Chapter 10
The Role of Macroinvertebrates on Plant Litter Decomposition in Streams

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Abstract Macroinvertebrate detritivores (i.e., shredders) in freshwaters are often a main driver of decomposition rates of terrestrial plant litter. Yet, the extent to which shredders drive this process depends on the specific functional traits and species present in the shredder community, which in turn are determined by the broader species pool, as well as a range of local environmental conditions, such as pH, substrate characteristics, water chemistry, water temperature, and current velocity. Projected global change will modify several of these environmental conditions, with potential consequences for litter decomposition rates and overall carbon cycling in freshwaters. In this chapter, we describe how a range of freshwater environmental conditions determines the presence of certain species (i.e., functional traits) and the characteristics of shredder communities (i.e., species composition and richness). We then discuss how these characteristics in turn may influence interactions among shredders, and between shredders and other freshwater organisms, to determine their influence on litter decomposition in streams.

10.1 Introduction

Litter-associated macroinvertebrates (i.e., shredders) are represented by a range of species, which are mainly insects in the orders Diptera, Plectoptera, and Trichoptera, but also include some crustaceans and molluscs that can locally occur in high densities and, as opposed to insect shredders, often have fully aquatic life cycles. Early studies on terrestrial plant litter and shredders in freshwater systems found clear positive associations between standing litter stock and shredder abundance (Anderson & Sedell, 1979; Cummins et al., 1973; Short et al., 1980). Yet, it was not until the landmark experiment by Wallace et al. (1982) that the direct role of shredders for

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plant litter decomposition was confirmed. Here, application of insecticides to an entire headwater reach resulted in a large reduction in shredder abundance, which dramatically reduced conversion of terrestrial leaf litter (CPOM; coarse particulate organic matter) to small particles (FPOM; fine particulate organic matter) and downstream transport of FPOM (Wallace et al., 1982). During this time, parallel energetic studies also revealed that invertebrate shredders have very low assimilation efficiency (Cummins & Klug, 1979; Golladay et al., 1983; McDiffet, 1970), and that their secondary production and respiration contribute little to the broader ecosystem energy budget (Fisher & Likens, 1973). Collectively, this research suggested that the role of shredders in the litter decomposition process is mainly in the conversion, via fragmentation, of CPOM to FPOM. This functional role is nevertheless critical, as it facilitates overall decomposition of terrestrially derived plant material (Cummins et al., 1989; Mulholland et al., 1985; Villanueva et al., 2012; Webster & Benfield, 1986), increases the availability of litter-based resources to other freshwater organisms (Cummins et al., 1973; Wallace & Webster, 1996), and underpins longitudinal connectivity in river systems (e.g., via FPOM transport; Wallace et al., 1982). As such, studies during this period set the stage for an actively developing and exciting research field over the coming decades (Graça, 2001; Marks, 2019; Tank et al., 2010).

Freshwater environmental conditions interact with regional pool of available species to determine which species (i.e., functional traits) and community characteristics (i.e., species composition and richness) are present or absent locally at any one site (Bonada et al., 2007; Jonsson et al., 2017; Poff, 1997; Poff et al., 2006). These characteristics in turn influence the rate at which the macroinvertebrate shredder community decomposes litter (Dangles & Malmqvist, 2004; Gessner et al., 2010; Jonsson & Malmqvist, 2000; McKie et al., 2008). Hence, altered environmental conditions will likely modify litter decomposition rates via changes in shredder community composition, with consequences for the role that shredders have for overall litter turnover rates. In this chapter, we will describe how certain traits may be present or absent in (or differ in abundance among) shredder communities due to variation in local environmental conditions. We will then go on to describe how such variation in community characteristics may regulate litter processing rates and trophic links between shredders and other freshwater functional feeding groups. As a synthesis, we present possible scenarios as to how predicted global change (i.e., changes in climate and land use) can affect litter decomposition in fresh waters via impacts on shredder communities, and will do so for tropical, temperate, boreal, and Arctic biomes.

All types of freshwater systems may contain macroinvertebrate shredder species, but their role is greatest in ecosystems that receive substantial seasonal inputs of terrestrial (e.g., riparian) plant material relative to the area of aquatic habitat, which is mostly in small to mid-sized streams surrounded by well-developed deciduous, riparian vegetation. Thus, while other types of riverine systems, as well as lakes and ponds, can receive terrestrial litter input and therefore may house shredders, we focus here on macroinvertebrate shredders and litter decomposition in small to mid-sized streams that are forested, which also represent the type of freshwater systems where most research relevant to this topic has been carried out.

10.2 Macroinvertebrate Shredder Functional Traits

Each species that can be classified as a freshwater macroinvertebrate shredder exhibits unique functional traits, or rather a set of traits, that make it more or less likely to exist under certain environmental conditions (Poff et al., 2006), and that determine its role in the litter decomposition process. In general, as all species classified as shredders per definition feed, at least partially, on plant litter, and their life cycle is often intimately tied to seasonal pulses in litter resource availability. In temperate and boreal systems, this means that most shredders time their presence and growth as larvae with autumn leaf senescence and subsequent peaks in litter input and increases in standing stocks (Richardson, 1991; Wallace et al., 1999). However, while this is true for insect shredders, other shredder/detritivorous taxa, such as crustaceans and gastropods, that are present throughout the year, are less responsive to seasonal variation in litter availability, but instead show a high level of feeding plasticity by foraging also on other types of food resources (MacNeil et al., 1997; Moore, 1975).

Plasticity in feeding traits can, however, also be found among insect shredders. In particular, the strategy to shred plant material for food can be mixed with scraping surfaces or collecting FPOM (Cummins & Klug, 1979). The level of plasticity, or the extent to which shredder species use another feeding strategy than shredding, can change with development (i.e., ontogenetic diet shifts: Feminella & Stewart, 1986; Tierno de Figueroa & López-Rodriguez, 2019), or with variation in water chemistry (e.g., pH: Dangles, 2002; Ledger & Hildrew, 2000). Further, it is possible that the inherently low quality of plant litter, and the additionally, successively (seasonally) diminishing quality of litter standing stocks (Chauvet, 1987; Gessner & Chauvet, 1994), promote a diet that includes also higher-quality, autochthonous resources, such as algae (Brett et al., 2017; Jonsson & Stenroth, 2016; Moore, 1975) as well as predation (Dangles, 2002). The reality of these dietary choices complicates the use of traditional, and overly simplistic, functional feeding group designations (Mihuc, 1997). Further, to understand the role of macroinvertebrates for litter decomposition, and how this role may be altered under changing environmental conditions, this potential flexibility in resource use has to be considered.

Shredders also exhibit traits that are directly related to variation in abiotic conditions, such as water chemistry (e.g., pH and nutrient concentrations), water temperature, current velocity, and bottom substrate complexity and grain size. Thus, depending on the local abiotic conditions, different shredder communities are found (Jonsson et al., 2017; Malmqvist & Mäki, 1994; Poff, 1997), and it is therefore to some extent possible to predict community characteristics in a particular freshwater habitat, based on prevailing, local abiotic conditions. For example, strong environmental filters are exerted directly by pH and nutrient concentrations (i.e., level of eutrophication) and, thus, indirectly by land use and land cover that shape water chemistry (e.g., Jonsson et al., 2017). Across a gradient in pH, euholognathan stoneflies tend to dominate in more acidic streams, while trichopterans and dipterans are less common, and crustaceans are very scarce (Dangles & Guérold, 1999). Conversely, in streams of higher pH, stonefly abundance is often lower, and crustaceans and other acid-sensitive species are more abundant (Dangles & Guérold, 1999; Griffith & Perry, 1993). Across a gradient in eutrophication, a similar—but opposite—change in community composition is typically observed (Woodiwiss, 1964). This is because stoneflies in general are sensitive to the low oxygen levels resulting from organic pollution (e.g., from agricultural runoff) and the subsequent high microbial oxygen consumption (Hilsenhoff, 1988). Moreover, some Trichoptera groups are fairly tolerant to low oxygen levels, and crustaceans tolerate, and often dominate, under these conditions (Metcalfe, 1994).

High oxygen (O_2) demand results in stoneflies and some other taxa being more abundant and species rich in colder waters at higher latitudes (and altitudes) when compared to more southern (and/or lowland) streams with higher temperatures, where O_2 saturation is often lower (Verberk et al., 2011). High water velocity promotes oxygenation, and is therefore an environment where more O_2 demanding species can be found, but can also in itself create habitats that are suitable for some (i.e., rheophilic) taxa and an obstacle to others, shaping communities across a gradient from slow- to fast-flowing water (Hart & Finelli, 1999). However, the impact of water velocity on a shredder community can interact with bottom substrate type and complexity (Huryn & Wallace, 1987). For example, high substrate complexity or large grain sizes may moderate potentially adverse effects of a fast current by creating refugia of lower current velocities (Franken et al., 2006). Because of this, and because substrates form the main living space for benthic macroinvertebrate communities, bottom substrate characteristics are important determinants of shredder community composition (Reice, 1980; Sponseller & Benfield, 2001; Williams & Mundie, 1978). In addition, bottom substrate characteristics influence stream retentiveness of terrestrial plant litter input (Ehrman & Lamberti, 1992; Lepori & Malmqvist, 2005), a pre-requisite for whether a rich and abundant shredder community can be found or not (Haapala et al., 2003; Richardson, 1991; Wallace et al., 1999).

10.3 Inter- and Intraspecific Interactions

The low assimilation efficiency of shredders reflects the inherently low quality of plant detritus as a food source. Although some studies have shown that detritivores can assimilate up to 40% of ingested plant biomass, others have found that the conversion rate of ingested leaf litter to shredder biomass more often is $\leq$ 20% (Golladay et al., 1983; McDiffet, 1970). Due to the low resource quality of leaf detritus, shredders are highly dependent on microbial colonization on and within the leaf tissue, as the microbes (primarily fungi) improve the nutritional quality to shredders (Bärlocher, 1985; Cummins & Klug, 1979). Accordingly, studies have shown that microbial colonization of leaf litter increases shredder assimilation efficiency considerably (Cummins & Klug, 1979; Golladay et al., 1983). Nevertheless, the generally low assimilation efficiency also means that feces produced are quite similar to the original detrital resource in terms of nutrient content. Frass and feces from shredder leaf consumption can therefore serve as an important pre-processed food resource to other shredders, collectors, and filter feeders (Dieterich et al., 1997; Grafius & Anderson, 1979; Jonsson & Malmqvist, 2005; Patrick, 2013; Short & Maslin, 1977). Thus, interactions between shredders and leaf-associated microbes are critically important for shredder secondary production, the availability and quality of litter-based resources to other freshwater organisms, and, thus, for overall plant litter processing in streams.

Interactions among shredder individuals within a shredder community may amplify or reduce their impacts on litter decomposition rates. For example, rates of litter decomposition have been found to decrease with increasing shredder density, due to strong interference competition (Jonsson & Malmqvist, 2003). In natural systems, such effects are likely absent initially when resources are abundant soon after leaf senescence, but may become increasingly apparent as the litter resource gradually is fragmented and consumed (Jonsson, 2006). Moreover, due to different species utilizing separate niches (i.e., 'niche complementarity'), competition is often weaker among species than within species (Loreau & Hector, 2001). Thus, total amount of interference competition may be lower in a species-rich community compared to in a community that consists of only one or a few species total (Gessner et al., 2010; Jonsson & Malmqvist, 2000, 2003, but see McKie et al., 2009). Hence, if shredder species are lost, litter decomposition rates may decrease despite compensatory increases in the abundance of remaining species, due to overall increased levels of interference (i.e., resource) competition (Jonsson & Malmqvist, 2000, 2003). Changes in shredder species richness can therefore alter their role as drivers of litter decomposition rates.

Different feeding modes, such as scraping the leaf surface to selectively consume fungal biomass, or ingesting pieces of the leaf matrix together with fungal biomass (Bloor, 2011), are a key aspect of niche complementary among invertebrate shredders. For example, isopods and stoneflies have mouthparts that are more suitable for scraping surfaces than biting bits off a leaf, as many trichopterans do (Graça et al., 1993; Jonsson et al., 2002). Such differences in feeding behavior may create situations of apparent niche complementarity, or cases where facilitation among species occur (Giller et al., 2004). Hence, a higher number of shredder species should, on average, result in higher decomposition rates (Gessner et al., 2010). These differences in feeding modes among distantly related shredder taxa are likely also the mechanistic explanation as to why mixing litter from different plant species may increase decomposition rates (Santonja et al., 2020; Swan & Palmer, 2006; Tonin et al., 2018). However, more subtle niche complementarity—whatever it may be—among closely related species (e.g., within the same family or genus) can also result in higher per-capita litter processing rates in mixed communities than for single species, if it lowers competition or promotes facilitative interactions (Jonsson & Malmqvist, 2000, 2003; McKie et al., 2008).

Changes in decomposition rates caused by a change in the shredder community will likely have consequences also for other organisms, such as litter-associated microbes (via nutrient excretion; Mulholland et al., 1985; Villanueva et al., 2012), filter feeders and collectors (via particle production; Dieterich et al., 1997; Grafius & Anderson, 1979; Jonsson & Malmqvist, 2005; Patrick, 2013; Short & Maslin, 1977, but see Heard & Richardson, 1995; Jonsson et al., 2018), and predators (via prey availability; Peckarsky, 1982). However, how a change in shredder community composition influences other freshwater organisms via altered litter processing rates has rarely been studied (but see Jonsson & Malmqvist, 2005; Patrick, 2013). Moreover, despite several studies showing that shredder species richness is important for rates of litter decomposition, there is ample evidence that the presence of particular shredder species, rather than a change in species richness per se, sometimes can be at least as important for rates of litter decomposition (Boyero et al., 2014; Dudgeon & Gao, 2010; Perkins et al., 2010; Santonja et al., 2018), indicating that dominant functional traits rather than shredder diversity per se (i.e., the 'mass ratio hypothesis'; Grime, 1998) determines litter mass loss (Creed et al., 2009; Stoker et al., 2017). Hence, future research should consider the importance of dominant traits in shredder communities rather than merely species richness, how environmentally induced variation in these trait values results in altered rates of decomposition, and what consequences this has for microbes and other invertebrate guilds.

10.4 Impacts of Global Change on Litter Decomposition via Effect on Invertebrate Shredders

In the face of current and future global change, freshwaters are among the most threatened ecosystems. In addition to potential direct and indirect effects of predicted climate change (IPCC, 2007; Moss et al., 2009; Settele et al., 2014), a long list of other anthropogenic changes, including different types of land uses, will continue to impact freshwater systems and their biodiversity in many ways (Dudgeon et al., 2006). These impacts will alter the rates of ecosystem processes, and in many cases lead to impaired ecosystem functioning (Dudgeon, 2010). Below, we explore how different types of global change may impact rates of litter decomposition via influences on invertebrate shredders (see also Table 10.1).

10.4.1 Warming

Global air temperature is expected to increase by 2–5 °C by the end of the twenty-first century, mainly due to effects of greenhouse gas emissions from human activities (IPCC, 2007). However, these warming trends will not be uniform globally. Instead, northern regions (i.e., the boreal and Arctic) are predicted to experience the greatest future temperature change, whereas considerably smaller increases may be observed in the tropics (IPCC, 2007; Settele et al., 2014). While stream water temperatures are regulated by a complex set of drivers (groundwater, shading, etc.), there is reason to expect that warmer air temperatures will increase water temperature, at least for some portion of the year (Morrill et al., 2005; Webb & Nobilis,

Table 10.1 Hypothesized effects of global change on shredder communities, and subsequent changes in plant litter decomposition rates due to altered importance of the shredder community, in four different biomes, each with expected biome-specific global changes. The hypothesized change ('Effects on decomposition rates') is based on the overview in the above text and cited literature within that text, and the presumed changed importance of shredders plant litter decomposition in fresh waters from before to after the impact of global change. The number of ' + ' or '–' represents the hypothesized strength of the effect

Biome	*Global change*	*Effect on freshwater system*	*Effect on the shredder community*	*Effect on decomposition rates*
Tundra	Warming	Increased water temperature	Reduced psychrophile species	– –
			Increased metabolic rates	+
	Shrubification	Increased litter input	Increased shredder abundance	+ +
Boreal forest	Warming	Increased water temperature	Reduced psychrophile species	– –
		Increased drought occurrence	Reduced shredder biomass and richness	–
	Precipitation	Increased flood stochasticity	Reduced shredder biomass and richness	–
			Removal of litter input	– –
		Increased N and dissolved C	Increased microbial biomass	+ +
	Forestry	Reduced litter quality	Reduced shredder biomass and richness	– – –
Temperate forest	Warming	Increased anoxic conditions	Reduced shredder biomass and richness	– – –
			Reduced microbial biomass	– –
		Increased drought occurrence	Reduced shredder biomass and richness	– – –
			Disconnect between land and water	– – –
	Precipitation	Increased flash floods	Reduced shredder biomass and richness	– – –
			Removal of litter input	– – –

(continued)

Table 10.1 (continued)

Biome	*Global change*	*Effect on freshwater system*	*Effect on the shredder community*	*Effect on decomposition rates*
	Agriculture	Reduced flows	Reduced shredder biomass and richness	– – –
			Disconnect between land and water	– – –
Tropical rain forest	Warming	Increased water temperature	Increased metabolic rates	+
	Precipitation	Reduced flows	Reduced shredder biomass and richness	–
			Disconnect between land and water	–
	Agriculture	Reduced flows	Reduced shredder biomass and richness	–
			Disconnect between land and water	– –

2007). As water temperature is a strong environmental filter that determines macroinvertebrate community composition (Jacobsen et al., 1997), such changes are likely to impact the distribution of freshwater organisms, their interactions, and thus the processes they carry out (Settele et al., 2014). Hence, warming-induced changes in shredder community composition will likely alter intra- and interspecific interactions, including the presence and strengths of facilitation and effects of niche complementarity, and interactions among different types of organisms that are associated with litter processing or products thereof. For example, warming has been shown to weaken facilitation between macroinvertebrate and microbial decomposers, presumably via increased metabolic demands and reduced nutrient excretion by the macroinvertebrates (Bernabé et al., 2018).

Warming of freshwaters will inevitably have the largest adverse impacts on cold-loving (i.e., psychrophile) macroinvertebrate species at higher latitudes, and if these species are important shredders, also the litter decomposition process will be severely affected (e.g., Perkins et al., 2010). As increases in temperature are likely to be greatest in high-latitude ecosystems, which often have species-poor communities dominated by only a few species that are adapted to colder conditions (e.g., stoneflies; Irons et al., 1994; Jacobsen et al., 1997; Li & Dudgeon, 2009; Masese et al., 2014), the impact of warming on the role of shredders for litter decomposition may be most pronounced in these systems (Table 10.1). Hence, in northern regions, the major effect of warming will likely be a changed shredder community composition due to taxon-specific temperature preferences and responses in metabolic rates to warming in relation to available resources (i.e., starvation; Perkins et al., 2010;

Sweeney, 1978; Sweeney & Schnack, 1977). The impact on litter processing may, however, be alleviated if more southern shredder species expand their ranges northward to fill vacant niches. Yet, the extent to which such species replacement can take place will depend on other environmental filters (e.g., local pH), geographic barriers, the rate at which warming occurs, as well as the migratory ability of the southern, more thermophilic species (Bilton et al., 2001). Moreover, climate-change induced alterations of riparian vegetation may counteract adverse effects of warming or even promote the role of shredders for litter decomposition in streams (Jonsson & Canhoto, 2017; Wondzell et al., 2019).

10.4.2 Climate-Induced Changes in Vegetation

Warming will also gradually change the terrestrial plant community composition (e.g., conifers will be replaced by broadleaf species; e.g., Walther et al., 2002) and functional trait representation, which in itself will further alter productivity on land as well as the quantity and quality of litter supplied to fresh waters during leaf senescence (Kominoski et al., 2013). Further, as tree species differ in phenology of leaf senescence (Dixon, 1976; Eckstein et al., 1999), and as phenology is coupled with litter quality (Campanella & Bertiller, 2008; Niinemets & Tamm, 2005), a gradual change in plant community composition in response to warming will also alter the temporal resource availability to shredders, and the quality of those resources (Jonsson & Canhoto, 2017). The most dramatic warming-induced shifts in vegetation are predicted to occur at high latitudes (i.e., in the tundra) and altitudes (i.e., above the current tree line), as trees will expand into these previously open areas, or, conversely, in regions that become too warm and dry for trees to persist (Table 10.1; Chen et al., 2011; Walther et al., 2002; Zhang et al., 2013). In the former situation, an increased shredder abundance, and thus an increased role of shredders for plant litter decomposition, may be expected, as the availability of litter resources will increase, whereas in the latter situation, shredders likely are lost, or severely reduced in abundance, reducing their role for plant litter processing.

Changes in terrestrial net primary productivity (NPP) are also expected in response to warming, especially in northern regions (i.e., boreal and Arctic) and at high elevations (e.g., Gao et al., 2013), as this is where temperature increases will be the greatest (IPCC, 2007; Settele et al., 2014). Mean annual temperature and NPP are generally positively correlated (Huston & Wolverton, 2009), so increased NPP as a consequence of climate warming is expected. However, lower latitudes may experience reduced NPP due to increasingly dry conditions caused by higher temperatures (IPCC, 2007; Settele et al., 2014; Walther et al., 2002). These potential changes in terrestrial NPP are important because this is tightly coupled to leaf litter production (Wardle et al., 2003), and therefore with amount of terrestrial plant litter that freshwater systems receive from the riparian zone, but also to shading that may counteract effects of warming on water temperature (Wondzell et al., 2019).

More subtle changes in litter quality may also be caused by warming, because in sufficiently warm and wet environments, where resources are abundant, plant strategies involve growing in height to escape intra- and interspecific competition for light (Hautier et al., 2009). This strategy requires allocation of resources to biomass production, and therefore results in lower investment into secondary compounds (i.e., defense against herbivores; Bazzaz et al., 1987; Coley, 1988), which then increases the quality (i.e., palatability) of the litter produced. However, contrastingly, higher concentrations of atmospheric carbon dioxide (CO_2), which is one main agent behind climate warming, and subsequent greater CO_2 uptake by vegetation, may result in poorer litter quality as the carbon (C)-to-nitrogen (N) ratio, as well as concentrations of lignin and phenolics, increase (Norby et al., 2001; Stiling & Cornelissen, 2007). In addition to differences in litter quality having strong effects on decomposition rates (Heal et al., 1997; Lidman et al., 2017; Ostrofsky, 1997), changes in litter quality may also exacerbate stochiometric mismatches between shredders and the litter resources (Norby et al., 2001; Tuchman et al., 2002). Such a change would have immediate consequences for freshwater secondary production, especially in combination with increased metabolic demands due to higher water temperature (Perkins et al., 2010; Sweeney, 1978; Sweeney & Schnack, 1977).

10.4.3 Direct and Indirect Effects of Changed Precipitation

Similar to the effects of increasing air temperature, precipitation patterns will change unevenly across the globe. Current models suggest that some regions will experience greater annual rainfall with positive effects on terrestrial NPP, whereas other areas are expected to experience lesser amounts with more severe and prolonged droughts and adverse effects on terrestrial NPP (Table 10.1; IPCC, 2007; Settele et al., 2014; Walther et al., 2002). Such effects on terrestrial NPP will in themselves affect the role of macroinvertebrates for plant litter decomposition in fresh waters, via changes in litter input quantity and quality (see 10.4.2). In addition, studies suggest that precipitation drives litter input dynamics to fresh waters in the tropics, whereas temperature in itself is a more important driver at higher latitudes (Tonin et al., 2017). However, greater stochasticity in precipitation, in terms of both amounts and frequency (Pendergrass et al., 2017), and thus frequency of floods and droughts in freshwater systems, is expected in a warmer climate (Trenberth, 2011). Hence, besides affecting NPP, altered precipitation may affect the role of shredders for litter processing by regulating litter input dynamics, and via impacts on the frequency and magnitude of floods, runoff of dissolved organic matter, and frequency and length of droughts.

Changes in both magnitude and frequency of floods due to climate change will influence freshwater macroinvertebrate community composition, and most invertebrate groups will exhibit a reduced abundance in response to altered flow regimes (Kakouei et al., 2018; McMullen & Lytle, 2012). In addition, spates due to extreme rainfall events can drive the exports of organic C and nutrients from freshwater systems, especially by reducing the retention of CPOM (Giling et al., 2015). Thus, if flooding events occur during or soon after leaf senescence, these will influence the spatial distribution of litter resources, with consequences for invertebrate shredders and other functional feeding groups that to some extent depend on this resource or products from the decomposition process (i.e., collectors and filter feeders). Such effects of high flow may be moderated by substrate characteristics that increase flow heterogeneity and promote litter retention, or be exacerbated by past human activities that have resulted in reduced structural complexity and increased channelization of streams (Ehrman & Lamberti, 1992; Koljonen et al., 2012; Lepori & Malmqvist, 2005).

Even moderately reduced flows may have large impacts on shredder-mediated litter decomposition rates, if they result in increased distance between riparian vegetation and the water body, reducing litter input and in-stream litter availability (Arroita et al., 2015; Giling et al., 2015), and thus shredder abundance (Richardson, 1991; Wallace et al., 1999). In the event of drastically reduced flows (i.e., extensive and prolonged droughts), invertebrate shredders (as well as other freshwater organisms) can be extremely vulnerable, as habitat conditions (e.g., oxygen levels and temperature) progressively deteriorate and habitats disappear (Bonada et al., 2007; Herbst et al., 2018). This habitat deterioration, in turn, will affect litter decomposition rates in streams where shredders are important actors in that process (Leberfinger et al., 2010; Monroy et al., 2016). It is important to note, however, that droughts (as well as spates) can have very different effects on the role of shredders for plant litter decomposition, depending on when during the year they occur and how they overlap with certain developmental stages of the locally important shredder species.

Runoff of dissolved organic matter (DOM), including critical nutrients (i.e., C, N, and phosphorus [P]), can stimulate litter-associated microbial biomass and activity in freshwater systems (Emilson et al., 2017), and thus increase the palatability of terrestrial plant litter and the rate at which it is decomposed by invertebrate shredders (sensu Heal et al., 1997; Rosemond et al., 2015). In regions where increased precipitation is expected as a consequence of climate change, freshwater systems will likely receive increased amounts of DOM from terrestrial runoff (Christensen et al., 2001; Larsen et al., 2011). In warmer regions, where increasingly dry conditions will have adverse effects of terrestrial vegetation, inputs of DOM may become more sporadic but of higher magnitude following rare, extreme rain episodes (Table 10.1; Alpert et al., 2002; Nunes et al., 2009). In addition to quantitative changes, DOM runoff may also change qualitatively, as a consequence of changed soil nutrient availability following climate-change induced alterations in plant physiology and community composition, and, thus, plant litter chemistry (Bazzaz et al., 1987; Niinemets & Tamm, 2005). Such qualitative changes may, as for quantitative changes, influence litter-associated microbial communities with consequences for litter palatability and the rate at which shredders decompose the plant litter.

Runoff of terrestrial organic matter may also reduce pH, which can be tightly coupled to concentrations of DOM (i.e., organic acidity). Thus, as opposed to positive effects of DOM via increased microbial biomass and litter palatability, runoff may also result in reduced shredder contributions to litter decomposition, and reduced overall decomposition rates, if important acid-sensitive shredder (and microbial) species are lost (Petrin et al., 2007; Schmera et al., 2013). However, in the boreal region, where precipitation and subsequent runoff are predicted to increase the most, many important shredder taxa are naturally tolerant to low pH (Dangles et al., 2004), so effects of DOM on shredder-mediated litter processing via changed shredder communities should be small in the north. However, besides bringing nutrients, or lowering the pH, runoff may also bring sediment other chemicals from land to water. The effect of such environmental change on the role of shredders for the litter decomposition process will depend on the causal agent (e.g., type of human activity) and the way in which catchment characteristics are altered (see 10.4.5).

10.4.4 Fire and Strong Winds

Climate change is expected to increase frequencies of forest fires and strong winds (Seidl et al., 2017). If large areas of a catchment are disturbed by either storm felling or fire, increased runoff (Verkaik et al., 2013) and subsequent effects on macroinvertebrate communities (Minshall, 2003) may persist until the forest has recovered. At smaller scales, fire and wind disturbance can result in increased inputs of dead wood, which in turn could alter water flow and promote retention of plant litter with positive effects on shredder abundance and their importance for litter decomposition. However, both fire and wind can also remove riparian vegetation and open the canopy, and thus change the resource base and the dominant functional feeding groups present in the freshwater system (Vannote et al., 1980). However, this effect is likely to be transient, provided that secondary succession proceeds in the absence of disturbance (Stone & Wallace, 1998). In fact, fire and wind disturbance may promote shredder abundance and shredder-mediated decomposition, if it allows for regeneration of early-successional deciduous vegetation, which produces higher-quality litter in a seasonal manner, as opposed to the often dominant late-successional, coniferous species.

10.4.5 Human Activities

Multiple types of land use will influence freshwater systems and their shredder communities in different ways (Table 10.1). Forestry, and in particular large-scale clear-cutting, affects vegetation and thus runoff of DOM (i.e., nutrients and pH) in a similar way as do large-scale disturbances (see 10.4.4), and may therefore mimic effects of forest secondary succession on freshwater invertebrate communities and plant litter decomposition. However, additional impacts on soils (i.e., damage from forestry machines and soil scarification to promote seedling growth and survival) create novel disturbance regimes, resulting in, for example, increased sediment inputs, with often adverse effects on freshwater invertebrate communities and litter decomposition rates (Gurtz & Wallace, 1984; Lecerf & Richardson, 2010).

Forestry also, typically, transforms the tree community composition, in favor of species (e.g., conifers and Eucalyptus) that produce lower-quality litter to freshwater systems (Ferreira et al., 2016; Laudon et al., 2011). Such changes in riparian vegetation is an important determinant of the presence of shredders; a reduced litter input quality will lessen the role of shredders in the decomposition process (Raposeiro et al., 2018), as shredders contribute more when litter is of higher quality, whereas microbes are more important for the decomposition of lower-quality litter (Hieber & Gessner, 2002; Raposeiro et al., 2018).

Effects of forestry may, however, also be small. In fact, macroinvertebrate abundance has in some cases been found to be higher in streams impacted by forestry, suggesting that other environmental filters, such as pH, override the impact of forestry on macroinvertebrate communities (Liljaniemi et al., 2002). This may be especially true for stream environments that are characterized by strongly limiting conditions in temperature and/or nutrients (i.e., in the boreal region, e.g., Lidman et al., 2017). Moreover, as suggested above, forestry may, in the absence of fire disturbance, emulate some beneficial aspects of natural disturbances, by creating young deciduous riparian vegetation that provide high-quality litter input to fresh waters and thus promote the abundance of shredders (Liljaniemi et al., 2002; McKie & Malmqvist, 2009). In any case, equivocal effects of forestry on freshwater macroinvertebrates may be due to the level of effects being mediated by other conditions, such as substrate type (Gurtz & Wallace, 1984), and will certainly differ among different management strategies. Thus, it is somewhat difficult to draw general conclusions as to how forestry affects the importance of invertebrate shredders for litter decomposition in freshwaters; these effects are likely transient in time and highly context dependent (Ferreira et al., 2016).

Agriculture can, in several ways, have large impacts on freshwater systems and their macroinvertebrate communities, and due to a growing human population, agricultural activities and their associated impacts are predicted to increase (Dudgeon et al., 2006; Laurance et al., 2014; Moss, 2008). When land is cultivated for agricultural purposes, there may be a complete removal of riparian vegetation, resulting in a more autochthonous resource base with subsequent changes in macroinvertebrate community composition (Allan, 2004; Vannote et al., 1980). Alternatively, there is a modified riparian plant community composition, which alters quantity and quality of litter input to streams (Stenroth et al., 2015), and thus likely the role of shredders for litter decomposition. However, one of the more dramatic impacts of agriculture is the runoff of nutrients, which stimulates microbial biomass and microbially mediated litter decomposition (Gulis & Suberkropp, 2003; Woodward, 2012), but thereby likely also litter palatability and shredder-mediated decomposition (Bärlocher, 1985; Cummins & Klug, 1979). However, this potentially positive effect on shredders may be counteracted, because reduced oxygen levels due to increased microbial activity have adverse impacts on some important shredder species, such as stoneflies, which therefore typically are absent in streams impacted by agriculture (Hilsenhoff, 1988;

Stenroth et al., 2015). Accordingly, effects of nutrient enrichment on litter decomposition have been found to be stronger in colder regions, suggesting that the initial importance of macroinvertebrates (higher in colder regions), and effects of nutrient enrichment on these, determine effects of nutrient enrichment on plant litter decomposition (Ferreira et al., 2014). Agricultural activities often also result in runoff of directly harmful substances, such as pesticides (Cooper, 1993; Willis & McDowell, 1982). These substances may influence the role of invertebrate shredders for litter decomposition, either by reducing litter palatability via impacts on the microbial community (i.e., microbial conditioning; Bärlocher, 1985; Cummins & Klug, 1979; Jonsson et al., 2015) or by directly affecting the shredder community (Liess & von der Ohe, 2005).

A reduction in microbial litter conditioning, independent of cause, may require compensatory feeding by shredders to maintain growth (Bärlocher, 1985; Cummins & Klug, 1979; Flores et al., 2014). Hence, despite adverse impacts on the microbial community, the importance of shredders for plant litter decomposition may *increase*. Conversely, the importance of shredders may *decrease* despite positive effects on the microbial community, e.g., via nutrient input, if consumption of less litter is required to sustain shredder growth (Zubrod et al., 2015). Hence, human-induced impacts on litter-associated microbial communities can either decrease or increase the role of shredders in the decomposition process, but the above described, unexpected effects are likely transient, as longer-term effects on per-capita feeding activity will act on shredder abundance. Accordingly, no effects on shredder activity from agricultural pesticides, despite reduced microbially mediated litter decomposition (Rasmussen et al., 2012), or compensatory feeding due to lower litter quality (Flores et al., 2014), will likely eventually result in reduced shredder contribution to the decomposition process (Bärlocher, 1985; Cummins & Klug, 1979).

Human activities also result in voluntary or involuntary introduction of nonnative species (Ricciardi, 2007), and these species may become invasive with potentially large impacts on native organisms and the processes they mediate (Ricciardi & Cohen, 2007; Mueller & Hellmann, 2008). With regard to plant litter decomposition in fresh waters, it is not well studied how introduced and invasive plant (Dangles et al., 2002) or shredder species may influence the role of shredders. Invasive crayfish are, however, a good example of how massive the effects of species introductions can be. Besides the signal crayfish (*Aphanomyces astaci*) being a carrier of the crayfish plague and, thus, reducing (or completely removing) populations of native crayfish (Strand et al., 2014), introduced and invasive crayfish species may impact litter decomposition and other processes in complex ways (Jackson et al., 2014; Turley et al., 2017). Thus, this area of global-change effects on litter decomposition in fresh waters definitely needs more research.

Besides the potentially large impact of each of the above presented global changes on freshwater macroinvertebrates and litter decomposition, freshwater systems are often influenced by several types of disturbances simultaneously (Dudgeon et al., 2006). Hence, it is difficult to predict consequences of global change in natural systems based on studies of isolated disturbance types (Jackson et al., 2016). Moreover, the ongoing loss of freshwater biodiversity (Dudgeon et al., 2006) may weaken the resistance and resilience of fresh waters to disturbances (i.e., the insurance hypothesis; Yachi & Loreau, 1999). For example, effects of an invasive terrestrial plant on shredder-mediated litter decomposition may differ depending on the diversity and composition of the shredder community feeding on litter from that plant (Dangles et al., 2002). Nonetheless, the large environmental variability that is inherent in many freshwater systems may have increased the tolerance of these systems to multiple disturbances, compared to more stable aquatic environments, such as marine systems (Jackson et al., 2016).

10.5 Conclusion

In summary, many types of global change have the potential to modify terrestrial and freshwater environmental conditions that will have consequences for shredder communities and their role as drivers of litter decomposition and overall organic matter dynamics in streams. These impacts are very likely to differ across biomes. Indeed, even the same type of global change, e.g., warming, will likely have different implications for freshwater systems depending on biome, resulting in different effects—in terms of magnitude and/or direction—on the role of shredders for rates of leaf litter decomposition (Table 10.1). For example, increases in water temperature due to climate change are expected to be much higher at northern latitudes than in the tropics (IPCC, 2007; Settele et al., 2014), resulting in losses of important psychrophile shredder species in the north, whereas tropical communities may remain intact. On the other hand, as a result of climate change, terrestrial vegetation may become more abundant in the north and at higher latitudes (Chen et al., 2011; Walther et al., 2002; Zhang et al., 2013), resulting in increased shading of streams and more terrestrial plant litter input; this may reduce water temperatures and promote shredder abundance and thus strengthen their importance as drivers of the decomposition process (e.g., Lagrue et al., 2011; Wondzell et al., 2019).

Overall, while global change may result in a weakened or strengthened role of macroinvertebrate shredders for plant litter decomposition in fresh waters, we hypothesize that the effect of warming will be small in the tropics, in part due to relatively low importance of shredders (as opposed to microbes) for litter decomposition in this biome (Li & Dudgeon, 2009), either negative or positive in the tundra and boreal regions, and the strongest—and only negative—in the temperate region, due to increased habitat fragmentation and deteriorating environment (Bonada et al., 2007; Herbst et al., 2018), and disconnected land–water systems (Arroita et al., 2015; Giling et al., 2015), resulting from greater drought frequencies from global warming and intensified human water use (Table 10.1). Nevertheless, how the role of shredders for organic matter processing in streams will be altered by current and future climate change is immensely difficult to predict. Moreover, other types of global-change drivers, such as land use, may also show biome-specific effects, but not in the same way as climate change. For example, effects of deforestation on plant litter availability and the shredder community may be more pronounced in the tropics than in northern regions, but this has yet not been comparatively studied. Therefore, future research on organic matter processing and C cycling in streams must consider the potentially altered role of shredders under changed environmental conditions, but at the same time also realize that alterations in this role will differ among different types of global change, and be specific depending on the biome that is studied (Table 10.1).

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