1 **Water flow regulation drives ecosystem functioning in a Mediterranean river**

2 **network**

3

4

5 Meritxell Abril[a*], Margarita Menéndez[a], Joan P Casas-Ruiz[b], Lluís Gómez-Gener[a], Milagros

6 Barceló[a], Francesc Oliva[c], and Isabel Muñoz[a]

7
8 [a]*Department of Ecology, Faculty of Biology, University of Barcelona, Barcelona, Spain*

9 [b]*Catalan Institute for Water Research, Girona, Spain*

10 [c]*Department of Statistics, Faculty of Biology, University of Barcelona, Barcelona, Spain*

11

12 *Corresponding author: Department of Ecology, Faculty of Biology, University of Barcelona.

13 Avda. Diagonal 643, 08028 Barcelona, Spain. Tel.: (+34) 934031188.

14 *E-mail address*: meritxell.abril@ub.edu (M. Abril).

15

16

17

18 HIGHLIGHTS

19

20 • Flow regulation transformed lotic reaches into lentic reaches along the river network.

21 • We assessed the differences in ecosystem functioning between lotic reaches and lentic

22   reaches using wood decomposition.

23 • The decomposition rates differed between lotic and lentic reaches in high-order

24   streams, especially in winter, with increased rates in lotic reaches compared with lentic

25   reaches.

26 • In high-order streams, flow regulation reduced decomposition rates and affected stream

27   ecosystem functioning along the river network.

28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

51 ABSTRACT

53 Mediterranean rivers are extensively modified by flow regulation practises along their courses.

54 An important part of the river impoundment in this area is related to the presence of small dams

55 and weirs constructed mainly for water storage and hydropower development. These projects

56 drastically modified the ecosystem morphology, transforming lotic reaches into lentic reaches

57 and increasing their alternation along the river. The aim of this study was to assess the effect

58 caused by the flow regulation on ecosystem functioning at the rivr network scale, using wood

59 decomposition as a functional indicator. We studied the mass loss from wood sticks during

60 three months in different lotic and lentic reaches located along a Mediterranean river basin, in

61 both winter and summer. The results revealed differences in the rates of the wood mass loss

62 between sites in summer and winter that were mainly related to the differences between stream

63 orders. The decomposition rates were related to temperature, nutrient concentrations (NO_2^-,

64 $NO_3^=$), water residence time, and the dissolved organic carbon concentration. High-order

65 streams with higher temperature and nutrient concentrations exhibited increased decomposition

66 rates compared with low-order streams. The effect of the flow regulation on the decomposition

67 rates only appeared to be relevant in high orders, especially in winter, when the hydrological

68 characteristics of lotic and lentic habitats widely varied. Lotic reaches with lower water

69 residence times and increased physical abrasion exhibited increased decomposition rates

70 compared with lentic reaches. Overall, our study revealed that the flow reduction caused by flow

71 regulation reduced organic matter decomposition in river ecosystems, and this effect was

72 enhanced in high-order streams.

85
86 **1. Introduction**

87

88   Many rivers and streams have been altered by different anthropogenic activities such as
89 water extraction, canalisation, or dam construction (Malmqvist and Rundle, 2002; Nilsson et al.,
90 2005). In Mediterranean areas, the presence of these impacts is particularly significant due to
91 the combination of a high population density, agricultural and industrial activities, and a high
92 natural variability of the flow regime (Grantham et al., 2012). Most of the flow regulation in this
93 area results from the construction of small dams and weirs (e.g. < 1 hm^3), mainly for water
94 abstraction purposes (Martin and Hanson, 1966; Marcé et al., 2012). In addition, flow variability
95 is predicted to increase with climate change (Schneider et al., 2013), increasing the need for
96 flow regulation.

97   Flow regulation interrupts the fluvial continuity, altering the natural structure of the ecosystem
98 along the river (Ward and Stanford, 1983). The hydro-morphology of the river network becomes
99 highly modified, increasing the water residence time and transforming lotic reaches into lentic
100 reaches (Sabater, 2008). The differences in water flow between these reaches also imply
101 differences in several physicochemical factors, such as water temperature (Poff and Hart, 2002)
102 and oxygen or nutrient concentrations (Friedl and Wüest, 2002), and ecosystem processes
103 such as sediment transport (Vericat and Batalla, 2005; Hupp et al., 2009) and organic matter
104 retention (Dewson et al., 2007). At the same time, these factors and processes potentially
105 shape the presence of biological communities in each habitat (Clavero et al., 2004; Strayer,
106 2006; Buffagni et al., 2009), directly affecting key ecosystem functions, i.e., the decomposition
107 of organic matter (Menéndez et al., 2012; Martínez et al., 2013) and metabolism (Baxter, 1977).
108 These forced differences between lotic and lentic habitats indicate that flow regulation can
109 trigger important changes in river ecosystem functioning (Elosegi and Sabater, 2012).
110 Moreover, given that flow regulation involves the interruption of the fluvial continuum,
111 consequences may be evident along the entire river network (Ward and Standford, 1983).

112   Different key ecosystem processes, such as organic matter decomposition (Gessner and
113 Chauvet, 2002; Feio et al., 2010), nutrient retention (Von Schiller et al., 2008), and metabolism
114 (Bunn et al., 1999; Young et al. 2008), have been used as indicators to assess ecosystem
115 functioning. Organic matter decomposition is a fundamental process in stream ecosystems

(Tank et al., 2010) and results from the interaction between several physical, chemical, and biological factors (Benfield, 1996; Gessner et al., 1999). Many researchers have demonstrated the effect of water temperature (Peterson and Cummins, 1974), dissolved nutrient concentration (Ferreira et al., 2014), or oxygen concentration (Webster and Benfield, 1986) on organic matter decomposition. At the same time, decomposition is influenced by alterations of the hydrological regime, such as drastic flow reductions (Dewson et al., 2007; Schlief and Mutz, 2009), variations in flow velocity (Ferreira and Graça, 2006; Santos Fonseca et al., 2012), and damming (González et al., 2012; Menéndez et al., 2012). The decomposition process integrates this complexity and is a good indicator of changes in the ecosystem.

At a watershed scale, decomposition rates depend on the river order, altitude, and/or different land uses (Benfield et al., 2000; Fleituch, 2001; Fonnesu et al., 2004; Pozo et al., 2011; Silva-Junior et al., 2014). As a consequence, several studies highlighted the importance of assessing the ecosystem response to an impact at this scale (e.g., Stanford and Ward, 1992; Allan et al., 1997; Poff and Zimmerman, 2010; Elosegi and Sabater, 2012). However, few studies considering organic matter decomposition have been performed at a catchment scale to date (see: Feio et al., 2010; Aristi et al., 2012).

Various studies used the litterbag method as an approach to quantify decomposition rates (Bärlocher, 2005). However, its utilisation allows high versatility in various aspects, such as mesh size, litter species, or the initial quality of the substrate, restricting the comparisons among studies (Lecerf and Chauvet, 2008). To overcome this issue, an alternative approach involves the use of commercial wood sticks (Young and Collier, 2009; Aristi et al., 2012; Arroita et al., 2012) that limits manipulation and allows standardisation of the initial chemical composition.

The aim of this study was to assess the variability caused by flow regulation on ecosystem functioning at the river netowrk scale using the organic matter decomposition process as a functional indicator. To achieve this objective, we studied the mass loss from wood sticks in different lotic and lentic reaches located in a diverse range of stream orders along a Mediterranean river network. Additionally, we identified the main environmental factors potentially affecting decomposition rates along the river orders. Due to the marked seasonality of Mediterranean areas, the experiment was conducted in summer and winter. We hypothesised that there would be differences in the decomposition processes between lotic and

lentic reaches along the river network given their environmental differences. We expected increased decomposition rates in lotic reaches based on increased physical abrasion due to higher flow. We predicted these rates to be particularly higher in summer when milder temperatures promote increased biological activity.

2. Materials and methods

2.1 Study area

This study was conducted in the Fluvià River watershed, located in the northeast of the Iberian Peninsula (Fig. 1). This sixth order watershed drains an area of 990 km^2. Its mainstream is 97 km in length and flows into the Mediterranean Sea. The climate is typically Mediterranean and is characterised by scarce precipitation occurring mainly in spring and autumn with drier and warmer summers. The mean annual precipitation in this region is 660 mm, and the monthly mean air temperature varies between 6°C in January and 23°C in July (ACA, http://aca-web.gencat.cat). The basin is relatively pristine and is covered mainly by mixed forests (78%); some agricultural (13%) and urban (3%) areas are present, mostly associated with the lowest altitudes (Land Cover Map of Catalonia 2009, CREAF). However, the flow is highly regulated by a total of 51 man-made watercourse interruptions of different dimensions (ACA, http:/aca-web.gencat.cat). Nevertheless, all of these interruptions have less than 1 hm^3 of capacity.

We selected a total of 10 experimental reaches of orders ranging from 2 to 5 (Strahler, 1957) within this catchment to ensure an appropiate representation of the river network heterogeneity (Table 1). These reaches were also classified as running water reaches (i.e., lotic habitats, n=6) and stagnant waters stored in small dams and weirs (i.e., lentic habitats, n=4). The experiment was conducted during winter (November 2012 to February 2013) and summer (June 2013 to September 2013).

2.2 Environmental parameters

175   During the study period, several physical, chemical, and hydrological parameters were

176   obtained monthly at each site (Table 2). Portable probes were used to measure the water

177   temperature, conductivity, pH (Cond 3310, WTW, Germany), and the dissolved oxygen

178   concentration (YSI ProODO Handheld, USA) on the field. The water samples were filtered

179   through pre-ashed glass fibre filters (0.7-µm pore size; Whatman GF/F, Germany), transported

180   to the laboratory under cooled conditions, and stored at 4°C in the dark until analysis. All water

181   samples were analysed the day after their collection. The concentrations of dissolved nitrite

182   (NO_2^-), nitrate (NO_3^{-2}), phosphate (PO_4^{-3}), chloride (Cl^-), and sulphate (SO_4^{-2}) were analysed by

183   ionic chromatography (IC5000, DIONEX, USA). The dissolved organic and inorganic carbon

184   concentrations in water (DOC and DIC, respectively) were measured with a total organic carbon

185   analyser (TOC-V CSH, Shimadzu, Japan). The sub-catchments associated with the

186   experimental reaches were characterised for the total area and percentage of land use cover by

187   a geospatial-processing software (ArcMap 10, ArcGIS, USA). The water residence time of the

188   lentic reaches was estimated from digitised bathymetric maps obtained with the same

189   geospatial-processing software. For the lotic reaches, the water residence time was obtained

190   from the reach distance and a reach average water velocity modelled by the hydraulic software

191   HecRas 2.2 (US Army Corps of Engineers, USA). To feed the model, we used hydraulic

192   parameters measured in the field with an acoustic-Doppler velocimeter (Sontek, YSI, USA) and

193   morphological data provided by the Catalan Water Agency (ACA, http:/aca-web.gencat.cat).

194   For each parameter, the average of the monthly measures was used as the representative

195   value of each study period.

196

197   *2.3 Decomposition experiment*

198

199   The decomposition rates were studied in all of the experimental reaches using commercial

200   wood sticks (15×1.8×0.22 cm) of Canadian poplar wood (*Populus nigra x canadienses*). Before

201   their placement in the reaches, each stick was marked with a pirographer, oven dried (70°C, 72

202   h), and weighed. A total of 15 (five groups of three) wood sticks were placed in each selected

203   site in November 2012 and June 2013 for the winter and summer experiments, respectively.

204   Each group was tied with nylon threads to metal bars, branches, or roots, and lead weights

205   were used to ensure that the sticks were completely submerged. One group of these sticks was

206   used at each site to prevent possible losses. An extra set of five sticks was transported to the

207   stream without being immersed in the water and returned to the laboratory to correct the initial

208   mass value for manipulation.

209   Five sticks (one per group) at each location were recovered after approximately 65 and 110

210   days in both winter and summer. After their retrieval, the sticks were placed in individual zip-lock

211   bags and transported in refrigerated containers to the laboratory, where they were immediately

212   processed. The recovered sticks were washed with tap water and brushed to remove adhering

213   material, oven dried (70°C, 72 h), and weighed. An aliquot of each stick was incinerated (500°C,

214   5 h) to remove the effect of the inorganic components and obtain an ash-free dry mass (AFDM).

215   A subsample of each recovered stick was ground into a fine powder (c.a 1-mm pore-size), and

216   the nitrogen (N) and carbon (C) contents were analysed. Both elements were determined using

217   a Perking Elmer series II CHNS/O elemental analyser.

218

219   *2.4 Data analysis*

220

221   The decomposition rates were estimated following the negative exponential model $M_t = M_0 e^{-kt}$

222   (Petersen and Cummins, 1974), where M_0 is the initial AFDM corrected for manipulation, M_t is

223   the remaining AFDM at time t, and k is the decomposition rate. A decomposition rate was

224   obtained for each site and period (summer and winter).

225   A linear mixed-effects model, using the R package *nlme* (Pinheiro et al., 2012), was used to

226   analyse differences in water characteristics and wood decomposition over time along the river

227   network. For wood decomposition, the proportion of the remaining AFDM was used as the

228   dependent variable; the elapsed time (co-variable), season (winter or summer), river order

229   (low=2-3, medium=4, high=5) and hydrologic habitat (lentic or lotic) served as the fixed-effects

230   factors. We used the natural logarithm of the proportion of remaining AFDM to achieve a linear

231   relationship with time. For the stream water characteristics, we applied a linear mixed-effects

232   model for each of these characteristics (dependent variable) using the same fixed-effects

233   factors indicated above as the independent variables, with the exception of elapsed time. The

234   full factorial model was employed; therefore, all of the interactions were assessed. For both

235 models, the site was fitted as a random factor with an effect on the intercept. This effect was

236 assessed using likelihood ratio tests to compare the linear regression model without random

237 factors (*gls* function) with the linear mixed model with all the fixed effects (*lme* function) and the

238 random effect. The final models were selected by Akaike's Information Criterion (AIC) and fitted

239 using the restricted maximum likelihood (REML). Model validation plots were used to assess the

240 assumptions of the analysis. We implemented a variance function (*varIdent* function) in the

241 model (Pinheiro and Bates, 2000; Zuur et al., 2009) to correct for residual heteroscedasticity.

242 For wood decomposition, the effects of the fixed factors on the response variable were

243 interpreted based on the statistical significance of the interaction among the fixed-effects

244 habitat, order, and season with time (Lagrue et al., 2011).

245   The relationship between wood decomposition and watershed characteristics was

246 determined by correlating the environmental variables with the decomposition rates to assess

247 linear relationships and to identify significant associations. A stepwise linear regression between

248 the water characteristics and rates was performed with the R package *MASS* (Venables and

249 Ripley, 2002) to identify which factors or factor combinations were the best predictors of the

250 decomposition rates. Model selection was done using a bidirectional elimination based on AIC.

251 Prior to the regression analysis, Pearson correlation coefficients between all of the variables

252 were examined for multicollinearity. Within the higher correlated predictor pairs, we selected the

253 pair that could provide the most ecological information. Sulphate, DIC, and phosphate were

254 discarded because they were highly correlated with conductivity, DOC, and NOx (NO_2^- + NO_3^{2-},

255 >90% in NO_3^{2-} form), respectively.

256   Before the statistical analysis, the distributional properties of the data were assessed to

257 identify outliers. The Shapiro–Wilk test was applied to assess normality for each variable, and a

258 log natural transformation was performed when necessary. All statistical analyses were

259 conducted using R version 2.15.3 (R Core Team, 2013), with a significance level set at a *p*<0.05

260 for all tests.

261

262 **3. Results**

263

264 *3.1 Stream water characteristics*

265

The stream water characteristics exhibited high variability between the sites along the river network in both seasons (Table 2). The interaction of habitat, order, and season was significant for NOx, dissolved oxygen, and the water residence time (Table 3). NOx concentrations varied widely between the orders with increased concentrations noted in sites from orders 4 and 5 (high orders) compared with sites from orders 2 and 3 (low orders) in both seasons. Within the high-order reaches, the sites located in the middle of the watershed exhibited the highest NOx concentrations, especially in summer. However, for all of the other high-orders sites, NOx concentrations increased in winter. The average residence time of water in summer was 8.9 ± 4 h, whereas it was 34.9 ± 18 h in winter. Lentic habitats exhibited a water residence time that was increased 4-fold compared with lotic habitats. These differences between the habitats were especially evident among the high orders in winter. Oxygen concentrations and pH were less variable among the sites. However, the oxygen concentration was generally higher in winter than in summer, and the highest values appeared in the high orders. The water temperature increased with stream order and exhibited higher values in summer compared with winter at all of the sites. The conductivity and Cl^- varied between orders and seasons, with the highest values noted in high-order reaches and winter. Regarding to the DOC, significant differences were only evident between seasons, with increased DOC in summer compared with winter (except in 4th order reaches).

3.2 Decomposition process

The decomposition rates differed significantly between seasons (interaction time x season, Table 4), with higher rates in summer (0.0027 ± 0.0004 d^{-1}) than in winter (0.0009 ± 0.0001 d^{-1}) at all of the sites (Fig. 2). Differences were also noted between orders (interaction time x order, Table 4). The decomposition rates were increased in high orders compared with low orders in both seasons. The differences between lotic and lentic habitats was only evident in high orders, with the highest decomposition rates in lotic habitats.

The seasonal variability in the decomposition rates was more important in high-order reaches compared with low-order reaches. In high orders, the decomposition rates were

295   increased 2.9-fold in summer compared with winter (0.001 ± 0.0003 d^{-1}), whereas the seasonal

296   differences in low orders were reduced until rates were only 1.57 times higher. Accordingly, the

297   variability among sites was more pronounced in summer, with rates 6.03 times higher in high-

298   order reaches (0.003 ± 0.0007 d^{-1}) compared with low-order reaches (0.0006 ± 0.00009 d^{-1})

299   (interaction time x order x season, Table 4).

300   Clear differences between lotic and lentic habitats were exclusively evident in high orders,

301   especially in winter (interaction time x habitat x order x season, Table 4). In high orders, lotic

302   habitats exhibited an average decomposition rate that was higher than that observed in lentic

303   habitats. This difference between habitats was especially remarkable in winter; decomposition

304   rates in lotic habitats (0.002 ± 0.0005 d^{-1}) were increased 2.5-fold compared with lentic habitats

305   (0.0007 ± 0.0002 d^{-1}). In summer, lentic habitats exhibited rates that were more similar

306   (0.003 ± 0.0011 d^{-1}) than the rates obtained for the lotic habitats. Conversely, low-order lentic and

307   lotic habitats presented similar decomposition rates in both seasons (Fig. 2).

308   The initial nitrogen content of sticks was 0.07% of dry mass, and an increase was observed

309   during decomposition in both periods. This increase was more pronounced in winter compared

310   with summer. After a loss of 20% of the initial mass, the amount of nitrogen in the sticks in

311   winter was approximately 0.4% of the dry mass, whereas it was approximately 0.2% in summer

312   (Fig. 3).

313

314   *3.3 Watershed characteristics and decomposition rates*

315

316   The stepwise regression revealed that the decomposition rates were significantly associated

317   with stream water characteristics. The final selected model included temperature, NOx, water

318   residence time, and DOC as the best combination of variables to predict the mass loss. The

319   proportion of variance in the rates explained by these predictors included in the model was

320   approximately 72% (Table 5).

321   At the same time, we identified a significant relationship between the decomposition rates

322   and the surface of agricultural land use in each sub-catchment in summer (Fig. 4). This

323   relationship was unimodal at the watershed scale from low to high orders, exhibiting increased

324   decomposition rates at intermediate levels of agricultural land use in both lentic and lotic

325   habitats. No significant relationship was observed during the winter period.

326

327   **4. Discussion**

328

329   Wood decomposition revealed differences in ecosystem functioning along the studied river

330   network that were more associated with differences between stream orders than with

331   differences between habitats (lentic-lotic). Flow regulation only affected decomposition rates in

332   high orders, where lotic and lentic habitats differed widely in their characteristics.

333

334   Contradictory results related to the decomposition of organic matter along stream orders or

335   altitudes are reported in the literature. Some authors report that the decomposition rates of leaf

336   litter increased in the downstream direction (Benfield et al., 2000; Fleituch, 2001; Fonnesu et al.,

337   2004), whereas others report a decrease (Cortes et al., 1995) or even no trend along the river

338   network (Tiegs et al., 2009). Regarding wood decomposition, the number of studies performed

339   at the watershed scale is even smaller, and these results are also inconsistent. Naiman and

340   Melillo (1987) reported increased rates in headwater streams, whereas other studies, including

341   our study, described faster decomposition downstream (Diez et al., 2002; Aristi et al., 2012).

342   The differences could be closely related to the characteristics of the study basin. In our basin,

343   the nutrient concentrations and water temperature differed widely between stream orders, with a

344   clear differentiation between high and low orders. The former exhibited higher temperature and

345   nutrient concentrations, and these factors were positively correlated with decomposition rates.

346   Previous studies have already indicated that elevated nutrient concentrations can accelerate

347   wood decomposition rates (Tank and Webster, 1998; Diez et al., 2002), mainly via fungal and

348   bacterial activity (Crenshaw et al., 2002). An increase in nutrient availability in the water column,

349   especially nitrogen and phosphorus, potentially provides an extra source of nutrients,

350   stimulating microbial activity on litter (Ferreira et al., 2014). At the same time, this stimulation

351   effect is more pronounced in substrates with low nutrients and high lignin content, such as

352   wood, because the microbial community is more limited by nutrients (Stelzer et al., 2003; Gulis

353   et al., 2004; Ferreira et al., 2006b). Thus, our results revealed an increase in the nitrogen

content in litter during decomposition, which was more pronounced in winter compared with summer likely due to differences in nutrient availability and microbial assemblages. Other researchers have found this increase (Menéndez et al., 2011) and attributed it to microbial nutrient uptake and immobilisation in the water column (Chauvet, 1987; Kuehn et al., 2000).

The effect of nutrient concentrations on litter decomposition also depends on water temperature (e.g., Ferreira and Chauvet, 2011). As we predicted, a clear effect of the temperature on the decomposition rates was detectable in our results, with increased decomposition rates noted in summer compared with winter at all of the sites. However, despite similar increases in temperatures between reaches of different orders, the effect of temperature on decomposition rates was much greater for high orders than low orders. Similarly, Fonnesu et al. (2004) studied the organic matter decomposition in a 5th order Mediterranean watershed and found that the seasonal variation in leaf decomposition was low in reaches with low decomposition rates and high in reaches with high decomposition rates. This finding is potentially related to a synergistic effect of nutrient concentration and temperature on decomposition (Ferreira and Chauvet, 2011). Temperature stimulates metabolic activity, allowing a faster decomposition process; however, stimulation only occurs if nutrients are available, especially in substrates such as wood. In high orders with relative nutrient availability, an increase in temperature in summer potentially enhances microbial activity. By contrast, in low orders, decomposition is limited by nutrients, and rates are less independent of the temperature (Graça and Canhoto, 2006).

Stream environmental parameters, such as nutrients and temperature, are strongly influenced by land uses within the watershed (Allan, 2004). Our watershed was primarily covered by forest, but increased agricultural land use was observed downstream. Agricultural activity as a consequence of runoff and deforestation is associated with elevated nutrient concentrations and increased water temperature (Townsend and Riley, 1999; Paul et al., 2006). In our study, summer decomposition rates exhibited a unimodal relationship with the amount of agricultural land use, revealing the highest decomposition rates at intermediate levels of agricultural land use. A similar relationship with leaf litter decomposition in streams was reported by Mctammany et al. (2008) along an agricultural land gradient and by Woodward et al. (2012) along a nutrient gradient. Moderate levels of agricultural runoff stimulate

decomposition, which is limited by nutrients, but extreme amounts may cause decreased decomposition rates due to other pollutants or sediment inputs (Hagen et al., 2006; Lecerf et al., 2006).

As we predicted, significant differences in decomposition rates between habitats were observed but only in high orders; increased rates were noted in lotic habitats compared with lentic habitats, especially in winter.

The only environmental variables with significant differences in the interaction among habitat, order, and season in the mixed-effects model and at the same time, related with decomposition rates in the final regression model were water residence time and NOx concentration. Given that lentic habitats are characterised by higher water residence time, we hypothesised that they experience less physical abrasion than lotic habitats. Similarly, different studies have demonstrated higher decomposition rates of leaves and twigs when flow velocity increases, suggesting that physical abrasion caused by flowing water along with transported sediment (Ferreira et al., 2006a) serves as an important breakdown factor (e.g., Chergui and Pattee, 1988; Vingada, 1995; Santos Fonseca et al., 2012). Flow is also a major determinant of biotic composition (Bunn and Arthington, 2002). Fungi are considered the main decomposers of submerged wood (Gulis et al., 2004), and the current velocity can serve as an important factor regulating their assemblage structure. Ferreira and Graça (2006) reported increased aquatic hyphomycete activity in leaves exposed to high, rather than low, current velocity. Water flow supplies a continuous source of fungal spores to detritus (Bärlocher, 1992) and promotes oxygen-rich waters, preferentially colonised by aquatic hyphomycetes (Chauvet, 1992). This colonisation primarily occurs in winter when the presence of leaf litter allows the maximum fungal production (Suberkropp, 1997). Therefore, in high orders, fungal activity in lotic habitats might be stimulated. In contrast, in lentic areas, where physical abrasion and fungal activity might be low, decomposition rates remain low. This notion is primarily true in winter. However, in summer, when no difference between habitats was noted, the temperature would homogenise their decomposition rates.

The wood decomposition rates measured along the river network integrated the effects of flow regulation. The reduction of flow due to small dams and weirs reduced the organic matter

413 decomposition capacity of the river, especially in high-order streams and in the winter season,

414 where the environmental differences between lentic and lotic reaches were more evident.

415   This study demonstrated that small dams and weirs modify ecosystem functioning along the

416 river network, affecting key ecosystem functions such as organic matter decomposition. These

417 types of impoundments are especially abundant in Mediterranean areas. Despite the

418 abundance of these impoundments, their ecological effects remain poorly understood.

419 Moreover, Mediterranean areas are experiencing a growth of urban areas and extension in

420 agriculture activities (Underwood et al. 2009), which could result in major flow regulation in the

421 future and more small dams and weirs in the river basins to guarantee water supply. Under this

422 scenario, it is especially relevant to further investigate the effects of these impacts on

423 ecosystem functioning, and to consider these results to promote effective river management.

430 **References**

431 Allan JD. Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. Annu Rev
432   Ecol Evol Syst. 2004; 35:257–84.
433 Allan JD, Erickson LD, Fay J. The influence of catchment land use on stream integrity across multiple
434   spatial scales. Freshw Biol. 1997; 37:149–61.
435 Aristi I, Díez JR, Larrañaga A, Navarro-Ortega A, Barceló D, Elosegi A. Assessing the effects of multiple
436   stressors on the functioning of Mediterranean rivers using poplar wood breakdown. Sci Total
437   Environ. 2012; 440:272–279.
438 Arroita M, Aristi I, Flores L, Larrañaga A, Díez J, Mora J, Romaní AM, Elosegi A. The use of wooden sticks
439   to assess stream ecosystem functioning: Comparison with leaf breakdown rates. Sci Total Environ.
440   2012; 440:115-122.
441 Bärlocher F. Leaf mass loss estimated by litter bag technique. In: Graça M, Bärlocher F and Gessner MO,
442   editors. Methods to Study Litter Decomposition. A Practical Guide. The Netherlands: Springer. 2005;
443   37–42.
444 Bärlocher F.Research on aquatic hyphomycetes: historical background and overview. In: Bärlocher F,
445   editor. The ecology of aquatic hyphomycetes. Berlin: Springer-Verlag. 1992.
446 Baxter, RM. Environmental effects of dams and impoundments. Annual Review of Ecology & Systematics.
447   1977; 8:255–283.

448 Benfield EF, Webster JR, Hutchens JR, Tank JL, Turner PA. Organic matter dynamics along a stream-
449   order and elevational gradient in a southern Appalachian stream. Verh Int Verein Limnol. 2000;
450   27:1–5.
451 Benfield EF. Leaf breakdown in stream ecosystems. In: Hauer FR, Lamberti GA, editors. Methods in
452   stream ecology. San Diego: Academic Press. 1996; 579–89.
453 Buffagni A, Erba S, Armanini DG. The lentic–lotic character of Mediterranean rivers and its importance to
454   aquatic invertebrate communities. Aquat Sci. 2009; 72:45–60.
455 Bunn SE, Arthington AH. Basic Principles and Ecological Consequences of Altered Flow Regimes for
456   Aquatic Biodiversity. Environ Manage. 2002; 30:492–507.
457 Bunn SE, Davies PM, Mosisch TD. Ecosystem measures of river health and their response to riparian and
458   catchment degradation. Freshw Biol. 1999; 41:333–45.
459 Chauvet E. De la biologie des hyphomycetes aquatiques à l'écologie des rivières. Cryptogamie
460   Mycologique. 1992; 13: 203–214.
461 Chauvet E. Changes in the chemical composition of alder, poplar, and willow leaves during decomposition
462   in a river. Hydrobiologia. 1987; 148: 35-44.
463 Chergui H, Pattee E.The effect of water current on the decomposition of dead leaves and needles. Verh Int
464   Verein Limnol.1988; 23:1294–1298.
465 Clavero M, Blanco-Garrido F, Prenda J. Fish fauna in Iberian Mediterranean river basins: biodiversity,
466   introduced species and damming impacts. Aquat Conserv Mar Freshw Ecosyst. 2004; 14(6):575–85.
467 Cortes RM, Graça M, Vingada J, Oliveira SV. Stream typology and dynamics of leaf processing. Ann
468   Limnol. 1995; 31: 119-131.
469 Crenshaw CL, Valett HM, Tank JL. Effects of coarse particulate organic matter on fungal biomass and
470   invertebrate density in the subsurface of a headwater stream. J North Am Benthol Soc. 2002; 21:
471   28–42.
472 Dewson ZS, James ABW, Death RG. Stream Ecosystem Functioning under Reduced Flow Conditions.
473   Ecol Appl. 2007;17(6):1797–808.
474 Diez J, Elosegi A, Chauvet E, Pozo J. Breakdown of wood in the Agüera stream. Freshw Biol. 2002;
475   47:2205–15.
476 Elosegi A, Sabater S. Effects of hydromorphological impacts on river ecosystem functioning: a review and
477   suggestions for assessing ecological impacts. Hydrobiologia. 2012; 712:129–43.
478 Feio MJ, Alves T, Boavida M, Medeiros A, Graça M. Functional indicators of stream health: a river-basin
479   approach. Freshw Biol. 2010; 55:1050–65.
480 Ferreira V, Castagneyrol B, Koricheva J, Gulis V, Chauvet E, Graça M. A meta-analysis of the effects of
481   nutrient enrichment on litter decomposition in streams. Biol Rev Camb Philos Soc. 2014. doi:
482   10.1111/brv.12125.
483 Ferreira V, Chauvet E. Synergistic effects of water temperature and dissolved nutrients on litter
484   decomposition and associated fungi. Glob Chang Biol . 2011; 17:551–64.
485 Ferreira V, Graça M. Do Invertebrate Activity and Current Velocity Affect Fungal Assemblage Structure in
486   Leaves? Int Rev Hydrobiol. 2006; 91:1–14.
487 Ferreira V, Graça M, de Lima JLMP, Gomes R. Role of physical fragmentation and invertebrate activity in
488   the breakdown rate of leaves. Archiv Hydrobiol.2006a; 165:493-513.
489 Ferreira V, Gulis V, Graça M. Whole-stream nitrate addition affects litter decomposition and associated
490   fungi but not invertebrates. Oecologia. 2006b; 149:718–29.
491 Fleituch T. Beech Leaf Breakdown and POM Storage along an Altitudinal Stream Gradient. Hydrobiologia.
492   2001; 86:515–26.
493 Fonnesu A, Pinna M, Basset A. Spatial and Temporal Variations of Detritus Breakdown Rates in the River
494   Flumendosa Basin (Sardinia, Italy). Int Rev Hydrobio. 2004; 89:443–52.
495 Friedl G, Wüest A. Disrupting biogeochemical cycles – Consequences of damming. Aquatic Sciences.
496   2002; 64:55–65.
497 Gessner M., Chauvet E. A Case for Using Litter Breakdown to Asses Functional Stream Integrity. Ecol
498   Appl. 2002; 12:498–510.
499 Gessner M, Chauvet E, Dobson M. A perspective on leaf litter breakdown in streams. Oikos. 1999; 85:
500   377-384 .
501 González JM, Mollá S, Roblas N, Descals E, Moya Ó, Casado C. Small dams decrease leaf litter
502   breakdown rates in Mediterranean mountain streams. Hydrobiologia. 2012; 712:117–28.
503 Graça M, Canhoto C. Leaf litter processing in low order streams. Limnetica. 2006; 25:1–10.

504 Grantham TE, Figueroa R, Prat N. Water management in mediterranean river basins: a comparison of
505   management frameworks, physical impacts, and ecological responses. Hydrobiologia. 2012; 719
506   :451–82.
507 Gulis V, Rosemond AD, Suberkropp K, Weyers HS, Benstead JP. Effects of nutrient enrichment on the
508   decomposition of wood and associated microbial activity in streams. Freshw Biol. 2004; 49:1437–47.
509 Hagen AEM, Webster JR, Benfield EF, Hagen EM. Are leaf breakdown rates a useful measure of stream
510   integrity along an agricultural landuse gradient. J N Am Benthol Soc. 2006; 25:330–43.
511 Hupp CR, Schenk ER, Richter JM, Peet RK, Townsend PA. Bank erosion along the dam-regulated lower
512   Roanoke River, North Carolina. In: James LA, Rathbun SL, and Whittecar GR, editors. Management
513   and Restoration of Fluvial Systems with Broad Historical Changes and Human Impacts: Geological
514   Society of America Special Paper. 2009; 451:97-108.
515 Kuehn KA, Lemke MJ, Wetzel RG, Suberkropp K. Microbial biomass and production associated with
516   decaying leaf litter of the emergent macrophyte *Juncus effusus*. Limnology and Oceanography.
517   2000; 45: 862–870.
518 Lagrue C, Kominoski JS, Danger M, Baudoin JM, Lamothe S, Lambrigot D, Lecerf A. Experimental
519   shading alters litter breakdown in streams of contrasting riparian canopy cover. Freshw Biol. 2011;
520   56: 2059-2069.
521 Lecerf A, Chauvet E. Intra-specific variability in leaf traits strongly affects alder leaf decomposition in a
522   stream. Basic and Applied Ecology.2008; 9:598-607.
523 Lecerf A, Usseglio-Polatera P, Charcosset JY, Lambrigot D, Bracht B, Chauvet E. Assessment of
524   functional integrity of eutrophic streams using litter breakdown and benthic macroinvertebrates.
525   Archiv Hydrobiol. 2006; 165:105-126.
526 Malmqvist B, Rundle S. Threats to the running water ecosystems of the world. Environ Conserv. 2002;
527   29:134–53.
528 Marcé R, Honey-Rose J, Manzano A, Moragas L, Catllar B, Sabater S. The Llobregat River Basin: A
529   Paradigm of Impaired Rivers Under Climate Change Threats. In: S. Sabater et al, editors. The
530   Llobregat: The Story of a Polluted Mediterranean River. Springer-Verlag, Berlin. 2012; 21:297–326.
531 Martin R, Hanson L. Reservoirs in the United States: U.S. Geological Survey, Water Supply Paper 1838.
532   1966.
533 Martínez A, Larrañaga A, Basaguren A, Pérez J, Mendoza-Lera C, Pozo J. Stream regulation by small
534   dams affects benthic macroinvertebrate communities: from structural changes to functional
535   implications. Hydrobiologia. 2013; 711:31–42.
536 Mctammany ME, Benfield EF, Webster JR. Effects of agriculture on wood breakdown and microbial biofilm
537   respiration in southern Appalachian streams. Freshw Biol. 2008; 53:842–54.
538 Menéndez M, Descals E, Riera T, Moya O. Effect of small reservoirs on leaf litter decomposition in
539   Mediterranean headwater streams. Hydrobiologia. 2012; 691:135–46.
540 Menéndez M, Descals E, Riera T, Moya O. Leaf litter breakdown in Mediterranean streams: effect of
541   dissolved inorganic nutrients. Hydrobiologia. 2011; 669:143–55.
542 Naiman R, Melillo J. Longitudinal patterns of ecosystem processes and community structure in a subarctic
543   river continuum. Ecology. 1987;68:1139–56.
544 Nilsson C, Reidy C, Dynesius M, Revenga C. Fragmentation and flow regulation of the world's large river
545   systems. Science. 2005; 308:405–8.
546 Paul MJ, Meyer JL, Couch C. Leaf breakdown in streams differing in catchment land use. Freshw Biol.
547   2006; 51:1684–95.
548 Petersen RC, Cummins KW. Leaf processing in a woodland stream. Freshw Biol.1974; 4: 343–68.
549 Pinheiro JC, Bates DM, Debroy S, Deepayan S, R Development Core Team. nlme: linear and nonlinear
550   mixed effects models. R package version 3. 2012; 1–105.
551 Pinheiro JC, Bates DM. Mixed-Effects Models in S and S-PLUS. New York: Springer Verlag; 2000.
552 Poff NL, Zimmerman JKH. Ecological responses to altered flow regimes: a literature review to inform the
553   science and management of environmental flows. Freshw Biol. 2010; 55:194–205.
554 Poff NL, Hart DD. How dams vary and why it matters for the emerging science of dam removal.
555   Biogeosciences. 2002; 52:659–738.
556 Pozo J, Casas J, Menéndez M, Mollá S, Arostegui I, Basaguren A, Casado C, Descals E, et al. Leaf-litter
557   decomposition in headwater streams: a comparison of the process among four climatic regions. J N
558   Am Benthol Soc. 2011; 30: 935-950.
559 R Core Team. R: A language and environment for statistical computing. Vienna: R Foundation for
560   Statistical Computing; 2013.

561   Sabater S. Alterations of the global water cycle and their effects on river structure, function and services.
562   Freshwater Reviews. 2008; 1:75-88.

563   Santos Fonseca AL, Bianchini I, Pimenta CMM, Soares CBP, Mangiavacchi N. The flow velocity as driving
564   force for decomposition of leaves and twigs. Hydrobiologia. 2012; 703:59–67.

565   Schlief J, Mutz M. Effect of sudden flow reduction on the descomposition of alder leaves (Alnus glutinosa
566   [L.]Gaertn.) in a temperate lowland stream: a mesocosm study. Hydrobiologia. 2009; 624:205–17.

567   Schneider C, Laizé CLR, Acreman MC, Flörke M. How will climate change modify river flow regimes in
568   Europe? Hydrol Earth Syst Sci. 2013; 17:325–39.

569   Silva-Junior EF, Moulton TP, Boëchat IG, Gücker B. Leaf decomposition and ecosystem metabolism as
570   functional indicators of land use impacts on tropical streams. Ecol Indic. 2014; 36:195–204.

571   Stanford JA, Ward JV. Management of aquatic resources in large catchments: Recognizing interactions
572   between ecosystem connectivity and environmental disturbance. In: Naiman R, editor. Watershed
573   Management. New York: Springer-Verlag; 1992; 91-124.

574   Stelzer RS, Heffernan J, Likens GE. The influence of dissolved nutrients and particulate organic matter
575   quality on microbial respiration and biomass in a forest stream. Freshw Biol. 2003; 48:1925–1937.

576   Strahler, AN. Quantitative analysis of watershed geomorphology. Transactions of the American
577   Geophysical Union. 1957; 38:913-920.

578   Strayer DL. Challenges for freshwater invertebrate conservation. J North Am Benthol Soc. 2006; 25:271-
579   87.

580   Suberkropp K. Annual production of leaf-decaying fungi in a woodland stream. Freshw Biol. 1997; 38:169-
581   178.

582   Tank JL, Rosi-Marshall EJ, Griffiths N, Entrekin S, Stephen ML. A review of allochthonous organic matter
583   dynamics and metabolism in streams. J North Am Benthol Soc. 2010; 29:118–46.

584   Tank JL, Webster JR. Interaction of Substrate and Nutrient Availability on Wood Biofilm Processes in
585   Streams. Ecology. 1998;79:2168–79.

586   Tiegs S, Akinwole P, Gessner M. Litter decomposition across multiple spatial scales in stream networks.
587   Ecosyst Ecol. 2009;161:343–51.

588   Townsend CR, Riley RH. Assessment of river health : accounting for perturbation pathways in physical and
589   ecological space. Freshw Biol.1999; 41:393–405.

590   Underwood E, Viers J, Klausmeyer K, Cox R, Shaw M. Threats and biodiversity in the mediterranean
591   biome. Diversity and Distributions. 2009; 15:188–197.

592   Venables WN, Ripley BD. Modern Applied Statistics with S. 4th ed. New York: Springer; 2002.

593   Vericat D, Batalla RJ. Sediment transport in a highly regulated fluvial system during two consecutive floods
594   (lower Ebro River, NE Iberian Peninsula). Earth Surf Process Landforms. 2005; 30:385–402.

595   Vingada, JVS. Decomposição de folhada num rio de montanha. Influência dos factores físicos e
596   biológicos. Master thesis. Faculdade de Ciências e Tecnologia da Universidade de Coimbra,
597   Coimbra.1995.

598   Von Schiller D, Martí E, Riera JL, Ribot M, Marks JC, Sabater F. Influence of land use on stream
599   ecosystem function in a Mediterranean catchment. Freshw Biol. 2008; 53:2600–12.

600   Ward JV, Standford JA. The Serial Discontinuity Concept of Lotic Ecosystems. In: Fontaine TD, Bartell
601   SM, editors. Dynamics of Lotic Ecosystems. Michigan: Ann Arbor Sci. 1983. 29-42.

602   Webster JR, Benfield EF. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology
603   Systems. 1986; 17:567-594.

604   Woodward G, Gessner MO, Giller PS, Gulis V, Hladyz S, Lecerf A, et al. Continental-scale effects of
605   nutrient pollution on stream ecosystem functioning. Science. 2012; 336:1438–40.

606   Young RG, Collier KJ. Contrasting responses to catchment modification among a range of functional and
607   structural indicators of river ecosystem health. Freshw Biol. 2009; 54:2155–70.

608   Young RG, Matthaei CD, Towsend CR. Organic matter breakdown and ecosystem metabolism: functional
609   indicators for assessing river ecosystem health. J North Am Benthol Soc. 2008; 27:605–25.

610   Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. Mixed Effects Model and Extensions in Ecology
611   with R. New York: Springer Science and Business Media; 2009.

612

613

614

Tables and Figures

Table 1.
Characterisation of the studied sites. The percentages of land use cover refer to the total sub-catchment area associated with each site.

Site	Latitude, N	Longitude, E	Altitude (m.a.s.l)	Order	Hydrologic Habitat	Catchment area (ha)	Land Use Cover (%) Forest	Land Use Cover (%) Agricultural	Land Use Cover (%) Urban
A	42°10'08"	3°03'18"	2	5	Lotic	96131	77,89	18,11	2,59
B	42°10'06"	3°01'48"	9	5	Lentic	94803	78,23	17,82	2,56
C	42°10'39"	2°50'11"	83	5	Lotic	80947	82,14	14,14	2,37
D	42°11'9"	2°45'36"	115	5	Lentic	78938	82,75	13,56	2,36
E	42°10'07"	2°43'47"	135	4	Lotic	11571	82,46	15,76	1,25
F	42°13'3"	2°34'29"	214	5	Lotic	29656	78,35	16,87	3,56
G	42°10'28"	2°28'71"	434	4	Lentic	10355	76,90	19,44	2,55
H	42°15'02"	2°28'49"	451	2	Lotic	155	96,58	3,03	0,10
I	42°18'03"	2°35'21"	356	3	Lotic	2476	95,15	0,13	0,01
J	42°18'06"	2°35'20"	358	3	Lentic	2475	95,17	0,01	0,13

Table 2.
Stream water characteristics of the studied sites. DIC=dissolved inorganic carbon, DOC=dissolved organic carbon, NOx=NO_2^-+NO_3^{-2}, PO_4^{-3}=phosphate, Cl^-=chloride, and SO_4^{-2}= sulphate. Values (mean ± SE) highlighted in bold correspond to the winter period, whereas non-bold values correspond to the summer period.

Stream water characteristics

Site	Temperature (°C)	Conductivity (µS / cm)	pH	Dissolved oxygen (mg/L)	DIC (mgC/L)	DOC (mgC/L)	NOx (mgN/L)	PO42- (mgP/L)	SO4 (mgS/L)	Cl- (mgCl/L)	Residence time (h)
A	**12.2 ± 1.1**	**926.5 ± 15.5**	**7.9 ± 0.1**	**9.3 ± 0.1**	**44.7 ± 0.3**	**0.8 ± 0.1**	**1.5 ± 0.1**	**0.004 ± 0.001**	**79.0 ± 4.1**	**49.1 ± 2.1**	**3.0 ± 0.7**
	22.0 ± 0.6	941.3 ± 27.7	8.0 ± 0.1	9.5 ± 0.8	43.2 ± 1.9	1.0 ± 0.1	1.1 ± 0.1	0.002 ± 0.001	90.3 ± 3.7	33.7 ± 1.4	1.1 ± 0.2
B	**10.0 ± 1.8**	**951.2 ± 21.0**	**8.3 ± 0.1**	**11.5 ± 0.3**	**44.9 ± 0.6**	**1.0 ± 0.1**	**2.1 ± 0.1**	**0.005 ± 0.003**	**86.4 ± 6.1**	**53.2 ± 2.9**	**7.3 ± 0.8**
	23.6 ± 0.5	936.2 ± 34.9	8.2 ± 0.1	10.8 ± 0.6	41.6 ± 2.1	1.1 ± 0.1	1.0 ± 0.1	0.002 ± 0.001	89.7 ± 4.9	34.4 ± 1.9	4.1 ± 1.2
C	**10.3 ± 1.1**	**1035.1 ± 20.1**	**8.1 ± 0.1**	**13.0 ± 0.9**	**52.6 ± 0.1**	**1.3 ± 0.1**	**2.0 ± 0.1**	**0.023 ± 0.007**	**92.5 ± 6.1**	**52.3 ± 3.6**	**2.5 ± 0.9**
	23.4 ± 0.8	1004.8 ± 52.8	8.2 ± 0.0	9.2 ± 0.1	45.7 ± 2.0	1.5 ± 0.1	1.2 ± 0.2	0.023 ± 0.019	91.4 ± 8.4	36.5 ± 2.0	1.8 ± 0.2
D	**11.6 ± 0.8**	**1122 ± 60.3**	**7.5 ± 0.0**	**8.6 ± 0.6**	**56.1 ± 1.0**	**1.3 ± 0.1**	**1.8 ± 0.1**	**0.051 ± 0.021**	**86.1 ± 4.2**	**51.9 ± 3.9**	**81.1 ± 9.2**
	23.1 ± 1.1	933.2 ± 44.8	8.1 ± 0.1	11.2 ± 1.2	47.1 ± 2.2	2.5 ± 0.3	1.3 ± 0.3	0.052 ± 0.022	72.9 ± 3.6	51.3 ± 5.1	33.8 ± 8.8
E	**6.7 ± 1.5**	**771.5 ± 37.2**	**8.1 ± 0.1**	**11.5 ± 0.7**	**58.1 ± 2.5**	**1.7 ± 0.3**	**2.0 ± 0.1**	**0.014 ± 0.008**	**55.9 ± 3.1**	**18.1 ± 0.2**	**7.6 ± 1.7**
	19.4 ± 0.6	1143.5 ± 193.7	8.1 ± 0.1	9.2 ± 0.4	49.2 ± 3.9	1.6 ± 0.2	1.9 ± 0.4	0.015 ± 0.006	154.4 ± 54.3	21.5 ± 2.8	2.2 ± 1.2
F	**9.8 ± 1.0**	**1216.7 ± 25.6**	**7.9 ± 0.0**	**13.7 ± 1.0**	**52.4 ± 0.9**	**1.3 ± 0.1**	**2.2 ± 0.1**	**0.046 ± 0.027**	**117.4 ± 5.1**	**81.2 ± 2.6**	**5.0 ± 0.4**
	21.0 ±1.1	919.5 ± 42.7	8.2 ± 0.1	10.7 ± 0.7	53.2 ± 0.8	1.9 ± 0.2	3.0 ± 0.1	0.194 ± 0.021	55.0 ± 5.9	63.9 ± 6.1	3.0 ± 0.3
G	**8.1 ± 0.9**	**606.5 ± 22.6**	**8.1 ± 0.0**	**11.6 ± 0.5**	**58.1 ± 2.6**	**1.7 ± 0.4**	**3.5 ± 0.3**	**0.038 ± 0.022**	**23.1 ± 5.2**	**15.9 ± 2.6**	**184.7 ± 8.6**
	17.1 ± 0.4	617.6 ± 57.0	8.1 ± 0.0	7.7 ± 0.4	63.2 ± 2.0	1.6 ± 0.1	4.8 ± 0.5	0.024 ± 0.004	14.3 ± 1.4	15.1 ± 1.5	25.7 ± 12.2
H	**5.5 ± 1.6**	**475.4 ± 47.8**	**8.1 ± 0.0**	**10.8 ± 0.3**	**50.8 ± 0.8**	**1.2 ± 0.1**	**0.03 ± 0.006**	**0.003 ± 0.001**	**19.8 ± 1.1**	**10.8 ± 0.2**	**34.1 ± 10.4**
	17.4 ± 0.9	512.3 ± 17.7	8.2 ± 0.0	8.9 ± 0.1	49.4 ± 1.3	1.5 ± 0.1	0.01 ± 0.007	0.003 ± 0.001	19.04 ± 0.71	7.6 ± 0.2	9.0 ± 2.7
I	**8.1 ± 1.3**	**939.2 ± 41.8**	**8.01 ± 0.1**	**10.3 ± 0.2**	**35.2 ± 0.4**	**0.5 ± 0.1**	**0.003 ± 0.0006**	**0.002 ± 0.001**	**127.4 ± 5.8**	**2.3 ± 0.1**	**10.4 ± 0.8**
	17.2 ± 0.6	671.7 ± 48.3	8.0 ± 1.1	8.8 ± 0.1	35.3 ± 0.8	0.7 ± 0.1	0.01 ± 0.006	0.002 ± 0.001	80.2 ± 7.8	1.8 ± 0.3	3.1 ± 0.5
J	**7.8 ± 1.5**	**951.7 ± 43.5**	**8.4 ± 0.1**	**11.3 ± 0.1**	**35.3 ± 0.4**	**0.5 ± 0.1**	**0.002 ± 0.006**	**0.002 ± 0.001**	**134.0 ± 6.9**	**2.2 ± 0.1**	**5.9 ± 0.4**
	16.7 ± 0.7	747.7 ± 40.1	8.4 ± 0.1	8.9 ± 0.2	34.1 ± 0.7	0.6 ± 0.0	0.01 ± 0.007	0.002 ± 0.001	82.5 ± 6.7	1.7 ± 0.3	4.8 ± 0.2

Table 3.
Summary of linear mixed-effect models of stream water characteristics of the studied sites along the river network in both seasons (n=20). DIC, PO_4^{-3}, and SO_4^{-2} values with correlation coefficients greater than 0.70 with DOC, NOx, and conductivity, respectively, were not included in the linear mixed-effects model. Data appearing in bold are statistically significant.

Dependent Variables

Fixed Factors	Temperature		NOx		Residence Time (log x)		DOC		Dissolved Oxygen		pH		Cl-		Conductivity	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Habitat	0.40	0.5526	6.02	0.0576	28.09	**0.0061**	0.21	0.6607	0.02	0.8711	1.88	0.2291	0.01	0.9475	0.02	0.8835
Order	35.27	**0.0011**	29.75	**0.0017**	15.16	**0.0136**	2.86	0.1481	1.03	0.4211	1.45	0.3177	21.56	**0.0035**	4.41	0.0787
Season	490.85	**<.0001**	1.02	0.3147	25.10	**<.0001**	8.17	**0.0058**	27.49	**<.0001**	1.76	0.1897	63.84	**<.0001**	10.16	**0.0220**
Habitat x Order	0.34	0.7245	5.44	0.0556	124.52	**0.0002**	0.24	0.7936	0.22	0.8074	1.92	0.2412	0.02	0.9735	0.54	0.6119
Habitat x Season	0.25	0.6140	0.01	0.92	0.55	0.4609	0.49	0.4851	2.40	0.1263	2.58	0.1134	29.96	**<.0001**	1.53	0.2199
Season x Order	1.41	0.2508	6.68	**0.0023**	5.53	**0.0072**	3.22	**0.0463**	3.89	**0.0254**	2.03	0.1402	14.69	**<.0001**	3.76	**0.0286**
Habitat x Order x Season	1.89	0.1594	6.99	**0.0018**	56.05	**<.0001**	0.62	0.5409	5.58	**0.0059**	0.31	0.7372	2.29	0.1093	3.08	0.0526
AIC (n=80)	352.29		150.75		336.54		131.19		293.06		4.71		416.56		892.014	

Table 4.
Summary of the linear mixed-effects model used to analyse differences in wood decomposition over time along the river network. The proportion of remaining AFDM was used as dependent variable. Season, hydrological habitat, river order, and time (co-variable) were used as fixed factors, whereas site was used as a random factor. Data appearing in bold are statistically significant.

Fixed Factors	AFDMr (log x)	
	F	p
Time	56.69	**<.0001**
Habitat	3.83	0.1219
Time x Habitat	0.46	0.4969
Order	10.27	**0.0266**
Time x Order	6.74	**0.0015**
Season	98.56	**<.0001**
Time x Season	35.30	**<.0001**
Habitat x Order	11.17	**0.0211**
Time x Habitat x Order	10.10	**0.0001**
Habitat x Season	18.52	**<.0001**
Time x Habitat x Season	0.09	0.7679
Order x Season	69.65	**<.0001**
Time x Order x Season	4.89	**0.0086**
Habitat x Order x Season	11.82	**<.0001**
Time x Habitat x Order x Season	5.49	**0.0049**

(n= 192, AIC = -351.90)

Table 5.
Multiple regression analyses of decomposition rates (day^{-1}) and stream water characteristics in winter and summer. T=temperature, NOx=NO$_2^-$+NO$_3^{-2}$, DOC=dissolved organic carbon. R=multiple regression coefficient. Note that residence time was negatively correlated with decomposition rates. Data appearing in bold are statistically significant.

Dependent Variable	Selected Independent Variables	Coefficient	Standard Error	t value	p
k (days^{-1}) n=20, R=0.72, F=13.55, p<0.001	**T**	0.060	0.024	2.470	**0.0260**
	NOx	0.242	0.104	2.318	**0.0350**
	Residence Time	-0.322	0.112	-2.873	**0.0116**
	DOC	0.687	0.3293	2.087	0.0543

Figure 1.
Locations of the study sites (letters from A to J) in the Fluvià River watershed (NE, Iberian Peninsula). Black dots denote lotic sampling reaches, whereas white dots denote lentic-sampling reaches.
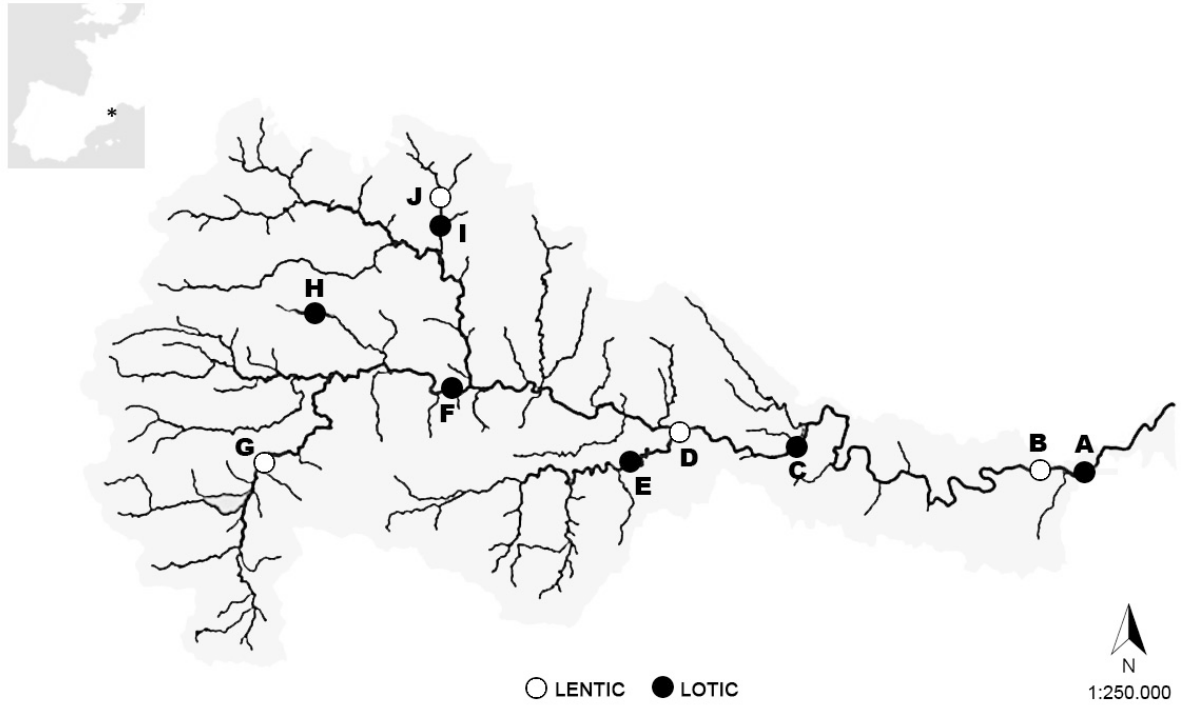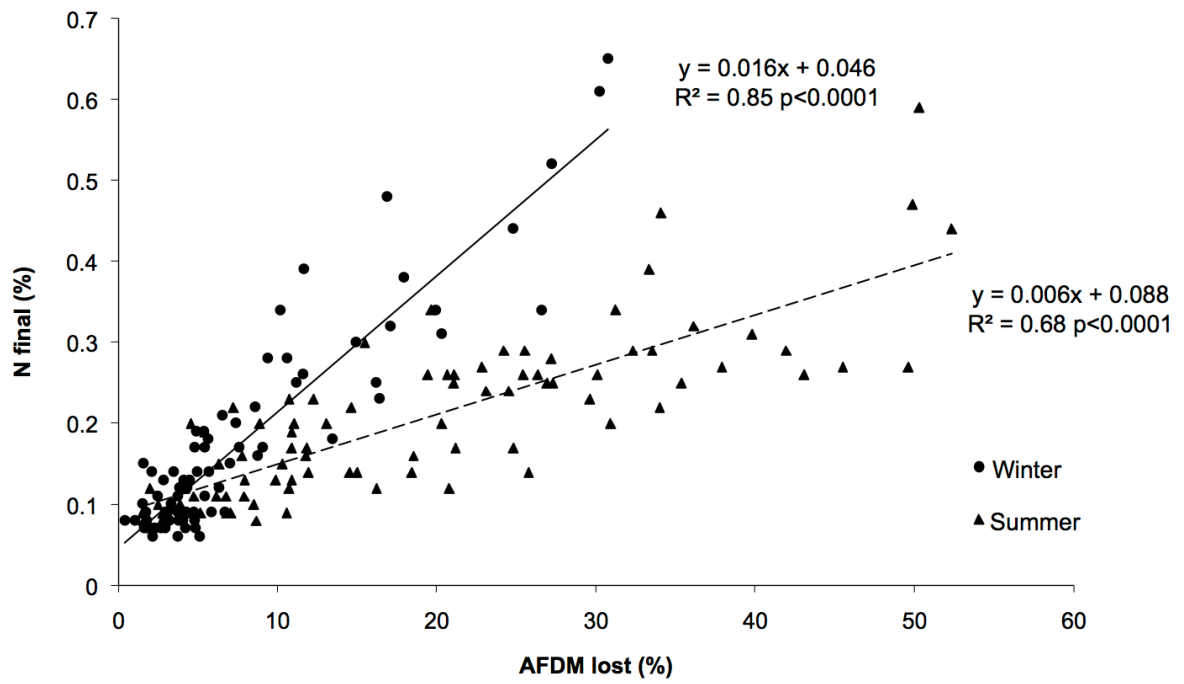
Figure 2
Decomposition rates (day^{-1}) of each site in winter and summer. Error bars indicate standard
error.
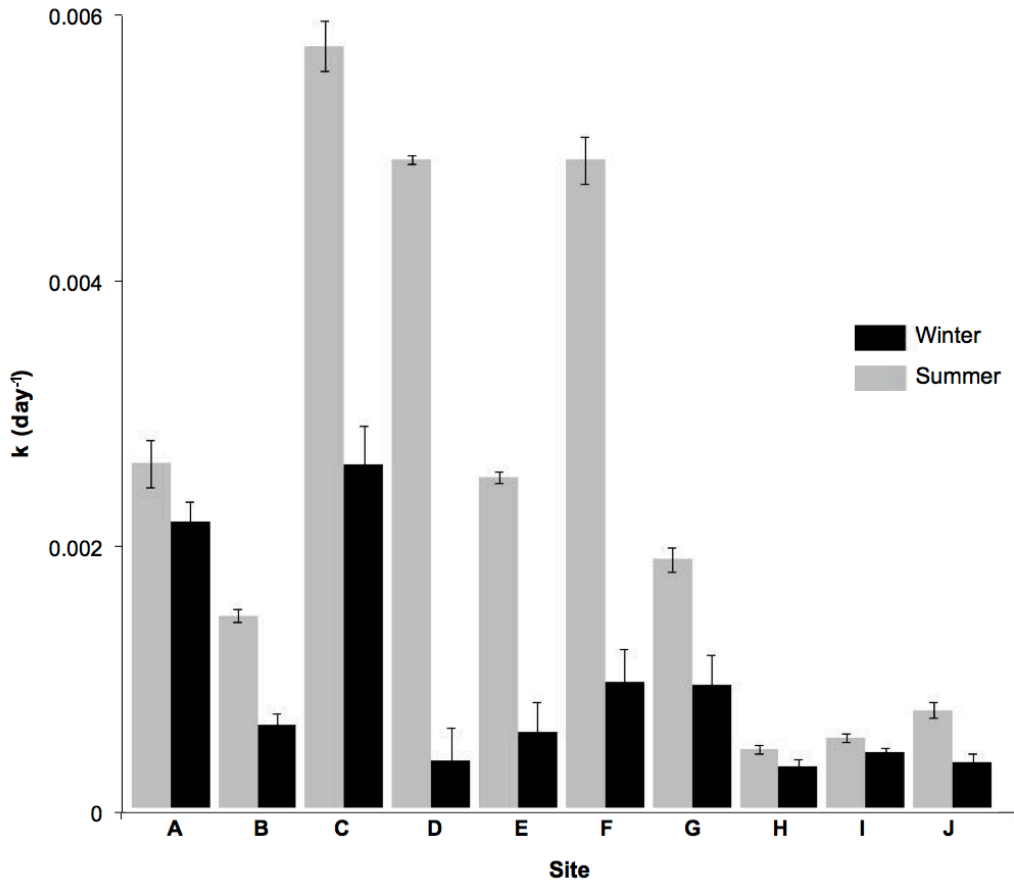
Figure 3.

Nitrogen (N) content in each stick as a percentage of stick dry mass and related to the total proportion of ash-free dry mass (AFDM) lost in each stick (n=192).

Figure 4.

Decomposition rates (day $^{-1}$) of each site (letters from A to J) in summer related to total hectares of agricultural land use presented in the sub-catchment associated with each site. White points indicate lentic habitats, whereas black points indicate lotic habitats (n=10).

$$y = -6E\text{-}11x^2 + 1E\text{-}06x + 0{,}0006$$
$$R^2 = 0.93 \quad p < 0.0001$$