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Invertebrate community structure and ecosystem functioning in European conifer plantation streams

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SUMMARY

1. Terrestrial leaf-litter is the dominant energy input to many headwater streams and consequently the nature of the riparian vegetation can have profound effects on in-stream processes. The impact of conifer plantations on community structure and ecosystem functioning (litter breakdown) was investigated in field experiments in three countries (Britain, Ireland, Poland), each representing a distinct European ecoregion. Twenty-six streams were used in the trial: half were bordered with broadleaved and the other half with conifer riparian vegetation.
2. In a leaf breakdown study using litter bags, two leaf types (oak and alder) were used to assess the impact of resource quality and two mesh sizes (10 and 0.5 mm aperture) were used to gauge the relative importance of invertebrate detritivores and microbial decomposers respectively. Comparisons were made between vegetation types and among regions; pH varied among individual streams but, unlike many previous studies, it was not confounded with vegetation type, enabling us to isolate the effect of vegetation more effectively.
3. Overall, riparian vegetation type did not affect breakdown rates but strong regional differences were observed. There was also a significant interaction between these two variables, but this disappeared after fitting pH as a covariable, demonstrating its importance in determining breakdown rates and raising the possibility that in previous studies the impacts of conifer plantations might have been confounded with pH.
4. Shredder species composition differed between vegetation types. Small stoneflies were most strongly associated with conifer streams; broadleaved streams generally had a higher proportion of larger taxa, such as limnephilid caddisflies and gammarid shrimps, although the latter were excluded from sites with low pH. However, breakdown rates were maintained irrespective of shredder community composition, suggesting a high degree of functional redundancy in these communities. Similar processing rates were observed between streams with high numbers of nemourids and those with only a few limnephilids or gammarids, suggesting that density compensation among consumers might stabilise process rates.

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5. Our results suggest that leaf-litter breakdown can be an effective proxy for assessing stream ecosystem functioning, as rates differed significantly across spatial scales, from between streams to across regions and responded to an environmental gradient (pH). The litter bag technique can also complement traditional assessment methods by providing valuable information on the composition of consumer guilds, thereby providing an important link between structure and function that is needed to help inform management practices.

Keywords: afforestation, breakdown rates, ecosystem processes, land-use, shredders

Introduction

Conifer forests cover large areas in the headwaters of river catchments in many countries, with commercial conifer plantations accounting for 215 million hectares in Europe alone (UNECE, 2005). The latter have been planted at a faster rate than they have been felled since the 1960s (UNECE, 2005), so potential impacts on water courses are likely to increase in the near future. Riparian trees are a major source of energy for headwater stream food webs, via inputs of leaf-litter and, to a lesser extent, coarse woody debris (CWD; Cummins *et al.*, 1989; Wallace *et al.*, 1997). It is therefore crucial to be able to assess the impacts of altering the vegetation in the riparian zone and the surrounding catchment (e.g. via planting exotic conifer forests) on stream ecosystems at both local and large scales (Hladyz *et al.*, 2009).

Many studies have reported negative impacts of exotic conifer monocultures on the composition of stream communities, particularly in Britain (e.g. Ormerod, Donald & Brown,1989; Ormerod *et al.*, 1993, 2004; Dobson & Cariss, 2000; Laitung *et al.*, 2002; Harriman *et al.*, 2003; Pretty & Dobson, 2004; Pretty, Giberson & Dobson, 2005), but the consequences for ecosystem functioning are less well-known (but see Friberg, 1997; Murphy & Giller, 2001; Collen, Keay & Morrison, 2004; Dangles, Malmqvist & Laudon, 2004b). Potentially, conifers can have several negative impacts on leaf-litter processing in headwater streams. Conifer needles are tough, poor in nutrients (Triska, Sedell & Buckley, 1975; Friberg & Jacobsen, 1994; Graça, 2001) and possess anti-fungal agents (Bärlocher, Kendrick & Michaelides, 1978; Bärlocher & Oertli, 1978), making them a poor quality food resource for both invertebrate detritivores and microbial decomposers. Consequently, replacing the native deciduous riparian vegetation with conifers has the potential to seriously impair detrital processing. Furthermore, conifer streams that run through plantations often suffer from poor detrital retention, due to commercial harvesting practices, so litter inputs are flushed rapidly from the system (Collen *et al.*, 2004). In addition, the elongated needles are rarely retained for sufficient time within the stream to allow microbial conditioning, an important early step in the breakdown process that stimulates subsequent shredder activity (Pretty & Dobson, 2004). These factors tend to result in poor food availability for shredders and thus impaired secondary production (Friberg & Jacobsen, 1999; Pretty & Dobson, 2004). Some of these negative effects may, however, be partially offset by the reduced seasonality of litter inputs, which do not arrive in a single pulse in autumn, as in deciduous streams (see Murphy & Giller, 2001).

Physicochemical variables that influence litter processing rates are often themselves altered by the riparian vegetation in conifer plantation streams. For instance, conifer plantations can exacerbate acidification via enhanced occult deposition, in addition to suppressing breakdown in topsoils (Stoner, Gee & Wade, 1984). They also alter temperature regimes through increased shading and change habitat structure by altering hydrology (Ormerod, Mawle & Edwards, 1987). All of these factors can operate at small scales (e.g. within streams), but even larger differences might be expected at larger scales, where, for instance, entire catchments have been afforested. Afforestation with conifers is therefore likely to alter breakdown rates since litter breakdown is determined by a suite of physicochemical variables, such as water temperature (Chauvet & Suberkropp, 1998), altitude (Fleituch, 2001), pH (Dangles & Guérold, 1999), nutrient availability (Stelzer, Heffernan & Likens, 2003) and current velocity (Suberkropp &

Klug, 1980). What is less well-known is how consistent these potential impacts are across very large, regional or continental scales and to what extent they are related to the often confounding effects of acidification, rather than to conifer afforestation *per se*.

This study describes a large-scale field experiment that was carried out as part of the pan-European consortium project RivFunction (see e.g. Lecerf *et al.*, 2006; http://www.ecolab.ups-tlse.fr/rivfunction/), in which the impact of conifer plantations on stream ecology was investigated in Britain, Ireland and Poland. Commercial forests account for 12%, 9% and 20%, respectively, of land surface area in Britain, Ireland and central Poland. The principal aim was to assess the impact of conifer plantations on the structure and functioning of stream communities in these three biogeographically distinct ecoregions in Europe (representing the E.U. Water Framework Directive ecoregions of 'Great Britain' (18), 'Ireland' (17) and 'The Carpathians' (10), (European Commission, 2000). Although Poland is covered by three distinct ecoregions, the term 'Poland' henceforth refers to the Carpathian ecoregion in that country. We tested the hypothesis that conifer plantations would have detrimental impacts on both the structure (abundance, richness and biomass of shredders) and functioning (as measured by litter breakdown rates) of stream ecosystems across the three regions. Breakdown rates were measured in a single co-ordinated field experiment that employed litter bags with two leaf types – alder (*Alnus glutinosa* (L.) Gaertn.) and oak (*Quercus robur* L.) – of differing palatability, with the former being a much faster decomposer than the latter (see e.g. Sampaio, Cortes & Leao, 2001; Hladyz *et al.*, 2009). We used two mesh apertures for the litter bags to assess the relative contribution of shredding invertebrate detritivores and microbial decomposers to total breakdown.

Methods

Site description

This study was carried out simultaneously in three regions at similar latitudes: south-central Britain (53.43°N, 1.65°W), western Ireland (53.95°N, 9.45°W) and Malopolska Province in the Western Carpathians of southern Poland (49.56°N, 20.15°E). All three regions have a high concentration of commercially managed conifer plantations and hence much of the surrounding landscape has been modified considerably by silviculture. In Britain, commercial conifer plantations are dominated primarily by Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Norway spruce (*Picea abies* (L.) Karsten), Scots pine (*Pinus sylvestris* L.) with occasional European larch (*Larix decidua* P. Mill.) and several other minor species (Forestry Commission, 2002). Sitka spruce is also common in Ireland, as is Lodgepole pine (*Pinus contorta* Dougl.) (Giller & O'Halloran, 2004). In the Carpathians of Poland, the most common species are Norway spruce (*P. abies*) and silver fir (*Abies alba* Mill.) (GUS 2007). However, each region also contains streams bordered by natural broadleaf vegetation and these were used to select reference sites. In the British broadleaved sites, the most common taxa were oak (*Q. robur*) and alder (*A. glutinosa*), whereas in Ireland, in addition to oak and alder, hawthorn (*Crataegus monogyna* Jaqc.), holly (*Ilex aquifolium* L.) and willow (*Salix* spp.) were also present. In Poland, the most common broadleaved species was beech (*Fagus sylvatica* L.).

Twenty-six streams were used in total: 10 streams (five bordered by conifer forests, five by native deciduous vegetation) were selected in Britain and Poland, plus six sites in Ireland (since only three sites where the entire catchment was covered with exotic conifers could be found within the same region, without being subjected to other confounding variables). All the streams were first- to fourth-order, with stony substrata (Table 1). *A priori* pairing of conifer and broadleaved sites was done to maximise statistical power and was based on overall similarities of site characterisations, e.g. width, depth and substrate structure (pairings in Table 1).

The riparian vegetation reflected the entire catchment vegetation for all sites in Ireland: deciduous woodland for the reference streams and conifer plantations for the impacted sites. In Britain, moorland was the principal vegetation type upstream of both reference and impacted sites. In Poland, most of the vegetation upstream of study sites was mixed woodland for reference sites and conifers for impacted sites. Riparian vegetation in the broadleaved sites was dominated by native species to each region. Among conifer sites, the dominant species in Britain and Ireland were exotic for both countries, whereas those in Poland were exotic within the experimental area,

Table 1 Summary of the main characteristics of the streams

Region	Stream	Riparian vegetation type	Stream pairs (within country)	$P–PO_4$ (ppm)	$N–NH_4$ (ppm)	Mean pH	Mean alkalinity	Mean conductivity (mS s^{-1})	The dominant riparian species
Britain	Widow	BL	1	7.34	7.8	6.8	21.7	141.3	*Quercus robur*
	Rochel	BL	2	4.0	0.0	6.4	14.6	169.0	*Q. robur*
	Agden	BL	3	2.8	54.4	5.4	0.0	77.0	*Alnus glutinosa*
	Strines	BL	4	3.8	23.3	5.4	4.4	80.1	*Q. robur*
	Emlin	BL	5	2.92	11.7	4.3	0.0	75.1	*Q. robur*
	Cote	CON	1	3.7	0.0	7.1	14.3	96.5	*Larix decidua*
	Fagney	CON	2	3.8	0.0	6.5	17.4	81.7	*Picea sitchensis*
	Linch	CON	3	3.4	23.3	5.0	2.3	53.4	*P. sitchensis/ Pinus sylvestris*
	Ouzelden	CON	4	3.3	0.0	6.1	6.5	74.4	*L. decidua*
	Lady	CON	5	3.5	0.0	6.5	7.4	96.1	*P. sitchensis*
Ireland	Glenisland	BL	1	10.7	18.5	7.1	49.13	211.0	*A. glutinosa*
	Cottage	BL	2	3.5	4.5	7.6	41.25	177.0	*Crataegus monogyna*
	Crumpaun	BL	3	9.5	53.0	7.5	43.68	176.2	*A. glutinosa*
	Altaconey	CON	1	1.0	13.0	7.7	22.4	111.0	*P. sitchensis*
	Rough	CON	2	4.0	14.0	7.5	7.1	214.0	*P. sitchensis*
	Bangor	CON	3	5.0	56.6	4.0	0.0	145.0	*P. sitchensis*
Poland	Turbacz	BL	1	34.0	245.0	7.8	80.2	187.8	*Fagus sylvatica*
	Ustępne	BL	2	33.3	245.0	8.2	82.6	193.1	*F. sylvatica*
	Kamienica	BL	3	53.0	196.7	7.8	75.7	166.8	*F. sylvatica*
	Olszowy	BL	4	35.3	235.0	8.3	84.9	180.0	*F. sylvatica*
	Roztoka	BL	5	37.9	242.5	8.3	96.1	208.0	*F. sylvatica*
	Czerwonka	CON	1	40.2	273.8	7.7	74.6	167.4	*Picea abies*
	Gorcowy	CON	2	67.4	262.5	8.2	77.7	170.7	*F. sylvatica*
	Lepietnica	CON	3	58.1	220.0	8.1	91.4	194.4	*P. abies*
	Furcówka	CON	4	40.1	245.0	8.3	87.2	196.4	*Abies alba*
	Sielski	CON	5	39.2	342.5	8.2	78.7	190.0	*P. sylvestris*

Water chemistry values are means of analyses from water samples collected at sampling times ($n = 3$). The most common riparian tree species in each site is also listed.
BL, broadleaved; CON, conifer.

in that they were only present at the study altitude due to artificial commercial planting on cleared natural beech forests. The sites differed with respect to the dominant riparian tree species present (Table 1).

Water quality

Conductivity and pH were measured on each sampling date using portable field meters: Hanna Instruments HI9024 and HI9835 in Britain (Hanna Instruments Ltd., Leighton Buzzard, U.K.); in Ireland Wissenschaftlich-Technische Werkstätten (WTW) Conduktometer LF 191 and pH 192 (see below); in Poland WTW Conduktometer LF 191 (WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) and Elmetron CX742 (Elmetron SPJ., Zabrze, Poland). Although all meters were calibrated prior to use where necessary, intercalibration between regions was not possible. Ammonium ($N–NH_4$), dissolved inorganic nitrogen (DIN) and phosphate ($P–PO_4$), were analysed from filtered water samples using standard laboratory techniques. Analyses in Britain and Poland were performed using ion chromatography (Dionex, Camberley, U.K.), while in Ireland a Lachat FIA (Lachat Instruments, Loveland, CO, U.S.A.) was used. Water temperature was measured every 2 h throughout the experiments using Smartbutton® temperature loggers (ACR Systems Inc., Surrey, BC, Canada) which were calibrated prior to use in each stream. Degree-days of exposure were calculated by multiplying the average water temperature by the number of days that the bags were left in each stream; this enabled us to correct for potential temperature dependency in breakdown rates among sites and over time.

Litter bag procedure

Freshly abscised alder and oak leaves were collected locally during autumn 2002 and air-dried to constant mass. Two mesh sizes were used, coarse (10 mm) and fine (0.5 mm) and each bag was individually labelled and filled with 5.0 g (±0.1 g) of either oak or alder leaves. Litter bags were secured by nylon twine to metal poles hammered into riffles. In total, 624 bags were used (6 replicates × 2 mesh apertures × 2 leaf species × 26 streams). A single collection was made for each leaf species at the estimated T_{50} (i.e. the time at which 50% of the initial leaf mass had been lost), which was calculated from additional bags placed in a reference stream in each region that were sampled repeatedly to derive breakdown rates over an extended time series (data not presented here; after Hladyz *et al.*, 2009). The experiments commenced at slightly different times of the calendar year in each region to standardise for seasonal differences in the timing of deciduous leaf-fall and collection times varied depending on the rate of breakdown. Due to the unusually warm and calm autumn of 2002, leaf-fall was severely delayed in Britain and Ireland and the field experiments could not therefore commence until January 2003. In Britain, the experiment started on 6 January 2003 and alder bags were collected after 35 and oak bags after 77 days; in Ireland, the litter bags were placed in the streams on 21 January 2003 and alder and oak bags were both collected on day 35 due to unexpectedly high breakdown rates. The Polish trial started on 4 November 2002, with alder bags collected on day 75 and oak bags on day 125, due to very low ambient temperatures and slow breakdown rates as the streams froze over.

The retrieved litter bags were transported in individual plastic bags to the laboratory, where invertebrates were removed and preserved in alcohol. The leaf material was washed to remove inorganic fractions, dried to constant mass at 105 °C and weighed. Ash-free dry mass was then estimated by ashing a subsample of leaf material in 500 °C for 4 h to correct for inorganic contamination. Leaf-litter breakdown rates were measured using the negative exponential model $M_t = M_i \times e^{-tk}$, where M_t is the remaining mass at time t, M_i is the initial mass and k is the breakdown rate constant (Petersen & Cummins, 1974; Castela, Ferreira & Graça, 2008). All invertebrates were identified (non-shredders to family and shredders to genus or species), counted and assigned to 'functional feeding groups', after Tachet *et al.* (2000). Shredder biomasses were determined directly by drying and weighing pooled samples in the U.K. and Ireland; in Poland published body length–biomass regressions applied to each individual shredder were used to calculate the total biomass in each sample (after Meyer, 1989; Wenzel, Meyer & Schwoerbel, 1990; Benke *et al.*, 1999; Baumgärtner & Rothhaup, 2005). Where length–mass regressions were not available for a particular genus, the closest relative was used instead (e.g. for *Nemurella* we used *Nemoura* and for *Capnia* we used *Allocapnia*).

Benthic samples

To quantify shredder abundance, taxon richness and biomass, five benthic samples were taken from each stream with a Surber sampler (quadrat area: 0.0625 m^2, 250 μm mesh aperture) at the time of alder litter bag collection. These samples were preserved in alcohol and later processed in the laboratory, where the invertebrates were identified to the lowest possible taxonomic level (usually species), counted, assigned to functional groups and their biomass estimated (see above). Benthic organic matter standing stocks were derived from these samples in Ireland and Britain.

Statistical analyses

Water chemistry was compared between regions and riparian vegetation types via two-way ANOVAS. Prior to analysis of breakdown rates, data were corrected for temperature differences among the regions by expressing mass loss rates in degree-days. These values were then transformed using the absolute value of the exponential breakdown coefficient (k), followed by a $\log(x + 1)$ transformation to normalise the data and to stabilise variances. The data were analysed using a nested, mixed Type III General Linear Model (GLM): litter bag replicates were nested within stream pairs, which in turn were nested within each region. The data were analysed twice, both with and without pH as a covariate, to assess its importance as a driver of breakdown rates. The following variables were selected as fixed factors in the analyses: region, vegetation type, mesh size, leaf type and stream pair (which were designated *a priori*, see Site description). Replicate was fitted as a random factor. The shredder data from litter bags and benthic samples were also analysed using GLM; to meet the assumptions of the model, shredder abundance and biomass were $\log_{10}(x + 1)$ transformed, whereas for shredder taxon richness a square-root transformation was used. Outliers with residuals >4 SD were excluded from the analyses.

The shredder assemblages in litter bags were related to physicochemical variables by direct gradient analysis using Canoco for Windows 4.5 (ter Braak & Šmilauer, 1999). Species counts were square-root $(x + 1)$ transformed prior to analysis and species with only single occurrences across the data set were removed to reduce the potential influences of very rare taxa, which are prone to being artefacts of rarefaction. Partial redundancy analysis (pRDA), with centering by species and samples, was used to determine which subset of physicochemical variables accounted for most variation in the shredder data. Leaf type was partialled out as a covariable so that species data could be examined independently of resource type. Forward-selection procedures were used to ensure only significant physicochemical variables were included in the final model ($P < 0.05$; using 9999 Monte Carlo permutations).

Results

Water chemistry

Overall, Ireland and Britain were more similar to each other in water chemistry than either was to Poland (Table 1). Water chemistry variables did not differ between vegetation types but differed among regions: phosphate ($F_{2,20} = 95.88$, $P < 0.001$), ammonium ($F_{2,20} = 225.71$, $P < 0.001$), pH ($F_{2,20} = 14.77$, $P < 0.001$) and conductivity ($F_{2,20} = 27.36$, $P < 0.001$) (Table 1).

Mass loss in litter bags

The two analyses performed on the mass loss data, excluding and including pH as a covariable, concurred in the majority of cases for the main effects in the model, with the notable exception of vegetation type (Table 2). Region, leaf type, mesh type and stream pair were all significant predictors in both analyses (see Table 2 for details). In general, leaf mass loss was faster from coarse litter bags than from fine litter bags, and from alder bags than from oak bags (Fig. 1), but regional differences resulted in significant region × mesh and region × leaf interactions (Table 2).

In the GLM, riparian vegetation type was not significant, although a region × vegetation type interaction was evident (Table 2). However, this interaction disappeared when pH was fitted as a covariate. Thus, there was no evidence for an overall suppression of breakdown rates in conifer streams, and in some instances the converse was true: both Britain and Poland, for instance, exhibited higher coarse alder breakdown rates in conifer streams than in broadleaved streams (Fig. 1).

Shredders in litter bags

Regional differences in shredder abundance, richness and biomass were evident (Table 3, Fig. 2), but the

Table 2 GLM analysis of leaf-litter breakdown rates (*k*-values), both including and excluding pH as a covariate

		No covariate		pH as covariate	
Source	d.f.	*F*-value	*P*-value	*F*-value	*P*-value
pH	1	–	–	21.98	0.000
Region	2	63.45	0.000	20.43	0.000
Riparian vegetation	1	0.25	0.616	1.68	0.195
Leaf	1	238.56	0.000	247.87	0.000
Mesh	1	164.96	0.000	165.82	0.000
Pair (Region)	10	8.44	0.000	4.70	0.000
Replicate (Region Pair)	65	0.71	0.958	0.69	0.967
Region × Vegetation	2	7.62	0.001	0.57	0.566
Region × Leaf	2	16.80	0.000	17.17	0.000
Region × Mesh	2	3.01	0.050	3.42	0.033
Vegetation × Leaf	1	0.26	0.608	0.24	0.623
Vegetation × Mesh	1	0.49	0.484	0.41	0.525
Region × Vegetation × Leaf	2	1.27	0.283	1.28	0.280
Region × Vegetation × Mesh	2	0.26	0.772	0.29	0.754

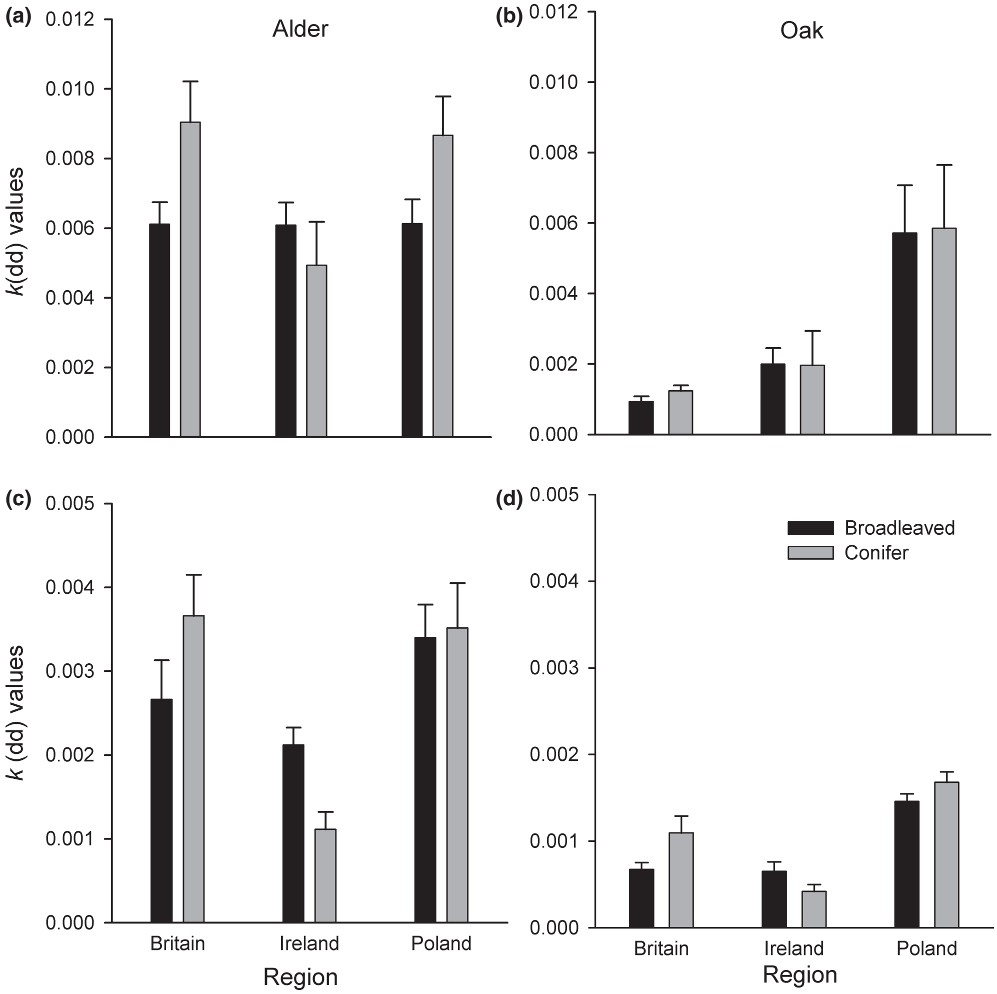

Fig. 1 *k*-values (corrected with degree-days) for alder (a, c) and oak (b, d) litter bags with two different mesh apertures: coarse (10 mm) (a, b) and fine (0.5 mm) (c, d) (±1 SE) in the three regions.

effects of vegetation type were not consistent across regions. For example, shredder abundance was similar in Britain and Ireland and it was higher in conifer streams than in broadleaved streams, but in Poland the opposite pattern was observed (Fig. 2a). Vegetation type affected shredder abundance but not shredder richness or biomass (Table 3). Although vegetation type on its own was not significant, the region × vegetation type interaction suggested significant within-region impacts of vegetation for both richness and biomass (Table 3). Shredder abundance and richness increased significantly with pH, but biomass did not (Table 3).

From the whole dataset, Britain had the highest shredder richness in the litter bags (Fig. 2b), but the overall richness in the data set was similar and relatively low. The number of shredder taxa found was similar in alder and oak bags. Conifer sites in Britain had consistently more taxa than broadleaved sites, whereas in Ireland the opposite held true, but only for alder bags (Fig. 2b). Shredder biomass was highest in the Irish broadleaved sites (alder bags) and Polish broadleaved sites (oak bags) (Fig. 2c), reflecting the significant differences among stream pairs and regions (Table 3).

The composition of the shredder assemblages in the litter bags differed both within and among regions, as revealed by the pRDA (Fig. 3). When added sequentially, conductivity explained most of the variation ($\lambda A = 0.08$, $F = 20.59$, $P < 0.001$), followed by pH ($\lambda A = 0.04$, $F = 13.58$, $P < 0.001$), phosphate ($\lambda A = 0.04$, $F = 13.96$, $P = 0.001$), vegetation type ($\lambda A = 0.04$, $F = 12.97$, $P < 0.001$) and ammonium ($\lambda A = 0.01$, $F = 2.84$, $P = 0.033$). According

Table 3 Summary statistics for GLMs comparing shredder abundance, richness and biomass

		Shredder abundance (bag^{-1})		Shredder species richness (bag^{-1})		Shredder biomass (mg bag^{-1})	
Source	d.f.	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
pH	1, 197	4.29	0.040	4.82	0.029	0.25	0.620
Region	2, 197	15.09	0.000	26.54	0.000	0.88	0.415
Vegetation type	1, 197	12.49	0.001	3.27	0.072	1.67	0.198
Leaf type	1, 197	4.53	0.035	3.58	0.060	2.46	0.118
Pair (Region)	19, 197	7.54	0.000	4.68	0.000	8.04	0.000
Replicate (Region Pair)	65, 197	0.49	0.999	0.53	0.998	0.53	0.998
Region × Vegetation	2, 197	15.94	0.000	3.34	0.037	3.26	0.041
Region × Leaf	2, 197	2.77	0.065	0.46	0.633	2.02	0.135

to the interset correlations, vegetation type was most strongly positively correlated with axis I (0.34), whereas the strongest negative correlation with axis I was with conductivity (−0.43), followed by phosphate (−0.35), ammonium (−0.34), alkalinity (−0.32), DIN (−0.17) and pH (−0.13). For axis II, the most strongly correlated environmental variables were alkalinity (−0.24), pH (−0.21) and phosphate (−0.17).

The stonefly genera *Amphinemura* and *Leuctra* spp. were most strongly associated with conifer site litter bags (Fig. 3). The stoneflies *Nemoura* and *Protonemura* and limnephilid caddis genera (*Chaetopteryx*, *Halesus* and *Potamophylax*) were associated with broadleaved vegetation sites. The amphipod shrimp *Gammarus*, *Nemoura* and *Protonemura* were the only taxa to show significant associations with individual environmental variables: *Gammarus* was found in high conductivity sites, whereas *Nemoura* preferred higher ammonium concentrations and *Protonemura* was associated with water pH (Fig. 3). Overall, the smaller plecopteran shredders (*Amphinemura* and *Leuctra*) were generally found in low conductivity, low alkalinity, conifer streams whereas other shredders (limnephilid caddis and *Gammarus*) had a stronger affinity towards higher conductivity, higher alkalinity, broadleaved streams. In Poland, however, *Gammarus* was also abundant in the circumneutral conifer stream. *Protonemura* was found in both riparian vegetation types in all the three regions.

Benthic invertebrates and organic matter

The patterns of shredder abundance seen in the litter bags were also evident in the benthic samples (Fig. 4), where highest abundances were found in British conifer streams and lowest in Irish broadleaved streams. Region had a significant effect on abundance ($F_{2,62} = 16.40$, $P < 0.001$), as did vegetation type ($F_{1,62} = 4.38$, $P = 0.040$), but shredder richness was only affected by the former ($F_{2,62} = 5.26$, $P = 0.008$). Differences between stream pairs for shredder abundance ($F_{10,62} = 10.07$, $P < 0.001$) and richness ($F_{10,62} = 3.46$, $P = 0.002$) were also evident. Benthic shredder biomass differed significantly between regions ($F_{2,62} = 19.95$, $P < 0.001$) and differences were also observed between pairs within regions ($F_{10,62} = 5.51$, $P < 0.001$).

Standing stocks of organic matter were measured only for Britain and Ireland. The lowest organic matter biomass was found in Irish broadleaved sites (0.5 g ±0.43 SE Surber^{-1}) but the organic matter retention was similar in Irish conifer sites (2.42 g ±2.94 SE) and British broadleaved (2.1 g ±0.53 SE) and conifer (1.8 g ±0.48 SE) sites. However, the average biomass in British broadleaved sites was heavily biased due to one sample containing a large quantity of CWD and after this outlier was removed, the average coarse particulate organic matter biomass was 1.5 g (±0.53).

Discussion

This study enhances our understanding of ecosystem functioning in streams affected by commercial conifer plantations. Results show that water chemistry, rather than vegetation type *per se*, had overriding influence on litter breakdown rates in forested headwater streams, even though riparian vegetation had a significant influence on the relative and absolute abundance of shredders. Strong impacts on community structure were therefore observed without

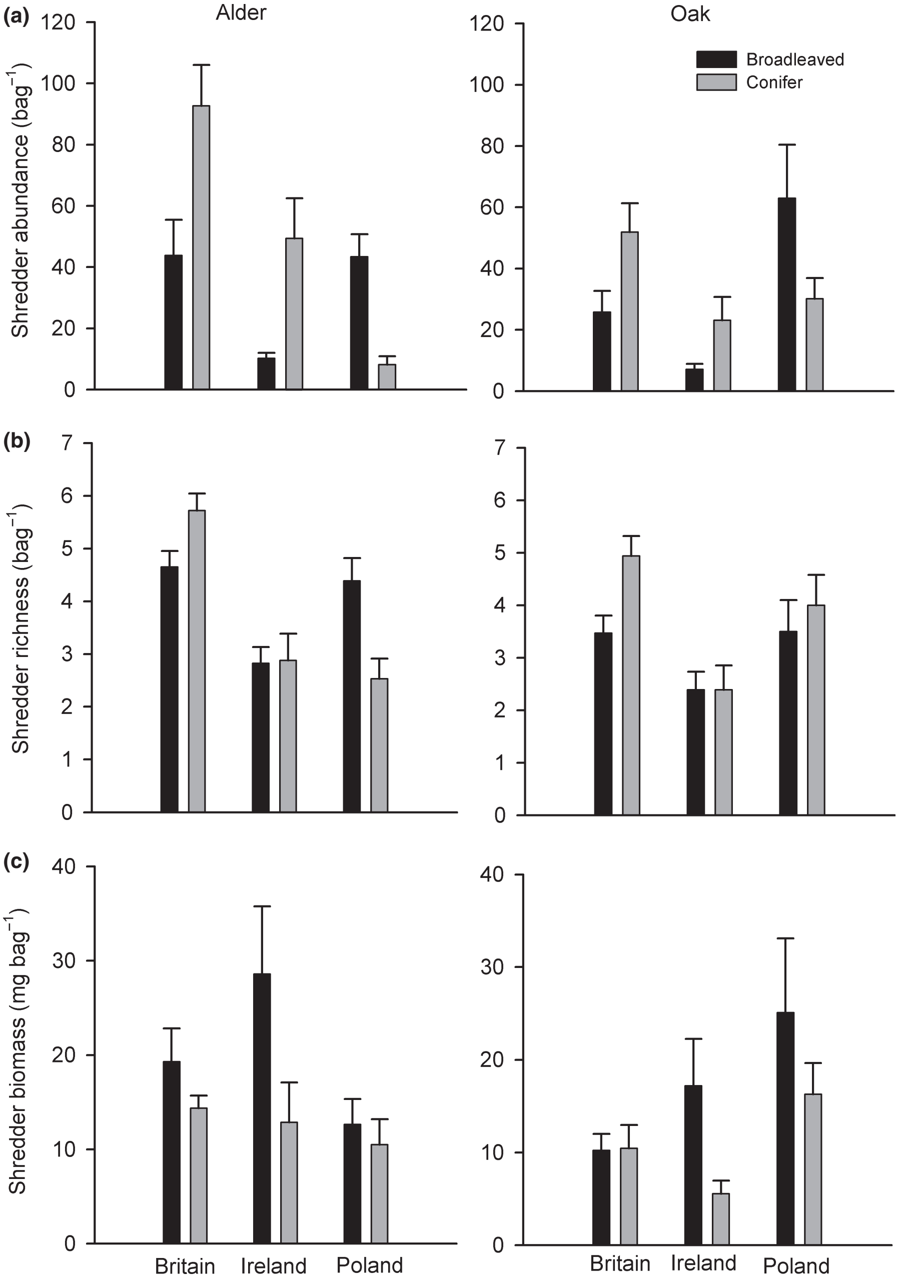

Fig. 2 Average shredder abundance (a), richness (b), biomass (c) in litter bags. Data are presented for two leaf types (alder and oak) in two riparian vegetation types (broadleaved and conifer) in the three ecoregions (±1 SE).

a corresponding difference in function. Ecosystem process rates were not impaired in streams with coniferous riparian vegetation. This suggests a high degree of functional redundancy and a loose coupling of structure and function (see Riipinen, Davy-Bowker & Dobson, 2008). Huryn *et al.* (2002) also previously found a high degree of redundancy in the shredder assemblage when comparing breakdown rates between forested, wetland, agricultural and urban systems, suggesting that this phenomenon might be ubiquitous.

As natural conifer forests mature, increased input of leaf-litter and CWD increases habitat complexity and provides increased habitat and food availability for shredders (Pretty & Dobson, 2004). This process is impaired in commercial forests due to the felling and

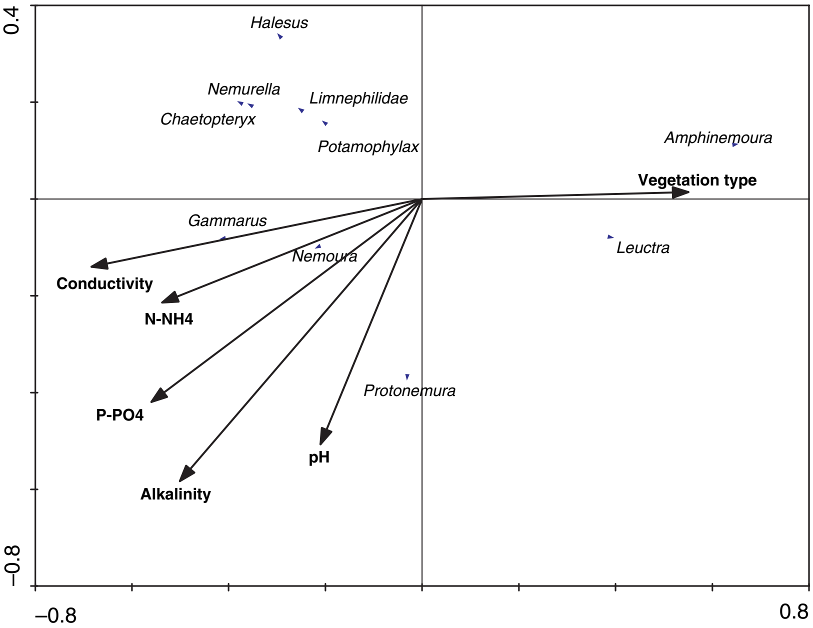

Fig. 3 Partial redundancy analysis of invertebrate genera of shredders in experimental leaf bags in the 26 streams differing in riparian vegetation type, with the effect of leaf type removed by fitting it as a covariate. Single occurrence species were removed prior analysis and only significant environmental variables are included in the analysis.

removal of the younger trees, so natural and commercial forest streams might be expected to differ markedly in terms of consumer and resource abundance and, by extension, ecosystem functioning (Friberg, 1997). However, the data for Britain and Ireland suggest that conifer sites did not suffer from reduced retention of organic matter in comparison to the broadleaved sites; on the contrary, conifer sites had higher benthic organic matter biomass than the broadleaved sites, suggesting that the level of organic matter retention is not necessarily a ubiquitous problem for stream function in coniferous streams. The higher benthic organic matter standing stocks may have caused the benthic shredder numbers to be higher, but this resulted in higher breakdown rates only in British conifer sites whereas the breakdown rates in Ireland were not affected.

Planting of conifer forests is often carried out in areas of low buffering capacity and therefore streams in these areas commonly suffer from the additional stress of acidification (Harriman & Morrison, 1982; Ormerod *et al.*, 1989; Clenaghan *et al.*, 1998). In Ireland, however, some previous studies have shown that acid pulses are not manifested in conifer sites during spates in well-buffered areas (Clenaghan *et al.*, 1998) although in other areas, such as County Mayo (where this study sites were located), this is not necessarily the case (Giller & O'Halloran, 2004).

The importance of pH on stream ecosystem functioning has been considered before (e.g. Dangles & Guérold, 1999, 2000). However, this study emphasises that vegetation effects should not be interpreted from pH effects in isolation when the two may be linked, especially at the community level of organisation. In fact, we found no significant effect of riparian vegetation in the overall analyses once the covarying effect of pH had been removed. However, we recognise that our few spot measurements were unlikely to represent the entire range of variation in pH at all our sites. Communities under episodic acidification may remain relatively impoverished even if the average pH remains relatively high (Kowalik *et al.*, 2007). Nevertheless, our pH measurements are probably broadly realistic considering the sampling coincided with the season when low pH due to acid pulses is most likely.

Acid-tolerant nemourid stoneflies (*Leuctra* and *Amphinemura*) were most strongly associated with conifers, whereas limnephilid caddisfly larvae were more common in broadleaved streams. This differs from the study by Friberg (1997), who found that larger shredders with longer life cycles were more strongly associated with coniferous than with mixed broadleaved streams in Denmark. Leaf-litter processing in streams with low pH could also be impacted via the loss of key taxa that contribute significantly to overall processing efficiency, such as *Gammarus* spp. (Dangles *et al.*, 2004a). *Gammarus* can have especially

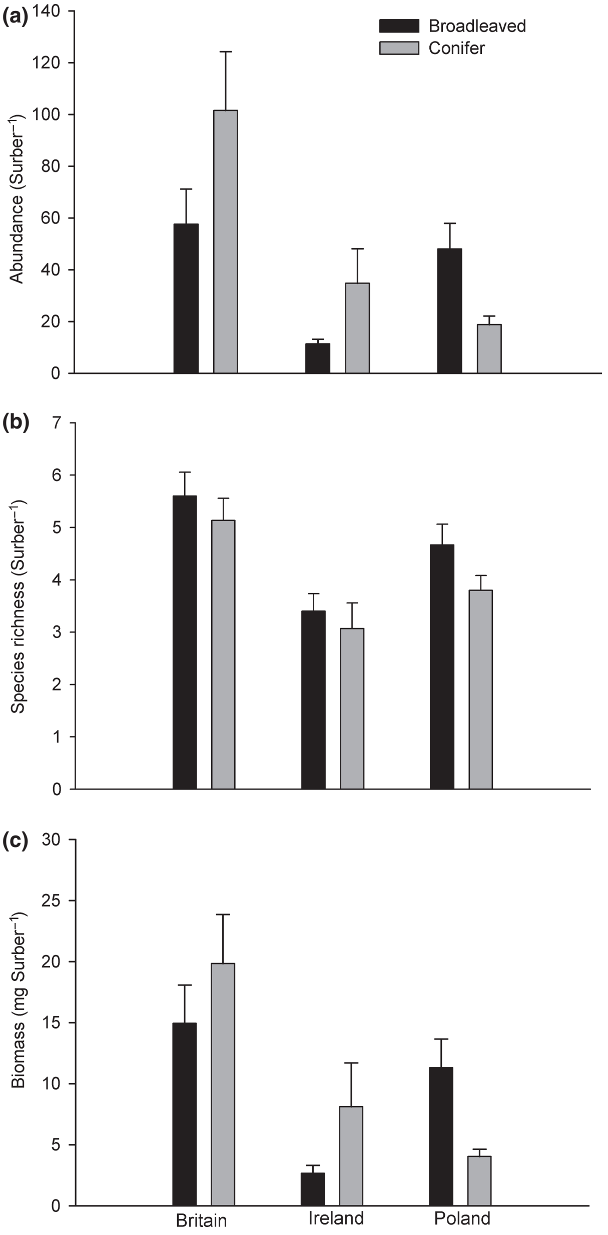

Fig. 4 Shredder abundance (a), number of shredder taxa (b) and shredder biomass (c) in the benthos of the study sites. Values are mean (±1 SE) for five samples, each covering an area of 25 × 25 cm (0.0625 m^2).

strong positive impacts on breakdown rates and where they occur, they can often dominate the invertebrate assemblage (Vought, Kullberg & Petersen, 1998; Maltby *et al.*, 2002; Dangles & Malmqvist, 2004; Woodward *et al.*, 2008). It is therefore a possibility that competitive release of generalist herbivore–detritivores (such as nemourid stoneflies) occurs in acidified systems, as proposed previously by Hildrew, Townsend & Francis (1984).

Shredder identity and abundance were important in determining breakdown rates. Larger caddis shredder taxa in broadleaved streams replaced *Amphinemura* and *Leuctra*, which are less effective *per capita* consumers (Dangles & Guérold, 2001) in conifer sites. Intriguingly, our data suggested that breakdown rates might be maintained at least partially by density compensation, indicating a degree of functional redundancy within the shredder guild. Given the strong potential for trophic redundancy amongst generalist detritivores in stream food webs (e.g. Friberg & Jacobsen, 1994; Ledger & Hildrew, 2000; Woodward, Speirs & Hildrew, 2005), the maintenance of equivalent ecosystem process rates in different assemblages might not be so surprising and merits further study, particularly as it has profound implications for the robustness of stream ecosystems that are exposed to perturbations (Woodward, 2009). Several authors have suggested that exotic conifer plantations are detrimental to stream community structure (e.g. Ormerod *et al.*, 1989, 1993, 2004; Dobson & Cariss, 2000; Laitung *et al.*, 2002; Harriman *et al.*, 2003) and/or ecosystem functioning (Pretty & Dobson, 2004; Pretty *et al.*, 2005). In relation to impacts on the former, reduced abundance, diversity, biomass, emergence and adult size of invertebrates have all been reported (Ventura & Harper, 1996; Thomsen & Friberg, 2002). It is possible, however, that many of the previous studies might have been confounded by acidity. This was not the case in this study; within regions, some large differences in breakdown rates were observed between the vegetation types but these were not consistently associated with impairment in conifer streams. Riparian vegetation did not significantly affect leaf-litter processing overall, although a significant region × vegetation type interaction was observed.

In summary, the results from this study suggest that: (i) stream pH is more important than riparian vegetation in determining litter breakdown rates; (ii) shredder identity and abundance drove breakdown rates and these variables were dependent primarily upon pH; (iii) although breakdown rates differed among regions, these differences were largely ascribed to water chemistry. Hence within these three European regions, conifer plantations might not be as deleterious to the structure and functioning of stream ecosystems as was previously thought. Clearly, the impacts of vegetation type and its possible interactions with water chemistry on shredder community structure and subsequent processing efficiency need to be considered in future studies. In particular, the potential role of functional redundancy within and across stream food webs (via feeding plasticity or density compensation) needs further investigation, as this could provide a mechanism by which ecosystem functioning is maintained even in the face of such seemingly profound disturbances as acidification or riparian alterations.

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