

WHY THE WORLD IS GREEN, THE WATERS ARE BLUE AND FOOD WEBS IN SMALL STREAMS IN THE ATLANTIC RAINFOREST ARE PREDOMINANTLY DRIVEN BY MICROALGAE?

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ABSTRACT

The question “Why is the world green?” has been debated and researched ever since the seminal paper of Hairston *et al.* (1960). Three main hypotheses were generated to explain why a large part of terrestrial plant biomass is not eaten by herbivores: (1) predators control herbivores (especially folivores), (2) plant defenses inhibit herbivores, and render the plant biomass relatively unavailable, and (3) different controls operate in regions of different productivity. Aquatic systems, especially those of plankton, tend to have much less plant biomass than terrestrial systems, and generally a much higher proportion of the living plant biomass is consumed by herbivores. Thus open-water aquatic systems appear transparent blue or green. They also often display cascading relationships in which changes at one trophic level have effects at two or more levels below. The orthodoxy for small streams shaded by forest is that they receive much organic matter from the surrounding forest and this provides the main source of energy and material for the food web. Some recent research in tropical streams shows that microalgae provide a greater proportion of the primary source than does allochthonous material. This may be a specifically tropical phenomenon, or perhaps a tendency that is more accentuated in the tropics. Exclusion experiments show trophic cascades and strong interactions between fauna (particularly shrimps) and allochthonous substrates. But the functional interactions (shredding of litter, removal of benthic material) are not trophic – the animals are herbivores or predators of herbivores based on microalgae. We can speculate that the apparent wastage of allochthonous material is at least partly due to the inherent costs that a detritivore would have in processing the more intractable and less nutritive food source (litter) in conditions of higher predation and competition, which are possibly more stringent in the tropics.

Key words: Food web, Herbivore control, Plant defense, Stable isotopes, Stream ecosystem.

RESUMO

PORQUE O MUNDO É VERDE, AS ÁGUAS AZUIS E OS PEQUENOS RIOS DA MATA ATLÂNTICA SÃO ALIMENTADOS PRINCIPALMENTE POR MICROALGAS? A questão “Porque o mundo é verde?” tem sido debatida e pesquisada desde a publicação seminal de Hairston *et al.* (1960). Três principais hipóteses foram levantadas para explicar porque uma grande parte da biomassa de plantas terrestres não é comida por herbívoros: (1) predadores controlam herbívoros (especialmente folívoros), (2) defesas das plantas inibem herbívoros e tornam a biomassa relativamente não disponível e, (3) diferentes controles operam em regiões com produtividades diferentes. Sistemas aquáticos, especialmente os de plâncton, tendem a ter muito menos biomassa de plantas que sistemas terrestres e, geralmente, uma porção bem maior da biomassa viva é consumida por herbívoros. Daí sistemas de águas abertas parecerem azul ou verde transparente. Tais sistemas muitas vezes mostram relações em cascata nas quais as mudanças em um nível trófico têm efeitos em dois ou mais níveis abaixo. A regra geral em pequenos rios sombreados de floresta é que recebam muita matéria orgânica proveniente da floresta ao redor, e isto fornece a fonte principal de energia e material para a rede trófica. Pesquisas recentes em pequenos rios tropicais mostram que microalgas fornecem uma parte maior da fonte primária do que a matéria alóctone. Isto pode ser um fenômeno especificamente tropical, ou talvez uma tendência, mais acentuada nos trópicos. Experimentos de exclusão mostram cascatas tróficas e interações fortes entre fauna (especialmente camarões) e substrato alóctone. Mas as interações funcionais

(e.g., rasgar serapilheira, remover matéria bêntica) não são tróficas – os animais são herbívoros ou predadores de herbívoros baseados em microalgas. Podemos especular que o desperdício aparente de matéria alóctone se deva em parte aos custos inerentes que o detritívoro teria que arcar por processar uma fonte menos tratável e menos nutritiva (serapilheira) em condições de predação e competição maiores, que possivelmente são mais exigentes nos trópicos.

Palavras chaves: Rede trófica, Controle de herbívoro, Defesa de planta, Isótopos estáveis, Ecossistema de córrego.

INTRODUCTION

The question “Why is the world green?” has been debated and researched ever since the seminal paper of Hairston, Smith and Slobodkin (1960) (henceforth abbreviated to HSS). HSS began with the observation that terrestrial ecosystems generally contain a large amount of living plant biomass – the material that makes the world appear green. Only a relatively small proportion of this biomass is consumed by herbivores in normal circumstances (Lowman & Heatwole 1992). Occasional outbreaks of insect herbivores may cause massive defoliation and indicate that some herbivores potentially could consume much larger portions of the living biomass. For example, stick insects (Phasmatidae) cause sporadic intensive damage to Australian eucalypt forests (Campbell 1961, Campbell & Hadlington 1967). This observation that herbivores could but do not consume the available biomass led HSS to conclude that herbivores must be controlled by predators, including parasites, parasitoids and disease. Terborgh *et al.* (2001, 2006) provide an interesting test and apparent agreement with the HSS conclusion.

HSS opens up two general lines of interest: (1) food chains and the control of one level by another, (2) the consumption of organic matter, and particularly the difficulty of assimilating terrestrial large woody biomass. The first was the original explanation of a green world which was given by HSS – that, in general, herbivores (and in particular folivores) are controlled by predators, parasites and disease. This is the classical “trophic cascade”, where changes in one trophic level can “cascade” down to two or more levels below. We will return to this below.

The second line of interest, and an alternative hypothesis, was initiated by Murdoch (1966) who observed that plants (and particularly terrestrial plants) protect their biomass by a number of means, and that

this biomass is not easily assimilated by herbivores. This hypothesis was dubbed “The World is Prickly and Tastes Bad” (Pimm 1991, chapter 12). The question has spawned a vast literature, particularly in the biochemical basis of plant defense (e.g., Hay & Fenical 1988, Coley & Barone 1996); here I will consider some of the consequences at the ecosystem level.

A third line of thought was introduced by Oksanen *et al.* (1981) who observed that the forces exerted on plant biomass might vary with the productivity of the environment. This hypothesis was called “The World is White, Yellow and Green” (Pimm 1991), where “white” characterizes biomes with little productivity such as arctic, high alpine and desert environments, ‘yellow’ environments have intermediate productivity and ‘green’ environments have high productivity.

KOALAS, SLOTHS AND SOUTHWOOD’S HERBIVOROUS INSECTS

We can note that mammalian folivores of forest trees are relatively rare. Koalas and sloths appear to be very specialized animals. In contrast, their relatives that eat fruit and seeds, the monkeys, opossums, possums, etc. are diverse.

On the other hand, insect herbivores are extremely diverse, both in overall numbers of species and in ways in which they exploit their hosts. Southwood (1961) was the first to attempt to explain this great diversity; he examined the diversity of herbivorous insects of trees in the British Isles and concluded that the evolutionary history of the plant-insect association explained a great deal of the relationship. That is, that species such as oaks (*Quercus* spp.) which had many records of occurrences during the Quaternary, have many more species of herbivorous insects than more recently introduced species. Subsequent analyses have

refined this picture (Strong *et al.* 1984) and the subject has been reviewed recently (Lewinsohn *et al.* 2005). We can note, however, that although there can be a high diversity of herbivores associated with a species, (about 300 in the case of Southwood's oak), and many of these species can be classified as 'leaf chewers', they do not generally consume a large part of the plant's phytomass, and indeed, the leaf-chewers on oaks tend to concentrate their activities on the newly-formed shoots, rather than the well-formed leaves (see also Coley & Barone 1996). This is because the leaves accumulate tannins and other polyphenolic substances that render the protein of the leaf difficult to digest.

Tannins are a general mechanism for making plant biomass less digestible and are a common defense of long-lived, woody vegetation – trees. Specific toxins such as alkaloids are favored by short-lived, fast-growing plants – weeds (Dearing *et al.* 2005). Tropical forests seem to have more diversity of defenses than temperate forests (Coley & Barone 1996). Physical impediments are used by many plants – spines, hairs, and general leaf toughness. Spicules of silica are common in grasses.

As well as the specific and apparently co-evolved deterrents to herbivory, herbivores have to contend with the fact that much of terrestrial plant biomass is relatively nutrient poor and composed of cellulose that is difficult to break down. Generally animals have co-opted bacteria and evolved specialized digestive structures to deal with this problem – as seen in the ruminants, lagomorphs and macropods within the mammals, and termites and many other groups within the insects.

All of this adds up to large costs to herbivores that try to partake of the biomass that the plants defend (Coley & Barone 1996). It is tempting to take the slowness and lethargy of the koala and sloth as a metaphor for the compromise that herbivores need to make for their specialization on leaves.

Along with the deterrents to herbivory, there have co-evolved between plants and animals many interactions in which animals are used for pollination and dispersal of seeds and are encouraged to visit flowers and gather fruits.

THE WATERS ARE BLUE

The open ocean and lakes are generally quite transparent from lack of biomass in the water column, and they take on the natural blue of the water (or a transparent green when looked into closer up). Biomass of planktonic algae is generally low, and indeed when it blooms as in 'red tides' and eutrophic water bodies, we become worried about the consequences for the ecosystem and for us.

In general, a much higher proportion of plant biomass is consumed by herbivores in aquatic systems compared to terrestrial systems. This is to a large extent due to the nature of plant biomass in aquatic systems and particularly in planktonic systems – the plants do not contain a large proportion of inert, woody, biomass, as trees do. Herbivores often consume the whole individual plant. Although phytoplankton do have defenses against herbivory by chemical and physical means, in general they co-exist with their herbivores by rapid reproduction. There are many cases of stable inverted pyramids of biomass in freshwater and marine systems, where the biomass of the herbivores is greater than that of the plants due to the high rate of grazing and the fast reproduction of the plants (phytoplankton).

The study of aquatic food chains has produced the most remarkable examples of trophic cascades and interactions between levels (Carpenter *et al.* 1987, Schindler 1990, Attayde & Hansson 2001). This abundance of examples coupled with the difficulty of finding species-level cascades in terrestrial systems lead to the question "Are trophic cascades all wet?" (Strong 1992). Subsequent reviews have revealed a diversity of trophic cascades including many in terrestrial systems (e.g., Pace *et al.* 1999) and led to questions of how they should be interpreted (Polis *et al.* 2000).

It is interesting to note in passing that shallow marine hard-substrate ecosystems often show interactive trophic cascades and strong grazing pressing on algae, (e.g., the recent review of limpet grazing by Coleman *et al.* 2006).

STREAM ECOLOGY

I will now turn our attention to rivers and streams (The term "stream" has been adopted in English for 'stream ecology', which is the study of small, wadable,

fluvial waterbodies – amongst the many other possible terms, such as ‘creek’, ‘brook’, ‘rivulet’. In Portuguese, there apparently has not been such a standardization, and we are open to using ‘riacho’, ‘córrego’, ‘arroio’, ‘igarapé’, ‘aimbim’ as the appendage to ‘ecologia’ to describe the this branch of study). The most used and cited model of how streams and rivers function ecologically is the River Continuum Concept (Vannote *et al.* 1980). As well as carbon flow, the model describes the functional feeding groups of animals that consume organic matter of the system. The model runs like this: in small, shaded, forest streams, the major input of organic matter comes from terrestrial sources, the surrounding forest; algal production is small because of the limitation of light due to shading. The community metabolism is, overall, heterotrophic (i.e., $P < R$ or gross primary productivity less than respiration). Amongst the animals, principally insects, that inhabit the system, the functional feeding group of ‘shredders’ is important because they process the leaves, twigs and other coarse particulate matter into fine particulate matter, which is collected and used by other functional feeding groups – the active and filtering collectors.

As the stream becomes larger downstream and the forest shades less, algal production becomes more important and grazing animals comprise a significant proportion of the fauna. The stream may become autotrophic, $P > R$. When the stream grows into a large river, it may revert to being heterotrophic as turbidity restricts light penetration and organic matter flows in from surrounding wetlands.

In recent years, the Riverine Continuum Concept has been called into doubt by Thorp & Delong (1994, 2002) and Delong & Thorp (2005) who studied the food webs of large heterotrophic rivers using stable isotope ratios of carbon and nitrogen to trace the flow of energy and biomass in the system. They found that although more energy entered the system from allochthonous sources and was indeed respired by the system, the associated carbon of the primary heterotrophs did not all flow into the metazoan food chain. Indeed, the primary carbon source for the metazoan food chain (i.e., the zooplankton, fish, etc.) derived from microalgae (phytoplankton) of the river, although the biomass of phytoplankton is very much smaller than the stock of allochthonous carbon (which is principally in the form of fine particulate matter and

dissolved organic carbon). More recent research has refined this picture to show that, at least for the large rivers of USA that were studied, the surrounding wetlands contribute relatively little to the metazoan food chain (Delong & Thorp 2005). Apparently a great deal of the respiration of allochthonous carbon is by bacteria, and their carbon is not proportionately transported to the zooplankton and fishes. This different model of river functioning has been termed the Revised Riverine Productivity Model.

This model is not so unexpected if we consider other aquatic systems in which the dominant source or stock of carbon is not the main source that flows through the system, but in which some other component, usually algal, which has a smaller biomass, is the major source for the higher levels in the food chain, e.g. Kitting *et al.* (1984) (seagrass), Hamilton *et al.* (1992) (Orinoco River floodplain), Bunn & Boon (1993) (billabongs), Forsberg *et al.* (1993) (Central Amazon River), Hecky & Hesslein (1995) (lakes).

Relatively little research of this kind has been published for small, forested tropical streams, but evidence is building up that they, too, might show this picture. The food webs of streams in Hong Kong (Salas & Dudgeon 2001, Mantel *et al.* 2004) and Puerto Rico (March & Pringle 2003) showed a predominance of algal sources, as did inland tropical rivers in Australia (Douglas *et al.* 2005) and our research in streams of the Mata Atlântica (Brito *et al.* 2006a, b; Detweiler 2005, Detweiler *et al.* 2005, Moulton 2006).

CÓRREGO DA ANDORINHA, ILHA GRANDE, RJ

Córrego da Andorinha is a medium order stream in well-preserved Atlantic rainforest at Ilha Grande, RJ, Brazil. It and its companion stream Rio Barra Pequena at Vila Dois Rios, have been the focus of experimental and descriptive stream research for the last 10 years. The research has uncovered three configurations of cascading trophic relationships, strong interactions of ‘environmental engineering’ by shrimps and ephemeropterans, and apparently a confirmation of the newly-emerging pattern of importance of microalgae in tropic stream food webs. I give a brief description of this work and relate it to the general questions of energy flow in ecosystems.

STRONG INTERACTORS, ORGANIC MATTER PROCESSING AND TROPHIC CASCADES IN TROPICAL STREAMS

Tropical streams in coastal regions have been intensively studied in Puerto Rico and Costa Rica. Catadromous shrimps of the families Palaemonidae, Atyidae and Xiphocaridae have been shown to be important in processing organic matter (Covich *et al.* 1999, Crowl *et al.* 2001, Pringle & Blake 1994, Pringle & Hamazaki 1998, Pringle *et al.* 1999, March *et al.* 2001, 2002). The different species work in different ways: *Xiphocaris elongata* (Xiphocaridae) shreds leaves and other organic matter and produces fine particles, *Atya lanipes* (Atyidae) collects fine particles with its modified chelae (Crowl *et al.* 2001). *Macrobrachium* spp. use their more robust chelae to pick material, and have some shredding action and a more obviously carnivorous diet (March & Pringle 2003). This suite of fauna process coarse particulate matter in the form of experimental leaf packs (e.g., March *et al.* 2001) and remove periphyton from hard substrates (Pringle & Blake 1994, March *et al.* 2002). In sites with fish fauna in addition to the shrimps, the fish were shown to also remove periphyton (Pringle & Hamazaki 1998).

In contrast to the activity of the shrimps (or perhaps because of it), insect shredders have been reported to be much less important in the processing of organic matter in tropical streams than in temperate streams (Covich *et al.* 1999). Thus there is a common but not universal observation in tropical streams of a lack of the shredding fauna that are given prominence in upstream sites in studies of temperate streams and in the Riverine Continuum Concept (Dudgeon & Wu 1999, Dobson *et al.* 2002, Wantzen 2002).

Additionally, Pringle & Hamazaki (1998) remarked on the lack of a trophic cascade between shrimps and fish as predators and their potential insect prey. They explained this as a consequence of the omnivory of these fauna, which by acting on both the primary consumers (herbivorous and detritivorous insects) and on the primary source (periphyton and detritus), prevented a cascading reaction from happening.

In experiments at our sites at Córrego da Andorinha, we have observed similarities and differences to the patterns described above. At a relatively high site (80

m a.s.l.) in Córrego da Andorinha, Souza (2002) and Souza & Moulton (2005) found that atyid shrimps (*Potimirim glabra*) reduced the quantity of periphyton on hard substrates – experimental exclusion of shrimps resulted in substrates with much higher organic and inorganic sediments. The atyids acted principally on the organic sediments not associated with algae.

This strong interaction on periphyton was expected from the dynamics of sites with high density of atyid shrimp in Puerto Rico (e.g., Pringle & Blake 1994) and was found in sites with *Paratya australiensis* in southeast Queensland, Australia (Moulton *et al.* 2003). But at a lower site, with shallow water depth, faster current and flat bedrock, the dynamic was the opposite – experimental exclusion of shrimps produced bare rock with little periphyton. At this site there is a strong trophic cascade between *Macrobrachium olfersi* shrimp, baetid ephemeropteran grazers and the periphyton substrate (Silveira & Moulton 2000, Silveira 2002, Moulton *et al.* 2004). Again, the “grazing” of the baetid ephemeropterans was particularly directed towards the organic sediments not associated with algae. Krsulovic (2004) found that the baetids removed over 90% of the material without ingesting it, thus causing a high ‘non-consumptive loss’ of periphyton.

We cannot say why a system with similar players – atyid and *Macrobrachium* shrimps, ephemeropterans and periphyton – would behave differently in a southeast Brazilian coastal stream compared to a Puerto Rican stream, but a dynamic model of the system can produce some ideas and a hypothesis. When we model the system, we can observe that the stability of the trophic cascade critically depends on the interaction strength of the predator-herbivore link compared to the omnivore link (predator-periphyton) (Silveira & Moulton 2000, Silveira 2002). Pursuing this logic, we can ask if the predator in Córrego da Andorinha, *M. olfersi*, is perhaps more carnivorous and less omnivorous than that in Puerto Rico (principally *Macrobrachium heterochirus*). We have no evidence to refute or support this hypothesis. An alternative hypothesis is that site characteristics determine the interactions; this appears the likely explanation for the difference between the dynamics of the two sites in Córrego da Andorinha.

A SECOND TROPHIC CASCADE

Further downstream in Córrego da Andorinha, the characteristics of the substrate change dramatically with a large increase in the quantity of periphyton and sediments. This stretch of stream has active predatory fish that are excluded from upstream areas by a large waterfall. We have correlational evidence that the change in substrate characteristics is caused by a trophic cascade of predatory fish that interact negatively on atyid shrimp that graze the periphyton (Souza *et al.* 2001, and unpublished data).

Again we can speculate why the trophic cascade exists in Córrego da Andorinha and was not observed in systems with fish and shrimp in Costa Rica (Pringle & Hamazaki 1998) and in downstream areas in Puerto Rico (e.g., March *et al.* 2002): Possibly the fish fauna of Córrego da Andorinha is dominated by predacious species (the characine *Bryconamericus microcephalus* and the poeciliid *Phalloceros caudimaculatus*) whereas in the other systems at least some of the fish are more omnivorous.

FUNCTIONAL VS TROPHIC RELATIONSHIPS IN STREAM FUNCTIONING

In the above description, we examined interactions among fauna and between fauna and periphyton without considering their trophic nature. The interactions were determined by experiments in which one element of the fauna was excluded and the resulting dynamic construed as the effect that the organism had on the system. (Most of the experiments in Puerto Rico, Costa Rica and Brazil used exclusion by electricity.) This did not show the movement of biomass through the food chain, although we could assume that there was some trophic basis to the interaction. In fact, the relationship between *Macrobrachium* and baetid ephemeropterans appears to be much more a potential predation than a transfer of biomass – we rarely observed baetids in the stomach contents of the *Macrobrachium*. Likewise, the atyid, *Potimirim*, was not found in the stomach contents of *Bryconamericus* (Resende & Mazzoni 2003, 2005).

Trophic relationships in food chains have been researched by tracing the occurrence of stable isotopes of carbon and nitrogen (Peterson & Fry 1987). This

was the basis of the work of Thorp & DeLong (1994, 2002), and it was applied to the stream food web in Puerto Rico by March & Pringle (2003), and to Córrego da Andorinha by Detweiler (2005), Detweiler *et al.* (2005), Brito *et al.* (2006a,b), and Moulton (2006). The technique is based on the observation that the ratio $^{13}\text{C}:^{12}\text{C}$ varies among sources of carbon and energy in food webs, and that the ratio is conserved in the different consumers of the different sources. Thus the food source of a consumer can often be deduced from this evidence. On the other hand, the ratio of ^{15}N to ^{14}N tends to increase by an approximately constant factor between trophic levels, and thus the position of a consumer in the trophic chain can be estimated.

March & Pringle (2003) found a high degree of incorporation of algal carbon in sites along an altitudinal gradient in Puerto Rico. The expectation based on the Riverine Continuum Concept model was that high elevation sites would be more shaded and dominated by the surrounding forest, and that the food web would be based primarily on allochthonous material. They found, however, that even at the highest elevation (300 m a.s.l.) the food web was dominated by algal sources. Salas & Dudgeon (2001) and Mantel *et al.* (2004) found a similar situation in shaded streams in Hong Kong.

A very surprising result within those of March & Pringle (2003) was the trophic position of the shrimp *Xiphocaris*. As mentioned above, *Xiphocaris* was found to shred leaves and other organic matter (Crowl *et al.* 2001), and was thought to be a classical “shredder” of the type described in the Riverine Continuum Concept. However the evidence from stable isotope analysis was that it derived its carbon principally from microalgae and as a secondary consumer. Obviously the functional role of this organism is different to its trophic position – presumably it shreds organic matter in search of animal prey which in turn are herbivores of algae. The atyid shrimp, *Atya lanipes*, also derived its carbon principally from microalgae (March & Pringle 2003), although it is functionally a filterer and collector of fine particles (Crowl *et al.* 2001). Yam & Dudgeon (2005) found a similar reliance on periphyton algae in the atyids *Caridina* spp. in shaded and unshaded streams in Hong Kong.

We observed a similar situation at Córrego da Andorinha (Detweiler 2005, Detweiler *et al.* 2005, Brito *et al.* 2006a,b, Moulton 2006). All of the consumers

sampled derived their carbon principally from microalgae. Atyid shrimps (*P. glabra*), which had been found to be 'ecosystem engineers' of material primarily not of periphyton origin (Souza 2002, Souza & Moulton 2005), were found to be trophically secondary consumers based on algae. *Macrobrachium olfersi* occupied a similar position to *Potimirim*. The baetid ephemeropteran *Cloedes* was found to be a trophic herbivore based on microalgae. The five fish species were all secondary consumers based on microalgae.

All of these results are at odds with the conventional feeding groups that have been allocated to these species based on stomach content analysis and direct observations. We observe that the shrimps and baetids have primarily detrital material in their stomach contents. A study of allochthonous material and diet of the characine fish *Bryconamericus* in Córrego da Andorinha concluded that the fish consumed a large proportion of allochthonous material in its diet (Resende & Mazzoni 2003, 2005).

The importance of microalgae in the food chain is quite incongruent with the proportion of microalgae in the stocks of biomass in Córrego da Andorinha (Figure 1). As expected for a forest stream, the majority of the organic material in the stream was of allochthonous origin – leaves, twigs and branches and particulate material. A small percentage of the organic material was in the periphyton (= organic material on hard substrate), and of this material, a small part was algal

biomass associated with chlorophyll (0.1 to 1% of total biomass, Figure 1). The standing stock of material does not represent the dynamics of the system, and for a complete analysis of the biomass available to consumers one would have to estimate the flux of material in each of the pools. We do not have these data, but we imagine from the static data that there is much more available allochthonous material than autochthonous.

Thus the food chain is seen to be supported by a small component of the available primary sources – the microalgae. It appears that the microalgae are a more nutritious and tractable source of food than the litter of forest plants. We can empathise with stream organisms who would find this material much more attractive – much as the monkeys, possums and birds find fruits and seeds more attractive than the green leaves of forest trees. But we can wonder why the resource of stream litter remains little incorporated into the food chain by adapted organisms such as insect larvae.

As mentioned above, various authors have noted the relative absence of shredding invertebrates in tropical streams (Dudgeon & Wu 1999, Dobson *et al.* 2002, Wantzen *et al.* 2002). There has been some speculation that the role of shredding is taken over by shrimps in coastal tropical streams (Covich *et al.* 1999). In a study that included Córrego da Andorinha and urban streams of Rio de Janeiro, Magalhães-Fraga (2002) observed

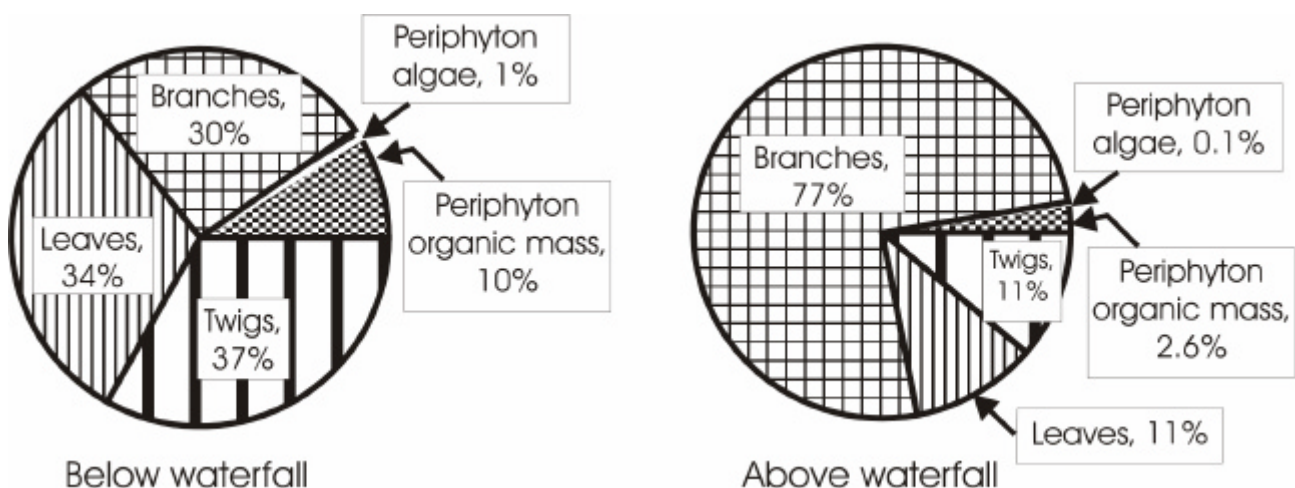


Figure 1. Carbon stocks in Córrego da Andorinha in sites just above and just below the waterfall at Mãe D'água expressed as percentage of total. Coarse material was collected in five 1 m transects across the stream, dried and sorted into categories branches, twigs and leaves. Benthic material was sampled with a plunger and syringe apparatus; the organic material was measured as ash-free dry mass; the algal mass was estimated from the measurement of chlorophyll using the assumption that chlorophyll makes up approximately 1% of total dry mass. Total dry mass below the waterfall was 46 g/m², and above, 59 g/m². Details are in Brito *et al.* (2006b).

faster leaf processing of leaf packs exposed to larger fauna compared to controls in which they were excluded, but she did not find a significant effect by smaller invertebrates. Insect shredder taxa were present, but apparently were not abundant and active enough to produce a significant effect in the experiment, although rates of decomposition were faster in intact streams compared to urban streams (Moulton & Magalhães 2003). Other studies have shown the presence of but low abundance of shredders in Neotropical streams, e.g., Callisto *et al.* (2001, 2004) (Serra do Cipó, MG, Brazil), Rosemond *et al.* (1998, 2001) (La Selva, Costa Rica).

FINALLY, WHY ARE THERE NOT MORE KOALAS AND SLOTHS?

Our picture is of tropical streams in which a disproportionate amount of the energy and material for the food chain comes from the small stock of microalgae of the periphyton. Tropical streams appear to be different to temperate streams in this, but this is possibly because so much emphasis has been given to the decomposer pathway in very shaded and small-order streams in the temperate. Temperate streams apparently do change to being dominated by microalgae when the streams become large and less shaded – at roughly 10 km² of catchment in the case of the Californian streams studied by Finlay (2001). Possibly tropical streams maintain algal production under higher vegetation cover than do temperate streams (Mosisch *et al.* 2001, Brito *et al.* 2006a).

It appears that the consumers as a group change towards the more nutritious and digestible algae when they are available, and spurn the less nutritious, more indigestible remains of terrestrial plants. This happens between species when more strictly herbivorous species occur in more open sites, and appears to happen within species that switch their diet away from litter and towards algae when they become available (Finlay 2001). If we accept this, we are still left with the question of why such an amount of allochthonous material remains uneaten. That is, why there are not more ‘koalas and sloths’ to take advantage of the available biomass which comes from the forest. Or why the existing specialist fauna of litter-eating insects are not more abundant and active. The specialists do

exist in Neotropical streams – we have found stable isotope evidence of the incorporation of allochthonous material in the trichopterans *Phylloicus* and *Triplectides* (unpublished data) and these are well-known leaf shredders.

From an armchair perspective, it seems that the HSS explanation must be operating – shredders are controlled by predators. Moreover, the white, yellow and green worlds of Oksanen *et al.* (1981) could also be invoked to explain the apparent exaggeration of this pattern in the ‘green’ tropics.

The experimental removal of potential predators has not generally shown this pattern, however – it generally does not provoke an increased rate of consumption of allochthonous material, as described above. At least part of the difficulty could be accounted for by the peculiar biology of the shrimps in some of these experiments, since they are apparently functional shredders but trophic predators (March & Pringle 2003, Brito *et al.* 2006b). Landeiro (2006) found abundant shredding trichopterans when larger fauna were excluded from leaf packs in small streams in Amazonia. On the other hand, Magalhães-Fraga (2002) found increased leaf processing in the presence of large fauna, but did not observe changes in the smaller invertebrate fauna associated with predator removal. Rosemond *et al.* (1998, 2001) excluded large fauna and did not observe an increase in shredding taxa, but they did find increase in non-shredding chironomid midges. The overall effects on organic matter consumption were greater in the presence of the shrimps and other large fauna; “the overriding negative effects of macroconsumers on organic-matter loss rates outweighed any potential positive cascading effect they may have had via consumption of smaller detritivores such as insect larvae and subsequent effects on leaf C” (Rosemond *et al.* 2001).

The same problem occurs in the experimental removal of ‘large omnivores’ from hard substrates with periphyton (Pringle & Blake 1994, Pringle & Hamazaki 1998, Souza & Moulton 2005) – the functional and trophic roles of the organisms are mixed. In the cases in which the larger fauna showed a strong trophic cascade (Moulton *et al.* 2004, Souza *et al.* 2001), the intermediate level (baetid ephemeropterans or atyids) acted functionally on allochthonous material, but were trophic herbivores of algae or predators of herbivores.

Notwithstanding this lack of evidence from experiments in a small scale of space and time, we can continue to speculate on why consumers apparently waste the available biomass of allochthonous material from the forest – except, apparently, when there is no alternative more nutritious food (algae) available. We can imagine that the adaptation to a diet of low nutritional quality (high C:N) and difficult digestion (due to protective chemicals, cellulose, and other structural difficulties) carries with it many costs, in terms of reduced speed of metabolism, slower growth rate, less disposable energy for flight and fight, etc. These costs would be particularly severe in a community of other organisms with more nutritious diet and with predators. In analogy with the terrestrial vertebrate herbivores, perhaps it makes for a slow, specialized lifestyle to adapt to folivory, as seen in the koalas and sloths, whereas the possums, opossums, rodents, monkeys, etc. that diversify on nutritious fruit and seeds and new shoots, comprise a much more diverse, abundant and metabolically fast community.

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REFERENCES

- ATTAYDE, J.L. & HANSSON, L.A. 2001. The relative importance of fish predation and excretion effects on planktonic communities. *Limnology and Oceanography*, 46: 1001-1012.
- BRITO, E.F.; DETWEILER, A.M.; KRSULOVIC, F.A.M.; SOUZA, M.L.; LIMA, V.N.; HERSHEY, A.E. & MOULTON, T.P. 2006a. Stable isotope analysis of food webs along a gradient of light and altitude in tropical forest streams, southeastern Brazil. *Bulletin of the North American Benthological Society*, 23: 125
- BRITO, E.F.; MOULTON, T.P.; SOUZA, M.L. & BUNN, S.E. 2006b. Stable isotope analysis indicates microalgae as the predominant food source of fauna in a coastal forest stream of Southeast Brazil. *Austral Ecology*, 31: 623-633.
- BUNN, S.E. & BOON, P.I. 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia*, 96: 85-94.
- CALLISTO, M.; GOULART, M.; MEDEIROS, A.O.; MORENO, P. & ROSA, C.A. 2004. Diversity assessment of benthic macroinvertebrates, yeasts, and microbiological indicators along a longitudinal gradient in Serra do Cipó, Brazil. *Brazilian Journal of Biology*, 64: 743-755.
- CALLISTO, M.; MORENO, P. & BARBOSA, F.A.R. 2001. Habitat diversity and benthic functional trophic groups at Serra do Cipó, southeast Brazil. *Brazilian Journal of Biology*, 61: 259-266.
- CAMPBELL, K.G. 1961. The effects of forest fires on three species of Stick Insects (Phasmatidae Phasmatodea) occurring in plagues in forest areas of south-eastern Australia. *Proceedings of the Linnaean Society of New South Wales*, 86: 112-121.
- CAMPBELL, K.G. & HADLINGTON, P. 1967. The biology of the three species of phasmatids which occur in plague numbers in forests of south eastern Australia. *Forestry Commission NSW Res. Note No. 20*, 38 pp.
- CARPENTER, S.R.; KITCHELL, J.F.; HODGSON, J.R.; COCHRAN, P.A.; ELSER, J.J.; ELSER, M.M.; LODGE, D.M.; KRETCHMER, D.; HE, X. & VON, ENDE C.N. 1987. Regulation of lake primary productivity by food web structure. *Ecology*, 68: 1863-1876.
- COLEMAN, R.A.; UNDERWOOD, A.J.; BENEDETTI-CECCHI, L.; ABERG, P.; ARENAS, F.; ARRONTE, J.; CASTRO, J.; HARTNOLL, R.G.; JENKINS, S.; PAULA, J.; DELLA SANTINA, P. & HAWKINS, J. 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia*, 147: 556-564.
- COLEY, P.D. & BARONE, J.A. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 27: 305-335.
- COVICH, A.P.; PALMER, M.A. & CROWL, T.A. 1999. The role of benthic invertebrate species in freshwater ecosystems - zoobenthic species influence energy flows and nutrient cycling. *Bioscience*, 49: 119-127.
- CROWL, T.A.; McDOWELL, W.H.; COVICH, A.P. & JOHNSON, S.L. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology*, 82: 775-783.
- DEARING, M.D.; FOLEY, W.J. & McLEAN, S. 2005. The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 36: 169-189.
- DELONG, M.D. & THORP, J.H. 2005. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. *Oecologia*, 147: 76-85.
- DEWEILER, A.M. 2005. The effects of urbanization on the food web of a mid-order stream in Rio de Janeiro, Brazil.

- Masters dissertation. University of North Carolina, Greensboro, NC, USA.
- DETWEILER, A.M.; HERSHEY, A.E.; MOULTON, T.P. & BRITO, E.F. 2005. The effects of urbanization on the food web of a mid-order stream in Rio de Janeiro, Brazil. *Bulletin of the North American Benthological Society*, 22: 263-264.
- DOBSON, M.A.; MAGANA, J.M.; MATHOOK, O. & NDEGWA, F.K. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshwater Biology*, 47: 909-919.
- DOUGLAS, M.M.; BUNN, S.E. & DAVIES, P.M. 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. *Marine and Freshwater Research*, 56: 329-342.
- DUDGEON, D. & WU, K.K.Y. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? *Archiv für Hydrobiologie*, 146: 65-82.
- FINLAY, J.C. 2001. Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology*, 82: 1052-1064.
- FORSBERG, B.R.; ARAUJO-LIMA, C.A.R.M.; MARTINELLI, L.A.; VICTORIA, R.L. & BONASSI, J.A. 1993. Autotrophic carbon sources for fish of the Central Amazon. *Ecology*, 74: 643-652.
- HAIRSTON, N.G.; SMITH, F.E. & SLOBODKIN, L.B. 1960. Community structure, population control, and competition. *American Naturalist*, 94: 421-425.
- HAMILTON, S.K.; LEWIS, W.M. & SIPPEL, S.J. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. *Oecologia*, 89: 324-330.
- HAY, M.E. & FENICAL, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics*, 19: 111-145.
- HECKY, R.E. & HESSLEIN, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society*, 14: 631-653.
- KITTING, C.L.; FRY, B. & MORGAN, M.D. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia*, 62: 145-149.
- KRSULOVIC, F.A.M. 2004. Avaliação de mecanismos de remoção de perifiton por ninfas de Ephemeroptera em um córrego, Ilha Grande, Brasil. Masters dissertation. Pós-graduação em Biologia, Universidade do Estado do Rio de Janeiro, RJ.
- LANDEIRO, V.L. 2006. Efeitos dos macroconsumidores (peixes e camarões) sobre a assembléia de insetos aquáticos e na taxa de degradação de folhas em riachos de floresta de terra firme, Amazônia Central. Masters dissertation. Pós-graduação em Entomologia, INPA, Manaus, AM.
- LEWINSOHN, T.M.; NOVOTNY, V. & BASSET, Y. 2005. Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution, and Systematics*, 36: 597-620.
- LOWMAN, M.D. & HEATWOLE, H. 1992. Spatial and temporal variability in defoliation of Australian eucalypts. *Ecology*, 73: 129-142.
- MAGALHÃES-FRAGA, S.A.P. 2002.. Efeitos do impacto por esgoto doméstico na decomposição e fauna associada em três rios do Parque Estadual da Pedra Branca, Rio de Janeiro, RJ. Doctoral thesis. Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, ICB, Universidade Federal de Minas Gerais, Belo Horizonte, MG.
- MANTEL, S.K.; SALAS, M. & DUDGEON, D. 2004. Foodweb structure in a tropical Asian forest stream. *Journal of the North American Benthological Society*, 23: 728-755.
- MARCH, J.G.; BENSTEAD, J.P.; PRINGLE, C.M. & RUEBEL, M.W. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 470-478.
- MARCH, J.G. & PRINGLE, C.M. 2003. Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. *Biotropica*, 35: 84-93.
- MARCH, J.G.; PRINGLE, C.M. & TOWNSEND, M.J. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. *Freshwater Biology*, 47: 377-390.
- MOSISCH, T.D.; BUNN, S.E. & DAVIES, P.M. 2001. The relative importance of shading and nutrients on algal production in subtropical streams. *Freshwater Biology*, 46: 1269-1278.
- MOULTON, T.P. 2006. Do we need a Revised Riverine Productivity Model for tropical streams? *Bulletin of the North American Benthological Society*, 23: 108.
- MOULTON, T.P. & MAGALHÃES, S.A.P. 2003. Responses of leaf processing to impacts in streams in Atlantic rainforest, Rio de Janeiro, Brazil — A test of the biodiversity-ecosystem functioning relationship? *Brazilian Journal of Biology*, 63: 87-95.
- MOULTON, T.P.; SILVEIRA, R.M.L.; SOUZA, M.L.; BRITO, E.F.; KRSULOVIC, F.A.M.; KOBLITZ, R.V. & BUNN, S.E. 2003. Strong interactors, ecosystem engineering and trophic cascades in coastal forest streams of southeast Brazil and southeast Queensland, Australia. *Bulletin of the North*

- American Benthological Society*, 20: 206.
- MOULTON, T.P.; SOUZA, M.L.; SILVEIRA, R.M.L. & KRSULOVIC, F.A.M. 2004. Effects of ephemeropterans and shrimps on periphyton and sediments in a coastal stream (Atlantic forest, Rio de Janeiro, Brazil). *Journal of the North American Benthological Society*, 23: 868-881.
- MURDOCH, W.W. 1966. Community structure, population control, and competition — a critique. *American Naturalist*, 100: 219-226.
- OKSANEN, L.; FRETWELL, S.D.; ARRUDA, J. & NIEMELÄ, P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, 118: 240-261.
- PACE, M.L.; COLE, J.J.; CARPENTER, S.R. & KITCHELL, J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14: 483-489.
- PETERSON, B.J. & FRY, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18: 293-320.
- PIMM S.L. 1991. *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago.
- POLIS, G.A.; SEARS, A.L.W.; HUXEL, G.R.; STRONG, D.R. & MARON, J. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution*, 15: 473-475.
- PRINGLE, C.M. & BLAKE, G.A. 1994. Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: Use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 1443-1450.
- PRINGLE, C.M. & HAMAZAKI, T. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology*, 79: 269-280.
- PRINGLE, C.M.; HEMPHILL, N.; McDOWELL, W.H.; BEDNAREK, A. & MARCH, J.G. 1999. Linking species and ecosystems: different biotic assemblages cause interstream differences in organic matter. *Ecology*, 80: 1860-1872.
- RESENDE, F.C. & MAZZONI, R. 2003. Aspectos da alimentação de *Bryconamericus microcephalus* (Characiformes, Tetragonopteridae) no córrego Andorinha, Ilha Grande RJ. *Biota Neotropica* 3, <http://www.biotaneotropica.org.br/v3n1pt?abstract?short+communication+BN01603012003>.
- RESENDE, F.C. & MAZZONI, R. 2005. Seasonal variation in the input of allochthonous matter in an Atlantic rain forest stream, Ilha Grande-RJ. *Acta Limnologica Brasiliensia*, 17: 167-175.
- ROSEMOND, A.D.; PRINGLE, C.M. & RAMIREZ, A. 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. *Freshwater Biology*, 39: 515-523.
- ROSEMOND, A.D.; PRINGLE, C.M.; RAMIREZ, A. & PAUL, M.J. 2001. A test of top-down and bottom-up control in a detritus-based food web. *Ecology*, 82: 2279-2293.
- SALAS, M. & DUDGEON, D. 2001. Stable-isotope determination of mayfly (Insecta : Ephemeroptera) food sources in three tropical Asian streams. *Archiv für Hydrobiologie*, 151: 17-32.
- SCHINDLER, D.W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos*, 57: 24-41.
- SILVEIRA, R. M. L. 2002. Modelo de matriz de comunidade em um córrego de Mata Atlântica. Doctoral thesis. Pós-graduação em Biologia, UERJ, Rio de Janeiro.
- SILVEIRA, R.M.L. & MOULTON, T.P. 2000. Modelling the food web of a stream in Atlantic forest. *Acta Limnologica Brasiliensia*, 12: 63-71.
- SOUTHWOOD, T.R.E. 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology*, 30: 1-8.
- SOUZA, M. L. 2002. Desenvolvimento de sistemas de exclusão elétrica e o papel funcional de camarão em um córrego da Mata Atlântica. Masters dissertation. Pós-graduação em Biologia, UERJ, Rio de Janeiro.
- SOUZA, M. L. & MOULTON, T.P. 2005. The effects of shrimps on benthic material in a Brazilian island stream. *Freshwater Biology*, 50: 592-602.
- SOUZA, M.L.; ASSIS, J.C.F.; FRANCISCHETTI, C.N.; MOULTON, T.P.; SILVEIRA, M.P. & SILVEIRA, R.M.L. 2001. Indirect effect of fish on shrimp determines sediments, periphyton abundance and macroinvertebrate diversity in two Atlantic forest streams in southeastern Brazil. *Bulletin of the North American Benthological Society*, 18: 260
- STRONG, D.R.J.; LAWTON, J.H. & SOUTHWOOD, T.R.E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific, Oxford.
- STRONG, D.R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, 73: 747-754.
- TERBORGH, J.; FEELEY, K.; SILMAN, M.; NUNEZ, P. & BALUKJIAN, B. 2006. Vegetation dynamics of predator-free land-bridge islands. *Journal of Ecology*, 94: 253-263.
- TERBORGH, J.; LOPEZ, L.; NUNEZ, P.V.; RAO, M.; SHAHABUDDIN, G.; ORIHUELA, G.; RIVEROS, M.; ASCANIO, R.; ADLER, G.H.; LAMBERT, T.D. &

- BALBAS, L. 2001. Ecological meltdown in predator-free forest fragments. (Reports). *Science*, 294: 19-23.
- THORP, J.H. & DELONG, M.D. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, 70: 305-308.
- THORP, J.H. & DELONG, M.D. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, 96: 543-550.
- VANNOTE, R.L.; MINSHALL, G.W.; CUMMINS, K.W.; SEDELL, J.R. & CUSHING, C.E. 1980. River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 130-137.
- WANTZEN, K.M. 2002. How do plant-herbivore interactions of trees influence coarse detritus processing by shredders in aquatic ecosystems of different latitudes? *Verhandlungen - Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 28: 815-821.
- YAM, R.S.W. & DUDGEON, D. 2005. Stable isotope investigation of food use by *Caridina* spp. (Decapoda: Atyidae) in Hong Kong streams. *Journal of the North American Benthological Society*, 24: 68-81.