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Impact of a set of environmental variables on the leaf litter breakdown rate in natural streams of the equatorial forest in Cameroon

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Abstract – This study assessed the environmental factors underlying the leaf litter decomposition rate in streams in the equatorial rainforest of Cameroon. To reach this goal we used the litterbag method and dead leaves of *Funtumia africana* (Benth) Stapf (Apocynaceae)in seven natural streams. Concomitantly, we measured biological (fungi and macroinvertebrates) and environmental parameters to highlight those that control the leaf litter breakdown rates. The breakdown rates ranged from 0.035 to 0.056 with an average of 0.042 ± 0.006 in the coarse-mesh litterbags (K_c) and from 0.018 to 0.059 with an average of 0.037 ± 0.01 in the fine-mesh litterbags (K_f). No significant difference was observed between seasons or sites, except for K_f. As in other tropical rainforests in South America and Asia, the breakdown rates are mainly resulted from microbial activity; the contribution of shredders was negligible, as confirmed by the K_c to K_f ratio and the litter fragmentation rate λ_F. Among environmental factors, only the distance from the source and the pH were positively correlated with the leaf litter breakdown rates.

Keywords: litter decomposition / macroinvertebrates / hyphomycetes / environmental factors / tropical streams / Central Africa

1 Introduction

Aquatic ecosystems are influenced by the landscape (Vannote *et al.*, 1980; Allan *et al.*, 2021a, 2021b) because they receive substantial inputs from surrounding lands (Fausch *et al.*, 2002; Townsend *et al.*, 2003). These inputs constitute a transfer of mineral and organic matter (Masese *et al.*, 2018). In forested ecosystems, the supply of mainly dead plant matter is quite significant. The decomposition of these organic matters is an important ecosystem process in the aquatic food web (Wallace and Webster, 1996; Covich *et al.*, 2004). They provide nutrients for aquatic plants and organic matter for aquatic organisms, mainly aquatic hyphomycetes and detritivorous invertebrates (Petersen and Cummins, 1974; Gessner *et al.*, 1999).

In temperate climate, many studies on the process of litter breakdown in streams have shown a strong contribution of detritivorous invertebrates to the litter breakdown process in streams (Gessner *et al.*, 1999; Gulis *et al.*, 2006; Piscart *et al.*, 2009, 2011; Chauvet *et al.*, 2016). This is particularly true in streams harbouring amphipods, which can be considered and a key species of leaf litter breakdown in temperate streams (Piscart *et al.*, 2017). However, many environmental factors mediate the breakdown rates, and this process is very sensitive to changes in environmental conditions (Dangles *et al.*, 2004; Boyero *et al.*, 2016; Follstad Shah *et al.*, 2017). Among physico-chemical factors, inorganic nutrients dissolved in water play a major role in litter breakdown (Jabiol *et al.*, 2019; Abelho and Descals, 2024) and limit its colonization by microorganisms (Madeiros *et al.*, 2015). The hydraulic conditions, the streambed roughness and other local heterogeneities also influence the breakdown rates of leaf litter (Omoniyi *et al.*, 2021), while the water temperature promotes decomposition, especially through microbial activity (Ferreira *et al.*, 2012; Boyero *et al.*, 2021). Among biological factors, the quality of litter (Foucreau *et al.*, 2013a, 2013b) and the diversity of shredder organisms also influence the breakdown process (Schindler, 2006; Schindler and Gessner, 2009; Gessner, 2010; Santonja *et al.*, 2018, 2020). This is why there has been growing interest in the use of leaf litter breakdown in recent years to assess the functional integrity of stream ecosystems (Gessner and Chauvet, 2002; Casas *et al.*, 2011; Chauvet *et al.*, 2016; Ferreira *et al.*, 2021; Omoniyi *et al.*, 2021).

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In tropical – especially rainforest – streams, plant production is greater within a much higher temperature range than in temperate zones (Wantzen *et al.*, 2008; Bruder *et al.*, 2014; Boyero *et al.*, 2015a). The climate, anthropogenic activities and the hydrological regime are very different (Bernhard-Reversat, 1982; McMahon *et al.*, 1992; Tiegs *et al.*, 2024). In South America (mainly Brazil, Panama), South Asia (China, Malaysia, Indonesia, India) and Oceania (Australia, Papua New Guinea), biological communities in streams differ from those of temperate zones (Benstead, 1996; Yule, 1996; Boyero *et al.*, 2009; Yule *et al.*, 2009). For example, shredders are scarce in tropical streams (Dobson *et al.*, 2002), whereas they are the main players of breakdown in European streams (Boyero *et al.*, 2006; Wantzen and Wagner, 2006; Boulton *et al.*, 2008; Bruder *et al.*, 2014).

In Sub-Saharan Africa, few studies on the process of leaf litter breakdown in streams have been led, mainly in Kenya (Mathooko *et al.*, 2000a, 2000b; Dobson *et al.*, 2004; Masese *et al.*, 2014a; Kadeka *et al.*, 2021), in Guinea Conakry (Tenkiano and Chauvet, 2017) and in Uganda (Fugère *et al.*, 2020). Among these studies, only the work of Fugère *et al.* (2020) was focused on equatorial rainforest and on only four sites, and the experimental design did not take microbial and/or macroinvertebrate communities and physico-chemical parameters into account. As a consequence, the role played by environmental factors in tropical rainforest in Africa remains almost unknown.

To address this question and identify the driving factors of the leaf litter breakdown in African streams, we selected 13 sites in the natural rainforest of South Cameroon. The main goals of this study were (1) to highlight the biological (macroinvertebrate and fungi assemblages) and physico-chemical determinants of leaf litter breakdown in equatorial streams in Cameroon, and (2) to discuss those factors to other factors found in temperate and other tropical streams in other regions.

2 Materials and methods

2.1 Study site

The study area was located in the equatorial rainforest of Cameroon, between 3°20'–3°37' N and 11°26'–11°34' E (Fig. 1). The climate is Guinean equatorial, with four seasons that are unequal and whose duration varies across years. They alternate as follows: a long dry season from December to April, a short rainy season from May to mid-July, a short dry season from mid-July to September, and a long rainy season from September to November. Rainfall varies from 1500 to 2000 mm, and the hydrographic network is dense (Ndam Ngoupayou *et al.*, 1998). Average annual air temperature is around 24.6 °C, with an annual average amplitude of 4.19 °C according to satellite data from the Amercian National Oceanic and Atmospheric Administration – Physical Sciences Laboratory (US NOAA, 2022) over the February 2019 to February 2020 period (https://psl.noaa.gov/data/timeseries/). In the study sites, soils can be one of three types: ferralitic soils located at the top of interfluves and at the bottom of slopes, hydromorphic soils in marshy valleys, or poorly evolved soils located on steep mountainous reliefs (Olivry, 1986). The vegetation is similar between sites, consisting of the dense secondary evergreen rainforest at medium and high altitudes, and a dense semi-deciduous rainforest at high altitude (Temgoua, 2007).

Thirteen sites located in seven forest streams were selected (Fig. 1). The sites varied in their geomorphology in order to represent the different types of stream in the study area. Table 1 shows the altitude, stream order, distance from the source, water depth, water width and main substrate of each sampling sites. Leaf litter exposure was measured in two different areas during the long dry season in six sampling sites at the North town of Mbalmayo town (K1, K2, K3, AN1, AN2, and N) in February/March 2020, and during the short dry season in the other seven sampling sites at South town (A, C, IM, NM, ON, OB, Z) in August 2020. Each sampling site was selected on the basis of the different stream orders and the hydrological variables in order to be representative of the local environmental conditions in headwater streams.

2.2 Environmental factors

The distances from the sampling stations to the source were measured directly with a 1:25,000 map, while the coordinates and the altitude of the sampling stations were taken with a Gamin® 60S geo-positioning system. The weather parameters were measured in the field using a Testo® 610 thermo-hygrometer for the humidity percentage and a Testo® 540 luxmeter for the light intensity between 08:00 am and 10:00 am. The hydrological variables were measured at each experimental site. The width of the water column was measured using a decameter stretched horizontally from one riverside to the other, depth was measured using a graduated stake, and the current velocity was determined by pouring methylene blue (a neutral and non-toxic dye) in the water and measuring the distance covered by the dye in one minute. Physico-chemical parameters (water temperature, dissolved oxygen, pH, and electrical conductivity) were measured using a Combo® Water Quality Meter 86031 multimeter in the field following standard protocols (Rodier *et al.*, 2009; American Public Health Association *et al.*, 2017).

2.3 Preparation of litterbags and leaf litter processing

The litter bags were made up of dead leaves of *Funtumia africana* (Benth) Stapf (Apocynaceae) collected just after abscission. We checked each leaf by naked eyes to remove damaged and parasitised leaves. In the laboratory, the leaves were spread over a large area for rapid drying in the open air for 15 days (Gessner and Chauvet, 2002). After drying, batches of 3 ± 0.01 g of litter were made up and placed in the litterbags. Prior moistening with distilled water was necessary to avoid damaging the leaves during field trips. The 10×10 cm bags were tetrahedron-shaped, and made of a coarse plastic mesh (5 mm mesh size) or a fine nylon mesh (0.5 mm mesh size) (Boulton and Boon, 1991; Cristiano *et al.*, 2019).

The litterbags were prepared the day before they were placed in the field, and stored in hermetically sealed plastic bags to retain humidity. In the field, they were fixed in pairs (one fine-mesh litterbag and one coarse-mesh litterbag) using metal stakes (10–15 mm in diameter and 1–1.5 m in length) using nylon cords (1 mm in diameter) of different lengths to guarantee independence between the litterbags. The metal

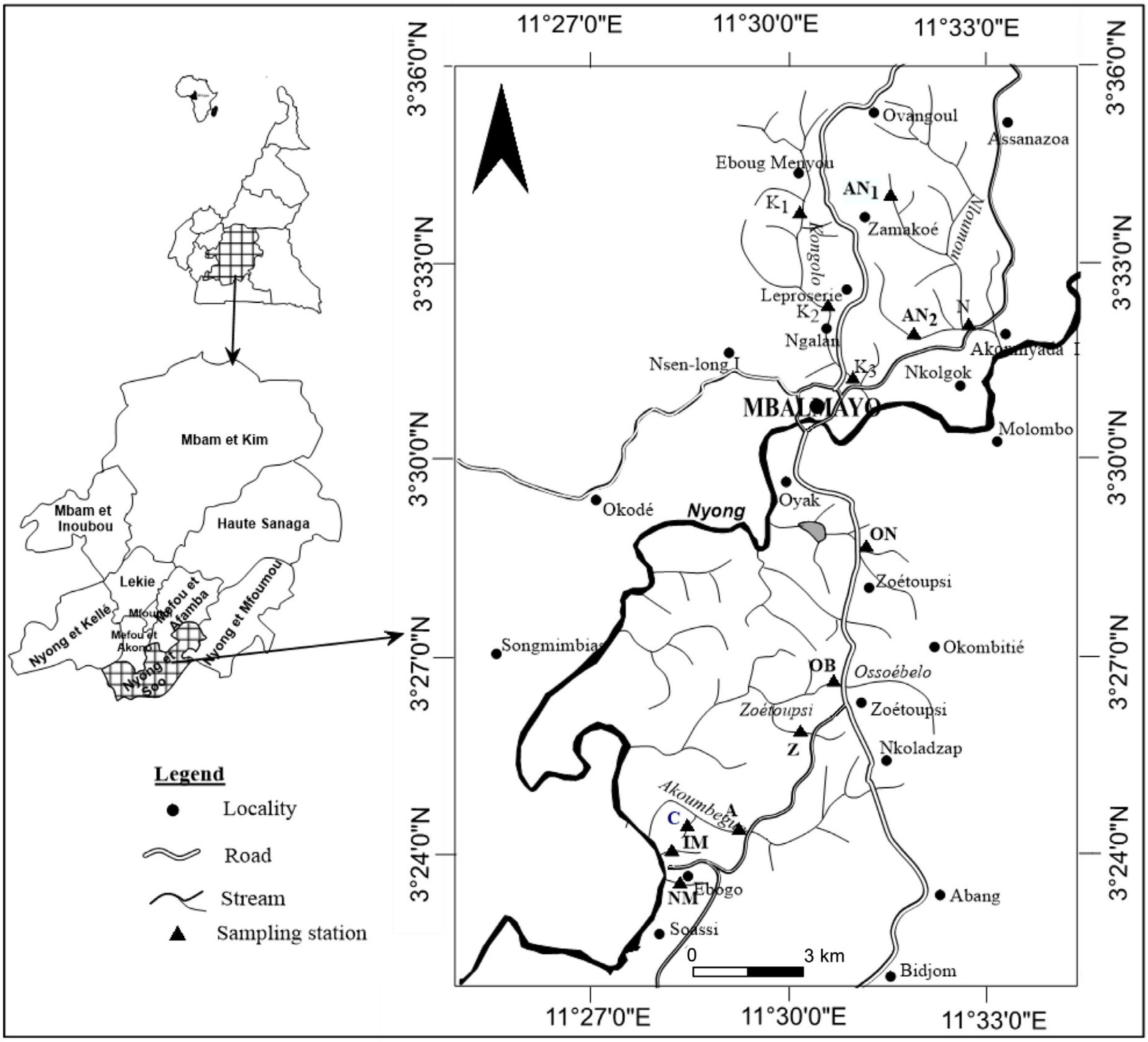

Fig. 1. Map of the study area showing the sampling and experimentation stations.

Table 1. Mean environmental characteristics of the study sites measured during leaf exposure.

Streams	Sites	Altitude (m a.s.l.)	Stream order	Distance from the source (km)	Water depth (m)	Water width (m)	Dominant Substrate
Akoumbegue	C	641	1	0.7	0.24 ± 0.12	2.93 ± 1.11	Mud
	A	643	2	5.86	0.31 ± 0.09	3.04 ± 0.86	Sand
Ibe-Mfeme	IM	644	1	1.3	0.30 ± 0.17	8.01 ± 9.10	Mud
Kongolo	K1	645	3	3.9	0.29 ± 0.06	3.88 ± 0.70	Sand
	K2	638	3	7.35	0.32 ± 0.13	2.95 ± 0.49	Sand
	K3	634	3	9.65	0.68 ± 0.29	7.52 ± 0.43	Mud
Nloumou	AN1	681	1	1.85	0.17 ± 0.05	2.68 ± 0.37	Sand
	AN2	645	1	3.4	0.40 ± 0.09	2.03 ± 0.53	Sand
	N	643	3	8.35	0.24 ± 0.06	3.56 ± 0.46	Sand
Nsoe-Mekok	NM	647	1	0.9	0.14 ± 0.10	2.99 ± 4.01	Rock
Ossoe-Nkoro	ON	645	1	1.5	0.23 ± 0.06	3.47 ± 2.11	Mud
Zoetoupsi	OB	651	1	2.7	0.25 ± 0.08	1.29 ± 0.23	Mud
	Z	653	1	0.9	0.32 ± 0.13	2.23 ± 0.43	Mud

stakes were deeply anchored to the bottom of the moderately flowing streams using a hammer, and the litterbags were stabilised by putting stones on the cord just upstream of the knot. Five pairs *per* sampling station were spaced out by 10 m linear distance from each other. This study took place between on February/March 2020 in the North town and on August 2020 in the South.

The litterbags were removed after 15 days of exposures. The macroinvertebrates that escaped when the coarse-mesh litterbags were collected were recovered using of kick net downstream of the litterbags. The litterbags were packaged individually in zip-lock plastic bags containing a little water from the stream, and stored in a cooler at ambient temperature for laboratory analysis.

The leaves from the exposed litterbags were rinsed one by one under running tap water to remove sediment. Accumulated organic particles and macroinvertebrates were collected in a 0.5 mm mesh sieve under a binocular microscope. The macroinvertebrates taken from the coarse-mesh litterbags were preserved in ethanol 70° and identified. Then, the litter batches were sub-sampled for laboratory culture of hyphomycetes. Sub-samples were taken from five representative leaves of each batch. Each sub-sample consisted of five 10–12 mm diameter discs (one per leaf) taken avoiding the midrib.

After sub-sampling, the remaining litter was oven-dried at 60 °C for 72 h, and weighed at room temperature after cooling in a desiccator to determine the dry mass (Piscart *et al.*, 2011).

2.4 Identification of aquatic hyphomycetes associated with litter

Each batch of 5 freshly cut discs was placed in a 100 mL wide-necked Erlenmeyer flask containing 25 mL of filtered (0.45 μm of porosity) stream water from the litter. The Erlenmeyer flasks were placed at ambient laboratory temperature (20–25 °C) for 48 h under rotary shaking to induce sporulation of the aquatic hyphomycetes that had colonised the discs. The resulting spore suspension was fixed with 2.5 mL of formalin (35%) and stored in a tube containing 35 mL of rinsing water from the Erlenmeyer flask. Ten mL of suspension were filtered through a cellulose membrane (0.45 μm of porosity) that was soaked in a vital dye – cotton blue – and mounted between slide and coverslip for observation under UpEdu® and Bresser® microscopes. Hyphomycetes were identified and counted based on the literature (Nilsson, 1964; Alasoadura, 1968; Iqbal, 1971; Ingold, 1975; Descals and Webster, 1982; Marvanová and Descals, 1985; Chen *et al.*, 2000; Gulis *et al.*, 2005; Braun, 2009).

2.5 Benthic macroinvertebrate sampling

Benthic macroinvertebrates were also collected in the streams before and at the end of the exposure period, with five replicates *per* kick-net sample in each sites following the multihabitat approach (Barbour *et al.*, 1999; Stark *et al.*, 2001). The 30-cm side kick-nets were square-shaped and equipped with a conical net of 500 μm mesh size over a surface area of 0.6 m^2. An equivalent of 3 m^2 was sampled in each sampling station. The organisms retained in the net were sorted and fixed in formalin 10%, and then cleaned and preserved in ethanol 70°.

All the specimens collected with the kick-net and those associated with the leaf litter were identified using a Bresser® Science ETD-101 binocular microscope at the family level using appropriate identification keys (Poisson, 1929; Durand and Levêque, 1980; Dethier, 1981; Testard, 1981; Day *et al.*, 2002; De Moor *et al.*, 2003, 2009; Stals and de Moor, 2007; Lowe, 2009).

2.6 Data analysis

Breakdown rates K_c (coarse-mesh litterbags) and K_f (fine-mesh litterbags) were calculated using the negative exponential decay model (Eq. (1)):

$$k = \frac{[\ln(Wt/Wo)]}{t}, \tag{1}$$

where t is the exposure time (days), W_t the weight at the end of exposure and W_0 the initial weight.

The rate (K) was expressed in g day^{-1} for both coarse mesh bags (K_c) and fine mesh bags (K_f). The K_c to K_f ratio was calculated to show the relative contributions of shredders and microbes. The litter fragmentation rate by shredder (λ_F) was calculated from K_c and K_f according to Lecerf (2017) (Eq. (2)):

$$\lambda_F = K_c - \frac{K_f - K_c}{\ln(K_f) - \ln(K_c)}. \tag{2}$$

We performed a three-way nested ANOVA using the breakdown rates as response variables, with site nested in streams and season as a random factor to test the variability of the breakdown rates among streams and across seasons. Pairwise comparisons were tested using Fisher's LSD test.

The taxonomic richness of hyphomycetes (S_h) and macroinvertebrates (S_m) and the mean abundance (Q) and Shannon-Weaver diversity (H') of macroinvertebrates were also computed for each site. The percentage of each trophic guild was calculated based on the literature (Cummins, 1973; Tachet *et al.*, 2010; Masese *et al.*, 2014b; Ramírez and Gutiérrez-Fonseca, 2014). We also performed a two-way nested ANOVA using biocenotic indices as response variables, with sites nested in streams to test the variability of biocenotic indices among sites and streams, with Fisher's LSD tests for pairwise comparisons.

We compared the sampling methods (litterbags *vs.* kick sampling) by comparing the composition of the macroinvertebrate communities collected by kick sampling with those collected in the litterbags using non-metric multidimensional scaling (NMDS) and two-way nested ANOSIM with habitat (litterbags *vs.* kick-net samples) nested in Stream. These analyses were made with Primer® 6 statistical software.

The links between environmental factors and breakdown rates were studied using a principal component analysis (PCA). Moreover, Pearson correlations between environmental factors and breakdown rates were tested.

3 Results

3.1 Breakdown rates

The breakdown rates were slightly low in stations AN2 and K1, but no statistical difference was observed between sites for

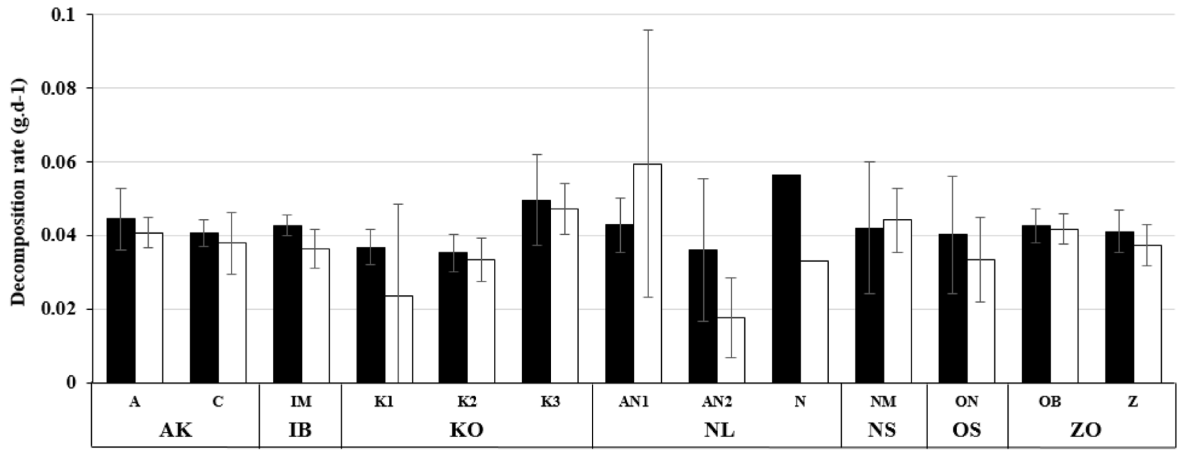

Fig. 2. Mean values (±SD) of total decomposition *Kc* (black bars) and microbial decomposition *Kf* (open bars) in each site for the seven streams (AK: Akoumbegue; IB: Ibe-Mfeme; KO: Kongolo: NL: Nloumou; NS: Nsoe-Mekok; OS: Ossoe-Nkoro; ZO: Zoetoupsi). For N, several bags destroyed and the SD was not computed.

Table 2. Mean values (± SD) of biocenotic indices in each site for aquatic hyphomycetes, macroinvertebrates from litterbags and kick samplings.

Streams	Sites	Hyphomycetes	Macroinvertebrates in Litterbags			Macroinvertebrates in Kick samplings		
		Richness (S_h)	Richness	Diversity	Abundance	Richness	Diversity	Abundance
Akoumbegue	A	6	2.2 ± 1.6	12.4 ± 15.2	0.48 ± 0.48	15.8 ± 1.9	2.6 ± 0.1	144 ± 74
	C	3	1.8 ± 0.4	6 ± 2.9	0.63 ± 0.41	11.3 ± 2.4	2.3 ± 0.2	53 ± 21
Ibe-Mfeme	IM	3	3 ± 1.9	5.6 ± 3	1.22 ± 1.01	12.6 ± 5.1	2.3 ± 0.4	56 ± 26
Kongolo	K1	1	2 ± 1.9	5.6 ± 3.8	0.78 ± 0.74	15.4 ± 2.1	2.5 ± 0.1	109 ± 43
	K2	5	4 ± 1.4	9.8 ± 5.7	1.73 ± 0.53	10.0 ± 4.1	2.1 ± 0.4	48 ± 26
	K3	2	2.2 ± 1.3	3.4 ± 1.3	0.9 ± 0.89	8.4 ± 1.8	2.0 ± 0.2	73 ± 51
Nloumou	AN1	3	5.2 ± 1.5	18 ± 11.2	1.54 ± 0.39	14.2 ± 2.9	2.5 ± 0.2	156 ± 98
	AN2	4	2.6 ± 2.4	6.2 ± 5.9	1.97 ± 0.2	13.8 ± 2.2	2.4 ± 0.1	111 ± 54
	N	5	0.6 ± 1.3	0.6 ± 1.3	1.58 ± 0	11.0 ± 4.1	2.2 ± 0.4	42 ± 20
Nsoe-Mekok	NM	3	1.4 ± 0.5	5.8 ± 2.4	0.37 ± 0.5	14.4 ± 4.4	2.4 ± 0.4	165 ± 57
Ossoe-Nkoro	ON	7	1.4 ± 1.1	5.8 ± 6.6	0.44 ± 0.52	12.0 ± 1.2	2.3 ± 0.1	62 ± 27
Zoetoupsi	OB	9	2.2 ± 1.8	9.4 ± 15.5	0.9 ± 0.06	12.2 ± 4.0	2.3 ± 0.3	40 ± 13
	Z	1	0.8 ± 0.4	1.2 ± 0.8	0 ± 0	8.8 ± 4.5	1.9 ± 0.6	47 ± 31

total breakdown *Kc* (Fig. 2, $F_{6,44} = 1.63$; $P = 0.162$). However, the microbial breakdown rate K_f varied slightly (Fig. 2, $F_{6,44} = 2.28$; $P = 0.053$): it was higher in site AN1 than in most of the other sites (P-values < 0.05), except K3, N, NM, and ON (Tab. 2).

The overall breakdown rates K_f and K_c did not differ (Fig. 2; paired samples *t*-test, $P = 0.506$). The K_c/K_f ratio ranged between 0.72 at AN1 and 2.03 at AN2, but there was no significant difference between sites, whether between the K_c/K_f ratios ($F_{6,43} = 0.73$; $P = 0.63$) or the litter fragmentation rates by shredders λF ($F_{6,44} = 1.64$; $P = 0.158$).

Similarly, the overall breakdown rates were similar between seasons, except for λF ($F_{1,44} = 4.32$; $P = 0.043$). The rate was higher in K3 than in all other sites (P-values < 0.045) except AN2 and N.

The specific richness of hyphomycetes associated with the litter varied sharply between sites from one species (stations Z and C) to nine species (station ON) (Tabs. 2 and S1). Similarly, the mean values of all biocenotic indices for benthic macroinvertebrates (Tab. 2) significantly differed between sites (P-values < 0.027) but not between streams (P-values $>$ 0.09). The macroinvertebrate community was dominated by shredders (mainly Atyidae) and predators in most of the sites (Tab. 3), except K3, ON, OB, and Z where the proportion of shredders was relatively low. In these sites, shredders were replaced by collectors (K3, ON and Z), except for OB.

3.2 Comparison of the benthic macroinvertebrates from kick sampling and litterbags

The results on the NMDS analysis (Fig. 3) showed a strong dissimilarity between the macroinvertebrate communities collected by kick sampling and those collected in the litterbags (ANOSIM R = 0.854, $P = 0.001$). The invertebrate community in litterbags is much reduced both in terms of abundance and diversity (Tab. 2). The trophic guilds are dominated by scrapers (mainly Atyidae) and predators (Odonata and

Table 3. Mean percentage (± SD) of trophic guilds between the benthic macroinvertebrates in litterbags and in kick samplings.

Streams	Sites	Macroinvertebrates in Litterbags					Macroinvertebrates in Kick samplings				
		Shredders %	Collectors %	Predators %	Scrapers %	Herbiv. %	Shredders %	Collectors %	Predators %	Scrapers %	Herbiv. %
Akoumbegue	A	–	96.4 ± 5	2.4 ± 1.1	2 ± 4.5	0.5 ± 1.2	5 ± 5.6	7.1 ± 5.2	22.7 ± 9.7	62.7 ± 13.8	2.6 ± 5.2
	C	10 ± 22.4	83.1 ± 13.4	–	8.9 ± 19.9	11.3 ± 13.1	6.8 ± 5.2	7.6 ± 3.2	41.4 ± 9.6	43.7 ± 14	0.6 ± 1.2
Ibe–Mfeme	IM	8.9 ± 14.5	72.4 ± 28.8	–	3.3 ± 7.5	18.7 ± 18.8	5.1 ± 3.6	19.5 ± 3.8	47.0 ± 18.9	27.8 ± 16.3	0.6 ± 1.4
Kongolo	K1	–	55 ± 44.7	–	5.6 ± 6.6	–	0.5 ± 1.1	10.6 ± 10.9	27.7 ± 13.9	61.2 ± 15.6	–
	K2	6.7 ± 10.9	76 ± 11	2 ± 0.9	2.2 ± 5	12.3 ± 14.1	2.4 ± 3.2	4.0 ± 4.1	45.9 ± 32.4	47.7 ± 33.8	–
	K3	–	72.6 ± 10.4	12.8 ± 7.4	45 ± 44.7	19.9 ± 11.8	0 ± 0	55.5 ± 27.4	33.7 ± 16.1	10.8 ± 14.7	–
Nloumou	AN1	0.9 ± 2	81.1 ± 25.9	–	9.8 ± 5.8	–	8.1 ± 7.7	11.5 ± 6.9	22.9 ± 7.5	57.5 ± 8.8	–
	AN2	–	83.3 ± 23.6	–	–	4.4 ± 9.9	3.9 ± 2.3	7.3 ± 2.8	26.2 ± 18.7	59.9 ± 19.7	2.7 ± 2.9
	N	66.7 ± 0.0	33.3 ± 0.0	–	–	–	2.2 ± 3.2	6.5 ± 8.8	62.6 ± 14.0	28.4 ± 15.8	0.3 ± 0.7
Nsoe–Mekok	NM	6.7 ± 14.9	53.3 ± 50.6	0 ± 0	–	40 ± 54.8	5.6 ± 8.6	1.0 ± 0.7	22.9 ± 13.3	70.3 ± 15.7	0.2 ± 0.5
Ossoe–Nkoro	ON	–	97.1 ± 5.9	5.9 ± 2.9	–	–	1.7 ± 2	25.9 ± 16.9	49.8 ± 25.3	17.4 ± 16.9	0.5 ± 1.1
Zoetoupsi	OB	8.3 ± 16.7	75.1 ± 11.9	4.1 ± 2	6.3 ± 12.5	8.3 ± 16.7	1.1 ± 1.5	11.0 ± 9.4	69.5 ± 14.3	22.7 ± 27.6	0.4 ± 0.8
	Z	–	100 ± 0.0	–	–	–	2.5 ± 3.7	23.8 ± 15.3	56.2 ± 25.6	17.2 ± 14.7	0.3 ± 0.6

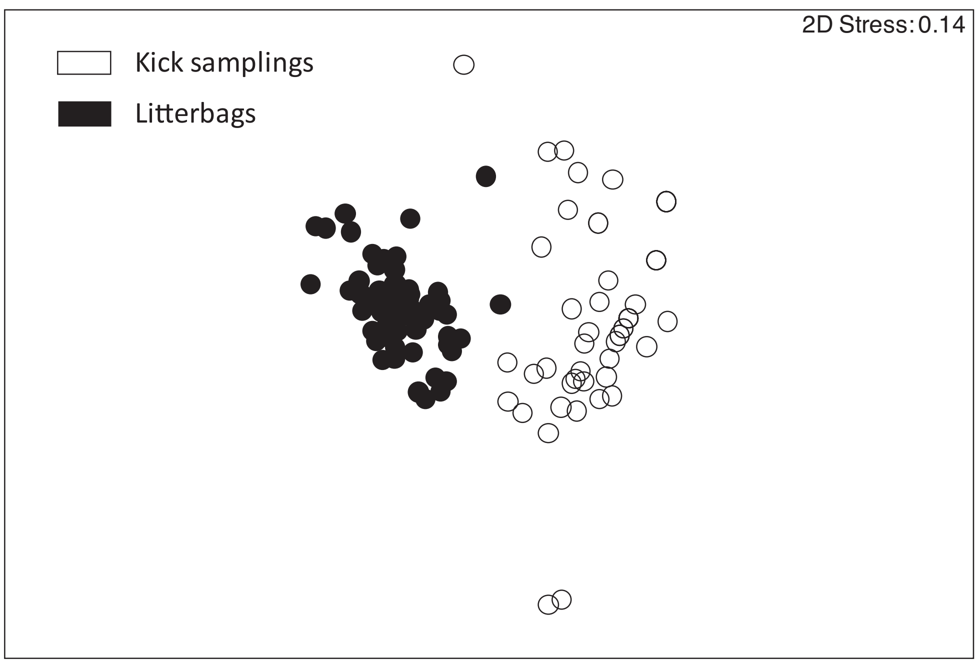

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of benthic macroinvertebrates in coarse-mesh litterbags (dark circles) and kick-net samples (open circles).

Heteroptera) in kick samplings whereas litterbags harbored mainly collectors (Chironomidae) (Tabs. 3 and S4). Finally, the relative abundance of shredders were low in all samples.

3.3 Analysis of the links between breakdown rates and environmental factors

The first two principal components of the PCA explained 36.5% and 20.7% of the total variance, respectively (Fig. 4). The first component was mainly explained by the longitudinal position of the sites, along with electrical conductivity (19.4%), water depth (17.9%), and the distance to the source (17.3%), water temperature (10.6%), and the channel width (10.5%). The second component was mainly explained by the meteorological factors with the % humidity (24.7%), water temperature (11.4%), and also the current velocity (11.5%).

The total breakdown rate (K_c) and the microbial decomposition rate (K_f) projected on the PCA were not clearly correlated with the principal components. This result was confirmed by the correlation matrix (Fig. 5) where only K_c was positively correlated with the distance to the source ($P = 0.0134$) and tended to be correlated with the pH ($P = 0.063$), whereas K_f was not correlated with environmental factors.

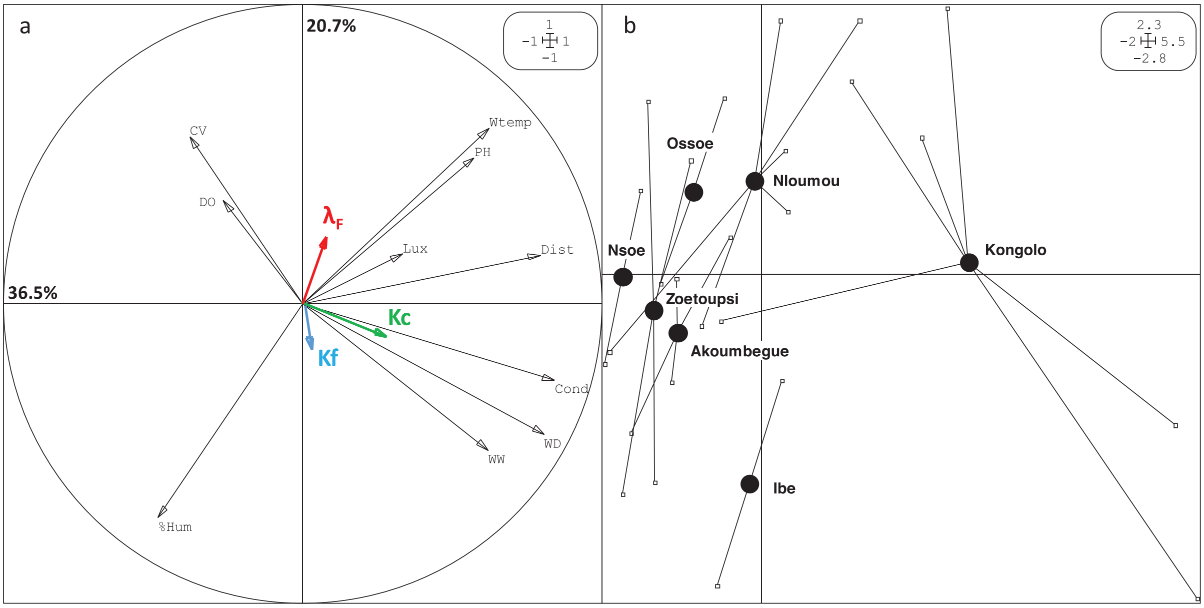

Fig. 4. Results of the PCA analysis with the correlation circle showing the correlations among the 10 environmental factors according to the different environmental factors (a). The breakdown rates K_c (green arrow), K_f (blue arrow) and λ_F (red arrow) are projected as quantitative supplementary variables. Black circles, distribution of the barycentres of each stream; solid lines link station to its different streams at each season (b). CV: current velocity; %Hum: percentage of air humidity; DO: dissolved oxygen; Lux: luminosity; WW: water width; WD: water depth; Cond: conductivity; Lambda: fragmentation rates; Dist: distance to the source.

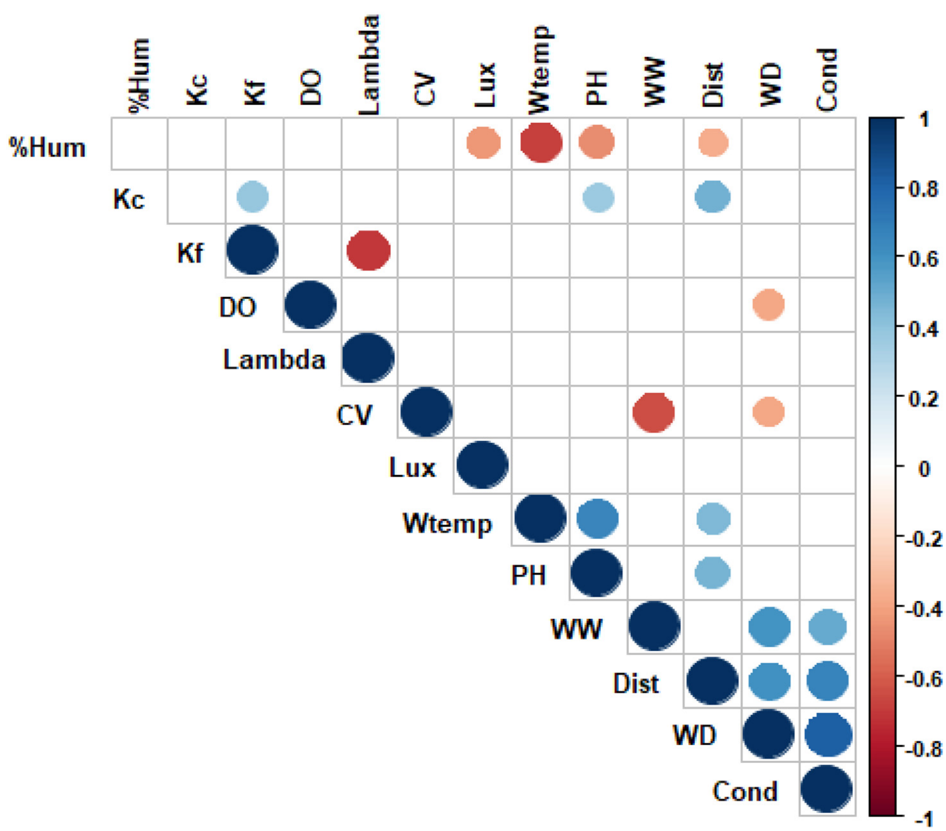

Fig. 5. Pearson correlations between decomposition metrics (K_c, K_f, λ_F) and environmental factors. The values represent the correlation coefficients. The coloured squares represent the significant coefficients (red or blue, P-value < 0.05) according to the scale of the value indicated on the right of the correlogram.

4 Discussion

The total breakdown rate remained similar across seasons and sites; only the microbial decomposition rate varied slightly between sites. This lack of variability may be related to the stability of environmental conditions in Cameroonian streams and more or less continuous inputs of leaf litter into tropical streams (Wantzen *et al.*, 2008). Our sites were located in the equatorial rainforest of Cameroon where seasonal variations of physicochemical parameters – except hydrology – are lower than in other climatic zones (Boulton *et al.*, 2008). These stable environmental conditions likely explain the stability of the leaf litter breakdown rate. Spatial stability of the breakdown rate has been reported in agricultural and forest streams of Kenya (Kadeka *et al.*, 2021). The authors explained their results by the presence and the good quality of the riparian zones in agricultural streams which maintain the quality of instream habitats, the canopy cover and the standing stocks of organic matter. These findings are congruent with our results obtained in an area free of significant anthropogenic pressure.

The total breakdown rate of *Funtumia africana* leaves found in our study (0.042 ± 0.006 g d^{-1}) is similar to those found in African streams, using other types of leaves and within the same range as in temperate climates, if we consider the tough species (e.g. *Q. robur*, *F. salvatica*, and *C. sativa*). However, the breakdown rates measured in Africa were higher than those measured in South America, but much lower than in Asia (Tab. 4). We also confirm the prominent role played by microbial activity, whereas the contribution of invertebrate shredders (λ_F) is rather limited (Tab. 4). The weak role of invertebrate shredders is confirmed by the low K_c/K_f ratio (1.21 ± 0.34) in our study and in other studies in Africa (Tab. 4). The contribution of invertebrates is commonly absent or scarce in tropical streams (Dobson *et al.*, 2002; Boyero *et al.*, 2021). The reason for this is the high temperature that limits the development of many shredders (Boyero *et al.*, 2021). Consequently, shredder diversity is negatively related with temperature (Boyero *et al.*, 2011b), whereas high temperature promotes microbial activity (Dobson *et al.*, 2002; Boyero *et al.*, 2011a, 2011b, 2015b; Tenkiano and Chauvet, 2017), especially bacterial activity (Ferreira *et al.*, 2012).

We noted a significant and positive correlation between the total breakdown rate (K_c) and the distance from the source and the pH, suggesting a higher contribution of invertebrate shredders downstream. This correlation could be explained by the role play by macrocrustacean shredders such as decapod Palaemonidae (Pringle *et al.*, 1993; Pringle and Hamazaki, 1998; Andrade *et al.*, 2017) or freshwater crabs (Dobson *et al.*, 2004), which play major roles in leaf breakdown in tropical streams where insect shredders are scarce or absent. Indeed, the abundance of such crustaceans increases in the lower parts of catchments (Saito *et al.*, 2012; Jacobsen *et al.*, 2008). Unfortunately, our data do not validate this hypothesis because these invertebrates are difficult to catch by kick sampling. Shredders can be abundant in our site, but their numbers are often underestimated by net samplings (Covich, 1988; Dobson, 2004; Dobson *et al.*, 2007; Boulton *et al.*, 2008; Camacho *et al.*, 2009; Kadeka *et al.*, 2021). Moreover, the potential underestimation of the shredder abundance is also observed by the invertebrate community sampled in litter bags that are very different than community if kick-samplings, especially by the lack of invertebrate shredders in litter bags in comparison with benthic kick samplings. The lack of correlation between invertebrate in litter bags and those if benthic layer was already been observed in a very different context in Europe (Piscart *et al.*, 2009). These authors observed a stronger correlation between the leaf litter breakdown rates and the invertebrate community in benthic layer than with invertebrates in litter bags. This result indicates with Serpa *et al.* (2020) and Sena *et al.* (2021) that invertebrates involved in leaf litter breakdown don't stay in litter bags but move from another microhabitat to consume leaf.

Microbial activity appeared as the driving force of tropical leaf litter breakdown. However, the influence of hyphomycetes species richness on the breakdown rate was negligible and no significant difference was observed between the breakdown rates in the different litterbags. The number of species (1–9 species) found on *Funtumia africana* leaves was lower than the number reported by Tenkiano and Chauvet (2017) on leaf litter in Guinean streams (18 species). Similar observations were reported by Bergfur and Sundberg in 2014. Ferreira *et al.* (2012) and David *et al.* (2024) found that the number of species and fungal activity were lower in tropical streams than in temperate streams, probably due to the high temperature. These authors also showed that litter colonisation by hyphomycetes decreases after a few days in tropical streams while it increases in temperate streams. This may have had an impact on the number of hyphomycete species found in our study. In addition, the steadily high temperature of tropical waters favours bacterial activity. Abelho *et al.* (2005) found a higher contribution of bacteria to microbial respiration, especially in the last stage of litter breakdown in a tropical stream.

By limiting shredder invertebrates and promoting microbial activity, temperature is the main factor controlling the overall breakdown of leaf litter (Boyero *et al.*, 2021). Similar observations have been reported in non-African tropical streams, particularly in southeastern Asia (Yule *et al.*, 2009), South America and Australia (Boulton *et al.*, 2008; Boyero *et al.*, 2015b; Cararo *et al.*, 2023).

In conclusion, the contribution of shredders to *Funtumia africana* breakdown is very weak in the streams of Cameroon. These results confirm those of previous studies carried out in other parts of the world, where the breakdown process is essentially microbial in tropical streams, particularly in Afrotropical streams. It is much lower in Cameroonian streams than in tropical Asian streams but higher than in South American streams. However, these results need to be put into perspective by the lack of information about the quality of leaves used in the previous studies. A meta-analysis of the data in the literature would be necessary to gain a better understanding of the mechanisms underlying this variability between tropical environments. Finally, our study showed that the leaf litter breakdown rates in Cameroon are mainly controlled by the distance from the source with also a potential contribution of the pH. Acidic waters may limit the breakdown rate, but the distance from the source increases leaf breakdown in Cameroonian forest streams. However, the link between

Table 4. Total decomposition rate (K_c) and ratio of total decomposition rate to microbial decomposition rate (K_c/K_f) in some tropical and temperate forest streams.

Countries	Regions	Leaf species	K_c (g.d^{-1})	K_c/K_f	References
Cameroon	Central Africa	*Funtumia africana*	0.035–0.056	1.21	Present study
Guinea	West Africa	*Albizia zygia*	0.001–0.051	1.51	Tenkiano and Chauvet, 2017
Guinea	West Africa	*Millettia zechiana*	0.062–0.080	1.42	Tenkiano and Chauvet, 2017
Kenya	East Africa	*Vernonia myriantha*	0.031–0.043	1.38	Kadeka *et al.*, 2021
Kenya	East Africa	*Syzygium cordatum*	0.004–0.009	1.1	Kadeka *et al.*, 2021
Kenya	East Africa	*Eucalyptus globulus*	0.006–0.01	1.36	Kadeka *et al.*, 2021
Kenya	East Africa	*Neoboutonia macrocalyx*		1.65	Masese *et al.*, 2014b
Kenya	East Africa	*Eucalyptus globulus*		1.48	Masese *et al.*, 2014b
Kenya	East Africa	*Syzygium cordatum*		1.52	Masese *et al.*, 2014b
Kenya	East Africa	*Eucalyptus saligna*	0.01 – 0.04	–	Tsisiche *et al.*, 2019
Kenya	East Africa	*Neoboutonia macrocalyx*	0.004–0.022	–	Tsisiche *et al.*, 2019
Kenya	East Africa	*Vangueria madagascariensis*	0.047	–	Dobson *et al.*, 2004
Kenya	East Africa	*Dombeya goetzenii*	0.010	–	Dobson *et al.*, 2004
Kenya	East Africa	*Syzygium cordatum*	0.022	–	Dobson *et al.*, 2004
Kenya	East Africa	*Rhus natalensis*	0.026	–	Dobson *et al.*, 2004
Kenya	East Africa	*Syzygium cordatum*	0.001	–	Mathooko *et al.*, 2000a
Kenya	East Africa	*Dombeya goetzenii*	0.711–0.789	–	Mathooko *et al.*, 2000b
Ouganda	East Africa	*Neoboutonia macrocalyx*		3.82	Fugère *et al.*, 2020
Brazil	South America	*Myrcia guyanensis*	0.006–0.007	–	Moretti *et al.*, 2007
Brazil	South America	*Ocotea* sp.	0.008–0.009	–	Moretti *et al.*, 2007
Argentina	South America	*Salix humboldtiana*	0.012	–	Capello *et al.*, 2004
Colombia	South America	*Tessaria integrifolia*	0.009–0.029	–	Rueda-Delgado *et al.*, 2006
Colombia	South America	*Symmeria paniculata*	0.001–0.010	–	Rueda-Delgado *et al.*, 2006
Colombia	South America	*Cecropia latiloba*	0.009–0.031	–	Rueda-Delgado *et al.*, 2006
Thailand	South Asia	*Acacia mangium*	0.068	–	Parnrong *et al.*, 2002
Thailand	South Asia	*Eucalyptus camaldulensis*	0.075	–	Parnrong *et al.*, 2002
Thailand	South Asia	*Hevea brasiliensis*	0.064	–	Parnrong *et al.*, 2002
France	Temperate	*Alnus glutinosa*	0.035–0.11	3.1–12.5	Rivière 2015
France	Temperate	*Castanea sativa*	0.017–0.038	1.69–4.7	Rivière 2015
France	Temperate	*Quercus robur*	0.010–0.017	0.9– 2.86	Rivière 2015
France	Temperate	*Fagus sylvatica*	0.007–0.068	1.7–17.8	Piscart *et al.*, 2009
Portugal	Temperate	*Alnus glutinosa*	0.047 – 0.052	2.76	Ferreira *et al.*, 2012
Portugal	Temperate	*Castanea sativa*	0.03	3.1	Ferreira *et al.*, 2012
Portugal	Temperate	*Quercus robur*	0.03	4.6	Ferreira *et al.*, 2012

breakdown rates and the environmental factors tested in our study remains quite limited, and further analyses would be required to gain a better understanding of leaf litter recycling in African rainforest streams.

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Supplementary Material

Table S1. Hyphomycetes associated with *Funtumia africana* (Benth) Stapf (Apocynaceae) leaf litter in fine-mesh litterbags exposed in the streams.

Table S2. Values of breakdown rates and environmental factors (K_c: rate in coarse mesh, K_f: rate in fine mesh, λ_F: fragmentation of leaf litter, Dist: distance to the source, CV: current velocity, WW: water width, WD: water depth, %Hum: percentage of air humidity, Lux: luminosity, Wtemp: water temperature, pH: potential Hydrogen, Cond: conductivity and DO: dissolved oxygen).

Table S3. Macroinvertebrates collected from kick samplings in the streams. Assignment of macroinvertebrates into FFGs according to literature: Sh = Shredders; Sc = Scrapers; Co = Collectors; Fi = Filters; He = Herbivores; Pr = Predators; Om = Omnivores.

Table S4. Macroinvertebrates collected from kick samplings in the streams. Assignment of macroinvertebrates into FFGs according to literature: Sh = Shredders; Sc = Scrapers; Co = Collectors; Fi = Filters; He = Herbivores; Pr = Predators; Om = Omnivores.

The Supplementary Material is available at https://www.limnology-journal.org/10.1051/limn/2024018/olm.

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