FORM AND FUNCTION

Small dams decrease leaf litter breakdown rates in Mediterranean mountain streams

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Abstract The damming of rivers and streams alters downstream habitat characteristics and biotic assemblages, and might thus alter stream functioning, although there is not much direct evidence of this impact. In this study we compared breakdown of alder leaves upstream and downstream from 4 small (<1 hm^3) dams in 4 Mediterranean mountain streams with no appreciable impact on water temperature and nutrient concentrations. Despite no effect on water characteristics, dams decreased leaf litter breakdown rates. Abundance and biomass of invertebrates and shredders and hyphomycete sporulation rates did not differ between upstream and downstream bags. However, the structure of invertebrate and hyphomycete assemblages did. Especially evident was a drop in limnephilids, which might explain the slower breakdown of leaf litter below dams. These results may help to explain some of the variability found in the literature on the effects of dams on decomposition rates. If dams increase water temperature and nutrient concentrations they may promote faster decomposition, but if dams do not change water characteristics, their impact on detritivore communities may cause slower decomposition rates.

Keywords Dams · Mediterranean streams · Leaf-litter breakdown · Aquatic invertebrates · Hyphomycetes · Stream functioning

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Introduction

Leaf litter from terrestrial ecosystems is the main food resource in forested headwater streams (Tank et al., 2010). For this reason, decomposition is a key process in these systems (Webster et al., 1999). When leaf litter enters the streams, microorganisms and detritivore invertebrates transform detritus into biomass, CO_2 and dissolved and fine particulate organic matter (Gessner et al., 1999) that may be used by other organisms at the site (Pettit et al., 2012), at downstream reaches (Wipfli et al., 2007) or in nearby terrestrial systems (Nakano &

Murakami, 2001). Changes in the mechanisms and rates of litter breakdown may thus influence communities and processes occurring elsewhere (Webster et al., 1999; Richardson et al., 2010).

In this study, we investigate the effects of damming headwater streams on leaf litter breakdown rates. The influence of dams on stream and river ecosystems has been studied extensively due to their abundance in most basins worldwide (Nilsson et al., 2005). Damming changes the timing and magnitude of river flow (Poff et al., 2007), reduces the downstream transport of sediments and other materials (Kondolf, 1997) and prevents aquatic migrations (Dudgeon, 2010). Currently, there is enough information to predict the effects of damming on many aspects of stream and river structure, including water chemistry, geomorphic characteristics, and aquatic communities (Ward & Stanford, 1983; Stanford & Ward, 2001; Bunn & Arthington, 2002; Elosegi et al., 2010). However, that is not the case with litter decomposition; among the 6 papers that, to our knowledge, have addressed the question, 3 reported that damming slows down breakdown (Nelson & Roline, 2000; Muehlbauer et al., 2009; Mendoza-Lera et al., 2012), but Short & Ward (1980) reported the opposite results and Casas et al. (2000) found no effect of damming on this parameter. Menéndez et al. (2012) assessed the effects of 4 dams in Mediterranean headwaters finding that the 3 dams releasing surface water decreased breakdown rates, whereas the other dam, discharging warmed and nitrogen-enriched water, enhanced breakdown.

These results suggest that dams may have two contrary effects on litter breakdown. First, they act as leaf litter traps, decreasing litter stocks downstream and making stream assemblages less dependent on detritus consumption. This effect of dams on functional organization of stream biota would hamper litter breakdown below them. However, when the water released is nutrient enriched and/or warmed, the effect of damming on decomposition can be minor or even reversed because both water temperature (as in Short & Ward, 1980) and nutrient concentrations (as in Casas et al., 2000) would increase litter breakdown.

In this study, we measured the effect of small surface-release dams on leaf litter breakdown dynamics in 4 cold oligotrophic mountain streams with little effect on water characteristics, channel form or riparian vegetation. Therefore, we hypothesized lower breakdown rates below the dams because of negative effects of dams on litter processing biota.

Methods

Study area

We studied 4 located on the southern slopes of the Guadarrama Mountains of central Spain, which drain small (maximum 952 ha, Table 1), siliceous basins devoted to forestry and ranching. The climate is continental with a dry summer characteristic from the Mediterranean region. Unregulated streams in the area flow throughout the year, but discharge tends to be lowest in summer, there are some floods in autumn and winter, and peak flows occur in late spring coinciding with snow melt. The 4 selected streams have each a small (<1 hm^3) surface-release dam for urban supply that only releases water when full, decreasing summer flows or even ceasing them in driest years. At each stream, 2 reaches approximately 50 m long were studied, one above (Up) and another below (Down) the dam. The distances between the dams and the Down sites were between 160 and 1250 m. The 2 reaches in the Guadarrama stream as well as Navacerrada-Up and Navalmedio-Up were surrounded by *Pinus sylvestris* L. forests. *Quercus pyrenaica* Willd. forests covered the banks of the 2 reaches studied in the Miraflores stream. The riparian vegetation of the Navacerrada-Down and Navalmedio-Down reaches consisted primarily of *Salix* spp.

Sampling protocol

Leaf litter breakdown was measured using mesh bags (15 × 20 cm, 5 mm mesh size) filled with approximately 5 g (± 0.25 g, air-dry mass) of alder, *Alnus glutinosa* (L.) Gaertn., leaves collected immediately after natural abscission. The experiments began on 25 November 2008 (Guadarrama and Navacerrada) and 9 January 2009 (Miraflores and Navalmedio) due to very low flows in November and December in the latter streams.

At each reach, 4 ropes, each with mesh bags tethered to it, were tied to nearby trees and anchored to the stream bottom by covering some sections of the ropes with boulders. Four bags per reach were

Table 1 Location of the studied sites and characteristics of their basins and dams

	Guadarrama		Miraflores		Navacerrada		Navalmedio	
	Up	Down	Up	Down	Up	Down	Up	Down
Latitude	40°46′28″N	40°45′43″N	40°49′29″N	40°49′10″N	40°45′26″N	40°45′9″N	40°45′11″N	40°44′45″N
Longitude	4°3′57″W	4°4′10″W	3°47′57″W	3°47′35″W	3°59′30″W	3°59′32″W	4°1′54″W	4°2′24″W
Altitude (m)	1381	1296	1322	1240	1420	1373	1322	1241
Basin area (Ha)	481	803	319	952	532	756	822	884
Land use								
% native vegetation	2.3	1.9	44.6	68.1	44.8	42.2	26.0	24.8
% tree plantations	97.7	98.1	51.6	29.6	42.9	41.2	69.8	68.4
% agriculture	0.0	0.0	3.8	2.1	5.4	3.8	4.2	6.4
Mean channel slope (%)	13.3	11.2	25.7	17.7	12.0	10.7	21.4	19.4
Distance to the dam (m)	680	550	360	500	500	60	400	480
Dam height (m)	18		36		–		41	
Volume impounded (hm³)	0.090		0.710		–		0.714	

retrieved (one bag from each rope) on 4 sampling occasions. Four additional bags were retrieved after only 1 day in the stream to measure the mass lost due to handling and leaching. The retrieved bags were placed inside individual plastic bags, transported in refrigerated containers to the laboratory and processed immediately (see below).

On each sampling date, pH, conductivity, percent oxygen saturation, oxygen concentration, and water discharge were measured with portable field meters. Water samples were taken on the same dates and transported under refrigeration to the laboratory in polyethylene bottles. Water temperature was recorded hourly at each study reach by Hobo Pendant data loggers (Onset Computer Corporation, Bourne, MA, USA). At each sampling occasion the mean channel width was determined from 5 random transects. Granulometric composition of the stream bed was assessed in 3 occasions using visual estimations of coverage by "boulders" (>25 cm), "cobbles" (6–25 cm), and "sand" (<6 cm) at 5 random transects. The characteristics of the riparian zones and stream channels were described with the QBR (Munné et al., 1998) and IHF (Pardo et al., 2002) indices, and the canopy cover was measured following Lemmon (1956).

Laboratory methods

The alder litter from each bag was rinsed on a 500 μm sieve with filtered (Whatman GF/F) stream water to dislodge fine detritus, sediment, and invertebrates. The remaining litter was dried (70°C, 72 h), weighed, ignited (500°C, 4 h) and weighed again separately to calculate ash-free dry mass (AFDM) and the AFDM/dry mass conversion factor needed to know the AFDM of alder litter used for the nutrient and sporulation determinations (see below). The content of C, N (Perkin Elmer series II CHNS/O elemental analyzer), and P (spectrophotometry following the molybdenum blue method after mixed acid digestion; Allen et al., 1974) was determined on random subsamples of approximately 0.5 g (dry mass) of leaf fragments taken before igniting the samples and milled to pass a 1 mm mesh. The chemical analyses of stream water were performed with the procedures specified in Pozo et al. (2011).

Hyphomycete sporulation rates were measured for the samples collected when the leaf litter had lost approximately 20% of its initial mass (i.e., at the expected peak of conidial production, Pascoal &

Cássio, 2004). Two sets of 5 leaf disks (diameter 12 mm) were punched out from 5 leaves with a cork borer. One set of disks was processed as explained above to determine the AFDM of the litter used for measuring sporulation. The other set of leaf disks was incubated separately in Erlenmeyer flasks with 25 ml of filtered stream water (Whatman GF/F) on a shaker (60 rpm, 10°C) for 48 h. The incubation media were fixed with 2 ml of 37% formalin and pre-stained with 2 drops of trypan blue in 0.05% lactic acid (TBLA) before filtering (5 μm pore size, Millipore SMWP) an aliquot of known volume. Each filter was stained with TBLA to facilitate conidium identification and counting.

All the invertebrates from the bags collected when the leaf litter had lost approximately 50% of its initial mass (the usual peak of invertebrate abundance, e.g., Hieber & Gessner, 2002) were sorted, identified to family (Oligochaeta to class) and counted under a dissecting microscope. They were classified into 3 functional feeding groups (Cummins, 1973): shredders, collectors, and "others" following the information provided in Pozo et al. (2011). The dry mass of each functional feeding group (70°C, 72 h) was also calculated.

Analysis of data

In all tests performed in this paper, the identity of the streams (hereafter, stream) and the reach (above and below the dams, hereafter, site) were treated as fixed factors. We were not interested in addressing the differences among the 4 studied streams, but the low number of streams in the study did not allow us to treat "stream" as a random factor (Bolker et al., 2009).

The null hypothesis of no differences among streams and sites in water characteristics (nutrient concentrations, pH, conductivity, alkalinity or oxygen saturation and concentration) was tested via a Permutational Multivariate Analysis of Variance (PERMANOVA), a multivariate analysis of variance based on permutations of an affinity matrix of samples that is constructed using many variables (Anderson, 2001). The water characteristics were standardized to a mean of 0 and a standard deviation of 1 before calculating the Euclidean distances between samples required for the PERMANOVA. The effects of stream and site on each characteristic cited above were evaluated using generalized linear models (GLMs) with a gamma

distribution (Zuur et al., 2009). Because the gamma distribution allows no zeros and nitrite and ammonium concentrations were below detection levels in certain samples, an arbitrary value of 0.001 was added to the values recorded in all samples. The daily mean water temperatures during the experiments were also compared among streams and sites using a gamma GLM.

Differences in mean stream channel width and discharge, IHF, QBR, grain size, and vegetation cover between Up and Down sites were also tested following the methods indicated above. However, in this case, due to the low number of permutations possible, the P value of the PERMANOVA was calculated using Monte Carlo procedures (Anderson & Robinson, 2003).

The effects of site and stream on leaf litter breakdown rates were tested by constructing linear models with the percentage of remaining AFDM as a dependent variable and degree days as a covariable. Previous research performed at these and other streams (e.g., Pozo et al., 2011) has shown that the linear model describes alder breakdown after leaching more accurately than the exponential one. Moreover, we did not observe deviations from the assumptions of linear models when we examined our models' residuals (Zuur et al., 2009). The same strategy was used to test the effects of site and stream on the percentage of C, N, and P remaining.

The effects of stream and site on the structure of the invertebrate assemblages that colonized the bags were also tested. First, the abundances of all of the taxa were square-root transformed to avoid the dominance of the results by the most abundant families. Then, a Bray-Curtis matrix measuring the pairwise dissimilarity between the assemblages was used to perform a non-metric multidimensional scaling (MDS) analysis that described the patterns in the assemblages. The same matrix was used to test the effects of site and stream on invertebrate assemblages via a PERMANOVA. The invertebrate families responsible for the bulk of the differences between the Up and Down sites were identified using the PRIMER similarity percentages routine (SIMPER, Clarke, 1993).

Invertebrate abundances (number of animals per bag) and richness (number of taxa per bag) were compared between the Up and Down sites with Poisson GLMs. Overdispersion was often detected in the invertebrate abundances; it was corrected by adjusting the standard errors with a quasi-GLM model

that included a dispersion parameter (Zuur et al., 2009). The patterns in invertebrate biomass (dry mass per bag) and diversity (1–Simpson's index) were analyzed using gamma GLMs.

The same overall procedure was followed for analyzing the aquatic hyphomycete assemblages in the bags. However, because the conidial counts were performed after filtering differing amounts of incubation medium, the GLMs testing for differences in conidial abundance and richness included the filtered volume as an offset variable (Zuur et al., 2009). MDS, PERMANOVA, and SIMPER analyses were performed on the conidial concentrations (number of conidia/ml).

Due to the high number of tests performed, the family-wise Type I error rate was controlled based on an acceptable level of 0.05 using false discovery rate (FDR) corrections (Benjamini & Hochberg, 1995). Those results that did not satisfy the conditions imposed by FDR corrections were considered non-significant in this paper.

All of the linear models and GLMs reported in this paper were constructed and analyzed with R 2.10.0 (R Development Core Team, 2009). MDS, PERMANOVA, and SIMPER were performed using PRIMER v. 6 (Clarke & Gorley, 2006).

Results

Habitat characteristics

The water characteristics were influenced by the stream (pseudo$F_{3,32} = 4.977$, $P = 0.0001$, PERMANOVA) where the samples were taken, but no effect of site (pseudo$F_{1,32} = 1.950$, $P = 0.0693$, PERMANOVA) or stream × site interaction (pseudo$F_{3,32} = 1.428$, $P = 0.1030$, PERMANOVA) was found.

Six of the 10 physical and chemical variables differed among streams, although differences were not large (Table 2). The only variable affected significantly by dams was alkalinity ($P < 0.0001$, GLM), but the differences were very small. No difference was found between Up and Down sites in any of the 8 variables describing the channel and riparian characteristics (pseudo$F_{1,6} = 0.404$, Monte Carlo $P = 0.782$, PERMANOVA; $P > 0.05$, GLMs).

Litter breakdown

The breakdown rates were higher at Up than at Down sites ($F_{1,107} = 32.416$, $P < 0.0001$, ANOVA; Fig. 1). The time required for complete breakdown at the Up sites (range, 105–229 degree days) was, on average, 59% of that required at the Down sites (219–454 degree-days).

No differences were detected among the mass, C, N, and P loss rates ($F_{3,382} = 0.931$, $P > 0.05$, ANOVA). This result indicates that the elemental composition of the decomposing leaf litter was not altered by the studied dams.

Invertebrate assemblages

A total of 2639 invertebrates belonging to 42 taxa were found in the 32 litterbags analyzed. Only 11 taxa had relative abundances greater than 1% (Table 3). Together, these 11 taxa represented 91.2% of all of the invertebrates found. Regardless of site, the most abundant families were Chironomidae and Limnephilidae, and most invertebrates were shredders (average: 42.2%) and collector-gatherers (39.1%). The dominance of shredders was greater in terms of biomass (84.6% of total); collector-gatherers represented only 6.4% of the total biomass.

The taxonomic structure of the invertebrate assemblages differed between sites (pseudo$F_{1,24} = 4.484$, $P = 0.0001$, PERMANOVA) and streams (pseudo$F_{3,24} = 3.593$, $P = 0.0001$, PERMANOVA), but a site × stream interaction was also found (pseudo$F_{3,24} = 4.097$, $P = 0.0001$, PERMANOVA). The estimates of the components of variation suggest that the pure effect of site on invertebrate assemblages (260) was smaller than that of stream (388) but also that the stream × site interaction (926) had a meaningful influence on the invertebrate assemblages. The main taxa responsible for the effect of site on the invertebrate assemblage structure were, in decreasing order of influence, Limnephilidae, Chironomidae, Hydropsychidae, Simuliidae, Leuctridae, Capniidae, and Sericostomatidae.

The MDS biplot that described the affinities among the invertebrate assemblages is not presented in this paper because its stress value of 0.22 indicates that it is not highly reliable (Clarke, 1993). It was however in accordance with the patterns described above.

Table 2 Means of the physical and chemical parameters recorded during breakdown experiments at the 8 studied sites and characteristics of stream channels and banks

	Guadarrama		Miraflores		Navacerrada		Navalmedio	
	Up	Down	Up	Down	Up	Down	Up	Down
Temperature (°C)^S	3.3 (0.5–5.4)	3.4 (1.6–5.4)	3.6 (0.7–5.8)	3.5 (1.6–6.1)	3.3 (0.9–5.7)	3.0 (1.6–5.2)	3.7 (0.9–5.6)	4.3 (1.0–7.2)
SRP (µgP/l)^S	11.7 (5.1–18.3)	10.1 (5.4–16.3)	3.3 (3–3.5)	2.5 (1.2–3.6)	5.4 (2.3–12)	4.6 (2.2–6.8)	4.1 (2.6–6.3)	4.5 (4.2–5)
Ammonium (µgN/l)	7.4 (0–18.4)	10.2 (0–28.6)	28.7 (26.4–31.4)	6.4 (0–14.1)	11.1 (0–20)	11.1 (0–24.1)	12.3 (0–25.5)	11.9 (0–31.2)
Nitrite (µgN/l)	1 (0.5–1.9)	0.9 (0.5–1.5)	1 (0.9–1.1)	1.3 (1–1.5)	0.9 (0.4–1.1)	1.1 (0.8–1.5)	1.4 (0.9–2.2)	1.1 (0.9–1.6)
Nitrate (µgN/l)^S	284.4 (157–377)	301.5 (84–475)	735.7 (667–821)	402.6 (270–485)	487.4 (314–759)	348.5 (264–557)	269.4 (213–355)	312 (255–364)
pH	6.7 (6.3–6.8)	6.9 (6.6–7.2)	6.3 (6–6.6)	6.6 (6.2–6.8)	6.6 (6.3–6.8)	6.7 (6.4–6.8)	6.8 (6.7–6.8)	6.7 (6.6–6.8)
Conductivity (µS/cm)^{S,*}	26 (19–29.4)	40.7 (22–55.7)	89.4 (67–100)	71.1 (63–84)	18.5 (15–20.8)	19.8 (15–22.6)	206.8 (199–223)	161.6 (111–198)
Alkalinity (meq/l)^{D,S}	0.3 (0.2–0.4)	0.3 (0.3–0.5)	0.1 (0.1–0.2)	0.2 (0.2–0.3)	0.2 (0.2–0.2)	0.2 (0.2–0.3)	0.2 (0.2–0.3)	0.4 (0.4–0.5)
Oxygen saturation (%)	102 (102–102)	106.4 (90–140)	107.2 (98–111)	108.5 (93–133)	101.2 (94–106)	96.8 (88–102)	110.6 (104–120)	101 (94–107)
Oxygen concentration (mg/l)	12 (11.7–12.2)	12.2 (10–16)	11.7 (10.7–12.5)	12 (10.2–15.3)	11.5 (10.3–12.4)	11.1 (10.1–11.6)	12.4 (11.2–13.1)	11.3 (10.4–12.2)
Discharge (l/s)	41.9 (12–58)	103.2 (6–220)	158.9 (51–260)	285.4 (52–557)	123.6 (39–241)	134.3 (6–216)	400.2 (133–495)	81.7 (4–283)
Mean channel width (m)	2.19	4.20	5.12	6.05	4.66	5.44	5.44	4.62
Boulders (%)	25.63	41.19	48.13	29.00	38.80	63.27	43.27	55.93
Cobbles (%)	37.56	21.25	25.44	47.50	35.00	30.93	11.33	30.20
Sand (%)	36.81	37.56	26.44	23.50	26.20	5.80	45.40	13.88
Canopy cover (%)	66.61	73.02	71.77	74.48	78.65	51.98	73.90	71.41
IHF	61	61	78	80	71	80	66	59
QBR	77.5	95	95	97.5	75	87.5	82.5	87.5

The ranges of the measures are indicated between *brackets*

SRP soluble reactive phosphorus

[S] Significant effect of stream detected, [*] significant location × stream interaction, [D] significantly higher in downstream sites
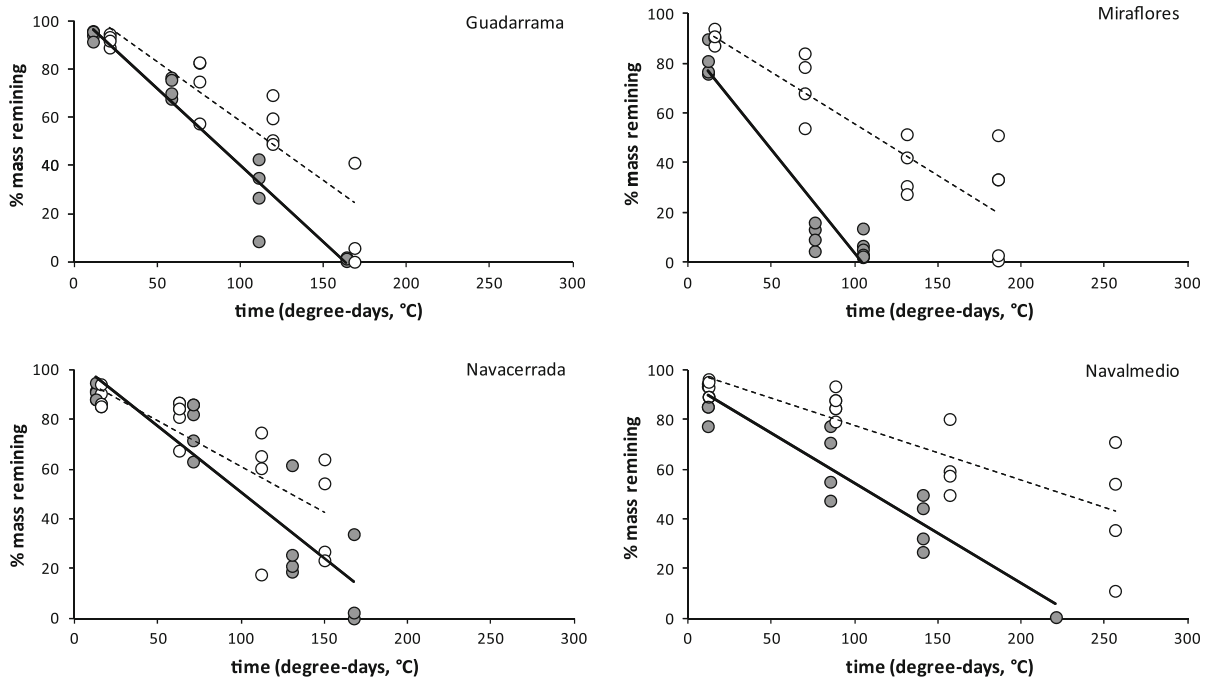
Fig. 1 Proportional mass remaining in the 4 sites upstream (*solid circles*, *continuous lines*) and downstream (*open circles*, *discontinuous lines*) from dams

Table 3 *P* values of the GLMs testing the effects of site and stream on the variables describing invertebrate assemblages and abundance (number of animals per litterbag) of the taxa that accounted for more than 1% of the assemblages

	Site	Stream	Site × stream
Richness	0.451	0.0511	0.0083
Diversity	0.21	0.0375	0.478
Chironomidae	0.0366	0.5524	**<0.0001**
Limnephilidae	**<0.0001**	0.0308	0.1481
Hydropsychidae	**0.0003**	**<0.0001**	**<0.0001**
Simuliidae	0.0842	0.0083	0.6061
Leuctridae	0.371	**<0.0001**	**0.0012**
Capniidae	0.811	**0.0004**	0.1805
Taeniopterygidae	**<0.0001**	**<0.0001**	0.0259
Sericostomatidae	0.129	**<0.0001**	0.0092
Leptophlebiidae	0.0059	**0.0006**	0.0278
Chloroperlidae	**0.0004**	**<0.0001**	**0.0003**
Oligochaeta	0.2977	**0.0014**	0.0179

Values highlighted in *bold* were found significant after False Discovery Rate corrections

The values of most of the descriptors of the invertebrate assemblages were not associated with site (Fig. 2; Table 3), although a significant site × stream interaction was detected for total invertebrate abundance and collector-gatherer biomass and abundance. Site had a significant effect only on the collector-gatherer biomass (highest downstream, *P* < 0.005, GLM). The effects of stream on assemblage descriptors were found more frequently, including an association with the abundance of total invertebrates, shredders and others.

The abundance of the most common invertebrate families was very variable among streams (Table 3). Four of these 11 families displayed significant differences in abundance between sites, being Limnephilidae and Chloroperlidae most abundant at Up reaches, and Hydropsychidae and Taeniopterygidae at Down reaches. The abundance of Leuctridae and, again, Chloroperlidae indicated a significant stream × site interaction. The stream factor had a more frequent effect on invertebrate abundance than the site factor or the site × stream interaction. It was significant in 8 of the 11 GLMs performed.

Hyphomycete assemblages

Conidia of 31 species of hyphomycetes were found in the leaf litter; these assemblages were dominated by
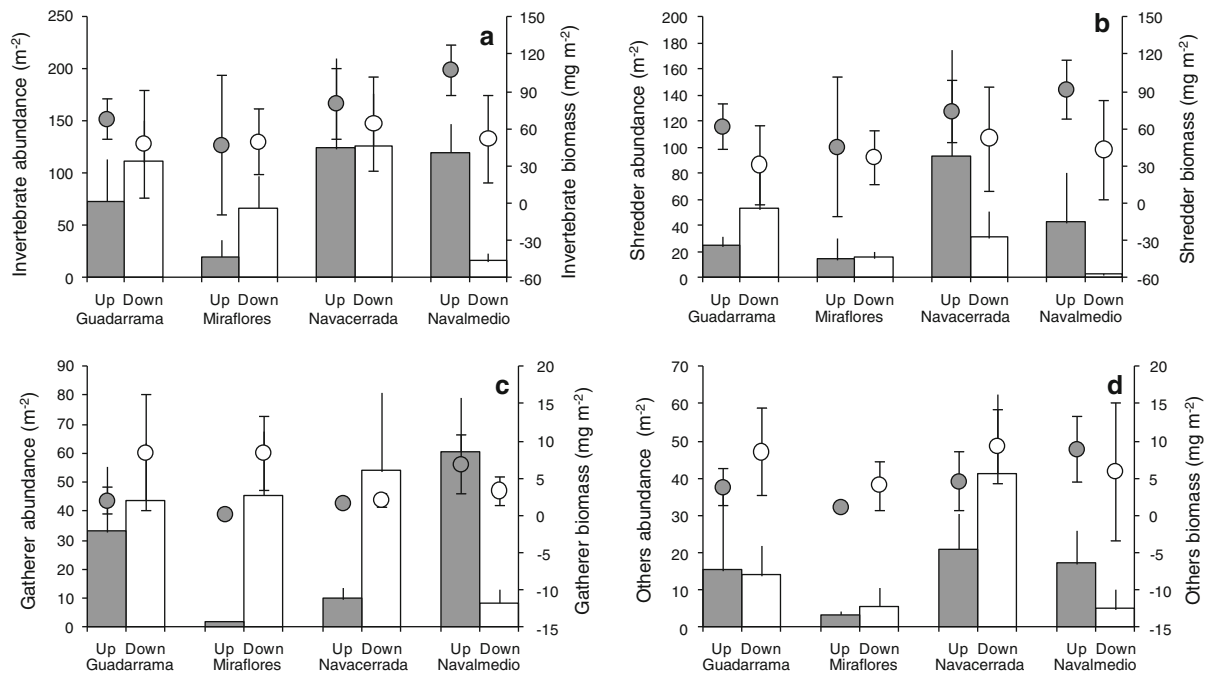
Fig. 2 Mean abundance (*columns*) and biomass (*points*) of invertebrates (**a**), shredders (**b**), gatherers (**c**) and others (**d**) that colonized the litterbags. Vertical lines are standard deviations

Flagellospora curvula Ingold (71.6% of all the conidia found), and only 6 other species had a proportional abundance greater than 1% (Table 4).

MDS results suggested that the hyphomycete assemblages from the 2 sites in the Miraflores stream and those collected at Navalmedio-Down differed from those at the other study sites (Fig. 3). Furthermore, the assemblages taken at the Up sites did not overlap in the biplot with those taken at the Down sites at the same stream. These observations were confirmed by the PERMANOVA. The structure of the hyphomycete assemblages differed between sites (pseudo$F_{1,23} = 8.082$, $P = 0.0002$, PERMANOVA) and among streams (pseudo$F_{3,23} = 15.101$, $P = 0.0001$, PERMANOVA). However, a site × stream interaction was also detected (pseudo$F_{3,23} = 4.681$, $P = 0.0001$). The species responsible for 50% of the differences observed between the Up and Down sites were, in order of decreasing influence, *F. curvula*, *Culicidospora aquatica* R.H. Petersen and *Lemonniera terrestris* Tubaki.

Site only influenced the abundance of *L. terrestris*, which was higher at Down sites. Species richness, total conidial abundance and the abundance of the 6 most abundant species differed among streams. These differences in species abundance were not due solely

to the low conidial abundance recorded in bags from the Miraflores stream (Table 4) because the site × - stream interaction was not significant in any test.

Discussion

The 4 dams studied here did not affect the nutrient concentrations in line with Mendoza-Lera et al. (2012), but contrasting with Casas et al. (2000) and Camargo et al. (2005) who reported increased nutrient concentrations below dams. The dams studied by Casas et al. (2000) and Camargo et al. (2005) release deep water, whereas those studied by us and by Mendoza-Lera et al. (2012) release surface water. In a recent study on small headwater dams in Iberian streams, Menéndez et al. (2012) reported that a dam releasing hypolimnetic water increased downstream water temperature and dissolved inorganic nitrogen, whereas 2 surface-release dams did not affect these variables. It thus seems that the effects of damming can be probably linked in part to their water-release mechanism; it is well known that hypolimnetic release can increase nutrient concentrations (Ward & Stanford, 1983; Marshall et al., 2006), but also that some

Table 4 Total abundance (number/ml), species richness and diversity of the hyphomycete conidia obtained from the litterbags plus abundance of those conidia that accounted for more than 1% in the assemblages

	Guadarrama		Miraflores		Navacerrada		Navalmedio	
	Up	Down	Up	Down	Up	Down	Up	Down
Total abundance[S]	3265.7 (1009.1)	6801.9 (3455.4)	3.3 (2.3)	16.0 (12.3)	2137.7 (605.2)	1312.4 (1092.4)	4861.9 (3274.5)	389.2 (172.4)
Richness[S]	13.5 (3)	17 (1.83)	3.67 (0.58)	5.25 (1.26)	11 (2.16)	12.5 (2.38)	14 (3.56)	8 (2.16)
Diversity	0.58 (0.08)	0.32 (0.09)	0.52 (0.22)	0.53 (0.1)	0.48 (0.09)	0.74 (0.07)	0.44 (0.1)	0.24 (0.17)
Flagellospora curvula Ingold[S]	1908.7 (884.6)	5533.9 (2939.1)	1.7 (2.3)	8.2 (7.1)	774.3 (228)	574.3 (638.2)	3478.1 (2487.5)	37.27 (40.5)
Culicidospora aquatica R.H. Petersen[S]	528.7 (203.3)	237 (169.4)	0 (0)	0 (0)	164.7 (138.2)	214 (191)	749.3 (527)	0 (0)
Lemonniera alabamensis Sinclair & Morgan[S]	365.5 (70.3)	126.8 (94.4)	0 (0)	0 (0)	10.3 (6.9)	181.7 (120.1)	285.5 (231)	0.4 (0.8)
Lemonniera terrestris Tubak[D,S]	0.5 (1)	258.1 (115.9)	0.2 (0.2)	4.6 (4.1)	0.6 (0.4)	0.7 (1.3)	4.7 (5)	330.8 (149.2)
Articulospora tetracladia Sv. Nilsson[S]	74.09 (54.9)	46.49 (40.1)	0.3 (0.4)	0.1 (0.1)	89.3 (58.2)	75.2 (39.8)	113.6 (98.1)	2.1 (2.4)
Tricladium chaetocladium Roldán[S]	28.7 (18.5)	158.1 (77.8)	0 (0)	0 (0)	14.3 (8.6)	22 (17.2)	6.7 (4)	0 (0)
Tetrachaetum elegans Ingold[S]	9.8 (7.2)	107.4 (89.1)	0 (0)	0.1 (0.1)	4.3 (3.3)	96.6 (95.5)	1 (2)	0 (0)

The numbers shown are means and, between brackets, standard deviations. The species are ranked in decreasing order of overall mean abundance

[S] Significant effect of stream on abundance, [D] significantly higher abundance at Down sites
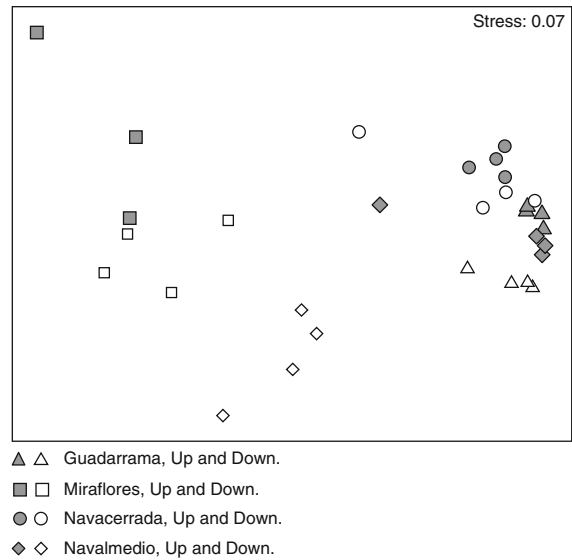

Fig. 3 MDS ordination of the hyphomycete assemblages that colonized the litterbags

dams may trap nutrients, thus promoting downstream reductions in their concentrations (Friedl & Wüest, 2002). All this suggests the effect of dams on downstream nutrient concentrations can be highly variable, depending probably on the water residence time, on depth of released water, the time of the year and also on the existence of a thermocline.

No evidence of the alteration of stream geomorphic characteristics by dams was found in the 4 streams analyzed here. This is a rather unexpected result since all the studied dams have been blocking sediment transport for more than 35 years, which should have caused some channel adjustment at Down sites. Mendoza-Lera et al. (2012), using our same study design and methods, also failed to detect any effect of 4 small dams on downstream channel morphology. We however think that this apparent lack of effects of dams on channel structure could be a consequence of the limited number of geomorphic variables or of the reduced sampling effort in both works (e.g., Baker et al., 2011).

The principal finding of our experiment is the significant and quantitatively important decrease in leaf litter breakdown rates below dams. Such decrease cannot be related to changes in water characteristics because stream water was not cooler or, as discussed above, nutrient-depleted below the dams. The only chemical parameter of the water that differed

consistently between the sites was alkalinity, but the magnitude of such difference was minute. Moreover, in our slightly acidic streams, if alkalinity had had any effect on breakdown rates it would have accelerated them at the Down sites where alkalinity was highest (Merrix et al., 2006), which was not the case. All these results agree with our main hypothesis: if dams do not alter the nutrient concentrations or water temperature below them, they may still cause lower breakdown rates of leaf litter.

The observed alterations in the detritivore assemblages below dams may be the cause of the slower breakdown. No differences were found between sites in either invertebrate and conidium abundance or invertebrate biomass, but the assemblage structure of both hyphomycetes and invertebrates colonizing litterbags were impacted by dams. Other studies have found that certain shredders contribute disproportionately to breakdown rates (e.g., Dangles & Malmqvist, 2004). In some cases, this disproportionate contribution makes the patterns of litter breakdown rates better explainable by the taxonomic composition of the detritivore assemblages than by their abundance (e.g., Simon et al., 2009). In our study, a noticeable portion of the difference between the invertebrate assemblages at the Up and Down sites corresponded to the lower abundance of limnephilids below dams. Because these caddisflies were the largest shredders found in the experiment, they may be the dominant detritivores in terms of leaf litter consumption rates (e.g., González & Graça, 2003; Reiss et al., 2011). In short, we propose that the shredder assemblages dominated by limnephilids above dams processed litter faster than the assemblages found below, where the most abundant shredders were small stoneflies.

The shifts detected in fungus assemblages might also have affected breakdown because hyphomycete species differ in their ability to process leaf litter (Gessner et al., 1999) and in their palatability to invertebrates (Chung & Suberkropp, 2009). However, we could not identify any key hyphomycete species that was more abundant at the Up sites than at the Down sites, and we have no evidence that L. terrestris (i.e., the only hyphomycete with a significantly greater abundance at the Down sites) is able to hamper litter decomposition. Thus, there is no strong evidence to support the idea that differences in breakdown rates were caused by differences in hyphomycete assemblages.

Our experiment cannot reveal the causes of the differences in biotic assemblages between sites above and below dams. As indicated previously, we found no effects of dams on water temperature, chemistry or stream channel characteristics, 3 factors with substantial influences on river biota (Giller & Malmqvist, 1998). However, these dams have an effect on the flow regime of the studied streams, increasing the length of the summer low flow period downstream. The direct effect of low flow on stream shredders has been measured by Leberfinger et al. (2010), who found that all 3 species present in their mesocosms fed at lower rate during experimentally decreased flow periods, and could therefore have decreased performance. Low-flow periods have also shown to result on decreased hyphomycete respiration, sporulation, and conidial germination, as well as on mycelial colonization (Schlief & Mutz, 2009). Such alterations during the low flow season might have driven the shifts in the invertebrate and fungus assemblages observed in this study.

The main result of our study is that dams may impact downstream rates of litter breakdown, a key ecosystem-level process, even if they do not alter water temperature, nutrient concentrations or stream channel and bank characteristics. The lower breakdown rates recorded below dams promoted a slower release of energy and nutrients from the benthic leaf litter. These effects may sum up the role of dams as traps of materials and nutrients, causing lower production downstream.

The 4 dams we studied have a strong effect on discharge and litter transport, especially in summer, and we hypothesize this is the reason why they impact detritivore assemblages. The effect of dams on decomposition may be, thus, proportional to their impacts on the natural flow regime.

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