist leaf-shredding invertebrate (shredder) found in the community.

FFG	Order	Lowest taxonomic grouping	Biomass (milligrams of dry mass per gram of *Cecropia* ± SE)		% biomass	
			KCG	KC	KCG	KC
Collector–filterer	Trichoptera	*Chimarra* spp.	7.09 (2.30)	0.00 (0.00)	8.16	0.00
Collector–gatherer	Coleoptera	Elmidae	1.27 (0.51)	5.48 (1.40)	1.46	9.19
	Diptera	Ceratopogonidae	0.90 (0.16)	0.17 (0.04)	1.04	0.28
		Chironomidae	3.56 (0.53)	7.17 (0.70)	4.10	12.01
		Tipulidae	0.00 (0.00)	0.03 (0.01)	0.00	0.04
	Ephemeroptera	*Baetis* spp.	0.15 (0.07)	0.65 (0.13)	0.17	1.08
		Baetodes spp.	0.04 (0.04)	0.82 (0.43)	0.05	1.38
		Leptohyphes spp.	0.36 (0.14)	2.83 (0.50)	0.42	4.75
		Tricorythodes spp.	0.40 (0.17)	0.19 (0.07)	0.47	0.32
	Trichoptera	Glossosomatidae	0.18 (0.07)	0.00 (0.00)	0.21	0.00
		Hydropsychidae	0.06 (0.03)	0.00 (0.00)	0.07	0.00
		Nectopsyche	0.10 (0.05)	0.00 (0.00)	0.12	0.00
Predator	Diptera	Tanypodinae	4.95 (3.57)	1.15 (0.24)	5.69	1.93
	Odonata	Argia	3.02 (0.94)	9.11 (1.97)	3.47	15.28
		Hetaerina	2.56 (0.48)	3.04 (0.82)	2.94	5.09
		Libellulidae	0.12 (0.09)	0.00 (0.00)	0.14	0.00
	Plecoptera	*Anacromeuria* spp.	0.20 (0.20)	2.25 (1.74)	0.23	3.77
Scraper	Ephemeroptera	*Thraulodes* spp.	0.30 (0.12)	1.93 (0.35)	0.35	3.23
Shredder	Trichoptera	*Phylloicus hansoni*	61.63 (31.87)	24.84 (5.57)	70.92	41.64
		Total	86.90 (31.57)	59.65 (9.07)		

contributor made up 2.5-fold less percentage of biomass (damselfly of the genus *Argia*; Table 1).

Phylloicus biomass and size structure.—We found no effect of macroconsumer presence or absence on *Phylloicus* biomass in any of the macroconsumer manipulation treatments in the downstream KCG reach ($F_{3,16} = 0.149$, $P = 0.94$; Fig. 3c). Conversely, in the upstream KC reach, *Phylloicus* biomass was significantly reduced in the presence of killifish and crabs ($F_{3,16} = 9.25$, $P = 0.001$; Fig. 3d). Tukey HSD post hoc tests showed that *Phylloicus* biomass was reduced 4× in controls relative to the three exclusion treatments ($P < 0.03$; Fig. 3d). *Phylloicus* abundance (total number per gram of leaf pack) also showed the same patterns as biomass in response to treatments. Similar to leaf decomposition findings, our results strongly suggest that killifish rather than crabs reduced *Phylloicus* biomass, because biomass was similar in treatments excluding either diurnal (killifish; 12-h daytime exclusion) or nocturnal (killifish + crabs; 12-h nighttime exclusion) macroconsumers ($P > 0.1$). Moreover, we should note that one of us (TNS) observed killifish readily consuming *Phylloicus* when dropped into the stream if the head capsule was exposed from the leaf case. Finally, in the presence of macroconsumers, *Phylloicus* were 70%

smaller (control treatments; length) relative to the three exclusion treatments ($F_{3,371} = 4.96$, $P = 0.002$; Fig. 4b), which mirrored trends in *Phylloicus* biomass, suggesting the largest individuals were preferentially consumed. In contrast, we found no significant differences in *Phylloicus* length between treatments in the downstream KCG reach ($P > 0.05$; Fig. 4a).

Finally, *Phylloicus* significantly increased the rate of leaf decomposition. In the downstream KCG reach, where *Phylloicus* abundance and biomass were high, we found a significant positive correlation between *Phylloicus* biomass and *Cecropia* litter decomposition rates ($R^2 = 0.41$, $P = 0.002$; Fig. 5a). In the upstream KC reach, one large outlier was identified in our data set (Cook's distance >1), and we report on a statistical test with the outlier removed (Cook 1977). In the upstream KC reach Phylloicus biomass was also positively correlated with decomposition rates ($R^2 = 0.30$, $P = 0.01$; Fig. 5b).

Landscape-scale study

Physiochemical characteristics.—We did not find any consistent differences in the physiochemical characteristics of pools in reaches above (KC) vs. below (KCG) waterfalls (Table 2), a result consistent with previous
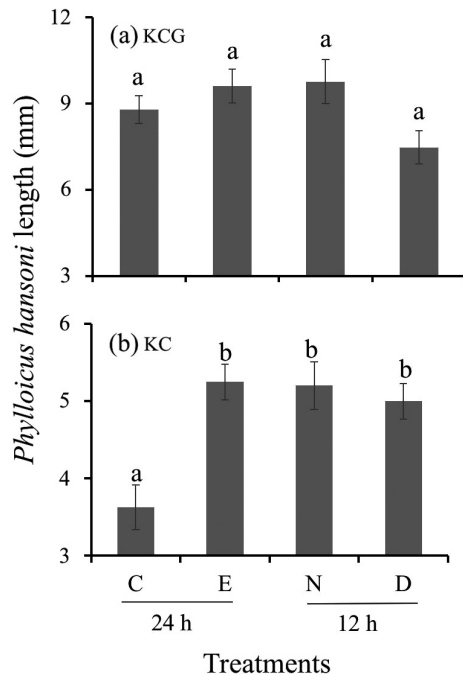
FIG. 4. Mean (±SE) for *Phylloicus* length (mm) for the focal stream experiment in downstream KCG or upstream KC reaches, where 24-h treatments allow full macroconsumer access [control (C)] or completely exclude macroconsumers [electric (E)]. Twelve-hour treatments exclude access to either diurnally active [day (D)] or nocturnally active [night (N)] macroconsumers. Different letters among bars indicate significance differences ($P < 0.05$) among treatments.

studies in this system (Walsh and Reznick 2009, Simon et al. 2017). This similarity indicates that differences in macroconsumer assemblage above and below waterfalls were not confounded with differences in physiochemical characteristics within streams. All abiotic characteristics varied much more among stream replicates than within streams (Table 2). Four of the eight physiochemical characteristics varied by more than an order of magnitude (Table 2), including canopy openness, discharge, standing stocks of coarse benthic organic matter (CBOM), and water velocity, and percent leaf litter cover within pools varied by more than fivefold among streams (Table 2).

Leaf decomposition and macroconsumer density/abundance.—*Cecropia* leaves decayed 2.5× faster in downstream KCG reaches relative to upstream KC reaches ($F_{1,5} = 9.85$, $P = 0.03$; Fig. 6a). We found similar crab density ($F_{1,5} = 0.78$, $P = 0.42$) in both downstream KCG and upstream KC reaches (Table 3). Killifish CPUE abundance was approximately 4× higher in upstream KC reaches relative to downstream KCG reaches ($F_{1,5} = 27.97$, $P = 0.003$; Table 3). Finally, in downstream KCG reaches we captured approximately 3× more individual guppies than killifish in baited traps (Table 3).
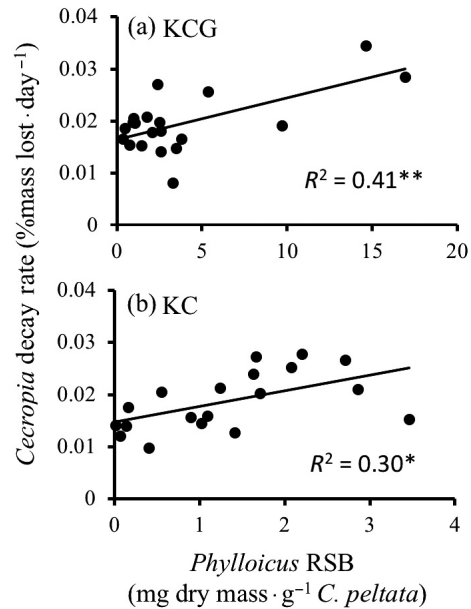

FIG. 5. Bivariate fit of decay rate for leaves of *Cecropia peltata* (percentage of mass lost per day) and resource-specific biomass (RSB) of *Phylloicus hansoni* (milligrams of dry mass per gram of *Cecropia*) from each focal stream experiment conducted in either (a) downstream killifish, crab, and guppy (KCG) reach or (b) upstream killifish and crab (KC) reach. Statistical significance of correlation noted by * ($P < 0.05$) and ** ($P < 0.01$).

Phylloicus abundance and biomass.—Across our six study streams, we found a total of 751 *Phylloicus* on leaf packs in downstream KCG reaches and just 26 total individuals on leaf packs above barrier waterfalls in KC reaches. *Phylloicus* biomass was 35× higher in downstream KCG reaches (below waterfalls) vs. upstream reaches ($F_{1,5} = 17.19$, $P = 0.009$; Fig. 6b). Finally, just as in the experimental study, we found a significant positive correlation between *Phylloicus* biomass and leaf litter decomposition rates in the downstream KCG reach, where *Phylloicus* biomass was high ($R^2 = 0.57$, $P = 0.01$; Fig. 7a), however, we found no relationship in the upstream KC reach where *Phylloicus* biomass was more than an order of magnitude lower ($P = 0.61$; Fig. 7b). Moreover, we should note that *Phylloicus* were so dense on leaf packs in downstream KCG reaches that one of us (TNS) frequently observed active shredding of leaf packs by *Phylloicus*.

DISCUSSION

We documented a strong, detrital-based trophic cascade in the upper headwater reaches of streams draining the southern slope of Trinidad's Northern Range mountains, which is contrary to our expectations based on previous studies in tropical streams. We also found no experimental or descriptive evidence to support our first prediction that omnivorous macroconsumers would

TABLE 2. Physiochemical characteristics [means ± SE (min, max)] of pools ($n = 6$) in paired reaches of six streams in the landscape study measured on the final day of the study.

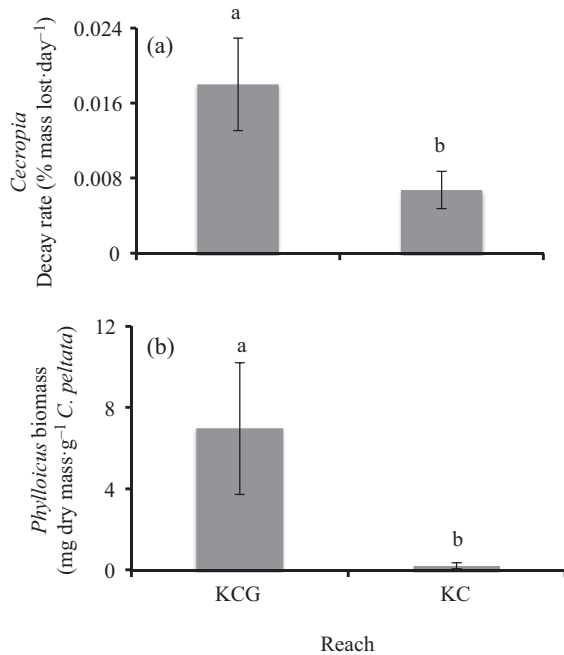|	Physiochemical characteristics							
Reach	Canopy openness (%)	Coarse benthic organic matter (g/m^2)	Depth (cm)	Q (m^3/s)	Dissolved oxygen (% saturation/L)	Leaf cover (%)	Temp (°C)	Velocity (m/s)
KCG	4.25 ± 1.41 (1.3, 15.86)	112.93 ± 21.46 (23.52, 394.86)	13.78 ± 1.09 (8.0, 18.0)	0.044 ± 0.012 (0.001, 0.008)	79.9 ± 43.16 (66.9, 89.9)	46.94 ± 8.08 (15, 80)	23.78 ± 0.16 (23.3, 24.4)	0.0049 ± 0.001 (0.00, 0.009)
KC	4.64 ± 1.13 (0.26, 12.48)	161.7 ± 25.71 (48.80, 480.25)	14.22 ± 1.0k1 (10.5, 18.5)	0.042 ± 0.011 (0.001, 0.007)	81.64 ± 3.30 (56.9, 91.7)	43.61 ± 8.04 (15, 80)	23.69 ± 0.18 (23.1, 24.4)	0.0047 ± 0.001 (0.00, 0.01)

FIG. 6. Mean (±SE) for (a) decay rate for *Cecropia peltata* leaves (percentage of mass lost per day) and (b) resource-specific biomass of *Phylloicus hansoni* (milligrams of dry mass per gram of *Cecropia*) in the landscape study ($n = 6$ streams). Different letters among bars indicate significance differences ($P < 0.05$) among treatments.
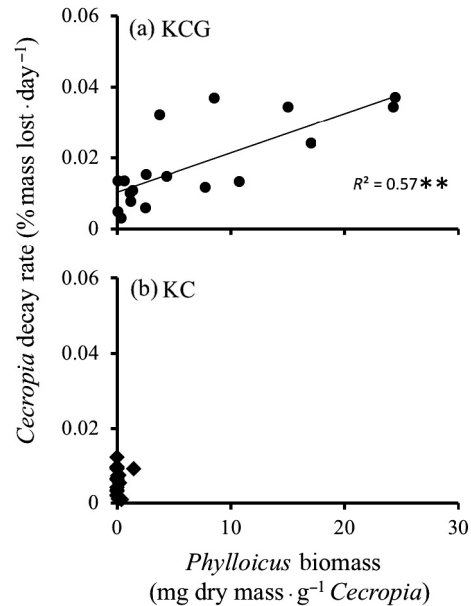

FIG. 7. Bivariate fit of decay rate for *Cecropia peltata* leaves (percentage of mass lost per day) and resource-specific biomass of *Phylloicus hansoni* (milligrams of dry mass per gram of *Cecropia*) in the landscape study across six streams with paired (a) downstream killifish, crab, and guppy (KCG) reaches and (b) upstream killifish and Crab (KC) reaches. Statistical significance of correlation noted by * ($P < 0.05$) and ** ($P < 0.01$).

TABLE 3. Mean macroconsumer abundance (killifish and guppies) and density (crabs) in the landscape study of paired reaches of six streams in the Caroni drainage. Abundance was estimated using catch per unit effort [CPUE (±SE)], for killifish and guppies, and transect observations [individuals per meter (±SE)] for crabs. Bolded values represent significant differences ($P < 0.05$) between KCG and KC reaches for each species, respectively.

	Macroconsumer density and abundance		
Reach	Killifish (CPUE)	Crab (individuals/m)	Guppy (CPUE)
KCG	**8.83 (2.81)**	3.32 (1.38)	23.00 (9.57)
KC	**30.61 (6.98)**	3.09 (1.35)	N.A.

directly increase leaf decomposition rates via direct consumption. We observed little shredding activity of crabs on *Cecropia* leaf packs, possibly because there were other more palatable food resources (i.e., fallen fruit) available in our focal stream during the study (TNS, *personal observation*). Leaf decomposition rates were significantly reduced where killifish were abundant (e.g., above barrier waterfalls) because of reductions in biomass of the only leaf-shredding insect, *Phylloicus*. Field observations (this study) and gut content analyses of killifish (Murray et al. 2018) confirm our experimental findings that killifish prey on leaf-shredding *Phylloicus*. Moreover, this trophic cascade was disrupted below barrier waterfalls because of the presence of a third omnivorous macroconsumer species (guppies) that significantly reduced killifish populations likely through predation on eggs and neonates. In fact, the presence of omnivorous guppies below barrier waterfalls resulted in an increase in the rate of leaf decomposition that was equivalent to

experimentally excluding all macroconsumers in upstream guppy-free reaches.

Indirect top-down effects of killifish predation on leaf decomposition rates were strong enough to reduce the inherent variability in our data that was caused by high natural environmental heterogeneity across the landscape. Four of eight physiochemical characteristics measured in our landscape study varied by more than an order of magnitude among streams; one varied by more than fivefold among streams (Table 2). Moreover, two of our six study streams (2b and 2f in Fig. 2) were characterized by a distinct exposed bedrock bottom (as opposed to gravel-dominated substrates), consisting of limestone complexes termed "tufa," which have been shown to cause P limitation in stream communities (Wetzel 2001, Day and Chenoweth 2004). Despite high environmental variation among streams, the variability (standard error) surrounding *Phylloicus* biomass and leaf decomposition rates was 20- and 5-fold lower, respectively, in upstream reaches where killifish exerted strong top-down control relative to downstream reaches where environmental heterogeneity among streams likely contributed to the higher observed variability in *Phylloicus* biomass and leaf decomposition rates.

One-third out of more than 30 studies documenting detrital-based trophic cascades in temperate ecosystems occurred in streams (Sitvarin et al. 2016). In contrast, we are aware of only one prior report of a detrital-based trophic cascade in a tropical stream (Andrade et al. 2017). The lack of reported detrital-based trophic cascades in tropical streams is typically attributed to the dearth of leaf-shredding insects in these systems. However, recent studies suggest that some taxa of leaf-shredding insects may instead have patchy distributions across large geographical regions and, when present, can have effects on leaf decomposition similar to those reported for temperate streams (Boyero et al. 2015). Our results suggest that the variation in leaf-shredding *Phylloicus* abundance is largely caused by discontinuities in macroconsumer community assemblages caused by barrier waterfalls. In the landscape component of our study, the biomass of leaf-shredding *Phylloicus* was more than an order of magnitude higher below barrier waterfalls, consequently increasing leaf decomposition rates by over twofold. Thus, although detrital-based trophic cascades may be less common in tropical streams because leaf-shredding insect species are often absent (e.g., Rosemond et al. 1998), our experimental and observational work conducted in two separate years across >420 ha suggest that they may be more common than previously thought.

The likelihood of observing detrital-based trophic cascades across other tropical streams will ultimately depend not only on the presence of leaf-shredding insects but also on the strength of the direct effects of large omnivores on detrital processing. For example, our study was conducted in streams across the Caroni drainage located on the southwestern slope of the Northern Range mountains; however, some drainages on the north slope of this mountain range contain large numbers of freshwater shrimps. Omnivorous shrimps have been shown to drive leaf decomposition rates on other Caribbean islands (March et al. 2001). Thus, it is possible that the detrital-based trophic cascades that we observed in the Caroni drainage would not be observed in other drainages in Northern Trinidad that contain large numbers of omnivorous shrimp.

Just as interactions between guppies and killifish appears to disrupt detrital-based trophic cascades in our study, previous studies have found that antagonistic interactions among competing predator species can reduce the strength of trophic cascades (Finke and Denno 2004, Bruno and O'Connor 2005, Wu et al. 2011, Karp and Daily 2014). For example, Finke and Denno (2004) found that adding hunting spiders to a predator community reduced overall predation on herbivores, because predators not only consumed herbivores but also consumed each other (i.e., intraguild predation), thereby indirectly reducing aboveground biomass of *Spartina* grass in a coastal salt marsh community. All of the above studies were conducted in "green" food webs (except see Wu et al. 2011), the bulk of which were done in terrestrial plant–herbivore systems. Our study extends these findings by providing evidence that antagonistic interactions among consumers can completely disrupt a detrital-based "brown" trophic cascade.

The exact mechanisms causing killifish density to decline in the presence of guppies remains unknown; however, Fraser and Lamphere (2013) reported that guppies readily consume killifish eggs and neonates in the laboratory and that introduced guppies reduce killifish densities in a replicated field experiment. Additionally, the presence of guppies has been shown to reduce killifish growth rates while not affecting survival in a field reciprocal transplant experiment (Walsh et al. 2011) and in a mesocosm experiment (Bassar 2017). Thus, interactions between guppies and killifish are likely both predatory and competitive in nature and, as such, their relationship may best be described as intraguild predation. Above all, these findings highlight the complex effects of omnivory on trophic cascades beyond those previously reported for tropical streams.

In summary, our findings are in contrast to previous studies in tropical streams and our own predictions, in that we found no experimental evidence that omnivorous macroconsumers directly increase rates of leaf decomposition. Although detrital-based trophic cascades have heretofore been considered rare in tropical streams, we reveal the mechanistic basis behind a strong trophic cascade in upper reaches of headwater streams in the Caroni drainage of northern Trinidad. These cascading trophic effects on leaf decomposition were consistently disrupted downstream of barrier waterfalls across six streams, where the presence of omnivorous guppies resulted in greater biomass of the leaf-shredding insect, *Phylloicus*, and significantly greater leaf decomposition

rates because of guppy predation on insectivorous killifish neonates. By combining in situ experiments in a focal stream, to isolate top-down effects of three different macroconsumers, with a landscape assessment across six streams, we found that macroconsumer effects were consistently strong enough to overwhelm the influence of high environmental variability on leaf decomposition rates, a key basal resource in headwater stream communities.

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