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Assessing the effects of irrigation and hydropower dams on river communities using taxonomic and multiple trait-based approaches

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A B S T R A C T

Rivers and streams have suffered multiple transformations to attend the increasing water demands worldwide. Among these, dams and reservoirs cause some of the most severe ecological impacts on rivers, altering the river flow and thermal regimens, nutrient and sediment fluxes, and network connectivity. However, in the context of the different dam purposes and operational schemes, knowledge of the ecological impacts on the riverine biota is still limited. In this study, our main goal was to assess dam-related effects (e.g. hydrological and thermal alteration, water quality changes) on river biological communities and identify key ecological responses associated to flow regulation. To achieve this, diatom, macroinvertebrate, and fish communities were surveyed in control ($n = 8$) and impacted ($n = 11$) streams (i.e. downstream of irrigation or hydropower dams) along three consecutive years. The study design aimed at minimising the environmental variability among control and impacts using previously established hydrological classifications. This allowed focusing primarily on the effects of dam operation schemes. In addition to traditional biotic indices based on the composition and structure of these communities, we assessed community-level responses using trait-based analyses with multivariate and fourth-corner analyses. The ecological changes varied with dam purpose and, in general, favoured disturbance-tolerant traits. Common biotic indices did not consistently respond to dam uses; trait-based analyses, in contrast, provided a more detailed picture of the dam-related effects on the studied river communities, with macroinvertebrate traits showing the strongest correlations to dam-related hydrological and physico-chemical variables, followed by diatoms and fish. Changes in the biological communities downstream of irrigation dams were mostly related to the inversion of the seasonal flow regimes (e.g. increases in the summer flows and magnitude of low flow extremes; decreases in the winter flows and in the frequency and magnitude of extreme high flow events) and the reduction of nutrient concentration. These changes favoured planktonic diatoms, macroinvertebrates with short life cycles and small body sizes, and fish feeding on the water column. Hydropower dams elevated significantly the rate of flow change and water temperature, favouring low profile adnate diatoms, multivoltine and passively dispersed macroinvertebrates, and scrapers. The key relationships identified in our study are useful to underpin river biodiversity conservation strategies and to set future research directions aiming at reducing the negative effects of dam operation schemes.

1. Introduction

Rivers and streams have been suffering a dramatic transformation to attend the increasing human freshwater demands worldwide. A significant part of this transformation is related to the construction of dams and other infrastructures for water diversion and storage, electricity generation, and risk management (Grill et al., 2019; Malmqvist and Rundle, 2002), with pervasive effects on riverine ecosystems (Richter et al., 2003; Vörösmarty et al., 2010). Therefore, one of the primary challenges for water resource managers is balancing these

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Abbreviations: IASPT, Iberian Average Score per Taxon; EPT, Ephemeroptera, Plecoptera, and Trichoptera; HI, Hydrological Index; NC, Natural hydrological Class; IPS, Specific Polluosensitivity Index; IBMWP, Iberian Biological Monitoring Working Party; LIFE, Lotic invertebrate Index for Flow Evaluation; EFI+, European Fish Index; ANOVA, Analysis of Variance.

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infrastructure's impacts on the verge of society development, while meeting ecological demands aggravated by global change (Arthington et al., 2010; Tickner et al., 2020).

Large dams represent the most prevalent form of hydrological alteration of river ecosystems worldwide (Arthington et al., 2010; Poff and Zimmerman, 2010; Rolls et al., 2013). Flow regulation caused by dams has been associated to the homogenisation of biological communities (e.g. Clavero & Hermoso, 2011; Oliveira et al., 2018), life cycle disruptions (e.g. Mims & Olden, 2013), and invasions of non-native species (e.g. Mathers et al., 2020). However, dams alter not only hydrological patterns, but also thermal regimes (Olden and Naiman, 2010; Poff and Zimmerman, 2010; Rolls et al., 2013), nutrient and sediment fluxes (Maavara et al., 2020; Syvitski, 2003), water quality (Scott Winton et al., 2019), and river longitudinal connectivity (Fagan, 2002; Grill et al., 2019). Despite the mitigation measures implemented worldwide to reduce dam impacts, such as fish passages, and environmental flow regimens (Arthington et al., 2010; Poff and Matthews, 2013; Schilt, 2007), global freshwater biodiversity still declines at alarming rates (Baker et al., 2020; Liermann et al., 2012). Therefore, understanding the ecological effects produced by dams in a systematic way is paramount for developing effective conservation strategies such as specific recommendations to restore key aspects of the flow regimen (Poff et al., 2010).

Dams tend to diminish peak flows and increase minimum flows, i.e. homogenise the flow regime, reducing channel complexity and, consequently, river biodiversity (Moyle and Mount, 2007; Poff et al., 2007). However, dam operational rules and storage capacity can influence specific hydrological and water quality variables (McManamay, 2014; Poff and Hart, 2002) and the ecological impact they produce. Despite numerous studies investigating how dams affect riverine assemblages (e.g. Chessman et al., 2010; Poff and Zimmerman, 2010; Sánchez-Pérez et al., 2020; Wu et al., 2019), the impacts associated to different dam operational schemes are seldom investigated simultaneously (but see Salmaso et al., 2018; Ko et al., 2020). Irrigation dams capture high flows and release the storage water depending on municipal and agricultural water demands, which can completely rearrange flow seasonality (Richter and Thomas, 2007) and therefore alter taxonomic and functional biological community structure (e.g. White et al. 2017). In contrast, hydropower dams can operate with little or no storage capacity, employing river's natural flow range (i.e. "run-of-river" operation) and generating minor flow regime alterations (Egré and Milewski, 2002; Richter and Thomas, 2007). However, downstream of these small hydropower plants, habitat degradation, water quality deterioration, and connectivity loss cause important ecological impacts (Kuriqi et al., 2021). Hydro-peaking dams are a different case, with frequent short-term flow fluctuations according to energy demands, which can have enormous short- and long-term impacts on river biota (e.g. increased macroinvertebrate drift; Schülting et al., 2019).

Biotic indices are widely used in the biological monitoring of water quality (Bonada et al., 2006) and have been also used to investigate the ecological effects of flow regulation. In general, most biotic indices (e.g. IASPT and EPT richness based on macroinvertebrate communities) were found to be sensitive to hydrological changes downstream of dams (e.g. Laini et al., 2018; Meißner et al., 2018; Mellado-Díaz et al., 2019), although these relationships lack a mechanistic or process-based background that limits their application to water management. Complementary, the biological communities' responses to dam-related disturbances (e.g. hydrological and physico-chemical changes) can also be approached through a trait-based analysis (Culp et al., 2011). Species traits, i.e. measurable organisms features describing, for example, body size, fecundity, and ecological preferences (McGill et al., 2006), have demonstrated consistent responses to environmental and hydrological variation across taxonomic boundaries (Frimpong and Angermeier, 2010; Göthe et al., 2017) and provide a better mechanistic understanding of the community responses to natural and anthropogenic stressors (Statzner and Bêche, 2010; White et al., 2017). For instance, the dominance of different macroinvertebrate feeding groups (Larsen et al., 2021) or different fish life strategies (Oliveira et al., 2018) are reported to vary significantly in response to flow alteration. These patterns can be readily translated into flow-ecology relationships (Craven et al., 2010; Rosenfeld, 2017) and, in combination with river classification, underpin conservation strategies applicable beyond the regional species pool (Arthington et al., 2018; Poff et al., 2010). These strategies (e.g. specific environmental flows) are critical to sustain fluvial ecosystems while addressing competing objectives such as water allocation for agriculture and energy production (Kuriqi et al., 2020; Poff and Matthews, 2013).

In this study, our main goal is to assess dam effects (e.g. hydrological and thermal alteration, water quality changes) on multiple river biological communities, focusing on dams primarily operated to attend irrigation demands or hydropower production. We aim to identify consistent community changes and trait-based ecological responses using diatom, macroinvertebrate and fish communities (i.e. organisms representing different levels of the river food web) in a control-impact design (natural vs regulated flow regime) in northern Spain. The selected streams are grouped in two natural hydrological classes (following Peñas & Barquín 2019), reducing environmental and hydrological variability. We hypothesise that (1) flow regulation will alter hydrological and physico-chemical characteristics depending on the dam purpose (i.e. irrigation vs hydropower dams), and (2) both biotic indices and ecological traits will respond to these changes, however, differently in each biotic group and depending on the intensity of hydrological or physico-chemical change. In general, we expect to identify key community shifts associated to the hydrological and physico-chemical changes, (3) with dams favouring disturbance-tolerant traits (e.g. generalist taxa, small body sizes, etc).

2. Methodology

2.1. Study design

Spain is among the top ten countries in dam building, with 1064 large dams (with a minimum height of 15 m or impounding >3 hm^3), according to the International Commission on Large Dams (ICOLD, 2021). River damming in the country has been motivated by the high water agriculture demands (3.8 million ha of irrigated lands; MAPAMA, 2020), low and irregular rainfalls, and high potential evapotranspiration (Fornés et al., 2021). Although hydropower expansion decelerated in the last decades due to environmental legislation and the exploitation of other energy sources (Fornés et al., 2021), 147 new hydropower plants are planned to be built in the country, mostly with small energy generation capacities (<10 MW; Baumüller et al., 2019).

In this study, we selected 19 permanent streams in northern Spain surveyed in three consecutive autumns (2017, 2018, 2019): 8 streams under natural flow regime (i.e. controls) and 11 streams affected by dams (i.e. altered flow regime; Fig. 1a and Table 1). We focused on dams operating with two main purposes: dams primarily used for irrigation (irrigation dams) and dams operated solely for hydropower production. Sampling sites were located in the Cantabric, Duero, and Ebro catchments, which drain to the Cantabric Sea, the Atlantic Ocean, and the Mediterranean Sea, respectively. The initial condition for site selection was to have an operational nearby gauge station. In potentially impacted sites (i.e. streams under a regulated flow regime caused by a reservoir located upstream), we selected river reaches affected by a minimum of one and a maximum of three upstream reservoirs.

Our sampling sites were restricted to streams that belong to natural hydrological classes 1 (NC1) and 2 (NC2). These two groups correspond, respectively, to NC10 and NC13 in the 20-level hydrological classification developed by Peñas and Barquín (2019) for the Spanish river network. The natural flow regime of NC1 streams was characterised by a large number of high flow events with short duration and low interannual variability on the timing and magnitude of low flows (Fig. 1b). NC2 was also characterised by a large number of high flow events, with a

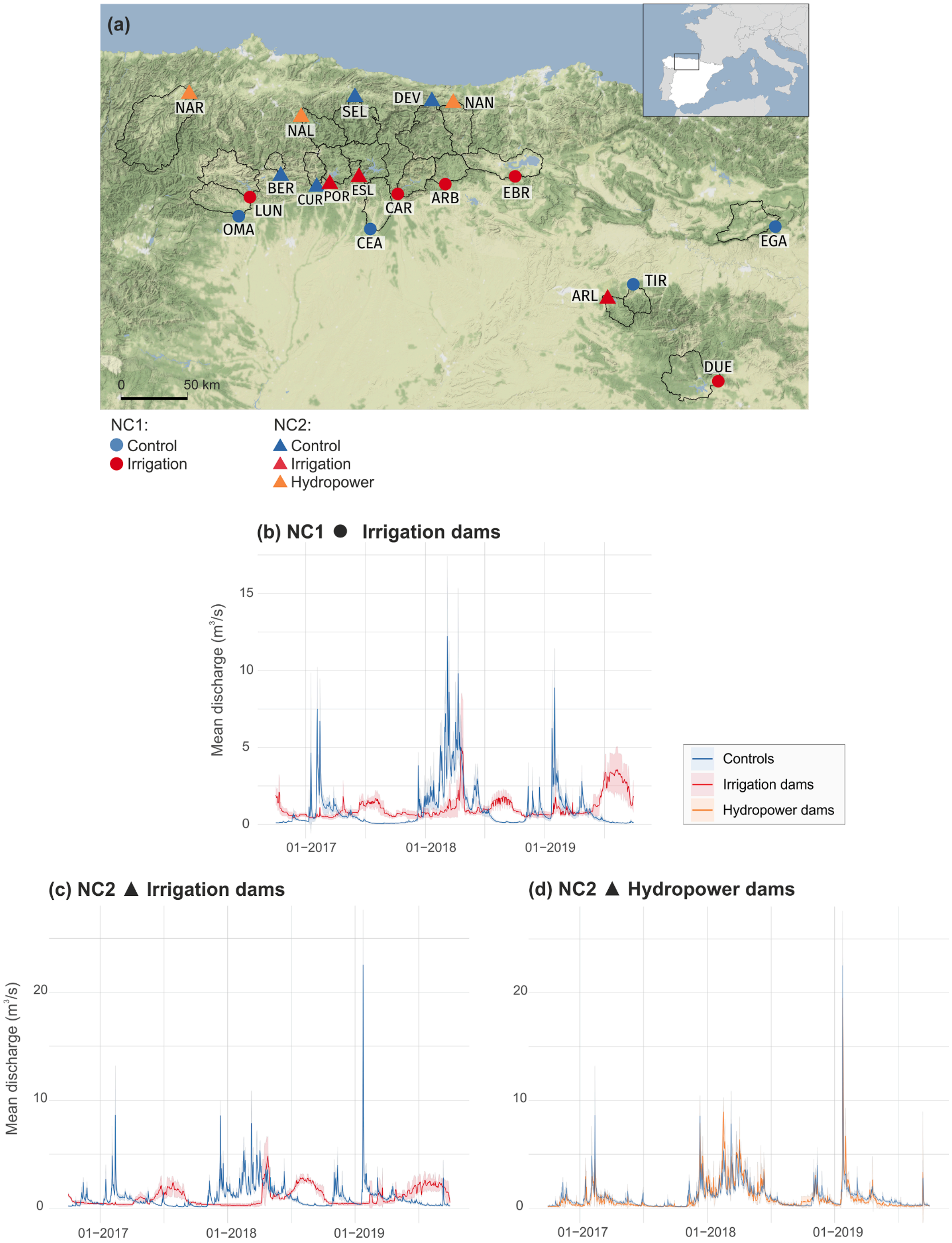

Fig. 1. (a) The 19 sampling locations and their catchment boundaries, classified according to the flow regime (i.e. unregulated (control) and altered flow regimes), and hydrological classes (i.e. NC1 and NC2). See Table 1 for site codes. Mean normalised daily discharge in (b) controls and sites impacted by irrigation dams in NC1, (c) controls and sites impacted by irrigation dams in NC2, and (d) controls and sites impacted by hydropower dams in NC2. Shaded areas represent 1SD confidence intervals.

peak in spring associated to snowmelt processes (Fig. 1c-d). Although the hydrological classes may not be a fixed product as their limits represent a trade-off between detail and interpretability (Poff et al., 2010), they reduce the noise associated to environmental and hydrological variability.

2.2. *Environmental and hydrological information*

Environmental characteristics describing climate, topography, geology, and land use and land cover at the catchment scale (Table S1 in Supplementary Material) were obtained from a synthetic river network (SRN), which was inferred from a 10-meter digital elevation model. The SRN is composed of virtual watersheds integrating the spatial river network with the environmental information at the national level (Barquín et al., 2015).

The river discharge was recorded in 19 gauge stations provided by the Spanish Ministry for Ecological Transition and Demographic Challenge (MITECO). We extracted the average daily discharge corresponding to the hydrological years of 2017, 2018, and 2019 (Fig. 1b-d). These years presented important meteorological differences, i.e. 2017

Table 1

Selected sampling sites divided between the hydrologic classes NC1 and NC2. Reservoir purpose.: Hydropower (HP), Irrigation (IR), Water Supply (WS). Storage index = storage volume/average annual runoff.

	Site code	River	Basin	Dam (year of construction)	Reservoir purpose	Storage Index
NC1	OMA	Omaña	Duero			
	CEA	Cea	Duero			
	TIR	Tirón	Ebro			
	EGA	Ega	Ebro			
	EBR	Ebro	Ebro	Ebro (1945)	IR/WS	3.71
	DUE	Duero	Duero	Cuerda del Pozo (1941)	IR/WS/HP	0.74
	LUN	Luna	Duero	Barrios de Luna (1956)	IR/HP	0.84
	ARB	Arbejal	Duero	Requejada (1935)	IR/HP	0.46
	CAR	Carrión	Duero	Camporredondo (1930) and Compuerto (1960)	IR/HP	0.72
NC2	SEL	Sella	Cantabric			
	DEV	Deva	Cantabric			
	CUR	Curueño	Duero			
	BER	Bernesga	Duero			
	NAN	Nansa	Cantabric	La Cohilla (1950) and Palombera (1955)	HP	0.06
	NAL	Nalón	Cantabric	Tanes and Rio Seco (1978)	HP	0.13
	NAR	Narcea	Cantabric	La Barca (1966)	HP	0.03
	POR	Porma	Duero	Juan Benet (1968)	IR/WS/HP	1.64
	ESL	Esla	Duero	Riaño (1987)	IR/HP	0.86
	ARL	Arlanzón	Duero	Arlanzón (1933) and Uzquiza (1988)	IR/WS	0.63

was considered a dry year, 2018 a wet year, and 2019 an average year according to the Spanish Governmental Agency of Meteorology (AEMET). Therefore, we computed 35 hydrological indices (HIs, Table S2 in Supplementary Material) annually using the normalised daily flow and describing the magnitude of monthly flows, the magnitude, duration, and timing of annual extremes, the frequency and duration of high and low pulses, and the rate of change (Richter et al., 1996).

2.3. Biological and physico-chemical data collection

Diatom, macroinvertebrate, and fish biological communities were surveyed annually, between September and October in 2017, 2018 and 2019, when all sites presented low flow conditions. This is crucial because low flow comparison is unfeasible at other times of the year since streams affected by irrigation dams usually have high flows in summer, whereas control sites typically have high flows in winter and spring.

Diatoms were surveyed following a standard procedure (UNE-EN ISO14407), selecting randomly-six cobbles from the benthos (approximately 100 cm^2 of exposed surface area) and scrubbing the upper part of the substratum with a dishwasher brush. The material was decanted in a sample bottle and preserved using formaldehyde. From each sample, 400 diatom valves were identified in laboratory using a microscope at the lowest feasible taxonomic level (species level in almost all cases).

Macroinvertebrates were surveyed from run and pool habitats using a Surber net. The stream substrate enclosed in the Surber sampling area (0.09 m^2) was disturbed and the material was swept into the net (0.5 mm mesh size) by the stream flow. Each sample (run and pool) was composed of three surbers. The taxonomic composition was completed with a kick hand-net sampling carried out in other habitats presented in the river stretch (e.g. roots, macrophytes, woody debris, etc.) with 10 kicks. Samples were preserved in 96% ethanol and identified in laboratory at the lowest feasible taxonomic level (mainly at species or genus level), except for Hydracarina, Nematoda, Ostracoda, Copepoda, and Oligochaeta.

Three days after the macroinvertebrate surveys, single-pass electrofishing was carried out in a representative area of the river reach (670 m^2 on average) using a portable electric fishing device (power 1.3 kW, current generation of 300–500 V or pulsations up to 940 V, and variable frequency 25–100 Hz). Nets or natural barriers were used to block upstream and downstream of the sampled area. After pass removal, the fish captured were kept in oxygenated boxes, anaesthetised with eugenol, counted, and identified at the species level. After a 30-minute recovery in containers with stream water, fish were returned alive to the stream. Brown trout (*Salmo trutta*) was classified into age classes: young of the year (0+), juvenile (1+) and adult (2+). Because of high flow conditions, Esla and Luna were not surveyed in 2018 and 2019, respectively.

To reduce the effect of rare taxa, we eliminated diatom and macroinvertebrate taxa representing less than 2% of total sampled individuals when considering the total number of occurrences (e.g. Lavoie et al., 2009). Regarding traits, we assigned diatom species to ecological guilds (high and low profile, planktonic, motile), life forms (colonial, stalked, adnate, pioneer), and cell sizes (biovolume in μm^3; Table S3 in Supplementary Material. Macroinvertebrates were assigned to traits describing their body size, life cycle duration, and feeding habits, among other characteristics (see Table S4 in Supplementary Material), using a fuzzy-coding approach. Last, fish species were assigned to traits describing maximum body length, habitat use, feeding habits and habitat, and migration patterns (see Table S5 in Supplementary Material). It is important to note that trait categories can overlap and species may belong to multiple trait categories (e.g. *Cocconeis euglypta* is considered, at the same time, a low profile and adnate diatom species).

Water physico-chemical measurements were collected during the field surveys. pH and conductivity were measured with Milwaukee pH55 and EC59 Portable Waterproof pH and EC/TDF Tester, respectively. Temperature was recorded with HOBO Pendant data loggers deployed in each site for at least 10 days between September and October each year. Nutrient concentrations were determined by continuous flow analysis (FIA and CFA) following standard protocols: UNE-EN ISO 15681-2:2005 for phosphates, UNE-EN ISO 13395:1997 for nitrite and nitrates, UNE-EN ISO 11732:2005 for ammonium, and UNE-EN ISO 77051:2019 for silicates.

2.4. Data analysis

An initial assessment of the relationships among the hydrological and physico-chemical variables in each hydrological class was performed using Spearman's rank correlations.

To identify significant differences in HIs, physico-chemical variables, and biotic indices between control and impacted sites in NC1 and NC2, we carried out a repeated-measure analysis of variance (ANOVA) using the R package *lme4* (Bates et al., 2015). Flow regulation was treated as a fixed factor, while the year of sampling as a random factor to account for potential temporal autocorrelation. In NC2, we further investigated the differences between controls, irrigation, and hydropower dams. The posthoc pairwise comparisons of the means were assessed by Tukey tests (*emmeans* R package; Lenth, 2021).

As the temperature is strongly influenced by altitude, the water temperature at sampling (T_{WATER}), the mean water temperature 14 days before biological sampling ($T_{14\text{-}DAY}$), and the degree-day accumulation in 10 days in October (Degree-day) were analysed in two groups in NC2: sites located at higher altitudes (>950 m; Bernesga, Curueño, Porma, Esla, and Arlanzón), and sites at lower altitudes (<400 m; Deva, Sella, Narcea, Nansa, and Nalón).

We calculated the taxa richness and Shannon-Wiener diversity index for the three biotic groups using the R package *vegan* (Oksanen et al., 2019). Additionally, we computed the Specific Polluosensitivity Index (IPS; CEMAGREF 1982) for diatoms, the Iberian Average Score per Taxon (IASPT; calculated as the value of the Iberian Biological Monitoring Working Party (IBMWP divided by the number of macroinvertebrate families) and the Lotic invertebrate Index for Flow Evaluation (LIFE; Extence et al., 1999) for macroinvertebrates, and the European Fish Index (EFI+; EFI+ Consortium, 2009). Statistically significant relationships ($p \leq 0.05$) among these biotic indices, HIs, and physico-chemical variables were assessed using Spearman's rank correlations.

To investigate community variation across hydrological and environmental gradients, we carried out the RLQ and fourth-corner analyses (Dray et al., 2014; Kleyer et al., 2012) using the R package *ade4* (Dray and Dufour, 2007). The combination of these methods constitutes a powerful approach to investigate trait-environment relationships in community ecology (Peres-Neto et al., 2017), with numerous examples in the literature (e.g. Brown et al., 2019; De Castro-Català et al., 2020; Wu et al., 2019). The RLQ analysis combines three tables: table R ($n \times m$), containing the measurement of m environmental variables at n sites, table L ($n \times p$), with the abundance of p taxa at n sites, and table Q ($p \times s$), describing s traits related to the same p taxa (Dolédec et al., 1996). This method is based on the computation of a cross-variance matrix weighted by taxa abundance, providing a broad overview of how traits and environmental characteristics are related (Brown et al., 2014; Thioulouse et al., 2018). The overall significance of the trait-environment relationship is assessed with 9999 permutations of the rows in tables R and Q sequentially to control type I error (ter Braak et al., 2012). Further, the fourth-corner analysis was used to identify significant individual trait-environment relationships using the three tables simultaneously. The method computes a matrix ($s \times m$) with the one-to-one trait-environment correlations (Dray et al., 2014).

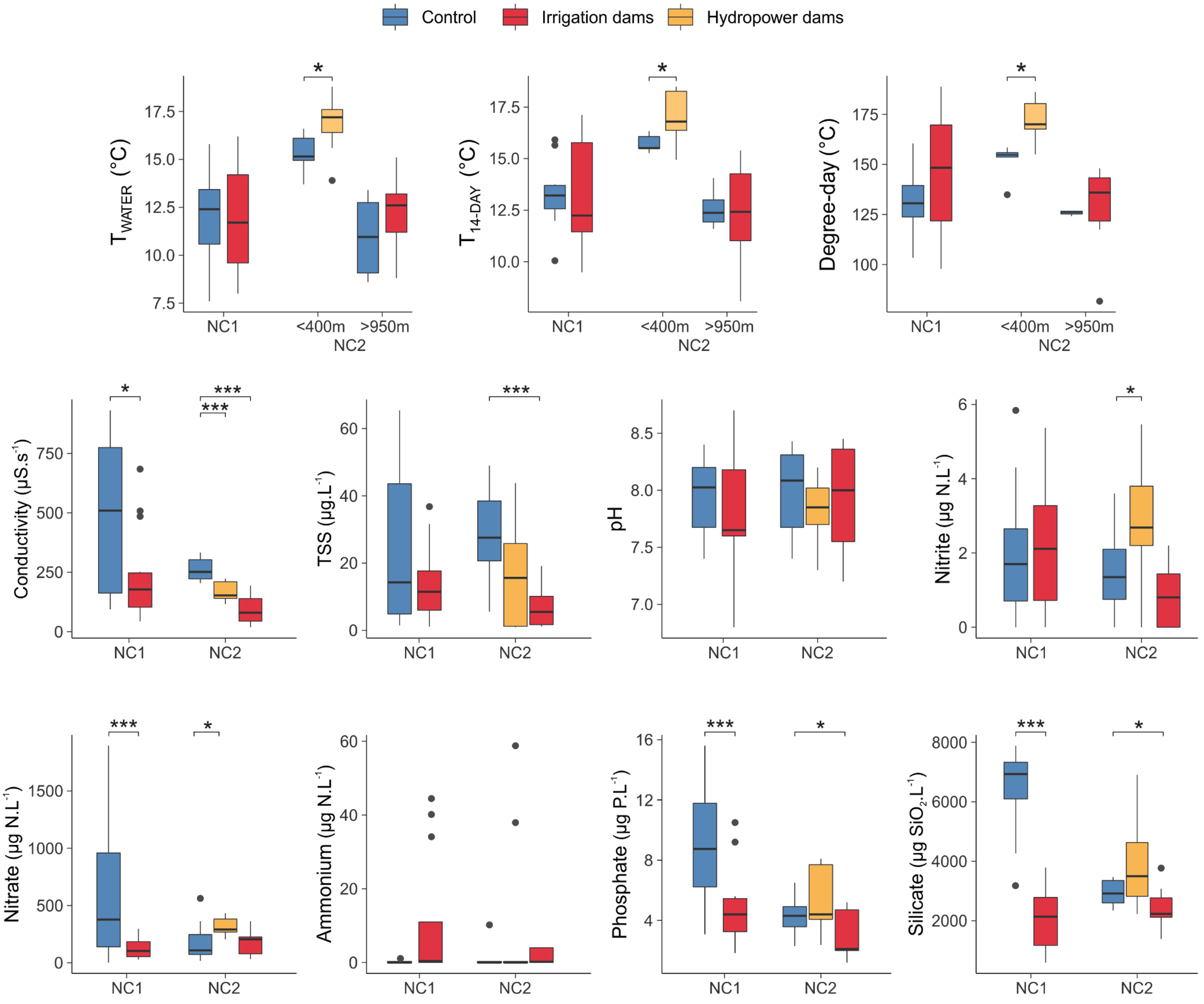

Fig. 2. Boxplots representing water temperature, nutrients, and other water quality variables in NC1 (12 samples for controls, 15 for irrigation dams) and NC2 (12 samples for controls, 9 for irrigation dams, 9 for hydropower dams). Significant p-values (Tukey pairwise comparisons) are represented as *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05.

Prior to the analyses, water physico-chemical and hydrological variables were standardised (zero mean and unit standard deviation). In this work, the statistically significant level for all the ANOVA tests, Spearman's rank correlation, and RLQ and fourth corner analyses was set to $p \leq 0.05$. All the analyses were performed in the R environment (R Core Team, 2020).

3. Results

3.1. Dam effects on hydrology and water quality

In general, hydrological (Table S6 and Fig. S1 in Supplementary Material) and water physico-chemical variables (Fig. 2 and Table S7) responded differently to the presence of irrigation and hydropower dams, but similar patterns of alteration were identified in both hydrological classes.

In both natural hydrological classes, the presence of irrigation dams generated significant increases in summer flows (+M7-10, see Table S6) and in the magnitude of daily to seasonal low flow extremes (+1-90LF in NC1; +1-30HF in NC2). These HIs were correlated (Spearman's rank correlations in Fig. S2 in Supplementary Material) to a higher number of days with increasing flows (+nPos), and lower nutrient concentrations (-Silicate, -Phosphate, -Nitrate in NC1; only -Silicate in NC2).

We also identified a significant decrease in winter flows (-M1-3 in NC1; -M1-3, -M12, in NC2), lower frequencies of high flow events (-FRE3-7), lower magnitudes of short-term high flow extreme events (-1,3HF in NC1; -1,3,7HF in NC2), the earlier timing of annual 1-day flow extremes (-JMax in NC1), and a lower water conductivity and nutrient concentrations (-Nitrate, -Phosphate, -Silicate in NC1; Table S7). These HIs were also correlated to lower flow rise (-meanPos)

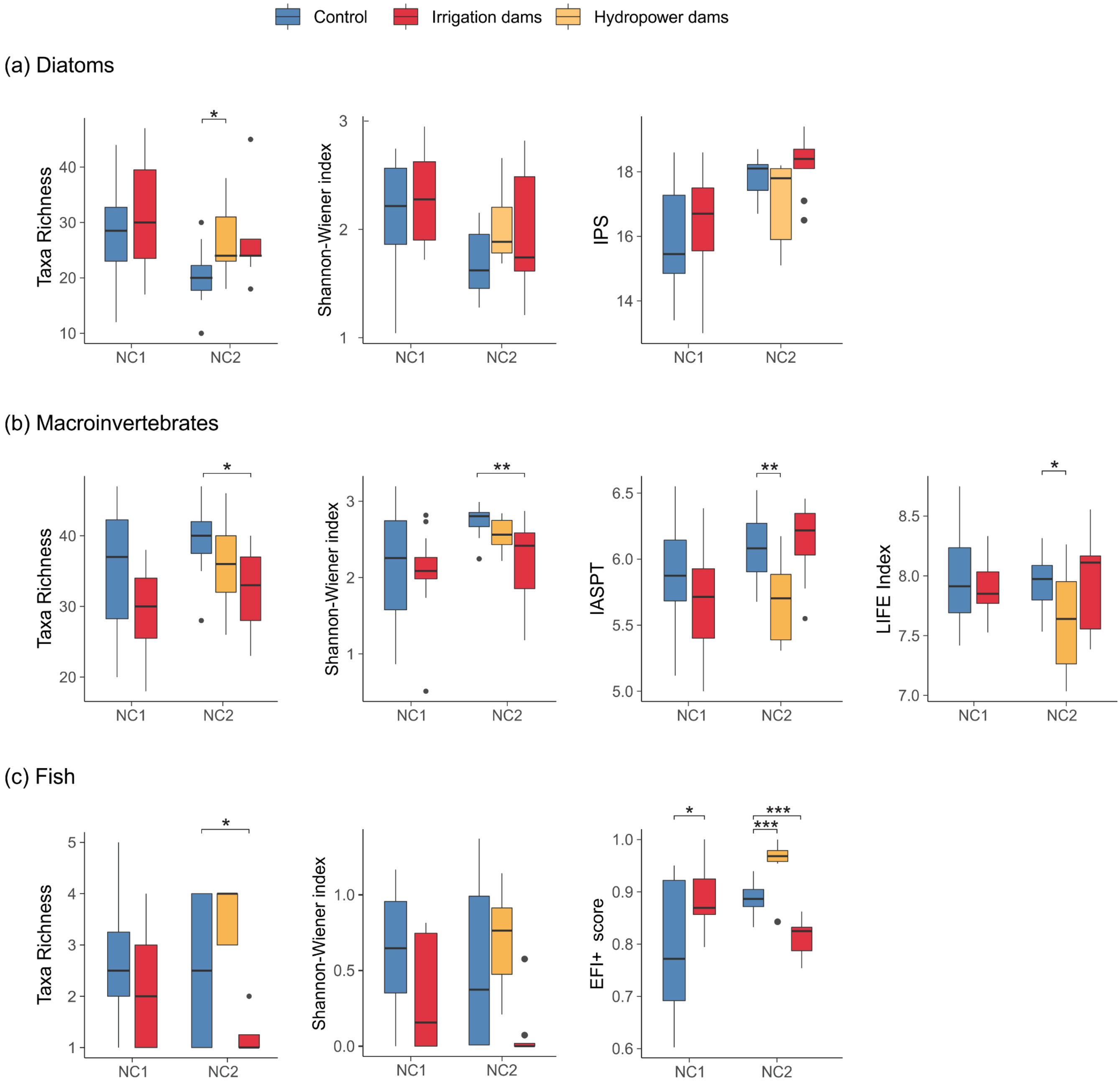

Fig. 3. Boxplots representing the taxonomic richness, Shannon-Wiener diversity index, and biotic indices based on (a) diatom, (b) macroinvertebrate, and (c) fish communities in NC1 (12 samples for controls, 15 for irrigation dams) and NC2 (12 samples for controls, 9 for irrigation dams, 9 for hydropower dams). Significant p-values (Tukey pairwise comparisons) are represented as *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05.

and less negative flow fall (+meanNeg) rates. Thus, the presence of irrigation dams resulted in an inversion of the seasonal flow patterns, decreases in the flow peak amplitude, and reductions in nutrient concentrations. These hydrological changes are clearly seen in the hydrographs (Fig. 1b-c), e.g. in 2018 (wet year), the magnitude of high flow events was strongly reduced, and in 2019 (average year), summer flows were substantially higher in comparison to controls.

In streams affected by hydropower dams in NC2, the flow regime alteration was less evident (Fig. 1d). A significantly higher number of low flow pulses within a year (+nPulsesLow; see Table S6) but with shorter duration (-meanDPLow) were detected downstream of these dams. These HIs were also linked to lower spring flows (-M4-6), a lower number of days with decreasing flows (-nNeg), and higher water temperature when compared to controls at similar altitudes (<400 m; Fig. 2 and Table S7). These alterations indicate a substantial day-to-day flow variation caused by hydropower dams.

3.2. *Dam effects on biotic indices*

Mean values of diatom biotic indices (Fig. 3a and Table S8 in Supplementary Material) increased in most of the impacted sites; however, only the taxonomic richness downstream of hydropower dams had a significant increase in comparison to controls. Nitrite, silicate, and water temperature were significantly correlated to the biotic indices in NC1 (Fig. S3a in Supplementary Material). In NC2, HIs and physico-chemical characteristics altered by irrigation dams (winter and summer flows, duration of high flow pulses, pH, silicate, and water temperature) showed significant correlations to taxonomic richness and IPS score (Fig. S3b).

The macroinvertebrate taxonomic richness and the Shannon-Wiener diversity index (Fig. 3b and Table S8) tended to decrease in impacted sites in comparison to controls, with significant differences downstream of irrigation dams in NC2 only. In general, they were significantly linked to HIs altered by irrigation dams (e.g. winter and summer flows, low flow extremes, number of flow increases and decreases) and by water temperature in NC1 (Fig. S3a in Supplementary Material). The LIFE and IASPT mean scores also tended to decrease in most altered sites, although only significant differences in IASPT score were detected downstream of hydropower dams (Fig. 3b). The indices showed few significant links to HIs and water quality in NC1, while in NC2, the IASPT score was significantly correlated to summer flows, seasonal low flow extremes, number and duration of annual low flow pulses, and water temperature (Fig. S3).

Fish communities (Fig. 3c and Table S8) in irrigation-impacted streams showed lower mean taxonomic richness and diversity in relation to controls; however, significant changes in taxonomic richness were observed downstream of irrigation dams in NC2 only. The fish taxonomic richness and diversity were significantly related to HIs and water quality variables altered by irrigation and hydropower dams (winter flows, flow change rates, high flows frequency, TSS, water conductivity, and temperature; Fig. S3 in Supplementary Material) in both hydrological classes. The EFI+ score showed significant changes in NC2, with increases downstream of hydropower dams and decreases in irrigation dams. This score was significantly related to monthly flows and physico-chemical variables in NC1, while in NC2, it was strongly influenced by irrigation- and hydropower-altered HIs and physico-chemical variables (e.g. summer and winter flows, high and low flow events, nutrient concentrations, water temperature; Fig. S3).

3.3. *Trait-based community responses to flow regulation*

3.3.1. *Diatoms*

The overall RLQ permutation test showed a non-significant trait-environment relationship (permutation across sites $p = 0.017$, across species $p = 0.258$) in NC1. The first two axes of the RLQ analysis explained 69.7% of the cross variance between diatom traits and the environment (Fig. 4a-d). Along the first axis (42.7%), sampling sites were segregated according to flow regulation. The planktonic guild and larger diatom cell sizes (+Biovolume) were significantly associated to the magnitude of daily to seasonal low flow extremes (+1-90LF; see fourth-corner analysis in Fig. S4 in Supplementary Material) and a low number of flow decreases (-nNeg), and stalked diatoms showed significant associations to lower winter flows (-M1), less negative flow fall rates (+meanNeg), and lower TSS and nitrite concentrations, i.e. some of the variables altered by irrigation dams in our study. In contrast, motile and adnate diatoms were associated to hydrological characteristics found in control sites (e.g. -90LF, -meanNeg).

In NC2, the overall RLQ trait-environment link was non-significant (permutation across sites $p < 0.001$, across species $p = 0.072$). The two first axes of the RLQ analysis (Fig. 4e-h) explained 91.1% of the cross variance between diatom traits and environmental variables. Along the first axis (50.2%), samples were segregated according to the flow regulation, with exception of the Nansa samples (NAN17, NAN19), which overlapped the control group. However, most of the trait-environment relationships were concentrated in the second RLQ axis (40.9%). Along this axis, planktonic diatoms showed significant positive relationships with autumn flows (+M9-10), the magnitude of daily low flow extremes (+1LF), and the mean duration of high flow pulses (+meanDPHigh; see fourth-corner analysis in Fig. S4 in Supplementary Material), i.e. HIs altered by irrigation dams in NC2. Larger diatom cell sizes, low profile, adnate, and motile diatoms were, in turn, significantly linked to hydrological and physico-chemical conditions found in controls and hydropower dams (e.g. lower summer and autumn flows, stronger flow changes, higher water temperature and nutrient concentrations). In addition, the position of controls and hydropower-impacted sites along the second axis was related to the hydrological year of the survey: samples collected in 2017 (dry year), 2019 (average year), and 2018 (wet year). This temporal pattern could be linked to a gradient of increasing flows (+meanPos, +nPulsesHigh) in 2018 samples in comparison to 2017 ones. In irrigation-impacted sites, however, this pattern was not clear.

3.3.2. *Macroinvertebrates*

The overall RLQ permutation test showed a significant macroinvertebrate trait-environment relationship (permutation across sites $p < 0.001$, across species $p = 0.018$) in NC1. The first two RLQ axes accounted for 93.2% of the total variance (Fig. 5a-d), with the first axis (86.8%) segregating control from impacted sites. Along this axis, macroinvertebrates with longer life cycles (Perennial), medium to large body sizes (MedLarge; >2–4 cm), adult aquatic stages (Adult), ovoviviparous, and shredders showed positive significant associations to hydrological and physico-chemical conditions found in NC1 control sites (e.g. increased winter flows and nutrient concentrations, higher magnitude and frequency of high flow events; see the fourth-corner analysis in Fig. S5 in Supplementary Material). These traits were replaced by macroinvertebrates with shorter life cycles (Ephem; life cycles ≤ 1 year), small to medium body sizes (SmallMed; >0.5–1 cm), deposit feeders (DepositFeeder), and taxa with eggs resistant to unfavourable conditions (DormantEggs) in sites marked by the inversion of seasonal flow patterns caused by irrigation dams (e.g. + M6-10, +90LF, +Reversals). The second axis (6.4%) was mainly linked to temperature and voltinism. Higher water temperatures (+$T_{14\text{-DAY}}$, +Degree-day), higher number of days with increasing flows (+nPos), and lower autumn flows (+M11) were significantly related to taxa with multiple reproductive cycles per year (Multivoltine), replacing crawlers, univoltine, and semivoltine taxa in streams with lower temperature.

In NC2 (Fig. 5e-h), the overall RLQ trait-environmental link was non-significant (permutation across sites $p < 0.001$, across species $p = 0.072$). Along the first axis (65.3%), macroinvertebrates with longer life cycles (Perennial), flyers, and gill respiration were significantly associated to unregulated flow conditions in NC2 (e.g. increased winter flows, more frequent high flow events, later timing of the annual minimum

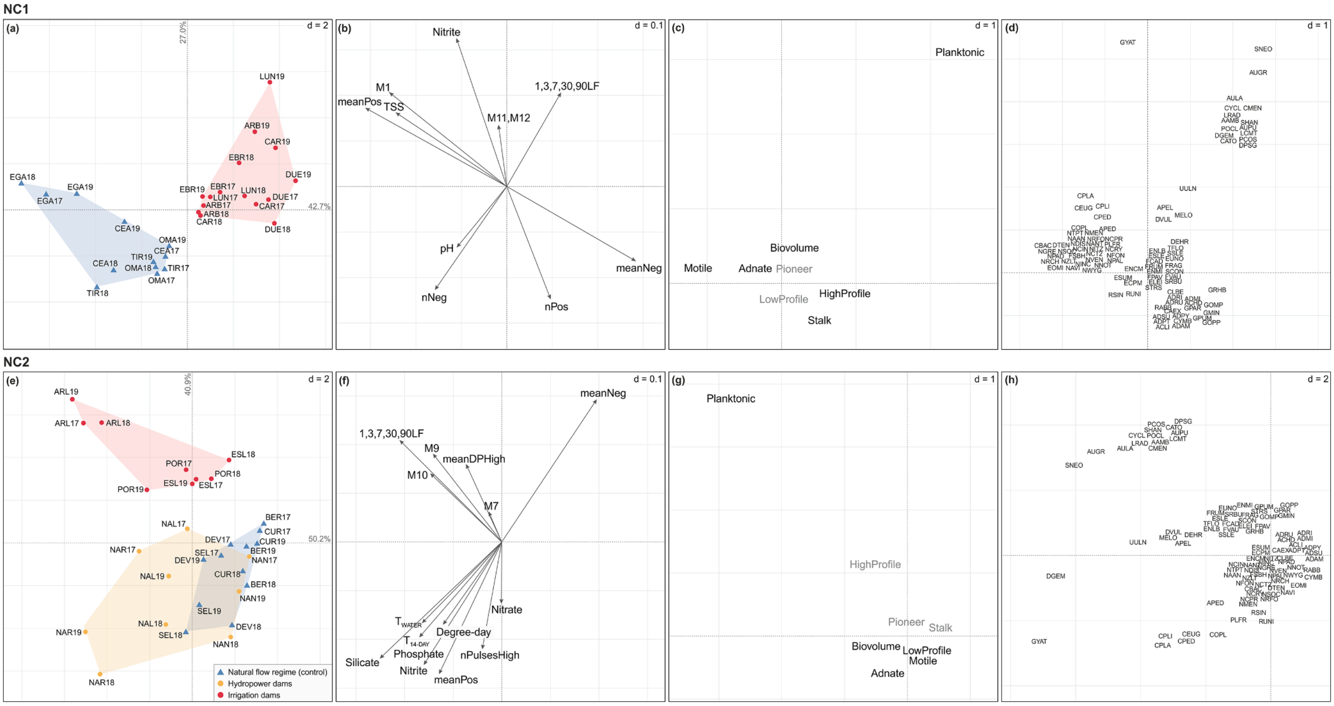

Fig. 4. Ordinations showing the first two RLQ axes on diatom communities in NC1 (top) and NC2 (bottom). (a, e) Sampling site scores according to flow regulation (site code and year of sampling, see Table 1). (b, f) Coefficients for key HIs and local environmental variables with strong links to traits (see Table S2 in Supplementary Material for codes). (c, g) Coefficients for traits (see Table S3 for codes). Traits with no significant relationships (see fourth-corner analysis, Fig. S4) are represented in grey. (d, h) Coefficients for species (see Table S9). The “d” values give the grid size for scale comparison across graphs.

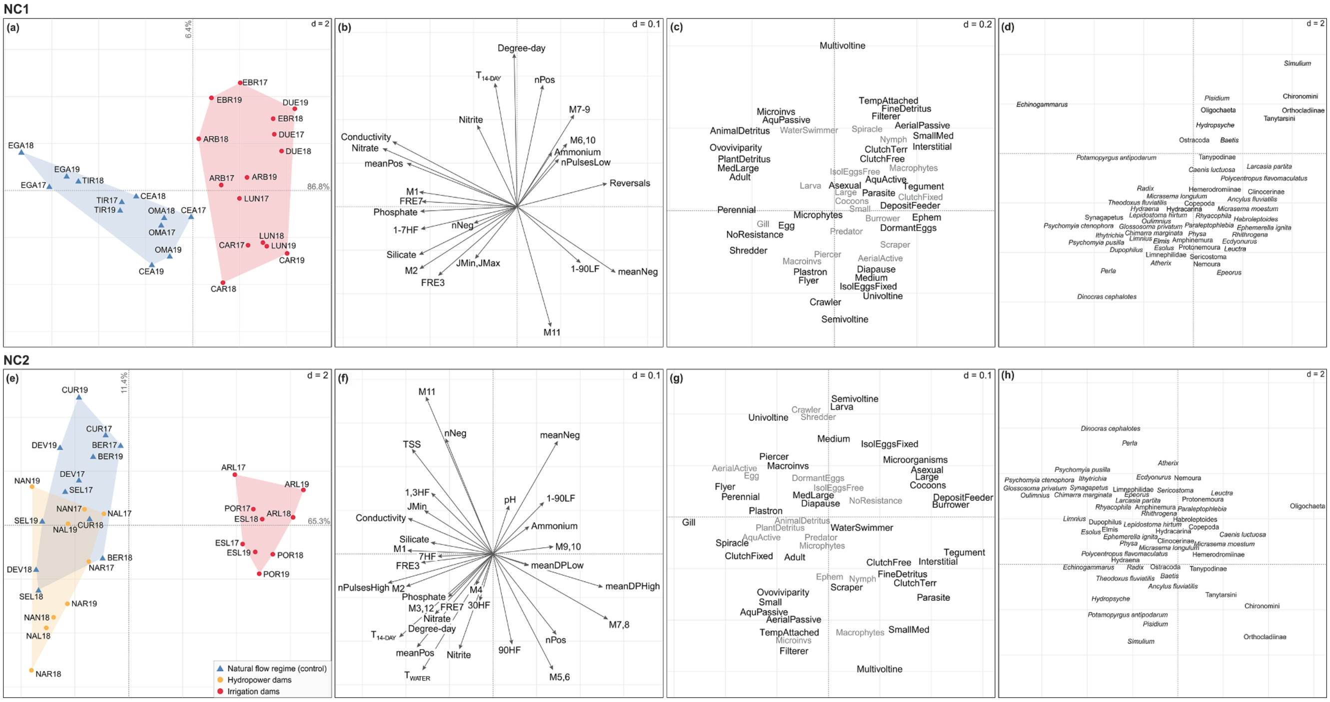

Fig. 5. Ordinations showing the first two RLQ axes on macroinvertebrate communities in NC1 (top) and NC2 (bottom). (a, e) Sampling site scores according to flow regulation (site code and year of sampling, see Table 1); (b, f) coefficients for key HIs and local environmental variables with strong links to traits (see Table S2 in Supplementary Material for codes). (c, g) Coefficients for functional traits (see Table S4 for codes). Traits with no significant relationships (see fourth-corner analysis, Fig. S5) are represented in grey. (d, h) Coefficients for species, see Table S10. The “d” values give the grid size for scale comparison across graphs.

flows, and higher nutrient concentrations; see the fourth-corner analysis in Fig. S6 in Supplementary Material). In contrast, sites impacted by irrigation dams were concentrated in the opposite direction, favouring burrowers, endobenthic organisms (Interstitial), tegument respiration, taxa with resistance strategies to unfavourable conditions (Cocoons), and asexual reproduction (Asexual). Along the second axis (11.4%), conditions characterising unregulated streams (e.g. + M11, +1-3HF, +JMin, +nNeg, +TSS) were significantly related to perennial and univoltine taxa. They were replaced by multivoltine taxa, aquatic passive dissemination (AquPassive), and scrapers in streams affected by hydropower dams (e.g. higher water temperatures, increased spring flows).

In addition, a gradient from the driest (2017 samples towards the upper part; Fig. 5e) to the most humid year (2018 samples towards the bottom) was present along the second axis in NC2. As such, univoltine and semivoltine taxa, medium body sizes (Medium; >1–2 cm), and cemented isolated eggs (IsolEggsFixed) tended to increase with more frequent flow decreases (+nNeg), less negative fall rates (+meanNeg), and higher November flows (+M11) toward the upper part of the graph. They were replaced by multivoltine, ovoviviparous taxa, aquatic passive dissemination, small to medium body sizes (SmallMed; >0.5–1 cm), and filter feeders and were, in turn, associated to higher water temperatures, increased nitrite and nitrate concentrations, higher magnitude and frequency of high flows (+30-90HF, +FRE7, +nPos), and higher spring flows (+M4-6).

3.3.3. Fish

In NC1, the overall trait-environment link was non-significant (permutation across sites $p = 0.007$, across species $p = 0.065$). The first two axes of the RLQ analysis (Fig. 6a-d) explained 96.9% of the total co-inertia linking fish traits and the environment. Most of this variability was concentrated in the first axis (87.3%), which represented a gradient of fish migration and flow change. Non-migratory species (e.g. *Phoxinus bigerri, Achondrostoma arcasii*) tended to be more abundant with higher flow rise rates (+meanPos), while potamodromous and piscivorous fish (e.g. *Salmo trutta*) were linked to less negative fall rates (+meanNeg significantly linked to Piscivory only; see fourth-corner analysis in Fig. S7). Across a gradient of flow regulation, benthic fish (e.g. *Barbatula quignardi*, *Gobio lozanoi*, *Cobitis calderoni*) were significantly linked to higher TSS concentrations, higher magnitude of daily floods (+1HF), and more frequent high flow events (+FRE3-7), which were conditions found in control sites. In contrast, species feeding at the water column (WaterColumn; e.g. *P. bigerri*) were significantly favoured by lower TSS concentrations and less frequent high flow events (-FRE7), that is, conditions found in streams affected by irrigation dams. Moreover, omnivorous fish species (e.g. *P. bigerri*) were significantly associated to increasing water temperatures (+Degree-day) but replaced by invertivorous ones at lower temperatures.

In NC2, the overall trait-environment link was non-significant (permutation across sites $p < 0.001$, across species $p = 0.148$). The first two axes of the RLQ analysis (Fig. 6e-h) explained 98.6% of the total co-inertia linking fish traits and the environment. Along the first RLQ axis (92.9%), samples were segregated according to flow regulation and dam purpose, with exception of the 2019 Sella sample (SEL19), which overlapped the hydropower-impacted group. In sites affected by irrigation dams (+M7-8, +meanDPHigh, +meanNeg), species feeding at the water column (e.g. *S. trutta*) and potamodromous fish (e.g. *S. trutta*) were significantly favoured. Species performing long-distance migrations (LongMigration, e.g. *S. salar*) and large-sized fish (MaxLength, e.g. *Anguilla anguilla*) seemed to be favoured by increasing flows (+meanPos, +nPulsesHigh) and higher silicate and nitrate concentrations, i.e. conditions found in control sites; however, these relationships were non-significant. Hydrological and physico-chemical conditions characterising sites affected by hydropower dams did not show positive associations to fish traits. Furthermore, in contrast to the diatom and macroinvertebrate ordinations, the interannual variation was unclear in fish communities.

4. Discussion

The combination of a control-impact design and three consecutive year surveys covering multiple biotic groups allowed us to identify key ecological responses to flow regime changes associated to different dam purposes. As hypothesised, the different dam operation schemes generated different biophysical responses in rivers. Irrigation dams were associated to the inversion of seasonal flow patterns and to a reduction

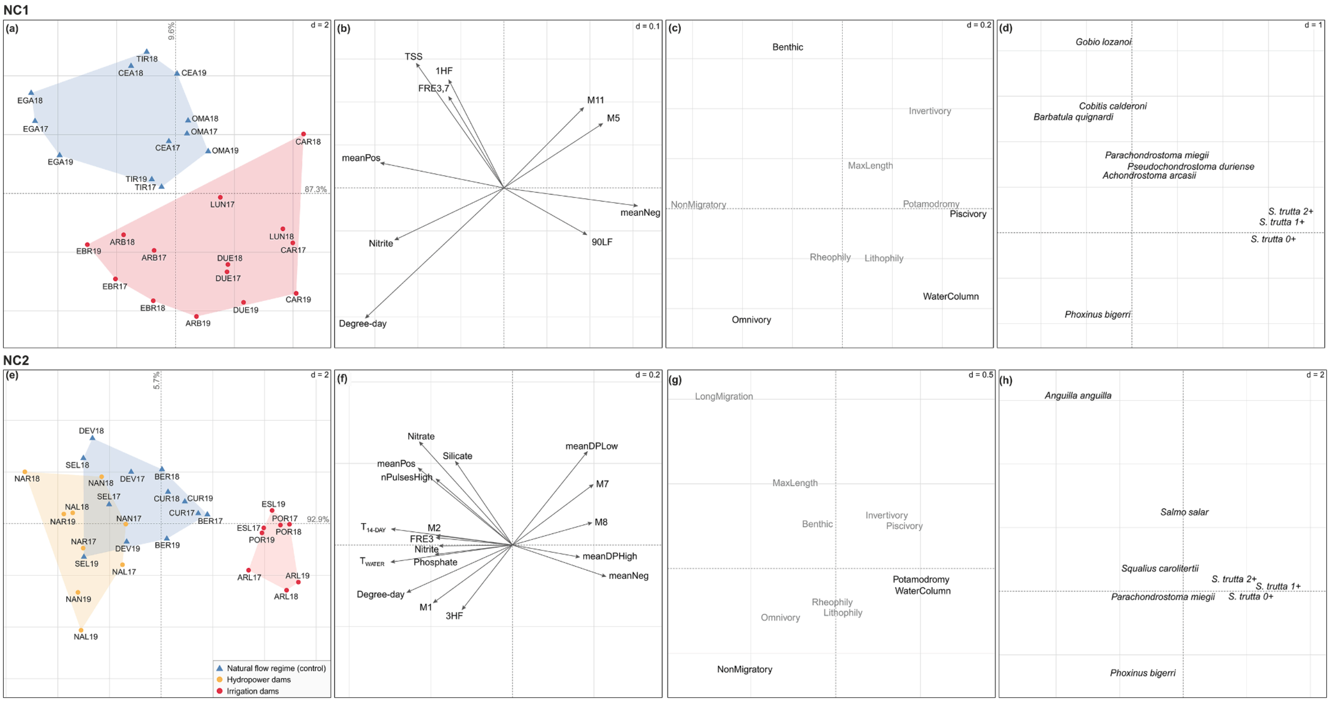

Fig. 6. Ordinations showing the first two RLQ axes on fish communities in NC1 (top) and NC2 (bottom). (a, e) Sampling site scores according to flow regulation (site code and year of sampling, see Table 1). (b, f) Coefficients for key HIs and physico-chemical variables with strong links to traits (see Table S2 for codes). (c, g) Coefficients for traits (see Table S5 for codes). Traits with no significant relationships (see fourth-corner analysis, Fig. S7) are represented in grey. (d, h) Coefficients for species, see Table S11. The "d" values give the grid size for scale comparison across graphs.

in nutrient concentrations, while hydropower dams were linked to higher rates of flow change and to increases in water temperature. Our second hypothesis also holds, as biological responses were community- and factor intensity-dependant. In this regard, it is worth noting that the taxonomic metrics were not always sensitive to dam impacts, while key trait-based community shifts emerged along the gradients of hydrological and physico-chemical dam-induced changes. Hydrological alteration (e.g. changes in low and high flow extremes, flow rise and fall rates, summer and winter flows, frequency and duration of low or high flow pulses), along with changes in water temperature and nutrient concentrations, showed significant relationships with trait-based community shifts, especially for macroinvertebrates and diatoms. Furthermore, dam-related impacts favoured a higher abundance of disturbance-tolerant traits (e.g. planktonic diatoms, multivoltine macroinvertebrates, non-migratory fish), as expected.

4.1. Environmental changes and dam purpose

Dam operational schemes (i.e. irrigation and hydropower) generated different changes in the hydrological and physico-chemical characteristics, as has been reported in previous studies (García de Jalón et al., 2019). Contrary to this result, Peñas and Barquín (2019) highlighted a lack of dependency between the hydrological alteration output and the purpose of the dam. Nonetheless, this discrepancy might relate to the contrasting spatial extent of both studies, as Peñas and Barquín (2019) covered the Iberian Peninsula and nine different hydrological classes. We found that river reaches affected by irrigation dams in both NC1 and NC2 showed increases in the summer flow magnitude and decreases in winter flows and in the frequency and magnitude of extreme high flow events. This result agreed with the observed inversion of river flow regimens to attend to urban and agricultural water demands (Richter and Thomas, 2007), which was also reported from Mediterranean rivers (e.g. García de Jalón et al., 2019).

The three dams used exclusively for hydropower generation (Narcea, Nalón, and Nansa) are located in Cantabric catchments, a region characterised by the confluence of coastal mountains and high precipitation levels (Esteban-Parra et al., 2003). They have relatively lower storage indices in comparison to other reservoirs included in this study (on average, 1.7 times smaller; Table 1) and their hydrological impact was mostly related to the frequent day-to-day or even sub-daily flow changes (Zimmerman et al., 2010). Sub-daily discharge information (unpublished data and not available in all gauges; CHC, 2022) indicated abrupt flow changes downstream of Narcea dam (hourly discharges), while Nalón (weekly discharges) and Nansa (run-of-river operation) had less pronounced short-term hydrological alteration. In agreement with previous studies (e.g. Kuriqi et al., 2021; van Looy et al., 2007) our study found significant impacts on aquatic ecosystems produced by hydropower dams. Moreover, biological responses to these flow regime alterations were more clear in macroinvertebrate and diatom communities (see Fig. 4e and 5e), as Narcea samples presented the largest deviation from the control group, while the Nansa ones showed to be more similar to controls. This result has potential implications when analysing biological responses to dam operation schemes, as hydropower dams can present drastic short-term flow changes caused by energy demand fluctuations (e.g. flood peaks occurring at the sub-daily or sub-hourly scale; Zimmerman et al., 2010). In this regard, finer-resolution hydrological information (e.g. hourly discharge) could be useful to unveil flow-ecology relationships that might not be captured when using daily hydrological datasets (Bevelhimer et al., 2015; Zimmerman et al., 2010).

Changes in water physico-chemical variables also varied with dam operational schemes, as highlighted in previous studies (Aristi et al., 2014; Kamidis et al., 2021; Ling et al., 2016). Irrigation dams considerably reduced the nutrient and TSS concentrations downstream. Previous studies have shown that the large storage volumes and extended residence times of irrigation dams are capable of retaining nutrients and suspended solids, causing disturbances in ecosystem structure and functioning downstream (Friedl and Wüest, 2002). Romero et al. (2016) gave further evidence on the effect of reservoirs with large regulatory capacity in Mediterranean climates, with nitrogen retention rates up to 90%. Hydropower dams presented significantly higher water temperatures in comparison to controls located at similar altitudes. Unlike large reservoirs, small dams present little or no thermal stratification, and water temperature downstream tends to rise due to the surface exposure to solar radiation, low flow velocities, and low magnitudes of short-term minimum flows (Bejarano et al., 2017; Chandesris et al., 2019). Thus, dam purpose (i.e. design) and operation schemes can significantly affect how these hydraulic infrastructures affect geophysical processes and river biodiversity.

4.2. Biotic indices responses to irrigation and hydropower dams

In general, biotic indices responses varied across dam types and natural classes. Diatom indices presented slightly higher scores in altered rivers and showed significant correlations to physico-chemical variables. Recent studies have pointed out similar results, for instance, Krajenbrink et al. (2019) found that the Trophic Diatom Index scored higher at impacted sites. These results indicate a possible community shift downstream of irrigation dams to adapt to lower nutrient and TSS concentrations and to more stable and permanent flows, conditions that have been shown to favour the development and growth of biofilm algae (Biggs et al., 1998). The reduction of grazers downstream of dams also contributes to a primary producer community shift towards more diverse communities (Liess and Hillebrand, 2004). Literature on diatom taxa richness in below dams is relatively scarce, but most research to date reported a greater number of taxa at dam downstream sites, similar to the results found in our study (Growns and Growns, 2001; Smolar-Žvanut and Mikoš, 2014). By contrast, our results indicated that the direction of community change would highly depend on which direction hydrological and water physicochemical characteristics are altered.

Macroinvertebrate richness and diversity showed important responses to HIs and physico-chemical variables significantly altered by the presence of irrigation dams (e.g. summer flows, low flow extremes, frequency of high flow events, nutrient concentrations). These results suggest that these indices may be good indicators of the biological impacts caused by these dams, although they have been rarely used for this purpose (but see Holt et al., 2015). In contrast, IASPT and LIFE scores showed weak responses to HIs and water quality variables altered by dams. This is not surprising since most biotic indices (e.g. IASPT, IPS) were originally designed to target organic pollution and water quality rather than other stressors (Bonada et al., 2006; Friberg et al., 2011). Conversely, the LIFE index, a macroinvertebrate metric designed to evaluate hydromorphological alteration (Extence et al., 1999), failed to detect any effect of irrigation dams on macroinvertebrate communities. Similar results have also been reported previously (e.g. Álvarez-Cabria et al. 2017; Laini et al. 2018). This limitation might be associated with different hydrological preferences of macroinvertebrates in Spanish streams (Armanini et al., 2011; Laini et al., 2018) and the effect of other relevant variables (e.g. temperature, water quality).

In relation to fish, it is important to remark that these communities in the studied streams are species-poor, with less than 4 species in any case. In fact, in NC2 streams impacted by irrigation dams, communities were composed exclusively by brown trout, decreasing taxonomic richness, diversity, and EFI+ scores (Fig. 3). In contrast, downstream of hydropower dams, the presence of Atlantic salmon and brown trout (i.e. salmonid species considered intolerant to oxygen depletion and habitat degradation) contributed substantially to increase EFI+ index scores. Thus, despite the significant changes found between dam types for taxa richness and EFI+ scores, we believe that these results are not consistent with the dam hydrological or water physicochemical changes. In contrast, we believe these results are more related to biogeographical and dispersion-connectivity issues related to metapopulational dynamics of few species, as it has been demonstrated in nearby catchments for brown trout and transversal obstacles (González-Ferreras et al., 2022, 2019). In fact, fish communities in poor-taxa rivers might not be a good indicator of changes in niche characteristics, as it has been pointed out in other studies (Colin et al., 2018; Maire et al., 2015; Vogel et al., 2019).

4.3. Trait-based responses to irrigation and hydropower dams

Most diatom community shifts in NC1 and NC2 were linked to dam-related changes in the flow regime and physico-chemical conditions (Fig. 2). Small-sized diatoms and low profile (adnate and pedunculate life forms, mostly represented in our dataset by *Cocconeis euglypta* and *Achnathidium pyrenaicum,* respectively) were replaced by planktonic and large-sized diatom cells in sites affected by irrigation dams, in agreement with Goldenberg-Vilar et al. (2021) and Wang et al. (2022). In NC2, the planktonic guild was linked to irrigation-impacted sites, while larger cell sizes and low profile adnate diatoms were more abundant in sites affected by hydropower dams. Planktonic diatoms are less resistant to high flow velocities and usually are found in higher numbers in lentic habitats (Rimet and Bouchez, 2012). Therefore, the more stable medium to low-flow conditions downstream irrigation impoundments may have facilitated the development of planktonic diatom assemblages (Growns, 1999; Krajenbrink et al., 2019; Petts, 1984). Adnate life forms are attached to the substrate by the whole valve area, i.e. adapted to the high flow velocities and scouring (Passy, 2007; Rimet and Bouchez, 2011; Wu et al., 2019). Due to high flow daily disturbance in hydropower dams in comparison to controls, adnate life forms are found in higher number in these impacted sites, whereas low profile pedunculated forms dominate in controls. It must be highlighted that recent studies have pointed out contrasting relationships between the diatom traits and flow regimes (e.g. Dalu et al., 2017; Krajenbrink et al., 2019; Stenger-Kovács et al., 2013). This could be associated to the added effect of other factors, such as nutrient and/or sediment loads. For instance, diatom size (biovolume), which showed contrasting results in NC1 and NC2, is a trait associated to nutrient availability but also to low flow velocities and lentic habitats. More research is needed to clarify if the response of different diatom guilds is a response to higher nutrient concentrations, hydrological conditions, or a combination of both, as the relationship of this trait with environmental variables is still not clear (Lavoie et al., 2006).

As expected, macroinvertebrate traits presented clear responses to the presence of dams and, in general, flow regulation favoured disturbance-tolerant traits, as seen elsewhere (Berger et al., 2018; Murphy et al., 2021). Maximum body sizes (small to medium sizes in NC1, larger sizes in NC2), life cycle duration ($\leq$1 year), respiration (tegument respiration in NC2), food and feeding habits (fine detritus feeders in NC1, deposit feeders in NC2), burrower and interstitial taxa in NC2 were favoured by hydrological and physico-chemical conditions altered by irrigation dams. In turn, macroinvertebrates with longer life cycles ($>$1 year), adult aquatic stage, and shredders were more abundant in natural streams. These results are aligned with previous works assessing the effect of hydrological alteration in Mediterranean streams. For instance, Belmar et al. (2019) detected the dominance of small-sized and multivoltine taxa and a decrease of shredders in regulated perennial rivers in Spanish Mediterranean rivers. Parallel, Mendoza-Lera et al. (2012) and González et al. (2013) also reported a lower abundance of shredders in communities below headwater dams, as the reservoirs retain leaf litter and reduce their food resources (i.e. detritus). Therefore, these traits might be considered key traits to assess the effects of irrigation dams on macroinvertebrate assemblages. Nonetheless, it must be pointed out that the response of the macroinvertebrate communities is also hydrological-class dependant as the association between shredders and flow regime or physico-chemical variables was only significant in NC1.

Although we found no significant variation in water temperature among controls and irrigation dams (i.e. the largest dams in our study), a thermal gradient in NC1 macroinvertebrate communities was significantly associated to voltinism, a trend also reported by Lawrence et al. (2010). Temperature plays a key role in organisms' growth and life cycle duration as their development depends on heat accumulation above a certain temperature threshold (Ward and Stanford, 1982; Woodward et al., 2010). These findings imply that macroinvertebrates might be particularly vulnerable to stressors other than flow regulation, such as water temperature (Chessman, 2009; Durance and Ormerod, 2007), causing important shifts in their life cycles and, as a consequence on macroinvertebrate community structure and composition.

The fish community shifts associated to hydrological and physico-chemical changes were less pronounced than in diatoms and macroinvertebrates (i.e. a lower number of significant trait-environment associations). As we pointed out earlier, we believe that the limited number of fish species (and hence traits) inhabiting the studied streams might limit the sensitivity of fish communities to establish niche-related changes generated by dams (Colin et al., 2018; Maire et al., 2015; Vogel et al., 2019). However, it is important to notice that flow regulation favoured generalists (e.g. omnivorous, non-migratory species) over specialists (e.g. benthic, migratory species). For instance, the absence of benthic invertivorous fish (a sensitive trait, e.g. *Barbatula quignardi*) in impacted sites can be linked to changes in substrate and macroinvertebrate communities (i.e. their main food source) downstream of dams (Wang et al. 2020), as it has been reported previously (Granzotti et al., 2018).

4.4. Implications for dam management

The current high irrigation demands (around 45% of the total annual water consumption in Spain; Fornés et al., 2021) and the increasing future water needs worldwide aggravated by climate change (Törnqvist et al., 2015) underline the urgency of investigating dam impacts on freshwater ecosystems. Few of the biotic indices covered in our study showed significant responses to dams. Most of them have been designed to assess water quality in terms of eutrophication and organic pollution, highlighting the limitations of the available biomonitoring tools to assess hydrological alteration (Ladrera and Prat, 2013; Wang et al., 2022). Moreover, the lack of a mechanistic understanding between the change on these biotic index and the key factors altered by dams (e.g. temperature, water quality, flow regime) limits their use to inform future management actions (De Castro-Català et al., 2020).

In this context, trait-based multivariate analyses allowed to establish a better mechanistic understading linking key traits and main environmental changes induced by dams and, therefore, this approach could provide a better conceptual framework to generate more accurate prescriptions for water managers (e.g. Fig. 7). In this regard, macroinvertebrate communities showed the strongest trait-based responses to irrigation and hydropower dams (i.e. more significant associations between traits and variables altered by these dams), followed by diatoms and fish. In hydropower dams, these responses were less evident, and fish traits did not show significant associations to hydropower-altered variables. Although the relationships identified in this study do not necessarily reflect direct cause-effect relationships, our findings emphasise the need to acknowledge the links between ecological components (e.g. multiple biological communities, ecosystem functions) and the main dam-related drivers of change (e.g. flow, temperature, water quality regimens). These conceptual framework might be very useful to develop effective biomonitoring programmes (e.g. identify sensitive traits to target specific impacts), conservation strategies (e.g. environmental flows or restoration of thermal and nutrient regimens), and to set future research priorities tackling dam impacts on river ecosystems.

Moreover, many environmental flow guidelines directed to diminish the ecological effects of dam operation schemes are designed worldwide using hydrobiological models, e.g. in Spain (Aguilar and Polo, 2016), Canada (Bradford et al., 2011), Australia (Gwinn et al., 2016), Korea

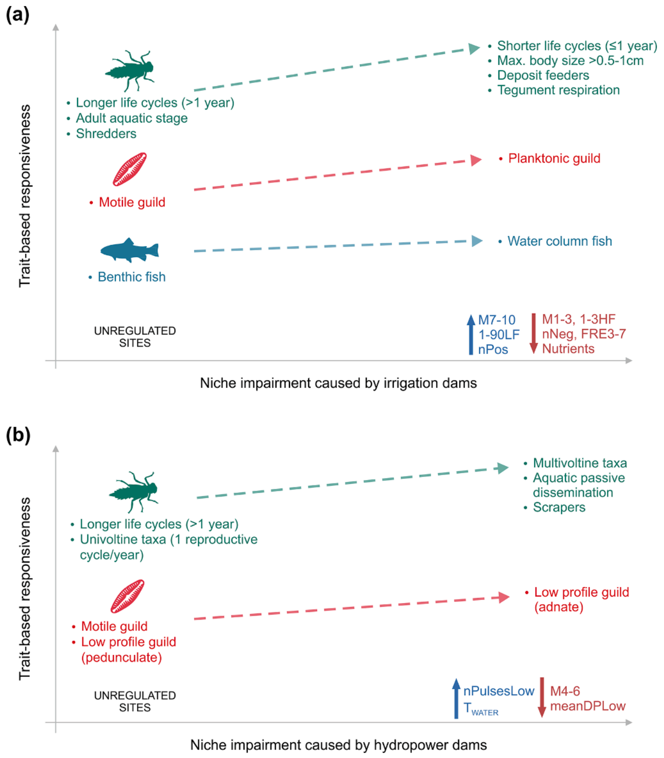

Fig. 7. Main trait-based community shifts (higher abundances of traits) in diatoms (in red), macroinvertebrates (in green), and fish (in blue) associated to dam-induced changes detected in sites impacted by (a) irrigation and (b) hydropower dams. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Park et al., 2020). These models evaluate the habitat suitability for specific fish species as a function of species tolerance to a given set of habitat conditions (mainly velocity, depth, and substrate; Poff et al. 2017). However, other factors (e.g. turbidity, nutrient concentration, water temperature, food availability, time of the day) might also impact species habitat selection, generating biased results (Armanini et al., 2011; Palau et al., 2016; Railsback, 2016). Furthermore, in species-poor rivers, the assessment of anthropogenic pressures is likely to be hampered when using methods sensitive to specific species, the presence/absence of rare taxa, and non-native species (Aparicio et al., 2011; Chen et al., 2020; Colin et al., 2018). In this context, as supported by our findings, macroinvertebrate and diatom communities, which are organisms ubiquitously found in rivers and with lower dependency on dispersal-connectivity (Shurin et al., 2009), could provide a more accurate biological information source for the assessment of dam impacts in terms of responsiveness to niche changes. These riverine communities seem to be suitable to develop specific cause-effect relationships with the key environmental factors (e.g. HIs, water quality) that control changes downstream of dams and, thus, better support adaptations to dam operation schemes towards sustainability. Lastly, these key relationships can also guide future research priorities and monitor the effectiveness of environmental flows or restoration of other niche characteristics (e.g. thermal or nutrient regimens).

Finally, it is worth noting some of the study limitations. Firstly, the three-year period of sampling in this study does not embrace the entire potential interannual hydrological and physico-chemical variability within these sites, which might provide an incomplete understanding of the long-term effects of dams on the studied river ecosystems. Nonetheless, previous works covering the same study area have found similar hydrological patterns (i.e. HI) between this three-year series and the long-term period series (Goldenberg-Vilar et al., 2021). In addition, other environmental factors (e.g. substrate composition, intrannual variability, sub-daily flow changes), which can be potentially relevant for the river biota, may be missing. Consequently, we consider that water agencies and dam operators should boost and provide resources to maintain long-term monitoring programs covering hydrological, physico-chemical, and biological sampling to disentangle the actual effect of dam operation schemes on river ecosystems, which could lead to an effective adaptive management cycle. Secondly, most of the results on this study and many others dealing with dam effects on river biota (e.g. Sánchez-Pérez et al., 2020; Wu et al., 2019) are based on correlations between biological response and potential environmental predictors. A major breakthrough in this research field that could contribute to test the effect of changes on dam operational schemes is long-term experiments on a real scale. Thus, we definitively encourage setting up experiments in partnership with dam operators (e.g. Consoli et al., 2022) to validate key ecological-environmental responses that could orientate future efforts to reduce negative effects of dams on river biodiversity.

5. Conclusions

In summary, our findings indicated that the seasonal flow regime inversion and nutrient reduction downstream of irrigation dams, as well as the elevated rate of flow change and water temperature associated to hydropower dams, caused significant trait-based community shifts in macroinvertebrate communities, followed in intensity by diatoms and fish. In contrast to biotic indices, traits describing body size, life cycle duration, respiration, feeding habits, and ecological guilds allowed to establish a better mechanistic understading linking traits and hydrological and physico-chemical changes. Our findings may help to provide prescriptions for water managers to design conservation programmes (e.g. environmental flows) that allow reducing the negative effects of dam operation; however, national/regional governments and water agencies must boost long-term monitoring programs that allow increasing our mechanistic understanding on the effects of dam operation in river ecosystems.

CRediT authorship contribution statement

Cássia Rocha Pompeu: Methodology, Software, Visualization, Formal analysis, Writing – original draft. **Francisco J. Peñas:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Alejandra Goldenberg-Vilar:** Data curation, Writing – review & editing. **Mario Álvarez-Cabria:** Data curation, Writing – review & editing. **José Barquín:** Conceptualization, Supervision, Project administration, Funding acquisition, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109662.

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