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Tropical shift in decomposers' relative contribution to leaf litter breakdown in two Guinean streams

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ABSTRACT

The hypothesis that leaf litter breakdown in Guinean streams is governed by microorganisms was confirmed, supporting the reported latitudinal shift in decomposers' contribution to this process. The large body size of dominant macroinvertebrate decomposers (shrimps) only partially compensated for their very low densities. In contrast with other tropical regions mostly dominated by insect larvae, the functional consequences of global warming on these stream ecosystems may be less severe due to the lower sensitivity of crustaceans to temperature increase.

Abstract in French is available with online material.

Key words: aquatic hyphomycete; decomposition; detritivorous macroinvertebrate; diversity; function; fungi; latitudinal pattern; shrimp.

Leaf litter breakdown is a crucial process for headwater streams (Wallace *et al.* 1997). Such ecosystems, at both high and low latitudes, receive large amounts of plant litter, *i.e.*, mainly dead leaves, which are at the basis of the stream detrital food web. Litter breakdown and the dynamics and relative contribution of decomposer types in temperate streams are now very well documented, While increasing information on litter breakdown from tropical streams is available, the relative implication of microorganisms and invertebrates has received less attention (Gonçalves *et al.* 2007, Jinggut & Yule 2015, and the inter-regional comparison in Boyero *et al.* 2015 are among exceptions). Microbial breakdown is assumed to be higher because of the higher temperatures, and possibly lower competition for the resource, prevailing in tropical streams (Irons *et al.* 1994). In contrast, the implication of leaf-shredding invertebrates in the tropics, due to their generally lower abundance and body size, particularly for insect larvae (but see Yule *et al.* 2009), is hypothesized to be weaker than that in temperate regions. Nevertheless it must be stressed that the contribution of tropical invertebrates may be underestimated due to the poor knowledge of their diet and local variability effects (Camacho *et al.* 2009). These latitudinal patterns tend to be well supported by the results of a global study (Boyero *et al.* 2011). However, like in other global studies, a limitation to generalization lies in the paucity of data from some tropical regions, with, *e.g.,* in the latter study for Africa only one site (Kenya—in Eastern Africa) also well documented by other studies (Dobson *et al.* 2002, Masese *et al.* 2014). In the present study conducted on two litter species in two streams in Guinea, we evaluated whether the relative contribution of microbial and invertebrate decomposers conformed to these patterns, *i.e.,* high microbial breakdown versus low invertebrate-driven breakdown in reference to their temperate counterparts. In addition to document the hypothesized discrepancy in decomposers' relative involvement across latitudes, our second objective was to evaluate the specific impact of global climatic changes on this ecosystem process. Because some tropical regions such as Western Africa are predicted to suffer severe warming during early and late 21st century (IPCC 2013) and leaf litter represents an important portion of the organic carbon stock, consequences on the fate of carbon may be substantial while different from those in temperate regions.

Our study was conducted in two headwater streams located in the vicinity of Macenta in Forested Guinea, a typically forested region at low-medium altitude in Southeastern Guinea (Western Africa) near the border with Liberia. Facély Mara and Noulava are first-order oligotrophic streams running under a diverse deciduous forest. Substratum consisted of sand, gravel and cobbles. Water temperature recorded over the leaf breakdown experiment was stable around 22°C. *Albizia zigia* (DC.) J.F.Macbr. and *Millettia zechiana* Harms are two common tree species in the vicinity of both streams and in Western Africa. Both species exhibit rather similar leaf traits even though the former had slightly higher N content than the latter (C:N ratios of 11.6 and 9.8, respectively). Five g (±0.05 g) of freshly-fallen leaves from either species were enclosed in coarse (CM, 9 mm) and fine mesh (FM, 0.5 mm) bags. A total of 96 leaf bags (2 leaf species × 2 mesh sizes × 2 streams × 3 blocks × 4 dates) were prepared and sets of 16 bags (2 leaf species × 2 mesh sizes × 4 dates) were exposed in each of three blocks along each stream on 11 June 2014. CM bags allowed access to both macroinvertebrate and microbial decomposers while FM bags restricted leaf decomposition to microorganisms. As shown by visual inspection, FM bags did not contain any invertebrates except on rare occasions where

TABLE 1. *Total, microbial, and invertebrate-driven litter breakdown rates of two leaf species in two Guinean streams, as determined from coarse-mesh bags, fine-mesh bags, and the difference in mass loss between coarse-mesh and fine-mesh bags, respectively. Average from* N = *3 per stream and leaf species (±Asymptotic Standard Error). Rates with the same letter are not significantly different (Tukey HSD,* P > *0.05)*

Stream	Leaf species	k_{total} (per d)	$k_{microbial}$ (per d)	$k_{invertebrate}$ (per d)
Facély Mara	*Albizia zigia*	0.03478 (±0.00245)^{a,b}	0.02080 (±0.00255)^{a}	0.00547 (±0.00104)^{b}
Facély Mara	*Millettia zechiana*	0.07646 (±0.00358)^{c}	0.04938 (±0.00189)^{b}	0.00223 (±0.00090)^{a}
Noulava	*Albizia zigia*	0.02545 (±0.02525)^{a}	0.01906 (±0.00098)^{a}	0.00318 (±0.00102)^{a,b}
Noulava	*Millettia zechiana*	0.06634 (±0.00400)^{b,c}	0.05121 (±0.00255)^{b}	0.00181 (±0.00048)^{b}

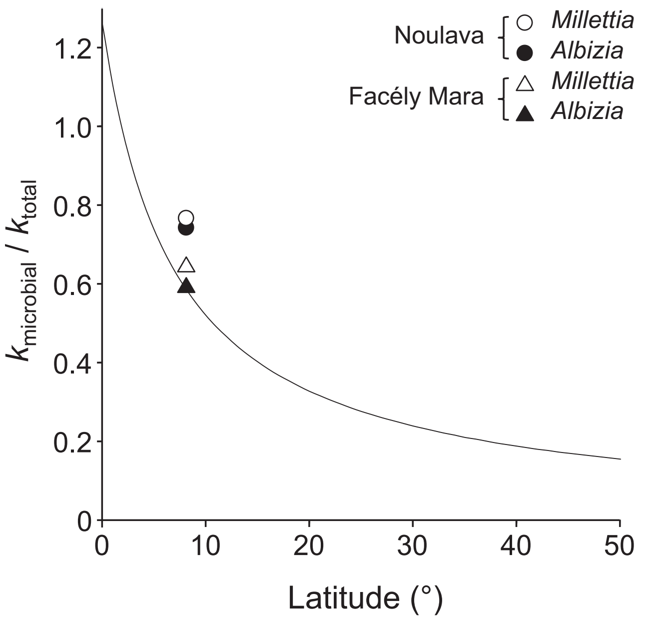

FIGURE 1. Ratio of microbial breakdown rate to total breakdown rate for two leaf litter species in two Guinean streams. The displayed relationship of this ratio against latitude [y = 8.83 / (latitude + 6.97)] is derived from two relationships determined in a global experiment and shown in Figs 2c and f in Boyero *et al.* (2011).

very few and tiny individuals occurred but did not, or only marginally, contribute to leaf breakdown. One leaf bag per leaf species, mesh size, block and stream was removed after 2, 4, 6 and 8 weeks. Biological and chemical determinations on retrieved litter material followed standard procedures (Graça *et al.* 2005, see Appendix S1). Breakdown rate, *k*, was determined according to the exponential model: $M_t = M_0 \cdot e^{-k.t}$, where M_t and M_0 are the remaining and initial ash free dry mass (AFDM) of leaves, respectively, and t the exposure time (in days), as derived from the decay model (Wieder & Lang 1982).

Both leaf species decomposed fast with breakdown rates being slightly, but not significantly, higher in Facély Mara (Table 1, k_{total}). In accordance with its very high N content (5.1%), *Millettia* decomposed significantly faster than *Albizia* ([N] = 4.1%) in both types of leaf bags and in both streams. Leaf C:N ratios continuously increased with breakdown time, from 11.6 to 14.2 and 14.7 for *Albizia* in Facély Mara and Noulava, respectively, and from 9.8 to 15.6 and 17.6 for *Milletia* in Facély Mara and Noulava, respectively (Fig. S1). Such a C:N increase with breakdown time is an uncommon pattern being probably due to the conjunction of high initial N leaf content and low dissolved inorganic N content in the stream water.

The same discrepancy between leaf species occurred for microbial breakdown rates in both streams (Table 1). Importantly, microbial breakdown rates ($k_{microbial}$) exceeded invertebrate-driven breakdown rates ($k_{invertebrate}$) by about one order of magnitude, and this pattern was exacerbated in *Millettia* possibly resulting from its higher N content. Leaf-associated sporulation by aquatic hyphomycetes showed low maxima (0.59 and 0.63/mg leaf AFDM/d for *Albizia* in Facély Mara and *Millettia* in Noulava, respectively) and late increases compared to the early peaks occurring in temperate streams (Fig. S1). The community structure of aquatic hyphomycetes on decomposing leaves was dominated by few species, mostly known for their tropical distribution (Table S1). Such consistently low reproductive activity and diversity have been reported from tropical streams (Jabiol *et al.* 2013, Graça *et al.* 2016). In the present study, the low peaks of sporulation rate may have been due to the very low dissolved inorganic N and P contents in the water of our streams, as shown in manipulative experiments on nutrient effect (Suberkropp & Chauvet 1995, Ferreira *et al.* 2006). It must, however, be underlined that the preeminence of fungal contribution to leaf breakdown is much more consistent across tropical regions than aquatic hyphomycete reproductive activity, with the latter being highly variable (*e.g.,* discrepancies of two orders of magnitude between Mathuriau & Chauvet 2002 and Ferreira *et al.* 2012). In contrast with temperate regions, sporulation rates in the tropics could thus not reflect fungal involvement in litter breakdown and be used as a reliable index of functional ecosystem impairment. The abundance of detritivore invertebrates peaked earlier than fungi but also at very low density (Fig. S1). The latter was, however, partially compensated for by the large individual body size and potentially substantial efficiency in leaf fragmentation as found in *Caridina africana*, a freshwater atyid shrimp that dominated detritivore assemblages (Table S1). The dominance of macroconsumer assemblages by shrimps is not uncommon in lowland streams of some regions, where they are shown to be efficient detritivores (*e.g.,* Crowl *et al.* 2001). As a result, such lowland streams tend to differ much more from temperate streams than do high-altitude tropical streams (Boyero *et al.* 2009). Interestingly the difference of leaf mass in FM and CM bags, *i.e.,* the mass loss due to macroinvertebrates, approximately equaled the consumption by *C. africana* as calculated from (i) individual density on *Millettia* at 2 weeks in Facely Mara and (ii) consumption rate determined for another species of Atyidae (*Atyaephyra desmarestii*, Callisto 2006), and (iii) a compensation factor for the between-taxa differences in per capita mass (McKie *et al.* 2008). Such a rough extrapolation must be used with caution as the contribution to leaf fragmentation may vary greatly among species of Atyidae (*e.g.*, *Atyia lanipes* and *A. desmarestii* in Crowl *et al.* 2001 and Callisto 2006, respectively). Nevertheless, this illustrates the potential implication of such freshwater shrimps in leaf litter breakdown, in particular when they dominate detritivore assemblages, even though they only contribute to a minor portion of total leaf mass loss in the present study.

Overall, the poor invertebrate diversity and their very low contribution to leaf breakdown relative to microorganisms, when compared to their temperate counterparts, were in accordance to reported global patterns (*e.g.*, Boyero *et al.* 2011) and even seemed to be exacerbated in our streams as reflected by very high $k_{microbial}$ / k_{total} ratios (Fig. 1), possibly due to the high litter content in N. As anticipated in previous studies (Boyero *et al.* 2011, 2012), the loss of species and climate warming may have serious implications on the trophic structure and the whole ecosystem functioning of such streams. The contribution of cool-adapted detritivore taxa that may be close to their thermal maxima in the tropics (and thus particularly vulnerable to climate warming) has been suggested to be further reduced, and the conversion of organic compounds into CO_2 through microbial breakdown to be stimulated leading to overall faster turn-over of organic C (Boyero *et al.* 2011). In the present streams of western Africa, such implications should nevertheless be tempered as the sensitivity of crustaceans to higher temperature as shown in *Caridina* (Hart 1983, de Silva 1989) may be lower than that of insect larvae many of which are cool-adapted. Whether *Caridina africana* is eurytherm remains unknown to our knowledge while the upper thermal tolerance appears somewhat inconsistent across *Caridina* species (Hart 1983, de Silva 1989), thus requiring complementary studies but still making our assumption plausible. Whereas the predominance of micro- versus macro-decomposers is confirmed by the present study, the impact of future temperature increase may be less severe than in other tropical streams, stressing that regional particularities preclude any generalization about the consequences of global warming on the functioning of tropical stream ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Characteristics of study sites—Experimental and analytical procedures.

FIGURE S1. Carbon-to-Nitrogen ratio of two leaf species decomposing in two Guinean streams, and litter-associated fungal sporulation rate and number of macroinvertebrate individuals.

TABLE S1. *Aquatic hyphomycete and macroinvertebrate taxa associated with two litter species decomposing in two Guinean streams.*

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