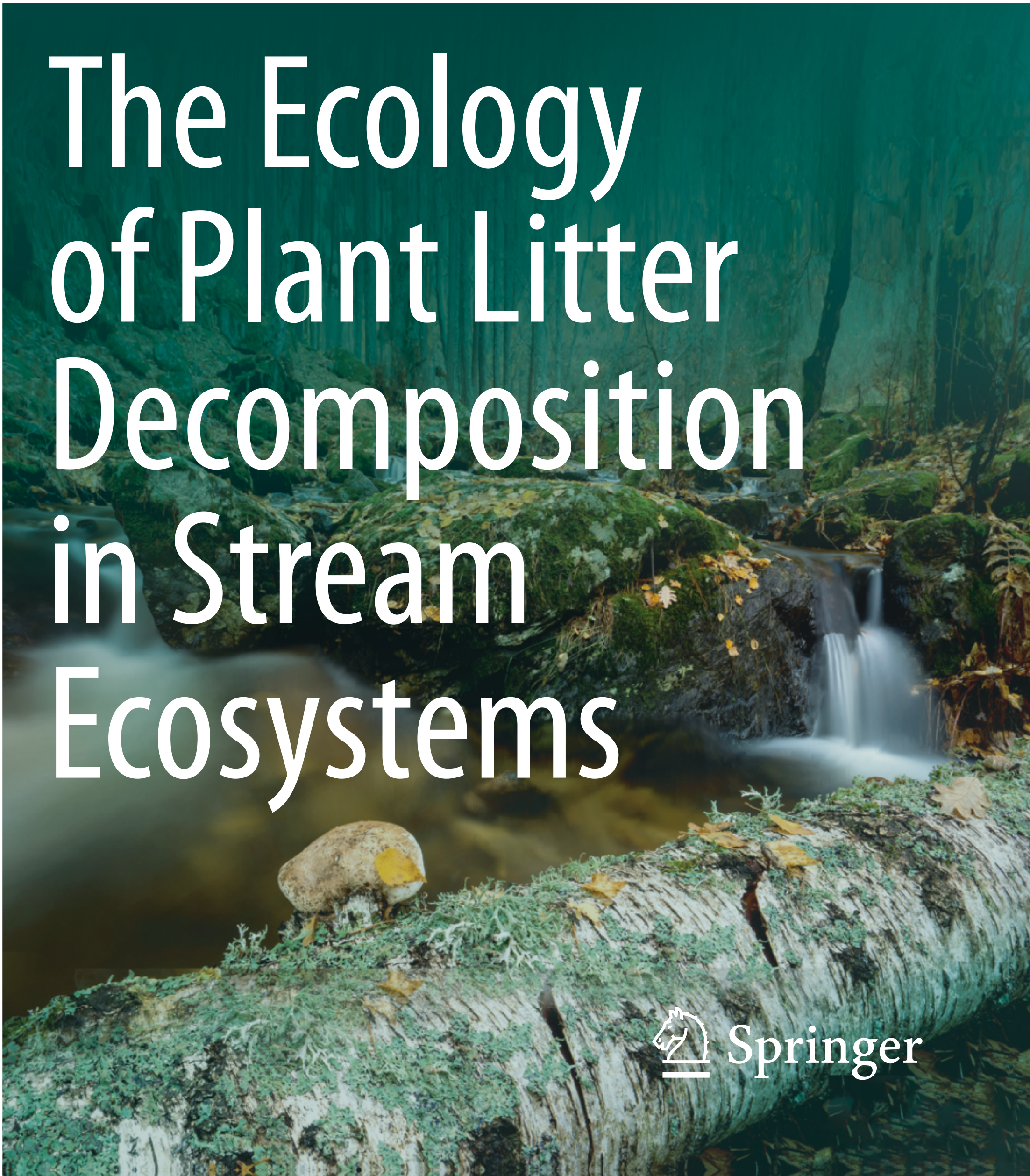
Christopher M. Swan
Luz Boyero
Cristina Canhoto *Editors*

The Ecology of Plant Litter Decomposition in Stream Ecosystems



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Editors
Christopher M. Swan
Geography and Environmental Sciences
University of Maryland Baltimore County
Baltimore, MD, USA

Luz Boyero
Faculty of Science and Technology
University of the Basque Country
Leioa, Bizkaia, Spain

Cristina Canhoto
Department of Life Sciences
University of Coimbra
Centre for Functional Ecology
Coimbra, Portugal

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Cover image: Stream flowing through birch forest in Canencia, Guadarrama Mountains, Spain
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Foreword

To what extent is knowledge about the plant litter decomposition process in streams important to the scientific community? Whoever reads this book probably knows that primary production in streams flowing through forest areas is limited, as a consequence of the scarcity of light under the tree canopy and the low concentration of dissolved nutrients. In contrast, unidirectional flows promoted by gravity move great amounts of dead plant organic matter from the terrestrial environment to the stream (vertical and lateral inputs) and within the stream (downstream transport). This plant litter represents the energetic basis to foodwebs in many streams, which are widely recognised as heterotrophic systems. The retentive capacity of a stream together with a series of physical, chemical and biological factors, determine the efficiency with which plant litter is used by detritivores and decomposers, its consequences on biodiversity, productivity and nutrient dynamics, and its interaction with global change drivers such as pollution and climate change. In consequence, it is not surprising that the plant litter decomposition process has attracted the attention of stream ecologists for decades.

The study of plant litter decomposition in stream ecosystems greatly developed since the last quarter of the past century, after the publication of several conceptual works that highlighted the relevance of terrestrial organic matter to stream functioning. Among these, “The stream and its valley” (Hynes, 1975) and “The river continuum concept” (Vannote et al., 1980) are worth mentioning. Later on, the impressive growth of research teams and scientific publications on this topic culminated in the organization of the first specialised scientific meeting in 1997: the Litter Breakdown in Rivers and Streams meeting (later renamed as Plant Litter Processing in Freshwaters, PLPF), which was held in Bilbao (Spain). The first edition was followed by others in Lunz (Austria, 1999), Szentendre (Hungary, 2002), Toulouse (France, 2005), Coimbra (Portugal, 2008), Cracow (Poland, 2011), London (United Kingdom, 2014) and, again, Bilbao (2017), coinciding with the 20th anniversary of the first meeting. The 9th edition should have already been celebrated in Braga (Portugal), but the Covid-19 pandemic has temporarily prevented it. These events have regularly and succesully joined together scientists from all over the world, demonstrating that the study of plant litter decomposition in streams continues to attract great attention from researchers, and underscoring the crucial role that this process has for our planet's biogeochemistry.

The PLPF meetings have been fruitful not only in sharing scientific findings, but also in promoting collaboration among scientists from around all the world, all working on plant litter decomposition but from different perspectives and scales, from molecular to global. This book is proof of such outcome: while not being the proceedings of a PLPF meeting, its idea came to light in the last meeting held in Bilbao. As a result, a selected group of experts has produced this state-of-the-art compendium, which reviews the basic knowledge and the progress being made in the last few decades about the process of plant litter decomposition in stream ecosystems, in the face of a changing world. Now it's time for you to enjoy it, learn from it and put it into practice!

Bilbao, Spain Jesús Pozo

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Part I

General Overview on Plant Litter Decomposition in Streams

Chapter 1
The Ecology of Plant Litter Decomposition in Stream Ecosystems: An Overview

Christopher M. Swan, Luz Boyero, and Cristina Canhoto

Abstract The decomposition of plant litter of terrestrial origin is a key process for the functioning of many stream ecosystems with notable relevance for global biogeochemical cycles. The process has received much attention in the literature but, since the iconic paper of Kaushik and Hynes (1971), we lack a comprehensive review of its patterns of variation and drivers. This book provides an updated compendium of the ecology of plant litter decomposition in streams, through 22 chapters grouped in four sections that focus on (I) the analysis of the patterns and drivers of decomposition, the importance of (II) biodiversity and (III) multiple aspects of global change, and (IV) the methodological approaches used to study litter decomposition and its applications. By summarizing decades of fruitful research, we hope this will be a reference textbook for ecologists and students that will stimulate further research and promote collaboration among researchers in this field.

Ninety percent of the global terrestrial plant biomass production ends up entering the detrital pool, supporting detritus-based food webs in both terrestrial and aquatic ecosystems (Gessner et al., 2010). Understanding how this organic matter is processed within ecosystems is of utmost importance, not only because this process underlies fundamental ecosystem services (Mancinelli & Mulder, 2015), but also

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C. M. Swan (✉)
Department of Geography and Environmental Systems,
University of Maryland, Baltimore County, Baltimore, MD 21250, USA
e-mail: chris.swan@umbc.edu

L. Boyero
Department of Plant Biology and Ecology, University of the Basque
Country (UPV/EHU), Leioa, Spain

Faculty of Science and Technology, University of the Basque Country, Leioa, Bizkaia, Spain
e-mail: luz.boyero@ehu.eus

C. Canhoto
Department of Life Sciences, Centre for Functional Ecology, University
of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
e-mail: ccanhoto@ci.uc.pt

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because it determines the amount of carbon (C) that is mineralized or sequestered, and hence potential feedbacks with the global climate (Heimann & Reichstein, 2008).

Stream ecosystems are estimated to receive, process, and transport nearly 1.9 Pg of terrestrially-derived C per year globally (Cole et al., 2007). Many streams rely on this allochthonous source of C for the maintenance of their food webs and various functions, given that primary production is often severely limited, due to the combination of high riparian shading and low nutrient availability (Vannote et al., 1980). In consequence, ‘the fate of dead leaves that fall into streams’ stands out as a major topic in stream ecology, that served as title for the seminal contribution of Kaushik and Hynes (1971), and was recently revisited in Jane Marks’ review paper (Marks, 2019).

This book intends to provide a comprehensive, contemporary compendium of the patterns (Part I), factors (Parts II and III) and approaches (Part IV) that govern the process of plant litter decomposition in streams, adding up to the several reviews available in the literature (e.g., Barlöcher & Sridhar, 2014; Boulton & Boon, 1991; Gessner et al., 1999; Graça et al., 2015; Marks, 2019; Royer & Minshall, 2003; Tank et al., 2010; Webster & Benfield, 1986), but going into much more detail, as allowed by a book format. The last few decades have seen an explosion of research addressing key questions about the ecological interactions at play in this process. A plethora of basic and applied ecological questions have been tested using plant litter decomposition as a study system, solely guided by a comprehensive book focused on litter decomposition methodological approaches, which has been recently re-edited (Bärlocher et al., 2020). The need for a complementary, more theoretical and updated approach was thought to be needed and is the rationale for this book.

The book integrates the many authors that shared and/or received the inputs of a common road of high-quality investigations presented and discussed in cozy, highly interactive and scientifically fruitful meetings—“Plant Litter Processing in Freshwaters” (PLPF). These triennially held meetings joined stream ecologists from all over the world and clearly contributed to stimulate stream ecological research, litter decomposition in particular, constituting grounds for the 22 chapters presented herein.

The expression “(plant/leaf) litter decomposition” is transversally used in this book by all authors. The majority of the book covers stream ecosystems, with a main focus on permanent headwater streams flowing through forested areas, because these are the streams that most rely on allochthonous plant litter as their main energy source (Vannote et al., 1980). However, some chapters deal with other types of streams (e.g., intermittent rivers and ephemeral streams), and some describe decomposition in terrestrial ecosystems for a comparative view.

This book is divided into four Parts that focus on different aspects of the plant litter decomposition process, namely its patterns and drivers (Part I), the role of biodiversity on litter decomposition outcomes (Part II) and on the consequences of the multiple facets and dimensions of global change on the process dynamics (Part III); the last Part considers the importance of methodological approaches and applications of this vital process, calling the attention to more mechanistic and future prospects of the presently used litter decomposition assessments and as a central tenet for human wellbeing (Part IV). We hope that this compendium of chapters, which overall review the knowledge on plant litter decomposition in streams that has resulted from decades of research, can serve as a reference textbook for ecologists and students. Furthermore, we hope that this book can stimulate further research, new lines of inquiry on this topic and promote collaboration among researchers in this field.

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Chapter 2
Multi-Scale Biophysical Factors Driving Litter Dynamics in Streams

Alan M. Tonin, José F. Gonçalves Júnior, Richard G. Pearson, Manuel A. S. Graça, Javier Pérez, and Luz Boyero

Abstract Terrestrial litter that decomposes in streams is critical to carbon and nutrient fluxes and aquatic food web dynamics. Litter dynamics is influenced by biogeochemical, morphological, environmental and climatic factors, making it challenging to understand how these factors relate to each other and to litter decomposition across different spatial scales. Here, we present a hierarchical framework that accommodates the links among a wide variety of local and regional factors (e.g., litter quality, water chemistry, flow) in relation to climate, geology, biogeography and phylogeny. These factors ultimately influence the agents or processes (e.g., microbes,

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A. M. Tonin (✉) · J. F. Gonçalves Júnior
Limnology-Aquaripária Lab, Department of Ecology, IB, University of Brasília (UnB), Brasília, Brazil

J. F. Gonçalves Júnior
e-mail: jfjunior@unb.br

R. G. Pearson
Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), James Cook University, Townsville, QLD, Australia

College of Marine and Environmental Sciences, James Cook University, Townsville, QLD, Australia

R. G. Pearson
e-mail: richard.pearson@jcu.edu.au

M. A. S. Graça
Department of Life Sciences and Marine and Environmental Sciences Centre (MARE), University of Coimbra, Coimbra, Portugal
e-mail: mgraca@ci.uc.pt

J. Pérez · L. Boyero
Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), Leioa, Spain
e-mail: javier.perezv@ehu.es

L. Boyero
e-mail: luz.boyero@ehu.eus

L. Boyero
IKERBASQUE, Bilbao, Spain

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detritivores, physical fragmentation, retention capacity) that govern litter inputs, storage and decomposition in streams. This framework highlights the dependence of litter dynamics on spatial scale and cautions against extrapolations across scales without quantifying the influence of biophysical variables on the different agents and processes. The framework can be used as a basis for experimental and observational studies of those interactions to develop broader mechanistic understanding of litter dynamics.

2.1 Streams as Hotspots of Organic Matter Processing

Fresh waters (i.e., wetlands, estuaries, lakes, rivers and streams) comprise only 0.01% of the Earth's water and approximately 0.8% of its surface area (Gleick, 1996). Yet this small fraction of global water supports a disproportionately high diversity of plants and animals (Dudgeon et al., 2006) and significantly contributes to the carbon cycle, at both regional and global scales (Cole et al., 2007; Hotchkiss et al., 2015; Raymond et al., 2013). Within fresh waters, 1st to 3rd order streams comprise over 75% of river network length (Raymond et al., 2013) and are closely linked to the terrestrial landscapes, so they are hotspots of organic matter processing because of the large amounts of terrestrial organic matter they receive, their typically low in-stream primary production, their high retentive capacity and their efficient decomposer communities (Battin et al., 2008).

Forest streams are typically net heterotrophic ecosystems, where overall stream respiration surpasses primary production (limited by riparian shading) and secondary production is fuelled by inputs of terrestrial organic carbon (Hall et al., 2000; Neres-Lima et al., 2017). Riparian vegetation, which supplies large amounts of plant litter streams and riparian soils (Tonin et al., 2017), also reduces light penetration and primary productivity in the stream, and may reduce water temperature extremes during the hottest and coldest periods of the year. The decomposition of this plant litter is the basis of key stream ecosystem processes, namely nutrient and carbon cycling and secondary production (Marks, 2019; Wardle et al., 2004). However, there are major gaps in our knowledge of organic matter dynamics in streams (e.g., timing and magnitude of inputs and biophysical factors acting on decomposition), especially in understudied areas of the world such as the tropics. For instance, little is known about the connection of litter fluxes with the otherwise well-known decomposition process, with only a few studies evaluating the inputs and outputs of litter (e.g., Fisher & Likens, 1972, 1973; Pozo et al., 1997; Webster & Meyer, 1997), despite their relevance for global carbon and nutrient cycling.

2.2 Dynamics of Litter Inputs and Storage in Streams

Terrestrial organic matter that enters streams is generally classified as coarse particulate organic matter, CPOM (>1 mm); fine particulate organic matter, FPOM

(0.45 μm–1 mm); and dissolved organic matter, DOM (<0.45 μm) (Webster et al., 1999). This material reaches streams via direct fall or lateral transport from the riparian zone. Most material is senescent, although large quantities of green leaves may reach streams in the tropics after storms (Wootton et al., 2019). In this chapter we focus on leaf litter because it is the dominant plant litter flux in streams (>60% of total fluxes of streams from different biomes, Abelho, 2001; Tonin et al., 2017), it is renewed annually, it has more rapid decomposition than woody material (Neres-Lima et al., 2017; Wallace et al., 1997) and it is the focus of most studies of decomposition in streams.

Litter falling from trees as a result of abscission or storm damage (hereafter 'litterfall') may reach the stream directly, but most litter falls to the ground, given its much larger area than that of streams. A proportion of this litter eventually is transported to streams by wind, water, gravity or animals, constituting lateral inputs to the stream. Although neglected in some litter studies, lateral inputs may represent a high proportion of total litter inputs to the stream (e.g., up to 55% in several tropical streams; Tonin et al., 2017), but not all streams (e.g., < 7%; Benson & Pearson, 1993). Lateral inputs and litterfall may differ in nutritional quality for stream consumers depending on the residence time on riparian soils, where litter undergoes physical and biological degradation (e.g., García-Palacios et al., 2016). Litter may also enter a stream reach by transport within the stream, here termed 'upstream input'.

After litter enters a stream, it can be retained by in-stream structures (e.g., rocks, roots, logs), increasing its residence time and enhancing decomposition by leaching and consumption by microbes and invertebrates. Litter may be redistributed or removed from streams by floods, although a considerable proportion may remain in pools, backwaters and debris dams. It may also be buried in sediments (e.g., in the hyporheic zone—the interface between surface stream and groundwater; Boulton et al., 1998). Here we refer to retained material as 'storage'. Litter accumulates in the streambed when inputs (i.e., litterfall, lateral inputs and upstream inputs) are higher than outputs (i.e., downstream transport and litter decomposition). The most complex of these litter fluxes is loss of litter mass by decomposition, resulting from chemical, physical and biological agents and their interactions.

2.3 Mechanisms of Litter Fluxes in Streams: Local and Regional Scales

Here, we present a framework describing the connections among litter inputs, storage and decomposition. We use a hierarchical spatial perspective to outline the links between biophysical factors that influence litter dynamics at different scales, like other frameworks of decomposition (Graça et al., 2015; Royer & Minshall, 2003), but differing in the inclusion of key related processes, components and the complexity of interactions across scales (Fig. 2.1). The framework is structured across three spatial

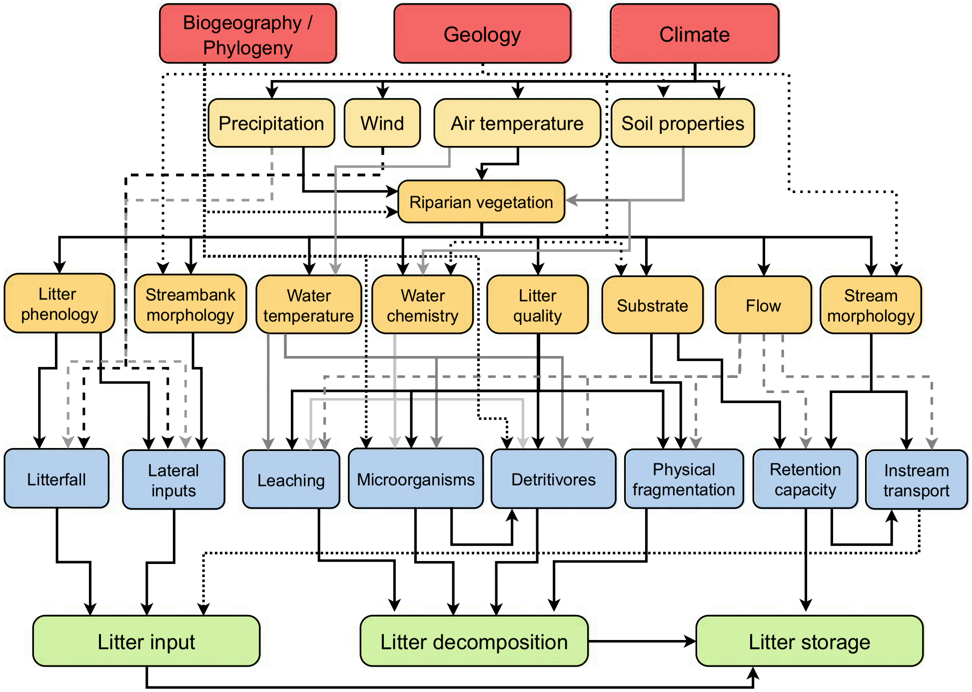

Fig. 2.1 Conceptual framework outlining the linkages of multiple biophysical factors driving litter dynamics (i.e., litter inputs, decomposition and storage; green boxes) at different spatial scales: regional (red boxes), local (orange boxes) and fine (blue boxes). Arrows of different shades or patterns (solid, dashed or dotted) are used to facilitate visual representation. This framework can apply to any chosen timeframe. Given the complexity of our conceptual framework, some linkages between factors may have not been depicted.

scales: regional, which accommodates variation in geology, climate and biogeography; local, including, for example, stream morphology, water quality and riparian vegetation identity; and fine, the scale at which many biophysical agents, such as litter fall, leaching, fragmentation consumption influence litter storage and decomposition. Most interactions within scales are not shown for simplicity (e.g., flow and stream morphology). The different components of the framework are described and expanded in the following sections. The framework is not explicitly linked to a particular timeframe, and could be applied at any time scale, from instantaneous to monthly, annual or multiannual.

2.3.1 Litter Inputs

Litter inputs are influenced by a variety of factors and their interactions, including litter phenology and production, stream and streambank morphology, precipitation, wind, retention capacity of streams and water flow. Firstly, litter production determines the amount of litterfall and depends on forest physiognomy, plant species diversity and vegetation composition and phenology, which are shaped by climatic factors, geomorphology, soils, and plant phylogeny and biogeography. Litter fall is caused by natural abscission (to conserve water or photosynthetic efficiency) and storms, which may release leaves, fruits, flowers and wood, especially in tropical regions (Benson & Pearson, 1993; Covich, 1988). Greater litterfall is expected in productive forests, which occur mostly on fertile soils and in warmer and wetter environments, such as rainforests (which also harbor higher plant diversity), than in less productive forests on infertile soils or in environments limited by water or temperature, such as cold dry forests, although the extended lifespan of leaves of evergreen tropical trees may reduce the inputs.

Secondly, streambank morphology (e.g., heterogeneity and slope) regulates lateral litter transport to the stream through its retention capacity, in relation to topography, hydrology (Leopold et al., 1992), and interactions with riparian vegetation. The heterogeneity of the streambank is determined by the presence of obstacles that hamper litter transport to the stream, such as depressions in the ground, living and dead trunks and buttresses, exposed roots, rocks and saplings and other small plants. Bank slope influences litter transport as steeper slopes facilitate litter movement by combinations of gravity, wind and enhanced surface runoff, especially during heavy rainfall. Thirdly, stream morphology and water flow affect litter inputs from upstream, through transport and retention mechanisms.

2.3.2 Litter Storage

The amount of litter stored on the streambed is regulated by interactions among three main factors: litter inputs, retention capacity of streams and litter decomposition.

Firstly, litter inputs would increase litter storage linearly if a stream retained all inputs. This might occur during periods of very low flow, but is otherwise unlikely because of high stream heterogeneity and the variable influence of flow and retention capacity.

Secondly, retention capacity determines litter storage as it reduces instream transport. The retention capacity of a stream is a function of stream morphology (e.g., width, depth, slope, sinuosity), water flow, substrate (including the type, size and quantity of retentive structures such as rocks and fallen tree trunks or branches, which may remain in the stream for years; Díez et al., 2000; Wallace et al., 1995), streambank structures (including roots and living trunks), and their interactions. Stream morphology is determined by geomorphological and hydrological processes, as well as riparian vegetation, which can provide flow resistance and increase bank strength by means of roots and woody debris (Hupp et al., 2016). Volume and velocity of water flow are influenced by precipitation and cross-sectional area and slope of the stream, which can determine whether retention structures are over-topped, and whether the stream has power to dislodge material from retention structures. In general, the retentive capacity of the streambed increases with substrate size—for example, boulders and cobbles are more efficient in retaining litter than gravel and sand (Jones, 1997). Large wood may greatly increase retention by redirecting flow and physically retaining litter directly or in pools.

Thirdly, litter decomposition decreases litter storage through the transformation of coarse litter into fine and dissolved material (Gessner et al., 1999), which is more easily transported by water flow, buried in the sediments (Webster et al., 1999) or incorporated into microbial and animal biomass. The components affecting litter decomposition are explored below. In summary, high retention is expected in small, shallow, sinuous and low-gradient streams; in low-flow conditions; and in streams with large substrates, high litter inputs and low decomposition rates. Retention is determined by the interactions among these variables.

2.3.3 Litter Decomposition

The processes that contribute to litter decomposition and affect its rate are leaching, physical fragmentation, microbial processing and detritivore consumption (Gessner et al., 1999; Marks, 2019).

2.3.3.1 Leaching

Leaching is the dissolution of water-soluble compounds from litter and may account for up to 40% of mass loss within a week of immersion, with the greatest loss typically occurring in the first 24–48 h (Gomes, 2015; Taylor & Bärlocher, 1996). However, greatest mass loss due to leaching may occur during the first 10 days of immersion in litter from some tropical plants (Gomes, 2015). Leaching is influenced by litter quality, and water chemistry, temperature, velocity and turbulence. Firstly, litter quality includes nutrient content (especially nitrogen and phosphorus), carbon recalcitrance (due to high content of lignin, cellulose and hemicellulose) and content of secondary metabolites (e.g., repellent or toxic substances such as phenols used in protection or competition by living plants). The degree of leaching may be determined by the concentration of soluble components, especially nutrients, low-mass carbon molecules and some secondary compounds, and their resistance to dissolution. For example, thick litter cuticles and superficial waxes may slow the dissolution of soluble compounds (Kuiters & Sarink, 1986; Schreeg et al., 2013). Litter quality is determined by the species composition of riparian vegetation and their physiological and morphological traits, which are influenced by climate, landscape, biogeography and phylogeny (Boyero et al., 2017; Siefert et al., 2015). Importantly, apparently similar plant communities may differ in litter quality as a result of soil characteristics (via different nutrient resorption efficiencies; Vergutz et al., 2012) or species interactions (e.g., competition for nutrients; Casper & Jackson, 1997).

Secondly, water chemistry affects leaching through variation in pH, hardness and mineral concentrations (Essington, 2005). Water hardness and mineral concentrations may affect different chemical compounds in different ways (e.g., polyphenols bind to hard-water minerals; Gebely, 2016). Water chemistry relates to lithology (i.e., characteristics of parent rock), soil properties and riparian vegetation (through regulation of dissolved inorganic and organic molecules). Thirdly, water temperature influences the solubility of molecules in the water (Chergui & Pattee, 1988). Water temperature is driven primarily by climate (through solar radiation), but riparian canopy density is also important in affecting stream shading. Finally, water flow enhances dissolution of water-soluble compounds. In summary, greater leaching is expected in litter with higher amounts of water-soluble compounds and lower protection from dissolution (e.g., absence of superficial waxes and low carbon recalcitrance), and in alkaline, warmer, faster and more turbulent waters. However, leaching is the least studied component of decomposition but compelling evidence of its importance is limited.

2.3.3.2 Microbial Decomposition

Fungi and bacteria are important contributors to decomposition and may have complementary roles (e.g., fungi facilitate the penetration of bacteria into leaf tissue). Fungi represent the largest proportion of microbial biomass (Findlay & Arsuffi, 1989; Hieber & Gessner, 2002). The contribution of microbes to decomposition is determined by biogeography and phylogeny, water temperature, water chemistry and litter quality. Firstly, biogeography and phylogeny may be responsible for community composition of fungi and bacteria (and, thus, different efficiencies in degrading leaf litter carbon), although there is controversy about the relative roles of the legacies of historical events (e.g., dispersal limitation and past environmental conditions) versus contemporary environmental conditions in shaping their communities (Martiny et al., 2006; O'Malley, 2007). Secondly, water temperature influences microorganisms by regulating the distribution of species (Dang et al., 2009), their metabolic and sporulation rates and their biomass (Ferreira & Chauvet, 2011). Thirdly, microbes increase their activity and biomass with increased availability of dissolved nutrients (through the maximization of carbon intake; Suberkropp & Chauvet, 1995), pH and alkalinity (by increasing the activity of different enzyme types associated with leaf softening and maceration; Chamier, 1987; Jenkins & Suberkropp, 1995). Microorganisms also perform better in softer litter, which is more susceptible to enzymatic degradation, and in litter that is rich in macro and micronutrients (such as calcium and magnesium) and not chemically defended (Schneider et al., 2012). Additionally, the selective feeding activity of detritivores on litter may affect microbial diversity and biomass by consuming some fungal species and rejecting others (e.g., Arsuffi & Suberkropp, 1989; Barlocher, 2005).

2.3.3.3 Fragmentation by Detritivorous Invertebrates

Detritivorous invertebrates are key organisms in litter decomposition, often responsible for a large proportion of total litter decomposition (e.g., 51–64% of litter mass loss; Hieber & Gessner, 2002), although this proportion is generally lower in tropical streams (Boyero et al., 2015; Gonçalves et al., 2007; Tonin, Hepp, et al., 2018). They consume litter directly and produce large amounts of FPOM via maceration and defaecation (Graça, 2001), which is consumed by other invertebrates (Cummins & Klug, 1979). Decomposition is affected by detritivore biogeography and phylogeny, water temperature, water chemistry, litter quality, water flow and streambed substrate. Large-scale drivers such as biogeography determine detritivore species distributions. For example, some taxa are more abundant and diverse in particular biogeographic realms (Boyero et al., 2011), including high abundance and diversity of caddisflies in the Australian realm; beetles in the Neotropics; and stoneflies and amphipods in the Palearctic. Detritivore contributions to decomposition tend to increase with their density, biomass and diversity (e.g., Jonsson & Malmqvist, 2000; Tonello et al., 2016; Tonin et al., 2014). Although detritivore density and diversity are typically higher in colder climates (Boyero et al., 2011), high biomass of efficient detritivores may compensate for lower diversity in some tropical streams (Cheshire et al., 2005; Tonin et al., 2014). Detritivore community composition may also have an effect on decomposition, mostly through the presence of efficient consumers (e.g., some caddisflies, stoneflies or amphipods; Tonin et al., 2014). Sometimes overlooked in studies of decomposition by detritivores are the larger crustaceans, which may be particularly abundant in tropical streams but not always clearly accounted for in field and laboratory experiments (Cogo & Santos, 2013). These animals may be of high biomass compared with insects and important consumers of litter in many systems (e.g., Coughlan et al., 2010; Crowl et al., 2001; Moulton et al., 2010).

Water chemistry may also shape detritivore communities. For example, some caddisfly and amphipod species are sensitive to acid waters (e.g., Dangles et al., 2004; Herrmann et al., 1993), whereas stoneflies are tolerant of them (e.g., Dangles & Guérold, 1999). Litter quality influences the consumption rates of detritivores and their C:N:P ratios, growth and survival (e.g., Graça et al., 2001; Tonin et al., 2017). They usually prefer litter that is soft and nutrient-rich (including macro and micronutrients), with low concentrations of secondary metabolites. Water flow and streambed substrate may also regulate detritivore distribution within streams, as different species occur in different substrate types (rocky *vs.* leaf litter substrates; Cheshire et al., 2005) and detritivores usually aggregate in areas of high litter accumulation, frequently in pools or backwaters, or behind retention structures (Heino et al., 2004). Therefore, litter storage and its spatial distribution often influence detritivore contribution to decomposition (e.g., Tonin, Hepp, et al., 2018). Finally, detritivores typically benefit from microbial colonization of litter (i.e., microbial conditioning; Casotti et al., 2019), because microbes increase the nutritional quality of litter and convert indigestible material into more labile compounds (Bärlocher, 1985), although fresh green leaves are consumed in some situations (Wootton et al., 2019).

2.3.3.4 Physical Fragmentation

Physical fragmentation is an important component of litter decomposition, but it can be difficult to separate its effects from those of other components, particularly from detritivore-mediated decomposition (Rader et al., 1994). Physical fragmentation depends on litter toughness, flow and flow-substrate interactions (Fonseca et al., 2013; Hoover et al., 2006). Litter toughness is increased by high concentrations of lignin, cellulose and hemicellulose. Flow affects physical fragmentation by abrading the litter surface with suspended particulate material, especially small particles, which are more likely to be transported by the current (Ferreira et al., 2006; Heard et al., 1999). Flow also causes turbulence, which may increase shear stress and enhance litter fragmentation, but there is limited information on this process.

2.4 Future Research Needs

The influence of scale is a major issue in ecology, both in terms of scientific understanding and subsequent management application (Levin, 1992). Frequently, local field studies and laboratory experiments are the only ones able to investigate patterns and processes in detail, so many decomposition studies have been undertaken at single stream sites. The major disadvantage is that conclusions cannot be confidently scaled up to generate broad conclusions. Similar studies undertaken at many sites help building a picture from which we can generalise, although the use of different methods can sometimes hinder comparisons. In response to such issues, in the last decade there has been a move to undertake parallel decomposition studies at multiple sites across the planet using standardised methods (Boyero & Pearson, 2017).

For development of general paradigms, understanding variability across scales is important (Tonin et al., 2019). Variability may be due to the physical environment operating at several scales, illustrated in the conceptual framework of Graça et al. (2015), but also to many biotic variables operating at fine scales, such as intraspecific competition (Boyero & Pearson, 2006), resource partitioning (Tonin, Pozo, et al., 2018), presence of large crustaceans (Coughlan et al., 2010), predation (Boyero et al., 2008), litter diversity (Bastian et al., 2008), decomposer diversity (Bastian et al., 2008), life cycle (Nolen & Pearson, 1992) and size or developmental stage (Nolen & Pearson, 1993). A hierarchical approach is required, preferably in several regions that may be regarded as representative globally. A limited number of detailed but biogeographically restricted studies of this nature have been undertaken in examination of diversity (e.g., Heino et al., 2018) and decomposition processes (Rezende et al., 2014; Tiegs et al., 2009; Tonin, Hepp, et al., 2018). Such hierarchical studies might provide a biogeographical, geomorphological and geological basis for developing a classification of streams relating to food webs, in a more globally inclusive scheme than, for example, the river continuum concept (Vannote et al., 1980), recognising that it is difficult to apply a single conceptual framework to all lotic systems.

Tank et al. (2010), in an extensive review, nominated a number of areas where more information was required on the dynamics of organic material in streams. A decade later, these gaps largely remain, particularly when considering issues at different scales. They include understanding of the dynamics and importance of dissolved organic matter, materials and energy budgets, inputs from floodplains and retention/transport generally. Those that we have highlighted above and others directly relevant to the decomposition process include: improved models of litter budgets (inputs, transport, storage) across scales; rates of organic matter decomposition across scales and biomes (mostly tropical ones), despite major advances in the last 10 years; multiple biophysical influences on decomposition; types of litter other than leaves (flowers, fruits and especially wood) across scales; fate of fine particulate organic matter (mineralization and incorporation in food webs); influence of variation within species and within individual trees in leaf chemistry on processing rates at different scales; effects of anthropogenic changes on litter inputs, decomposition and storage, which is an expanding field but has no systematic approach at the global scale (includes vegetation clearing, exotic species, species invasion, agriculture, urbanisation and changes in temperature and hydrology with climate); development of spatially explicit models at large scales (e.g., ecoregions, biomes), which provide the opportunity to formulate new hypotheses; and development of general models/frameworks of litter dynamics across scales, as elucidated in this paper. We look forward to future global experiments, meta-analyses and syntheses towards developing a more comprehensive framework that will enhance our understanding of the variable importance of organic matter and its sources in stream ecosystems, providing the capacity to predict effects of environmental change and inform improved management.

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Chapter 3
Stoichiometry of Plant Litter Decomposition in Stream Ecosystems

Michael Danger, Julio Arce-Funck, Miriam Beck, Clément Crenier, Vincent Felten, Ziming Wang, and Florence Maunoury-Danger

Abstract Ecological stoichiometry is an approach of ecology aimed at understanding the causes and consequences of elemental imbalances in nature (mainly focusing carbon, nitrogen, and phosphorus), from molecular to ecosystem levels. Like most detritus in nature, plant litters are nutrient depleted, and both microbial decomposers and detritivores are exposed to large stoichiometric constraints. These nutritional constraints will ultimately control litter decomposition rates, nutrient mineralization, and affect, in turn, decomposers' community structures. To consider such stoichiometric constraints could greatly help understanding the functioning of detritus-based ecosystems. In this chapter, focused on leaf litter, diverse examples of stoichiometric constraints at play at the detritus-decomposer interface in aquatic ecosystems are presented. The different steps involving stoichiometric processes and ultimately conducting to litter decomposition, from the production of leaf litter in the riparian zones of freshwater ecosystems to its incorporation in aquatic food webs and its potential recycling in freshwater ecosystems are discussed. Stoichiometric constraints arising between detritus and decomposers in freshwater ecosystems are then placed into the context of current global change. Finally, we highlight

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M. Danger (✉) · J. Arce-Funck · M. Beck · C. Crenier · V. Felten · Z. Wang ·
F. Maunoury-Danger
Université de Lorraine, CNRS, LIEC, 57000 Metz, France
e-mail: michael.danger@univ-lorraine.fr

LTSER France, Zone Atelier du Bassin de La Moselle, Vandoeuvre-lès-Nancy, France

M. Beck
e-mail: miriam.beck@univ-lorraine.fr

V. Felten
e-mail: vincent.felten@univ-lorraine.fr

Z. Wang
e-mail: ziming.wang@univ-lorraine.fr

F. Maunoury-Danger
e-mail: florence.maunoury-danger@univ-lorraine.fr

M. Danger
Institut Universitaire de France, Paris, France

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the limits of the stoichiometric approach as well as some complementary approaches and perspectives of work are proposed.

3.1 Ecological Stoichiometry: Conceptual Bases in Detritus-Based Ecosystems

Ecological stoichiometry is an approach of ecology aimed at understanding the causes and consequences of imbalances between several chemical elements during organisms' interactions and ecological processes, from molecular to ecosystem levels (Elser et al., 1996; Sterner & Elser, 2002). It relies on the observation that all living organisms are composed of the same chemical elements (e.g., carbon (C), nitrogen (N), phosphorus (P), iron (Fe), silica (Si), potassium (K), etc.) in more or less important and variable amounts. Ecological stoichiometry approaches then consider the elemental compositions (often expressed as molecular elemental ratios, for example C:N or N:P ratios) of basal resources and living organisms involved in ecological interactions. Any mismatch between consumer requirements and elements available in their resources constitutes a stoichiometric constraint that can alter consumers' life history traits (survival, growth, reproduction), nutrient transfer efficiency and ecosystem productivity, but also nutrient recycling (Cebrian et al., 2009; Sterner & Elser, 2002; Vanni, 2002). It can also be efficiently applied to community ecology, since stoichiometric constraints alter competitive interaction outcomes between species and participate to shape community structures (Moe et al., 2005; Tilman, 1982). Taking explicitly into account the couplings between biogeochemical cycles and organisms via chemical elements, ecological stoichiometry permits to relate several sub-disciplines of ecology, such as ecophysiology, population and community ecology, and ecosystem ecology.

Although formalized quite recently (Sterner & Elser, 2002), ecological stoichiometry finds its origin in much older approaches. As early as 1925, Lotka in his book entitled *Elements of Physical Biology*, evoked the importance of considering the elemental composition of living organisms in the study of their interactions and their impacts on their environment. Results from Redfield (1958) then largely questioned the couplings between elements in organic matter and their importance for biogeochemical cycles. In 1986, Reiners first proposed a mechanistic view of the connections between the elemental composition of organisms, environmental constraints, and ecosystem processes. This approach has then been successfully tested into diverse ecosystems, from lakes and rivers to marine and terrestrial ecosystems (Sterner & Elser, 2002). Despite the apparent generality of ecological stoichiometry concepts, most studies have been restricted to the plant—herbivore interface. Fewer studies investigated the importance and the impacts of stoichiometric constraints for upper trophic levels (predators) and for detritus consumers. While stoichiometric constraints are expected to be reduced at higher trophic levels due to the higher