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RESEARCH PAPER

A conceptual model of litter breakdown in low order streams

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The detrital-based food web of many streams and rivers plays a fundamental role in the cycling and retention of carbon and nutrients. However, we still need to understand which global mechanisms underlie the biogeochemical pathways that control energy transfer from the detrital pool through local food webs into nutrient and energy cycles and storage. Previous attempts to understand the variability in litter breakdown rates have included the search for latitudinal variation patterns and analysis of the influence of different factors. Here we complement those studies by developing a conceptual model to predict litter breakdown dynamics in low order streams. According to the model, litter breakdown rates and the relative role of microbial decomposers and shredder detritivores on this process are hierarchically governed by interactions between climate/hydrology and geology acting upon plant traits, nutrient and leaf availability to decomposers, and metabolism of microbial decomposers and shredders. The model explains variations in leaf litter breakdown rates and shredder abundance across large geographic areas, allowing the formulation of predictions of how anthropogenic pressures may affect litter breakdown rates.

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1 Introduction

1.1 Litter breakdown is an important ecosystem process

Typically ~90% of the energy fixed by primary producers in terrestrial systems and many fresh waters falls into the detrital pool (Cebrian, 1999; Abelho, 2001). Food webs relying strongly on detrital pathways are known as "brown food webs" (Kaspari, 2004). Brown food webs are directly involved in the mineralization of organic matter, a key ecosystem process.

The detrital-based food web of many streams and rivers plays a fundamental role in the cycling of C. Battin et al. (2009) estimated that organic carbon inputs from land to freshwater ecosystems is 2.7 Pg C year^{-1}; freshwaters in turn would be responsible for carbon dioxide (CO_2) emissions of about 1.2 Pg C year^{-1}. A critical role for forested low-order streams in those land–water–atmosphere C-fluxes should be expected for two reasons. First, due to their size, low order streams

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are widely spread across the terrestrial landscape representing an active zone of exchange of materials between land, water, and atmosphere. Second, the amount of energy flowing through the detrital food web is typically larger than that generated *in situ* by primary producers. This condition is due to the abundant leaf litter subsidies from the riparian tree vegetation and the limited solar irradiation in the stream bed (Fisher and Likens, 1973; Abelho, 2001 but see Lau et al., 2009). Once in the stream, terrestrial detrital inputs (e.g., leaf litter) undergoes physical and chemical transformations, largely mediated by microorganisms and invertebrate consumers. An important number of these transformations are collectively studied as leaf litter breakdown (Gessner et al., 1999). Invertebrate consumers include leaf shredding, scraping, and mining detritivores, hereafter treated as 'shredders'.

Leaf litter breakdown has been recognized as a complex process in both terrestrial and aquatic ecosystems and conceptual models to describe it in an ecosystem context have been formulated based on hierarchy theory (e.g. McIntire and Colby, 1978; Lavelle et al., 1993; Royer and Minshall, 2003). For streams Royer and Minshall (2003) proposed a hierarchical model that distributes the sources of variability of litter breakdown rates between several factors across spatial scales, ranging from leaf pack accumulations to biomes. This approach has the conceptual advantage of linking mechanistically the influence of large-scale factors (e.g., climate, geology) to processes occurring at smaller scales through other intermediate factors with an increasing local influence. Intermediate factors include riparian vegetation and the quality of litter inputs, water quality, water velocity and others.

In spite of the appeal of a hierarchical model for litter breakdown in terms of synthesis and holism, its applicability relies on the availability of information about the mechanisms connecting large to small scale processes. Although small-scale studies are abundant, (e.g. reach scale, single streams, see Tank et al., 2010 for a review), larger-scale studies are less common. Two exceptions include two recent studies at continental (Woodward et al. 2012) and global scales (Boyero et al., 2011b), which give some insights about large-scale controls on litter breakdown. While Boyero et al. (2011b) provided evidence of the importance of temperature-driven microbial litter breakdown on a global-scale, Woodward et al. (2012) showed a significant nutrient effect on invertebrate-mediated breakdown rates on a continental scale in a pan-European experiment. These studies highlight the influence of large scale factors on leaf litter breakdown, a key ecosystem process.

Leaf litter breakdown is a patch-scale process (Pringle et al., 1988; Royer and Minshall, 2003) and litter breakdown rates are evaluated at the leaf-pack scale. Therefore any predictions about this process in response to global change will require the downscaling of the potential effects of varying large scale controls (e.g. climate) to the relevant scale of the process (patch). Here we review, discuss, and synthesize the mechanisms and pathways involved in a hierarchical model for leaf litter breakdown. We develop Royer and Minshall's (2003) framework further by describing different sources of variability in litter breakdown rates using recent literature. Furthermore, we establish several scenarios based on different mechanistic pathways for leaf breakdown in streams. In each case we make theoretical predictions about litter breakdown rates.

1.2 Litter breakdown in streams vs. terrestrial ecosystems

Here we will use the term "litter breakdown" to refer to the transformation of large particles of organic matter into smaller particles, and to the incorporation of some of its carbon into secondary production. Although the terms "litter breakdown" and "litter decomposition" are frequently used as synonymous, "litter decomposition" refers to the total mineralization of organic matter. Global analyses of leaf litter breakdown experiments have shown that, in terrestrial ecosystems, breakdown is constrained by: (i) climate (moisture and temperature); and (ii) chemical and physical properties of plants (Aerts, 1997). High breakdown rates are observed under warm and humid conditions (Aerts, 1997; Gholz et al., 2000; Salinas et al., 2011) and for nutrient-rich plants with low lignin (Aerts, 1997; Cornwell et al., 2008; Bakker et al., 2011) and tannin concentrations (Makkonen et al., 2012). In contrast, plant chemical and physical defenses against desiccation, herbivory and fungal infections may retard litter breakdown. Physical barriers include leaf toughness and surface waxes (Read and Stokes, 2006), while chemical defenses include polyphenolics, particularly condensed tannins (Stout, 1989; Wantzen et al., 2002; Coq et al., 2010). Many such compounds are long lived and remain active after senescence, and thus are likely to affect microbial decomposers and invertebrate consumers, retarding decomposition and therefore nutrient cycling, with consequences for ecosystem productivity.

Although litter breakdown in low order streams is generally constrained by the same factors (e.g., Stout, 1989; Bärlocher et al., 1995; Canhoto and Graça, 1999; Wantzen et al., 2008), streams have several fundamental differences from terrestrial systems which preclude generalizations. These include: (i) temperature ranges, which are buffered in streams; (ii) water availability, not limiting in streams; (iii) oxygen levels, occasionally limiting in streams but not in the superficial soil layer of terrestrial systems; (iv) abrasion by sediment transport; and (v) unidirectional transport of organic matter in streams.

1.3 There is large-scale variability in litter breakdown in low order streams

Leaf litter breakdown is the result of leaching of soluble compounds, the activity of microbial decomposers and shredder detritivores, and physical abrasion. Physical settings and biological communities are highly variable over large spatial scales, hence this variability is translated to breakdown rates. In the following paragraphs, we briefly report on the variability of litter breakdown patterns across wide geographical areas and the biological agents of the process: microbial decomposers and shredder detritivores.

1.3.1 Breakdown rates

Because of global temperature gradients, we would expect a biological process such as litter breakdown to be faster towards warmer (tropical) climates. However, according to the literature, there is wide variation in litter breakdown rates within the tropics, at least at the stream reach scale: some tropical streams hold some of the fastest breakdown rates recorded (~50% initial mass lost in 7–14 days; e.g., Stout, 1989; Irons et al., 1994; Mathuriau and Chauvet, 2002; Abelho et al., 2005; Rincón and Santelloco, 2009; Dudgeon and Gao, 2010), while others show very slow rates (10–15% initial mass loss in 75–120 days; (Abelho, 2001; Gonçalves et al., 2006; Rueda-Delgado et al., 2006; Chará et al., 2007). In contrast, ranges of litter breakdown are generally less extreme in temperate streams, with 50% mass loss in 84 days (median of 100 k values reported by (Abelho, 2001); 25% C.L. = 41 days). Differences in litter breakdown rates between tropical and temperate regions are even stronger when rates are corrected for temperature, resulting in particularly slow rates in certain tropical streams where litter breakdown can even be slower than in forest soils (e.g., Capps et al., 2011; Santos, 2011; Ferreira et al., 2012).

A relevant question in this context is whether the low litter breakdown rates observed in some tropical streams are due to the poor quality of resources (local tree species), to unfavorable environmental conditions (e.g., water chemistry, physical habitat) and/or to the lower abundance or biomass of microbial decomposers and shredders. Reciprocal incubation experiments designed to address this question have produced contrasting results, suggesting that all these factors may interact to determine litter breakdown rates (e.g., Gonçalves et al., 2006; Wantzen and Wagner, 2006; Ferreira et al., 2012). Our model below addresses this variation.

1.3.2 Microbial decomposers

Literature from temperate zones consistently shows that, once in the water, leaves are rapidly colonized by a diverse array of saprophytes, particularly aquatic hyphomycetes, which typically may account for up to 12–16% of the detrital mass (Gessner and Chauvet, 1997; Pascoal and Cássio, 2004; Duarte et al., 2006). Litter breakdown rates have also been related to aquatic hyphomycete taxonomic richness and reproductive activity (e.g., Pérez et al., 2011; Pérez et al., 2012), but few studies have addressed the diversity and/or biomass of aquatic hyphomycetes in tropical forest and savanna streams. Opposite to the general trend of increased biological diversity towards the tropics (Willig et al., 2003), aquatic hyphomycete biomass and diversity seem to be low in some streams outside the temperate zones, such as in the Brazilian Cerrado (Gonçalves et al., 2007), the Ecuadorian Andes (Encalada et al., 2010), French Guyana (Jabiol et al., 2013), and the Amazon (Capps et al., 2011; Ferreira et al., 2012). However, high fungal biomass, activity or diversity has been observed in other tropical systems in Venezuela (Smits et al., 2007; Rincón and Santelloco, 2009), Panama (Bärlocher et al., 2010), Puerto Rico (Santos-Flores and Betancourt-López, 1998) and Colombia (Mathuriau and Chauvet, 2002). As with litter breakdown rates, it seems that tropical streams vary considerably in terms of the importance (presence and abundance) of aquatic hyphomycetes. When aquatic hyphomycetes are absent (e.g., Ferreira et al., 2012), a relevant question is whether any other microorganisms are replacing them in their functional role of enzymatic maceration of leaf litter.

Irons et al. (1994) suggested that microbial activity decreases while shredder biomass increases with latitude in relation to the temperature decrease. As a result, the relative importance of microbes on litter decomposition should increase towards the tropics, with shredders showing the opposite trend (see below). However, the slower microbial decomposition and lower microbial biomass observed in many streams at lower latitudes suggest that, in many cases, the potential stimulatory effect of higher temperature on microbial activity is overruled by other factors such as poor litter quality or low dissolved nutrient availability.

1.3.3 Shredder detritivores

Feeding activities of shredders are facilitated by the presence of aquatic hyphomycetes through fungal enzymatic maceration of leaves and fungal high nutrient concentration and biomass (Chung and Suberkropp, 2009). In many temperate low order streams, shredders frequently account for ≥40% of total invertebrate biomass (e.g. Graça et al., 2001) and abundance (Boyero et al., 2011b). Shredders greatly contribute to litter breakdown by consuming up to 64% of stream leaf biomass (e.g. Hieber and Gessner, 2002; González and Graça, 2003; Azevedo-Pereira et al., 2006; Leberfinger and Herrmann, 2010). Shredders are therefore important elements promoting litter breakdown in most temperate zones, with only one exception reported: in New Zealand streams hydraulic disturbance may inhibit shredder activity (Winterbourn et al., 1981; Linklater, 1995).

The role of shredders is, however, variable in tropical climatic zones. Shredders have been reported as locally abundant and/or important for litter breakdown in Puerto Rico (Crowl et al., 2001; Cross et al., 2008), the Australian wet tropics (Cheshire et al., 2005; Camacho et al., 2009), Hong Kong (Li and Li, 1996), Malaysia (Yule et al., 2009), montane Ecuador (Encalada et al., 2010), Costa Rica (Benstead, 1996), Sri Lanka (Walpola et al., 2011) and the Colombian Andes (Chará-Serna et al., 2012). However, they seem to be absent or scarce in other regions, mostly in tropical rain forests and savannas in Costa Rica (Irons et al., 1994; Rosemond et al., 1998), Colombia (Mathuriau and Chauvet, 2002; Rueda-Delgado et al., 2006), the Brazilian Cerrado (Wantzen and Wagner, 2006; Gonçalves et al., 2007), Hong Kong (Li et al., 2009; Dudgeon and Gao, 2010), Papua New Guinea (Yule, 1996) and Hawaii (Larned et al., 2003), and in some Mediterranean streams of the Iberian Peninsula (Gonçalves et al., 2006; Pérez et al., 2011).

In a global study in which 1295 leaf litter samples from 147 streams in 16 regions located in six continents were analyzed (Boyero et al., 2011a,b; 2012) it was found that temperate streams as a whole have shredder densities $\sim$2.5 times higher and species richness 2.2 times higher than tropical streams. Moreover, in some tropical streams, gut content and stable isotope analyses have revealed that, despite the presence of dense riparian forest and high organic matter availability, invertebrates appear to gain the bulk of their energetic requirements from autochthonous sources (Brito et al., 2006; Lau et al., 2008; Dudgeon et al., 2010). Consequently, some authors have suggested that neotropical shredders seem to be more generalist than species from temperate areas (Wantzen and Wagner, 2006).

The lower abundance of shredders in the tropics could be partially explained by the high activity of microbial decomposers (given the temperature - metabolism relatioship depriving shredders of their resources (Irons et al., 1994) or by evolutionary constraints, since most shredders belong to the orders Plecoptera and Trichoptera, which evolved in cold environments (Wantzen and Wagner, 2006; Pearson and Boyero, 2009). Another explanation for the scarcity of shredders in many tropical areas deals with plant defenses. Herbivory is assumed to be more intense in the tropics than in temperate regions (e.g. Wantzen et al., 2002; Salgado and Pennings, 2005; Pennings et al., 2009; but see Moles et al., 2011). Accordingly, plants from low latitudes should be better defended against consumers than plants from high latitudes, and most of such defenses remain active after senescence (Coley and Barone, 1996; Marquis et al., 2012). Therefore, Wantzen, Wagner & Junk (2002) proposed that this difference across latitudes results in litter being recalcitrant for microbes and detritivores and, consequently, in low litter breakdown rates at lower latitudes. However, reciprocal incubation experiments have shown that high-quality temperate leaves also decompose slowly in some tropical streams (e.g. Ferreira et al., 2012), suggesting that plant defenses are not the only factor in play.

2 Predicting litter breakdown rates: moving downwards within a hierarchical framework for litter breakdown in streams

In large-scale experiments, a significant portion of the variability observed in litter breakdown rates cannot be explained by the simple analysis of individual factors, because of interactions among factors operating at smaller scales. Woodward et al. (2012) found a great variability in breakdown rates at intermediate dissolved nutrient concentrations, in contrast with the low breakdown rates at very high or very low nutrient concentrations. Boyero et al. (2011b) suggested that factors other than temperature likely influenced litter breakdown rates across sites at a global scale and accounted for the considerable residual variability observed. Although Royer and Minshall (2003) proposed a hierarchical framework for litter breakdown to deal with those scale-dependencies and interactions; finding straightforward connections between large-scale factors and processes operating at the patch scale (i.e., the scale at which leaf breakdown occurs) is complicated due to the confounding effects of intermediate-scale variables. Understanding the mechanisms behind those hierarchical effects and interactions is fundamental for the development of predictive models for litter breakdown. In this section we illustrate several pathways by which hierarchical factors influence leaf litter breakdown. Starting with factors at the top of the hierarchy, we move downwards to explore possible mechanisms involved in the integration of large-scale constraints into small-scale constraints. We have numbered those pathways (1 to 5) in Figure 1 as described in the following paragraphs.

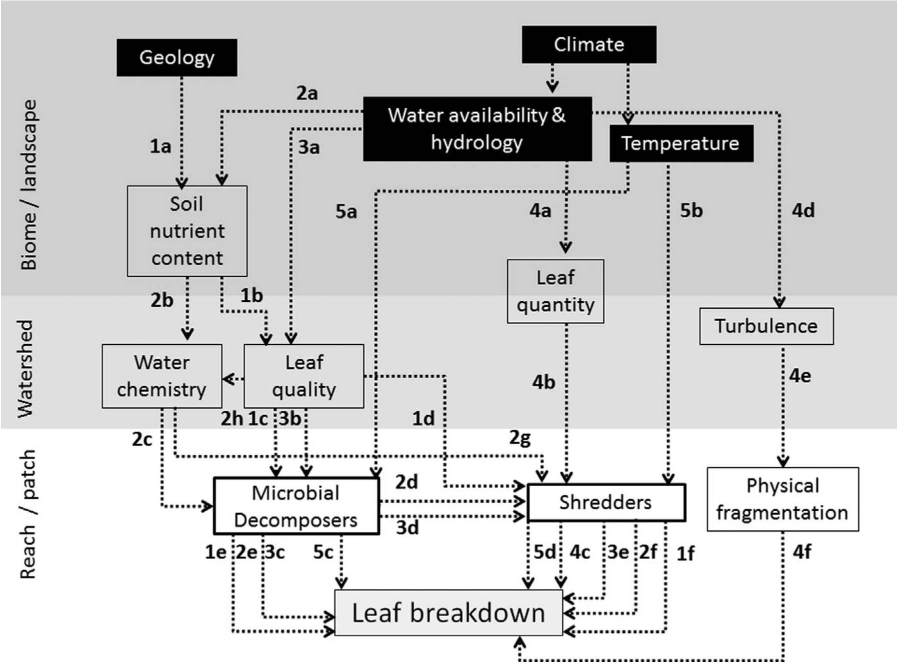

Figure 1. Conceptual model of biologically-induced litter breakdown drivers in streams from a hierarchical perspective. Arrows indicate influence of one factor over the next one. Letters and numbers correspond to 'pathways' referred to in the text. There are five pathways, which are ultimately controlled by geology (pathway 1), water chemistry resulting from the interaction between geology and hydrology (pathway 2), water stress (pathway 3), hydrological regime (pathway 4) and temperature (pathway 5).

2.1 Geology selects for leaf traits relevant to litter breakdown and establishes scenarios for leaf quality inputs to stream reaches (Pathway 1)

Geology determines soil elemental composition (Fig. 1, 1a), which may control litter breakdown through two pathways. Firstly, soil nutrient availability affects nutrient concentration in plants (Fig. 1, 1b). Secondly, geology affects nutrient concentration in stream water (Fig. 1, 2b). We start by reviewing the first mechanism.

Low levels of nutrients in soils can limit nutrient concentrations in plants (Ordoñez et al., 2009; Alvarez-Clare and Mack, 2011). Moreover, plants from nutrient-poor soils are generally better defended against herbivory (Coley et al., 1985; Coley, 1987; Coley and Barone, 1996; Fine et al., 2006; Silva and Batalha, 2011). Defenses may be in the form of synthesis of chemical anti-feeding compounds, or tough/leathery leaves (c.f. Coley et al., 1985; Coley and Barone, 1996; Wantzen et al., 2002; Ardón and Pringle, 2008; Wantzen et al., 2008). Given the high retention and low rates of litter drift in headwaters (Elosegi, 2005), streams running through nutrient poor soils are likely to be dominated by low quality litter (Fig. 1, 1b). Low quality leaves (high defenses, low nutrients) are likely to render detritus more recalcitrant (Bakker et al., 2011) for microbial decomposers (Sridhar and Bärlocher, 2000; Ferreira et al., 2006b; Li et al., 2009) and for shredders (Coq et al., 2010; Coughlan et al., 2010; Graça and Cressa, 2010; Fig 1, 1c, 1d), limiting their assimilation, activity, and growth.

Therefore our first prediction is that, other factors (e.g., climate, temperature, hydrological regime) being similar, low order streams flowing through soils with low nutrients will show slower litter breakdown rates and lower biomass of microbial decomposers and shredders, whereas low order streams running through nutrient rich soils are likely to receive high quality leaf litter, that is rapidly used as a resource by microbial decomposers and shredders (Fig 1, 1e, 1f).

2.2 Climate and geology, through hydrological regimes and soil properties respectively, establish scenarios for water chemistry (Pathway 2)

Climate-driven hydrological regime and geology-defined soil properties (Fig 1, 2a and 1a, respectively) affect the levels of dissolved nutrients in streams (Fig 1, 2b). Aquatic hyphomycetes and other microbial decomposers retrieve a proportion of their nutrient requirements from the water, where nutrients are already in their mineral form and thus require less energy expenditure for uptake than nutrients in litter that require the production of enzymes (Suberkropp, 1998; Fig. 1, 2c).

Hence, dissolved nutrients are an important limiting factor for fungal growth and activity, as shown in laboratory experiments (Gulis and Suberkropp, 2003; Berggren et al., 2010; Ferreira and Chauvet, 2011b), field correlative studies (Rosemond et al., 2002; Niyogi et al., 2003; Gulis et al., 2006), and whole-stream nutrient enrichment experiments (Gulis and Suberkropp, 2003; Ferreira et al., 2006b; Benstead et al., 2009).

In streams running through poor soils, the joint action of low nutrients in leaves (see above) and low nutrients in the water are likely to limit fungal activity and biomass (Stelzer et al., 2003), with potential negative consequences for shredder feeding (Fig 1, 2d) and detrital breakdown (Fig 1, 2e, 2f). Besides nutrients, water parameters such as pH, calcium concentration, and hardness may also affect fungal enzymes (Clivot et al., 2013) and the identity and abundance of shredders such as gastropods and crustaceans (Fig. 1, 2g; Dangles and Guerold, 2001; Wantzen and Butakka, 2011).

We predict that low dissolved nutrient concentration in many areas, particularly in tropical streams, may limit microbial activity, despite the warmer temperatures. It has been proposed that, if at least one factor that influences litter breakdown is below or above optimal thresholds, litter breakdown will be retarded despite all other factors being optimal (Prescott, 2010).

Within this context, riparian vegetation may overrule the geology effect since it also has the potential to affect water chemistry and therefore the activity of aquatic hyphomycetes (Fig 1, 2h). Riparian vegetation dominated by fast-growing tree species or N-fixers are likely to produce high quality litter subsidizing soil and run-off water with nitrogen, which in turn accelerates litter breakdown (Shaftel et al., 2012). The invasion of riparian corridors by N-fixing riparian trees (with no anti-feeding defenses) is likely to' increase litter breakdown rates and the biomass and activity of microbial decomposers and shredders.

2.3 Climate-driven precipitation patterns establish scenarios for leaf quality inputs to stream reaches (Pathway 3)

An important component of climate is hydrology, chiefly water availability, which affects the composition of vegetation and, particularly, leaf traits (Fig. 1, 3a). Plants from dry zones generally have smaller, leathery leaves with high mass: surface ratios and thicker cuticles (Gallardo and Merino, 1993; Wright et al., 2001).

Recalcitrant litter is more difficult for fungal enzymes to break down (Fig 1, 3b, 3c), which may result in low fungal biomass and therefore low palatability to shredders (Fig. 1, 3d). Tough leaves are also more difficult for shredders to chew (Fig. 1, 3e; Graça and Cressa, 2010; Walpola et al., 2011). Assuming that the quality of litter is proportional to the quality of living plant tissues, the prediction here is that in areas subjected to water stress, litter quality will be low, its breakdown will be slow and the abundance of microbial decomposers and shredders will be low.

2.4 Climate defines precipitation patterns and hydrological regimes and establishes scenarios for organic matter retention and ultimately, leaf litter availability (Pathway 4)

The hydrological regime, driven by the amount and temporal dynamics of rainfall, establishes a physical setting with important effects on litter retention and thus the amount of resources available for shredders and their role in litter breakdown, particularly when decomposition is slow (Fig. 1, 4a, 4b). In the presence of medium- and fast-decomposing leaves, and continuous litter supply, leaves at several stages of microbial conditioning can co-occur and therefore shredders have access to good-quality resources. Hence, shredders can occur in large numbers and be important for litter breakdown (Fig.1, 4d). Spates can remove or diminish these resources but soon litter of good quality will be available again (Fig. 2, top).

However, if spates are frequent, retention is low, and the litter standing stock is of low quality, litter does not have time to be fully colonized by microbial decomposers and to become tender. Under these conditions, spates will be an important fragmentation agent of litter, which may be

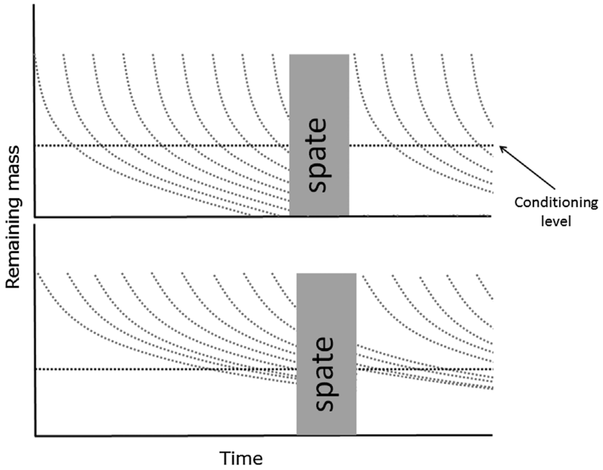

Figure 2. Conceptual representation of leaf litter dynamics in streams under constant litter supply and ocasional spates and two scenarios of litter quality/decomposition rates, with remaining mass of leaves reaching streams represented by dotted lines. When leaves fall in the water they are colonized by aquatic hyphomycetes which macerate the leaf matrix, causing its decomposition and facilitating feeding by shredders. The horizontal dotted line indicates the hypothetical moment in which leaves are fully conditioned (colonized by microorganisms and macerated) and can be consumed by shredders. In the top panel, decomposition is fast; spates may remove leaves, but soon the stream is again supplied with fully-conditioned leaves. In the low panel decomposition is slow; most of the leaves are removed from the system by spates before they are palatable for shredders.

removed from the systems before it achieves a stage capable of being used by shredders (Yule, 1996). Hence, there may not be enough time for the establishment of shredder assemblages, or enough resources to support large shredder populations. Leaf packs may then become flushed out of the system (e.g., transported downstream, deposited on banks or buried), before they are processed (Fig. 2, bottom; Fig. 1, 4d) and therefore physical fragmentation becomes the most important element of litter degradation in these systems (Fig. 1, 4e, f; Rueda-Delgado et al., 2006; Boulton et al., 2008; Wantzen et al., 2008).

2.5 Temperature affects metabolism and the rate at which microbial decomposers operate (Pathway 5)

Since rates of biological activity (e.g., metabolism) increase exponentially with temperature up to optimal temperature values (other factors being non-limiting), ecological process rates should increase towards the tropics. Indeed, litter breakdown rates are reported to be higher in warmer waters within the same region (Fabre and Chauvet, 1998; Pérez et al., 2011; Pérez et al., 2012; Martinez et al., 2014) and during the warmer seasons (Graça et al., 2001; Swan and Palmer, 2004; Ferreira et al., 2006b).

Increases in water temperature under laboratory conditions stimulate the enzymatic activity of aquatic hyphomycetes (Chandrashekar et al., 1991), fungal biomass accrual and carbon mineralization (Fig. 1, 5a; Ferreira and Chauvet, 2011b; Ferreira and Chauvet, 2011b), invertebrate food intake (Fig. 1, 5b; Vannote and Sweeney, 1980; González and Graça, 2003; Azevedo-Pereira et al., 2006) and, therefore, the rate at which leaf litter breaks down (Fig. 1, b, c; Dang et al., 2009; Fernandes et al., 2009; Ferreira and Chauvet, 2011b; Ferreira and Chauvet, 2011b). We therefore predict that, for the same conditions of resource quality and chemical environment, litter breakdown will increase with temperature, according to the metabolic theory of ecology (Brown et al., 2004).

3 Biodiversity

A large number of papers have recently investigated the function-diversity relationship (e.g., Gessner et al., 2010 and references therein), arising the question of whether diversity could be a predictor of litter breakdown. However, as we show below, the relation ship between environmental conditions, diversity of litter, fungi, shredders and litter breakdown remains unclear.

According to the 'complementarity niche hypothesis' (Loreau et al., 2001), systems with higher litter diversity would be able to support higher species richness of decomposers and detritivores than systems with lower diversity of litter resources. According to the same hypothesis, we can expect a positive relationship between species richness and function such as litter breakdown. Field and laboratory studies have found positive relationships between litter diversity and aquatic hyphomycete diversity (Rajashekhar and Kaveriappa, 2003; Laitung and Chauvet, 2005; Lecerf et al., 2005) and activity (Woodeggenschwiler and Bärlocher, 1983), as well as between litter diversity and detritivore diversity activity (Swan and Palmer, 2006). Differences in litter diversity have therefore the potential to affect heterotrophic pathways by altering decomposer and first-order consumer diversity and activity, which in turn might have an effect on breakdown rates (Lecerf et al., 2005; Riipinen et al., 2009).

However, the effect of increasing fungal species richness on litter decomposition is not clear, with laboratory studies reporting either no effect (Dang et al., 2005; Duarte et al., 2006) or a positive relationship (Bärlocher and Corkum, 2003). Changes in fungal identity seem to affect litter decomposition more than changes in fungal diversity (Duarte et al., 2006). Similarly, the effect of increases in detritivore diversity on litter consumption is often species-specific, with reports of no effects, likely due to interspecific competition (Jonsson et al., 2002; Bastian et al., 2008), or of stimulation of litter consumption (Jonsson and Malmqvist, 2000; Jonsson, 2006; Boyero et al., 2007), which can be attributed to release from intraspecific interference, niche complementarity, and/or facilitation.

In summary, we can predict how diversity of leaf substrates varies in small streams across biomes, but we cannot predict yet how diversity of litter, decomposers, and detritivores controls litter breakdown rates.

4 Conclusions

All the above evidence allows us to predict rates of litter breakdown in low order streams at large geographic scales based on climate and geology. Streams with continuous supplies of high-quality litter and streams with high dissolved nutrient concentrations (which are ultimately driven by climate and geology) may support high aquatic hyphomycete activity on leaves, thus increasing their palatability for shredders and the relative importance of this guild within the benthic community and in litter breakdown. This is the situation of most temperate deciduous and some tropical forest streams. In contrast, the predominance of poor-quality litter in streams with low nutrient levels will limit the activity of hyphomycetes on leaves, making this litter less attractive for shredders, which will become less important within the invertebrate community. This is the situation reported for several tropical streams.

The model can explain the observed differences in litter breakdown rates and the importance of shredders across wide geographic areas. It also allows for testable predictions regarding non-adjacent compartments on Fig. 1. Note that, at the local scale, other human-induced factors such as pollution (Niyogi et al., 2003; Del Arco et al., 2012) may overrule these settings. Particularly important in this context is organic pollution in nutrient-limited environments. However, these factors need specific analyses.

The extrapolation of breakdown rates from patch scale to larger geographic areas could serve as a basis to estimate the contribution of litter breakdown to large scale C fluxes. However, it is necessary to know how much of the leaf breakdown C is being converted into the forms considered in global balances (e.g., Particulate Organic Carbon-POC, Dissolved Organic/Inorganic Carbon-DOC/DIC). This important question needs to be addressed by future research efforts.

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