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Drought and detritivores determine leaf litter decomposition in calcareous streams of the Ebro catchment (Spain)

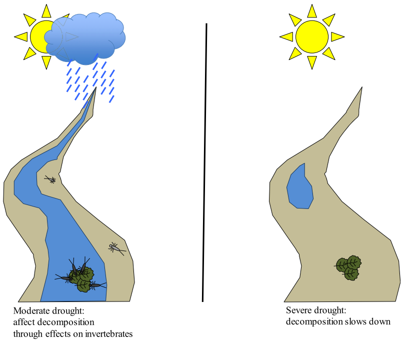
Silvia Monroy [a,*], Margarita Menéndez [b], Ana Basaguren [a], Javier Pérez [a], Arturo Elosegi [a], Jesús Pozo [a]

[a] *Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country, P.O. Box 644, 48080 Bilbao, Spain*
[b] *Department of Evolutionary Biology, Ecology and Environmental Sciences, Ecology Section, Faculty of Biology, University of Barcelona, Av. Diagonal, 643, 08028 Barcelona, Spain*

HIGHLIGHTS

- Drought will be more prevalent in the Mediterranean region as a consequence of climate change and human activities.
- We assessed decomposition of leaf-litter of contrasting quality across a regional-scale drought gradient.
- Decomposition rates showed no general pattern but declined sharply in streams subject to severe water stress.
- Drought affected detritivores, which in turn were the main drivers of decomposition rates.

GRAPHICAL ABSTRACT



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ABSTRACT

Drought, an important environmental factor affecting the functioning of stream ecosystems, is likely to become more prevalent in the Mediterranean region as a consequence of climate change and enhanced water demand. Drought can have profound impacts on leaf litter decomposition, a key ecosystem process in headwater streams, but there is still limited information on its effects at the regional scale. We measured leaf litter decomposition across a gradient of aridity in the Ebro River basin. We deployed coarse- and fine-mesh bags with alder and oak leaves in 11 Mediterranean calcareous streams spanning a range of over 400 km, and determined changes in discharge, water quality, leaf-associated macroinvertebrates, leaf quality and decomposition rates. The study streams were subject to different degrees of drought, specific discharge ($L\ s^{-1}\ km^{-2}$) ranging from 0.62 to 9.99. One of the streams dried out during the experiment, another one reached residual flow, whereas the rest registered uninterrupted flow but with different degrees of flow variability. Decomposition rates differed among sites, being lowest in the 2 most water-stressed sites, but showed no general correlation with specific discharge. Microbial decomposition rates were not correlated with final nutrient content of litter nor to fungal biomass. Total decomposition rate of alder was positively correlated to the density and biomass of shredders; that of oak was not. Shredder density in alder bags showed a positive relationship with specific discharge during the decomposition experiment. Overall, the results point to a complex pattern of litter decomposition at the regional scale, as drought affects decomposition directly by emersion of bags and indirectly by affecting the functional composition and density of detritivores.

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* Corresponding author.
E-mail address: silvia.monroy@ehu.eus (S. Monroy).

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1. Introduction

Global climate models forecast widespread shifts in temperature and precipitation patterns in the next decades, including increased temperature, reduced rainfall and higher frequency of extreme climate events in the Mediterranean area (IPCC, 2014). Because of the linkages between climate and hydrological processes (Papadaki et al., 2016), these changes are expected to affect flow regime in different ways, such as reducing average flow or increasing the frequency and magnitude of extreme flow events (Huang et al., 2016).

Flow is a key driver of the structure and function of aquatic ecosystems, as it affects water quality, physical habitat, energy resources and biotic interactions (Allan and Castillo, 2007; Dewson et al., 2007; Poff et al., 1997). Drought, in particular, is an important environmental stressor for freshwater ecosystems (Sabater, 2008). It reduces water velocity and depth, reduces hydrological connectivity, promotes sedimentation (Dewson et al., 2007), alters water physicochemical conditions (Schäfer et al., 2012; von Schiller et al., 2011) and affects the inputs, storage and quality of organic matter (Sanpera-Calbet et al., 2015; Ylla et al., 2010). Therefore, it can affect not only stream biological assemblages (Bonada et al., 2007; Filipe et al., 2013), but also ecosystem processes (Acuña et al., 2005; Martínez et al., 2015). Semiarid regions such as the Mediterranean are particularly vulnerable to drought disturbances (Milly et al., 2005; Sabater and Tockner, 2010). The Mediterranean climate is characterized by high inter-annual variability and pronounced seasonality with hot, dry summers (Gasith and Resh, 1999), and climate models forecast reduced precipitation and more severe drought events (Milly et al., 2005). Therefore, to predict the consequences of oncoming climate change, it is important to understand the effects of drought on river ecosystem functioning.

Organic matter decomposition is a key process which transfers energy and matter across trophic levels (Perkins et al., 2010), controls nutrient cycling (Cheever et al., 2012) and contributes greatly to the global carbon cycle (Battin et al., 2009; Kominoski and Rosemond, 2012). It is a complex process that includes the leaching of soluble compounds, physical abrasion, microbial conditioning and invertebrate fragmentation, and which depends on a complex array of both intrinsic (e.g. litter quality) and extrinsic (e.g. temperature, dissolved nutrients, discharge) factors (Tank et al., 2010). Therefore, decomposition rate has been proposed as an integrative indicator of ecosystem functional status (Gessner and Chauvet, 2002; Young et al., 2008). Previous studies have shown decomposition in streams to occur more slowly during periods of residual flow (Leberfinger et al., 2010; Mora-Gómez et al., 2016), being also slower in temporary than in perennial streams (Langhans and Tockner, 2006), and the effects of drying events to extend long after flow resumption (Datry et al., 2011). Nevertheless, most information so far existing on the effects of drought on litter decomposition derives from studies at a few sites (Martínez et al., 2015) and there is not yet a clear consensus on whether the patterns observed also hold for larger, regional scales subject to other confounding factors.

Additionally, it is still unclear whether the effects of drought differ among groups of consumers. Reduced decomposition rates in temporary streams have been attributed to reduced macroinvertebrate activity (Langhans and Tockner, 2006; Martínez et al., 2015), whereas microbial decomposition seems to recover from drought faster than invertebrate activities (Datry et al., 2011), although fungi and bacteria also differ in their sensitivity to environmental stress (Mora-Gómez et al., 2016). Also, it is still unclear whether the effects of drought differ among leaf species. Leaf species show a wide range of degradability (Petersen and Cummins, 1974), determined in part by their contents in nutrients and structural molecules such as lignin (Hladyz et al., 2009), although intra-specific variations can be large (Graça and Poquet, 2014). The most palatable leaves can be readily consumed by shredding invertebrates, whereas the decomposition of more recalcitrant species is more driven by microbes (Martínez et al., 2016). Therefore, it is likely that the differential impact of drought on microbes and invertebrates could result in contrasting effects on the decomposition of different leaf species.

The aim of our study was to examine the effect of drought on leaf litter decomposition across a regional gradient of aridity, to check whether microbial or detritivore activities are more affected, and whether the effects are consistent for leaves with contrasting quality. We performed a decomposition experiment with a fast-decaying (alder) and a slow-decaying species (oak) along an aridity gradient in 11 streams in the Ebro river basin (Spain). We hypothesized that 1) drought reduces the decomposition rate; 2) detritivore activity is more affected than microbial activity; 3) fast-decaying, high-quality leaf litter is more affected than slow-decaying, low-quality one; and 4) differences in decomposition rate between species are higher where detritivore activity is most affected.

2. Methods

2.1. Study sites

We performed a first screening of potential sites for experiments in the Ebro basin (Spain) by checking the information on hydrology and ecological status available at the Ebro Hydrographic Confederation (CHE; http://www.chebro.es). We selected streams of the Mediterranean calcareous mountain typology, which are characterised by limestone substrate, catchment slope > 2%, specific discharge (Qs) < 16.5 L s^{-1} km^{-2} and conductivity >320 μS cm^{-1} (CEDEX, 2004; CHE). In spring 2014, we visited over 40 calcareous mountain streams with good ecological status according to the monitoring network of CHE, where we analyzed the physical habitat and determined basic physico-chemical characteristics. Based on all this information, we performed a principal component analysis from which we selected 11 sites with similar habitat and water quality but spatially distributed along a precipitation gradient, which ranged from 311.2 up to 621.4 mm y^{-1}, with average annual temperature ranging from 8.2 to 14.2 °C (Fig. 1; Table 1). The sites spanned a distance of over 400 km. Given that inter-annual variability of the Mediterranean climate is high and hydrological conditions in a given period can depart markedly from historic averages, we used the accumulated rainfall for a year prior to sampling as a surrogate of the climate conditions at the sampling site. We used the specific discharge (Qs), calculated as the mean annual discharge per unit catchment area (L s^{-1} km^{-2}) (Munné and Prat, 2004) as a proxy for drought. Moreover, we also calculated the monthly coefficient of variation of water flow (CV_Q) as the standard deviation of monthly flow divided by annual average flow, since it yields information about intra-annual flow variability. All flow variables were calculated using daily mean flows from a common 10-y period (Qs_{10}; CV_{Qs10}) and from 1-y prior to the study period ($Qs_{13/14}$; $CV_{Qs13/14}$) (Table 1). Daily mean flow values for all study sites were obtained from nearby gauging stations for the period 2005–2015 (data from CHE; http://www.chebro.es).

2.2. Environmental variables

During the study period (autumn-winter 2014–2015), water temperature was recorded hourly with two ACR Smart-Button temperature loggers (ACR Systems Inc) at each site placed at different depths, thus also allowing to detect reductions in flow. Conductivity, pH and oxygen saturation were measured on three occasions with a multiparametric sensor (WTW Multi 350i). Discharge was estimated on these occasions from instantaneous water velocity measured by a current metre (MiniAir 2, Schiltknecht Co). Furthermore, following the calculation procedure in the precedent section, Qs and CV_Q were determined for the experimental period (Qs_{exp}, $CV_{Qs,exp}$) for both total and microbial decomposition periods. Water samples for nutrient analyses were collected at all streams on each sampling date, immediately filtered (Millipore, 0.45 μm pore) and frozen (−20 °C). Nitrate, chlorine and

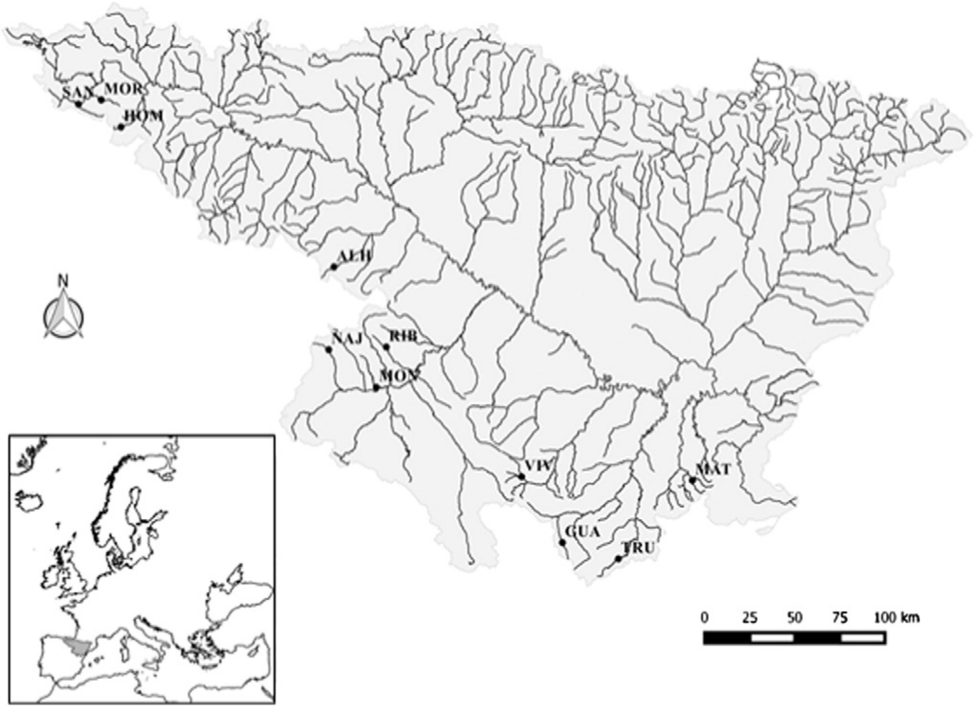

Fig. 1. Location of the study sites.

Table 1
Location, reach characterization and hydrological and climatic attributes for all studied streams. Streams arranged along the longitudinal gradient W–E. For air temperature, mean values and their range (in parenthesis) are shown. Data for hydrological variables of SAN and MOR and NAJ and MON were estimated from the same gauging station. Specific discharge (Qs) and monthly coefficient of variation of water flow (CV_Q) from a common 10-y period (Qs_{10}; CV_{Qs10}) and from 1-y prior to the study period ($Qs_{13/14}$; $CV_{Qs13/14}$).

	SAN	MOR	HOM	ALH	NAJ	MON	RIB	VIV	GUA	TRU	MAT
Latitude (N)	42° 41′ 06.5″	42° 42′ 24.9″	42° 34′ 36.5″	41° 53′ 56.5″	41° 29′ 54.1″	41° 18′ 57.0″	41° 30′ 28.3″	40° 52′ 12.2″	40° 32′ 52.8″	40° 27′ 42.0″	40° 49′ 37.0″
Longitude (W)	3° 52′ 46.3″	3° 43′ 33.8″	3° 35′ 20.4″	2° 09′ 34.5″	2° 11′ 58.5″	1° 53′ 11.5″	1° 48′ 59.9″	0° 56′ 12.8″	0° 40′ 48.1″	0° 18′ 57.6″	0° 11′ 07.8″ E
Altitude (m a.s.l.)	764	786	755	920	918	661	822	954	1251	1124	565
Basin area (km^2)	47.9	59.1	55.6	45.0	41.5	88.2	54.0	45.3	55.9	165.0	48.7
Width (m)	3.3 ± 0.7	3.0 ± 0.34	2.9 ± 0.5	3.5 ± 0.9	1.9 ± 0.3	2.1 ± 0.8	2.9 ± 0.5	4.9 ± 1.2	1.7 ± 0.2	6.7 ± 1.8	7.6 ± 0.8
Riparian vegetation											
Tree canopy cover(%)	83	62	93	73	79	33	72	30	46	1.6	24
Substrate composition(%)											
Boulder (>256 mm)	20	5	5	20	(+)		(+)	20	5	30	5
Cobble (64–256 mm)	50	40	10	60	10		30	0	45	45	40
Pebble (16–64 mm)	10	35	5	5	40		50	0	40	20	45
Gravel (2–16 mm)	10	10	5	10	25		10	0	5	5	10
Sand (<2 mm)	10	10	5	5	25	100	10	80	5	0	0
Travertine substrate		70									
Hydrological variables											
Qs_{10} ($L\ s^{-1}\ km^{-2}$)	9.99	9.99	3.41	1.3	0.62	0.62	2.96	0.66	5.73	1.09	6.58
CV_{Qs10}	0.72	0.72	0.62	0.81	0.1	0.1	0.46	0.63	0.49	1.19	0.59
$Qs_{13/14}$ ($L\ s^{-1}\ km^{-2}$)	10.08	10.08	3.21	0.84	0.69	0.69	2.58	0.67	5.25	0.31	4.18
$CV_{Qs13/14}$	0.94	0.94	0.78	0.71	0.16	0.16	0.27	0.45	0.48	0.74	0.4
Climatic variables											
Annual mean air temperature (°C)	8.2 (3.3–14.4)	10.0 (3.3–14.4)	12.5 (7.3–17.6)	10.6 (6.9–14.9)	12.4 (5.9–19.4)	8.9 (5.1–13.9)	13.4 (4.7–17.0)	13.8 (8.5–17.6)	10.5 (4.4–16.4)	9.7 (6.2–21.4)	14.2 (8.1–19.5)
Annual mean precipitation from 2005 to 2015 (mm)	621.4	543	503.9	379.6	311.2	349	419.3	408.5	451.8	509.5	508.5
Coefficient of variation of monthly precipitation (%)	43.4	49	44.7	35.9	42.9	40.7	37.1	43.5	42.1	43.8	50.3
Annual mean precipitation 2013/14 (mm)	523.2	476	521.4	386.6	266.7	401.8	454.4	238	350.8	411.4	–
Coefficient of variation of monthly precipitation 2013/14 (%)	100	56.2	68.6	55.4	80.7	63.7	44.6	69.8	69.4	88.7	–

SAN: San Antón; MOR: Moradillo; HOM: Homino; ALH: Alhama; NAJ: Nájima; MON: Monegrillo; RIB: Ribota; VIV: Vivel; GUA: Guadalope; TRU: Truchas; MAT: Matarraña.

sulphate concentration were determined by capillary ion electrophoresis (Agilent CE), and the rest of the nutrients were analyzed colorimetrically (Spectrophotometer Jasco V-630): nitrite by the sulphanilamide method, ammonium by the salicylate and dichloroisocyanurate method and dissolved reactive phosphorus (SRP) by the ascorbic acid method (APHA, 1998). Dissolved inorganic nitrogen (DIN) was computed as the sum of nitrate, nitrite and ammonium.

2.3. Leaf litter decomposition

In October 2014 we collected freshly-fallen leaves of two native species from the Iberian Peninsula contrasting in quality, the highly palatable black alder, *Alnus glutinosa* (L.) Gaertner, and the recalcitrant pedunculate oak, *Quercus robur* L. Approximately 5.0 g (±0.1 g) of air-dried leaf litter were enclosed in either fine (12 × 15 cm, 0.5 mm mesh size) or coarse (20 × 25 cm, 5 mm mesh size) mesh bags and deployed in the 11 streams on 2nd to 4th December 2014. At each site, 5 iron bars were anchored randomly to the streambed in riffle sections along 50 m of the channel and 4 bags (2 species × 2 mesh size) were tied to each bar by nylon lines, making a total of 20 bags per site (5 samples per species and mesh bag type). An extra set of five bags per species and type of mesh bag were used to correct initial mass values for manipulation loss and estimate air dry to oven-dry (72 h at 60 °C), to ash free dry mass (AFDM, 12 h at 500 °C) conversion factors.

On 13th to 18th January 2015, when alder was expected to have lost approximately 50% of the initial mass, we retrieved all (alder + oak) coarse mesh bags to evaluate total decomposition rate. We retrieved all fine bags on 9th to 11th March 2015 to calculate microbial decomposition. Retrieved litter bags were enclosed individually in zip-lock bags and transported in a refrigerated cooler to the laboratory. The leaf litter material from each bag was rinsed with distilled water on a 200-μm sieve to remove sediments and associated invertebrates. For each fine-mesh bag, a set of five leaf disks was punched out with a cork borer (12 mm diameter) and frozen at −80 °C for later fungal biomass determination. The remaining material was oven-dried (60 °C, 72 h) and weighed to determine leaf dry mass. A portion of leaf material from each bag retrieved was ground (1 mm pore sieve) and stored (−20 °C) for later nutrient analyses and the rest was combusted (500 °C, 12 h) and weighed to determine the remaining ash free dry mass (AFDMr). The collected fauna was preserved in 70% ethanol for later analyses.

2.4. Leaf litter stoichiometry

Carbon (C) and nitrogen (N) concentrations were determined with a Perkin Elmer II CHNS/O elemental analyser and phosphorus (P) colorimetrically after autoclave-assisted extraction (APHA, 1998). Results were expressed as a percentage elemental content of leaf dry mass (%C, %N, %P).

2.5. Fungal biomass

The sets of five leaf disks from each fine-mesh bag were freeze-dried and weighed to later determine ergosterol concentration as a measure of fungal biomass (Gessner and Chauvet, 1993). Lipid extraction and saponification were performed using KOH methanol 0.14 M (8 g L^{-1}) at 80 °C for 30 min in a shaking bath. Extracted lipids were purified using solid-phase extraction cartridges (Waters Sep-Pak®, Vac RC, 500 mg, tC18 cartridges, Waters Corp.), and ergosterol was eluted using isopropanol. Ergosterol was detected and quantified via high pressure liquid chromatography (HPLC) by measuring absorbance at 282 nm. A Jasco HPLC system equipped with a Gemini-NX 5 μm C18 250 × 4.6 mm column was used. The mobile phase was 100% methanol and the flow rate was set to 1.2 mL min^{-1}. Ergosterol was detected at 33 °C and converted to fungal biomass using a conversion factor of 5.5 mg ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). The results were expressed in mg of fungal biomass per gram of leaf litter AFDM.

2.6. Associated invertebrates

Invertebrates removed from coarse-mesh bags were identified to family level (except Oligochaeta which was identified to the order level), counted and sorted into 2 groups: the functional feeding group of shredder invertebrates according to Tachet et al. (2002) and Merritt et al. (2007), and the other invertebrates as non-shredders. Shredders and non-shredders were dried (60 °C, 72 h) and combusted (500 °C, 12 h) to determine AFDM. Results were expressed as number of total invertebrates and shredders per gram of litter AFDM and mg of total invertebrates or shredders per gram of litter AFDM.

2.7. Statistical analysis

Differences in physicochemical characteristics were analysed by one-way ANOVA with stream as factor. Leaf litter decomposition rates were estimated by fitting the remaining AFDM to the negative exponential model. The rates were expressed in terms of degree-days to correct for the influence of temperature (Graça et al., 2005). The decomposition rates and final litter nutrient contents were compared separately for each bag type by two-way ANOVA (factors: stream, leaf species). Fungal biomass and invertebrate density and biomass were tested by two-way ANOVA (factors: stream, leaf species). Bivariate relationships between decomposition rates and biological variables and between decomposition rate or biological variables and both hydrological (Qs, CV_{Qs}) and environmental variables (conductivity, pH, SRP, DIN, riparian canopy cover, annual precipitation) were tested by linear regression. When necessary, data were log10 or log10(x + 1) transformed to achieve requirements for parametric analyses. All statistical analyses were performed with R statistical program (version 3.0.3; R Development Core, 2014).

3. Results

3.1. Environmental variables

The characteristics of the streams differed markedly (Tables 1 and 2). In general, the riparian vegetation was scarce and dominated by *Populus nigra* L. and *Salix* sp., except stream MON, which was dominated by sedges (*Scirpus* sp.). The canopy cover, an indicator of potential leaf litter inputs to streams, was rather variable, depending mainly on channel width (Table 1).

Rainfall was low during the first part of the study period (from 2nd December 2014 to 18th January 2015), which included the whole coarse mesh bags experiment, followed by intense rain and floods afterwards. Only one site (VIV) was dry when the bags were deployed, and from information recorded by dataloggers, it remained dry for 19 d. Another site (TRU) suffered a strong reduction in water level after the 4th d of incubation, and flow there remained marginal for 87 d. Average discharge during the experimental period ranged from 14.6 to 679.9 L s^{-1} (Table 2). All streams presented well oxygenated waters and alkaline pH. Water temperature differed about 9 °C from the coldest to the warmest stream, differences being statistically significant (one-way ANOVA, $F_{10,1023}$: 328.4, $p < 0.00001$), and conductivity ranged from 430 to 812 μS cm^{-1} ($F_{10,21}$: 26.2, $p < 0.00001$). DIN concentration ranged from 168 to 11,284 μg N L^{-1} (Table 2), differences among sites being statistically significant ($F_{10,21}$: 29.8, $p < 0.00001$); it was dominated by NO_3^-. SRP concentration was relatively low (from 2.3 to 18.8 μg P L^{-1}) and showed no significant differences among streams ($p = 0.8$) (Table 2).

Table 2
Water physical and chemical characteristics of the studied streams throughout experiment period (mean ± SE; $n = 3$). For water temperature, daily mean values and their range (in parenthesis) are shown. $Q_{s\ exp.}$ and $CV_{Qs\ exp.}$ calculated for the experimental period of the fine mesh ($Q_{s\ exp.,\ fine}$; $CV_{Qs\ exp.,\ fine}$) and coarse mesh ($Q_{s\ exp.,coarse}$; $CV_{Qs,\ exp.,\ coarse}$).

	SAN	MOR	HOM	ALH	NAJ	MON	RIB	VIV	TRU	GUA	MAT
Discharge (L s^{-1})	281.6 ± 68.4	267.8 ± 96.5	143.4 ± 77.7	355.3 ± 223.1	41.9 ± 2.2	14.6 ± 0.9	94.2 ± 12.0	10.2 ± 7.4	679.9 ± 659.4	237.4 ± 77.9	586 ± 191.1
$Q_{s\ exp.,\ fine}$ (L s^{-1} km^{-2})	28.75	28.75	8.21	3.76	0.7	0.7	3.11	0.59	1.28	–	6.31
$CV_{Qs\ exp.,\ fine}$	0.8	0.8	0.95	1.29	0.11	0.11	0.75	0.19	1.4	–	0.53
$Q_{s\ exp.,\ coarse}$ (L s^{-1} km^{-2})	14.95	14.95	2.53	4.97	0.75	0.75	4.11	0.53	1.86	–	7.37
$CV_{Qs,\ exp.,\ coarse}$	0.49	0.49	0.3	1.34	0.07	0.07	0.8	0.05	1.32	–	0.57
Water temperature (°C)	7.8 (10–5.5)	8.6 (10.2–7.1)	5.7 (10.2–3.1)	4.3 (9.4–0.5)	6.6 (9.9–3.2)	9.4 (12.2–7.4)	6 (10.6–2.5)	5.8 (9.6–2.9)	3.7 (12.7–1.7)	5.2 (9.2–1.7)	12.9 (14.1–11.3)
Conductivity (μS cm^{-1})	443 ± 7	430 ± 8	568 ± 49	505 ± 13	659 ± 21	801 ± 27	35 ± 2	812 ± 73	449 ± 20	545 ± 7	460 ± 6
pH	8.3 ± 0.1	8.1 ± 0	8.4 ± 0	8.5 ± 0	8.0 ± 0	8.1 ± 0	8.1 ± 0	7.9 ± 0.3	8.0 ± 0.2	8.3 ± 0.1	8.3 ± 0.1
Oxygen saturation (%)	102.3 ± 4.4	112.0 ± 7.6	106.3 ± 4.8	106.1 ± 4.7	90.1 ± 1.7	91.1 ± 1.3	97.6 ± 2.4	66.9 ± 27.1	95.4 ± 3.1	101.7 ± 2.5	106.4 ± 1.2
DIN (μgN L^{-1})	1213.2 ± 282.5	570.2 ± 89.7	11,284.9 ± 4460.1	4416.1 ± 148.3	5667.5 ± 773.9	835.8 ± 210.7	4494.4 ± 676.5	426.0 ± 164.9	167.8 ± 14.5	766.2 ± 277.4	314.9 ± 68.8
SRP (μgP L^{-1})	6.5 ± 3.7	4.7 ± 0.7	14.7 ± 10.5	6.4 ± 5.0	2.3 ± 1.2	12.0 ± 9.2	18.8 ± 8.6	14.8 ± 7.3	15.2 ± 13.4	15.1 ± 7.9	13.8 ± 7.7
Chloride (mg L^{-1})	4.9 ± 0.7	3.0 ± 0.5	10.9 ± 0.3	8.8 ± 0.7	19.8 ± 0.8	34.3 ± 4.1	32.6 ± 5.0	39.0 ± 0.2	3.7 ± 0.9	7.9 ± 2.0	4.1 ± 0.7
Sulphate (mg L^{-1})	5.3 ± 0.5	2.5 ± 0.6	15.2 ± 0.8	27.9 ± 4.3	28.8 ± 2.1	82.1 ± 5.8	33.3 ± 4.6	77.2 ± 7.2	16.7 ± 6.2	51.3 ± 8.0	11.3 ± 1.3

3.2. Litter decomposition

For alder leaves, the AFDM remaining ranged across streams from 30.3% to 69.2% in fine mesh bags and from 20.1% to 79.4% in coarse bags. For oak, it ranged from 69.8% to 84.3% in fine bags and from 70.1% to 95.8% in coarse bags. Decomposition rates for alder ranged from 0.00062 to 0.00162 dd^{-1} in fine mesh bags and from 0.00102 to 0.00585 dd^{-1} in coarse mesh bags; the range for oak was from 0.00025 to 0.00071 dd^{-1} and from 0.00018 to 0.00082 dd^{-1}, respectively (Fig. 2). Decomposition rates differed significantly among sites for both species and mesh type (two-way ANOVAs; Table 3) the interaction between site and species being statistically significant for coarse but not for fine mesh bags (Table 3).

Decomposition rates in coarse mesh bags were lowest in stream VIV, which dried out, and stream TRU, where flow was marginal for part of the experiment, but no differences were found among these streams and the rest in fine mesh bags (Fig. 2). No general relationship was found between decomposition rate and any hydrologic (Qs) or climatic variables, except for a positive correlation between oak microbial decomposition and $CV_{Qs,exp}$. The decomposition rate of both litter species in coarse bags was positively correlated with riparian canopy cover (alder: $r^2 = 0.38$; $p = 0.043$; oak: $r^2 = 0.68$; $p = 0.002$).

3.3. Nutrients in leaf litter

The initial C, N and P concentrations in alder litter were 51.8%, 2.9% and 0.11%, respectively, and 50.1% C, 1.3% N and 0.05% P for oak litter. The final carbon concentration was around 40.2–51.2% for all mesh and species.

The final N concentration was higher than initial values in both species. In alder litter it ranged from 3.57 to 4.23% in fine bags and from 2.19 to 4.35% in coarse bags; in oak litter it ranged from 1.36 to 1.79% in fine bags and from 1.25 to 1.58% in coarse bags (Fig. 3). Differences among streams were statistically significant for both leaf species and mesh sizes, the interaction between site and species being statistically significant for %N in coarse bags (Table 3).

In general, the final P concentration was lower or similar to initial values in both species. For alder litter it ranged from 0.04 to 0.08% in fine bags and from 0.06 to 0.11% in coarse bags. For oak litter it ranged from 0.04 to 0.08% in fine and from 0.08 to 0.12 in coarse bags (Fig. 3). Differences were statistically significant among sites for both leaf species and mesh sizes, the interaction between site and species being also statistically significant (Table 3).

The final N and P concentrations were not correlated to the hydrologic nor climatic descriptors. Only for oak in fine bags the final N concentration appeared to be positively correlated to dissolved nitrogen availability ($r^2 = 0.58$), but only when excluding the 4 richest sites (NAJ, ALH, RIB and HOM, with DIN > 1500 μg-N L^{-1}).

In general, the leaf ash content for alder and oak litter was around 15 and 10% in coarse and fine bags respectively, although these values were greater in SAN, HOM and GUA (Fig. 3).

3.4. Fungal biomass

Fungal biomass ranged from 2.8 to 68.9 mg g^{-1} AFDM for alder litter and from 15.2 to 65.4 mg g^{-1} AFDM for oak litter (Fig. 4). Differences were statistically significant among sites, values being highest in GUA and lowest in MON, but not between species (Table 3). Fungal biomass was not correlated to any hydrological (Qs and CV_{Qs}) or other environmental variables. There were no relationships neither with decomposition rate nor with litter nutrient content.

3.5. Associated invertebrates

Total invertebrate richness in bags ranged from 6 to 16 taxa; the lowest values were found at TRU and VIV in oak and in TRU, VIV and

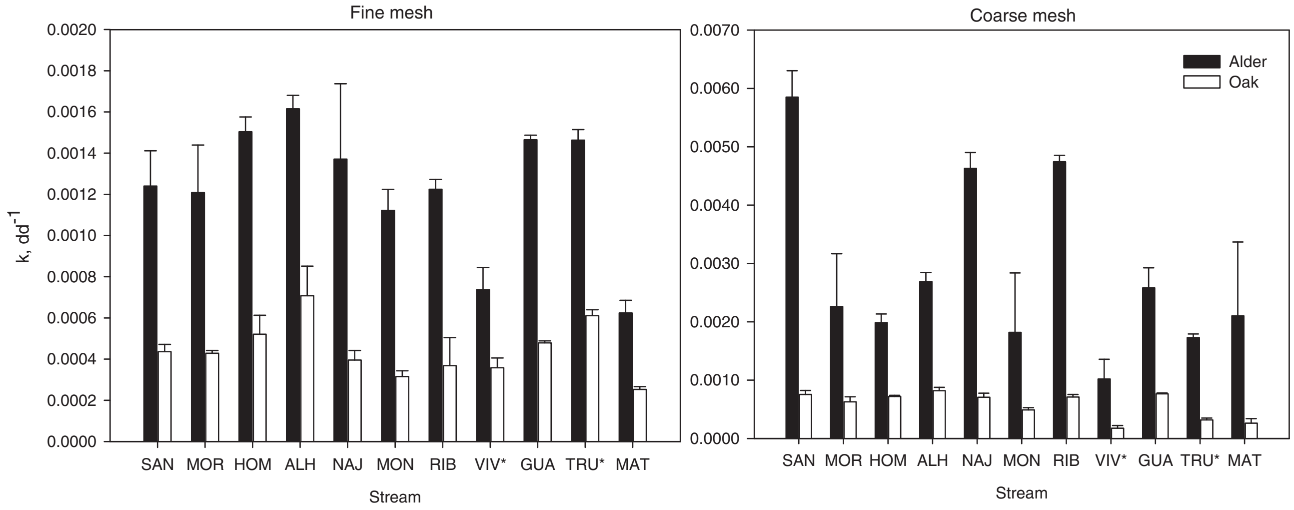

Fig. 2. Decomposition rates (k, dd^{-1}) in fine (left) and coarse mesh bags (right) along longitudinal gradient from west to east (mean ± SE; $n = 5$). Note the different scales. Streams that suffered strong reduction in water flow throughout experiment are marked with asterisk.

MON in alder, all them streams with very low Qs (Table 1). Total invertebrate density ranged from 2.3 to 118.5 individuals g^{-1} AFDM for alder and from 2.2 to 51.6 individuals g^{-1} AFDM for oak, the lowest values occurring at TRU. Total invertebrate biomass ranged from 0.05 to 113.9 mg g^{-1} AFDM for alder and from 1.07 to 23.2 mg g^{-1} AFDM for oak, with the lowest values also occurring at TRU. Invertebrate density and biomass were statistically different among streams for both species (Table 3). Shredder density ranged from zero (VIV, TRU and GUA) to 42.3 individuals g^{-1} AFDM for alder litter and to 11.8 individuals g^{-1} AFDM for oak litter. Shredder biomass ranged from zero in both litter species to 110.8 mg g^{-1} $AFDM^1$ for alder litter and 18.0 mg g^{-1} AFDM for oak. Shredder density and biomass differed significantly among streams and between species and tended to be more abundant in alder bags, the interaction between site and species being statistically significant (Table 3).

Only shredder density showed a significant relationship with one of the descriptors of drought (Qs_{exp}, positive). Among all other environmental variables measured, total invertebrate density (alder: $r^2 = 0.53$; $p = 0.01$; oak: $r^2 = 0.37$; $p = 0.046$) and biomass (alder: $r^2 = 0.68$; $p = 0.002$; oak: $r^2 = 0.38$; $p = 0.044$) in both species only showed a significant relationship with riparian canopy cover. The decomposition rate of alder litter was positively correlated with both density and biomass of shredders in litter bags, whereas that of oak was not correlated with any invertebrate variable (Fig. 5).

4. Discussion

The flow regime in the Mediterranean region can be seriously altered in the coming decades following changes in rainfall and temperature (Milly et al., 2005). Our experiment across a precipitation gradient aimed at gaining knowledge on the likely consequences of such changes for stream ecosystem functioning. We hypothesized drought to reduce decomposition rate, but, although decomposition was slowest at the sites suffering most intense drought, no general pattern could be

Table 3
Summary table for two-way ANOVAs performed on decomposition rate (k, dd^{-1}), final nitrogen and phosphorus concentration (%N, % P), fungal biomass and invertebrate variables (density and biomass of total invertebrates and of shredders). Significant values are highlighted in bold.

		Coarse mesh bags			Fine mesh bags		
		df	F	*p*	df	F	*p*
k (dd^{-1})	Stream	10, 88	21.0	**<0.0001**	10, 84	10.0	**<0.0001**
	Species	1, 88	596.1	**<0.0001**	1, 84	413.5	**<0.0001**
	Stream × Species	10, 88	3.2	**0.0016**	10, 84	0.8	0.583
%N	Stream	10, 87	11.2	**<0.0001**	10, 84	2.8	**0.005**
	Species	1, 87	1608.1	**<0.0001**	1, 84	1382.0	**<0.0001**
	Stream × Species	10, 87	3.4	**0.00086**	10, 84	1.0	0.481
%P	Stream	10, 87	23.1	**<0.0001**	10, 84	20.4	**<0.0001**
	Species	1, 87	473.6	**<0.0001**	1, 84	1007.3	**<0.0001**
	Stream × Species	10, 87	6.2	**<0.0001**	10, 84	5.6	**<0.0001**
Fungal biomass	Stream				10, 80	9.5	**<0.0001**
	Species				1, 80	2.3	0.1371
	Stream × Species				10, 80	1.1	0.389
Total invertebrate density	Stream	10, 87	12.4	**<0.0001**			
	Species	1, 87	12.0	**0.001**			
	Stream × Species	10, 87	0.9	0.526			
Shredder density	Stream	10, 87	19.2	**<0.0001**			
	Species	1, 87	14.7	**0.0002**			
	Stream × Species	10, 87	3.4	**0.0008**			
Total invertebrate biomass	Stream	10, 87	9.9	**<0.0001**			
	Species	1, 87	19.0	**<0.0001**			
	Stream × Species	10, 87	3.3	**0.001**			
Shredder biomass	Stream	10, 87	14.0	**<0.0001**			
	Species	1, 87	20.7	**<0.0001**			
	Stream × Species	10, 87	4.0	**0.0001**			

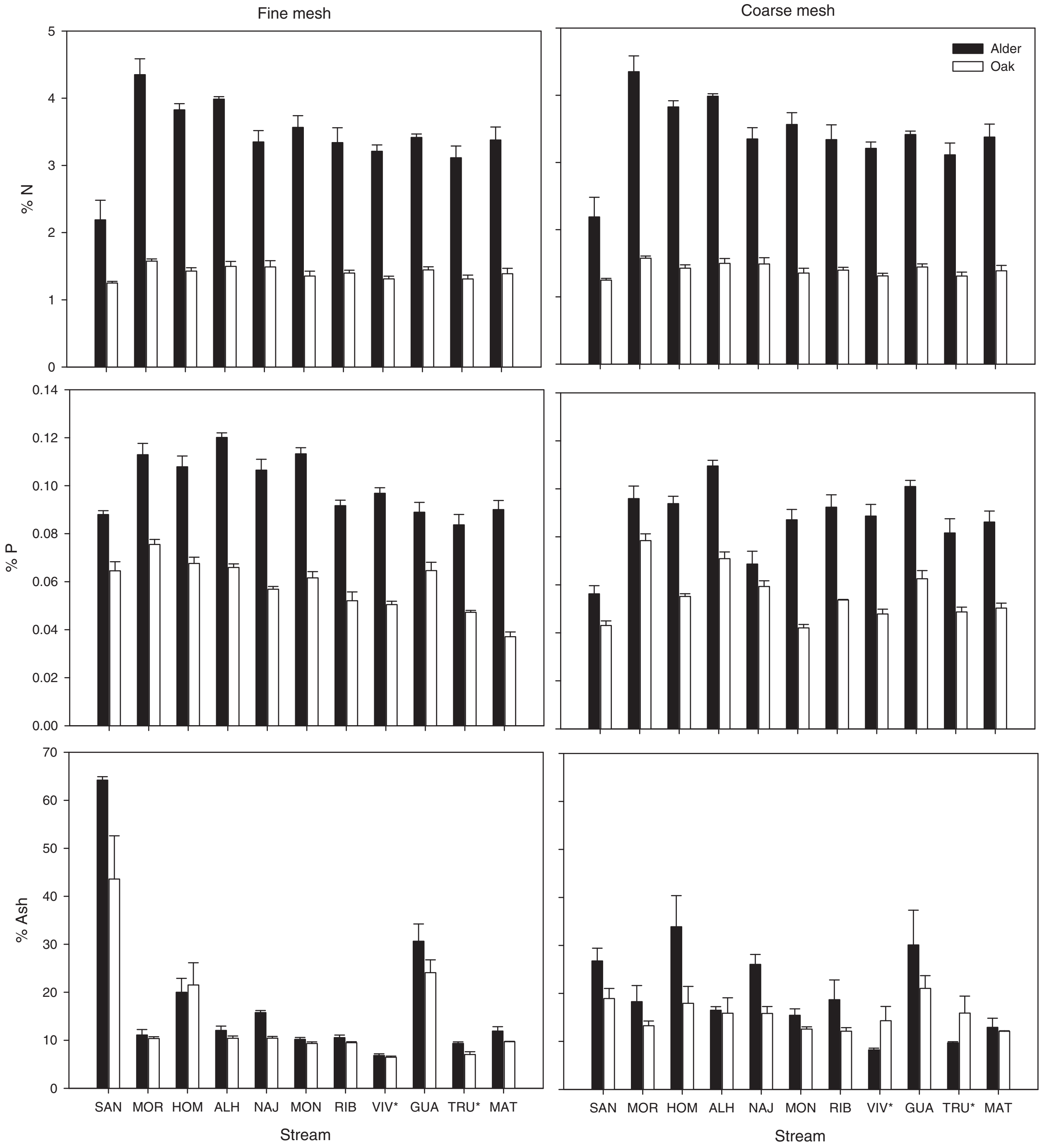

Fig. 3. Leaf nitrogen, phosphorus and ash concentration (% DM) at the end of experiment in fine (left) and coarse mesh bags (right). Streams arranged in longitudinal gradient order from west to east (mean ± SE; n = 5). Streams that suffered strong reduction in water flow throughout experiment are marked with asterisk.

found between decomposition rate of both litter species and any of the proxies for drought we determined.

In the two streams where drought was most intense (VIV, where the stream dried out during part of the experiment, and TRU, where residual flow occurred) decomposition rates were lower than in the rest of the sites in both species, a result consistent with the literature, that shows decomposition to be slower in temporary than in perennial streams (Richardson, 1990; Datry et al., 2011; Martínez et al., 2015), and also slower under residual flow (Acuña et al., 2005; Leberfinger et al., 2010). Furthermore, this severe level of drought seemed to affect more total than microbial decomposition confirming the second hypothesis and as has also been shown in elsewhere (Martínez et al., 2015). Microbes can survive drought if there is some residual humidity in the field (Abril et al., 2016; Bruder et al., 2011; Sridhar and Bärlocher, 1993), and microbial activity recovers quickly after flow resumption (Langhans and Tockner, 2006), unlike invertebrates, which take longer to recover (Datry et al., 2011). Drying events usually reduce the functional and taxonomic richness of invertebrate communities, and although permanent streams are highly resilient to hydrological fluctuations (Schriever et al., 2015), the recovery of communities in intermittent streams can be slower, as it depends on a few resistant species (Leigh et al., 2016) or on re-colonization from other water bodies.

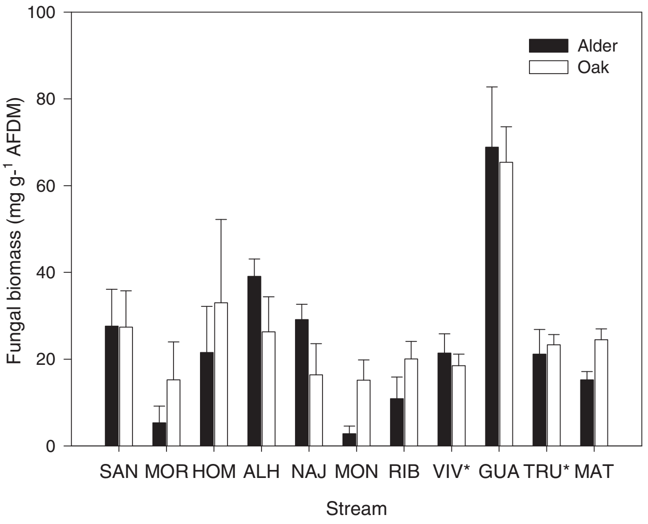

Fig. 4. Fungal biomass on alder and oak leaf litter incubated in fine-mesh bags at the end of the study. Streams arranged in longitudinal gradient order from west to east (mean ± SE; *n* = 4–5). Streams that suffered strong reduction in water flow throughout experiment are marked with asterisk.

Severe drought events would, thus, show a slower functional recovery, what would explain the lower decomposition rates measured in VIV and TRU.

Microbial decomposition of both species was not correlated with fungal biomass. In the literature there are examples of positive significant relationship (e.g. Foulquier et al., 2015) as well as of lack of correlation (Casas et al., 2011). Nutrient content, which is usually taken as a proxy of nutrient change caused by microbial activity (Cheever et al., 2012; Webster et al., 2009), was also not related to microbial decomposition. However, microbial decomposition of both species tended to increase with $CV_{Qs,exp.}$, although the relationship was only statistically significant for oak leaves. Other environmental variables could be driving the microbial decomposition, such as water nutrient availability, as suggested by the relationship between N content of oak litter and dissolved N.

Total decomposition rate of alder, the leaf material with the best quality, was mainly determined by detritivore density and biomass. Among the invertebrate variables, only shredders seemed to be limited by specific discharge throughout the experiment. Flow stability, minimum flow and flow permanence are important drivers of macroinvertebrate assemblages (Belmar et al., 2013; Datry et al., 2011), and affect leaf litter processing. On the other hand, the existence of a clear link between total decomposition of alder and detritivore community suggests

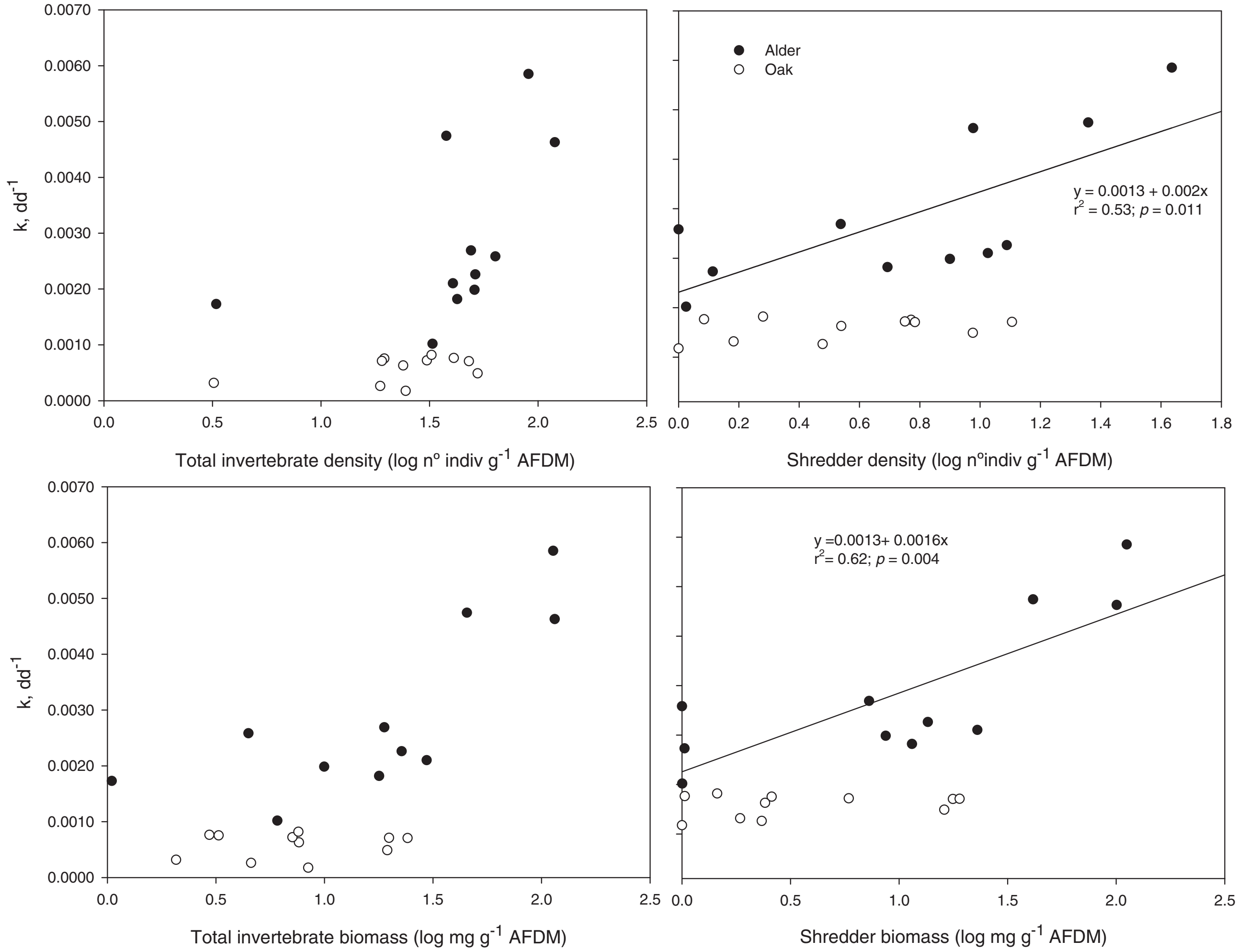

Fig. 5. Relationships between breakdown rates (k, dd^{-1}) in coarse bags and density and biomass of total invertebrates and of shredders g^{-1} AFDM. The equation, r^2 and *p*-values of the relationship and fitted lines are also shown.

that the impact of hydrological conditions on invertebrate community could result in contrasting effects on the decomposition of leaf species with different quality, fast-decaying and high-quality leaf litter being more affected than slow-decaying and low-quality one, as we hypothesized (third hypothesis).

We found a strong positive correlation between total decomposition rate and stream canopy cover, an indirect indicator of litter inputs to streams, which was also correlated with the density and biomass of invertebrates in litter bags. This link suggests the abundance of detritivore invertebrates in Mediterranean streams to be also controlled by the supply of riparian detritus, which is in part dependent on rainfall (Sanpera-Calbet et al., 2015). Changes in the identity and timing of leaf inputs as a consequence of climate change or human activities could, thus, alter decomposition in the near future (Kominoski and Rosemond, 2012; Kominoski et al., 2013).

The lack of statistically significant relationship between decomposition rate and the variables we used to quantify drought could derive from other factors such as human activities, as litter decomposition responds to multiple factors such as nutrient concentration (Woodward et al., 2012), pesticides (Brosed et al., 2016), siltation (Niyogi et al., 2003) or hydraulics (Elosegi and Sabater, 2013). Besides, travertine precipitation, which occurred in some of our streams, can either enhance or slow decomposition, depending on the continuity of the travertine layer (Casas and Gessner, 1999; Miliša et al., 2010). Therefore, the effects of drought could be not easily disentangled given the concomitant variation in other environmental variables and the particular responses of decomposers and detritivores.

5. Conclusion

In short, our results point to a complex pattern of litter decomposition at the regional scale, as drought affects decomposition directly by emersion of bags and indirectly by affecting the functional composition and density of invertebrates. Decomposition rate was determined by the macroinvertebrate community, which was affected by hydrology as well as by riparian vegetation. Other studies (e.g., Pozo et al., 2011) have also shown leaf decomposition to reflect geographic differences in macroinvertebrate communities, thus highlighting the role of invertebrates as drivers of leaf decomposition. By contrast, microbial-mediated decomposition might be less affected by drought.

Seasonality in precipitation and temperature is expected to increase in oncoming years in the Mediterranean region, resulting in more intense and frequent drought events (e.g. low flows, droughts), as well as an increase in the number of intermittent streams. Future efforts are needed to identify factors and their interactions affecting stream ecosystem processes, such as organic matter decomposition, to predict and monitor the consequences of future hydrologic change under a shifting mosaic of abiotic and biotic conditions.

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