Oecologia (2005)
DOI 10.1007/s00442-005-0212-3

ECOSYSTEM ECOLOGY

Antoine Lecerf · Michael Dobson · Christian K. Dang
Eric Chauvet

Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems

Received: 4 February 2005 / Accepted: 5 July 2005

Abstract Riparian vegetation is closely connected to stream food webs through input of leaf detritus as a primary energy supply, and therefore, any alteration of plant diversity may influence aquatic ecosystem functioning. We measured leaf litter breakdown rate and associated biological parameters in mesh bags in eight headwater streams bordered either with mixed deciduous forest or with beech forest. The variety of leaf litter types in mixed forest results in higher food quality for large-particle invertebrate detritivores ('shredders') than in beech forest, which is dominated by a single leaf species of low quality. Breakdown rate of low quality (oak) leaf litter in coarse mesh bags was lower in beech forest streams than in mixed forest streams, a consequence of lower shredder biomass. In contrast, high quality (alder) leaf litter broke down at similar rates in both stream categories as a result of similar shredder biomass in coarse mesh bags. Microbial breakdown rate of oak and alder leaves, determined in fine mesh bags, did not differ between the stream categories. We found however aquatic hyphomycete species richness on leaf litter to positively co-vary with riparian plant species richness. Fungal species richness may enhance leaf litter breakdown rate through positive effects on resource quality for shredders. A feeding experiment established a positive relationship between fungal species richness per se and leaf litter consumption rate by an amphipod shredder (*Gammarus fossarum*). Our results show therefore that plant species richness may indirectly govern ecosystem functioning through complex trophic interactions. Integrating microbial diversity and trophic dynamics would considerably improve the prediction of the consequences of species loss.

Keywords Trophic interactions · Microbial diversity · Ecosystem functioning · Shredders · Leaf litter breakdown

Communicated by Roland Brandl

A. Lecerf (✉) · E. Chauvet
Laboratoire Dynamique de la Biodiversité
UMR 5172 CNRS-UPS, 29 rue Jeanne Marvig
31055 Toulouse, France
E-mail: lecerf@cict.fr
Tel.: +33-562-269993
Fax: +33-562-269999

M. Dobson
Department of Environmental Geographical Sciences
Manchester Metropolitan University, Chester St.,
M1 5GD Manchester, UK

C. K. Dang
EAWAG, Limnological Research Center
CH-6047 Kastanienbaum, Switzerland

Introduction

Confronted with the dramatic species extinction rate on Earth (Pimm et al. 1995), ecologists have spent the past decade addressing the potential consequences of species loss on ecosystem function (Chapin et al. 2000; Loreau et al. 2002). Since the first experiments on the diversity–productivity relationship, there has been recent growing interest for understanding how plant diversity effects can be propagated through food webs (Hooper et al. 2000; Raffaelli et al. 2002; Thébault and Loreau 2003). Particularly relevant to this issue is the effect of altered food resources, caused by changed plant diversity, on first-order consumers (e.g., Loreau 2001; Thébault and Loreau 2003). However, this remains poorly understood, and is difficult to study, requiring simultaneous consideration of interacting multiple trophic levels (Polis et al. 1997; Raffaelli et al. 2002).

Stream detritus food webs are ideal systems in which this question can be explored. In most low order heavily shaded streams, detritus derived from terrestrial riparian vegetation represents the dominant energy supply (Vannote et al. 1980; Wallace et al. 1997). This creates a strong unidirectional link between terrestrial primary producers and aquatic consumers (Vannote et al. 1980;

Cummins et al. 1989; Bärlocher 1992; Polis et al. 1997; Wallace et al. 1997). Leaf litter is the most abundant and most predictable food supply of high quality to large-particle invertebrate detritivores ('shredders') and microbial decomposers (Webster and Benfield 1986; Graça 2001). Aquatic hyphomycetes fungi are the dominant microbial component in detritus food webs (Bärlocher 1992; Gessner and Chauvet 1994; Hieber and Gessner 2002). In addition to direct breakdown, aquatic hyphomycetes enhance leaf quality for shredders through conditioning (see reviews in Suberkropp 1992, 2003), involving both leaf tissue softening by fungal enzymes (Bärlocher and Kendrick 1975; Graça et al. 1993a) and providing mycelia as food (Cargill et al. 1985; Arsuffi and Suberkropp 1988).

Dynamics of stream detritus food webs are, therefore, based on the interaction between the basal resource, aquatic hyphomycetes and shredders. However, despite interest directed towards the role of species diversity among shredders and fungi in leaf litter breakdown (e.g., Jonsson and Malmqvist 2000; Bärlocher and Corkum 2003), the possible influence of diversity within the leaf litter resource per se has been neglected (Swan and Palmer 2004). Furthermore, while differences in the conditioning ability of different fungal species have been documented (e.g., Bärlocher and Kendrick 1973; Arsuffi and Suberkropp 1984, 1988; Graça et al. 1993a), the influence of fungal diversity on leaf consumption rate by shredders remains unexplored (Suberkropp 2003).

Some theoretical stream ecosystem models predict that a reduction in riparian tree diversity — and therefore in diversity of leaf litter input — will have a strong bottom-up influence on both structure and function of detritus food webs (Pringle et al. 1988; Cummins et al. 1989). Scattered evidence partly supports this statement. Composition and diversity of riparian forest vegetation was found (1) to influence aquatic hyphomycetes assemblages (Bärlocher and Graça 2002; Laitung et al. 2002; Laitung and Chauvet 2005), (2) to affect secondary production of shredders in streams (Stout et al. 1993; Friberg et al. 2002), and (3) to have an impact on leaf litter breakdown rate (Swan and Palmer 2004). Despite these individual lines of evidence, there has been no attempt to assess how leaf litter diversity may influence detritus food webs and therefore affect stream ecosystem functioning.

The aim of this study was to test the hypothesis that altering resource diversity entering a detritus-based stream would influence ecosystem functioning through effects on shredders and aquatic hyphomycetes. For this purpose, we compared leaf litter breakdown in headwater streams running through either mixed forests or forests dominated by beech. We used a fast and slow decomposing leaf species as, respectively, high- and low-quality food resource for shredders to assess how differences in species composition of litter inputs between both forest types influence resource–consumer links. To limit the effects of confounding factors such as litter fall timing and input amount, which might co-vary with riparian plant diversity, we focused on fully deciduous riparian vegetation comprising only native species. In addition, a feeding experiment was conducted in the laboratory to test whether changes in fungal composition and richness alter leaf consumption rate by shredders, and thus, indirectly, litter breakdown.

Materials and methods

Field experiment

Study sites

The experiment was carried out in the Montagne Noire, South-Western France, a 1,450-km^2 highland region covered by a mixed broadleaf forest. Climatic conditions are marked by high rainfall (average 1,500 mm year^{-1}). Eight first- or second-order permanent streams with similar physical characteristics (Table 1) were selected in forested areas, situated between 2°05′19″E and 2°26′27′E longitude and 43°24′44′N and 43°29′23″N latitude. In all catchments, forestry management was the only major anthropogenic disturbance, without however any marked alterations of stream habitats (Laitung et al. 2002). Some areas were still under traditional forest management, in which riparian vegetation remains a diverse mixture of species; in contrast, a significant area was converted during the twenteeth century to intensive production of beech (*Fagus sylvatica* L.). Even-aged pure beech stands had been created by selective cutting of non-commercial trees during forest rotation; this kind of treatment has little effect on the quantity of litter fall (Hölscher et al. 2002), but reduces the diversity of leaf litter inputs considerably. The effect of riparian plant diversity was assessed by comparing four reference streams (Fraissègne, Ladoux, Oréval, Montaud), chosen in mixed deciduous forests, with four streams (Lestrèpe, Linon, Prune, Rieusoul) located in mature

Table 1 Physical and chemical characteristics of study streams according to forest type; range of stream values for altitude, slope, catchment area, discharge (determined once at medium water level during the winter 2003) and degree-days (cumulative temperature during the time of alder and oak exposure); range of mean stream values ($n = 3$ monthly samples) for other factors

Factor	Mixed forest	Beech forest
Altitude a.s.l. (m)	500–800	500–800
Slope (m m^{-1})	0.05–0.25	0.05–0.19
Catchment area (km^2)	0.4–2.3	0.6–1.1
Discharge (l s^{-1})	14–67	5–62
Degree-days (alder)	264.1–300.9	313.6–327.6
Degree-days (oak)	496.5–607.4	597.0–655.9
Mean temperature (°C)	6.5–7.8	7.8–8.6
pH	6.3–6.5	5.7–7.3
Conductivity (μS cm^{-1})	38–62	27–210
Alkalinity (mg $CaCO_3$ l^{-1})	2.5–7.3	0.9–68.9
P-PO_4 (μg l^{-1})	2.0–3.1	1.6–4.0
N-NO_3 (μg l^{-1})	1,151–1,803	395–2,239

beech forests. For each of our study streams, the whole water course from the source to the sampling station ran under the same forest type, thereby avoiding any bias due to upstream–downstream linkage.

Stream characterization

During the breakdown study (from mid-December 2002 to February 2003), water temperature was recorded every 2 h (SmartButton, ACR System Inc.) and water chemistry was assessed monthly. Conductivity and pH were measured in the field (WTW pH-meter 320i; WTW Cond 320i). Alkalinity, nitrate, nitrite and ammonia concentrations were determined following colorimetric standard methods (APHA 1989), while orthophosphate concentration was determined by the malachite green method, which is appropriate when quantifying extremely low concentrations (Motomizu et al. 1983).

Riparian plant diversity and composition were estimated by sampling ten naturally accumulated leaf packs with a hand net in each stream (*ca.* 100 m around the study site), and then pooling these to provide approximately 5 l of leaf material. Leaves were washed, sorted, oven-dried at 105°C for 48 h and weighed by species. Leaf species were then assigned to three categories (i.e., fast, medium or slow decomposing leaf species; Petersen and Cummins 1974) according to their breakdown rate in streams as determined in the literature (Webster and Benfield 1986; Gessner and Chauvet 1994) and from personal observations. Natural leaf packs were sampled on two occasions: immediately prior to beginning of the field experiment in mid-December 2002 and at its termination when the final mesh bags were removed in late February 2003.

Leaf litter breakdown

The litter bag method (Boulton and Boon 1991) was used to assess breakdown rate and the litter-associated biological parameters of two leaf litter species belonging to two distinct decomposing categories. Oak (*Quercus robur* L.) was preferred to beech, a tree species belonging to the same slow decomposing category, to avoid confounding effects because of beech leaf dominance in beech forest streams. Alder [*Alnus glutinosa* (L.) Gaertn.] leaf litter was selected to represent the fast decomposing species.

Freshly fallen leaves of both species were collected at abscission during autumn 2002 and placed into single-species mesh bags. About 5 g (± 0.05) of air-dried leaves were enclosed in fine (0.5-mm nylon) and coarse (10-mm plastic) mesh bags closed in a tetrahedral shape (Jonsson et al. 2001). The coarse mesh allowed large shredders such as limnephilid caddisflies to enter, whereas fine mesh excluded most of the invertebrates without interfering with microbial colonization (Boulton and Boon 1991). An experimental unit consisted of the combination of both leaf species and both types of mesh bags. Six replicates of each bag type were installed on December 13, 2002 in each of the eight streams and secured by a rebar anchored in the sediments. Prior to transporting to the field, leaf litter was sprayed with distilled water to prevent breakage during handling and transport. Four additional fine mesh bags of each leaf species were constructed but kept in the laboratory as controls to determine initial leaf ash-free dry mass (AFDM). Alder and oak bags were retrieved after 36–37 and 77–78 days, respectively, and stored individually in plastic zip-lock bags at stream temperature during transport to the laboratory.

Upon retrieval the leaves were washed individually with tap water to remove sand, exogenous organic matter and invertebrates. Two sets of five 12-mm diameter discs were cut in five leaves from fine mesh bags, avoiding the central veins, and used latter to analyse the aquatic hyphomycetes assemblage. The remaining leaf material from both tree species was dried at 105°C for 48 h and weighed to the nearest 0.01 g. Samples were then ground using a Culatti micro hammer mill with 0.5-mm mesh. Portions of about 500 mg were ashed at 550°C for 4 h, then weighed to determine the organic matter content of leaf litter dry mass.

Fungi

Because slow decomposing leaves were naturally present in both mixed and beech forest streams, only oak was used for fungal analysis. Five oak leaf discs were frozen at −18°C until processing for ergosterol extraction. The other five were placed into 100-ml Erlenmeyer flasks filled with 25 ml filtered stream water (Whatman glass fibre GF/F) and used to induce sporulation (production of asexual fungal spores) by gently shaking (100 rpm, 25.4 mm orbital path) at 10°C (Gessner et al. 2003). After 48 h, spore suspensions were transferred into 50-ml polyethylene centrifuge tubes, the flask and discs were rinsed with distilled water to collect spores no longer in suspension, and the volume was adjusted to 35 ml with 2 ml of 37% formalin and distilled water as required. The sets of discs were then oven-dried and weighed to the nearest 0.1 mg. Tubes were stored in the dark until counting and identification of the fungal spores. For that purpose, samples were treated with 1 ml of Triton X-100 (0.01% solution) and stirred for at least 10 min. Then, 5 ml of suspension was filtered through a membrane filter (5 μm pore size), and the spores on the filter were stained with 0.02% Trypan blue in lactic acid. At least 200 spores were identified and counted under the microscope (× 320). Sporulation rate was calculated as the number of spores released per milligram leaf litter AFDM and per day.

The frozen leaf discs were used to determine ergosterol content as a measure of fungal biomass (Gessner et al. 2003). Leaf material was freeze-dried, weighed to the nearest 0.1 mg and then lipids were extracted with

5 ml hot alkaline ethanol (KOH: 8 g l^{-1}) at 80°C for 30 min. We used solid-phase extraction (SPE) and the high-performance liquid chromatography method, slightly modified from Gessner and Schmitt (1996) to use more convenient cartridges (Waters Oasis HLB, 60 mg, 3 cc). After acidification of the extract (1 ml HCl 0.65 N), 3 ml was passed by gravitation through a conditioned cartridge and ergosterol was recovered with 1.4 ml isopropanol. Extraction efficiency (90.8 – 98.1%) was monitored for each series using control samples to calculate the ergosterol content in leaf litter. Fungal biomass in litter was expressed as ergosterol mass per milligram leaf litter AFDM.

Invertebrates

Invertebrates from coarse mesh bags were preserved in 70% ethanol, identified to genus level, assigned to functional feeding groups (Tachet et al. 2000) and counted. The biomass of each group was determined by weighing dried animals (60°C, 48 h) to the nearest 0.1 mg, and then expressed per gram AFDM of the remaining leaf litter.

Feeding experiment

Litter conditioning

Following the procedure of Suberkropp (1991), autoclaved packs of twenty 10-mm diameter leaf discs of oak were inoculated for 42 days in stream-simulating microcosms consisting of aeration chambers containing unconstrained leaf discs in 40 ml of nutrient-enriched water [per litre: 100 mg $CaCl_2$ $2H_20$, 10 mg $MgSO_4$ $2H_20$, 0.5 g morpholino propane sulfonic acid (MOPS), 100 mg KNO_3, and 5.5 mg K_2HPO_4] with aeration and pH adjusted to 7.0 with NaOH. The leaf discs were then freeze-dried (Sridhar et al. 2001) and weighed to the nearest 0.001 mg per set of two. The discs used for the feeding experiment were selected randomly among unfragmented discs.

Nine multi-species hyphomycetes combinations for each of the four richness levels (2, 4, 6 and 8 species) were drawn at random from a pool of 12 species. In addition, all species were grown in monoculture. This translated into a total of 49 treatments including one non-inoculated treatment. The fungal species used were *Alatospora acuminata* Ingold, *Anguillospora longissima* (Sacc. and Sid.) Ingold, *Articulospora tetracladia* Ingold, *Flagellospora curvula* Ingold, *Goniopila monticola* (Dyko) Marvanová and Descals, *Heliscus lugdunensis* Saccardo and Thérry, *Lemonniera aquatica* de Wildeman, *Lemonniera terrestris* Tubaki, *Tetrachaetum elegans* Ingold, *Tetracladium marchalianum* de Wildeman, *Tricladium chaetocladium* Ingold and *Tumularia aquatica* Ingold (Descals and Marvanová). All strains originated from streams in the Montage Noire and these fungal species were among the most common representatives from the study streams.

Feeding trial

The feeding experiment was conducted in the laboratory to assess the link between aquatic hyphomycetes diversity and leaf consumption rate by *Gammarus fossarum* Koch amphipods. Animals were collected from the Montaud stream and acclimated for 1 week to the laboratory (10°C in the dark, in stream water). They were provided with conditioned leaf litter for 6 days, but starved for 24 h prior to the beginning of the experiment. One sexually mature male (9.3 ± 0.6 mm: total length ± SD) was placed in an 80-ml plastic tray filled with 60 ml filtered water from the stream (Whatman glass fibre GF/F) after the addition of a set of two pre-wetted leaf discs. Every 2 days, one-third of the water was renewed to remove excreted compounds and to add oxygen. After 5 days, the animal was removed, killed by freezing and measured to determine mass using a length–mass relationship (body mass $= 0.0609 \times (\text{length})^2 + 0.2897 \times \text{length} + 0.4291$, where body mass is expressed in milligrams AFDM and body length in millimetres: Felten 2003). Leaf fragments were freeze-dried and weighed to the nearest 0.001 mg. The treatments of the feeding experiment were run on two successive occasions, each run consisted of two replicates and one control (without animal). Thus a total of 294 experiments were run: [(49 treatments × 2 replicates) + 49 controls] × 2 times. Consumption rate (CR) was calculated as follows:

$$\text{CR} = \frac{(\%\ \text{leaf mass loss with amphipod} - \%\text{leaf mass loss without amphipod})}{\text{amphipod body mass}},$$

where leaf mass loss without amphipod is derived from the control treatment.

Data analysis

The effect of forest type on stream temperature, water chemistry (mean parameters over three sampling dates) and diversity of leaf litter standing stocks was investigated using the Mann-Whitney test (*U*-test). Both mean stream temperature and cumulative temperature (degree-days) during the exposure period of alder and oak leaves were determined. Leaf litter diversity was defined here as leaf species richness (for each sampling date and cumulative over both sampling dates), Shannon-Wiever index (Shannon 1948) and percentage of fast plus medium decomposing species.

Leaf litter breakdown rate k was calculated for each bag by Petersen and Cummins (1974) formula: $k = \frac{1}{t} \times \ln\left(\frac{M_f}{M_i}\right)$ where M_i is the initial leaf litter AFDM (g), M_f is the leaf litter AFDM (g) remaining after exposure and t is the cumulative temperature during the time

of exposure (degree-days). Breakdown rates were calculated for coarse mesh bags (k_c) and fine mesh bags (k_f).

Differences in shredder genus assemblages between streams were assessed using correspondence analysis on square-root transformed abundance data. We used the scores from the first axes to explain more than 50% of total inertia as a synthetic variable in ANOVA. A similar procedure was applied to aquatic hyphomycetes species assemblages. These analyses were performed using ADE 4 software (Thioulouse et al. 1997).

Data were analysed using a General Linear Model procedure from Statistica 6.0 (StatSoft 2001). Type III sum of squares (SS) was used for nested designs and type I SS for multiple linear regression. We performed three-way nested-crossed ANOVAs to test whether leaf litter breakdown rates (k_c and k_f) and shredder descriptors (biomass, genus richness and axis score of correspondence analysis) depended on the leaf species used, forest type and streams. Leaf species effect (fixed) was crossed with the forest type (fixed) and the stream effect (random), which is nested within forest type. Breakdown rate k_c was also tested against shredder biomass using regression analysis, including the effect of leaf species and the leaf species × shredder biomass interactive term. Because the fungal assemblage was studied only in oak, we used two-way nested ANOVAs to test for the effect of forest type (fixed) and stream (random) on fungal descriptors (ergosterol, sporulation rate, species richness and axis score of correspondence analysis). Consumption rate (arcsinus-transformation) from the feeding experiment was analysed by two-way nested ANOVA, in which the species identity effect (random) is nested in the richness effect (fixed) of aquatic hyphomycetes. Significant differences were considered at $P < 0.05$ in all cases.

Results

Field experiment

Site characterization

Streams were circum-neutral or slightly acidic with low to moderate conductivity and buffering capacity (Table 1). While orthophosphate concentration was normally low, relatively high nitrate concentration suggested substantial atmospheric deposition in the Montagne Noire. Forest conversion into pure beech forest had no consistent effect on water chemistry (*U*-test for all chemical parameters: $P > 0.20$), but water temperature was significantly higher in beech forest streams (mean difference 2.1°C; *U*-test: $P < 0.05$; Table 1).

There were clear differences in the relative composition of leaf litter between forest types (Table 2). Mixed forest streams provided a high diversity, and here natural leaf packs in December were relatively diverse and contained a large proportion of fast and medium decomposing species. During the same period, beech forest streams had a significantly lower diversity of leaf litter, and fast and medium decomposing species were rare (*U*-test for all descriptors: $U = 0$, $P = 0.021$), their inputs being dominated by *F. sylvatica* and, to a lesser extent, *Quercus* spp. (Table 2).

There were consistent reductions in leaf species richness, Shannon-Wiever diversity and percentage of fast and medium decomposing species in leaf packs in mixed forest streams between December and February, whereas no changes were observed in the beech forest streams (Table 2).

Leaf litter breakdown

Leaf litter breakdown rate in coarse (k_c) and fine (k_f) mesh bags was primarily dependant on leaf species; hence breakdown rate of alder was around twice as fast as that of oak (Fig. 1a, b). In coarse mesh bags, the most striking result was the appreciably lower oak litter breakdown rate in beech forest streams, which was approximately one-third that in mixed forest streams (Fig. 1a). However this effect resulted from a leaf species-by-forest type interaction (Table 3). No forest effect was found for alder leaf litter (Fig. 1a, b), and forest type was not significant per se (Table 3). In the fine mesh bags, microbial breakdown rate (k_f) did not show the same pattern (Fig. 1b), with no effect of either forest type or leaf species-by-forest type interaction (Table 3). Stream, and to a less extent, leaf species-by-stream interaction determined leaf litter breakdown in coarse (k_c) and fine (k_f) mesh bags (Table 3).

Shredders accounted for more than 90% of the macroinvertebrate biomass in both alder and oak coarse mesh bags. Shredder biomass varied with forest type following the same pattern as breakdown rate k_c (Fig. 2), and hence we found a significant leaf species-by-forest type interaction (Table 3). There were also consistent differences in shredder biomass across streams (Table 3). At bag-level, shredder biomass was related to leaf litter breakdown rate k_c, independently of leaf species used. Thus, after suppressing the leaf species effect (GLM type I SS: $F_{1,81} = 20.1$, $P < 0.0001$), shredder biomass appeared to be positively related to k_c ($F_{1,81} = 21.4$, $P < 0.0001$, normalized coefficient of regression = 0.37). The leaf species-by-shredder biomass interaction was not significant ($F_{1,81} = 2.0$, $P = 0.16$).

Taxonomic structure of shredder assemblage, as determined by the first axis of the correspondence analysis, differed significantly between the two leaf species used (Table 3). The amphipod *G. fossarum* was the dominant shredder in oak, and to a less extent, in alder leaf bags; other common shredders were Plecoptera, mainly *Nemoura* in alder and *Protonemura* in oak, and Trichoptera, mainly *Potamophylax* (Table 4). There was no effect of forest type per se or of leaf species-by-forest type interaction on shredder genus richness or assemblage structure, although both parameters showed significant variations with stream and leaf species-by-stream interaction (Table 3).

Table 2 Leaf species composition in mixed and beech forest streams in December and February; LC = leaf decomposing category: slow (S), medium (M) and fast (F) decomposing leaves; for each species, the range of percentage occurrence (by dry mass) across the four study streams in each forest type is given for each collection period. Ranges of stream values are also presented for percentage (by dry mass) of fast and medium decomposing leaf species (F + M), leaf species richness, and Shannon-Wiever index scores; total species richness refers to cumulated value by stream over the two sampling dates

Leaf species	LC	Mixed forest		Beech forest	
		December	February	December	February
Fagus sylvatica L.	S	12.0–28.6	6.2–59.5	86.4–95.7	79.9–95.4
Hedera helix L.	S	0.0–1.3	0.0–5.5	0.0–2.4	0.0–3.7
Ilex aquifolium L.	S	0.0–1.1	0.0–1.2	0.0–2.2	0.0–0.7
Platanus hybrida Brot.	S	0.0–0.3	0.0–0.8		
Quercus petrea Lieblein	S	0.0–44.0	7.2–80.9	0.6–3.8	0.9–18.2
Q. robur L.	S	0.0–21.6	3.9–12.3	0.0–1.1	
Q. rubra L.	S	0.0–0.4			
Acer campestre L.	M	0.0–0.5			
Betula pendula Roth	M	0.0–22.0			
Castanea sativa Miller	M	0.0–49.7	0.0–26.4	0.0–0.6	
Corylus avellena L.	M	0.3–52.1	0.0–8.4		
Crataegus monogyna Jacq	M	0.0–0.1			
Robinia pseudoaccacia L.	M	0.0–0.3			
Sorbus aria (L.) Crantz	M	0.0–1.6	0.0–0.4		
Alnus glutinosa (L.) Gaertn.	F	0.0–16.9			
Fraxinus excelsior L.	F	0.0–9.2			
Rubus futicosus L.	F	0.0–0.5	0.0–1.9	0.3–2.6	0.4–1.2
Salix caprea L.	F	0.0–1.4			
S. cinerea L.	F	0.0–15.5	0.0–0.1		
Sorbus aucuparia L.	F	0.0–2.3			
Tilia cordata M.	F	0.0–0.3	0.0–0.9		
F + M		37.8–72.5	1.0–27.1	0.6–5.3	0.7–2.5
Species richness		10–14	4–11	4–6	3–4
Shannon-Wiever index		2.05–2.28	0.91–1.99	0.30–0.75	0.30–0.83
Total species richness		10–16		4–6	

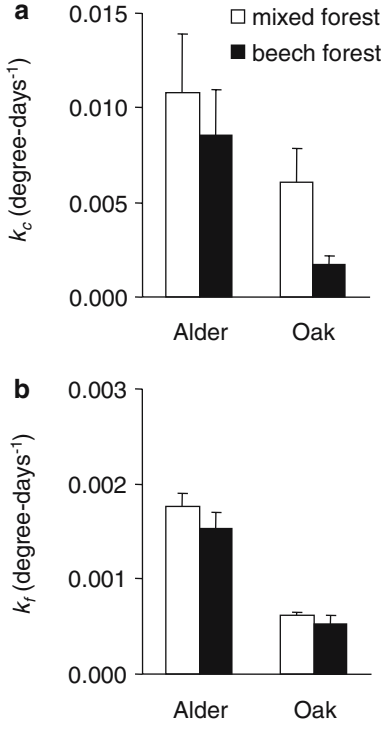

Fig. 1 Alder and oak litter breakdown rate in degree-days^{-1} (+1SE) in streams surrounded by mixed forest (*open bars*) and beech forest (*black bars*); **a** breakdown rate in coarse mesh bags (k_c); **b** breakdown rate in fine mesh bags (k_f)

Although microbial breakdown rate (k_f) of oak leaves did not differ between forest types (Fig. 1b), aquatic hyphomycetes species richness varied consistently (Table 5). Total species richness per stream (combining the six replicated bags) ranged from 20 to 28 in mixed forest streams and 12–18 in beech forest streams. Total fungal and leaf species richness were positively related by a log-linear function ($r^2 = 0.656$, $F_{1,6} = 11.5$, $P = 0.015$; data not shown). In contrast, fungal biomass

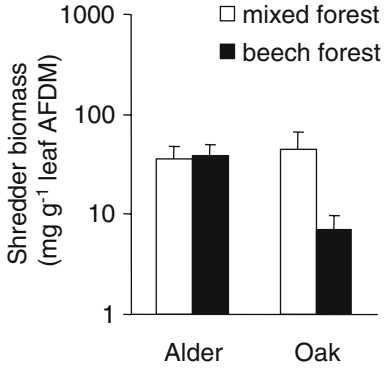

Fig. 2 Shredder biomass per gram leaf litter AFDM (mean +1SE) in alder and oak coarse mesh bags in streams surrounded by mixed forest (*open bars*) and beech forest (*black bars*); note the logarithmic scale on the vertical axis

Table 3 ANOVA for total leaf breakdown rate (k_c), microbial leaf breakdown (k_f) and shredder assemblage descriptors (transformations are indicated in parentheses) in the litter bags in mixed and beech forest streams; shredder biomass was standardized by litter AFDM remaining in coarse mesh bag; shredder assemblage structure was tested using score from axis 1 of correspondence analysis (CA) summarized as 58.3% of total inertia of the table (shredder genus × litter bag)

Factor	Leaf species		Forest type		Leaf species × forest type		Stream		Leaf species × stream	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
k_c (degree-days^{-1}; ln x)	109.7	< 0.0001	2.3	0.1782	7.1	0.0376	15.2	< 0.0001	2.1	0.0659
k_f (degree-days^{-1}; ln x)	1079	< 0.0001	1.1	0.3412	0.3	0.6138	27.2	< 0.0001	3.6	0.0033
Shredder biomass (mg^{-1} g leaf AFDM; ln $x+1$)	9.8	0.0025	2.8	0.1450	6.5	0.0431	3.5	0.0044	0.7	0.6769
Shredder genus richness	0.2	0.6858	2.9	0.1377	0.0	0.9920	3.1	0.0096	3.9	0.0020
Shredder assemblage structure (CA axis 1)	9.6	0.0027	0.1	0.7774	0.4	0.5255	5.4	0.0001	2.7	0.0189

(ergosterol content) and sporulation rate on oak leaves were not significantly affected by forest type surrounding the stream (Table 5). Significant differences among streams occurred for ergosterol, sporulation rate and fungal species assemblage according to the two first axes of correspondence analysis (Table 5).

Feeding experiment

The feeding experiment showed that consumption of oak leaf litter by *G. fossarum* was positively related to fungal species richness. After 5 days, leaf consumption by the amphipods ranged over the treatments between 1 and 18.4% (Fig. 3a). Because the results did not differ significantly between the two experimental runs (one-way ANOVA: $F_{1,194} = 0.66$; $P = 0.42$), the nested ANOVA did not include this effect. Consumption rate of leaves increased substantially when inoculated with aquatic hyphomycetes compared to non-inoculated leaves (*t*-test: $t_{4,198} = 3.0$, *P*-one-side-tail = 0.001; Fig. 3a). Leaves inoculated with a monoculture of *G. monticola* were consumed at least two times faster than all other treatments (Fig. 3a). As a result, a first nested ANOVA highlighted a significant fungal species identity effect on consumption rate ($F_{43,144} = 1.74$, $P = 0.048$), caused by the monoculture of *G. monticola* (Tukey's test: $P < 0.05$). This obviously hid the fungal species richness effect ($F_{4,43} = 1.40$, $P = 0.25$), finally highlighted in a second nested ANOVA excluding the monoculture of *G. monticola* ($F_{4,42} = 3.36$, $P = 0.0178$). Fungal species richness and consumption rate were then related by a positive log-linear relationship (Fig. 3b). Fungal species identity effect was removed without the monoculture of *G. monticola* ($F_{42,141} = 0.88$, $P = 0.68$; statistical power = 0.81).

Discussion

Riparian plant species reduction alters resource quality for shredders

Leaf litter breakdown in the study streams was apparently mainly mediated by invertebrate activity, as shown by the breakdown rates that are five times higher in coarse mesh compared with fine mesh bags (Fig. 1a, b). As in Hieber and Gessner's (2002) mathematical model, shredder biomass primarily determined invertebrate activity in coarse mesh bags. Hence, the six-fold difference in shredder biomass in oak leaves between the two stream categories (Fig. 2) probably accounted for the three-fold difference in litter breakdown rate (Fig. 1a). The difference in shredder biomass between forest types was not associated with a shift in shredder genus assemblage. Thus variations in leaf litter breakdown rate were a simple consequence of variations in shredder abundance and body mass (Jonsson and Malmqvist 2000; Zhang et al. 2003). As a result, we can expect direct effects of riparian plant species loss on shredder populations as suggested by Cummins et al. (1989).

Difference in shredder biomass on oak leaves between forest types was associated with species diversity and composition of leaf litter inputs. As the fast and medium decomposing species were greatly depressed in beech forest, our results suggest a bottom-up control on shredders by leaf litter quality. Such a relationship has rarely been established at stream ecosystem-level, although it is supported by results from microcosm experiments (Ward and Cummins 1979; Canhoto and Graça 1995; Yanoviak 1999; González and Graça 2003). The highest shredder biomasses were recorded in litter bags placed in mixed forest streams, where litter inputs included a large amount of fast and medium decomposing leaf species. These leaves represent high quality resources to shredders because of their low concentration of refractory compounds and high nutrient (N and P) content (Webster and Benfield 1986; Graça 2001; Gjerløv and Richardson 2004). Exploitation of a high quality food resource is likely to lead to higher secondary production of shredders and hence greater biomass (Stout et al. 1993; Friberg et al. 2002). Water temperature is probably not a confounding factor in this study because high temperature would normally be expected to increase shredder biomass and fungal activity (Ward and Cummins 1979; Chauvet and Suberkropp 1998; González and Graça 2003), whereas these were lowest or unaltered in the warmest streams. The leaf species-by-forest type interaction in determining litter breakdown rate and shredder biomass (Table 4) suggested aggregation of

Table 4 Shredder assemblages identified at genus level, in alder and oak coarse mesh bags; mean (SE) relative abundances (%) calculated separately for alder and oak bags

Taxa	Alder	Oak
Amphipoda		
Gammarus	33.9 (5.6)	57.3 (5.7)
Plecoptera		
Nemoura	19.2 (4.2)	7.1 (2.4)
Protonemura	7.1 (3.3)	10.0 (3.3)
Leuctra	4.6 (1.1)	3.8 (1.5)
Amphinemura	0.9 (0.5)	1.5 (0.9)
Trichoptera		
Potamophylax	15.3 (3.5)	9.3 (2.6)
Sericostoma	1.1 (0.8)	0.3 (0.2)
Odontocerum		0.7 (0.5)
Cryptothrix		0.4 (0.4)
Hydratophylax		0.2 (0.2)
Lasiocephala		0.2 (0.1)
Diptera		
Tipula	0.2 (0.2)	0.1 (0.1)
Coleoptera		
Elodes	1.3 (0.6)	2.1 (1.3)

Table 5 ANOVA for descriptors (data not transformed) of aquatic hyphomycetes species assemblages colonizing oak leaves in fine mesh bags in mixed and beech forest streams; ergosterol content represented the fungal biomass on leaves; sporulation rate represented the reproductive activity of aquatic hyphomycetes; fungal assemblage structure was tested using score from axis 1 and 2 of correspondence analysis (CA) summarized respectively as 35.1 and 15.0% of total inertia of the table (aquatic hyphomycetes species × litter bag)

Factor	Forest type		Stream	
	F	*P*	*F*	*P*
Ergosterol content (μg mg^{-1} leaf AFDM)	0.6	0.4599	3.5	0.0069
Fungal sporulation rate (no mg^{-1} leaf AFDM day^{-1})	4.1	0.0884	10.7	< 0.0001
Fungal species richness	7.0	0.0385	1.2	0.3201
Fungal assemblage structure (CA axis 1)	1.1	0.3161	59.9	< 0.0001
Fungal assemblage structure (CA axis 2)	1.5	0.2562	15.8	< 0.0001

animals onto alder leaves placed in beech forest streams. Alder bags hence formed 'resource islands' of high quality that the most mobile shredders are likely to track and exploit (Rowe and Richardson 2001; Zhang et al. 2003). Thus rapid breakdown of alder leaves, even in beech forest streams, would provide additional evidence for food quality limitation to shredders.

Fungal diversity on leaf litter alters shredder performance

If shredders in streams select resource patches with the highest quality, the significantly higher biomass of shredders on oak bags in mixed forest rather than beech forest streams would imply that shredder response is not determined simply by initial chemical composition of leaf litter. Nutritional quality of a slow decomposing leaf species such as oak will vary across forest types as a result of microbial conditioning effects. Evidence for this comes from the observed differences in fungal diversity colonizing such leaf litter. Litter conditioning by aquatic hyphomycetes can consistently enhance resource quality for shredders (Arsuffi and Suberkropp 1988; Graça et al. 1993b). Likewise fungal species identity can influence leaf consumption rate (see reviews by Suberkropp 1992, 2003). However, the relationship between aquatic hyphomycetes species richness and shredder consumption rate was unexpected.

Our feeding experiment suggests that fungal species richness is likely to regulate leaf consumption rate by keystone shredders such as *G. fossarum*, particularly of slow decomposing leaf species. Therefore, fungal species richness could control shredder growth rate and fitness (Graça et al. 1993b; Suberkropp 2003). A species-rich assemblage of aquatic hyphomycetes may enhance resource quality for shredders in two ways. First, as invertebrates consume fungal mycelia, the diversity of nutritional elements provided by a multi-species mycelia patch (Cargill et al. 1985) may increase its nutritional quality relative to a single-species patch (Scheu and Simmberling 2004). Second, the enzymes secreted by different species of aquatic hyphomycetes may complement each other (Bärlocher and Corkum 2003; Treton et al. 2004), improving digestibility of leaf tissue for shredders (Bärlocher and Kendrick 1975; Graça et al. 1993a). Even though most aquatic hyphomycetes species are able to degrade the main leaf litter compounds such as cellulose, it is probable that differences occur between the enzymes involved in partial hydrolysis of leaf tissue (Arsuffi and Suberkropp 1984; Chamier 1985; Bärlocher 1992). Shredders such as amphipods tend to eat hydrolysed plant tissue rather than mycelia (Bärlocher and Kendrick 1975; Graça et al. 1993a), so enhanced diversity of enzymes probably affect nutritional quality of leaf litter.

Riparian plant species richness indirectly influences leaf breakdown rate

Riparian vegetation composition and structure are some of the most important determinants of diversity among aquatic hyphomycetes assemblages (Gulis 2001; Bärlocher and Graça 2002; Laitung et al. 2002; Laitung and Chauvet 2005). Recently, Laitung and Chauvet (2005) found a positive relationship between woody plant species richness and richness of free conidia of aquatic hyphomycetes in adjacent streams. The present study corroborates this result and extends it to leaf-associated assemblages. It therefore provides evidence for the indirect functional importance of riparian plant species richness on leaf litter breakdown in streams, as fungal richness enhances shredder performance.

Mechanisms underlying the richness covariance between plants and heterotrophic microorganisms, already

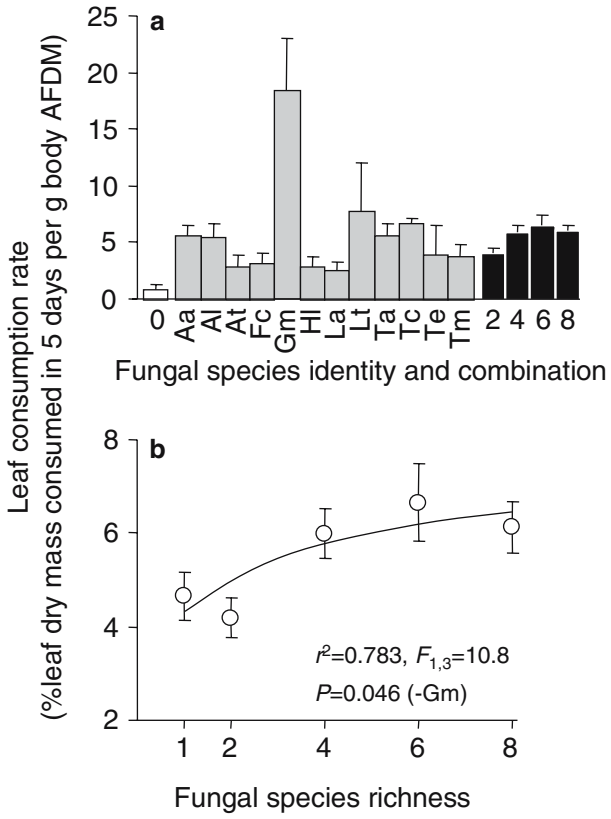

Fig. 3 **a** consumption rate (mean +1SE) of *G. fossarum* on oak leaf discs in relation to fungal species identity and combination: non-inoculated treatment (0 = sterile discs; *open bar*); conditioned by different fungal monoculture (*Aa Alatospora acuminata*, *Al Anguillospora longissima*, *At Articulospora tetracladia*, *Fc Flagellospora curvula*, *Gm Goniopila monticola*, *Hl Heliscus lugdunensis*, *La Lemmoniera aquatica*, *Lt Lemmoniera terrestris*, *Te Tetrachaetum elegans*, *Tm Tetracladium marchalianum*, *Tc Tricladium chaetocladium* and *Ta Tumularia aquatica*; *grey bars*); multi-species fungal combinations for the richness level 2, 4, 6 and 8 (*black bars*); **b** log-linear regression curve was adjusted for fungal species richness and mean consumption rate (±1SE) by richness level; the monoculture of *Gm* was excluded in Fig. 3b

reported in terrestrial ecosystems, remain largely unknown despite being potentially numerous (Hooper et al. 2000). In addition to few cases of preference of aquatic hyphomycetes for particular leaf species (Gulis 2001), we suggest three non-exclusive mechanisms to explain the close relationship between fungal and riparian plant richness, niche differentiation, energy availability and host specificity. The two former mechanisms assume direct trophic determinism by litter and the latter a biotic association between living trees and fungi. Thus niche differentiation may allow more species to coexist in streams under the richest riparian vegetation as organic compound richness increases with plant richness (Loreau 2001). At the same time, local extinction of rare species would be avoided by higher energy availability (Wright 1983) related to the presence of plant species producing high quality leaf litter. The host-specificity explanation is supported by the fact that more tree species may lead to an increase in terrestrial fungal richness through host-specificity of some endophytes (Kowalski and Kehr 1996; Petrini 1996), and these terrestrial species are suspected to inoculate streams. Although the origin of aquatic hyphomycetes in streams remains partially obscure (Bärlocher 1992), their regular occurrence in the terrestrial environment (Bandoni 1981), often as endophytes of riparian vegetation (Fisher et al. 1991; Sridhar and Bärlocher 1992), makes this hypothesis plausible.

Conclusion

Our results clearly illustrate the need to integrate trophic dynamics into diversity-ecosystem function research (Loreau et al. 2002; Raffaelli et al. 2002; Thébault and Loreau 2003). The indirect effect of plant species richness on leaf litter breakdown is certainly the most relevant finding emerging from this study. We provide some of the clearest evidence to date that microbial diversity can regulate decomposition through trophic interactions. Finally our study demonstrates the importance of conserving the riparian zone diversity, and especially woody plant species richness. However, methodological limitation of our study area resulted in a covariance of quality of litter input and riparian plant richness. Therefore, the relative importance of species composition and overall richness per se in explaining differences in leaf litter breakdown between mixed and beech forest streams remains unclear.

Acknowledgements This research was supported by the European Commission through the Framework 5 programme (Rivfunction: contract EVK1-CT-2001-00088) and the French national programme ECOFOR "Ecosystèmes forestiers. Biodiversité et Gestion forestière". We thank S. Millot, D. Lambrigot and J.-Y. Charcosset for their technical assistance. We are grateful to three anonymous referees for their useful suggestions and to M.O. Gessner for his helpful comments on an earlier version of the manuscript.

References

APHA (American Public Health Association) (1989) Standard methods for examination of water and wastewater, 17th edn. American Public Health Association, Washington DC

Arsuffi TL, Suberkropp K (1984) Leaf processing capabilities of aquatic hyphomycetes: interspecific differences and influence on shredder feeding preferences. Oikos 42:144–154

Arsuffi TL, Suberkropp K (1988) Effects of fungal mycelia and enzymatically degraded leaves on feeding and performance of caddisfly (Trichoptera) larvae. J N Am Benthol Soc 7:205–211

Bandoni RJ (1981) Aquatic hyphomycetes from terrestrial litter. In: Wicklow OT, Carroll GC (eds) The fungal community: its organization and role in the ecosystem. Marcel Dekker, New York

Bärlocher F (1992) Community organization. In: Bärlocher F (ed) The ecology of aquatic hyphomycetes. Springer, Berlin Heidelberg New York, pp 38–76

Bärlocher F, Corkum M (2003) Nutrient enrichment overwhelms diversity effects in leaf decomposition by stream fungi. Oikos 101:247–252

Bärlocher F, Graça MAS (2002) Exotic riparian vegetation lowers fungal diversity but not leaf decomposition in Portuguese streams. Freshwat Biol 47:1123–1136

Bärlocher F, Kendrick B (1973) Fungi and food preferences of *Gammarus pseudolimnaeus*. Arch Hydrobiol 72:501–516
Bärlocher F, Kendrick B (1975) Leaf-conditioning by microorganisms. Oecologia 20:359–362
Boulton AJ, Boon PI (1991) A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? Aust J Mar Freshwater Res 42:1–43
Canhoto C, Graça MAS (1995) Food value of introduced eucalypt leaves for Mediterranean stream detritivore: *Tipula lateralis*. Freshwat Biol 34:209–214
Cargill ASI, Cummins KW, Hanson BJ, Lowry RR (1985) The role of lipids as feeding stimulant for shredding aquatic insects. Freshwat Biol 15:455–464
Chamier A-C (1985) Cell-wall-degrading enzymes of aquatic hyphomycetes: a review. Bot J Lin Soc 91:67–81
Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 480:234–242
Chauvet E, Suberkropp K (1998) Temperature and sporulation of aquatic hyphomycetes. Appl Environ Microbiol 64:1522–1525
Cummins KW, Wilzbach MA, Gates DM, Perry JB, Taliaferro WB (1989) Shredders and riparian vegetation. Bioscience 39:24–30
Felten V (2003) Effets de l'acidification des ruisseaux vosgiens sur la biologie, l'écologie et l'écophysiologie de *Gammarus fossarum* Koch, 1835 (Crustacea Amphipoda): Approche intégrée à différents niveaux d'organisation. Ph-D Thesis, University of Metz
Fisher PJ, Petrini O, Webster J (1991) Aquatic hyphomycetes and other fungi in living aquatic and terrestrial roots of *Alnus glutinosa*. Mycol Res 95:543–547
Friberg N, Larsen AD, Rodkaer A, Thomsen AG (2002) Shredder guilds in three Danish forest streams contrasting in forest type. Arch Hydrobiol 153:197–215
Gessner MO, Bärlocher F, Chauvet E (2003) Biomass, growth and sporulation of aquatic hyphomycetes. In: Tsui CKM, Hyde KD (eds) Freshwater mycology. Fungal diversity Press, Hong Kong, pp 127–157
Gessner MO, Chauvet E (1994) Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75:1807–1817
Gessner MO, Schmitt AL (1996) Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. Appl Environ Microbiol 62:415–419
Gjerløv C, Richardson JS (2004) Patchy resources in a heterogeneous environment: effects of leaf litter and forest cover on colonisation patterns of invertebrates in a British Columbian stream. Arch Hydrobiol 161:307–327
González JM, Graça MAS (2003) Conversion of leaf litter to secondary production by a shredding caddis-fly. Freshwat Biol 48:1578–1592
Graça MAS (2001) The role of invertebrate on leaf litter decomposition in streams — a Review. Int Rev Hydrobiol 86:383–393
Graça MAS, Maltby L, Calow P (1993a) Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*. I: feeding strategies. Oecologia 93:139–144
Graça MAS, Maltby L, Calow P (1993b) Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*. II: Effects on growth, reproduction and physiology. Oecologia 96:304–309
Gulis V (2001) Are there any substrate preferences in aquatic hyphomycetes? Mycol Res 105:1088–1093
Hieber M, Gessner MO (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038
Hölscher D, Hertel D, Koenies H (2002) Soil nutrient supply and biomass production in a mixed forest on a skeleton-rich soil and an adjacent beech forest. J Plant Nutr Soil Sci 165:668–674
Hooper DU, Bignell DE, Brown VK, Brussaard L, Dangerfield JM, Wall DH, Wardle DA, Coleman DC, Giller KE, Lavelle P, Van der Putten WH, de Ruiter PC, Rusek J, Silver WL, Tiedge JM, Wolters V (2000) Interaction between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. Bioscience 50:1049–1061
Jonsson M, Malmqvist B, Hoffsten PO (2001) Leaf litter breakdown rates in boreal streams: does shredder species richness matter? Freshwat Biol 46:161–171
Jonsson M, Malmqvist B (2000) Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. Oikos 89:519–523
Kowalski T, Kehr RD (1996) Fungal endophytes of living branch bases in several European tree species. In: Redlin SC, Carris LM (eds) Endophytic fungi in grasses and woody plants: systematics, ecology and evolution. APS Press, St Paul Minnesota, pp 67–86
Laitung B, Chauvet E (2005) Vegetation diversity increases species richness of leaf decaying fungal communities in woodland streams. Arch Hydrobiol (in press)
Laitung B, Pretty JL, Chauvet E, Dobson M (2002) Response of aquatic hyphomycete communities to enhanced stream retention in areas impacted by commercial forestry. Freshwat Biol 47:313–324
Loreau M (2001) Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. Proc R Soc Lond B 268:303–309
Loreau M, Naeem S, Inchausti P (eds) (2002) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford United Kingdom
Motomizu S, Wakimoto T, Toei K (1983) Spectrophotometric determination of phosphate in river waters with molybdate and malachite green. Analyst 108:361–367
Petersen RC, Cummins KW (1974) Leaf processing in a woodland stream. Freshwat Biol 4:343–368
Petrini O (1996) Ecological and physiological aspects of host-specificity in endophytic fungi. In: Redlin SC, Carris LM (eds) Endophytic fungi in grasses and woody plants: systematics, ecology and evolution. APS Press, St Paul Minnesota, pp 87–100
Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Ann Rev Ecol Syst 28:289–316
Pimm SL, Russel GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. Science 269:347–350
Pringle CM, Naiman RJ, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourn MJ (1988) Patch dynamics in lotic systems: the stream as a mosaic. J N Am Benthol Soc 7:503–524
Raffaelli D, van der Putten WH, Persson L, Wardle DA, Petchey OL, Koricheva J, van der Heijden M, Mikola J, Kennedy T (2002) Multi-trophic dynamics and ecosystem processes. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, United Kingdom, pp 147–154
Rowe L, Richardson JS (2001) Community responses to experimental food depletion: resource tracking by stream invertebrates. Oecologia 129:473–480
Scheu S, Simmberling F (2004) Growth and reproduction of fungal feeding Collembola as affected by fungal species, melanin and mixed diets. Oecologia 139: 347–353
Shannon CE (1948) A mathematical theory of communication. ATT Tech J 27:379–423
Sridhar KR, Bärlocher F (1992) Endophytic aquatic hyphomycetes of roots of spruce, birch and maple. Mycol Res 96:305–308
Sridhar KR, Krauss G, Bärlocher F, Raviraja NS, Wennrich R, Baumbach R, Krauss GJ (2001) Decomposition of alder leaves in two heavy metal-polluted streams in central Germany. Aquat Microb Ecol 26:73–80
StatSoft (2001) STATISTICA (data analysis software system). Version 6. www.statsoft.com
Stout BM, Benfield EF, Webster JR (1993) Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. Freshwat Biol 29:59–69
Suberkropp K (1991) Relationships between growth and sporulation of aquatic hyphomycetes on decomposing leaf litter. Mycol Res 95:843–850

Suberkropp K (1992) Interaction with invertebrates. In: Bärlocher F (ed) (1992) The ecology of aquatic hyphomycetes. Springer, Berlin Heidelberg New York, pp 118–134
Suberkropp K (2003) Methods for examining interactions between freshwater fungi and macroinvertebrates. In: Tsui CKM, Hyde KD (eds) Freshwater mycology. Fungal diversity Press, Hong Kong, pp 159–171
Swan CM, Palmer MA (2004) Leaf diversity alters litter breakdown in a piedmont stream. J N Am Benthol Soc 23:15–28
Tachet H, Bournand M, Richoux P, Usseglio-Polatera P (eds) (2000) Invertébrés d'eau douce. CNRS Publishers, Paris
Thébault E, Loreau M (2003) Food web constraints on biodiversity–ecosystem functioning relationships. Proc Natl Acad Sci USA 100:14949–14954
Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. Stat Comput 7:75–83
Treton C, Chauvet E, Charcosset JY (2004) Competitive interaction between two aquatic hyphomycete species and increase in leaf litter breakdown. Microb Ecol 48:439–446
Vannote RL, Minshall GW, Cummins JR, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137
Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial inputs. Science 277:102–104
Ward GM, Cummins KW (1979) Effect of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ecology 60:57–64
Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. Ann Rev Ecol Syst 17:567–594
Wright DH (1983) Species-energy theory: an extension of species-area theory. Oikos 41:496–506
Yanoviak SP (1999) Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in Neotropical tree hole microcosms. Oecologia 120:147–155
Zhang Y, Negishi JN, Richardson JS, Kolodziejczyk R (2003) Impact of marine-derived nutrients on stream ecosystem functioning. Proc R Soc Lond B 270:2117–2123