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Editor's choice

Diets of leaf litter-associated invertebrates in three tropical streams

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Abstract – Shredders play a major ecological role in temperate streams, but their numerical importance is highly variable within the tropics. Detailed studies on the diets of tropical stream invertebrates are advisable to be able to better describe and understand this variation. Here, we examined the diets of invertebrates collected from the leaf litter of three tropical streams in Colombia, using gut content analysis. Fine and coarse particulate organic matter were the main food resources for invertebrates, which could be divided into four main dietary groups: predators, shredders, specialist collectors and generalist collectors. While the specialist collectors were the most numerically abundant group (54%), shredder biomass accounted for 63% of total invertebrate biomass, suggesting that shredders play a significant ecological role in the study streams. We describe the diets of 12 out of 47 taxa that were previously unknown, which indicates that knowledge about the feeding ecology of tropical stream invertebrates is still incipient.

Key words: Aquatic invertebrates / gut contents / shredders / dietary groups / trophic guilds

Introduction

Invertebrate shredders play a major role in the biological decomposition of leaf material in temperate streams (Webster and Benfield, 1986; Allan, 1995; Boyero *et al.* 2011a). Their feeding activities produce large amounts of fine particulate organic matter (FPOM; Cummins, 1974), which is used by other detritivore guilds (Heard and Richardson, 1995), and they incorporate allochthonous carbon and nutrients into animal biomass (Chung and Suberkropp, 2009), thus making it available for higher trophic levels (Wallace *et al.*, 1997).

The importance of shredders in tropical streams, however, is not so clear. Several studies have suggested that tropical shredders are scarce (Dobson *et al.*, 2002; Rueda-Delgado *et al.*, 2006; Wantzen and Wagner, 2006; Gonçalves *et al.*, 2007), while others have shown the opposite (Cheshire *et al.*, 2005; Wright and Covich, 2005; Chará *et al.*, 2007; Camacho *et al.*, 2009; Ríos-Touma *et al.*, 2009; Yule *et al.*, 2009). A recent global study has demonstrated not only that shredder diversity increases with latitude (Boyero *et al.*, 2011b) but also that variability in shredder abundance and diversity within the tropics is higher than within temperate areas (Boyero *et al.*, 2011c).

Information on tropical stream food webs and the feeding ecology of tropical stream invertebrates is still incipient (Boyero *et al.*, 2009), except for a few locations such as Hong Kong (Mantel *et al.*, 2004) and north Queensland (Cheshire *et al.*, 2005). Some information also exists for Kenya (Dobson *et al.*, 2002), Brazil (Motta and Uieda, 2004), Bolivia (Tomanova *et al.*, 2006) and Indonesia (Yule *et al.*, 2010). There is evidence that related species occurring in different regions often have different diets (Cheshire *et al.*, 2005; Tomanova *et al.*, 2006), so detailed studies on tropical stream invertebrate diets are advisable. Here, we describe the diets of multiple invertebrate species from three Colombian streams through gut content analysis. We predict that classification of invertebrates into trophic guilds based on their diets will provide evidence of the important ecological role of shredders in these tropical streams.

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Table 1. Physical and chemical parameters recorded in the study sites.

	Paloblanco	La Hacienda	Marianela
Altitude (m asl)	1792	1858	1911
Mean width (m)	2.4	2.4	3.8
Mean depth (cm)	16.5	9.3	18
% Canopy cover	60	70	50
% Pool habitats	42	57	67
% Riffle habitats	58	43	33
% Leaf litter in pools	33	50	40
% Leaf litter in riffles	54	54	25
Substrate composition:			
% Boulder (> 256 mm)	0	15	60
% Cobble (64–256 mm)	15	60	0
% Pebble (16–64 mm)	80	15	20
% Gravel (2–16 mm)	0	10	20
% Sand (< 2 mm)	5	0	0
Water temperature (°C)	15.5	14.9	14.3
Conductivity (μS.cm^{-1})	48	41	35
pH	7.1	7.3	7.5
Alkalinity (mg $CaCO_3$.L^{-1})	24.9	21.3	17.9
Total phosphorus (μg P-PO_4.L^{-1})	70	60	40
Total nitrogen (mg N.L^{-1})	< 1.6	< 1.6	< 1.6
Nitrites (mg N-NO_2.L^{-1})	< 0.01	< 0.01	< 0.01
Nitrates (mg N-NO_3.L^{-1})	0.8	0.7	0.7

Materials and methods

The study sites were Paloblanco (4°43'45"N, 75°34'49"W), La Hacienda (4°43'23"N, 75°34'1"W) and Marianela (4°44'19"N, 75°33'19"W), three first-order forest streams located in the middle watershed of the Otún River (Central Andes of Colombia), between 1792 and 1911 m above sea level. Physical and chemical characteristics of the streams were recorded in a single measurement and summarized in Table 1. Five riffles and five pools were sampled in each stream during the dry season (February) of 2007; ten replicate leaf-litter samples were taken from leaf packs, by extracting litter from within a 20 × 20 cm frame with a dip net (0.5 mm mesh) placed immediately downstream.

Invertebrates were sorted from the leaf litter in the field, preserved in 85% ethanol and transported to the laboratory, where they were identified to the lowest possible taxonomic level (generally genus). Excess moisture was removed from the invertebrates with tissue paper, and individuals from each taxon were separately weighed to obtain a relative measure of biomass. Leaves were oven dried at 60 °C for 5 days and weighed.

In order to assign the collected invertebrates to trophic guilds, the gut contents of 1–15 individuals of each taxon were examined following the methods proposed by Cheshire *et al.* (2005) and Tomanova *et al.* (2006). Guts were removed and mounted in glycerin to create semi-permanent slides, which were examined under a microscope (up to 100 × magnification). The proportion of each food item was estimated from the relative area of food particles in 20 randomly chosen fields on each slide. Gut contents were divided into six categories: (1) FPOM, (2) coarse particulate organic matter (CPOM), (3) algae (ALG), (4) animal tissue (AT), (5) mineral material (MM), and (6) fungi (FUNG).

Principal components analysis (PCA) was used to describe variation in invertebrate assemblages based on their diets, using the average percentage of each food item in the guts of individuals (arcsin-square-root transformed). We further used cluster analysis (Euclidean distance and Ward's clustering method) to classify invertebrate taxa into groups with similar gut contents. Only taxa with at least three individuals examined were included in these analyses (individuals from different streams and habitats were pooled to have a sufficient number of individuals). Both analyses and graphical presentation were performed using SPSS 12.0 for Windows and XLSTAT.

Results

Sample composition

A total of 2300 invertebrates from 71 taxa were collected, including 56 genera, 33 families, 13 orders and 3 classes. Insecta was the most important class, comprising 98% of the collected organisms. Average invertebrate abundance ranged from 2.4 (± 2.1 SD) to 5.5 (± 6.1 SD) individuals per gram of leaf litter, at La Hacienda and Marianela streams, respectively. Invertebrate biomass varied between 17.2 (± 10.9 SD) and 22.4 (± 29.1 SD) mg of invertebrate wet mass per gram of leaf litter dry mass, at Paloblanco and Marianela streams, respectively.

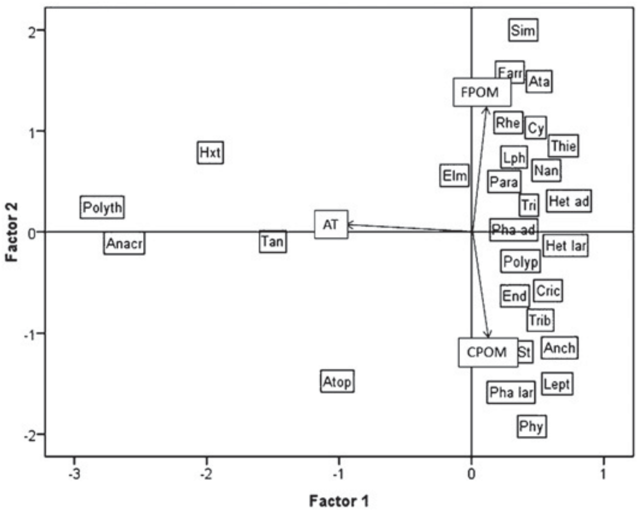

Fig. 1. Principal components analysis (PCA) of the diet composition of 26 invertebrate taxa from three Colombian streams. Factors 1 and 2 explain 53 and 38% of the variance, respectively. FPOM, fine detritus; CPOM, coarse detritus; AT, animal tissue. For abbreviations of taxa see Table 2.

Gut contents analysis

PCA and cluster analysis were performed on 26 taxa for which we had data for three or more individuals. However, we present the results for all 47 taxa with gut contents, as it may be useful information for future studies in the region (Appendix 1 available online). FPOM was the only food item found in high proportion in all individuals. The second most ingested food type was CPOM. The PCA identified two principal factors: F1, mainly determined by AT, which decreased along the axis; and F2, mainly determined by CPOM and FPOM, with CPOM decreasing and FPOM increasing along the axis. F1 and F2 explained 53 and 38% of the data variation, respectively (Fig. 1).

Four dietary groups (I–IV) were identified with the cluster analysis (Fig. 2). Mean percentages of food types in each group are presented in Figure 3. Group I contained four taxa with an average of 51% of AT in their guts, and was therefore called "predators". FPOM and CPOM were also important food resources in this group; taxa in this category included Polythoridae and Tanypodinae. Group II included nine taxa with an average of 52% of CPOM in their gut content, and were denominated "shredders". Taxa like *Phylloicus*, *Leptonema* and *Anchytarsus* where classified in this category. Groups III and IV were closely related and contained taxa with high proportions of FPOM. Group III contained four taxa with very high percentages of FPOM (82%) and lower proportions of other food resources; they were called "specialist collectors". Some of the most representative taxa grouped in this category were *Farrodes* and *Simulium*. Group IV contained 11 taxa with an average of 70% of FPOM, and considerable amounts of CPOM and ALG; thus it was named "generalist collectors" and included *Leptohyphes, Parametriocnemus* and *Heterelmis*.

Relative importance of the dietary groups in the leaf-litter-associated community

The most abundant dietary group in the community was the specialist collectors, with 54% of the collected individuals. They were followed by the generalist collectors and the shredders, which accounted for 18 and 17% of the individuals, respectively. In terms of biomass, however, the relative importance of the trophic groups changed substantially. Shredders were the dominant dietary group, representing 63% of total biomass. The second most important dietary group was the predators, which comprised 17% of total biomass, even though they represented only 4% of individuals. Specialist and generalist collectors were the groups with less biomass with 7 and 3%, respectively. Taxa that were not considered in the statistical analyses due to low number of individuals or empty guts comprised 6% of the abundance and 10% of total biomass.

Discussion

This is the first study addressing the trophic structure of invertebrate communities associated with submerged leaf litter in Colombian streams, and one of the few that have described the diets of tropical stream invertebrates based on gut content analysis. Such studies are crucial, as previous records suggest that genera previously allocated into a given FFG in the temperate region can exhibit different feeding habits in the tropics (*e.g.* Dobson *et al.*, 2002). Although we did not attempt to classify invertebrates into FFGs, as we did not examine mouth parts, we were able to identify differences in the diets of leaf litter-associated invertebrates, compared to those previously reported by Merritt and Cummins (1996) for North American insects. For example, 60% of the gut contents of *Leptonema*, previously described as a collector and filterer, were composed of CPOM; *Atopsyche*, previously described as a predator, had some AT in their guts but presented high percentages of CPOM; and *Tribelos*, described as a collector in the temperate region, showed evidence of shredding activity (Table 2).

FPOM was the most important food resource for the leaf litter-associated community, as it was found in substantial proportions in the guts of all individuals. This is in agreement with results of Palmer *et al.* (1993) and Tomanova *et al.* (2006), and studies reviewed by these authors. FPOM is primarily generated from the decomposition of CPOM by shredders, micro-organisms and physical abrasion (Allan, 1995). FPOM constitutes a mostly continuous resource in the streams, and its ubiquity in the guts of leaf litter-associated invertebrates may be explained by its high availability in the habitat.

CPOM was the second most important food resource for the leaf litter invertebrate assemblage, being present in high percentages in 18 taxa. This fact, and the relative importance of shredders in terms of biomass (63%) in leaf

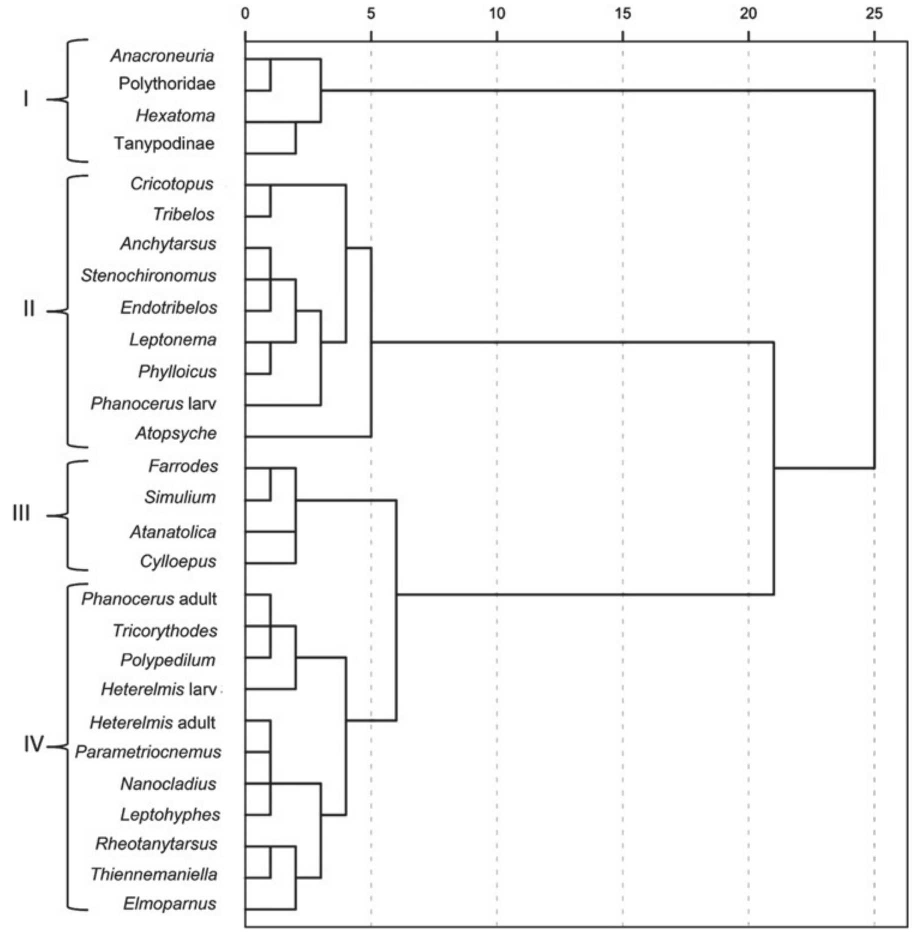

Fig. 2. Cluster analysis of 26 invertebrate taxa associated with leaf-litter packs in three Colombian streams, based on proportions of different food types in their guts. Four groups were identified: I, Predators; II, Shredders; III, Specialist collectors; IV, Generalist collectors.

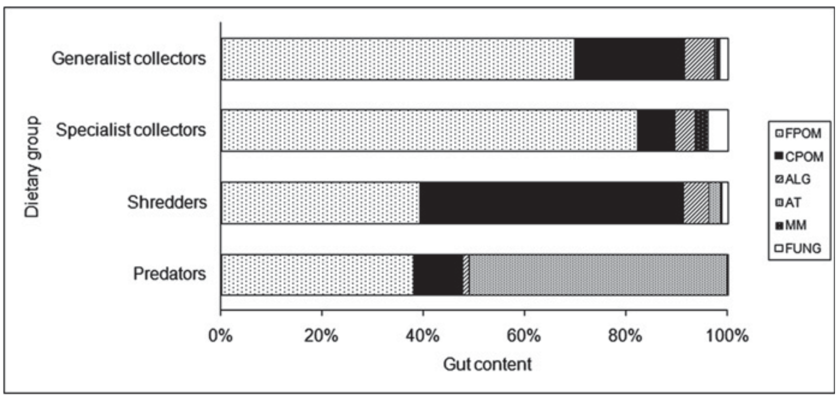

Fig. 3. Mean percentages of the different food types ingested by each dietary group found in leaf-litter packs in three Colombian streams. Dietary groups derived from cluster analysis. FPOM, fine detritus; CPOM, coarse detritus; ALG, algae; AT, animal tissue; MM, mineral material; FUNG, fungi.

litter packs, indicates that invertebrates are playing an important role in leaf litter processing in these tropical streams. This is in agreement with previous studies: Cheshire *et al*. (2005) found that shredders represented 20% of the species richness and 24% of the biomass (up to 40% in pools) of invertebrate assemblages (all microhabitats included) in Australian tropical streams; Chará *et al*. (2007), who classified FFGs based on the literature,

Table 2. Dietary groups identified in the present study, compared to previous reports in the literature.

Taxa	Abbreviation	Dietary group present study	FFG reported in literature
Anacroneuria	Anacr	Predators	–
Anchytarsus	Anch	Shredders	Shredders[1]
Atanatolica	Ata	Specialist collectors	–
Atopsyche	Atop	**Shredders**	**Predators**[1]
Cricotopus	Cric	Shredders	Shredders[1]
Cylloepus	Cy	Specialist collectors	–
Elmoparnus adult	Elm	Generalist collectors	–
Endotribelos	End	Shredders	–
Farrodes	Farr	Specialist collectors	–
Heterelmis larvae	Het lar	Generalist collectors	Shredders, collectors[2]
Heterelmis adult	Het ad	Generalist collectors	–
Hexatoma	Hxt	Predators	Predators[1,2]
Leptohyphes	Lph	Generalist collectors	–
Leptonema	Lept	**Shredders**	**Collectors-filterers**[1,2]
Nanocladius	Nan	Generalist collectors	Collectors[1]
Parametriocnemus	Para	Generalist collectors	Collectors[1]
Phanocerus adult	Pha ad	Generalist collectors	Shredders, collector-scrapers[2]
Phanocerus larvae	Pha lar	Shredders	–
Phylloicus	Phy	Shredders	Shredders-detritivores[1]
Polypedilum	Polyp	Generalist collectors	Collectors, predators[1]
Polythoridae	Polyth	Predators	–
Rheotanytarsus	Rhe	Generalist collectors	Collectors[1]
Simulium	Sim	Specialist collectors	Collectors[1,3]
Stenochironomus	St	Shredders	Shredders, collectors[1]
Tanypodinae	Tan	Predators	–
Thiennemaniella	Thie	Specialist collectors	–
Tribelos	Trib	**Shredders**	**Collectors**[1]
Tricorythodes	Tri	Generalist collectors	Collectors[1]

[1]Merritt and Cummins (1996), [2]Tomanova *et al.* (2006), [3]Cheshire *et al.* (2005). Major contrasts are highlighted in boldface.

found that shredders represented 13% of the abundance and 68% of the biomass of invertebrates colonizing leaf litter bags in Andean Colombian streams; and Yule *et al.* (2009) found that shredders were 25% of the abundance and 82% of the biomass of benthic macroinvertebrates in Malaysian streams. However, these results contrast with those of Dobson *et al.* (2002), Rueda-Delgado *et al.* (2006) and Wantzen and Wagner (2006), who reported low numbers of shredders in several tropical streams. A more recent global study has explored variation in shredder abundance and diversity in ~150 streams from 14 regions across a latitudinal gradient, showing that shredder numbers are indeed quite variable within the tropics, but generally less important than in temperate streams (Boyero *et al.* 2011a, 2011b, 2011c). Although the reasons for this variation are largely unknown, water temperature and leaf litter characteristics are likely to be important (Boyero *et al.*, 2011c).

Our study highlights the importance of considering biomass in future studies of the ecological role of different FFGs in stream food webs. We found that most collectors (*e.g.* *Simulium*, *Farrodes* and several genera of Chironomidae) were small-sized and abundant, while shredders (*e.g.* *Phylloicus*, *Leptonema* and *Anchytarsus*) and predators (*e.g.* Polythoridae and *Anacroneuria*) were generally larger and less numerous taxa. Our study also provides new information on the diets of 12 invertebrate Neotropical taxa. This kind of research is necessary to avoid misclassification of species into FFGs and to allow a proper description of tropical stream food webs. We provided information only for invertebrates associated with leaf litter, as our main interest was to identify shredder species and to assess their ecological importance. Future studies should describe the diets of invertebrates found in other types of microhabitat and potential diet shifts during larval development (Basaguren *et al.*, 2002). The examination of mouthpart morphology is also desirable to classify species into FFGs and describe food webs. Our results, while limited in scope, demonstrate that shredders are an important component of leaf litter invertebrate assemblages in highland Colombian streams.

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