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Additional Information

# **Fish community responses to antecedent hydrological conditions based on long-term data in Mediterranean river basins (Iberian Peninsula)**

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## **1 Introduction**

In recent decades, many studies have proven the paramount impact of flow regimes on the structure of lotic ecosystems (Lytle and Poff, 2004; Resh et al., 1988), both through extreme events such as floods (e.g. Robertson *et al.*, 2015) and droughts (e.g. Fenoglio *et al.*, 2007) but also during moderate flows, which temporarily and spatially regulate the habitat availability (e.g. White *et al.*, 2018). Freshwater organisms have evolved and adapted specifically to the natural flow regime (Poff et al., 1997; Townsend and Hildrew, 1994) that ultimately select specific life-history strategies of freshwater organisms (Mims and Olden, 2012). Consequently, changes in the frequency, magnitude, timing and duration of the different flows may lead to remarkable changes or to populations collapses (Piniewski et al., 2017).

Nowadays, unregulated free-flowing rivers are largely restricted to remote regions of the Arctic, Amazon and Congo basins (Grill et al., 2019) and the Iberian Peninsula is not excluded of this global phenomenon (Hermoso et al., 2018). For instance, Spain currently harbours more than 1200 large dams located in its river systems, with a total capacity of 56,000 hm<sup>3</sup>, which corresponds to the fifth highest number of large dams per country worldwide and it exceeded only by China, the

United States, India and Japan (Magdaleno and Fernández, 2011). While removal of regulation facilities such as large dams has been stressed to be a paramount action to re-naturalise flow regimes, it is often unfeasible due to socioeconomic constraints (Hermoso et al., 2018). Consequently, it has been rarely addressed in this territory and management actions must try to emulate specific aspects of river flow regimes (e.g. spring floods) (Schiermeier, 2018; Yarnell et al., 2015).

A direct or unintended effect of human activities related to fresh waters exploitation is the introduction and thriving of alien species (Westphal et al., 2008), which often turned into invasive species that harmed the recipient ecosystems (e.g., Radinger et al., 2019). In Mediterranean ecosystems, the loss of the natural intra- and inter-annual flow variability, together with the creation of lentic habitats related to flow regulation facilities (e.g. reservoirs and weirs), have favoured the establishment of a number of alien species (Muñoz-Mas et al., 2016a; Vinyoles et al., 2007). Mediterranean fish communities are known for their high endemism and the predominance of Cyprinids, which possess high specific diversity and show morpho-functional and physiological adaptations to fluctuating environments (Granado-Lorencio, 2000, 1996). For instance, the presence of the endemic Eastern Iberian barbel (*Luciobarbus guiraonis*) as well as the native fish richness have been negatively related with the percentage of alien species, smaller distance between barriers and the reduction of the mean annual flow (Olaya-Marín et al., 2016). The Iberian Peninsula is climatologically and hydro-geomorphologically heterogeneous (Benito-Calvo et al., 2009). Therefore, in addition to the introductions occurred in regulated lotic systems, this heterogeneity has favoured the establishment of a larger number of alien species in unregulated ecosystems as they found suitable habitats to thrive (Sheppard et al., 2018).

Apart from foreign introductions, inter-basin water transfers are recognized as one of the major corridors for species translocations (*i.e.* species transferred across river basins within a

political border) (Gallardo and Aldridge, 2018). Translocated species have traditionally been viewed acquiescently, although there is evidence that they can produce negative impacts in the same way as aliens (Muñoz-Mas et al., 2017). A good example is the Iberian straight-mouth nase (*Pseudochondrostoma polylepis*), which moved along the Tagus-Segura river transfer and for whom it has been demonstrated —empirically (Alcaraz et al., 2014) and theoretically (Muñoz-Mas et al., 2017)— to have a dramatic negative impact on the native Júcar nase (*Parachondrostoma arrigonis*).

Some experiences demonstrated that flow regime re-naturalisation displaces alien species in favour of that native in rivers where alien and native species coexist (Kiernan et al., 2012). Although, once an alien species is established, coexisting with the native species is, unfortunately, the most habitual outcome in the colonised area (Muñoz-Mas et al., 2019; Strayer, 2010). In the Iberian Peninsula, like in other parts of the world, water demands are steadily increasing, essentially for hydroelectric power production and agricultural purposes (de Fraiture and Wichelns, 2010), which is a process that is likely to be exacerbated if the expected decrease in water yield caused by the projected climate change occurs (Alvar et al., 2017). In this context, scientists are challenged to define ecosystem needs clearly enough to guide policies and management strategies in order to optimize water uses (Poff et al., 2003).

Although imperfect, the transposition of the EU Water Framework Directive into national contexts has supposed a great step forward in the development of legislative body compelling managers and stakeholders to mitigate the negative impacts of river regulation (Voulvoulis et al., 2017). For instance, the Spanish environmental flow legislation can be considered more progressive than in other territories because it is not restricted to hydrological methods (e.g. Tennant, 1976) and alludes to physical habitat methods that consider specific biotic needs (Muñoz-Mas et al., 2016b). However, it is still focused on sustaining a discharge exceeding a minimum threshold value, although it is broadly recognized that focusing on low flows, and neglecting high flows, during the

process of decision-making ignores relevant aspects controlling biotic communities, which may lead to uncertain ecosystem management outcomes (Arthington et al., 2006).

In this context of native and alien species co-existence, focusing not only on a discharge exceeding a minimum threshold value requires extensive knowledge about potential species responses (Piniewski et al., 2017). However, even when species autecology is known, the morphologic characteristics of the river may interact with flow regimes leading to different responses of species communities (Turner and Stewardson, 2014), especially for regulated river segments (Chen and Olden, 2018). Therefore, although numerous studies have been performed (Muñoz-Mas et al., 2019, 2016a), there is still need for more river science research to complement former studies that often focused on few species of recreational and economic value (Tonkin et al., 2019).

It is well recognized that the distribution and abundance of fishes are strongly influenced by flow velocity, resources' availability, and thermal regime, all of which are under hydrological influence (White et al., 2018). In addition to flow regimes, a variety of interacting factors such as competition for space, predation (Olaya-Marín et al., 2016) and biological stochasticity are known to naturally affect fish abundance and distribution. Hence, a suite of other biotic and abiotic factors not related to hydrology can also influence the composition of freshwater fish assemblages (Jackson et al., 2001). Thus, it is often very difficult to disentangle the different causes of variation in the organism density and abundance along environmental gradients. Methods testing hypotheses about central tendency (e.g. ANOVA) or central responses (e.g. ordinary least square regression, generalised linear or generalised additive models) set aside the concurring role of other unmeasured factors (Austin, 2007). From the ecological viewpoint, testing hypotheses about the environmental gradients (*e.g.* gradients of hydrological indicators), as limiting factors or constraints on the density of organisms, could be more informative than testing them about mean responses (Downes, 2010).

Limiting factors typically result in wedge-shaped relationships with small changes in the mean value of the response variable along the gradient of the independent variable, but with large changes at the upper end of the distribution (Kail et al., 2012).

Quantile regression allows the association of the different rates of change (slopes) to the different parts of the response distribution, being a method for estimating functional relationships among variables for all the portions of a probability distribution (Koenker and Bassett, 1978). This statistical tool was introduced in ecology by Cade et al. (1999) and can be used to test the role of environmental factors as limiting factors. Moreover, its application allows to predict not only the most probable values of the studied biological metric, but also the maximum or minimum values that could be expected in environmental conditions comparable to the ones used for the model fitting (Cade and Noon, 2003; Doll, 2011; Fornaroli et al., 2016).

The collection of hydrological time series and information on biological communities for several years using a standardized methodology allows to assess the effects of the antecedent hydrological conditions on lotic ecosystems. This sampling scheme becomes essential for the evaluation of those variables that do not show negligible inter-annual variations, such as hydrological characteristics (Wilding et al., 2018). Biological monitoring data, together with hydrological time series provide the opportunity to develop quantitative models that can guide policy and management of water resources (Poff et al., 2010). This work, through quantile regression, tested hypotheses to elucidate the effect of antecedent hydrological conditions (characterised as 48 hydrological indicators) over fish community metrics (species richness, Capture Per Unit Effort/CPUE and CPUE ratio over the total CPUE) which were reclassified taking into account the life-history strategies of the different species (i.e. periodic, opportunistic or equilibrium) and their origin (i.e. native, translocated or alien) in the Júcar River Basin District (JRBD), Eastern Iberian Peninsula. The present work aimed at: i) quantifying the hydrological alterations of the studied

rivers; ii) determining the functional characteristics of fish communities with a special focus on introduced species; iii) determining the flow-ecology relationships that describe richness, proportion and abundance of fish functional groups (*life-history strategies x origin*).

## **2 Material and Methods**

### **2.1 Fish community**

A large monitoring database collecting and homogenizing the existing information on fish fauna in the JRBD (Eastern Iberian Peninsula) (Costa Balaguer, 2017) was updated with authors' personal data and used to derive fish community metrics. The database covers an area of 42,000 km<sup>2</sup> and represents different river typologies, from small mountain streams to large lowland rivers, in five river basins. We identified 15 river sectors (i.e. sector of rivers with similar environmental and biological conditions) where data on fish community and gauging site were coupled. The location of the different river sectors, sampling sites and gauging stations are reported in Figure 1. Different sampling efforts were used by the numerous agencies working on different river types over thirty years, but it was possible to retrieve the abundance (Catch Per Unit Effort - CPUE) for each sampled species collected by electrofishing. Each species was classified as native, translocated and alien (i.e. non-Iberian) to investigate separately on these three groups of species.

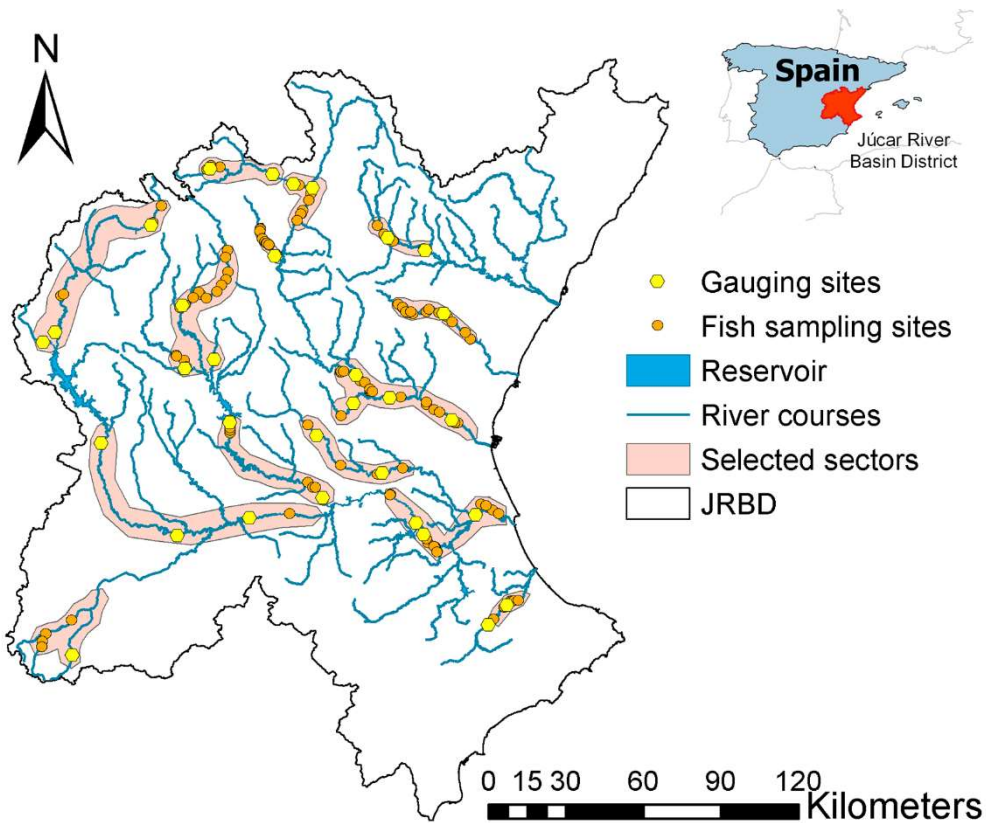


Figure 1 – Map of the Júcar River Basin District (JRBD) displaying the sampling sites, gauging stations and rivers sectors (i.e. sector of rivers with similar environmental and biological conditions) used as categorical factor in the quantile regression models.

Auto-ecological attributes such as fecundity, female maturation age, body size and affinity for lentic waters allowed us to classify ecologically relevant groups of organisms that can show different responses. Thus, in addition to classifying fish species as native, translocated or alien, they were grouped as a function of their life-history strategies (opportunistic, equilibrium and periodic *sensu* Mims & Olden, 2012), assigned on the basis of auto-ecological characteristics retrieved from the databases at *freshwaterecology.info* (FAME Consortium, 2002; Grenouillet and Schmidt-Kloiber, 2006; Pont et al., 2006; Schmidt-Kloiber and Hering, 2015), *FishBase* (Froese & Pauly, 2019) and other sources (Table 1). Opportunistic strategists correspond to small-bodied species with early maturation and low juvenile survivorship and often are associated with habitats defined by frequent



and intense disturbance, mirroring the classic *r* strategy. Periodic strategists are characterized by medium to large body size, late maturation, high fecundity, and low juvenile survivorship and are likely to be favoured in highly periodic (seasonal) environments. Equilibrium strategists are typically small to medium in body size with intermediate times to maturity, low fecundity per spawning event, and high juvenile survivorship largely due to high parental care and small clutch size, closely aligned with the *K* strategy. Equilibrium strategists are predicted to be favoured in more stable habitats with low environmental variation. Finally, the two salmonids — the native brown trout (*Salmo trutta*) and the alien rainbow trout (*Oncorhynchus mykiss*) — were considered separately. The complete list of the sampled species with their attributes is reported in Table 1.

A total of 25 metrics (reported in Table S1), representative of richness, incidence and CPUE were calculated for each sample considering either the origin of the species or their origin and life-history strategy. For all the analyses we included only sites with a representative gauging site and the river reaches represented by 9 samples or more. The final dataset comprised 274 sampling events from 2000 to 2017 throughout the JRBD.

1 Table 1 – List of native, translocated and alien fish species with the respective life-history strategy (opportunistic, periodic or equilibrium) and main references.

Family Name	Scientific Name	Common Name	Native	Translocated	Alien	Opportunistic	Periodic	Equilibrium	Citation(s)
Anguillidae	<i>Anguilla Anguilla</i> (Linnaeus 1758)	European eel	X					X	Fernández-Delgado <i>et al.</i> , 1989
Bleniidae	<i>Salaria fluviatilis</i> (Asso 1801)	Freshwater blenny	X			X			Vinyoles & De Sostoa, 2007
Centrarchidae	<i>Lepomis gibbosus</i> (Linnaeus 1758)	Pumpkinseed			X			X	Gutiérrez-Estrada <i>et al.</i> , 2000; Vila-Gispert & Moreno-Amich, 2000
	<i>Micropterus salmoides</i> (Lacépède 1802)	Largemouth bass			X			X	Rodríguez-Sánchez <i>et al.</i> , 2009
Cobitidae	<i>Cobitis paludica</i> (de Buen 1930)	Southern Iberian spined-loach	X			X			Soriguer <i>et al.</i> , 2000
Cyprinidae	<i>Achondrostoma arcasii</i> (Steindachner 1866)	Bermejuela	X			X			Rincon & Lobon-Cervia, 1989
	<i>Alburnus alburnus</i> (Linnaeus 1758)	Common bleak			X	X			Almeida <i>et al.</i> , 2014
	<i>Barbus haasi</i> (Mertens 1925)	Iberian redfin barbel	X				X		Aparicio & de Sostoa, 1998
	<i>Carassius auratus</i> (Linnaeus 1758)	Goldfish			X			X	Ribeiro <i>et al.</i> , 2008
	<i>Cyprinus carpio</i> (Linnaeus 1758)	Common carp			X			X	Fernández-Delgado, 1990
	<i>Gobio lozanoi</i> (Doadrio & Madeira 2004)	Pyrenean gudgeon				X			Lobon-Cervia, Montañes & Sostoa, 1991
	<i>Luciobarbus graellsii</i> (Steindachner 1866)	Ebro barbel			X		X		Doadrio <i>et al.</i> , 2011; Oliva-Paterna <i>et al.</i> , 2007
	<i>Luciobarbus guiraonis</i> (Steindachner 1866)	Easter Iberian barbel	X				X		Doadrio <i>et al.</i> , 2011
	<i>Parachondrostoma arrigonis</i> (Steindachner 1866)	Júcar nase	X			X			Doadrio <i>et al.</i> , 2011
	<i>Parachondrostoma turiense</i> (Elvira 1987)	Turia nase	X			X			Doadrio <i>et al.</i> , 2011

Family Name	Scientific Name	Common Name	Native	Translocated	Alien	Opportunistic	Periodic	Equilibrium	Citation(s)
	<i>Pseudochondrostoma polylepis</i> (Steindachner 1864)	Iberian straight- mouth nase		X		X			Doadrio <i>et al.</i> , 2011; Granado Lorenzo, Guillen Hortal & Cuadrado Gutierrez, 1985
	<i>Squalius alburnoides</i> (Steindachner 1866)	Calandino		X		X			Doadrio & Carmona, 2006; Herrera & Fernández-Delgado, 1994
	<i>Squalius valentinus</i> (Doadrio & Carmona 2006)	Easter Iberian chub	X			X			Doadrio & Carmona, 2006; Alcaraz-Hernández <i>et al.</i> , 2015
Esocidae	<i>Esox lucius</i> (Linnaeus 1758)	Northern pike			X			X	Vila-Gispert & Moreno-Amich, 2002; Doadrio <i>et al.</i> , 2011
Percidae	<i>Sander lucioperca</i> (Linnaeus 1758)	Zander			X			X	Vila-Gispert, Alcaraz & García-Berthou, 2005; Doadrio <i>et al.</i> , 2011
Poeciliidae	<i>Gambusia holbrooki</i> (Girard 1859)	Eastern mosquitofish			X	X			Vargas & De Sostoa, 1996; Fernández-Delgado, 1989
Salmonidae	<i>Oncorhynchus mykiss</i> (Walbaum 1792)	Rainbow trout			X		X		Doadrio <i>et al.</i> , 2011
	<i>Salmo trutta</i> (Linnaeus 1758)	Brown trout	X				X		Nicola & Almodóvar, 2002
Valenciidae	<i>Valencia hispanica</i> (Valenciennes 1846)	Samaruc	X			X			Doadrio <i>et al.</i> , 2011

## 3 2.2 Hydrological characterization

4 Within the study area 33 gauging sites (i.e. station or dam) that recorded daily discharge  
5 were selected, for each of them, a benchmark period of 20 years (1997–2017) of data was set for  
6 river flow analyses. This 20-year period was considered sufficient to reflect the range of flow  
7 conditions experienced by biological communities, including extreme events (i.e. floods and  
8 droughts) (Laizé et al., 2013). To avoid any bias caused by differences in the cumulated basin areas  
9 during the process of classifying the river flow (Monk et al., 2006) daily discharge values from each  
10 gauging site were transformed to z-scores  $N(0, 1)$ .

11 Following previous studies (Poff and Zimmerman, 2010), 48 hydrological indicators that: (i)  
12 collectively describe the full range of natural hydrologic variability, including the magnitude,  
13 frequency, duration and timing of flow events (Mathews and Richter, 2007; Olden and Poff, 2003;  
14 Poff et al., 1997; Richter et al., 1996), (ii) are ecologically relevant and can be extrapolated from  
15 ecological principles (Arthington et al., 2006; Monk et al., 2007) and (iii) are amenable to  
16 management, were selected (see Table 2). Among them, 12 indicators are representative of average  
17 monthly conditions (1-12, Table 2), 10 represent the magnitude and duration of annual minima and  
18 maxima (13-22, Table 2), and two the timing of minima and maxima (23 & 24, Table 2). Each of those  
19 indicators were independently evaluated for each of the two antecedent years; the monthly average  
20 data of the month when the sampling took place were excluded, and for all the other indicators one  
21 year of data up to the day (or one year and one day) before the sampling was considered.

22 Before the analyses, the hydrological indicators underwent a unit-based standardization  
23 ( $X' = (X - X_{min}/X_{max} - X_{min}) + 0.01$ ) and outliers identified from Inter Quartile Range (IQR)  
24 values (defined as observations that fall below  $Q1 - 1.5 \times IQR$  or above  $Q3 + 1.5 \times IQR$ ) were  
25 removed. Hydrological indicators with heavily skewed distributions (visualized from inspection of

26 histograms) and few unique values (<20) were also excluded from the analyses. Finally, the  
27 hydrological indicators describing the antecedent hydrological conditions derived from the  
28 standardised daily historic discharges (z-scores) were paired to the 25 fish community metrics  
29 described in section 2.1.

30 Table 2 – Hydrological Indicators used to characterise the hydrology in the Jucar River Basin District (JRBD).  
 31 The table indicates which indicators were evaluated with Quantile Regression (QR), for the first (year before  
 32 sampling) and second antecedent year to the fish sampling.

Number	Used in QR	Q group	Q index	Description (units: z-score)
1	Yes	Winter Months	QDec	Average December discharge
2	Yes		QJan	Average January discharge
3	Yes		QFeb	Average February discharge
4	Yes	Spring Months	QMar	Average March discharge
5	Yes		QApr	Average April discharge
6	Yes		QMay	Average May discharge
7	Yes	Summer Months	QJun	Average June discharge
8	Yes		QJul	Average July discharge
9	Yes		QAug	Average August discharge
10	Yes	Fall Months	QSep	Average September discharge
11	Yes		QOct	Average October discharge
12	Yes		QNov	Average November discharge
13	Yes	Annual Minima	Q1Min	Minimum 1-day average discharge
14	Yes		Q3Min	Minimum 3-day average discharge
15	Yes		Q7Min	Minimum 7-day average discharge
16	Yes		Q30Min	Minimum 30-day average discharge
17	Yes		Q90Min	Minimum 90-day average discharge
18	Yes	Annual Maxima	Q1Max	Maximum 1-day average discharge
19	Yes		Q3Max	Maximum 3-day average discharge
20	Yes		Q7Max	Maximum 7-day average discharge
21	Yes		Q30Max	Maximum 30-day average discharge
22	Yes		Q90Max	Maximum 90-day average discharge
23	Yes	Timing Extreme	QJulianMin	Julian date of minimum discharge
24	Yes	Events	QJulianMax	Julian date of maximum discharge
25	No	Frequency and duration of high and low pulses	QLPC	Number of daily flow events <Q75
26	No		QLPD	Average number of days flow events <Q75
27	No		QHPC	Number of daily flow events >Q75
28	No		QHPC	Average number of days flow events >Q25
29	No	Rate and frequency of water condition changes	QnoRises	Number of consecutive days flows increased
30	No		QRR	Average rate of flow increases on consecutive days
31	No		QnoFalls	Number of consecutive days flows decreased
32	No		QFR	Average rate of flow decreases on consecutive days

33

## 34 **2.3 Fish community and hydrological data exploration**

35 Fish community composition —taking into account the three life-history strategies and the  
36 three species origins, as well as brown and rainbow trout (*i.e. S. trutta and O. mykiss*)— and the  
37 hydrological indicators were explored with Self and Super-Self Organizing Maps (*i.e. SOM and Super-*  
38 *SOM*), respectively for the fish community groups and the hydrological indicators. The SOMs  
39 (Kohonen, 1982) are a type of artificial neural network used for dimensionality reduction and data  
40 exploration that demonstrated proficient to carry out a number of studies involving fish and  
41 macroinvertebrates assemblages, as well as hydrological data (Kalteh et al., 2008; Tsai et al., 2017;  
42 Zhang et al., 2018). SOM and Super-SOM (*i.e. multi-layered SOM*) rely in the development and  
43 ordination of a series of prototypes (unit neurons) that minimize their distance to the training  
44 samples (in this case the CPUEs of fish community groups and hydrological indicators). The resulting  
45 unit neurons or prototypes are usually ordinated onto a bi-dimensional map and the optimizing of  
46 the SOM is conducted so that the unit neurons that are located near to each other in the map have  
47 similar associated input samples (Zhang et al., 2018). The input samples are assigned to the closest  
48 unit neuron. Therefore, after the optimisation, the resulting map can be used to inspect the  
49 existence of distribution patterns and gradients within the simplified version of the input dataset —  
50 and hence within the training dataset — or to cluster the unit neurons to relate the resulting groups  
51 with additional features.

52 The development and visualization of the SOMs was performed using the functionalities  
53 implemented within the *R* package *kohonen* (Wehrens and Kruisselbrink, 2018), while the  
54 parameters selection followed the methods described in Zhang et al. (2018). Thus, input samples  
55 were properly standardised prior to developing the SOMs and a hexagonal lattice was selected. The  
56 dimensions of the map (number of neurons in X and Y) were those that simultaneously minimised

57 the quantization and topographic errors (Zhang et al., 2018). For both SOMs the number of unit  
58 neurons for each dimension varied between 2 and 20. However, whilst the SOM applied to the  
59 CPUEs of the fish community had a single layer, the SOM for the hydrological indicators involved  
60 two different layers to accommodate the different groups of indicators (i.e. Super-SOM). The first  
61 layer included the unit neurons that prototyped the flow regime (indicators 1-12 in Table 2) whereas  
62 the second layer included those that prototyped the remained indicators (indicators 13-24 in Table  
63 2).

64 Once the optimal dimensions of the (Super-)SOMs were determined, the resulting maps  
65 were plotted to inspect distribution patterns among input variables and the Ward linkage method  
66 was used on the distances between the prototypes of the (Super-)SOMs to cluster the unit neurons  
67 and, consequently, the input sample data (Tsai et al., 2017; Zhang et al., 2018). The function *NbClust*  
68 included in the homonymous *R* package (Charrad et al., 2014) was used to determine the optimal  
69 number of clusters (Zhang et al., 2018). Finally, the resulting clusters were used to inspect spatial  
70 and temporal differences among groups.

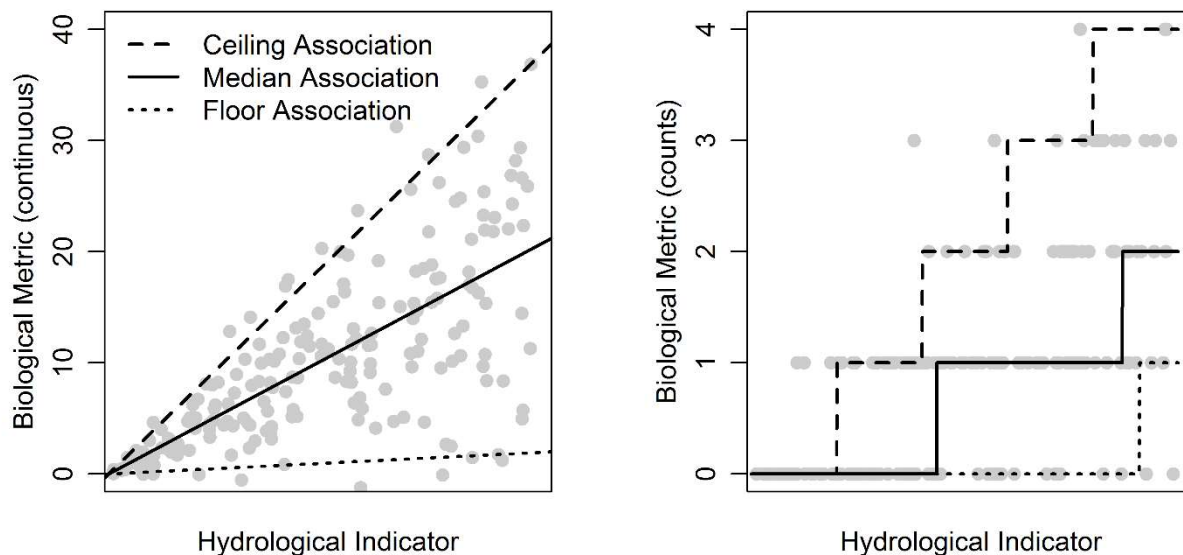
71

## 72 **2.4 Community responses to hydrological indicators**

73 In the context of quantile regression, the significant associations between the hydrologic  
74 indicators and fish metrics can be defined either as median or as limiting (upper and lower),  
75 depending on the tested quantiles. Significant associations across multiple quantiles groups indicate  
76 that a hydrologic indicator is an important predictor of that metric. The limiting associations in which  
77 only the upper or lower quantiles groups are significant correspond to hydrologic indicators acting  
78 as “ceilings” and/or “floors” (Konrad et al., 2008). That means those hydrological indicators



79 constrain the fish metric, although other ecological factors (*e.g.* food availability or presence of alien  
80 species) likely play an additional role and cause the observed spread on the data (Figure 2).



81

82 Figure 2 - Conceptual representation of the use of quantile regression to show the median and limiting  
83 actions of hydrological indicators on continuous (left) and discrete (right) biological metrics.

84 Ceiling, median and floor associations were examined using a series of quantile regressions  
85 (QRs) and quantile mixed-effect regression (QRMs), to account for potential spatial autocorrelation  
86 between samples. To do so, a suite of statistical models ( $n = 12$ , see Table 3) were created for each  
87 combination of fish metric and hydrological indicator and were compared with the corresponding  
88 null models ( $n = 3$ , see Table 3). Each hydrological indicator was modelled via 4 statistical functions  
89 (linear, exponential, logarithmic and quadratic) in separate models to account for both linear and  
90 non-linear ecological responses to hydrological influences (see Rosenfeld, 2017). Moreover, three  
91 model structures were used to account for potential spatial autocorrelation among samples  
92 collected in the same river sector. Therefore, for each model shape, the QR model did not account  
93 for the spatial autocorrelation among samples (*i.e.* with no variable for river sector), the QR model  
94 accounted for the non-independence of the sampling sites as a different intercept for each river

95 sector (i.e. the fixed effects of 15 river sectors) and, finally, the QRM models accounted for the non-  
96 independence of the sampling sites as the variation among river sectors (i.e. river sector as random  
97 effect). The QRMs involved subject-specific random intercepts which is analogous to the random  
98 intercepts described for standard linear mixed-effect models (Bolker et al., 2009; Fornaroli et al.,  
99 2015).

100 Comparisons with null models were used to assess the performance of hydrological  
101 indicators as predictors, similarly to a likelihood ratio test; for each model structure a null model  
102 was created and consisted of a constant model (i.e. with no hydrologic indicator) with the same  
103 variance structure described above. The different models were implemented using the *lqm* and  
104 *lqmm* functions (respectively for QRs and QRMs) within the '*lqmm*' package (Geraci, 2014; Geraci  
105 and Bottai, 2014). Such regressions were performed across various quantiles (from 0.05 to 0.95 in  
106 0.05 increments) to test responses of fish metrics across a range of data values. Akaike weights ( $w_i$   
107 - derived from corrected Akaike Information Criteria values) were calculated and averaged across  
108 all quantiles constructed for each QR and QRM (see Fornaroli et al., 2019). Subsequently, for each  
109 community response metric, each hydrological indicator was paired to the optimal function (the QR  
110 or QRM exhibiting the highest average  $w_i$  value).

111 Table 3 – Formulas of statistical models underpinning the quantile regression (QR) and quantile mixed-effect  
 112 regression (QRM) models constructed.  $x$  denotes the hydrological indicator; random effects within QRMs are  
 113 denoted by '1|'. Null models (those not comprising a hydrological metric) are highlighted in grey.

Number	Model type	Statistical function	Rivers Effect	Function
1	QR	-	None	$y = a$
2	QR	-	Fixed	$y = a + (b \times \text{River})$
3	QRM	-	Random	$y = a + (1   \text{River})$
4	QR	Linear	None	$y = a + (b \times x)$
5	QR	Exponential	None	$y = a + (b \times \exp(x))$
6	QR	Logarithmic	None	$y = a + (b \times \log_{10}(x))$
7	QR	Quadratic	None	$y = a + (b \times (x)) + (c \times (x^2))$
8	QR	Linear	Fixed	$y = a + (b \times x) + (c \times \text{River})$
9	QR	Exponential	Fixed	$y = a + (b \times \exp(x)) + (c \times \text{River})$
10	QR	Logarithmic	Fixed	$y = a + (b \times \log_{10}(x)) + (c \times \text{River})$
11	QR	Quadratic	Fixed	$y = a + (b \times (x)) + (c \times (x^2)) + (d \times \text{River})$
12	QRM	Linear	Random	$y = a + (b \times x) + (1   \text{River})$
13	QRM	Exponential	Random	$y = a + (b \times \exp(x)) + (1   \text{River})$
14	QRM	Logarithmic	Random	$y = a + (b \times \log_{10}(x)) + (1   \text{River})$
15	QRM	Quadratic	Random	$y = a + (b \times (x)) + (c \times (x^2)) + (1   \text{River})$

114

115 The optimal model for each combination of community response metrics and hydrological  
 116 indicators was subsequently analysed for three sets of quantiles (0.02-0.10, 0.45-0.55, 0.90-0.98 all  
 117 with 0.01 step width) respectively representative of “floor”, “median” and “ceiling” action. The  
 118 choice of quantiles represents an arbitrary selection both in terms of the number of quantiles and  
 119 the position of quantiles throughout the distribution. It is likely that the chance of a Type I error  
 120 increases with the number of quantiles tested. We calculated the averaged  $w_i$  across each set of  
 121 quantiles to explore a range of quantiles throughout the distribution whilst limiting the probability  
 122 of Type I error. The range of reliable extreme quantile estimates is ultimately limited by the sample  
 123 size ( $n$ ). For our study, we used the guidelines of  $n > 5/q$  and  $n < 5/(1 - q)$ , where  $q$  is the  
 124 quantile proposed by Rogers (1992) to determine the limits of reliable extreme quantiles. The  
 125 average  $w_i$  of qualifying models were then separately compared against null models (Table 3) for

126 each set of quantiles, with significant models being considered as those with an average  $w_i$  value  
127 greater than 0.999 ( $w_i$  of null model  $< 0.001$ ).

128 For count metrics (those representative of species richness), the statistical procedure used  
129 in the QR and QRM approach described above was applied to quantile count models, after Cade &  
130 Dong (2008). In this case however, it is necessary to transform the count metric by adding a random  
131 uniform number in the interval 0-1, ( $Y' = (Y + U[0,1])$ ). The QRs and QRMs were then  
132 implemented using the same procedure as described above, although each QR and QRM was  
133 estimated  $m = 500$  times using  $m$  random samples from  $U[0,1)$ . The estimated coefficients were  
134 averaged to remove the source of additional variation introduced by adding random numbers to  $Y$   
135 (see Machado & Silva, 2005; Cade & Dong, 2008).

136

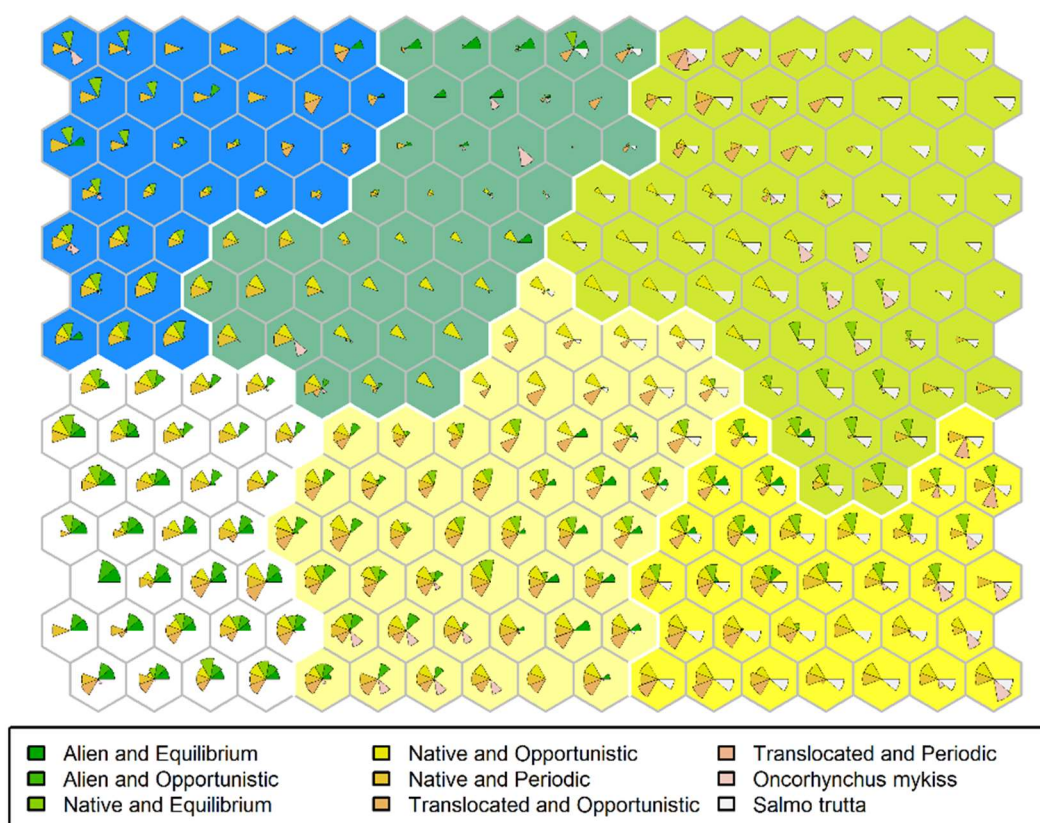
## 137 **3 Results**

### 138 **3.1 Fish community and hydrological data exploration**

#### 139 *3.1.1 Fish community*

140 The Self-Organising Map (SOM) identified six clusters according to their species composition,  
141 origin and life-history strategy (Figure 3). Cluster 1 (Figure 3 – bottom left) included samples with  
142 abundant alien species (equilibrium and opportunistic) and, to a lesser extent, samples with  
143 abundant native (opportunistic and periodic) and translocated species (opportunistic). Cluster 2  
144 (bottom centre) included those samples with abundant native species of any kind, which cohabit  
145 with translocated (opportunistic) species. Cluster 3 (bottom right) encompassed the samples with  
146 abundant native species that coexist with brown trout and, occasionally, with rainbow trout. Cluster  
147 4 (top right) includes the samples where brown trout dominates fish assemblages, although it also

148 includes samples where the rainbow trout or translocated (opportunistic) species are present.  
 149 Cluster 5 (top centre) encompasses samples with low CPUEs, although among them that including  
 150 native (opportunistic and periodic) and alien equilibrium were preponderant. Finally, Cluster 6 (top  
 151 left) involved samples with moderate values of CPUE for the native groups of species, although the  
 152 values of the CPUE of the native equilibrium and periodic were relatively higher.



153  
 154 Figure 3 – Self-Organising Map (SOM) obtained for the fish community composition (Captures Per Unit Effort  
 155 - CPUEs) taking into account the three life-history strategies (Equilibrium, Opportunistic and Periodic) and  
 156 the three species origins (Native, Alien and Translocated). The SOM was trained considering the brown and  
 157 rainbow trout (*Salmo trutta* and *Oncorhynchus mykiss*) separately.

158  
 159 The different clusters defined by the SOM did not show any temporal patterns, although the  
 160 samples included in cluster 4 and 5 (top right and top centre, respectively) were slightly more

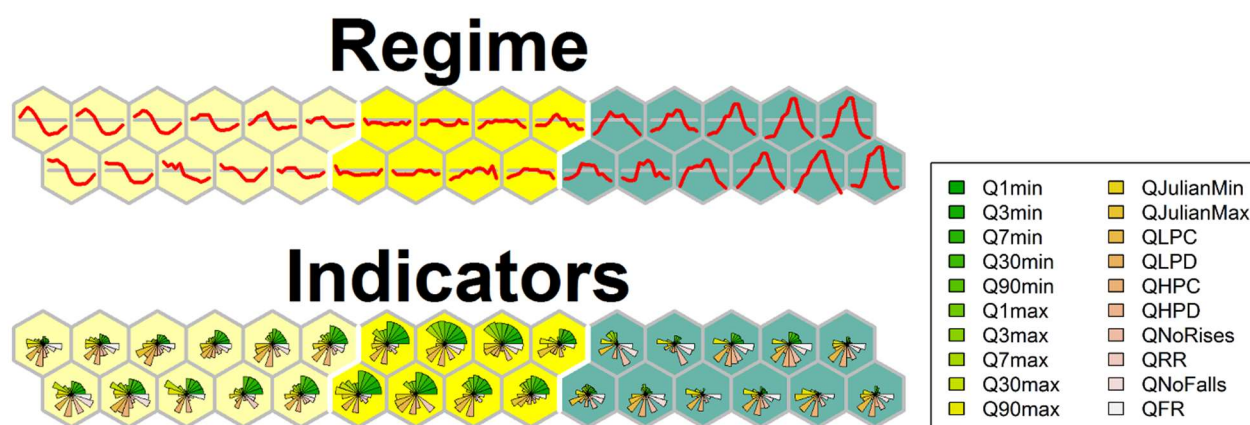
161 contemporary than those included in the remaining clusters (see Figure S1 left). Conversely,  
162 regarding the geographic position of the clusters, marked differences existed. Cluster 1, which  
163 comprises sampling sites where alien species dominate, involved southeaster samples (Figure 5),  
164 which coincides with the sampled lowland river segments. Cluster 3, which included the samples  
165 with abundant native species and brown trout, mainly corresponded with sampling sites located  
166 north- and westwards, which coincides geographically with the upper segments of the most well  
167 conserved rivers of the JRBD. Cluster 4, which included the sampling sites where both salmonids  
168 coexist with translocated (opportunistic) species, are located in the northern- and western-most  
169 sampling sites. Finally, clusters, 2, 5 and 6 involved samples located at intermediate latitudes and  
170 longitudes (Figure S1).

### 171 3.1.2 *Hydrological characterization*

172 The Super-Self-Organising Map (Super-SOM) identified 3 clusters according to the flow  
173 regime and hydrological indicators (Figure 4). These were based on a clear gradient from gauging  
174 sites with inverted flow regime, which present the maxima in summer and minima in winter (Cluster  
175 1 - top left), to sites with natural flow regime where maxima occur in winter/spring and minima in  
176 summer (Cluster 3 - top right). In intermediate position the Super-SOM ordinated the gauging sites  
177 with no marked seasonal differences (Cluster 2- top centre). Regarding the remaining hydrological  
178 indicators (in layer 2, Figure 4 bottom) their distribution patterns matched the gradients observed  
179 in the top layer (Regime, Figure 4 top). Therefore, cluster 1 (bottom left) was characterised by higher  
180 values of the number of daily flow events below  $Q_{75}$  (QLPC), average number of days with flow  
181 events above  $Q_{25}$  (QHPC), average rate of flow decreases on consecutive days (QFR), and number of  
182 consecutive days with no flow decreases (QNoFalls). Cluster 2 (top and bottom centre) did not  
183 included gauging sites with marked difference across the flow regime. Therefore, it encompassed

184 sites with relatively high values of the indicators characterising the minima. Finally, Cluster 3  
 185 encompassed gauging sites with a varied mixture of indicators without a clear pattern of  
 186 preponderant indicators, which is coherent with the variability expected in Mediterranean natural  
 187 flow regimes.

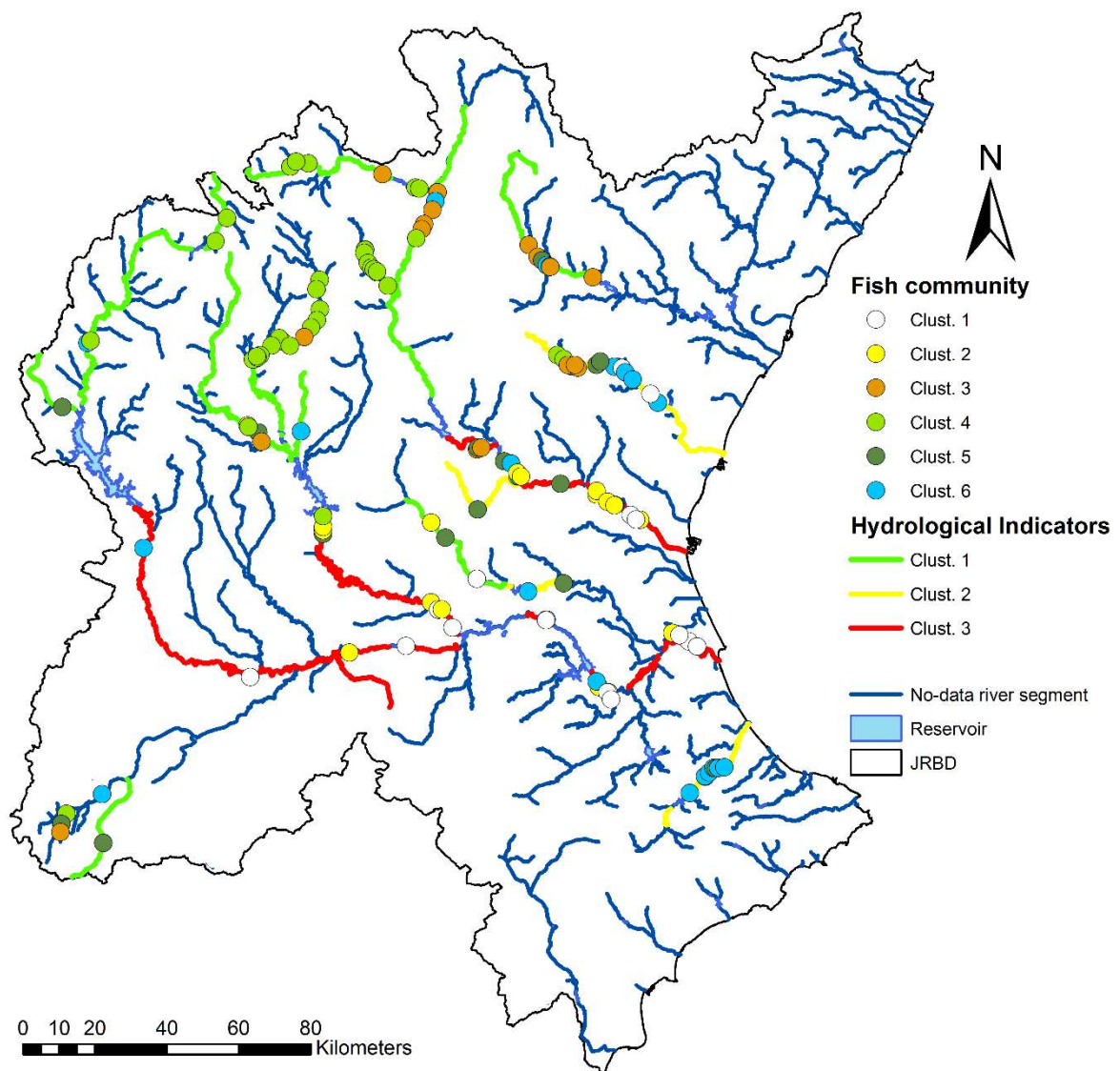
188 The different clusters defined by the Super-SOM showed a clear spatial pattern (Figure 5, Figure S2).  
 189 Cluster 1 involved gauging sites located north- and westwards, corresponding with the upstream  
 190 segments of the target rivers, while Cluster 3 involved southeaster samples, i.e. the lowland river  
 191 segments.



192

193 Figure 4 - Super-Self-Organising Map (Super-SOM) obtained considering two groups of hydrological indicators  
 194 separately. Layer 1 (top) prototyped the flow regime (indicators 1-12 in Table 2) whereas layer 2 (bottom)  
 195 prototyped the remaining indicators (indicators 13-24 in Table 2). See Table 2 for a complete description of  
 196 the hydrological indicators.

197



198  
 199 Figure 5 – Map of the Jucar River Basin District (JRBD) displaying the clusters defined with a Self-Organising  
 200 Map (SOM) of the fish community composition and hydrological indicators.

201

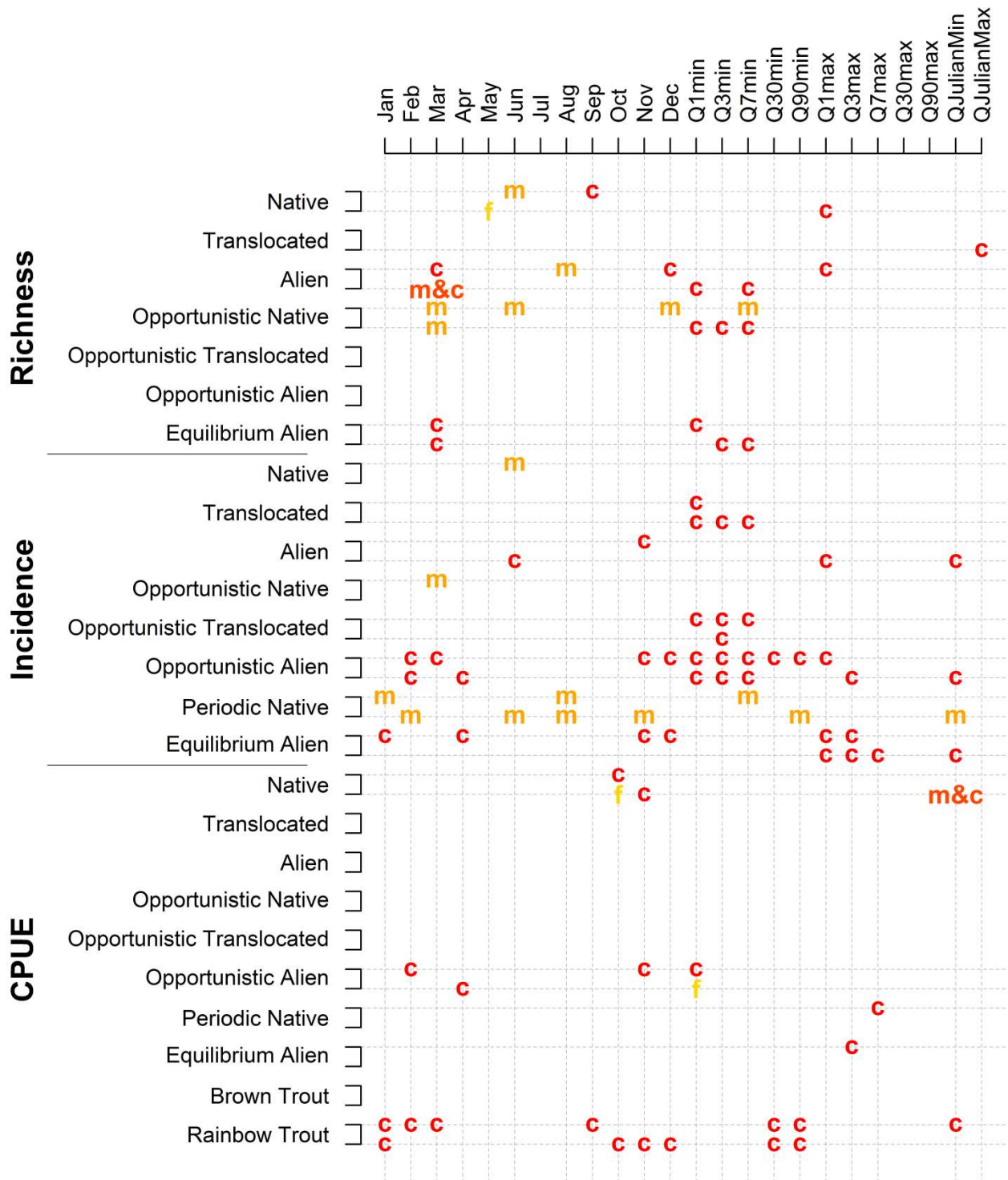
202 **3.2 Relationships among hydrological indicators and fish community**  
 203 **characteristics**

204 Amongst 102 significant relationships identified by the quantile regression analyses, 77%  
 205 represent ceiling relationships, 20% represent median relationships, and 3% are floor relationships



206 (Figure S3); only in two cases the same association was identified for different sets of quantiles.  
207 Most of the selected models did not include any effect of river sector (81%), although its addition  
208 to the models was often better represented by a random effect (18%) rather than a fixed effect  
209 (1%). We accounted for non-linearity in the relationships (see Table 3); thus the logarithmic shape  
210 was selected in 63% of the instances, the linear in 19%, quadratic in 12% and the exponential in 6%.

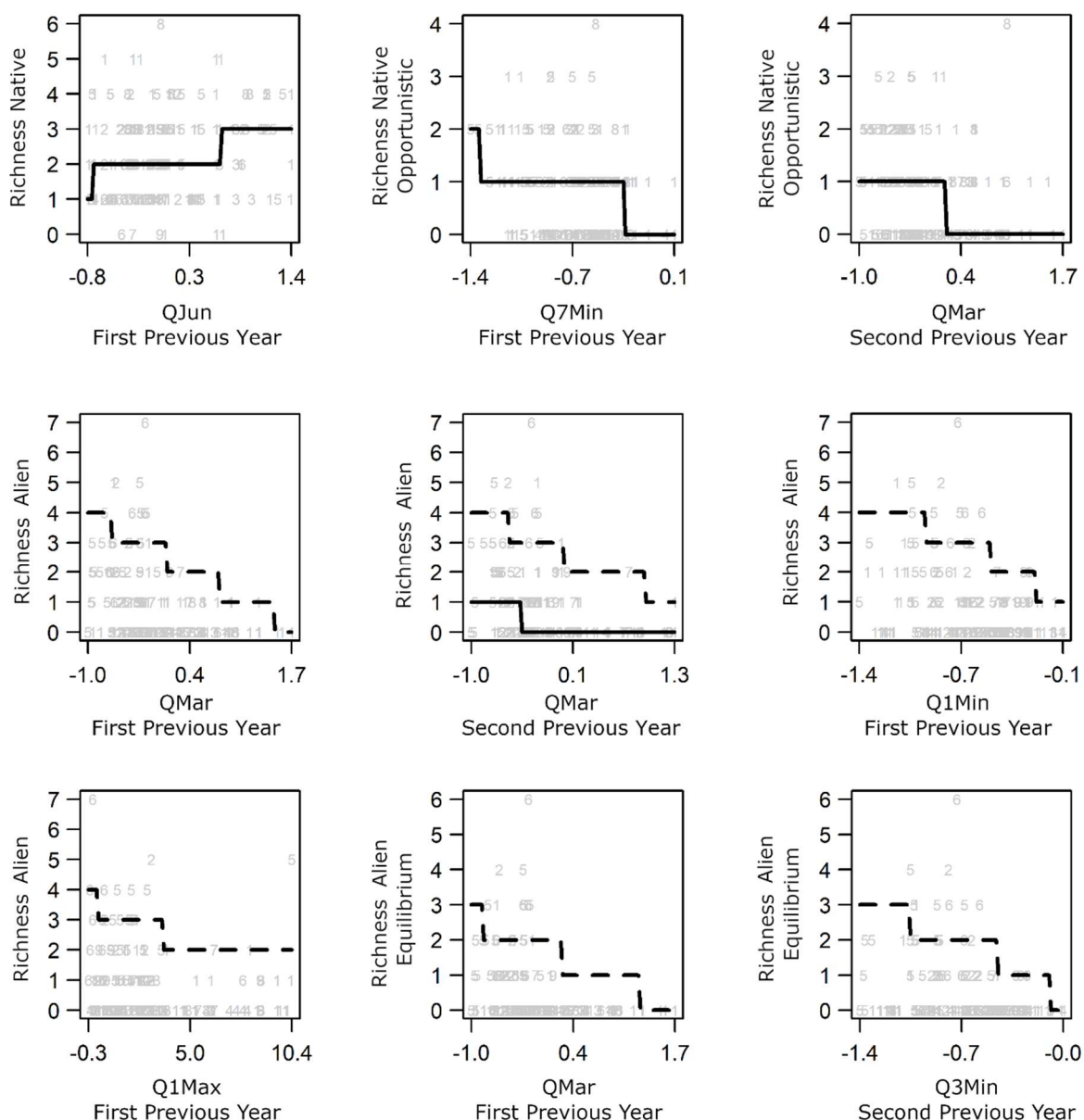
211 First and second antecedent hydrological years (one year before sampling and two years  
212 before, respectively) were associated with fish community metrics with similar performance ( $n =$   
213 100; first, 49%; second, 51%) and within a coherent pattern because the same hydrological indicator  
214 evaluated for the two years showed similar associations (e.g. positive or negative effect) with the  
215 same biological metric (see Figures 5 to 7). Metrics related to richness, ratio (proportion) and CPUE  
216 of alien species showed the higher proportion of significant associations in comparison with the  
217 native and translocated ones (native, 6.5%; translocated, 3.1%; alien, 13.1%). Looking at each  
218 combination of origin and life-history strategy group, the native and periodic showed 10.4% of  
219 significant relationships, the native and opportunistic 6.3% and no significant relationships were  
220 identified for brown trout. Amongst the alien species, rainbow trout showed the greatest proportion  
221 of significant associations with hydrological indicators (27.1%), followed by the other two groups of  
222 alien species; alien and opportunistic (16.0%) and alien and equilibrium (11.1%). The group of  
223 translocated and opportunistic was less influenced by antecedent hydrological conditions (2.8%).  
224 The hydrological indicators describing the annual minima, magnitude and duration, were more  
225 often associated with fish community characteristics than others (Figure S3-H).



226  
 227 Figure 6 – Summary of the quantile regression models. Yellow, orange and red colour denote significant ( $w_i$   
 228  $> 0.999$ ) floor (f), median (m) and ceiling (c) association, respectively. Two lines for each fish community  
 229 metric refer to the first antecedent year (top line) and second antecedent year (i.e., two years before, bottom  
 230 line).

231

232 Figures 7 and 8 show a selection of quantile regression models that considered the range of  
 233 the effect of the hydrological indicator, the ecological significance of the association (e.g. positive  
 234 or negative effect) and the relevance to management (e.g. possibility of establishing specific flow  
 235 regulations), while the complete results are reported in Figures S4 – S6.



236  
 237 Figure 7 – Selection of quantile regression relationships between the hydrologic indicators (x-axis) and  
 238 species richness metrics (y-axis) with significant ( $w_i > 0.999$ ) regression lines (solid and dashed lines represent  
 239 median and ceiling associations, respectively). The plots for all the selected models are in Figure S4; this

240 selection of plots (among the significant models) considered the range of the effect of the hydrological  
241 indicator, the ecological significance and the relevance to management.

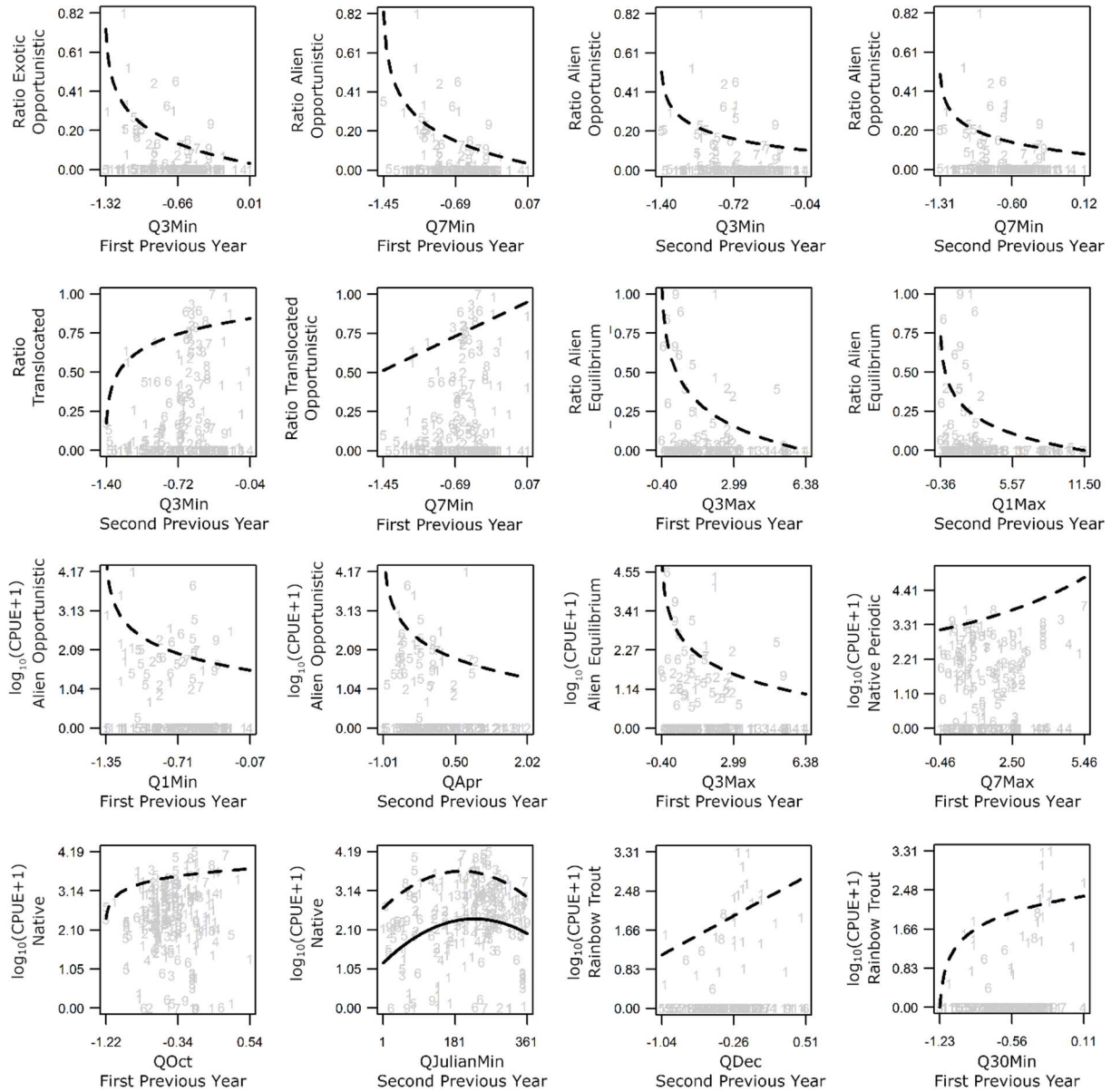
242 Native species richness was positively influenced by the average flow in June of the  
243 antecedent year (Figure 6). Moreover, the richness of native opportunistic species was positively  
244 associated with lower minimum flows and relatively low March flows. A wider range of positive  
245 response was generally observed in the alien species richness, in relation with March low flows and  
246 annual 1-day minima. In addition, the maximum number of alien species that can be expected where  
247 annual maxima are high (z-score > 5) was two times lower compared to sites with really small (z-  
248 score < 0) annual maxima. Coherent responses were specifically observed for alien equilibrium  
249 species.

250 The proportion of alien individuals showed strong association with some hydrological  
251 indicators (Figure 8); moreover, the different life-history strategies responded to different features  
252 of hydrological regime. Higher proportions of alien opportunistic fish (up to 80%) in the community,  
253 e.g. *Alburnus alburnus* and *Gambusia holbrooki* (see Table 1), were associated with lower annual  
254 minima; this pattern was consistent for different duration time and within years (Figure 7-8).  
255 Similarly, the abundance of this group (CPUE) was positively associated with lower April flow and  
256 lower annual minima. In addition, higher proportions (up to 100%) of alien equilibrium species (i.e.  
257 *L. gibbosus*, *M. salmoides*, *C. auratus*, *C. carpio*, *E. lucius* and *S. lucioperca*, see Table S1) were  
258 associated with lower spring flows and annual maxima; in this case the patterns are also coherent  
259 for different duration time (1, 3 and 7 days) and within years (first vs. second antecedent year). All  
260 the associations among the magnitude of annual maxima and proportion of equilibrium alien  
261 individuals were described by a logarithmic function; substantial increases of proportion of alien  
262 species are described for annual maxima below the 20-year annual average (Figure 8, negative  
263 values of x-axis). Similarly, there was a positive response in the abundance of alien fish with annual

264 maxima below the 20-year annual average. Higher proportions of translocated individuals were  
265 associated with relatively high annual minima of the antecedent years. It was also remarkable the  
266 positive response of the rainbow trout (in terms of CPUE) to some hydrological indicators, namely,  
267 mean flow in December and magnitude of annual minima (Figures 8, S6).

268         The CPUE of native species showed some relationships with antecedent hydrological  
269 conditions, specifically with higher annual maxima (7-day Max) and October flow. Concerning the  
270 timing, the median and maximum values of abundance increased where annual minima occur  
271 during summer or early fall (matching the general pattern of the natural flow regime). In addition,  
272 the CPUE of native species with periodic life-strategy that spawn during spring (*B. haasi* and *L.*  
273 *guiraoinis*, see Table S1) displayed a positive response to higher magnitudes of the annual maxima.  
274 With regard to the abundance of brown trout, no significant relations were found.

275         For the group of translocated species, the richness was associated only with the timing of  
276 high flows (Figure S4) because winter or early spring maxima triggered lower richness, whereas  
277 higher minimum flows relate with a higher ratio of the group (Figure 8).



278

279 Figure 8 – Selection of quantile regression relationships between the hydrologic indicators (x-axis) and fish  
 280 community metrics (y-axis) with significant ( $w_i > 0.999$ ) regression lines (solid and dashed lines represent  
 281 median and ceiling associations, respectively). The plots for all the selected models are in Figure S5 – S6; this  
 282 selection of plots (among the significant models) considered the range of the effect of the hydrological  
 283 indicator, the ecological significance and the relevance to management.

284

## 285 **4 Discussion**

286 In this work robust flow-ecology relationships have been identified, most of the significant  
287 relationships described a limiting (ceiling) effect of the analysed hydrological indicators, confirming  
288 that antecedent hydrological conditions are one of the limiting factors that constrain fish  
289 community, although other biotic or abiotic factors further impact species abundance causing the  
290 observed spread on the modelled data.

291 Based on the results obtained with the (Super-)SOMs, the Jucar River Basin District (JRBD)  
292 can be considered a paradigmatic example of the typical spatial distribution of native, translocated  
293 and alien (invasive) species and hydrological alteration in the Iberian Peninsula. In this territory,  
294 native fish communities are increasingly being cornered to the upper part of stream networks —  
295 being isolated from one to another by impermeable barriers (Alcaraz et al., 2014; Aparicio et al.,  
296 2000)— while alien species proliferate in the lowland rivers segments favoured by flow regime  
297 homogenization and morphological alteration (Muñoz-Mas et al., 2016a). Although habitat  
298 fragmentation distorts a little this general pattern (Muñoz-Mas et al., 2017), it can be concluded  
299 that the guidelines resulting from this study should be transferable to other Mediterranean basins  
300 and districts of the Iberian Peninsula.

301 Our results on quantile regression indicated that native species proved to be well adapted  
302 to the naturally variable and stochastic flow regime of Mediterranean rivers. The native populations  
303 inhabit a wide range of geographical conditions with community characteristics varying from  
304 richness 1 to 6 and a range of CPUE that span over 4<sup>th</sup> order of magnitude. At some extent, our  
305 results indicate the large resilience of the populations, given that our data cover five river basins  
306 and 18 years of biological data. Such capacity for adaptation is reflected in the fact that only few  
307 (6.5 %) significant associations were detected despite the many hypotheses tested (432).

308 Conceivably, other factors such as hydromorphology, water chemistry, biogeographical region, river  
309 size, or inhomogeneity between surveys could mask some existing relationships between  
310 antecedent hydrologic conditions and response of fish community. For instance, previous studies in  
311 the JRBD indicated that the distance between smaller barriers control native species richness  
312 (Olaya-Marín et al., 2012) while the density of the Eastern Iberian barbel (*L. guirao*) was related  
313 to the flow variability, proportion of alien fish species and flow minima (Olaya-Marín et al., 2016).  
314 Nonetheless, the general response to the timing of the minimum annual flow (QJulianMin) indicates  
315 the relevance of considering not only the magnitude but the month when the minimum  
316 environmental flows are implemented. This is crucial in Mediterranean regulated rivers where there  
317 is an inversion of the intra-annual variability pattern with summer maxima and winter minima  
318 (Aparicio et al., 2011). Furthermore, as most of the significant relationships identify ceiling  
319 associations and not median ones, our results point that the implementation of environmental flows  
320 requires further improvements (*e.g.* river connectivity) to be effective. Our results suggest that the  
321 positive effect of managing low and high flows may be greatly influenced by other factors (that mask  
322 the median but not the limiting response) controlling river habitat and hydraulics at smaller scales,  
323 *e.g.* presence of barriers and impaired connectivity. On the contrary, a positive relationship was  
324 found between the maximum abundance of native-periodic species (Iberian redfin barbel and Eastern  
325 Iberian barbel) and the magnitude of annual maxima (ceiling relationship, Figure 6). Other studies  
326 support this result showing a lack of disruptive effects on the number and CPUE of native fish  
327 following severe floods (Marchetti and Moyle, 2001; Pires et al., 2008). More specifically, different  
328 studies demonstrated that artificial river regulation has a strong influence on recruitment (Copp,  
329 1990; Konečná et al., 2009); therefore, the specific role of spring flows during the cyprinids spawning  
330 and larva development deserve a special attention in further studies.



331 The causes of the poor association between the translocated species and the antecedent  
332 hydrological conditions may be twofold. On the one hand, those species have been moved from  
333 Iberian river basins; they are therefore acclimatised to the natural flow regime of these unregulated  
334 recipient river segments. On the other hand, the most successful species of this group often have  
335 characteristics typical of invasive species, which allowed them to colonise regulated river segments  
336 as foreign alien species did (Muñoz-Mas et al., 2016a). Consequently, water administration should  
337 be particularly diligent to avoid further translocations as they often proved to be perfectly fitted to  
338 occupy Iberian river segments of any type (Alcaraz et al., 2014; Muñoz-Mas et al., 2016a).

339 From a management perspective, one of the most innovative results is the strong association  
340 among antecedent flow condition and the success of alien species. In summary, opportunistic alien  
341 species (e.g. common bleak and eastern mosquitofish), proved to be favoured by lower annual  
342 minima, and equilibrium alien (e.g. pumpkinseed or northern pike) are favoured by smaller annual  
343 maxima.

344 Opportunistic species such as common bleak and eastern mosquitofish are aligned to *r*  
345 strategy with early maturation and low juvenile survivorship; juveniles can overcome very low  
346 annual minima with limited loss compared to other groups of species, thus benefitting of reduced  
347 competition for space and predation. Previous studies demonstrated how minimum flow, by  
348 reducing the available habitat and altering water temperature extremes, negatively affected a  
349 higher percentage of native fish species than aliens (e.g. Bernardo et al., 2003; Leuven et al., 2011).  
350 Equilibrium species are closely aligned with the *K* strategy and the juvenile survivorship is largely  
351 due to high parental care, high flows or flood events can be an important stressor that the juvenile  
352 cannot overcome (Bernardo et al., 2003). Displacement of alien fishes during high flow events has  
353 been already reported (e.g. Valdez et al., 2012), and high flow releases have been effectively  
354 employed to restore native fish species or assemblages in highly variable lotic ecosystems (e.g.

355 Kiernan et al., 2012). Our results with alien fish and the aforementioned positive relationship  
356 between native-periodic species and annual maxima confirm the potential role of high-flows and  
357 flushing flows in the implementation of environmental flows counteracting the presence of alien  
358 species as demonstrated in other Mediterranean regions (Scoppettone and Rissler, 1995).  
359 Moreover, the elimination of floods following impoundment was already identified as a driver that  
360 promotes the dominance of alien fishes (Muñoz-Mas et al., 2016a). The alien fish species present in  
361 the JRBD, especially these belonging to the equilibrium group, are adapted to aquatic ecosystems  
362 with different environmental conditions and have the higher performance in the lentic ecosystems  
363 of reservoirs. That confirms the importance of fully retaining specific process-based components of  
364 the hydrograph or functional flows to reduce their incidence, rather than attempting to mimic the  
365 full natural flow regime with lower magnitudes (Yarnell et al., 2015). Pires et al. (2008), suggest that  
366 the seasonal, and highly variable floods in Mediterranean rivers may be viewed as primary  
367 landscape filters that reduce the species pool to those possessing life-history and behavioural  
368 attributes to cope with high flows. This is supported by evidence that aliens are strongly affected by  
369 floods, probably because they are not evolutionarily adapted to the prevailing hydrological regime.

370           Consequently, although the Spanish environmental flow legislation can be considered more  
371 progressive than in other territories because it considers some hydrological analysis of the flow  
372 regime as well as physical habitat methods that consider specific biotic needs (Muñoz-Mas et al.,  
373 2016b), it can be considered incomplete regarding the consideration of flow-ecology responses  
374 from a holistic perspective, as well as concerning the management of alien (invasive) species,  
375 because it mainly focuses on the minimum environmental flow. The experiences concerning flow  
376 releases are scarce in the Iberian river basins and the reported results generally cover only  
377 morphological aspects, although the benefits of considering high flows during the process of  
378 environmental flow determination has been highlighted in renowned studies (Arthington et al.,

379 2006). Nevertheless, given the interaction between species ecologies, morphologic characteristics  
380 and flow regimes (Turner and Stewardson, 2014), the finale magnitude of the higher flows should  
381 be calculated following additional approaches to avoid favouring any aspect of the alien species  
382 present. In this regard, habitat simulation and habitat time series should be great tools to investigate  
383 the critical periods in terms of habitat and the relations between hydraulic variables and juveniles  
384 development (De-Miguel-Gallo et al., 2019).

385         The CPUE of rainbow trout, contrary to brown trout's CPUE, showed a strong association  
386 with the flow conditions during the spawning season (higher flow is associated with higher CPUE)  
387 and with the magnitude of annual minima (higher minima are associated with higher CPUE)  
388 confirming that alien species can be more sensitive to antecedent hydrological condition than  
389 natives. However, contrary to what has been inferred from the results obtained for the alien species,  
390 it can be concluded that water managers would be in the wrong direction by promoting increases  
391 of low and high flows for native fish conservation as they could favour in a higher proportion the  
392 rainbow trout. Consequently, as it has been indicated for translocated species, water administration  
393 should be particularly diligent to avoid further introductions of this species, this should be combined  
394 with elimination programmes and detailed studies about population dynamics during the process  
395 of environmental flow assessment.

396         Environmental flow concept is already well known (Jowett, 1997), but not always  
397 implemented, and can be well applied to our results with a different perspective: benefit the native  
398 population disadvantaging the alien ones. To achieve this goal, environmental flows must be  
399 implemented and they must account for the complete hydrological regime (Poff et al., 2010; Poff  
400 and Schmidt, 2016), our results highlight that, in Mediterranean rivers, the management of annual  
401 maxima below large dams can be one of the key aspects of this framework. A suite of dam operation  
402 strategies that simultaneously meet both societal and environmental water needs underscored the

403 potential benefits provided by time-varying environmental flow rules. Ensuring human water  
404 security versus supporting ecosystems services via natural hydrology have long been considered  
405 conflicting objectives in water-resource management (Naiman et al., 2002), a perspective that has  
406 been reinforced by previous optimization studies (Chen and Olden, 2017; Haro et al., 2014; Shiau  
407 and Wu, 2013). Many multi-objective optimization studies have focused on balancing human water  
408 needs with the goal of releasing environmental flows to mimic specific aspects of a natural flow  
409 regime that solely benefit native fish species (Kiernan et al., 2012). By contrast, our results suggest  
410 that looking beyond the natural flow paradigm and considering the effects on native and alien  
411 species explicitly in the design of environmental flows can be very relevant to improve the ecological  
412 status of Mediterranean rivers.

413         The flow–ecology relationships provided in this study represents essential information for  
414 the application of holistic approaches of E-flows (e.g. BBM, King et al., 2008; ELOHA, Poff et al., 2010;  
415 Eco-engineering decision scaling, Poff et al., 2015) and can be incorporated along with a dam  
416 operation model into a multi-objective optimization framework (e.g. Paredes-Arquiola et al., 2014)  
417 that ensure human needs while benefiting populations of native fishes and inhibiting populations  
418 of alien fishes (Chen and Olden, 2017).

419         River ecosystem management based on empirical flow-ecology relationships can be  
420 particularly useful both to reduce ecological alterations and to maximise the environmental benefit  
421 of reducing anthropogenic exploitation of water resources (Gillespie et al., 2015), especially under  
422 the current climate change scenario (Palmer et al., 2008). Furthermore, it can be instrumental to  
423 support the development and implementation of regional environmental flow standards (Poff et al.,  
424 2010). This study highlighted the importance of avoiding new translocations and considering high  
425 flows in the process of environmental flow assessment. Consequently, we expect this study to  
426 promote further prevention programmes and the review of the actual legislation as well as the

427 implementation priorities, to account for high flows in order to properly manage the pervasive  
428 presence of alien fish species in Iberian rivers.

429

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