Energy flow and the trophic basis of macroinvertebrate and amphibian production in a neotropical stream food web

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SUMMARY

1. Despite the typically high taxonomic and functional diversity of tropical habitats, little is known about the roles of individual consumers in their ecosystem structure and function. We studied the trophic basis of production in a tropical headwater stream by identifying major sources of energy, measuring energy flow through consumers and characterising interactions among trophic levels and functional groups.

2. We examined gut contents of 18 dominant macroinvertebrate and two tadpole taxa and used these data, along with previously published estimates of secondary production, to quantify food-web structure and energy flow pathways. We also examined the prevalence of omnivory and patterns of resource consumption across seasons and habitats.

3. Non-algal biofilm, a heterogeneous polysaccharidic matrix, was the most utilised food resource in the stream. Contrary to some studies of Old World tropical stream food webs, detrital energy sources were consumed at relatively high rates and contributed significantly to overall energy flow, although much of this was attributable to a single shredder taxon. Algal consumption rates were similar to values reported for temperate streams and were highest during the dry season.

4. Omnivory was prevalent across all functional groups, particularly predators, suggesting traditional functional and trophic assignments based on temperate regions may not be appropriate for tropical systems. Seasonal patterns of resource consumption appeared linked to hydrological disturbance.

5. This is the first study to provide quantitative estimates of energy flow through a neotropical stream food web. Extirpation and extinction rates in tropical freshwater habitats are high; our study provides baseline information for conservation and management of remaining systems, and for quantifying the consequences of further losses of biodiversity such as ongoing amphibian declines.

Keywords: energy flow, gut contents, non-algal biofilm, omnivory, tropical stream

Introduction

Freshwater habitats in the tropics are typically diverse, but this diversity is increasingly threatened by pollution, habitat destruction, climate change and disease (Dudgeon, 2000; Jenkins, 2003). Current global extinction rates are estimated to be 10–100 times higher than background rates, and many organisms, particularly amphibians, are experiencing higher losses in the tropics than in temperate regions (Dirzo & Raven, 2003; Barnosky *et al.*, 2011). Without basic natural history information on declining and threatened species, it is difficult to predict the ecological consequences of their losses, and many species are lost before much is known of their ecological roles (Crawford, Lips & Bermingham, 2010).

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Quantifying energy fluxes through food-web components across time and space is central to understanding ecosystems. Patterns of energy flow and the associated roles of consumers have been examined to a much greater extent in temperate streams (e.g. Benke & Wallace, 1997; Hall, Likens & Malcom, 2001; Stagliano & Whiles, 2002) than in the tropics. Apart from the general predictions of the River Continuum Concept (RCC; Vannote *et al.*, 1980), which was developed for temperate-forested streams, there are few conceptual models of tropical stream ecosystem structure and function (Dudgeon, Cheung & Mantel, 2010; but see Greathouse & Pringle, 2006; Tomanova, Goitia & Helešic, 2006). Further, recent studies suggest that the RCC does not accurately predict the relative importance of energy sources along tropical stream continua. For example, the RCC predicts that allochthonous resources are the dominant energy sources in forested headwater streams, but autochthonous energy sources can be more important in tropical headwaters than in temperate streams (e.g. March & Pringle, 2003; Brito *et al.*, 2006; Lau, Leung & Dudgeon, 2009). The relative importance of these resources may also vary across habitats within a stream reach, since riffles and pools provide differential resource availability because organic matter storage, algal production and prey encounters vary with water velocity, substratum size, depth and tractive force (Dudgeon, 2000; Colón-Gaud *et al.*, 2008; Meissner *et al.*, 2009).

While some qualitative information on food-web structure in neotropical headwaters is available, quantitative information on biomass and secondary production, and particularly energy flow pathways (e.g. the trophic basis of production), is lacking (but see Ramírez & Pringle, 1998; Cross *et al.*, 2008; Colón-Gaud *et al.*, 2009). Flooding during the tropical wet season reduces detrital resources and algal standing stocks in stream channels (Dudgeon, 2000; Yang, Tang & Dudgeon, 2009), which may limit secondary production (Colón-Gaud *et al.*, 2009) and influence the type of resources consumed. In contrast, relatively stable conditions during the dry season favour development of algal communities and animal populations (Dudgeon, 2000; Yang *et al.*, 2009). Omnivory is hypothesised to be more prevalent in tropical streams than in temperate streams, as it allows for diet shifts as relative availability of resources fluctuates with seasonal hydrology (Covich, 1988; Jepsen & Winemiller, 2002; Wantzen, Ramírez & Winemiller, 2006).

Our primary objective was to estimate the trophic basis of production in a neotropical headwater stream. We performed detailed gut analyses of macroinvertebrates and tadpoles from a Panamanian stream. This information, along with secondary production estimates from the same stream and sampling period, allowed us to quantify energy flow through the food web. We also examined patterns of consumption across habitat types and season. Given that coarse particulate organic matter (CPOM) storage and shredder production are low in these streams (e.g. Rosemond, Pringle & Ramírez, 1998; Colón-Gaud *et al.*, 2009; Boyero *et al.*, 2011), we predicted that autochthonous energy sources would be more important overall than in temperate forested systems, particularly during the dry season when algal abundance peaks. We further predicted that omnivory would be prevalent because of reduced and variable food resource availability associated with frequent flooding and scouring events (e.g. Lancaster *et al.*, 2005). At the time of our study, the stream had an intact amphibian population, but was in the path of a *Batrachochytrium dendrobatidis* (chytrid fungus) disease wave (Lips *et al.*, 2006; Whiles *et al.*, 2006). Thus, our study provides a quantitative assessment of food-web structure and energy flow in a healthy neotropical headwater stream, prior to the subsequent loss of its amphibians.

Methods

Study site

Río Guabal is a second-order stream located in Parque Nacional G. D. Omar Torríjos near El Copé, Coclé, Panama that flows into the Caribbean ocean. Elevation of the stream along the study reach ranged from 700 to 900 m above sea level. Water temperatures were nearly constant during the study at *c*. 21 °C. Río Guabal is a high-gradient stream with distinct pool, run and riffle habitats and heterogeneous substrata ranging from boulders to silt. Average canopy cover along the reach was 70% (Colón-Gaud *et al.*, 2008). Climate in this region is characterised by a distinct wet season that results in frequent scouring floods and high stream flows (average discharge = 208 L s^{-1}), with a relatively stable dry season (average discharge = 46 L s^{-1}) occurring from January to March (Colón-Gaud *et al.*, 2008). Samples were collected from two physically similar and representative 100 m reaches of Río Guabal that were located *c*. 500 m apart.

Macroinvertebrate and tadpole sampling

We used macroinvertebrate and tadpole samples and production estimates from a prior study (Colón-Gaud *et al.*, 2009, 2010). Macroinvertebrates were sampled monthly from June 2003 to May 2004 using a stovepipe

corer (0.0314 m² sampling area) in three randomly selected pools and a Surber sampler (250-μm mesh, 0.0949 m² sampling area) in four randomly selected riffles within each stream reach on each sample date. Samples were preserved in *c.* 8% formalin solution. One species of fish, *Brachyrhaphis roswithae,* and crabs of the genus *Ptychophallus* were present in the stream, but were not included in this study.

Invertebrates in samples were identified to genus, except for Chironomidae, which were categorised as predatory Tanypodinae or non-Tanypodinae (primarily non-predatory subfamilies Chironominae, Orthocladiinae and Tanytarsini). Functional feeding group (FFG) assignments were based on Merritt, Cummins & Berg (2008). Individuals were measured (total body length) to the nearest mm, and length–mass regressions were used to estimate biomass (Benke *et al.*, 1999). Production of most taxa was estimated using the size frequency method; the instantaneous growth method was used for some taxa with short development times and unclear cohort structure (Benke & Huryn, 2007; Colón-Gaud *et al.*, 2008, 2009). Instantaneous growth rates were derived from *in situ* growth chamber studies in the study stream (Colón-Gaud *et al.*, 2009).

Tadpoles were sampled during 2003–04 monthly from riffles, pools and isolated side pools along each study reach using a 250-μm mesh dip net and a stovepipe corer (Colón-Gaud *et al.*, 2010). The most abundant grazing species in the stream were the ranid, *Lithobates warszewitschii,* and the hylid, *Hyloscirtus colymba* (Ranvestel *et al.*, 2004; Whiles *et al.*, 2006; Colón-Gaud *et al.*, 2010). Length–mass relationships were developed to estimate tadpole biomass following the procedures of Benke *et al.* (1999). Tadpole production was estimated using the instantaneous growth method (Benke & Huryn, 2007; Colón-Gaud *et al.*, 2010).

Gut content analyses

We performed gut content analyses on common macroinvertebrate taxa from all FFGs that constituted 1% or more of total invertebrate production, with more than 90% of total macroinvertbrate production included. We examined 18 invertebrate taxa, including three from each FFG, except for predators (six taxa). Oligochaeta and Tricladida were not examined because dissection was difficult and/or gut contents were not well preserved. We analysed gut contents of six *Lithobates* and 14 *Hyloscirtus* tadpoles.

We used individuals collected during two dry season months (February and March) and two wet season months (October and December). When present in sufficient quantities, five individuals of each taxon per month were analysed. Entire gut tracts were removed from macroinvertebrates. For tadpoles, which have long, coiled guts, only the foregut was examined. Using methods adapted from Parker & Huryn (2006), we suspended gut contents from each individual in water and sonicated them for 30 s. Suspensions were filtered onto a nitrocellulose membrane filter (0.45 μm pore size). Filters were dried at 60 °C for 15 min, placed on microscope slides, cleared with Type B immersion oil, enclosed with a cover slip and sealed with nail polish.

We photographed ten randomly selected fields of view on each mounted filter using a Leica DMLS compound microscope and a Leica DFC320 camera (Leica Microsystems Ltd., Heerbrugg, Switzerland) at 400× magnification. We used the Leica Application Suite (LAS) Software version 3.3.0 (Leica Microsystems Ltd., Heerbrugg, Switzerland) to identify particles and measure the area of individual particles (μm²). After summing individual particle areas of each food type from the ten pictures, per cent of each food type consumed was calculated relative to total food cover in ten pictures for each individual. Particles were classified as algae, amorphous detritus, animal material, fungal hyphae, non-algal biofilm or vascular plant material. Non-algal biofilm is a translucent, heterogeneous matrix composed mainly of dissolved organic polysaccharides, bacteria and heterotrophic and autotrophic exudates. Amorphous detritus included indistinct detrital materials that did not show characteristics of vascular plants. Amorphous detritus and vascular plant material were classified as allochthonous resources, while algae and fungal hyphae were categorised as autochthonous materials. Animal material and non-algal biofilm were classified separately, since non-algal biofilm can include both allochthonous and autochthonous resources.

Trophic basis of production

Annual secondary production estimates from Colón-Gaud *et al.* (2009, 2010), mean annual per cent of each food category consumed (based on percentage of total area of food items in the gut) and gross production efficiency estimates for each FFG were used to estimate the trophic basis of production for each taxon. Gross production efficiency is the product of net production efficiency (NPE) and assimilation efficiency (AE). We used NPE estimates of 38% for shredders (Perry *et al.*, 1987), 50% for predators (Lawton, 1970), 33% for collectors (filterers and gatherers) and 50% for scrapers (Benke &

Wallace, 1980). Colón-Gaud *et al.* (2010) used an NPE value of *c.* 50% for tadpoles, which is an average value for ectothermic vertebrates (Burton & Likens, 1975). We used AE estimates of 10% for vascular plant detritus and amorphous detritus, 30% for algae and non-algal biofilm, 50% for fungi and 70% for animal material, based on Benke & Wallace (1980, 1997), and Cross, Wallace & Rosemond (2007).

The relative contribution of each food type (*i*) to production (CP$_i$) was estimated by multiplying the mean annual percentage of each food type consumed (% G$_i$) by its respective AE$_i$ and by NPE.

$$\text{CP}_i = \% \, G_i \times \text{AE}_i \times \text{NPE} \qquad (1)$$

To estimate the percentage of production attributed to each food type (% CP$_i$), each CP$_i$ was divided by the sum of all CP$_n$.

$$\% \, \text{CP}_i = \text{CP}_i \div (\text{CP}_i + \text{CP}_j + \ldots \text{CP}_n) \quad (\%) \qquad (2)$$

To calculate the production attributed to each food type (P$_i$), we multiplied the production estimate of each taxon (TP) by the percentage of production attributed to each food type (% CP$_i$).

$$P = \text{TP} \times \% \, \text{CP}_i \quad (\text{g m}^{-2}\text{year}^{-1}) \qquad (3)$$

This value was then divided by the gross production efficiency (AE$_i$ × NPE) to estimate the amount of each food type consumed (CA$_i$).

$$\text{CA}_i = P_i \div (\text{AE}_i \times \text{NPE}) \quad (\text{g m}^{-2}\text{year}^{-1}) \qquad (4)$$

Estimates were generated for FFGs and applied to all taxa in a given group, weighed by the annual production of each taxon (Benke & Wallace, 1980). Values were then used to construct quantitative food webs for macroinvertebrate FFGs and tadpoles.

Statistical analyses

We used a two-tailed *t*-test to assess differences between allochthonous and autochthonous materials consumed, with taxa as replicates. Non-algal biofilm was excluded from this comparison because it is a mixture of allochthonous and autochthonous materials. To meet assumptions of normality, we log$_{10}$-transformed data prior to analyses. We used a paired one-tailed *t*-test to examine differences in consumption rates of allochthonous and autochthonous material between the wet and dry seasons because we had developed an *a priori* directional hypothesis. Per cent production attributed to each food type was used for this analysis instead of amount of food type consumed, because secondary production val-

ues were annual estimates. Percentage values were square root arcsine-transformed prior to analyses.

Taxa with the highest secondary production value for each FFG were used to examine differences between habitats because they had high abundances in both pool and erosional habitats. A two-tailed *t*-test was performed to assess differences between habitats, with months sampled as replicates (*n* = 4). A Chi-squared test was performed to examine omnivory. A value of 50% animal and 50% plant material consumed was used for the expected percentage. If the observed percentages did not differ from the expected, the taxon was considered to have a high degree of omnivory. An alpha of 0.05 was used for all statistical tests. *T*-tests across habitats and season were not run for tadpoles due to low sample size available.

Results

Annual consumption

Consumption rates varied within and among functional feeding groups (see Appendix S1 for per cent production attributed to each food type across taxa and Appendix S2 for average annual amount of each food source consumed). Consumption by shredders ranged from 0.90 to 12.10 g m^{-2} year^{-1}, and the dominant shredder, *Anchytarsus*, had the highest consumption rate among all taxa across all functional feeding groups (12.10 g m^{-2} year^{-1}). Shredders, scrapers and filterers mostly consumed non-algal biofilm and vascular plant material, followed by amorphous detritus and animal material (Fig. 1). The filtering caddisfly, *Macronema*, had the second highest overall consumption rate among the 18 taxa examined (4.67 g m^{-2} year^{-1}), four times higher than the other two filterers. Predators had the lowest total consumption rate, with the stonefly *Anacroneuria* having the lowest total consumption among the 18 taxa (0.05 g m^{-2} year^{-1}). Predators consumed mainly animal material, followed by vascular plant material, amorphous detritus and non-algal biofilm. Although each FFG consumed one or two dominant food sources, almost all fed on every food type to some degree (Fig. 1). Tadpoles showed a similar generalist feeding behaviour; total annual consumption was 0.15 g m^{-2} year^{-1} for *Lithobates* and 1.87 g m^{-2} year^{-1} for *Hyloscirtus* (Fig. 2). Both tadpole taxa consumed mostly non-algal biofilm, followed by animal material, diatoms and vascular plant detritus.

Overall, allochthonous food sources were consumed at a significantly higher rate than autochthonous across all macroinvertebrate taxa (*P* < 0.001). An average of 40.7%
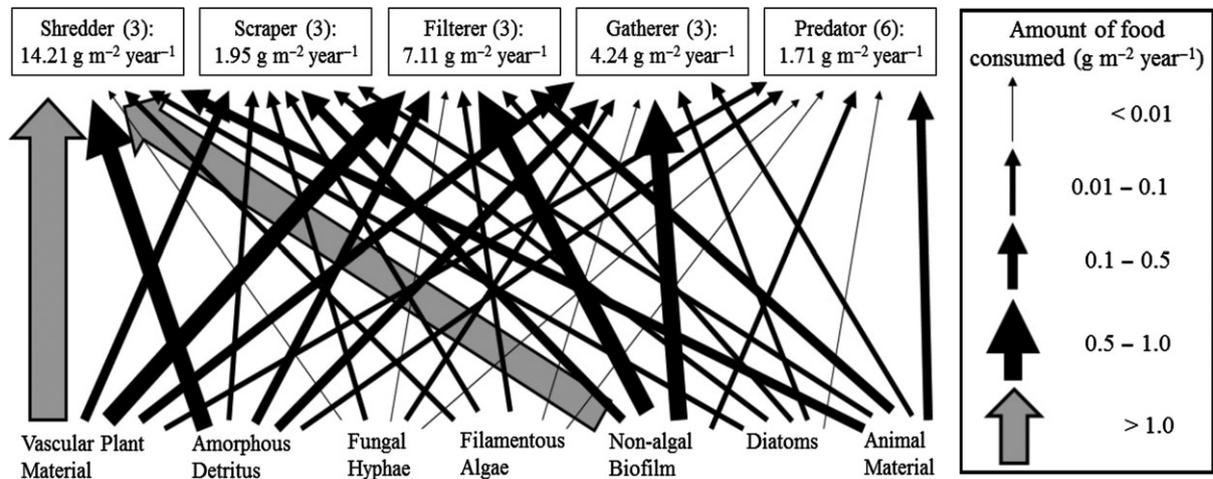
Fig. 1 Food resource consumption (g Ash free dry mass m^{-2} $year^{-1}$) by macroinvertebrate functional feeding groups in Río Guabal, Panama. Numbers in brackets indicate total number of taxa analysed in each functional feeding group. Numbers after colons indicate total annual consumption by each functional feeding group.
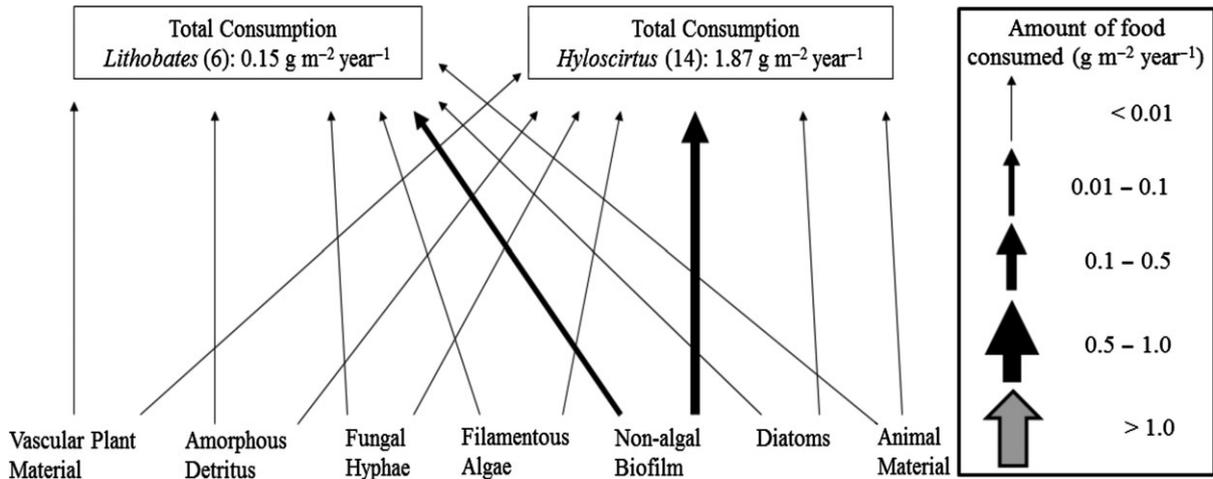

Fig. 2 Annual consumption of each food type (g AFDM m^{-2} $year^{-1}$) by two common tadpole species, *Lithobates warszewitschii* and *Hyloscirtus colymba*. Numbers in boxes at the top are total annual consumption; values in brackets indicate total number of individuals analysed.

of food consumed was allochthonous in origin, ranging from 0.014 g m^{-2} $year^{-1}$ (*Anacroneuria*) to 4.727 g m^{-2} $year^{-1}$ (*Anchytarsus*), compared with 4.0% autochthonous materials. Consumption rates of autochthonous materials among taxa ranged from 4.6×10^{-4} g m^{-2} $year^{-1}$ (*Hexatoma*) to 0.460 g m^{-2} $year^{-1}$ (*Anchytarsus*). Consumption of non-algal biofilm and animal material combined averaged 55.3% across taxa. Consumption patterns among tadpoles differed from invertebrates; *Lithobates* consumed around twice as much autochthonous (6.5%) materials as allochthonous (3.6%) sources, and *Hyloscirtus* consumed about equal amounts of autochthonous (3.1%) and allochthonous (3.7%) resources (Appendix S3).

Seasonality

Consumption of autochthonous food resources varied most with season. Allochthonous food source consumption did not differ significantly between wet (average = 12.5%) and dry (13.7%) seasons ($P = 0.11$). In contrast, consumption of autochthonous materials was significantly higher during the dry season (5.9%) than in the wet season (2.6%; $P < 0.001$). Fungal hyphae were the most important autochthonous food source consumed, and consumption of this material was significantly higher during the dry season ($P = 0.04$, Fig. 3). Algae and diatoms were also consumed at a signifi-
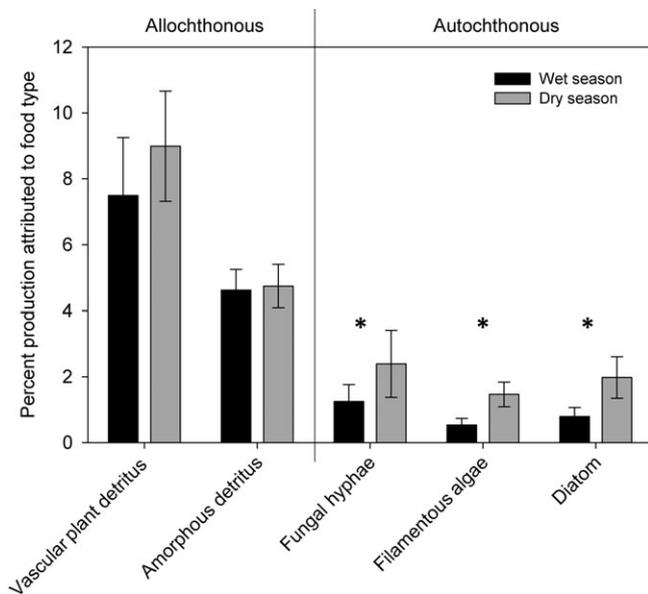
Fig. 3 Percent of total macroinvertebrate production attributed to each type of autochthonous and allochthonous foods during the wet and dry season. Values were averaged across common macro-invertebrate taxa (n = 18 taxa; mean ± 1 SE). Asterisks indicate significant differences between wet and dry season values for a given food type (P < 0.05).

cantly higher rate during the dry season (P = 0.003 and P = 0.04, respectively).

Consumption of diatoms was highly variable between seasons, with a significantly greater diversity of diatom taxa consumed in the wet season (P = 0.03). During both seasons, the most common diatom genera in macroinvertebrate guts were *Eunotia* and *Nupela* (up to 60%), except for predators during the wet season, which consumed mostly *Cocconeis* (89%). Other diatom genera found in macroinvertebrate guts across all taxa included *Achnathidium*, *Diadesmis*, *Gomphonema*, *Gyrosigma*, *Luticola*, *Navicula*, *Pinnularia*, *Planothidium*, *Rhopalodia*, *Synedra* and *Terpsinoë* (Appendix S4). Tadpoles consumed a higher diversity of diatom taxa than macroinvertebrates. A total of 15 diatom genera were found in *Hyloscirtus* guts and 13 in *Lithobates* guts, while the most genera found in any macroinvertebrate taxon were eight. Tadpoles mostly consumed *Nupela*, *Nitzschia* and *Achnanthes* diatoms (Appendix S5).

Habitat

Resource consumption rates were generally higher in pool habitats, with the exception of scrapers. The shredder, *Anchytarsus*, consumed mostly non-algal biofilm, vascular plant material, amorphous detritus and algae in pools (Fig. 4a), and other dominant food sources were

consumed at similar rates between habitats. Filterers and gatherers consumed more food in pools, with significantly higher non-algal biofilm consumption in pools than in riffles (P = 0.006, P < 0.001, Fig. 4c,d, respectively). The filterer, *Macronema*, also consumed vascular plant material at a significantly higher rate in pools (P = 0.047), while non-Tanypodinae chironomids consumed significantly more amorphous detritus in pools than in riffles (P < 0.001). The scraper, *Farrodes*, consumed overall more food in riffles, with significantly higher consumption of non-algal biofilm in riffles compared with pools (P < 0.001, Fig. 4b). Predatory midges consumed more animal material, non-algal biofilm, amorphous detritus and algae in pools than in riffles, but only differences in animal material were significant (P = 0.002, Fig. 4e). Predators in pool habitats did not consume diatoms.

Omnivory

Omnivory was evident across all 18 taxa (Fig. 5). Predators had the highest degree of omnivory, indicated by *c.* 1 : 1 ratios of plant and animal materials consumed. For example, *Anacroneuria* consumed nearly equal amounts of plant and animal materials (χ^2 = 1.79, d.f. = 1). Other functional feeding groups had lower degrees of omnivory, with ratios much greater than 1 : 1 (plant:animal material). *Phylloicus* (10 : 1) had the highest degree of omnivory among shredders. Scrapers and gatherers showed similar degrees of omnivory across taxa (average = 21 : 1). Among filterers, *Macronema* had the highest (5 : 1). Tadpoles had a plant:animal material ratio of 10 : 1 for *Lithobates* and 60 : 1 for *Hyloscirtus*.

Seasonal differences in omnivory were most pronounced among predators. Both *Hexatoma* and *Anacroneuria* (predators) showed no difference in plant and animal material consumption during the dry season (i.e. 50% plant and 50% animal material consumed; χ^2 = 0.097, d.f. = 1 and χ^2 = 0.188, d.f. = 1, respectively) and had higher degrees of omnivory during the dry season than in the wet season (Fig. 6). The other predators showed a similar trend, except for *Heteragrion* and *Phylogenia*, which had the least seasonal differences in plant and animal consumption. Other functional feeding groups showed no consistent patterns in degrees of omnivory between wet and dry seasons.

Discussion

As the first comprehensive assessment of energy flow from basal resources through consumers in a neotropical
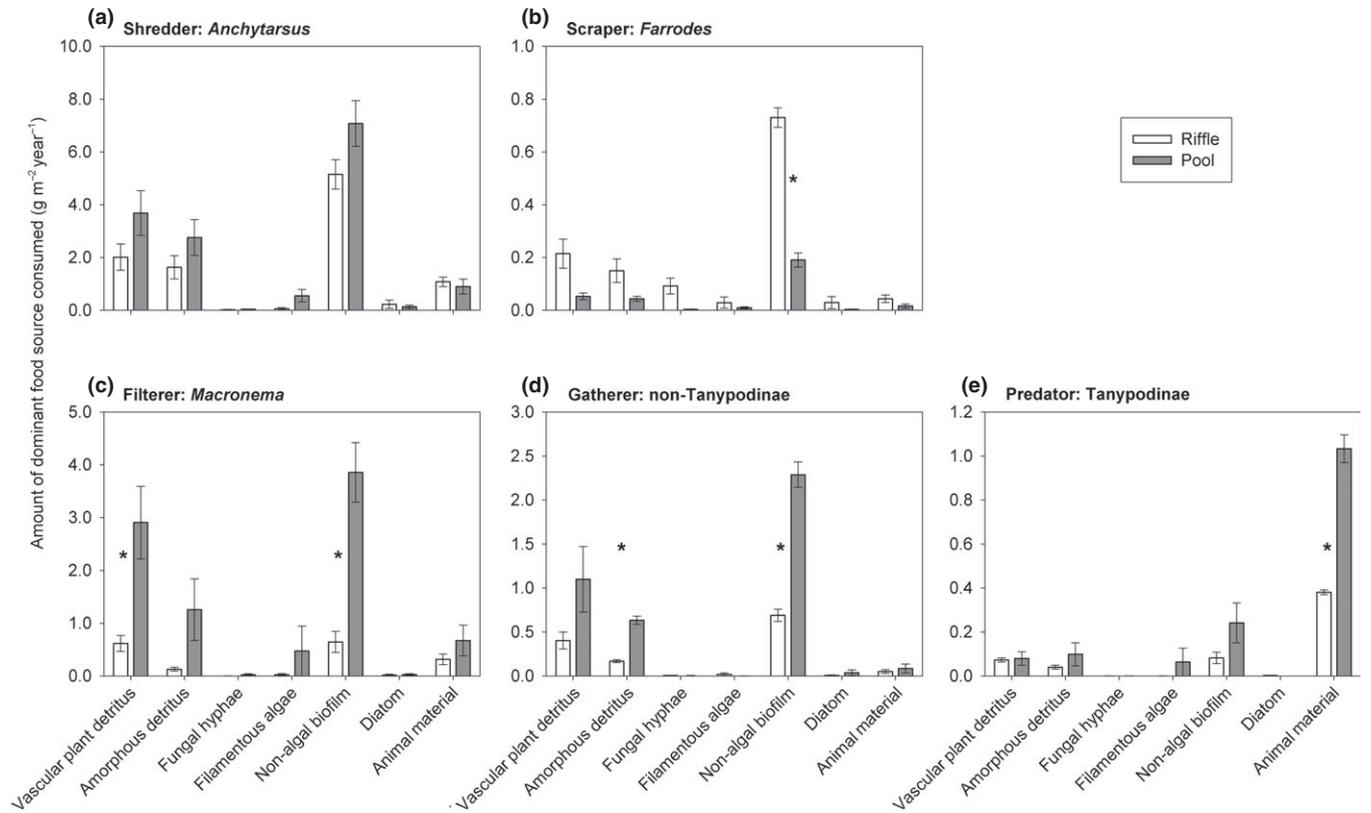
Fig. 4 (a–d) Average annual consumption (g AFDM m^{-2} year^{-1}) of food types by common macroinvertebrate taxa in each functional feeding group in riffles and pools (mean ± 1 SE). Asterisks indicate significant differences between riffle and pool habitats for a given food type and group ($P < 0.05$). Note differences in scale on individual panels.
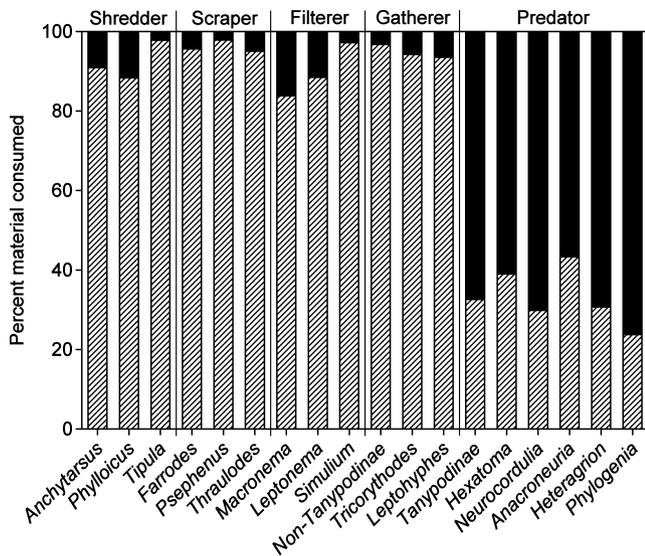

Fig. 5 Average per cent plant (hashed bars) and animal (black bars) material consumed by common macroinvertebrate taxa within each functional feeding group. Plant material includes vascular plant and amorphous detritus. Microbial material consumed is not included.
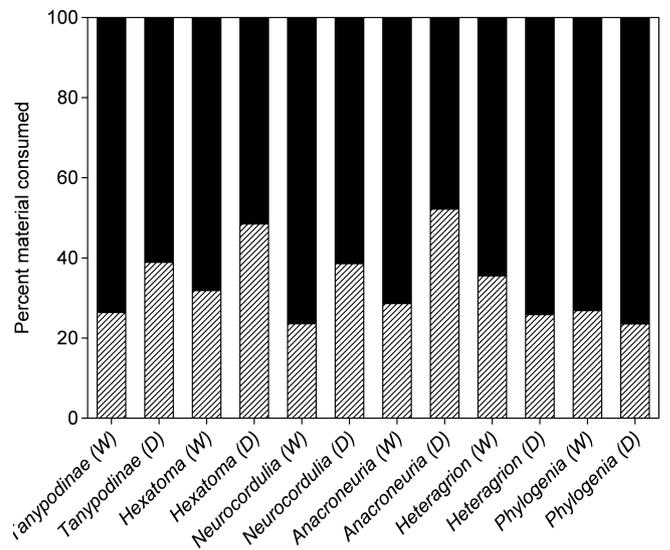
Fig. 6 Consumption of plant (hashed bars) and animal (black bars) materials by predators during the wet (W) and dry (D) seasons. Percentages are habitat weighted averages. Plant material includes vascular plant and amorphous detritus. Microbial material is not included.

headwater stream, this study represents an important baseline model of food-web structure and energy flow for neotropical headwaters. In particular, our results will allow assessment of the ecological consequences of current amphibian declines in the region. Río Guabal is part of an ongoing, long-term study assessing the consequences of disease-driven amphibian declines in Central America (e.g. Lips *et al.*, 2008; Cheng *et al.*, 2011). The chytrid fungus, *Batrachochytrium dendrobatidis*, arrived shortly after this study, decimating the amphibian population (Lips *et al.*, 2006; Whiles *et al.*, 2006). Subsequent studies documented shifts in algal biomass and production of shredders and scrapers following the loss of the amphibian community in Río Guabal (Connelly *et al.*, 2008; Colón-Gaud *et al.*, 2009). Based on our results, we predict that the loss of amphibians in this and other similar streams will decrease the relative importance of detrital pathways through consumers, while increasing the significance of autochthonous pathways because of increases in algal resource availability and potential compensatory responses by grazing invertebrates.

Resource consumption patterns

The tropics are generally considered highly productive systems relative to temperate regions. However, the sum of consumption rates by all invertebrate functional feeding groups measured in Río Guabal was low (30 g m^{-2} year^{-1}) compared with estimates from temperate streams (e.g. 116 g m^{-2} year^{-1}; Cross *et al.*, 2007). Low consumption rates in our study are a product of low invertebrate production, which is probably related to frequent hydrological disturbances that reduce invertebrate biomass and resource availability (e.g. result in low in-stream storage of benthic organic matter; Colón-Gaud *et al.*, 2008, 2009). Thus, although many aspects of tropical headwaters might enhance productivity (e.g. relatively warm and stable temperatures, perennial flow, high leaf litter inputs), hydrological disturbance appears to override these factors and limit production, consumption and energy flow through the food web. A single shredder taxon, *Anchytarsus*, was the sole reason for the importance of the detrital energy pathway in Río Guabal. *Anchytarsus* accounted for the majority of energy flow through the detrital pathway and had twice the production of all other shredding taxa combined (Colón-Gaud *et al.*, 2009). Shredders are often poorly represented in tropical streams, which has been attributed to adaptations of many shredder taxa to lower temperatures and the lower palatability of tropical leaves

(Dobson *et al.*, 2002; Boyero *et al.*, 2011). For example, shredders in Chinese tropical streams constitute ≤10% of total macroinvertebrate abundance and are of little importance to leaf litter breakdown (Lau *et al.*, 2009). Compared with many estimates from temperate-forested streams, shredder abundance and production values in Río Guabal were low, but densities of all functional groups in Rio Guabal were low, and thus shredder abundance and production values were comparable with other functional groups in the stream. Provided there were no compensatory responses by other shredders, loss or declines of *Anchytarsus* from these streams could significantly alter energy flow pathways.

The importance of non-algal biofilm in Río Guabal may be related to habitat characteristics and our methods for analysing guts. Low algal abundance and relatively warm, stable temperatures in Río Guabal may have provided optimal conditions for development of non-algal biofilm, enhancing its importance as the primary energy source for consumers in the system (average contribution to production across all taxa = 43%). Non-algal biofilm is an aggregation of fungi, bacteria, dissolved organic polysaccharides and exopolymer secretions (Decho, 1990). Elevated and stable stream temperatures in addition to higher rainfall and incident light can explain differences in biofilm composition in the tropics (Romaní & Sabater, 2000). Non-algal biofilm has not been considered in many prior studies, since few sonicated gut contents prior to analysis (but see Parker & Huryn, 2006; Cross *et al.*, 2011), and most used metricel or polycarbonate membrane filters rather than nitrocellulose (e.g. Rosi-Marshall & Wallace, 2002; Parker & Huryn, 2006; Cross *et al.*, 2007). Sonication of our samples presumably separated non-algal biofilm attached to detritus, and nitrocellulose membranes have high binding capacities for nucleic acids and proteins. Given its importance as an energy source in Río Guabal, further examination of the specific composition and spatiotemporal developmental patterns of this resource in streams is warranted.

Some aspects of the Río Guabal food web resembled patterns observed in temperate stream food webs, with some notable exceptions. Vascular plant material and amorphous detritus were important resources in Río Guabal, as has been observed in numerous studies of forested temperate stream food webs (e.g. Rosi-Marshall & Wallace, 2002; Cross *et al.*, 2011). However, diatoms and wood, which are often important food sources in temperate streams (Hall *et al.*, 2001; Rosi-Marshall & Wallace, 2002; Cross *et al.*, 2007), appeared much less important in Río Guabal. Wood, in particular, was virtually absent from guts of consumers in Río Guabal,

probably due to the frequent scouring (Colón-Gaud et al., 2008). Frequent scouring events combined with heavy shading also limit diatom abundances in neotropical headwaters, potentially explaining the lack of relative importance of diatoms in tropical stream food webs compared with temperate counterparts (Dudgeon, 1999).

Autochthonous food resource contributions to production in Río Guabal were more similar to estimates from temperate streams (Rosi-Marshall & Wallace, 2002; Cross et al., 2007) than estimates from Asian tropical headwaters (Salas & Dudgeon, 2001; Lau et al., 2009). Dense canopy cover over Río Guabal presumably decreases algal production, shifting the importance to allochthonous sources (e.g. Lamberti & Steinman, 1997; Doi, 2009). In addition to shading, frequent high discharge events in tropical streams like Río Guabal result in significant scouring of algal resources (Salas & Dudgeon, 2003). Studies in a Chinese subtropical river found percentages of autochthonous material in macroinvertebrate diets similar to those we observed in Río Guabal, and attributed both canopy cover and scouring to lower overall consumption of autochthonous resources (Wen et al., 2010).

We used NPE and AE estimates derived from studies in temperate regions, and thus, we may not have accounted for some potential differences between tropical and temperate resource consumption patterns. Future studies that examine ecological efficiencies of tropical stream taxa will enhance our ability to compare tropical and temperate systems, and better assess roles of consumers in energy flow.

Seasonality

Autochthonous food sources were ingested at higher rates during the dry season, a pattern driven primarily by consumption of diatoms and other algae. These results are consistent with prior studies showing higher availability of algal food sources and consumption rates in tropical streams during the dry season (Mosisch & Bunn, 1997; Salas & Dudgeon, 2001; Lau et al., 2009). Higher abundance of algae during the dry season is a function of reduced flooding, which allows time for algal growth and reproduction (Mosisch & Bunn, 1997). The lack of differences in consumption of allochthonous materials between seasons can be attributed to similar amounts of CPOM standing stocks during both seasons (Colón-Gaud et al., 2008). Studies of tropical streams that have found seasonal differences in consumption of allochthonous food sources were conducted in systems, where autochthonous pathways are more important

(Salas & Dudgeon, 2001; Lau et al., 2009), which was not the case in Río Guabal.

Habitats

With the exception of scrapers, invertebrate consumption rates were generally higher in pool habitats. These differences were a function of both variations in production and resource availability between habitats. Compared with riffles, Río Guabal pools had 2–3 times higher benthic organic matter standing stocks (Colón-Gaud et al., 2008), which resulted in higher resource availability and presumably higher consumption rates in pool habitats. Predators can also have higher success rates with prey encounters in pools and spend less energy coping with higher water velocities while searching for prey (Lancaster & Hildrew, 1993). In addition, more abundant CPOM in pools could increase cover for ambush predators and provide more habitat and resources for potential prey.

Unlike temperate systems, the dominant food source for scrapers in Río Guabal was non-algal biofilm. This food resource may be more available to scrapers in riffle habitats since other groups, particularly tadpoles, are more abundant in pools (Ranvestel et al., 2004). Given the abundance of predatory invertebrates and tadpoles in pools, relatively small-bodied scrapers may face less competition and predation risk in riffles.

Omnivory

Omnivory can be an adaptive response to nutritional limitations, competition and frequent disturbance (Jepsen & Winemiller, 2002; Loeuille & Loreau, 2005; Wilder & Eubanks, 2010); these mechanisms may be particularly relevant to predators in Río Guabal, which had the highest degree of omnivory. Predators consumed less animal material during the dry season, indicating that prey encounter rates may be lower during low flow periods and alternative food sources were consumed to supplement the shortfall. During the wet season, macroinvertebrates can be tolerant of rapidly changing flow regimes by moving to low flow microhabitats, or refugia (Lancaster & Hildrew, 1993). Prey abundances and predation pressure can be higher in refugia at high flow compared with any habitat during baseflow (Lancaster, 1996; Lake, 2000), which may explain lower degrees of omnivory by dominant predators in Río Guabal during the rainy season.

Incidental ingestion of detritus and other non-animal material (e.g. material on prey or in prey guts) may

contribute to apparent omnivory by predatory taxa. Studies in European streams have used various methods and criteria to resolve this issue and found that up to 54% of detrital material in predator guts was actively ingested (Bo & Fenoglio, 2005; Lancaster *et al.*, 2005; Fenoglio *et al.*, 2007). We also observed an ontogenetic shift in predators from a relatively high detritus to low detritus diet in Río Guabal, indicating that at least early instars actively feed on detritus (e.g. Céréghino, 2002). Our results build on evidence suggesting that omnivory is more prevalent in tropical food webs compared with temperate systems for both predatory and non-predatory taxa (Wantzen *et al.*, 2006; Coat *et al.*, 2009).

Animal material was among the top four food sources for non-predatory macroinvertebrates and tadpoles in Río Guabal. In comparison with temperate stream food webs, overall consumption rates of animal material were much higher (Rosi-Marshall & Wallace, 2002; Cross *et al.*, 2011). In particular, the two dominant filter-feeding caddisfly taxa were highly carnivorous, a pattern that has been observed to some degree in temperate headwater streams (Benke & Wallace, 1980). Nets of some hydropsychids may not be efficient for catching drifting algae and detritus, making animal material a necessary and nutritious alternative food source (Lancaster *et al.*, 2005).

Given that neotropical headwaters are only recently studied systems and very few analyses of gut contents or feeding ecology of tropical species having been performed (e.g. Cheshire, Boyero & Pearson, 2005), we often depend on information from other regions to interpret the results (Wantzen *et al.*, 2006). As with most studies of tropical stream invertebrates, we used functional feeding group classifications based on feeding methods from studies in temperate regions. However, tropical streams receive leaf litter input throughout the year, peak litter fall occurs in the warmer season, the diversity of riparian vegetation is high and the frequency of stochastic flow events is high compared with temperate headwaters (Cheshire *et al.*, 2005). Therefore, temperate FFG classifications may not be appropriate for neotropical streams, and new categories specific to the tropics may be necessary (see Cheshire *et al.*, 2005; Tomanova *et al.*, 2006).

Our study provides quantitative information on the contributions of various stream consumers to energy flow in a tropical headwater stream, information that is central to understanding and managing these relatively poorly studied systems. This information is also valuable for understanding the consequences of ongoing losses of consumer diversity. Biodiversity losses

such as amphibian declines are influencing ecosystems across the planet, and predicting the consequences of these losses is difficult (Hooper *et al.*, 2012). Freshwater habitats, particularly streams, have some of the highest rates of species losses (Jenkins, 2003; Warren *et al.*, 2005; Vaughn, 2010) and are therefore logical focal systems to study the consequences of declining biodiversity and extinction.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Average annual percent of production attributed to each food type (mean $\pm$ 1 SE) for 18 common macroinvertebrate taxa across all functional feeding groups (FFG). Numbers in parentheses indicate total number of individuals analysed.

Appendix S2. Average annual consumption of each food type (g AFDM m^{-2} year^{-1}, mean $\pm$ 1 SE) by 18 common macroinvertebrate taxa across all FFG. Numbers in parentheses indicate total number of individuals analysed.

Appendix S3. Consumption of various food types (mg AFDM m^{-2} year^{-1}) by two common tadpole species ($n = 6$ *Lithobates*, $n = 14$ *Hyloscirtus*) and percent contribution of each food type to annual production.

Appendix S4. Percentages of diatom taxa found in gut contents of common macroinvertebrate taxa across all FFG during the wet and dry seasons.

Appendix S5. Percentages of diatom taxa found in gut contents of two common tadpole species.

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