



Response of community structure to sustained drought in Mediterranean rivers

Dani Boix^a, Emili García-Berthou^a, Stéphanie Gascón^a, Lluís Benejam^a, Elisabet Tornés^{a,b}, Jordi Sala^a, Josep Benito^a, Antoni Munné^c, Carolina Solà^c, Sergi Sabater^{a,b,*}

^a Institute of Aquatic Ecology, University of Girona, 17071 Girona, Spain

^b Catalan Institute for Water Research (ICRA), Scientific and Technologic Park of the University of Girona, 17003 Girona, Spain

^c Catalan Water Agency (ACA), Provença 204-208, 08036 Barcelona, Spain

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SUMMARY

Mediterranean rivers are characterized by frequent hydrological disturbances, including floods, droughts, and human impacts like water abstraction. During 2008 an exceptionally long drought in NE Spain was irregularly interrupted by rainfall events. We analyzed the relationships between the biological community structure with the ongoing and preceding hydrological patterns during the drought and recovery periods. We aimed: (1) to assess the role of hydrology on different biological assemblages (diatoms, macroinvertebrates and fish), (2) to determine which measures of community structure could be better related to hydrology, and (3) to determine the effects of water abstraction on river communities. Three subsets of variables (hydrological, spatial and environmental) were selected to determine the relative importance of hydrological alterations. Variation partitioning analysis and ordination methods were used to determine which subset of variables had higher effects on 20 parameters and six matrices (taxonomic and functional) of the biological communities. The analyses revealed that both parameters and matrices were significantly related to hydrological effects. Reservoirs intensified the effect of drought on downstream community composition and structure, as a result of the competition between human uses of water and environmental values.

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Introduction

Mediterranean rivers are characterized by a flashy regime, with dry summers and large winter floods, compounded by a large inter-annual variability in rainfall, which sometimes results in dry winters and consequently long supra-seasonal droughts. Depending on duration of dry periods, as well as on basin and reach characteristics, drought intensity ranges from declines in discharge below average baseflow levels, to intermittency, and even to total drying of the river channel, with increasing effects for the biota. Additionally, most areas with Mediterranean climate are densely populated, what often leads to large impacts on river hydrology, caused by water abstraction and regulation, thus compounding the effects of drought. After the Water Framework Directive (WFD) (2000/60/EC), the main management goal of aquatic environments in Europe

is to achieve and maintain the ecological status of natural water bodies. Thus, management decisions in drought situations that would alter water flow should not worsen the ecological status. Also, extremely drought events can originate temporary deterioration on water bodies that cannot be considered in breach of Water Framework Directive objectives, and those can occasionally be reduced due to exceptional circumstances which can not reasonably be foreseen (Art. 4.6 of the WFD). However, little is known about the effects on the aquatic communities due to anthropic water flow alterations during drought or flood events (Boulton and Lake, 2008; Death, 2008).

Low water flows related to extended drought episodes have manifold consequences. The residence water time increases and leads to an average 'ageing' of water (Vörösmarty and Sahagian, 2000). Alteration of natural hydrological conditions reduces the strength and frequency of flooding and of meander migration, and lowers the incidence of post-disturbance succession (Margalef, 1997). Abnormal hydrological stability homogenizes river habitats, and this obviously affects organisms' performance and distribution. River habitats change from lotic (flowing waters) to lentic (standing waters) in a process that can be named "lenticification" (Sabater, 2008). Slow-flowing waters may promote higher water temperature and evaporative losses that may be particularly relevant in arid and semi-arid areas (Hamilton et al., 2005). Overall,

* Corresponding author. Address: Catalan Institute for Water Research (ICRA), Scientific and Technologic Park of the University of Girona, 17003 Girona, Spain. Tel.: +34 972418375; fax: +34 972418150.

E-mail addresses: dani.boix@udg.edu (D. Boix), emili.garcia@udg.edu (E. García-Berthou), stephanie.gascon@udg.edu (S. Gascón), lluisbenejam@hotmail.com (L. Benejam), etornes@icra.cat (E. Tornés), js.genoher@gmail.com (J. Sala), josepbenito@gmail.com (J. Benito), anMunne@gencat.cat (A. Munné), csolao@gencat.cat (C. Solà), sergi.sabater@udg.edu (S. Sabater).

changes extend to the biogeochemical processes as well as to the biological community within the river.

Many organisms have adaptive mechanisms that allow them to survive droughts and to recover quickly after water returns (Lake, 2003). However, human-caused alterations derive on rapid or unpredicted drying that does not provide sufficient time for production of desiccation-resistant structures or physiological adjustments (Stanley et al., 2004). The ability to recover after drought also depends on the existence of reservoirs of propagules, stored in areas that did not dry out, or in the sediments, which facilitates the processes of recolonization (Robson et al., 2008). Responses or adaptations are specific of groups of organisms. Many benthic algal species have physiological adaptations consisting of thick cell walls or resisting propagules to withstand desiccation (Steinman and McIntire, 1990). The metabolism of primary producers is sensitive to changes in water temperature and hydrology (Hill et al., 1995; Acuña et al., 2004; Uehlinger, 2006). The macroinvertebrate assemblage structure is deeply affected by droughts (e.g. Acuña et al., 2005; Bonada et al., 2006), though the extent of changes depends on the biological adaptations and trophic role of the species within the community (Boulton and Lake, 1992a; Closs and Lake, 1994). Relevant changes in macroinvertebrate assemblage structure have been related to critical thresholds (i.e. isolation from littoral vegetation, loss of riffle areas, loss of surface waters, etc.; Boulton, 2003). Droughts are selective forces that increase fish local density, alter food resources and affect the strength of interspecific interactions on fish communities (Magoulick and Kobza, 2003; Davey and Kelly, 2007). These changes affect population size and species richness, especially of native and intolerant species (Lake, 2003; Matthews and Marsh-Matthews, 2003; Magalhães et al., 2007). The recovery of biological communities from drought depends on the type of hydrological event (i.e. seasonal versus supra-seasonal; Lake, 2003), the environment characteristics (e.g. substratum type; Wright et al., 2003), the existence of refugia (e.g. Magoulick and Kobza, 2003), and the taxonomic group concerned (Acuña et al., 2005; Adams and Warren, 2005; Magalhães et al., 2007; Ledger et al., 2008). Community post-recovery processes could extend over a few months after the drought or extend for much longer (McKnight et al., 1999; Mosisch, 2001; Lake, 2003; Death, 2008).

This study aims to analyse the recovery of biological communities after a supra-seasonal drought that extended for a year and a

half (winter 2006–spring 2008) in rivers of NE Iberian Peninsula. During this period, human demand nearly depleted the available water reserves, and the rivers run unusually low. Furthermore, the recovery of normal flows was delayed at reaches downstream from reservoirs. This scenario offered the opportunity to analyse the effect of hydrology on communities. We hypothesized that the impact of drought would be greatest at reaches downstream from reservoirs, and thus, affected by water abstraction and regulation. Specifically, the objectives of this study were: (1) to assess the role of hydrology on different biological assemblages (diatoms, macroinvertebrates and fish), (2) to determine which measures of community structure could be better related to hydrology, and (3) to determine the effects of water regulation and abstraction on river communities.

Material and methods

Study area

The study area included 13 river sites distributed along three watersheds (Muga, Fluvià and Ter Rivers) in the NE Iberian Peninsula (Fig. 1). Ter River is the largest (2955 km²) of the systems analyzed. It has its headwaters in the Pyrenees and in its upper course is partially subject to a snow fed regime. Fluvià River (974 km²) and Muga River (758 km²) are smaller watersheds that have their headwaters located in mountainous areas. The middle and lower parts of the three watersheds are subject to Mediterranean climate, implying higher hydrological variability in these sections.

Four of the sites studied were located in the river headwaters (F1, M1, T1 and T2). Two of the rivers (Muga and Ter) are regulated and have reservoirs for drinking and agricultural uses (Puig et al., 1987). Five sites of these two rivers were located upstream of reservoirs (M1, T1, T2, T3 and T4), whereas six other were located downstream of reservoirs (M2, M3, T5, T6, T7 and T8). The studied sites corresponded to permanent river reaches that did not dry, even under drought conditions. In the case of Ter River, two main reservoirs have a total water storage capacity of 398 million m³ (47% of the annual discharge), whereas the reservoir located in the Muga River has a total water storage capacity of 61 million m³ (41% of the annual discharge) (ACA, 2009). During the period 1996–2007 a mean of 205 million m³ y⁻¹ was derived which represents a 44% of the mean discharge (ACA, 2009). Two sections were

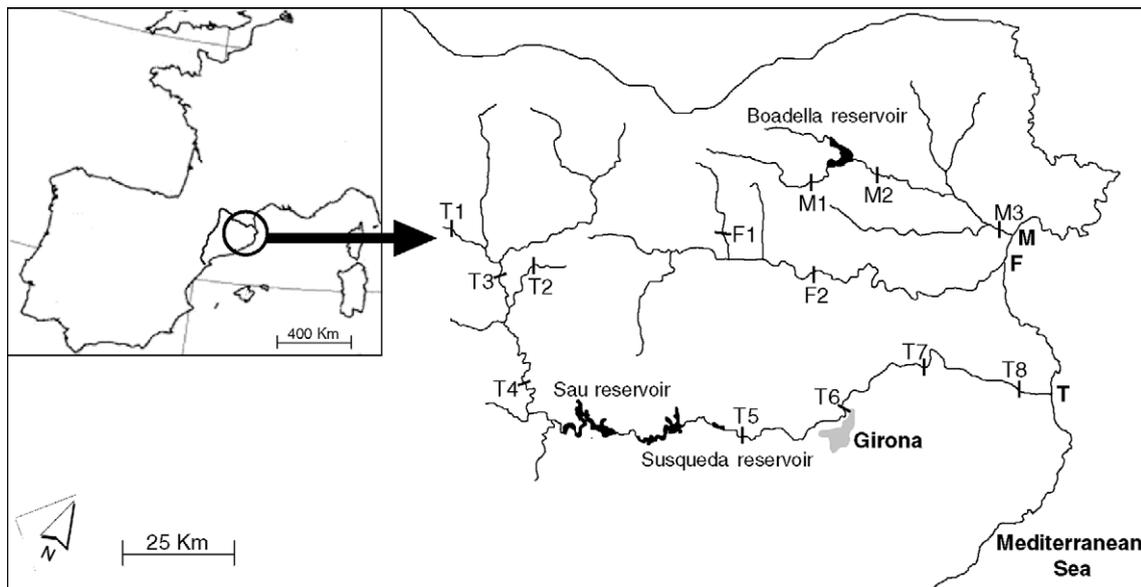


Fig. 1. Location of sampling sites, reservoirs and main towns in the three studied Mediterranean rivers. M, Muga; F, Fluvià; T, Ter.

separated in Ter River – upstream of the reservoirs system (hereafter, Ter-unregulated) and downstream of the reservoirs system (hereafter, Ter-regulated). These sections not only allowed the comparison between regulated and unregulated sites in the same river, but also the comparison among different flow recovery times in the different sites, since the temporal pattern of the drought was different between them (more details in Results section). Muga River has also a reservoir, but the entire basin was under drought conditions along the studied year. Moreover, our sampling design (only one site unregulated) did not allow an adequate comparison between regulated and unregulated sites. For these reasons Muga River was not divided in two sections as was done in the Ter River.

Sampling

Four sampling surveys were conducted on April, May, July and September 2008 after a severe drought period that extended for two years. In May 2008 the drought period progressively finished and flow recovered, though this return was not simultaneous in all watersheds. Diatoms and macroinvertebrates were sampled in the four sampling periods, whereas fish were not sampled in May. Conductivity, water temperature, percent oxygen saturation, and pH of the water were measured in all sampling surveys using WTW meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). A cross-section of the river channel was made in each site, and water depth profiles and water velocity estimates (current meter MiniAir2 Schiltknecht 43221, Gossau, Switzerland) were used to measure water flow. Incident light was measured using a Li-Cor quantum sensor (Li-192SB, Lincoln, NB, USA).

Diatom sampling, preparation and counting followed CEN standards (CEN, 2000, 2001). Three cobbles were randomly collected from the river bottom in riffle sections. The cobbles were scraped with a knife to a final area of 3 cm² in order to detach the algal communities. Samples were rinsed in 5 ml of river water (not filtered) and preserved in 4% formaldehyde until analysis. Diatom frustules were cleaned from organic material in 34% hot hydrogen peroxide. Permanent slides were prepared by mounting the cleaned frustules in Naphrax (r.i. 1.74; Brunel Microscopes Ltd., Chippenham, Wiltshire, UK). Up to 400 valves were counted per slide in random microscopy fields under a light microscopy. A Nikon Eclipse E600W light microscope equipped with Nomarski differential interference contrast optics was used for diatom counts at a magnification of 1000×. Taxa were identified at the species level following mainly Krammer and Lange-Bertalot (1991–1997) and Lange-Bertalot (2001). Macroinvertebrates were collected at each sampling site using a Surber sampler of 0.1 m² surface area with 500 μm mesh net. Samples were collected using the quantitative method of Hering et al. (2004) adapted to Mediterranean rivers. The method consisted in sampling 12 subsamples, collected according to the relative abundance of the potential substratum type. Eight subsamples were performed in the dominant (>5%) and four in the marginal substrata (<5%). The considered substrata were bryophytes, submerged hydrophytes, helophytes, algae, submerged roots, coarse particulate organic matter, flat bedrock, boulders (>250 mm), cobbles and pebbles (25–250 mm), gravels (2–25 mm), coarse and medium sands (<2 mm), and fine sands (<0.1 mm). The 12 subsamples were merged in one sample, then preserved with 4% formaldehyde, sorted and identified to family level in the laboratory. Fish were sampled by electrofishing 100-m stretches (200–350 V, 2–3 A, fully-rectified triphasic DC), following CEN standards (CEN, 2003) to estimate richness, abundance and composition of the assemblage at each site. A single pass in rivers of this region generally captures about 31–67% of the fish individuals and 77–100% of the species present (Benejam et al., in press). All fishes stunned were collected with nets, anaesthetized with tricaine methanesulfonate (MS-222), identified to

species, counted, measured (fork length in mm) and then returned to the river.

Hydrological variables

Daily streamflow during 2008 was obtained from the closest gauging station (Catalan Water Agency; <http://www.gencat.cat/aca>). We calculated two measures of hydrologic stress. Drought ratio was calculated as the average flow during the month prior to sampling, relative to the monthly mean flow for 2000–2008. Abstraction rate was calculated for each site by means of the Sacramento Soil Moisture Accounting (SAC-SMA) model. The SAC-SMA is a flexible model (Burnash et al., 1973) widely used by the US National Weather Service (e.g. Hartmann et al., 2002) and by the Catalan Water Agency (ACA, 2002; Benejam et al., in press). It is a conceptually based rainfall–runoff model, with areal precipitation and areal potential evapotranspiration as inputs, and has been previously calibrated by the Catalan Water Agency (ACA, 2002). We considered that there was “strong drought” when drought ratio was >50%, and “strong abstraction” when abstraction rate was >90%. Two other hydrological variables used were the 2008 monthly flow and the accumulated rain of the month before the sampling.

Biological community parameters and functional matrices

Six community parameters were calculated for each assemblage (diatoms, macroinvertebrates and fish): species richness (SR); Shannon-Wiener diversity (D); Pielou's evenness (J) in base-two logarithm (Pielou, 1969); taxonomic distinctness, TD; average taxonomic distinctness, ATD; and variation in taxonomic distinctness, VTD. The last three taxonomic parameters were calculated following Clarke and Warwick (1998, 2001a). Density was also calculated for macroinvertebrates (individuals m⁻²) and fish (individuals CPUE⁻¹).

Two matrices using abundances of individuals of each assemblage (diatoms, macroinvertebrates and fish) were created. The first matrix classified individuals according to the taxonomic level in each assemblage (species for diatoms and fish, families in the case of macroinvertebrates). The second matrix classified the individuals according to their assignment to functional groups. The functional matrix for the diatom assemblage was created using the trophic indicator value of van Dam et al. (1994) classification, which integrates qualitative species classifications into a seven-grade scale according to their trophic preferences. Those species not given a rank in the list were assigned according to our own expertise. Differences in feeding strategies (Tachet et al., 2000; Usseglio-Polatera et al., 2000) were used for macroinvertebrates. Eight functional feeding groups (FFG) were considered. These were absorbers, deposit feeders, shredders, scrapers, filter-feeders, piercers, predators and parasites. Family FFG affinity was transcribed into fuzzy codes scaled from 0 (no taxon affinity to a particular FFG) to 3 (strong affinity) after Chevenet et al. (1994) and Tomanova et al. (2007). The FFGs for each sample FFG were obtained by multiplying the taxa code by the taxon density. The functional fish matrix was created after considering the characteristics of flow affinity, feeding habitat, trophic guild, reproductive guild, and tolerance to environmental degradation (Benejam et al., in press). When literature was contradictory or ambiguous, fish species were not assigned to any category.

Data analyses

Similarity analyses

The comparison of the taxonomic assemblage composition (diatoms, macroinvertebrates and fish) between unregulated and

regulated sites of Ter River was performed by means of ANOSIM analyses (Clarke and Warwick, 2001b). Differences in assemblage composition between drought and post-drought periods for each catchment or river segment (Muga, Fluvià, Ter-unregulated and Ter-regulated) were also determined with ANOSIM analyses. ANOSIM operates on a resemblance matrix and is similar to a standard univariate ANOVA, but does not require normality or homoscedasticity of data. Similarity percentages (SIMPER) tests were used to determine the assemblage similarity in each catchment/river segment, as well as the dissimilarity between drought and post-drought periods for each catchment/river segment. The diatom, macroinvertebrate and fish taxa contributing to the dissimilarity between the two periods were identified also by SIMPER analyses.

Non-parametric multidimensional scaling (MDS) were performed with the Ter River samples to analyse the relationship between diatoms, macroinvertebrates and fish assemblage structure with respect to their location (upstream or downstream the reservoirs) and their global hydrological stress. Taxa abundances were square-root transformed and Bray–Curtis was selected as a similarity distance. ANOSIM and SIMPER tests, MDS and calculations of the assemblage parameters were performed by PRIMER v. 6.0 for Windows.

Variation partitioning

The effects of flow regime on the different biotic components were also analyzed by means of variation partitioning (Borcard et al., 1992; Legendre and Legendre, 1998), using the 'vegan' package (Oksanen et al., 2009) of the R language (R Development Core Team, 2008). Variation partitioning decomposes the variation of dependent variables in unique (or pure) and shared (or joint) effects of a set of predictors. Variation partitioning is achieved by partial regression and redundancy analysis for single (community parameters) and multiple dependent variables (species or functional matrices), respectively. The vegan package primarily uses adjusted R squares to assess the partitions explained by the predictors and their combinations, because this is the only unbiased method (Peres-Neto et al., 2006).

The community parameters of each assemblage were used as single dependent variables. The taxonomic (species-abundance) and functional (functional trait-abundance) matrices were used as multiple dependent variables. The species-abundance matrix was square-root transformed. The variation partitioning procedure was carried out separately for each assemblage (diatoms, macroinvertebrates and fish) and matrix (taxonomic and functional).

Three sets of predictors were considered: hydrological, spatial and environmental. This allowed to decompose the variation in the following components: pure hydrological effects ($H|(S+E)$), pure spatial effects ($S|(H+E)$), pure environmental effects ($E|(H+S)$), non-hydrological spatially-structured environmental effects ($(S\cap E)|H$), non-environmental spatially-structured hydrological effects ($(H\cap S)|E$), non-spatial joint hydrological–environmental effects ($(H\cap E)|S$), spatially-structured joint hydrological–environmental effects ($(H\cap E\cap S)$), and unexplained variation ($1 - (H +$

$E + S)$). We also report the overall (i.e. unique plus shared with other components) hydrological effects (H).

The set of hydrological variables included drought ratio, abstraction rate, monthly flow and accumulated rain of the month before the sampling. Spatial variables included catchment (two dummy binary variables, representing Muga, Fluvià and Ter Rivers), altitude, stream order, distance to the source, and location (upstream or downstream of reservoirs). Finally, fourteen variables were included in the environmental data set: pH, conductivity, water temperature, percent oxygen saturation, incident light, DIN (dissolved inorganic nitrogen), phosphate, riparian vegetation type, water transparency and percentages of substrata (boulders, cobbles and pebbles, gravels, coarse and medium sands, uniform natural surfaces, other substrata). Riparian vegetation type had four ordinal values: closed canopy, open canopy, narrow vegetation strip and riparian vegetation absent. Water transparency had three ordinal values: transparent water, low turbidity and high turbidity. All concentrations and water flow were \log_{10} transformed, whereas percentage estimates were arcsin transformed (Legendre and Legendre, 1998). A principal component analysis (PCA) was conducted with the results (adjusted coefficient of determination of the seven independent components (i.e. the first seven listed above)) of the variation partitioning (i.e. in order to determine which community parameters or matrices were more related to hydrology).

Results

Hydrological variation: drought and post-drought periods

While in most rivers water flow increased with 2008 spring rains, Muga River remained in drought conditions throughout 2008 (Table 1). Fluvià River and Ter-unregulated recorded rapid flow increases after the rains. Ter-unregulated in the post-drought period had a higher flow than the annual 2000–2008 mean flow. In this period, more than 50% of the days had a higher flow than the monthly mean (Table 1). However, flow recovery was observed one month later in the Ter-regulated, because water was retained by reservoirs (Fig. 2). Sites in Ter-regulated showed an extended drought and a low flow (<50% of the 2000–2008 annual mean flow; daily flow below the monthly mean) after the return of rains. Thus, whereas Fluvià and Ter Rivers were sampled during drought (April and May) and post-drought (July and September) conditions, water flow of Muga River did not recover during all the studied period. Moreover, between both sections of Ter River, unregulated and regulated, the post-drought conditions were markedly different. Therefore, in the unregulated section water flow was near the double of the annual mean flow, while in the regulated section was less than the half of the annual mean flow (Table 1). Fluvià River was in an intermediate situation, being the water flow in the post-drought period similar to the annual mean flow.

Table 1
Hydrological parameters of four representative sites in the catchments or river segments studied (Muga, Fluvià, Ter-unregulated and Ter-regulated). The annual mean flow for the period 2000–2008 and the date for the initial flow recovery are indicated. The percentage of days with flow under the monthly mean flow for 2000–2008 ($F < MMF$) is given in the drought and post-drought periods. The mean flow for each period in 2008 is also shown.

Catchment/river segment	Site	Date initial of flow recovery	Annual mean flow ($\text{m}^3 \text{s}^{-1}$)	Drought		Post-drought	
				$F < MMF$ (% days)	Mean flow ($\text{m}^3 \text{s}^{-1}$)	$F < MMF$ (% days)	Mean flow ($\text{m}^3 \text{s}^{-1}$)
Muga	M2	n.r.	1.26	100	0.54	–	–
Fluvià	F2	11/05	4.40	100	0.66	82	3.79
Ter-unregulated	T3	11/05	8.82	93	4.28	44	14.82
Ter-regulated	T8	06/06	10.60	99	2.02	92	4.19

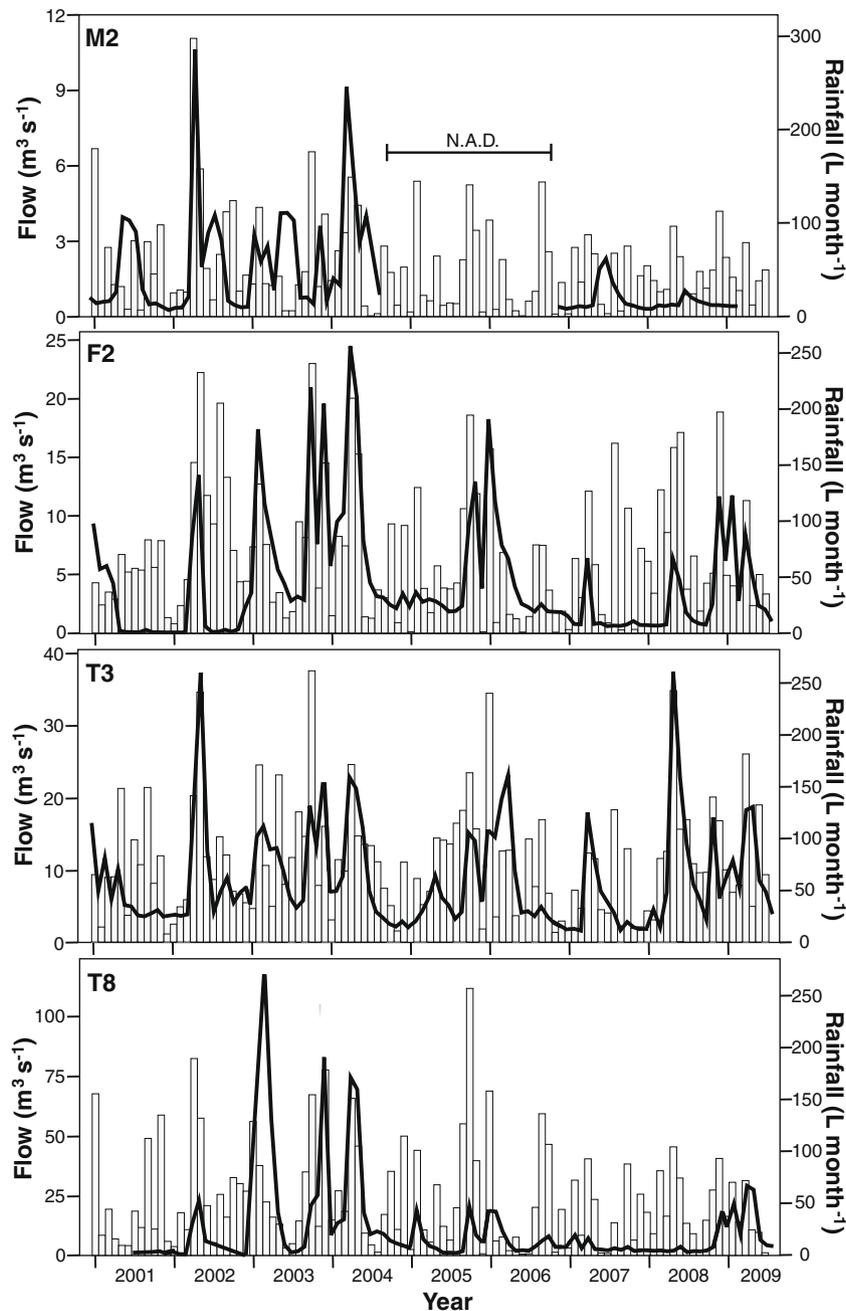


Fig. 2. Monthly flow average and rainfall for the period 2001–2009 in four sites representative of the catchments or river segments studied. Muga (M2), Fluvià (F2), Ter-regulated (T3) and Ter-unregulated (T8). Bars indicate the accumulated monthly rain ($L y^{-1}$), and the line the flow ($m^3 s^{-1}$). Flow data were not available (N.A.D.) in the Muga River for 2005 and 2006.

Biological assemblage variation between drought and post-drought periods

Only two diatom taxa, *Achnanthes minutissima* and *Amphora pediculus* explained dissimilarity in the three river sections between drought and post-drought phases. *Fragilaria construens* var. *venter*, *Nitzschia inconspicua* and *Navicula subminuscula* explained dissimilarity in the Fluvià and Ter-regulated, *Nitzschia dissipata* was found to explain dissimilarity in the 2 sections of River Ter, and *Cymbella microcephala* in the Fluvià and the Ter-unregulated. However, the pattern of increment/diminution between drought and post-drought phases of the different taxa was not always the same in the three river sections. For example, the abundance of

A. minutissima and *A. pediculus* in the post-drought phase diminished with respect to the drought phase in the Fluvià and Ter-regulated, but incremented in the Ter-unregulated. On the other hand, *C. microcephala* decreased in the Fluvià and in the Ter-unregulated (Table 2).

Chironomidae, Baetidae, Naididae, Simuliidae, Tubificidae and Caenidae were the macroinvertebrate taxa experiencing higher differences between drought and post-drought periods in Fluvià, Ter-unregulated and Ter-regulated (Table 2). Analogously to the fact described in the diatom assemblage, changes in abundance between the drought and post-drought periods were not coincident for the particular taxa. There was a higher proportion of filter-feeding taxa (i.e. Simuliidae and Hydropsychidae), or a general

Table 2
SIMPER analysis of dissimilarity between drought and post-drought periods. The taxa of each assemblage (diatoms, macroinvertebrates and fish) contributing most to the dissimilarity between periods are shown together with their percentage contribution in dissimilarity. Legend: I, taxa which increased in the post-drought period; D, taxa which decreased in the post-drought period.

Fluvià (D versus Pd)			Ter-unregulated (D versus Pd)			Ter-regulated (D versus Pd)		
Taxa	(%)	I/D	Taxa	(%)	I/D	Taxa	(%)	I/D
Diatoms								
<i>Cymbella microcephala</i>	8.53	D	<i>Cymbella microcephala</i>	5.78	D	<i>Navicula subminuscula</i>	3.89	I
<i>Amphora pediculus</i>	6.73	D	<i>Achnanthes minutissima</i>	5.47	I	<i>F. contruens var. venter</i>	3.34	D
<i>F. construens var. venter</i>	5.82	I	<i>Achnanthes biasoletiana</i>	4.69	I	<i>Achnanthes minutissima</i>	3.17	D
<i>Anomoeoneis vitrea</i>	4.70	I	<i>Cymbella minuta</i>	4.09	D	<i>Cyclotella meneghiniana</i>	3.15	D
<i>Achnanthes minutissima</i>	3.88	D	<i>Nitzschia fonticola</i>	2.74	D	<i>Amphora pediculus</i>	3.15	D
<i>Navicula minima</i>	3.39	I	<i>Nitzschia dissipata</i>	2.74	I	<i>Cocconeis placentula</i>	2.90	I
<i>Nitzschia inconspicua</i>	2.39	D	<i>Amphora pediculus</i>	2.70	I	<i>Nitzschia frustulum</i>	2.47	I
<i>Navicula cryptotenella</i>	2.37	D	<i>Cymbella affinis</i>	2.44	I	<i>Nitzschia inconspicua</i>	2.37	I
<i>Fragilaria delicatissima</i>	2.32	D	<i>Diatoma moniliformis</i>	2.28	D	<i>Nitzschia dissipata</i>	2.15	D
<i>Navicula subminuscula</i>	2.18	I	<i>Navicula gregaria</i>	2.13	D	<i>Thalassiosira pseudonana</i>	2.02	I
Macroinvertebrates								
Chironomidae	15.40	D	Naididae	20.68	D	Chironomidae	19.45	D
Baetidae	14.01	I	Chironomidae	9.73	I	Naididae	10.89	D
Naididae	12.08	D	Tubificidae	7.43	I	Tubificidae	7.07	D
Simuliidae	7.96	I	Leuctridae	4.91	D	Baetidae	6.10	I
Tubificidae	6.33	D	Caenidae	4.51	D	Simuliidae	5.61	I
Ceratopogonidae	6.28	D	Baetidae	3.90	I	Lumbriculidae	5.38	D
Caenidae	3.86	I	Elmidae	3.71	D	Gammaridae	3.90	D
Empididae	2.57	D	Lumbriculidae	3.58	D	Dugesidae	3.89	I
Physidae	2.23	I	Simuliidae	3.11	I	Caenidae	3.85	I
Hydroptilidae	1.97	I	Hydropsychidae	2.50	I	Coenagrionidae	2.72	I
Fish								
<i>Barbus meridionalis</i>	26.22	D	<i>Phoxinus phoxinus</i>	24.54	I	<i>Lepomis gibbosus</i>	19.92	D
<i>Squalius laietanus</i>	24.40	I	<i>Barbus meridionalis</i>	19.40	I	<i>Barbus graellsii</i>	17.44	D
<i>Gambusia holbrooki</i>	23.18	D	<i>Rutilus rutilus</i>	18.00	D	<i>Carassius auratus</i>	10.10	D
<i>Anguilla anguilla</i>	15.08	D	<i>Barbatula barbatula</i>	17.67	D	<i>Barbus meridionalis</i>	9.44	I
<i>Cyprinus carpio</i>	11.13	I	<i>Pseudorasbora parva</i>	8.01	I	<i>Anguilla anguilla</i>	8.79	D

decrease of Oligochaeta (i.e. Naididae and Lumbriculidae) in the post-drought period.

The fish assemblage strongly varied along the longitudinal gradient. Upstream reaches were dominated by *Phoxinus phoxinus*, *Salmo trutta*, and *Barbatula barbatula*, while *Barbus meridionalis* and *Squalius laietanus* were more common in downstream reaches. The last sampling site of Ter River also had presence of native marine species (*Liza ramada* and *Atherina boyeri*) and many exotics (*Lepomis gibbosus*, *Carassius auratus*, *Micropterus salmoides*, and *Sander lucioperca*). This spatial variation was linked to that of

hydrological and environmental conditions. Fish abundance (and secondarily richness) increased after drought, though less remarkably in the sites most affected by water abstraction (downstream of reservoirs).

Differences in the assemblage composition between Ter-unregulated and Ter-regulated were confirmed by means of ANOSIM analyses: diatoms ($R = 0.653$; $p < 0.001$), macroinvertebrates ($R = 0.249$; $p < 0.001$) and fish ($R = 0.862$; $p < 0.001$). Assemblages had different maximum values of similarity within river segments (Muga, Fluvià, Ter-unregulated and Ter-regulated): diatoms were more similar in Ter-regulated, macroinvertebrates were more similar in Ter-unregulated, and fish were more similar in Fluvià (Table 3). The different effect of the post-drought conditions for each river and assemblage were expressed in the dissimilarity between drought and post-drought periods: diatoms had the minimum dissimilarity in Ter-unregulated and that of fish occurred in the Fluvià, while macroinvertebrates had similar dissimilarities in all rivers studied.

MDS analyses showed differences between regulated and unregulated reaches of Ter River for diatoms and fish, but not for macroinvertebrates (Fig. 3). The different result obtained by macroinvertebrates could be explained, at least partially, by the lower taxonomic resolution. The MDS solution obtained for the diatom assemblage distinguished not only two groups of samples (upstream and downstream of the reservoirs system), because a third group with the samples from headwater sites (T1 and T2) was also distinguished (Fig. 3A and B).

Variation partitioning

Hydrological effects were significantly related to community parameters of the three assemblages (diatoms, macroinvertebrates and fish). Four parameters were significantly related to hydrology:

Table 3

Comparison of the similarity between the three assemblages (diatoms, macroinvertebrates, fish) for each catchment/river segment (Muga, Fluvià, Ter-unregulated and Ter-regulated) and dissimilarity between periods (drought and post-drought), by means of SIMPER analysis. Dissimilarity percentages between drought and post-drought periods are indicated in italics.

	Diatoms	Macroinv.	Fish
Muga	29	36	30
Drought (% similarity)	29	63	30
Post-drought (% similarity)	–	–	–
<i>Drought versus Post-drought (% dissimilarity)</i>	–	–	–
Fluvià	30	37	52
Drought (% similarity)	32	66	58
Post-drought (% similarity)	27	57	51
<i>Drought versus Post-drought (% dissimilarity)</i>	63	43	37
Ter-unregulated	38	48	39
Drought (% similarity)	36	61	32
Post-drought (% similarity)	40	56	40
<i>Drought versus Post-drought (% dissimilarity)</i>	63	45	55
TER-regulated	56	45	35
Drought (% similarity)	56	62	38
Post-drought (% similarity)	56	52	35
<i>Drought versus Post-drought (% dissimilarity)</i>	45	45	58

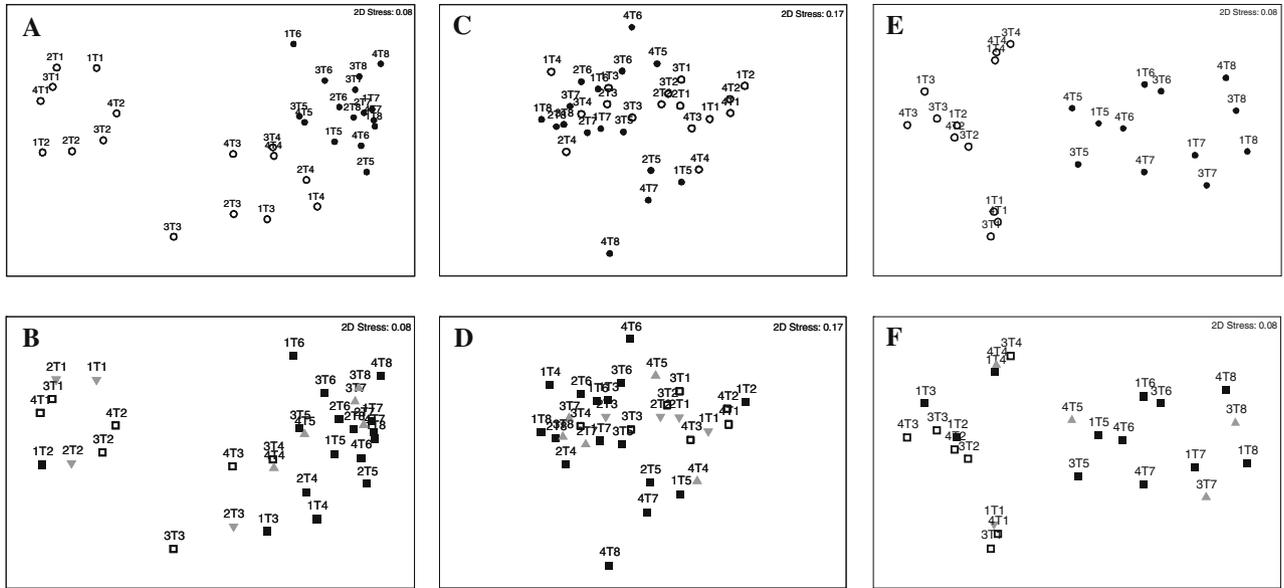


Fig. 3. MDS plots of the samples of the diatom assemblages (plots A and B), macroinvertebrates (plots C and D) and fish (plots E and F). Upper plots (A–E) show the location of the sample upstream (open circles) or downstream of the reservoir system (black circles). Bottom plots (B–F) show the types of hydrological stress for each sample: strong abstraction (upper triangles), strong drought (bottom triangles), presence (black squares) and absence (open squares) of both hydrological stress types. Each sample was coded adding a number before the site code (see Fig. 1). This number corresponds to the sampling survey (1, April; 2, May; 3, July; 4, September). Sites 1 and 2 correspond to sites located in headwater streams, while the rest of the sites were located in the main river course.

Table 4

Variation partitioning of the response variables (proportion of variance explained; |: unique effects, +: common effects, ∩: shared effects) per hydrological (H), spatial (S) and environmental (E) factors (see Methods for further details). Response variables include six diatoms parameters, seven macroinvertebrates parameters and seven fish parameters. Legend: SR, species richness; J, evenness; D, Shannon–Wiener diversity; TD, taxonomic distinctness; ATD, average taxonomic distinctness; VTD, variation in taxonomic distinctness; N, abundance in numbers. Negative proportions of variance explained are indicated as zero. Bold figures indicate significant proportions of variance explained (permutation tests, $P < 0.05$); only overall and unique components can be tested.

	H	H S + E	S H + E	E H + S	H∩S E	S∩E H	H∩E S	H∩S∩E	1 – [H + S + E]
<i>Diatoms</i>									
Diatoms_SR	0.37	0.00	0.11	0.09	0.40	0.11	0.12	0.00	0.33
Diatoms_J	0.57	0.05	0.05	0.00	0.23	0.09	0.06	0.23	0.29
Diatoms_D	0.53	0.03	0.10	0.05	0.31	0.09	0.07	0.13	0.23
Diatoms_TD	0.22	0.08	0.15	0.18	0.22	0.14	0.07	0.00	0.30
Diatoms_ATD	0.00	0.00	0.24	0.45	0.07	0.00	0.05	0.00	0.37
Diatoms_VTD	0.00	0.20	0.23	0.23	0.00	0.12	0.00	0.00	0.46
<i>Macroinvertebrates</i>									
Macroinv_SR	0.57	0.06	0.04	0.00	0.23	0.09	0.07	0.22	0.31
Macroinv_N	0.24	0.05	0.00	0.00	0.11	0.07	0.06	0.01	0.69
Macroinv_J	0.11	0.00	0.06	0.00	0.09	0.12	0.07	0.05	0.81
Macroinv_D	0.13	0.00	0.25	0.01	0.05	0.14	0.03	0.08	0.47
Macroinv_TD	0.37	0.03	0.05	0.01	0.00	0.03	0.03	0.32	0.54
Macroinv_ATD	0.41	0.04	0.02	0.01	0.02	0.24	0.01	0.34	0.33
Macroinv_VTD	0.06	0.13	0.00	0.00	0.01	0.22	0.08	0.00	0.92
<i>Fish</i>									
Fish_SR	0.26	0.02	0.34	0.29	0.22	0.00	0.02	0.00	0.16
Fish_N	0.21	0.00	0.00	0.18	0.04	0.15	0.06	0.12	0.58
Fish_J	0.30	0.00	0.20	0.19	0.30	0.19	0.00	0.00	0.34
Fish_D	0.29	0.00	0.29	0.11	0.29	0.20	0.00	0.00	0.21
Fish_TD	0.31	0.06	0.54	0.28	0.05	0.00	0.00	0.20	0.27
Fish_ATD	0.26	0.06	0.66	0.33	0.00	0.00	0.00	0.20	0.32
Fish_VTD	0.20	0.20	0.39	0.50	0.00	0.00	0.00	0.00	0.46

species richness, evenness, diversity and taxonomic distinctness. Moreover, numerical abundance and average taxonomic distinctness were also related to hydrology in the case of macroinvertebrates and fish (Table 4). Only two diatom parameters (taxonomic distinctness and variation in taxonomic distinctness) were related to pure hydrological variability.

The results obtained with the six organism matrices (taxonomic and functional classification) were similar to those obtained using community parameters. Although all six matrices were signifi-

cantly related to the overall hydrological effects, none was related to pure hydrological effects (Table 5). When pure effects of hydrology were considered, environmental and spatial variables were more clearly related to assemblage matrices than hydrology.

The first axis of PCA analysis performed with the result of all variation partitioning analyses (using community parameters and assemblage matrices) explained the 38% of variability. The second axis explained the 19% of variability (Fig. 4). The first axis showed a gradient from shared effects (mainly shared effects of space and

Table 5
Results of the variation partitioning (proportion of variance explained; |: unique effects, +: common effects, \cap : shared effects) per hydrological (*H*), spatial (*S*) and environmental (*E*) variables. Response variables include six assemblage matrices, two (one classifying organisms by its taxonomic identity, another classifying them by its functional group) for each assemblage used in the study (diatoms, macroinvertebrates and fish). Negative proportions of variance explained are indicated as zero. Bold figures indicate significant proportions of variance explained (permutation tests, $P < 0.05$); only overall and unique components can be tested.

	<i>H</i>	<i>H</i> <i>S</i> + <i>E</i>	<i>S</i> <i>H</i> + <i>E</i>	<i>E</i> <i>H</i> + <i>S</i>	<i>H</i> \cap <i>S</i> <i>E</i>	<i>S</i> \cap <i>E</i> <i>H</i>	<i>H</i> \cap <i>E</i> <i>S</i>	<i>H</i> \cap <i>S</i> \cap <i>E</i>	1 – [<i>H</i> + <i>S</i> + <i>E</i>]
<i>Taxonomic matrix</i>									
Diatoms	0.27	0.00	0.10	0.12	0.09	0.11	0.04	0.14	0.39
Macroinv.	0.13	0.05	0.10	0.14	0.02	0.02	0.01	0.05	0.61
Fish	0.13	0.02	0.15	0.22	0.00	0.19	0.05	0.06	0.31
<i>Functional matrix</i>									
Diatoms	0.23	0.01	0.10	0.18	0.06	0.14	0.00	0.17	0.35
Macroinv.	0.19	0.08	0.03	0.13	0.06	0.04	0.01	0.04	0.62
Fish	0.21	0.00	0.07	0.20	0.03	0.16	0.07	0.11	0.36

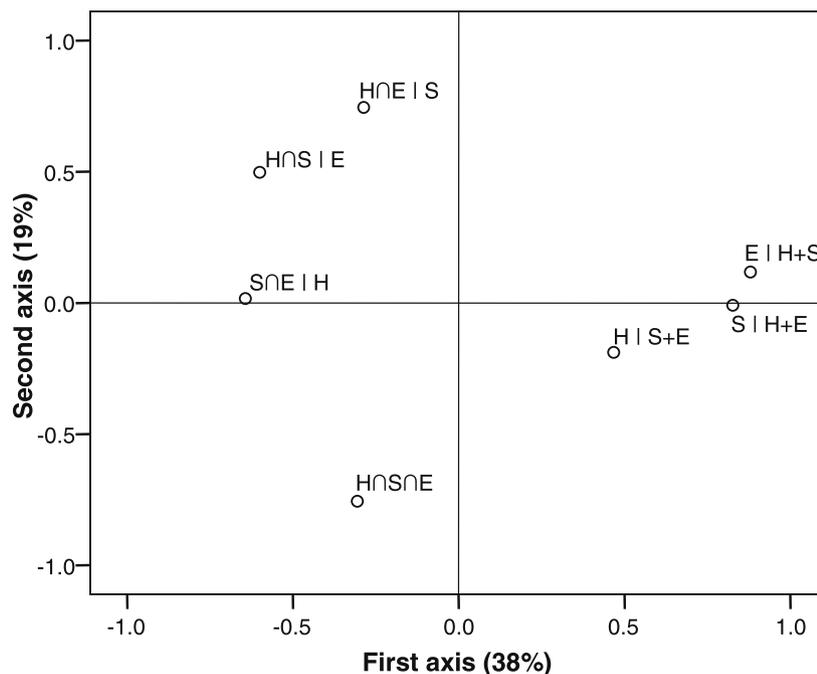


Fig. 4. Principal components analysis (PCA) performed using the variation partitioning data of the 20 community parameters and six assemblage matrices. Factor loadings of the variation partitioning fractions in the final PCA solution are shown. Labels of variation partitioning proportions are the same as those in Tables 4 and 5.

environment) to pure effects. The second axis arranged from triple shared effects (hydrology + space + environment) to shared effects of hydrology with both space and environment. Community parameters were distributed in all the space determined by both axes, while all assemblage matrices were located near one to each other (Fig. 5). The three groups of community parameters (diatoms, macroinvertebrates and fish) were distributed in the PCA solution following different patterns. While macroinvertebrate parameters had negative coordinates for both axes, fish parameters had positive coordinates for the first axis (with one exception: numerical abundance), and diatom parameters had not a spatial pattern in the PCA solution.

Discussion

Hydrology and composition of biological communities

Changes in community composition due to hydrology have been mostly described in the extremes of the hydrological continuum (i.e. floods and droughts; e.g. Boulton and Lake, 2008; Death,

2008; Liu and Wang, 2008). Hydrology has also been related to population structure (e.g. Cowx et al., 1984; Resh, 1992) and ecosystem function (Cuffney and Wallace, 1989; Boulton and Lake, 1992b). The alterations in hydrological connectivity account for changes in the ecosystem functioning, community composition and population structure. Droughts represent a disruption in hydrological connectivity, whereas floods amplify hydrological connectivity (Lake, 2003). However, some responses are stream- and community-specific (e.g. Argerich et al., 2004; Dewson et al., 2007). Death et al. (2009) observed that flow reduction in three New Zealand streams caused significant changes in community structure at only one of the streams. Functional processes also show varying responses. Leaf breakdown rates decreased after flow reduction (and associated lower physical abrasion) in some studies, but not in others (e.g. Rader et al., 1994; Casas et al., 2000).

The three groups studied (diatoms, invertebrates and fish) in the Catalan Rivers differed in their response to hydrologic alterations. Diatom assemblages were sensitive to the frequency and timing of hydrological disturbances, which increase their tolerance and even cause diverging responses (Ledger et al., 2008). Diatom species differ in their success to withstand emersion (Peterson,

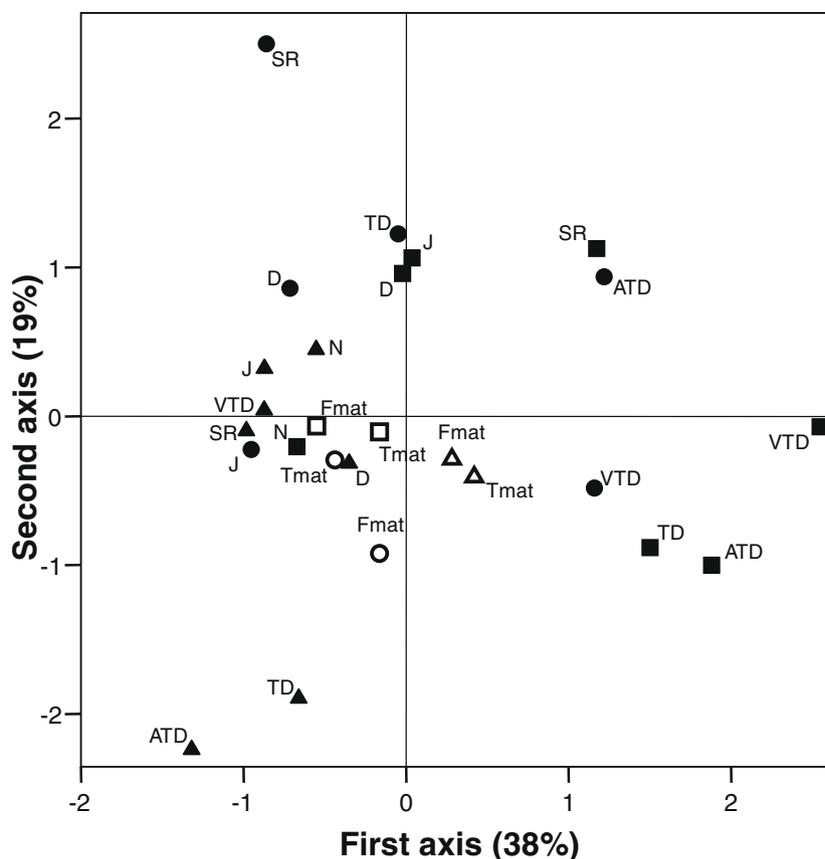


Fig. 5. Principal components analysis (PCA) performed using the variation partitioning of the 20 community parameters and six assemblage matrices. The location of each community parameter and each assemblage matrix in the final PCA solution is shown. Symbols: circles (diatoms), triangles (macroinvertebrates) and squares (fish). Solid symbols correspond to community parameters, while open ones to matrices. Legend: SR, species richness; J, evenness; D, Shannon–Wiener diversity; TD, taxonomic distinctness; ATD, average taxonomic distinctness; VTD, variation in taxonomic distinctness; N, abundance in numbers; Tmat, taxonomic matrix; Fmat, functional matrix.

1996), and gradual drying allows much higher desiccation resistance of diatoms than those subjected to rapid drying since physiological acclimation is time-dependent (Hostetter and Hoshaw, 1970). Further, diatoms are extremely sensitive to chemical characteristics of the water (e.g. nutrients, water conductivity; Leira and Sabater, 2005; Tornés et al., 2007), sometimes due to dilution and therefore to water scarcity. As a result, changes in taxonomic composition and physiognomy of the diatom community were not linear or uniform. Composition of macroinvertebrate assemblages can gradually change with the decrease of flow. The sequential loss of connectivity (lateral and longitudinal) and the severity of pool conditions favour tolerant or lentic species (Boulton, 2003; Bonada et al., 2007; Boulton and Lake, 2008). Changes in macroinvertebrate assemblage are not only taxonomic. Some feeding strategies were more affected than others, filter-feeders decreased in response to reduced flows (Death et al., 2009). Different biological traits were more prevalent in drought conditions, associated to those described in intermittent and ephemeral streams (e.g. high power of dispersal, short life-span or generalistic feeding; Williams, 1996). Drought also has strong effects on fish assemblages. Although fish of arid or semi-arid regions are well adapted to hydrological changes (Lake, 2003; Matthews and Marsh-Matthews, 2003), drought reduces population size and community richness (Magoulick and Kobza, 2003). The last downstream sites of the Ter River, severely affected by drought and water abstraction, displayed high richness and abundance of exotic fish such as mosquitofish, pumpkinseed sunfish, common carp or goldfish. Water regulation tends to favour limnophilic fish (i.e. spe-

cies that prefer standing waters), which often are exotic in the Iberian Peninsula (e.g. Vila-Gispert et al., 2005).

The decrease of flood frequency and the occurrence of extended droughts under water scarcity facilitate the invasion of exotic species (Lake, 2003). Even though drought sometimes causes higher death rate of exotic than native fish (Scott and Helfman, 2001; Closs and Lake, 1996), accentuated droughts facilitate the extension of invasive riparian plants (e.g. Busch and Smith, 1995). River regulation and the associated slow flows facilitate species invasions, causing severe food web disturbances (e.g. *Azolla filiculoides*, *Procambarus clarkii*; Janes et al., 1996; Geiger et al. 2005). These two species were present in the studied rivers, and the arrival of new exotic species is being documented (e.g. *Anodonta woodiana* in 2006 and *Misgurnus anguillicaudatus* in 2007; Franch et al., 2008; Pou-Rovira et al., 2009).

There was a significant relationship between hydrology and the structural measures (community parameters and assemblage matrices) of the three assemblages analyzed. However, the effects of hydrology were not analogous. There were similar values of dissimilarity between drought and post-drought periods in the macroinvertebrate assemblage of the three rivers. Instead, minimum differences were recorded for diatoms and fish. Some of the observed changes between drought and post-drought periods could be attributed to the more lotic conditions in the latter (i.e. filter-feeders increased and lentic taxa decreased in the post-drought period). The PCA performed with the proportions of the variation partitioning analysis confirmed both the different relationship between each assemblage and the hydrological descriptors, as well as

the relative importance of environment and spatial factors. Although assemblage structural measures (community parameters and assemblage matrices) were related to hydrology, significant differences in assemblage composition between drought and post-drought periods did not occur. In addition, pure hydrological effects were not significantly related to community structural measures. These different facts suggest both the resilient nature of these assemblages as well as the complexity of the biological response, not restricted to the influence of hydrology.

Relationship between community structure measures and hydrology

Assemblage matrices and community parameters were the two main approaches used in this study. The two have been previously used to identify stream community changes related to hydrological situations as droughts or floods (e.g. Acuña et al., 2005; Bonada et al., 2006; Snyder and Johnson, 2006). Coincident results obtained by the two approaches were observed in both lotic (Acuña et al., 2005; Bonada et al., 2006) and lentic systems (Boix et al., 2008; Ruhí et al., 2009). Nevertheless, some differences exist because the assemblage matrix approach had more natural variability though better resolution. For example, Boix et al. (2008) distinguished two types of invertebrate assemblages using species richness as community parameter (saline and freshwater assemblages), while the assemblage matrix approach could distinguish three types: saline, freshwater temporary and freshwater permanent. The results obtained in this study by means of the two approaches were in agreement: matrices and parameters were significantly related to overall hydrological effects but not to pure hydrological effects. However, the two assemblage matrices types (taxonomic and functional) provided a more similar result than that of community parameters.

Results obtained by the traditional community parameters (i.e. SR, *J* and *D*) and those of taxonomic distinctness (i.e. TD, ATD and VTD) differed in the three assemblages. The position in the PCA performed using the variation partitioning of the community parameters and assemblage matrices indicated that the taxonomic distinctness parameters in diatoms and fish were mostly associated to the environmental and spatial characteristics. Instead, the traditional parameters were preferentially associated to the spatial variability related to changes in habitat characteristics (the shared effects of environment and space; Figs. 4 and 5).

The complementarity between both types of parameters (Heino et al., 2005) accounts for the variability included in the biodiversity. Studies using a partial account of the biological community obtained similar results with both types of parameters (Campbell et al., 2008; Ruhí et al., 2009). Even though it has been described that traditional parameters respond more clearly to human disturbances (e.g. Abellán et al., 2006), it has also been shown that taxonomic distinctness parameters are more sensitive to these disturbances (e.g. Marchant, 2007; Gascón et al., 2009), or that no relationship between anthropogenic impacts and community parameters exists (e.g. Heino et al., 2007).

Spatial variability as a result of drought and reservoir management

Our study showed the relevance of hydrology alterations on most of the community structural measures, but also confirmed that pure hydrological effects were only slightly significant. Other factors which covariate with hydrology can be equally relevant for biological communities (e.g. Cobb et al., 1992; Biggs et al., 1999; Snyder and Johnson, 2006). A remarkable proportion of variation was explained by shared effects of hydrological and spatial and/or environmental variables. Hydrological disturbances may imply changes on the environment characteristics (e.g. substratum) relevant to the community structure (Wright et al., 2003). Our study

revealed that the shared effects of hydrology and spatial variables were more relevant than those of hydrology and environmental variables in affecting the community parameters of the three assemblages.

The analysis of Ter River revealed that the discontinuity in the hydrological patterns caused by the reservoirs differentially affected the assemblage structure of diatoms and fish between upstream and downstream segments of the river. The reservoirs system located in the middle of Ter River main course imply both damming and water diversion. Nearly half of the flow discharge (approximately 205 million m³ y⁻¹) is canalized for human water supply mostly to the Barcelona region. Reservoirs significantly alter water flow, channel morphology, habitat structure, water temperature, dissolved oxygen levels, nutrient, and sediment and debris loads (Kanehl et al., 1997). Their presence benefit nonnative fish species at the expense of native species and anadromous fish populations are declining rapidly (Schmidt et al., 1998). The important shared effects between hydrology and space were also observed in the MDS results, especially when global drought stress and human abstraction jointly occurred (downstream of the reservoirs). In contrast, situations without any of these stresses, or those with only global drought stress were characteristic of sites upstream of the reservoirs (Fig. 3). Reservoirs intensified the effect of drought on downstream community composition and structure, as a result of the competition between human uses of water and environmental values.

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