Macroinvertebrates and leaf litter decomposition in a neotropical lowland stream, Quebrada Negra, Costa Rica

Macroinvertebrados y descomposición de residuos de hojas en un curso de agua de tierras bajas neotropical, Quebrada Negra, Costa Rica

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Abstract: The Quebrada Negra, a first order tropical lowland stream within the Piedras Blancas National Park, Costa Rica, is a heterogeneous environment with a high diversity of habitats where environmental characteristics vary drastically over small distances. The taxonomic composition of stream benthic fauna and its trophic structure (functional feeding group -FFG) within riffle and pool sites were distinguished. At riffle sites, Ephemeroptera was the dominant insect order (37%), followed by Coleoptera and Diptera. Collector-filterers were mainly represented by Philopotamidae and Hydropsychidae (Trichoptera). These two families were not present at pool sites. The macrozoobenthos of pools was dominated by Diptera (36%) and Ephemeroptera (31.9%), including the family of Caenidae (11%) which were not found at riffle sites. In terms of species numbers, representing the different trophic guilds, the fauna is mostly made up of collector-gatherers (53%), followed by predators (16.5%) and filter-feeders (14.5%). Shredders, such as Leptoceridae and Calamoceratidae were rare.

Leaf litter decomposition in tropical lotic systems has received less attention than in streams in the temperate region. In view of various defence mechanisms against herbivory (polyphenols – especially tannins) of plants in tropical rainforests, leaf decay rates and macroinvertebrate colonisation of 4 plant species, representing a range of life history and defence strategies, were investigated using litter bags. Leaf material of 4 common tree species, *Acalypha diversifolia* (Euphorbiaceae), *Cecropia obtusifolia* (Cecropiaceae), *Tetrathylacium macrophyllum* (Flacourtiaceae) and *Sloanea medusula* (Elaeocarpaceae) were exposed in the stream. Peaks of macrozoobenthos colonisation (total individuals and abundance of major taxa) occurred between 10 and 20 days of exposure on *A. diversifolia*, *C. obtusifolia*, *T. macrophyllum*. Colonisation on *Sloanea medusula* increased slowly within exposure time and showed the lowest population density. Most of the variation in colonist densities and species composition was explained by leaf type and time of exposure. The invertebrate community which colonised litter bags was dominated by taxa of mayflies (mainly Leptohyphidae), caddisflies and Chironomidae.

Key words: neotropical rainforest stream, aquatic macroinvertebrates, small scale distribution, riffle-pool sites, trophic structure, leaf litter decomposition.

Resumen: El Quebrada Negra, es un curso de agua tropical del primer orden de tierras bajas, que atraviesa el Parque Nacional Piedras Blancas, en Costa Rica, es un medio ambiente heterogéneo con una gran diversidad de hábitat, donde las características ambientales varían drásticamente en distancias pequeñas. Se determinó la composición taxonómica de la fauna béntica del río y su estructura trófica (grupo funcional de alimentación, FFG) en los sitios de rápidos y en los remansos. En los sitios de rápidos, el orden de insectos dominante fue Ephemoroptera (37%), seguido por Coleoptera y Diptera. Los recolectores filtradores estuvieron representados por las Philopotamidae y las Hydropsychidae (Trichoptera). Estas dos familias no se hallaron en los sitios de remansos. El macrozoobentos dominante en los remansos fueron Diptera (36%) y Ephemeroptera (31,9%), que incluía la familia Caenidae (11%), la cual no se halló en los sitios de rápidos. En términos de números de especies, representando los diferentes grupos tróficos, la fauna está constituida principalmente por recolectores (53%), seguido de predadores (16,5%) y filtradores (14,5%). Los trituradores como Leptoceridae y Calamoceratidae fueron escasos.

La descomposición de residuos de hojas en sistemas lóticos tropicales ha recibido poca atención en comparación con los cursos de agua de las regiones templadas. Debido a los diferentes sistemas de defensa vegetales de las selvas tropicales contra los herbívoros (polifenoles – especialmente taninos), se investigó mediante el uso de bolsas de residuos vegetales, la tasa de descomposición de las hojas y la colonización de macroinvertebrados de 4 especies vegetales, representantes de un amplio margen de historia vital y estrategias defensivas. Se expusieron en el río muestras de 4 especies de árboles comunes: *Acalypha diversifolia* (Euphorbiaceae), *Cecropia obtusifolia* (Cecropiaceae), *Tetrathylacium macrophyllum* (Flacourtiaceae) y *Sloanea medusula* (Elaeocarpaceae). Los pun-

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tos máximos de densidad de colonizadores (total de individuos y abundancia de taxa principales) ocurrieron entre los 10 y 20 días de exposición en *A. diversifolia*, *C. obtusifolia* y *T. macrophyllum*. La colonización en *Sloanea medusula* aumentó lentamente con el tiempo de exposición y mostró una menor densidad de población. La mayor parte de la variación en la densidad de colonización y composición de especies fue explicada en función del tipo de hoja y el tiempo de exposición. Las comunidades de invertebrados que colonizaron de manera dominante las muestras de residuos fueron: efímeras (principalmente Leptohyphidae), frigáneas y Chironomidae.

Palabras clave: cursos de agua neotropicales, macroinvertebrados aquáticos, distribución en pequeña escala, remansos y rápidos, estructura trófica, descomposición de residuos de hojas.

Introduction

The present paper consists of two parts. The first deals with the distribution of macroinvertebrates in the Quebrada Negra, a 1st order, tropical lowland stream within the Piedras Blancas National Park, Costa Rica. The second deals with the role of macrozoobenthos in leaf litter decomposition. The neotropical benthic macroinvertebrate fauna is still poorly known, although the abundance, small scale distribution, drift patterns and functional organisation of macroinvertebrates in streams has been studied by various authors (eg. PRINGLE & RAMIREZ 1998, FÜREDER 1994, FENOGLIO et al. 2004, JACKSON & SWEENEY 1995).

Streams are highly heterogeneous environments in which habitat characteristics vary drastically over small distances (FENOGLIO et al. 2004). The heterogeneity of stream bed structures is a major factor in the maintenance of a diverse macroinvertebrate fauna (SCHIEMER & ZALEWSKI 1992). Local variations of abiotic factors, such as current velocity, substrate composition and water depth shape the distribution patterns of the biota. In the present survey, the composition of the macrozoobenthos within riffle-pool sequences as well as local variations of density and functional composition in relation to selected environmental characteristics like current velocity and water depth were analysed.

Stream communities in forested catchments are generally dependent on allochthonous organic matter as a trophic base. It is generally accepted that leaf litter is one of the major energy sources of food webs in forested headwater streams (VANNOTE et al. 1980, CUMMINS et al. 1989). The shading effect of riparian vegetation effectively limits in situ primary production. Allochthonous sources, especially litter fall is therefore of primary importance in the energy budgets (CUMMINS et al. 1973, 1974, FISHER & LIKENS 1973). Leaf litter entry into neotropical streams is controlled mostly by the seasonality of the precipitation (DE LA ROSA 1995), which is an important difference from temperate streams. Peaks in leaf fall have been reported during the dry season for Central American forests. On Barro Colorado Island (Panama) the peak in fall occurs from January to April (HAINES & FOSTER 1977), while in Santa Rosa (in the northern dry zone of Costa Rica) it takes place between November and May (HARTSHORN 1983). The rate of decomposition is determined by specific differences among leaves, environmental variables (e.g. temperature) and the feeding activity of detrivores (ALLAN 1995). Water temperature has been cited widely as an important controlling variable for stream ecosystem processes and enhances breakdown rates (KAUSHIK & HYNES 1971, ANDERSON & SEDELL 1979, WEBSTER & BENFIELD 1986, PRINGLE 1994).

Some trees in tropical rainforests can maintain their leaves for periods exceeding a year, and they are exposed to longer periods of herbivory and other physical damage than of decidious forests in mid-latitudes. Thus tropical lowland rainforest leaves contain on the average, more defensive compounds as protection against herbivory (see JANZEN 1974, STOUT 1980). Tropical lotic systems have received less attention in the processing of leaf litter than temperate streams. One further objective of the present study was therefore to determine differences in decay of four plant species of the Quebrada Negra riparian forest in the context of patterns of colonising macroinvertebrates. A study on the plant anatomy and histological analyses of the exposed leaves shows the varying nature of the leaf structure, elucidated the differences in "toughness" and tannin content and supports the results of the differences in decay (RIEMERTH et al. 2008).

Material and methods

Sampling of macrozoobenthos and litter decomposition experiments were conducted at the Quebrada Negra in March and April 2004 under conditions of low discharge. The Quebrada Negra, a first order tropical lowland forest stream within the Piedras Blancas National Park, Costa Rica, is a highly heterogeneous, dynamic and unregulated stream course. Current velocity, stream depth, stream bed width and sediment size fluctuate within short distances (100 m). A sequence of riffle and pool sites are the two most distinguishable (micro)habitats within the defined 100m sector of Quebrada Negra (see also "The River Network of the Piedras Blancas National Park, Costa Rica" TSCHELAUT et al.

2008). Riffle environments were selected in relatively shallow turbulent areas (0.1 m deep) where the water flow was high (approx. 0.5 ms^{-1}). Pools had a mean depth of 0.24 m and low flow (0.15 ms^{-1}). Samples of the benthic invertebrate fauna were collected by disturbing the substrate manually to a depth of about five centimetres for approximately five minutes. Depending on the physical characteristics of the sites, either a Surber sampler with a defined surface area or a Kick sampler was used. Macroinvertebrates from each sample were hand sorted under a binocular microscope, identified to taxonomic units, counted and placed in 70% ethanol. The keys of MERRITT & CUMMINS (1996) were used for identification of the taxa to the level of families. Invertebrates were assigned to functional feeding groups (FFG), according to MERRITT & CUMMINS (1996): collector-gatherers (Co), filterers (F), predators (P), scrapers (Sc) piercers (Pi) and shredders (Sh).

Leaf decay rates and macroinvertebrate colonisation of exposed leaf litter from four different plant species from the riparian vegetation of the Quebrada Negra were investigated. The four plant species were selected according to life history strategies and abundance after a survey of the riparian vegetation (see TSCHELAUT et al. 2008). Litter bags of *Acalypha diversifolia* (Euphorbiaceae), *Cecropia obtusifolia* (Cecropiaceae), *Tetrathylacium macrophyllum* (Flacourtiaceae) and *Sloanea medusula* (Elaeocarpaceae) (see Plate 1), were placed over a 28 day period in the Quebrada Negra. For simplicity, the fast growing plants are further called r-strategists and the slow growing K-strategists. All four chosen plant species are common and typical for the riparian vegetation in this area of Costa Rica. Only old leaves, prior to abscission, were exposed in the stream. Litter bags were made out of nylon mesh (10 × 10 mm) and small stones were added to each bag to ensure that contents were in contact with the stream bed. 16 litter bags of each species (8 g of leaves) were tied on strings and placed in the stream parallel to the current. The experimental sites were located in riffles of moderate depth and velocity (approximately 0.08 m deep and 0.2 ms^{-1}). Two bags of each species were collected after 4, 8, 14, 21 and 28 days by placing a net (200 µm) under each so as not to lose the colonising macroinvertebrates. After cutting the attachment string, the litter bags were transferred to a plastic tube and transported to the laboratory. Invertebrates were washed from the leaves, sorted and preserved in 70% ethanol. Macroinvertebrates were later counted and determined to family level. Insects were assigned to functional feeding groups following MERRITT and CUMMINS (1996). Leaves were dried to constant weight at 70°C and weighed. The experiment ran from the 28th of February 2004 to the 27th of March 2004. The study came to a premature end due to a flash flood event and loss of the remaining litter bags.

Analysis of data

WEBSTER and BENFIELD (1986) argue that a simple exponential model provides a general and utilitarian description of the breakdown process. The exponential model $W_t = W_o e^{-kt}$ (where W_t is the amount of leaf litter remaining after time, t, of the initial amount W_o, and k is the processing coefficient) was used to calculate processing coefficients. The exponent k (in units $days^{-1}$), which is the slope of the plot of $\log_e$ of leaf mass versus time, provides a single measure of breakdown rate. This model assumes that there is a constant fractional loss of material present at any given time.

The DCA (detrended correspondence analysis) is a procedure of analysis of gradients. This was performed on the basis of the macroinvertebrate distribution in context with the time of exposition of the leaf material. The results are represented as a biplot.

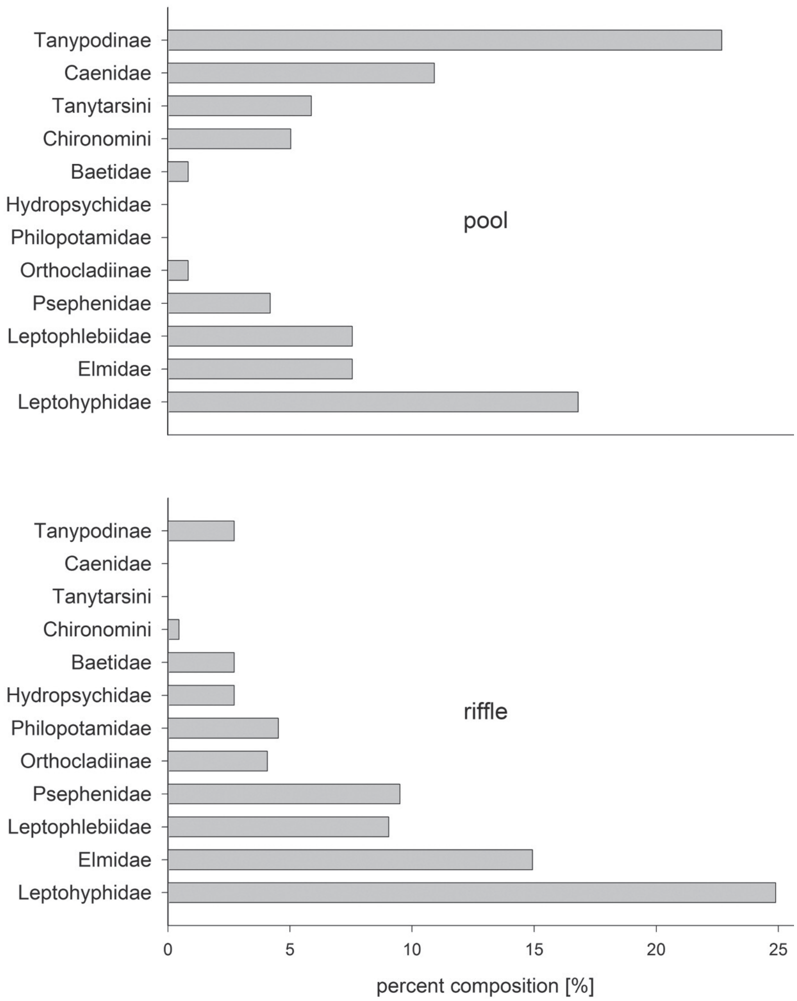

Fig. 1: Percent composition [%] of major Ephemeroptera, Diptera, Trichoptera and Coleoptera families at riffle and pool sites of the Quebrada Negra, arranged according to their preference for lotic habitats.

Results

Distribution of macroinvertebrates at riffle and pool sites of the Quebrada Negra

The distribution of the macroinvertebrate communities in the Quebrada Negra shows the effects of current velocity and depth. Fifty taxa were identified (major taxa can be seen in Tab. 1 and Fig. 1) within pools and riffle sites. Aquatic insects represent the dominant component of stream benthos.

Tab. 1 and Fig. 1 reflect the clear differences of the macroinvertebrate composition at riffle and pool sites. At riffle locations, Trichoptera (caddisflies) were represented by the two filter-feeding families: Hydropsychidae and Philopotamidae, which are always associated with higher current velocities. Ephemeroptera (mayflies) was the dominant insect group (36.7%), mainly represented by Leptohyphidae (24.9%) and Leptophlebiidae (9%). Coleoptera (beetles) – mainly Elmidae and Psephenidae – and Diptera (flies) followed in abundance. Chironomidae (Orthocladiinae, Tanypodinae, Chironomini) was the dominant family of Diptera, which were supplemented by the shredder Tipulidae and the collector-filterer Simuliidae (blackflies). The predators Odonata are represented by Zygoptera (damselflies) and Anisoptera (dragonflies).

In pools, Diptera (36.1%) was the most abundant insect order, of which 34.5% was made up by Chironomidae, including Tanytarsini (6%), which were not present at riffle sites. Ephemeroptera (31.9%) were second in dominance, with Leptohyphidae (16.8%) the most abundant family, followed by Caenidae (10.9%). Members of the family Caenidae are not found at riffle sites and are always associated with low flow. Coleoptera were represented by Elmidae and Psephenidae.

Tab. 1: Number and percent composition [%] of the macroinvertebrate fauna within riffle and pool sites of the Quebrada Negra and FFG (Fi: filterer; Pr: predator; Co: collector-gatherer; Sh: shredder; Pi: piercer; Sc: scraper).

	riffle total individuals = 221 n = 3		pool total individuals = 119 n = 5		Feeding group
taxon	number	percent	number	percent	
EPHEMEROPTERA	81	36,7	38	31,9	Co
Baetidae	6	2,7	1	0,8	Co
Caenidae	0	0	13	10,9	Co
Leptohyphidae	55	24,9	20	16,8	Co
Leptohlebiidae	20	9,0	9	7,6	Co
TRICHOPTERA	19	8,6	1	0,8	
Hydropsychidae	6	2,7	0	0	Co-Fi
Hydroptilidae	1	0,5	0	0	Pi
Philopotamidae	10	4,5	0	0	Co-Fi
others	2	0,9	1	0,8	
PLECOPTERA	2	0,9	0	0	
Perlidae	2	0,9	0	0	Pr
DIPTERA	28	12,7	43	36,1	
Chironomidae	16	7,2	41	34,5	
Chironomini	1	0,5	6	5,0	Co
Orthocladiinae	9	4,1	1	0,8	Co
Tanypodinae	6	2,7	27	22,7	Pr
Tanytarsini	0	0	7	5,9	Co-Fi
Simuliidae	3	1,4	0	0	Co-Fi
Tipulidae	9	4,1	0	0	Sh
Ceratopogonidae	0	0	1	0,8	Pr
MEGALOPTERA	1	0,5	0	0	Pr
Corydalidae	1	0,5	0	0	Pr
COLEOPTERA	54	24,4	14	11,8	
Elmidae	33	14,9	9	7,6	Co
Psephenidae	21	9,5	5	4,2	Sc
LEPIDOPTERA	4	1,8	0	0	Sh
ODONATA	11	5,0	4	3,4	Pr
HYDRACHNELLAE	10	4,5	6	5,0	
TURBELARIA	4	1,8	1	0,8	
HETEROPTERA	1	0,5	2	1,7	Pr
REST	6	2,7	10	8,4	

Macrozoobenthos colonisation during litter decay

A total of 3339 individuals of macroinvertebrates were collected from litter bags. A marked feature of the macrobenthos colonisation was the dominance by insects. Thirteen orders and about 39 families colonised the litter bags during the course of study. The number of Ephemeroptera, Diptera (mainly Chironomidae), Trichoptera, Coleoptera and Odonata species was particularly high. By contrast, Plecoptera (stoneflies) were few and constituted only 0.03% of total colonizers. Abundant families and species within this study resemble the picture of the findings from riffle and pool sites of the Quebrada Negra. The assemblage was dominated by Diptera (44.7% of the total fauna), mostly made up of Chironomidae (41.4%), particularly the subfamily Orthocladiinae (23.1%). Ephemeroptera (39.4% of the total fauna) were the following major group, comprising Baetidae (6.8%), Leptohyphidae (27.7%), Leptophlebiidae (4.3%) and Caenidae (0.6%). Trichoptera (8.1%), mostly Leptoceridae (2.7%) and Hydropsychidae (2.4%), were also abundant. Odonata, Coleoptera and Turbellaria were the only other orders that made up more than 1% of the total assemblage. Colonist densities (total individuals and abundance of major taxa) were highest on *Cecropia obtusifolia* and *Tetrathylacium macrophyllum* leaves and lowest on *Sloanea medusula*. Macroinvertebrate numbers increased steadily in the first 14 days of leaf exposition (Fig. 2) at all plant species except at *Sloanea medusula*. Abundance at *Acalypha diversifolia*, *Tetrathylacium macrophyllum* and *Cecropia obtusifolia* declined after longer exposures, when most of the plant material had been broken down and mainly the lignified, unpalatable parts of the leaves remained in the bags. By day 28, species richness has declined. The K-strategist *Sloanea medusula* does not show the rapid increase of colonisation seen in the other three plants.

Fig. 3 represents the sequence of a succession and shows the patterns of the macroinvertebrate feeding group assemblage within time of leaf exposure. Axis 1 can be interpreted as the time axis. The macroinvertebrates were assigned to feeding groups after MERRITT & CUMMINS (1996). The seperation into functional feeding groups revealed considerable differences between the colonisation dynamics of filter-feeders and shredders. In real time, colonisation of the plants by collectors and filterers was rapid in the first days of exposition. Leaf-cutting shredders appeared when litter became more palatable after being conditioned for a certain time. Figure 4 exemplifies the biofilm development on the leaves of *Cecropia obtusifolia* (Cecropiaceae) after approximately 14 days of exposition. Collector species existed throughout the study, along with predators which were present throughout the study within the community.

Differences of the four plant species in decay and loss of weight within exposure time are shown in Figure 5. Weight loss from leaf packs was clearly dependent on litter type. The weight loss of *Tetrathylacium macrophyllum* (e.g. 47.2% loss after 14 days) was consistently faster than that of *S. medusula* (e.g. 13.6% loss after 17 days). *S. medusula* had lost only 20.1% on day 24 where as by day 28, *Tetrathylacium macrophyllum* packs had lost 72.3% of their initial weight, *Acalypha diversifolia* had lost 67% and *Cecropia obtusifolia* had lost 54.7%. *T. macrophyllum* was almost decomposed to the leaf nervation by the end of the study (Fig. 6). The weight loss of *Sloanea medusula* was clearly slower.

The relationship between the leaf litter remaining (W_t) of each plant species and their values for daily litter decomposition rates (k) is presented in Table 2. According to the "hierarchy of species along a processing continuum" of PETERSEN & CUMMINS (1974) and the known decomposition rates, *Acalypha diversifolia* (0.0395), *Cecropia obtusifolia* (0.0234), and *Tetrathylacium macrophyllum* (0.0458) can be assigned to the "fast" group. *Sloanea medusula* (0.0094) can be placed into the slow group.

Discussion

The fauna of the riverbed of Quebrada Negra resembles the taxonomical and functional composition of other neotropical lowland streams (PRINGLE & RAMIREZ 1998, FENOGLIO et al. 2004, COVICH 1988, RAMIREZ & PRINGLE 2001, BENSTEAD 1996, ROSEMOND et al. 1998, 2002). Ephemeroptera (esp. Leptohyphidae and Leptophlebiidae), Coleoptera (esp. Elmidae and Psephen-

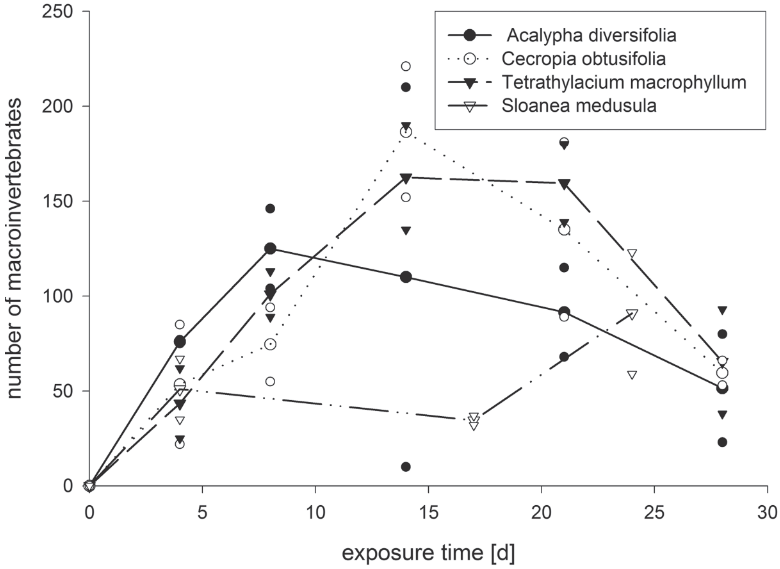

Fig. 2: Mean number of macroinvertebrates colonising four different types of leaf packs (*Acalypha diversifolia*, *Cecropia obtusifolia*, *Tetrathylacium macrophyllum*, *Sloanea medusula*) within exposure time [d], bags n=2.

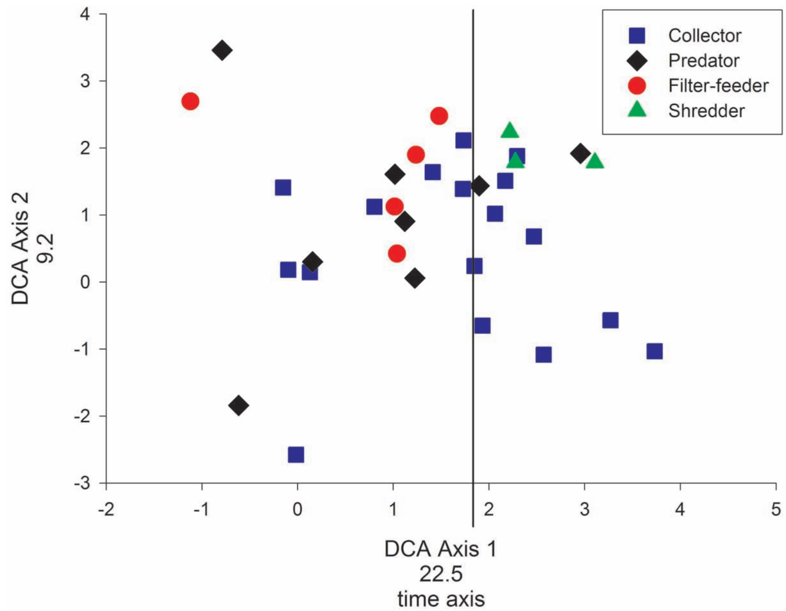

Fig. 3: Ordination biplot resulting from a DCA (Detrended Correspondence Analysis) of the fauna collected from four types of leaf packs (*Acalypha diversifolia*, *Cecropia obtusifolia*, *Sloanea medusula*, *Tetrathylacium macrophyllum*) placed in the Quebrada Negra. The macroinvertebrates were assigned to functional feeding groups. (Filter-feeder = red, predator = black, collector-gatherer = blue, shredder = green).

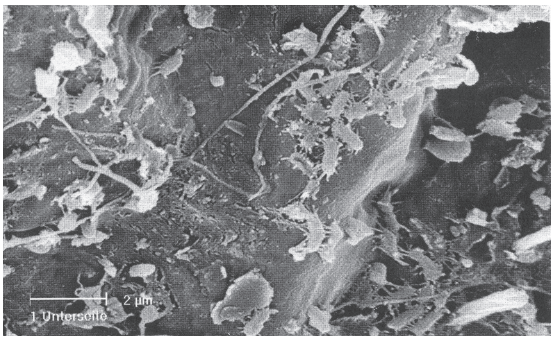

Fig. 4: Biofilm development on *Cecropia diversifola* (Cecropiaceae) after approx. two weeks of exposure.

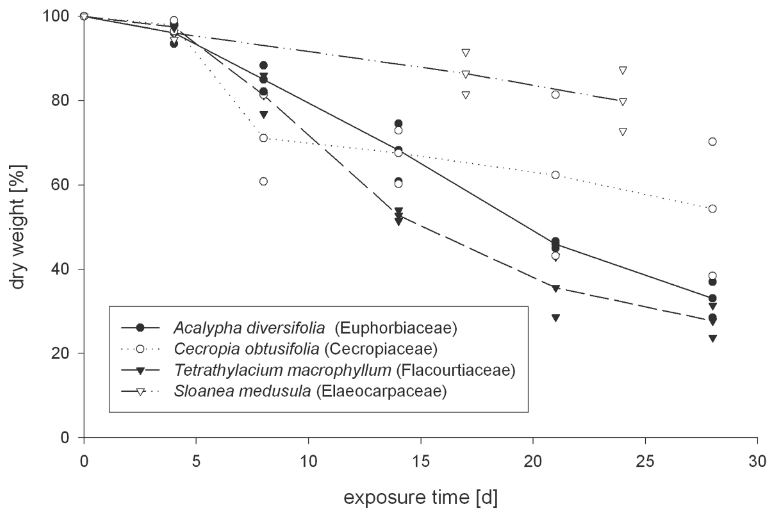

Fig. 5: Single values of percentage loss [%] and mean percentage [%] loss of weight from four different types of leaf packs (*Acalypha diversifolia*, *Cecropia obtusifolia*, *Tetrathylacium macrophyllum*, *Sloanea medusula*) exposed in the Quebrada Negra for 28 days.

idae) and Chironomidae were the dominant taxa within this study. This specific assemblage of benthic insect larvae is in accordance with the above mentioned authors. COVICH (1988) pointed to the fact that the taxonomic composition of neotropical stream communities is characterised by a high endemicity of certain groups coupled with a paucity of species (e.g. Plecoptera) in others (see BENSTEAD 1996, ROSEMOND 1998, FÜREDER 1994).

In the Quebrada Negra, the density and taxonomic diversity of macrozoobenthos varied greatly between pool and riffle locations. Current velocity is an important factor in shaping benthic communities, both in structural and functional composition: density and taxonomic richness of the invertebrate assemblage increased with higher current velocities. Substrate influences invertebrate abundance: riffle sites with boulders and pebbles were richer than sandy habitats (pools). In general, all the dominant species are collector-gatherer or filter-feeder (both feeding on fine particulate matter) with their associated predators. Shredders are rare and this absence has also been stressed in other studies on Central American lowland streams (PRINGLE & RAMIREZ 1998). Shredders (Calamoceratidae, Leptoceridae) encountered within the experiment on leaf litter decomposition in the Quebrada Negra (TSCHELAUT et al. 2008) did not occur in the samples of riffle and pool sites. This rarity of shredders found, contradicts a study of BENSTEAD (1996) in a Costa Rican stream, where two species of trichopteran shredders made up over 30% of litter bag colonists (and 98% of all shredders).

Shredders play an important role in the decay of particulate organic matter in temperate streams (KAUSHIK & HYNES 1971, PETERSEN & CUMMINS 1974, WALLACE & WEBSTER 1996). Studies have shown that in general, the abundance of shredding invertebrates and decay rates of leaves are positively correlated (WALLACE et al. 1982, BENFIELD & WEBSTER 1985, MALMQVIST 1993).

Under the hypothesis that stream macroinvertebrates are using leaf litter as a source of food, we would expect a higher proportion of shredders as leaf-pack colonists. As seen in most studies of litter breakdown in streams (DUDGEON 1991, DUDGEON & WU 1999, WEBSTER & BENFIELD 1986, BENSTEAD 1996), leaf colonisation by macroinvertebrates increased during the initial exposition time. Indeed, time and leaf type explained most of the variation in macroinvertebrate densities on leaf packs in a study of DUDGEON & WU (1999). In the present study, filter-feeders and shredders showed a different time sequence of colonisation. Filter-feeder colonisation was initially fast in comparison to shredders, which appeared only when the leaf material had been exposed and conditioned for a certain time. One explanation of this sequence could be that shredders, using leaf material as a food resource, cause a loss of substrate which leads to a decline of filter-feeders.

This is in accordance with STOUT (1980) who suggested that, in addition to serving as a nutrient input source, leaves serve as substrata for aquatic invertebrates; slowly decomposing, long-lasting leaves in particular would serve primarily as attachment sites for some insects and other invertebrates. BENSTEAD (1996) found that the balance of immigration and emigration of shredders was strongly dependent on the mass of leaf litter remaining. Collector species were present throughout the field experiments. Their colonisation appeared to be a more passive process and independent of the amount of leaf litter remaining in the bags. Macrobenthic predators rapidly colonised the litter bags, but by the end of the study period, the number of predators

Tab. 2: Values of daily litter decomposition rate (k) from four different types of leaves (*Acalypha diversifolia*, *Cecropia obtusifolia*, *Tetrathylacium macrophyllum*, *Sloanea medusula*) exposed in the Quebrada Negra, obtained from the slopes of regression equations between log W_t and t.

taxon	W0	Wt	t	k
Acalypha diversifolia (Euphorbiaceae)	3,16	1,05	28	0,0395198
Cecropia obtusifolia (Cecropiaceae)	3,30	1,71	28	0,0234255
Tetrathylacium macrophyllum (Flacourtiaceae)	3,18	0,88	28	0,0458265
Sloanea medusula (Elaeocarpaceae)	4,67	3,73	24	0,0093646

had declined. This decrease may indicate the importance of leaf litter as a microhabitat for predators. This finding is similar to our own observations.

Plant-specific differences in leaf breakdown rates are well documented (PETERSEN & CUMMINS 1974, PADGETT 1976). PETERSEN & CUMMINS (1974) distinguished three categories of leaf species – from slow to fast – according to breakdown rates in temperate streams. Species with a processing coefficient, k, of greater than 0.01 day^{-1} were placed in the "fast" group. According to this category *Sloanea medusula* has a slow breakdown rate, whereas *Tetrathylacium macrophyllum* leaves lost weight considerably faster. This matched our hypothesis on leaf palatibility to macroinvertebrates and was revealed by higher colonisation on *Tetrathylacium macrophyllum*. The high rates of leaf litter decomposition for *Acalypha diversifolia*, *Cecropia obtusifolia* and *Tetrathylacium macrophyllum*, in comparison to *Sloanea medusula*, may be attributed to the differences in leaf structure, i.e. thickness and presence or absence of cuticularised cell walls as well as the differences in their tannin content. *Sloanea medusula* leaves are thicker than the leaves of the three other plants (see RIEMERTH et al. 2008). These factors may explain the relatively slow weight loss of *Sloanea medusula* observed in this study. The relationship between leaf lifetime relating to life history strategy and the type of defence (fibre as well as immobile defences like condensed tannin) has been documented by COLEY (1985, 1988) for trees in Panama. The palatable litter will serve mainly as a food source and support high densities of macroinvertebrates, while lower densities of animals will be associated with less palatable litter which is used mainly as a substrate. Leaf litter needs to be conditioned by microbial activities (e.g. by bacteria and aquatic hypomycetes (BÄRLOCHER 1985) before it is made more palatable and availible for the consuming invertebrates). PRINGLE (1993) proposed the hypothesis that, due to the lack of insect shredders, the decomposition of plant material in neotropical streams is either carried out by macroconsumers, such as crustaceans and fish, or by enhanced microbial activity.

Potential detrivores present such as fish (e.g. Poecilidae – see PICHLER & SCHIEMER 2008) or crayfish might have partial access to the contents of the litter bags, but their contribution to litter decomposition has not been evaluated (see WOOTON & OEMKE 1992).

We concur with BENSTEAD (1996) that high water temperatures are an important contributing factor and give rise to rapid microbial conditioning of leaf litter, with a potential subsequent increase in the rate of consumption by the shredder community. The low percentage of shredders (3.5%) during the study is an interesting finding which requires further attention.

Fig. 6: *Tetrathylacium macrophyllum* (Flacourtiaceae) on the 21st day of exposure in the stream.

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References

ALLAN J.D. (1995): Stream Ecology – Structure and function of running waters. — Chapman and Hall, New York.

ANDERSON N.H., ANDERSON S.E. & J.R. SEDELL (1979): Detritus processing by macroinvertebrates in stream ecosystems. — Ann. Rev. Entomol. **24**: 351-377.

BÄRLOCHER F. (1985): The role of fungi in the nutrition of stream invertebrates. — Bot. J. Linnean Society **91**: 83-94.

BENSTEAD J.P. (1996): Macroinvertebrates and the processing of leaf litter in a tropical stream. — Biotropica **28**: 367-375.

CAMPBELL C.I. & L. FUCHSHUBER (1995): Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. — J. N. Am. Benthol. Society **14**: 174-182.

COLEY D.P. (1988): Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. — Oecologia **74**: 531-536.

COVICH A.R. (1988): Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. — J. N. Am. Benthol. Soc. **7**: 361-386.

CUMMINS W.K. (1973): Trophic relations of aquatic insects. — Ann.Rev.Entomol. **18**: 183-206.

CUMMINS W.K. & H.G. LAUFF (1968): The influence of substrate particle size on the microdistribution of stream macrobenthos. — Hydrobiol. **34**: 145-181.

DE LA ROSA C. (1995): Middle American streams and rivers. Pp. 189-218. — In: CUSHING C.E., CUMMINS K.W. & G.W. MINSHALL (eds), Ecosystems of the world 22 – River and stream ecosystems. Elsevier Science B.V.

DUDGEON D. (1991): An experimental study of abiotic disturbance effects on community structure and function in a tropical stream. — Arch. Hydrobiol. **122** (4) 403-420.

DUDGEON D. & Y.K.K. WU (1999): Leaf litter in a tropical stream: food or substrate for macroinvertebrates? — Arch. Hydrobiol. **146**: 65-82.

FENOGLIO S., BO T.& M. CUCCO (2004): Small scale macroinvertebrate distribution in a riffle of a neotropical rainforest stream (Rio Bartola, Nicaragua). — Caribbean Journal of Science **40**: 253-257.

FISHER S.G. & G.E. LIKENS (1973): Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. — Ecol. Monogr. **43**: 421-439.

FÜREDER L. (1994): Drift patterns in Costa Rica streams. — Ph.D. Thesis, Leopold-Franzens-University Innsbruck, Austria.

GILLER P.S. & H. TWOMEY (1993): Benthic macroinvertebrate community organisation in two contrasting rivers – between-site differences and seasonal patterns. Biology and Environment. — Proceedings of the Royal Irish Academy **93B**: 115-126.

GONÇALVES J.J.F., FRANÇA J.S. & M. CALLISTO (2006): Dynamics of allochthonous organic matter in a tropical Brazilian headstream. — **49**: 967-973.

GRAÇA M.A.S., BÄRLOCHER F. & M.O. GESSNER (2005): Methods to study litter decomposition – A practical guide. — Springer.

HAINES B. & R.B. FOSTER (1977) in DE LA ROSA C. (1995): Middle American streams and rivers. Pp. 189-218. — In: CUSHING C.E., CUMMINS K.W. & G.W. MINSHALL (eds), Ecosystems of the world 22 – River and stream ecosystems. Elsevier Science B.V.

HARTSHORN G.S. (1983) in DE LA ROSA C. (1995): Middle American streams and rivers. — In: CUSHING C.E., CUMMINS K.W. & G.W. MINSHALL (ed.), Ecosystems of the world 22 – River and stream ecosystems. Elsevier Science B.V.: 189-218.

IRONS J.G., OSWOOD M.W., STOUT R.J. & C.M. PRINGLE (1994): Latitudinal patterns in leaf litter breakdown: is temperature really important? — Freshwater Biology **32**: 401-411.

JACKSON K.J. & W.B. SWEENEY (1995): Egg and larval development times for 35 species of tropical stream insects from Costa Rica. — J. N. Am. Benthol. Society **14**: 115-130.

JANZEN D.H. (1974): Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. — Biotropica **6**: 69-103.

KAUSHIK N.K. & H.B.N. HYNES (1971): The fate of the dead leaves that fall into streams. — Arch Hydrobiol. **68**: 465-515.

MATHOOKO J.M. & C.O. OTIENO (2002): Does surface textural complexity of woody debris in lotic ecosystems influence their colonization by aquatic invertebrates? — Hydrobiol. **489**: 11-20.

MERRITT R.W. & K.W. CUMMINS (1996): An introduction to the aquatic insects of North America. — Third Edition, Kendall/Hunt Publishing Company.

PICHLER C. & F. SCHIEMER (2008): Ecology of fishes of Quebrada Negra, Costa Rica, a first order neotropical lowland stream. — In this volume.

PETERSEN R.C. & K.W. CUMMINS (1974): Leaf processing in a woodland stream. — Freshwater Biol. **4**: 343-368.

PRINGLE C.M. & A. RAMIREZ (1998): Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. — Freshwater Biology **39**: 359-373.

PRINGLE C.M., ROSEMOND A.D. & A. RAMIREZ (1998): Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. — Freshwater Biology **39**: 515-523.

RAMIREZ A. & C.M. PRINGLE (1998): Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica. — Hydrobiol. **386**: 19-26.

RAMIREZ A. & C.M. PRINGLE (2001): Spatial and temporal patterns of invertebrate drift in streams draining a neotropical landscape. — Freshwat. Biol. **46**: 47-62.

RIEMERTH A., GUSENLEITNER M., DRAXLER G., WANEK W.& F. SCHIEMER (2008): The role of leaf anatomy and tannins in litter decay in a tropical stream. — In this volume.

ROSEMOND A.D., PRINGLE C.M. & A. RAMIREZ (1998): Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. — Freshwat. Biol. **39**: 515-523.

ROSEMOND A.D., PRINGLE C.M., RAMIREZ A., PAUL J.M. & J.L. MEYER (2002): Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. — Limnol. Oceanogr. **47** (1): 278-289.

SCHIEMER F. & M. ZALEWSKI (1992): The importance of riparian ecotones for diversity and productivity of riverine fish communities. — Netherlands Journal of Zoology **42**: 323-335.

STOUT J. (1980): Leaf decomposition rates in Costa Rican lowland tropical rainforest streams. — Biotropica **12(4)**: 264-272.

TSCHELAUT J., PICHLER C., WEISSENHOFER A. & F. SCHIEMER (2008): The river network of the Piedras Blancas National Park, Costa Rica. — In this volume.

VANNOTE R.L., MINSHALL G.W., CUMMINS K.W., SEDELL J.R. & C.E. CUSHING (1980): The River Continuum Concept. — Can. J. Fish. Aquat. Sci. **37**: 130-137.

WEBSTER J.R., BENFIELD E.F., EHRMAN T.P., SCHAEFFER M.A., TANK J.L., HUTCHENS J.J. & D.J.D'ANGELO (1999): What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. — Freshwater Biology **41**: 687-705.

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Plate 1: (**a**) *Cecropia obtusifolia* (Cecropiaceae); (**b**) *Sloanea medusula* (Elaeocarpacea); (**c**) *Acalypha diversifolia* (Euphorbiacae); (**d**) *Tetrathylacium macrophyllum* (Flacourtiacae).

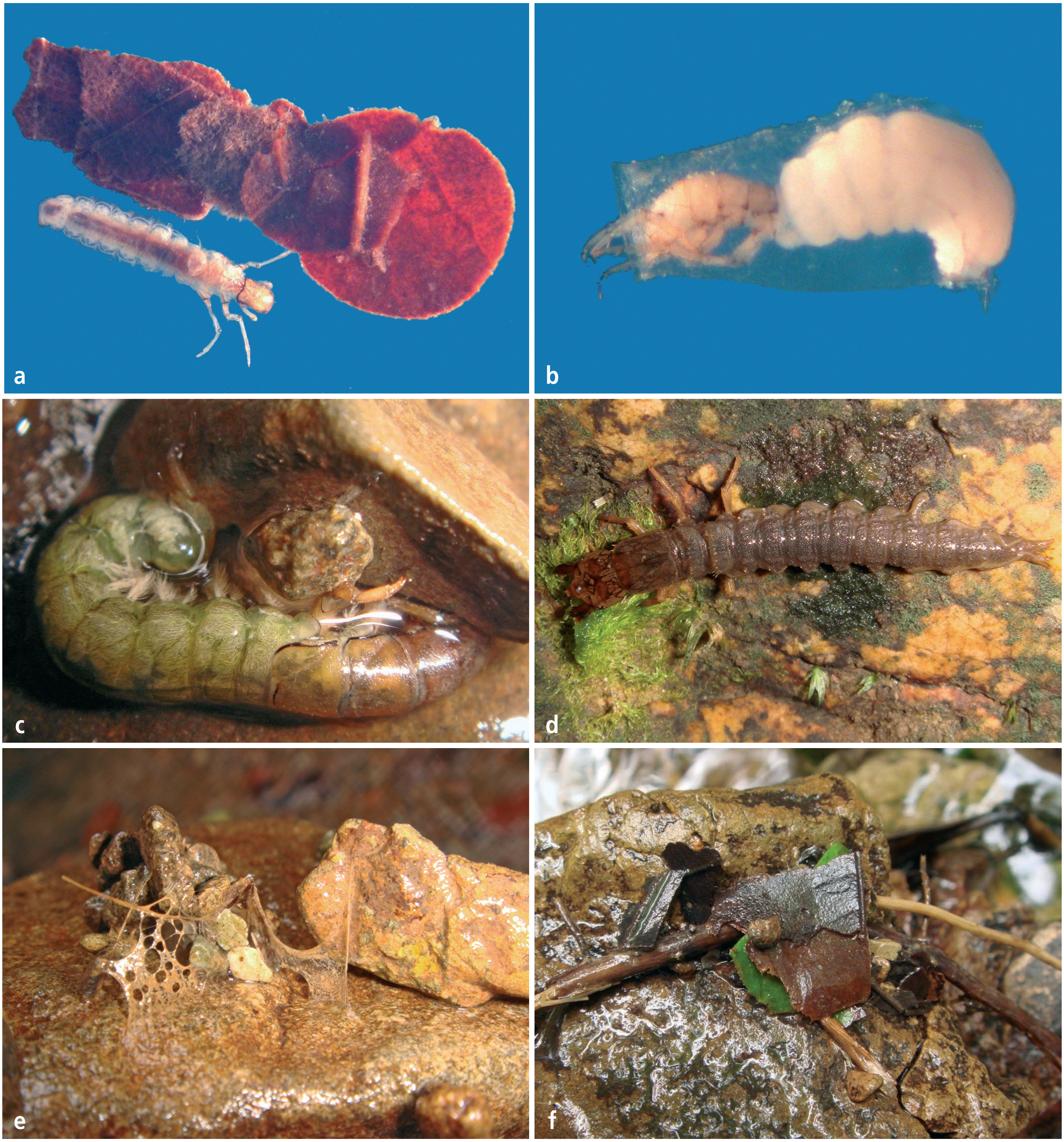

Plate 2: (**a**) Trichoptera – Calamoceratidae with larval case; (**b**) Trichoptera – Hydroptilidae with portable case; (**c**) Trichoptera – Hydropsychidae; (**d**) Megaloptera – Corydalidae; (**e**) Trichoptera net; (**f**) Trichoptera retreat.