Chapter 8
The Role of Key Plant Species on Litter Decomposition in Streams: Alder as Experimental Model

Javier Pérez, Ana Basaguren, Naiara López-Rojo, Alan M. Tonin, Francisco Correa-Araneda, and Luz Boyero

Abstract A key or keystone species is defined as a species with disproportionately large effects on the ecosystem relative to its abundance. In freshwater ecology it is often used with a bottom-up perspective, to refer to riparian plant species whose litter resources are of particular importance for invertebrate communities and ecosystem processes. This includes fast-decomposing species that represent an important litter supply in terms of nutrients (e.g., alder) and slow-decomposing species that last for long in the stream and are able to sustain communities in periods were preferred resources have disappeared (e.g., oak). This chapter will focus on the major role that litter of the genus *Alnus* (i.e., alder) plays in the decomposition process, a crucial component of stream ecosystem functioning. Alder litter often determines overall decomposition rates and how these are affected by factors such as plant diversity as well as rates of nutrient cycling or secondary production. We take advantage of the wide use of alder litter in multiple studies conducted at different spatial scales (from

---

J. Pérez (✉) · A. Basaguren · N. López-Rojo · L. Boyero
Department of Ecology and Plant Biology, Faculty of Science and Technology,
University of the Basque Country (UPV/EHU), 48940 Leioa, Spain
e-mail: javier.perezv@ehu.eus

A. Basaguren
e-mail: ana.basaguren@ehu.eus

N. López-Rojo
e-mail: naiara.lopez@ehu.eus

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

A. M. Tonin
Department of Ecology, IB, Universidade de Brasília, Asa Norte, Brasília, Distrito Federal CEP 70910-900, Brazil

F. Correa-Araneda
Unidad de Cambio Climático y Medio Ambiente, Instituto de Estudios Del Hábitat, Facultad de Arquitectura y Construcción, Universidad Autónoma de Chile, Temuco, Chile
e-mail: francisco.correa@uautonoma.cl

L. Boyero
IKERBASQUE, Basque Foundation for Science, Bilbao, Spain

C. M. Swan et al. (eds.), *The Ecology of Plant Litter Decomposition in Stream Ecosystems*, https://doi.org/10.1007/978-3-030-72854-0_8

local to global) and with different approaches (from laboratory to field studies) to illustrate how the presence and abundance of a key riparian plant species can drive stream ecosystem functioning.

8.1 The Key Species Concept

The concept of keystone species was coined by Robert T. Paine, a zoologist and ecologist at the University of Washington (USA), to describe the role of a predator species for shaping community structure in a rocky intertidal zone. In his words, *"…the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time… are determined by their activities and abundances"* (Paine, 1969). That was the first time this author used the keystone term, although he had previously described the important role of the starfish *Pisaster ochraceus* as predator of mussels in an intertidal community (Paine, 1966).

The keystone species term has been broadly applied since its first use, but its meaning has often varied (Mills et al., 1993). Key and keystone species have been generally used with similar meaning (but see Higdon, 2002), and we use them here as synonymous. While the original definition referred to top predators with large influence in the maintenance of community diversity and organization, in conservation ecology it has been typically used as synonym of the umbrella species concept, which implies the protection of overall communities or ecosystems through the management of a single species (e.g., Rohlf, 1991). Moreover, Mills et al. (1993), in a review about this concept, considered five categories of key species depending on the community compartment mainly affected by their loss: (1) predators (with effects on their prey or their competitors), (2) prey (with effects on their predators or other prey), (3) plants (with effects on animal consumers), (4) links (e.g., pollinators or seed dispersers, with effects on plants) and (5) modifiers (e.g., beavers, with effects on the habitat). In recent years, as a consequence of the growing rate of biodiversity loss (Barnosky et al., 2011; Loh & Wackernagel, 2004), the probability of extinction of key species has increased. Given the main ecological role of these species, their loss generally has important repercussions for ecosystem functioning, with the term keystone process species *sensu* Folke et al. (1996) also being used to refer to species that can drive critical ecosystem processes. Again, this term usually refers to players more than resources, with a top-down perspective (Davic, 2003).

However, in freshwater ecology the key species concept is often used with a bottom-up perspective, referring to riparian plant species whose litter is of particular importance for stream communities and ecosystem processes such as decomposition. Several studies have pointed out the key importance of certain riparian plant species in stream ecosystems. For example, Piccolo and Wipfli (2002) and Wipfli and Musslewhite (2004) highlighted the role of red alder (*Alnus rubra*) in upland stream reaches in Alaska to increase invertebrate and detritus subsidies to downstream sites and support higher salmonid biomass through trophic linkages. Swan and Palmer (2004) studied litter diversity effects on decomposition and concluded that the presence of a single key species, the American sycamore (*Platanus occidentalis*), caused non-additive effects in the decomposition of litter mixtures. These authors reported in a subsequent study that the loss of individual riparian species could influence consumer production and material processing, and suggested that the presence of this single slow-decomposing species (*P. occidentalis*) could inhibit detritivore growth and thus control consumer secondary production (Swan & Palmer, 2006). Also with a bottom-up perspective, França et al. (2009) studied litter inputs to a Brazilian stream in order to identify key riparian species for energy fluxes and nutrient cycling in tropical headwaters.

The review by Woodward (2009) about freshwater biodiversity, ecosystem functioning and food webs discussed the importance of litter variability in terms of ecological stoichiometry; thus, the presence of more recalcitrant litter types (e.g., oak) could enable consumers to persist once higher-quality resources (e.g., alder) have been depleted (see also Haapala et al., 2001). Kominoski et al. (2011) studied the effects of riparian species composition on stream ecosystem functioning, which was driven by high-quality litter inputs. The revision by Swan and Kominoski (2012) on plant biodiversity and decomposition highlighted several bottom-up effects on aquatic food webs. Boyero et al. (2014) showed that the identity of species that are lost from communities and of those that remain is a key driver of decomposition. The conceptual model of litter decomposition in low-order streams by Graça et al. (2015) suggested that riparian vegetation dominated by nitrogen (N) fixers (such as alder) accelerates overall decomposition in streams. Tonin et al. (2017a) assessed plant diversity effects on decomposition and identified different underling mechanisms (following Loreau & Hector, 2001), one of them being positive selection (i.e., positive diversity effects arising when the presence of a particular species with high decomposition rate dominates the decomposition rate of the mixture).

As shown in the above examples, the effects of key plant species on stream ecosystem functioning have been commonly explored in the literature. In these studies, the key species concept refers mainly to two types of species: (1) fast-decomposing species that represent an important litter supply in terms of nutrients (e.g., alder); and (2) slow-decomposing species that last for long in the stream and are able to sustain communities in periods when preferred resources have disappeared (e.g., oak). The latter species are not riparian species, at least in temperate areas, but they are abundant in the surrounding forest; thus, they might be dominant but not keystone species (*sensu* Higdon, 2002). The presence of alder litter often determines overall decomposition rates, or associated processes such as nutrient cycling or secondary production, and how these are affected by factors such as plant diversity or detritivore community density. A large number of plant litter decomposition experiments have used alder litter for two main reasons: (1) alder species are often dominant riparian species (mostly in Europe but also present in other areas; Fig. 8.1); and (2) they provide ecosystems with fast decomposing litter, hence being particularly suitable for short-term experiments lasting a few weeks. In this chapter, we mainly

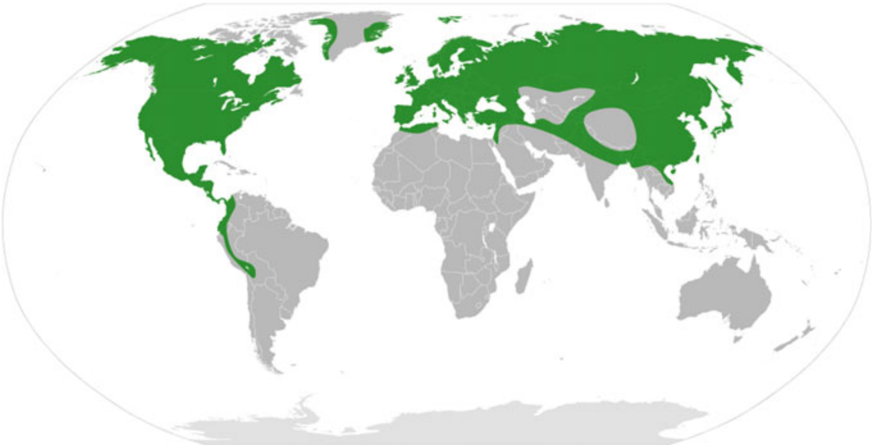


Fig. 8.1 Natural distribution of the alder species (genus *Alnus*) (*Image credit* Ninjatacoshell—commons.wikimedia.org/w/index.php?curid=27474274—based on Silvester [1977])

focus on the major role that alder litter plays in the process of litter decomposition in temperate streams.

8.2 Alder Litter in Field Experiments

Alder is the common name of a genus of riparian plants (*Alnus*) belonging to the family Betulaceae. The genus comprises about 35 species, some of which are dominant riparian species in Eurasia (mainly black alder, *Alnus glutinosa*, but also grey alder, *A. incana*). Moreover, the genus is also present in the American continent, including grey alder but with some endemic species such as Andean alder (*A. acuminata*), red alder (*A. rubra*) or Arizona alder (*A. oblongifolia*); and in Asia, including Japanese alder (*A. japonica*) and Manchurian alder (*A. hirsuta*). The N fixation capacity is the most relevant functional trait of alder trees, through the symbiotic relationship with *Frankia alni*, a filamentous actinomycete, N-fixing bacterium (Franche et al., 2008). Thus, they are scarcely limited by soil N content. These bacteria, found in tree root nodules, absorb atmospheric N_2, making it available to the tree in exchange of sugars. Therefore, alder (through roots and litter) improves the fertility of the soil where it grows, boosting ecological succession in poor soils. In aquatic ecosystems it constitutes an allochthonous resource of key importance, reaching to the stream in the form of litter with relatively low carbon (C):N and C:P ratios (Hladyz et al., 2009). Hence, hereafter we will mainly focus on alder species as examples of fast-decomposing, nutrient-rich litter that is of key importance in their distribution areas.

Taking advantage of the wide use of alder in multiple field studies using the litter bag technique (Bärlocher, 2005) at different spatial scales (from local to global; Table 8.1), we illustrate how the presence and abundance of this key riparian tree (as an example of fast-decaying species) can drive overall stream ecosystem functioning.

8.2.1 Alder and Stream Litter Processing Capacity

Alder litter is commonly used in studies dealing with land use (which implies the replacement or removal of riparian and/or surrounding vegetation), as it usually reflects the processing capacity of the stream detritivore community better than lower-quality litter. Thus, in Northern Spain, decomposition of black alder (*A. glutinosa*) was 20% lower in streams flowing through exotic pine plantations (*Pinus radiata*) than in streams flowing through mixed deciduous forests, possibly in relation to the lower detritivore densities in the former; in contrast, decomposition of pine needles was lower than that of alder and did not differ between stream types (Martínez et al., 2013). Similarly, litter of Andean alder (*A. acuminata*) decomposed faster than that of another N-fixing local tree species (cutlass guaba, *Inga spectabilis*) in forest and pasture streams of Ecuador; the difference was greater for coarse-mesh than for fine-mesh bags in forest streams (1.9- *vs.* 1.3-fold,) and in pasture than forest streams (1.8- *vs.* 1.4-fold), and alder litter harboured almost twice more species of microbial decomposers and showed higher sporulation rates (Encalada et al., 2010).

The above pattern, however, is not general, as other studies have shown higher sensitivity of poorer-quality litter to land use changes. For example, black alder decomposition did not differ between streams running through mixed deciduous forests and beech forests in France (Lecerf et al., 2005), in contrast to common oak litter (*Quercus robur*) decomposition, which was higher in mixed forest streams in coarse-mesh bags; still, alder decomposed faster than oak, in both coarse-mesh and fine-mesh bags. In a regional scale study, black alder also decomposed much faster than common oak in coarse-mesh and fine-mesh bags in 11 Mediterranean streams in Northeastern Spain with varying environmental conditions in terms of hydrology, water quality and invertebrate assemblages; alder decomposition was related to detritivore density and biomass, but that was not the case for oak (Monroy et al., 2016).

8.2.2 Dissolved Nutrients and Alder Decomposition

Alder litter has lower nutrient stoichiometric imbalance for stream consumers than most other litter types (Hladyz et al., 2009), so the availability of dissolved nutrients or the stream trophic status (*sensu* Dodds, 2007) generally has less effect on alder decomposition than on that of nutrient-poorer species. In consequence,

Table 8.1 Examples of field decomposition studies (streams and rivers) using leaf litter of alder and other species (also other substrates: wood and sticks). A brief statement about alder-derived results is given

References	Plant species	Alder-related result
Lecerf et al. (2005)	*Alnus glutinosa*	Decomposition rate of alder litter was around twice as fast as that of oak litter
	Quercus robur	
Ferreira et al. (2006)	*Alnus glutinosa*	Nitrate enrichment did not stimulate alder litter decomposition rates (as did for oak litter)
	Ochroma pyramidale (wood)	
	Quercus robur	
Gulis et al. (2006)	*Alnus glutinosa*	Low levels of eutrophication stimulated decomposition less for alder than for oak litter
	Quercus robur	
Abelho (2008)	*Alnus glutinosa*	Alder litter was colonized earlier and then macroinvertebrates shifted towards harder litter
	Castanea sativa	
	Quercus ilex	
Arroita et al. (2012)	*Alnus glutinosa*	Shedders were more abundant in alder bags and almost absent from poplar sticks. Poplar and alder litter belong to the fast processing group
	Fagus sylvatica	
	Eucalyptus camaldulensis	
	Platanus × *hispanica*	
	Populus nigra (leaves & sticks)	
	Quercus robur	
Ferreira et al. (2012)	*Alnus glutinosa*	Alder seemed to drive the decomposition of litter packs
	Castanea sativa	
	Inga punctata	
	Quercus robur	
	Triplaris dugandii	
	Zygia cataractae	
Martínez et al. (2013)	*Alnus glutinosa*	Pine plantations reduced litter processing capacity of streams
	Pinus radiata	
Pérez et al. (2014)	*Alnus glutinosa*	Transplantation to a nutrient-richer site enhanced eucalypt litter processing (but not alder one)
	Eucalyptus globulus	
Boyero et al. (2016)	*Alnus glutinosa*	Temperature had a large positive influence on microbial decomposition of alder litter
	+70 local species	
Monroy et al. (2016)	*Alnus glutinosa*	Alder litter decomposition was positively correlated to the density and biomass of shredders; that of oak litter was not
	Quercus robur	

using alder in comparison with poorer-quality litter allows examining the magnitude of such effects. In a Portuguese stream experimentally subjected to different levels of N enrichment across a stream reach, decomposition of black alder was not affected by enrichment, while decomposition of common oak (which was lower than that of alder) was enhanced by N enrichment (Ferreira et al., 2006). Similarly, in another study, decomposition of black alder did not consistently differ between 5 pairs of reference/eutrophic Portuguese streams, in contrast to the consistently faster decomposition of common oak in eutrophic streams (Gulis et al., 2006); the authors suggested that this could be due to a higher susceptibility of alder litter to mechanical fragmentation and erratic detritivore colonisation and feeding, and to the lower nutrient content of oak litter, which may trigger a more rapid microbial response to eutrophication. Similar results were observed in a litter-bag transplantation experiment in Northern Spain (Pérez et al., 2014), where black alder decomposition was less affected by the stream trophic status than that of blue gum eucalypt (*Eucalyptus globulus*); while eucalypt decomposed faster in a midstream than a headwater reach (the former being more affected by agroforestry), alder decomposition was similar between reaches, even when litter had been transplanted from the other reach. Nonetheless, other studies have shown that dissolved nutrient availability can influence variables related to alder decomposition such as the conditioning level reached [i.e., the microbially-mediated quality change; e.g., Pozo et al. (2011)].

8.2.3 Alder: The Top of the Class

Alder litter is often a preferred resource of decomposers, being usually the one that is decomposed fastest in studies comparing different types of litter (Casas et al., 2013). For example, in a Portuguese stream, black alder decomposed more than 3-times faster ($k = 0.033\ \mathrm{d}^{-1}$) than sweet chestnut (*Castanea sativa*) or common oak ($k = 0.011\ \mathrm{d}^{-1}$ in both cases) in coarse-mesh bags in a 2-month experiment; this study showed that detritivores colonized alder earlier (with a peak at day 28) than the other species (day 65), suggesting that they exploited their preferred resource first and then shifted to less palatable resources (Abelho, 2008). Similarly, in a pristine stream in Northern Spain, black alder and black poplar (*Populus nigra*) decomposed at a similar rate ($k = 0.012\ \mathrm{d}^{-1}$ for both) and were faster than 4 other species [common oak, beech (*Fagus sylvatica*), London plane (*Platanus* × *hispanica*) and river red gum eucalypt (*Eucalyptus camaldulensis*): $k = 0.002$ to $0.008\ \mathrm{d}^{-1}$] in coarse-mesh bags; furthermore, detritivore densities and fungal sporulation rates were highest in alder (Arroita et al., 2012). However, in the same study, the decomposition rate of alder in a nearby polluted stream was reduced by 48%, a greater reduction than that for most other species (5% for poplar, 24% for oak, 26% for beech and 36% for eucalypt), suggesting that deleterious effects of pollutants on detritivores were not compensated by nutrient subsidies for alder litter as they did for nutrient-poor litter types (Arroita et al., 2012).

8.2.4 Alder Is Always Welcome

Given the known palatability of alder litter, this substrate is a good candidate when aiming to select a common substrate for decomposition studies conducted at large spatial scales. For example, black alder decomposition rates were similar between a temperate (Portugal) and a tropical (Ecuador) stream, but faster in the temperate stream when data were adjusted by water temperature (Ferreira et al., 2012); it decomposed faster in coarse-mesh than in fine-mesh bags, and it showed higher fungal biomass, taxonomic richness and sporulation rates than other species, and higher densities of detritivores than common oak, in the temperate stream. In the same study, litter of other species incubated with alder in 3-species mixtures decomposed faster than in monoculture, so the presence of alder seemed to enhance decomposition; in contrast, the presence of oak in mixtures had the opposite effect (Ferreira et al., 2012).

In a large-scale study across Europe, decomposition of black alder and common oak in coarse-mesh bags (and less so in fine-mesh bags) showed a humped-shaped response (i.e., a subsidy stress response) to increasing nutrient concentrations; rates were low at the extremes, and low to high at intermediate concentrations, where nutrients were not limiting and other stressors were not too high, so other drivers became important (Woodward et al., 2012). In another large-scale study including multiple tropical sites around the world, black alder litter decomposed faster than most native litter mixtures, with few exceptions; differences between alder and mixtures occurred for both coarse-mesh and fine-mesh bags, and variation across sites was larger for alder than for mixtures, possibly reflecting differences in detritivore and microbial assemblages (Boyero et al., 2015).

In other global-scale studies, decomposition of black alder was mainly driven by temperature, mostly through its direct influence on microbial decomposition rate (Boyero et al., 2011, 2016). Alder decomposition was higher in more alkaline waters in warmer streams (possibly through effects on microorganisms and detritivores that are sensitive to low pH), but higher in more acidic waters in cooler streams (where detritivores typical of acidic waters dominate).

8.3 Alder Litter in Laboratory Experiments

Here we mainly refer to litter decomposition experiments conducted in microcosms, which are enclosed, simplified and relatively small ecological systems containing a reduced assemblage of living organisms (Canhoto et al., 2005). While artificial stream facilities (which are in between field and microcosms approaches) are also used sometimes (e.g., Zubrod et al., 2017), the low number of studies so far precludes any generalization. Microcosms can be of very different sizes, from little flasks or test tubes to big tanks; however, for litter decomposition studies, microcosms often consist of glass jars filled with stream water, sediment and litter as the main resource for detritivores and microorganisms, and provided with a natural photoperiod and aeration to mimic streams conditions (for further details see chapter 20 in this volume). The present section draws some generalizations derived from the use of alder litter in microcosm experiments using a selection of ten stream microcosm studies (Table 8.2).

8.3.1 Alder Is a Good Resource for Consumers

As occurred in field studies, alder litter usually is the highest-quality resource in microcosm experiments, due to its low C:N ratio. This implies that it is usually the resource preferred by detritivores, resulting in higher consumption, and rendering higher detritivore growth rates. Most microcosm experiments have measured consumption rates (and other associated variables) of litter types of contrasting quality, which are generally offered separately to consumers (monocultures). Thus, in most cases [but see Solagaistua et al. (2019)], alder has shown the highest consumption rate. This is despite the fact that different detritivorous consumers have been used, with caddisflies (e.g., *Sericostoma pyrenaicum, S. vittatum, Limnephilus atlanticus*) and amphipods (e.g., *Gammarus pullex, G. fossarum, Echinogammarus berilloni*) being the most common ones; an exception is Fidalgo et al. (2013), who used the red swamp crayfish *Procambarus clarkii.* All these microcosm experiments have allowed the study of variables associated with the decomposition process that are very difficult or impossible to measure in the field. This includes, for example, detritivore growth and survival rates (Balibrea et al., 2017; Larrañaga et al., 2014a), or nutrient assimilation efficiency (Santonja et al., 2018), all of which are usually higher when invertebrates feed on alder. These physiological variables appear to be accurate short-term ecological indicators of different stressors (Landeira-Dabarca et al., 2019; Pérez et al., 2021).

8.3.2 Alder Is a Key Driver of Litter Diversity Effects on Decomposition

Even if some relevant studies have focused on detritivore consumption preferences (e.g., Balibrea et al., 2017; Foucreau et al., 2013; Graça & Cressa, 2010), the majority of experiments conducted in the last couple of decades have examined the consequences of losing litter diversity on decomposition. These studies have shown that litter diversity loss significantly alters the rates of decomposition and other related processes, such as nutrient cycling and the production of fine particulate organic matter (Fernandes et al., 2015; López-Rojo et al., 2018, 2019). Some diversity effects might be driven by a small supply of alder (Larrañaga et al., 2020), stimulating the consumption of low quality litter. Furthermore, the simultaneous assessment of

Table 8.2 Examples of laboratory decomposition studies (stream microcosms mainly) using alder and other litter species. A brief statement of alder-derived results is given

References	Plant species	Alder related result
Villanueva et al. (2011)	*Alnus glutinosa* *Quercus robur* *Eucalyptus globulus*	Larvae lost phosphorus at higher temperature when fed oak or eucalypt litter, but not when fed alder litter
Jabiol and Chauvet (2012)	*Alnus glutinosa* *Betula pendula* *Juglans regia* *Quercus robur*	Mixing litter increased walnut consumption but not that of alder or oak litter
Foucreau et al. (2013)	*Alnus gutinosa* *Carpinus betulus* *Quercus robur*	Consumption rates on alder litter were significantly higher
Larrañaga et al. (2014a)	*Alnus glutinosa* *Eucalyptus globulus* *Quercus robur*	Detritivores feeding on alder litter had higher growth rate and recovered the mass lost in reproduction in short time
Campos et al. (2014)	*Alnus glutinosa* *Eucalyptus globulus*	Cadmium exposure only affected the mass loss of alder litter, reducing detritivore feeding
Arce-Funck et al. (2016)	*Acer pseudoplatanus* *Alnus glutinosa*	Consumption and energetic storage, but not consumer tolerance to silver, was higher on alder litter
Tonin et al. (2017a)	*Alnus glutinosa* *Populus nigra* *Robinia pseudoacacia* *Salix atrocinerea*	Alder litter decomposed faster than other species. Detritivores fed preferentially on alder litter
Santonja et al. (2018)	*Alnus glutinosa* *Quercus robur*	Consumption was higher in alder than in oak litter. Assimilation was twofold higher
López-Rojo et al. (2018)	*Alnus glutinosa* *Corylus avellana* *Ilex aquifolium* *Quercus robur*	Alder litter monocultures showed the highest consumption and growth rate. Plant diversity effect increased in presence of alder litter
Solagaistua et al. (2019)	*Alnus glutinosa* *Corylus avellana* *Fagus sylvatica* *Fraxinus excelsior* *Quercus robur*	Alder litter was the second preferred resource; consumption of European ash litter was higher, following a quality index

microcosms containing monocultures and mixtures has enabled to understand the mechanisms underlying such diversity effects. Nutrient-poor species such as oak can benefit from the presence of nutrient-rich species such as alder, which suggests possible mechanisms. For example, alder leaching could enhance microbial colonization and detritivore-mediated consumption of poor resources; thus, the presence of alder can increase the magnitude of diversity effects on decomposition and associated processes (López-Rojo et al., 2018).

Results of microcosm studies are not always consistent or easily comparable. This could be related to different methodological procedures, such as the use of different substrates, even within the same species, which might differ in nutrient contents (e.g., litter from different areas or years, Lecerf & Chauvet, 2008), or consumers with different conditions (e.g., life stage, physiological status, acclimation period). For example, some studies found alder consumption to be variable (sometimes lower than expected) when offered together with lower-quality litter in mixture (Jabiol & Chauvet, 2012; Little & Altermatt, 2018). Solagaistua et al. (2019) suggested that special care should be taken when comparing microcosm experiments with different incubation times.

8.3.3 Alder Can Inform About Early Effects of Environmental Change

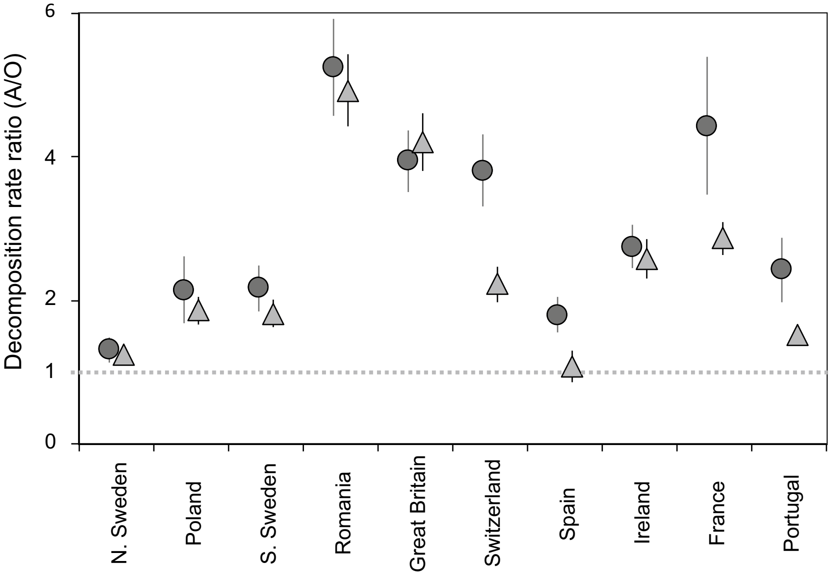
As alder litter is a fast-decomposing litter, it can be used to detect early ecological consequences of environmental change such as increases in water temperature, dissolved nutrients or pollutants, using experiments of relatively short duration. For example, Villanueva et al. (2011) examined the metabolic rates of *Sericostoma vittatum* larvae feeding on black alder, blue gum eucalypt and common oak at two different temperatures, concluding that litter type modulated the effects of temperature; while larvae fed poor-quality litter lost P and reduced N assimilation efficiency at higher temperature, this did not occur for larvae fed alder. Also, Tonin et al. (2017a) showed that microbial activity was enhanced by dissolved N availability on N-poor poplar, but not on N-rich alder. Similarly, studies assessing effects of other pollutants on decomposition have been usually conducted using a single litter type, often black alder (e.g., Zubrod et al., 2017). Campos et al. (2014) examined the decomposition of black alder and eucalyptus that were pre-incubated in water with cadmium; alder, but not eucalyptus, was decomposed more slowly at higher cadmium concentrations. In contrast, Arce-Funck et al. (2016) conducted and experiment where *G. fossarum* previously fed black alder or sycamore maple (*Acer pseudoplatanus*) were exposed to different water silver concentrations; although consumption rate and energetic storage was higher for individuals fed alder, this did not increase their tolerance to dissolved silver, so alder litter was unable to compensate for the negative effects of this metal. Therefore, taking these studies into account, some toxicological effects could be litter type-dependent (Arce-Funck et al., 2018; Cornejo et al., 2020).

8.4 Comparisons Between Alder and Poor-Quality Litter

Some of the above sections have mentioned the utility of analysing patterns of decomposition of high-quality, fast-decomposing alder in comparison with those of poor-quality, slow-decomposing species (mainly oak). Here we explore the usefulness of calculating ratios between alder and oak decomposition rates (hereafter A/O) for different purposes. The use of decomposition ratios as indices of stream ecosystem functioning was suggested by Gessner and Chauvet (2002), who proposed the use of ratios between impact and reference sites as indicators of impairment, or between coarse-mesh and fine-mesh bags as indicators of detritivore activity. They also suggested that ratios of fast-decomposing and recalcitrant litter could be useful; for example, they could inform about different mechanisms contributing to decomposition, or about the different time scales required for impact assessment. Still, the use of such ratios is scarce, even if the experimental comparison of litter types of contrasting quality is a common practice. An exception is Larrañaga et al. (2014b), who explored black alder (A) and eucalyptus (E) decomposition rates and associated detritivore densities and presented both of them as A/E ratios.

While ratios cannot replace original data on decomposition rates of different species, they provide complementary information. For example, they can reflect the influence of different factors or the relative importance of different decomposition agents (e.g., alder may better reflect the processing capacity of detritivores, and oak the degree of microbial conditioning). Here, taking advantage of the abundance of decomposition field studies using black alder and common oak, especially deriving from the RivFunction European project (Chauvet et al., 2016), we present A/O ratios from coarse-mesh and fine-mesh bags (representing total and microbial decomposition, respectively) and explore the potential of such ratios to provide useful information about stream ecosystems. The following comments should be considered only as tentative explanations of the patterns evidenced by A/O ratios, supported by the empirical observations of studies revised here.

Firstly, we plotted mean values of A/O ratios of decomposition rates for the different regions (Fig. 8.2) included in Woodward et al. (2012), who explored effects of nutrient enrichment in 100 streams greatly differing in dissolved nutrient availability (the 1st workpackage of RivFunction). In most cases, alder decomposed considerably faster than oak. Only sites in Northern Sweden (with very low temperature and dissolved nutrient availability) presented A/O ratios below 2 in coarse-mesh and fine-mesh bags, meaning that decomposition of alder and oak was very similar; these low ratios (and rates) suggested biotic limitation, usually observed in such environmental conditions. In general, A/O ratios from both coarse-mesh and fine-mesh bags showed values between 2 and 6. Several regions of Europe, all of them within the upper range of water temperature values (Switzerland, Spain, France and Portugal), showed marked differences between coarse-mesh and fine-mesh A/O ratios, the latter being lower; this suggests a higher preference of detritivores for alder, while microbial decomposers appeared to be less determined by litter quality, as usually observed. The A/O ratios within each of these regions were rather similar,



	N. Sweden	Poland	S. Sweden	Romania	Great Britain	Switzerland	Spain	Ireland	France	Portugal
Temperature	0.6 ± 0.1	2.3 ± 0.3	3.2 ± 0.2	4.0 ± 0.5	5.5 ± 0.2	7.6 ± 0.3	7.9 ± 0.2	8.3 ± 0.3	8.8 ± 0.3	10.9 ± 0.2
DIN | SRP	89 | 7	2379 | 125	3507 | 22	2624 | 202	2115 | 78	1921 | 36	745 | 43	6549 | 114	4035 | 28	1076 | 20

Fig. 8.2 Mean A/O ratios (±SE, n = 10 sites per region) of exponential decomposition rates in coarse-mesh (dark circles) and fine-mesh bags (light triangles), with regions ordered by mean water temperature (ºC). Mean dissolved nutrient availability (μg L^{-1}) in terms of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP). The grey dot line means no difference between alder and oak decomposition rate (i.e., A/O = 1) (Data credit Woodward et al. [2012])

with only French sites showing high intra-regional variability in coarse-mesh ratios. Regional similarity in A/O ratios could be related to ecogeographic features (e.g., climate, hydrology, biological communities, etc.) determining the processing capacities of the different regions, and intra-regional variability of the ratio might point to high environmental variability among sites.

Secondly, we discuss some coarse-mesh A/O ratios from studies derived from the 2nd workpackage of RivFunction, which was focused on the effects of riparian forest modification. Lecerf et al. (2005) compared effects of forest type (beech *vs.* mixed) on decomposition across sites in France. These authors indicated that there were significant differences in decomposition rates of coarse-mesh bags only when considering the interaction between forest type and litter type. Using data from this study, we obtained A/O ratios of ca. 4.0 in mixed forest sites and 1.8 in beech forest sites, indicating the important influence of riparian vegetation in supporting detritivore assemblages. Riipinen et al. (2010) examined alder and oak decomposition at 30 sites in 3 European regions; the A/O ratios in coarse-mesh bags were ca. 6.0 in England, but much lower in Ireland and Poland (2.5–3.0 and 1.0–1.5, respectively), regardless of the surrounding vegetation type. Similar results were found in a study comparing litter decomposition in streams surrounded by deciduous forest or pasture in 3 European regions (Hladyz et al., 2010): the A/O ratio of coarse-mesh bags was independent of riparian vegetation in Ireland (3.8 *vs.* 3.9 in forest and pasture, respectively) and Romania (4.3 *vs.* 4.5), but not in Switzerland (2.5 *vs.* 1.0). The latter was the only region showing differences in decomposition between land use types, possibly due to differences in detritivore assemblages (Hladyz et al., 2010). Ferreira et al. (2015) found differences in alder and oak decomposition in coarse-mesh bags between streams sites surrounded by mixed forest and eucalyptus plantations in Spain and Portugal; we observed A/O ratios of 2.9 and 2.5 in mixed forest streams (Spain and Portugal, respectively) and 1.1 and 2.0 in eucalyptus streams, suggesting greater effects of plantations on detritivores at the Spanish sites (which held higher invertebrate densities than the Portuguese sites), as discussed by the authors.

Finally, we consider studies other than those from RivFunction. A study in Northern Spain found that decomposition of litter differing in quality (black alder, beach and common oak) had similar sensitivity to temperature along an altitudinal gradient, possibly due to small variations in detritivore assemblages along the gradient (Martínez et al., 2016); A/O ratios derived from this study ranged from 4.5 to 4.7, supporting their conclusions. Monroy et al. (2016) found high variability in decomposition rates across 11 streams of the Ebro river basin in Northeastern Spain; A/O ratios from these streams were in general high but also highly variable (2.8–8.0), possibly reflecting the effects of high environmental variation in terms of hydrology, water quality and invertebrate assemblages.

8.5 Conclusions

We have reviewed knowledge about key riparian species, in particular alder, which presence and/or abundance are often main drivers of stream ecosystem functioning. This information may help with the selection of litter types to be used in decomposition experiments, depending on the study design and hypotheses to be tested in each case. Thus, the use of alder litter may be particularly useful when short-term patterns are of interest, while slow decomposers such as oak (or any other local recalcitrant species) may be more informative in the long term. Moreover, alder litter, which is a highly preferred resource, could act as 'bait' for detritivores in a reach depleted of good-quality litter (e.g., Martínez et al., 2015); this could be useful in some cases, but may also lead us to biased conclusions. Alder litter also has characteristics, other than its fast decomposition, which make it useful in experiments; this includes high nutrient concentrations derived from the N-fixing capacity of the tree, which makes this species particularly suitable for studies exploring the role of litter quality on decomposition, or the role of functional trait diversity (as alder presents special traits such as the N-fixing capacity).

The same could apply to other fast-decomposing species in areas where alder is not present. For example, in tropical regions (e.g., França et al., 2009), a similar role may be played by other (N-fixing or non-fixing) species, and most likely by a variety of species, as tropical riparian forests are more diverse (Boyero et al., 2017; Tonin et al., 2017b). Lianas (woody vines), which are structural parasites of shade-tolerant trees with fast-growing capacity, might be a good example of key plant species in tropical moist forest (van der Heijden et al., 2013) and also for litter decomposition in streams. Some fast-decaying *Ficus* species might play a similar key role in the tropical streams, as its decomposition rate is similar to that of *Alnus* species (López-Rojo et al., 2020). Overall, key plant species (alone or in combination with other species) deserve special consideration in studies assessing litter decomposition and related processes that are fundamental components of stream ecosystem functioning.

References

Abelho, M. (2008). Effects of leaf litter species on macroinvertebrate colonization during decomposition in a Portuguese stream. *International Review of Hydrobiology, 93,* 358–371.

Arce-Funck, J., Crenier, C., Danger, M., Billoir, E., Usseglio-Polatera, P., & Felten, V. (2018). High stoichiometric food quality increases moulting organism vulnerability to pollutant impacts: An experimental test with *Gammarus fossarum* (Crustacea: Amphipoda). *Science of the Total Environment, 645,* 1484–1495.

Arce-Funck, J., Crenier, C., Danger, M., Cossu-Leguille, C., Guérold, F., & Felten, V. (2016). Stoichiometric constraints modulate impacts of silver contamination on stream detritivores: An experimental test with *Gammarus fossarum. Freshwater Biology, 61,* 2075–2089.

Arroita, M., Aristi, I., Flores, L., Larrañaga, A., Díez, J., Mora, J., Romani, A. M., & Elosegi, A. (2012). The use of wooden sticks to assess stream ecosystem functioning: Comparison with leaf breakdown rates. *Science of the Total Environment, 440,* 115–122.

Balibrea, A., Ferreira, V., Gonçalves, V., & Raposeiro, P. M. (2017). Consumption, growth and survival of the endemic stream shredder *Limnephilus atlanticus* (Trichoptera, Limnephilidae) fed with distinct leaf species. *Limnologica, 64,* 31–37.

Bärlocher, F. (2005). Leaf mass loss estimated by litter bag technique. In M. A. S. Graça, F. Bärlocher, & M. O. Gessner (Eds.), *Methods to study litter decomposition: A practical guide* (pp. 37–42). Springer.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature, 471,* 51–57.

Boyero, L., Cardinale, B. J., Bastian, M., & Pearson, R. G. (2014). Biotic vs. abiotic control of decomposition: A comparison of the effects of simulated extinctions and changes in temperature. *PLoS One, 9*(1), e87426.

Boyero, L., Graça, M. A. S., Tonin, A. M., Pérez, J., Swafford, A. J., Ferreira, V., Landeira-Dabarca, A., Alexandrou, M. A., Gessner, M. O., McKie, B. G., Albariño, R. J., Barmuta, L. A., Callisto, M., Chara, J., Chauvet, E., Colon-Gaud, C., Dudgeon, D., Encalada, A. C., Figueroa, R., … Pearson, R. G. (2017). Riparian plant litter quality increases with latitude. *Scientific Reports,* 7, 10562.

Boyero, L., Pearson, R. G., Gessner, M. O., Barmuta, L. A., Ferreira, V., Graça, M. A. S., Dudgeon, D., Boulton, A. J., Callisto, M., Chauvet, E., Helson, J. E., Bruder, A., Albariño, R. J., Yule, C. M., Arunachalam, M., Davies, J. N., Figueroa, R., Flecker, A. S., Ramírez, A., … West, D. C. (2011). A global experiment suggests climate warming will not accelerate litter decomposition in streams but may reduce carbon sequestration. *Ecology Letters, 14*, 289–294.

Boyero, L., Pearson, R. G., Gessner, M. O., Dudgeon, D., Ramírez, A., Yule, C. M., Callisto, M., Pringle, C. M., Encalada, A. C., Arunachalam, M., Mathooko, J., Helson, J. E., Rincón, J., Bruder, A., Cornejo, A., Flecker, A. S., Mathuriau, C., M'Erimba, C., Gonçalves, J. F., … Jinggut, T.

(2015). Leaf-litter breakdown in tropical streams: Is variability the norm? *Freshwater Science, 34,* 759–769.

Boyero, L., Pearson, R. G., Hui, C., Gessner, M. O., Pérez, J., Alexandrou, M. A., Graça, M. A., Cardinale, B. J., Albariño, R. J., & Arunachalam, M. (2016). Biotic and abiotic variables influencing plant litter breakdown in streams: A global study. *Proceedings of the Royal Society B: Biological Sciences, 283,* 20152664.

Campos, D., Alves, A., Lemos, M. F., Correia, A., Soares, A. M., & Pestana, J. L. (2014). Effects of cadmium and resource quality on freshwater detritus processing chains: A microcosm approach with two insect species. *Ecotoxicology, 23,* 830–839.

Canhoto, C., Graça, M. A., & Bärlocher, F. (2005). Feeding preferences. In: *Methods to study litter decomposition* (pp. 297–302). Springer.

Casas, J. J., Larrañaga, A., Menéndez, M., Pozo, J., Basaguren, A., Martínez, A., Pérez, J., González, J. M., Mollá, S., & Casado, C. (2013). Leaf litter decomposition of native and introduced tree species of contrasting quality in headwater streams: How does the regional setting matter? *Science of the Total Environment, 458,* 197–208.

Chauvet, E., Ferreira, V., Giller, P. S., McKie, B. G., Tiegs, S. D., Woodward, G., Elosegi, A., Dobson, M., Fleituch, T., & Graça, M. A. (2016). Litter decomposition as an indicator of stream ecosystem functioning at local-to-continental scales: Insights from the European RivFunction project. *Advances in Ecological Research*, *55*, 99–182. Elsevier.

Cornejo, A., Pérez, J., Alonso, A., López-Rojo, N., & Boyero, L. (2020). A common fungicide impairs stream ecosystem functioning through effects on aquatic hyphomycetes and detritivorous caddisflies. *Journal of Environmental Management, 263*, 110425.

Davic, R. D. (2003). Linking keystone species and functional groups: A new operational definition of the keystone species concept. *Conservation Ecology, 7*.

Dodds, W. K. (2007). Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology & Evolution, 22,* 669–676.

Encalada, A., Calles, J., Ferreira, V., Canhoto, C., & Graça, M. A. S. (2010). Riparian land use and the relationship between the benthos and litter decomposition in tropical montane forest streams. *Freshwater Biology, 55,* 1719–1733.

Fernandes, I., Duarte, S., Cássio, F., & Pascoal, C. (2015). Plant litter diversity affects invertebrate shredder activity and the quality of fine particulate organic matter in streams. *Marine & Freshwater Research, 66,* 449–458.

Ferreira, V., Encalada, A. C., & Graça, M. A. S. (2012). Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. *Freshwater Science, 31,* 945–962.

Ferreira, V., Gulis, V., & Graça, M. A. S. (2006). Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia, 149,* 718–729.

Ferreira, V., Larrañaga, A., Gulis, V., Basaguren, A., Elosegi, A., Graça, M. A., & Pozo, J. (2015). The effects of eucalypt plantations on plant litter decomposition and macroinvertebrate communities in Iberian streams. *Forest Ecology and Management, 335*, 129–138.

Fidalgo, M. L., Ferreira, C., & Sampaio, A. (2013). Assessment of the preferences of red swamp crayfish (*Procambarus clarkii*) fed with riparian tree leaves: A microcosm study. *International Review of Hydrobiology, 98,* 183–190.

Folke, C., Holling, C. S., & Perrings, C. (1996). Biological diversity, ecosystems, and the human scale. *Ecological Applications, 6,* 1018–1024.

Foucreau, N., Puijalon, S., Hervant, F., & Piscart, C. (2013). Effect of leaf litter characteristics on leaf conditioning and on consumption by *Gammarus pulex*. *Freshwater Biology, 58,* 1672–1681.

França, J. S., Gregório, R. S., de Paula, J. D. A., Júnior, J. F. G., Ferreira, F. A., & Callisto, M. (2009). Composition and dynamics of allochthonous organic matter inputs and benthic stock in a Brazilian stream. *Marine & Freshwater Research, 60,* 990–998.

Franche, C., Lindström, K., & Elmerich, C. (2008). Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. *Plant and Soil, 321,* 35–59.

Gessner, M. O., & Chauvet, E. (2002). A case for using litter breakdown to assess functional stream integrity. *Ecological Applications, 12,* 498–510.

Graça, M. A., & Cressa, C. (2010). Leaf quality of some tropical and temperate tree species as food resource for stream shredders. *International Review of Hydrobiology, 95,* 27–41.

Graça, M. A., Ferreira, V., Canhoto, C., Encalada, A. C., Guerrero-Bolaño, F., Wantzen, K. M., & Boyero, L. (2015). A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology, 100,* 1–12.

Gulis, V., Ferreira, V., & Graça, M. A. S. (2006). Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: Implications for stream assessment. *Freshwater Biology, 51,* 1655–1669.

Haapala, A., Muotka, T., & Markkola, A. (2001). Breakdown and macroinvertebrate and fungal colonization of alder, birch, and willow leaves in a boreal forest stream. *Journal of the North American Benthological Society, 20,* 395–407.

Higdon, J. (2002). Functionally dominant herbivores as keystone species. *Conservation Ecology, 6*.

Hladyz, S., Gessner, M. O., Giller, P. S., Pozo, J., & Woodward, G. (2009). Resource quality and stoichiometric constraints on stream ecosystem functioning. *Freshwater Biology, 54,* 957–970.

Hladyz, S., Tiegs, S. D., Gessner, M. O., Giller, P. S., Risnoveanu, G., Preda, E., Nistorescu, M., Schindler, M., & Woodward, G. (2010). Leaf-litter breakdown in pasture and deciduous woodland streams: A comparison among three European regions. *Freshwater Biology, 55,* 1916–1929.

Jabiol, J., & Chauvet, E. (2012). Fungi are involved in the effects of litter mixtures on consumption by shredders. *Freshwater Biology, 57,* 1667–1677.

Kominoski, J. S., Marczak, L. B., & Richardson, J. S. (2011). Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology, 92,* 151–159.

Landeira-Dabarca, A., Pérez, J., Graça, M. A., & Boyero, L. (2019). Joint effects of temperature and litter quality on detritivore-mediated breakdown in streams. *Aquatic Sciences, 81,* 1–10.

Larrañaga, A., Basaguren, A., & Pozo, J. (2014a). Resource quality controls detritivore consumption, growth, survival and body condition recovery of reproducing females. *Marine & Freshwater Research, 65,* 910–917.

Larrañaga, A., de Guzmán, I., & Solagaistua, L. (2020). A small supply of high quality detritus stimulates the consumption of low quality materials, but creates subtle effects on the performance of the consumer. *Science of the Total Environment, 726*, 138397.

Larrañaga, S., Larrañaga, A., Basaguren, A., Elosegi, A., & Pozo, J. (2014b). Effects of exotic eucalypt plantations on organic matter processing in Iberian streams. *International Review of Hydrobiology, 99,* 363–372.

Lecerf, A., & Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology, 9,* 598–605.

Lecerf, A., Dobson, M., Dang, C. K., & Chauvet, E. (2005). Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia, 146,* 432–442.

Little, C. J., & Altermatt, F. (2018). Species turnover and invasion of dominant freshwater invertebrates alter biodiversity–ecosystem-function relationship. *Ecological Monographs, 88,* 461–480.

Loh, J., & Wackernagel, M. (2004). *Living planet report 2004.* WWF-World Wide Fund for Nature.

López-Rojo, N., Martínez, A., Pérez, J., Basaguren, A., Pozo, J., & Boyero, L. (2018). Leaf traits drive plant diversity effects on litter decomposition and FPOM production in streams. *PLoS One, 13,* e0198243.

López-Rojo, N., Pozo, J., Pérez, J., Basaguren, A., Martínez, A., Tonin, A. M., Correa-Araneda, F., & Boyero, L. (2019). Plant diversity loss affects stream ecosystem multifunctionality. *Ecology, 100*, e02847.

López-Rojo, N., Pérez, J., Pozo, J., Basaguren, A., Apodaka-Etxebarria, U., Correa-Araneda, F., & Boyero, L. (2020). Shifts in key leaf litter traits can predict effects of plant diversity loss on decomposition in streams. *Ecosystems.*

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature, 412,* 72.

Martínez, A., Larrañaga, A., Pérez, J., Descals, E., Basaguren, A., & Pozo, J. (2013). Effects of pine plantations on structural and functional attributes of forested streams. *Forest Ecology and Management, 310,* 147–155.

Martínez, A., Monroy, S., Pérez, J., Larrañaga, A., Basaguren, A., Molinero, J. & Pozo, J. (2016). In-stream litter decomposition along an altitudinal gradient: Does substrate quality matter? *Hydrobiologia, 766,* 17–28.

Martínez, A., Pérez, J., Molinero, J., Sagarduy, M., & Pozo, J. (2015). Effects of flow scarcity on leaf-litter processing under oceanic climate conditions in calcareous streams. *Science of the Total Environment, 503,* 251–257.

Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience, 43,* 219–224.

Monroy, S., Menendez, M., Basaguren, A., Pérez, J., Elosegi, A., & Pozo, J. (2016). Drought and detritivores determine leaf litter decomposition in calcareous streams of the Ebro catchment (Spain). *Science of the Total Environment, 573,* 1450–1459.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist, 100,* 65–75.

Paine, R. T. (1969). The Pisaster-Tegula interaction: Prey patches, predator food preference, and intertidal community structure. *Ecology, 50,* 950–961.

Pérez, J., Correa-Araneda, F., López-Rojo, N., Basaguren, A., & Boyero, L. (2021). Extreme temperature events alter stream ecosystem functioning. *Ecological Indicators, 121,* 106984.

Pérez, J., Galan, J., Descals, E., & Pozo, J. (2014). Effects of fungal inocula and habitat conditions on alder and eucalyptus leaf litter decomposition in streams of northern Spain. *Microbial Ecology, 67,* 245–255.

Piccolo, J. J., & Wipfli, M. S. (2002). Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences, 59,* 503–513.

Pozo, J., Casas, J., Menéndez, M., Mollá, S., Arostegui, I., Basaguren, A., Casado, C., Descals, E., García-Avilés, J., González, J. M., Larrañaga, A., López, E., Lusi, M., Moya, O., Pérez, J., Riera, T., Roblas, N., & Salinas, M. J. (2011). Leaf-litter decomposition in headwater streams: A comparison of the process among four climatic regions. *Journal of the North American Benthological Society, 30,* 935–950.

Riipinen, M. P., Fleituch, T., Hladyz, S., Woodward, G., Giller, P., & Dobson, M. (2010). Invertebrate community structure and ecosystem functioning in European conifer plantation streams. *Freshwater Biology, 55,* 346–359.

Rohlf, D. J. (1991). Six biological reasons why the Endangered Species Act doesn't work—And what to do about it. *Conservation Biology, 5,* 273–282.

Santonja, M., Pellan, L., & Piscart, C. (2018). Macroinvertebrate identity mediates the effects of litter quality and microbial conditioning on leaf litter recycling in temperate streams. *Ecology and Evolution, 8,* 2542–2553.

Silvester, W. B. (1977). Dinitrogen fixation by plant associations excluding legumes [Nitrogen]. *Treatise on Dinitrogen Fixation.*

Solagaistua, L., Elosegi, A., & Larrañaga, A. (2019). Consumption and performance responses of the amphipod *Echinogammarus berilloni* change during laboratory incubation. *Annales de Limnologie-International Journal of Limnology* (p. 25). EDP Sciences.

Swan, C. M., & Kominoski, J. S. (2012). Biodiversity and ecosystem function of decomposition. *eLS*. John Wiley & Sons.

Swan, C. M., & Palmer, M. A. (2004). Leaf diversity alters litter breakdown in a piedmont stream. *Journal of the North American Benthological Society, 23,* 15–28.

Swan, C. M., & Palmer, M. A. (2006). Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. *Oecologia, 147,* 469–478.

Tonin, A. M., Boyero, L., Monroy, S., Basaguren, A., Pérez, J., Pearson, R. G., Cardinale, B. J., Gonçalves, J. F., & Pozo, J. (2017a) Stream nitrogen concentration, but not plant N-fixing capacity, modulates litter diversity effects on decomposition. *Functional Ecology, 31,* 1471–1481.

Tonin, A. M., Gonçalves, J. F., Bambi, P., Couceiro, S. R. M., Feitoza, L. A. M., Fontana, L. E., Hamada, N., Hepp, L. U., Lezan-Kowalczuk, V. G., Leite, G. F. M., Lemes-Silva, A. L., Lisboa, L. K., Loureiro, R. C., Martins, R. T., Medeiros, A. O., Morais, P. B., Moretto, Y., Oliveria, P. C. A., Pereira, E. B., … Boyero, L. (2017b). Plant litter dynamics in the forest-stream interface: Precipitation is a major control across tropical biomes. *Scientific Reports, 7*, 10799.

van der Heijden, G. M., Schnitzer, S. A., Powers, J. S., & Phillips, O. L. (2013). Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica, 45,* 682–692.

Villanueva, V. D., Albariño, R., & Canhoto, C. (2011). Detritivores feeding on poor quality food are more sensitive to increased temperatures. *Hydrobiologia, 678,* 155–165.

Wipfli, M. S., & Musslewhite, J. (2004). Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia, 520,* 153–163.

Woodward, G. (2009). Biodiversity, ecosystem functioning and food webs in fresh waters: Assembling the jigsaw puzzle. *Freshwater Biology, 54,* 2171–2187.

Woodward, G., Gessner, M. O., Giller, P. S., Gullis, V., Hladyz, H., Lecerf, A., Malmqvist, B., McKie, B. G., Tiegs, S. D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graça, M. A. S., Fleituch, T., Lacoursière, J. O., Nistorescu, M., Pozo, J., Risnoveanu, G., … Chauvet, E. (2012). Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science, 336,* 1438–1440.

Zubrod, J. P., Englert, D., Wolfram, J., Rosenfeldt, R. R., Feckler, A., Bundschuh, R., Seitz, F., Konschak, M., Baudy, P., & Lüderwald, S. (2017). Long-term effects of fungicides on leaf-associated microorganisms and shredder populations—An artificial stream study. *Environmental Toxicology and Chemistry, 36,* 2178–2189.