

## Local Variation in Shredder Distribution can Explain their Oversight in Tropical Streams

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### ABSTRACT

Stream shredders play an important role in the breakdown of allochthonous leaf litter—a well-known, key process in temperate headwater streams. In contrast, it has been suggested that litter breakdown in tropical streams is driven by microorganisms, shredders being scarce or absent. We propose that shredders have been overlooked in some tropical streams for two reasons: (1) assuming that tropical shredders belong to the same taxa as temperate ones, without determining the diet of tropical litter fauna; and (2) the small spatial scale of most tropical stream studies, which do not account for intra- and inter-site comparisons. We explored shredder abundance and species richness in six streams in each of two tropical regions, the Australian wet tropics (AWT) and Panama (PAN), finding 734 individuals of 12 shredder species in AWT and 391 individuals of 16 species in PAN. Shredder species richness was positively related to altitude in AWT, but not in PAN. Shredder contribution to total leaf breakdown in the field was  $24 \pm 3$  SE percent in AWT and negligible in PAN, but this was probably due to the unsuccessful colonization of experimental cages by PAN shredders. In the laboratory, shredder contribution to total leaf breakdown was higher than in the field ( $35\% \pm 2$  SE in AWT and  $64\% \pm 3$  SE in PAN) and varied with leaf decomposability. Our results support earlier indications that shredders are not scarce or functionally unimportant in the tropics, and suggest that their contribution to litter processing should be determined along altitudinal gradients.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

**Key words:** altitude; Australian wet tropics; latitude; leaf litter breakdown; macroinvertebrates; Panama.

THE BREAKDOWN OF LEAF LITTER IS OF MAJOR importance in the functioning of headwater forest streams, providing the main energy source for the ecosystem (Wallace & Webster 1996). Leaf breakdown is the result of several processes, including leaching of soluble organic and inorganic materials, colonization by fungi and bacteria, mechanical fragmentation caused by water movement and the activity of the animals that fragment and feed on the leaf tissue (shredders) (Graça 2001). In north temperate streams, leaf fall occurs predominantly during autumn (Webster & Benfield 1986), and dense packs of litter accumulate in the stream and are colonized by numerous shredders (Wantzen & Wagner 2006). In contrast, several studies from tropical areas have suggested that shredders are scarce in the tropics (*e.g.*, Costa Rica: Rosemond *et al.* 1998; Hong Kong: Dudgeon & Wu 1999; Kenya: Dobson *et al.* 2002). Although some other patterns have been described (*e.g.*, Australian wet tropics: Pearson & Tobin 1989, Cheshire *et al.* 2005; Malaysia: Yule *et al.* 2009), shredder contribution to leaf breakdown in tropical streams has generally been considered negligible, and leaf litter breakdown is attributed to leaching of soluble compounds, microbial decomposition and physical fragmentation (Irons *et al.* 1994).

One explanation for latitudinal differences might be that insect orders that contain most species of known shredders (mostly Plecoptera and Trichoptera), which have evolved in cool running waters (Hynes 1970), are apparently largely missing in the tropics. However, this assumes that tropical shredders belong to the same

taxa as temperate shredders, which may not be the case. Although tropical and temperate streams do not show consistent differences in food web structure and organic matter processing (Boulton *et al.* 2008), it is possible that similar functions are performed by different taxa in streams from contrasting latitudes.

We suggest that shredders are not scarce in the tropics as a general pattern, and that they might have been overlooked in some tropical areas due to two factors related to methodology. Firstly, some tropical studies could have failed to identify the local shredders because they have used the functional feeding group (FFG) classification proposed for temperate areas. For example, studies in South America (Mathuriau & Chauvet 2002; Gonçalves *et al.* 2006, 2007) and other tropical areas (Tumwesigye *et al.* 2000, Ndaruga *et al.* 2004) have often used Merritt and Cummins' (1996) classification of North American aquatic insects. We propose that the identification of novel shredders in tropical streams through analysis of gut contents would reveal a higher abundance and species richness of this FFG. For example, while most baetid and leptophlebiid mayflies are scrapers in temperate streams, the genera *Barba* (Leptophlebiidae) from Papua New Guinea (Yule 1996), *Acanthiops* (Baetidae) from Kenya (Dobson *et al.* 2002), *Andesiops* (Baetidae) from Bolivia (Molina 2004) and *Atalophlebia* (Leptophlebiidae) from the Australian wet tropics (Cheshire *et al.* 2005), were found to be shredders through examination of gut contents.

Secondly, intra- and inter-site comparisons of tropical streams are rare, which would miss altitudinal effects on shredder abundance and species richness as well as local variability due to the patchy nature of leaf packs in streams. Shredder abundance and

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species richness are likely to vary with altitude due to variation in temperature as well as inputs (quantity and diversity) and retentiveness of leaf litter. Tropical streams at higher altitudes may be more similar to temperate streams than to lowland tropical streams (see Yule *et al.* 2009), and thus shredder numbers are likely to vary through altitudinal gradients as much as they vary with latitude.

We examined the local variation in shredder numbers (abundance and species richness) and the contribution of shredders to leaf litter breakdown in two tropical regions, the Australian wet tropics (AWT) and Panama (PAN), using local leaf species and reciprocally transferred leaves. We hypothesized that the local variation in shredder numbers would be high and related to altitude, and that the contribution of shredders to leaf breakdown would not be negligible and would vary at local scales in relation to internal factors such as leaf decomposability (defined as their susceptibility to break down by microbial activity, leaching and/or physical fragmentation).

## METHODS

Hypothesis 1: Shredder numbers are locally variable and depend on altitude.

We sampled six streams at each of the AWT (18° S) and PAN (9° N; see Table S1). The surveys were conducted in the late dry season for both regions: October–November 2005 in AWT and February–March 2006 in PAN. The average daily air temperature during this time of the year is 25.5°C for AWT (Bureau of Meteorology, Australia) and 26.5°C for PAN (Gerencia de Hidrometeorología, Panama). All surveyed stream reaches were well shaded, headwater forest streams of second or third order and were located across an altitudinal gradient. We measured the pH, conductivity, dissolved oxygen and water temperature using a Hydro-lab multi-probe meter, air temperature, average channel width and water depth (at 10 and 50 locations, respectively); we noted the altitude, latitude and longitude; and we visually estimated percent canopy cover and percent of substrate covered by leaf litter (Table S1).

At each stream, 12 leaf litter samples were haphazardly collected from pool habitats. Each sample consisted of leaves taken from the surface of litter packs, sufficient to fill a 5-L tray. Known or potential shredders were sorted from the litter samples, preserved in 70 percent ethanol and identified to species or morphospecies. The rest of the sample was preserved for further examination.

AWT shredders were well known from Cheshire *et al.* (2005). They are all relatively large invertebrates (mostly cased caddisflies) that can be easily picked by eye. In PAN, we picked those cased caddisflies similar to AWT shredders (calamoceratids and leptocerids), plus other conspicuous animals that were considered potential shredders (tipulids, snails and crabs). The gut contents of these animals (up to 10 individuals/morphospecies/site, depending on availability) were examined following the methods of Cheshire *et al.* (2005). Individuals with > 40 percent of their gut contents composed of vascular plant tissue (particles > 1 mm) were considered to be shredders, following the criteria of Cheshire *et al.* (2005). Several PAN samples were later checked in the laboratory (the

gut contents of all invertebrates were examined following the same methods), producing no further shredders.

Altitudinal variation of shredder abundance (number of individuals per liter of leaf litter) and species richness (number of species or morphospecies per liter of leaf litter) was explored with linear regression for each of the regions studied.

Hypothesis 2: Shredder contribution to leaf breakdown is not negligible and is related to leaf decomposability.

We conducted a field and a laboratory experiment to address this hypothesis. Firstly, we explored the contribution of shredders to leaf breakdown in one stream in each study region, and the effect of leaf decomposability on breakdown rates. The experiment was conducted at Camp Creek (AWT) and Quebrada Juan Grande (PAN), where the average water temperatures were 20°C and 24°C, respectively. These streams were chosen as typical forest streams in the study areas and had a well-known, abundant shredder fauna. While such streams may not be representative of all streams in the region, they should provide a clear estimate of shredder activity in those streams where shredders are abundant.

At each location, we used leaves from three riparian tree species, which were the most abundant leaves in the study streams (Bastian *et al.* 2007), and that differed in decomposability (high, medium and low; determined from previous work in the AWT [Boyero *et al.* 2006, Bastian *et al.* 2007] and PAN [R. Camacho, L. Boyero and R. G. Pearson, unpubl. data]). The most decomposable species were *Apodytes brachystylis* Muell. (Icacinaceae) (AWT) and *Hirtella triandra* Sw. (Chrysobalanaceae) (PAN); those with medium decomposability were *Endiandra bessaphila* Hyland (Lauraceae) (AWT) and *Guarea guidonia* L. (Meliaceae) (PAN); and the least decomposable were *Cryptocarya leucophylla* Hyland (Lauraceae) (AWT) and *Zygia longifolia* (Willd.) Britton & Rose (Fabaceae) (PAN). We used green leaves collected from randomly selected trees. Although senescent leaves are commonly used in breakdown experiments, green leaves are rapidly decomposed in streams and have been shown to be important food sources for shredders due to their high nitrogen content, relatively soft tissue and high availability in the streambed at certain times of the year (see Bastian *et al.* 2007). Leaves were oven-dried at 50°C for 48 h and weighed to the nearest gram.

At each location, 40 plastic containers (14.5 × 9.5 cm) with six leaves each (two/species) were placed in the stream. All containers had a 13.5 × 7.5 cm window on the top, with 20 covered by a fine mesh (1.0 × 1.5 mm) and the other 20 by a coarse mesh (15 × 20 mm) (see Boyero *et al.* 2006). Pairs of containers (one coarse- and one fine-meshed) were haphazardly placed in stream pools. After 2 weeks, 10 pairs were randomly selected and removed from the stream. Shredders were separated, preserved in 70 percent ethanol and taken to the laboratory for identification. Leaves were oven-dried at 50°C for 48 h and re-weighed. Two weeks after the first collection, the other 10 pairs of containers were collected and processed similarly. We recognize that there might have been some difference in the water movement between fine- and coarse-meshed containers; however, as the experiment was conducted in pools with virtually zero current velocity, it is unlikely that this had any major effect.

Leaf breakdown rates ( $k$ ) for each leaf species in each container were determined using the exponential decay model  $W_t = W_0 e^{-kt}$ , where  $W_t$  is the nal mass of leaf material,  $W_0$  is the initial mass of leaf material and  $t$  is the time in days (Gonçalves *et al.* 2006). A two-way ANOVA model was used to explore the variation of  $k$  with leaf decomposability and treatment (coarse/fine mesh), for each region. Finally, we explored the relationship between  $k$  and shredder abundance for each leaf decomposability level and region to investigate whether the breakdown rates were density-dependent.

Secondly, we performed a laboratory experiment to further explore the contribution of shredders to leaf breakdown and to assess any effect of leaf origin (native vs. exotic species). The experiment was conducted with the most common shredder species present in the AWT or PAN streams. Late-instar shredders of similar size were exposed to combinations of leaves from both regions that varied in decomposability. Water temperatures mimicked natural conditions in the streams where shredders were collected (20°C in AWT and 24°C in PAN). Because of this difference in temperature, the results were analyzed separately. We used the same six leaf species as in the field experiment. Leaves from both regions were collected from trees near the surveyed streams, oven-dried at 80°C for 48 h (due to Australian Quarantine Inspection Service requirements for imported leaves) and weighed. Although this high temperature might affect the internal structure and composition of the leaves, all leaves were treated similarly and so it was unlikely to affect comparisons among them.

Plastic containers identical to those used in the field experiment, but open on the top and filled with 500 mL of bottled local spring water, were used. In AWT, we had a total of 80 containers, 40 with AWT leaves and 40 with PAN leaves. Each container had a total of three leaves, one leaf of each of the three AWT or PAN species mentioned above. In 20 containers (10 with AWT and 10 with PAN leaves), we introduced three individuals of *Lectrides varians* Mosely (Leptoceridae); in another 20, three individuals of *Anisocentropus kirramus* Neboiss (Calamoceratidae); in another 20, one individual of each of three species: *L. varians*, *A. kirramus* and *Triplectides gonetalus* Morse & Neboiss (Leptoceridae); and in the final 20 containers, there were no shredders (controls). Controls allowed us to separate leaf breakdown due to shredder consumption from that due to microbial processing. In PAN, one treatment was omitted because there were not enough individuals of a second shredder species available at the time. In 20 containers, we introduced three individuals of *Phylloicus* sp. 1 (Calamoceratidae); another 20 contained one individual of each of three species: *Phylloicus* sp. 1, *Phylloicus* sp. 2 (Calamoceratide) and *Triplectides* sp. (Leptoceridae); and 20 were the controls. All containers were replenished with bottled water when necessary. After two weeks, the experiment was terminated. Leaves were oven dried at 50°C for 48 h and reweighed. Shredders were preserved in 70 percent ethanol.

Leaf breakdown was quantified as the decay rate ( $k$ ), calculated for each leaf  $\times$  shredder combination. For each experiment (AWT or PAN), we used a four-way ANOVA model to explore the variation of  $k$  with leaf origin (native/exotic), leaf decomposability (high/medium/low), treatment (shredders/controls) and shredder

species (nested within treatment), including all second-order interactions.

The average contribution of shredders to total leaf breakdown was calculated as

$$k_{\text{coarse-mesh containers}} - k_{\text{fine-mesh containers}} / k_{\text{coarse-mesh containers}} \times 100.$$

## RESULTS

Hypothesis 1: shredder numbers are locally variable and depend on altitude.

A total of 734 shredder individuals of 12 species (one mayfly, 10 caddisflies and one dipteran) were found in AWT, while 391 individuals of 16 species (13 caddisflies, one dipteran, one crab and one snail) were found in PAN (Table S2). In AWT, shredder abundance and species richness were positively related to altitude (abundance:  $F_{1,4} = 7.72$ ,  $P = 0.0499$ ; richness:  $F_{1,4} = 15.9$ ,  $P = 0.016$ ; Fig. 1). In PAN, the opposite pattern was apparent for abundance, which decreased with altitude ( $F_{1,4} = 21.5$ ,  $P = 0.01$ ), but species richness showed no clear pattern ( $F_{1,4} = 0.17$ ,  $P = 0.704$ ). Species richness was not related to abundance for AWT ( $y = 5.493 + 0.020x$ ;  $R^2 = 0.30$ ,  $P = 0.151$ ) or PAN ( $y = 5.926 + 0.024x$ ;  $R^2 = 0.15$ ,  $P = 0.243$ ).

Hypothesis 2: shredder contribution to leaf breakdown is not negligible and is related to leaf decomposability

A total of 69 individuals from seven species colonized coarse-mesh containers in AWT after 14 d, with numbers subsequently decreasing to 53 individuals from six species after 28 d. In PAN, colonization of containers was much lower, with 11 individuals from five species after 14 d, and five individuals from four species after 28 d. The average contribution of shredders to total leaf breakdown was  $24 \pm 3$  SE percent in AWT and negligible in PAN.

The total leaf breakdown rates were directly related to decomposability, both in the AWT and in PAN, with the most decomposable leaves showing the highest rates, as expected (Table 1; Fig. 2). Breakdown rates were higher in coarse- than in fine-mesh bags in AWT, but not in PAN, where the interaction leaf decomposability  $\times$  treatment was significant (Table 1): breakdown rates were higher in the fine-mesh treatment for highly decomposable leaves, while the opposite occurred for leaves with medium decomposability, and there was no difference for those with low decomposability (Fig. 2). Shredder abundance was not correlated to breakdown rates, for any region or decomposability level ( $P > 0.05$  in all cases).

In the AWT laboratory experiment (Table 2; Fig. 2), breakdown rates were higher in shredder treatments than in controls. The rates varied with leaf decomposability as expected (high  $>$  medium  $>$  low decomposability). Native (AWT) leaves broke down faster than exotic (PAN) leaves, and the rates were higher in treatments with only *A. kirramus* or with the three shredder species than in treatments with only *L. varians*.

Shredder contribution to total breakdown was  $33 \pm 2$  percent on average, being lower for the most decomposable leaves ( $24\% \pm 2$ ), intermediate for the least decomposable leaves

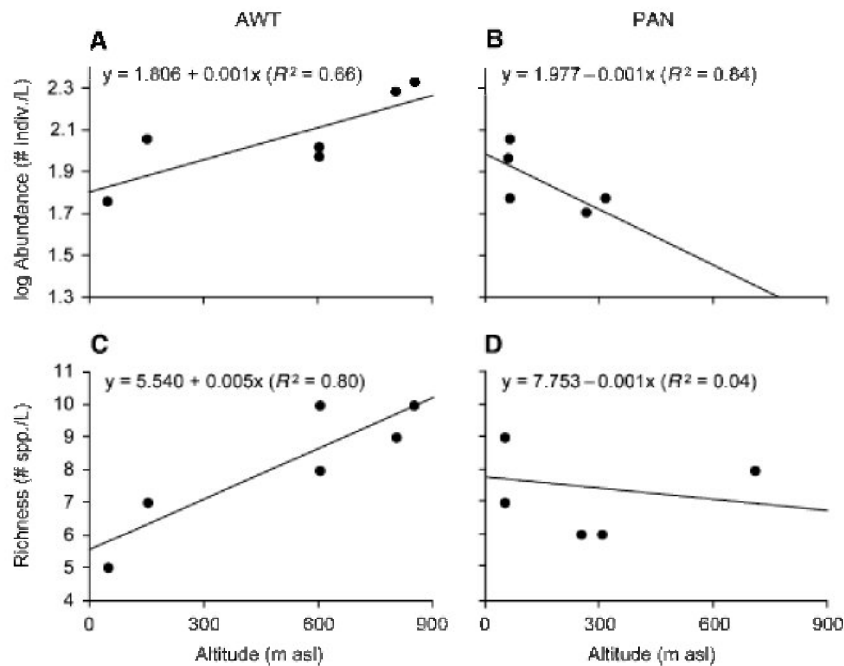


FIGURE 1. Linear regressions showing variation of shredder abundance (A–B) and species richness (C–D) with altitude (m asl) in AWT (A and C) and PAN (B and D).

(33% ± 3) and higher for leaves with medium decomposability (41% ± 2).

In the PAN laboratory experiment (Table 2; Fig. 2), the breakdown rates were also higher in shredder treatments than in controls. Again, the rates varied with leaf decomposability as expected (high > medium > low decomposability). Exotic (AWT) leaves broke down faster than native (PAN) leaves, but this was only true for controls (significant interaction leaf origin × treatment). There were no differences among shredder species treatments.

TABLE 1. Results of two-way ANOVA exploring variation of leaf breakdown rates (k) with leaf decomposability (high/medium/low) and treatment (coarse/fine mesh) in the field, in the Australian wet tropics (AWT) and Panama (PAN). Degrees of freedom (df), sums of squares (SS), F-statistic and P-values are shown (significant values at α = 0.05 level in bold).

Source of variation	df	SS	F	P
AWT				
Leaf decomposability (Ld)	2	0.00219	106	< <b>0.0001</b>
Treatment (Tr)	1	0.00035	34.1	< <b>0.0001</b>
Ld × Tr	2	0.00006	3.06	0.0510
Error	114	0.00118		
PAN				
Leaf decomposability (Ld)	2	0.00295	42.4	< <b>0.0001</b>
Treatment (Tr)	1	0.00002	0.50	0.4812
Ld × Tr	2	0.00057	8.21	<b>0.0005</b>
Error	114	0.00396		

Shredder contribution to total breakdown was 63 ± 3 percent on average, being lower for leaves with high decomposability (54% ± 4), followed by leaves with medium (57% ± 4) and low decomposability (78% ± 4).

DISCUSSION

Our results suggest that shredder numbers in tropical forest headwater streams are highly variable, with altitude possibly being an important source of variation. In a limited number of stream sites in the Australian wet tropics, shredders were more diverse at higher altitudes, a pattern that has also been found in other tropical areas such as Malaysia (Yule *et al.* 2009) and Colombia (J. Chará, pers. comm.), and confirms previous records of higher trichopteran diversity at higher altitudes in the Australian wet tropics (Pearson 2005). In Panama, shredders were more abundant at lower altitudes, but we did not find a relationship between diversity and altitude, although our lack of replication at higher altitudes precludes any conclusions based on these data.

The River Continuum Concept suggests that shredders are numerically and functionally dominant in forested headwater streams (Vannote *et al.* 1980), and this pattern is supported by some tropical studies (*e.g.*, Greathouse & Pringle 2006). However, this model does not account for differences among headwater streams, such as altitudinal variation and factors that co-vary with altitude (*e.g.*, water temperature, composition of riparian vegetation). Given that most known insect shredders (mainly Plecoptera and Trichoptera) are animals typical of cool waters, abundance gradients in temperate streams may not be as important as those in

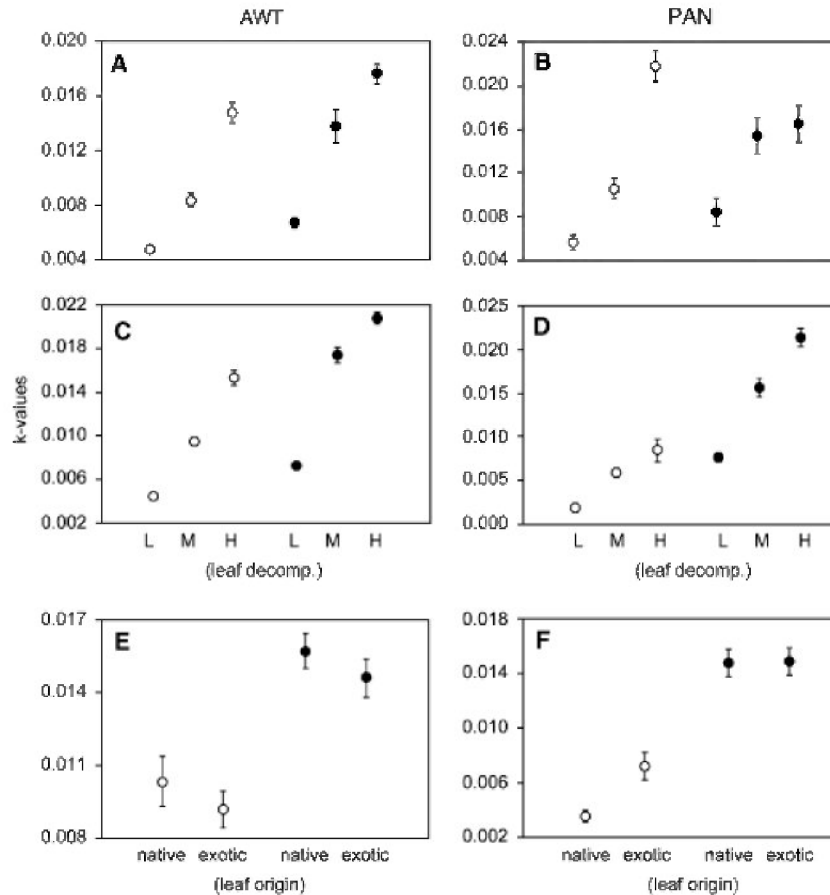


FIGURE 2. Leaf breakdown rates ( $k$ -values, in day<sup>-1</sup>) in the field (A–B) and laboratory (C–F) experiments performed in each study region, showing variation in fine (open circles) and coarse (closed circles) treatments in AWT (A, C and E) and PAN (B, D and F) at varying decomposability levels (L, low; M, medium; H, high) and with native vs. exotic leaves. Bars indicate SE.

tropical streams, because of their overall smaller gradients in temperature from headwaters to stream mouths. In the tropics, the higher temperatures reached in the lowlands may be responsible for the scarcity of shredders, which may still be abundant in the highlands. Jacobsen *et al.* (1997) found that the number of insect families increased with water temperature resulting in higher insect diversity in lowland tropical streams (Ecuador) than highland tropical (Ecuador) or lowland temperate (Denmark) streams. We suggest that gradients in macroinvertebrate species richness are accompanied by gradients in the taxonomic and functional composition of communities, including shredder relative abundance, as suggested by our data from the Australian wet tropics.

To determine patterns of distribution of shredders, we must first determine which species are shredders by means of gut content analysis and, if possible, stable isotope analysis. Most studies have relied on the FFG classification proposed for temperate areas, mostly for North America (Merritt & Cummins 1996). Thus, Rosemond *et al.* (1998), Ramírez *et al.* (2006) and Benstead (1996) reported zero, one and three shredder taxa, respectively, for some Costa Rican streams, and Mathuriau and Chauvet (2002) reported four species in a Colombian stream. These and other studies (*e.g.*,

Shieh & Yang 2000, Gonçalves *et al.* 2007) partly or totally used Merritt and Cummins' (1996) FFG classification, rather than analyzing the diets of the local fauna found in leaf litter.

In contrast, most studies that have described tropical food webs through gut content analysis have found that shredders are not scarce. Yule (1996) found nine shredder taxa in two streams on Bougainville island (Papua New Guinea), Cheshire *et al.* (2005) found 14 taxa in two streams of the Australian wet tropics, and Yule *et al.* (2009) found 24 shredder taxa in 13 Malaysian streams. Although gut content analysis (Mantel *et al.* 2004) and stable isotope analysis (Lau *et al.*, 2009) revealed that shredders were scarce in Hong Kong, this observation does not conflict with our hypothesis of altitudinal gradients in shredder species richness in the tropics, as streams in Hong Kong are all lowland. Our limited Panamanian data are equivocal in this regard.

A general latitudinal gradient in shredder species richness is not supported by various reports from temperate streams, which have a similar range of richness as reported for tropical streams: for example, Jaarsma *et al.* (1998) found only two shredder taxa in two New Zealand streams; Fenoglio and Bo (2004) found six shredder taxa in three study sites in the Italian Alps; Hawkins and Sedell

TABLE 2. Results of three-way ANOVA exploring variation in leaf breakdown rates (k) with leaf origin (native/exotic), leaf decomposability (high/medium/low), treatment (coarse/fine mesh), and shredder species (nested within treatment), in the laboratory (including second order interactions), in the Australian wet tropics (AWT) and Panama (PAN). Degrees of freedom (df), sums of squares (SS), F-statistic and P-values are shown (significant values at  $\alpha = 0.05$  level in bold).

Source of variation	df	SS	F	P
AWT				
Leaf origin (Lo)	1	$5.57 \times 10^{-5}$	4.17	<b>0.0424</b>
Leaf decomposability (Ld)	2	$4.48 \times 10^{-3}$	167	< <b>0.0001</b>
Treatment (Tr)	1	$1.30 \times 10^{-3}$	97.1	< <b>0.0001</b>
Shredder species (Sp)	2	$1.10 \times 10^{-4}$	4.11	<b>0.0176</b>
Lo $\times$ Ld	2	$4.52 \times 10^{-5}$	1.69	0.1871
Lo $\times$ Tr	1	$1.43 \times 10^{-8}$	0.001	0.9739
Ld $\times$ Tr	2	$1.97 \times 10^{-4}$	7.37	<b>0.0008</b>
Lo $\times$ Sp	2	$1.38 \times 10^{-4}$	5.14	<b>0.0066</b>
Ld $\times$ Sp	4	$5.42 \times 10^{-5}$	1.01	0.4017
Error	222	$2.97 \times 10^{-3}$		
PAN				
Leaf origin (Lo)	1	0.00014	6.10	<b>0.0145</b>
Leaf decomposability (Ld)	2	0.00280	59.6	< <b>0.0001</b>
Treatment (Tr)	1	0.00356	152	< <b>0.0001</b>
Shredder species (Sp)	1	0.00002	1.04	0.3090
Lo $\times$ Ld	2	0.00006	1.28	0.2805
Lo $\times$ Tr	1	0.00012	5.25	<b>0.0232</b>
Ld $\times$ Tr	2	0.00034	7.30	<b>0.0009</b>
Lo $\times$ Sp	1	0.00010	4.20	<b>0.0419</b>
Ld $\times$ Sp	2	0.00001	0.19	0.9233
Error	166	0.00389		

(1981) reported eight shredder taxa in four North American streams; and Pretty *et al.* (2005) found ten shredder taxa in an English acidic stream. A common explanation for the reported scarcity of shredders in the tropics is that this feeding mechanism has been developed by insect orders evolutionarily adapted to cool waters and largely absent from warmer tropical streams (*e.g.*, stoneflies) (Irons *et al.* 1994). However, recent studies have shown that other macroinvertebrates or insect orders occupy the shredder feeding guild. These include crabs in Kenya (Dobson 2004), crayfish in Australia (Boyero *et al.* 2007), shrimps in Puerto Rico (Greathouse & Pringle 2006), snails, crabs, mayflies and semi-terrestrial cockroaches in Malaysia (Yule *et al.* 2009), and mayflies in Papua New Guinea (Yule 1996), Kenya (Dobson *et al.* 2002), Bolivia (Molina 2004) and Australia (Cheshire *et al.* 2005).

It has been proposed that fewer shredders in the tropics reduce their contribution to leaf breakdown, which would be mainly driven by microorganisms (Irons *et al.* 1994). Leaf breakdown rates may depend on several factors, including temperature, water chemistry, leaf palatability (determined by decomposability and levels of nutrients and toxic compounds) and shredder abundance and species richness (Nolen & Pearson 1993, Irons *et al.* 1994, Jonsson &

Malmqvist 2000, Pearson & Connolly 2000, Boyero *et al.* 2007, Bastian *et al.* 2008). In the AWT, shredder contribution to total leaf breakdown (24%) was within the range reported for several temperate streams; for example, 10 percent (Petersen *et al.* 1989), 24 percent (Petersen & Cummins 1974) or 27 percent (Webster 1983) in various North American streams. Other temperate studies have reported higher or lower contributions of shredders to leaf breakdown, *e.g.*, 51–64 percent in Germany (Hieber & Gessner 2002) or 3 percent in oligotrophic and mesotrophic streams in France (Baldy *et al.* 2007). Although these studies used various methods to calculate shredder contribution to total litter breakdown, they clearly illustrate the existence of a range of situations among temperate streams and do not support the idea of a widespread prevalent role of shredders in these streams in contrast with tropical streams.

It is likely that shredder contribution to leaf breakdown depends more on their biomass than their numeric abundance. This may be especially true in the tropics, where many shredders have large body sizes, *e.g.*, shrimps (March *et al.* 2001), crabs (Dobson 2004) or semi-terrestrial cockroaches (Yule *et al.* 2009). We did not measure biomass, but note that the shredders that we recorded in PAN and AWT were not especially large in comparison with those of temperate streams. If these larger animals had been included in our studies, we expect that the contribution of shredders to leaf breakdown would have been much higher than we recorded.

Breakdown rates are also directly related to temperature; for example, Nolen and Pearson (1993) found that shredder processing of leaf litter increased with temperature, while the microbial rates did not vary. In another laboratory experiment, both microbial and shredder rates were significantly higher at 20°C than 15°C, but the increase was higher for shredders (M. Bastian, R.G. Pearson and L. Boyero, unpubl. data). These findings contradict the hypothesis that higher temperatures could increase microbial rates to the extent that leaves become unavailable for shredders, which has been proposed as an explanation for shredder scarcity in the tropics (Irons *et al.* 1994). The effect of temperature on microbial vs. shredder breakdown rates should be explored further to test this hypothesis. Other factors such as leaf properties or water quality, which may affect breakdown rates (Graça 2001), were not investigated in this study.

The difference in the relative importance of shredders and microbes in leaf breakdown in our laboratory experiments is interesting. It is possible that the difference in temperatures between regions differentially affected breakdown due to microbes and shredders, as suggested above. But as we used different shredder species in each region, it is possible that interspecific differences influenced the results. It is also likely that an interplay between variation in microbial and leaf characteristics had an effect. We do not have data to investigate these possibilities.

In conclusion, we propose that shredders are not scarce or functionally unimportant in the tropics as a whole, in contrast to some previous indications. Further research in the tropics is required to investigate this contention. Spatial variability in shredder species richness and abundance and in their contribution to leaf litter breakdown needs to be determined at appropriate scales,

especially among headwater streams and along altitudinal gradients. Additionally, the diets of the leaf litter fauna should be determined through gut content analysis and, if possible, stable isotope analysis, rather than relying on existent FFG classifications for temperate areas, as it has been shown that closely related taxa may use different food sources.

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## SUPPORTING INFORMATION

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

TABLE S1. *Environmental characteristics of the study sites surveyed in the Australian wet tropics (AWT) and Panama (PAN).*

TABLE S2. *Species/morphospecies found in the field survey and field experiment in the Australian wet tropics (AWT) and Panama (PAN).*

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