Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream

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Abstract: We examined whether a tropical stream in Puerto Rico matched predictions of the river continuum concept (RCC) for macroinvertebrate functional feeding groups (FFGs). Sampling sites for macroinvertebrates, basal resources, and fishes ranged from headwaters to within 2.5 km of the fourth-order estuary. In a comparison with a model temperate system in which RCC predictions generally held, we used catchment area as a measure of stream size to examine truncated RCC predictions (i.e., cut off to correspond to the largest stream size sampled in Puerto Rico). Despite dominance of generalist freshwater shrimps, which use more than one feeding mode, RCC predictions held for scrapers, shredders, and predators. Collector–filterers showed a trend opposite to that predicted by the RCC, but patterns in basal resources suggest that this is consistent with the central RCC theme: longitudinal distributions of FFGs follow longitudinal patterns in basal resources. Alternatively, the filterer pattern may be explained by fish predation affecting distributions of filter-feeding shrimp. Our results indicate that the RCC generally applies to running waters on tropical islands. However, additional theoretical and field studies across a broad array of stream types should examine whether the RCC needs to be refined to reflect the potential influence of top-down trophic controls on FFG distributions.

Résumé : Nous examinons si un cours d'eau tropical à Porto Rico s'accorde aux prédictions du concept du continuum fluvial (« river continuum concept (RCC) ») en ce qui a trait aux groupes alimentaires fonctionnels (FFG) de macro-invertébrés. Les points d'échantillonnage des invertébrés, des ressources de base et des poissons s'échelonnent des eaux de tête du bassin jusqu'à 2,5 km de l'estuaire, un cours de quatrième ordre. Lors de notre comparaison avec un système modèle des régions tempérées dans lequel les prédictions du RCC se réalisent généralement bien, nous utilisons la surface du bassin versant comme mesure de la taille du cours d'eau afin d'évaluer les prédictions du RCC tronqué (c'est-à-dire amputé de manière à correspondre à la taille maximale de rivière échantillonnée à Porto Rico). Malgré la dominance des crevettes d'eau douce généralistes, qui utilisent plus d'un mode alimentaire, les prédictions du RCC s'appliquent aux râcleurs, aux déchiqueteurs et aux prédateurs. Les collecteurs–filtreurs affichent une tendance inverse à celle prédite par le RCC, mais la répartition des ressources de base indique que cela est compatible avec le thème central du RCC qui veut que la répartition longitudinale des FFG suive les patrons longitudinaux des ressources de base. La répartition des filtreurs pourrait aussi s'expliquer par la prédation par les poissons qui affecte les répartitions des crevettes qui se nourrissent par filtration. Nos résultats indiquent que le RCC s'applique généralement bien aux eaux courantes des îles tropicales. Il faudra, cependant, des études théoriques et des travaux de terrain dans une gamme élargie de types de cours d'eau afin de savoir si le RCC doit être raffiné de manière à refléter l'influence potentielle des contrôles trophiques descendants sur les répartitions des FFG.

[Traduit par la Rédaction]

Introduction

Research on tropical streams and rivers has been critical to the development of stream ecosystem theory (sensu Minshall 1988). For example, Junk et al. (1989) based much of the flood-pulse concept on undisturbed conditions of the Amazon River. Tropical stream ecology can also contribute to clarification and refinement of the river continuum concept (RCC); for example, features of tropical streams and

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rivers have been used to make key points in several theoretical RCC papers (e.g., Minshall et al. 1985; Statzner and Higler 1985). The RCC (Vannote et al. 1980) is a widely used model for interpreting longitudinal patterns in lotic food webs. The concept examines longitudinal changes in the relative importance of autochthonous and allochthonous basal resources, as well as distributions of macroinvertebrate functional feeding groups (FFGs). For example, the RCC predicts that in forested regions, the proportion of total macroinvertebrate biomass attributable to shredders decreases downstream because of a decline in availability of coarse particulate organic matter.

Despite its wide use, the global applicability and utility of the RCC is uncertain because the development of RCC predictions was largely based on river systems draining forested basins of high relief in North America where river–floodplain connections are severely disrupted by hu-

man activities (e.g., Winterbourn et al. 1981; Minshall et al. 1985; Junk et al. 1989). Alternatively, the RCC may simply need to be further refined and developed to reflect the diversity of river systems in different biomes (Minshall et al. 1985, 1992; de la Rosa 1995). Very little RCC-related or other longitudinal work has been done in the tropics. Tropical data on longitudinal patterns and FFGs are rare (Nair et al. 1989; Dudgeon and Bretschko 1996; Melo and Froehlich 2001). The data that do exist are inadequate for testing the RCC because they (*i*) are based on FFG abundances not biomass, (*ii*) are from a single habitat type such as riffles, and (*iii*) exclude decapod macroinvertebrates and (or) are from highly impacted systems. Whether the RCC is viewed as a narrow construct of temperate North American research or as a broadly useful but not yet fully refined concept for understanding longitudinal biotic patterns, it is clear that more tropical systems need to be examined for comparison to the RCC and its specific predictions.

Tropical island streams and rivers have several unique characteristics that may affect whether they conform to RCC predictions. First, tropical island drainages are often short, entering the ocean as low- or mid-order streams (Smith et al. 2003). As in other regions dominated by small streams that flow directly into oceans (Petersen et al. 1995; Dodds 2002), longitudinal patterns on tropical islands could differ from RCC predictions by being truncated. Second, lotic assemblages of macroinvertebrates on tropical islands are generally dominated by diadromous freshwater shrimps, fishes, and snails (Smith et al. 2003). Because diadromous organisms require a migration between freshwater and salt water to complete their life cycles, waterfalls, which are also common on tropical islands, can cause dramatic longitudinal variation in faunal abundances. Additional characteristics often observed in all types of tropical river systems are poor retention of organic matter because of frequent and unpredictable flash floods (Covich and McDowell 1996; Smith et al. 2003) and an abundance of leaves of poor food quality (e.g., with high concentrations of secondary compounds; Stout 1989). Poor retention and quality of organic matter are thought to cause nonconformance to classic RCC predictions (Winterbourn et al. 1981).

In this study, we describe longitudinal variation in benthic community structure of a tropical stream draining the Luquillo Experimental Forest / Caribbean National Forest (LEF/CNF) on the island of Puerto Rico. Our main objective was to examine whether longitudinal patterns in biomass of macroinvertebrate FFGs follow RCC predictions. We also examined longitudinal patterns in presence or absence of predatory fishes, abundance of algivorous fishes, and standing stocks of algal biomass (chlorophyll *a*), coarse and fine benthic organic matter, and fine benthic inorganic matter. Based on previous qualitative observations of freshwater shrimp and predatory fish distributions in relation to LEF waterfalls (e.g., above waterfall barriers to predatory fish migration, shrimps are at extremely high abundances), we hypothesized that collector–filterers, scrapers, and predators would not conform to classic RCC predictions, whether truncated or not. We reasoned that high abundances of shrimps above waterfalls should result in skewed patterns of macroinvertebrate FFGs because shrimps feed by filtering, gathering, scraping, and predation.

Materials and methods

Study area

The study was conducted at nine sites along a continuous, 13 km stream from its headwaters in an unnamed tributary of Río de la Mina to within 2.5 km of the Río Mameyes estuary (Fig. 1). Río Mameyes enters the ocean as a fourth-order stream, and at mid- and high elevations, the drainage basin contains numerous small and large waterfalls. The five upstream study sites occur in the LEF. The Río Mameyes drainage within the LEF includes the largest tracts of undisturbed primary forest left in the Caribbean (Weaver 1994). The remainder of the drainage occurring within LEF borders is dominated by forest affected by past human activity (i.e., secondary forest that has regrown after agricultural activity early in the 20th century and forest affected by selective harvest; Foster et al. 1999; Clark and Wilcock 2000). The lower four sites occur in surrounding lowlands dominated by secondary forest, pasture and residential areas, and a predominantly forested riparian zone. Río Mameyes is the only river system draining the LEF with no dam on its main stem; however, the lowest elevation site is located at a municipal water intake, which was designed to minimize impact and appears to have no major physical, chemical, or biotic effect on the stream (March et al. 2003). The study region shows only slight seasonal variation in rainfall and allochthonous inputs (Reagan and Waide 1996; Larsen 2000). Unpredictable flash flood events, in which discharge increases up to 10-fold in less than 1 h, occur throughout the year (Covich and McDowell 1996).

Study sites were categorized as being either high elevation and high gradient or low elevation and low gradient (Table 1). High-elevation – high-gradient sites occur above a waterfall or gradient break. High gradients block upstream migration by fishes that prey on freshwater shrimps; however, shrimps can climb waterfalls and maintain large abundances upstream (Covich 1988*a*). Low-elevation sites have lower gradients, and predatory fishes are present. In terms of abundance and biomass, macroinvertebrate assemblages in Puerto Rico are dominated by snails (native Neritinidae and exotic *Thiara granifera*) and three families of migratory shrimps (Xiphocarididae (*Xiphocaris elongata*), Atyidae (*Atya lanipes*, *A. innocous*, *A. scabra*, and *Micratya poeyi*), and Palaemonidae (*Macrobrachium carcinus*, *M. crenulatum*, *M. heterochirus*, *M. faustinum*, and *M. acanthurus*)) (Covich and McDowell 1996). Atyid shrimps often dominate macroinvertebrate communities of headwater streams in Puerto Rico (Pringle 1996), but in mid- to low-elevation streams below waterfalls, adult atyids occur only at low densities (Covich and McDowell 1996). Neritinid and thiarid snails are similarly known to vary in abundance with elevation: they are at high densities in mid- and low-elevation sites and absent at higher elevations (March et al. 2002; Pyron and Covich 2003).

Freshwater shrimps in Puerto Rico have been found to have dramatic effects on algal biomass and species composition, quantity and quality of benthic organic matter, quantity

Fig. 1. The Río Mameyes drainage (●, study sites). The upper inset shows the location of the study drainage in Puerto Rico in relation to the capital city, San Juan. The lower inset shows the location of Puerto Rico in relation to Florida, USA, and other islands of the Greater Antilles. Latitude and longitude coordinates of sites are listed (also see Table 1 for site numbers).
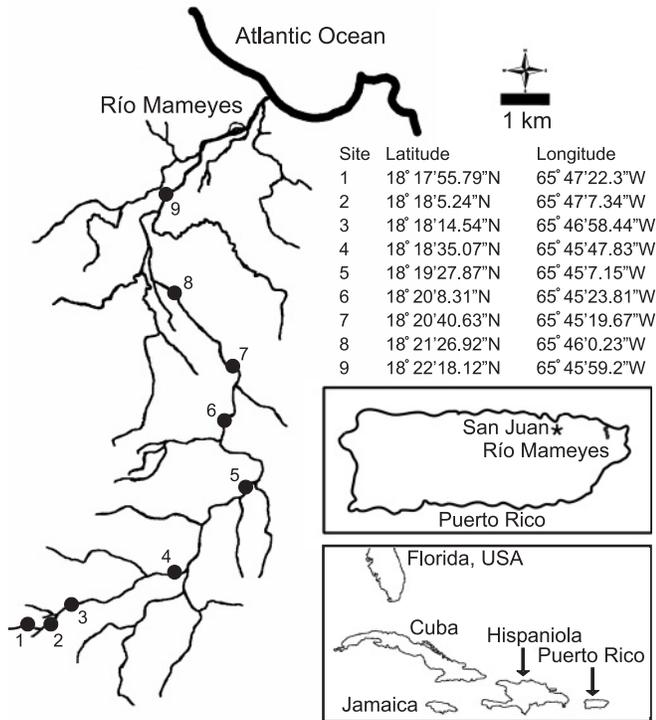
of epilithic fine sediments, leaf decomposition rates, and abundance and biomass of benthic invertebrates (e.g., Pringle et al. 1999; Crowl et al. 2001; March et al. 2002). *Sicydium plumieri*, the algivorous green stream goby, is the only fish species that occurs above waterfalls in LEF streams. In Costa Rica, algivorous gobies have been found to affect algal biomass, quantity and quality of benthic organic matter, and abundance of benthic insects (Barbee 2002). Predatory fishes in the Río Mameyes catchment (*Agonostomus monticola*, *Gobiomorus dormitor*, *Eleotris pisonis*, *Awaous tajasica*, and *Anguilla rostrata*) feed primarily on shrimps and other invertebrates (Nieves 1998). Except for the catadromous American eel (*A. rostrata*) and a diadromous eleotrid capable of forming landlocked populations (*G. domitor*), all native freshwater shrimps, neritinid snails, and fishes in Puerto Rico are thought to be amphidromous, with adult females releasing larvae that passively drift downstream to the estuary before migrating back upstream as juveniles (March et al. 1998; Nieves 1998; Bacheler et al. 2004). Other aquatic fauna of the Río Mameyes catchment are aquatic insects dominated by Baetidae, Leptophlebiidae, Chironomidae, Elmidae, Hydroptilidae, and Simuliidae, benthic invertebrates including Oligochaeta, Copepoda, and Acari, and the crab *Epilobocera sinuatifrons* (Covich and McDowell 1996; Zimmerman and Covich 2003).

Methods

At each site, we established a reach that was 10 times the channel width and visually identified major habitats (Ta-

ble 1). Proportional availability of major habitats was determined using occurrence frequency of mesohabitats (riffles, pools, and runs, based on measured lengths) combined with occurrence frequency of substrates (based on 54 random measurements in each major mesohabitat type). All measurements and samples were taken during base flow from June through August 2001. Epilithic chlorophyll *a* was sampled using a suction device modified from Loeb (1981). We collected a pooled sample of four individual and randomly located Loeb samples in each of three pools and three riffles at each site. Chlorophyll *a* samples were brought back to the lab on ice, filtered, frozen, and analyzed fluorometrically according to standard methods (American Public Health Association 1985).

To measure non-shrimp benthic invertebrate densities and standing stocks of very fine (VF, <250 µm) and medium fine (MF, 250 µm – 1 mm) benthic inorganic matter (BIM) and VF, MF, and coarse (C, >1 mm) benthic organic matter (BOM), three randomly located samples per major habitat were collected and processed using methods modified from Lugthart and Wallace (1992) and Grubaugh et al. (1996). Macrophytes in runs, as well as sand habitats in pools, were sampled using a core of known area. Pools with boulders and interstitial cobble and gravel were sampled using the "benthic block net" method described by Greathouse and Pringle (2005); the benthic block net apparatus functions similarly to a core. Bedrock–boulder cascades were sampled by scrub-brushing invertebrates and benthic matter from a known area into a hand net or into a Surber sampler with foam rubber tied around the frame to create a seal with the substrate. Cobble–coarse gravel riffles were sampled with an unmodified Surber net. In cobble runs, a sample consisted of a single cobble placed into a downstream D net, scrubbed on the bank to remove invertebrates and benthic matter, and measured to determine surface area. Because hand, Surber, and D nets were 250 µm mesh, we further modified methods of Lugthart and Wallace (1992) and Grubaugh et al. (1996) by using the Loeb sampler to collect VFBOM and VFBIM in Surber and hand-net samples, and we used the Loeb sampler on nearby cobbles to estimate VFBOM and VFBIM in D-net samples. An additional modification is that we did not separate macrophytes from coarse detritus when measuring standing stocks of CBOM; however, macrophytes only occurred in run and riffle samples at the lowest-elevation site (*Hydrilla*) and in a single riffle sample at site 3 (filamentous algae). Invertebrate samples were preserved in the field in ethanol.

Samples intended for estimating VFBOM/BIM (from Loeb, core, and benthic block net sampling) were sieved to remove material >250 µm before filtration onto pre-ashed, pre-weighed glass fiber filters (Whatman GF/F, 0.7 µm). Non-decapod invertebrate samples were separated into MF and C fractions using nested 1 mm and 250 µm sieves before sorting for macroinvertebrates. After sorting, we subsampled the MFBOM/BIM for filtration onto a pre-ashed, pre-weighed glass fiber filter. CBOM and filters of VFBOM/BIM and MFBOM/BIM were dried for 24 h at 50 °C, weighed, ashed for 3 h at 500 °C, and reweighed to determine ash-free dry mass (AFDM) for VFBOM, MFBOM, and CBOM and inorganic dry mass for VFBIM and MFBIM. Non-decapod invertebrates were identified to the lowest practicable level

Table 1. Study site physical characteristics.

Site	Stream	Stream type[a]	Stream order[b]	Catchment area (ha)	Elevation (m asl)[c]	Slope (%)	Mean width[d] (m)	Canopy cover[e] (%)	Major habitats
1	Unnamed	High	0	4	720	16.8	3.0	89.5	Sand pools, boulder–bedrock riffles
2	Unnamed	High	1	32	660	14.8	4.5	83.2	Boulder pools, cobble riffles
3	Río de la Mina	High	2	136	590	12.7	8.3	43.3	Boulder pools, boulder–bedrock riffles
4	Río de la Mina	High	2	506	250	7.8	11.0	40.3	Boulder pools, boulder–bedrock riffles
5	Río Mameyes	Low	3	1574	105	4.0	21.0	15.5	Boulder pools, boulder–bedrock riffles
6	Río Mameyes	Low	3	2025	65	1.6	14.5	29.7	Boulder pools, boulder–bedrock riffles
7	Río Mameyes	Low	3	2225	42	1.8	16.6	33.9	Boulder pools, boulder–bedrock riffles
8	Río Mameyes	Low	3	2422	16	0.8	15.0	22.2	Boulder pools, cobble riffles
9	Río Mameyes	Low	3	3455	5	0.7	13.0	22.7	Cobble runs, macrophytes,[f] cobble riffles

[a]High, high elevation – high gradient; low, low elevation – low gradient.
[b]Based on blue lines from US Geological Survey 1:20 000 topographic maps. Stream order 0 site is a headwater stream without a blue line.
[c]Units are metres above sea level (m asl).
[d]Bankfull measurements.
[e]Spherical densiometer measurements.
[f]Macrophytes were *Hydrilla* in runs.

(generally family or subfamily for insects and class or order for other non-decapod invertebrates; note that we consider potential bias of FFG designation from this level of identification in the Discussion). Length–mass regressions, determined from individuals preserved in ~10% formaldehyde, were used to determine snail biomass (Appendix A). Published (Benke et al. 1999) and unpublished (W. Cross, Institute of Ecology, University of Georgia, Athens, GA 30602, USA, personal communication) length–mass regressions were used to determine biomass of other non-decapod invertebrates. Functional feeding group designations of non-decapod invertebrates followed those of March (2000) and were based on Buzby (1998) and Merritt and Cummins (1996).

We obtained quantitative estimates of shrimp and crab biomass and fish abundance by electroshocking and snorkeling. A minimum of one pool or run habitat and one riffle habitat per site were electroshocked using depletion or removal sampling methods (White et al. 1982; Fièvet et al. 1996, 1999). Block and dip nets were 0.635 cm mesh. Captured shrimps and crabs were identified to genus or species and measured to the nearest millimetre for postorbital carapace length (Hobbs 1991). Electroshocking was ineffective for capturing gobies (*Sicydium* and *Awaous*) and sleepers (Eleotridae) in pools, as has been observed by other researchers for Puerto Rico (E. García, US Department of Agriculture Forest Service, Southern Region, Atlanta, GA 30309, USA, and N. Hemphill, Trinity County Resource Conservation District, Weaverville, CA 96093, USA, personal communication). Thus, in one pool or run per site, we snorkeled a known area, counting all gobies and sleepers ob-

served. Visibility was similar across sites. Carapace length–mass regression equations for shrimps and crabs, determined from individuals preserved in ~10% formaldehyde, were used to determine shrimp and crab biomass (Appendix A). In determining biomass of macroinvertebrate functional feeding groups, we apportioned biomass of shrimp taxa equivalently to each known functional feeding group membership (Table 2).

Data analysis

For both our analytical approach and our basis for comparison with RCC functional group predictions, we used a model study demonstrating that the RCC generally applies to macroinvertebrate communities along a continuous, 65 km reach from the headwaters of Ball Creek to the Little Tennessee River (via Coweeta Creek) in North Carolina, USA (Grubaugh et al. 1996). The analytical approach consisted of linear regressions of arcsine-transformed percentages of habitat-weighted functional group biomass against catchment area. We also used linear regression against catchment area to analyze other ecosystem and community structure parameters.

To compare results from the Little Tennessee River drainage with results from the Río Mameyes drainage, regression lines from Grubaugh et al. (1996) were included in plots of habitat-weighted biomass of functional groups vs. catchment area and percent functional group biomass vs. catchment area. Although our data are from sampling at only one time of year, whereas regressions from Grubaugh et al. (1996) are based on annual means from seasonal sampling, we consider ours to be reasonable estimates of annual means because

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Table 2. Decapod functional feeding group (FFG) apportionment used for this study.

Taxa	Scraper	Shredder	Gatherer	Filterer	Predator	References for known FFGs
Shrimp						
Xiphocaris elongata	1/3	1/3	1/3	—	—	Fryer 1977; Crowl et al. 2001; March et al. 2001
Atya scabra	—	—	—	1	—	Fryer 1977; Covich 1988*a*
Atya lanipes	1/3	—	1/3	1/3	—	Fryer 1977; Covich 1988*a*
Atya innocous	1/3	—	1/3	1/3	—	Fryer 1977; Covich 1988*a*
Micratya poeyi	1/3	—	1/3	1/3	—	Fryer 1977
Juvenile *Atya* spp.	1/3	—	1/3	1/3	—	(Ambiguous atyids likely *A. lanipes* or *A. innocous*)
Macrobrachium spp.	—	—	1/2	—	1/2	Crowl and Covich 1994; Covich and McDowell 1996; March et al. 2001
Crab						
Epilobocera sinuatifrons	—	—	1/2	—	1/2	Covich and McDowell 1996; Henry 2000

Note: For each taxon, apportionments were split into equivalent proportions for each mode of feeding known from references in the literature. Gatherer, collector–gatherer; filterer, collector–filterer.

intra-annual variation in climate (Ramírez and Melendez-Colom 2003) and standing stocks of algae (C. Pringle, E. Greathouse, K. Smith, unpublished data), organic matter (C. Pringle, E. Greathouse, K. Smith, unpublished data), and macroinvertebrates (Masteller 1993; Covich et al. 2003) in Puerto Rico is inconsistent, with no clear seasonal patterns.
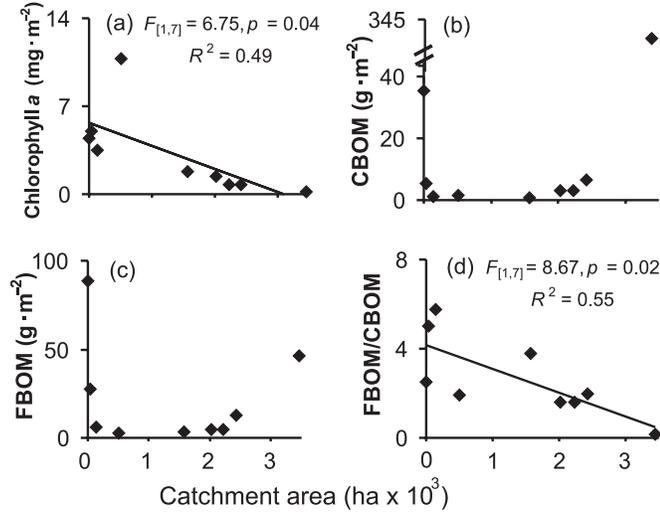
We presupposed that examining whether the Río Mameyes drainage follows RCC predictions requires comparison of our data with RCC predictions cut off at mid-orders. For example, the RCC predicts a hump-shaped pattern for scrapers because of low representation in forested headwaters, maximum importance in mid-orders (~3rd to 5th order), and low representation in high orders (>6th order). But for a stream entering the ocean at 4th order, the proportional representation of scrapers should increase along the entire stream length from headwaters to ocean. Thus, in comparing patterns of percent functional group biomass vs. catchment area, our primary focus was to compare our data with the portion of the regression lines from Grubaugh et al. (1996) that would correspond to truncation at a catchment area of 3500 ha (equivalent to a 3rd-order stream based on blue lines of a US Geological Survey (USGS) 1:25 000 topographic map) to exclude portions of the regression that correspond to sites of much greater size than our sampling sites (i.e., truncation excludes areas where catchment area, order, width, depth, discharge, etc., indicate a stream size much larger than our largest sampling site). However, the figure of percent functional group biomass vs. catchment area shows the full nontruncated regression lines from Grubaugh et al. (1996) to also allow examination of the Río Mameyes pattern in a broader context. The figure of habitat-weighted biomass of functional groups vs. catchment area does not include full nontruncated regression lines from Grubaugh et al. (1996); regression lines from Grubaugh et al. (1996) in this figure were truncated at ~4000 ha because a nonlogarithmic *x* axis with a maximum value of 4000 ha was necessary to clearly illustrate the patterns in the Río Mameyes data (i.e., extending the *x* axis to 125 000 ha to correspond to the largest catchment area from Grubaugh et

al. (1996) makes the Río Mameyes data too small to see and extending the *x* axis to 1 000 000 ha and making it logarithmic obscures the patterns in the Río Mameyes data).

Truncation at 3500 ha excludes all portions of the regressions corresponding to sampling sites on the Little Tennessee River. Moreover, regressions in each study are based on data from sites located along our definition of a "continuum": a continuous length of stream that spans several orders (i.e., sites were along a single channel from upstream to downstream). Thus, when describing and discussing the results of our comparison, we use "Río Mameyes continuum", "Coweeta Creek continuum", and "Little Tennessee River continuum" to distinguish between the two drainages and truncated ("Coweeta Creek continuum") and nontruncated ("Little Tennessee River continuum") portions of the Little Tennessee River drainage.

Geomorphic features are broadly comparable between the drainages of the Río Mameyes (outlet at site 9) and Coweeta Creek (outlet at site M-5 from Grubaugh et al. 1996). Both outlets are 3rd order (based on blue lines from USGS topographic maps). The continuums also have similar basin lengths (Coweeta, 9.2 km; Mameyes, 9.8 km), relief ratios (Coweeta, 0.10; Mameyes, 0.10), average stream slopes (Coweeta, 0.05; Mameyes, 0.05), and elongation ratios (Coweeta, 0.8; Mameyes, 0.7; an indicator of basin shape) (see Gordon et al. (1992) for equations used to calculate geomorphic characteristics). Annual runoff is ~2 times higher in the Río Mameyes drainage (~2.6 m) than in the Coweeta drainage (~1.1 m). Similarly, bankfull widths are somewhat higher on average in the Río Mameyes (~12 m) than in the Coweeta drainage (~8 m). In comparing FFG patterns between the Río Mameyes and Coweeta Creek continuums, we decided against using other measures of stream size (or position along the continuum) in our figures because other measures either would have given very similar results (e.g., high correspondence between catchment area and order between the two drainages suggests that results would have been similar if data were plotted against order) or are inadequately characterized in Grubaugh et al. (1996) and (or) the Río

Fig. 2. Patterns in standing stocks of basal resources along the Río Mameyes continuum: (*a*) epilithic chlorophyll *a*, data points are means from three pools and three riffles at each site; (*b*) habitat-weighted coarse (C, >1 mm) benthic organic matter (BOM); (*c*) habitat-weighted fine (F, <1 mm) BOM; (*d*) ratio of F to C habitat-weighted BOM.

Fig. 3. Habitat-weighted biomass of atyid decapods (■), gastropods (△), and other macroinvertebrates (● and broken line) along the Río Mameyes continuum. Solid black bar on *x* axis indicates region containing waterfall barrier to upstream migration of predatory fishes. AFDM, ash-free dry mass.
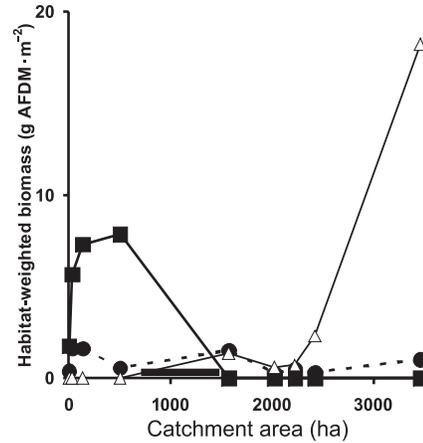

Table 3. Habitat-specific densities of the green stream goby, *Sicydium plumieri*, along the Río Mameyes continuum.

| Site	*Sicydium* in pools[a] (no.·m^{-2})	*Sicydium* in riffles[b] (no.·m^{-2})
1	0.00	0.00
2	0.00	0.21
3	2.93	0.44
4	1.65	1.44
5	0.60	0.21
6	0.52	0.20
7	0.50	0.10
8	0.00	0.01
9	0.00	0.00

[a]Snorkeling data.
[b]Electroshocking data.

Mameyes basin. For example, there are only two gauges along the Río Mameyes continuum, and thus, to compute mean annual runoff or discharge, we would have had to have used a linear regression between catchment area and flow. Grubaugh et al. (1996) also had to use such a regression to estimate mean annual discharge at several of their sites. Thus, if we had plotted figures against runoff, Mameyes data points would simply have been shifted to the right relative to Grubaugh et al. (1996) regression lines.

We used linear regressions among shrimps and ecosystem and community properties (standing stocks of chlorophyll *a*, BOM, BIM, macroinvertebrates) to examine whether there are negative correlations between shrimps and ecosystem and community properties that are consistent with previous shrimp exclusion experiments (e.g., Pringle et al. 1999; March et al. 2002). Because these past shrimp exclusions were conducted in pools, we conducted separate regressions for pools (and runs) and for riffles. We also examined linear regressions between total non-decapod invertebrate biomass and BOM. For simplicity of data presentation, VF and MF size fractions were generally combined into a single "fine" size fraction. For statistical analyses, we used JMP 3.2.6 (SAS Institute Inc. 1999) and a significance level of 0.05. All percentages were arcsine-transformed before statistical analyses. For nonpercentage data, the Shapiro–Wilk test was used to test for normality, and when appropriate, $\log_{10}(x + 1)$ transformations were conducted.

Results

Standing stocks of chlorophyll *a* in periphyton decreased along the Río Mameyes continuum (Fig. 2*a*), as did the ratio of habitat-weighted FBOM to CBOM (Fig. 2*d*). Absolute standing stocks of FBOM and CBOM showed no longitudinal trend but were highest at the extremes of the continuum (Figs. 2*b* and 2*c*). Habitat-weighted atyid shrimp biomass was dramatically higher in high-elevation sites (Fig. 3). In

contrast, habitat-weighted biomass of gastropods was dramatically higher at the two lowest-elevation sites, whereas habitat-weighted biomass of other macroinvertebrates was more even across the continuum (Fig. 3). Predatory fishes were not present in electroshocking samples and during snorkeling observations at sites with catchments smaller than approximately 1000 ha (Fig. 3; Appendix B, Table B1). Highest densities of the green stream goby occurred in mid-elevation sites, and no *Sicydium* were found at the highest- and lowest-elevation sites (Table 3). Macroinvertebrate biomass, standing stocks of basal resources, and proportional representation of habitats used in habitat weighting are listed by habitat unit and site (Appendix B, Tables B2–B5).

For habitat-specific analyses, macroinvertebrate functional feeding groups showed variable trends in dominance along the continuum (Fig. 4). Relative dominance of scrapers increased and shredders decreased along the continuum in boulder–bedrock pools, but both functional groups showed no trend in boulder–bedrock riffles. Percentages of collector–gatherers decreased with catchment area in boulder–bedrock pools but increased in boulder–bedrock riffles. Percentages

Fig. 4. Relative dominance of macroinvertebrate functional feeding groups in bedrock–boulder pools, bedrock–boulder riffles, and cobble riffles along the Río Mameyes continuum. Data are arcsine-transformed percentages of total habitat-specific biomass at each sampling site. Note that gatherers denotes collector–gatherers and filterers denotes collector–filterers. AFDM, ash-free dry mass.
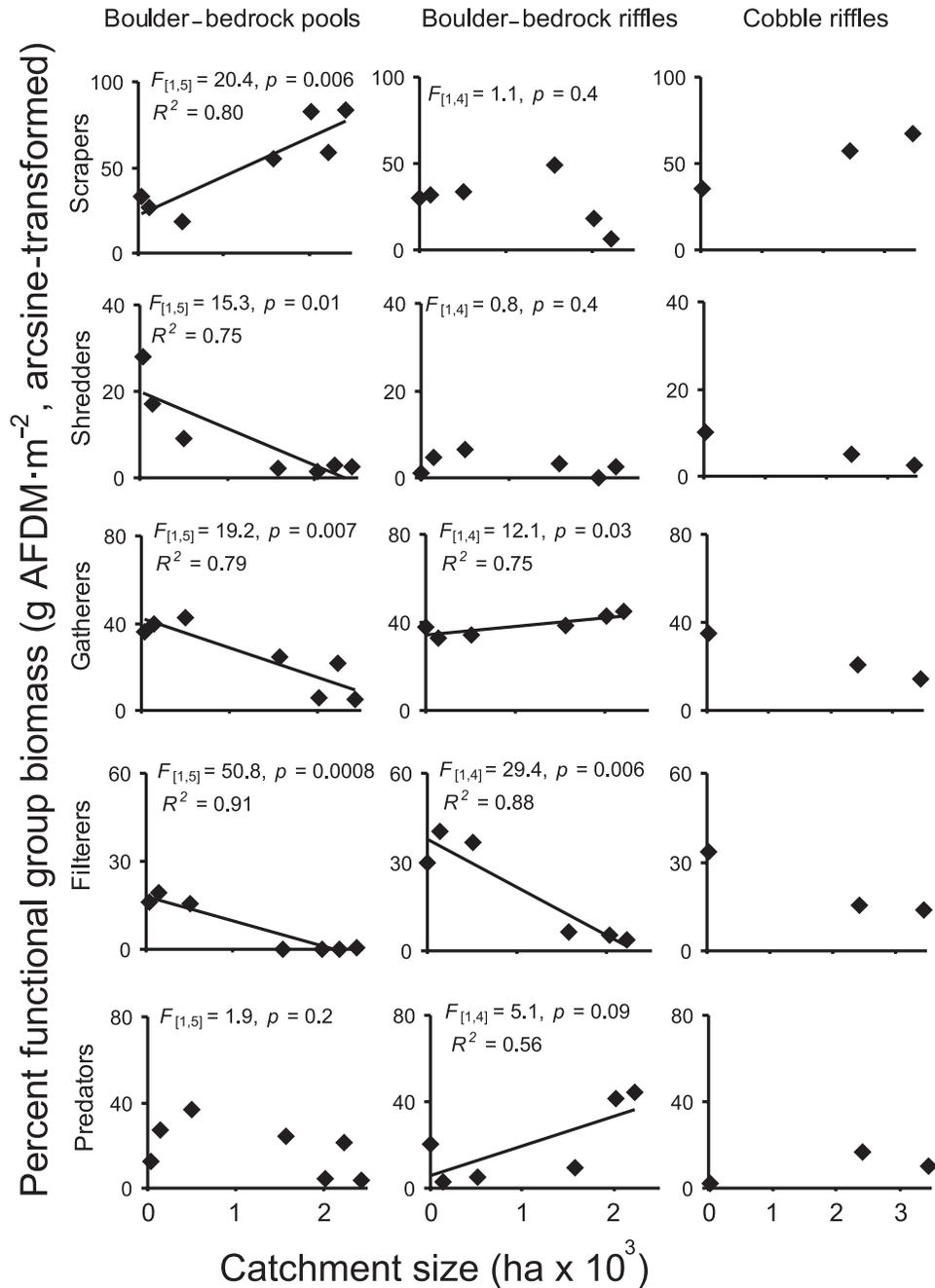

of collector–filterers in both boulder–bedrock pools and boulder–bedrock riffles decreased with catchment area. Predators showed no trend in boulder–bedrock pools and a marginally significant trend of increasing with stream size in boulder–bedrock riffles. Cobble riffle data are presented but not analyzed for statistical trends because cobble riffles occurred at only three sites (Fig. 4, third column). Cobble–macrophyte runs at the lowest-elevation site were dominated by scrapers (scrapers were 97% of total invertebrate biomass in runs). Sand pools at the highest-elevation site were dominated by collector–gatherers, collector–filterers, and scrapers

(33%, 29%, and 32% of total invertebrate biomass, respectively). Total macroinvertebrate biomass was highest in cobble–macrophyte runs at the lowest-elevation site where mean total biomass was 24.9 g AFDM·m^{-2}. Among the three other habitat types, total macroinvertebrate biomass was fairly equivalent (mean total biomass: boulder–bedrock pools, 4.2 g AFDM·m^{-2}; boulder–bedrock riffles, 3.9 g AFDM·m^{-2}; cobble riffles, 5.8 g AFDM·m^{-2}; sand pools at highest-elevation site, 3.3 g AFDM·m^{-2}).

Longitudinal patterns in absolute values of habitat-weighted biomass in the Río Mameyes continuum generally

Fig. 5. Habitat-weighted biomass of macroinvertebrate functional feeding groups along the Río Mameyes continuum (◆ and solid regression lines) and the Coweeta Creek continuum (broken regression lines, from Grubaugh et al. 1996; regression lines are truncated at ~4000 ha). Total biomass of (*a*) macroinvertebrates, (*b*) scrapers, (*c*) collector–gatherers, (*d*) collector–filterers, (*e*) predators, and (*f*) shredders. AFDM, ash-free dry mass.
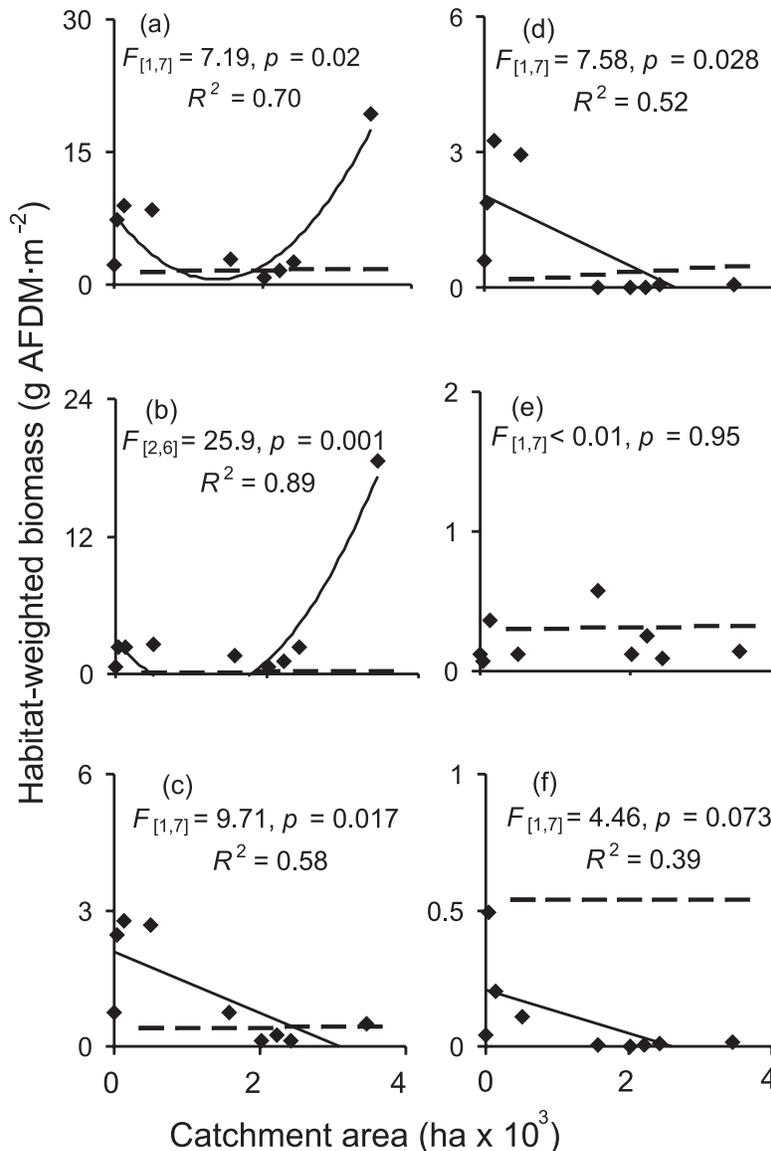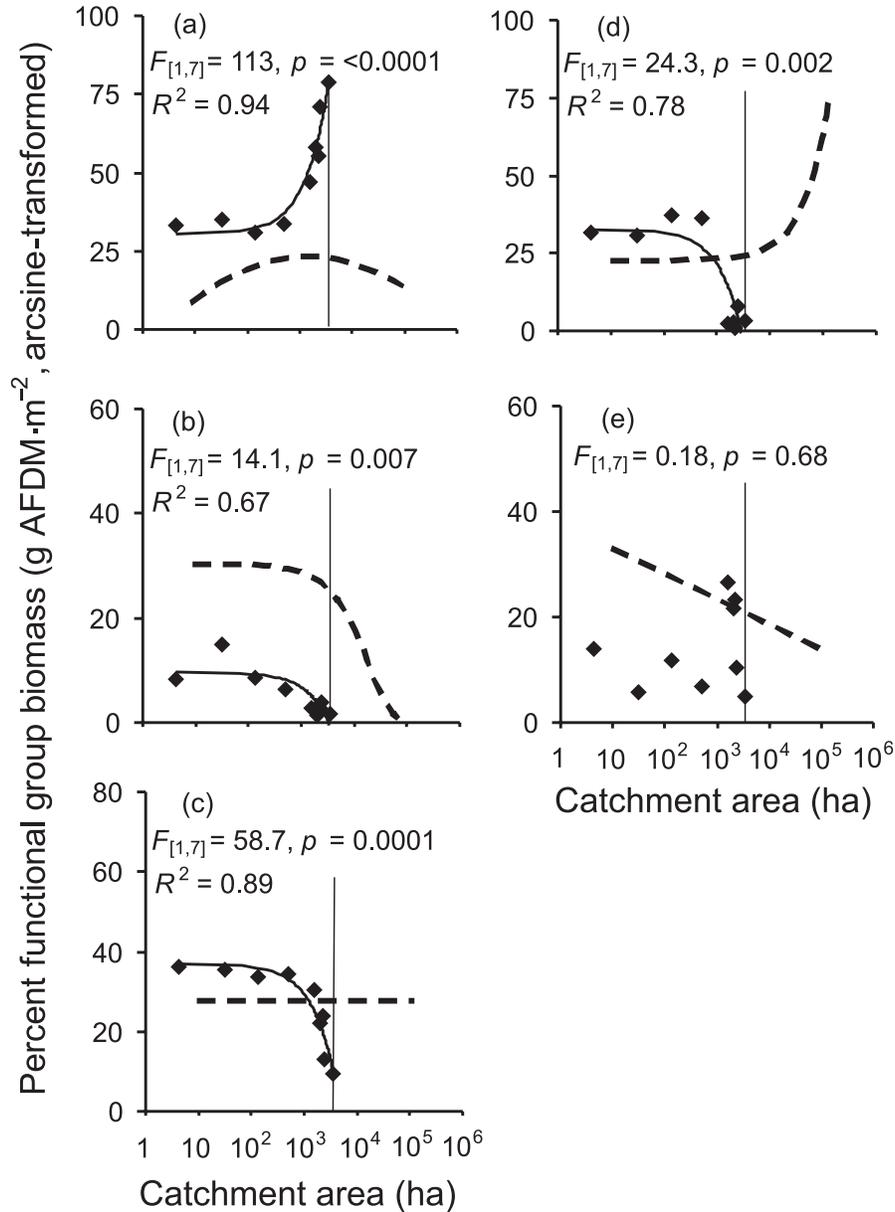

did not match patterns in the Coweeta Creek continuum, which usually showed little to no variation over the spatial scale of comparison (Fig. 5). Predators were the only functional feeding group in the Río Mameyes continuum to closely match the Coweeta Creek pattern. Mean habitat-weighted biomass of predators in the Río Mameyes continuum was 0.2 g AFDM·m^{-2} compared with ~0.3 g AFDM·m^{-2} in the Coweeta Creek continuum (Fig. 5). Total habitat-weighted biomass in the Río Mameyes continuum showed a polynomial trend with catchment area, and the mean across all sites was 6.0 g AFDM·m^{-2}, a much higher value than the ~1.4 g AFDM·m^{-2} in the Coweeta Creek continuum. In the Río Mameyes continuum, a polynomial function fit the pattern for habitat-weighted biomass of scrapers, which reached much higher values compared with the Coweeta Creek regression line (Fig. 5). Habitat-weighted biomass of both

collector–gatherers and collector–filterers decreased along the Río Mameyes continuum, from values much above the Coweeta Creek regression at high-elevation sites to values comparable to the Coweeta Creek continuum at low-elevation sites. For shredders, habitat-weighted biomass showed a marginally significant trend of decreasing along the Río Mameyes continuum and was generally much lower than shredder biomass in the Coweeta Creek continuum (Fig. 5).

No regressions between percent functional group biomass and catchment area in the Río Mameyes continuum closely matched regressions in the Coweeta Creek continuum, but the directions of some trends did match (Fig. 6). Along both the Río Mameyes and Coweeta Creek continuums, percent functional group biomass increased for scrapers and decreased for shredders (note that the entire Little Tennessee River

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Fig. 6. Relative dominance of macroinvertebrate functional feeding groups along the Río Mameyes continuum (♦ and solid regression lines) and the Little Tennessee River continuum (broken regression lines, from Grubaugh et al. 1996). Vertical lines indicate the catchment area where truncating the Little Tennessee River continuum allows comparison of the Río Mameyes continuum with the Coweeta Creek continuum. Plots are arcsine-transformed percentages of habitat-weighted biomasses at each sampling site: (a) scrapers, (b) shredders, (c) collector–gatherers, (d) collector–filterers, and (e) predators. Note that significant regression lines for Mameyes data appear curved because of the log scale of the x axis. AFDM, ash-free dry mass.

continuum showed a hump-shaped pattern) (Fig. 6; Table 4). Percent contribution of shredders in the Río Mameyes continuum was less than 7% at all sites (Table 4) and was much lower than the percent contribution of shredders in the Coweeta Creek continuum (Fig. 6). Relative dominance of collector–gatherers and collector–filterers decreased along the Río Mameyes continuum, whereas collector–gatherers and collector–filterers showed little to no change along the Coweeta Creek continuum and collector–filterers showed a large increase along the entire Little Tennessee River continuum (Fig. 6; Table 4). Percent contribution of macroinvertebrate predators showed no trend along the Río

Mameyes continuum but decreased along the Coweeta Creek continuum (Fig. 6; Table 4).

In pools–runs, the only correlations between any of the shrimp genera and ecosystem properties were marginally significant and positive. In riffles, biomass of atyids and *Xiphocaris* were positively correlated with chlorophyll *a* (atyids, $F_{[1,7]} = 23.0$, $P = 0.002$; *Xiphocaris*, $F_{[1,7]} = 6.5$, $P = 0.036$). Biomass of riffle atyids was also positively correlated with VFBOM ($F_{[1,7]} = 28.8$, $P = 0.001$), and biomass of *Xiphocaris* shrimp was positively correlated with FBOM ($F_{[1,7]} = 8.8$, $P = 0.021$) and VFBIM ($F_{[1,7]} = 11.8$, $P = 0.011$). Total biomass of non-decapod invertebrates was pos-

Table 4. Percent of habitat-weighted biomass in each macro-invertebrate functional feeding group at sites along the Río Mameyes continuum.

Site	Scrapers	Shredders	Gatherers	Filterers	Predators
1	29.8	2.0	34.8	27.6	5.8
2	32.7	6.7	33.7	25.9	1.0
3	26.3	2.2	31.0	36.4	4.1
4	30.4	1.3	31.9	35.0	1.4
5	53.9	0.2	25.8	0.2	19.9
6	71.8	0.1	14.3	0.2	13.6
7	67.9	0.2	16.2	<0.1	15.7
8	89.2	0.5	5.0	2.0	3.3
9	96.2	0.1	2.6	0.3	0.7

Note: Gatherers, collector–gatherers; filterers, collector–filterers.

itively correlated with CBOM in pools and runs ($F_{1,7}$ = 77.6, P < 0.0001). Total biomass of non-decapod invertebrates in riffles showed no correlations with BOM, regardless of size fraction. Chlorophyll *a* was negatively correlated with habitat-weighted biomass of snails ($F_{[1,7]}$ = 9.91, P = 0.016). Habitat-weighted biomass of atyid shrimp was also dramatically higher where habitat-weighted snail biomass was zero ($F_{[1,7]}$ = 57.81, P < 0.0001). Sampled snail biomass was zero at all high-elevation sites (sites with catchment areas smaller than ~1000 ha); however, we did observe that snails were present during fieldwork at high-elevation site 4.

Discussion

Do macroinvertebrate FFGs match RCC predictions?

Functional groups in the Río Mameyes continuum conform broadly to truncated RCC predictions for some FFGs but not others. Relative contributions of shredders and scrapers clearly fit RCC predictions and match the Coweeta Creek trends (Grubaugh et al. 1996) by decreasing and increasing, respectively, from headwaters to mid-orders. We expected the shredder pattern because the dominant shredder in Puerto Rico, *X. elongata*, is known to have high abundances above waterfalls (March et al. 2001). We did not expect the scraper pattern because we did not anticipate snail biomass at low elevations overwhelming contributions from high densities of shrimp scrapers at high elevations.

Relative contributions of predators, gatherers, and filterers do not match trends in the Coweeta Creek continuum. Predators were the only FFG for which the Coweeta Creek continuum did not conform to the RCC prediction (Grubaugh et al. 1996). Our findings do conform to the RCC prediction that relative contributions of predators do not change with stream size (Vannote et al. 1980). However, we hypothesized that predators would decrease downstream (as observed in the Coweeta Creek continuum), because in both systems, there are downstream increases in densities of predatory fishes, which have the potential to competitively exclude invertebrate predators. For gatherers, it is difficult to make conclusions regarding whether the decrease in relative contributions along the Río Mameyes continuum conforms to the RCC or not because the exact RCC prediction is unclear. Grubaugh et al. (1996) found no change in percent gatherer biomass with stream size. The original RCC (Vannote et al.

1980) did not make a separate and clear prediction for gatherers: gatherers were grouped with filterers in a single collector category, and collector representation was predicted to remain constant from headwaters to mid-orders. In their revision of the RCC, Minshall et al. (1985) characterize gatherers as decreasing slightly from headwaters to mid-orders. Filterers are the one FFG in the Río Mameyes continuum that clearly does not conform to RCC predictions. We found that filterers decrease in relative dominance downstream, but the RCC prediction is that contributions of filterers either do not change substantially (Vannote et al. 1980; Grubaugh et al. 1996) or increase (Minshall et al. 1985) from headwaters to mid-orders. The filterer pattern matches our hypothesis that dominance of atyid shrimps in headwaters would cause a downstream decrease in filterers.

The direction of regression slopes for relative contributions in the Río Mameyes continuum match those of the Coweeta Creek continuum and RCC predictions for several FFGs. However, actual percent representation and standing stocks of FFG biomass are strikingly different from patterns observed by Grubaugh et al. (1996). The Río Mameyes continuum has low representation of shredders, which is thought to be typical of many tropical regions including Asia (Burton and Sivaramakrishnan 1993; Yule 1996*b*; Dudgeon 1999), the Pacific islands (Resh and de Szalay 1995), Africa (Minshall et al. 1985), and the neotropics (Wootton and Oemke 1992; Mathuriau and Chauvet 2002). Shredders appear to be largely replaced by scrapers, gatherers, and filterers.

Our findings do not support the hypothesis that low representation of shredders in tropical streams is an artifact of macroinvertebrate-focused FFG analyses that only consider insect shredders and exclude other biota, such as crustaceans and fishes, that may be important leaf feeders in the tropics (Ramírez and Pringle 1998; Dudgeon and Wu 1999; Moss 2005). We found that shredder biomass is poorly represented despite the fact that we included all potential shredders and leaf feeders (calamoceratid caddisflies, the elmid beetle *Phanocerus* (Buzby 1998), and leaf-mining chironomids (E. Greathouse, personal observation); *X. elongata*; no stream fishes are CPOM detritivores in Puerto Rico).

Ours is the first tropical study to our knowledge that evaluates FFG predictions of the RCC using appropriate methods. Regional reviews of stream ecology have noted the lack of adequate longitudinal and functional group data for tropical Asia (Dudgeon 1999), the Pacific islands (Resh and de Szalay 1995), the Caribbean and Central America (de la Rosa 1995), South America (Lewis et al. 1995), and Africa (Cooper 1996). Valid evaluation of RCC predictions and use of the RCC as a comparative tool require methods of sampling and analysis similar to those used in the development of the RCC (Barmuta and Lake 1982). Tropical FFG data that do exist are from Asia (e.g., Dudgeon 1984; Burton and Sivaramakrishnan 1993), the Pacific islands (Dudgeon 1994; Yule 1996*b*), Africa (Cooper 1996; Tumwesigye et al. 2000), and Central America (Ramírez and Pringle 1998). However, existing data are problematic for evaluating RCC predictions because, similar to most FFG studies in the temperate zone, these tropical studies have (*i*) been based on macroinvertebrate abundances, (*ii*) excluded decapods, (*iii*) been conducted in systems highly modified by humans, and (or) (*iv*) limited sampling to a single type of habitat (e.g., riffles).

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Conclusions from functional group analyses can vary substantially with the metric used (Fisher 1995). Biomass and production are appropriate metrics to use for evaluating the RCC and indicating ecosystem attributes (Barmuta and Lake 1982; Cummins and Merritt 2001). Abundance and taxonomic diversity can be misleading (Grubaugh et al. 1996). Excluding shrimps and crabs from analyses, or not sampling them with appropriate methods, is especially problematic in the tropics because these decapods often represent important primary consumers and detritivores. Analyses of highly impacted tropical systems confound biome and human impact and are problematic because the RCC attempted to describe unperturbed longitudinal patterns.

Functional group RCC analyses also must examine average or characteristic fauna at each site; this requires sampling of all major habitats (Minshall et al. 1985; Grubaugh et al. 1996). Our data support this contention. Río Mameyes trends in relative contributions of habitat-weighted FFGs match habitat-specific trends for pools but not for boulder–bedrock riffles. Macroinvertebrate sampling is often limited to riffles, but if we had limited our sampling to boulder–bedrock riffles, we would have erroneously concluded that the Río Mameyes continuum does not match any RCC predictions for FFGs.

Why does the Río Mameyes continuum not follow the RCC prediction for filterers?

Our finding that filterers do not conform to RCC predictions may be due to several challenges in our application of the FFG approach. First, we generally identified non-decapod invertebrates to the family or subfamily level. Several researchers have argued that genus- or species-level identifications are necessary to assess FFGs (Plague et al. 1998; Lenat and Resh 2001). However, greater resolution of identifications would be unlikely to alter our results because biomass of decapods and snails outweighed other invertebrate biomass by two orders of magnitude.

A second and more important challenge is the high abundance of shrimps, which are capable of more than one mode of feeding. Applying FFGs to these generalists is problematic because solid data on which to base apportionment of FFG membership are lacking (c.f., Hawkins and MacMahon 1989). We apportioned shrimp biomass equivalently among each feeding mode known for adults; however, our analysis could be improved with detailed studies on shrimp FFG apportionments. Our feeding mode apportionment also assumes that the proportion of time spent by shrimps in each feeding mode does not vary between juveniles and adults or longitudinally. However, feeding mode is known to vary with age for many macroinvertebrates (Cummins 1973; Davies et al. 1995; Ladle and Westlake 1995), and shrimp diets may change with elevation because of longitudinal variation in predators or food resources (Cushing and Allan 2001; March et al. 2001).

We found broad agreement with many RCC predictions, despite high abundances of generalist shrimps. These findings contrast with current thinking about generalist feeders. Facultative relationships with food categories are thought to make generalist macroinvertebrates less reliable indicators of ecosystem conditions (e.g., autotrophy vs. heterotrophy,

CPOM vs. FPOM; Mihuc and Minshall 1995; Cummins and Merritt 2001), indicative of shifting availability of different types of food resources (Dodds et al. 2004), and problematic in efforts to evaluate the RCC (Cooper 1996; Plague et al. 1998; Cushing and Allan 2001). In fact, dominance by generalists is a major feature of regions such as New Zealand (Winterbourn 1995) and Australia (Lake 1995), which are the focus of classic debates about the applicability of the RCC to non-northern-temperate streams.

A third consideration in our application of FFGs is that we excluded fishes from our analysis. Excluding fishes in FFG- and RCC-related studies may be particularly problematic in the tropics where fishes are often important herbivores and detritivores (Lowe-McConnell 1987; Wootton and Oemke 1992; Lévêque 1995). The algivorous goby, *Sicydium plumieri*, is abundant in the middle of the Río Mameyes continuum and including it in the scraper category could alter our findings. However, a preliminary analysis, based on (*i*) visual estimates of *Sicydium* lengths from snorkeling, (*ii*) measured *Sicydium* lengths from electroshocking, and (*iii*) a *Sicydium* length – wet mass regression (Nieves 1998), indicates that including algivorous gobies as scrapers would not alter our overall longitudinal patterns in proportional representation of FFGs.

A fourth challenge in our analysis is the relative degree of human disturbance of the Río Mameyes drainage. It is one of the least human-modified drainages in the Caribbean and thus one of the closest indicators of unperturbed longitudinal patterns possible for running waters in the Caribbean. However, the drainage is affected by human activities (e.g., past agricultural land use at low and mid-elevations and present urban–suburban land use in the lowlands (Thomlinson et al. 1996; Clark and Wilcock 2000; Grau et al. 2003), the exotic snail, *T. granifera*, introduced in the 1950s (Pyron and Covich 2003), and freshwater shrimp harvest (Greathouse et al. 2005)). Thus, it may be problematic to use the Río Mameyes continuum to evaluate the RCC, which is generally regarded as a theory applying to pristine rivers, but this challenge is inherent in many RCC studies, including the use of human-modified systems of North America in the development of the RCC (Statzner and Higler 1985) and the use of human-modified systems of New Zealand in criticisms of the RCC (Davies et al. 1995).

Despite the aforementioned challenges, we believe our results are reliable and the decrease in filterers downstream is not due to a problem in our methods or analysis. This leads to the question of whether the pattern of filterers represents a contradiction of the RCC. We suggest that it is not a contradiction but instead a potential refinement of the RCC (sensu Minshall et al. 1992). The pattern appears to fit the framework outlined by Minshall et al. (1985) for a biome-related variation on the central RCC theme of longitudinal FFG patterns following longitudinal patterns in basal resources, which in turn reflect the physical gradient. Based on our data, we cannot draw conclusions about overall organic matter dynamics in light of RCC predictions on ratios of fine vs. coarse allochthonous resources because we did not measure organic matter in transport. However, we found that the ratio of fine to coarse BOM decreases downstream, which is opposite of the RCC prediction for the ratio of fine to coarse

particulate organic matter (POM) in temperate forested streams. This suggests that low availability of coarse detritus relative to availability of fine POM in headwaters may explain the high representation of filterers in the Río Mameyes headwaters.

Patterns in detrital resources (and thus FFGs) of Río Mameyes may differ from those in temperate systems because tropical climates likely cause different patterns in organic matter inputs, retention, and decay (de la Rosa 1995). Terrestrial inputs of FPOM vs. CPOM to other tropical streams are thought to be skewed towards fines. CPOM inputs may be reduced because tropical temperatures and humidity and retention of CPOM in rainforest canopy structures (e.g., hyphae networks, bromeliads) cause high terrestrial decay rates of leaves (Minshall et al. 1985; Covich 1988b; Yule 1996b). In fact, our results are similar to those of Yule (1996a, 1996b) who studied proportional abundances of FFGs in a headwater vs. a lowland site in Papua New Guinea. Filterers decreased downstream in New Guinea, and their dominance in the headwaters was attributed to terrestrial decomposition causing stream inputs to be dominated by FPOM rather than CPOM. Puerto Rico's tropical climate may also affect the relative availability of fine vs. coarse POM by affecting in-stream processes (e.g., poor retention and high in-stream abrasion of CPOM and debris dams due to flash floods and warm temperatures; Buzby 1998; Merriam et al. 2002). Alternatively, the food quality of leaf inputs may be similar to those of other tropical streams, where high concentrations of secondary compounds are thought to limit shredder biomass (Stout 1989).

The truncated continuum patterns that we observed for scrapers and shredders match findings on longitudinal patterns in autotrophic vs. allochthonous resources in relation to canopy cover (Ortiz-Zayas et al. 2005). This is additional evidence that Río Mameyes FFG patterns follow patterns in basal resources. The drainage is heterotrophic along its entire length (ratios of primary production to community respiration (P/R) < 1; Ortiz-Zayas et al. 2005). However, there is a large increase in primary production and only a small increase in community respiration downstream. Thus, P/R increases along the gradient consistent with the downstream decrease in canopy cover and the RCC prediction for P/R from headwaters to mid-orders.

For possible explanations of the filterer pattern, effects of predators are an alternative to filterers tracking basal resources. This alternative would represent a major and perhaps long overdue refinement of the RCC, which is essentially a "bottom-up" theory (i.e., food resources control consumer distributions) (Dettmers et al. 2001). Attributing the filterer pattern to patterns in fine vs. coarse basal resources would imply that high atyid shrimp abundances at high elevations are a consequence of these patterns. However, there is a long-standing hypothesis that waterfalls blocking upstream migration of predatory fishes cause observed atyid distributions. If high atyid abundance upstream from waterfalls is due to a release from fish predation, then the Río Mameyes drainage may be a system in which longitudinal patterns in FFGs are also controlled by top-down factors. Other systems in which a downstream increase in fish predation is thought to affect longitudinal FFG patterns are the headwaters of the Medway River (an acid stream system in southeast England; Townsend and Hildrew 1984) and the Little Tennessee River – Coweeta Creek continuum (Grubaugh et al. 1996).

Do shrimps cause longitudinal variation in benthic resources?

In situ manipulative experiments (e.g., Pringle et al. 1999; Crowl et al. 2001; March et al. 2001) have demonstrated dramatic effects of atyid and *Xiphocaris* shrimps on leaf decay rates and standing stocks of epilithic chlorophyll *a*, FBOM, FBIM (i.e., fine sediments), and aquatic insects. Thus, we examined whether chlorophyll *a*, FBOM, FBIM, CBOM, and aquatic insects are at low levels where atyid and *Xiphocaris* biomass is high (above the waterfall) and are increased below the waterfall where these shrimps are at low abundances and biomass. We found no negative correlations between any benthic resources and biomass of atyids and *Xiphocaris*, and we did not observe clear increases in any benthic resources below the waterfall barrier to predatory fish. In fact, epilithic chlorophyll *a* showed a significant downstream decrease. Moreover, there were positive correlations between biomass of invertebrates, BOM, and chlorophyll *a* similar to those observed by Grubaugh et al. (1996). These correlations indicate that invertebrates are tracking food resources.

Along a longitudinal gradient encompassing a waterfall in a neighboring drainage, March et al. (2002) found that effects of shrimp exclusion on algae, organic matter, and insects varied. There were no effects in a low-elevation site with abundant grazing snails (primarily native), whereas effects at mid- and high-elevation sites were significant. A downstream decrease in chlorophyll *a* was also observed. The negative correlation we observed between chlorophyll *a* and snail biomass (~95% native snails) suggests that grazing by abundant snails at low elevations is causing the chlorophyll *a* pattern. Likewise, the negative correlation between atyid shrimps and snails is consistent with the hypothesis of March et al. (2002) that high abundances of shrimps at high elevations may be due to a release from competition with snails. This hypothesis and hypotheses about snail grazing maintaining low standing stocks of algae, organic matter, and insects deserves detailed experimental study in the tropics.

We further hypothesize that grazing by the high abundance of algivorous gobies in the middle reaches of Río Mameyes is an important factor in maintaining low standing stocks of epilithic chlorophyll *a*, FBOM, and FBIM. In other Puerto Rican streams where *Sicydium* are not prevalent, epilithic FBOM and FBIM show a dramatic pattern in relation to predatory fish barriers: thick layers of fines occur on rocks in pools with predatory fishes immediately below the waterfall, and rocks in pools above the waterfall are clean (E. Greathouse, personal observation). In contrast, rocks appeared clean at all of our sites both above and below the predatory fish barrier.

Significance

Our findings on FFGs, FBOM, and CBOM combined with those of Ortiz-Zayas et al. (2005) on P/R indicate that the Río Mameyes drainage conforms to the central theme of the

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RCC: changes in stream size determine changes in basal resources and consumers. However, our results also indicate that longitudinal patterns in FFGs in the Río Mameyes are influenced by top-down control, a mechanism that is not currently considered in RCC literature. Findings for the Río Mameyes likely have wide application because the basic geomorphology and longitudinal distributions of diadromous fauna (fishes, decapods, and snails) in the Río Mameyes are characteristic of tropical insular and coastal streams throughout the world (Smith et al. 2003). As in the Río Mameyes, tropical insular and coastal streams across the Caribbean, Latin America, the Pacific islands, and Asia have high abundances of snails and algivorous gobies at low and mid-elevations and high shrimp abundances above waterfalls that block upstream migration of predatory fishes (e.g., Hunte 1978; Lyons and Schneider 1990; Craig 2003).

Comparing the Río Mameyes and Coweeta Creek continuums provides a more detailed understanding of how a model tropical island stream differs from a model temperate continuum. However, the extent to which these findings can be generalized, and applied to refining the RCC, is unclear because our study represents a comparison of only two case studies, and we focused on using catchment area as a measure of stream size in our comparisons. For example, it is unknown whether the FFG equations in the Coweeta Creek – Little Tennessee River continuum are representative of other temperate systems. It is also unclear the extent to which results would have differed had we made comparisons using other possible measures of position along the continuums, such as stream order, runoff, distance, slope, etc.

Differences among the Río Mameyes, the Little Tennessee River, and the RCC may be due to the Río Mameyes being an island stream or a tropical stream or they may be due to another reason. Comparing a single tropical island stream with a single temperate stream limits our ability to determine which factors cause observed differences. This limitation is not only attributable to our study design, but also reflects a paradox in RCC research. On the one hand, the RCC is an important concept in research on the ecology of streams: the original paper introducing the concept (Vannote et al. 1980) is the most-cited paper in benthic science (Resh and Kobzina 2003). On the other hand, the extent to which the RCC has made a difference in our understanding of aquatic ecology has been greatly debated since its original publication (e.g., Winterbourn et al. 1981; Minshall et al. 1985). Many have questioned whether the concept provides predictive power for making comparisons among sites or understanding system responses to disturbance at different points in stream networks. Proponents argue that the most powerful idea from the RCC is simply its provision of an organizing framework and a standard set of methods and measurements for conducting comparative longitudinal studies across biomes and stream types (e.g., Barmuta and Lake 1982; Minshall et al. 1985; Ortiz-Zayas et al. 2005). However, this potential power is unrealized because there are actually few longitudinal studies testing RCC predictions (especially on FFG biomass) in any biome, let alone comparative longitudinal studies using similar methods across a broad array of biomes. Comparisons across multiple examples of tropical, temperate, island, and continental streams,

using multiple types of measures of position along the continuum (e.g., order, runoff, distance, etc.), would be necessary to determine the causes of the differences between the Río Mameyes and the Little Tennessee River, as well as the true potential of the RCC as an organizing concept in stream ecology. Such comparisons would also benefit conservation and management because they would allow us to incorporate insular tropical systems into our general understanding of lotic structure and function (Smith et al. 2003). Improved conservation and management of these systems is critical because the biological integrity of many tropical island streams, including Río Mameyes and its headwaters, is threatened by growing water demands (March et al. 2003), land use change (Brasher 2003), and our minimal understanding of insular tropical stream ecology (Smith et al. 2003).

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Appendix A

Table A1. Carapace and shell length–mass regressions determined for decapods and snails preserved in ~10% formaldehyde.

Taxon	L	a	b	% ash	R^2	N
Xiphocaris elongata	Carapace length	0.0001	3.042	9.1	0.97	64
Atya lanipes	Carapace length	0.0004	2.579	15.1	0.95	55
Non-gravid *Atya scabra*	Carapace length	0.0004	2.479	26.2	0.68	24
Gravid *Atya scabra*	Carapace length	0.0005	2.500	23.1	0.82	23
Non-gravid *Atya innocous*	Carapace length	0.0001	2.904	27.5	0.95	21
Gravid *Atya innocous*	Carapace length	0.0001	3.179	24.2	0.93	17
Juvenile *Atya* spp.	Carapace length	0.0012	1.450	19.0	0.47	12
Micratya poeyi	Carapace length	0.0006	1.881	13.8	0.74	57
Non-gravid *Macrobrachium*	Carapace length	0.0004	2.636	12.7	0.96	39
Gravid *Macrobrachium* spp.	Carapace length	0.0002	3.016	13.3	0.98	18
Epilobocera sinuatifrons	Carapace length	0.00005	3.324	47.6	0.98	35
Thiara granifera	Shell length	0.00002	2.618	87.6	0.95	78
Neritina spp.	Shell length	0.000008	3.532	83.2	0.94	73

Note: AFDM = aL^b, where L is either carapace length or shell length in mm and AFDM is ash-free dry mass in grams; % ash, percent ash content (includes shells for snails); N, number of individuals used in determining regression. Carapace length was the postorbital carapace length (Hobbs 1991).

Appendix B. Predatory fishes, standing stocks of macroinvertebrates and basal resources, and proportional representation of habitats in sampled sites (1–9) along the Río Mameyes continuum.

Tables B1–B6 appear on pages 150–152.

Table B1. Predatory fishes.

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Anguilla rostrata					×	×	×	×	×					×	×	×	×	×
Agonostomus monticola					×	×	×	×	×					×	×	×	×	×
Eleotridae					×	×	×	×	×					×	×	×	×	×

Note: ×, present in electroshocking samples or observations.

[a]Site number.

Table B2. Decapods (g AFDM·m⁻²).

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Atyidae	1.0	7.6	8.8	10.1	<0.1	<0.1	<0.1	0.1	0.1	2.9	1.1	2.4	0.1					<0.1
Xiphocaris elongata		0.8	0.2	0.4	<0.1	<0.1	<0.1	<0.1	<0.1	0.3	3.0	1.9	<0.1					<0.1
Macrobrachium spp.			<0.1			0.3		0.3	0.3			0.3	0.5	2.9				0.2
Epilobocera sinuatifrons	0.3	<0.1		<0.1	<0.1		<0.1	0.3	<0.1	0.4		2.7	<0.1			0.6		0.2

Note: Atyidae, *Atya lanipes*, *A. innocous*, *A. scabra*, *Micratya poeyi*, and juvenile *Atya* spp. AFDM, ash-free dry mass.

[a]Site number.

Table B3. Non-decapod invertebrates (mg AFDM·m⁻²).

	Riffle									Pool									Cobble	*Hydrilla*
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	9	9
Phanocerus spp. Elmidae (C)	<1	3		<1	1				6	1	<1	<1	<1	<1		<1	<1	<1	1	
Other Elmidae (C)			5					2	159	159	<1	<1	1	<1	3	4	1		11	69
Blephariceridae (D)					65							<1							<1	
Chironomidae (D)	6	2	216	1	8	7	2	17	13	15		1	14	6	4			2	<1	80
Simuliidae (D)	31	<1	1	3	<1	<1		<1	<1	<1		<1							<1	<1
Baetidae (E)	<1	5	<1	<1	<1	<1	<1	61	16	6	13	7	<1	1	6	<1			2	741
Leptophlebiidae (E)	<1	15	<1	1	12	<1						3	1	1	6	<1			7	1
Crambidae (L)		124		<1	4	26	2	1		<1	<1		<1		<1					
Libellulidae (O)	1	<1							79	<1		<1		<1	<1	<1			<1	
Hydropsychidae (T)	<1	4	49																	
Hydroptilidae (T)	52	<1	66	6	585	29	<1	20	36	<1		2		<1		<1			<1	94
Philopotamidae (T)	<1		13	6	1	<1	<1	235	299					<1		<1			<1	<1
Neritina spp. (snail)								2388	4500					5694	1758	1476	3890		9631	24 922
Thiara granifera (snail)								2	42					112	228	183	3		63	1 736
Others	17	9	1	3	7	16	<1	10	6	4	<1	12	<1	1	6	3	3	<1	<1	4

Note: AFDM, ash-free dry mass; cobble, cobble habitat in runs; *Hydrilla*, *Hydrilla* macrophytes in runs; C, Coleoptera; D, Diptera; E, Ephemeroptera; H, Hemiptera; L, Lepidoptera; O, Odonata; T, Trichoptera.

[a]Site number.

Table B4. Functional feeding group biomass.

	Riffle									Pool								Run
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Scrapers, D	0.3	2.8	2.5	3.3	<0.1	<0.1	<0.1	<0.1	<0.1	1.1	1.4	1.4	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Scrapers, N	37	16	161	6	365	41	3	2512	4655	<1	3	10	5	5809	1991	1665	3900	17.7
Shredders, D	<1	0.3	<0.1	0.1	<0.1		<0.1	<0.1	<0.1	0.1	1.0	0.6	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Shredders, N	<1	3	3	<1	1		<1	6	<1	<1	<1	1	<1	<1	<1	<1	2	<1
Collector–gatherers, D	0.5	2.8	2.5	3.4	<0.1	0.2	0.2	0.3	0.2	1.1	1.6	2.9	0.3	1.4	<0.1	0.3	<0.1	0.2
Collector–gatherers, N	39	14	252	5	304	22.3	3	145	128	18	4	20	8	16	9	10	11	0.3
Collector–filterers, D	0.3	2.5	3.9	3.8	<0.1	<0.1	<0.1	<0.1	<0.1	1.0	0.4	0.8	<0.1					<0.1
Collector–filterers, N	32	<1	62	1	9	2	1	244	299	<1	<1	9	<1	<1	<1	<1	<1	<1
Predators, D	0.2	<0.1	<0.1	<0.1	<0.1	0.2	0.2	0.3	0.2	<1	0.2	1.5	0.2	1.4	<0.1	0.3	<0.1	0.1
Predators, N	3	6	<1	<1	1	15.4	<1	2	1	81	<1	1	5	<1	4	3	4	<1

Note: AFDM, ash-free dry mass; D, decapods (g AFDM·m⁻²); N, non-decapod invertebrates (mg AFDM·m⁻²).
[a]Site number.

Table B5. Basal resources.

	Riffle									Pool								Cobble	Hydrilla
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	9
Chlorophyll a (mg·m⁻²)	4.3	7.9	5.4	15.3	1.5	0.9	0.9	0.7	0.2	4.4	2.2	1.5	6.2	2.0	1.8	0.6	0.7	0.2	—
VFBOM (g AFDM·m⁻²)	1.0	2.8	2.2	2.1	0.7	0.8	1.3	1.2	0.8	73.2	7.1	20.6	5.8	11.3	13.4	9.7	26.2	0.7	68.7
MFBOM (g AFDM·m⁻²)	5.4	46.2	2.6	0.2	0.6	0.2	<0.1	1.2	5.6	249	1.3	1.1	0.5	0.2	0.9	0.5	0.4	0.2	5.4
CBOM (g AFDM·m⁻²)	88.6	9.3	0.4	<0.1	1.5	0.3	0.1	18.8	12.4	26.9	3.2	5.7	9.6	0.4	9.5	6.9	5.2	3.2	558
VFBIM (g·m⁻²)	1.9	11.5	2.2	0.6	0.4	0.6	0.1	0.3	0.8	255	11.9	18.9	9.4	3.3	20.2	11.1	19.2	0.8	381
MFBIM (g·m⁻²)	203	599	0.7	<0.1	0.5	0.2	0.1	10.7	25.2	6736	0.4	1.0	0.8	0.1	0.2	0.2	0.1	0.4	9.6

Note: VF, very fine (<250 µm); MF, medium fine (<1 mm, >250 µm); C, coarse (>1 mm); B, benthic; OM, organic matter; IM, inorganic matter; AFDM, ash-free dry mass.
[a]Site number.

Table B6. Proportional representation of habitats.

	Riffle									Pool								Run		
	1[a]	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9	Cobble	*Hydrilla*
For decapod sampling	0.59	0.70	0.77	0.78	0.61	0.61	0.40	0.27	0.24	0.41	0.30	0.23	0.22	0.39	0.39	0.60	0.73	0.76		
For non-decapod invertebrate sampling																				
Boulder–bedrock	0.32		0.60	0.76	0.52	0.53	0.29				0.17	0.15	0.14	0.23	0.30	0.43	0.46			
Sand										0.27										
Cobble		0.53						0.21	0.19										0.13	
Hydrilla macrophytes																				0.61

Note: Cobble, cobble habitat in runs; *Hydrilla*, *Hydrilla* macrophytes in runs.

[a]Site number.