Fundam. Appl. Limnol. Vol. 184/2 (2014), 109–124
Stuttgart, April 2014

Article

Colonisation of leaf litter by lotic macroinvertebrates in a headwater stream of the Phachi River (western Thailand)

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With 5 figures, 4 tables and 1 appendix

Abstract: Leaf litter decomposition has been widely studied during the last 60 years. However, the relative importance of various processes, such as physical abrasion, microbial activity and macroinvertebrates consumption, remains unclear in tropical streams. The aim of this study was to gain insights into the ecological processes leading to the decomposition of leaf litter in headwater streams of Thailand, with a particular focus on the role played by macroinvertebrates. The breakdown rate of two leaf species, *Bambusa bambos* and *Lagerstroemia floribunda*, was investigated in a 1st order tropical stream of Ratchaburi province (western Thailand) using litter bags submerged over an 8-week period. Litter bags were retrieved after 2, 14, 28, 42 and 56 days of immersion and characterised by two metrics, remaining AFDM and faunal composition of macroinvertebrates. Most rapidly decomposed leaves were those of *B. bambos* placed in riffles and most slowly decomposed were those of *L. floribunda* placed in pools ($k = 0.030$ and $0.006\ d^{-1}$, respectively). The highest amount of invertebrates per leaf bag were found after 14 days of immersion for *B. bambos* (174 individuals, SE = 10.0, n = 4) and after 28 days of immersion for *L. floribunda* (174 individuals, SE = 15.8, n = 5). Faunal composition of invertebrates differed between pools and riffles but not within leaf species. The low influence of shredders (accounting for maximum 5 % of total invertebrate abundance in leaf bags) is in accordance with previous findings in tropical zones, while there is a new thought that physical abrasion may play an important role in leaf decay. Nevertheless, non-shredder invertebrates may indirectly contribute to the decomposition of leaf material. In both pools and riffles, macroinvertebrate communities varied with time, showing a diminution of stream habitability, correlated with progressive water withdrawal.

Key words: leaf breakdown, tropical streams, macroinvertebrates, ecosystem functioning, headwater streams.

Introduction

Researching the fate of allochthonous organic matter in streams has been an important topic of investigation for aquatic ecologists over the last 60 years (Tank et al. 2010). Noteworthy are many studies focused on organic matter inputs in streams (Webster & Meyer 1997, Abelho 2001, Allan & Castillo 2007, Wantzen et al. 2008) and decomposition mechanisms of leaf litter (Cummins 1974, Webster & Benfield 1986, Abelho 2001, Tank et al. 2010). It is now widely understood that terrestrial inputs are critical to fuelling stream food webs, especially in headwater streams where riparian vegetation reduces autotrophic production by shading and produces large amount of organic detritus (Vannote et al. 1980, Allan & Castillo 2007, Wantzen et al. 2008). Decomposition of leaf litter is generally considered as the result of successive or simultane-

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DOI: 10.1127/1863-9135/2014/0596
www.schweizerbart.de
1863-9135/14/0596 $ 4.00

ous processes including leaching of soluble contents, physical abrasion and fragmentation due to transport and retention, colonisation and degradation by microorganisms (also called conditioning), and consumption by invertebrates or fish (Webster & Benfield 1986, Allan & Castillo 2007).

Nevertheless, the processes leading to the inclusion of leaf litter into trophic chains remain insufficiently known in tropical streams. Various studies revealed a scarcity or even a lack of shredder invertebrates and assume that leaf decomposition may be essentially dependent on physical fragmentation and microbial activity (reviewed by Wantzen et al. 2008). Some authors suggested that this scarcity could be due to leaf properties of tropical forests, showing low palatability for macroinvertebrates due to high contents of tannins and secondary compounds (Boyero et al. 2009, Boyero et al. 2011). However, high diversity of shredder invertebrates has been found in Malaysia, which is the closest region to Thailand for which data are available (Yule et al. 2009, Che Salmah et al. 2013). In other tropical regions, some authors highlighted possible replacement of insect shredders present in temperate zones by bigger shredders such as crabs or shrimps, which may process large quantities of organic material despite a low number of individuals (March et al. 2001, Dobson et al. 2002, Abdallah et al. 2004).

The objective of this study was to gain insights into the various pathways used by detrital material to integrate in trophic chains, and to acquire data concerning decomposition rates of different leaf species in Thailand. Breakdown rates and macroinvertebrate colonisation of two leaf species differing in quality (toughness) were measured after different times of immersion and locations (pools and riffles) within a low order stream. The two species, *Bambusa bambos* (Poaceae) and *Lagerstroemia floribunda* (Lythraceae), were chosen because of their abundance in vertical leaf fall and differences in expected decomposition rate. Leaves of the perennial plant *B. bambos* were expected to decompose rapidly due to low toughness and high surface/weight ratio, favouring gas and nutrient exchanges with the water column. Moreover, *B. bambos* produces a sweet siliceous substance that may be attractive for macroinvertebrates (Kaikini Aakruti et al. 2013). Leaves of the deciduous tree *L. floribunda* are thick, tough and probably contain high levels of tannins and secondary compounds, similar to the close species *L. speciosa* studied in Philippines (Laruan et al. 2013), making them resistant to decomposition. On the other hand, previous studies showed that leaves placed in riffles were decomposed faster than those placed in pools (Webster & Benfield 1986, Benfield et al. 2000).

Methods

Study site

The study was conducted in a 1st order tributary of the Phachi river, situated in Ratchaburi province in western Thailand, ~150 km west of Bangkok (altitude: 230 m, latitude 13° 28.6′ N, longitude 99° 14.5′ E), between February and March 2013. The selected site was located approximately 20 km down from the source and was not impacted by human activity. The stream was characterised by a high slope (25 % on the 210 m of the study site) and an alternation of riffles, pools and waterfalls up to 10 m high. The stream bed was mostly composed of boulders, cobbles, sand and leaf litter. Additional suitable habitat for invertebrates was afforded by many trees whereby their roots were directly immersed in the water, and a few macrophytes located in shallow calm waters downstream of the falls. The riparian vegetation, largely shading the stream bed, consisted of a secondary forest dominated by *Bambusa* sp., *Dillenia* sp., *Caryota* sp. and *Lagerstroemia* sp.

Litter bags were divided in five different stations along the 210 m of the study site. Each station was considered as a replicate and consisted in an alternation of riffle, pool and waterfall. Only two habitats were evaluated, pools and riffles (a total of 10 micro-habitats), because waterfalls were not considered to be habitats where leaves are retained and decomposed. At the beginning of the experiment, width, depth and current velocity were taken for every micro-habitat where litter bags were placed. Conductivity, pH, dissolved oxygen concentration and water temperature were measured on each sampling date within every micro-habitat. Concentrations of PO_4-P were determined within 24 h after sample collection, using standard ascorbic acid method provided by Hach Company (1992). The concentration of NO_3-N was measured once in the middle of the study by Research and Development Institute of Kasetsart University, using cadmium reduction method. Both analyses were based on 3 samples of water randomly taken along the stream portion and stored on ice.

During the experiment (hot season), air temperature ranged from 23.5 to 36.5 °C during the day. Only one notable day of precipitation was recorded, 29 days after the beginning of the experiment, corresponding to 60 mm of rainfall (according to Thai Meteorological Department at Ratchaburi Station; http://www.tmd.go.th). Discharge of the stream was near 50 L s^{-1} at the beginning of the experiment and almost reached its lowest (about 10 L s^{-1}) by the end of March.

Experimental design

Freshly fallen leaves were collected in November 2012, dried for 48 h at 60 °C and stored in sealed plastic bags until needed. Litter bags consisted of 5.0 ± 0.1 g of leaves enclosed in nylon bags (15 cm × 25 cm) made of 9 mm mesh screen to allow access to the largest shredder invertebrates, which were the hollow twig cased caddisfly *Ganonema* (Calamoceratidae) and decapods (35–50 leaves for *B. bambos* and 6–10 leaves for *L. floribunda*).

A total of 100 litter bags were introduced into the stream on 31 January 2013, consisting in equal proportion of either leaf species. The experiment encompassed 4 treatments, including two leaf species and two locations. Litter bags were randomly distributed within each pool and riffle, in groups of five on 1.5 m lines. Lines were placed following natural accumulations of leaves in pools, and parallel to the flow in riffles. They were anchored to the stream bed with stones attached to both extremities. Moreover, cobbles were placed over the lines to maintain all bags in contact with the stream bottom and ensure natural invertebrate colonisation.

The experiment lasted 56 days, corresponding to 1441 degree-days. One litter bag was randomly retrieved within each micro-habitat and for each leaf species after 2, 14, 28, 42 and 56 days of immersion (a total of 20 litter bags for each sampling date). Before being removed from the water, litter bags were placed in a 500 µm mesh size kick net to minimise loss of invertebrates. Harvested bags were placed into individual plastic bags with water from the stream and stored on ice until processing in the laboratory. On every collecting date, two samples of natural accumulations of leaves randomly distributed along the study site were taken with a 500 µm mesh size kick net for each habitat (a total of 20 samples of natural leaf litter accumulations, 10 in pools and 10 in riffles). These samples were considered as representing an average community structure in natural accumulations of leaves.

Samples processing

Litter bags were processed within 12 h after retrieving. Sediment and invertebrates were rinsed with tap water over a 250 µm mesh size sieve and preserved in 90 % ethanol for further determination. Remaining leaf material was dried for 48 h at 60 °C (long enough to reach a stable dry mass) and weighed to the nearest 0.01 g. Two sub-samples of 300–400 mg of every litter bag were combusted for 2 h at 550 °C in a furnace to estimate ash-free dry mass (AFDM). At the initial time of the experiment, four sub-samples of each leaf species were combusted similarly to obtain initial AFDM. Samples of natural leaf litter accumulations were processed similarly to allow the analysis of invertebrate communities per constant dry mass of leaf litter. AFDM of natural accumulations of leaves ranged from 8 to 17 g.

Invertebrates were sorted using an appropriate binocular microscope and identified with available taxonomic keys (Morse et al. 1994, Yule & Hoi Sen 2004, Sangpradub & Boonsoong 2006). Most insect taxa were identified to family level, except Ephemeroptera, Plecoptera and Trichoptera taxa (EPT) that were identified to genus level, and Chironomidae, that were identified to sub-family level. Non-insect taxa were identified to family (molluscs and crustaceans), order (water mites) or class level (worms). Taxa were assigned to functional feeding groups (FFG) according to Morse et al. (1994) and Dudgeon (1999).

Statistical analyses

Data of chemical and physical parameters of the stream were compared using two-way analysis of variance (ANOVA) for groups meeting required assumptions (normal distribution and equal variances) and Kruskal-Wallis non parametric test for other groups.

Loss of AFDM through time was fitted to an exponential decay model

$$M_t = M_i e^{-kt}$$

where M_t is the remaining AFDM at time t, M_i the initial AFDM and k the breakdown rate constant in days or degree days (Webster & Benfield 1986). Breakdown rates were estimated by linear regression on natural log-transformed data and slopes were compared using two-way analysis of covariance (ANCOVA; Crawley 2007). The linearizations were accomplished despite the recommendations of Bärlocher (2005), in order to obtain homogeneity of variances that gradually increased with sampling date. Loss of AFDM after 48 h of immersion was compared using two-way ANOVA, considering leaf species and location as grouping factors.

Abundance and taxa richness of macroinvertebrates were compared using three-way ANOVA, considering leaf species, location and time of immersion as grouping factors. A first analysis included only litter bags data and a second one compared litter bags and natural accumulations of leaves. To be compared with litter bags, data corresponding to natural leaf accumulations were expressed for 5.0 g of litter dry mass. The ANOVA was performed on treatments with non null value only, to fit with required assumptions. Data were square root +1 transformed for the comparison of shredder abundances and unmodified for the comparison of all invertebrates abundances and diversity. For all univariate analysis, differences between treatments were detected using Tukey's honest significant difference (HSD) *post hoc* comparisons, with alpha error level of 0.05.

Invertebrate assemblage changes in response to litter bags treatments were visualised by performing principal component analysis (PCA) on abundance data matrices. It required an initial transformation of data, which was performed by the Hellinger method (Legendre & Gallagher 2001). A Bray-Curtis distance matrix, using presence/absence data of taxa, was analysed by metric dimensional scaling (MDS) to be compared with results shown by PCA.

All statistical analyses were performed using R software version 2.15.1 (R Development Core Team, 2012).

Results

Physical and chemical characteristics of the stream

Parameters of pools and riffles of the stream were significantly different only for physical characteristics (Table 1). However, both chemical and physical parameters varied among time in correlation with the progressive water withdrawal, implying increase of temperature, conductivity and total dissolved solids, and decrease of oxygen concentration, current velocity and area of submerged substrate. pH also slightly varied through time but without showing any particular pattern.

Decomposition rates

A total of 12 litter bags were vandalised during the experiment. Due to their complete disappearance, 5 of them were removed from all analysis, while 7 were kept only for decomposition rates calculation. Evi-

Table 1. Physical and chemical characteristics of pools and riffles of the stream. Range and mean are based on all data collected during the experiment.

Parameter	Pool		Riffle		p
	Mean	Range	Mean	Range	
Water temperature (°C)	25.3	22.5–30.6	25.2	22.5–28.3	d
pH	6.9	6.2–7.4	6.9	6.1–7.8	d
Conductivity ($\mu S\ cm^{-1}$)	74	37–182	74	37–208	d
Dissolved oxygen ($mg\ L^{-1}$)	5.0	2.5–6.1	5.2	2.4–6.8	d
Dissolved oxygen (%)	60.9	31.9–76.5	62.3	30.8–78.5	d
Total dissolved solids ($mg\ L^{-1}$)	50	25–114	50	25–129	d
Current velocity ($m\ s^{-1}$)	< 0.05		0.32	0.10–0.50	–
Width (m)	2.6	1.0–3.5	1.1	0.3–2.0	d, l
Depth (m)	0.36	0.20–0.60	0.10	0.05–0.20	d, l
$N\text{-}NO_3^-$ ($mg\ L^{-1}$)	0.29 (0.28–0.29)				–
$P\text{-}PO_4^{3-}$ ($mg\ L^{-1}$)	0.26 (0.14–0.45)				–
Number of leaf bags recollected	48		47		
Number of natural accumulations recollected	10		10		

p indicates the significance of differences between groups of measures (ANOVA with sampling date and location as factors or Kruskal-Wallis test)
(–) not tested; (d) p-value (sampling date) < 0.05; (l) p-value (location) < 0.05

Table 2. Breakdown rate coefficient k (day^{-1}/degree day^{-1}, mean ± SE) of leaves exposed to the four experimental treatments as revealed by linear regression on natural log transformed data.

Location	Species	k per day				k per degree day			
		k (day^{-1})	R^2	T_{50}	T_{90}	k (degree day^{-1})	R^2	T_{50}	T_{90}
Riffle	*B. bambos*	0.030 ± 0.0026^{a}	0.86	23	76	0.0012 ± 0.00010^{a}	0.86	576	1912
	L. floribunda	0.019 ± 0.0009^{b}	0.95	37	123	0.0007 ± 0.00003^{b}	0.95	931	3093
Pool	*B. bambos*	0.012 ± 0.0007^{bc}	0.92	59	195	0.0005 ± 0.00003^{bc}	0.92	1489	4946
	L. floribunda	0.006 ± 0.0002^{c}	0.96	113	376	0.0002 ± 0.00001^{c}	0.96	2862	9507

Different letters indicate significant differences between treatments (ANCOVA plus HSD *post hoc* comparisons, $\alpha = 0.05$).
T indicates theoretical time (day^{-1}/degree day^{-1}) to decompose the corresponding percentage of AFDM.

dences were found that these 5 samples were moved a short time before retrieving and it was assumed that AFDM was not significantly modified by the perturbation. However, at least 3 replicates were available for every experimental treatment on the last sampling date. AFDM represented 74 % of dry mass for *B. bambos* and 92 % for *L. floribunda*. Leaves of *B. bambos* showed a significantly higher decomposition rate than leaves of *L. floribunda* (ANCOVA, $F_{2,91} = 13.9$, $p < 0.001$) and decomposition rates were significantly higher in riffles compared to pools (ANCOVA, $F_{1,91} = 42.3$, $p < 0.001$; Table 2). Leaching during the first 48 h was significantly different among leaf species (ANOVA, $F_{1,17} = 72.8$, $p < 0.001$), but was not influenced by location in the stream (ANOVA, $F_{1,17} = 0.7$, $p = 0.41$). It represented a mean of 10.9 % of initial AFDM for *B. bambos* and 2.8 % for *L. floribunda* (Fig. 1). For a more concrete representation of differences, theoretical time to decompose completely leaves of *L. floribunda* in pools was greater than 1 year, while leaves of *B. bambos* placed in riffles would be decomposed in less than 3 months.

Abundance and diversity of macroinvertebrates

A total of 9975 individuals were collected during the experiment, belonging to 75 taxa (complete list in Appendix). Macroinvertebrates were counted in 88 samples, 33 of litter bags placed in pools, 35 of litter bags placed in riffles and 20 of natural accumulations of leaves. In litter bags recollected after two days of immersion, invertebrates were not counted because of their scarcity and insufficient time to allow a complete colonisation. EPT taxa represented 44 % of total abundance, with 30 taxa identified. Other insect taxa accounted for 47 % of total abundance (including 38 %

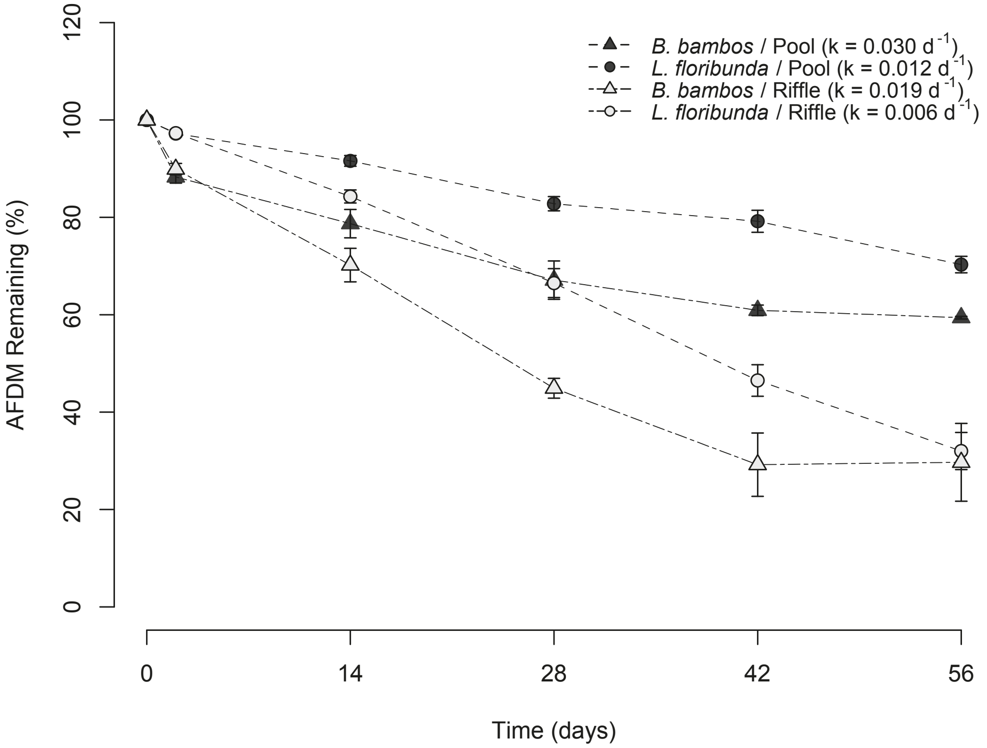

Fig. 1. Mass remaining (% AFDM, mean ± SE) of leaves exposed to the four experimental treatments among time in Phachi's tributary.

of Chironomidae) and belonged to 33 families. Remaining abundance corresponded to non insect taxa. Only 3 taxa were exclusively found in pools, accounting for 0.1 % of total abundance, while 19 were found only in riffles, representing 4.9 % of total abundance.

On average, the highest abundance of invertebrates was found in riffles, after 14 days of immersion for *B. bambos* leaves (174 individuals per litter bag; Fig. 2A) and after 28 days of immersion for *L. floribunda* (174 individuals per litter bag; Fig. 2A). Litter bags placed in riffles showed a significantly higher abundance of invertebrates than those placed in pools (ANOVA, $F_{1,62} = 30.9$, $p < 0.001$), but leaf species and time of immersion did not influence the amount of individuals found in litter bags (ANOVA, respectively $F_{1,62} = 1.0$, $p = 0.33$ and $F_{3,62} = 1.2$, $p = 0.32$). Natural leaf accumulations significantly supported a lower number of individuals in both riffles and pools (ANOVA, respectively $F_{1,43} = 27.4$, $p < 0.001$ and $F_{1,41} = 7.7$, $p = 0.01$). The richness of taxa showed a similar trend as abundance, with the highest value found in riffles after 28 days of immersion (respectively a mean of 19.4 and 20 taxa per leaf bag for *B. bambos* and *L. floribunda*; Fig. 2B). Litter bags placed in riffles presented significantly higher richness of invertebrate taxa than those placed in pools (ANOVA, $F_{1,62} = 61.7$, $p < 0.001$) and leaf species did not influence the amount of taxa in litter bags (ANOVA, $F_{1,62} = 0.0$, $p = 0.86$). However, unlike results of abundance, time of immersion significantly affected the number of taxa found in litter bags, with lower values at the beginning and at the end of the experiment (ANOVA, $F_{3,62} = 6.1$, $p = 0.01$, plus HSD *post hoc* comparisons). Natural leaf accumulations showed a lower diversity of macroinvertebrates in riffles but no significant difference in pools (ANOVA, respectively $F_{1,43} = 12.1$, $p = 0.01$ and $F_{1,41} = 2.24$, $p = 0.14$).

The assignment of macroinvertebrates to FFG revealed the presence of only 4 shredder taxa, the plecopteran *Cryptoperla* (Peltoperlidae), the dipteran Tipulidae and the two trichopterans *Ganonema* and *Lepidostoma* (Calamoceratidae and Lepidostomatidae). Their abundance in litter bags showed a similar trend as total abundance, with a maximum reached in riffles after 28 days of immersion for *B. bambos* and after 14 days for *L. floribunda* (representing 4.4 % of total abundance in litter bags for both treatments; see Fig. 3). Litter bags placed in riffles showed a significantly higher abundance of shredders than those placed in pools (ANOVA, $F_{1,43} = 9.5$, $p < 0.01$). Time

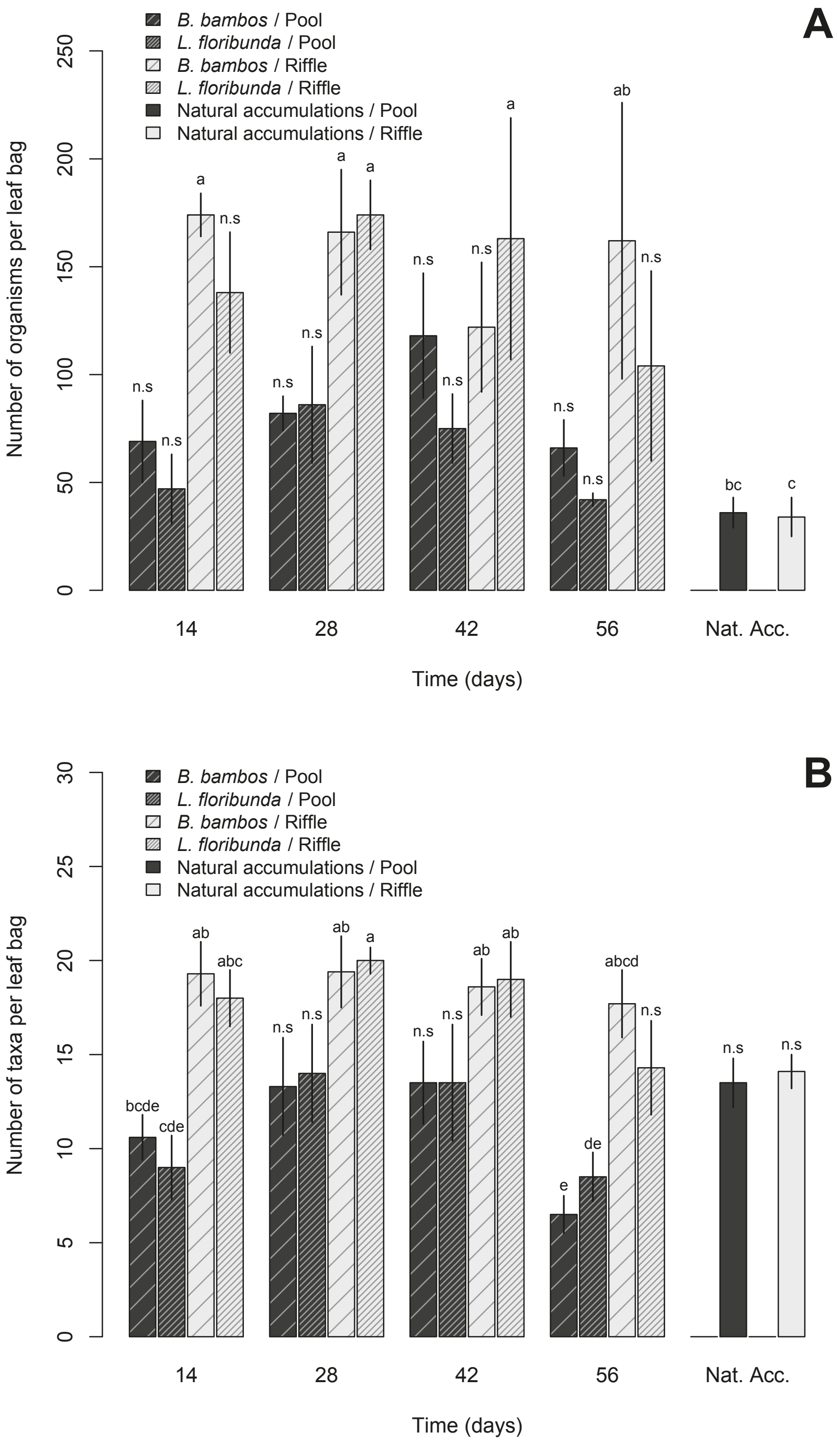

Fig. 2. **(A)** Abundance and **(B)** richness of macroinvertebrates in leaf bags exposed to the four experimental treatments (mean ± SE). Different letters indicate significant differences between treatments (ANOVA plus HSD *post hoc* comparisons, $\alpha = 0.05$). Groups not differing from any other are indicated by letters n.s.

of immersion influenced amount of shredders found in litter bags (ANOVA, $F_{3,43} = 4.0$, $p < 0.05$) but not leaf species (ANOVA, $F_{1,43} = 1.0$, $p = 0.32$). However, no significant differences were highlighted between any of the treatments with non null value (ANOVA plus HSD *post hoc* comparisons, $\alpha = 0.05$). Within all samples collected during the experiment, collector taxa represented 75.2 % of total abundance of invertebrates, predator taxa accounted for 13.8 %, scraper taxa for 7.7 %, shredder taxa for 2.1 % and finally, piercer taxa represented 1.2 % of total abundance of invertebrates.

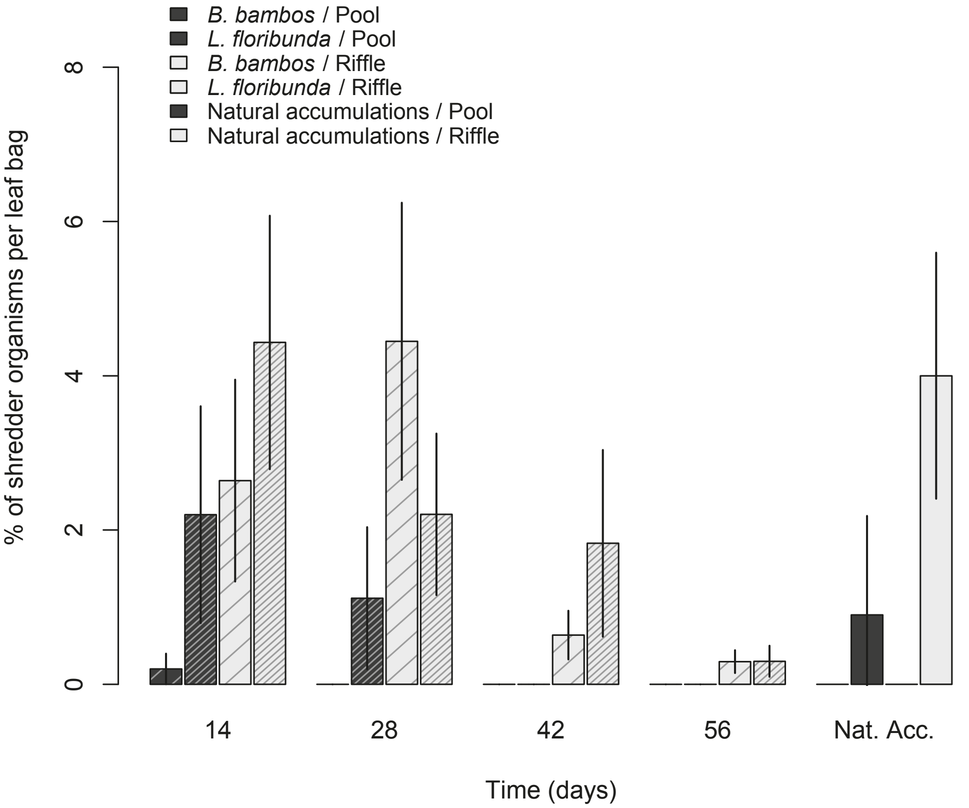

Fig. 3. Proportion of shredder macroinvertebrates in leaf bags exposed to the four experimental treatments (% of abundance, mean ± SE). No significant differences were found between treatments with non null value (ANOVA plus HSD post hoc comparisons, $\alpha = 0.05$).

Community structure of macroinvertebrates

The first axis of PCA separated two groups of samples based on their location in the stream (Fig. 4A). Variability conserved by first two axes accounted for 38 % of total. Best represented taxa on the first axis of the PCA were Orthocladiinae (Diptera) and *Etrocorema* (Perlidae), both negatively correlated with the axis, while *Caenis cornigera* (Caenidae) and Oligochaeta were the best represented taxa on the second axis (Table 3). The MDS on Bray-Curtis distance matrix confirmed the distinction of groups revealed by PCA, with a similar dispersion within samples collected in pools and those collected in riffles (Fig. 4B). However, none of the analysis highlighted a clear separation between leaf species and with natural accumulations of leaves.

In order to identify changes in community structure through time, samples collected in pools and in riffles were further analysed separately. Moreover, taxa found in less than 30 % of leaf bags were removed to reduce interferences induced by rarely occurring taxa. In pools, a total of 13 taxa were conserved to seek for changes in community structure (Table 4). These taxa occurred in a minimum of 9 leaf bags among the 33 considered and accounted for 90.2 % of total abundance of macroinvertebrates collected in pools. The dominant taxon was *Caenis cornigera* (Caenidae), except on day 56 where oligochaetans were more abundant. A higher number of taxa were conserved in riffles, with 24 taxa occurring in a minimum of 10 leaf bags among the 35 considered, representing 93.5 % of the total abundance of macroinvertebrates collected in riffles (Table 4). The dominant taxon was Chironominae (Chironomidae), except on day 56 where *Caenis cornigera* (Caenidae) were more abundant. A total of 9 taxa were common to both habitats in the stream. The PCAs were performed on communities occurring in litter bags only. Communities found in natural accumulations of leaves were removed to prevent their influence in the definition of axis and maximize the differences between litter bag treatments. However, natural accumulations samples were posteriorly positioned, being considered as supplementary rows (Fig. 5A & 5B).

Variability conserved by the first two axis of PCA performed on pool selected data accounted for 60 % of the total. Best represented taxa on the first axis of

Table 3. Percentage of variability conserved by taxa on the first two axis of the different PCAs.

Taxon		All data		Pool selected data		Riffle selected data	
		1st axis	2nd axis	1st axis	2nd axis	1st axis	2nd axis
% of total variability		22	16	43	17	29	15
O. Plecoptera							
	g. Cryptoperla	–	–	–	–	54 (–)	–
	g. Etrocorema	56 (–)	–	–	–	64 (–)	–
	g. Phanoperla	–	–	–	–	48 (–)	–
O. Ephemeroptera							
	g. Nigrobaetis	–	–	44 (–)	–	–	51 (–)
	Caenis cornigera	–	54 (+)	82 (–)	–	62 (+)	–
	g. Teloganopsis	–	–	–	–	52 (–)	–
	Teloganodes tristis	–	–	–	–	52 (–)	–
O. Diptera							
	sf. Chironominae	–	–	–	85 (+)	–	–
	sf. Orthocladinae	54 (–)	–	–	–	42 (–)	–
	sf. Tanypodinae	–	–	–	–	48 (+)	–
Cl. Oligochaeta		–	60 (–)	87 (+)	–	–	44 (+)

(+/–) indicates positive/negative correlation with the axis
Only taxa with more than 40 % of variability conserved on any of the first two axes are indicated.

the PCA were *Caenis cornigera* (Caenidae) and Oligochaeta, respectively negatively and positively correlated with the axis (Table 3). The PCA performed on riffle selected data conserved 44 % of total variability on the first two axes. Best represented taxa on the first axis of the PCA were *Caenis cornigera* (Caenidae), the plecopterans *Etrocorema* (Perlidae), *Cryptoperla* (Peltoperlidae) and *Phanoperla* (Perlidae), and the ephemeropterans *Teloganopsis* (Ephemerellidae) and *Teloganodes tristis* (Teloganodidae). The first of them was positively correlated with the axis and all others negatively correlated (Table 3).

Discussion

Decomposition of leaf litter

Breakdown rate coefficients measured in this experiment were lower than those previously reported by Parnrong et al. (2002), which constitute the only available data for Thailand. Their experiment was conducted in riffles of three 2nd order streams of southern Thailand with similar temperatures as the one in our study. According to reported references at plant family level (Webster & Benfield 1986), decomposition rates of all 6 leaf species considered in their experiment were expected to be relatively similar to those found in the present study. The authors obtained decay coefficients ranging from 0.024 to 0.075 day^{-1} (0.019 to 0.030 day^{-1} in riffles of the present study) and concluded that only leaf species influenced processing rates, not streams, seasons (wet/dry) or sites (forested/agricultural). The main parameter which appeared to be different between both studies was water velocity, ranging from 0.43 to 0.85 m s^{-1} (depending on season), in the experiment of Parnrong et al. (2002), and always less than 0.50 m s^{-1} in our study. Although Parnrong et al. (2002) did not highlight significant influence of season on leaf decay (influencing water velocity), they found an interaction effect between stream and season, suggesting that there may be a contrasting response to seasonal change within streams.

Our study supports the hypothesis that water velocity is an important factor affecting leaf decay coefficient in tropical headwater streams, as it has already been shown by artificial reduction of stream flow in Hong Kong (Niu & Dudgeon 2011). Our results are similar to other studies comparing pools and riffles in temperate streams, always revealing higher breakdown rate in riffles (Webster & Benfield 1986, Benfield et al. 2000). As shown by comparison of AFDM loss after 2 days of immersion, leaching is not influenced by location in the stream. However, the relative importance due to the changing of current velocity on the three other main processes contributing to leaf de-

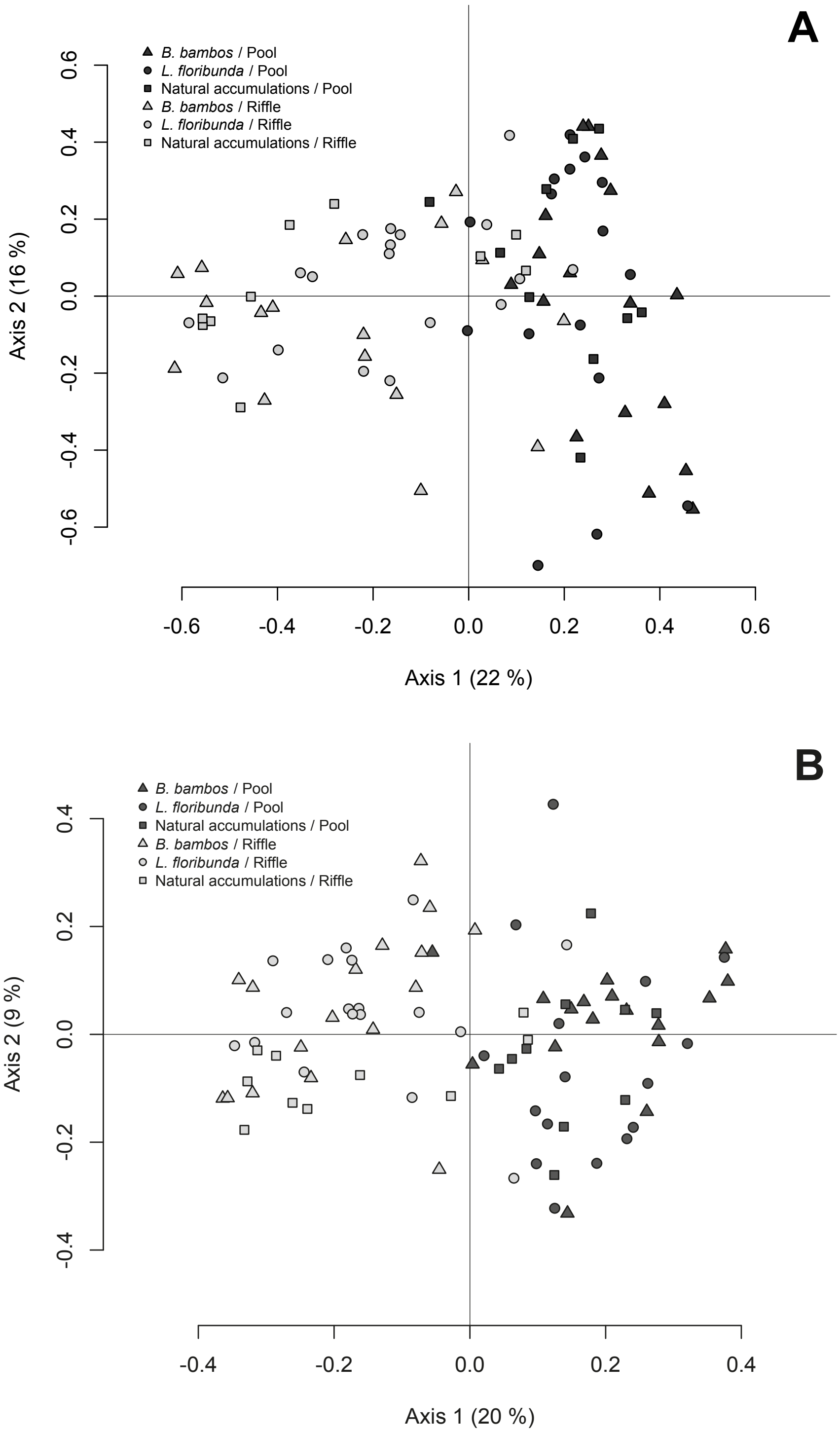

Fig. 4. Biplot of sample coordinates on the first two axis of PCA with **(A)** Hellinger transformed data and **(B)** MDS with Bray-Curtis distance matrix, including all 88 samples for those a faunal list was established.

cay, namely physical abrasion and fragmentation, microbial conditioning and direct consumption, remains unclear. In temperate stream pools, absence of physical abrasion, lower gas and nutrients exchange rates and lower shredder invertebrates are assumed to be responsible for lower decomposition rates (Webster & Benfield 1986). The low abundance of shredder invertebrates in both pools and riffles of the present study suggests that they play a minor role in the decomposition of leaf material. Given that leaves remained entire

Table 4. Mean abundance and percentage of total (in parenthesis) of most frequently occurring taxa of macroinvertebrates in leaf bags exposed to the four experimental treatments.

Taxon		**Pool**					**Riffle**				
	FFG	**Day 14**	**Day 28**	**Day 42**	**Day 56**	**Nat. Acc.**	**Day 14**	**Day 28**	**Day 42**	**Day 56**	**Nat. Acc.**
O. Plecoptera											
g. Cryptoperla	Shr	–	–	–	–	–	1.0 (1)	5.2 (3)	0.2 (0)	0.0 (0)	0.3 (1)
g. Etrocorema	Pre	–	–	–	–	–	3.3 (2)	5.6 (3)	0.3 (0)	0.7 (1)	1.3 (4)
g. Phanoperla	Pre	–	–	–	–	–	3.3 (2)	6.6 (4)	0.9 (1)	1.6 (1)	0.1 (0)
O. Ephemeroptera											
g. Baetis	Col	–	–	–	–	–	3.2 (2)	0.2 (0)	0.7 (0)	0.0 (0)	0.1 (0)
g. Cloeon	Col	0.1 (0)	1.9 (2)	3.3 (3)	2.5 (5)	1.4 (4)	–	–	–	–	–
g. Nigrobaetis	Col	3.6 (6)	1.6 (2)	1.9 (2)	0.1 (0)	1.1 (3)	18.2 (12)	9.5 (6)	6.3 (5)	1.3 (1)	2.1 (6)
Caenis cornigera	Col	**28.7 (48)**	**28.8 (34)**	**28.5 (30)**	3.6 (7)	**12.1 (34)**	19.8 (13)	11.7 (7)	20.7 (15)	**29.0 (23)**	4.4 (13)
g. Teloganopsis	Col	–	–	–	–	–	6.2 (4)	9.6 (6)	1.2 (1)	0.1 (0)	0.0 (0)
g. Dipterophlebiodes	Scr	1.0 (2)	1.3 (1)	0.6 (1)	0.1 (0)	0.5 (1)	11.4 (7)	3.2 (2)	13.4 (10)	3.7 (3)	0.5 (1)
Isca janiceae	Col	–	–	–	–	–	7.1 (5)	2.3 (1)	8.4 (6)	0.1 (0)	0.5 (1)
Thraulus demoulin	Col	1.1 (2)	3.0 (4)	7.3 (8)	8.3 (15)	1.9 (5)	–	–	–	–	–
Teloganodes tristis	Col	–	–	–	–	–	2.3 (2)	7.1 (4)	2.3 (2)	0.3 (0)	0.2 (1)
O. Trichoptera											
g. Cheumatopsyche	Col	–	–	–	–	–	3.6 (2)	1.8 (1)	0.3 (0)	0.1 (0)	0.2 (1)
g. Hydroptila	Pi	–	–	–	–	–	0.1 (0)	3.4 (2)	0.3 (0)	0.4 (0)	0.0 (0)
g. Lepidostoma	Shr	–	–	–	–	–	2.7 (2)	0.8 (0)	1.7 (1)	0.0 (0)	0.2 (0)
O. Coleoptera											
f. Elmidae	Scr	0.9 (2)	1.3 (1)	1.8 (2)	2.4 (4)	1.0 (3)	2.8 (2)	2.0 (1)	6.8 (5)	4.6 (4)	0.8 (2)
f. Dryopidae	Col	–	–	–	–	–	0.9 (1)	2.9 (2)	0.6 (0)	0.4 (0)	0.2 (1)
f. Hydrophilidae	Pre	–	–	–	–	–	2.3 (2)	4.0 (2)	2.3 (2)	1.0 (1)	0.7 (2)
f. Scirtidae	Col	–	–	–	–	–	1.8 (1)	0.9 (1)	4.6 (3)	1.3 (1)	0.0 (0)
O. Diptera											
f. Ceratopogonidae	Pre	0.2 (0)	0.6 (1)	0.5 (1)	0.1 (0)	0.3 (1)	0.2 (0)	0.5 (0)	1.3 (1)	2.1 (2)	0.2 (1)
sf. Chironominae	Col	13.3 (23)	19.1 (23)	25.8 (27)	11.5 (21)	7.0 (19)	**32.7 (21)**	**46.4 (27)**	**35.8 (25)**	24.0 (19)	**11.8 (35)**
sf. Orthocladinae	Col	1.1 (2)	5.3 (6)	3.8 (4)	0.1 (0)	0.6 (2)	10.3 (7)	25.2 (15)	4.4 (3)	1.9 (1)	2.5 (7)
sf. Tanypodinae	Pre	2.2 (4)	2.3 (3)	4.0 (4)	1.4 (3)	0.5 (1)	13.1 (9)	10.9 (6)	10.4 (7)	21.1 (16)	1.3 (4)
O. Odonata											
f. Gomphidae	Pre	–	–	–	–	–	0.4 (0)	0.2 (0)	1.8 (1)	1.4 (1)	0.1 (0)
O. Decapoda											
f. Atyidae	Col	2.4 (4)	2.1 (3)	0.8 (1)	0.3 (0)	0.2 (1)	–	–	–	–	–
O. Hydracarina	Pre	0.3 (1)	0.9 (1)	0.6 (1)	0.1 (0)	0.0 (0)	–	–	–	–	–
Cl. Turbellaria	Pre	–	–	–	–	–	0.0 (0)	0.5 (0)	2.8 (2)	5.7 (4)	0.0 (0)
Cl. Oligochaeta	Col	0.6 (1)	3.0 (4)	10.9 (11)	**22.0 (41)**	2.6 (7)	1.0 (1)	1.8 (1)	6.4 (5)	16.4 (13)	0.2 (1)
Sum		55.6 (94)	71.0 (85)	89.5 (93)	52.5 (97)	29.2 (81)	147.9 (96)	162.3 (95)	134.1 (96)	117.4 (91)	27.5 (82)

Col = collectors; Pre = predators; Scr = scrapers; Shr = shredders; Pi = piercers
Values in bold indicates the most abundant taxa

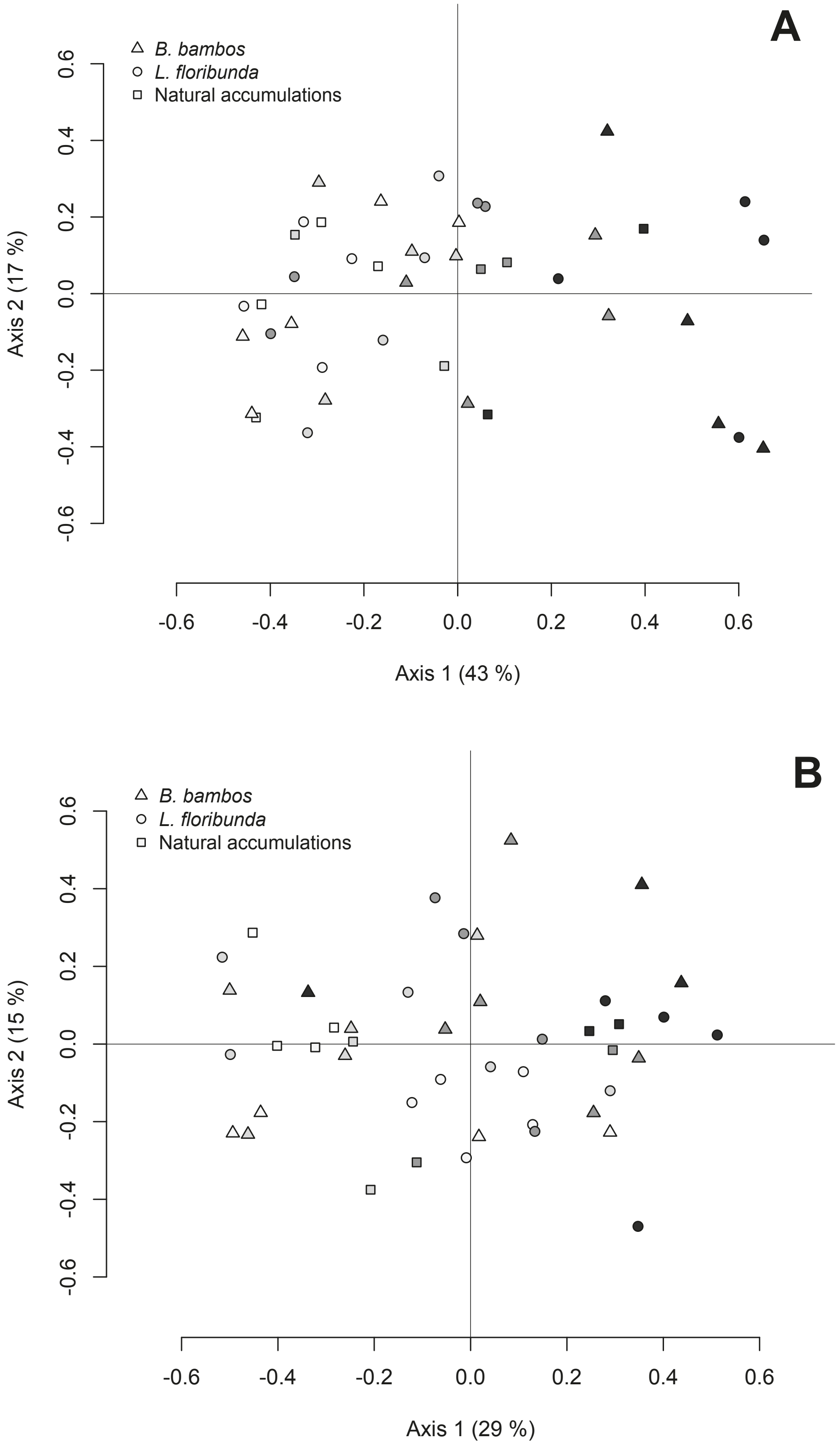

Fig. 5. Biplot of sample coordinates on the first two axis of PCA with **(A)** 33 faunal lists of pool selected data and **(B)** 35 faunal lists of riffle selected data. Intensity in grey scale indicates increasing evolution of sampling date

in leaf bags during most of the breakdown process, physical fragmentation of leaf material may account for a small proportion of leaf mass loss. However, abrasion due to collisions with mineral particles transported by the current may be important since headwater streams are erosion zones providing mineral material downstream (Allan & Castillo 2007). A highly aerated structure was provided by the wavy shape and great size of *L. floribunda* leaves. This structure suggested maximal exchange possibilities of gas and nutrients with the water column, even in pools, with the presence of very low current. Although we did not measure microbial activity during the experiment, there is no reason to think that microbial activity could have been favoured in riffles due to higher current velocity, at least for *L. floribunda* leaves.

The exponential decay model was used to provide breakdown coefficients that can be compared with other studies. However, data of the present study appeared to fit better to a linear decay model ($R^2 > 0.91$ for all treatments; data not provided). This correlation implies that leaf decomposition may not depend on the amount of organic material remaining, as assumed by the employment of exponential decay model, but on the initial mass of organic material. Biologically, it suggests that leaves are decomposed according to their exchange surface with the water column, which remains relatively stable during most of the decomposition process. Nevertheless, even if the proportion of leaves retained in both locations of the stream was not measured, it appeared to be much higher in pools, where leaf decay is slower. As shown by leaves of *L. floribunda*, the completion of the decomposition process in pools may need more than one year. Thus, it is highly probable that most of the leaf material is not decomposed in the headwater stream but exported downstream during flooding periods, as suggested by Wantzen et al. (2008), and that much litter breakdown is a result of physical fragmentation.

Macroinvertebrates associated with leaf litter

Previous studies have shown that shredder invertebrates have a significant role in leaf litter decomposition in temperate streams, and could even constitute the main component influencing the decomposition rate of leaves (Sponseller & Benfield 2001, Hieber & Gessner 2002), while contrasted results were found in tropical streams (March et al. 2001, Dobson et al. 2002, Abdallah et al. 2004, Wantzen et al. 2008, Yule et al. 2009, Che Salmah et al. 2013).

The amount of shredder invertebrates never exceeded 5 % of total abundance in the present study. Some taxa that were not reported as primarily shredders, such as Chironomidae and Oligochaeta, may act as miners and contribute to the decomposition of leaves (Chauvet et al. 1993, Wantzen & Wagner 2006). However, abundance of these taxa was about 10 times greater in previous studies than in the present experiment. In a study conducted in Puerto Rico, March et al. (2001) highlighted faster decomposition rates of leaf litter in sites where shrimps of families Atyidae and Xiphocaridae were present. However, their activity was reduced when shrimps of family Palaemonidae were also present. Given that families Atyidae and Palaemonidae occurred in headwater streams of the Phachi River, along with crabs of the family Potamidae that may have comparable life traits as Palaemonidae, a similar interaction process may be suspected. As reported by Rosemond et al. (1998) in Costa Rica, omnivorous fish may cause loss of weight from leaf bags, although the cause (feeding or/and physical disruption) was not determined. Moreover, scrapers taxa could possibly act indirectly on leaf decay by their consumption of biofilm. The reduction of its thickness may increase gas and nutrient exchanges with hyphomycetes in contact with leaf material and increase their activity. Nonetheless, despite the fact that obligate shredders seemed to play a minor role in the decomposition of leaf material in Phachi headwater stream, a large bulk of invertebrates (and possibly fish or even amphibians) may contribute in several ways to leaf decay.

As previously reported in temperate streams (Logan & Brooker 1983, Kobayashi & Kagaya 2002), diversity and abundance of macroinvertebrates were lower in pools compared to riffles. Differences in community structure highlighted by PCA were essentially due to higher abundance of two taxa in riffles, *Etrocorema* (Plecoptera) and Orthocladiinae (Diptera). However, taxa of orders Plecoptera, Trichoptera and Coleoptera also occurred more frequently in riffles, while only a few ephemeropterans and non-insect taxa were more common in pools. Considering only the presence of taxa, without taking into account their abundance, the MDS confirmed different patterns in pools compared to riffles. Kobayashi & Kagaya (2002) suggested two reasons to explain differences in community structure of invertebrates between pools and riffles. First, higher current velocity may enable invertebrates that do not possess adaptive morphology to penetrate and attach to patches of leaf litter in riffles, such as cased caddisfly shredders or shrimps. Second, taxa that have high oxygen requirements may not find suitable conditions in pools. Only a few cased caddisfly shredders were found in the present study, as well as taxa that were not considered to be adapted to high current velocity, such as shrimps or some dipterans. This low abundance of pool-specific taxa may be linked with the hydrology of the stream, characterised by a high slope and high flooding periods that flush away invertebrates along with patches of leaf litter, leading to the "reset" of the system, as described by Wantzen et al. (2008). Due to their aerial respiration, coleopterans taxa are not concerned by low oxygen levels. Nevertheless, they occurred more frequently in riffles compared to pools, which may be due to lower water depth and higher stream margins proximity, allowing them to reach more easily oxygen supplies.

A progressive modification of invertebrate community structure in leaf bags was identified by PCA in both pools and riffles. In pools, the progression was essentially an increased abundance through time of Oligochaeta and decreased abundance of *Caenis cornigera* (Caenidae). In riffles, it was essentially due to increasing abundance of *Caenis cornigera* (Caenidae) and a decreasing of Plecoptera, *Teloganopsis* (Ephemerellidae) and *Teloganodes tristis* (Teloganodidae) through time. However, analysis of natural accumulations of leaves revealed the same trend as leaf bags in both pools and riffles. It suggests that this progression may be related to a global modification of community structure within the stream instead of a leaf decay advancement effect. Decreasing abundance of plecopterans and ephemeropterans and an increase in tolerant taxa such as Oligochaeta are correlated with diminution of water quality in Thai streams (Boonsoong et al. 2009). Given that the progressive water withdrawal caused by dry season leads to an increase of water temperature and a decrease of dissolved oxygen content, a diminution of streams habitability for invertebrates is to be expected. Mean water temperature increased from 22.7 °C at the beginning of the present experiment to 28.5 °C at the end and dissolved oxygen content fell from 5.5 to 3.3 mg L^{-1}, which may confer extreme conditions for many invertebrates taxa, especially plecopterans and ephemeropterans, that are known to be more adapted to temperate streams (Merritt et al. 2008, Wantzen et al. 2008).

Acknowledgments

The project was funded by the research fund for DPST graduate with first placement from the Institute for the Promotion of Teaching Science and Technology (IPST 033/2555). We are most grateful to our colleagues for assistance during field trips. We would like to thank Assoc. Prof. Dr. Narumon Sangpradub for project advice and Department of Zoology for facilities and assistance. We would especially like to thank Dr. Michael T. Barbour for critically reading the manuscript.

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Submitted: 26 November 2013; accepted: 09 April 2014.

Appendix 1. Complete list and relative abundance of taxa collected during the experiment.

Taxon		Natural accumulations		Litter bags	
	FFG	Pool	Riffle	Pool	Riffle
O. Plecoptera					
f. Peltoperlidae					
g. *Cryptoperla*	Shr	–	X	*	X
f. Perlidae					
g. *Etrocorema*	Pre	–	X	*	X
g. *Phanoperla*	Pre	–	x	x	X
O. Ephemeroptera					
f. Baetidae					
g. *Baetis*	Col	–	x	x	x
g. *Cloeon*	Col	X	x	X	–
g. *Nigrobaetis*	Col	X	X	X	X
f. Caenis					
Caenis cornigera	Col	X	X	X	X
f. Ephemerellidae					
g. *Teloganopsis*	Col	*	–	x	X
f. Ephemeridae					
g. *Ephemera*	Col	*	–	–	–
f. Polymitarcyidae					
g. *Polyplocia*	Col	–	–	*	–
f. Heptageniidae					
g. *Thalerosphyrus*	Scr	x	X	*	x
f. Leptophlebiidae					
g. *Choroterpes*	Col	x	*	x	–
g. *Dipterophlebiodes*	Scr	X	X	X	X
Isca janiceae	Col	–	X	*	X
Thraulus demoulin	Col	X	–	X	x
f. Teloganodidae					
Teloganodes tristis	Col	x	x	x	X
O. Trichoptera					
f. Calamoceratidae					
g. *Ganonema*	Shr	x	X	x	x
f. Ecnomidae					
g. *Ecnomus*	Col	*	–	x	x
f. Helicopsychidae					
g. *Helicopsyche*	Scr	–	–	–	x
f. Hydropsychidae					
g. *Cheumatopsyche*	Col	–	x	*	X
f. Hydroptilidae					
g. *Hydroptila*	Pi	x	–	x	x
g. *Orthotrichia*	Pi	–	–	–	x
g. *Oxyethira*	Pi	–	–	–	x
f. Leptoceridae					
g. *Leptocerus*	Col	–	–	x	x
g. *Oecetis*	Col	x	*	x	x
g. *Setodes*	Col	x	*	x	x
f. Lepidostomatidae					
g. *Lepidostoma*	Shr	*	x	x	x
f. Odontoceridae					
g. *Marilia*	Col	–	–	*	*
f. Psychomyidae					
g. *Psychomyia*	Col	x	–	x	x
O. Heteroptera					
f. Corixidae	Pi	X	x	*	*
f. Hebridae	Pre	–	–	–	x
f. Helotrephidae	Pre	–	–	–	x
f. Naucoridae	Pre	–	–	–	x
f. Pleidae	Pre	–	–	*	x
f. Veliidae	Pre	–	x	–	x

Appendix 1. Continued.

Taxon		Natural accumulations		Litter bags	
	FFG	Pool	Riffle	Pool	Riffle
O. Coleoptera					
f. Carabidae	Pre	–	–	–	*
f. Dryopidae	Col	–	x	x	x
f. Dytiscidae	Pre	–	–	–	x
f. Elmidae	Scr	X	X	X	X
f. Hydraenidae	Scr	–	–	–	x
f. Hydrophilidae	Pre	x	X	–	X
f. Psephenidae	Scr	x	–	–	x
f. Scirtidae	Col	–	*	–	X
f. Torridincolidae	Scr	–	–	x	x
O. Megaloptera					
f. Corydalidae	Pre	–	–	–	x
O. Diptera					
f. Athericidae	Pre	*	–	x	x
f. Ceratopogonidae	Pre	x	x	x	x
f. Culicidae	Col	–	*	x	–
f. Chironomidae					
sf. Chironominae	Col	X	X	X	X
sf. Orthocladinae	Col	X	X	X	X
sf. Tanypodinae	Pre	X	X	X	X
f. Dixidae	Col	–	*	–	–
f. Psychodidae	Col	–	–	–	x
f. Phoridae	Col	x	x	*	x
f. Simuliidae	Col	–	X	–	x
f. Tipulidae	Shr	*	*	–	x
O. Odonata					
f. Calopterygidae	Pre	x	–	x	x
f. Corduliidae	Pre	x	–	x	x
f. Euphaeidae	Pre	–	–	–	x
f. Gomphidae	Pre	x	x	x	x
f. Libellulidae	Pre	*	*	x	x
f. Protoneuridae	Pre	–	–	x	x
O. Decapoda					
f. Atyidae	Col	x	x	X	*
f. Palaemonidae	Col	X	x	x	x
f. Potamidae	Col	–	x	–	*
Cl. Bivalva					
f. Sphaeriidae	Col	x	–	*	–
Cl. Gastropoda					
f. Ancylidae	Scr	–	*	X	x
f. Thiaridae	Scr	x	–	*	*
f. Valvatidae	Scr	x	X	x	x
O. Hydracarina	Pre	*	*	x	x
Cl. Hirudinea	Pre	–	–	–	*
Cl. Turbellaria	Pre	–	–	x	X
Cl. Oligochaeta	Col	X	x	X	X
Ph. Nematoda	Pre	*	*	–	x

Col = collectors; Pre = predators; Scr = scrapers; Shr = shredders; Pi = piercers
(X) indicates common taxa, (x) rare taxa (abundance < 1 %), (*) anecdotic taxa (only one individual found) and (–) absent taxa