Stream Ecosystem Functioning in an Agricultural Landscape: The Importance of Terrestrial–Aquatic Linkages

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SUMMARY

The loss of native riparian vegetation and its replacement with non-native species or grazing land for agriculture is a worldwide phenomenon, but one that is prevalent in Europe, reflecting the heavily-modified nature of the continent's landscape. The consequences of these riparian alterations for freshwater ecosystems remain largely unknown, largely because bioassessment has traditionally focused on the impacts of organic pollution on community structure. We addressed the need for a broader perspective, which encompasses changes at the catchment scale, by comparing ecosystem processes in woodland reference sites with those with altered riparian zones. We assessed a range of riparian modifications, including clearance for pasture and replacement of woodland with a range of low diversity plantations, in 100 streams to obtain a continental-scale perspective of the major types of alterations across Europe. Subsequently, we focused on pasture streams, as an especially prevalent widespread riparian alteration, by characterising their structural (e.g. invertebrate and fish communities) and functional (e.g. litter decomposition, algal production, herbivory) attributes in a country (Ireland) dominated by this type of landscape modification, via field and laboratory experiments. We found that microbes became increasingly important as agents of decomposition relative to macrofauna (invertebrates) in impacted sites in general and in pasture streams in particular. Resource quality of grass litter (e.g., carbon : nutrient ratios, lignin and cellulose content) was a key driver of decomposition rates in pasture streams. These systems also relied more heavily on autochthonous algal production than was the case in woodland streams, which were more detrital based. These findings suggest that these pasture streams might be fundamentally different from their

native, ancestral woodland state, with a shift towards greater reliance on autochthonous-based processes. This could have a destabilizing effect on the dynamics of the food web relative to the slower, detrital-based pathways that dominate in woodland streams.

I. INTRODUCTION

A. Impacts of Agriculture on European Streams: Pollution, River Engineering and Clearance of Riparian Zones

Europe's landscape has been altered profoundly by human activity for millennia. Since the Industrial Revolution (ca. 1840), and particularly after the Second World War (1945), agricultural practices have intensified across the continent, and now operate at truly industrial scales (Feld *et al.*, 2011; Friberg *et al.*, 2011; Mulder *et al.*, 2011). The consequences of this are manifested in the continent's freshwaters which, as typically small and relatively isolated water bodies in a largely agricultural landscape, are particularly sensitive to the land use in their catchments. Europe's streams and rivers receive runoff loaded with agrochemicals, pesticides, sewage and other pollutants (Feld *et al.*, 2011; Friberg *et al.*, 2011) and they have also been channelised, deepened and straightened for land drainage, flood management and the transport of humans and goods (e.g. timber floating). In recent years, increasing attempts have been made to restore water quality through enhanced pollution legislation (e.g. EU Habitats Directive and EU Water Framework Directive—WFD), more enlightened catchment management regimes, and even river restoration schemes (Feld *et al.*, 2011; Friberg *et al.*, 2011). In addition to this primarily post-industrialisation intensification of agriculture, many catchments have been stripped of their native deciduous woodland; a process that has been ongoing since the Neolithic. Of these three main types of perturbation, the most is known about the ecological impacts on running waters of pollutants (mostly in the form of organic pollution), less about the effects of river engineering (but see Feld *et al.*, 2011; Harrison *et al.*, 2004), and least about the consequences of altering the riparian vegetation (but see Hladyz *et al.* 2010; Riipinen *et al.*, 2010): it is this latter anthropogenic impact that forms the focus of this chapter.

Most biomonitoring and bioassessment in running waters to date has focussed on measuring the impacts of organic pollution on community structure (Bonada *et al.*, 2006; Woodward, 2009), but the need to measure the impacts of a wider range stressors and to consider the functional responses of ecosystems is now being recognised (Gessner and Chauvet, 2002), even if it is yet to be formally incorporated into environmental legislation, such as the EU Water Framework Directive (Friberg *et al.*, 2011). Bioassessment of 'ecological status' for freshwaters in the WFD is predominately based on structural indicators (e.g. measures of diversity, or indices based on sensitive taxa). This implies that the WFD assessment of 'ecological status' assumes that the biological structure of an ecosystem directly relates to the functioning of an ecosystem, which is not necessarily the case (Friberg *et al.*, 2011; Gessner and Chauvet, 2002). A more integrated structural–functional approach, which also considers the influence of the surrounding terrestrial environment, is needed if we are to move beyond primarily descriptive biomonitoring towards developing a deeper understanding that can help to predict, and ultimately mitigate future change in what is already a heavily modified landscape (Hladyz *et al.*, 2011; Moss 2008; Perkins *et al.* 2010a,b; Woodward, 2009). Recent studies have started to address the current lack of knowledge by investigating how environmental perturbations affect the decomposition rate of terrestrial leaf litter in streams (Hladyz *et al.*, 2010; Huryn *et al.*, 2002; McKie and Malmqvist, 2009; Riipinen *et al.*, 2010; Young and Collier, 2009). Allochthonous leaf litter is the dominant basal resource in many stream food webs (Cummins *et al.*, 1989; Wallace *et al.*, 1999; Woodward *et al.*, 2005) and its decomposition represents a key component of ecosystem functioning.

Woodland has been cleared to provide pasture for livestock grazing across Europe for millennia, long before the advent of artificial fertilisers, agrochemicals or river engineering: as such, this is arguably the earliest form of large-scale alteration of land use, although its impacts on terrestrial–aquatic riparian zones and the attendant implications for stream food webs remain largely unknown (but see Hagen *et al.*, 2010; Hladyz *et al.*, 2010, 2011; Young *et al.*, 1994). The fact that this dramatic land-use change started so early in human history might explain the otherwise surprising lack of studies into its ecological impacts in running waters—it is now so ubiquitous that it is widely viewed as simply being an integral part of the familiar European landscape, even to the extent that many of our moorland, heathland, fell, pastures and meadows are regarded as having high conservation status, despite not being natural climax communities (Friberg *et al.*, 2011). In Ireland, where much of the current study is based, this process of removing large tracts of the native vegetation began as early as 5400 years ago, with extensive and widespread forest clearance starting about 600 years ago (Dodson and Bradshaw, 1987). Agricultural or semi-natural pasture, moorland and heathland now dominate many European, and most Irish, catchments, and this is also increasingly true of many other parts of the world (Fujisaka *et al.*, 1996; Menninger and Palmer, 2007; Reid *et al.*, 2008). The vegetation of riparian zones has also been altered in many other ways, but typically to a lesser extent, than conversion to pasture, including, for instance, the introduction or invasion of exotic plants used for forestry (e.g. conifer plantations, Riipinen *et al.*, 2010; eucalyptus plantations, Ferreira *et al.*, 2006), the creation of monospecific forests for forestry (e.g. Lecerf *et al.*, 2005), forest clear-cutting (McKie and Malmqvist, 2009), biofuel production, ornamental purposes, or the provision of shelter for livestock (e.g. *Rhododendron* invasion Hladyz *et al.*, 2011).

These riparian alterations have the potential to trigger significant changes in stream ecosystem functioning (Figure 1). For instance, Hladyz *et al.* (2011) examined the influence of three vegetation types on community structure and

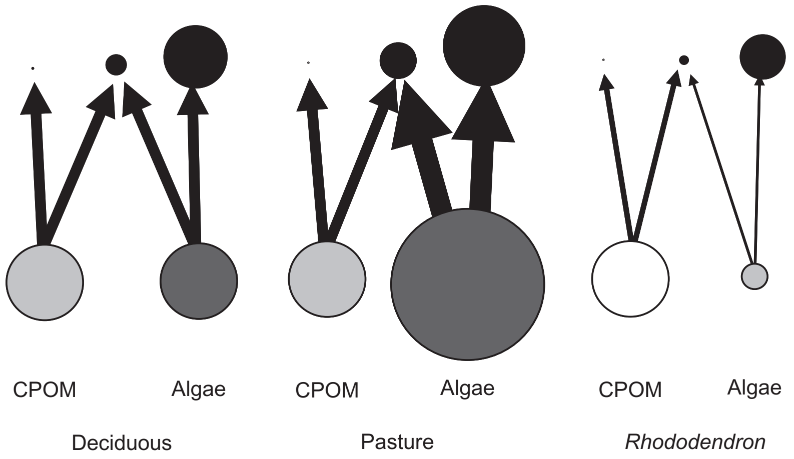


Figure 1 Schematic representations of simplified food webs linking the primary consumers to the dominant basal resources in three vegetation types. Among the basal resources, the diameter of the circles denoting algae is scaled linearly to primary production per degree day per unit area of stream bed, and the diameter of the CPOM circles scales linearly to the standing biomass per unit area of stream bed. Among the primary consumers, grazers (e.g. *Baetis* spp.), generalists (e.g. *Gammarus* spp.) and shredders (e.g. Limnephilidae caddis larvae), the diameter of each circle scales linearly to the standing biomass per unit area of stream bed. The intensity of the colour of each circle denotes tissue C:N (black = 0–5; dark grey = 5–10; mid-grey = 10–100; white = 100–1000 [molar ratios]). The arrows denote energy flux from resources to consumers: the width of each arrow indicates whether the flux is degraded in terms of quality (thin arrows) or quality and magnitude (thinnest arrows) or if it is enhanced in quality and magnitude (thick arrows), relative to conditions in the deciduous woodland 'reference' streams. Redrawn after Hladyz *et al.* (2011).

three key ecosystem processes (decomposition, primary production and herbivory) in nine Irish streams bordered by three characteristic vegetation types, deciduous woodland, pasture or *Rhododendron ponticum* L. (an aggressive riparian invader). Community structure and ecosystem processes differed among vegetation types, with autochthonous pathways being relatively more important in the pasture streams than in the woodland reference streams (Figure 1). However, in *Rhododendron*-invaded streams overall ecosystem functioning was compromised because both allochthonous and autochthonous inputs were impaired, that is, *Rhododendron*'s poor quality litter and densely shaded canopy suppressed decomposition rates and algal production, and the availability of resources to consumer assemblages (Figure 1). In general, the consequences of riparian vegetation changes, for stream ecosystems are therefore potentially profound, yet still largely unknown, as few studies have investigated these processes in 'pasture' streams or other altered riparian zones relative to those bordered by native vegetation (but see Hladyz *et al.*, 2010, 2011; Riipinen *et al.*, 2010).

B. Impacts of Riparian Clearance on Stream Ecosystem Functioning: Detrital Decomposition, Primary Production and Consumption Rates

Detritus dominates the basal resources of many stream food webs, particularly in the upper reaches of river networks (Cummins *et al.*, 1989; Wallace *et al.*, 1999; Webster and Benfield, 1986; Woodward *et al.*, 2005). It is derived mostly from allochthonous subsidies of riparian leaf litter, which are broken down to produce CO_2 and other inorganic compounds, dissolved and fine-particulate organic matter, and consumer biomass (Gessner *et al.*, 1999). The principal biological agents of litter decomposition are detritivorous invertebrate 'shredders' and microbial decomposers (bacteria and aquatic hyphomycete fungi; Hieber and Gessner, 2002), and decomposition rates are mediated via the combined influences of resource quality, temperature, and consumer abundance (Figure 2; Boyero *et al.* 2011; Gessner *et al.*, 2010; Hladyz *et al.*, 2009; Reiss *et al.*, 2010). Shredders often account for the majority of leaf mass loss, at least in the temperate woodland streams that have been most intensively studied (Hieber and Gessner, 2002; Hladyz *et al.*, 2009; Irons *et al.*, 1994); their abundance and activity are determined by the quality, quantity and timing of litter inputs. There are, however, suggestions that microbial decomposers can be more important in pasture streams because invertebrate shredders may be scarce or absent, even though total decomposition (i.e. consumption by invertebrates + microbes) rates may be similar to those in woodland streams (Hladyz *et al.*, 2010).

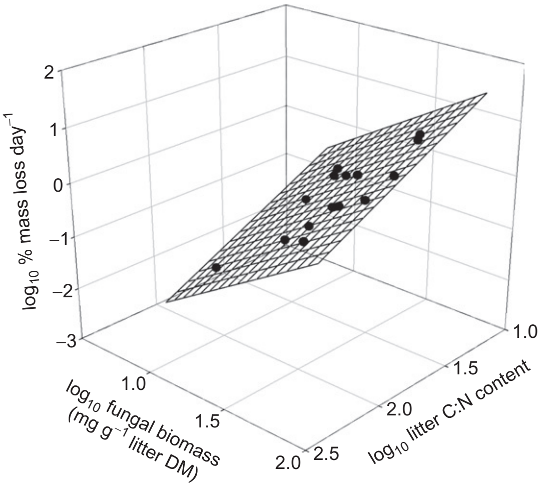


Figure 2 Within-stream constraints on leaf-litter decomposition rates. 91% of variance in litter decomposition rates within a single woodland stream as a function of resource quality for invertebrate shredders, as measured by the degree of microbial conditioning and C:N content of litter—91% of the variance is accounted for by these two variables alone. Redrawn after Hladyz *et al.* (2009).

In theory, because pasture streams lack a dense, overhanging canopy and significant leaf litter inputs (Campbell *et al.*, 1992; Reid *et al.*, 2008), algal production could underpin a greater proportion of secondary production, via autochthonous-based pathways in food webs, relative to the role of detritus in woodland streams (Figure 1; Delong and Brusven, 1998; Hladyz *et al.*, 2011). In this way, pasture systems could retain the potential to process leaf litter (Gessner *et al.*, 1998), even though that ability might not normally be expressed (Hladyz *et al.*, 2011). Although leaf litter *per se* may be scarce, these systems can receive appreciable terrestrial inputs of grass litter as an alternative detrital resource (Hladyz *et al.*, 2011; Leberfinger and Bohman, 2010; Menninger and Palmer, 2007). Surprisingly, little is known about how grass litter is processed in pasture streams (but see Menninger and Palmer, 2007; Young *et al.*, 1994), but there are indications that it is used primarily by microbes rather than invertebrate consumers (Dangles *et al.*, 2011; Hladyz *et al.*, 2010; Niyogi *et al.*, 2003). This suggests a fundamental shift in the driving agents of decomposition in particular and overall ecosystem functioning in general, in terms of reliance on autochthonous versus allochthonous pathways, at the base of the food web (Hladyz *et al.*, 2010). In other words, the structure and dynamics of these systems might be very different from their woodland counterparts.

One of the principal aims in this chapter was to compare litter decomposition rates in a set of 100 European streams, half of which were reference sites bordered by native vegetation, and the other half had altered riparian vegetation. These were selected to represent the major types of riparian alteration, on a continental-scale, with the 10 regions representing the major European ecoregions as defined in the WFD: the alterations investigated included riparian zones that had been cleared for pasture (in Ireland, Romania and Switzerland) or forestry (N. Sweden), and a range of low diversity plantations (e.g. monospecific beech forests in France; eucalypt plantations in Portugal and Spain). We then sought to characterise community structure and ecosystem functioning in a set of nine pasture streams in Ireland, to gain a better understanding of how these systems operate in their own right, using a combination of survey and experimental approaches (Table 1; Figure 3).

Table 1 Outline of the tiered approach to the study, ranging from an extensive pan-European field bioassay experiment (Tier I) through to increasingly more controlled field-based (Tiers II–III) and laboratory studies (Tier IV)

	Tier I	Tier II	Tier III	Tier IVa	Tier IVb
Number of study sites	100	9	1	n/a	n/a
Water chemistry characterised/controlled	✓/×	✓/×	✓/✓	✓/✓	✓/✓
Oak litter decomposition	✓	✓	✓	×	✓
Grass litter decomposition	×	✓	✓	✓	✓
Grass litter quality controlled	×	×	✓	✓	✓
1° consumer assemblage composition characterised/controlled	×/×	✓/×	✓/✓	✓/✓	✓/✓
1° consumer abundance characterised/controlled	×/×	✓/×	✓/✓	✓/✓	✓/✓
1° consumer—basal resource stable isotope signatures characterised	×	✓	×	×	×
2° consumer assemblage composition characterised/controlled	×/×	✓/×	✓/✓	×/×	×/×

Tier I: RIVFUNCTION pan-European study (including 15 pasture streams—5 in Ireland); Tier II: Irish multiple sites field experiments; Tier III: Irish single site (Dripsey River) field experiments; Tier IVa: Irish laboratory mesocosm experiment (multiple-choice feeding trial); Tier IVb: Irish laboratory microcosm experiment (single-choice feeding trial). See Section II for full details and Figure 3 for a schematic depiction of the connections between the drivers and responses for Tiers II–IV.

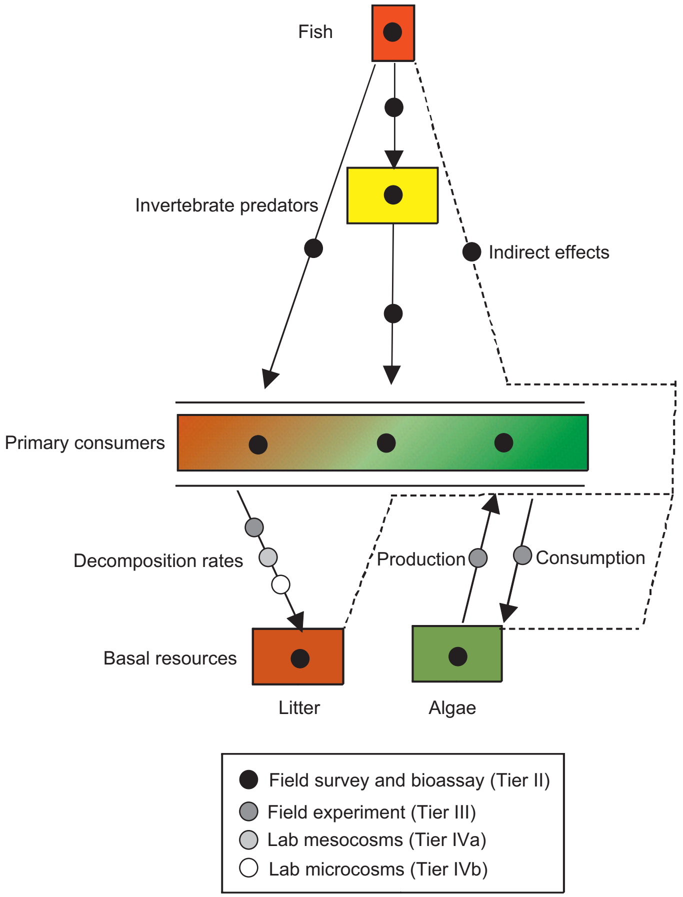


Figure 3 Generalised schematic representation of the putative main drivers of community structure and ecosystem functioning in the intensive studies carried out in the Irish pasture streams (Tiers II–IV of the study design—see Table 1 for details).

C. The Potential for Indirect Food Web Effects to Influence Stream Ecosystem Functioning

The vast majority of ecosystem process studies in running waters have focussed on trophic interactions at the base of the food web (i.e. litter decomposition by detritivores and decomposers). However, ecosystem processes can also be affected indirectly via top-down effects exerted by the higher trophic levels, including, for instance, predatory fishes. Focussing on basal resources and their primary consumers, therefore, provides only a partial picture of the potential biological drivers (Power, 1990; Woodward *et al.*, 2008). Indirect food web effects could also interact with the effects of riparian clearance. For instance, fishes can induce trophic cascades by altering the density and/or behaviour of primary consumers (Nakano *et al.*, 1999), which in turn can affect the use of algae and detritus by consumers at lower trophic levels (Abrams, 1995; Holomuzki and Stevenson, 1992; Oberndorfer *et al.*, 1984; Peacor and Werner, 1997; Power, 1990; Short and Holomuzki, 1992; Turner, 1997; Woodward *et al.*, 2008).

Food web structure and ecosystem functioning are clearly inextricably linked and hence need to be considered in parallel to obtain a complete picture of how these higher levels of organisation operate (Gessner *et al.*, 2010). This interconnection underpinned our reasons for considering the wider community food web in the intensive studies in the Irish systems. Surveys are often the first step when investigating these higher level patterns and processes since appropriate experimental approaches tend to be logistically unfeasible to implement, especially as the drivers and responses often operate at larger spatiotemporal scales that cannot be manipulated easily (e.g. reaches, years; Woodward, 2009). By decreasing in scale and simplifying complexity from field conditions to tightly controlled laboratory experiments, one might move closer to identifying potential drivers, which are far harder to resolve in the field as they may be modulated by a complex array of variables (e.g. water chemistry, community differences).

To date most of the research on food webs and ecosystem processes has focussed on small spatial scales in isolated studies of single, or a few, systems, rather than employing multiple-scales of investigation in replicated systems across environmental gradients (Woodward, 2009; but see Brown *et al.*, 2011; Layer *et al.*, 2010b; Ledger *et al.*, 2011). We attempted to integrate field and laboratory experiments with empirical survey data in a standardised manner across multiple sites to explore the connexions between structure and function and to explore potential links between different organisational levels.

D. Linking Ecosystem Structure and Functioning Across Multiple Levels of Organisation via Experimental and Empirical Approaches

In the first part of this chapter, we compared a range of different anthropogenic alterations to riparian zones, including replacement of natural woodland with pasture and plantations, in a continental-scale study of 100 streams across multiple ecoregions as part of the pan-European RIVFUNCTION research project (e.g. Hladyz *et al.*, 2010; Riipinen *et al.*, 2010). This involved conducting field-based bioassays of leaf litter decomposition rates in response to a range of different riparian alterations (Table 2), with the specific type of impact representing a dominant perturbation in each of the nine countries.

Table 2 Geographical co-ordinates and physicochemistry of the 100 European reference and impacted streams, mean (min/max) given per region

European region	Stream types	Longitude °E/W	Latitude °N	Temp. (°C)	TON (μg L^{-1})	SRP (μg L^{-1})	pH	Conduc. (μS cms^{-1})
Ireland[a]	Reference	−9.56/−9.39	53.90/53.96	5.7–6.0	121(55/220)	4(4/18)	7.32(6.99/7.64)	166(114/211)
	Impact (pasture)	−9.57/−9.31	53.92/54.00	5.1–5.7	42(19/61)	6(3/18)	7.36(7.27/7.48)	124(87/150)
Switzerland[a]	Reference	7.93/9.65	53.90/48.08	4.9–8.4	1870(669/2636)	5(6/8)		449(323/517)
	Impact (pasture)	8.03/9.57	47.18/47.83	6.3–8.0	1800(560/3261)	5(5/7)		394(287/502)
Romania[a]	Reference	25.03/25.32	63.88/44.92	3.7–6.3	341(117/679)	5(1/10)	7.69(7.30/7.91)	249(218/320)
	Impact (pasture)	25.10/25.73	44.68/45.09	2.5–6.7	1230(163/2074)	5(1/24)	7.81(7.49/8.05)	398(218/670)
N. Sweden[b]	Reference	19.86/20.38	44.86/64.39	0.3–0.9	39(9/129)	7(2/9)	6.49(5.65/7.03)	54(39/85)
	Impact (forest clearfell)	19.88/20.60	63.94/63.34	0.3–0.5	23(7/57)	9(4/16)	6.32(5.81/6.84)	39(30/47)
S. Sweden	Reference	13.07/14.07	55.73/56.04	1.8–4.8	3386(1247/7760)	21(12/32)	7.44(7.25/7.86)	268(149/519)
	Monospecific forest (Beech)	13.12/14.08	55.71/56.07	1.8–4.9	3120(1184/7747)	18(9/39)	7.27(6.85/7.64)	213(96/478)
France[c]	Reference	2.09/2.41	43.41/43.49	6.4–8.4	1384(1064/1804)	3(2/3)	6.41(6.32/6.51)	43(33/62)
	Monospecific forest (Beech)	2.21/2.44	43.41/43.49	7.7–9.1	954(396/2239)	3(2/5)	6.44(5.71/7.26)	82(27/210)
Great Britain[d]	Reference	−1.95/−1.61	53.42/54.40	3.9–5.7	1042(294/2680)	4(3/7)	5.67(4.33/6.79)	83(75/169)

(*continued*)

Table 2 (*continued*)

European region	Stream types	Longitude °E/W	Latitude °N	Temp. (°C)	TON (μg L^{-1})	SRP (μg L^{-1})	pH	Conduc. (μS cms^{-1})
	Conifer forest	−1.84/−1.75	53.41/53.44	3.9–5.7	606(456/790)	4(3/4)	6.24(5.00/7.10)	80(53/96)
Poland[d]	Reference	20.07/20.63	49.47/49.61	1.5–2.7	792(521/1288)	39(33/53)	8.06(7.77/8.28)	187(167/208)
	Conifer forest	20.02/20.53	49.42/49.60	1.1–3.0	548(340/914)	49(39/67)	8.10(7.73/8.26)	184(167/196)
Portugal[e]	Reference	−8.30/−8.21	40.06/40.51	8.3–12.5	230(110/356)	3(3/4)	6.47(6.29/6.72)	31(23/41)
	Eucalyptus plantation	−8.37/−8.22	40.45/40.52	11.3–13.0	250 (137/388)	3(2/5)	6.49(6.18/6.68)	48(34/81)
Spain[e,f]	Reference	−3.33/−3.23	43.21/43.32	7.8–10.9	861(245/1560)	6(3/9)	7.00(6.44/7.55)	92(68/141)
	Eucalyptus plantation	−3.33/−3.23	43.17/43.35	8.7–10.6	5734(428/767)	9(8/10)	6.81(6.07/7.19)	116(67/214)

Superscript denotes previous published data comparing reference and impacted streams: [a]Hladyz *et al.* (2010), [b]McKie and Malmqvist (2009), [c]Lecerf *et al.* (2005), [d]Riipinen *et al.* (2009, 2010), [e]Ferreira *et al.* (2006) and [f]Elosegi *et al.* (2006).

This 100-stream dataset included 50 reference (native woodland) and 50 impacted sites, of which 15 were pasture streams in three countries, Ireland, Switzerland and Romania (Hladyz *et al.*, 2010). Leaf litter decomposition rates in all 100 streams were measured in coarse and fine-mesh bags, as proxy measures of the relative importance of invertebrates and microbes, respectively, as the agents of decomposition (after Hladyz *et al.*, 2010).

In the following year, we focussed on a set of nine pasture streams in Ireland, three of which were also included in the earlier pan-European project, in a more intensive case study. Here, we took a more in-depth and holistic view of overall ecosystem functioning and the potential for indirect food web effects to influence process rates, in addition to characterising community assemblages directly, rather than using proxy measures. These field experiments were complemented with a range of laboratory trials, in which we attempted to identify the key drivers of litter decomposition. We have subdivided the study into four tiers of approach (Table 1), which follow a logical progression from the most extensive but least detailed field experiment in 100 European streams (Tier I: RIVFUNCTION study), to a more intensive field-based study in nine Irish streams (Tier II), followed by better controlled field experiments in a single focal stream in Ireland (Tier III) and finally to highly controlled laboratory experiments (Tier IV).

In the Irish studies, we expanded the range of both responses and predictors considered in the pan-European study. We quantified three key ecosystem processes (decomposition, primary production and herbivory) and community structure (invertebrate and fish population abundance and biomass) in nine pasture streams across a gradient of intensity of agricultural land use using a suite of field and laboratory experiments. Resource quality, in terms of nutrient status (C:N:P ratios) and physical toughness (% lignin and % cellulose content), of grass litter was characterised from each stream, to assess its influence on process rates. We also compared decomposition rates among streams in parallel using a single, standardised source of oak litter (*Quercus robur* L.), as in the pan-European field experiment, as this species constitutes a widespread and significant component of the detrital pool in many woodland ‘reference’ streams. The other major energy input to the food webs, autochthonous primary production, was assayed using algal colonisation tiles, and top-down effects of herbivores were gauged by excluding crawling grazers from half of these (after Hladyz *et al.*, 2011; Lamberti and Resh, 1983). Finally, we quantified the abundance and biomass of invertebrate and fish populations, which we used to make inferences about the potential for indirect food web effects to influence process rates at the base of the web (e.g. Woodward *et al.*, 2008). In summary, our key objectives were as follows:

1. Compare leaf litter decomposition rates in reference sites versus those with altered riparian zones using a standardised pan-European bioassay experiment in 100 streams. We predicted that, overall, impacted streams would be impaired and therefore have slower decomposition rates than reference streams.
2. Characterise ecosystem functioning (litter decomposition rates, algal production and herbivory) and community attributes (abundance and species composition of fish and invertebrate assemblages) of pasture streams. We predicted the more nutrient-enriched streams would exhibit faster process rates at the base of the food web and that this would be reflected by increased consumer abundance.
3. Determine relationships between resource quality and decomposition rates of grass and leaf litter. We predicted that grass litter provides, in general, a poorer quality resource than leaf litter, but that in addition its quality will vary considerably across sites, with a general increase associated with agricultural improvement (e.g. anthropogenic fertilisation of pasture catchments and riparian zones).
4. Assess the potential for subtle indirect food web effects to be manifested, to test the hypothesis that top-down effects (e.g. herbivory) would also increase with agricultural intensification (as with bottom-up effects), because detrital subsidies should support more consumers per unit biomass with increasing litter quality (e.g. carbon:nutrient ratios in grasses). Additionally, predatory fish were predicted to influence the abundance of organisms at lower trophic levels and, hence, to affect process rates indirectly, via predation on invertebrate grazers and detritivores.

II. METHODS

A. Tier I. RIVFUNCTION Field Experiment: Impacts of Riparian Alterations on Decomposition Rates in 100 European Streams

Ten research teams from nine countries (France, Great Britain, Ireland, Poland, Portugal, Romania, Spain, Northern Sweden, Southern Sweden and Switzerland) carried out a single co-ordinated field experiment to assess the effects of altered riparian vegetation on leaf litter decomposition rates in 100 streams across Europe (Table 2; Figure 4). Stream characteristics (other than riparian vegetation) were standardised as far as possible between impacted and reference sites, both within and among regions, in order to isolate the effects of alterations to the riparian zone. Dissolved nutrient concentrations within each country reflected regional baselines that were relatively free of agricultural

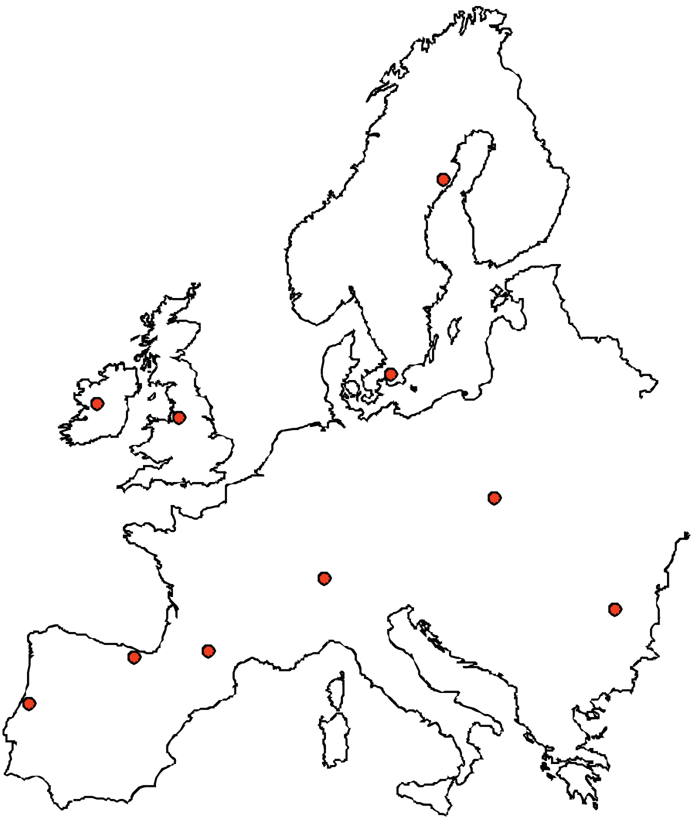


Figure 4 Tier I: Location of the 100 stream sites used in the pan-European RIVFUNCTION study (see Section II).

runoff and sewage effluents, and all streams were <5 m wide, <50 cm deep at winter baseflow, 1st–4th order, with a stony substrate and reference sites were all bordered with native woodland (after Hladyz *et al.*, 2010; Riipinen *et al.*, 2010). Water samples filtered over Whatman GF/F glass fibre filters (average pore size 0.7 μm) were analysed in the laboratory for total oxidised nitrogen ($NO_3^- + NO_2^-$) and soluble reactive phosphorus ($SRP \sim PO_4^{3-}$). Conductivity, pH and stream temperature were measured in the field.

Decomposition rates of alder (*Alnus glutinosa* (L.) Gaertn.) and oak (*Q. robur* L.) leaf litter, sourced locally in each country, were measured in a single large-scale trial conducted during autumn/winter 2002/2003. Mesh bags, each containing 5.00 ± 0.25 g of air-dried leaves, were deployed in 10 streams per region (Hladyz *et al.* 2010; Riipinen *et al.* 2010). Mesh apertures of 10 (‘coarse mesh’ hereafter) or 0.5 mm (‘fine mesh’) were used to permit or prevent invertebrate colonisation, respectively. In total, over 2400 leaf bags were exposed (6 replicates × 2 mesh sizes × 2 leaf species × 10 streams × 10 regions), which were retrieved when additional coarse-mesh bags (sampled repeatedly at reference sites; data not shown here—see Hladyz *et al.*, 2010 for details) had lost approx. 50% of their initial mass (T_{50}) to standardise for the degree of decomposition, rather than exposure time, among regions and leaf species (after Hladyz *et al.*, 2010; Riipinen *et al.*, 2010). The retrieved leaf litter was frozen at $-20\,°\mathrm{C}$, and subsequently oven-dried at 105 °C, with a subsample combusted at 550 °C to calculate ash-free dry mass (AFDM).

Litter decomposition rates were expressed as the exponential decay rate coefficient, k, in the model $(m_t/m_0) = \mathrm{e}^{-kt}$, where m_0 is the initial AFDM and m_t is AFDM at time t (Boulton and Boon, 1991). Both types of rate coefficient were calculated for total decomposition in the coarse-mesh bags (k_{total}) and for microbial decomposition in fine-mesh bags ($k_{\mathrm{microbial}}$). Invertebrate-mediated decomposition was calculated as the difference between percent mass remaining in coarse-mesh and fine-mesh bags, and this was also then converted to a decomposition coefficient (k_{invert}; after McKie *et al.*, 2006). Finally, a dimensionless metric was calculated as the ratio of invertebrate-mediated decomposition coefficient to microbial decomposition coefficient (i.e. $k_{\mathrm{invert}}/k_{\mathrm{microbial}}$). To correct for potential temperature differences among streams and regions, t was also expressed in terms of thermal sums (degree days).

B. Tier II. Irish Field Experiments and Surveys: Decomposition, Algal Production and Herbivory Rates and Community Structure in Nine Pasture Streams

The same source of air-dried oak litter that was used in the pan-European field experiment was employed in the subsequent Irish studies described below (Tiers II–IV, inc.), to provide a standardised detrital resource base for comparative purposes. In addition, senescent grass litter was collected from the banks of each stream and used in the Irish trials to examine the effects of local differences in resource quality. Litter was weighed to 5.00 ± 0.25 g per ‘coarse’ or ‘fine’ mesh bag, as described for the RIVFUNCTION trial. Each grass litter pack was tied into a cylindrical bundle using two cable ties, to mimic natural benthic ‘litter-packs’.

The extensive field experiments and surveys that comprised the Tier II study in nine Irish streams were carried out in winter (November–December) 2003 and spring (April–May) 2004, to coincide with the seasonal peaks in leaf litter inputs and algal production, respectively. Streams were standardised as far as possible to fall within the same criteria for physical characteristics used in the RIVFUNCTION study: that is, all nine streams were 1st–2nd order, <5 m wide, with stony substrata. The streams were chosen to span a gradient of agricultural activity, from unimproved rough pasture (in the six northern sites in Co. Mayo) to improved pasture. All catchments were dominated by pasture ($>90\%$ areal coverage), as is typical of much of Ireland. Three of the less agriculturally productive sites in Co. Mayo (Srahrevagh, Goulaun and Yellow) were also used previously in the Tier I RIVFUNCTION experiments. The three additional Clare Island sites, also in Co. Mayo, are located in a very low density agricultural area (approx. 7.8 people km^{-2}) of high conservation value (Guiry *et al*., 2007) and, like the three nearby mainland Mayo sites, are rough pasture as is typical of much of the north of the country. The three sites in Cork were more productive, improved pasture with higher densities of livestock, which is typical of the southern counties: that is, overall, the nine sites represented a general gradient of increasing agricultural intensity (Clare Island → Mayo → Cork) (Table 3).

Conductivity and pH were measured in the field and filtered (0.7 μm pore size) water samples were analysed in the laboratory for a suite of chemical variables (Table 3): all nine streams were pH >7, with similar temperature ranges, and all were below the median values of SRP for Europe (Figure 5) and not showing any obvious signs of organic pollution. Stream temperatures were measured continuously throughout the experiment using data loggers (ACR Systems Inc., BC Canada).

Nine replicate leaf bags were used per stream in a nested, randomised block design (i.e. 2 mesh types $\times$ 2 litter types [oak/local grass] $\times$ 9 replicates $\times$ 3 streams $\times$ 3 regions $\times$ 2 seasons $=$ 648 litter bags). After 28 days exposure the bags were collected and frozen at $-20°$ C. After thawing, invertebrates were separated from the litter in the laboratory (using a 500-μm sieve), preserved in 70% ethanol, assigned to functional feeding groups (after Cummins and Klug, 1979) and counted. The remaining litter was processed and decomposition rates calculated as described for the RIVFUNCTION study above.

Resource quality of the different litter types was assessed by measuring initial C:N:P ratios and lignin and cellulose content of oven-dried litter (Table 4). Samples were ground into a fine powder (Culatti DFH48 mills, 1 mm screen), and carbon and nitrogen content was determined using a Perkin Elmer Series II CHNS/O analyser. Phosphorus was determined spectrophotometrically at 700 nm, after mixed acid digestion (15 min at 325 °C; Allen 1989). C:N:P ratios were expressed as molar ratios, whereas lignin and cellulose concentrations were determined gravimetrically (after Gessner, 2005).

Table 3 Geographical co-ordinates and physicochemistry of the nine Irish pasture streams over two seasons (winter 2003/spring 2004)

Region	Stream	Stream code	Longitude °W	Latitude °N	Temp. (°C)	TON (μg L^{-1})	NH$_4$ (μg N L^{-1})	SRP (μg L^{-1})	pH	Conduc. (μS cms^{-1})
Clare Island	Bunnamohaun	Bu	−10.04	54.80	6.5/10.9	181/218	15/8	4/4	8.11/8.05	471/579
	Owenmore	Ow	−10.01	53.79	6.6/10.5	103/73	11/21	1/5	8.06/7.92	245/343
	Dorree	Do	−9.98	53.81	6.8/11.8	33/99	33/120	2/4	8.02/7.54	220/332
Mayo	Yellow	Ye	−9.55	53.93	6.6/9.3	104/24	11/0	4/2	7.82/7.21	76/91
	Goulaun	Go	−9.58	54.00	6.9/9.7	39/8	19/0	4/<1	7.94/7.05	80/85
	Srahrevagh	Ro	−9.56	53.98	6.2/9.3	68/40	30/4	16/8	8.17/8.01	113/183
Cork	Dripsey	Dr	−8.76	51.97	8.5/9.1	5921/4743	8/10	27/16	7.31/7.46	221/225
	Morning star	Ms	−8.37	52.40	7.8/9.5	2407/1749	16/15	28/32	8.35/8.21	481/463
	Aherlow	Ah	−8.30	52.37	7.1/9.1	2214/1126	18/75	31/47	8.39/8.90	316/288

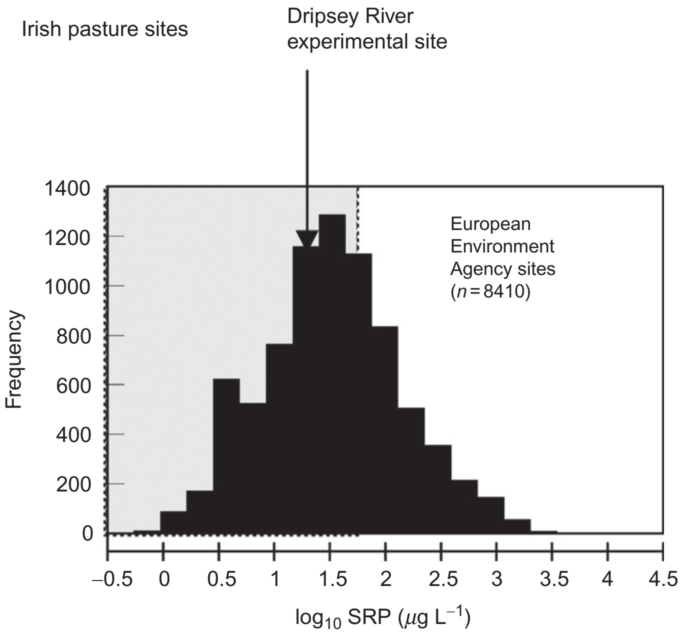


Figure 5 Europe-wide SRP concentrations in 8410 running waters (EEA database), with the range included in the nine Irish pasture streams study (Tier II) delimited by the shaded box bounded within the dashed lines and the position of the Dripsey River focal experimental site (Tier III) highlighted with an arrow.

Algal production and herbivory rates were measured over 28 days exposure of colonisation tiles (10 cm × 10 cm unglazed quarry tiles) attached in pairs to house bricks. The vertical edges of one tile per brick were coated with petroleum jelly to deter crawling gazers, and the other was left as a control, to obtain a proxy measure of grazing pressure (after Hladyz *et al.*, 2011). Algal samples were frozen within 1 h of collection and chlorophyll *a* concentration was determined subsequently using standard spectrophotometric techniques, after overnight ethanol extraction (Jespersen and Christoffersen, 1987).

Nine Surber samples (25 cm × 25 cm quadrat, 500-μm mesh size) were taken per stream per season to quantify benthic invertebrate abundance, and processed as per the litter bags. Invertebrate body mass data were obtained by applying published length–mass regression to linear dimensions (e.g. head capsule width, body length), after Layer *et al.* (2010a,b) measured under a dissecting microscope. A 50-m reach in each of the nine sites was electrofished during the spring sampling period (this could not be done in the winter because these sites were subject to legal protection at this time), using

Table 4 Measures of resource quality for grass and oak litter (mean ± S.E.) used in the Irish studies (Tiers II–IV as described in Section II)

Region	Stream code	Litter	%C	%N	%P	C:P	C:N	N:P	% lignin	% cellulose
Cork		Oak	49.00	2.24	0.11	1122	26	44	40.5 ± 0.7	31.1 ± 1.0
Clare Island	Bu	Grass	40.52 ± 4.39	1.04 ± 0.11	0.04 ± 0.02	4389 ± 2917	47 ± 10	85 ± 45	8.7 ± 0.6	36.0 ± 1.3
	Do		41.68 ± 1.90	1.22 ± 0.28	0.05 ± 0.04	5048 ± 3923	43 ± 12	101 ± 65	11.8 ± 0.4	42.7 ± 3.5
	Ow		42.84 ± 2.57	1.36 ± 0.22	0.06 ± 0.00	1706 ± 131	37 ± 4	47 ± 8	12.2 ± 2.2	35.7 ± 1.5
Mayo	Go		45.50 ± 0.16	1.13 ± 0.05	0.03 ± 0.02	4735 ± 2497	47 ± 2	99 ± 49	7.8 ± 0.6	36.8 ± 0.6
	Ro		44.40 ± 0.35	1.29 ± 0.24	0.08 ± 0.02	1460 ± 284	42 ± 8	35 ± 0	6.9 ± 0.4	31.8 ± 0.9
	Ye		45.82 ± 0.04	1.25 ± 0.00	0.05 ± 0.01	2468 ± 349	43 ± 0	58 ± 8	11.5 ± 0.8	34.1 ± 1.0
Cork	Ah		45.17 ± 0.30	1.32 ± 0.17	0.07 ± 0.02	1906 ± 615	41 ± 6	46 ± 9	7.1 ± 0.6	35.5 ± 2.0
	Dr		44.21 ± 0.04	1.69 ± 0.34	0.11 ± 0.01	1048 ± 87	32 ± 6	34 ± 4	3.2 ± 0.2	20.5 ± 0.9
	Ms		43.97 ± 1.72	1.65 ± 0.05	0.12 ± 0.02	960 ± 173	31 ± 2	31 ± 3	3.7 ± 0.4	25.4 ± 0.2

three depletion runs between stop-nets (after Bohlin *et al*., 1989). All captured fishes were identified to species, measured (fork length and body mass) and released.

Stable isotope analyses (SIA) of primary consumers and basal resources within each food web were used to assess consumer–resource interactions among regions and between seasons. Five replicates of CPOM, epilithic biofilm and the dominant invertebrate taxa from the main functional feeding groups were collected from each stream during winter and spring sampling for isotopic determination. For instance, the freshwater shrimp *Gammarus duebeni* (Liljeborg) was used as a representative generalist ('shredder-grazer') able to exploit both algae and detrital food chains (cf. Hladyz *et al*., 2011), and the mayflies Heptageniidae and *Baetis* spp. represented 'grazers' (after Cummins and Klug, 1979). SIA samples were frozen within 1 h of collection. The SIA samples were combusted in a PDZ Europa ANCA-GSL preparation model and passed through a PDZ Europa 20–20 stable isotope analyser (PDZ Europa Ltd., Sandbach, UK). Pee Dee Belemnite was used as the standard ratio for C and atmospheric N for N. All isotope values are given in per mille, and standard δ notation is used to describe the relative difference in isotope ratio between the samples and known standards.

C. Tier III. Intensive Experimental Study of Grass Litter Decomposition Within a Single Field Site

In addition to the extensive field experiments carried out in the nine Irish streams, a complementary intensive field trial was carried out in a single site (the Dripsey River), in which we used all nine grass types from the different streams during winter (February–March) 2005 (Table 4). In this experiment, we used coarse and fine-mesh bags in a randomised block design, with five replicates per treatment, which were deployed simultaneously for 28 days to quantify decomposition rates whilst controlling for potential site-specific differences in community composition and physicochemical parameters. The Dripsey River was selected because it was the most nutrient-rich site within the Irish study, and hence had the largest range of potential consumer species that could respond to differences in resource quality, and because it lay closest to the mean, median and modal values for European streams (Figure 5). Consumer abundance and identity were thus controlled for, unlike in the multiple sites study, insofar as each litter bag was exposed to an identical regional pool of potential colonists, so any differences in decomposition rates could be ascribed to differential local-scale responses among the consumers to litter quality: that is, shredders were free to choose which litter type to exploit (cf. Hladyz *et al*., 2009).

D. Tier IV. Laboratory Experiments: Resource Quality and Decomposition Rates

To complement the field experiments and to identify the drivers of decomposition rates under more tightly controlled conditions, we carried out two laboratory experiments that examined the feeding preferences of two detritivore consumers, the caddis larvae *Halesus radiatus* Curtis (Order Trichoptera) and the freshwater shrimp *G. duebeni* Liljeborg (Order Amphipoda), common taxa in Irish pasture streams (e.g. Hladyz *et al.*, 2011). The taxa were offered either a single resource (single-choice) or a choice of the nine types of grass litter resources (multiple-choice) used in the Tier II and III studies, respectively, and we hypothesised that the shredders would feed preferentially on the better quality resources. In general, the more intensively farmed Cork grass litters were characterised by higher %P and %N content, whereas the rough pasture grasses were characterised by higher % lignin and % cellulose. These experiments were designed to complement the previous studies, by focussing on specific drivers and responses: that is, we controlled for consumer species identity and abundance and also the physicochemical environment (temperature, light regime, water chemistry) in order to isolate the effects of resource type *per se*.

The first (Tier IVa) of these laboratory experiments measured consumer preference of grass litter (multiple-choice trials) using 60 L mesocosms. In this study, 3 g (±0.25 g) of air-dried grass litter from all nine sites was preconditioned for 2 weeks in Dripsey River water and subsequently added to arenas containing different consumer assemblages (monocultures which consisted of either 90 *Gammarus* individuals or 90 *Halesus* individuals and a microbial-only control treatment) in a C–T room at 10 °C. Five replicate arenas were used per consumer treatment and in each arena a paired control of each grass litter type was used to assess microbial-only decomposition (grass litter enclosed in 500-μm fine-mesh bag versus the equivalent litter in a coarse-mesh bag). The experiment ran for 2 weeks after the initial preconditioning period, over the same period as the Dripsey River field experiment (Tier III). The mesocosms were examined daily for dead animals, which were removed and replaced. Survival rates were between 89% and 93% for *Gammarus* and *Halesus*, respectively. At the end of the trial, invertebrates were separated from the litter, and litter was dried to constant mass at 105 °C and decomposition rates, $-k$, were calculated for each replicate.

The second (Tier IVb) laboratory trial was carried out using standardised consumer assemblages composed of 10 individuals of either the cased caddis *Halesus* or the freshwater shrimp *Gammarus*, in which we measured decomposition rates of grass litter and oak litter in 1 L microcosms (after McKie *et al.*, 2008; single-choice trials). Grass or oak litter were air-dried to constant mass, weighed to 3 g (±0.25 g), and then one of each of the 10 resource types (nine grasses, or oak) was conditioned in streamwater collected from the Dripsey River in each microcosm for 2 weeks, prior to the introduction of the invertebrates (five replicates of each). The entire study was conducted in a C–T room at 10 °C under a 12-h light:dark regime for 2 weeks after the initial conditioning period. Microcosms were examined daily for dead animals, which were removed and replaced. Survival rates over the duration of the trial were 88% and 91% for *Gammarus* and *Halesus*, respectively. At the end of the trial, invertebrates were removed and the remaining litter was oven-dried to constant mass at 105 °C and a decomposition rate, *k*, was calculated for each microcosm.

1. Statistical Analyses

Two analyses were performed on the RIVFUNCTION Tier I dataset: first, we examined differences in decomposition coefficients and ratios between impact and reference streams among regions. We then tested for differences in decomposition coefficients and ratios between pasture streams and other riparian impacts. Linear mixed effects models (LMEM) were used to account (i) for the hierarchical nature of the experimental design, with litter bags nested within individual streams and streams nested within pairs and (ii) for the incorporation of both fixed and random effects in the design. The following variables were fitted as fixed effects in the analyses: region, impact, leaf species and mesh type. We treated region as a fixed effect in the following analyses: regions were chosen *a priori* to include the different types of the major riparian alteration impacts commonplace across Europe, and they also represented the main ecoregions defined within the WFD. Streams and stream pairs were fitted as random effects. Since our experimental design was unbalanced because of the loss of some litter bags during field exposure, we used the restricted maximum likelihood method (REML) to estimate error terms (after Hladyz *et al.*, 2011). The optimal model structure was determined using the hypothesis testing approach (e.g. likelihood ratio test) following the mixed effects model selection procedure outlined in Zuur *et al.* (2009). Pairwise comparisons on main fixed effects were performed using Bonferroni *post hoc* tests. Decomposition coefficients and ratios were $\log_{10}$ transformed to normalise the data. If homogeneity was violated separate LMEMs analyses were carried out. The statistical analyses were performed with PASW Statistics Version 18.0 (SPSS Inc., Chicago, IL).

In the Irish Tier II study, decomposition rates, algal production and grazing rates and invertebrate abundances in the extensive field trial were analysed using LMEMs and also partial least squares (PLS) regression (after Eriksson *et al.*, 1999). In the former, region and season were fitted as fixed effects in all analyses. We treated region as a fixed effect in these analyses as we were interested in examining differences among the regions which represented a general gradient of increasing agricultural intensity (Clare

Island → Mayo → Cork). In addition the decomposition rates analysis included litter type and mesh type and the algal production analysis included grazing treatment. Sample-units and streams were fitted as random effects. REML was used to estimate error terms due to our unbalanced designs as a result of losses of a few litter-bags or tiles in the field. Data were $\log_{10}$-transformed (or $\log_{10}x+1$ where zero counts were present) to meet the assumptions of the tests, where appropriate.

Relationships between ecosystem process rates and water chemistry variables and/or resource quality and/or biotic variables were examined using PLS regression. PLS extracts components from a set of variables which, as in principal components analysis, are orthogonal and so eliminates multi-colinearity. In addition, PLS maximises the explained covariance between the variables. The constructed components are used to create a model for the response variable with the relative importance of the predictor variables ranked with variable importance on the projection (VIP) values (Eriksson *et al.*, 1999). The VIP values reflect the importance of terms in the model both with respect to y and with respect to x (the projection). VIP is normalised and the average squared value is 1, so terms in the model with a $\text{VIP} > 1$ are important. PLS analyses were conducted using SIMCA-P (version 11.5; Umetrics AB, Umeå, Sweden). Additional components were extracted until the increase in explained variance fell below 10%.

Multi-variate analyses of water chemistry, resource quality and community structure among regions was analysed using PRIMER 6 (v 6.1.13) and PERMANOVA (v.1.0.3) (PRIMER-E Ltd., Plymouth, UK) (after Anderson *et al.*, 2008). PERMANOVA is more robust than MANOVA since calculations of P-values are via permutations, thus avoiding the assumption of data normality. To visualise patterns evident from PERMANOVA, we used metric multi-dimensional scaling, principal coordinate analysis (PCO), which is an unconstrained ordination method. In order to highlight patterns in the PCO, we used vectors based on Spearman correlations (greater than 0.5 to target variables with high correlations) which highlights the overall increasing or decreasing relationships of individual variables across the plot ignoring all other variables.

Carbon isotope signatures of biofilm and terrestrial detritus were overlapping in many of our streams or were outside the limits of the consumer isotope signatures, so we were unable to use mixing models to discern their relative contributions to diet. Instead of using mixing models the δ^{13}C signatures for consumers were related to values of biofilm and CPOM via PLS regression analysis with both biofilm and CPOM used as predictor variables on consumer signatures.

The data from the Tier III field experiment study was analysed with PLS regression. In the laboratory studies for the multi-choice treatments (Tier IVa), we evaluated food preferences (using untransformed decomposition rates, $-k$)

Table 5 pan-European RIVFUNCTION field experiment (Tier I): Linear mixed effects model results of comparisons of standard (k_d) and temperature-normalised (k_{dd}) decomposition rate coefficients of litter in coarse-mesh and fine-mesh bags among regions and impacts

			F-ratio	
Comparison	df_N	df_D	$\log_{10} k_d$	$\log_{10} k_{dd}$
Region	9	39.98/39.56	10.30***	29.36***
Impact	1	39.64/39.17	0.053^{ns}	0.012^{ns}
Mesh	1	251.67/251.81	776.58***	748.29***
Leaf	1	252.59/252.77	805.21***	587.31***
Impact × mesh	1	251.67/251.81	10.64**	10.48**
Region × impact	9	39.52/39.05	1.22^{ns}	2.50*
Impact × leaf	1	252.31/252.48	0.823^{ns}	0.611^{ns}
Region × mesh	9	251.67/251.81	12.51***	11.97***
Mesh × leaf	1	251.67/251.81	3.89^{ns}	3.84^{ns}
Region × leaf	9	252.44/252.61	14.24***	13.23***
Region × impact × mesh	9	251.67/251.81	3.12**	3.04**
Region × mesh × leaf	9	251.67/251.81	2.55**	2.45*

Non-significant interactions and parameters omitted. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns: $P > 0.05$.

using Friedman's test, which is based on ranks (after Canhoto *et al.*, 2005) and also analysed decomposition rates using PLS regression. In the single-choice treatment (Tier IVb), where consumers were presented with only a single resource type, decomposition rates ($-k$) were analysed using PLS regression.

III. RESULTS

A. Tier I. RIVFUNCTION Field Experiment: Impacts of Riparian Alterations on Decomposition Rates in 100 European Streams

Decomposition rates differed among regions, mesh types and leaf types, with faster decomposition in coarse mesh and for alder litter (Table 5; Figure 6). There was no main effect of riparian alterations *per se*, but there were significant two-way and three-way interactions, indicating that these impacts were contingent upon other factors. For instance, the impact × mesh interaction revealed that decomposition rates were similar for fine mesh between treatments whereas for coarse-mesh rates were generally faster in reference streams than in impacted streams. After correction for temperature effects all significant effects remained and regional differences actually increased,

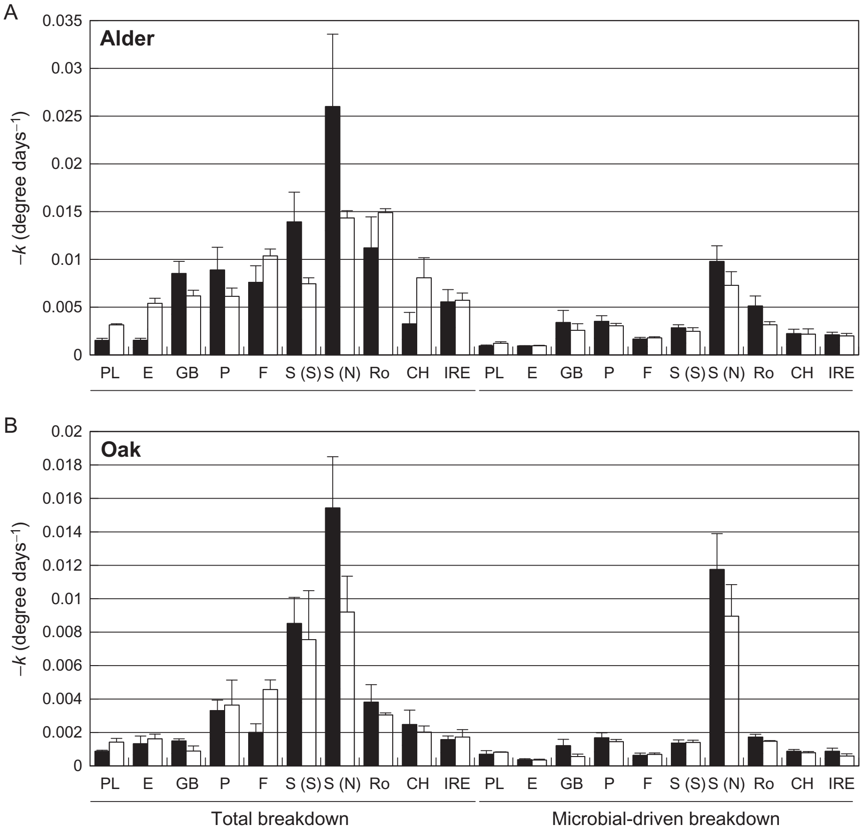


Figure 6 Tier I: Impacts of anthropogenic alterations to riparian zones on alder (A) and oak (B) litter decomposition rates in 100 European streams across 10 regions in nine countries, grouped by type of alteration. Portugal (PL) and Spain (E) impacted sites were invaded by *Eucalyptus* spp.; Great Britain (GB) and Poland (P) were impacted by conifer plantations; France (F) and southern Sweden (S (S)) were impacted by replacement of native forest with beech (*Fagus sylvatica*) plantations and four sites had their native riparian woodland cleared for forestry (northern Sweden (S (N))) or pasture (Romania (Ro), Switzerland (CH) and Ireland (IRE)). Shaded bars represent impacted streams, white bars denote reference streams (means per region ± S.E.).

suggesting that these were not simply due to variation in latitudinal or altitudinal thermal regimes. The region × impact interaction further highlighted the regional contingency, which might reflect differences in the type of impact and/or consumer communities (Table 5). Invertebrate:microbial decomposition rates differed among regions and were lower in impacted versus reference streams, although this outcome was also dependent upon region (Table A1).

The subsequent analysis between pasture land use and other riparian impacts revealed faster decomposition rates in pasture streams than in streams

Table 6 pan-European RIVFUNCTION field experiment (Tier I): Linear mixed effects model results of comparisons of standard (k_d) and temperature-normalised (k_{dd}) decomposition rate coefficients of litter in coarse-mesh and fine-mesh bags between pasture and other riparian impacts

			F-ratio	
Comparison	df_N	df_D	$\log_{10} k_d$	$\log_{10} k_{dd}$
Impact	1	48.16/±	4.49*	
Mesh	1	145.03/145.99	177.32***	177.55***
Leaf	1	145.79/146.32	208.31***	164.67***

±, non-significant interactions and parameters omitted. *$P < 0.05$; ***$P < 0.001$.

subjected to other types of riparian impact (Table 6). Decomposition was also fastest for alder litter and coarse-mesh bags. After correcting for temperature effects, the differences between pasture streams and streams subjected to other riparian impacts became non-significant (Table 6). Invertebrate:microbial decomposition rates were lower in pasture streams compared with streams subjected to other riparian impacts (LMEM F df_{N1} $df_{D48.43} = 6.87$, $P < 0.05$), but there was no differences between oak and alder litter.

B. Tier II. Irish Field Experiments and Surveys: Decomposition, Algal Production and Herbivory Rates and Community Structure in Nine Pasture Streams

1. *Tier II.i. Chemical Characteristics of Regions*

Physicochemical parameters (SRP, TON, NH_4, pH and conductivity) differed among streams, revealing a general gradient of agricultural intensity: the first axis of a PCO explained 59.5% of the chemical data and was associated with SRP, TON, pH. The second axis explained a further 18.7% and was associated with TON and NH_4 (Figure 7A).

2. *Tier II.ii. Ecosystem Functioning: Detrital Pathways*

The spring grass resource quality measures (%C, %N, %P, % lignin and % cellulose) differed among streams (Figure 7B). This separation was evident on the first axis of an associated PCO which explained a total of 91.8% of the variation in the resource quality matrix. In general, the more intensively farmed

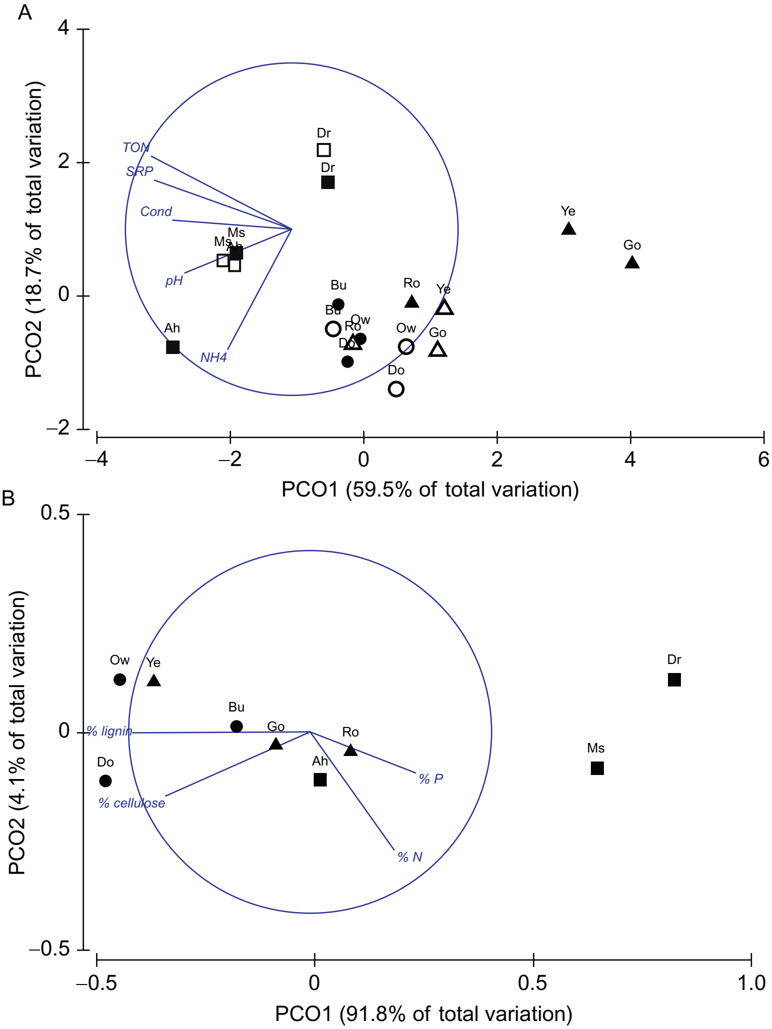


Figure 7 Tier II: PCO of physicochemical variables among Irish pasture streams for two seasons (A) and PCO of grass resource quality variables among Irish pasture streams in spring (B). Open symbols denote winter and closed denote spring. Squares denote Cork streams, triangles denote Mayo streams and circles denote Clare Island streams, respectively. Vector overlay denotes Spearman correlations, showing vectors longer than 0.5 in length (see Section II). Labels denote stream names; Bu, Bunnamohaun; Ow, Owenmore; Do, Dorree; Ye, Yellow; Go, Goulaun; Ro, Srahrevagh; Dr, Dripsey; Ms, Morning Star; Ah, Aherlow.

Table 7 Irish multiple sites field experiments (Tier II): Linear mixed effects model results of comparisons of standard (k_d) and temperature-normalised (k_{dd}) decomposition rate coefficients of litter in coarse-mesh and fine-mesh bags among regions and between seasons

				F-ratio	
Comparison	Mesh size	df_N	df_D	$\log_{10} k_d$	$\log_{10} k_{dd}$
Region	C	2	5.99	3.44^{ns}	2.72^{ns}
Leaf	C	1	298.00/296.00	33.30***	33.71***
Season	C	1	298.06/296.06	152.24***	81.75***
Region × leaf	C	2	298.00/296.00	5.30**	5.40**
Region × season	C	2	±/296.06		3.43*
Leaf	F	1	282.33/282.32	260.73***	261.12***
Season	F	1	282.40/282.39	77.75***	34.99***

±, non-significant interactions and parameters omitted. $*P<0.05$; $**P<0.01$; $***P<0.001$; ns: $P>0.05$.

Cork sites were characterised by higher %P and %N content, whereas the rough pasture grasses were characterised by higher % lignin and % cellulose.

In general, litter decomposition in coarse and fine-mesh bags was fastest in spring and for grass litter (Table 7; Figure 8). For coarse-mesh bags, there was no main effect of region, though there was a significant interaction with region × litter type: oak decomposition in Cork streams was 3.7× and 2.4× faster than in Mayo and Clare Island streams, respectively; whereas for grass litter these regional differences were about 30% less marked. Microbial-only decomposition did not differ among regions. After correcting for temperature effects, seasonal differences were reduced but still significant for both coarse and fine-mesh bags (Table 7). The ratio of $k_{invert}/k_{microbial}$ was highest in spring and on oak litter, with no main effect of region (LMEM Season, F df_{N1}, $df_{D25} = 5.02$, $P < 0.05$, Leaf, F df_{N1}, $df_{D25} = 52.15$, $P < 0.001$; Figure 8). PLS regression revealed that in winter grass decomposition in coarse mesh was driven by litter quality (e.g. C:P, %P) and shredder abundance; whereas, in spring, abiotic variables (e.g. pH, SRP, TON) were also significant in addition to the previously mentioned drivers in winter (Table 8; Figures 9 and 10A). Similar patterns occurred with oak litter decomposition in coarse-mesh bags, with shredders being important drivers in winter and the same abiotic variables (e.g. pH, SRP, TON) primarily associated in spring (Table 8; Figures 9 and 10A). For fine mesh, a combination of abiotic and resource quality attributes were important for grass litter decomposition in both seasons (e.g. temperature, pH, N:P). For oak litter, SRP and temperature in winter and TON in the spring, respectively, were important for decomposition rates (Table 8). Correcting for temperature effects in general

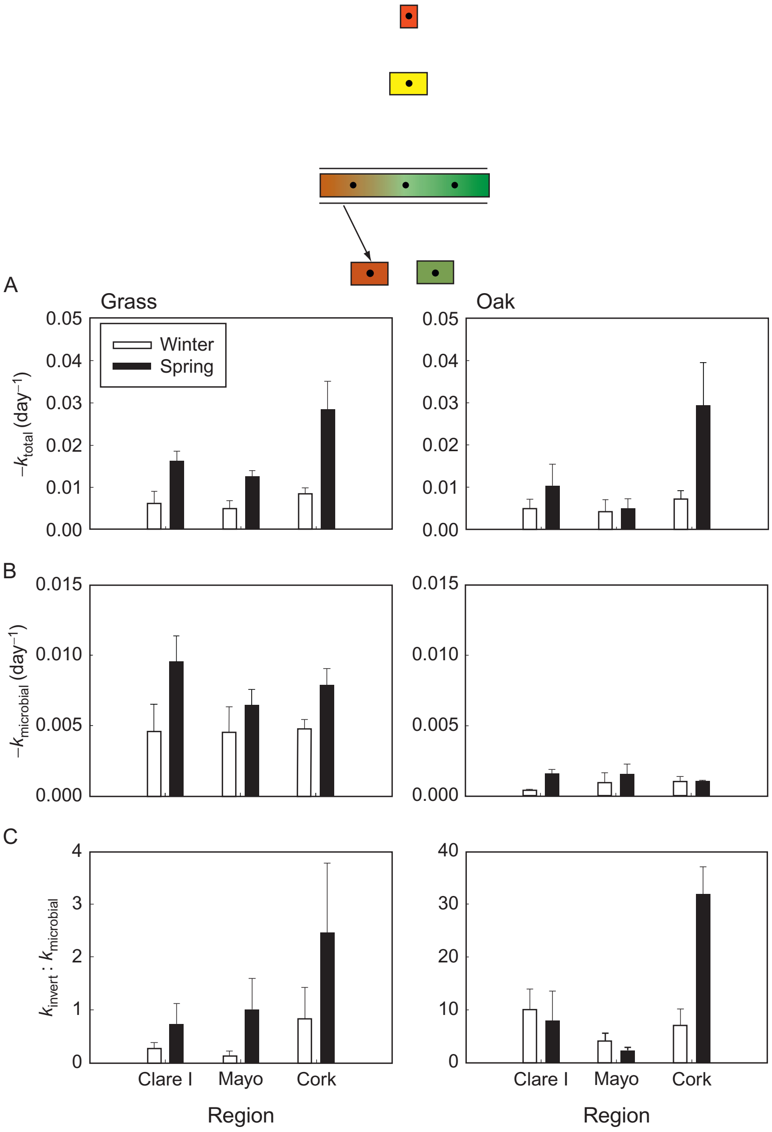


Figure 8 Tier II. Grass and oak litter decomposition among Irish pasture streams in winter and spring: (A) total decomposition rates (coarse mesh), (B) microbial decomposition rates (fine mesh), (C) ratio of invertebrate-mediated to microbial decomposition rates. Individual values were averaged using streams as replicates and data presented show mean values of streams ± 1 S.E.

Table 8 Summary table of partial least-squares (PLS) regression output for litter decomposition rates ($-k_d$) from Irish large-scale field (Tier II) trials, Irish single site field experiment (Tier III) and laboratory trials (IVa,b) (see Tables A2, A3, A10–A12 for VIP, slope for all variables and k_{dd} results when applicable)

Tier	Response	Season	Variables[a]	R^2Y
II	Grass total	Winter	C:P, %P, N:P, B.ShrA, %Gra, %N, C:N, Temp., %Pre	0.93
		Spring	pH, SRP, Grass Shr g^{-1}, TON, N:P, C:P, Temp., %P	0.77
	Oak total	Winter	Oak Shr g^{-1}, B.ShrA	0.81
		Spring	pH, SRP, Oak Shr g^{-1}, TON	0.83
	Grass microbial	Winter	Temp, N:P, %P, C:P	0.85
		Spring	pH, Temp., %C, TON, N:P, conduc.	0.87
	Oak microbial	Winter	SRP, Temp., conduc.	0.72
		Spring	TON	0.33
III	Grass total		Lig, cell, Shr g^{-1}, N:P	0.87
	Grass microbial		Lig, cell, N:P	0.84
IVa	*Halesus*		Lig, cell, N:P, %P	0.72
	Gammarus		Lig, cell, N:P	0.77
	Microbes		Lig, cell, N:P	0.84
IVb	*Halesus*		Lig, N:P, cell, C:P, %P	0.52
	Gammarus		Lig, N:P,%P, cell, C:P	0.72
	Microbes		Lig, %P, N:P, cell, C:P	0.79

[a] Predictor variables: *biotic attributes*: fish biomass (spring only; FishB), fish abundance (spring only; FishA), invertebrate biomass (spring only; InvB), Grass shredders g^{-1} (Grass only), Oak shredders g^{-1} (Oak only), benthos shredder abundance (B.ShrA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4. *Resource quality attributes* (Grass only): %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

did not markedly increase the amount of explained variance in decomposition rates (Tables A2 and A3).

Shredder abundance g^{-1} litter was highest in spring (LMEM F df_{N1} $df_{D146.69} = 19.93$, $P < 0.001$). There was no main effect of region (LMEM F df_{N2} $df_{D6.00} = 2.21$, $P > 0.05$) or litter type (LMEM F df_{N1} $df_{D151.68} = 0.198$, $P > 0.05$) but there were significant two-way interactions with region × leaf (LMEM F df_{N2} $df_{D151.63} = 6.38$, $P < 0.01$) and region × season (LMEM F df_{N2} $df_{D146.67} = 11.95$, $P < 0.001$): Cork streams had higher abundances on oak litter than Clare Island and Mayo streams; whereas, grass litter abundances were similar among regions. Cork streams had higher abundances in spring than Clare Island and Mayo streams; whereas, in winter, abundances were similar among regions, as revealed by a region × season interaction.

Invertebrate assemblages g^{-1} litter varied among sites, seasons and litter types (Table A4; Figure A1). The shredder guild in the Mayo streams were

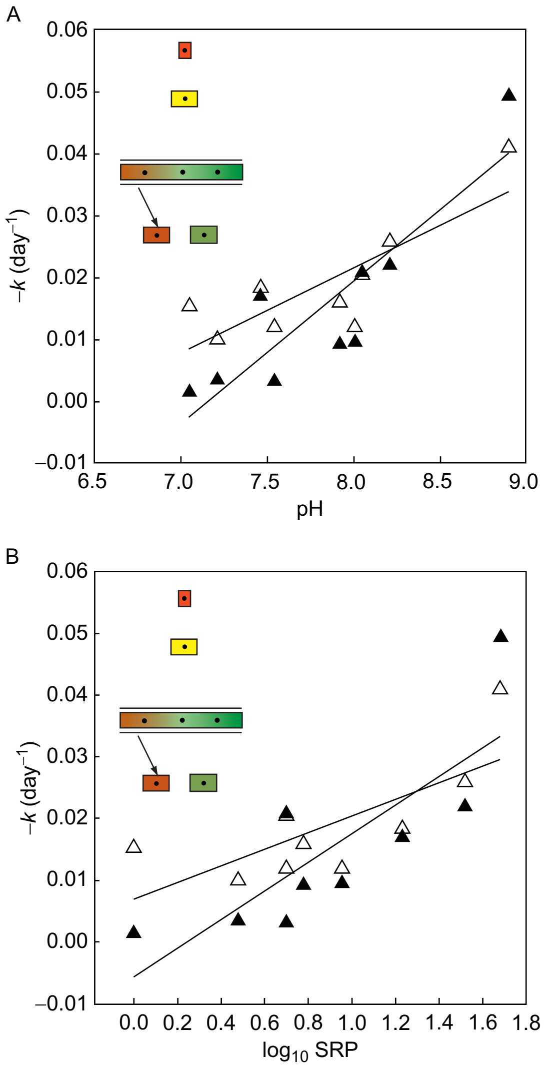


Figure 9 Tier II: Bottom-up effects of pH (A) and SRP on litter decomposition rates in spring ($-k_{d\text{total}}$) in Irish pasture streams (B). Figures denote linear relationships of daily litter decomposition and two measures of stream water chemistry (pH and SRP) for the nine Irish pasture streams (closed triangle denotes oak litter decomposition rates; SRP, $r^2 = 0.65$, $P < 0.01$; pH, $r^2 = 0.77$, $P < 0.01$; open triangle denotes grass litter decomposition rates; SRP, $r^2 = 0.54$, $P < 0.05$; pH, $r^2 = 0.66$, $P < 0.01$).

characterised by mostly stonefly species (e.g. from the genera *Leuctra*, *Protonemura* and *Amphinemura*) whereas Cork streams were distinguished by a range of shredder consumers (e.g. Limnephilidae caddis larvae, *Gammarus* spp.

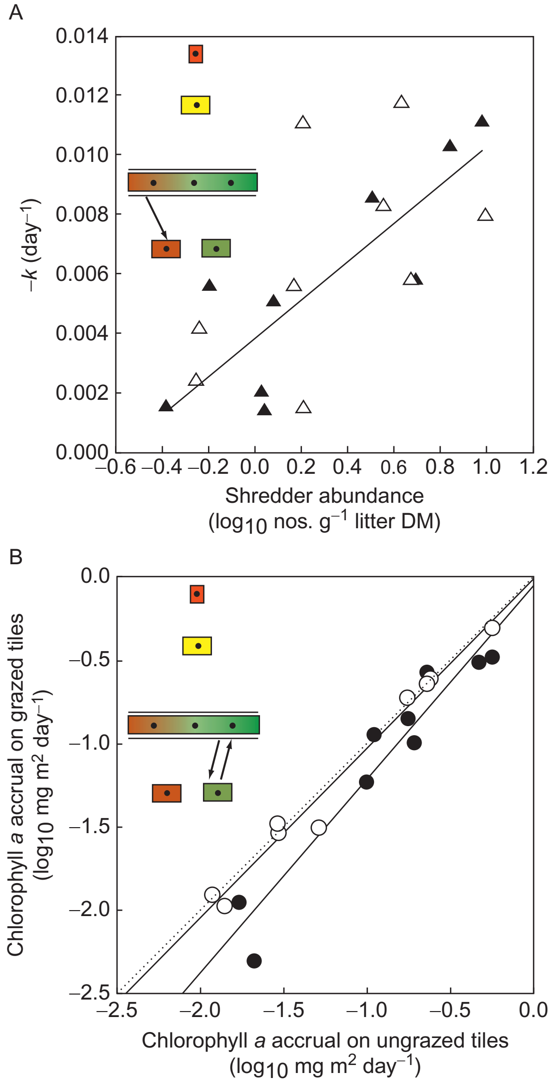


Figure 10 Tier II: Top-down effects of primary consumers on decomposition rates in winter (A) (closed triangle; Oak $r^2 = 0.71$, $P < 0.01$, open triangle; Grass non-significant as a bivariate relationship in winter, as depicted here, although it is a significant predictor in PLS regression during spring; Table 8) and direct top-down effects of primary consumers on chlorophyll production (B): distance below the 1:1 line reveals the strength of herbivory. Daily chlorophyll *a* production in nine streams for two seasons. Open circles denote winter values, closed circles denote spring values.

Table 9 Irish multiple sites field experiments (Tier II): Linear mixed effects model results of comparisons of standard (A_d) and temperature-normalised (A_{dd}) algal production ($\log_{10}$ chlorophyll *a* mg m^{-2}) on grazed and ungrazed tiles among regions and between seasons

			F-ratio	
Comparison	df_N	df_D	$\log_{10} A_d$	$\log_{10} A_{dd}$
Region	2	6.04/6.04	15.36**	18.07**
Treatment	1	150.00/150.00	38.93***	38.93***
Season	1	144.12/142.13	8.50**	0.17^{ns}
Region × treatment	2	150.00/150.00	3.80*	3.80*
Treatment × season	1	150.00/150.00	13.50***	13.50***
Region × season	2	±/142.13	±	4.95**

±, non-significant interactions and parameters omitted. *$P<0.05$; **$P<0.01$; ***$P<0.001$; ns: $P>0.05$.

Table 10 Summary of table of partial least-squares (PLS) regression output for algal tiles and ratio from Irish large-scale field trial (Tier II) (A_d) (see Table A5 for VIP, slope for all variables and A_{dd})

Tier	Response	Season	Variables[a]	R^2Y
II	Grazed tiles	Winter	%Pre, conduc., %Gra	0.67
		Spring	%Gra, Temp., %Pre	0.78
	Ungrazed tiles	Winter	%Pre, %Gra, conduc., Temp.	0.65
		Spring	%Gra, Temp., B.GraA	0.87
	Ungrazed: Grazed	Winter	B.GraA, conduc.	0.93
		Spring	B.GraA, FishA, conduc., NH_4, TON	0.85

[a] Predictor variables: *biotic attributes*: fish biomass (spring only; FishB), fish abundance (spring only; FishA), invertebrate biomass (spring only; InvB), benthos grazer abundance (B.GraA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4.

amphipods), with Clare Island streams being intermediate between the two (Figure A2).

3. *Tier II.iii. Ecosystem Functioning: Algal Pathways and Herbivory*

Algal production increased across the gradient of agricultural intensity (Clare Island < Mayo < Cork) and was highest on ungrazed tile surfaces and in spring (Table 9; Figure 10B). A significant season × grazing treatment interaction revealed that the proportion of production consumed was lower in

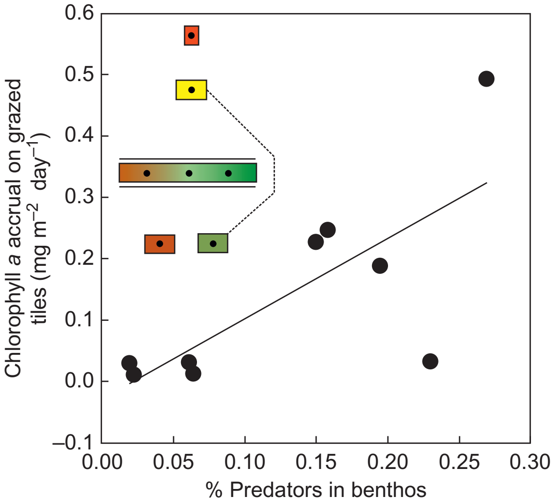


Figure 11 Tier II: Potential for indirect food web effects on ecosystem processes—algal production on grazed tiles versus invertebrate predator relative abundance in winter ($r^2 = 0.54$, $P < 0.05$).

spring (70.3%) than in winter (93.2%). After correcting for temperature effects, however, the main effect of season was no longer significant, although its interactions were. There was also a region × grazing treatment interaction, with Mayo (92.1%) streams having markedly higher proportions of production consumed compared with Cork (71.6%), with both regions having a high supply rate, and Clare Island streams, which had both low supply and consumption rates (59.7%). PLS regressions indicated the importance of the invertebrate community in relation to algal accrual on tiles, with % grazers in the benthos in spring (negative association) and % invertebrate predators (positive association) in the winter being significant predictors (Table 10; Figure 11; Table A5), with stream conductivity and temperature being significant abiotic drivers (Table 10; Table A5). Important variables predicting the ratio of algal accrual on ungrazed:grazed tiles were grazer and fish abundance, conductivity, NH_4, and TON (Table 10; Table A5).

4. Tier II.iv. Community Structure and Ecosystem Functioning: Effects of Consumer Assemblages

The composition and absolute abundances of the invertebrate assemblages in the benthos differed among sites, as revealed on the PCO (Table A6; Figure A3). Benthic abundances of shredders were highest in spring (LMEM F df_{N1} $df_{D150} = 14.26$, $P < 0.001$), and no main effect of region was evident (LMEM F df_{N2} $df_{D6} = 1.34$, $P > 0.05$). There was, however, a significant

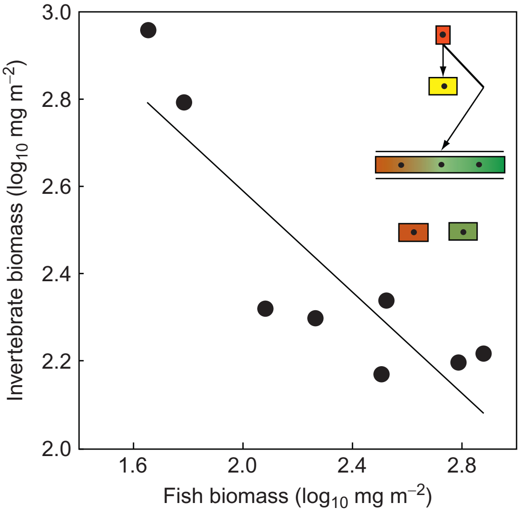


Figure 12 Tier II: Potential top-down food web effects: invertebrate biomass versus fish biomass ($r^2 = 0.77$, $P < 0.01$).

season × region interaction (LMEM F df_{N2} $df_{D150} = 5.76$, $P < 0.01$): Cork streams had higher abundances than the other sites in spring, whereas abundances in winter were more similar among regions, and the same was true for grazers (LMEM F df_{N2} $df_{D150} = 5.26$, $P < 0.01$). There was, however, no main effect for region (LMEM F df_{N2} $df_{D6} = 0.83$, $P > 0.05$) or season for grazers (LMEM F df_{N1} $df_{D150} = 0.87$, $P > 0.05$). Invertebrate biomass declined as fish biomass increased, suggesting the potential for top-down control of the former by the latter (Figure 12; Table A7) and invertebrate-mediated decomposition for oak litter was also reduced as fish biomass increased (negative association; Figure 13A; Table A8). Fish abundance was also an important predictor of herbivory on the algal tiles: invertebrate grazing pressure declined as fish biomass increased (Table 10; Figure 13B).

The mass–abundance scaling plots of the consumer communities revealed that the general direction of energy flux in the food web was smaller, more abundant taxa to larger, rare and less diverse consumers. The number of nodes increased across the gradient of agricultural intensification, particularly among the higher trophic levels (i.e. the predatory fishes), which were more prevalent in the Cork sites and least so in the rough pasture streams on Clare Island, one of which was the only fishless stream (Figure 14).

The stable isotope data were highly variable among streams (Figure 15). PLS regression confirmed that the grazing mayflies *Baetis* spp. and Heptageniidae fed mostly on algal biofilm (Table A9). In contrast, one of the dominant consumers, *Gammarus* spp., appeared to exploit both biofilm and

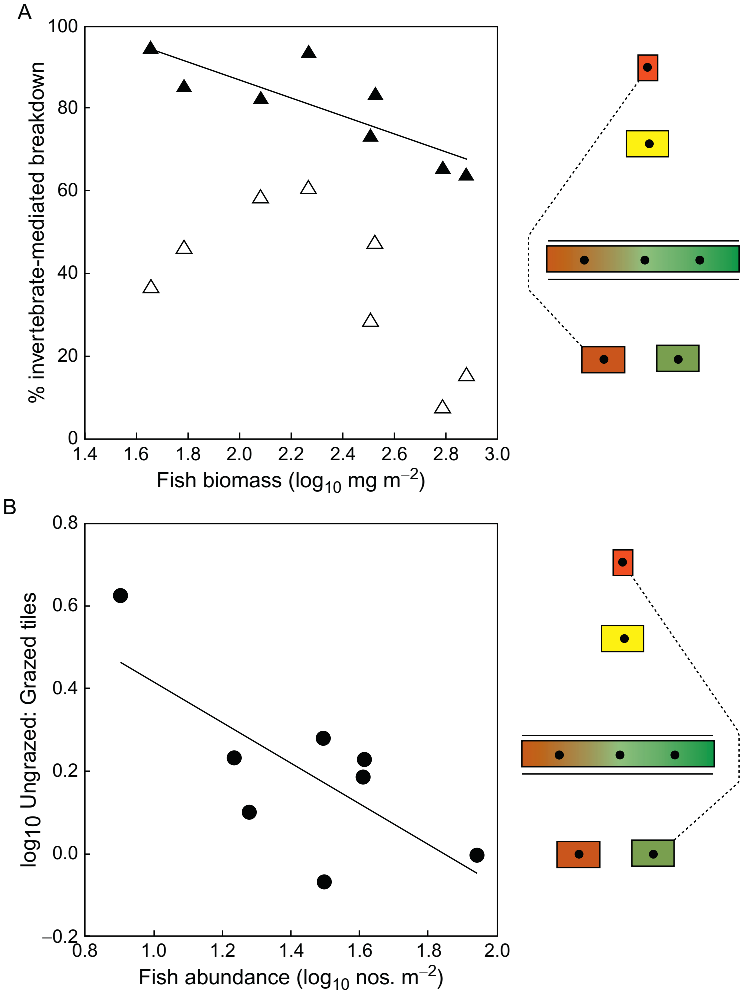


Figure 13 Tier II: Potential cascading indirect (e.g. mediated via fish predation on invertebrate predators) top-down effects: (A) detritivory versus fish biomass (closed symbols denote oak decomposition rates, $r^2 = 0.68$, $P < 0.05$; open symbols denote grass decomposition rates, non-significant as a bivariate relationship, as depicted here, although it is a significant predictor in PLS regression; Table A8) and (B) invertebrate algal grazing versus fish abundance ($r^2 = 0.52$, $P < 0.04$).

CPOM (cf. Hladyz *et al.*, 2011) as revealed by the close match to the 1:1 line (assuming no carbon fractionation; after Nyström *et al.*, 2003), with the latter being more important in the winter and the former in the spring, tracking changes in resource availability (Figure 15; Table A9).

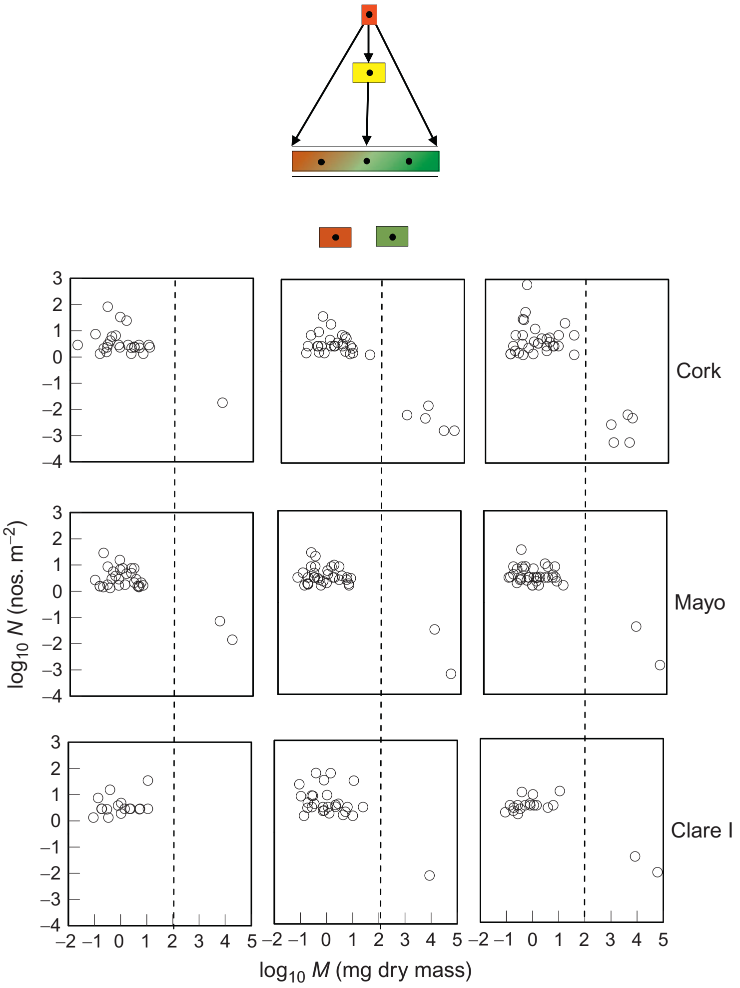
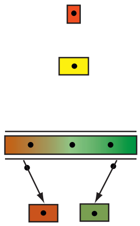


Figure 14 Tier II: Food web structure in the nine food webs, showing mass–abundance scaling relationships among fish and invertebrate consumers. The fish assemblage in each panel occurs to the right of the dashed line.

C. Tier III. Intensive Experimental Study of Grass Litter Decomposition Within a Single Field Site

In the intensive field trial where all nine grass litter types were placed within the Dripsey River, PLS regression analysis identified litter quality (in this instance % lignin content, % cellulose content and N:P) and shredder



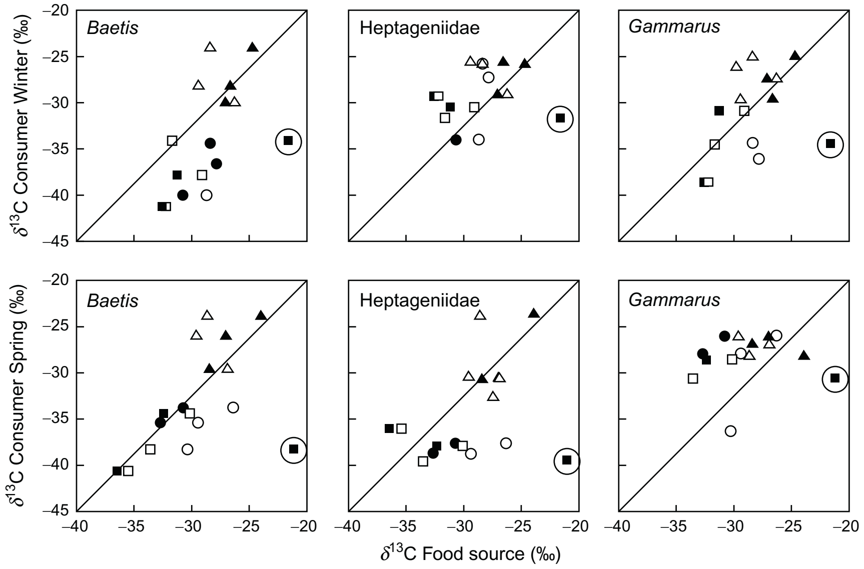
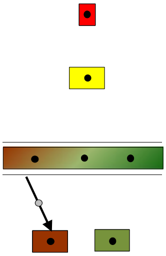


Figure 15 Tier II: Stable isotope signatures (δ^{13}C) of consumers in relation to two potential basal resources: epilithic biofilm (solid symbols) and CPOM (open symbols) among regions and between seasons. Squares represent Cork streams, triangles Mayo streams and circles Clare Island streams. Outlier circled in plots and excluded from analyses. Identical values on the *x* and *y* axes would lie on the diagonal 1:1 line (assuming no fractionation) (see Section III).

abundance as significant predictors of decomposition rates (Figure 16; Table 8; Table A10), as in the Tier II study in multiple sites.

D. Tier IV. Laboratory Experiments: Resource Quality and Decomposition Rates

In the Tier IVa multiple-choice feeding trial decomposition rates were driven by resource quality, and declined with increasing % lignin content (Figure 17). *Gammarus* preferred higher quality grasses (Friedman's test $P < 0.001$; pairwise comparisons Ms, Ah, Dr > Do; Dr, Ms > Ye) and similar



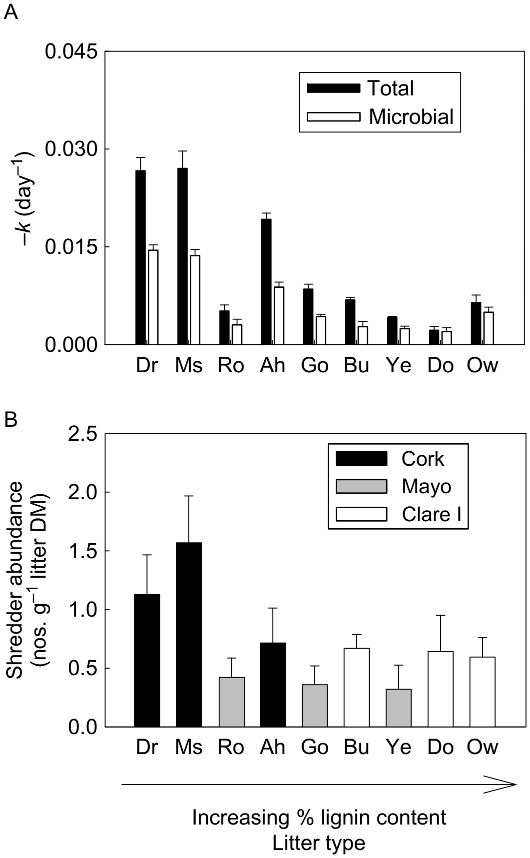
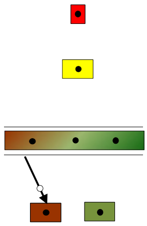


Figure 16 Tier III: Dripsey River field trial of decomposition rates of all nine grass litter types in a single stream (A) and shredder abundance in litter bags (B). Data displayed are mean values ± S.E. Litter is ranked from lowest to highest in % lignin content.

patterns were evident for *Halesus* (Friedman's test $P < 0.001$; pairwise comparisons Ms, Ah, Dr > Do; Dr, Ms > Ye; Ro > Do). In the final experiment (Tier IVb), where only a single resource was given (single-choice), *Halesus*



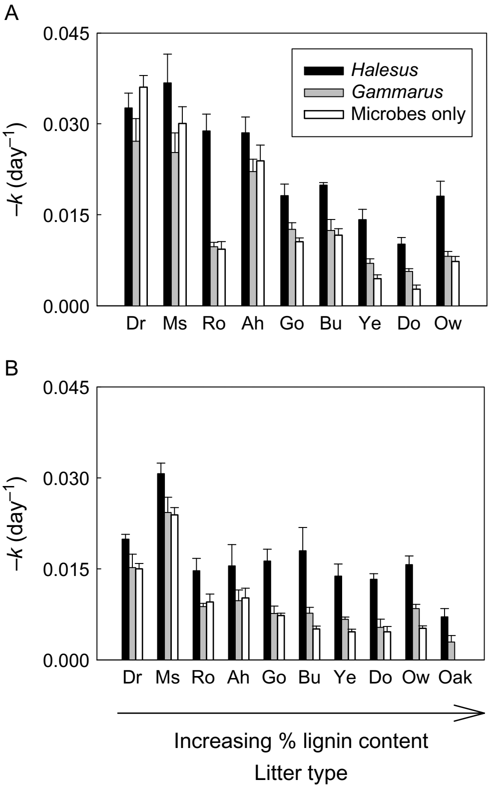


Figure 17 Laboratory experiments (Tier IV): (A): Multiple-choice grass litter preference trials with 90 shredders consumers (*Halesus* or *Gammarus*) and microbial-only decomposition and (B) single-choice grass and oak litter decomposition trials with 10 shredder (*Halesus* or *Gammarus*) consumers and microbial-only decomposition. Litter is ranked from lowest to highest in % lignin content.

and *Gammarus* decomposition rates were also highly correlated suggesting that they were feeding on litter types in a comparable manner ($r^2 = 0.92$, $P < 0.001$). PLS regressions from both laboratory experiments confirmed the importance of % lignin content to decomposition rates, other measures of

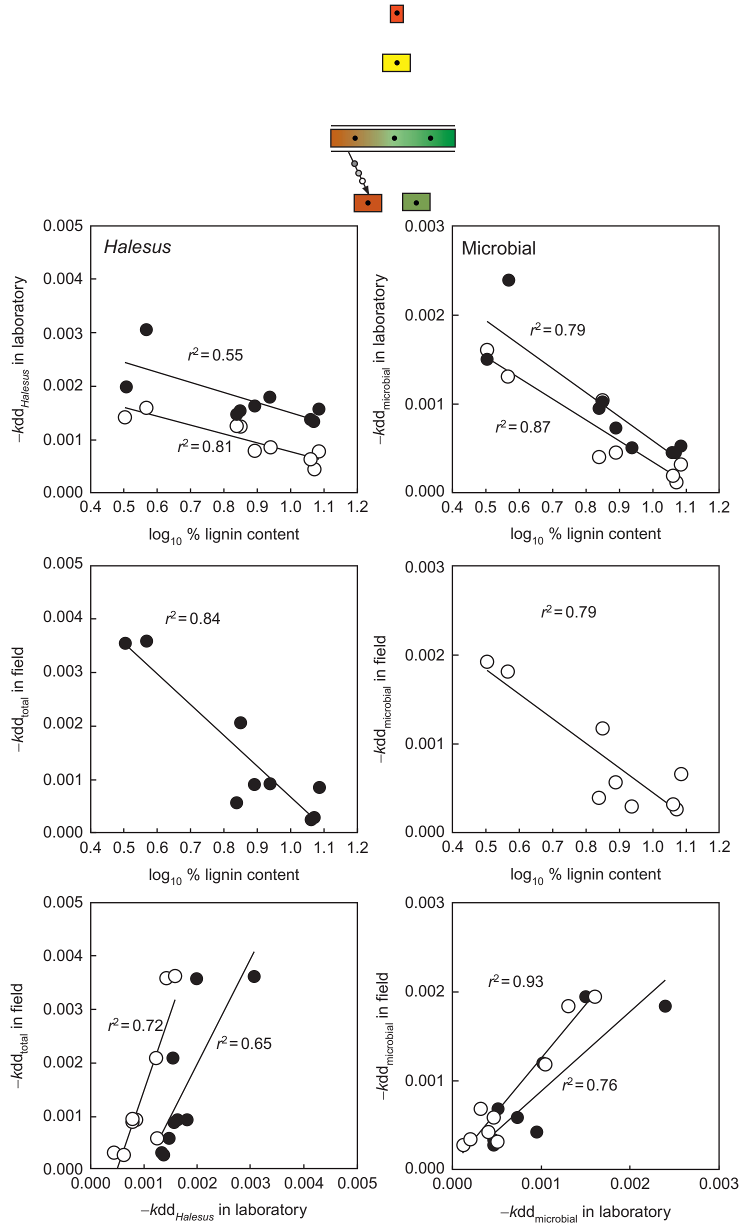


Figure 18 Summary comparison of field and lab experiments, with decomposition rates expressed per degree day to normalise for temperature differences among sites and trials (*Halesus* and microbial only). Note the high degree of congruence across the different experimental tiers, from field experiments (Tier III) to laboratory mesocosms (Tier IVa, open circles) to laboratory microcosms (Tier IVb, closed circles). All regressions were significant ($P < 0.05$).

quality that were also identified included % cellulose content, %P and N:P and C:P ratios (Table 8; Tables A11 and A12).

In summary, our pan-European RIVFUNCTION experiment revealed that in many (but not all) instances, total litter decomposition rates were faster in reference streams, but microbial-mediated decomposition was similar in absolute terms: that is, the relative importance of microbes tended to be higher in impacted sites, and especially so in pasture streams. In our more intensive studies on pasture systems in Ireland, experiments and surveys revealed that resource quality was a fundamental driver of decomposition rates, but that its effect was modulated by other drivers, particularly as complexity and realism increased from laboratory microcosms to field conditions. In the latter, there were a range of additional underlying drivers which influenced process rates, including water chemistry variables (e.g. SRP, pH) and local differences in community abundance and composition. When we focussed on one stream (Tier III) as a model system to control for differences in water chemistry and community composition and abundance *per se*, the importance of resource quality (e.g. % lignin content and nutrient content) was more marked than in the Tier II studies, as was also the case in the simplest, most tightly controlled Tier IV laboratory experiments (Figure 18). Figure 18 demonstrates this high degree of congruence, using linear regression, across the different experimental tiers, for grass litter decomposition in response to resource quality, from field experiments to laboratory experiments with *Halesus* and microbes. This congruence in results across these different scales and levels of organisation suggested that similar fundamental drivers were operating and that their effects were relatively direct, given that similar responses were observed in simple single-species microcosms and under less controlled field conditions.

IV. DISCUSSION

We found marked differences between ecosystem process rates in native woodland (i.e. reference) streams and those with altered riparian vegetation, although the magnitude and direction of these differences varied with the type of impact across Europe. Overall, there was no consistent main effect of altered riparian zones *per se*, since some impacts increased overall decomposition rates (McKie and Malmqvist, 2009), whereas others had no effect or decreased rates. Effects on total decomposition rates were contingent upon the type of impact and/or the particular European region of study, although the general effects of riparian alterations were broadly consistent among regions where similar types of impact (i.e. pasture vs. woodland in Switzerland, Ireland and Romania) were compared (cf. Hladyz *et al.*, 2010; Riipinen *et al.*, 2010). This is perhaps not surprising, given that riparian alterations could potentially cover a vast range of scenarios, from improving to impairing the quality and magnitude of litter inputs, suggesting that a blanket effect of riparian degradation is perhaps a somewhat naïve and unrealistic expectation. Although this large-scale field study was focussed on decomposition rates, inferences could be made about the roles of different consumer types by proxy, based on the mesh aperture used, as in other recent studies (e.g. Dangles *et al.*, 2011; Hladyz *et al.*, 2009, 2010; Riipinen *et al.*, 2010). This revealed more consistent effects of riparian alterations, especially via the mesh type × impact interaction, with a general increase in the importance of microbes relative to invertebrates as important agents of decomposition in impacted streams, especially in pasture compared to woodland streams. Although invertebrates were still important, and in many cases still *the* most important agents, this response suggests that the invertebrate detritivores were more sensitive to perturbations than the microbial decomposers.

The apparent decline in the relative importance of invertebrates as agents of decomposition in pasture streams has been suggested previously (Bird and Kaushik, 1992; Danger and Robson, 2004; Huryn *et al.*, 2002) and may be because grass litter is generally a poorer quality resource than leaf litter, being less accessible or palatable to shredders. A recent laboratory study using two shredder species (the caddis larvae *Limnephilus bipunctatus* and stonefly *Nemoura* sp.) from open-canopy streams revealed that senescent grass, despite being the most abundant food source year round, was relatively unfavoured when compared with leaf litter of terrestrial trees and shrubs, fresh grass litter, moss and benthic algae (Leberfinger and Bohman, 2010). Another potential reason for the decline in the role of invertebrates is that food webs in pasture streams rely more on inputs from autochthonous algal production than on allochthonous terrestrial detritus (Delong and Brusven, 1998; England and Rosemond, 2004; Hladyz *et al.*, 2010, 2011; McCutchan and Lewis, 2002; but see Leberfinger *et al.*, 2011). Therefore, not only is the detrital resource base impaired in pasture streams, but there is also greater availability of higher quality algal food as a more palatable alternative than terrestrial leaf litter.

The results of the intensive studies we conducted in Ireland are among the first attempts to characterise structural and functional attributes in a standardised manner across multiple sites via the integration of experiments with empirical survey data. One key point that emerged from this study was the high level of congruence in results obtained at different spatial scales in the field and the laboratory, which suggested that similar mechanisms were operating and that key system properties could be replicated under controlled conditions (e.g. Figure 18). It was apparent, for instance, that essentially the same drivers (i.e. measures of resource quality) of decomposition rates in the laboratory experiments were also evident in the field, despite the vast increase in the complexity of the systems under study.

1. Ecosystem Functioning: Bottom-Up Effects and Direct Consumer–Resource Interactions

The laboratory and field experiments in Ireland all revealed strong effects of resource quality on decomposition rates. There were also significant influences of consumer identity in response to resource quality, with oak litter being processed primarily by invertebrates, and with grass litter, particularly the higher quality litter, being processed to a greater extent by microbial activity. The fact that oak is itself not a particularly favoured resource relative to other types of leaf litter (Hladyz *et al*., 2009) further highlights the apparent poor quality of grass as a food source.

In general, the results obtained in the laboratory and the intensive field trial in the Dripsey River mirrored those from the extensive trials across all nine streams. For instance, the sites with higher stream nutrient concentrations and better quality grass litter were associated with enhanced litter decomposition rates and algal production, and higher invertebrate abundance, which, when taken together, are suggestive of bottom-up driven systems. These positive associations between stream nutrient concentrations and decomposition rates are also in line with our initial predictions based on previous studies (cf. Niyogi *et al*., 2003; Pearson and Connolly, 2000; Robinson and Gessner, 2000). Rates of microbial decomposition, however, showed no clear and consistent response among the nine streams: thus, differences in total decomposition are more likely to be attributable to the shredder guild, as suggested by the strong positive correlation between their abundance and decomposition rates.

It is intriguing that resource quality was a powerful predictor of microbial decomposition in the laboratory experiments. The fact that the same pattern was not so evident in the field is certainly suggestive of the role of shredders as key modulators of process rates: some shredders turned out to be particularly reliant on microbial conditioning to improve litter palatability, but others (e.g. *Halesus* in the Tier IV experiments) appeared to be far less dependent (Figure 17). Initial resource quality prior to microbial conditioning, as measured, for instance, by concentrations of leaf nutrients (Gessner 1991; Petersen and Cummins, 1974; Quinn *et al.* 2000; Suberkropp *et al*., 1976; Webster and Benfield, 1986) and physical toughness (Gessner and Chauvet, 1994; Melillo *et al*., 1982; Royer and Minshall, 2001) of litter also determines decomposition rates, and indeed the higher quality grasses broke down especially rapidly in both the laboratory and field trials, with shredders consuming more of the better quality resources per unit time.

In other controlled laboratory studies species richness, consumer abundance and body size have been positively correlated with decomposition rates (Jonsson *et al*., 2001; McKie *et al*., 2008). The more nutrient-enriched sites in

Ireland were indeed characterised by an abundant and diverse guild of large shredders, including caddis and *Gammarus* species, whereas the Mayo sites had slower decomposition rates and a distinct shredder guild dominated by small stoneflies (Figure A2). It is often difficult to disentangle the effects of size and species identity *per se*, as they tend to be confounded in experimental studies, but some recent research indicates that the former, rather than the latter, is the key driver in freshwater assemblages (Reiss *et al.*, 2009, 2010). In the context of the current study, this suggests that similar process rates might be maintained in taxonomically different assemblages, so long as consumer sizes are comparable (cf. Figure 14).

Despite differences in the relative importance of microbes versus invertebrates, total decomposition rates for grass and oak litter were often similar. Shearer and Webster (1985) and Metwalli and Shearer (1989) found that the composition of fungal assemblages in forested streams differed from those in sparsely vegetated areas. Gulis (2001) found in a study of 92 streams that grass blades had different fungal assemblages from those supported by leaf litter, and inferred that pasture sites might contain aquatic fungal species adapted to processing grass litter. In our study, the invertebrate-mediated: microbial decomposition ratio was higher for oak than for grass litter, even though the former had far higher lignin content, which is a strong predictor of decomposition rates (Gessner and Chauvet, 1994; Hladyz *et al.*, 2009). However, oak litter had lower C:N and N:P ratios than most of the grass litters, which implies that invertebrates respond to more than one aspect of resource quality (Hladyz *et al.*, 2009). Further, the grass litter used in our experiments, like most grasses, probably had a higher silica content (e.g. Lanning and Eleuterius, 1987) than the oak litter, and this could also have contributed to lower rates of invertebrate-mediated decomposition and shredder colonisation. Similarly, a study examining decomposition of herbs and grasses in an open-canopy stream found lower colonisation of grasses by shredders compared to herb leaf litter and inferred that this reflected the lower resource quality of grass litter (Menninger and Palmer, 2007).

Taken together, our results indicate that pasture streams have an impaired detrital base, in terms of the rate at which energy per unit mass of resource is transferred to higher trophic levels. This appears to be a result not only of reduced litter inputs but also, in accordance with a few previous studies have also suggested that grass litter might indeed be a relatively poor food resource (Leberfinger and Bohman, 2010; Niyogi *et al.*, 2003; Young *et al.*, 1994). Nonetheless, even though pasture streams receive limited leaf litter inputs, the ability of these ecosystems to process this resource was clearly retained by the microbes and some shredders that consumed grass litter. Similar observations have been made in alpine streams above the tree line (Gessner *et al.*, 1998; Robinson *et al.*, 1998). This could confer a degree of inbuilt resilience upon the maintenance of overall ecosystem functioning, whereby the potential for the food web to switch to a detrital resource base is retained should conditions change (e.g. via successional reversion of pasture to woodland). Despite the lack of significant leaf litter inputs, standing crops of detritus can still be large in pasture streams, although they are composed primarily of grasses, macrophytes and herbs (e.g. Hladyz *et al.*, 2011; Leberfinger and Bohman, 2010; Menninger and Palmer, 2007). Our results suggest that pasture streams can support shredder biomass, particularly in winter, as suggested by the apparent switching by *Gammarus* from reliance on detritus (e.g. CPOM) in the winter, to increased biofilm consumption in the spring, as resource availability changed (Figure 15). Several other studies have shown that detrital resources can be of importance in open-canopy streams, and potentially more so than algal resources for particular consumers (e.g. shredding caddis larvae; Hladyz *et al.*, 2011; Leberfinger *et al.*, 2011).

Seasonal effects on ecosystem functioning were also important, with litter decomposition, algal production and grazing pressure all being higher in spring than in winter. These differences were often still apparent, albeit less so, after temperature correction of process rates, suggesting that seasonal differences were due to more than simply different thermal regimes. Shredder abundance was higher in the spring, and in combination with higher temperature rates most likely accounted for the elevated decomposition rates. In contrast, grazer abundance did not change seasonally, suggesting that per capita algal consumption was higher in spring during its peak in primary production (Cox, 1990; Francoeur *et al.*, 1999; Minshall, 1978). Overall the enhanced process rates observed in spring generally reflected a combination of increased temperatures, consumer abundance, per capita consumption and availability of algae.

2. Higher-Level Drivers: The Potential for Trophic Cascades and Indirect Food Web Effects

Most studies into ecosystem functioning have tended to focus on the lower trophic levels, namely primary producers, detritus and primary consumers, rather than the higher, predatory levels (Woodward, 2009). This is a potential shortcoming because predators can exert powerful indirect effects on primary production and herbivory (e.g. Power, 1990; Scheffer, 1998) and there is increasing evidence that both fish and invertebrate predators can reduce leaf litter decomposition rates by influencing the abundance and/or activity of shredders (e.g. Oberndorfer *et al.*, 1984; Woodward *et al.*, 2008). Alterations to riparian vegetation could therefore modulate these indirect predator impacts, as suggested by the presence of ‘apparent trophic cascades’ in streams where inputs of terrestrial detritus had been curtailed (Nakano *et al.*, 1999).

The combined effects of reduced detrital resource quality and increased algal availability could, in theory, result in less dynamically stable food webs in pasture streams, due to a reduction in the damping effect of 'slow' detritus-based food chains relative to the 'faster' algal-based food chains (Rooney *et al.*, 2006). This could increase the possibility of trophic cascades arising because interaction strengths should increase, at least at the base of the web, as the system becomes less donor-controlled (Woodward, 2009; Woodward and Hildrew 2002). The increase in the diversity and abundance of predatory fish across the gradient of agricultural intensity and nutrient enrichment in the Irish streams also suggests that the food webs may be less dynamically stable than those in the less productive agricultural regions, since this is likely to further increase interaction strengths within the food web (cf. Layer *et al.*, 2010b, 2011).

Very few studies have assessed both community structure and the contribution of detrital and algal food chains to overall ecosystem functioning in pasture streams, which is surprising given the ubiquity of these systems in both Europe and elsewhere (Fujisaka *et al.*, 1996; Huryn *et al.*, 2002; Young *et al.*, 1994), and these suggestions still remain to be tested more rigorously via a full characterisation of the trophic networks of these types of streams. Nonetheless, the correlational data presented here indicate the potential for decreased food web stability in these systems relative to their native woodland counterparts, and also as they become more enriched.

Further manipulative experiments are required to identify causal mechanisms behind the potential impact of predators on basal processes (e.g. litter decomposition, algal consumption). Nonetheless, we can still make some inferences about their possible importance in pasture streams based on literature, correlations in our data, and the structure of the communities we observed. The potential for fish to exert indirect effects on the base of the food web (e.g. via suppressed rates of litter decomposition and herbivory when they are abundant; Figure 13) are hinted at in correlations in the data: for instance, the negative correlation between fish and invertebrate biomass is opposite to the positive relationship that would be expected if bottom-up effects took precedence. Top-down effects could thus account for at least some of the increased variability in the data and the weakening of resource quality constraints in the field versus the lab, even though the pattern and direction of responses was consistent. This generally high congruence between the results from the field and laboratory studies suggests that, overall, decomposition rates were most likely driven primarily by short, direct pathways within the food web (i.e. consumption by primary consumers). Indirect effects (e.g. via trophic cascades), although potentially more prevalent than in woodland streams, were likely to be of secondary importance. To explore these suggestions further, it would be instructive to perform large-scale and long-term experimental manipulations of multiple trophic levels and ecosystem processes under field conditions. The results of such experiments could provide critical information to understand and predict the structure and dynamics of stream ecosystems in general.

3. *Caveats, Conclusions, and Future Directions*

Although the replacement of forests by human-modified vegetation is a worldwide phenomenon, our understanding of the community and ecosystem-level consequences of the loss of riparian woodland is clearly far from complete (Dodds, 1997; Hladyz *et al.*, 2010). Several lines of evidence presented here, however, suggest that streams with altered riprarian zones might, in general, be functionally fundamentally different from those in their ancestral woodland (i.e. 'reference') state, as revealed, for instance, by the significant interaction between mesh type x vegetation types. In particular, in many instances microbes played an increasingly important role as agents of decomposition, compared with the predominance of invertebrate detritivores in woodland sites, even though total decomposition rates were similar. This could have wider implications for the transfer of energy and nutrients in perturbed systems, since the capacity of microbes to correct for impaired detritivore activity might ultimately be somewhat limited (i.e. shredders are far larger consumers and many can macerate even very tough litter very effectively). In addition, microbial-mediated decomposition might operate via different routes of carbon and nutrient cycling, which might, for instance, benefit other types of invertebrate consumers (e.g. collector-gatherers vs. shredders). Further studies are clearly needed to assess how widespread this phenomenon of (relative) increased microbial decomposition is on a global scale, how consistent it is across different types of riparian modification (including those arising from the wide range of exotic plants that are invading riparian zones across the world). It is also important to develop a better understanding of the mechanisms that underpin the observed responses, and particularly to unravel the relative roles of different microbial and invertebrate consumers experimentally (Reiss *et al.*, 2010).

Differences between streams that flowed through woodland versus those that flowed through altered riparian zones were especially evident in systems dominated by pasture. Firstly, within pasture streams, algal pathways were relatively more important, due to a combination of increased light availability and poor detrital food quality, as grass litter was clearly not a favoured food among the invertebrate primary consumers (cf. Hladyz *et al.*, 2011).

Further investigations are required to quantify the extent to which increased algal contributions might compensate for, or even potentially exceed, those of allochthonous carbon, especially as this could have wider implications for carbon cycling and food web stability in freshwaters (Woodward *et al.*, 2010). Secondly, resource quality of grass litter exerted strong effects on consumption rates of both invertebrates and microbes, even though it was generally of poorer quality than the leaf litter that dominates native woodland streams (cf. Hladyz *et al.*, 2009). Thirdly, microbial decomposers become increasingly predominant relative to the invertebrate detritivores that are the principal agents of litter decomposition in woodland streams (Cummins *et al.*, 1989; Hladyz *et al.*, 2011; Wallace *et al.*, 1999). Similar responses have been reported from a recent study in 30 Swiss, Romanian, and Irish streams (Hladyz *et al.*, 2010), in an Australian pasture stream (Danger and Robson, 2004), 12 New Zealand streams in which fungal biomass was strongly correlated with grass litter decomposition rates (Niyogi *et al.*, 2003), and also in 24 high-altitude grassland streams in Ecuador (Dangles *et al.*, 2011). This suggests that the responses observed and described here might be global phenomena. Further studies in pasture streams would also clearly benefit from a closer focus on the microbial component of the food web, and it could be instructive to apply some of the new molecular and metagenomic approaches and next-generation sequencing techniques to identify the drivers behind these processes *in situ*, in terms of the identity, abundance and, potentially, the activity of both bacteria and fungi (Bärlocher *et al.*, 2009; Purdy *et al.*, 2010).

Much of our understanding of ecosystem processes and food web dynamics in running waters is derived from studies of (a few) wooded headwater streams (e.g. Cummins *et al.*, 1989; Fisher *et al.*, 1982; Gregory *et al.*, 1991; Wallace *et al.*, 1999; Woodward *et al.*, 2005). Far less attention has been paid to those in more obviously human-modified environments, where most studies have focussed on biomonitoring of the invertebrate assemblage (i.e. the nodes in part of the food web) in response to organic pollution. Other stressors, including the alteration of riparian vegetation have been largely overlooked in terms of their impacts on the higher levels of organisation and the links between community structure and ecosystem functioning (Hladyz *et al.*, 2010, 2011; Leberfinger and Bohman, 2010; Menninger and Palmer, 2007). It is also becoming increasingly clear that alterations to riparian zones and their allochthonous inputs to freshwater food webs could have important, but still largely unknown, synergies with the impacts of climate change in the near future (Boyero *et al.*, 2011; Perkins *et al.*, 2010a,b; Woodward *et al.*, 2010). It is of vital importance to understand the patterns and processes that operate in these altered streams if we are to improve stream ecosystem management, restoration and/or rehabilitation schemes, as well as to gain insight into the ecology of these systems in their own right, and we hope that the current study goes some way towards redressing this imbalance.

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APPENDIX

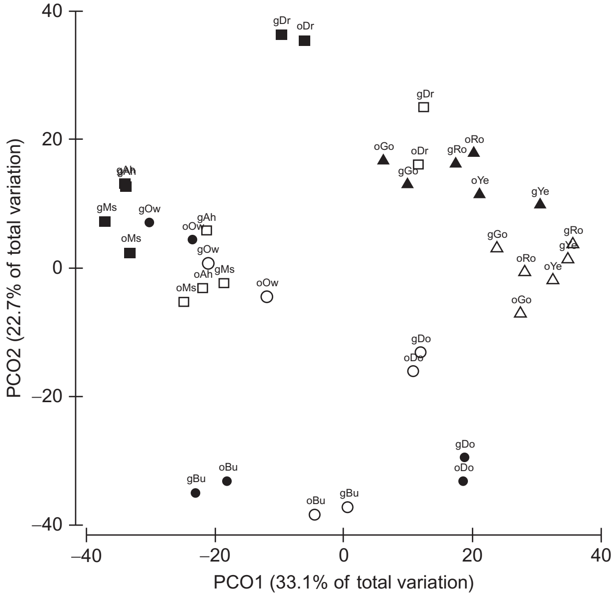

Figure A1 Tier II: Two factor PCO plot of the centroids of the macroinvertebrate assemblages in mesh bags on the basis of the adjusted Bray–Curtis dissimilarity measure, showing the factors of region (squares denote Cork streams, triangles denote Mayo streams and circles denote Clare Island streams, respectively) and season (closed symbols denote spring samples and open symbols denote winter samples, respectively). 'g' denotes grass litter bags and 'o' denotes oak litter bags, respectively. Labels denote stream names (see Table 3 for legend).

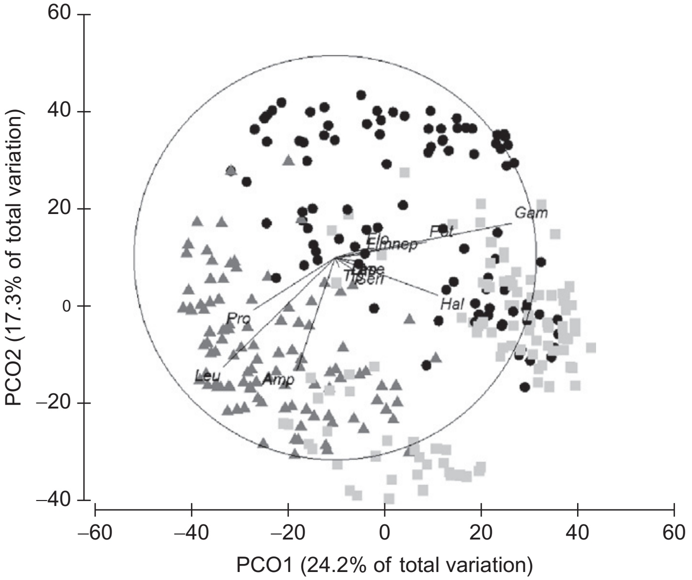

Figure A2 Tier II: One factor PCO plot of the macroinvertebrate assemblages in mesh bags on the basis of the adjusted Bray–Curtis dissimilarity measure, showing the factor region (squares denote Cork streams, triangles denote Mayo streams and circles denote Clare Island streams, respectively). Vector overlay denotes Spearman correlations, displaying the shredder guild. Gam, *Gammarus* spp., Ase, *Asellus aquaticus* (L.), Pot, *Potamophylax* spp., Hal, *Halesus* spp., Lim, *Limnephilus* spp., Limnep, Limnephilidae indet., Seri, *Sericostoma personatum* (Kirby and Spence), Lep, *Lepidostoma* spp., Elo, *Elodes* spp. larvae, Pro, *Protonemura* spp., Amp, *Amphinemura sulcicollis* (Stephens), Leu, *Leuctra* spp., Tip, *Tipula* spp.

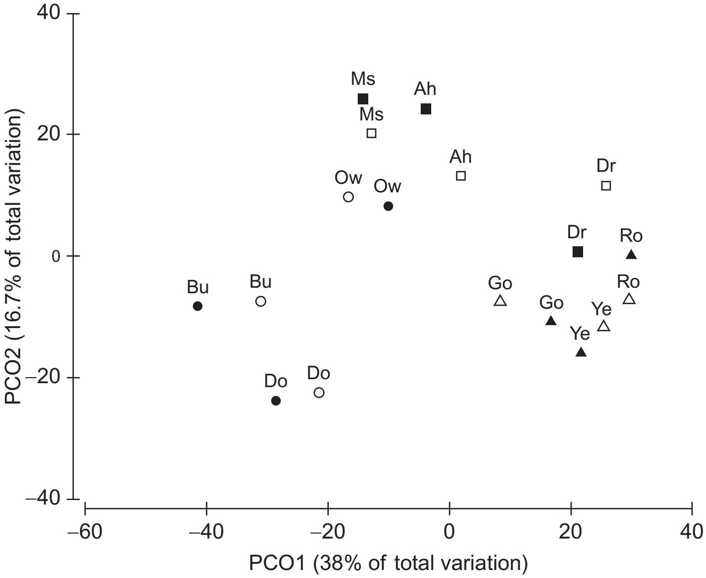

Figure A3 Tier II: Two factor PCO plot of the centroids of the macroinvertebrate assemblages in stream benthos on the basis of the adjusted Bray–Curtis dissimilarity measure, showing the factors of region (squares denote Cork streams, triangles denote Mayo streams and circles denote Clare Island streams, respectively) and season (closed symbols denote spring samples and open symbols denote winter samples, respectively). Labels denote stream names (see Table 3 for legend).

Table A1 pan-European RIVFUNCTION field experiment (Tier I): Linear mixed effects model results of comparisons of the ratio of invertebrate-mediated decomposition rates and microbial decomposition rates ($\log_{10}\ k_{\mathrm{invert}}{:}k_{\mathrm{microbial}}$) among European regions and impact

Comparison	Leaf	df_N	df_D	*F*-ratio
Region	A	9	40.90	3.13**
Impact	A	1	39.45	14.59***
Region × impact	A	9	39.33	4.15**
Region	O	9	85.00	7.37***
Impact	O	1	84.98	4.82*

Non-significant interactions and parameters omitted. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

Table A2 Tier II: Partial least-squares (PLS) regression output for litter decomposition rates ($-k$) in coarse-mesh bags from Irish large-scale field trial

$-k$	Season	Variable[a]	VIP	Slope	Components	R^2Y
Grass total	Winter	C:P/B.ShrA	1.26/1.25	−0.26/−0.71	3/4	0.93/0.96
		%P/N:P	1.25/1.17	0.25/−0.49		
		N:P/%Gra	1.21/1.16	−0.29/−0.36		
		B.ShrA/%Pre	1.16/1.14	−0.33/−0.32		
		%Gra/Grass Shr g^{-1}	1.14/1.14	−0.18/0.55		
		%N/C:P	1.13/1.12	0.11/−0.34		
		C:N/%P	1.13/1.12	−0.12/0.34		
		Temp./%Shr	1.1/1.00	−0.39/0.002		
		%Pre/SRP	1.07/1.00	−0.17/−0.38		
		Constant		1.81/1.84		
Grass total	Spring	pH	1.82/1.79	0.3/0.32	2/2	0.77/0.76
		SRP	1.44/1.45	0.2/0.23		
		Grass Shr g^{-1}	1.21/1.23	0.19/0.22		
		TON/%C	1.18/1.16	0.15/0.19		
		N:P/TON	1.17/1.16	0.06/0.17		
		C:P	1.15/1.12	0.11/0.07		
		Temp./N:P	1.04/1.12	−0.18/0.06		
		%P/	1.04/	0.04/		
		Constant		1.98/1.80		
Oak total	Winter	Oak Shr g^{-1}	1.62/1.60	0.41/0.45	2/2	0.81/0.73
		B.ShrA	1.26/1.17	0.32/0.32		
		Constant		1.54/1.51		
Oak total	Spring	pH	1.51/1.43	0.32/0.36	2/2	0.83/0.86
		SRP	1.33/1.28	0.23/0.28		
		Oak Shr g^{-1}	1.14/1.13	0.22/0.27		
		TON	1.11/1.04	0.17/0.19		
		Constant		1.01/0.97		

$-k_d$ and k_{dd} are separated by '/'. Variables are listed with their regression slopes in descending VIP (variable importance to the projection) index order. Slope coefficients are not independent (unlike MLR), as the variables may be collinear. The VIP values reflect the importance of terms in the model both with respect to y and with respect to x (the projection). VIP is normalised and the average squared value is 1, so terms in the model with a VIP > 1 are important (other variables are not shown). R^2Y is the % of the variation of y explained by the model.

[a] Predictor variables: *biotic attributes*: fish biomass (spring only; FishB), fish abundance (spring only; FishA), invertebrate biomass (spring only; InvB), Grass shredders g^{-1} (Grass only), Oak shredders g^{-1} (Oak only), benthos shredder abundance (B.ShrA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4. *Resource quality attributes* (Grass only): %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell). Temperature was excluded from DD analyses.

Table A3 Tier II: Partial least-squares (PLS) regression output for litter decomposition rates ($-k$) in fine-mesh bags from Irish large-scale field trial

$-k$	Season	Variable[a]	VIP	Slope	Components	R^2Y
Grass microbial	Winter	Temp./N:P	1.52/1.23	−0.37/−0.52	2/3	0.85/0.83
		N:P/SRP	1.34/1.20	−0.33/−0.49		
		%P/pH	1.2/1.18	0.26/0.28		
		C:P/TON	1.19/1.14	−0.25/−0.41		
		/%C	/1.10	/0.16		
		/%P	/1.04	/0.36		
		/C:P	/1.03	/−0.36		
		Constant		1.98/1.82		
Grass microbial	Spring	pH	1.32/1.78	−0.82/−0.97	4/4	0.87/0.83
		Temp./%C	1.29/1.32	0.36/−0.45		
		%C/TON	1.2/1.04	−0.32/0.83		
		TON/SRP	1.11/1.03	0.76/0.13		
		N:P/	1.02/	0.36/		
		Conduc./	1/	−0.14/		
		Constant		3.13/3.67		
Oak microbial	Winter	SRP	1.32/1.82	0.98/0.53	3/1	0.72/0.37
		Temp./	1.15/	−0.92/		
		Conduc./	1.06/	0.15/		
		Constant		1.14/1.08		
Oak microbial	Spring	TON/pH	1.7/1.18	−0.58/−1.10	2/4	0.33/0.81
		/TON	/1.07	/−2.47		
		Constant		1.31/1.27		

$-k_{\mathrm{d}}$ and k_{dd} are separated by '/'.

[a] Predictor variables: *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4. *Resource quality attributes* (Grass only): %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell). Temperature was excluded from DD analyses.

Table A4 Irish multiple sites field experiments (Tier II): Permutational MANOVA (PERMANOVA) of 74 invertebrate species abundance variables in mesh bags (√transformed nos. g^{-1} litter DM), based on the adjusted Bray–Curtis dissimilarity measure

Comparison	df_{N}	df_{D}	Pseudo *F*-ratio
Region	2	6	2.97*
Leaf	1	6.01	3.79*
Season	1	6	5.02**
Region × leaf	2	6	1.09$^{\mathrm{ns}}$
Region × season	2	6	2.73*
Leaf × season	1	6	4.49***

Three-way interactions were non-significant and therefore omitted. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns: $P > 0.05$.

Table A5 Tier II: Partial least-squares (PLS) regression output for algal tiles and ungrazed/grazed ratio from Irish large-scale field trial

Algal response	Season	Variable[a]	VIP	Slope	Components	R^2Y
Grazed tiles	Winter	%Pre	1.34/1.37	0.28/0.30	2/2	0.67/0.68
		Conduc.	1.27/1.34	−0.41/−0.47		
		%Gra	1.22/1.24	−0.17/−0.18		
		Constant		0.86/0.94		
	Spring	%Gra	1.86/1.70	−1.16/−0.98	3/3	0.78/0.75
		Temp./%Pre	1.29/1.15	−0.07/−0.07		
		%Pre/NH_4	1.2/1.02	−0.3/−0.04		
		Constant		1.19/1.18		
Ungrazed tiles	Winter	%Pre	1.28/1.36	0.26/0.29	2/2	0.65/0.63
		%Gra	1.17/1.24	−0.15/−0.17		
		Conduc.	1.14/1.21	−0.38/−0.42		
		Temp./	1.05/	0.24/		
		Constant		0.83/0.91		
	Spring	%Gra	1.82/1.84	−1.21/−1.15	3/3	0.87/0.87
		Temp./FishB	1.23/1.09	0.01/−0.33		
		B.GraA	1.15/1.09	−0.24/−0.22		
		Constant		1.1/1.1		
Ungrazed: Grazed	Winter	B.GraA	1.75	0.59	2	0.93
		Conduc.	1.24	0.17		
		Constant		4.5		
	Spring	B.GraA	1.21	0.61	3	0.85
		FishA	1.19	−0.55		
		Conduc.	1.14	−0.51		
		NH_4	1.08	0.47		
		TON	1.05	−0.46		
		Constant		1.78		

A_d and A_{dd} are separated by '/'.

[a] Predictor variables: *biotic attributes*: fish biomass (spring only; FishB), fish abundance (spring only; FishA), invertebrate biomass (spring only; InvB), benthos grazer abundance (B.GraA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4. Temperature was excluded from DD analyses.

Table A6 Permutational MANOVA (PERMANOVA) of 73 invertebrate species abundance variables in stream benthos ($\log_{10}$ nos. 0.0625 m^{-2}), based on the adjusted Bray–Curtis dissimilarity measure

Comparison	df_N	df_D	Pseudo *F*-ratio
Region	2	6	3.35**
Season	1	6	3.26*
Region × season	2	6	0.107^{ns}

$*P < 0.05$; $**P < 0.01$; ns: $P > 0.05$.

Table A7 Tier II: Partial least-squares (PLS) regression output for potential indirect food web effects on invertebrate biomass from Irish large-scale field trial

Response	Variable[a]	VIP	Slope	Components	R^2Y
Invertebrate biomass	FishB	1.60	−0.29	3	0.96
	B.GraA	1.54	0.24		
	B.ShrA	1.49	0.28		
	FishA	1.32	−0.15		
	%Pre	1.06	−0.21		
	SRP	1.06	−0.14		
	Conduc.	1.02	0.06		
	Grass Shr g^{-1}	1.01	0.09		
	Constant		8.17		

[a] Predictor variables: *biotic attributes*: fish biomass (FishB), fish abundance (FishA), Grass shredders g^{-1}, Oak shredders g^{-1}, benthos shredder abundance (B.ShrA), benthos grazer abundance (B.GraA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4, mg chlorophyll *a* accrual on ungrazed tiles day^{-1} (A_dU), mg chlorophyll *a* accrual on grazed tiles day^{-1} (A_dG). *Resource quality attributes* (Grass only): %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

Table A8 Tier II: Partial least-squares (PLS) regression output for potential indirect food web effects on % invertebrate-mediated decomposition from Irish large-scale field trial

Litter type	Variable[a]	VIP	Slope	Components	R^2Y
Grass	NH_4	1.53	0.31	3	0.80
	FishA	1.38	−0.32		
	Grass Shr g^{-1}	1.28	0.11		
	Cell	1.24	0.08		
	FishB	1.21	−0.18		
	Temp.	1.12	−0.04		
	pH	1.11	0.24		
	TON	1.07	0.18		
	Lig	1.05	−0.15		
	Constant		1.94		
Oak	FishB	1.30	−0.30	3	0.90
	Oak Shr g^{-1}	1.26	0.22		
	%Gra	1.21	−0.62		
	B.GraA	1.17	−0.04		
	InvB	1.08	0.32		
	B.ShrA	1.06	0.08		
	pH	1.03	0.33		
	Constant		6.87		

[a] Predictor variables: *biotic attributes*: fish biomass (FishB), fish abundance (FishA), Invertebrate biomass (InvB), Grass shredders g^{-1}, Oak shredders g^{-1}, benthos shredder abundance

(B.ShrA), benthos grazer abundance (B.GraA), % invertebrate predators in benthos (%Pre), % invertebrate grazers in benthos (%Gra), % invertebrate shredders in benthos (%Shr); *abiotic attributes*: stream temperature (Temp.), TON, SRP, pH, conductivity (conduc.), NH_4, mg chlorophyll *a* accrual on ungrazed tiles day^{-1} (A_dU), mg chlorophyll *a* accrual on grazed tiles day^{-1} (A_dG). *Resource quality attributes* (Grass only): %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

Table A9 Tier II: Partial least-squares (PLS) regression output for consumer carbon isotope signatures in relation to potential food sources in winter and spring

Consumer	Season	Variable	VIP	Slope	R^2Y
Baetis	Winter	CPOM	0.58	0.25	0.58
		Biofilm	1.29	0.55	
		Constant		−5.99	
	Spring	CPOM	0.81	0.35	0.72
		Biofilm	1.16	0.51	
		Constant		−5.79	
Heptageniidae	Winter	CPOM	0.92	0.33	0.50
		Biofilm	1.08	0.39	
		Constant		−6.99	
	Spring	CPOM	0.54	0.24	0.58
		Biofilm	1.31	0.58	
		Constant		−6.23	
Gammarus	Winter	CPOM	0.50	0.19	0.40
		Biofilm	1.32	0.49	
		Constant		−9.83	
	Spring	CPOM	1.35	0.47	0.27
		Biofilm	0.41	0.14	
		Constant		−8.56	

All models contained one component.

Table A10 Tier III: Partial least-squares (PLS) regression output for litter decomposition rates ($-k$ day^{-1}) from Irish single site (Dripsey River) field experiment

Type of decomposition	Variable[a]	VIP	Slope	Components	R^2Y
Grass total	Lig	1.33	−0.31	2	0.87
	Cell	1.21	−0.29		
	Shr g^{-1}	1.15	0.23		
	N:P	1.01	−0.11		
	Constant		1.21		
Grass microbial	Lig	1.34	−0.33	2	0.84
	Cell	1.31	−0.34		
	N:P	1.07	−0.18		
	Constant		1.29		

[a] Predictor variables used in this model included: Shredders g^{-1} (Coarse-mesh only, Shr g^{-1}), % P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

Table A11 Tier IVa: Partial least-squares (PLS) regression output for litter decomposition rates ($-k$ day^{-1}) from multiple-choice mesocosm grass litter trials

Consumer	Variable[a]	VIP	Slope	Components	R^2Y
Halesus	Lig	1.36	−0.18	1	0.72
	Cell	1.21	−0.16		
	N:P	1.14	−0.15		
	%P	1.10	0.15		
	Constant		2.57		
Gammarus	Lig	1.47	−0.37	2	0.77
	Cell	1.26	−0.31		
	N:P	1.02	−0.14		
	Constant		1.76		
Microbes	Lig	1.43	−0.37	2	0.84
	Cell	1.31	−0.35		
	N:P	1.04	−0.16		
	Constant		1.27		

[a] Predictor variables used in this model included: Grass litter quality: %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

Table A12 Tier IVb: Partial least-squares (PLS) regression output for litter decomposition rates ($-k$ day^{-1}) from single-choice microcosm grass litter trials

Consumer	Variable[a]	VIP	Slope	R^2Y
Halesus	Lig	1.29	−0.15	0.52
	N:P	1.18	−0.13	
	Cell	1.12	−0.13	
	C:P	1.1	−0.13	
	%P	1.09	0.12	
	Constant		3.29	
Gammarus	Lig	1.23	−0.16	0.72
	N:P	1.18	−0.16	
	%P	1.14	0.15	
	Cell	1.12	−0.15	
	C:P	1.08	−0.14	
	Constant		1.83	
Microbes	Lig	1.26	−0.18	0.79
	%P	1.14	0.16	
	N:P	1.12	−0.16	
	Cell	1.09	−0.15	
	C:P	1.03	−0.14	
	Constant		1.48	

All models consisted of component.

[a] Predictor variables used in this model included: Grass litter quality: %P, %C, %N, C:P, C:N, N:P, % lignin content (lig), % cellulose content (cell).

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