

# Macroconsumer effects on insect detritivores and detritus processing in a tropical stream

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## SUMMARY

1. Few studies have assessed the effects of macroconsumers, such as fishes and shrimps, on detritus and detritivores.
2. We used an underwater electric field to prevent macroconsumers from feeding in and on leaf packs in a lowland stream in Costa Rica and thus to determine their effects on the density of insect detritivores and decay rates of leaves.
3. Exclusion of macroconsumers resulted in significantly higher densities of small invertebrates inhabiting leaf packs. Most of these were collector–gatherers, none were shredders.
4. Despite the increase in invertebrate density, decay rates of leaves were not statistically different. These findings contrast with results from temperate streams showing that increases in the density of invertebrates in leaf packs typically result in an increased rate of decay.
5. Leaf decay rates and invertebrate densities were also compared between leaf packs placed in electric exclusion treatments and those placed in coarse (2 cm) plastic net bags (as used in many previous studies). Our results suggest that using such netting in tropical streams may deter macroconsumers, which can affect insect density and, potentially, decay rates of organic matter.

## Introduction

Macroconsumers, such as fish and decapod crustaceans (e.g. shrimp, crayfish), can be ‘strong interactors’ (*sensu* Paine, 1992) in both temperate and tropical streams by affecting the abundance of basal food resources and populations of small consumers (Power, 1984a, 1984b; Cooper, Walde & Peckarsky, 1990; Power, 1990; Covich *et al.*, 1991; Flecker, 1992; Gelwick & Matthews, 1992; Pringle *et al.*, 1993; Creed, 1994; Pringle & Blake, 1994; Flecker, 1996; Pringle, 1996; Pringle & Hamazaki, 1997, 1998). In temperate streams, insectivorous fishes are the dominant macroconsumers, whereas many more species of fish that are algivorous, detritivorous, and omnivorous are found in tropical streams (Angermeier & Karr, 1983; Bowen, 1983; Covich, 1988; Goulding, Carvalha & Ferreira, 1988; Wootton & Oemke, 1992). In addition, tropical streams can have large populations of shrimps, which are often omnivorous (Covich *et al.*, 1991; Pringle *et al.*, 1993; Pringle & Blake, 1994). Thus, macroconsumers

in temperate streams may primarily affect small consumers (e.g. insect larvae), but the omnivorous nature of many macroconsumers in tropical streams may result in effects at several trophic levels.

Studies of macroconsumers in streams have focused primarily on their effects in food webs based on primary production (Allan, 1981; Power, 1984a, 1984b, 1990; Cooper *et al.*, 1990; Pringle *et al.*, 1993; Creed, 1994; but see Flecker, 1992, 1996). However, macroconsumers may also have effects in detritus-based food webs. Coarse particulate detritus can be a limiting food resource to in-stream consumers (Richardson, 1991; Dobson & Hildrew, 1992). We know very little, however, about trophic interactions in detritus-based food webs in streams or other ecosystems (Polis, 1991, 1996; Bengtsson *et al.*, 1995). Many studies have shown that large consumers in tropical streams are dependent on detrital food resources (see references in Covich, 1988). Macroconsumers may be more important in

processing organic matter than are small consumers in tropical streams. The biomass of insect shredders, which are primarily responsible for decay of organic matter in temperate streams, may be lower in the tropics (Irons *et al.*, 1994). For example, plecopteran larvae, some of which are important leaf shredders in temperate streams, are relatively rare in the tropics (Baumann, 1982; Covich, 1988). Thus, in tropical streams, macroconsumers may play an analogous role to insect shredders in many temperate streams, by accelerating decay rates of leaves.

Experimental manipulations of macroconsumers (fishes and shrimps) in tropical streams have shown that they decrease the abundance of basal food resources [algae and fine particulate organic matter (FPOM)], as well as small insect consumers. Studies of shrimp-dominated montane streams in Puerto Rico showed that exclusion of shrimps resulted in increased abundance of both algae and FPOM (Pringle *et al.*, 1993; Pringle & Blake, 1994). In Costa Rica, experimental exclusion of macroconsumers resulted in a greater mass of algae and organic and inorganic materials and higher abundance of small consumers (e.g. insect larvae) than in controls (Pringle & Hamazaki, 1997, 1998). Exclusion of fishes and shrimps did not result in a 'trophic cascade' (*sensu* Carpenter, Kitchell & Hodgson, 1985) (e.g. an increase in herbivorous insects and a decrease in algal abundance), but rather in an increase in the abundance of both insects and algae (Pringle & Hamazaki, 1997, 1998). This work supported the hypothesis that large-sized omnivorous consumers (e.g. fishes and shrimps) negatively affect the abundance of two trophic levels (small consumers and basal food resources) simultaneously (Diehl, 1995). Studies by Flecker (1992, 1996) in a tropical stream in Venezuela showed similar effects of fish feeding on invertebrates and fine particulate detritus: exclusion of fish resulted in increased abundance of both.

In this study, we tested whether macroconsumers feeding on coarse particulate organic matter had similar effects to those observed when macroconsumers fed on algae or FPOM from hard substrata (see references above). Specifically, we tested whether macroconsumers reduced the abundance of small consumers (insect larvae) inhabiting leaf packs. We also examined whether macroconsumers consumed leaves, thus increasing their decay rate, or whether macroconsumers decreased decay rates via a trophic cascade by removing insect detritivores from leaf packs. In

addition, we compared decay rates of leaf packs incubated in coarse plastic net bags to those of controls (no netting) to determine the effects of this method of leaf incubation on leaf decay in a tropical stream.

## Materials and methods

The study was conducted in the Sabalo (10°26' N, 84°01' W), a fourth-order stream bordering La Selva Biological Station on the Caribbean slope of Costa Rica. The study reach was bordered by pasture on one side and by primary lowland rainforest on the other, although most of the catchment was forested. Substrata consisted of small cobbles and gravel in riffles and gravel and sediment in runs. The river had a relatively constant temperature (diel range between 24 and 26 °C, annual range, approximately 24–27 °C, C. M. Pringle, unpublished data). La Selva has an approximate annual precipitation of 4 m, most of which occurs from June to December (Sanford *et al.*, 1994). This experiment was conducted in May 1994 at the end of the 'dry' season.

Eight species of omnivorous shrimp (*R. Tiffer*, Universidad de Costa Rica, unpublished) and forty-three taxa of fish (Bussing, 1994) have been identified from streams draining La Selva. Of the fishes, twenty-six species have been recorded in the Sabalo (Burcham, 1988). Most of these species are considered to be omnivores, consuming both plant and animal material (Burcham, 1988; Wootton & Oemke, 1992). For example, *Astyanax fasciatus* (Cuvier), which is abundant in the Sabalo, feeds on algae, detritus and terrestrial and aquatic insects (Burcham, 1988; Bussing, 1994; C. M. Pringle, unpublished data). *Astyanax fasciatus* and two other species, *Alfaro cultratus* (Regan) (an omnivore/insectivore) and *Neotroplus nematopus* (Gunther) (an omnivore/herbivore) (Burcham, 1988) made up 80% of the 'feeding pressure' (number of fish × time spent feeding) on substrata in a fast-flowing riffle of the Sabalo (Pringle & Hamazaki, 1997). In a study 1 year later, Pringle & Hamazaki (1998) showed that *A. fasciatus* alone comprised 80% of the 'feeding pressure' by fish in slow-moving runs in the Sabalo. Nocturnally feeding shrimps [*Macrobrachium digueti* (Bouvier), *M. faustinum* (De Saussure) and *M. heterochirus* (Wiegmann)] were also present in the stream runs at densities of 2–6 m<sup>-2</sup>. In this previous study, shrimps had measurable effects on benthic communities, but were less abundant and had fewer

effects on insect densities, sediment and algal resources than fishes (which feed diurnally) (Pringle & Hamazaki, 1998). The present work was conducted in these same runs, one month after completion of the study by Pringle & Hamazaki (1998).

In May 1994, macroconsumers (both fishes and shrimps) were experimentally excluded from tethered leaf packs along a 200 m stretch of the Sabalo. Electric fields within PVC 'hoops', as described by Pringle & Hamazaki (1997), and modified from those used by Pringle & Blake (1994), were used to exclude macroconsumers. The enclosures consisted of copper wire suspended within a PVC frame (45 cm diameter) that was placed on legs, so that it rested a few centimetres above the stream bottom. The copper wire was connected to solar-powered electric fence chargers installed on posts on the stream bank. The chargers emitted electrical pulses (55/min), with a pulse duration of 2 ns. In the study stream, these electrical pulses deterred all organisms >1 cm in length, but allowed colonization by smaller organisms. The electric pulse affected an area that extended about 4–6 cm beyond the edge of the hoop.

We determined the effects of macroconsumer exclusion on decay of *Ficus insipida* Willd. (= *glabrata* HBK) leaves and on the abundance and taxonomic composition of invertebrates that colonized them. *Ficus insipida* is a dominant riparian tree of rivers in Central America and at La Selva (Stout, 1980; Hartshorn, 1983), and is found on the banks of the Sabalo. We collected newly abscised leaves from trees near the Sabalo and dried them at approximately 40 °C. Leaf packs were individually weighed [4.5–5 g dry mass (DM)], wetted, bound together at the base of the leaves with binder clips and tethered in the stream.

We used two treatments: (i) macroconsumer exclusion (4.5–5 g DM leaf packs placed within an electrified hoop) and (ii) control (leaf packs within a hoop with no electricity). Another group of leaf packs were incubated in the stream within litter bags made of bird netting (2 cm plastic mesh) to compare leaf decay rates using this method to controls (above). We set up three treatment groups (consisting of an exclusion, control and 'bagged' treatment) in four different areas of the stream. Four replicate leaf packs for each treatment (one from each of the four runs) were collected on days 1, 3, 7, 11 and 15 after being placed in the stream. The experiment ran from 6 May to 20 May 1994. Previous work showed 50–100% loss of

*F. glabrata* (= *insipida*) leaf packs placed in the Sabalo after 16 days *in situ* (Stout, 1980).

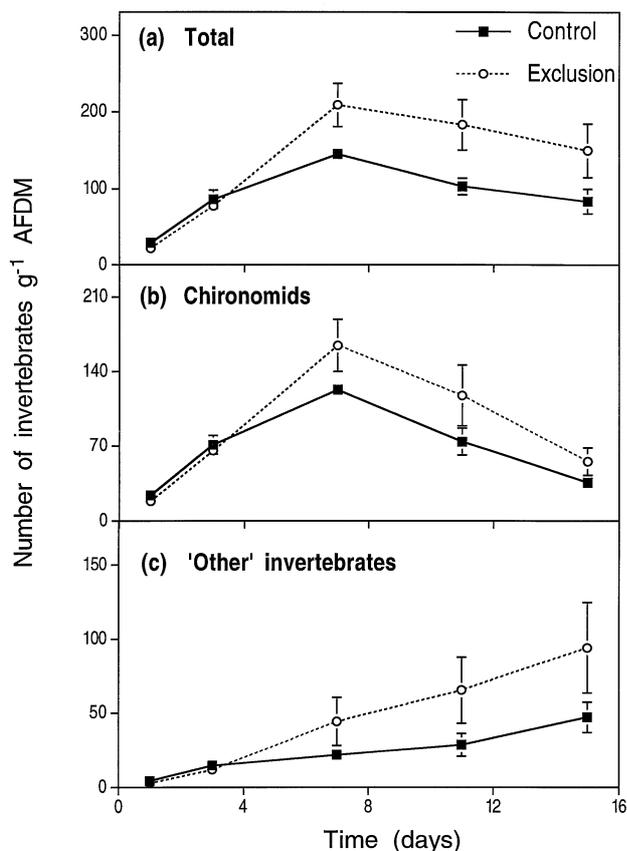
Leaf packs were collected into a 250- $\mu$ m-mesh net in the stream, so as not to lose colonizing invertebrates. Leaf packs were refrigerated until they were processed (within 24 h). Invertebrates were rinsed from leaf surfaces and stored in 70% ethanol. Leaves were dried to constant weight at 60 °C and a subsample was ashed at 500 °C to determine ash-free dry mass (AFDM) remaining. A negative exponential model of AFDM remaining vs. time was used to determine decay coefficients (*k*) (Webster & Benfield, 1986; Boulton & Boon, 1991). Invertebrates were identified to the lowest practical taxonomic unit (typically genus, except Chironomidae, which were identified to family) and assigned to functional feeding groups based on Merritt & Cummins (1996) and/or gut content analysis. Insect densities were normalized to abundance/g AFDM of the leaf packs from which they were collected.

The effect of macroconsumer exclusion on decay rate was determined using analysis of covariance on natural log percentage AFDM remaining (using day as the covariate) (Boulton & Boon, 1991). Differences in insect density, proportion of nonchironomids to chironomids and proportion of different functional groups between treatments were determined with repeated measures analysis of variance (anova) (Sokal & Rohlf, 1981) using Statistical Analysis Systems (SAS, 1988).

## Results

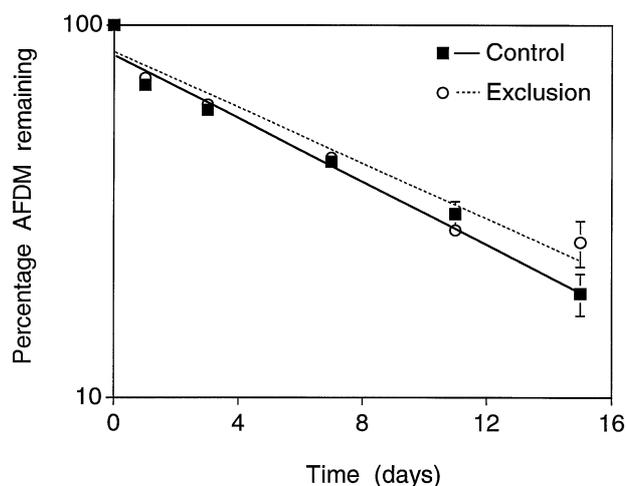
Exclusion of macroconsumers resulted in significantly higher densities of invertebrates inhabiting leaf packs (Fig. 1a,  $P < 0.02$ , repeated measures anova). Densities were similar between treatments on days 1 and 3 of the experiment, but had diverged by day 7. Larval chironomids (Diptera: Chironomidae) dominated insect abundance for the first few days, but their numbers declined after day 7 (Fig. 1b). Differences in the density of chironomids in enclosure and control treatments were not significant. Densities of insect taxa other than chironomids [primarily collector-gathering mayflies (Ephemeroptera) and caddisflies (Trichoptera)] continuously increased during the study (Fig. 1c).

When macroconsumers were present, assemblages consisted primarily of chironomids, and secondarily of some nonchironomid taxa: Ephemeroptera



**Fig. 1** (a) Total invertebrate densities normalized per g AFDM of leaves in macroconsumer exclusion and control treatments. (b) Densities of Chironomidae (Diptera) (= Chironomids) normalized per g AFDM of leaves in exclusion and control treatments. (c) Densities of invertebrates other than chironomids ('other' invertebrates) normalized per g AFDM of leaves in exclusion and control treatments. Points are means ( $n = 4$ )  $\pm$  1 SE.

(Leptohiphidae, Baetidae, Leptophlebiidae) and Trichoptera (primarily Hydroptilidae and some Hydropsychidae). In the exclusion treatment, invertebrate assemblages were progressively dominated by mayflies (primarily *Baetis* sp. and *Leptohyphes* sp.) and caddisflies (primarily hydroptilids) and, to a lesser extent, chironomids. At the beginning of the study (days 1 and 3), the proportion of nonchironomid taxa to chironomids was about 1 : 5 in both treatments. By the end of the study, nonchironomid taxa outnumbered chironomids by a proportion of 2.2 : 1 in the exclusion treatment, but occurred in a proportion of 1.3 : 1 in control treatments; however, treatment differences were not significant. Other Diptera (Simuliidae, Ceratopogonidae), Coleoptera (larval Elmidae), Odonata (Coenagrionidae), small gastropods, shrimp larvae



**Fig. 2** Decay rates of leaf packs in exclusion and control treatments. The linear equation for decay in the control treatment is  $y = (-0.091)x + 4.36$ ,  $R^2 = 0.91$ , and the equation for decay in exclusion treatment is  $y = (-0.082)x + 4.35$ ,  $R^2 = 0.90$ , where  $x$  is time in days and  $y$  is the natural logarithm of percentage AFDM remaining.

(Decapoda), mites and Oligochaeta also colonized leaf packs, but were always found in low abundance (<5 individuals/leaf pack).

Leaf packs were dominated by collector-gatherers, which comprised 84–88% (range: 83–90% for any treatment average) of abundance on days 1–11 and 71% of abundance on day 15 on average between treatments. Scrapers (e.g. hydroptilid caddisflies) were slightly more abundant on day 15 than previous days. No taxa could be classified as shredders (except for incidental 'physical' shredding potentially caused by leaf-mining chironomids) and predators were rare. There were no treatment effects on the proportion of invertebrates belonging to different functional groupings based on repeated measures anova.

Decay was extremely fast, and there was no significant difference in rate between the treatments (Fig. 2). Instantaneous decay rate ( $k$ ) was  $9.1\% \text{ day}^{-1}$  ( $\pm 0.7$  SE) under control conditions, and  $8.2\% \text{ day}^{-1}$  ( $\pm 0.7$  SE) when macroconsumers were excluded.

Enclosing leaves in coarse plastic mesh 'bags' resulted in insect densities ( $120 \text{ g}^{-1} \text{ AFDM} \pm 46$  SE) and decay rates (26.4% AFDM remaining  $\pm 3.1$  SE) that were more similar to macroconsumer exclusion treatments ( $150 \text{ g}^{-1} \text{ AFDM} \pm 35$  SE and 25.7% AFDM remaining  $\pm 4.4$  SE) than to controls ( $83 \text{ g}^{-1} \text{ AFDM} \pm 16$  SE and 19.2% AFDM remaining  $\pm 2.8$  SE) at the end of the experiment; however, differences were not significant.

## Discussion

Invertebrate consumers contribute to the decay of organic matter in temperate streams (Kaushik & Hynes, 1971; Petersen & Cummins, 1974; Wallace & Webster, 1996). Studies have shown that abundance of shredding invertebrates and decay rates of leaves are positively related (Wallace, Webster & Cuffney, 1982; Oberndorfer *et al.*, 1984; Benfield & Webster, 1985; Mulholland *et al.*, 1985; Malmqvist, 1993; Tuchman, 1993). In contrast, we showed that an increased density of invertebrates, which resulted from exclusion of macroconsumers, was not associated with higher rates of leaf decay. This may be largely due to the fact that the invertebrates present in our leaf packs were primarily collector–gatherers and not shredders, as defined by traditional functional feeding group classification (*sensu* Cummins & Klug, 1979). Irons *et al.* (1994) hypothesized that decay rates of leaves in the tropics are driven more by microbial breakdown than insect shredding, compared to temperate streams. Our results are in general agreement with this hypothesis. Our data show that total invertebrate densities in leaf packs were not low relative to temperate streams, but there was a conspicuous lack of shredders. Invertebrate densities reported here were 25–150/g AFDM of leaf, which is comparable to those reported from some temperate streams (2–111/g DM, Sedell, Triska & Triska, 1975; 6–30/g DM, Short, Canton & Ward, 1980; 10–250/g AFDM, Cowan *et al.*, 1983; 0–120/g DM, Mutch & Davies, 1984; 100–550/g AFDM, Richardson, 1992). However, there may be fewer shredding insects that contribute to decay processes of leaf accumulations in tropical compared to temperate streams. In our study, leaf-pack dwelling invertebrates consisted primarily of collector–gatherers. Other studies in lowland tropical streams have similarly noted an abundance of collector–gatherers and a lack of insect shredders (Walker, 1987; Yule, 1996; Pringle & Ramírez, 1998; Ramírez & Pringle, unpublished). Also, in tropical streams, whole orders of insects that are typical of the shredding fauna of temperate streams (e.g. Plecoptera) are rare (Baumann, 1982).

The chironomids present in leaf packs in this study may have functioned in a manner similar to that of shredders by affecting leaf decay through ‘physical’ rather than ‘trophic’ means; they ‘mined’ leaves by getting in between layers of the leaf mesophyll, although their gut contents were com-

prised of small particulate detritus, not leaf fragments (A. D. Rosemond, personal observation). Their densities did not increase in response to the experimental exclusion of macroconsumers, suggesting that they may have been less vulnerable to predation or dislodgement compared to other invertebrates (mobile mayflies and caddisflies) due to their ‘mining’ behaviour. Pringle & Hamazaki (1998) previously showed that macroconsumers had relatively greater impacts on mobile prey than on chironomids on hard substrata in the Sabalo. The ‘mining’ behaviour we report may function similarly to other forms of habitat construction/modification (e.g. tube or case building) that have been shown to similarly protect chironomids from fish predation (Goyke & Hershey, 1992; Power, Marks & Parker, 1992).

Macroconsumers had no discernible net effect on decay rates of leaves in this study, yet several lines of evidence indicate that there is a capacity for such effects in the Sabalo. Previous work indicated that terrestrial plant material can comprise up to 60% of gut contents of fishes in the Sabalo and in a nearby stream, the Sura (Burcham, 1988). Also, a previous study in the Sabalo showed direct consumption of leaves by fishes (Wootton & Oemke, 1992). Wootton & Oemke’s (1992) study showed that fresh *Ficus insipida* leaves were consumed by fishes within 48 h (most within 24 h and once within 10 min); however, the effects of herbivory on fresh leaves used by Wootton & Oemke (1992) may not reflect fish herbivory on naturally shed leaves. There may also be different habitats within the stream where fish herbivory is more important. The fishes, *Brycon guatemalensis* (Regan), *Cichlasoma tuba* (Meek), and *C. alfari* (Meek) were responsible for leaf consumption in the study by Wootton & Oemke (1992). These species, particularly large *Brycon*, primarily inhabit deep pools in the Sabalo and were not observed feeding in the relatively shallow runs (average depth  $c.<1$  m) where our study was conducted. In the present study, we observed fish ‘pecking’ at leaves in the control treatments, suggesting that they were feeding on invertebrates and disrupting leaves in the process. We did not observe whole leaves or large portions of leaves being removed by macroconsumers. These indirect effects of macroconsumers on organic matter loss were small compared to losses from direct consumption of leaves by fishes previously reported from the Sabalo (Wootton & Oemke, 1992); however, both processes may be

important to organic matter dynamics on the scale of the whole stream.

Our experimental design did not allow us to distinguish between the effects of invertebrates and macroconsumers on leaf decay; if both insects and macroconsumers had significant effects on leaf decay, and macroconsumers reduced insect abundance, the effects would have effectively canceled each other out. The net effect of macroconsumers on decay of organic matter would depend on: (i) how much macroconsumers directly accelerated leaf decay (via consumption of leaves or activity associated with feeding on insects) and (ii) how much removal of insects resulted in decreased leaf decay. Because macroconsumers affected insect densities in this study, we were unable to separate these effects. However, exclusion of fish and shrimp macroconsumers resulted in: (i) an overall nonsignificant effect on organic matter standing stocks and (ii) an increase in the abundance of insect taxa that did not fall within the 'shredder' functional feeding group. These results are consistent with insects having little or no effect on decay rate in our system. In essence, no 'trophic cascade' was observed, in which the exclusion of macroconsumers would be predicted to lead to an increase in insect abundance and a subsequent increase in decay of organic matter. Such effects have been observed in temperate studies in which insect predators controlled shredder abundance, which in turn controlled rates of leaf decay (Oberndorfer *et al.*, 1984; Malmqvist, 1993), but were not observed in this study. Despite the lack of insect shredders in leaf packs in this study, decay rates ( $k$ ) based on the exponential model (Webster & Benfield, 1986) were extremely fast ( $k_{\text{day}} = 0.09$  and  $0.08$ , based on AFDM) relative to rates from temperate streams ('fast' rates reported as  $k_{\text{day}} = > 0.010$ , 'slow' rates reported as  $k_{\text{day}} < 0.005$  based on DM, Petersen & Cummins, 1974) and are in the range reported from other studies in tropical streams ( $k_{\text{day}} = 0.025$ , based on DM (Benstead, 1996),  $k_{\text{day}} = 0.02$  and  $0.56$ , based on DM; Irons *et al.*, 1994). These data also support the hypothesis that leaf decay in tropical streams may be driven primarily by factors such as microbial activity, rather than insect shredding.

The effects of macroconsumers in stream ecosystems, and specifically their effects on smaller invertebrate prey, may depend on the dominant basal food source (e.g. leaf litter or periphyton) present in the stream. Compared to periphyton on hard substrata,

leaves may provide better refugia for vulnerable insects, but may be a lower quality food resource. We compared the density of insects found on leaves in this study with densities on substrata dominated by periphyton and FPOM (Pringle & Hamazaki, 1998). We also compared the magnitude of the effect that macroconsumers had in reducing densities on different substrata in these two studies which were conducted in the same stream, one month apart. We found that, in general, insect densities on leaves (normalized per g AFDM) were lower than those found on a mixture of periphyton and FPOM (average over all dates with macroconsumers present, 89/g vs. 249/g, respectively). In addition, percentage reduction of insects by macroconsumers was less on leaves than on substrata covered with periphyton and FPOM (average reduction over all dates, 30% vs. 49%, respectively). In other tropical studies in which the effects of macroconsumers on insects were tested and the dominant basal food resource consisted of fine detritus and periphyton, insect densities were much higher than found in this study (when Flecker's data is converted to number per g sediment AFDM, numbers are on the order of  $>1000/\text{g}$  AFDM) (Flecker, 1992, 1996). In addition, the percentage reduction of insects by macroconsumers in Flecker's studies (on the order of 40–50%) is similar to that found by Pringle & Hamazaki (1998) and higher than that found in this study. Although these are very general comparisons (not accounting for surface area, food quality, etc.), they suggest that the 'top-down' effects of macroconsumers may depend on substratum type and the relative vulnerability of invertebrates to predation (see Flecker, 1984; Richardson, 1992; Power *et al.*, 1992).

Because macroconsumers are abundant in many streams, their effects should be considered in latitudinal comparisons of leaf decay. Measurements of insect densities and decay rates of leaves enclosed in mesh bags in this study were only suggestive of this enclosure method affecting access by macroconsumers. However, we feel that such enclosure methods (Benfield, 1996) have the potential to reduce the accessibility of leaves to macroconsumers and result in underestimates of decay rates and overestimates of natural invertebrate densities in streams where macroconsumers are common. A similar mesh was used in the study by Irons *et al.* (1994) to enclose leaf packs in a latitudinal study of leaf decay. They found that, when normalized per degree day, decay rates actually

increased with latitude. However, macroconsumers that feed on plant material are much more common in tropical than in temperate streams (Angermeier & Karr, 1983; Bowen, 1983; Burcham, 1988; Wootton & Oemke, 1992). If macroconsumers contribute more to leaf decay in the tropics, latitudinal differences in their effects would not have been observed using mesh bags. Future latitudinal comparisons of decay rates of organic matter should consider effects of macroconsumers, since our results show that they can affect insect densities and potentially, organic matter dynamics in tropical streams.

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