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Evaluating the response of current biotic indices and functional metrics to natural and anthropogenic predictors in disconnected pools of temporary rivers

Zeynep Ersoy^{a,b,*}, Nieves López-Rodríguez^{a,b,c}, Raúl Acosta^{a,c}, Maria Soria^{a,b,d,e}, Joan Gomà^{a,b}, Francesc Gallart^c, Cesc Múrria^{b,f}, Jérôme Latron^c, Pilar Llorens^c, Pau Fortuño^{a,b}, Guillermo Quevedo-Ortiz^{a,b}, Núria Cid^{g,a}, Narcís Prat^{a,h}, Miguel Cañedo-Argüelles^c, Núria Bonada^{a,b}

^a FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Barcelona, Catalonia, Spain

^b Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain

^c SHE2 group (Surface Hydrology, Ecology and Erosion), Institute of Environmental Assessment and Water Research, IDAEA, CSIC, Barcelona, Catalonia, Spain

^d Centre d'Estudis dels Rius Mediterranis - Universitat de Vic - Universitat Central de Catalunya, Museu del Ter, Manlleu, Catalonia, Spain

^e Aquatic Ecology Group - Universitat de Vic - Universitat Central de Catalunya, Vic, Catalonia, Spain

^f ZooSysEvo (Zoological Systematics and Evolution), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Barcelona, Catalonia, Spain

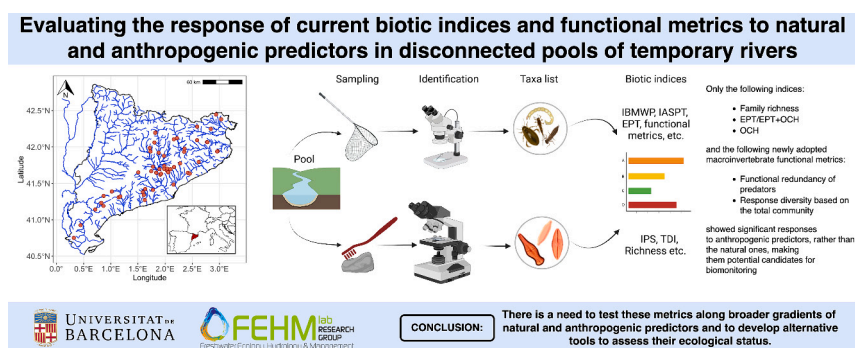
^g IRTA Marine and Continental Waters Programme, La Ràpita, Catalonia, Spain

^h Institut de Recerca de l'Aigua (IdRA), Universitat de Barcelona, Barcelona, Catalonia, Spain

HIGHLIGHTS

- Current biomonitoring programs often neglect disconnected pools of temporary rivers.
- Disconnected pools serve as biodiversity refugia and provide a suitable habitat for sampling.
- We tested whether current biotic indices and functional metrics detect anthropogenic and natural predictors in pools.
- Most biotic indices and functional metrics did not perform well in detecting anthropogenic impacts.
- We need to test these metrics along broader gradients of predictors and develop alternative assessment tools.

GRAPHICAL ABSTRACT



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ABSTRACT

Temporary rivers, forming the majority of river networks worldwide, are key biodiversity hotspots. Despite their great value for maintaining biodiversity and ecosystem functioning, they are often neglected in biomonitoring programs due to several challenges, such as their variable hydromorphology and the difficulty of establishing

* Corresponding author at: FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Diagonal, 643, 08028 Barcelona, Catalonia, Spain.

E-mail address: zzeynepersoy@gmail.com (Z. Ersoy).

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reference conditions given their dynamic nature, resulting in highly variable communities. Disconnected pools often form in temporary rivers when flow ceases, providing refuge for aquatic taxa. Given their importance for biodiversity conservation, revising and adapting biotic indices are needed. Here, we evaluate the performance of current biological indices designed for perennial rivers (macroinvertebrates, diatoms) and functional metrics (macroinvertebrates) in assessing biological quality of disconnected pools. We sampled 55 disconnected pools in Catalonia, NE Spain, covering local (e.g., physico-chemical variables, water chemistry) and regional (e.g., human influence, hydrological variables at the water body level) natural and anthropogenic gradients. Only a few macroinvertebrate biotic indices (e.g., family richness, EPT/EPT + OCH and OCH) showed strong responses to anthropogenic predictors and were unaffected by natural predictors at both local and regional scales, making them suitable for biomonitoring. Of the newly adopted functional metrics of macroinvertebrate communities tested, only two (i.e., functional redundancy of predators and response diversity based on the total community) responded strongly to anthropogenic predictors. The rest showed varying responses to the interactive effect of anthropogenic and natural predictors, requiring calibration efforts. Models assessing these metrics explained <40 % of the total variation, likely due to the interplay of colonization/extinction dynamics and density-dependent trophic interactions governing community assemblages in disconnected pools. Although some existing biological metrics could potentially be used to monitor the ecological status of disconnected pools, we call for further development of biomonitoring tools specifically designed for these habitats since they will become more widespread with global change.

1. Introduction

Temporary rivers, also known as intermittent rivers and ephemeral streams, make up the majority of the world's river networks (Datry et al., 2014; Messenger et al., 2021) and are known to be hotspots of freshwater biodiversity (Cid et al., 2017; Myers et al., 2000). They naturally experience periodic flow cessation or drying, and typically shift between different aquatic phases (i.e., flowing, disconnected pool, and dry; Gallart et al., 2017), displaying highly variable and distinct biological communities (Cid et al., 2017; Tonkin et al., 2017). Temporary rivers are expected to become more widespread globally and experience longer dry periods due to climate change, increased flow regulation and demand for water extraction (Datry et al., 2017; Messenger et al., 2021). However, they have been largely neglected in environmental management and biodiversity conservation planning worldwide because all efforts were focused on perennial rivers (Datry et al., 2023a; Leigh et al., 2019). This is mainly due to the difficulty of hydrological classification of temporary rivers and establishing their reference conditions, as they are highly dynamic ecosystems in space and time (Gallart et al., 2017; Munné et al., 2021; Skoulikidis et al., 2017). Moreover, there is usually a mismatch between the timing of regular sampling by water authorities and the flowing phase in these ecosystems, resulting in sites without biological data (Munné et al., 2021). In the context of the European Water Framework Directive (WFD), many temporary rivers have small catchment areas (<10 km²) and low mean natural flow, which makes them not eligible as official water bodies and are therefore excluded from biomonitoring programs (Munné and Prat, 2004; Stubbington et al., 2018; Munné et al., 2021). Their management also still depends on the classification of the water bodies into the different natural flow regime existing in each river basin district (Munné et al., 2021).

Current biotic indices have been developed to assess anthropogenic factors in perennial rivers, but they may fail when flow intermittence is present (Buffagni et al., 2020; Datry et al., 2023b). Also, their validity for assessing the ecological status of temporary rivers is under debate. These indices often rely on sensitive lotic taxa that may be absent in temporary rivers, and their applicability may be inadequate given the generalist taxa found in pools, especially during dry years (Bogan et al., 2017a; Cid et al., 2016; Lobera et al., 2019; Prat et al., 2014). During the disconnected pool phase, low values in biotic indices may be due to flow intermittence and the disappearance of species with greater affinity to riffles, rather than anthropogenic factors (Mazor et al., 2014; Munné and Prat, 2011; Soria et al., 2020). Recently, several studies have explored the development of biotic indices and functional metrics that can capture anthropogenic factors on these dynamic ecosystems (Crabot et al., 2021; Soria et al., 2020), either through calibrating current indices by

removing drying-sensitive macroinvertebrate taxa (Arias-Real et al., 2022) or using flow response guilds (White et al., 2019).

Disconnected pools are widespread in temporary rivers of Mediterranean climate regions (Bonada et al., 2020; Gallart et al., 2017; Munné et al., 2021). These rivers experience dramatic changes in the environmental and habitat conditions, which in turn, influence the structure and functioning of their biological communities (Bonada et al., 2020). At the regional scale, they can be highly vulnerable to human disturbance and pollution (Chiu et al., 2017; Gómez et al., 2017) through direct or indirect impacts. They can be fed solely by runoff and precipitation, or connected to groundwater, depending on the hydroclimatic conditions of the catchment (Bonada et al., 2020; Bourke et al., 2023), which could have consequences on temperature and oxygen levels (Woelfle-Erskine et al., 2017). However, disconnected pools are typically characterized by high temperatures and concentrations of solutes, organic matter, and low oxygen levels (Boulton, 2003; Bonada et al., 2020; Sarremejane et al., 2022), and can be governed by biotic interactions resulting from decreasing habitat and resource availability at the local scale (Bonada et al., 2020; Cid et al., 2016). They can be present in riverbeds year-round even during dry periods and thus offer an opportunity to assess the ecological status of temporary rivers. Disconnected pools also have a high conservation value because they provide resources for terrestrial taxa and act as refugia for aquatic organisms during dry periods (Bonada et al., 2020). This way they support the persistence of the native taxa (Bogan et al., 2019; Hill and Milner, 2018; Sánchez-Montoya et al., 2022) or even rare and endemic taxa adapted to their potentially extreme environmental conditions, such as anoxia (Datry et al., 2017).

In the last decade, there have been several attempts to define new ecotypes for Mediterranean temporary rivers based on their hydrology (Gallart et al., 2017). For example, the inclusion of a new typology categorized as "temporary rivers with disconnected pools" (i.e., intermittent-stagnant ecotype) could be a first step towards a definition of the reference conditions for this category (Munné et al., 2021). Despite all efforts to establish this new ecotype, reliable indicators to determine its biological quality are still lacking. Thus, there is a need to obtain information to assess if calibration of current indices is possible or if alternative methods are needed to assess the biological quality of disconnected pools (Munné et al., 2021).

In this study, we sampled 55 disconnected pools with varying degrees of anthropogenic and natural predictors to (1) assess whether current biotic metrics of benthic macroinvertebrate and diatom communities can be used to detect anthropogenic predictors during the disconnected pool phase at local and regional scales, and (2) test the potential use of newly developed functional metrics (i.e., functional redundancy, response diversity) to assess biological status of disconnected pools using macroinvertebrate biological traits. We hypothesized

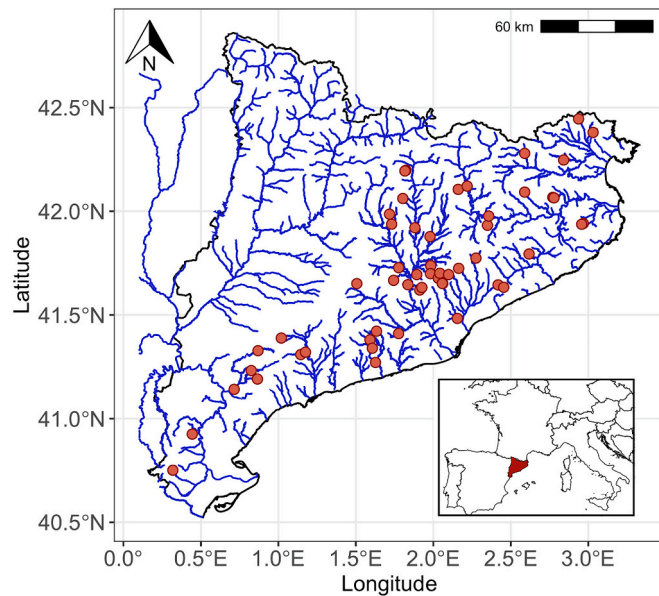


Fig. 1. Map of 55 disconnected pools sampled across Catalonia, NE Spain. Red dots indicate the sampling locations and blue lines indicate the main fluvial networks in Catalonia.

that current biotic indices would respond to the natural intrinsic predictors of disconnected pools (e.g., environmental predictors such as organic matter concentration, temperature and extreme natural conditions such as hypoxia and hydrological predictors such as zero-flow permanence) at both local and regional scales rather than to anthropogenic predictors (e.g., nutrient concentrations, human population density and number of wastewater treatment plants) because environmental niche filtering conditions dominate after pools disconnect. Thus, we expect that the current macroinvertebrate and diatom indices would not adequately capture anthropogenic predictors at both local and regional scales. In contrast, macroinvertebrate functional metrics could have a potential to capture anthropogenic predictors, as metrics derived from functional trophic groups have shown to be not affected by natural flow intermittence in temporary rivers having disconnected pools (Soria et al., 2020).

2. Material and methods

2.1. Sampling and laboratory analyses

We selected 90 pools in temporary rivers using our own experience and previous hydrological data introduced by the Catalan Water Agency (ACA) in the Temporary Rivers Ecological and Hydrological Status (TREHS) software (Gallart et al., 2017). To determine when disconnection occurs, we visited the connected pools often based on the water level of the previous visit to determine when disconnection occurs. Once pools were disconnected (i.e., from May to September 2021, ranging from 3 to 64 days, average of 20 days), we collected environmental and biological samples from the 55 pools belonging to nine hydrographic basins in Catalonia, NE Spain (Fig. 1 and Table S1), covering most river catchments in one of the most heavily populated regions of Spain (Damásio et al., 2011; Prat and Rieradevall, 2006). The remaining 35 pools never got disconnected and were therefore removed from the analyses. The size of pools was measured as surface area by multiplying the length by the width of the pool. Their size ranged from 0.6 to 96.4 m² with an average of 19.41 m², covering a wide variety of sizes and depths.

When pools were disconnected, we sampled macroinvertebrates using a standardized protocol for perennial streams (Jáimez-Cuéllar, 2002) adapted to disconnected pools. To do this, we selected all available habitats in half of the disconnected pool, leaving the other half

Table 1

List of biotic indices and metrics calculated.

Indices and metrics	Abbreviation	References
Iberian Biological Monitoring Working Party	IBMWP	Alba-Tercedor et al., 2004
Iberian Average Score Per Taxon (IBMWP value /number of families)	IASPT	Alba-Tercedor and Sánchez-Ortega, 1988
Number of macroinvertebrate families	Family richness	AQEM Consortium, 2002
Number of families of Ephemeroptera, Plecoptera and Trichoptera	EPT	Munné and Prat, 2009
Number of families of Odonata, Coleoptera and Hemiptera	OCH	Bonada et al., 2007
Ratio between Ephemeroptera, Plecoptera and Trichoptera taxa to the sum of Ephemeroptera, Plecoptera and Trichoptera taxa, and Odonata, Coleoptera and Hemiptera taxa	EPT/EPT + OCH	Bonada et al., 2006; Cid et al., 2016
1 - GOLD metric, where GOLD stands for Gastropoda, Oligochaeta and Diptera	1-GOLD	Pinto et al., 2004
ICM-9 (ICM-Med), multimetric index proposed by the Mediterranean Geographical Intercalibration Group, based on qualitative data	ICM-Med	Buffagni and Erba, 2004; Buffagni et al., 2005
ICM-11a (IMMi-L), multimetric index for Mediterranean rivers, based on qualitative data	IMMi-L	Munné and Prat, 2009
Number of diatom taxa	Taxa richness	Blanco et al., 2012
Pollution Sensitivity Index	IPS	Coste, 1982
Trophic Diatom Index	TDI	Kelly and Whitton, 1995
Sladeczek index	SLA	Sládeček, 1986
LOBO Index	LOBO	Lobo et al., 2002
Descy Index	DES	Descy, 1979

unsampled to reduce the impact on the community. We then sampled the selected microhabitats in the available half of the pool with a 250 µm mesh kick-net until no more different taxa were detected. This protocol (Jáimez-Cuéllar, 2002) is characterized by its exhaustive and semi-quantitative nature: the microhabitats are sampled until no taxa different from those previously sampled are detected, and the number of passes made in each habitat is recorded to obtain the sampling effort per site sampled. We did not account for the area sampled as we adopted this semi-quantitative approach for the calculation of quality indices and metrics. We preserved the samples in 96 % ethanol, and sorted, counted and identified macroinvertebrates to the family level (i.e., except for Oligochaeta at the sub-class level and Hydracarina at the order level) in the laboratory under a Olympus SZX7 stereomicroscope at magnification ranging from 0.8 to 5.6 following Tachet et al., 2010 and Osorio Álvarez et al., 2021. For diatoms, following the sampling and laboratory protocol from the Ministry of Agriculture, Food and Environment (MAAMA, 2013), we brushed the surface and edges of the stones, cobbles, bedrock and different substrates found in each pool, comprising seven substrates per pool and preserved the samples in 96 % ethanol. In the laboratory, we treated the samples with hydrogen peroxide to remove organic matter and rinsed with distilled water to obtain a clean frustule suspension. We then added drops of hydrochloric acid to remove calcium carbonate and mounted permanent slides with Naphrax® resin (CEN, 2003). We counted samples until we had at least 400 valves from the entire sample and identified them to the species level using taxonomic keys (Hofmann et al., 2011; Lange-Bertalot and Krammer, 2000-2011) under a POLYVAR light microscope with DIC at 1000× magnification.

2.2. Calculation of biotic indices and functional metrics

After a literature screening of biotic indices widely used in the Iberian Peninsula and Europe under the WFD that have potential to be used in disconnected pools (see Table 1), we selected and calculated nine qualitative and semi-quantitative biotic indices for macroinvertebrates

(i.e., IBMWP, IASPT, family richness, EPT, OCH, EPT/OCH + EPT, 1-GOLD, ICM-Med and IMMI-L) and five for diatoms (i.e., taxa richness, IPS, TDI, SLA, LOBO, DES). To calculate indices for macroinvertebrates, we used the “*biomonitor*” package (Laini et al., 2022), while for diatoms we used the “*diaThor*” package (Nicolosi Gelis et al., 2022) in R version 4.0.2 (R Core Team, 2020).

Additionally, previous studies (Soria et al., 2020; Crabot et al., 2021) showed that functional metrics of macroinvertebrates can potentially be used in temporary rivers. Based on this, we also calculated 12 functional metrics, out of which five metrics based on the number of taxa that contribute similarly to each functional feeding group (i.e., functional redundancy or FR) and seven metrics based on how taxa functionally respond to natural and anthropogenic predictors (i.e., traits related to resilience and resistance strategies; response diversity or RD), following the methodology of Soria et al. (2020). To do so, we first characterized the effect and response traits of macroinvertebrates at the family level coded using a fuzzy approach (except for Oligochaeta and Hydracarina) as these can be easily implemented by water monitoring agencies, collecting mean trait values at the genus level from Tachet et al. (2010). Effect traits describe how organisms contribute to ecosystem functioning by transferring resources and energy through the food web (Suding et al., 2008). On the other hand, the response traits reflect organism resistance and resilience to natural and anthropogenic predictors, providing information on how communities respond to environmental changes (McLean et al., 2019; Suding et al., 2008). For the effect traits, trophic functional group information (i.e., predators, grazers, shredders, gatherers, filterers, piercers, and parasites) were collected. Response traits, categorized by resistance and resilience traits, including asexual reproduction, resistance forms, respiration and locomotion types, life cycle duration, and dispersal methods, were selected based on Lytle and Poff (2004), Bogan et al. (2017b), and Stubbington et al. (2017). For FR, we used effect traits (i.e., functional trophic group) to calculate the trait richness (presence-absence, pa) or average abundance (ab) for the whole community level and each functional group: predators, grazers, shredders, omnivorous and piercers (see Table S2). For RD, we used resilience

and resistance traits to calculate functional richness (FRic) (Villéger et al., 2008), RD metrics of the whole community level and each functional group using average abundance (ab).

2.3. Natural and anthropogenic predictors

We determined the predictors affecting each pool using local (on-site) and water body (hereafter referred to as “regional”, i.e., catchment or sub-catchment area of at least 10 km² or corresponding to a stretch of >5 km in length, McCluney et al., 2014) scale that are detailed below. Additionally, we considered regional hydrological parameters using TREHS software (Gallart et al., 2017), as this is already implemented by water monitoring agencies.

2.3.1. Local natural and anthropogenic predictors

At the local scale, we considered physico-chemical parameters and water depth as predictors of natural and anthropogenic predictors. We measured water temperature (°C), conductivity (µS/cm) and dissolved oxygen (% and mg/L) in-situ using a multi-parameter probe (YSI Pro Plus). Water depth was measured at 10 different points in each pool and then the average was taken. Additionally, we filtered water samples using glass microfiber filters (Grade GF/C) for nutrient analysis and stored them frozen in 0.5 L sterilized plastic bottles until further analysis. Nitrates (NO₃), nitrites (NO₂), ammonium (NH₄), phosphates (PO₄) and total organic carbon (TOC) were then determined using standard protocols in the Environmental Laboratory of the Technical Office of Environmental Assessment and Management (Area of Territory and Sustainability) of the Provincial Council of Barcelona (UNE-EN ISO/IEC 17025:2005).

2.3.2. Regional environmental and hydrological predictors

At the regional scale, we considered the number of wastewater treatment plants (WWTP), the Human Influence Index (HII) extracted from Wildlife Conservation Society and Center For International Earth Science Information Network database (WCS-CIESIN) as anthropogenic

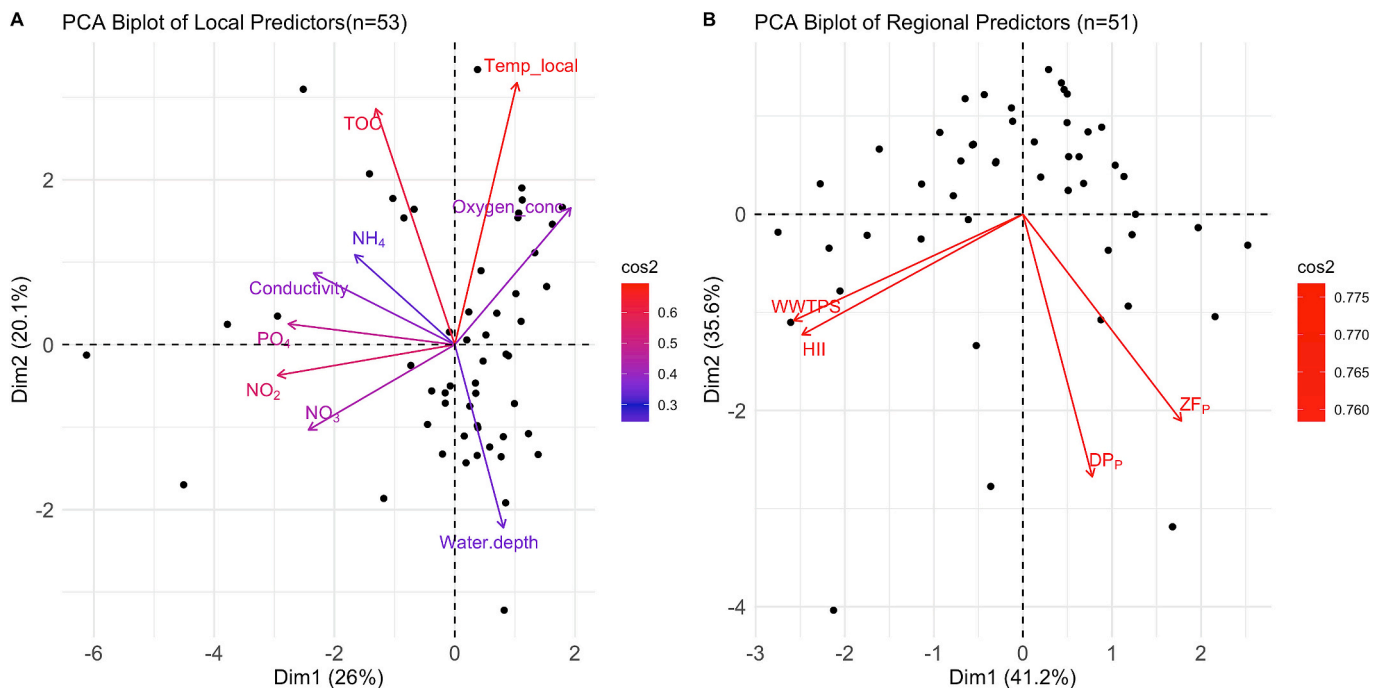


Fig. 2. PCA biplots of the local (A) and regional (B) natural and anthropogenic predictors. In (A) the local predictors were: Temp_local: local temperature, TOC: total organic carbon, Oxygen_conc: oxygen concentration, NO₃: nitrates, NO₂: nitrites, and PO₄: phosphates concentration. In (B) the regional predictors were: WWTPs: number of WWTPs in 10 km buffer zones, HII: human influence index, DP_p: disconnected pool permanence, ZF_p: zero-flow permanence. Dim1: PC1 axis, Dim2: PC2 axis. Higher cos2 values indicate a good representation of the variable on the principal component.

predictors, and the zero-flow permanence (ZF_p) and the disconnected pool permanence (DP_p) as natural predictors (Gallart et al., 2017). For WWTPs, we collected information from the HydroWASTE dataset (Ehalt Macedo et al., 2022) in a 10 km buffer zone around the study sites using QGIS (version 3.22.5). We determined the average HII, normalized by biome and biogeographic realm, based on human population pressure (population density), human land use and infrastructure (built-up areas, dams, night-time lights, land use/land cover) and human access (coastlines, roads, railroads, navigable rivers) around 10 km buffer zone around the study sites using WCS-CIESIN database (WCS-CIESIN, 2005). The ZF_p and DP_p metrics correspond to the values of flow and disconnected pools' permanence metrics from the TREHS software database (Gallart et al., 2017). Note that due to the nature of the data available, the TREHS database was created by incorporating in situ and Google StreetView observations of the three aquatic phases of each water body (i.e., flowing, disconnected pool or dry riverbed phases every 100–200 m) as well as interviews with local residents into the software (i.e., frequency and duration of the three aquatic phases for each water body).

2.4. Statistical analyses

We conducted all statistical analyses using R version 4.0.2 (R Core Team, 2020) and plotted graphs using the “ggplot2” package (Wickham, 2009). First, to characterize natural and anthropogenic predictors at local and regional scales, we conducted two principal component analyses (PCA) using the “prcomp” function of the “stats” package. All local (NO₃, NO₂, NH₄, PO₄, TOC, conductivity, dissolved oxygen and water depth) and regional (HII, WWTPS, ZF_p, DP_p) predictors were standardized and centered before the analysis. When data were unavailable for any sampling site ($n = 2$ for local, $n = 4$ for regional predictors, $n = 3$ for missing diatom samples) due to missing sampling or data in the databases, these sites were excluded from further analysis. The scores on the first and second axes of PCA (PC1 and PC2) were used as a proxy for the natural and anthropogenic predictors, separately at the local (PC1_{local} and PC2_{local}) and the regional (PC1_{regional} and PC2_{regional}) scales. To determine the effects of local and regional natural and anthropogenic predictors on all biotic and functional metrics, we ran generalized linear regression models (GLMs) with Gaussian, Poisson, or Gamma distribution families depending on the response variable ($n = 52$ for macroinvertebrates and $n = 48$ for diatoms), using the biotic indices and functional metrics as response variables, and the four PCA axis scores (PC1_{local}, PC2_{local}, PC1_{regional} and PC2_{regional}) and the interactions between them (PC1_{local}: PC1_{regional}, PC1_{local}: PC2_{regional}, PC2_{local}: PC1_{regional}, PC2_{local}: PC2_{regional}) as predictors. The most parsimonious models were selected through backward selection using the “stepAIC” function (MASS package; Venables and Ripley, 2002) based on Akaike information criteria values. We visually checked model residuals for normality and homogeneity of variance and then applied log or square-root transformation for some of the response variables to improve the model residuals. For the most parsimonious models, we visualized model predictions using the “effectplot” function and “interactplot” from the “jtools” and “interactions” packages (Long, 2022a, 2022b).

3. Results

Using the local natural and anthropogenic predictors ($n = 53$) (Fig. 2A), the first two axes explained 26 % and 10.1 % of the variation, respectively, and all axes together explained 46.1 % of the total variation. Nitrites (NO₂) had the highest contribution to PC1, followed by phosphates (PO₄) and nitrates (NO₃), showing lower PC1 scores with higher concentrations of the nutrients attributed to anthropogenic predictors. Local temperature (Temp_{local}) contributed the most to PC2, followed by TOC (total organic carbon) and water depth, indicating lower PC2 scores with higher temperatures, higher TOC and lower water depth attributed to the natural pool dynamics. Using the regional

Table 2

GLM results showing the relationship between the biotic indices tested for macroinvertebrates and diatoms, and the local and regional gradients of natural and anthropogenic predictors. For each index, only the most parsimonious models with the corresponding predictors selected are shown. Adj. R²: adjusted R².

Response variables	Predictors	Estimate	p-value	Adj. R ²		
Macroinvertebrates IBMWP	PC1 _{local}	4.33	0.08	0.25		
	PC2 _{local}	-4.60	0.12			
	PC1 _{regional}	5.55	0.07			
	PC2 _{regional}	3.83	0.26			
	PC1 _{local} :PC2 _{regional}	2.66	0.17			
IASPT	PC1 _{local}	0.10	0.09	0.11		
	PC2 _{regional}	0.10	0.18			
	PC1 _{local} :PC2 _{regional}	0.06	0.17			
Family richness	PC1 _{local}	0.05	0.08	0.27		
	PC2 _{local}	-0.06	0.05			
	PC1 _{regional}	0.08	0.01			
	PC2 _{regional}	0.03	0.46			
	PC1 _{local} :PC1 _{regional}	-0.04	0.75			
EPT	PC1 _{local} :PC2 _{regional}	0.03	0.11	0.27		
	PC1 _{local}	0.21	<0.01			
	PC2 _{local}	-0.18	<0.01			
OCH	PC1 _{local}	0.02	0.63	0.19		
	PC1 _{regional}	0.14	<0.001			
	PC2 _{regional}	0.02	0.69			
	PC1 _{local} :PC1 _{regional}	-0.04	0.15			
EPT/EPT + OCH	PC1 _{local} :PC2 _{regional}	0.05	0.09	0.22		
	PC1 _{local}	0.04	0.01			
	PC2 _{local}	-0.03	0.07			
	PC1 _{regional}	-0.02	0.29			
1-GOLD	PC2 _{local} :PC1 _{regional}	0.02	0.16	0.20		
	PC1 _{local}	0.12	0.06			
	PC2 _{local}	-0.01	0.87			
	PC1 _{regional}	0.08	0.14			
	PC2 _{regional}	-0.12	0.14			
ICM-Med	PC2 _{local} :PC1 _{regional}	0.09	0.1	0.29		
	PC1 _{local}	0.33	0.14			
	PC2 _{local}	-0.84	<0.001			
	PC2 _{regional}	0.51	0.16			
IMMi-L	PC2 _{local} :PC2 _{regional}	-0.46	0.09	0.30		
	PC1 _{local}	0.29	0.17			
	PC2 _{local}	-0.85	<0.001			
	PC2 _{regional}	0.45	0.18			
Diatoms Taxa richness	PC2 _{local} :PC2 _{regional}	-0.45	0.08	0.18		
	PC1 _{local}	0.72	0.50			
	PC2 _{local}	1.05	0.41			
	PC1 _{regional}	-0.51	0.72			
	PC2 _{regional}	-0.39	0.83			
	PC1 _{local} :PC1 _{regional}	-1.14	0.16			
	PC2 _{local} :PC2 _{regional}	2.78	0.05			
	IPS	PC1 _{local}	0.05		0.01	0.36
		PC2 _{local}	-0.02		0.43	
		PC1 _{regional}	0.02		0.31	
PC2 _{regional}		-0.05	0.06			
PC1 _{local} :PC1 _{regional}		-0.02	0.03			
TDI SLA	PC2 _{local} :PC1 _{regional}	-0.03	0.04	0.06		
	PC _{regional}	0.87	0.09			
DES	PC1 _{local}	-0.03	0.15	0.28		
	PC2 _{local}	0.03	0.39			
	PC1 _{regional}	-0.01	0.86			
	PC2 _{regional}	0.09	0.02			
	PC1 _{local} :PC1 _{regional}	0.04	0.02			
	PC2 _{local} :PC1 _{regional}	0.04	0.08			
	PC1 _{local}	0.06	0.25			
PC1 _{regional}	-0.06	0.38				
PC1 _{local} :PC1 _{regional}	-0.10	<0.01				

environmental and hydrological predictors ($n = 51$) (Fig. 2B), the first two axes explained 41.2 % and 35.6 % of the variation, respectively, and all axes together explained 76.8 % of the total variation. The number of WWTPs within 10 km buffer zones (WWTPS) contributed the most to PC1, followed by human influence index (HII), showing lower PC1

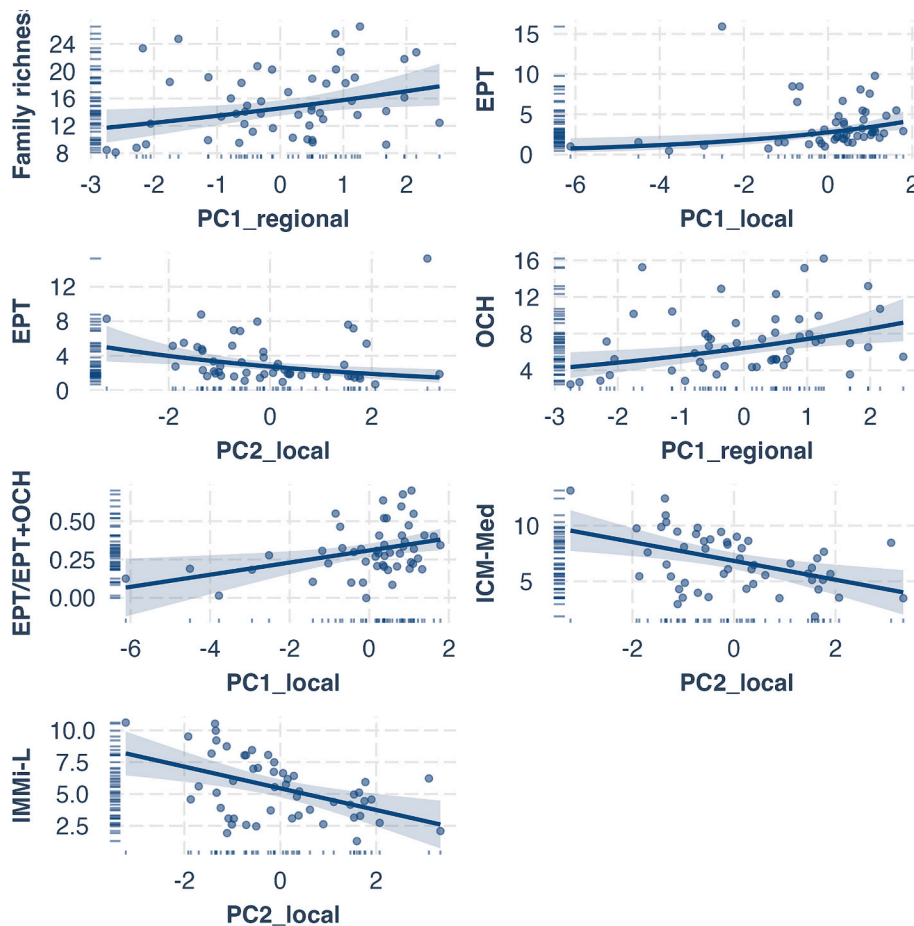


Fig. 3. GLM prediction plots showing relationships between biotic indices of macroinvertebrates (Family richness, EPT, OCH, EPT/EPT + OCH, ICM-Med, IMMI-L) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Shaded regions represent the 95 % confidence intervals and rug plots in the margins show the distribution of the response and predictor variables.

scores with a higher number of WWTPS and human influence attributed to anthropogenic predictors. Disconnected pool permanence (DP_p) had the greatest effect on PC2, followed by zero-flow permanence (ZF_p), indicating higher PC2 scores with higher pool and zero-flow permanence that are highly related to natural pool dynamics. Additionally, as the time since disconnection differed among the pools sampled, we checked for the relationship between disconnection time and some of the biotic indices tested, but no effect was found (Fig. S1).

Because not all GLMs retained the tested predictors, we reported the results for only the ones that retained any of the tested variables. GLMs showed that the PC1 axis of the regional predictors (PC1_{regional}) was positively and significantly related to macroinvertebrate family richness and OCH (Table 2, Fig. 3), which indicates the relation between high levels of anthropogenic impact and lower values of indices. EPT was positively and significantly related to PC1_{local} being lower with low nutrient levels, but negatively to PC2_{local}, thus being higher at higher temperatures and TOC levels (Table 2 and Fig. 3). However, EPT/EPT + OCH showed only positive relationship with PC1_{local} and ICM-Med and IMMI-L were negatively related to PC2_{local} (Table 2, Fig. 3). From diatom biotic indices, IPS was negatively related to interaction between PC1_{local}: PC1_{regional} and PC2_{local}: PC2_{regional}, whereas DES was negatively related to PC1_{local}: PC1_{regional} interaction (Table 2 and Fig. 4). SLA was positively related to PC2_{regional} and PC1_{local}: PC1_{regional} interaction (Table 2, Fig. 5). The remaining biotic indices did not respond significantly to the local and regional predictors ($p > 0.05$, Table 2).

GLMs using macroinvertebrate functional metrics showed significant and positive relationships between PC1_{regional} and PC1_{local}:

PC2_{regional} interaction for FR.predators.pa and logFR.predators.ab, while FR.shredders.pa and logFR.shredders.ab were negatively related to PC2_{local} (Table 3, Figs. 6 & 7). Moreover, we found negative relationship between logFR.omnivoros.ab and PC2_{local}: PC1_{regional} interaction, and between logFR.piercers.ab and PC2_{local}, whereas this relationship was negative between logFR.piercers.ab and PC1_{local}: PC2_{regional} interaction (Table 3, Fig. 7). LogFR.grazers.ab was positively and significantly related to PC1_{local}: PC2_{regional} and PC2_{local}: PC1_{regional} interactions (Table 3, Fig. 8). LogRD was positively related to PC1_{local} and PC2_{local}: PC1_{regional} interaction, and logRD.grazers was positively related to PC1_{local}, but negatively to PC2_{regional} (Fig. 8).

4. Discussion

Despite their high value and vulnerability, temporary rivers have been overlooked in conservation and management plans (Acuña et al., 2014). Understanding how different aquatic phases can inform about ecological quality has been challenging so far due to the complex and dynamic nature of temporary rivers (Datry et al., 2023a; Soria et al., 2020; Stubbington et al., 2022). In our study, we show that most widely used biotic indices for both macroinvertebrates and diatoms and newly adopted functional metrics for macroinvertebrates had low performance in detecting local and regional anthropogenic predictors in disconnected pools of temporary rivers.

In line with our hypotheses, most biotic indices for macroinvertebrates and diatoms did not respond to anthropogenic predictors. Among the biotic indices tested for macroinvertebrates, only family

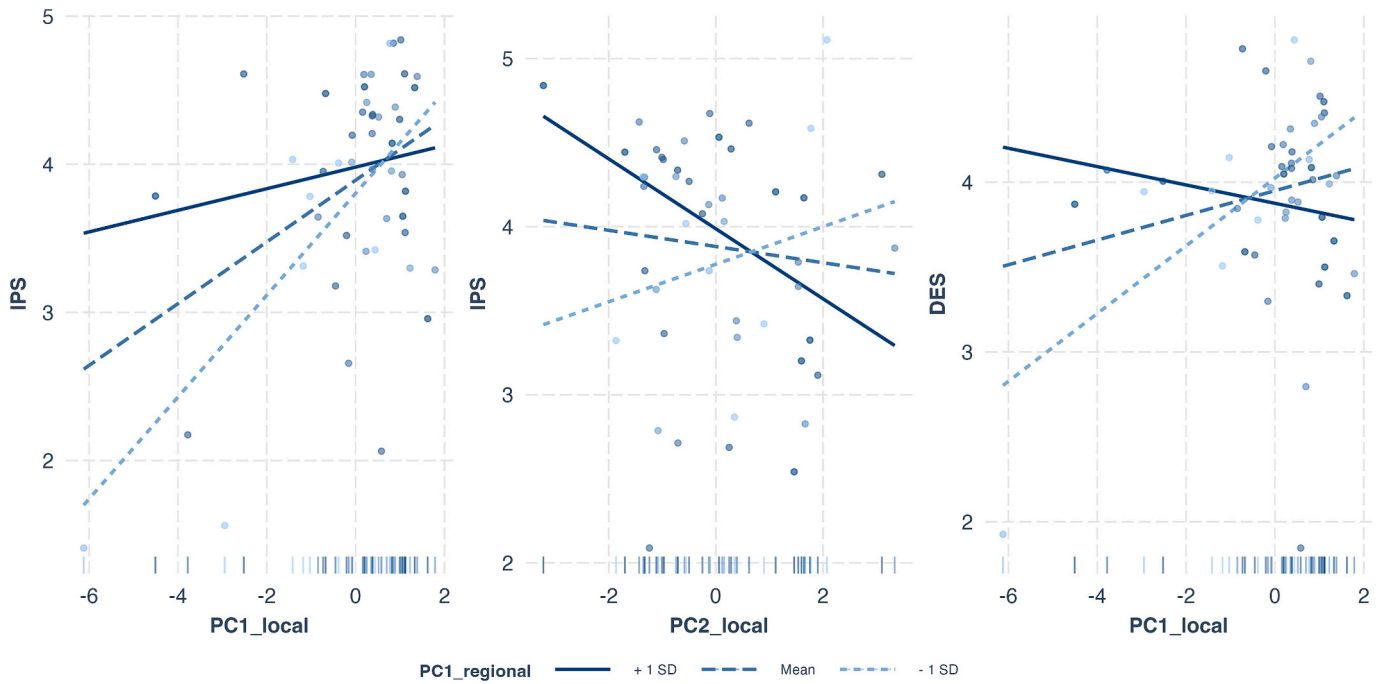


Fig. 4. GLM prediction plots showing simple and interactive relationships between biotic indices of diatoms (IPS and DES) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Rug plots in the margins show the distribution of the response and predictor variables. Legend shows the moderator variable involved in the interaction, and the different dashed lines indicate mean of the moderator variable (here PC_{1_regional}), 1 standard deviation above and below the mean.

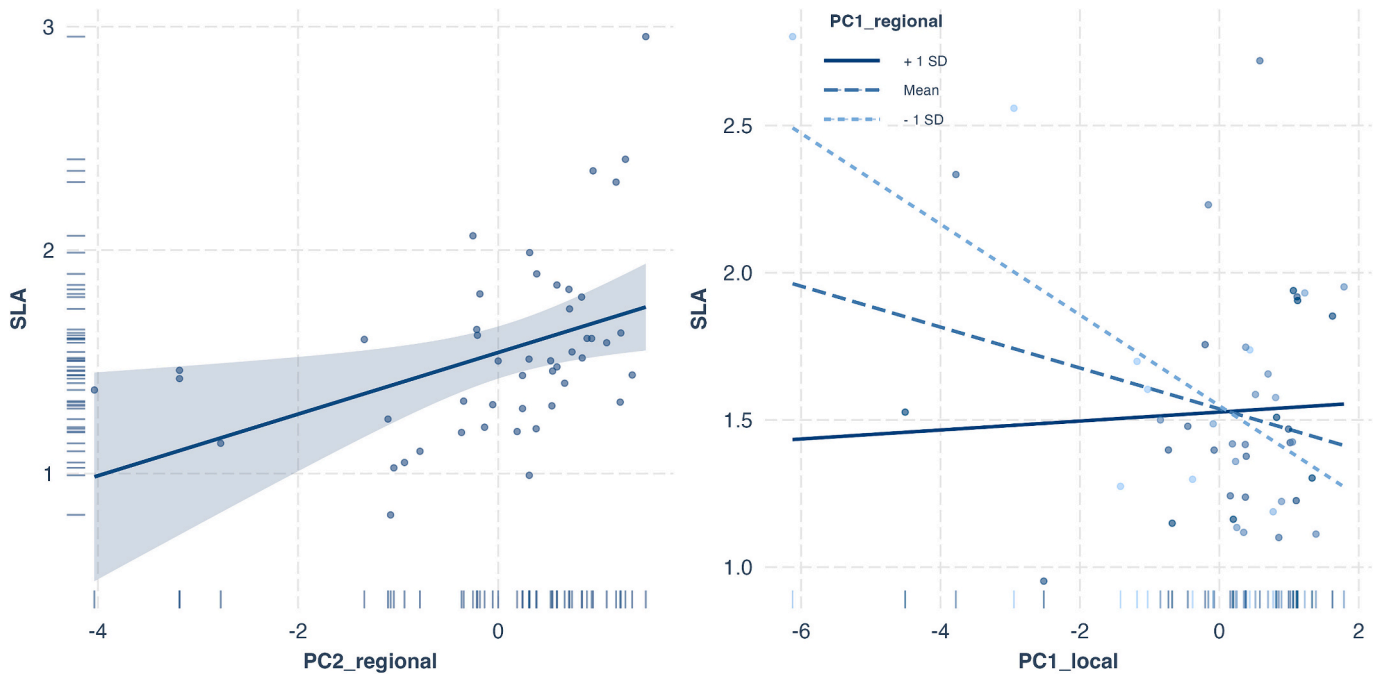


Fig. 5. GLM prediction plots showing simple and interactive relationships between biotic index of diatoms (SLA) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Shaded regions represent the 95 % confidence intervals and rug plots in the margins show the distribution of the response and predictor variables. Legend shows the moderator variable involved in the interaction, and the different dashed lines indicate mean of the moderator variable (here PC_{1_regional}), 1 standard deviation above and below the mean.

richness, OCH and EPT/EPT + OCH varied significantly along the PCA axis of anthropogenic impact (PC1_{local} or PC1_{regional}) but did not show significant differences across the natural impact gradient (PC2_{local} and/or PC2_{regional}). This is supported by previous studies in temporary rivers showing higher correspondence of the value of these

indices with anthropogenic gradient (Prat et al., 2014; Soria et al., 2020; Wilding et al., 2018). The decline in EPT/EPT + OCH ratio in response to anthropogenic predictors can be explained by the replacement of the lotic taxa (e.g., EPT) by the lentic (e.g., OCH) taxa adapted to dominant environmental conditions in disconnected pools such as increased

Table 3

GLM results showing the relationship between the functional indices tested for macroinvertebrates, and the local and regional gradients of natural and anthropogenic predictors. For each index, only the most parsimonious models with the corresponding predictors selected are shown. Adj. R²: adjusted R².

Response variables	Predictors	Coefficients	p-value	Adj. R ²
Functional redundancy				
FR.pa	PC1_local	0.02	0.28	0.10
	PC1_regional	-0.02	0.37	
	PC1_local:	-0.03	0.11	
FR.predators.pa	PC1_regional			0.23
	PC1_local	0.14	0.19	
	PC1_regional	0.30	0.02	
	PC2_regional	0.11	0.36	
FR.grazers.pa	PC1_local:	0.22	<0.01	0.10
	PC2_regional			
	PC1_local	0.23	0.08	
FR.shredders.pa	PC2_local	-0.21	0.15	0.25
	PC2_regional	-0.45	<0.01	
FR.omnivores.pa	PC2_regional	0.39	0.06	0.30
	PC2_local:	-0.29	0.06	
	PC1_local	0.00	0.99	
	PC2_local	-0.10	0.72	
	PC1_regional	0.37	0.20	
FR.piercers.pa	PC2_regional	0.69	0.08	0.18
	PC1_local:	-0.30	0.10	
	PC1_regional			
	PC2_local:	-0.48	0.11	
	PC2_regional	-0.05	0.44	
log(FR.predators.ab)	PC2_local	-0.16	0.07	0.36
	PC1_regional	0.16	0.07	
	PC2_regional	-0.05	0.56	
	PC1_local:	0.08	0.12	
	PC2_regional	0.12	0.29	
log(FR.grazers.ab)	PC2_local	0.11	0.43	0.30
	PC1_regional	0.51	<0.001	
	PC2_regional	-0.12	0.52	
	PC1_local:	0.32	<0.01	
	PC2_regional	0.21	0.15	
log(FR.shredders.ab)	PC2_regional	0.09	0.51	0.20
	PC1_local	-0.13	0.41	
	PC2_local	0.21	0.20	
	PC1_regional	0.04	0.82	
	PC2_regional	-0.17	0.09	
log(FR.omnivores.ab)	PC1_local:	0.29	<0.01	0.19
	PC2_regional			
	PC2_local:	0.26	0.02	
	PC1_regional	0.28	0.07	
	PC2_local	-0.51	<0.01	
log(FR.piercers.ab)	PC2_regional	0.22	0.19	0.24
	PC1_regional	0.02	0.91	
	PC2_local:	0.27	0.23	
	PC2_local:	-0.30	0.01	
	PC1_regional	-0.24	0.17	
RD	PC2_regional	-0.09	0.30	0.35
	PC1_local	-0.21	0.04	
	PC2_local	0.15	0.15	
	PC1_regional	-0.05	0.65	
	PC2_regional	0.14	0.03	
Response diversity	PC1_local	0.01	0.02	0.35
	PC2_local	-0.01	0.05	
	PC1_regional	0.01	0.07	
	PC2_regional	-0.00	0.38	

Table 3 (continued)

Response variables	Predictors	Coefficients	p-value	Adj. R ²
sqrt(RD.predators)	PC2_local:	0.01	0.03	0.14
	PC1_regional			
	PC2_local:	0.01	0.17	
	PC2_rgeional			
	PC1_local	0.02	0.19	
log(RD.grazers)	PC1_regional	0.04	0.11	0.23
	PC2_regional	0.03	0.30	
	PC1_local:PC2:	0.02	0.13	
	regional			
	PC1_local	0.02	<0.01	
sqrt(RD.shredders)	PC2_local	-0.01	0.39	0.13
	PC2_regional	-0.02	0.03	
	PC1_local:	-0.01	0.10	
	PC2_regional			
	PC2_local:	0.01	0.16	
RD.omnivores	PC2_regional	0.03	0.09	0.05
	PC2_local	-0.04	0.06	
log(RD.piercers)	PC1_regional	0.00	0.12	0.11
	PC1_local	-0.01	0.23	
	PC1_regional	0.01	0.23	
FRic	PC1_local:	-0.01	0.10	0.07
	PC2_regional	-0.02	0.07	

nutrient concentrations, temperature increase, and oxygen depletion. For example, as local conditions deteriorate, pools are typically colonized by lentic taxa such as Odonata, Coleoptera and Hemiptera (OCH), which are rarely found in riffles (Boulton, 2003; Bonada et al., 2006; Cid et al., 2016). In contrast, lotic taxa like Ephemeroptera, Plecoptera and Trichoptera (EPT) disappear because they are adapted to flow conditions with lower temperatures and higher oxygen levels and are highly susceptible to drying (Bonada and Resh, 2013), leading to an overall decrease in EPT and EPT/EPT + OCH. Thus, these results should be interpreted with caution, since the replacement of EPT by OCH could be more related to natural hydrological changes than to pollution. However, we also found a decrease only in OCH only with increasing regional anthropogenic predictors, such as the number of WWTPs and human influence index (HII). This does not align with the high pollution tolerance values of OCH (Chang et al., 2014) and calls for a deeper investigation into the response of the EPT/EPT + OCH to anthropogenic predictors in disconnected pools along hydrological gradients. Therefore, these indices could be considered as potential candidates for use in disconnected pools, compared to other analyzed metrics. However, in contrast to our expectations, we did not find that most metrics respond to natural dynamics of the pool. For example, one of the widely used metrics IBMWP did not show any response to both natural and anthropogenic predictors, as it was previously shown to be an effective indicator only in the flowing phase of temporary rivers during wet years (Soria et al., 2020). In the case of diatoms, IPS, SLA and DES showed different responses to the interactive effects of anthropogenic and natural predictors at local and regional scales, showing that the effect of regional impact predictors varied depending on the local impact gradient. Although being consistent with previous studies where local anthropogenic and natural conditions such as nutrients and conductivity are the main drivers of diatom communities (Potapova and Charles, 2003; Yuan et al., 2022), further exploration of these interactions with regional predictors are needed. Moreover, explained variances of the models tested were low, indicating high variability in the composition of communities across disconnected pools. These results are consistent with the previous findings in temporary rivers (Soria et al., 2020; Stubbington et al., 2018) and the low coherence with biological indices could be related to density-dependent factors (i.e., species interactions) and changes in the habitat condition over time during drought periods (e.g., size and permanence of disconnected pools; Bonada et al., 2020), among other things.

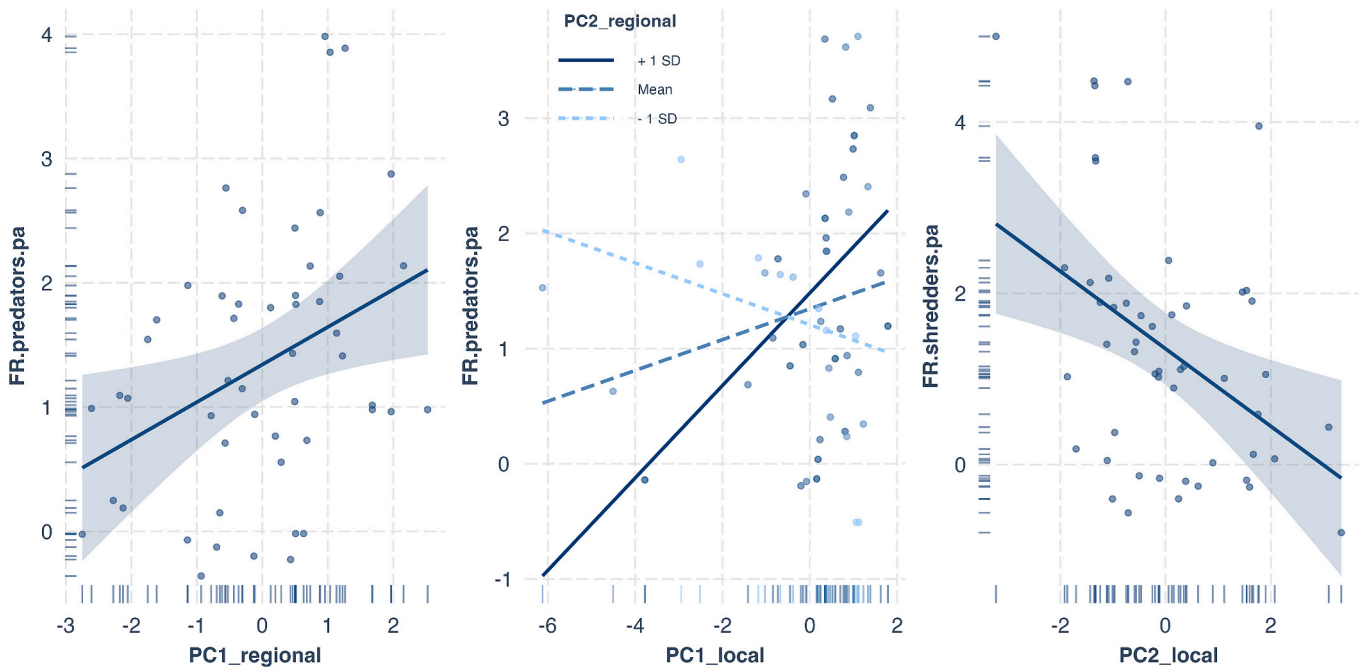


Fig. 6. GLM prediction plots showing relationships between macroinvertebrate functional metrics (FR.predators.pa, FR.shredders.pa) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Shaded regions represent the 95 % confidence intervals and rug plots in the margins show the distribution of the response and predictor variables. Legend shows the moderator variable involved in the interaction, and the different dashed lines indicate mean of the moderator variable (here PC_{2_regional}), 1 standard deviation above and below the mean.

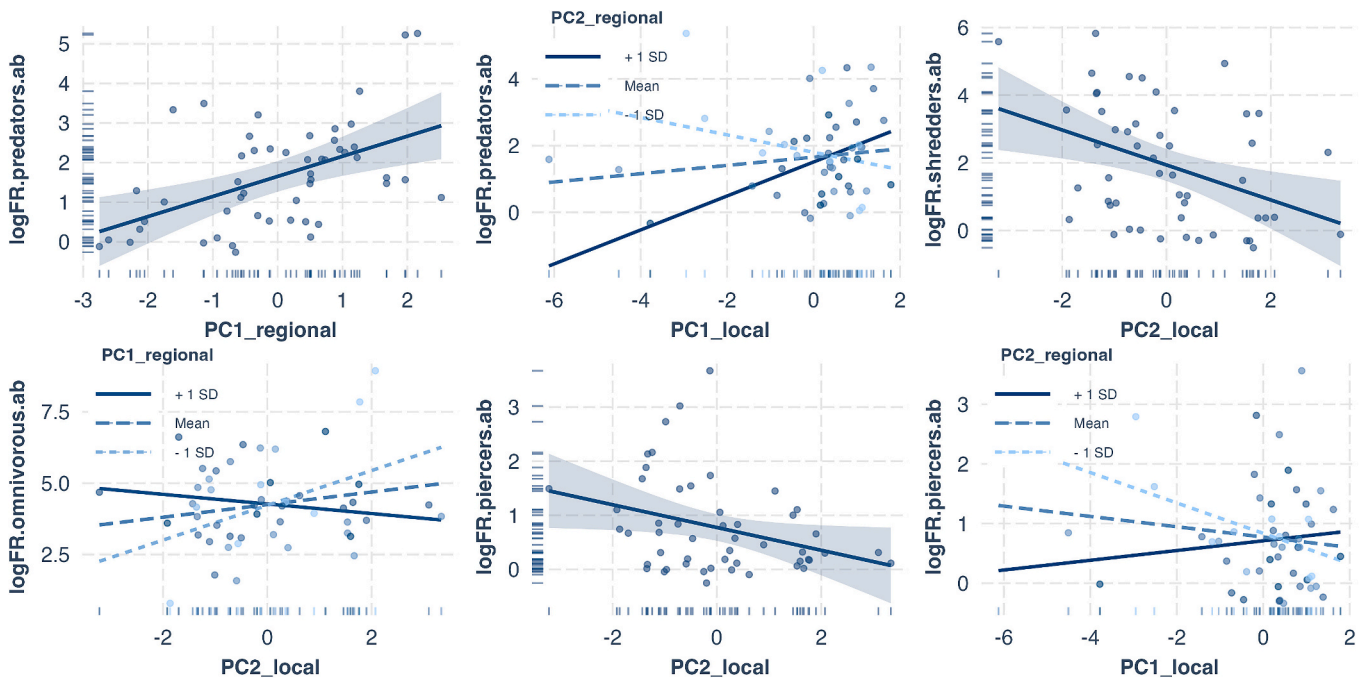


Fig. 7. GLM prediction plots showing relationships between macroinvertebrate functional metrics (logFR.predators.ab, logFR.shredders.ab, logFR.omnivoros.ab, logFR.piercers.ab) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Shaded regions represent the 95 % confidence intervals and rug plots in the margins show the distribution of the response and predictor variables. Legends show the moderator variable involved in the interaction, and the different dashed lines indicate mean of the moderator variables 1 standard deviation above and below the mean.

In line with our expectations, some functional metrics of macroinvertebrate communities showed response to anthropogenic predictors. Only functional redundancy of predators (pa and ab) and response diversity based on the total community varied significantly along the PCA axis of anthropogenic impact. This indicated fewer predator taxa were able to perform similar functions in the ecosystem and most taxa

respond similarly to environmental stressors as human impact increased, which could have important consequences for ecosystem stability and resilience. Moreover, most functional metrics showed significant changes with interaction between local and regional predictors of anthropogenic and natural predictors, showing complex patterns and thus requiring calibration to be used in biomonitoring. Moreover, in our

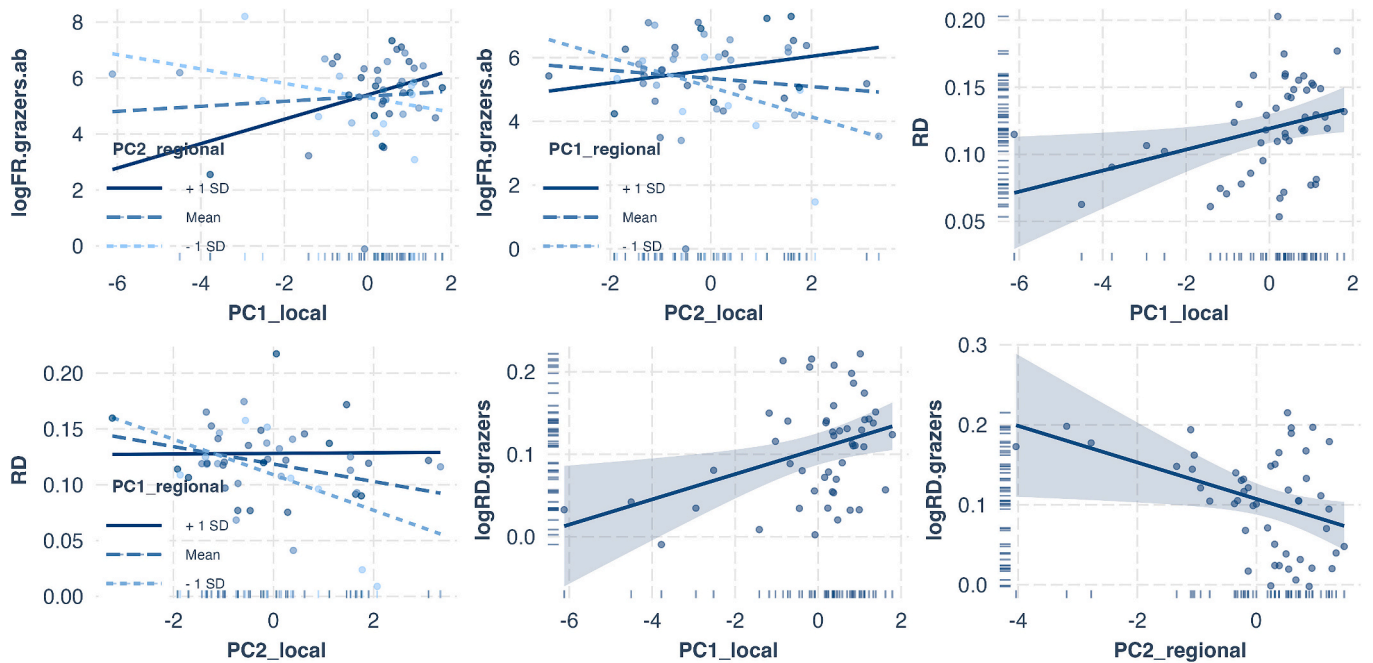


Fig. 8. GLM prediction plots showing relationships between macroinvertebrate functional metrics (logFR.grazers.ab, RD, logRD.grazers) and PC_{local} and PC_{regional} axes from PCAs of local and regional predictors. Shaded regions represent the 95 % confidence intervals and rug plots in the margins show the distribution of the response and predictor variables. Legends show the moderator variable involved in the interaction, and the different dashed lines indicate mean of the moderator variables 1 standard deviation above and below the mean.

study, most of the significant functional metrics (FR.shredders.pa, FR.shredders.ab, FR.piercers.ab, RD.grazers) showed response to natural predictors, representing natural dynamics of pools such as temperature, organic matter and water depth. The functional trophic group of shredders and piercers became poorer, and response of grazers to environmental stressors became similar as a result of local natural predictors such as an increase in depth and decrease in temperature. These results are consistent with previous findings (Pineda-Morante et al., 2022; Soria et al., 2020). All of these changes in functional groups could have implications for biotic interactions (especially predation and competition) and ecosystem functioning, as biotic interactions are critical for shaping community composition in small water bodies (Datry et al., 2017; McIntosh et al., 2017) due to reduced habitat availability and reduced flow permanence.

In our results, responses of biotic and functional metrics to anthropogenic predictors were mostly weak and the explained variance was minimal for most of the biotic indices probably because these indices are not particularly designed to capture the hydrological variability of the system (Alcaraz-Hernández et al., 2022; Magand et al., 2020). For example, when sampling benthic diatoms, according to WFD protocols the areas with low flow and areas of deposition should be ideally avoided, because these habitats limit the colonization of epilithic diatoms (CEN, 2003). This was not the case when sampling disconnected pools, which are areas with no to low flow and of high deposition. The minimal variance explained by the models could also be due to high variation across communities over time as sites show high hydrological variation (Lobera et al., 2019; Sarremejane et al., 2017; Stubbington et al., 2018). However, as there have been complex responses to interactions between natural and anthropogenic predictors, further research on the interaction between local hydrological variability and the responses to environmental impacts in disconnected pools are needed.

We acknowledge the limitations of our study. For example, among our sampled sites, only three had human influence index (HII) >50, of which 65 is the highest HII. However, the human influence index only tells part of the story as we sampled heavily disturbed catchments. For example, a site with a low HII could be heavily polluted due to human

activities taking place upstream. Moreover, although we use the proximity of WWTPs as a proxy for chemical pollution, there are emergent contaminants that we might be failing to capture with our predictor variables (De Castro-Català et al., 2015). In our sampling survey, we also did not account for the distance from pools to nearby pools or perennial river reaches, which can be a strong determinant of dispersal distance on macroinvertebrate community composition (Marshall et al., 2006) and dissimilarity in temporary rivers (Cañedo-Argüelles et al., 2020). In fact, spatial connectivity could be one of the main drivers of metacommunity assembly in temporary rivers (Cañedo-Argüelles et al., 2020; Pineda-Morante et al., 2022). Thus, there is also a need to integrate spatio-temporal heterogeneity into effective ecosystem assessment and conservation practices in temporary rivers (Bruno et al., 2022; Cunillera-Montcusí et al., 2023). In this regard, the metacommunity framework can be helpful, as it captures regional-scale processes driven by landscape connectivity and dispersal (Cid et al., 2022; Cid et al., 2020). Furthermore, we cannot disregard the interactive effect of the local hydrological variables (e.g., time since disconnection, number of zero-flow days) as they have clear effects on the key physico-chemical characteristics (e.g., temperature, conductivity, dissolved organic matter) as the pool shrinks (Bonada et al., 2020). This could have influenced our results because biological communities undergo secondary succession in disconnected pools (Bonada et al., 2020). However, we could not find any effect of the time since disconnection in the biotic indices tested. As we did not collect biological samples before the disconnection period, we were unable to address changes in the biological indices before and after the flow cessation, but further research is needed to test the interaction between hydrological and other local anthropogenic predictors.

Overall, our results suggest that using current biotic indices adopted by the WFD and the newly adopted functional metrics for disconnected pool states could result in flawed management decisions in Mediterranean temporary rivers because there are complex patterns underlying natural and anthropogenic predictors at local and regional scales. However, there are some potential indices to be further explored for use in biomonitoring, such as the richness of Odonata + Coleoptera +

Heteroptera (i.e., OCH). As global change will continue to shape river networks worldwide, there is an urgent need to reevaluate and refine the current biotic indices. These evaluations should be tested along broader spatial scales of anthropogenic and natural predictors to ensure their applicability and effectiveness under varying environmental conditions and novel adaptations such as the inclusion of other lentic taxa (e.g., microcrustaceans) should be explored and integrated into the bio-monitoring programs.

CRedit authorship contribution statement

Zeynep Ersoy: Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation, Conceptualization. **Nieves López-Rodríguez:** Writing – review & editing, Methodology, Investigation, Data curation. **Raúl Acosta:** Writing – review & editing, Investigation, Data curation. **Maria Soria:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Data curation. **Joan Gomà:** Writing – review & editing, Investigation, Data curation. **Francesc Gallart:** Writing – review & editing, Methodology, Investigation, Data curation. **Cesc Múrria:** Writing – review & editing, Investigation, Data curation. **Jérôme Latron:** Investigation, Data curation. **Pilar Llorens:** Investigation, Data curation. **Pau Fortuño:** Writing – review & editing, Investigation, Data curation. **Guillermo Quevedo-Ortiz:** Writing – review & editing, Investigation, Data curation. **Narcís Prat:** Writing – review & editing, Investigation, Data curation. **Miguel Cañedo-Argüelles:** Writing – review & editing, Supervision, Investigation. **Núria Bonada:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

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.scitotenv.2024.174825>.

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