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Litter Decomposition as an Indicator of Stream Ecosystem Functioning at Local-to-Continental Scales: Insights from the European *RivFunction* Project

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Abstract

RivFunction is a pan-European initiative that started in 2002 and was aimed at establishing a novel functional-based approach to assessing the ecological status of rivers. Litter decomposition was chosen as the focal process because it plays a central role in stream ecosystems and is easy to study in the field. Impacts of two stressors that occur across the continent, nutrient pollution and modified riparian vegetation, were examined at >200 paired sites in nine European ecoregions. In response to the former, decomposition was dramatically slowed at both extremes of a 1000-fold nutrient gradient, indicating nutrient limitation in unpolluted sites, highly variable responses across Europe in moderately impacted streams, and inhibition via associated toxic and additional stressors in highly polluted streams. Riparian forest modification by clear cutting or replacement of natural vegetation by plantations (e.g. conifers, eucalyptus) or pasture produced similarly complex responses. Clear effects caused by specific riparian disturbances were observed in regionally focused studies, but general trends across different types of riparian modifications were not apparent, in part possibly because of important indirect effects. Complementary field and laboratory experiments were undertaken to tease apart the mechanistic drivers of the continental scale field bioassays by addressing the influence of litter, fungal and detritivore diversity. These revealed generally weak and context-dependent effects on decomposition, suggesting high levels of redundancy (and hence potential insurance mechanisms that can mitigate a degree of species loss) within the food web. Reduced species richness consistently increased decomposition variability, if not the absolute rate. Further field studies were aimed at identifying important sources of this variability (e.g. litter quality, temporal variability) to help constrain ranges of predicted decomposition rates in different field situations. Thus, although

many details still need to be resolved, litter decomposition holds considerable potential in some circumstances to capture impairment of stream ecosystem functioning. For instance, species traits associated with the body size and metabolic capacity of the consumers were often the main driver at local scales, and these were often translated into important determinants of otherwise apparently contingent effects at larger scales. Key insights gained from conducting continental scale studies included resolving the apparent paradox of inconsistent relationships between nutrients and decomposition rates, as the full complex multidimensional picture emerged from the large-scale dataset, of which only seemingly contradictory fragments had been seen previously.



1. INTRODUCTION

Although its roots can be traced back deep into the ecological literature (e.g. even indirectly in [Darwin, 1881](#)), interest in what we now call ecosystem functioning and its relationship with biodiversity gained momentum particularly towards the end of the 20th century ([Jax, 2010](#)). This was prompted by the increasing recognition that species can have strong effects on their environments ([Lawton, 1994](#); [Wallace and Webster, 1996](#)) and growing concerns that population declines and high rates of species extinctions could eventually lead to the loss of key ecosystem functions, ultimately threatening human life support mechanisms ([Ehrlich and Ehrlich, 1981](#)). The argument is based on the recognition that organisms in ecosystems ultimately regulate biogeochemical cycles and provide resources essential to humans, such as clean water, timber or fish ([Jackson et al., 2016](#)). Three decades of intensive research have established that biodiversity loss can indeed have important repercussions on ecosystem functioning ([Cardinale et al., 2012](#); [Hooper et al., 2005](#)), but also that many idiosyncrasies exist, partly because some species show a larger degree of redundancy than others ([Rosenfeld, 2002](#)).

Riverine ecosystems are especially vulnerable to the loss of both biodiversity and ecosystem functioning via a wide range of stressors, on local-to-global scales, yet it is only in the last decade or so that the full implications of these threats have become appreciated. The majority of drainage pathways in river catchments worldwide are small wooded streams ([Allan and Castillo, 2007](#)), where the closed riparian vegetation limits instream primary production but supplies large amounts of litter ([Vannote et al., 1980](#)), and this is where much of riverine biodiversity is concentrated in the landscape. Consequently, aquatic food webs in these streams obtain most of their energy and

carbon from land-derived allochthonous organic matter, which ultimately also fuel the lower reaches into which the headwaters flow (Hladyz et al., 2011a*; Wallace et al., 1997). The decomposition of this litter is mainly a biological process, driven by microbial decomposers (fungi and bacteria) and macroinvertebrate detritivores (Gessner et al., 1999; Hieber and Gessner, 2002; Webster and Benfield, 1986), and it is highly sensitive to changes in environmental conditions (Ferreira et al., 2015a; Rosemond et al., 2015; Webster and Benfield, 1986). The central role of litter decomposition in streams, which represents the major ‘brown pathways’ in the food web, means that this process needs to be considered in order to capture and assess the broader ecological status of these ecosystems (Gessner and Chauvet, 2002*).

Despite seminal work by Odum (1956), for many years stream ecosystems have been considered mere conduits instead of biologically active ecosystems in their own right (Battin et al., 2009; Raymond et al., 2013). This view is changing and the necessity to incorporate ecosystem functioning into stream assessment and environmental management schemes has become increasingly evident (Christensen et al., 1996; Giller, 2005). The *RivFunction* initiative developed against this backdrop and evolved into a large-scale EU-funded project that aimed at elaborating a novel methodology for assessing the ecological status of European rivers in functional terms by focusing on leaf litter decomposition as a key ecosystem-level process. The goal was to unravel the relationships between environmental drivers, community structure and litter decomposition in streams at unprecedented scale.

This was achieved by conducting coordinated large-scale field experiments and bioassays across Europe (Hladyz et al., 2011a*; Woodward et al., 2012*), as well as smaller-scale field studies and controlled microcosm experiments (e.g. McKie et al., 2008*) within five Workpackages (Fig. 1). Emphasis of the large-scale field studies was on two types of widespread impacts in European streams: pollution by high nutrient inputs and modification of riparian vegetation. Two potential pathways affecting ecosystem functioning as indicated by leaf litter decomposition were examined, where: (i) stressors directly affect the activities of organisms and (ii) shifts in community structure towards species with intrinsically different activity potentials lead to changes in the emergent properties of the community (Fig. 1).

The importance of the second pathway was elucidated in microcosm and field experiments, especially by focusing on the diversity of plant litter, fungi and litter-consuming macroinvertebrates as one important aspect of

References marked with an “” are derived from the *RivFunction* project.

Core activities of the original RivFunction Workpackages

(Note: Further cross-links and new directions emerged as the project evolved—see Table 8 for examples of follow-on work that bridged these gaps)

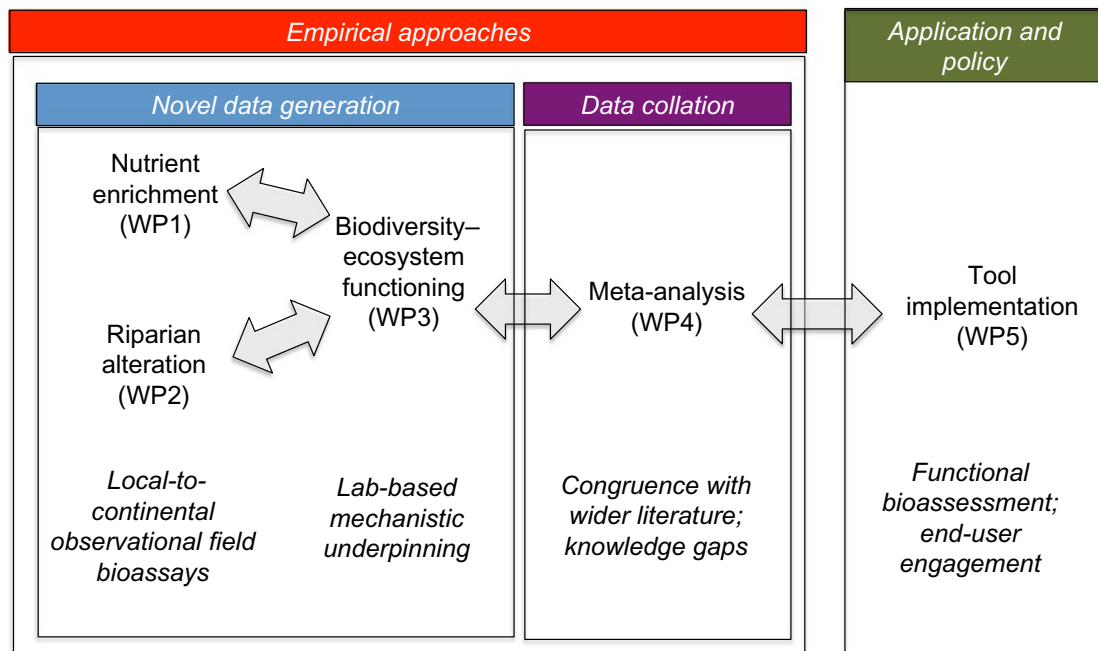


Fig. 1 A schematic highlighting the interconnections among the five original RivFunction Workpackages, from field-based surveys and bioassays to laboratory experiments, meta-analysis and tool development and implementation.

community structure that drives functioning at local scales (e.g. [McKie et al., 2008*](#)). This information, together with published data and results from studies addressing important sources of variability in decomposition served as the basis for elaborating a methodology to assess the ecological status of European streams and rivers from a functional point of view at local-to-continental scales ([Hladyz et al., 2011a*](#); [Woodward et al., 2012*](#)).

Standardising RivFunction Protocols for Pan-European Comparisons

A key challenge when designing field studies across large and heterogeneous areas such as Europe is ensuring that differences among ecoregions are due to the anthropogenic impacts of interest, rather than intrinsic biogeographical or other differences. To avoid bias due to plant litter species and quality, decomposition studies were carried out using leaves from two tree species—alder (*Alnus glutinosa* (L.) Gaertn.) and oak (*Quercus robur* L.)—that both occur nearly throughout the continent ([Graça and Poquet, 2014](#)). Alder and oak have contrasting physical and chemical characteristics (greater softness, greater concentrations of nutrients and lower concentrations of structural and secondary compounds in alder than in oak; [Gulis et al., 2006*](#); [Hladyz et al., 2009*](#)), differ greatly in their palatability to

litter-consuming detritivores (greater for alder than oak; [Canhoto and Graça, 1995](#)) and decompose at different rates (faster for alder and slow for oak; [Gulis et al., 2006*](#); [Riipinen et al., 2010*](#)), thus allowing assessment of whether the effects of change in nutrient concentration or riparian forest modification on litter decomposition are moderated by litter quality.

The same set of response variables was assessed at each study site (i.e. individual streams nested and replicated across ecoregions) following standardised field and laboratory protocols to investigate impacts along a gradient of nutrient enrichment (Workpackage 1), as well as impacts of various types of riparian forest modification (Workpackage 2), in addition to enabling pairwise comparisons of impacted and corresponding reference streams within individual ecoregions. The coordinated and standardised field experiments were carried out by 10 research teams from 9 European ecoregions and countries (England, France, Ireland, Poland, Portugal, Romania, Spain, Sweden and Switzerland) and included a total of >200 streams across north–south and east–west gradients in Europe ([Figs 2 and 3](#)). All streams were <5 m wide, <50 cm deep at winter baseflow, first to fourth order, with a stony substrate and bordered with native deciduous riparian vegetation except where riparian forests were clear-cut or replaced by pasture, exotic invaders or plantations. A range of other measurements to characterise streams were standardised. Water samples were analysed in the laboratory for NH_4^+ , NO_3^- , NO_2^- (total dissolved inorganic nitrogen (DIN) = nitrogen in NH_4^+ + NO_3^- + NO_2^-) and soluble reactive phosphorus (SRP \approx phosphorus in PO_4^{3-}).

Detailed protocols describing the preparation, field placement and retrieval of litter bags from streams, as well as subsequent laboratory procedures were implemented to ensure comparable data across the entire study and to enable integrated analyses of data gathered at all sites. Alder and oak leaf litter were collected locally after senescence and used in both large-scale coordinated litter decomposition experiments conducted during autumn and winter 2002/2003. Both litter species were incubated in coarse- and fine-mesh bags, and litter mass remaining and decomposition rates were determined based on six replicate litter bags collected once from each stream. Mesh bags, each containing 5.00 ± 0.25 g of air-dried leaves, were deployed in at least 10 streams per ecoregion for each Workpackage, with apertures of 10 (coarse) or 0.5 mm (fine) to permit or prevent macro-invertebrate colonisation, respectively. This enabled us to quantify total, microbial and macroinvertebrate-driven decomposition rates of oak (slow-decomposing) and alder (fast-decomposing) litter. Litter bags were collected

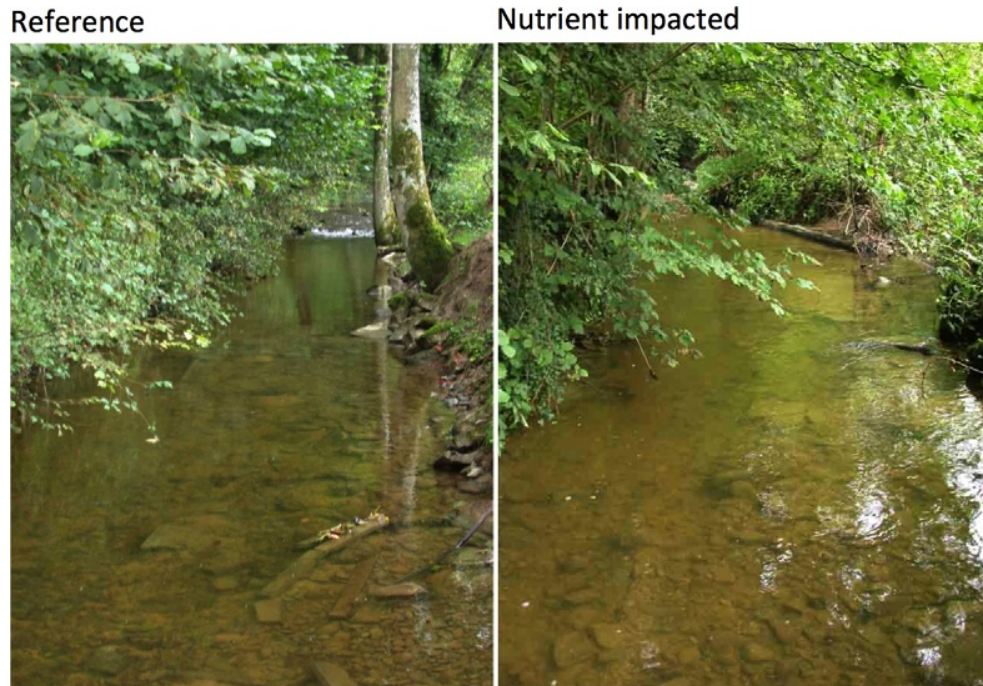


Fig. 2 Types of reference and impacted streams from Workpackage 1, designed to isolate the effects of nutrient enrichment while standardising for riparian coverage and other physicochemical properties of the system. An example of a pair of sites in the Alps (Switzerland) with reference and nutrient-impacted streams on *left* and *right*, respectively. Average water temperature (15°C) and depth (0.1 m), and substratum composition (*gravel, cobble*) were identical. Electrical conductivity (449 and 513 $\mu\text{s}/\text{cm}$, respectively), water discharge (150 and 250 L/s, respectively) and stream width (2.5 and 1.7 m, respectively) were similar. *Photo credit: M.O. Gessner.*

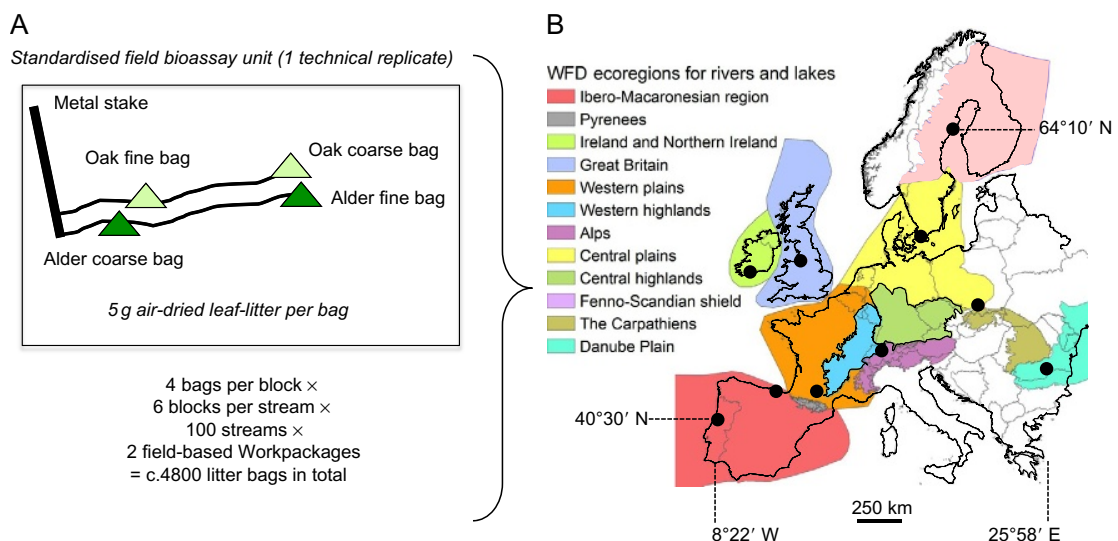


Fig. 3 The standardised field bioassay unit (A) and (B) regions and locations (*dots*) where the litter bioassay units were used in the initial continental-scale surveys in Workpackages 1 and 2. This basic design was adapted in subsequent studies: for instance in the follow-up Workpackage 2 studies, algal processes were also explored via the addition of a colonisation tile adjacent to each litter bag, or different types of litter were also added. The positioning of the fine (0.5 mm aperture mesh) vs coarse (1 cm aperture mesh) litter bags per leaf type per rebar was randomised within blocks.

when additional coarse-mesh bags (sampled on several occasions at reference sites) had lost $\sim 50\%$ of their initial mass (T_{50}) (see Riipinen et al., 2009*). Thus, we standardised among regions and leaf species for the degree of decomposition rather than for exposure time. The retrieved leaf litter was oven-dried and ash-free dry mass (AFDM) determined after ashing of sub-samples. Correction factors derived in the laboratory for leaching losses and moisture content were applied to the initial air-dry mass and AFDM (Hladysz et al., 2009*).

Litter decomposition rates were expressed as the exponential decay rate coefficient, k , in the model $(m_t/m_0) = e^{-kt}$, where m_0 is the initial AFDM and m_t is AFDM at time t (see, e.g. Riipinen et al., 2009*). Macroinvertebrate-driven decomposition was derived by calculating the difference in the mean percent mass remaining in coarse- and fine-mesh bags in each stream and then subtracting the difference from the initial 100% mass before calculating a k value (k_{inv}) indicating the contribution of litter-consuming macroinvertebrates to mass loss (Woodward et al., 2012*). To correct for potential temperature differences among streams and regions (Fig. 4), t was expressed in terms of thermal sums (degree-days).

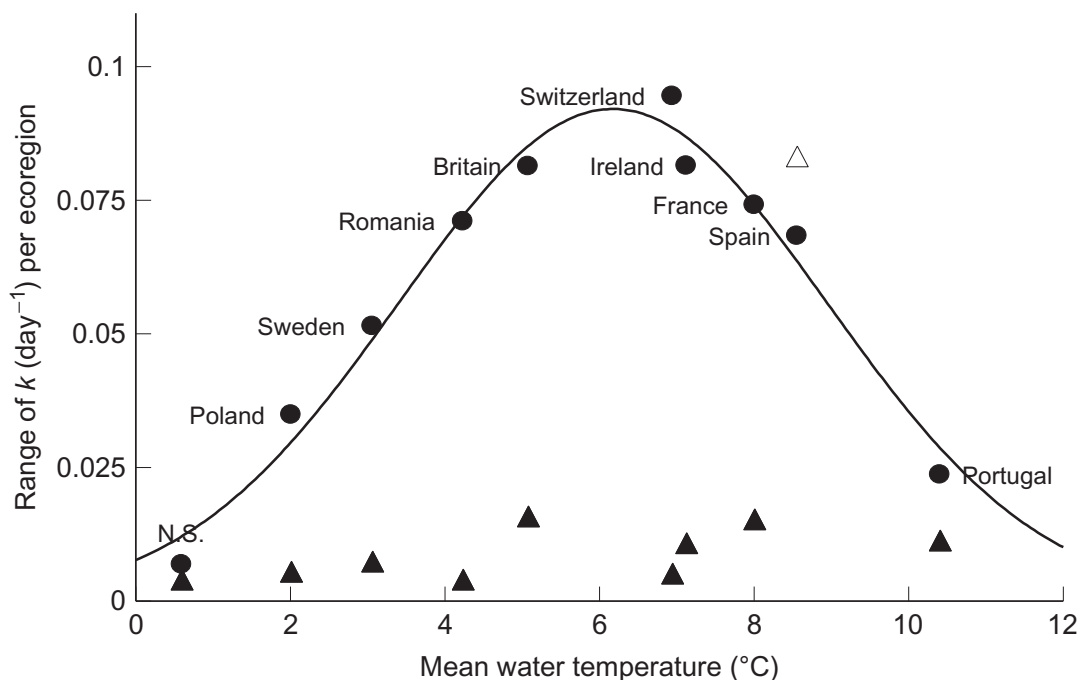


Fig. 4 Among-stream variation in total and microbial-mediated decomposition rates among reference sites within the study regions across Europe as a function of stream temperature. The range was compressed at either extreme, with the greatest apparent potential for biotic responses, especially those driven by macroinvertebrates, evident in the mid-range. The *circles* represent total decomposition in coarse-mesh bags (1 cm mesh aperture) and the *triangles* microbial-only mediated decomposition in fine-mesh bags (0.5 mm mesh aperture).



2. NUTRIENT ENRICHMENT EFFECTS ON LEAF LITTER DECOMPOSITION

The susceptibility of freshwater ecosystems to anthropogenically derived pollutants and nutrient enrichment is now well known and the impacts are likely to intensify in the future (Ferreira et al., 2015a; Friberg et al., 2016; Gessner and Chauvet, 2002*; Jackson et al., 2016; Stamm et al., 2016; Young et al., 2008). Impacts in rivers in particular are exacerbated by their intimate terrestrial linkages in dendritic networks, such that almost any activity within a river catchment has the potential to cause environmental change within the river system, and any significant pollutant entering a river may exert some effect for large distances downstream (Malmqvist and Rundle, 2002; Thompson et al., 2015). The wide range of stressors that can affect freshwater systems can be classified into four major types: ecosystem destruction, physical habitat alteration, water chemistry alteration and direct species additions and removals (Malmqvist and Rundle, 2002) resulting in 14 major threats that interact with the 6 major services provided by freshwater systems (Giller et al., 2004a; Fig. 5). There is a strong regional influence in this context, dependent largely on economic activity and state of development.

In Europe, nutrient enrichment from agricultural run-off, sewage inputs and nitrogen deposition have been occurring in surface waters for centuries, but the dramatic increases evident from the second half of the 20th century have placed the continent's vulnerable freshwaters in a precarious position (Woodward et al., 2012*). Attempts to reverse the damage done to these ecosystems and to the 'goods and services' they provide has triggered the introduction of far-reaching international legislation, such as the EU Water Framework Directive (WFD) (Hering et al., 2010). The US Clean Water Act was implemented for similar reasons (Adler et al., 1993), and ambitious environmental legislation is currently being drawn up in many other parts of the world to protect global water resources (such as New Zealand's National Policy Statement (NPS) for Freshwater Management). These legislative provisions stress the need to consider environmental impacts on processes as well as structural elements and to include assessment of such processes in bio-monitoring and restoration.

Biodiversity and ecosystem functioning are intimately linked and both are vulnerable to environmental stressors. Aquatic ecosystems and freshwater ecosystems in particular are impacted by multiple stressors (Giller et al., 2004b) and experimental studies have begun to explore the range

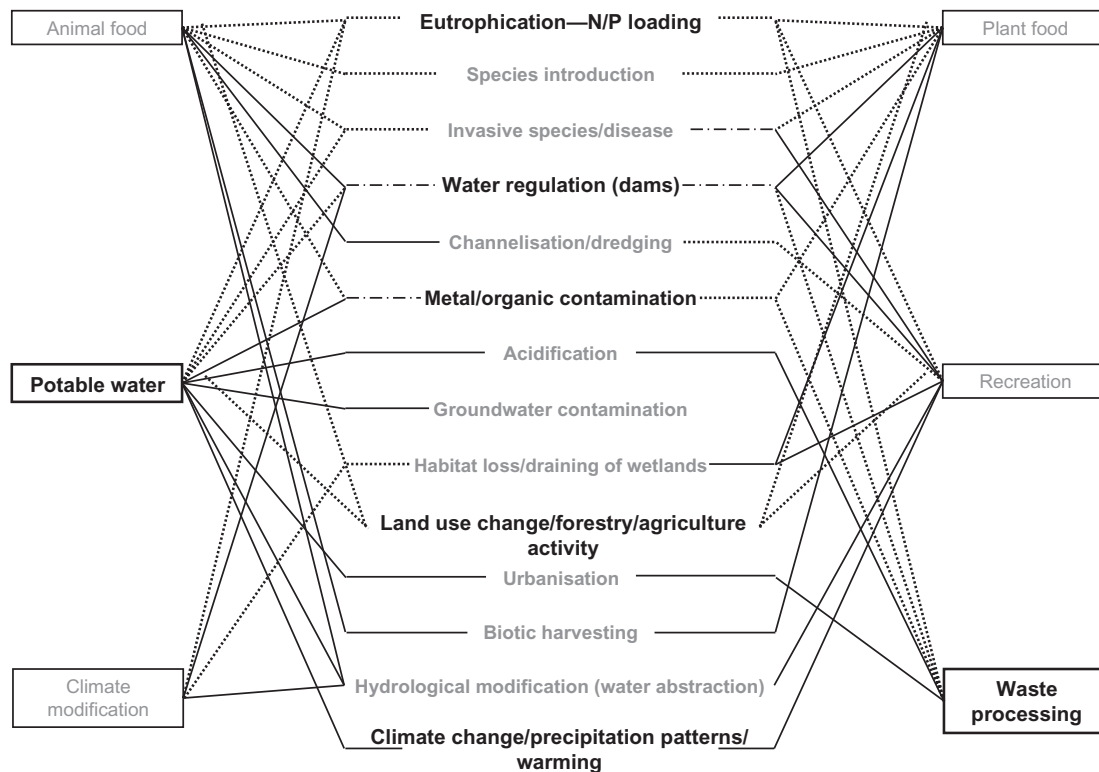


Fig. 5 A schematic diagram illustrating the interaction between 6 major ecosystem services provided by freshwater systems and 14 potential threats and stressors affecting the freshwater domain. Those threats and services related to the research associated with *RivFunction* are highlighted. Dotted lines indicate possible mediation through the benthos. Modified from Giller, P.S., Covich, A.P., Ewel, K.C., Hall, R.O., Merritt, D., 2004a. *Vulnerability and management of ecological services in freshwater systems: case studies of freshwater ecosystem services*. In: Wall, D.H. (Ed.), *Sustaining Biodiversity and Functioning in Soils and Sediments*. SCOPE Series, vol. 64, © Island Press, Washington, DC, pp. 137–160.

of synergistic and antagonistic impacts (e.g. McKie et al., 2009*; Piggott et al., 2015; Tolkkinen et al., 2013, 2015). Assessing and understanding the consequences of biodiversity change on ecosystem functioning are critical, given the threats to ecosystem processes and, in turn, to the associated ecological goods and services (e.g. drinking water quality, fisheries) (Giller et al., 2004a), especially since many of the ‘ecological surprises’ that often arise can be linked to the indirect effects of biotic interactions among different species in the food web (Gray et al., 2016). In the present context, we are concerned explicitly with the important ecosystem process of litter decomposition in streams, and both its direct and indirect drivers. As the trophic state of many streams is likely to deteriorate in the future due to the continuing increase in human-induced nutrient availability

(Jackson et al., 2016), it is of fundamental importance to understand how nutrient enrichment affects litter decomposition.

At large biogeographical scales, litter decomposition rates are strongly influenced by temperature and, consequently, they are likely to vary markedly across latitudinal and climatic gradients (Fig. 4). The few studies that have compared tropical and temperate freshwaters, however, have revealed that although microbial activity increases with temperature, macro-invertebrate leaf-shredders, which drive leaf litter decomposition rates at higher latitudes, are often missing from tropical streams (Boyero et al., 2011; Dobson et al., 2002; Graça et al., 2015; Irons et al., 1994; Rosemond et al., 1998). Decomposition rates are also governed indirectly by the nutrient status of the water, which is itself affected by environmental factors, including anthropogenic inputs of domestic sewage and agricultural run-off (e.g. Gulis et al., 2006*; Lecerf et al., 2006*; Niyogi et al., 2003; Pascoal et al., 2003; Stamm et al., 2016). A meta-analysis of 99 studies suggests that the effect of nutrient enrichment might be strongest in cold oligotrophic streams driven by patterns of biogeography of invertebrate decomposers which may be modulating the effect of nutrient enrichment on litter decomposition (Ferreira et al., 2015a). At more local scales, the availability and quality of leaf litter, in addition to the abundance, diversity and activity of aquatic consumers, combine to determine the rate of decomposition and energy flux to the higher trophic levels (Dangles et al., 2004*; Fleituch, 2013*; Gessner and Chauvet, 1994, 2002*; Gulis et al., 2006*; Hladysz et al., 2011a*). Decomposition by purely physical forces, such as sediment abrasion, is generally trivial relative to these biotic drivers (e.g. Ferreira et al., 2006b*; Hieber and Gessner, 2002; Hladysz et al., 2009*). Some evidence of synergistic effects of nitrogen and phosphorus has also been identified from field manipulative experiments (Ferreira et al., 2015a; Kominoski et al., 2015; Rosemond et al., 2015).

Experimental studies have reported elevated decomposition rates in nutrient-enriched systems, reflecting concomitant increases in both litter quality (i.e. lower carbon-to-nutrient ratios that enhance microbial conditioning and/or litter stoichiometry) and consumer abundance and activity (e.g. Bergfur et al., 2007; Ferreira et al., 2006c*; Greenwood et al., 2007; Gulis et al., 2006*; Halvorson et al., 2016; Manning et al., 2015; Rosemond et al., 2002). Nevertheless, there may be no clear effect of nutrient enrichment of stream water on the leaf decomposition rate where levels of eutrophication are relatively low, as in headwater streams (Pérez et al., 2013) or where nitrogen levels may not in fact be limiting (Royer and

Minshall, 2001; Stallcup and Ardón, 2006). In addition, such monotonic responses are unlikely to be ubiquitous, as many streams receive considerable inputs of domestic sewage and agricultural run-off that can induce anoxia, mobilise heavy metals and physically smother the benthos by so-called ‘sewage fungus’ (in fact a filamentous bacteria in the *Sphaerotilus* genus) (Curtis and Harrington, 1971; Lecerf et al., 2006*; Niyogi et al., 2003; Pascoal and Cássio, 2004). Such direct and indirect, potentially toxic, effects will also lead to community-level changes related to physiological tolerance of species, multistressor impacts (Giller et al., 2004b) and the well documented negative impacts on stream communities (e.g. Wright et al., 2000), including widespread species loss and catastrophic fish kills. Thus, some form of unimodal relationship between nutrient concentrations and decomposition rates in streams and rivers is predicted, with slow decomposition at both extremes, due to nutrient limitation in oligotrophic systems and toxic effects of other pollutants in hypertrophic systems.

Most studies have been conducted at relatively small scales and over a limited range of nutrient concentrations, thus the seemingly monotonic (and occasionally contradictory—positive and negative) responses that have often been reported to date (e.g. Ferreira and Chauvet, 2011; Gulis and Suberkropp, 2003; Ramírez et al., 2003; and those above) might simply reflect a truncated portion of an underlying unimodal response that is only evident at much larger scales and/or across a larger nutrient gradient. The picture is complicated further at large scales, as climatic and biogeographical effects come into play, and if we are to develop the new generation of ecosystem-based approaches to bioassessment, as required under current and emerging legislative provisions, we need to know how eutrophication—functioning relationships are influenced by these factors. The *RivFunction* project was able to present the results of a pan-European experiment that measured this crucial ecosystem process across a gradient that spans three orders of magnitude in nutrient concentrations and several biogeographic areas (Figs 6 and 7). We were also able to quantify the relative importance of microbial and macroinvertebrate-driven decomposition, by measuring both simultaneously. This was the first and to date only study where such comparisons have been made at multiple sites at a truly continental scale.

The objective of Workpackage 1 was to assess the impacts of nutrient loading (eutrophication) on river ecosystem functioning through the quantification of leaf litter decomposition and associated parameters. The underlying hypothesis was that increases in nutrient levels through pollution (eutrophication) fundamentally alters the functioning of the river ecosystem,

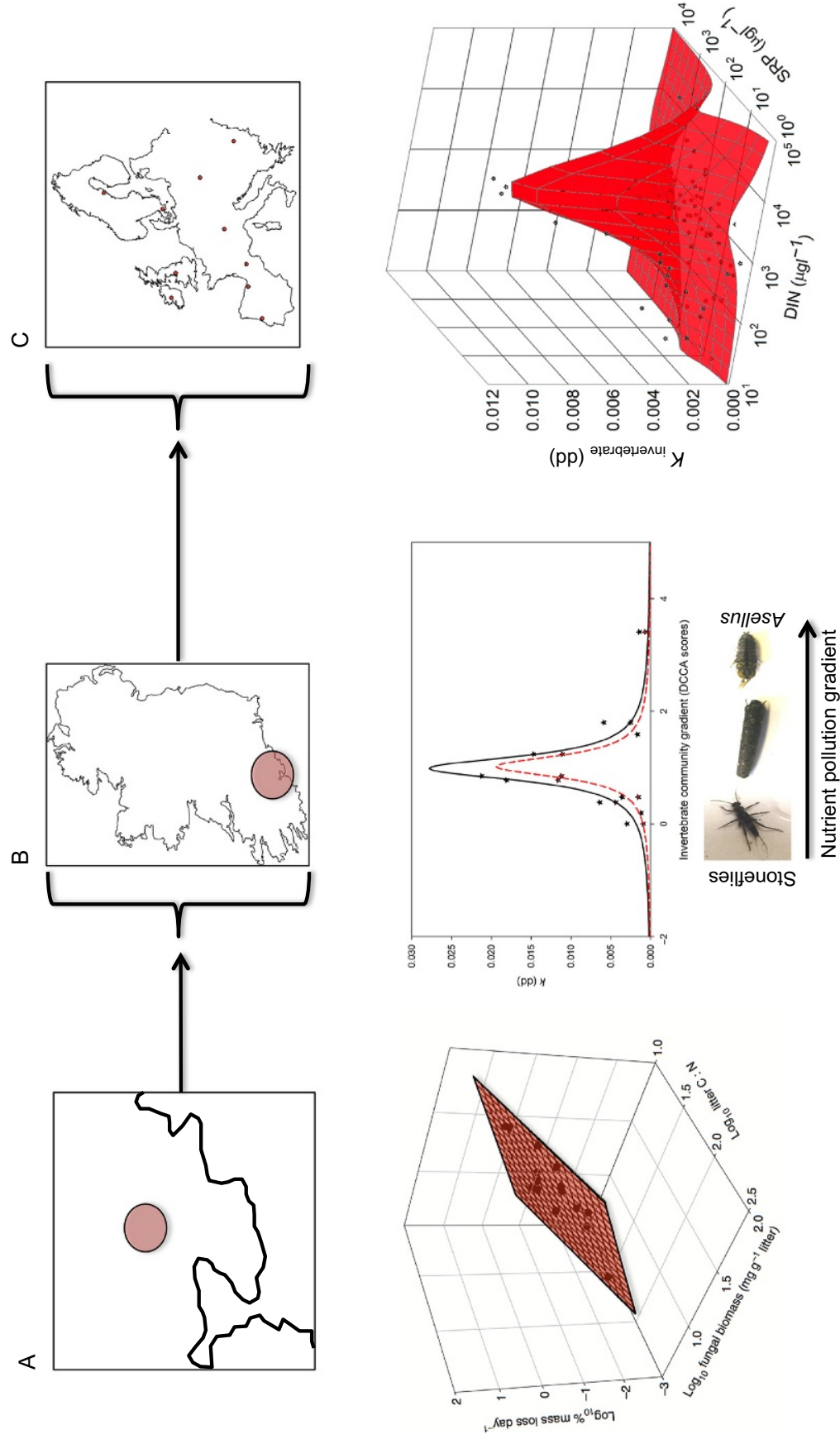


Fig. 6 Workpackage 1: Nutrient enrichment and environmental filters—from local-to-continental scales. (A) Decomposition rates as a function of litter quality (CN content) and fungal conditioning among 15 species of trees' litter in a single site in Ireland; (B) total (black solid line) and invertebrate-mediated decomposition (red (grey in the print version) dashed line) rates of alder in 10 streams across Ireland, as a function of invertebrate assemblage composition, from pristine to heavily-polluted systems; (C) volume-filling relationship between two major macronutrients and alder litter decomposition in the 100 streams across Europe.

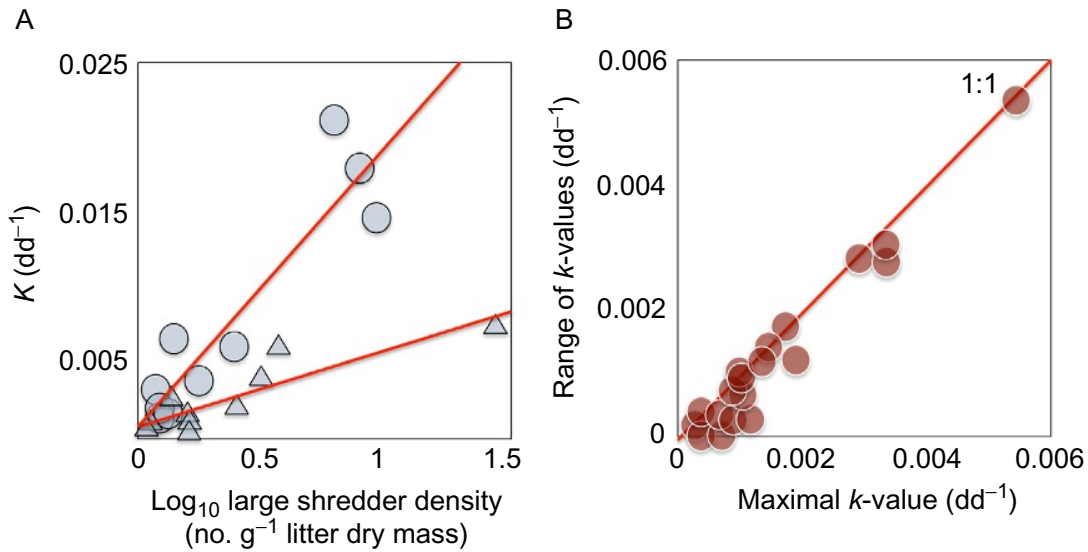


Fig. 7 Workpackage 1: (A) Decomposition rates as a function of consumer density in 10 streams in Ireland, providing mechanistic insight into the potential drivers behind the unimodal curve in Ireland in Fig. 6B. Total decomposition rates in coarse-mesh bags per degree-day plotted as a function of the abundance of large litter-consuming detritivores (Limnephilidae+Gammaridae) per gram of leaf litter ash-free dry mass in oak (triangles) and alder (circles). Equations for the regression lines are: (1) alder k_{total} : $y = -0.0007 + 0.019x$; $r^2 = 0.86$, $F_{1,9} = 50.0$, $P < 0.001$; (2) oak k_{total} : $y = -0.0009 + 0.0049x$; $r^2 = 0.80$, $F_{1,9} = 32.2$, $P < 0.001$. (B) The range of decomposition rates vs maxima across Europe, showing that within the grid of combinations of SRP and DIN across Europe that describes the volume-filling relationship in Fig. 6C, even at the highest peak rates decomposition can also be extremely slow. The 1:1 line shows where the range is equal to the maximum. This suggests the potentially key role of local and contingent community-level effects related to the abundance, size and identity of the consumer assemblages (e.g. as per Fig. 7A and B). Redrawn from Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., 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., Schindler, M., Vadineanu, A., Vought, L.B.-M., Chauvet, E., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science*, 336, 1438–1440.

and that this impairment can be quantified and evaluated by following changes in a key ecosystem-level process, litter decomposition, with a simple assay. Suitable indicators of, and critical thresholds for, proper river ecosystem functioning were identified based on litter decomposition experiments conducted under field conditions. We hypothesised that rates of litter decomposition are constrained by microbial nutrient limitation on the rising limb along nutrient pollution gradients and by the effects of environmental degradation and other accompanying pollutants on invertebrates on the falling limb of a unimodal relationship between nutrient levels and leaf litter decomposition.

Key Findings

The effects of nutrient (nitrogen and phosphorus) loading on river functioning were examined through a single, large scale, pan-European experiment, by comparing decomposition rates of leaf litter at impacted and corresponding reference sites in which both point source and nonpoint source pollution were considered. The 100 investigated streams across Europe spanned 1000-fold differences in nutrient concentrations on both axes (SRP: $<1\text{--}926\ \mu\text{g L}^{-1}$, DIN: $13\text{--}15,700\ \mu\text{g L}^{-1}$). Elevated dissolved nutrient concentrations relative to regional baselines were due to agricultural run-off and sewage effluents. The validity of the representativeness and scalability of this approach is highlighted by a clear positive relationship between BOD₅ (5-day biochemical oxygen demand) and nutrient concentrations in over 8000 European streams, and the comparable frequency distributions of nutrient concentrations between these and our study sites (Woodward et al., 2012*). In total, over 2400 leaf bags were exposed in the 100 streams (6 replicates \times 2 mesh sizes \times 2 leaf species \times 10 streams \times 10 regions), of which 2161 were retrieved at the end of the experiment. Results from these core Workpackage 1 studies have been published in a variety of journals over the past decade (e.g. Gulis et al., 2006*; Lecerf et al., 2006*; Woodward et al., 2012*) and the key findings are summarised and revisited below (see also Figs 6 and 7).

Across the nine ecoregions, total decomposition was considerably faster than microbial-mediated decomposition only, and the higher quality alder litter decomposed considerably faster than oak litter. The ratio of invertebrate-only to microbial-only k -values was close to two for both leaf species: thus, invertebrates were the main drivers of decomposition across Europe as a whole, although their relative contribution varied among ecoregions. Many of the patterns reported for oak were also evident in alder, although variability was higher in the latter, reflecting this species' faster decomposition rate vs, whereas the more refractory oak leaves gave a more integrated signal over a far longer exposure time in each stream.

Decomposition rates varied markedly among ecoregions, being suppressed at both high and low latitudes and in the more eastern sites, as the climate became less maritime and more continental. Similar latitudinal and longitudinal patterns were evident in the ratio of invertebrate: microbially driven decomposition, with invertebrates being less important at the extremes and in the more eastern ecoregions. Simple linear regression models using ecoregions as replicates (i.e. removing the lower levels of nesting) yielded significant relationships between mean temperature and

k -values, when outliers were excluded (northern Sweden for fine-mesh bags, Portugal for coarse-mesh bags). The slope of the line was also steeper for total decomposition than for microbial-only and, consequently, invertebrate-only decomposition also increased with temperature, when the two warmest ecoregions were excluded ($y = 0.0022x - 0.0005$; $R^2 = 0.76$). The fact that the outliers to these fits were always at the extremes of the temperature gradient suggests that other factors, in addition to temperature, were influencing decomposition rates. Multiple regression models on the full dataset revealed significant effects of water quality, temperature and geographical location: i.e. the spatial and environmental context of the ecoregions explained some of the variation not accounted for by temperature. When normalised per degree-day, [Irons et al. \(1994\)](#) found that decomposition rates actually increased with latitude and that shredders become progressively more important as agents of decomposition as latitude increases. However, many of the previous studies have compared a small set of sites clustered together in a temperate setting, with a similar set in the tropics, rather than a true gradient-based approach. Thus, many of the more subtle shifts within temperate regions identified in the present study have been previously obscured: although shredders were the main drivers of decomposition across Europe as a whole ([Fig. 4](#)), they did not become progressively more important with latitude, as suggested by other studies ([Boyer et al., 2011](#); [Irons et al., 1994](#); [Rosemond et al., 1998](#)). In fact, most of the decomposition in northern Sweden, close to the arctic circle, appeared to be driven almost entirely by microbial activity.

In addition to the responses in mean decomposition rates, there were further temperature-related patterns within the data that were also not evident at smaller spatial scales. For instance, the range of variation in total decomposition among streams within ecoregions followed a unimodal Gaussian curve ($R^2 = 0.97$) in response to temperature ([Fig. 4](#)). The range of microbial decomposition, however, was much lower and effectively constant across the temperature gradient, with the possible exception of the more variable Spanish sites.

Intriguingly, microbially driven decomposition did not display any clear or consistent response to nutrient concentrations, whereas, in contrast to the monotonic changes in decomposition rates in response to nutrients that have been described in previous studies (e.g. see references earlier), our overall invertebrate-driven spatial data for decomposition rates were best described by a unimodal surface in two dimensions and a unimodal volume in three dimensions—as we predicted at the outset ([Fig. 6C](#)). This applied for both

leaf species and as a function of SRP and DIN concentrations. The rising limb of the unimodal curve was likely due to nutrient stimulation of microbes and subsequent increased consumption by invertebrates (Woodward et al., 2012*). In contrast, the falling limb was likely due to deteriorating environmental conditions accompanying excessive nutrient supply (e.g. low oxygen concentrations, presence of other pollutants), which suppressed invertebrate-driven decomposition. Rates were always low at the extremes, but ranged from low-to-high at intermediate nutrient concentrations and were bounded by a hump-shaped envelope (Fig. 6C). Within a given range of nutrient concentrations, the spread of decomposition rates was almost equal to the maximum: i.e. there was an upper, but not a lower, limit to decomposition rates (Fig. 7B). Essentially, there was a bounding envelope that delimited maximal decomposition rates, but within that envelope a broad distribution of process rates was possible, such that at any given nutrient concentration the maximum rate was almost equal to the range. The wide range of decomposition rates at intermediate nutrient concentrations were likely found due to a combination of site-specific differences in environmental parameters, particularly water temperature, and intrinsic ecosystem properties, such as the taxonomic composition, abundance and (functional) activity of the shredder assemblage, in turn related to other environmental gradients. Indeed, within one of the Irish sites we found that >90% of the variance in litter decomposition rates was explained by litter resource quality and the degree of microbial conditioning (Fig. 6A), which in turn determined the density of large shredders that drove overall consumption rates (Fig. 7A). The communities at the extreme ends of the nutrient gradient will fall within a more constrained range of possible configurations than those in more mesotrophic waters, where enrichment effects are more modulated and community structure is determined to a larger extent by additional factors, such as hydrology, pH and the biogeographical filtering of the species pool.

In addition to the responses to nutrients, there was considerable scale-dependent spatial variation in decomposition rates. In particular, larger-scale effects reflected temperature differences among ecoregions but within ecoregions, where temperature differences among streams were minimal, changes in macroinvertebrate community structure were important. This is highlighted by the data from Ireland, which provided a useful subset of sites because they spanned the entire nutrient gradient across Europe (Fig. 6B). Condensing the principal gradient of invertebrate community structure across these sites into a single α -axis, via detrended correspondence

analysis, enabled us to plot invertebrate community structure against decomposition rate (Woodward et al., 2012*). The species scores reflected the classic community response to eutrophication, with indicators of ‘pristine’ conditions (e.g. nemourid stoneflies) at one end of the gradient and indicators of organic pollution (e.g. *Asellus* isopods) at the other end. The moderately enriched sites exhibited the highest decomposition rates and were characterised by the largest consumer taxa (i.e. gammarid shrimps and limnephilid caddisflies). As a result, this integrated, biotic gradient yielded a clearer unimodal relationship than for nutrient concentration alone, with R^2 values of 0.96 and 0.95 for total and invertebrate-mediated decomposition, respectively. The abundance of large detritivores was the most powerful predictor of decomposition rate across the Irish sites (Fig. 7A), whereas no significant relationship emerged for the smaller, but far more abundant taxa such as stoneflies, suggesting that consumer body size was the key functional trait driving the patterns in the field and when multiplied by abundance this gave a measure of the total functional capacity of the assemblage, in ways analogous to what we found in the subsequent laboratory studies (e.g. Perkins et al., 2010; Reiss et al., 2011).

The concentrations of individual nutrients thus represented only part of what is a more complex and multifaceted stressor in the real world. Indeed, gradients in community structure, rather than nutrient concentrations per se, provide a more holistic measure of the trophic status of freshwaters, as evidenced by the widespread use of diversity indices rather than chemical analysis to detect organic pollution (Friberg et al., 2011; Karr, 1999; Wright et al., 2000). The problem with this approach, though, is that the species composition of communities differs across countries and ecoregions, due to underlying biogeographical effects, making it difficult to standardise taxonomic-based bioassessment metrics at large scales (see chapter “Recommendations for the next generation of global freshwater biological monitoring tools” by Jackson et al.; Wright et al., 2000).

It is instructive that the intermediate ‘mesotrophic’ study sites were characterised by shredders and that the peak decomposition rates corresponded to a subset of these sites with communities dominated by large taxa, particularly Gammaridae shrimps and Limnephilidae and other cased caddis (Figs 6B and 7A). This suggests that body size and abundance of the consumer assemblage is a more important driver of stream ecosystem functioning than other aspects of community structure, including species richness (e.g. Huryn et al., 2002). Indeed, decomposition rates in Ireland were some of the fastest recorded across the entire European range, yet this country has a relatively

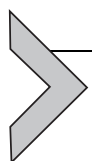
depauperate invertebrate fauna (Giller et al., 1998), with only about 70% of the species found in Great Britain, which in turn possesses a similar percentage of the species found in continental Europe. The importance of body size within ecological systems has become a major focus of recent food web research (Brose et al., 2005; Mancinelli et al., 2013; Woodward et al., 2005b), in contrast to the field of biodiversity–ecosystem functioning (B-EF), which has traditionally focused mainly on taxonomic diversity. These two previously disparate fields are now converging, and there is increasing interest in the role of functional diversity and species traits, such as body size, in the more recent literature (Woodward et al., 2005a,b, 2010).

A potential bias in the broader literature is that terrestrial grassland ecosystems have dominated much of the B-EF research until recently (e.g. Hector et al., 2002; Spehn et al., 2005; Tilman et al., 2014), whereas freshwaters may be fundamentally different. For example, the importance of vertical consumer–resource interactions, as opposed to horizontal competitive interactions, within aquatic food webs has been strongly emphasised (Kohler and Wiley, 1997; Petchey et al., 2004; Woodward, 2009). The fact that the most marked changes in decomposition rates occurred in the mid-portion of the nutrient gradient where structural measures of community composition are often least sensitive, suggests that this functional approach is a potentially important complement to the traditional structural-based biomonitoring techniques in current usage (Gessner and Chauvet, 2002*). The next logical step is to develop integrated structural–functional metrics for assessing ecological integrity that combine community descriptors (consumer traits and abundance) with ecosystem data (process rates). The advantage of using a trait-based structural–functional approach is that it is effectively independent of taxonomy, and could therefore be applied across large biogeographical regions (Dolédéc et al., 1999; Friberg et al., 2011; Usseglio-Polatera et al., 2000; Woodward and Hildrew, 2002). This would be a major leap forward and would serve to unite the community and ecosystem approaches to ecology that have developed in parallel, but in relative isolation, over the last century.

Our results also raise fundamental questions about how to determine ecosystem health in the context of eutrophication. Firstly, water resource managers normally aspire to naturally low-nutrient conditions, and yet ecosystem functioning in such systems, as assessed by leaf litter decomposition rates, was indistinguishable from that of heavily polluted streams (Fig. 6B and C). This suggests that ensuring both low-nutrient water and effective resource use in stream food webs (from leaf litter to detritivores to fish) coupled with high

process rates might be irreconcilable goals in stream management. Second, stream managers currently rely primarily on structural bioassessment measures to assess stream ecosystem health because they provide a reliable time-integrated response to stressors such as organic pollution or acidification. Biogeographical constraints can be overcome using litter decomposition to monitor nutrient loading because biogeography is a minor issue (for example, black alder or similar species of the genus are common throughout most of Europe and the Holarctic), and marked changes in decomposition rate occurred in the rising portion of the pollution gradient, in which established structural measures (such as metrics based on fish, invertebrate or algal communities) are typically least sensitive.

As in many other parts of the world, Europe is a highly industrialised, intensively managed continent, with a large proportion of the landscape characterised by agriculture and other human land-uses leading to the significant pollution of receiving freshwater environments ([Hilton et al., 2006](#); [Vörösmarty et al., 2010](#)). Our study reveals that as Europe's freshwaters drift away from their natural conditions, along with rapid biodiversity losses, ecosystem functioning is changed, too—and on a continental scale. The natural controlling factors appear to have been altered so fundamentally that drivers and responses might not continue to operate in easily predictable ways. Given the huge uncertainties surrounding human environmental impacts it will be challenging to manage European surface waters sustainably and meet the demands of biodiversity conservation and environmental legislation. As eutrophication is recognised as one of the major threats to water quality throughout Europe, the outcomes of Workpackage 1 of the *RivFunction* project can play an important role in the context of overall social objectives of understanding and improving quality of the water resources in the future.



3. EFFECTS OF RIPARIAN FOREST MODIFICATIONS ON LEAF LITTER DECOMPOSITION

Small forest streams constitute the majority of water courses in undisturbed catchments ([Downing et al., 2012](#)) and are often densely shaded by riparian vegetation, deriving most of their energy and carbon from the decomposition of litter of terrestrial origin, rather than instream primary production ([Wallace et al., 1997](#)). Given their strong dependence on litter resources, aquatic communities and processes can be very sensitive to changes in riparian forests driven by forestry practices, invasion by exotic tree species or conversion to pasture. The replacement of native forests

by plantations or invasion by exotic tree species has the potential to affect aquatic communities and processes, especially when invasive tree species or those used in plantations introduce novel traits or strongly alter the composition of functional traits (leading to litter of different quality), relative to an undisturbed assemblage (Kominoski et al., 2013). In such cases, even when a closed canopy is maintained, the allochthonous trophic pathway may still be affected (Hladyz et al., 2011b*; Murphy and Giller, 2001). When the native forest is clear-cut or converted into pasture, the increase in solar irradiation can promote instream primary production and autochthonous trophic pathways (Hladyz et al., 2011b*), while the reduction in organic matter input to streams can inhibit allochthonous trophic pathways, although aquatic communities may still retain the capacity to decompose terrestrially derived leaf litter (Hladyz et al., 2011b*)—thus there can be fundamental shifts between the roles of the green vs brown pathways at the base of the food web as a result of land-use change.

In this context, the overarching goal of *RivFunction* Workpackage 2 was to assess the impacts of riparian forest modifications on leaf litter decomposition in streams. Four broad types of forest change were assessed: (i) replacement of native forests by commercial tree plantations (deciduous plantations, conifer plantations and eucalyptus plantations), (ii) invasion of native forests by exotic tree species, (iii) forest clear cutting and (iv) replacement of native forests by pasture (Fig. 8). In the main coordinated litter decomposition experiment, each of 10 research teams selected 5 stream pairs (eight stream pairs for Ireland), each composed of a stream with native riparian forest (reference stream) and a partner with altered riparian vegetation (altered stream), making a total of 53 reference—altered stream pairs across Europe. A total of 2544 bags ($10 \text{ regions} \times 10 \text{ streams (+6 in Ireland)} \times 2 \text{ leaf litter species} \times 2 \text{ mesh sizes} \times 6 \text{ replicates}$) were thus deployed in European streams for the main Workpackage 2 experiment. In contrast to the Workpackage 1 sites, all these streams were selected to be minimally impacted by agricultural run-off, sewage effluents or other human disturbances (apart from changes in riparian vegetation in altered streams), and thus variation in water chemistry primarily reflected regional context (e.g. geology, atmospheric nitrogen deposition). Within each pair, streams were as similar as possible regarding environmental characteristics other than riparian vegetation to isolate the effect of forest change. Riparian forests in reference streams were representative of the natural vegetation and riparian vegetation in altered streams was representative of the major anthropogenic alteration to riparian forests in each region (Table 1).

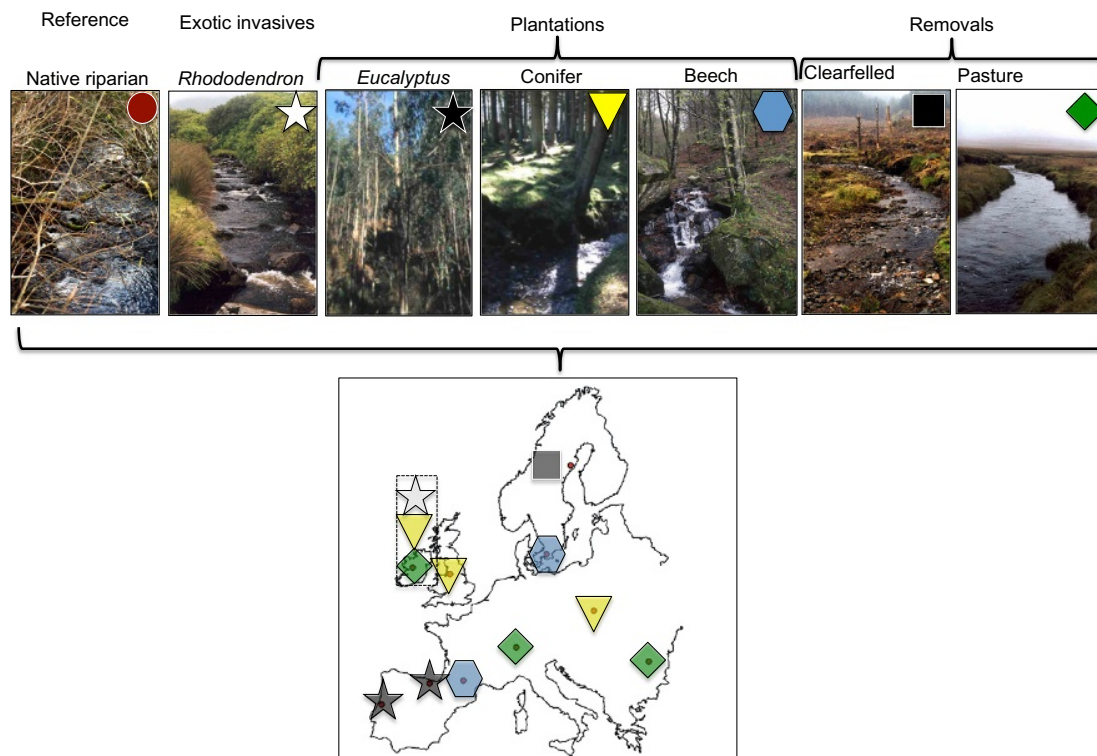


Fig. 8 Workpackage 2: The major riparian alterations investigated across Europe—note, some were unique to particular regions, others were repeated across Europe and in other instances several were studied in the same place (e.g. Ireland).

The experimental design used in Workpackage 2 was otherwise broadly similar to that used in Workpackage 1 (Fig. 3), bar the use of categorical treatments in the former as opposed to the gradient approach in the latter (cf. Fig. 6 vs Fig. 8). In some regions, detailed macroinvertebrate (e.g. taxa richness, density, biomass) and microbial (e.g. fungal biomass and reproductive activity) parameters associated with decomposing litter were also determined (Ferreira et al., 2015b*; Lecerf et al., 2005*; Riipinen et al., 2010*). However, to better understand the dynamics of litter decomposition and of associated parameters (e.g. macroinvertebrate and aquatic hyphomycete colonisation, litter chemical composition) under forest alteration, a complementary coordinated experiment was carried out simultaneously to the main litter decomposition experiment, in one reference—altered stream pair per region (10 reference—altered stream pairs across Europe). In this experiment, additional alder and oak litter bags were deployed in the streams, sampled on up to five occasions over time (i.e. the ‘complete time series’), and AFDM remaining and associated variables were determined (Ferreira et al., 2006a*; Lecerf and Chauvet, 2008a*). Additional experiments were also carried out in three European regions to assess

Table 1 European Region and Terrestrial Ecoregion, and Riparian Vegetation in Altered Streams for the Main and Complementary Coordinated Experiments in *RivFunction* Workpackage 2

Region	Ecoregion ^a	Altered Streams	Additional Information
Central England	Celtic broadleaf forests	Conifer plantations	Riipinen et al. (2009*, 2010*) and Hladyz et al. (2011a)*
South-western France	Western European broadleaf forests	Beech plantations	Lecerf et al. (2005)*, Lecerf and Chauvet (2008a)* and Hladyz et al. (2011a)*
Western Ireland	Celtic broadleaf forests	Pasture	Hladyz et al. (2010*, 2011a*,b*)
	Celtic broadleaf forests	Conifer plantations	Riipinen et al. (2010)*
Southern Poland	Central European mixed forests	Conifer plantations	Riipinen et al. (2010)* and Hladyz et al. (2011a)*
Central Portugal	Cantabrian mixed forests	Eucalyptus plantations	Ferreira et al. (2006a*, 2015b*) and Hladyz et al. (2011a)*
Romanian Danube plains	Pontic steppe	Pasture	Hladyz et al. (2010*, 2011a*)
Northern Spain	Cantabrian mixed forests	Eucalyptus plantations	Ferreira et al. (2006a*, 2015b*) and Hladyz et al. (2011a)*
Northern Sweden	Scandinavian and Russian taiga	Forest clear cutting	McKie and Malmqvist (2009)* and Hladyz et al. (2011a)*
Southern Sweden	Sarmatic mixed forests	Beech plantations	Hladyz et al. (2011a)*
Swiss plateau	Alps conifer and mixed forests	Pasture	Hladyz et al. (2010*, 2011a*)

^aEcoregions defined on the basis of climatic, topographic and geobotanical European data (European Environment Agency; <http://www.eea.europa.eu/data-and-maps/figures/dmeer-digital-map-of-european-ecological-regions>).

the effects of invasion of riparian forests by exotic woody species of major concern in these regions on litter decomposition in streams (Hladyz et al., 2011b*; Lecerf et al., 2007a*) (Fig. 8).

When the 10 regions were considered together, modifications of riparian forests (i.e. replacement by conifer, beech and eucalyptus plantations, forest

clear cutting and replacement by pasture) did not have an overall significant effect on leaf litter decomposition (Hladyz et al., 2011a*). However, strong effects associated with specific disturbances were observed in more regionally focused studies (Hladyz et al., 2011b*; McKie and Malmqvist, 2009*). These contrasting findings at the pan-European and regional scales are not surprising since different types of forest modification have contrasting effects on leaf litter provision and decomposition, which also depends on leaf litter species and type of decomposer community. Nevertheless, at the European scale, total litter decomposition was generally slower in altered than in reference streams, while microbially driven litter decomposition was not significantly affected by forest change (Hladyz et al., 2011a*) suggesting that these alterations affected macroinvertebrates more strongly. Also, the response of litter decomposition to forest change depended on the region (Hladyz et al., 2011a*), indicating that effects on litter decomposition were contingent upon the type of forest change, aquatic communities and/or environmental conditions. Differences between regions were exacerbated further when temperature-corrected litter decomposition rates (k , dd^{-1}) were considered, suggesting that differences other than in temperature are responsible for the observed differences among regions (Hladyz et al., 2011a*). The effects of different types of forest modification on litter decomposition in streams are discussed in more detail below.

3.1 Deciduous Broadleaf Plantations

The effects of the replacement of native deciduous broadleaf forests by deciduous broadleaf plantations on litter decomposition were assessed in south-western France where plantations of beech (*Fagus sylvatica* L.) have replaced large areas of native forests where hazel (*Corylus avellana* L.), chestnut (*Castanea sativa* Mill.), oaks (*Quercus petraea* (Mattuschka) Liebl, *Q. robur*) and beech were previously common (Lecerf et al., 2005*) (Table 2). Total oak leaf litter decomposition was inhibited in streams flowing through beech plantations (altered streams) compared with streams in native forests (reference streams), which was likely due to reduced shredder biomass in litter bags in the former. However, no significant differences were found for total alder leaf litter decomposition or both alder and oak microbially driven leaf litter decomposition between stream types (decomposition rates determined based on the simplified time-series experiment; Lecerf et al., 2005*). Aquatic hyphomycete species richness was also reduced in plantation compared with reference streams, but this did not

Table 2 Summary Table of the Literature Assessing the Effects of the Replacement of Native Deciduous Broadleaf Forests by Deciduous Broadleaf Plantations on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate	Decomposer Community ^b	No. Reference/ Altered Streams or Sites	Response to Forest Change ^c
*Lecerf et al. (2005)	South- western France	Alder leaves	Microbial	4/4	~
			Total	4/4	~
		Oak leaves	Microbial	4/4	~
			Total	4/4	—
*Lecerf and Chauvet (2008a)	South- western France	Alder leaves	Total	1/1	—
			Microbial	1/1	—
Menéndez et al. (2013)	North-eastern Spain	Alder leaves	Total	3/3	+

^aReferences marked with an “*” are derived from the *RivFunction* project.

^bTotal decomposer community: microbes + macroinvertebrates.

^cResponse of litter decomposition to forest change: —, significant inhibition of litter decomposition in altered streams; ~, no significant effect of forest change on litter decomposition and +, significant stimulation of litter decomposition in altered streams.

translate into slower microbially driven litter decomposition in the plantation streams (Lecerf et al., 2005*), suggesting some degree of functional redundancy among fungal species (Dang et al., 2005*; Ferreira and Chauvet, 2012). However, reduced aquatic hyphomycete species richness may have limited leaf litter palatability to shredders, indirectly contributing to the lower total oak leaf litter decomposition in altered streams. No effect of forest change on alder leaf litter decomposition was found, possibly because alder litter formed ‘islands’ of high quality resource in a stream bed dominated by nutrient-poor beech litter, which could attract shredders over small microhabitat scales within a given stream (Lecerf et al., 2005*). A similar explanation was invoked by Menéndez et al. (2013) in relation to faster decomposition of alder leaf litter in streams flowing through plane (*Platanus hybrida (hispanica)* Brot.) plantations compared with reference streams.

When data from the complete time-series experiment was used, total and microbially driven alder leaf litter decomposition rates were slightly lower in the altered vs reference streams (Lecerf and Chauvet, 2008a*), which may have reflected the greater fungal species richness associated with decomposing litter per date in reference sites (Lecerf et al., 2005*).

Differences in the effect of beech plantations on alder leaf litter decomposition between simplified and complete time-series experiments demonstrated the need to consider multiple sampling dates when using leaf litter decomposition to assess impacts of forest change on stream ecosystem functioning, as results based on a single sampling date are likely conservative (Lecerf et al., 2005* vs Lecerf and Chauvet, 2008a*). Nevertheless, leaf litter decomposition was sensitive to forest change, showing its potential to be used as a bioassessment tool of stream functional integrity, although the small number of studies investigating the replacement of native forests by deciduous plantations on litter decomposition (Table 2) currently limits the development of specific management recommendations.

3.2 Conifer Plantations

The effects of replacing native broadleaf forests with conifer plantations on litter decomposition in streams were assessed in central England, western Ireland and southern Poland (Table 3). In England, conifer plantations are dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.), while native broadleaf forests are dominated by oak, hazel (*C. avellana* L.), lime (*Tilia* spp.) and alder. In Ireland, Sitka spruce and Lodgepole pine (*Pinus contorta* Douglas) are common species in conifer plantations, and oak, alder, hawthorn (*Crataegus monogyna* Jacq.) and holly (*Ilex aquifolium* L.) are common in native forests. In Poland, the most common species in conifer plantations are Norway spruce and silver fir (*Abies alba* Mill.), while native forests are dominated by beech. No overall effect of the replacement of native broadleaf forests by conifer plantations on leaf litter decomposition in the standardised leaf litter bags was found when considering 13 reference—altered stream pairs in the three regions (Riipinen et al., 2010*). However, a significant vegetation \times region interaction revealed that the effect of conifer plantations on leaf litter decomposition was contingent on the region (Riipinen et al., 2010*). It is important to note that this interaction subsequently disappeared after fitting pH as a covariable, indicating its overall importance in controlling litter decomposition (Riipinen et al., 2010*). In central England, total and microbially driven litter decomposition rates were faster in streams flowing through conifer plantations (altered streams) than through broadleaf forests (reference streams), which can be partially attributed to the greater shredder abundance in the former (Riipinen et al., 2009*,

Table 3 Summary Table of the Literature Assessing the Effects of the Replacement of Native Broadleaf Forests by Conifer Plantations on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate	Decomposer Community ^b	No. Reference/ Altered Streams or Sites	Response to Forest Change ^c
Whiles and Wallace (1997)	North Carolina, USA	White pine needles	Total	2/2	+
		Red maple leaves	Total	2/2	+
Riipinen et al. (2009*, 2010*)	Central England	Alder leaves	Microbial	5/5	+
			Total	5/5	+
		Oak leaves	Microbial	5/5	+
			Total	5/5	+
Riipinen et al. (2010)*	Western Ireland	Alder leaves	Microbial	3/3	–
			Total	3/3	~
		Oak leaves	Microbial	3/3	–
			Total	3/3	~
	Southern Poland	Alder leaves	Microbial	5/5	~
			Total	5/5	+
		Oak leaves	Microbial	5/5	~
			Total	5/5	~
Hisabae et al. (2011)	South- western Japan (winter)	Japanese cedar needles	Total	1/1	+
		Fusazakura leaves	Total	1/1	+
	South- western Japan (summer)	Japanese cedar needles	Total	1/1	~
		Fusazakura leaves	Total	1/1	~
Martínez et al. (2013)	Northern Spain	Alder leaves	Total	3/3	–
		Pine needles	Total	3/3	~

^aReferences marked with an ‘*’ are derived from the *RivFunction* project.

^bTotal decomposer community: microbes + macroinvertebrates.

^cResponse of litter decomposition to forest change: –, significant inhibition of litter decomposition in altered streams; ~, no significant effect of forest change on litter decomposition and +, significant stimulation of litter decomposition in altered streams.

2010*). In southern Poland, total alder leaf litter decomposition was faster in altered than in reference streams, despite the greater abundance, species richness and biomass of shredders in reference streams (Riipinen et al., 2010*), which suggests that structure and function are not always closely linked. In western Ireland, there was a tendency for slower microbially driven leaf litter decomposition in altered than in reference streams (Riipinen et al., 2010*).

Differences in the magnitude and direction of the effect of conifer plantation on litter decomposition among regions suggest that the identity of the conifer species, local communities and/or environmental conditions may be of prime importance. Shredder species composition differed between vegetation types, with small stoneflies most strongly associated with conifer streams while broadleaved streams generally had a higher proportion of larger taxa, such as limnephilid caddisflies and gammarid shrimps (echoing the main drivers of breakdown seen in Workpackage 1), although the latter were excluded from sites with low pH. The maintenance of decomposition rates irrespective of shredder community composition suggested a high degree of functional redundancy: indeed, similar decomposition rates were observed between streams with high numbers of nemourids and those with only a few limnephilids or gammarids, suggesting that density compensation among consumers might stabilise process rates (Riipinen et al., 2009*).

Despite conifer plantations being the most common plantations worldwide, only five studies have so far addressed their effects on litter decomposition in streams (Hisabae et al., 2011; Martínez et al., 2013; Riipinen et al., 2009*, 2010*; Whiles and Wallace, 1997; Table 3). The effects vary within and among studies suggesting that they depend on the type of plantation, environmental context, identity of litter and type of decomposer community. Given the potential for effects of conifer plantations on stream processes, more studies are needed to support the development of future management recommendations.

3.3 Eucalyptus Plantations

The effects of the replacement of native deciduous broadleaf forests by eucalyptus (*Eucalyptus globulus* Labill.) plantations on litter decomposition in streams were assessed in central Portugal and northern Spain (Table 4). Eucalyptus plantations cover > 1.5 million ha in the Iberian Peninsula and in many cases these replace native deciduous broadleaf forests dominated

Table 4 Summary Table of the Literature Assessing the Effects of the Replacement of Native Broadleaf Forests by Eucalyptus Plantations on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate	Decomposer Community ^b	No. Reference/ Altered Streams or Sites	Response to Forest Change ^c
Pozo (1993)	Northern Spain	Alder leaves	Total	2/1	~
		Eucalyptus leaves	Total	2/1	+
Abelho and Graça (1996)	Central Portugal	Chestnut leaves	Total	3/3	–
		Eucalyptus leaves	Total	3/3	–
Molinero et al. (1996)	Northern Spain	Chestnut leaves	Total	2/2	~
		Oak leaves	Total	2/2	~
		Eucalyptus leaves	Total	2/2	~
Pozo et al. (1998)	Northern Spain	Alder leaves	Total	1/1	~
		Eucalyptus leaves	Total	1/1	~
Díez et al. (2002)	Northern Spain	Alder branches	Total	1/1	~
		Alder heartwood	Total	1/1	~
		Oak branches	Total	1/1	~
		Eucalyptus branches	Total	1/1	~
		Pine branches	Total	1/1	~
Bärlocher and Graça (2002)	Central Portugal	Chestnut leaves	Microbial	2/3	~
			Total	2/3	~
		Eucalyptus leaves	Microbial	2/3	~
			Total	2/3	~

Continued

Table 4 Summary Table of the Literature Assessing the Effects of the Replacement of Native Broadleaf Forests by Eucalyptus Plantations on Litter Decomposition in Streams—cont'd

Reference	Region	Litter Substrate	Decomposer Community	No. Reference/ Altered Streams or Sites	Response to Forest Change
*Ferreira et al. (2006a)	Central Portugal	Alder leaves	Total	1/1	~
		Oak leaves	Total	1/1	~
	Northern Spain	Alder leaves	Total	1/1	~
		Oak leaves	Total	1/1	+ ^d
Laćan et al. (2010)	California, USA	Native litter mixture	Total	3/3	~
		Eucalyptus leaves	Total	3/3	~
Larrañaga et al. (2014)	Northern Spain	Alder leaves	Total	2/2 ^e	—
		Eucalyptus leaves	Total	2/2 ^e	—
*Ferreira et al. (2015b)	Central Portugal	Alder leaves	Microbial	5/5	~
			Total	5/5	—
		Oak leaves	Microbial	5/5	~
			Total	5/5	~
	Northern Spain	Alder leaves	Microbial	5/5	~
			Total	5/5	—
		Oak leaves	Microbial	5/5	~
			Total	5/5	~

^aReferences marked with an ‘*’ are derived from the *RivFunction* project.

^bTotal decomposer community: microbes + macroinvertebrates.

^cResponse of litter decomposition to forest change: —, significant inhibition of litter decomposition in altered streams; ~, no significant effect of forest change on litter decomposition and +, significant stimulation of litter decomposition in altered streams.

^dStimulation of litter decomposition in the altered stream attributed to a flood event (alder litter bags had all been sampled by this time).

^eThe reference and altered stream sites resulted from the experimental addition of native broadleaf and eucalyptus litter, respectively, in each of two streams.

by oak and chestnut. Total alder leaf litter decomposition was slower in streams flowing through eucalyptus plantations (altered streams) than through native forests (reference streams), which was attributed to lower macroinvertebrate and shredder colonisation in altered streams (Ferreira et al., 2015b*). Total oak leaf litter decomposition was not significantly affected by forest change (Ferreira et al., 2015b*), likely due to the lower contribution of macroinvertebrates to the decomposition of nutrient-poor litter (Hieber and Gessner, 2002). Microbially driven alder and oak leaf litter decomposition were generally not affected by forest change (Ferreira et al., 2015b*), despite differences in aquatic hyphomycete community structure between stream types (Bärlocher and Graça, 2002; Ferreira et al., 2006a*), suggesting again a degree of functional redundancy among microbes (Dang et al., 2005*). The replacement of native deciduous broadleaf forests with eucalyptus plantations had stronger negative effects on aquatic communities in central Portugal than in northern Spain (Ferreira et al., 2006a*, 2015b*), likely due to the drier climate in the former promoting summer droughts in eucalyptus streams and limiting the development of an understory of deciduous vegetation. The maintenance of a native riparian buffer may thus partially mitigate the negative effects of eucalyptus plantation on aquatic communities.

The effects of eucalyptus plantations on litter decomposition vary within and among studies (Abelho and Graça, 1996; Bärlocher and Graça, 2002; Díez et al., 2002; Ferreira et al., 2006a*, 2015b*; Laćan et al., 2010; Larrañaga et al., 2014; Molinero et al., 1996; Pozo, 1993; Pozo et al., 1998; Table 4), but a recent meta-analysis has found an overall 20% inhibition of litter decomposition in streams flowing through eucalyptus plantations compared with reference streams (Ferreira et al., 2016a). Eucalyptus plantations cover >20 million ha worldwide (Iglesias-Trabado et al., 2009), but their impacts on litter decomposition in streams have been addressed mostly in the Iberian Peninsula and thus generalisation to other regions is limited due to differences in the type of native forest, eucalyptus species used in plantations, climate, etc. A new collaborative experiment is currently underway to assess the effects of the replacement of native forests by eucalyptus plantations on alder leaf litter decomposition in streams in eight locations distributed across seven countries in the Iberian Peninsula, East Africa and South America to widen our understanding of the effects of eucalyptus plantation on stream functioning.

3.4 Invasion of Riparian Areas by Exotic Woody Species

The effects of the invasion of riparian forests by exotic woody species were assessed in northern England, south-western France and western Ireland, where native riparian vegetation is being invaded in the former two regions by Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr.) and in the latter by *Rhododendron* (*Rhododendron ponticum* L.) (Table 5). Lecerf et al. (2007a)* found no significant differences in total oak and knotweed leaf litter decomposition between a reference stream and a stream flowing through a riparian forest invaded by knotweed (altered stream) in north-central England, likely due to the low level of invasion, while leaf litter decomposition was stimulated in the altered stream in south-western France likely due to the greater abundance of larger shredders in the invaded stream. Hladysz et al. (2011b)* found slower total alder and oak leaf litter decomposition in streams where riparian forests were invaded by *Rhododendron* (altered streams) than in reference streams, reflecting the overall lower shredder abundance in altered streams (Fig. 9). In contrast, total *Rhododendron* leaf litter decomposition was not significantly affected by forest change, probably because its decomposition was already slow in reference streams as a result of the overriding effect of poor resource quality (Hladysz et al., 2011b*). Thus, even though the canopy cover was maintained in altered streams, the allochthonous trophic pathway was negatively affected by *Rhododendron* invasion of riparian forests (Hladysz et al., 2011b*). As altered streams have closed canopies resulting from dense stands of *Rhododendron*, the autochthonous trophic pathway was also negatively affected (Hladysz et al., 2011b*).

The invasion of riparian forests by exotic plant species is a serious problem in many regions of the world (e.g. Friedman et al., 2005; Lorenzo et al., 2010), which can affect aquatic systems by multiple pathways (Hladysz et al., 2011b*; Roon et al., 2014; Schulze and Walker, 1997; Serra et al., 2013). However, results from the few studies that have addressed the effects of the invasion of riparian forests by exotic tree species on litter decomposition in streams are conflicting (Table 5), which suggests that the effect may depend on multiple factors, e.g. the identity of invasive species and/or of the quality of decomposing litter, type of decomposer community involved in the process, environmental conditions, etc. Thus, there is urgent need to increase our knowledge on the response of aquatic communities and processes to plant species invasions to better manage aquatic resources (Hladysz et al., 2011b*).

Table 5 Summary Table of the Literature Assessing the Effects of the Invasion of Native Forests by Exotic Woody Species on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate ^b	Decomposer Community ^c	No. Reference/ Altered Streams or Sites	Response to Forest Change ^d
Schulze and Walker (1997)	South Australia	Redgum leaves	Microbial	3/3	~
			Total	3/3	~
		*Weeping willow leaves	Microbial	3/3	~
			Total	3/3	~
*Lecerf et al. (2007a)	North-central England	Oak leaves	Total	1/1	~
		*Japanese knotweed leaves	Total	1/1	~
	South-western France	Oak leaves	Total	1/1	+
		*Japanese knotweed leaves	Total	1/1	+
*Hladysz et al. (2011b)	Western Ireland	Alder leaves	Total	3/3	—
		Oak leaves	Total	3/3	—
		*Rhododendron leaves	Total	3/3	~
Roon et al. (2014)	Alaska, USA	Thin-leaf alder leaves	Total	1/1	—
		*European bird cherry leaves	Total	1/1	—

^aReferences marked with an ‘*’ are derived from the *RivFunction* project.

^bSubstrates marked with an ‘*’ originated from the exotic invader.

^cTotal decomposer community: microbes + macroinvertebrates.

^dResponse of litter decomposition to forest change: —, significant inhibition of litter decomposition in altered streams; ~, no significant effect of forest change on litter decomposition and +, significant stimulation of litter decomposition in altered streams.

3.5 Forest Clear Cutting

The effects of forest clear cutting on leaf litter decomposition were assessed in northern Sweden (Table 6). Leaf litter decomposition was stimulated in

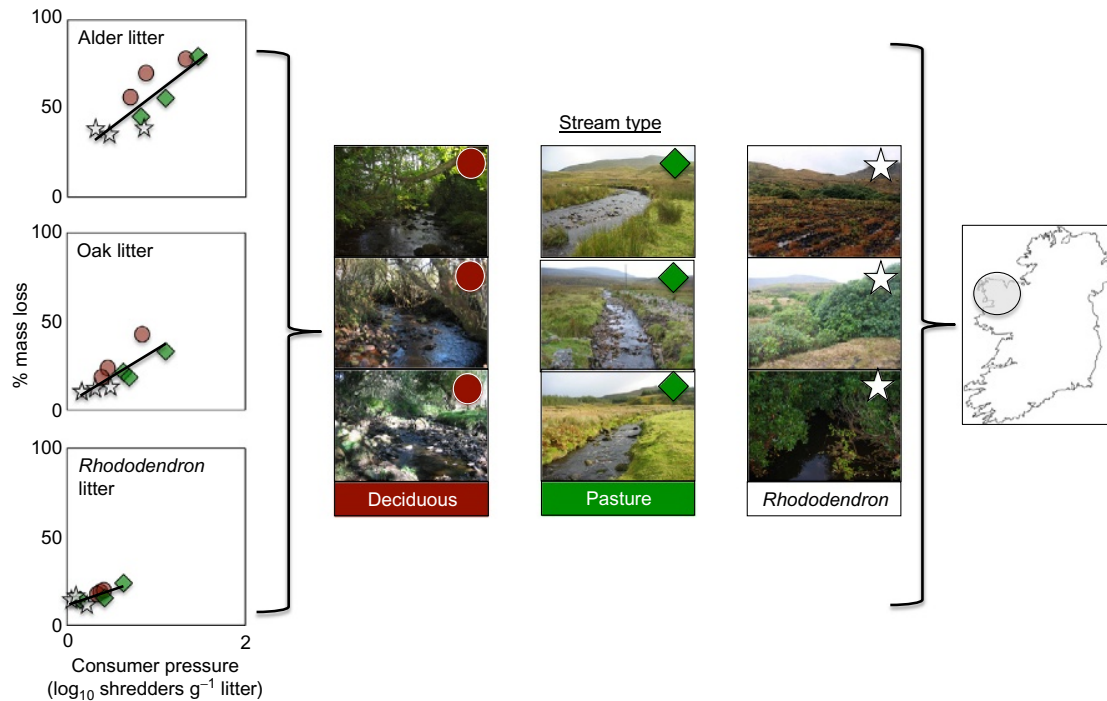


Fig. 9 Decomposition of different litter types in different stream types in Ireland, representing the three major land uses in the locale—native deciduous woodland, land cleared for unimproved pasture, and *Rhododendron* invasion. Note, in each of the nine streams invertebrate consumer abundance was quantified per gram of litter (cf. Fig. 7A), as well as mass loss, which revealed strong differences due to both bottom-up effects of resource quality and top-down effects. Redrawn after Hladyz, S., Tiegs, S.D., Gessner, M.O., Giller, P.S., Rîșnoveanu, 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. *Freshw. Biol.* 55, 1916–1929.

streams flowing through forest clear-cuts (altered streams) compared with streams flowing through old mixed boreal forests (reference streams), mostly for alder in coarse-mesh bags (McKie and Malmqvist, 2009*). No significant differences were found for macroinvertebrate abundance, diversity, assemblage composition or functional feeding groups abundances and species densities between reference and altered streams (except for scraper species density that was higher in reference streams), suggesting that macroinvertebrate community structure was not tightly coupled to variability in leaf litter decomposition (McKie and Malmqvist, 2009*). Rather, higher decomposition rates in the clear-cut streams were associated with an increase in decomposition efficiency by microbes and shredders compared with reference streams (McKie and Malmqvist, 2009*). Notably, this increase in decomposition efficiency occurred even though mean temperatures were actually lower in the clear-cut sites during the study period. This can be explained by the joint effects of three variables that differed between clear-cut and forested streams: increased nutrient concentrations, a shift in the

Table 6 Summary Table of the Literature Assessing the Effects of Forest Logging on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate	Decomposer Community ^b	No. Reference/ Altered Streams or Sites	Response to Forest Change ^c
Benfield et al. (1991)	South Appalachian Mountains, USA	Dogwood leaves	Total	1–3/1	+
		Red maple leaves	Total	1–3/1	+
		White oak leaves	Total	1–3/1	+
		Rhododendron leaves	Total	1–3/1	+
Kreutzweiser et al. (2008)	Canada	Speckled alder leaves	Total	9/12	–
*McKie and Malmqvist (2009)	Northern Sweden	Alder leaves	Microbial	5/5	+
			Total	5/5	+
		Oak leaves	Microbial	5/5	+
			Total	5/5	+
Lecerf and Richardson (2010b)	Canada	Red alder leaves	Total	13/3	–

^aReferences marked with an “*” are derived from the *RivFunction* project.

^bTotal decomposer community: microbes + macroinvertebrates.

^cResponse of litter decomposition to forest change: –, significant inhibition of litter decomposition in altered streams and +, significant stimulation of litter decomposition in altered streams.

composition of litter inputs, and increased shredder biomass. Firstly, phosphate concentrations were slightly greater in the clear-cut streams (McKie and Malmqvist, 2009*), which might have stimulated decomposition from the bottom-up by favouring increased microbial activity (Ferreira et al., 2006c*, 2015a; Gulis and Suberkropp, 2003; Robinson and Gessner, 2000). Secondly, benthic litter standing stocks in the clear-cut streams were dominated by broadleaf (*Betula* spp.) litter, while the forested streams were dominated by refractory conifer needles, reflecting the dominance of birch saplings in the recovering riparian vegetation of the clear-cut streams. This greater incidence of broadleaf litter coupled with higher phosphorus

concentrations together likely resulted in greater availability of nutrient rich and palatable litter in the clear-cut streams, in turn explaining why shredder biomass was overall higher in these streams (McKie and Malmqvist, 2009*). Higher shredder biomass in turn increased the resource-processing potential of detritivore assemblages, providing a further potential explanation for elevated decomposition rates in the clear-cut streams. Additionally, the potential increase in primary production in clear-cut streams may have stimulated litter decomposition by the release of labile carbon that could have stimulated the use of leaf litter by decomposers in a case of priming effect (Danger et al., 2013). Increased primary production may have also contributed to the increased shredder biomass at clear-cut streams if these were feeding on algal resources associated with decomposing litter (Franken et al., 2005).

Again, there are conflicting results among studies addressing the effects of forest harvest on litter decomposition in streams (Benfield et al., 1991, 2001; Kreutzweiser et al., 2008; Lecerf and Richardson, 2010a; McKie and Malmqvist, 2009*; Table 6) suggesting that effects are context dependent and in particular related to the clear-cut type (deciduous/broadleaf vs coniferous). A recent meta-analysis addressing the effects of forest harvest on several stream parameters also found contradictory results among primary studies, i.e. negative and positive responses of the same parameter to forest harvest among studies, highlighting the ‘need to consider site-specific mechanisms by which such changes occur’ (Richardson and Béraud, 2014).

3.6 Pasture

The effects of the long-term conversion of native broadleaf forests to grazing pasture on leaf litter decomposition were assessed in western Ireland, the Romanian Danube plains and the Swiss plateau where this type of forest change is widespread (Hladyz et al., 2010*) (Fig. 8; Table 7). When the three regions were considered together, no significant overall effects of forest change on litter decomposition were found (Hladyz et al., 2010*). However, in some regions macroinvertebrate-driven leaf litter decomposition was faster in streams flowing through deciduous forests (reference streams) and microbially driven leaf litter decomposition was faster in streams flowing through pastures (altered streams), although a significant difference in leaf litter decomposition between stream types was found only for total alder leaf litter decomposition—which was slower in altered than in reference streams in the Swiss plateau (Hladyz et al., 2010*). This suggests a shift in the relative contribution of macroinvertebrates and microbes to leaf litter decomposition between reference and altered

Table 7 Summary Table of the Literature Assessing the Effects of the Conversion of Native Forests to Pasture on Litter Decomposition in Streams

Reference ^a	Region	Litter Substrate	Decomposer Community ^b	No. Reference/ Altered Streams or Sites	Response to Forest Change ^c
Bird and Kaushik (1992)	Canada	Maple leaves	Total	1/1	~
Danger and Robson (2004)	South-eastern Australia	Eucalyptus leaves	Total	2/2	~
Encalada et al. (2010)	North-western Ecuador	Alder leaves	Microbial	3/3	~
			Total	3/3	—
		Guaba leaves	Microbial	3/3	~
			Total	3/3	—
*Hladysz et al. (2010)	Western Ireland	Alder leaves	Microbial	5/5	~
			Total	5/5	~
		Oak leaves	Microbial	5/5	~
			Total	5/5	~
	Romanian Danube plains	Alder leaves	Microbial	5/5	~
			Total	5/5	~
		Oak leaves	Microbial	5/5	~
			Total	5/5	~
	Swiss plateau	Alder leaves	Microbial	5/5	~
			Total	5/5	—
		Oak leaves	Microbial	5/5	~
			Total	5/5	~
*Hladysz et al. (2011b)	Western Ireland	Alder leaves	Total	3/3	~
		Oak leaves	Total	3/3	~
		Rhododendron leaves	Total	3/3	~

^aReferences marked with an ‘*’ are derived from the *RivFunction* project.

^bTotal decomposer community: microbes + macroinvertebrates.

^cResponse of litter decomposition to forest change: —, significant inhibition of litter decomposition in altered streams; ~, no significant effect of forest change on litter decomposition and +, significant stimulation of litter decomposition in altered streams.

streams. In fact, the ratio between macroinvertebrate- and microbially driven leaf litter decomposition was generally greater in reference than in altered streams, suggesting that reduced performance by macroinvertebrates in altered streams is compensated for by stimulated microbial activity (Hladyz et al., 2010*). These results are consistent with those of some previous studies comparing streams flowing through forest and pasture with comparable water characteristics (Ontario: Bird and Kaushik, 1992; Australia: Danger and Robson, 2004; Ecuador: Encalada et al., 2010; Table 7).

Altogether these results suggest that decomposition rates may, in some cases, not be very useful as simple indicators of stream functional impairment due to forest change, whereas the ratio between macroinvertebrate- and microbially driven leaf litter decomposition may be more sensitive to environmental change (Gulis et al., 2006*; Hladyz et al., 2010*), and there are some clear similarities, as well as notable differences, to the responses to nutrient enrichment in the other large-scale bioassay (e.g. Fig. 10 for comparison of main results from the Irish sites for both Workpackages).

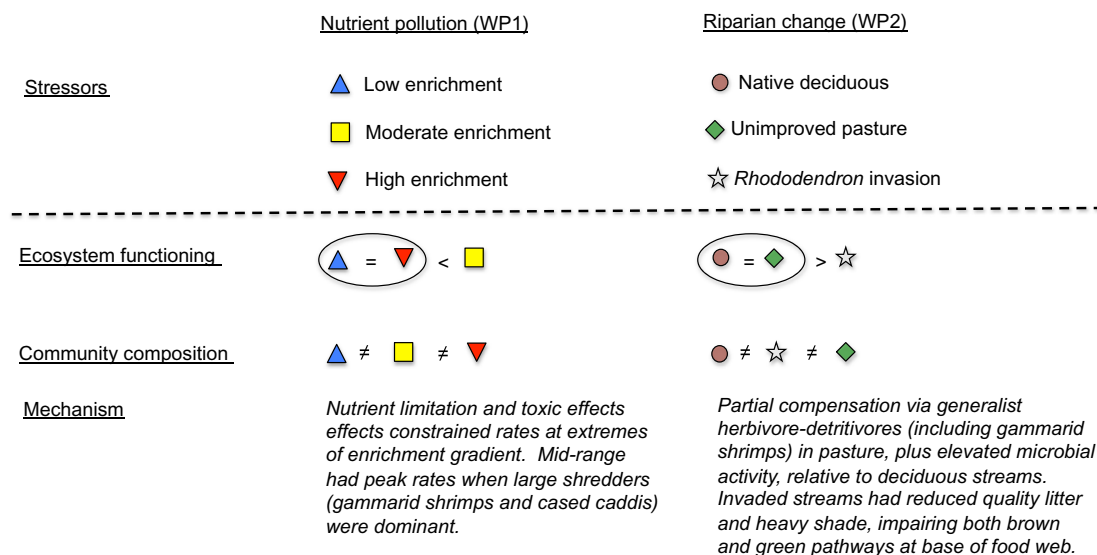


Fig. 10 Summary of contrasts of results from the two major field-based Workpackages (1 and 2) in Ireland, where both consumer assemblages (structure) and decomposition rates (function) were quantified. Note identical rates were observed in highly polluted vs pristine conditions, which were both markedly lower than in moderately enriched sites, with community composition changing progressively along this gradient. Under riparian change, there was similar but less extreme patterns of community turnover, but here pasture and woodland sites had comparable breakdown rates, and both were higher than those invaded by *Rhododendron*.

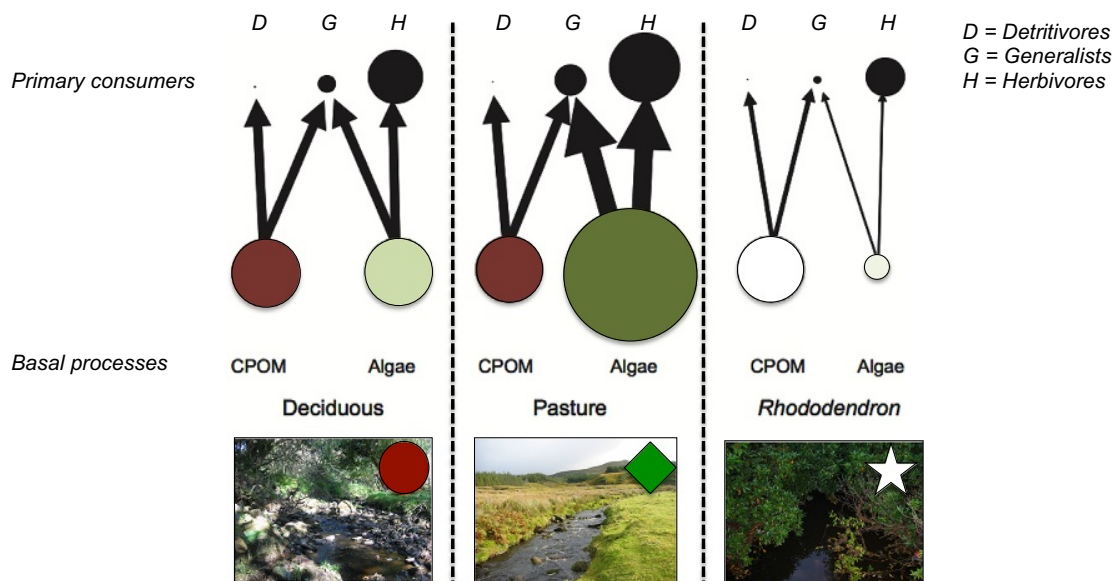
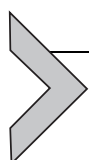


Fig. 11 Beyond decomposition: in the 10 Irish *RivFunction* sites we expanded beyond focusing on decomposition in the ‘brown pathways’ of the food web to include algal processes in the ‘green pathways’ and the links to the consumers of both sets of dominant basal resources, as a function of riparian land-use change. Here, we found evidence of compensation for the partial loss of detrital pathways in pasture streams, via elevated algal production and resource quality, whereas in *Rhododendron* streams both pathways were severely compromised. This was due to reduced resource quality and availability, due to the high C:N content of the litter and the heavy shade cast by the canopy: the transfer of energy through the food web therefore collapsed as the compensation of one pathway by the other was not possible. The area of the *circles* are scaled by standing stocks of consumers and resources, the *arrows* by process rates as measured using litter bags and algal colonisation tiles, both in the presence and absence of macroinvertebrates. Redrawn after Hladyz, S., Tiegs, S.D., Gessner, M.O., Giller, P.S., Rîşnoveanu, 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. *Freshw. Biol.* 55, 1916–1929.

It is also clear that the brown and green pathways in the food web are often intimately connected and one may partly compensate for impairment of the other, especially if generalist consumers are present that can access both major basal energy inputs (Fig. 11).



4. BIODIVERSITY-RELATED MECHANISMS UNDERLYING ALTERED LITTER DECOMPOSITION

Accurate diagnosis of the underlying causes of changes in functional integrity, whether under anthropogenic or natural disturbance, requires a sound mechanistic understanding of the abiotic and biotic factors driving variation in ecosystem processes (Truchy et al., 2015). A key component

of the *RivFunction* framework is the idea that anthropogenic pressures can alter leaf decomposition both by affecting the activities and hence resource-processing potential of decomposing organisms, and by favouring consumer species with intrinsically different resource-processing characteristics. Such trait-mediated and indirect effects could also arise from a loss of diversity, which could impair ecosystem functioning if key species are lost, or if important interactions among species or groups of organisms that underpin ecosystem processes are compromised (Gessner et al., 2010; Truchy et al., 2015).

Much of the variation in leaf litter decomposition along anthropogenic stressor gradients can be attributed to direct influences of abiotic drivers on activities of organisms, such as the initially positive effects of increasing nutrients and temperature on processing rates (Ferreira and Chauvet, 2011; Gulis and Suberkropp, 2003; Salinas et al., 2011). Even so, clear associations between changes in biodiversity and community composition of detrital food webs and rates of leaf decomposition were frequently detected in the *RivFunction* field studies. For example, declines in leaf litter decomposition seen at very high levels of nutrient enrichment appeared partly driven by the loss of (large) detritivore species (Woodward et al., 2012*). Disentangling interactions between abiotic and biotic drivers are often challenging, but may be crucial for interpreting and managing the effects of human disturbances on ecosystem functioning (Frainer and McKie, 2015; Giller, 2005; McKie et al., 2006*). In a study of the effects of a stream-liming program on acid streams in Sweden, microbially mediated decomposition was stimulated by the addition of calcium, which otherwise limits microbial activity in these systems (McKie et al., 2006*). However, this increase was completely offset by reductions in detritivore-driven litter decomposition in limed stream sections, which was associated with declines in the species richness and evenness of shredders, and an increase in the dominance of less efficiently feeding stoneflies at the expense of more efficient caddisflies (McKie et al., 2006*). The net result was that overall rates of leaf decomposition did not differ between limed and unlimed stream sections, although it would be erroneous to conclude that there were no direct or indirect effects of liming on the decomposition process.

A limitation of field-based studies is that while associations between ecosystem functioning and community composition and diversity can be detected, often with the aid of sophisticated statistical approaches, such associations remain essentially correlative (Frainer and McKie, 2015).

A substantial portion of the research conducted within *RivFunction* focused on the role of biodiversity, with Workpackage 3 dedicated to understanding the roles played by the community composition and diversity of litter-decomposing invertebrates, microbes and of the litter resource itself, in regulating decomposition rates.

The approach taken in *RivFunction* for investigating these relationships drew heavily on the theoretical and empirical framework developed within the wider field of B-EF research. Until *RivFunction* was launched in 2002, B-EF research had focused on two main questions: (1) is there a general relationship between increasing biodiversity of producers or consumers and key ecosystem processes and (2) what is the importance of biodiversity per se relative to the presence of particular species for ecosystem functioning (Loreau et al., 2002)? A consensus on both issues was developing, which would be reflected subsequently in key meta-analyses and review papers (e.g. Balvanera et al., 2006; Cardinale et al., 2006, 2007): increasing biodiversity was often, but not universally, associated with increasing ecosystem process rates (especially the primary productivity of grassland plants), and these relationships were often driven by both nonadditive effects of multiple species (i.e. complementarity) and the presence of particular, highly influential species (i.e. the selection effect). However, more subtle and sophisticated questions were increasingly being posed when *RivFunction* was launched, including those related to the roles of other measures of biodiversity than species richness (e.g. evenness, functional diversity), interactions between biodiversity and other environmental variables, and the role of biodiversity in maintaining the stability of ecosystem functioning, including under environmental stress (Cardinale and Palmer, 2002; Giller et al., 2004b; Loreau et al., 2002; Wilsey and Polley, 2004). These and other questions informed the development of B-EF research in *RivFunction* (Fig. 12).

Each of the three main groups involved in the decomposition of litter—macroinvertebrate detritivores, aquatic hyphomycetes and the litter resource itself—were considered in turn, none of which had been extensively studied previously in B-EF research. The role of aquatic hyphomycetes in particular had been barely investigated and remains limited to this day. The logistical and statistical challenges involved in working with these organism groups were substantial, whether it be in restraining mobile aquatic insects in realistic experimental units or inoculating leaf discs with known spores of different fungal species, all at predefined levels of biodiversity. A further challenge arose from the impossibility of exactly

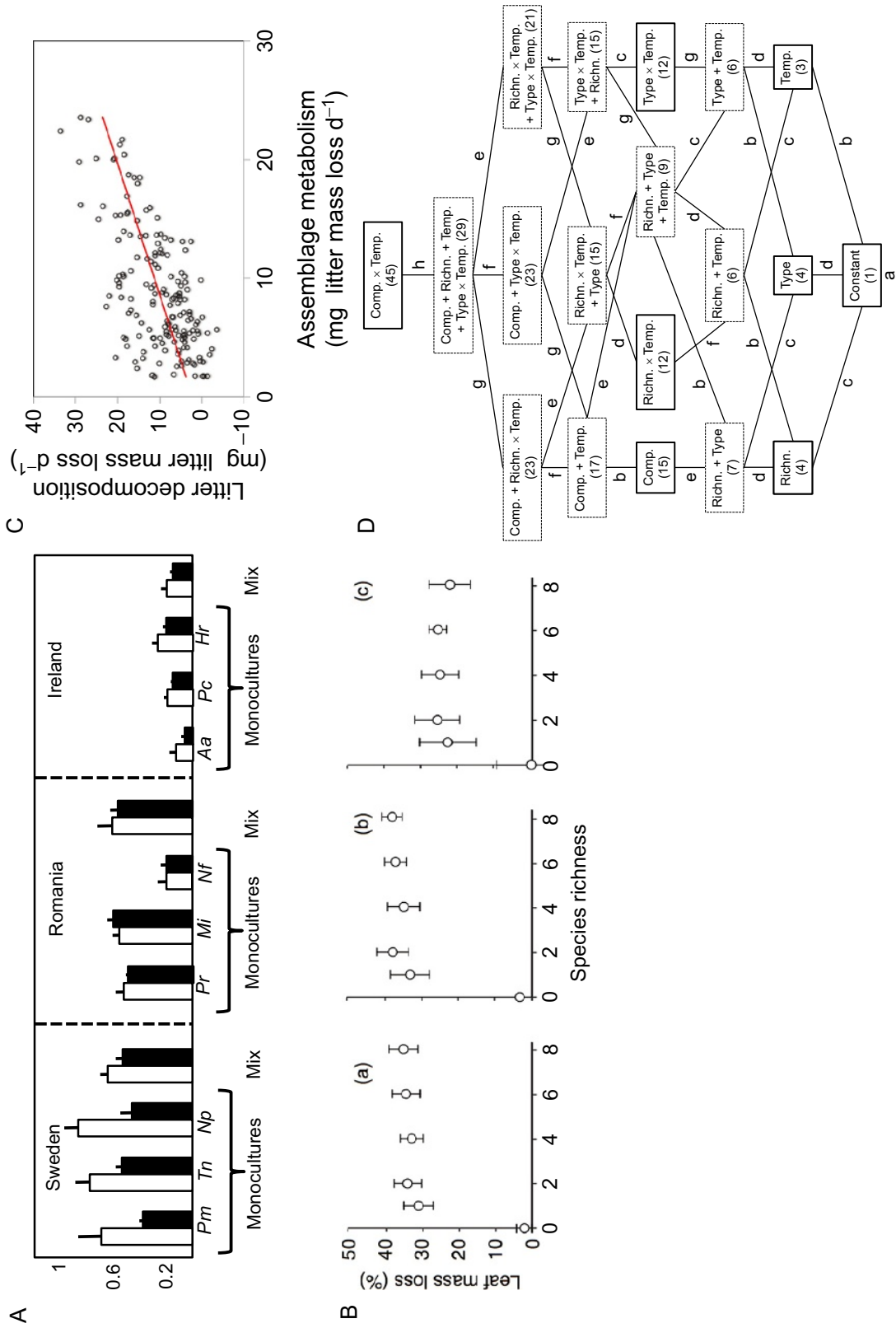


Fig. 12 See legend on next page.

quantifying the contribution of individual consumer species to decomposition rates in species mixture, complicating the assessment of the effects of diversity per se vs individual species (e.g. by using the [Loreau and Hector \(2001\)](#) diversity effect partition). Finally, litter decomposition is an integrative process involving the interplay among organisms at different trophic levels, and capturing this complexity is logistically very challenging in manipulative experiments, not least because of the degree of replication required to vary diversity across two or more trophic groups ([Jabiol et al., 2013](#)). To overcome these and other challenges, *RivFunction* employed a number of novel experimental designs and innovative statistical approaches.

Results from the *RivFunction* diversity experiments were a component of the landmark paper by [Gessner et al. \(2010\)](#), which focused on reviews of B-EF relationships separately at leaf litter, microbial, and detritivore levels, and multitrophic relationships. Here, we discuss the *RivFunction* results in the context of two broad research questions: (1) *Is there a general relationship between biodiversity and leaf decomposition, and which aspects of diversity are most important?* (2) *How does biodiversity influence the stability of decomposition rates, including under variable environmental conditions?* This section

Fig. 12 The ever increasing complexity of biodiversity–ecosystem functioning experiments (Workpackage 3), during and after *RivFunction*. Here we show experiments involving a range of invertebrate shredder and microbial species. The early Workpackage 3 studies revealed evidence of both idiosyncrasy and redundancy among and within assemblages, with weak or inconsistent richness effects (Panels A and B), though effects of species evenness were stronger, but still inconsistent ([McKie et al., 2008*](#)). Subsequent work that followed after *RivFunction* highlighted how body size and the metabolic capacity of the assemblage could account for much (>40%) of this variance, irrespective of richness (Panel C). More recent work suggested richness was more important when multiple processes were considered, especially in a heterogeneous environment, using far more complex experimental designs (Panel D). *Panel A:* A subset of data redrawn after [McKie, B.G., Woodward, G., Hladyz, S., Nistorescu, M., Preda, E., Popescu, C., Giller, P.S., Malmqvist, B., 2008. Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. *J. Anim. Ecol.* 77, 495–504.](#) *Panel B:* [Dang, C.K., Chauvet, E., Gessner, M.O., 2005. Magnitude and variability of process rates in fungal diversity-litter decomposition relationships. *Ecol. Lett.* 8, 1129–1137.](#) *Panel C:* [Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S.G., Reiss, J., Woodward, G., 2010. Environmental warming and biodiversity-ecosystem functioning in freshwater microcosms: partitioning the effects of species identity, richness and metabolism. *Adv. Ecol. Res.* 43, 177–209.](#) *Panel D:* [Perkins, D.M., Bailey, R.A., Dossena, M., Gamfeldt, L., Reiss, J., Trimmer, M., Woodward, G., 2015. Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. *Glob. Chang. Biol.* 21, 396–406.](#)

concludes with a discussion of implications of the findings of Workpackage 3 for development of leaf decomposition as a tool in environmental assessment.

4.1 Is There a General Relationship Between Biodiversity and Ecosystem Functioning, and Which Aspects of Biodiversity Are Most Important?

In line with most previous B-EF research, the *RivFunction* biodiversity manipulations focused primarily on whether general relationships between increasing biodiversity and ecosystem functioning could be detected (cf. [Gessner et al., 2010](#)). This was motivated by the large number of drivers of diversity loss in streams that could potentially affect organisms within the detrital food web ([Gessner et al., 2010](#)). However, many of the *RivFunction* studies emphasised other aspects of biodiversity than species richness within a single functional guild, such as evenness and diversity across multiple trophic levels, and the idea of species traits was also investigated ([McKie et al., 2008*](#); [Sanpera-Calbet et al., 2009*](#); [Schindler and Gessner, 2009*](#)).

Broadly, the functional traits of an organism are those that regulate its responses to environmental variability and its effects on ecosystem processes ([Violle et al., 2007](#)). The potential for species traits to underpin a predictive framework linking environmental and community change with ecosystem processes is being recognised increasingly ([Reiss et al., 2009](#); [Truchy et al., 2015](#)), but research on these linkages was still nascent when *RivFunction* started. Similarly, relationships between species evenness and ecosystem functioning remain poorly investigated for most ecosystem processes, even though human activities affect relative abundances of species far more often than their presence ([Chapin et al., 2000](#)). Increases in species dominance can in turn increase the concentration of particular traits associated with those species in functional guilds, which may either increase the importance of those traits for functioning per se, or alter the strength of key species interactions associated with them ([Hillebrand et al., 2008](#); [Truchy et al., 2015](#)). Finally, although most B-EF studies focused on variation in diversity within a single trophic level, interactions across levels can shape the effects of species loss on ecosystem functioning ([Raffaelli et al., 2002](#)). Biodiversity changes within one trophic level not only affect species richness and composition at other levels, but can also alter ecosystem processes, via both top-down and bottom-up drivers ([Jabiou et al., 2013](#); [Mancinelli and Mulder, 2015](#); [Srivastava et al., 2009](#)).

The potential importance of the species evenness of detritivores for litter decomposition was demonstrated by [Dangles and Malmqvist \(2004\)](#) in their analysis of decomposition datasets from field studies conducted in France and Sweden. They found that decomposition rates generally increased with increasing species richness, but also observed contrasting relationships between assemblages of differing evenness ([Dangles and Malmqvist, 2004](#)). Leaf litter decomposition rates were always higher in the dominated communities, but also plateaued sooner, with no further increases in species richness effects (i.e. redundancy) beyond four species. In contrast, although decomposition rates were lower in more even communities, rates were still increasing at higher levels of richness (6–7 species). [Dangles and Malmqvist \(2004\)](#) further documented spatiotemporal variation in species dominance patterns, which was associated with substantial variability in decomposition rates, especially across seasons.

[McKie et al. \(2008\)*](#) expanded on this work by conducting a microcosm experiment in Sweden, Romania and Ireland to investigate effects of the species richness, evenness and density of detritivores on leaf decomposition. Assemblage composition at each laboratory was chosen to reflect the main species comprising natural stream communities in the autumn. Across all three experiments, there was no general relationship between increasing diversity and leaf decomposition rates ([Fig. 12; McKie et al., 2008*](#)). Rather, effects of both species richness and evenness varied according to the composition of each species pool.

Decomposition in the Romanian study was generally enhanced as richness—but not evenness—increased, whereas in Ireland it was affected by evenness but not richness, with the effects of the former further depending on the identity of the dominant species. There was no relationship between any diversity parameter and decomposition rates in Sweden. The mechanisms underlying these diversity effects contrasted markedly among the regions. The Romanian results were predominantly attributable to the selection effect (i.e. driven by the presence of particular species), whereas there was evidence for positive complementarity among species in Ireland, particularly when the isopod crustacean *Asellus aquaticus* was dominant. Overall, the occurrence of B-EF relationships depended on the degree of taxonomic heterogeneity within each assemblage: the Swedish assemblage consisted of three closely related stoneflies, while the other experiments consisted of detritivores from two orders ([McKie et al., 2008*](#)). This points towards the importance of heterogeneity in the functional traits of species in regulating the occurrence and strengths of

relationships between biodiversity and ecosystem functioning, a key topic of later B-EF research (e.g. [Flynn et al., 2011](#); [Frainer and McKie, 2015](#); [Frainer et al., 2014](#)).

[Schindler and Gessner \(2009\)*](#) focused more explicitly on the role of species trait heterogeneity in regulating relationships between the diversity of the litter resource and decomposition rates. Litter packs of species that contrast strongly in nutrient concentration or structural carbon compounds might decompose more rapidly than single-species packs, due to detritivores optimising nutrient and energy acquisition among multiple species, or microbially mediated transfers of nutrients from nutrient rich to recalcitrant species ([Gessner et al., 2010](#)). Both mechanisms could potentially suggest species complementarity enhances ecosystem process rates (e.g. [Cardinale, 2011](#); [Tylianakis et al., 2008](#)). However, despite the plausibility of these mechanisms, subsequent studies have generally not found consistent effects of increasing litter diversity per se on decomposition ([Gessner et al., 2010](#)). Nevertheless, particular species combinations have been associated with nonadditive outcomes for decomposition ([Handa et al., 2014](#); [Lecerf et al., 2007b*, 2011](#)), with higher or lower rates than derived from the component species in isolation. This suggests that there may be specific combinations of litter species traits that might be particularly influential in regulating decomposition, and that more consistent effects of diversity might emerge when it is quantified in its 'functional' rather than taxonomic form.

[Schindler and Gessner \(2009\)*](#) studied nine deciduous tree species, which were categorised into three categories (three species per category) according to their expected decay rate, as the focal functional 'effect' trait: fast, medium and slow-decomposing species. They also quantified differences in litter chemistry traits: phosphorus, nitrogen and lignin concentration. They mixed the 9 species in a total of 40 species combinations, including replication of 'homogenous' (where all species represent the same litter decay class) and 'heterogeneous' (where the species are drawn from different decay classes). Contrary to their hypotheses, they did not find generally elevated rates of litter decomposition between heterogeneous and homogenous litter packs, with decomposition rates largely controlled by a trait–litter lignin concentration. However, they did find that the most recalcitrant and most labile species decomposed slower and faster, respectively, in litter mixtures comprising different decay categories than in homogenous mixtures, or in single-species litter bags. [Schindler and Gessner's \(2009*\)](#); also see [Frainer et al., 2015](#)) results thus point towards the value of litter traits in a

framework for predicting not only purely additive effects on decomposition, but also nonadditive effects arising from particular litter species combinations (e.g. [Handa et al., 2014](#)).

[Sanpera-Calbet et al. \(2009\)*](#) specifically examined the interaction across trophic levels, between diversity of litter resources vs that at microbial and detritivore consumer levels. They found that for two rapidly decomposing species, hazel (*C. avellana*) and ash (*Fraxinus excelsior* L.), rates were strongly elevated when either or both species were mixed with a refractory species, beech (*F. sylvatica*). Intriguingly, this interaction was not driven primarily by the qualities of beech as a food resource, but rather as habitat, and as a material for the construction of protective cases by particular group of highly efficient consumers in the limnephilid caddisfly genus *Potamophylax* ([Sanpera-Calbet et al., 2009*](#)). Litter packs including beech supported higher than expected abundances and biomasses of leaf-shredding invertebrates, including higher abundances of *Potamophylax*, and this resulted in accelerated decomposition of other species mixed with beech (but not beech itself). This represents a form of facilitation, whereby beech leaf litter facilitates the activities of a key consumer and thereby enhances the decomposition process ([Bruno et al., 2003](#); [Gessner et al., 2010](#)). There was no evidence that interactions between litter species composition and microbial consumers influenced decomposition rates.

The importance of the diversity of aquatic fungi was also investigated in *RivFunction*. There is particularly strong potential for increasing microbial species diversity to elevate decomposition rates, since species possess different litter degrading enzymes which may complement one another, and some types of microbes may facilitate penetration of the litter matrix by others ([Gessner et al., 2010](#)). Despite this, studies conducted within *RivFunction* and elsewhere have found scant evidence that increases in fungal diversity have consistent general effects on microbially mediated decomposition, although a laboratory microcosm study ([Lecerf et al., 2005*](#)) found increasing aquatic hyphomycete diversity stimulated consumption rates by the crustacean *Gammarus fossarum* Koch. This finding suggests that complementary interactions and chemical or functional differences among multiple fungal species increase the availability of nutrients or otherwise enhance the palatability of the litter to *Gammarus*, and further emphasise the importance of interactions across trophic levels for regulating B-EF relationships ([Lecerf et al., 2005*](#)). This was even more thoroughly investigated in an experiment partly conceived during the *RivFunction* project, and ultimately conducted by [Jabiol et al. \(2013\)](#). They found that rates of leaf litter decomposition were maximised when diversity of both fungi and

invertebrate decomposers was the highest, and when fish predator cues were present, with the cumulative effects of species loss within and across trophic levels reducing process rates. This partly reflected both bottom-up effects of fungal diversity and top-down effects of fish cues on the performance of detritivores, including increased feeding by a caddisfly species which was both an efficient leaf-shredder and predation-resistant (Jabiol et al., 2013). Results from this and other experiments (e.g. O'Connor and Donohue, 2013; Perkins et al., 2015), suggest that functional ecosystem impairment resulting from widespread biodiversity loss could be more severe than inferred from previous experiments confined to varying diversity within single trophic levels (Lecerf and Richardson, 2010a).

Other aspects of the functional diversity of litter, microbes and detritivores were also assessed within *RivFunction*. Lecerf and Chauvet (2008b)* focused on intraspecific diversity of a single, key riparian species—*A. glutinosa*—collected from five widely spaced source populations across Europe. They found wide variation in phosphorus and lignin concentrations, which together explained much of the variability in litter decomposition rates. Significantly, intraspecific variation in leaf decomposition rate was within a similar range to that reported for interspecific variation among cooccurring riparian plant species in Europe (Lecerf and Chauvet, 2008b*). Rather than litter nutrient concentrations per se, Hladyz et al. (2009)* focused on the degree of stoichiometric imbalance between the nutrient ratios (e.g. C:N and C:P) of different litter species and the stoichiometric requirements of the main shredder consumers (Fig. 6A). They exposed different single-species litter bags in a stream field experiment, and quantified nutrient ratios of both leaf litter and consumers, and found that litter stoichiometric ratios indeed predicted a significant portion of variability in decomposition, with decomposition rates generally declining as the degree of stoichiometric imbalance with the main consumers in a stream increased (also see Frainer et al., 2016). Finally, McKie et al. (2008)* and McKie et al. (2009)* built on previous research (Jonsson and Malmqvist, 2003; Ruesink and Srivastava, 2001) on the interplay between detritivore density, biomass and biodiversity in regulating B-EF relationships. This ultimately contributed to refinements in the definition of ‘density-dependent diversity effects’ (Gessner et al., 2010), and approaches for unifying B-EF research with metabolic theory (Perkins et al., 2010). The results of Lecerf and Chauvet (2008b)*, Hladyz et al. (2009)* and McKie et al. (2008, 2009)* point towards additional aspects

of biodiversity which can strongly regulate decomposition rates at local and regional scales, and thus need to be incorporated into a more complete framework for understanding variability in functioning, including variability attributable to human activities.

Following on from the suggestions that emerged from the correlative field studies in *RivFunction*, that body size was a key trait for detritivore consumption rates, and that assemblage total abundance and biomass could be a strong predictor of decomposition rates (Hladysz et al., 2011a,b*; Woodward et al., 2012*), the next generation of B-EF experiments (e.g. Perkins et al., 2010) and field studies (e.g. Frainer et al., 2014) explored these drivers in more detail. Many of these post-*RivFunction* studies turned to metabolic frameworks and (supposedly) universal allometric scaling relationships to develop the theoretical underpinning of the novel experimental designs in what became evermore complex and sophisticated laboratory experiments aimed at disentangling these different drivers, and how they responded to environmental change—with a strong focus on climate change and global warming (Table 8). These studies were natural extensions of the pioneering *RivFunction* work and many of them unearthed new insights—for instance, the role of species richness per se appeared to have been overemphasised, and in most cases the majority of variation in the data could be explained by the distribution of biomass among and within species in the assemblage, and the resulting metabolic capacity of the consumers as a whole. This tallied with the observations in the field, in which large detritivores, when abundant, dominated processing rates (e.g. Frainer and McKie, 2015), with cased caddis and *Gammarus* shrimps being keystone species in the regard and important conduits to the higher trophic levels. It also emerged from many of these studies that effects were often simply additive—at least when a single process was measured and diversity quantified as taxonomic richness—but that more complex biodiversity effects were manifested as environmental conditions changed and more processes were quantified (Fig. 12C and D; Perkins et al., 2010, 2015; Reiss et al., 2011), or when diversity was quantified as functional diversity of species traits rather than taxonomic richness (Frainer et al., 2014). For instance, ‘multifunctionality’ became an important consideration across a thermal gradient, in which species richness became important for delivering a range of process rates closer to their maxima across but not within temperature regimes (Perkins et al., 2015).

Table 8 Beyond *Rivfunction*—Illustrative Examples of the Next Generation of Research Based on the *RivFunction* Approach, from 2005 Onwards

Study	Approach	Drivers	Responses	
Water characteristics (extension of WP1)				
Ferreira et al. (2015a)	MA	Nutrients	Algal production Benthic invertebrates Community respiration Carbon cycle	
Ferreira et al. (2015c)	WEM	Temperature and litter species		
Ferreira and Chauvet (2011)*	LME	Temperature and nutrients		
Ferreira et al. (2016b)	MA	Heavy metals		
Dossena et al. (2012)	FME	Temperature		
Rosemond et al. (2015)	WEM	Nutrients	DNA-based assessment of fungal community Cotton strip tensile strength loss Bacterial production Breakdown rate of wooden stick DNA-based assessment of fungal and bacterial communities	
Land-use (extension of WP2)				
Ferreira et al. (2015b)	MA	Changes in forest composition		
Tolkkinen et al. (2015)	FS	Forest drainage and pH		
Burrows et al. (2014)	WEM	Forest clear-felling		
Jinggut et al. (2012)	FS	Deforestation		
Arroita et al. (2013)	FS	Agriculture/irrigation		
Kominoski et al. (2011)	FS	Changes in forest composition		
Biotic controls (extension of WP3)				
Dangles et al. (2011)	FS, Mod	Detritivore richness	Meiofauna community Trophic cascade Consumer–resource elemental imbalance Constancy of diversity–function relationship Algal production Algal production Trophic cascade	
Majdi et al. (2014)	FME	Invertebrate predators		
Frainer et al. (2016)	LME	Stoichiometric traits of leaf litter and shredders		
Frainer et al. (2014)	FS	Shredder functional diversity		
Danger et al. (2013)	LME	Algae		
Woodward et al. (2008)	FME	Fish predator		

Table 8 Beyond *Rivfunction*—Illustrative Examples of the Next Generation of Research Based on the *RivFunction* Approach, from 2005 Onwards—cont'd

Study	Approach	Drivers	Responses
Reiss et al. (2011)	LME	Evenness and body size of detritivores	
Alp et al. (2016)	FS, Mod	Biological invasion	Ecosystem phenology
Macroscale patterns (extension of WP4)			
Handa et al. (2014)	FME	Biome, ecosystem type, and litter diversity	Carbon and nitrogen cycling
Boyero et al. (2011)	FS	Temperature, latitude	Activation energy of litter breakdown
Boyero et al. (2016)	FS	Specific leaf area, litter phylogenetic diversity, channel width, and pH	
Graça and Poquet (2014)	FS	Climatic and edaphic factors	Litter palatability
Biomonitoring (extension of WP5)			
Young and Collier (2009)	FS	Land-use, nutrients	Ecosystem metabolism Leaf toughness loss Cotton strip tensile strength loss Breakdown rate of wooden stick Invertebrate-based biotic index
Clapcott et al. (2012)	FS	Land-use	Ecosystem metabolism Cotton strip tensile strength loss ¹⁵ N natural abundance Invertebrate-based biotic index
Thompson et al. (2015)	FS	Pesticide	Algal production Nutrient cycling Ecosystem metabolism Genes
Feio et al. (2010)	FS	Land-use, pollution	Sediment respiration rate
FWB			Periphyton biomass
Lepori et al. (2005)	FS	Stream restoration	

The table illustrates work that built on the original sets of drivers examined in the five project Work-packages (WP). The different approaches are: *FME*, field microcosm/mesocosm experiment; *LME*, laboratory microcosm/mesocosm experiment; *EM*, whole ecosystem manipulation; *MA*, meta-analysis; *FS*, field survey; *Mod*, modelling. Displayed responses are other than litter breakdown rate and “standard” metrics related to microbial decomposers and shredders associated to litterbags.

4.2 How Does Biodiversity Influence the Stability of Decomposition Rates, Including Under Variable Environmental Conditions?

Theory suggests that more species-rich communities may better be able to buffer environmental variability and maintain ecosystem processes within 'normal' bounds due to (i) statistical averaging, also called the portfolio effect, whereby functioning is inherently more stable for species-rich systems, as the responses of extreme species are diluted over a more diverse assemblage and (ii) insurance effects, or the greater likelihood that a more species-rich assemblage will include species with some level of tolerance to the altered conditions (Doak et al., 1998; Loreau et al., 2002). These scenarios had scarcely been tested when *RivFunction* was launched.

Two key studies from *RivFunction* focused on the potential for the portfolio effect to stabilise ecosystem process rates. In a microcosm experiment, Dang et al. (2005)* found that while increased fungal species diversity was not associated with any systematic increase in leaf decomposition rates (Fig. 12B), it was associated with reduced levels of variability. This effect was weakened by increased levels of species dominance in microbial assemblages. Lecerf et al. (2007b)* observed similar phenomena at the level of the litter resource in a field study, with no overall relationship between increased litter diversity and decomposition rates; however, higher litter diversity was associated with reduced variability of decomposition. Together, these results point towards the potential for losses of not only species richness but also species evenness to increase variability in leaf decomposition rates, and hence reduce stability in the processing of litter at local and regional scales.

Other *RivFunction* studies focused on interactions between community change and abiotic environmental parameters. McKie et al. (2009)* investigated how variation in detritivore species richness and two environmental perturbations interacted to affect litter decomposition and detritivore growth. The assessed environmental perturbations were nutrient enrichment, which was expected to enhance decomposition from the bottom-up by stimulating microbial activity, and stream liming, which also stimulates microbial activity by increasing availability of limiting cations, but which has been associated with reduced decomposition by stonefly (Plecoptera) detritivores in Swedish boreal streams (McKie et al., 2006*). Both treatments constituted perturbations for the naturally acidic and nutrient-poor streams of the Swedish boreal region. McKie et al. (2009)* expected the effects of liming on decomposition by the selected detritivore species to range from positive to negative, reflecting

differences in their pH preferences ([Lillehammer, 1988](#); [McKie et al., 2006*](#)), implying potential for species mixtures to buffer the effects of liming on ecosystem functioning, in line with the insurance effect hypothesis. Replicate enclosures containing litter and the detritivore assemblages were deployed in the field, with liming manipulated at the whole reach scale, and nutrients varied at the level of the individual enclosure. Surprisingly, increased detritivore richness reduced both leaf decomposition and detritivore growth. These negative effects of richness in our field study were opposite to previous laboratory observations ([Jonsson, 2006](#)), further illustrating the importance of environmental context for B-EF relationships (discussed in detail by [McKie et al., 2009*](#), also see [Cardinale, 2011](#); [Cardinale et al., 2000](#)). Effects of the abiotic manipulations were similar in magnitude to these diversity effects, but positive, with leaf decomposition increasing by 18% and 8% following liming and nutrient enrichment, respectively. Finally, the effects of liming were reduced in most species mixtures relative to the monocultures, suggesting increased functional stability when multiple species were present under an anthropogenic perturbation.

Temperature is a basic driver of metabolic processes ([Brown et al., 2004](#)), with the chemical reactions underpinning respiration, resource assimilation and organismal growth all generally increasing with temperature, in line with Van't Hoff's rule ([Myers, 2003](#)). Mean temperatures as well as daily and seasonal variability are increasingly being altered worldwide in aquatic environments as a result of thermal pollution and hydropeaking, and these changes are expected to intensify as a result of global climate change ([Céréghino and Lavandier, 1998](#); [Salinas et al., 2011](#)). [Dang et al. \(2009\)*](#) investigated how shifts in both mean temperatures and the degree of diel temperature oscillations affected the community composition of aquatic hyphomycetes and litter decomposition rates. They tested the effect of 5°C warming with and without diel oscillations on litter decomposition by fungal communities in stream-mimicking laboratory microcosms. Five temperature regimes with identical thermal sums (degree-days) were applied: constant 3°C (representing an ambient scenario) and 8°C (representing a warming scenario); diel temperature oscillations of 5°C around each mean and oscillations of 9°C around 8°C. Temperature oscillations around 8°C but not 3°C accelerated decomposition markedly, by 18% (5°C oscillations) and 31% (9°C oscillations), respectively, compared to the constant temperature regime at 8°C. These outcomes for decomposition were regulated by a combination of both direct (the effect of temperature on

processing rates of individual species, reflecting their individual temperature response curves) and indirect (the effect of an increase in mean temperature on dominance by a functionally important species) pathways (Dang et al., 2009*).

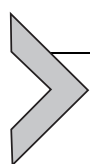
4.3 Implications for the Use and Interpretation of a Litter Decomposition Assay in Bioassessment

The *RivFunction* Workpackage 3 experiments provided several key insights with important bearings on the inferences that can be drawn from decomposition assay studies in both the lab and the field:

- (1) Variation in species composition, reflecting the presence of functionally significant traits, is frequently associated with variation in decomposition at local scales (see also Jonsson and Malmqvist, 2000, 2003).
- (2) Variation in biodiversity per se, can also be associated with significant variation in leaf decomposition rates, but these effects are inconsistent and contingent (Fig. 12) on the composition of regional species pools and environmental context.
- (3) Strong impacts of species loss on ecosystem functioning can be expected when linkages among food web compartments are weakened or lost, and overall trophic complexity reduced.
- (4) Nonadditive effects associated with particular species combinations, rather than increasing diversity per se, may also be common, especially at the level of the litter resource.
- (5) Variability in leaf decomposition regulated by biotic factors (biodiversity, species composition, biomass and density) can equal that regulated by abiotic factors. Litter decomposition assays which only consider abiotic drivers risk missing interactions with biotic drivers that can dampen or amplify the effects of human pressures.
- (6) Biodiversity per se might assist in maintaining the inherent stability of ecosystem functioning under stress, particularly reflecting the portfolio effect, but these relationships remain poorly assessed empirically.
- (7) Other attributes of the functional diversity of detrital food webs also appear to have strong potential predictive power at both local and larger scales, including intraspecific diversity, and stoichiometric characteristics of litter and consumers.

A clear limitation of the *RivFunction* Workpackage 3 manipulations, despite being at the cutting-edge of the field at the time, is that they were often still limited in scope (e.g. number of species or trophic levels considered, spatiotemporal scale) and/or conducted under experimental settings with

varying degrees of realism. However, recently, more spatiotemporally extensive field and mesocosm studies have been conducted which draw on insights partly derived from the *RivFunction* experiments to disentangle interactions between abiotic and biotic drivers and their effects on ecosystem functioning (e.g. [Dangles et al., 2011](#); [Frainer and Mckie, 2015](#); [Frainer et al., 2014](#); [Tolkkinen et al., 2013](#); Table 8). Further scope for doing so can only be enhanced as leaf decomposition is more frequently incorporated into environmental assessment schemes and more extensive datasets are generated.



5. ACCOMODATING NATURAL VARIABILITY WHEN USING LITTER DECOMPOSITION IN STREAM ASSESSMENT

Natural or background variation in process rates is a key consideration when using ecosystem processes such as litter decomposition to evaluate human impacts on streams. This variation can be broadly assigned to two sources: extrinsic environmental conditions and consumer activity, and intrinsic litter quality. These factors need to be understood if human impacts are to be evaluated accurately. Important extrinsic factors include temperature, dissolved nutrients (e.g. N, P, Ca) and pH of the stream water. The biomass and composition of litter-consuming detritivore communities respond to these abiotic drivers and form a bridge to the intrinsic drivers of breakdown inherent in the litter itself. Intrinsic factors that relate primarily to intra- and interspecific variation in litter quality, include their stoichiometric and biochemical composition—especially in terms of CNP ratios and lignin and cellulose content (e.g. [Fig. 6A](#)). Overlain on these sources of biotic and abiotic variation are those stemming from methodological choices and experimental design of the study itself (cf. [Gessner et al., 2007](#)). Many of these factors vary over broad temporal and spatial scales and some of this variation is relevant for using decomposition to evaluate human impacts on ecosystem functioning. While sometimes considerable in aggregate, extrinsic and intrinsic variation in decomposition can be minimised or accommodated to develop a more-sensitive decomposition-based tool ([Gessner and Chauvet, 2002*](#)).

5.1 Extrinsic Factors

Extrinsic factors vary widely across a range of spatial scales, from large scale, such as those that span continents and latitudinal gradients ([Boyero et al., 2011](#); [Woodward et al., 2012*](#)) to local habitat scale within a stream

(Frainer et al., 2014; Langhans et al., 2008*; Tiegs et al., 2008*). Variation across these scales acts as filters that often need to be partitioned to detect human impacts, depending on the goals of the assessment. At the largest spatial scales, variation stemming from climatic and geological differences matters for streams by influencing water quality (e.g. nutrient concentrations and temperature) and hydrologic conditions. For example, regional variation in water quality can be reflected in the nutrient-limitation status of microbial heterotrophs (Reisinger et al., 2016). Additionally, biogeographic variation in species pools can influence decomposition (e.g. litter-consuming macroinvertebrate taxa). For example, invertebrate shredding is often insignificant in many low-latitude streams, due to the absence or rarity of invertebrate detritivores, but elevated microbial activity due to warmer temperatures may compensate for this effect (Boyero et al., 2011; see also Section 2). Variation at spatial scales smaller than regions, such as drainage networks, may be significant especially in geologically heterogeneous areas (Casas et al., 2011; Pozo et al., 2011), but not necessarily so. For example, litter decomposition rates were highly consistent among drainage networks in a geologically uniform region of the Black Forest (Germany) with minimal human impacts when efforts were made to control for stream size, and within stream habitats (Tiegs et al., 2009*). In the same study, decomposition rates were also highly consistent among reaches within streams and among riffles. Taken together, these results suggest that even though decomposition rates are inherently spatially variable among different habitats (Frainer et al., 2014; Langhans et al., 2008*) or longitudinal temperature gradients (Griffiths and Tiegs, 2016), when study design controls for a few extrinsic factors, highly consistent background values can be obtained (Tiegs et al., 2009*). These values provide a useful backdrop against which changes in decomposition due to human activities can be evaluated.

5.2 Temporal Variability

Like spatial variation in decomposition, unaccounted for temporal variation in decomposition can compromise the detection of human impacts on ecosystem functioning. Leaf litter decomposition in streams is typically measured over weeks to months, thereby integrating variation over (relatively) small temporal scales. However, temporal variability over longer timescales poses a problem as a source of statistical noise. While many decomposition studies have been conducted in temperate latitudes where there is a strong seasonality in stream environmental factors, most have been conducted in autumn to

coincide with peak leaf fall. For this reason, we have a more limited understanding of decomposition in other seasons (but see, e.g. [Bergfur, 2007](#); [Ferreira et al., 2006b*](#); [McKie et al., 2006*](#)), and temporal variation in general. Studies during other seasons have typically found that organic matter decomposition varies through time, and tracks water quality attributes such as nutrients and temperature, as well as shifts in consumer assemblages (e.g. [Griffiths and Tiegs, 2016](#); [Hladyz et al., 2011a,b*](#); [Mora-Gómez et al., 2015](#)). In temperate zones, decomposition appears to be more rapid in warmer seasons, probably due to both higher metabolic activity of consumers, but also particularly to the phenology of large shredders ([Dangles and Malmqvist, 2004](#); [McKie et al., 2006*](#)) and a general scarcity of high-quality litter in streams resulting in detritivores aggregating in artificially inserted litter bags ([Murphy et al., 1998](#); [Murphy and Giller, 2000](#)). Unless accommodated in experimental designs or accounted for in statistical analyses, such temporal background variation can impair the sensitivity of assessments of ecosystem functioning.

Several solutions are available to address these issues. The first is to assume that effects brought on by human activities will swamp natural temporal background variability, and thus simply ignore the latter. A more satisfactory approach is to use temporally stratified designs whereby sampling is conducted only during specified times of the year to control for seasonal variability, preferably including periods of peak organic matter input. A logistically more involved option is to repeat decomposition experiments on multiple sampling dates to integrate temporal variability and/or to use slow-decomposing litter, such as oak leaves, that integrates decomposer activities over larger timespans. These latter two options may be less critical in ecoregions where there is little seasonality, and rates of decomposition might be relatively consistent throughout the year. However, many tropical areas experience significant seasonality.

An important downside of using recalcitrant organic matter is the greater potential for loss of experimental units during floods, thus fast-decomposing leaf species are preferable in streams with unpredictably variable flow regimes. High flow also removes litter naturally deposited on stream beds: a consequence of this is that the release of fungal spores from decomposing leaves into the water diminishes, thus slowing fungal colonisation of leaves freshly submerged in streams and, by extension, microbial decomposition. Conversely, aggregations of litter-consuming macroinvertebrates on small patches of experimental litter introduced into streams after flow recedes could artificially elevate decomposition rates. Consequently, the timing of

leaf litter exposure in streams relative to flow events, including their legacy, is an important consideration for sensitive assessment of stream ecosystem functioning.

Variation in decomposition rates across large time scales (i.e. years–decades), is likely, but poorly understood given the small number of decomposition studies that are repeated on an annual basis, or even resampled many years apart (but see Fig. 13). Long-term variation might be related to periodic events such as El Niño–Southern Oscillation (ENSO), and therefore predictable to some extent, or be independent of known meteorological or other events. This variation might stem from long-term fluctuations in hydrology (e.g. above- or below-average discharges), water quality (e.g.

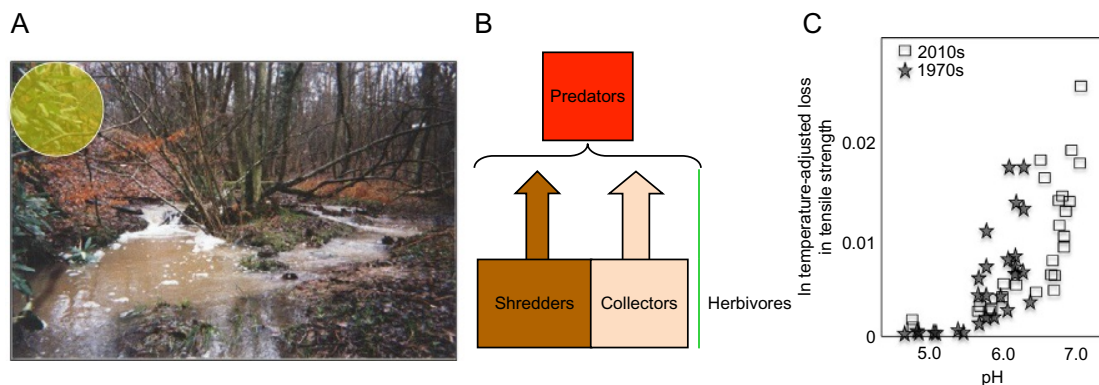


Fig. 13 The next steps beyond *RivFunction*: towards a consideration of multiple stressors, multiple responses and long-term trends. The image (A) shows one of the most intensively studied model stream systems in the world—Broadstone Stream in S. England—highlighting how it, like many other systems, is exposed to a mix of natural and anthropogenic drivers. The image (B) shows a simplified version of the food web, in which the trophic basis of total secondary production via detrital vs algal pathways is drawn to scale. The stream has had little exposure to direct human modification, and its high retentiveness and large amounts of woody debris and leaf litter represent close to the ancestral state for this part of the world, as revealed by the dominance of detrital inputs to the food web. Despite its limited land-use modification, it has been exposed to diffuse acidification for many decades from which it and adjacent sites are now recovering, as revealed using cotton-strip assays (Panel C). In addition, the vegetation is now a mix of native and nonnative species, with *Rhododendron* (cf. Fig. 11) and other exotic evergreens having invaded in recent decades (highlighted in (A) within the yellow (light grey in the print version) inset circle), and it has also been subjected to extreme events, including floods (A) and droughts, over a similar timespan. Combining the use of such model systems with larger-scale comparative approaches (e.g. Figs 3, 6 and 11) will improve future understanding of the drivers of stream ecosystem functioning at larger scales in both space and time, and across multiple stressor gradients. *Panel B: Data derived from Woodward, G., Speirs, D.C., Hildrew, A.G., 2005b. Quantification and resolution of a complex, size-structured food web. Adv. Ecol. Res. 36, 85–135. Panel C: Jenkins et al. (2012).*

temperature) and be reflected in biotic communities (e.g. invertebrates). Long-term studies in decomposition are very rare, but needed in order to better understand natural temporal variation in decomposition, and to track human impacts to ecosystem functioning that occur gradually at large spatial scales.

Another approach to accommodate temporal variability is to normalise decomposition data with environmental data that have a well-understood influence on decomposition. In particular, if temporal variability stems from variation in temperature, the use of ‘temperature-corrected’ decomposition rates should minimise noise in the dataset. This is commonly done by assuming a linear relationship between temperature and decomposition rate and replacing elapsed time with degree–days in regression analyses to calculate decomposition rates (e.g. [Woodward et al., 2012*](#)). A key drawback with this approach, however, is that there may be instances when the environmental factor that is being controlled for, such as temperature, is also confounded with and altered by human activity, and is of interest in bioassessment.

Lastly, it may be possible to derive a ‘disturbance index’ to assess the degree to which any human-induced disturbance has impacted a stream over and above the degree of natural variability in decomposition under normal conditions (cf. [Johnson et al., 2005](#)). This approach allows for the objective assessment of the occurrence and direction of change as well as the duration of an impact. The disturbance index can be applied at different scales—for a single stream, a catchment or a region.

5.3 Intrinsic Factors: Partitioning and Minimising Variability in Leaf Litter Resource Quality and Potential Alternatives

While leaf litter is a logical choice as a type of organic matter to use in assessment and monitoring programs ([Gessner and Chauvet, 2002*](#)), its use in projects that span large temporal or spatial scales presents considerable methodological and logistical challenges ([Tiegs et al., 2013](#)). Leaf litter is the largest source of organic matter that enters many stream ecosystems ([Abelho, 2001](#)), and it therefore constitutes an environmentally realistic material for use in decomposition assays. Additionally, there is a large body of literature on decomposition, providing considerable background information for interpreting data. In order for leaf litter decomposition to be directly comparable among sites, however, a single homogenous batch of leaf litter is required. In studies that span large spatial scales, a homogenous batch of leaf litter could seemingly be amassed choosing litter from a broadly

distributed tree species that grows near each site, therefore ruling out the interspecific variability in litter quality (Webster and Benfield, 1986). However, researchers have recently also documented considerable intraspecific variability in leaf litter quality among biogeographic regions (Graça and Poquet, 2014; Lecerf and Chauvet, 2008b*; LeRoy et al., 2007), confounding such experimental designs if the goal is to compare the decomposition rates among streams using locally collected batches of leaf litter. Even within a region, researchers have documented variability within a species and species–hybrid complexes (LeRoy et al., 2007). This solution of amassing a single batch of litter is additionally limited by several factors, including the fragility of air-dried litter, which tends to become fragmented during transport, and the use of fresh (i.e. not dried) litter presents additional problems (e.g. decomposition prior to incubation in the field). For long-term interannual projects, the need for prolonged storage of the litter presents further logistical difficulties, as when the original batch has been used up subsequent batches collected on other dates are unlikely to be identical matches.

An approach to overcome the problem of variable litter quality is the use of other standardised forms of organic matter instead of natural leaf litter. For example, agar-based pellets containing ground leaf litter and referred to as DecoTabs (Kampfraath et al., 2012) are consumed by litter-consuming macroinvertebrates, and also act as a viable substrate for microbes. Advantages of this approach are that DecoTabs are highly standardised, inexpensive and easy to prepare and deploy. Moreover, chemicals, whether in dissolved or particulate form, can be added, so that to DecoTabs can be used to test for specific effects of nutrients, metals, xenobiotics or other substances in the field. A potential disadvantage is that the texture of DecoTabs greatly differs from that of natural leaf litter, suggesting that the assay can at best be used as a proxy of natural leaf litter decomposition.

A second alternative to measuring decomposition with organic matter other than leaf litter is the cotton-strip assay (Jenkins et al., 2013; Slocum et al., 2009; Tiegs et al., 2007*, 2013). Advantages are that the material is made of cellulose—the most abundant organic polymer on Earth and the primary constituent of leaf litter—in the form of highly standardised woven cotton fabric. In contrast to assays using DecoTabs or natural leaf litter, in which mass loss is the standard response variable, the cotton-strip assay relies on loss of tensile strength, a measure that corresponds to cellulose degradation. Advantages of the cotton-strip assay are that the incubation period is short (i.e. often around 20–30 days) relative to most

assays using natural leaf litter, and that the material is durable. Furthermore, being small, light and nonliving, or previously living, cotton strips can be readily shipped across the globe in large numbers (Fig. 14). For example, the assay was recently deployed in over 500 streams as part of a global-scale experiment, CELLDEX (Cellulose Decomposition EXperiment). In this experiment, more than 5000 cotton strips were prepared from cotton in the form of artist's fabric, following a protocol detailed in Tiegs et al. (2013). Each strip was 27 threads in width and 8 cm in length, and loss of tensile strength was compared to cotton strips that were not incubated in the field. Data were expressed in percent tensile strength loss per day. This assay has been shown to be sensitive to several environmental parameters, including those that are impacted by human activities, including concentrations of dissolved nutrients and water temperature (Griffiths and Tiegs, 2016) and geomorphic alterations (Wensink and Tiegs, 2016). A key drawback is that the assay does not explicitly include the impact of litter-consuming macroinvertebrates, which, as discussed earlier, are often more sensitive to perturbations than microbial decomposers. Also, it is essential that details of the cloth's density and thread number per unit area are standardised as this can have strong effects on its loss of tensile strength (Jenkins et al., 2013). Future



Fig. 14 The next steps beyond *RivFunction*: towards global-scale biomonitoring. The CELLDEX Project builds on the *RivFunction* Project by measuring decomposition rates using a standardised field bioassay—here this involves cotton strips, rather than leaf litter, as a trade-off between capturing the reality of local litter types and standardisation is unavoidable at these large scales. Each red (dark grey in the print version) dot represents a location where the cotton-strip assay was deployed in four streams.

work is needed to establish the degree to which microbial communities colonising cotton strips resemble those of natural leaf litter.

A third alternative is to incubate commercially available tea bags containing tea leaves of varying nutrient quality in the field for determination of mass loss ([Keuskamp et al., 2013](#)). As with the cotton-strip and DecoTab assays, key advantages are ease of use, low cost and high standardisation. Moreover, although fragmented, the material resembles natural leaf litter much more closely than cotton strips and especially DecoTabs. A noteworthy aspect of the tea-bag assay is the simultaneous use of two different types of tea that vary in their carbon-to-nitrogen ratios. The idea is that the different tea types will decompose at different rates, depending on the nutrient status of the ecosystem, as *RivFunction* revealed in its simultaneous use of alder and oak (and other) leaves (e.g. [Hladysz et al., 2009*](#)). Major drawbacks are that the assay currently remains untested in aquatic environments, and given the fragile nature of the materials involved (e.g. a delicate rope for attaching the bags to an anchor), may not be suitable for high-energy streams. Additionally, given the very fine mesh used, problems with sedimentation inside the tea bags need consideration, especially under high concentrations of suspended sediments.

A fourth alternative to leaf litter is standardised pieces of wood, which are inexpensive, can be stored for long periods prior to deployment without suffering decay, are readily sent to collaborating laboratories and are easily deployed in the field. The most commonly used wood substrata are ice cream, popsicle sticks or medical tongue depressors, and wood veneers have also been used. Although little comparative data are currently available, wood appears to respond to environmental factors in ways that are consistent with responses of leaf litter ([Arroita et al., 2012](#); [Díez et al., 2001](#); [Ferreira et al., 2006c*](#); [Gulis et al., 2004](#)). A further advantage of wood is that its decomposition rate varies with the surface-to-volume ratio of individual pieces ([Spänhoff and Meyer, 2004](#)) and thus, by using pieces of different size and shape, it is possible to perform decomposition experiments that last and integrate environmental conditions from weeks to years. [Aristi et al. \(2012\)](#) detected a 50-fold variation in the decomposition rate of tongue depressors deployed at 66 sites across the Iberian Peninsula, thus demonstrating large differences in ecosystem functioning. Currently, the approach is used for routine monitoring of the functional status of rivers in New Zealand ([Collier and Hamer, 2014](#)). However, it is unclear the extent to which the efficacy of this method is dependent on the presence of xylophagous invertebrates.

In aggregate, these alternatives to the use of leaf litter provide solutions to most of the limitations associated with litter bag assays, and especially those identified during and after the *RivFunction* project. While each has certain advantages that can be exploited to meet the needs of particular research projects, an overarching goal of stream assessment is to rely on a recognised standard approach to facilitate comparisons among studies conducted by different teams at different times and different places. Although the development of numerous alternative assays, irrespective of their individual strengths, could undermine this goal, none of the alternatives is compelling enough at present to abandon further testing of the strengths and limitations of different approaches.



6. TOWARDS THE INTEGRATION OF ECOSYSTEM FUNCTIONING INTO STREAM MANAGEMENT

6.1 Ecosystem Functioning and Stream Management

River management and restoration are a worldwide practice of growing importance as we attempt to redress the problems that have arisen from our longstanding use and misuse of freshwater habitats and resources (Giller, 2005). The interest of managers for ecosystem functioning is at least twofold. On the one hand, they may be interested in a given ecosystem-level process, such as fish production or nutrient retention, and thus, manage the ecosystem to maximise this process, or in more modern terms, the associated ecosystem services (Corvalan et al., 2005; Costanza et al., 1997). This approach is increasingly taken into account, for instance, in river restoration projects, in which desired outcomes are not necessarily determined by the guiding image of an unrealistically pristine situation (Palmer and McDonough, 2013; see chapter “Effective river restoration in the 21st century: from trial and error to novel evidence-based approaches” by Friberg et al.). The full implementation of this type of restoration project would require *measuring* the ecosystem process of interest, or some other highly related proxy, but does not imply determining what the ‘natural’ or ‘reference’ conditions should be, nor whether ‘more is necessarily better’ in relation to the overall efficient functioning of the system as a whole. For instance, river managers in some regions may deliberately elevate nutrient pollution to increase fish yield, even at the cost of decreasing water quality or reducing biodiversity (Stevenson and Esselman, 2013). On the other hand, managers may be interested in maintaining ‘natural’ or ‘healthy’ ecosystems, which usually involves *assessing* the status of the ecosystem against a

specific benchmark. This is, for instance, the prism of the ecological status in the EU Water Framework Directive (WFD, 2000), which explicitly includes functioning as one goal for ecosystem management (ecological status is an expression of the quality of the structure and functioning of aquatic ecosystems associated with surface waters). This is a more controversial area, since it implies that ecosystems are entities whose limits and status can be clearly delimited, what is often not the case (Jax, 2010). Nevertheless, the implementation of the WFD clearly shows that, although ecosystems can be open systems with undefined boundaries, highly variable in time and space, and affected by humans since prehistoric times, they can be described in typologies consistently enough (but see, Friberg et al., 2011) that their status assessed accurately enough across an entire continent (Hering et al., 2010).

As with a growing number of other regulatory frameworks worldwide, the EU WFD explicitly includes ecosystem functioning in the definition of ecological status, but does not include clear definitions of what the functional properties among the assessment elements might be for streams and rivers. This contradiction led Gessner and Chauvet (2002)* to their initial advocacy for using litter decomposition for functional assessment and has later been expanded by other authors to include additional functional metrics (e.g. Palmer and Febria, 2012). From the outset, the *RivFunction* project involved environmental managers concerned by the challenge of introducing ecosystem functioning into river management. To date, some progress has been made based on individual initiatives, but there have been diverse responses among managers across Europe, ranging from scepticism to approval and, even more than a decade later, we are still far from its general implementation. The causes for this are multiple, and include the difficulties in defining ‘reference’ conditions for ecosystem functioning, the specialised skills and equipment necessary to determine some ecosystem-level processes, as well as the frequent nonlinearities of ecosystem processes vs environmental stressors (Woodward et al., 2012*). Nevertheless, the general success of structural biomonitoring techniques (Birk et al., 2012), despite the inherent spatial and temporal variability of river communities, suggests that there is a priori circumspection for similar techniques to be developed for functional assessment.

River ecosystem functioning and services are based on multiple processes, which include nutrient retention, secondary production, decomposition of organic matter, pollutant attenuation or whole-stream metabolism (Giller et al., 2004a; Truchy et al., 2015). They offer a

potentially powerful and flexible toolbox to gauge functional impairment and recovery (Young et al., 2008). Each one of these integrates different spatiotemporal scales, from minutes to months and from millimetres to entire river sections, and responds to different environmental stressors (Elosegi and Sabater, 2013), thus offering managers the possibility to tailor their monitoring programs according to the functional variables of most relevance or interest.

6.2 Rationale and Steps in the Use of Litter Decomposition for Functional Assessment

An essential prerequisite for any project within the Fourth European Framework Programme (Key Action EESD-1999-1: *Sustainable Management and Quality of Water*)—which was the key driver of *RivFunction* from a legislative and management perspective—was to respond to social expectations in terms of water quality improvement. The RTD Priorities EESD-1999-1.2.1 and 1.2.2 were dedicated to *Ecosystem functioning* and *Ecological quality* targets, respectively. *RivFunction* was thus designed to acquire new knowledge and summarise existing knowledge on decomposition responses to environmental disturbances. Information on the two major sources of alteration, water quality degradation (nutrient enrichment) and land-use change (riparian forest modification), was obtained within the project from 100 European streams for each of both impairment sources. In addition, the compilation of published data provided information on litter decomposition sensitivity to other local environmental stresses and/or global scale environmental changes. The rationale for this was to underpin a robust and widely applicable functional assessment tool, with the potential to be universally applicable, far beyond the borders of the EU and EEA.

In terms of its implementation as a monitoring tool an inherent limitation can be summarised by the following paradox: (i) to be routinely used, authorities need evidence that a tool is reliable, applicable to a wide variety of situations, and fully finalised, whereas (ii) the refined parametrisation of the tool before regional or national implementation would require an adoption by authorities at very large scales, requiring generation of a greatly expanded dataset both in terms of scale and representativeness. As an illustration, compared with the 200 streams sampled in *RivFunction* Workpackages 1 and 2, a target site number for Europe would need to be higher by at least one order of magnitude given the number of sites routinely monitored for biological assessment, i.e. several tens of thousands on the European continent alone. The fact that litter decomposition (like most

functional processes) responds to environmental stressors in nonlinear ways (Woodward et al., 2012*) also complicated the implementation of such a tool.

Two developments have, however, strengthened the case for such a functional assessment tool. Firstly, a large body of literature has appeared in the last decade, often from outside the original *RivFunction* consortium and in many cases inspired by the project rationale and outcomes (Table 8): more publications on leaf litter decomposition response to environmental disturbances were produced during the last 10 years than the 30 preceding years. This recent interest is even more pronounced when examining litter decomposition specifically as an assessment tool, including those generated from within *RivFunction* (e.g. Arroita et al., 2012; Castela et al., 2008*; Lecerf et al., 2006*; Riipinen et al., 2009; Tiegs et al., 2007*), but also from elsewhere (Bergfur, 2007; Pascoal et al., 2003), North America (Fritz et al., 2011; Hagen et al., 2006; Johnson et al., 2014), including tropical regions (Lopes et al., 2015; Silva-Junior et al., 2014). Secondly, following these scientific advances, interest has grown among end-user representatives, together with a sufficient investment, in the litter decomposition prototype tool, e.g. as designed in Gessner and Chauvet (2002)* and documented in *RivFunction* and other case studies.

6.3 An Example of National Adoption

An example from France is illuminating within this context, where the functional approach has rapidly gained in popularity over the last 10 years with river basin and national water agencies in charge of water quality assessment/improvement. This enthusiasm may have been caused by the apparent simplicity of its practical implementation, especially at a time when water authorities have had to face new challenges (i.e. all waters reaching ‘good ecological status’ by 2015, as stipulated in the European WFD). From 2011, the Onema (The French National Agency for Water and Aquatic Environments) initiated an ambitious research programme on the testing and application of alternative functional quality indicators of water bodies, e.g. including isotopic approaches to evaluate food web integrity, cellulose decomposition and associated enzymatic activities, biofilm production and photosynthetic activity, and leaf litter or cotton strip decomposition, together with the comparison of such indicators (F. Guérol, Y. Reyjol and J.-M. Baudoin, pers. comm.). The need for functional bioassessment tools to complement classical WFD-compliant tools is illustrated in two specific situations: (i) streams from overseas European territories, typically in

tropical regions, where no or poor biomonitoring information is available and (ii) when attempting to restore ecosystem integrity (Castela et al., 2008). A recent illustration of the Onema support is the application of the litter decomposition assay to 85 headwater stream sites across France, corresponding to various stages and types of hydromorphological disturbance or restoration, i.e. dam removal, remeandering, pond disconnection and sedimentary recharge (Colas et al., 2016). At the regional scale, several programmes have been initiated by river basin agencies, including those for the Loire-Bretagne and Adour-Garonne. The latter recently funded a project aiming at the comparison of structural indicators, as currently used in river quality monitoring, and the newly developed functional indicators based on litter decomposition (Brosed et al., 2016). The 84 regularly monitored stream sites were subjected to various degrees of single to multiple stressors, mostly including point source and diffuse pollution. Even though the functional metrics and thresholds were still tentative, this project identified the complementarity of both types of indicators.

The success of the *RivFunction* project can also be measured by the currently growing interest in applying the litter-bag approach to assess other types of ecosystems beyond streams and rivers. In France, the project communication has been sufficiently broad to reach stakeholders engaged in the management of novel (man-made) ecosystems for which there is an urgent need to develop indicators of ‘good ecological potential’ and to define relevant ecological thresholds. Litter breakdown metrics have served as benchmark in the Onema-funded project *IsoLac* focusing on gravel-pit lakes to measure the performances of promising food web level indicators based on stable isotope analyses. *RivFunction*’s basic premise that litter breakdown rate can characterise ecosystem health has also been embraced in a research project aiming to develop cost-effective biotic indicators for soil functions in brownfields and old-abandoned mines (*Ifons* project funded by the ADEME, The French National Agency for Environmental Management and Sustainable Development).

In contrast to France, there is no sign yet that the other European countries (at least those involved in the EU *RivFunction* consortium) are fully engaged in formally applying the litter-bag approach to evaluate the functional integrity of streams and rivers, although there is growing interest on a more ad hoc basis at regional scales (e.g. Jackson et al., 2016). Importantly, it must be stressed that the initial arguments for the introduction of litter decomposition in ecological assessment originated from outside Europe: as early as 1986, Webster and Benfield pointed out the potential

of litter decomposition to assess the effect of anthropogenic stresses on stream integrity, and in conjunction with complementary functional approaches it has already been implemented to some extent in New Zealand (Young et al., 2004).

6.4 Proposed Metrics

By exploring the various European situations examined within *RivFunction*, the application of the simplest metric proposed in Gessner and Chauvet (2002)*, i.e. the ratio of decomposition rates at impacted and reference site, has provided promising results (Table 9). Although tentatively proposed, the thresholds were sensitive enough to detect responses even to weak environmental changes, as far as the anthropogenic stressor was not complicated by background perturbations and other confounding factors. The situations where reference conditions are unknown or not documented (or even do not exist) are, however, still commonplace. This becomes especially critical when working at the scale of small hydrocoregions, which multiplies the number of cases to consider before carrying out any comparison. In France, for instance, there are 120 level 2-ecohydroregions, with distinct abiotic settings that can induce substantial variability in decomposition even between reference conditions. Ideally, a database covering reference situations from all such hydrocoregions would be needed to standardise stream functional assessment across a heterogeneous territory like France. In the absence of such a database, the ratio of decomposition rates in fine-mesh and coarse-mesh bags can be used as an indicator of the shift in the contributions of microbial and invertebrate decomposers, resulting from differential, possibly compensatory, responses (Gessner and Chauvet, 2002*). Indeed, the ratio of total to microbially driven decomposition rates was useful for detecting the functional impairment of pesticide-affected streams along a gradient of toxicity due to the strongly deleterious effects of pesticides on macro-invertebrates contrasting with the relatively insensitive leaf-associated microflora both in SW France (Brosed et al., 2016) and in the UK (Thompson et al., 2015). No compensatory decomposing activity of micro-organisms was observed in the impacted streams in France, and there was only a weak and partial compensation in the UK study. This means that total decomposition rates were also dramatically reduced, thus enabling reliance on either decomposition rate ratios or absolute decomposition rates to quantify the functional impairment of such stream ecosystems. In addition to litter decomposition parameters, several fungal-based metrics have been proposed (e.g. Castela et al., 2008; Colas et al., 2016; Lecerf and Chauvet, 2008a*) and other new molecular microbial-based tools may also serve a complementary

Table 9 Summary Table of *RivFunction* Case Studies Assessing the Functional Impairment of Stream Ecosystems by Various Stressors, Based on Ratio of Decomposition Rates in Coarse-Mesh Bags at Impacted (k_i) and Reference (k_r) Sites

Stressor	Study Reference	$k_i:k_r$
Nutrient enrichment		
Moderate	Gulis et al. (2006)*	2.3–2.7
Moderate	Elosegi et al. (2006)*	1.2–8.9
Moderate	Castela et al. (2008)*	1.5–4.7
High	Lecerf et al. (2006)*	0.11–0.36
Nitrate addition (0.9 mg L ⁻¹)	Ferreira et al. (2006c)*	1.3–1.4
Riparian forest modification		
Spruce monoculture	Riipinen et al. (2010)*	0.88–0.92
Beech monoculture	Lecerf et al. (2005)*	0.31–0.77
Eucalypt monoculture, Portugal	Ferreira et al. (2006a)*	0.75–0.79
Eucalypt monoculture, Spain	Ferreira et al. (2006a)*	1.0–2.1
Plant invasion (<i>Rhododendron ponticum</i>)	Hladysz et al. (2011b)*	0.44–0.51
Plant invasion (<i>Fallopia japonica</i>)	Lecerf et al. (2007a)*	1.0–1.5
Others		
Acidification	Dangles et al. (2004)*	0.09–0.18
Acidification	Baudoin et al. (2008)*	0.16–0.38
Liming of humic streams	McKie et al. (2006)*	0.50–0.75
Mine pollution	Lecerf and Chauvet (2008a)*	0.58
Mine pollution	Medeiros et al. (2008)*	0.36–0.84
Copper contamination (75 µg L ⁻¹)	Roussel et al. (2008)*	0.28–0.73

Three classes [(0.75–1.33)], [(0.50–0.75), (1.33–2.00)] and [(<0.50), (>2.00)] represent high, moderate and low levels of stream functional resilience to impact, respectively (Gessner and Chauvet, 2002)*, as illustrated by *light grey* to *black shading*. Note that the response to nutrient enrichment has been shown to display bell-shape along the nutrient concentration gradient, in contrast to other stressors, tending to cause monotonic changes in decomposition rate ratios.

role here (see chapter “Recommendations for the next generation of global freshwater biological monitoring tools” by Jackson et al.; Thompson et al., 2015). Maximum leaf-associated spore production was found to be the most sensitive indicator of human impacts on streams, including eutrophication, pollution from mine drainage and alteration of riparian vegetation (Lecerf and Chauvet, 2008a*). Intriguingly, the ratio of microbial to total breakdown

was also a clear indicator of the switch from deciduous forest to pastureland (Hladysz et al., 2011a*), especially where grass litter as opposed to leaf litter was used as the resource, suggesting this metric has potential to pick up both instream and riparian impacts.

Finally, further work could also incorporate the idea of providing a more ‘robust’ reference value through application of the concept of a disturbance index (cf. Johnson et al., 2005). This approach was developed to take on board natural variability of macroinvertebrate community metrics and hydrochemical parameters for assessing the impact of land-use change (e.g. clearfelling) on stream ecosystems. It allows for objective assessment of the occurrence and direction of change as well as the duration of an impact and should be readily applicable to monitor and assess changes in ecosystem processes such as litter decomposition rates.

In conclusion, the *RivFunction* project has generated wide range important and novel insights into the functioning of freshwater ecosystems and also laid the foundations for a stronger coupling of pure and applied research, as well as advancing ecological understanding in each respective discipline. It has opened several exciting new avenues of research, from understanding how biodiversity shapes ecosystem functioning in a changing environment to providing a template for developing the next generation of global bio-monitoring tools.

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