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Revisiting the Fates of Dead Leaves That Fall into Streams

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Abstract

As terrestrial leaf litter decomposes in rivers, its constituent elements follow multiple pathways. Carbon leached as dissolved organic matter can be quickly taken up by microbes, then respired before it can be transferred to the macroscopic food web. Alternatively, this detrital carbon can be ingested and assimilated by aquatic invertebrates, so it is retained longer in the stream and transferred to higher trophic levels. Microbial growth on litter can affect invertebrates through three pathways, which are not mutually exclusive. First, microbes can facilitate invertebrate feeding, improving food quality by conditioning leaves and making them more palatable for invertebrates. Second, microbes can be prey for invertebrates. Third, microbes can compete with invertebrates for resources bound within litter and may produce compounds that retard carbon and nitrogen fluxes to invertebrates. As litter is broken down into smaller particles, there are many opportunities for its elements to reenter the stream food web. Here, I describe a conceptual framework for evaluating how traits of leaf litter will affect its fate in food webs and ecosystems that is useful for predicting how global change will alter carbon fluxes into and out of streams.

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1. INTRODUCTION

Fluxes: transfers between pools; also known as flows

Leaves and branches that fall from riparian trees dominate the carbon budgets of most streams (Marcarelli et al. 2011) (**Figure 1**). Although algae also pump carbon into these systems through photosynthesis, annual respiration exceeds photosynthesis in most freshwaters, and microbial decomposition of terrestrial detritus in streams drives a net global efflux into the atmosphere of 2.1 Pg C/year (Battin et al. 2009, Raymond et al. 2013). Most detrital carbon entering streams is respired by stream microorganisms (Marcarelli et al. 2011), but a small yet vital flux fuels a macroscopic food web (Wallace et al. 2015), from detritivores and predatory invertebrates to fish and amphibians within the stream, and to amphibians, reptiles, birds, and mammals in the surrounding riparian landscape (see the sidebar titled Detritivores and Decomposers). Detrital inputs profoundly influence both the food webs and the carbon and nutrient economy of streams and rivers. How this influence unfolds depends on the "Fate of Dead Leaves That Fall into Streams," the title of a perspective published nearly half a century ago (Kaushik & Hynes 1971), revisited here to emphasize that alternative pathways to different fates are shaped by traits and interactions of leaves, microbes, and macroinvertebrates, all sensitive to a changing environment.

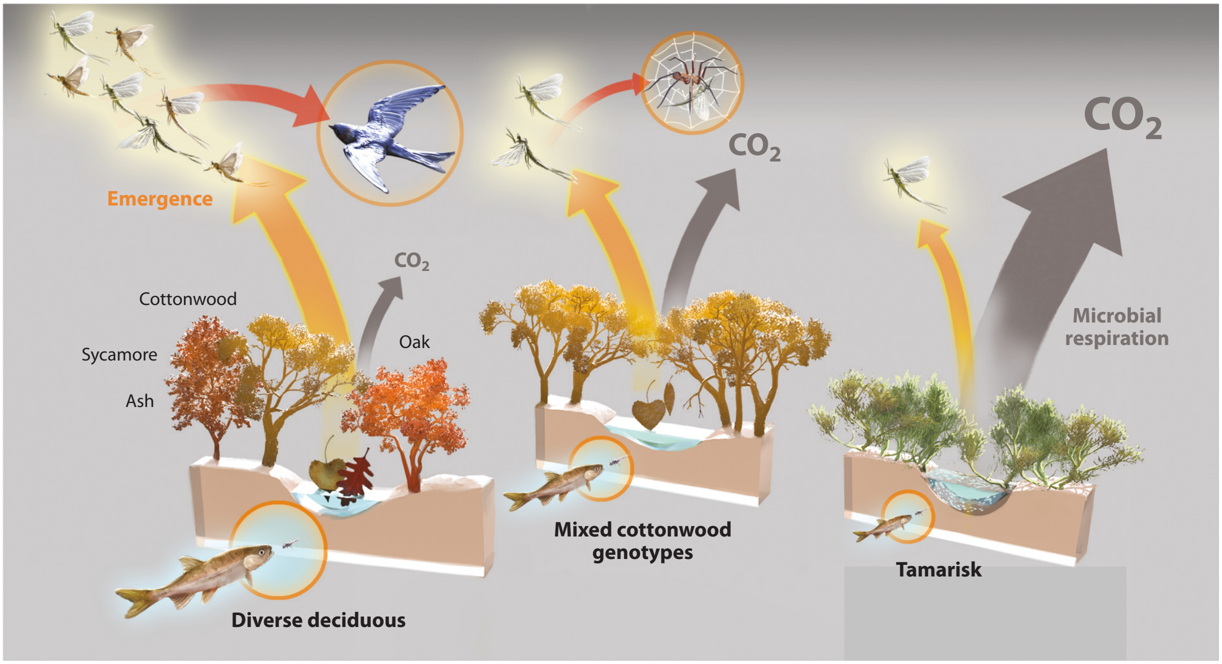

Figure 1

Terrestrial and aquatic ecosystems are linked by inputs of terrestrial litter and exports of aquatic insect emergence to watersheds. The traits of dead leaves that fall into rivers affect the rates and pathways of element loss from decomposing litter. These rates and pathways in turn determine the fate of leaf elements: whether they are sequestered in stream sediments, respired off as carbon dioxide (CO_2) by rapid microbial respiration, or transferred up food webs to nourish macroscopic stream biota. Diverse plant assemblages have both labile and refractory litter and can provide a more continuous resource supply for macroinvertebrates throughout their life cycles. Enhancing carbon fluxes to freshwater food webs not only supports aquatic predators but also fuels increasing insect emergence, an important energy flux to predators in riparian zones. In some cases (e.g., hybrid zones of riparian cottonwood forests), intraspecific genetic diversity affecting the lability of leaves is high enough to prolong carbon fluxes to macroinvertebrates (Compson et al. 2018). As riparian plant diversity decreases (e.g., when diverse native vegetation is replaced by rapidly decomposing invasive plants, like tamarisk in the southwestern United States), fluxes of carbon to stream invertebrates decrease, with concurrent increases in microbial respiration and loss of litter carbon as CO_2 to the atmosphere. Illustration by Victor Leshyk and Abigail Downard.

DETRITIVORES AND DECOMPOSERS

Detritivores are primarily insects, crustaceans, and protists that feed on detritus using mouth parts to macerate and transform material into smaller particles. Detritivores are also classified into functional feeding groups based in part on the size of the particles that they ingest (see **Figure 2**).

Decomposers are organisms that use dead organic matter (detritus) as an energy source and for minerals and nutrients, in the process breaking the detritus down into smaller particles or minerals. In streams, the primary decomposers are microbes (fungi and bacteria) that secrete extracellular enzymes to biochemically transform the organic matter into forms assimilable by the cell, where they are further transformed during metabolism. Both detritivores and decomposers are important in the process of decomposition, the breakdown of dead organic matter.

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Despite the complexity of controls and outcomes of the interactions between dead leaves and the micro- and macroorganisms that shape the ecology and biogeochemistry of streams (**Figure 2**), most research on the fates of leaves in streams has focused just on rates of litter decomposition. This rate has been well studied because it can be easily measured and its controls can be consistently detected (Boyero et al. 2016, Tiegs et al. 2019). Yet, this integrated rate masks the variety of the fates of the elements in litter as they follow different pathways through food webs and ecosystems. Both rates and pathways determine the fates of detritus in streams and its contribution to higher trophic levels, food webs, and ecosystem processes (Gessner et al. 1999). Rates of element loss from litter and the pathways these elements follow vary among leaf types (Compson et al. 2018, Siders et al. 2018) (**Figure 1**). Vascular plants living near or along the water's edge can differ markedly in biochemical, physical, and ecological traits in ways that strongly influence elemental fluxes through stream ecosystems (Ferreira et al. 2016, Siders et al. 2018) (**Figure 1**). Differences in the chemical and mechanical properties of different leaves

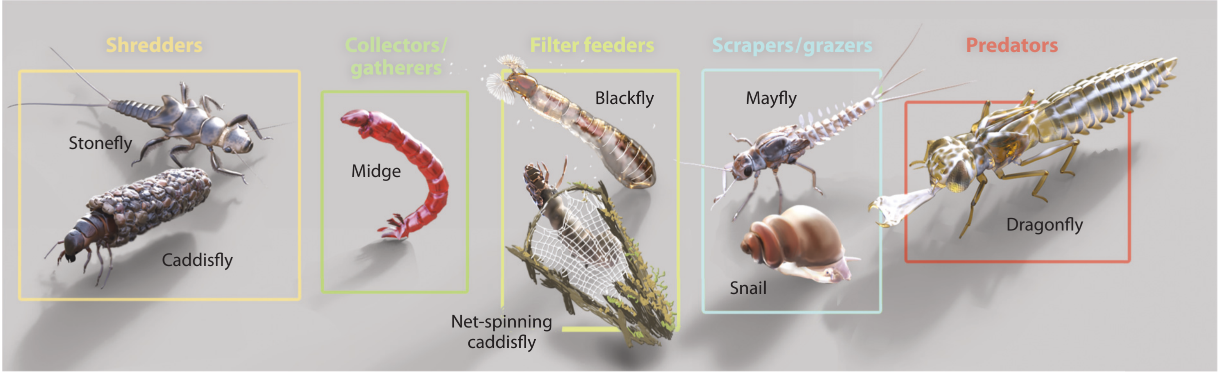

Figure 2

Stream macroinvertebrates are classified into functional feeding groups on the basis of the size and type of food they consume. Many macroinvertebrates have mouth parts or feeding structures that help them consume specific foods. For example, net-spinning caddisflies collect particles in their nets, and predatory dragonflies capture prey with prehensile mouthparts. Particulate organic matter is classified by particle diameter as coarse (CPOM, >1 mm), fine (FPOM, 0.5 μm—1 mm), or dissolved (DOM, <0.5 μm). Shredders consume CPOM (primarily leaves), collectors/gatherers consume FPOM deposited on the stream bed, and filter feeders consume FPOM and DOM from the water column. Scrapers/grazers eat attached biofilms such as algae, and predators eat other animals. Taxa shown are representative members of each group. Although diet and stable isotope studies indicate that many invertebrates are omnivores that feed opportunistically on detritus, other invertebrates, and algae, functional feeding groups remain useful for investigating their ecology. Illustration by Victor Leshyk and Abigail Downard.

affect how they are processed by different microorganisms, which in turn affects losses to the atmosphere and transfers to higher trophic levels (Wallace et al. 2015) along with residence times of carbon in the stream (Rosemond et al. 2015).

Here, I review our current knowledge about the rates and pathways of element losses from leaf litter in streams. First, I consider the ecological and ecosystem consequences of variation in detrital inputs to streams and rivers. I revisit some old concepts and terms that warrant rethinking. Second, I review more recent results derived from new tools that combine stable isotope tracers with genomics and molecular biology to elucidate the rates and pathways of element flow through microbes in natural environments. Third, I discuss how rates and pathways of element flow from litter inputs to streams may shift under global change, with marked consequences for food webs and the carbon and nutrient economy of running waters. Finally, I present future issues that will advance our understanding of stream ecosystems.

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2. RETHINKING LITTER QUALITY

Leaf litter is broken down by microbes, macroinvertebrates (**Figure 2**), and sometimes vertebrates, and differences in litter characteristics can determine whether elements bound in litter fuel higher trophic levels or are lost from the ecosystem via export, burial, or respiration. Traditionally, in both terrestrial and aquatic biogeochemistry literature, more rapidly decomposing leaves have been considered to be of higher quality (Melillo et al. 1982, Hobbie 2000). By associating quality with decomposition rate, however, the apparent value of litter increases with its rate of disappearance, regardless of its fate: transfer to higher trophic levels, to sediment organic matter reservoirs, to microbial biomass, to dissolved organic matter (DOM), or to the atmosphere as carbon dioxide (CO_2). The word "quality" is value-laden and does not address that quality may differ for bacteria, fungi, and invertebrates; that elements bound in litter (e.g., carbon, nitrogen, phosphorus) typically cycle somewhat independently (Halvorson et al. 2017a); and that different organisms may be limited by different elemental resources. For these reasons, the term litter quality should be abandoned. It oversimplifies and fails to distinguish the multiple pathways and fates of elements in leaf litter and their effects on organisms. Moving beyond litter quality, research can focus on how traits of litter influence the subsequent flow paths of its elements through aquatic food webs. In contrast to the commonly held view that slowly decomposing leaves are of poor quality, recent research has demonstrated that leaf traits that slow decomposition can promote more transfer of carbon to macroscopic consumers, whereas rapidly decomposing high-quality litter supports microbial rather than macroscopic productivity (Fuller et al. 2015, Siders et al. 2018).

2.1. Beyond the Peanut Butter on the Cracker Analogy

A common analogy among stream ecologists is that the microbial biofilm that develops on decomposing leaves is the nutritious peanut butter on the less nutritious cracker, so conditioning (growing this biofilm) increases element flow from litter to insects (Cummins 1974). Element ratios (C:N, C:P) of microbes are much lower than those of the litter itself and better meet macroinvertebrate stoichiometric demands (Cross et al. 2003). Invertebrates often prefer and grow faster on litter after it has been colonized by microbes. But the analogy fails for several reasons. First, peanut butter does not eat the cracker in the way that microbes eat the leaves. Microbes compete with invertebrates for carbon and other elements and can produce defensive compounds that deter macroinvertebrate feeding (Bärlocher 1982, Suberkropp 1992, Danger et al. 2016). Rapid microbial decomposition can also cause rapid element loss from litter to the atmosphere or water column, short-circuiting its transfer to higher trophic levels. If leaves are crackers, the microbial spreads in reality might range from high-fat peanut butter to sugar-laden jams, vitamin-rich vegemite, or inedible or toxic axle grease, with a broad range of nutritional values. Understanding interactions between microbes and invertebrates feeding on leaves requires that we recognize their diverse roles, as facilitators, as prey, or as competitors.

Litter toughness: the physical strength (resistance to fracture) of a senesced leaf; increased by factors like cuticle size or the amount of lignin

2.2. Microbial Sinks or Links

In all ecosystems, microbes can function as sinks or links (Sherr et al. 1987). Microbial sinks divert carbon and nitrogen in detritus to sediments or to the atmosphere and away from macroscopic food webs. Microbial links, in contrast, facilitate the transfer of these elements to macroscopic consumers at higher trophic positions (Sherr et al. 1987). Identifying the microbial and macroorganismal taxa, traits, and interactions, as well as the environmental contexts that make microbes sinks or links for litter-based stream food webs, is another important research direction. If microbes deplete the energy and nutrient content of decomposing litter and are also inaccessible as prey to higher trophic levels (i.e., trophic cul-de-sacs), they will function as sinks in food webs. If, however, decomposing microbes are packaged into units that larger invertebrates can eat, they could be links fueling higher trophic levels. In lakes and oceans, pelagic bacteria act as links. They flocculate dissolved organic compounds, primarily from algal exudates, making them available to small eukaryotic filter feeders (Pomeroy 1974), which shunt energy and nutrients back into the macroscopic food web. Benthic microbial assemblages processing organic material along heterogeneous stream beds likely live in a more complex world. Steep redox, flow velocity, and light gradients cause these benthic microbes to play more diverse roles as they shunt organic matter into or out of the macroscopic food web (Meyer 1994).

3. RATES AND PATHWAYS OF ELEMENT LOSS FROM LITTER

3.1. The Rate of Decomposition

Decomposition rates vary predictably with the physical and chemical traits of the litter itself, and this variation occurs both between and within plant species (e.g., Webster & Benfield 1986, LeRoy et al. 2007, García-Palacios et al. 2016). Refractory carbohydrates (lignin, tannin, and phenol) slow decomposition, whereas decomposition speeds up with increased labile carbohydrates (sugars) as well as macronutrients (nitrogen and phosphorus), micronutrients (calcium and magnesium), and specific leaf area, an inverse measure of leaf toughness (Cornwell et al. 2008). Litter toughness reduces decomposition and is postulated to be one factor explaining the paucity of shredders in tropical rivers (Graça & Cressa 2010). Litter traits are also influenced by the plant's environment. Like herbivores, the growth of decomposers is often limited by nitrogen or phosphorus rather than by carbon (Sterner & Elser 2002). Higher litter C:N caused by increases in atmospheric CO_2 concentration can reduce decomposition in streams, whereas nutrient enrichment of soils generates litter with higher nitrogen concentration and lower C:N, stimulating aquatic decomposition (Tuchman et al. 2002, LeRoy et al. 2012). Phylogenetically determined leaf traits can, however, override environmental factors in determining how leaf traits affect decomposition rates (LeRoy et al. 2012).

Hundreds of studies have documented differences in decomposition rates in streams caused by variation in leaf type. The consequences of these differences for the fate of litter-derived elements in ecosystems, however, are not as well studied, despite calls to go beyond mass loss and quantify the pathways that decomposition products follow after their release from litter (Gessner et al. 1999, Hieber & Gessner 2002). Partitioning element fluxes into different products is challenging, because complex primary and secondary pathways sequentially transform one product into another (**Figure 3**). What rules govern the fate of elements released from leaf litter?

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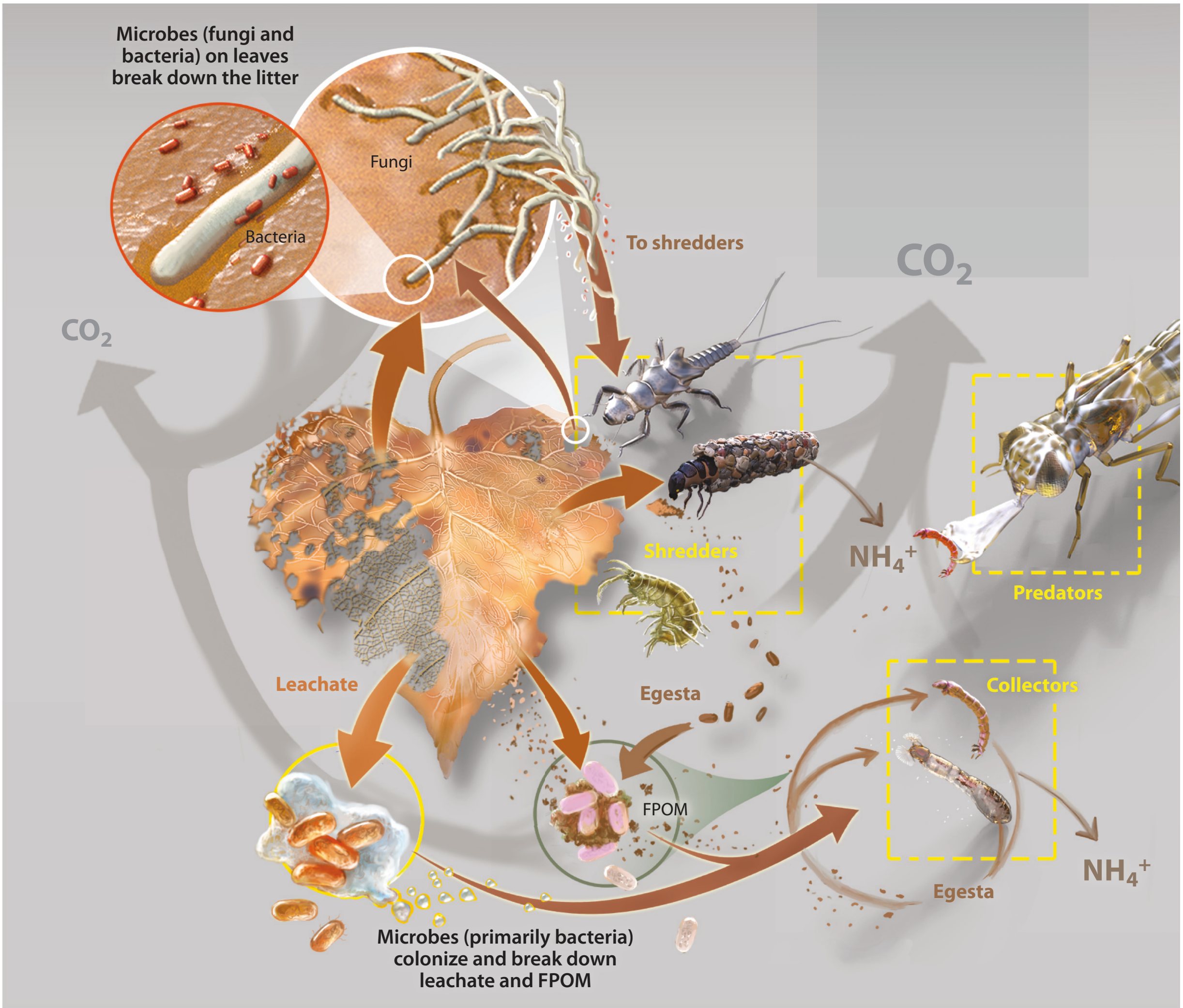

Figure 3

Carbon and nitrogen bound in litter follow multiple pathways, ultimately ending in mineralization [conversion of organic molecules to inorganic carbon dioxide (CO_2) and ammonium NH_4^+]. Prior to mineralization, elements pass through one or many decomposition products that include leachate, fungi, bacteria, protists, macroinvertebrates, and fine particulate organic matter (FPOM). Organically bound atoms can be recycled multiple times through alternative pathways before being mineralized. Most carbon bound in litter is quickly respired by microbes that break down leaves, leachate, and FPOM, but the small fraction that is taken up by protists or invertebrates supports a diverse and productive food web. Shredders feed directly on leaves and associated microbes, but their assimilation is low, and most detritus that passes through their guts is egested, entering the pool of FPOM. Microbes feeding on FPOM or leachate function either as sinks by mineralizing elements or as links by recapturing elements and transferring them to collectors/gatherers or filter feeders. Leaf litter traits and environmental conditions influence the relative strengths of these pathways. Illustration by Victor Leshyk and Abigail Downard.

3.2. Where Does It Go? Pathways of Element Flow

Litter breaks down or decomposes via processes that occur sequentially or simultaneously, including leaching, mineralization by microbes, macroinvertebrate consumption, and fragmentation (**Figure 3**). The three primary breakdown products—leachate, fine particulate organic

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matter (FPOM, 0.5 µm–1 mm diameter), and inorganic matter (e.g., CO_2, NH_4)—and the three agents—bacteria, fungi, invertebrates—are ubiquitous across leaf types, but the relative amount of each differs with litter type and stream environment (Gessner et al. 1999). In addition, meiofauna, particularly protists, are now recognized as important components of decomposer guilds (Dopheide et al. 2011, Risse-Buhl et al. 2012). Ultimately all elements are mineralized and recycled, but the rate of mineralization depends on the route that elements take through living organisms and abiotic pools. Understanding how rate affects fate is germane to predicting which litter and decomposer traits will promote different pathways.

Transfers and transformations from one pool to another can be rapid. Leachate can turn into bacterial biomass or be respired as CO_2 within hours. Microbes are consumed by meiofauna or macroinvertebrates, which incorporate elements into their tissues but also excrete, egest, or respire them. Macroinvertebrates are eaten by predators or emerge as winged adults and can enter terrestrial food webs. Because decomposition is relatively rapid in streams, much of the carbon and nitrogen bound in leaves is mineralized within a year of leaf fall. Once mineralized, nutrients spiral as they are advected downstream as solutes, captured and assimilated from the water column into benthic biomass, temporarily retained, then mineralized back into solutes to travel farther downstream in the water (Newbold et al. 1981). Below, I summarize major breakdown products of dead leaves (sensu Gessner et al. 1999), with an emphasis on pathways that create microbial sinks or links and discuss how litter type affects these pathways.

Mineralization: the biological process converting organic matter to mineral forms; mineralization generates carbon dioxide (CO_2), ammonium ($NH_4{}^+$), phosphate ($PO_4{}^{3-}$), sulfate ($SO_4{}^{2-}$), and other molecules

Leachate: the suite of organic compounds that dissolve when a leaf is immersed in water (e.g., leachate is produced when making tea)

Pools: reservoirs of materials (elements, compounds, energy) in an ecosystem

Deposit feeders: animals that feed on material associated with benthic sediments

Quantitative Stable Isotope Probing (qSIP): a technique for measuring the isotopic composition of specific nucleic acid sequences that can be used to estimate microbial species growth rates

3.2.1. Leachate.

Leachate (DOM) is rapidly generated, quickly decomposed, and believed to be primarily a trophic sink because dissolved compounds are unavailable to shredders (**Figure 2**). Most labile leachate is quickly respired by microbes. Labile organic molecules are lost as DOM within the first 48 hours after litter immersion, accounting for almost one-third of low-molecular-weight DOM in streams in the fall and winter (Meyer et al. 1998). The fluxes connecting dissolved organic carbon (DOC) from leaves to higher trophic levels may be underestimated, however (Meyer 1994). When bacteria that consume DOM are preyed upon by meiofauna, some of this energy may be shunted back into the food web (Meyer 1994). Low-molecular-weight compounds are a small fraction of the total DOC pool but may account for most of bacterial productivity transferred up aquatic food chains by heterotrophic flagellates and ciliates (Berggren et al. 2010). Leachate with more recalcitrant molecules can be exported downstream (Kaplan & Bott 1983, Wymore et al. 2015). Across litter types, leaching accounts for 5–45% of the dry mass lost to decomposition (Strauss & Lamberti 2002). DOC molecules can form aggregates large enough to reenter the macroscopic food web through filter feeders; these aggregates are also more susceptible to sinking into sediments where they can be stored or picked up by deposit feeders. The chemical composition of leachate differs across leaf types, affecting its lability (Strauss & Lamberti 2002, Wymore et al. 2015). Bacterial species discriminate among leachate types, determining in part whether carbon is respired, transferred to higher trophic levels, or transported downstream (Wymore et al. 2018).

3.2.2. Microbes.

Microbes (bacteria, fungi, and protists) are integral to litter breakdown at every stage (**Figure 3**). Fungi account for 60–99% of total microbial biomass on large litter particles, with most estimates at more than 90% (Baldy et al. 1995, Findlay 2010). Microbes enter the water with the leaf or colonize quickly after leaf fall, having first access to the energy and elements contained in the litter before invertebrates colonize (Suberkropp & Klug 1980). Quantitative stable isotope probing (qSIP), which differentiates microbes that are actively replicating from dormant cells (Hungate et al. 2015, Hayer et al. 2016), revealed in one study that 80% of growing fungi were species that entered the stream with the leaf (J.C. Marks, unpublished data), giving these species a head start before other aquatic consumers arrive. Fungi produce many extracellular enzymes that break down complex compounds (Suberkropp 1992) and contain essential nutrients for invertebrates not found in the dead plant tissue (Torres-Ruiz et al. 2007, Wallis et al. 2012, Funck et al. 2015, Danger et al. 2016). Bacteria, in contrast, mostly colonize from the sediments or water column after fungal breakdown commences (J.C. Marks, unpublished data). Fungi facilitate colonization by bacteria by breaking down recalcitrant molecules into more labile compounds and by causing leaves to disintegrate into smaller particles with higher surface areas (Suberkropp 1992, Gessner & Chauvet 1994). As they penetrate leaves, fungal mycelia can also deliver bacteria to otherwise inaccessible leaf tissue (Kohlmeier et al. 2005). As leaf particle size decreases, bacteria become more dominant in the decomposer guild (Findlay 2010). Extracellular polysaccharides (also known as exopolysaccharides) produced by bacteria, fungi, and algae are ubiquitous in freshwaters. They form the amorphous slime that binds cells together in biofilms. Exopolysaccharides are typically overlooked in stream food webs but can account for ten times more biomass than actual cells, dominating the carbon pool of microbial mats and forming a significant flux of organic matter to invertebrates (Couch et al. 1996, Hall & Meyer 1998).

Mycelia: fungal filaments that grow on the surface and interior of dead leaves

Conidia: spores produced by fungi through mitosis (asexual reproduction); traditionally, aquatic fungal species were identified by the shape of their conidia

Microbial biomass and productivity are generally higher on faster decomposing litter (Gessner & Chauvet 1994, Pastor et al. 2014). Different litter types promote the growth of different microorganisms (Nikolcheva & Bärlocher 2005, Marks et al. 2009), with some evidence that bacteria:fungi ratios are higher on rapidly decomposing litter types (Wymore et al. 2013, Pastor et al. 2014). These differences likely affect pathways of element flow to higher trophic levels and as such are central to predicting the roles of microbes as sinks or links in stream food webs. Molecular tools are revealing far more diversity in fungal taxa than was described by identifying fungi by the conidia/spores they produce (Nikolcheva & Bärlocher 2005, Duarte et al. 2015, Seena et al. 2019). Results from qSIP, however, indicate that, of the 150 fungal species living on submersed leaves and identified with next-generation sequencing, only 34% were actively dividing, demonstrating that many fungal cells on leaves are dormant (J.C. Marks, unpublished data). Molecular databases for aquatic fungi are rapidly growing (Seena et al. 2019) and will be instrumental in discerning the influence of different taxa on the pathways of element flow during decomposition.

Protists (unicellular eukaryotes including ciliates, flagellates, and amoebae) graze biofilms or capture particles in the water (Weitere et al. 2018). Protist grazing reduces microbial biomass, particularly bacteria, but can also indirectly increase microbially mediated decomposition by rapidly recycling nutrients (Ribblett et al. 2005, Wang et al. 2009). Protists alter the morphology of microbial mats, stimulating bacterial turnover by burrowing, digging, and increasing rugosity, porosity, and surface area, thereby promoting nutrient and gas exchange (Böhme et al. 2009, Dopheide et al. 2011, Risse-Buhl et al. 2012). Protists become a conduit transferring elements from leaves to higher trophic levels if macroinvertebrate collectors (**Figure 2**) feed on them (Ptatscheck et al. 2017).

Many microbes, however, are defended against grazing. Filamentous growth forms and large colonies allow bacteria to escape in size from small protozoan grazers. Exopolysaccharide capsules protect bacterial cells from consumption and digestion in the gut (Matz & Kjelleberg 2005), and the same mechanism is likely effective in open environments as well. Some bacteria produce defensive compounds internal to cells or released into the environment (Matz & Kjelleberg 2005). Through quorum sensing, bacteria cells communicate by secreting and sensing chemical signals, enabling populations to produce and excrete defensive compounds collectively to deter grazing (Matz & Kjelleberg 2005). Small protists and large macroinvertebrate shredders can detect and avoid defensive compounds in bacteria and fungi, preferentially eating more palatable taxa (Suberkropp 1992).

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3.2.3. Invertebrates. Macroinvertebrates consume and recycle organic matter and are the primary link to higher trophic levels, particularly fish (reviewed in Graça 2001). Shredders, macroinvertebrates that consume the particles larger than 1 mm (e.g., leaves) (**Figure 2**), initiate the breakdown process. When macroinvertebrates are abundant, they ingest 50–65% of available leaf litter (Hieber & Gessner 2002), comminuting it into smaller particles that accelerate breakdown and consumption by microbes. Assimilation rates are much lower (approximately 1%) because invertebrates are inefficient feeders (Siders et al. 2018). Once ingested, elements derived from the litter can be incorporated into animal tissue, respired, excreted, or egested. Symbiotic gut microbes further break down organic matter in the gut, promoting assimilation and altering compounds prior to egestion. Excretion promotes nutrient cycling through mineralization, whereas egestion forms fecal pellets that enter FPOM to be broken down by microbes, reingested by invertebrates, or deposited and stored in stream sediments (Halvorson et al. 2017b). To the extent that macroinvertebrates directly assimilate litter-derived elements into their own biomass, they serve as major potential links of leaves to aquatic food webs. Most of the flux mediated by macroinvertebrates, however, is the conversion of litter to FPOM (Evans-White & Halvorson 2017, Halvorson et al. 2017b). This transformation can produce either links or sinks for elements in aquatic ecosystems, depending on whether FPOM is consumed by higher trophic levels (link) or lost to sedimentation, export, or gas production (sink).

Symbiotic gut microbes: microbes that contribute to decomposition of detritus in the guts of detritivores, producing small-molecular-weight compounds that the detritivore utilizes in metabolism

Microorganisms influence how litter-derived elements flow through macroinvertebrates. As mentioned previously, macroinvertebrates prefer and grow faster on litter that has been colonized by microbes and partially converted to microbial biomass, or conditioned (Suberkropp 1992). Yet, it is not well known which particular assemblages of microorganisms, and which traits of litter, are more or less effective at facilitating element assimilation from leaves by macroinvertebrates. Past work assessing growth on—or preference for—different litter types provides some insight into the traits of litter that influence macroinvertebrate growth, but these studies have yielded mixed results (Graça 2001). In some cases, rapidly decomposing litter types disproportionately support invertebrates (Golladay et al. 1983, Motomori et al. 2001), but the opposite can also occur (Fuller et al. 2015, Halvorson et al. 2017b), and in other cases, no clear patterns are apparent (Graça 2001, Fogelman et al. 2018). Growth studies, typically conducted in the laboratory, usually do not address the role of microbes as competitors, because litter is provided in unlimited supply. Preference studies may not last long enough to detect preference shifting, biasing results toward apparent preference for rapidly decomposing litter (Compson et al. 2018).

Hundreds of studies have compared invertebrates on different leaf types, yet it remains difficult to predict how leaf type affects stream invertebrates, despite a persistent view that rapidly decomposing litter is of higher quality. Recent studies using leaves grown with isotopic labels to follow carbon and nitrogen through multiple pathways challenge this view, demonstrating that in some cases, slowly decomposing litter transfers a higher proportion of leaf carbon to macrobiota at higher trophic levels, whereas rapidly decomposing litter supports more microbial productivity that is lost to macrobiota (Compson et al. 2018, Siders et al. 2018) (**Figure 4**). The rate of litter decomposition may influence whether micro- or macroorganisms benefit from dead leaves that fall into streams.

3.2.4. Fine particulate organic matter. FPOM is generated from leaf litter by several processes (**Figure 3**). Some is generated physically (e.g., abrasion), but most is produced biologically. Fungal enzymes break down large particles, releasing FPOM (Suberkropp 1992). Shredders create FPOM, some as a byproduct of sloppy feeding, most through egesta or feces (Petersen & Cummins 1974, Graça 2001). FPOM, the primary food resource for collectors, is not as well studied as CPOM (Bundschuh & McKie 2016). The species composition of both consumers and

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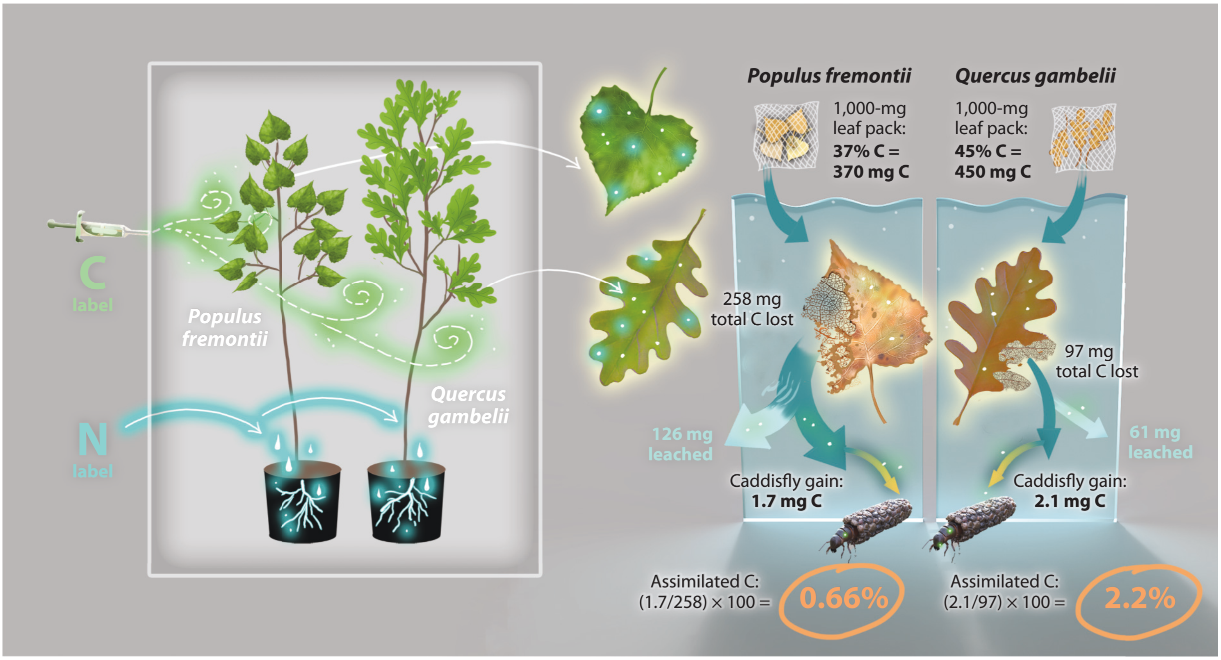

Figure 4

Labeling trees with stable isotopes of carbon (C) and nitrogen (N) allows direct measurements of C and N flow to different pathways. Enriched molecules are depicted as fluorescent dots. Leaf packs are constructed with labeled leaves and incubated in streams. In the example shown here (Siders et al. 2018), more C was assimilated by a shredding caddisfly from slowly decomposing oak litter than from rapidly decomposing Fremont cottonwood litter. In contrast, more C was lost to leachate and to microbial biomass from the Fremont cottonwood leaf packs than from the oak litter. These and similar results from other invertebrate taxa (Fuller et al. 2015) challenge the view that faster decomposing leaves provide more nourishment for macroinvertebrates in streams. Illustration by Victor Leshyk and Abigail Downard.

leaves affects the amount of FPOM produced, the size of particles generated, and their stoichiometry (Bundschuh & McKie 2016). FPOM production can vary 20-fold across macroinvertebrate species and is directly related to their rates of litter consumption (Santonja et al. 2018).

When detritus passes through the guts of invertebrates, particles are stripped of nutrients and labile carbon, creating packets of organic matter with higher C:N ratios and lignin concentrations than the original leaf litter (Yoshimura et al. 2008, Santonja et al. 2018). Decomposition rates of FPOM by microbes correlate with rates of decomposition of the original CPOM, preserving the signal of the leaf litter, but FPOM breaks down more slowly (Webster et al. 1999, Wurzbacher et al. 2016), probably because higher C:P or C:N ratios more than counteract higher surface:volume ratios.

Egesta or fecal pellets constitute as much as two-thirds of FPOM and have their own natural history (Malmqvist et al. 2001). Although FPOM is transferred farther downstream than larger particles (Webster et al. 1999), it also accumulates in depositional areas and slowly decomposes over months to years (Joyce et al. 2007, Yoshimura et al. 2008). Egesta leave the gut after acquiring high bacteria loads (Joyce et al. 2007, Callisto & Graça 2013). Egesta can be strong sinks for carbon and inorganic nutrients when they are deposited in sediments or broken down by microbes (Halvorson et al. 2017b), but they can also catalyze microbial loops if they reenter macroscopic food chains via filter feeders or collectors/gatherers. Extracellular polysaccharides maintain the shape and size of pellets, contributing to their sinking and storage (Joyce et al. 2007). For example, feces of amphipods, common shredders, remain stored in sediments in the winter but begin to decompose in the spring as water warms, providing a food resource when most CPOM has disappeared (Joyce et al. 2007). Many invertebrates eat their own and each other's fecal pellets (Wotton & Malmqvist 2001). Chironomid (midge) larvae, ubiquitous in streams, empty their guts up to 20 times per day, recycling organic matter from their own feces which some also use to build tubes in which they live (Hirabayashi & Wotton 1998). Filter-feeding blackfly larvae aggregate small particles from the water column with their labral fans, turning small particles into larger fecal pellets that are deposited and stored in sediments (Malmqvist et al. 2001). Densities of blackflies can be so high (up to 600,000 individuals per m^2) that they form visible black mats on rocks, profoundly affecting organic matter cycling (Wotton & Malmqvist 2001). Little information is available about how litter type affects the relative strength of these FPOM pathways, but the enormous quantity of egesta in streams suggests that small shifts toward microbes that are fed upon by filter feeders or collectors could significantly alter the amount of energy and nutrients that link to higher trophic levels.

Labral fans: feeding structures resembling foldable fans that surround the mouth of blackfly larvae (Simuliidae), capturing particles from the water column

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4. RETHINKING BIASES: IS FASTER BETTER? NEW EVIDENCE FROM STABLE ISOTOPES

Elements originally bound in litter follow fast and slow pathways into and out of the macroscopic food web. Rapidly decomposing litter yields up its elements more quickly, but this does not necessarily mean that, over the longer term, it contributes more carbon or nutrients to the macroscopic food web. Sampling schedules in laboratory and field experiments tend to bias findings: Short-term sampling documents more breakdown products of litter from rapidly decomposing leaves, when slowly decomposing litter is still in early phases of decomposition, with most elements still bound in more refractory litter. Sampling regimes of short duration overestimate the contribution from rapidly decomposing litter to litter breakdown products and underestimate those from litter that breaks down more slowly. Experimental and natural litter packs host so many invertebrates that it is difficult to discern which insects are using the litter as a food source and which are using it as habitat. Stable isotope labeling offers a sensitive, quantitative way to follow carbon and nitrogen from leaf litter into microorganisms and macroinvertebrates, determining which organisms rely on leaf matter for food by quantifying both rates and pathways of element flow (**Figure 4**). This approach also demonstrates how carbon and nitrogen from litter of different plant species follow distinct pathways, differences that standard community analyses have failed to detect (Compson et al. 2015). Three strong patterns emerge from stable isotope tracer studies of these rates and pathways: First, slowly decomposing litter often transfers more litter carbon and nitrogen to higher trophic levels than rapidly decomposing litter (Compson et al. 2015, Siders et al. 2018) (**Figure 4**). Second, rapidly decomposing litter supports more microbial biomass and higher bacterial productivity, whereas slowly decomposing litter tends to promote fungal growth (Wymore et al. 2013, Pastor et al. 2014), which may be a better food resource than bacteria for some invertebrates (Arsuffi & Suberkropp 1989, Findlay 2010). Third, more carbon and nitrogen are lost as leachate from rapidly decomposing litter compared with more slowly decomposing litter (Wymore et al. 2015, Siders et al. 2018). In preference experiments, shredders initially preferred rapidly decomposing litter, but after a few weeks of decomposition, their preference shifted toward more slowly decomposing litter (Compson et al. 2018). Although plant structural compounds may retard nutrient cycling, the slower release rates of energy and nutrients bound in complex chemicals may increase the efficiency and the long-term rate of elemental transfers to invertebrates.

Compson et al. (2018) found carbon and nitrogen assimilation by a shredding caddisfly feeding on different cottonwood genotypes to be decoupled from decomposition rate. Tannin and lignin both slowed the rate of decomposition, but higher lignin concentrations correlated with higher rates of element assimilation—particularly nitrogen—by macroinvertebrates. In contrast, tannin appeared to suppress element assimilation by macroinvertebrates. This contrast illustrates how the rate of element loss from decomposing litter is decoupled from the pathways through which elements flow: Both defensive and structural compounds slow the rate of decay. But defensive compounds like tannin retard element assimilation by macroinvertebrates and appear to retain anti-insect properties even after the death of the leaf. In contrast, structural compounds in leaves retard the rate of decay but can promote element transfer throughout food webs, possibly because of better congruence between leaf litter decay and the life cycle of macroinvertebrates.

Riparian zones: the vegetated areas surrounding streams that function as the link between terrestrial and aquatic habitats

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5. GLOBAL CHANGE AND STREAM FOOD WEBS

Riparian zones and streams are hotspots of biodiversity but have been degraded through river channelization, dewatering, dam building, deforestation, and invasions of non-native species. Degradation or loss of riparian vegetation reduces wildlife habitat and corridors, increases temperature, reduces water quality, and depletes river food webs of leaves (Sweeney et al. 2004). Globally, the species composition of riparian plants is changing, with increases in drought-tolerant plants, agricultural species, and non-native species (Ashton et al. 2005, Kominoski et al. 2013). Stream restoration projects allow practitioners to shape the species composition of vascular plants in riparian zones. Understanding how leaves function in rivers is integral to predicting responses to global change and designing restoration and conservation programs to conserve biodiversity and sustain ecosystem services. The rates and pathways of litter loss are both sensitive to primary drivers of global change, including loss of biodiversity, warming, nutrient deposition, and pollution with synthetic chemicals.

5.1. Diversity of Leaves and Macroinvertebrates

Global loss of biodiversity has motivated studies testing for relationships between biodiversity and ecosystem function (Hooper et al. 2012). Perhaps the most important effect of functional diversity in litter type in streams was recognized decades ago. Leaves that decompose at different rates provide a continuum of resources for shredders throughout their life cycles (Sedell et al. 1975, Grubbs & Cummins 1994) (**Figure 1**). Recent studies support this finding, showing that rapidly decomposing litter provides a pulse of carbon and nitrogen to invertebrates shortly after leaf fall, whereas slowly decomposing litter makes carbon and nitrogen available later in the season (Ferreira et al. 2016, Siders et al. 2018) (**Figure 5**). In experimental studies, effects of plant species richness on decomposition, measured using mixed litter leaf packs, are variable, but higher litter richness tends to accelerate decomposition (Handa et al. 2014). Furthermore, effects of invertebrate diversity, accelerating decomposition through facilitation and niche partitioning (Jonsson et al. 2001, Jabiol et al. 2013, Handa et al. 2014), are larger and more consistent in diverse leaf packs. Diversity of functional feeding groups increases both the rate and the size of the flux toward higher trophic levels, because consumers capitalize on different size classes of organic matter (Tonin et al. 2018). As invertebrate species decline, more organic matter will be processed by microbes, increasing carbon export out of streams as CO_2.

5.2. Impacts of Warming and Nutrients

In lakes and oceans, small increases in nutrients or temperature increase food web productivity, but larger increases in nutrients and warming tip ecosystems to alternative states, reducing

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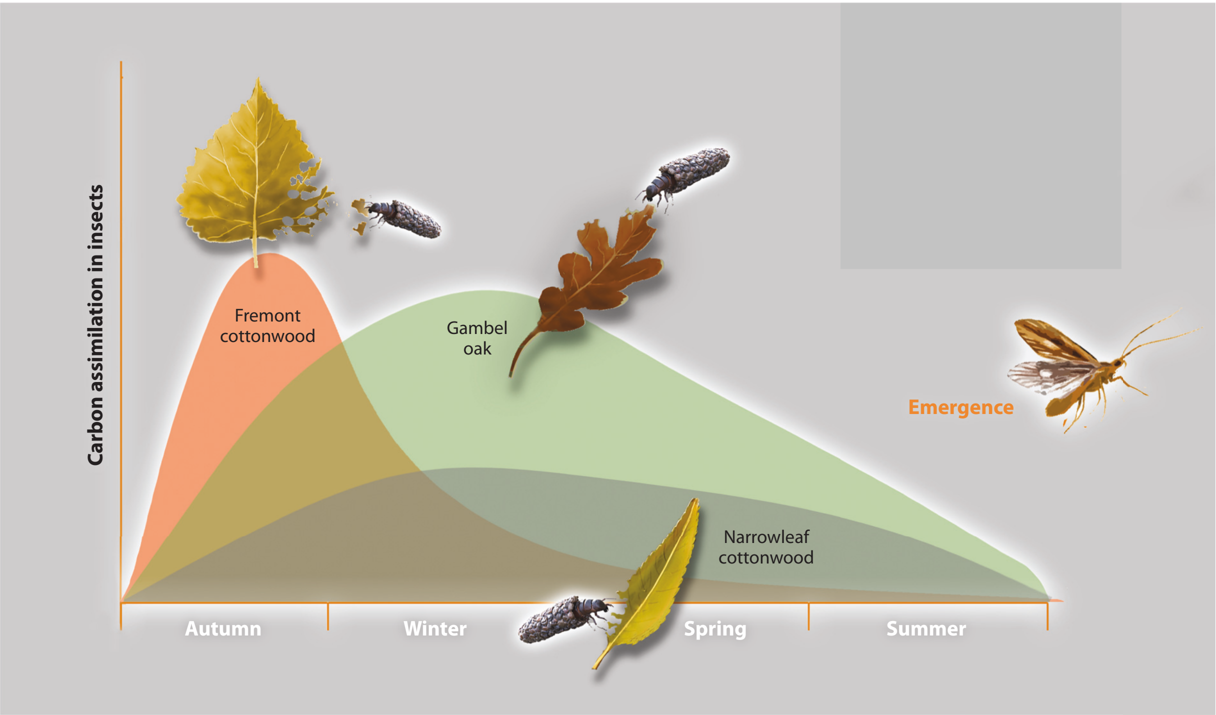

Figure 5

Phenology of carbon assimilation by invertebrates from leaves in a southwestern United States ecosystem over a hypothetical year. Total carbon assimilated is the area under each curve. Stable isotope studies indicate that rapidly decomposing litter types, such as Fremont cottonwood, provide a rapid but brief pulse of carbon and nutrients to invertebrates within weeks after litter fall. In contrast, litter that decomposes more slowly provides a more sustained flux, with some leaf types (e.g., oak) transferring more carbon than others (e.g., narrowleaf cottonwood), depending on the leaf concentrations of structural versus defensive compounds (e.g., Siders et al. 2018). Illustration by Victor Leshyk and Abigail Downard.

trophic complexity and food chain length (Folke et al. 2004). These trends may also prove true in detrital-based stream food webs. A recent meta-analysis of rivers and streams found that warming by 1.4°C accelerated decomposition (mediated by both microbes and macroinvertebrates) by 5–21% (Follstad Shah et al. 2017). More warming might shift the balance between the two pathways, favoring microbial processing, if streams follow trends documented in lakes and oceans. Climate warming is predicted to increase microbially mediated litter decomposition but decrease macroinvertebrate-mediated decomposition, because shredder densities decrease with temperature (Boyero et al. 2011a, 2016). Increases in temperature could create tipping points, particularly at low latitudes where the species diversity of shredders is low, shredder taxa are close to their thermal maxima, and small declines in diversity may be irreversible and could eliminate most of the shredder guild (Boyero et al. 2011b, 2016) (**Figure 6**). Strong coupling of predators and prey in detrital streams (Wallace et al. 2015) indicates that depletion of the shredder guild compromises invertebrate and vertebrate predators, resulting in trophic downgrading, in which top-down controls are diminished (Estes et al. 2011). Because tropical streams and rivers produce a large fraction of the global CO_2 flux from freshwater ecosystems into the atmosphere, shifts toward microbial respiration would decrease the capacity of these waters to store carbon, measurably affecting the global carbon cycle (Battin et al. 2009, Raymond et al. 2013).

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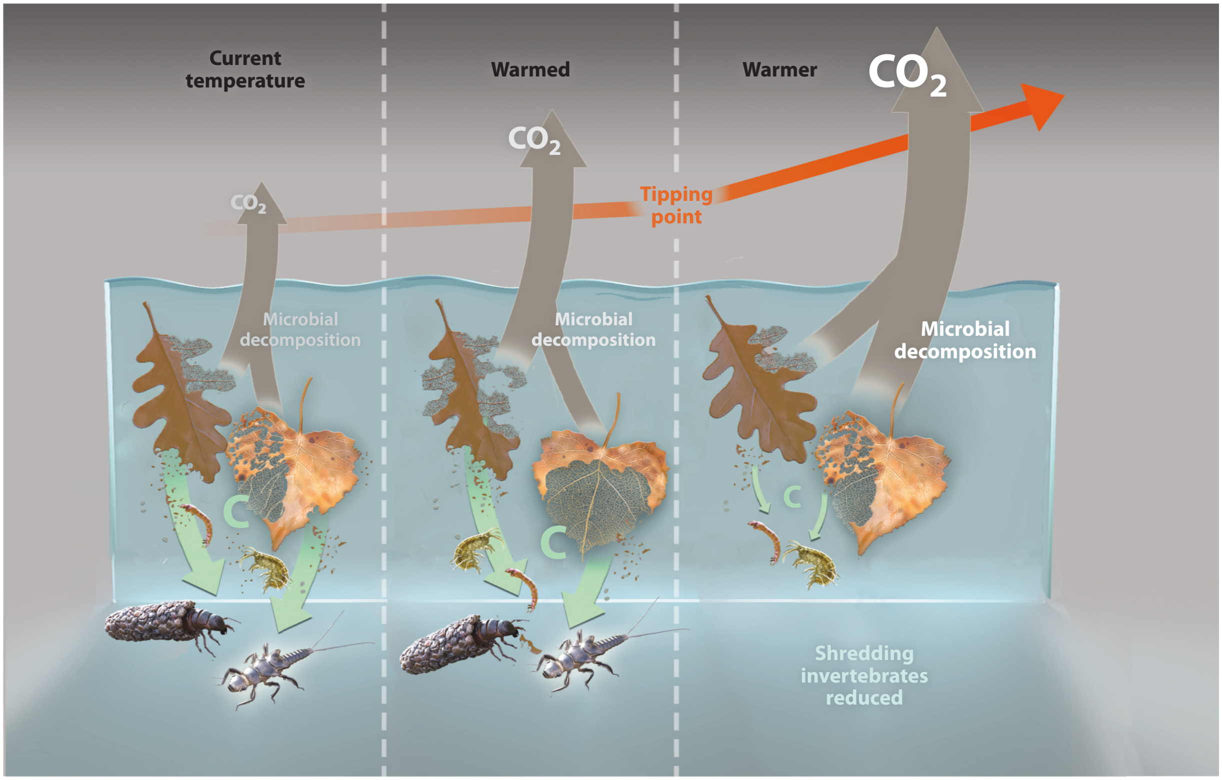

Figure 6

Shifts in carbon flows through detrital-based stream food webs caused by increased temperature. Small increases in temperature will accelerate both microbial and macroinvertebrate activity, increasing decomposition and the rate of element loss, but with minor effects on pathways or fluxes of carbon. In contrast, larger increases driving temperatures toward thresholds that exceed temperature tolerance of shredders would shift energy away from shredding invertebrates and toward microbial respiration, increasing carbon dioxide (CO_2) fluxes from streams to the atmosphere. If shredders are lost from the ecosystem, decomposition rates may not change because increases in microbial decomposition are offset by decreases in macroinvertebrate decomposition, but there would be a large shift of carbon fluxes away from stream food webs and toward microbial respiration and CO_2 production (Boyero et al. 2011a). Illustration by Victor Leshyk and Abigail Downard.

Nutrient enrichment, primarily nitrogen and phosphorus, also stimulates decomposition (Ferreira et al. 2015) by increasing microbial activity, because microbes acquire nutrients from the water column (Cheever et al. 2013, Pastor et al. 2014). Microbes have lower C:N and C:P ratios than leaf litter (Cross et al. 2003), and nutrient uptake helps resolve the mismatch. Nutrient uptake by bacteria and fungi also aligns the stoichiometry of the detrital matrix with requirements of invertebrates (Cross et al. 2003), which consume more litter, further accelerating decomposition (Manning et al. 2015, Halvorson et al. 2018). Nutrient loading in extreme cases (hypereutrophic streams) depletes oxygen, which slows decomposition and excludes invertebrates and other aerobic organisms (Woodward et al. 2012, Ferreira et al. 2015).

Low levels of nutrient enrichment increase food web productivity by reducing elemental imbalances between basal resources and consumers (Cross et al. 2006, Demi et al. 2018). Macroinvertebrate abundance and shredding increase after whole-stream nutrient enrichment (Cross et al. 2006, Manning et al. 2015, Demi et al. 2018), but microbial respiration and carbon loss through

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export of particulate materials also increase (Rosemond et al. 2015, Kominoski et al. 2018). The increased flux to invertebrates could be reversed as carbon storage decreases and invertebrates become limited by the quantity of detrital resources rather than their nutrient content (Halvorson et al. 2017a). Although carbon storage may buffer streams for a couple of years, ultimately sustained increases in respiration and export would limit the quantity of litter (Wallace et al. 2015, Halvorson et al. 2017a). Nutrient enrichment reduces differences in decomposition rates across plant species by disproportionately accelerating decomposition of slowly decomposing species (Gulis & Suberkropp 2003, Manning et al. 2015), which limits food availability for invertebrates later in the season. Ecosystems where invertebrates are limited more by phosphorus than by nitrogen may be more susceptible to large changes in food web structure, because human activities are shifting ecosystems away from nitrogen limitation and toward phosphorus limitation (Peñuelas et al. 2013). Stochiometric ratios across fungal species are more variable than in invertebrates, and changes in fungal species could preserve microbial respiration rates as N:P ratios increase (Danger et al. 2016). Carbon compounds bound in litter may bypass macroscopic food webs if decomposition shifts more toward microbial, rather than macroinvertebrate, pathways in ecosystems with increased nitrogen but not phosphorus (Demi et al. 2018).

5.3. Xenochemicals

Many pollutants impact microbes or macroinvertebrates, reducing decomposition. Fungicides, commonly used in agriculture, reduce fungal biomass and the palatability and assimilation of litter by invertebrates, slowing down decomposition (Zubrod et al. 2011, Fernández et al. 2015). Pesticides that target invertebrates reduce macroinvertebrate densities and activity, shunting energy away from the macroscopic food web (Schäfer et al. 2012). Pharmaceuticals and personal care products are an emerging problem, with biologically active compounds found in rivers worldwide, which tend to suppress microbial activity, slowing decomposition (Rosi-Marshall et al. 2013).

5.4. Changes in Riparian Vegetation

Changes in plant species composition of riparian zones have variable effects on stream food webs. Responses are dramatic if plants produce lethal compounds novel to the invaded ecosystems (Custer et al. 2017). More prevalent but subtle consequences occur through changes in the nutritional content of leaves, because invasive species often have higher concentrations of nitrogen than natives (Ashton et al. 2005). Increased nutrient content could lead to more productive food webs, but not if energy is disproportionately channeled through microbial decomposition. Tamarisk, a widespread invasive species, presents a compelling example. Litter from tamarisk has high nutrient content and decomposes faster than many native riparian plants (Going & Dudley 2008). In short-term laboratory experiments, insects fed tamarisk litter grew more quickly than insects fed native cottonwood or willow litter (Going & Dudley 2008, Moline & Poff 2008). Yet, field experiments show tamarisk reduces aquatic invertebrate diversity and abundance (Bailey et al. 2001, Kennedy & Hobbie 2004). Its rapidly decomposing litter is associated with decreases in invertebrates and fish (Kennedy et al. 2005) (**Figure 1**). Tamarisk leaves are hard to find in the river just a few weeks after leaf fall (Moline & Poff 2008). Overall, the ephemeral nature of tamarisk litter appears to have negative effects on stream invertebrate production, because most of its energy is going to microbial respiration. In addition, dense tamarisk thickets shade the stream, limiting algal growth (Going & Dudley 2008, Hultine et al. 2013). Removal of tamarisk allows macroinvertebrates and fish to rebound (Kennedy et al. 2005).

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Operational taxonomic units (OTUs): describes bacterial groups in lieu of the term "species," because species concepts for bacteria are complex and poorly defined

Eucalypt plantations outside of the native range of eucalypts present a counter example. The decomposition rate in leaves of eucalypts is slowed by structural and defensive compounds. The thick cuticles of eucalypts limit fungal colonization of leaf surfaces to stomatal openings. Fungal breakdown occurs beneath the waxy cuticle in areas where invertebrates cannot access, greatly depressing energy flow to invertebrates (Graça et al. 2002). Therefore, introduction of slowly decomposing non-native eucalypt litter inhibits macroinvertebrates in streams (Graça et al. 2002). The contrast between tamarisk and eucalypts demonstrates that non-native plants can decompose more rapidly or more slowly than native flora, and in both cases can alter pathways of element flow, depending on specific traits of the leaves and their impacts on microbial and macroinvertebrate decomposers.

6. SUMMARY

Energy and nutrients bound in litter can follow multiple pathways during decomposition in streams, but a few branch points determine the fates of dead leaves that fall into streams. First, to what extent are the elements contained in litter directly assimilated by macroconsumers or by microbes? Second, of the portion taken up by microbes, to what extent are these assimilated by macroconsumers that transfer them throughout food webs? What portion of microbial biomass is respired as CO_2, stored in stream sediments or exported downstream? Models to predict these fates and pathways must take into account: (*a*) traits of leaves (nutrient content, structural and defensive compounds, timing of litter fall, etc.), which vary with species and even genotype in ways that constrain consumption and decomposition; (*b*) life history and feeding style of the macro- and microheterotrophs consuming litter; and (*c*) environmental conditions in streams that accelerate (nutrients, temperature) or decelerate (pollutants) decomposition.

7. FUTURE ISSUES

Quantitative models are needed to predict both the pathways of elemental fluxes triggered by litter inputs to specific stream ecosystems and the regional or global trends in stream carbon budgets. The fate of DOM and FPOM in river food webs is poorly understood, although they dominate carbon pools in rivers. Small shifts of carbon fluxes toward or away from macroorganismal food webs could profoundly affect stream food web productivity. More research focusing on how litter type affects the fate of DOM and FPOM is needed to reveal and classify leaf traits that affect these fluxes. Research that integrates microbial and ecosystem ecology by exploring the biogeochemical significance of individual microbial taxa will bring the power of the molecular revolution to biogeochemistry. New techniques such as qSIP can bridge these fields to define the roles of genetically determined species [or operational taxonomic units (OTUs)] in ecosystem processes. Microbes, like macroorganisms, can then be classified into: (*a*) dominants, taxa that are high in abundance with a large influence on element fluxes through the system; (*b*) keystones, taxa whose influence on element fluxes are disproportionately large compared with their abundance (sensu Power et al. 1996); and (*c*) weak interactors, taxa that are present and may be growing and assimilating elements but whose abundances and growth rates have little influence on ecosystem processes.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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