



Water availability and biological interactions shape amphibian abundance and diversity in Mediterranean temporary rivers

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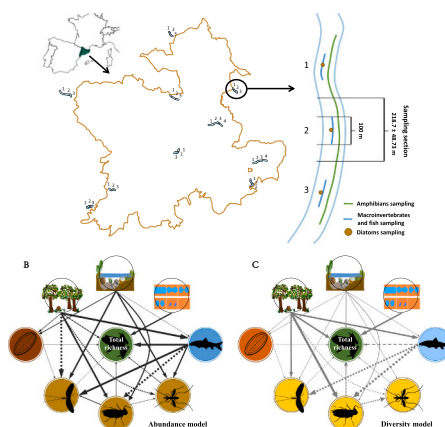
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HIGHLIGHTS

- The lack of research underscores the importance of studying amphibians in temporary rivers, especially in the climate change context.
- Water availability is crucial for shaping amphibian abundance and diversity.
- Amphibians in temporary rivers depend more on top-down than bottom-up interactions.
- Multi-trophic interactions, hydroperiod, and habitat heterogeneity are vital for amphibian conservation strategies.

GRAPHICAL ABSTRACT



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ABSTRACT

Amphibians, the most threatened vertebrates globally, face risks due to climate change, habitat loss, and fragmentation. Their sensitivity to environmental changes highlights their importance as ecological indicators. Temporary rivers, influenced by geological, climatic, and anthropogenic factors, play a critical role in shaping biodiversity and community structure. Some species of amphibians may be adapted to these temporary waters, a

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Freshwater fish
Hydroperiod
Macroinvertebrates
Riparian habitat

fact reflected in their life cycles and various biological traits. However, to develop effective conservation strategies for amphibians, it is essential to address the knowledge gaps surrounding the complex interactions between biological dynamics and fluvial habitat conditions. In this study, we investigated how trophic interactions between amphibians and other aquatic organisms (diatoms, macroinvertebrates, and fish), coupled with environmental factors (water availability and riparian structure), can affect amphibian abundance and diversity in temporary rivers. The study was conducted in a Mediterranean river network located in Sant Llorenç del Munt i l'Obac Natural Park (Catalonia, Spain). Our expectations were that habitats suitable for egg deposition, lacking predators (e.g. tadpole-predators and fish), and abundant in food sources would likely support higher amphibian abundance and diversity. However, water availability was identified as a crucial factor shaping abundance and diversity in the studied amphibian communities, even if it correlated with fish presence, and especially impacting amphibian species usually linked to permanent water bodies. Concerning biotic interactions, while our results suggested that amphibian populations in temporary rivers are more dependent on top-down than bottom-up interactions, the presence of aquatic predators was not as conclusive as expected, suggesting that in temporary rivers the fish-avoiding amphibian species can survive using microhabitats or breeding opportunities linked to natural river dynamics. Overall, our findings highlight the importance of considering multi-trophic interactions, hydroperiod and habitat heterogeneity in temporary river ecosystems for effective amphibian conservation.

1. Introduction

Biodiversity loss is a major problem worldwide, especially pronounced in freshwater ecosystems, which cover <1 % of Earth's surface but host a large fraction of species (Bruno et al., 2022; Reid et al., 2019). Amphibians are the most threatened vertebrate group globally, with 41 % of described species at risk (IUCN, 2023) mainly due to agriculture, timber and plant harvesting, infrastructure development, pollution, climate change, fire, diseases, invasive species, among others (Falaschi et al., 2019; Gardner et al., 2007; Stuart et al., 2004; Luedtke et al., 2023). Their sensitivity to environmental disturbances makes them excellent ecological indicators (Puig-Gironès and Real, 2022). Furthermore, they play a key role in trophic networks, acting as both predators and prey (Eby et al., 2006). Therefore, the current amphibian declines (Green et al., 2020; Hof et al., 2011; Stuart et al., 2004) may affect the biological interactions and subsequently affect biodiversity, due to the crucial role they play in food webs, and their loss may alter nutrient cycling, and impact predator-prey relationships, leading to changes in biodiversity (Whiles et al., 2006). With a biphasic cycle, usually transitioning from aquatic larvae to terrestrial adults (Wells, 2010), amphibians can inhabit ecosystems subjected to wet and dry phases (Smith et al., 2019) such as temporary rivers (Sánchez-Montoya et al., 2017), making them important connectors between freshwater and terrestrial environments.

Temporary rivers are very dynamic ecosystems, with strong spatial and temporal variations in hydrological connectivity, which determine their biodiversity (Bogan et al., 2013; Bonada and Resh, 2013). These variations are influenced by geological characteristics, climate and human activities (Acuña et al., 2014; Datry et al., 2014; Leigh et al., 2016). In Mediterranean regions, temporary rivers represent about 60 % of the total river network (Stubbington et al., 2018) and are expected to become more abundant in the future due to climate change, with the alterations in precipitation patterns resulting in less regular rainfall and more extreme events (Döll and Schmied, 2012). Moreover, future predictions indicate longer dry periods and intense but infrequent rainfall (Tramblay et al., 2021). Thereby, temporary rivers are likely to experience longer dry phases in the future. This is important because flow reduction affects habitat size, intensifying competition, and restricting organisms' dispersal (Bogan et al., 2017). The prolongation of dry periods represents a challenge to the survival of temporary river communities (Smith and Wood, 2002), especially if organisms lack resistance strategies or their weak dispersal abilities challenge the colonisation of available habitats (Bogan et al., 2013; Bogan et al., 2017).

Some amphibian species adapt their life cycles to temporary waters, mostly related to their hydroperiod (water volume maintenance over time) and flow characteristics (Sillero and Skidmore, 2009). Consequently, the presence of ephemeral, intermittent, and permanent water

bodies within temporary rivers are expected to foster higher diversities (Richter-Boix et al., 2011; Sánchez-Montoya et al., 2017; Werner et al., 2007). In the Mediterranean region, species with brief or plastic larval periods can minimise mortality under desiccation risk in ephemeral ponds (Enriquez-Urzelai et al., 2013; Escoriza and Boix, 2014; Richter-Boix et al., 2006). However, species adapted to ephemeral or temporary ponds are usually not well adapted to the presence of competitors and predators (Beja and Alcazar, 2003; Richter-Boix et al., 2006; Richter-Boix et al., 2007). On the other hand, species adapted to inhabit permanent water bodies which typically host diverse biota must be capable of dealing with increased competition and predation (Cruz and Rebelo, 2007; García-Muñoz et al., 2010). While this general framework may apply for most species, other complex interactions may be important for each species. For instance, food resources available (Enriquez-Urzelai et al., 2013) (e.g. benthic algae, or aquatic invertebrates), and the canopy cover, which influences water temperature, may play important roles in amphibian diversity and community composition (Werner et al., 2007). Although amphibians are known to inhabit watercourses, the preferences of this group in these habitats have been scarcely addressed (Dalbeck et al., 2020). Specifically, amphibian diversity, preferences, and community structure have been rarely studied in temporary rivers (Manenti and Pennati, 2016; Sánchez-Montoya et al., 2017).

In this study, we aimed to understand how biological interactions and local abiotic variables affect amphibian abundance and diversity in temporary rivers. We considered biological variables: (1) benthic algae (i.e. diatoms), (2) macroinvertebrates grouped in three trophic categories (tadpole-predators, grazers and others), (3) fish, and local abiotic variables: (1) water availability (i.e. the hydroperiod), (2) instream habitat heterogeneity and (3) riparian habitat quality. Our hypotheses were the following: (1) the use of the hydroperiod gradient by amphibians in temporary rivers will be similar to what is commonly reported for ponds. Since water availability is the primary variable affecting amphibian abundance and diversity (Richter-Boix et al., 2006; Richter-Boix et al., 2007; Werner et al., 2007), we expected species usually linked with permanent ponds to be mostly detected in more permanent rivers, whereas species adapted to temporary ponds would be mostly detected in temporary ones. (2) The abundance of the different amphibian species will vary specifically in each case along a gradient of riparian forest quality; due to their differing sensitivities to environmental disturbance, water and soil temperature, and a different habitat preference for complex sites for shelter (Battaglin et al., 2016). (3) Adult amphibian abundance and diversity would be higher in habitats suitable for egg deposition, characterised by fewer predators (e.g. tadpole-predators and fish) and abundant possible food sources (invertebrates and/or diatoms) (Enriquez-Urzelai et al., 2013; Werner et al., 2007).

2. Materials and methods

2.1. Study area and sampling design

The study area was located in the Sant Llorenç del Munt i l'Obac Natural Park in the north-east Iberian Peninsula (Fig. 1). This area has a Mediterranean climate characterised by its variability, with an annual rainfall range of 355.8–897.9 mm and an average annual temperature range of 12.4–14.0°C (between 2006 and 2021) (Puig-Gironès et al., 2023). This protected area (13,694 ha) consists of mid-altitude mountain ranges (300–1104 m a.s.l.) covered by stands of mixed Mediterranean oak and pine forests. The Natural Park's underlying geology is dominated by karst limestones, with a permeable conglomerate matrix of clay and limestone (Rieradevall et al., 1999), making it a highly permeable substrate. Consequently, the surface flow of streams can last only hours or days after rainfall. During the summer, nearly all streams in the Natural Park stop flowing and shift to disconnected pools or completely dry riverbeds until few resumes with the autumn rains (Pineda-Morante et al., 2022). In this area, permanent streams are mostly associated with springs from the karst aquifer and are located at low elevations (Bonada et al., 2007).

Eight temporary rivers that uniformly occupy the entire Natural Park area (Fig. 1) and cover a wide range of hydrological conditions in the geographical context were selected. These temporary rivers are distributed across two different river basins: Llobregat and Besòs. This has implications for the fish species found in each temporary river; for example, the mountain barbel (*Barbus meridionalis* Risso) is native to the Besòs basin, whereas the red-finned barbel (*Barbus haasi* Mertens) is native to the Llobregat basin. During the sampling period, these conditions ranged from perennially flowing water with continuous flow and

low-flow to non-flowing water with disconnected pools or dry riverbeds. In each temporary river, we established three or four amphibian transects ranging from 184 to 384 m (mean \pm SD = 218.7 ± 48.73), obtaining a total of 27 sampling sections. Into these sections, diatoms, macroinvertebrates and fish were also sampled (Fig. 1). The majority of these transects were sections with very little anthropogenic influence due to the difficult access to the riverbed, steep slopes in some sections, and ruderal vegetation. At each of the 27 sampling sections, specific surveys were conducted to obtain both the abundance and diversity of diatoms, macroinvertebrates, amphibians and fish, as well as a set of local abiotic variables detailed below.

2.2. Biological sampling

In each of the 27 sampling sections, diatom and macroinvertebrate sampling was carried out once per season (summer, spring, autumn and winter) to capture the entire diversity. Each site consisted of a 100-m long reach and was located 100–500 m from the nearest site (Fig. 1). Diatom sampling was conducted by selecting 4 rocks or cobbles (minimum size of 10×10 cm) located in submerged areas of the stream. Substrates submerged for more than eight weeks were selected to ensure a fully mature biofilm (Quevedo-Ortiz et al., 2024). Data loggers (HOBO Pendant® Temperature/Light loggers) installed in various sections of the river confirmed that all substrates were submerged at the specified time (Pineda-Morante et al., 2022). Samples were collected from substrates using a hard toothbrush and stored in plastic vials with tight-fitting lids with water. All samples were preserved in the freezer using 70 % ethanol. In the laboratory, hydrogen peroxide at 100 % was used to eliminate traces of organic matter. Finally, the sample was washed with distilled water and fixed on a microscope slide with Naphrax® resin.

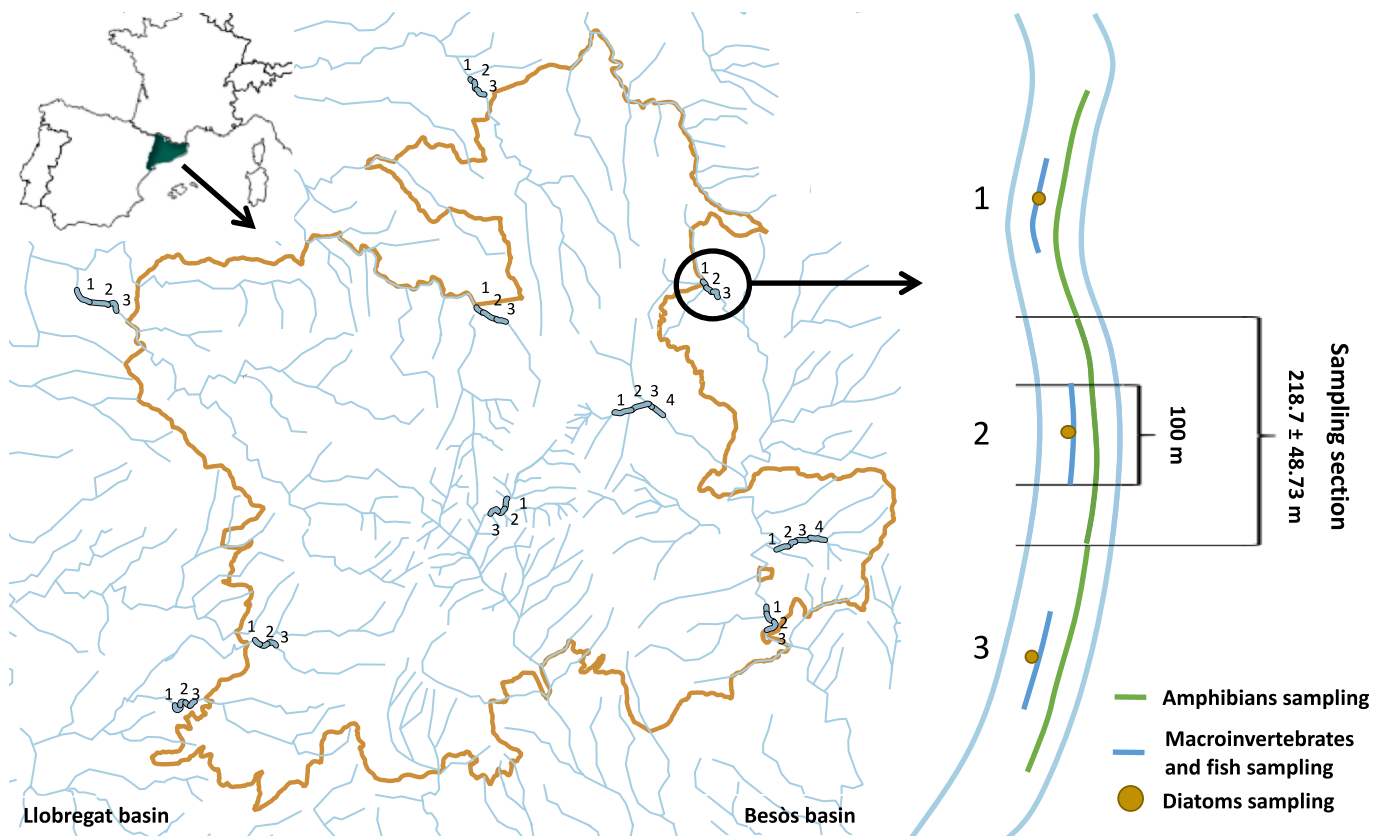


Fig. 1. Location of the Sant Llorenç del Munt i l'Obac Natural Park and the sampling sections. Each sampling section consisted of 3 to 4100-m transects for aquatic macroinvertebrates, separated from the next by 100 to 300 m. Within the macroinvertebrates transects, different stable substrates located in submerged areas and larger than 10×10 cm were selected for diatom sampling. The macroinvertebrate transects were within the amphibian transects, which averaged 218.7 ± 48.73 m in length.

Taxonomic identification (Table S1) was performed under a POLYVAR light microscope with DIC at 1000× magnification. For each sample, a minimum of 400 valves were counted and identified to the species level using taxonomic keys (Lange-Bertalot and Krammer, 2000), which demonstrated a good representation of the aquatic communities of the rivers (MAAMA, 2013). The information on species richness and abundance was expressed in terms of the relative number of species and valves identified per sample. To ensure accurate representation, the species richness was calculated based on the total number of valves counted per sample, not extrapolated from a specific surface area of the river.

Macroinvertebrates were sampled following a multihabitat approach, which involved covering all available habitats within each site in proportion to their presence. Specifically, we employed a kick-net with a 250-µm mesh to collect macroinvertebrates from various substrate types, including gravel, sand, leaf litter, and submerged vegetation. Samples were preserved in 96 % ethanol and specimens were identified at the lowest possible taxonomic level, mostly genus (for more details see Pineda-Morante et al., 2022). After their identification, macroinvertebrates were grouped in three feeding groups following biological traits of feeding habits in Tachet et al. (2010): macroinvertebrates capable of depredating on vertebrates (hereafter tadpole-predator macroinvertebrates), herbivores capable to compete with tadpoles (hereafter grazing macroinvertebrates) and others that do not appear in the previous two categories, like invertebrate-predators or filter-feeding (hereafter other macroinvertebrates) (Table S2). The tadpole-predator macroinvertebrates group are large predators (carver/engulfer/swallower) that primarily consume animal tissue, including vertebrates. The grazing macroinvertebrates group include scrapers, which feed on periphyton or attached algae; shredders, which break down decomposing plant tissue, feed living macrophytes or gouge decomposing wood; and gatherers, which consume fine particulate organic matter deposited in streams (Tachet et al., 2010; Bonada and Dolédec, 2011; Boix et al., 2024; Kaczmarek et al., 2024).

Fish sampling was performed in each river along a reach of 100 m long (Fig. 1) using a portable electrofishing equipment (HONDA model ELT60IIH, 300–500 V). Once caught, fish were anaesthetised with tricain metasulfonate (MS-222, 50 mg/L), species identified, counted and measured (in fork length, mm) and weighed (g). After that, fish were recovered, and finally released at the same point they were captured. We captured five species of fish in the study area. Three were native *Cyprinidae*: the *B. meridionalis*, the *B. haasi*, and the Catalan chub (*Squalius laietanus* L.). The other two were invasive species: the minnow (*Phoxinus* sp.), and the sunfish (*Lepomis gibbosus* L.). Fish were totally absent in two of the temporary rivers explored. The most abundant species were the two *Barbus* species, whereas *S. laietanus* was only found sporadically in one stream. *Barbus* species are mainly insectivores, feeding on aquatic macroinvertebrates. *S. laietanus* is omnivorous; feeding on aquatic macroinvertebrates, aquatic plants and algae, but larger individuals can prey on small fish (Aparicio et al., 2016; Rodríguez-Lozano et al., 2016). *Phoxinus* sp. is also omnivorous, consuming macroinvertebrates, filamentous algae and diatoms. The *L. gibbosus* is an insectivorous predator that additionally preys on vertebrate larvae and juveniles (Aparicio et al., 2016). The density of each fish species (n° individuals per hectare) was estimated by applying the Zippin's (1956) method, adapted to a single catch and applying an average catchability value of 0.5 validated for Catalonia by Benejam et al. (2012).

Amphibian surveys were conducted in spring 2022, coinciding with the reproductive period for most amphibians in the area. Three samplings were carried out in the second half of March, April and May, to cover the phenology of the different species present in the Sant Llorenç del Munt i l'Obac Natural Park and obtain realistic maximum numbers. The survey consisted of a night-time linear transect survey along the riverbed (starting 30 min after sunset and continuing until an hour after the solar midnight at most), using acoustic (adult frogs) and visual counts (adults, larvae, tadpoles, and egg clutches). The transects were

covered by walking at an approximate speed of 2 km/h. Acoustic counts of adult frogs recorded individuals calling in and around the sampling sections both in the stream and in its immediate surroundings. As for visual counts, all adults that were sighted during the sampling, both in and out of the water were recorded. For each sampling section, the maximum number of individuals seen or heard was recorded. For larvae and tadpoles, visual counts were quantitative except for large aggregations (over 50 individuals), where we used a semi-quantitative estimate with three classes: a) 50–250; b) 250–500; and c) > 500 individuals. This approach allows the abundance of individuals to be managed within count limits and, at the same time, provides a more general estimate for higher values, facilitating data collection in situations where precise counts may be more difficult. All equipment in contact with water was thoroughly cleaned to prevent the spread of emerging amphibian diseases.

Amphibian surveys were carried out a year and a half after the end of diatom, macroinvertebrate and fish sampling. Despite the delay, several factors support the robustness of the results even with the delay. Juvenile and adult amphibians sampled were likely born at the site of the study (Smith and Green, 2006); and although they may move between alternative aquatic habitats available at distances of a few hundred metres (Denöel et al., 2018; Schabetsberger et al., 2004). They are expected to form stable population numbers in the absence of great changes in habitat structure. That is, in the absence of great recent traumatic events in the area (e.g. wildfires, great floods), the amphibian communities are expected to be mostly stable across years, with only slight variations but with a very similar species structure (Richter-Boix et al., 2007). The study area experienced a drought period from mid-2020 to early 2024. Our study was conducted over 1.5 years, however, all data were collected within the same drought period but at different times. Therefore, climatic conditions during this period could affect the generalisation of our results to non-drought periods (Moss et al., 2021, see Discussion). Therefore, while our data provide valuable insights, they should be interpreted with caution. Nonetheless, this study offers a significant start on the understanding of trophic relationships in temporary rivers. This combination of data and experimental design may provide us an excellent representation for understanding more accurately how amphibians respond to environmental conditions and resources within riverine habitats. This understanding is essential for future conservation and management initiatives for amphibians and intermittent aquatic ecosystems.

2.3. Local abiotic variables

Local abiotic variables consisted in water availability, the instream habitat heterogeneity and the quality of the riparian habitat. Our water availability variable was derived from field observations of the aquatic state (i.e. flowing, non-flowing with disconnected pools or dry) during each of the three amphibian sampling events. For simplicity, this resulted in a proportion measure indicating the presence or absence of water in each river section. Sections with water always present were assigned a value of 1, those where water was present during one or two sampling events were assigned values of 0.5, and sections that were dry during all sampling events were assigned a value of 0.

Instream habitat heterogeneity was obtained by applying the IHF index (Índice de Hábitat Fluvial; Pardo et al., 2002). The IHF measures the capacity of the physical habitat to support a diverse macroinvertebrate assemblage through the heterogeneity of stream habitats (Prat et al., 2009). Maximum values of this index (max of 100 points) indicate high habitat heterogeneity, which potentially support a high macroinvertebrate diversity; while low values (min of 0) indicate a lack of heterogeneity by natural or human-driven processes, which results in low macroinvertebrate diversity. To calculate it, the characteristics of both riffles and slow waters must be recorded, including substrate inclusion, sedimentation degree, substrate composition (i.e. the percentage of blocks, sand, mud, etc.), velocity and depth regimes, shade

percentage on the riverbed, aquatic vegetation cover, and other organic elements that contribute to habitat heterogeneity. In our study the IHF index scores ranged from 79.5 to 93.5.

Lastly, the quality of riparian habitat was obtained by applying the QBR (Qualitat del Bosc de Ribera; Munné et al., 2003), an easy-to-calculate index that assesses the riparian status of streams and rivers. This index scores between 0 and 100 points based on the sum of four components: riparian vegetation cover, canopy structure, canopy quality, and channel alterations. Each component is initially scored based on specific criteria, with adjustments made according to additional factors. Each component contributing equally to the final score, with a maximum of 25 points per component. The component for riparian vegetation cover evaluates the cover percentage provided by trees and shrubs in the riparian zone. For canopy structure component, a more diverse and complex structure (i.e., multiple layers) results in a higher score. The canopy quality component awards higher scores for diverse and native vegetation. Lastly, channel alterations component assesses physical modifications to the river channel, such as dams or riverbank ripraps, which affect the natural flow and habitat. Here, lower scores are given based on the extent and impact of these structures (Munné et al., 2003). In our study the QBR scores ranged from 87 to 100.

2.4. Statistical analyses

The relative abundance of amphibians was calculated by dividing the number of adult amphibians counted in each sampling section by the length of the sampling section (Fig. 1). For larvae and tadpoles, relative abundance was assessed using a combination of quantitative (below 50 individuals) and semi-quantitative counts. The latter was based on the previous explanation criterion using the midpoint of each class, i.e., a) corresponding to 150 individuals, b) to 375 individuals, and c) to 1000 individuals. Additionally, the logarithmically transformed total counts of diatoms, tadpole-predator, grazing and other macroinvertebrates were summed to derive relative abundance per sampling section. Amphibian species richness was measured in each sampling section in three categories: adult, larvae, and total richness (adults and larvae) detected.

To ensure independence of sampling sections, a chi-square test of independence was performed, which revealed no significant association (Pearson's chi-square test p -value = 0.2841; Kruskal-Wallis rank sum test p -value = 0.4631), i.e., amphibian abundance was independent among sampling sections. Subsequently, permutational analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities was used to assess the effects of the eight-predictor variables, on biological interactions (the relative abundance of diatoms, tadpole-predators, grazing and other macroinvertebrates, and fish) and local abiotic variables (water availability, IHF, QBR), on the taxonomic composition of the adults and larvae amphibian communities. This analysis, with 999 permutations for robust results, was complemented by Redundancy Analysis (RDA) to identify and summarise linear relationships between the community composition and explanatory variables. The RDA included the eight predictor variables as explanatory variables, and their significance was calculated by ANOVA-like permutation tests (9999 permutations), using the R vegan package (Oksanen et al., 2019).

Lastly, structural equation modelling (SEM) analysis was used to assess the strength of biological interactions of temporary rivers food webs while controlling for potential confounding variables. SEM simultaneously examines dependence/cause relationships, provides a holistic view by analysing the interdependent relationships between variables, thus elucidating the underlying processes or fundamental than cause theses dependent relations analysed in the SEM model. Initially, a comprehensive SEM model to assess main interactions was formulated, both direct and indirect, affecting amphibian variables (adult density, adult richness, larval density, larval richness, and total richness). The model included the eight predictor variables focusing on both biological interactions with freshwater biota (diatoms tadpole-

predators, grazing and other macroinvertebrates, and fish), as well as local abiotic variables (water availability, IHF, QBR). Subsequently, ten different SEM models were generated, each corresponding to one of five amphibian variables in relation to the abundance (five models) or diversity (five models) of freshwater biota, while local abiotic variables remain unchanged in the different models. Models were running, eliminating non-significant variables and retaining only models that demonstrated a good fit, i.e., a significant p -value (<0.05), a comparative fit index (CFI) >0.95 and a standardised root mean square residual (SRMR) <0.08 , were retained (Table S3). All models met these conditions. These analyses were carried out using the R Lavaan package (Rosseel, 2012). Before testing the SEMs, multicollinearity diagnostics were performed and outliers were identified (Zuur et al., 2009). Multicollinearity was detected by quantifying variance-inflation factors (VIF) calculated for each fixed factor (Fox and Monette, 1992) using the R software (R Development Core Team, 2017). Large VIF values (arbitrary threshold of ≤ 5 suggesting collinearity) were sequentially dropped from further analysis, however, no multicollinearity was detected.

3. Results

A total of eight amphibian species were identified. Seven of them were identified as adults and five of them as larvae, with some species detected in both life stages. Among the species found in the adult stage (totalling 350 adult individuals), Iberian Green Frog (*Pelophylax perezi* López-Seoane) was the most abundant and widespread, constituting a 46.86 % of the total and being observed in 23 out of 27 sampling sections. The Mediterranean Tree Frog (*Hyla meridionalis* Boettger) was the second most abundant species detected in the adult stage, accounting for 23.71 % of the observations and being found in 12 sites. The Spiny Common Toad (*Bufo spinosus* Daudin) and the Catalan Midwife Toad (*Alytes almogavarii* Arntzen & García-París) were present in 11 and 14 sites, making up 15.14 % and 10 % of the detected adult population, respectively. Lastly, the Natterjack Toad (*Epidalea calamita* Laurenti, 1.43 %), the Marbled Newt (*Triturus marmoratus* Latreille, 2.29 %) and the Common Parsley Frog (*Pelodytes punctatus* Daudin, 0.57 %) were clearly less common in the transects, with only sporadic occurrences in the sampling sections. Conversely, among the amphibians in the juvenile stage (approximately 4726 individuals count), *B. spinosus* dominated, comprising 64.96 % of all counted individuals in only eight sites. Fire salamander (*Salamandra salamandra* L.) larvae were the second most abundant, representing 16.62 % detections across 20 sites. The *E. calamita* larvae were present in only three sites, accounting for 10.59 %, while *A. almogavarii* and *P. punctatus* larvae were found in 2 and 1 sites, comprising 2.88 % and 4.89 %, respectively.

The RDA analysis revealed distinct patterns for adult and larval amphibians. In adults, the first component (50.25 % of the variability explained) showed a correlation between fish abundance and tadpole-predator macroinvertebrate abundance, whereas the second component (25.11 % of the variability) separated sections with high diatom abundance from those with a higher water availability, QBR and IHF (Fig. 2a; model significance = 0.19). Adult amphibians clustered into three groups: the two Bufonid species (*B. spinosus* and *E. calamita*); *P. perezi* and *H. meridionalis*, associated with abundant water and vegetation; and *A. almogavarii* associated with tadpole-predator macroinvertebrates. On the other hand, for larval amphibians, the first component of the RDA (40.24 % of the variability) separated the sampling sections based on fish abundance and QBR, while the second component (28.43 % of the variability) distinguished the sampling sections with fish from those with macroinvertebrates (Fig. 2b; model significance = 0.02). High abundances of *P. perezi* and *B. spinosus* larvae were found in sections with higher fish abundances and QBR, while *S. salamandra* were more abundant in sections with low water availability. *A. almogavarii* larvae preferred sections with abundant macroinvertebrates, particularly grazing macroinvertebrates and other macroinvertebrates. *E. calamita* showed no clear preference, and

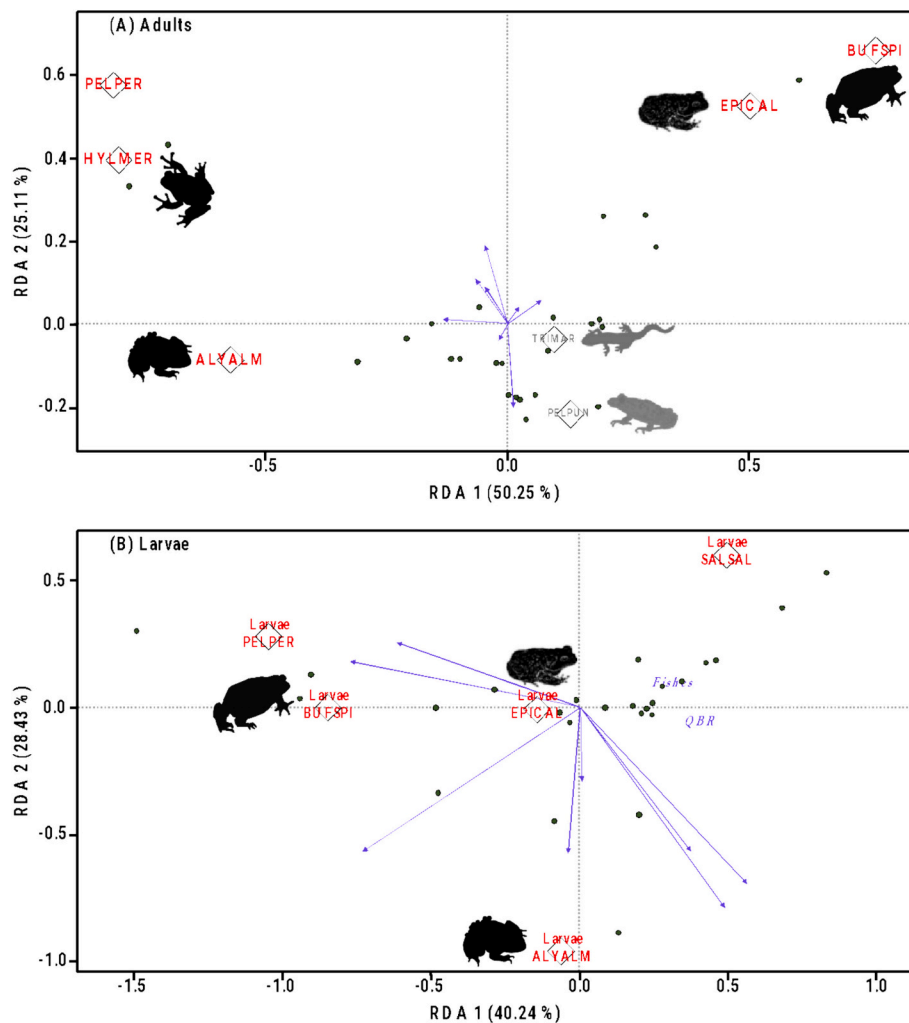


Fig. 2. Redundancy analysis (RDA) for adult and larvae amphibians. The redundancy analysis plots above represent adult amphibian species (A), while those below represent larvae amphibian species (B) in the Sant Llorenç del Munt i l'Obac Natural Park. Black circles correspond to each sampling section. Grey silhouettes correspond to species that were found in fewer than 3 sampling sections. Acronyms for species are as follows: ALYALM for Catalan midwife toad (*Alytes algogavarii* Arntzen & García-París); BUFSP1 for spiny common toad (*Bufo spinosus* Daudin); EPICAL for natterjack toad (*Epidalea calamita* Laurenti, 1.43 %); HYLMER for Mediterranean tree frog (*Hyla meridionalis* Boettger); PELPER for Iberian Green Frog (*Pelophylax perezi* López-Seoane); PELPUN for common parsley frog (*Pelodytes punctatus* Daudin); SALSAL for fire salamander (*Salamandra salamandra* L.); and TRIMAR for marbled newt (*Triturus marmoratus* Latreille).

H. meridionalis larvae were not found (Fig. 2b).

Structural equation models (SEM) revealed significant associations between faunistic and local abiotic variables and amphibian parameters. The models were highly explanatory (Table S4) for amphibians (R^2 ranged between 0.54 and 0.72), fish (0.49 to 0.82), tadpole-predator macroinvertebrates (0.45 to 0.69), moderately for grazing macroinvertebrate (0.31 to 0.72), and lower for other macroinvertebrates (0.26 to 0.44) and diatoms (0.05 to 0.17). Water availability had the largest standardised total effect on total amphibian richness, followed by fish abundance and QBR ($R^2 = 0.69$). Total amphibian richness showed the highest positive direct effects from fish abundance and water availability (Table 1, Fig. 3b), and the lowest effects from other macroinvertebrates, tadpole-predator macroinvertebrates, and diatom abundance. Conversely, negative effects were observed for QBR and grazing macroinvertebrate abundance (Table 1, Fig. 3b). When considering organism diversity ($R^2 = 0.64$), we observed that the relationships between species lose importance on total amphibian richness, with QBR and water availability being the positive and largest standardised total effect (Table 2, Fig. 3c). IHF and other macroinvertebrate diversity had the lowest positive effects. However, most faunal diversity interactions are negatively related, with fish diversity and predatory tadpole

macroinvertebrate predators having the largest negative direct effects, while the diversity of grazing macroinvertebrates and diatoms had the smallest negative effects (Table 2, Fig. 3c).

The direct effects of the local abiotic variables on the abundance and richness of adult amphibians (Fig. 4) and larvae (Fig. 5), also showed that water availability had the largest positive effect (Table 1 and Table 2). QBR also played an important role in determining the abundance and richness of both adults and larvae, whereas IHF only influenced larval abundance. Unexpectedly, there was a notable positive relationship between fish abundance and adult richness (Fig. 4), larval abundance and larval richness (Fig. 5), although it was strongly negative for adult amphibian abundance (Table 1). Fish diversity also showed negative effects on adult abundance and richness (Table 2). Tadpole-predator macroinvertebrate abundance positively affected larval abundance, whereas the diversity of tadpole-predator had a negative relationship with adult richness and larvae abundance. Diatoms, grazing macroinvertebrates, and other macroinvertebrates abundance and diversity presented less direct effects, usually being in an opposite relationship between adults and larvae. Although diatom abundance also showed similar relationships, their diversity was positively related to both adult and larval abundance but negatively correlated with their

Table 1
SEM modelling results on the relationships of environment and biota abundances on each of the amphibian parameters. The explanatory variables in each SEM model include fish abundance and the abundance of macroinvertebrate groups (tadpole-predator macroinvertebrates, grazing macroinvertebrates, and others) and diatoms on total amphibian richness, adult and larval abundance, as well as adult and larval species richness. The table shows the coefficient (b) of the model parameter with its standard error (\pm SE) and associated p-values. The relationships between the explanatory variables (fish, macroinvertebrates, and diatoms) remain constant across models, so they are only represented in the total richness column. The grey spaces correspond to non-significant variables that do not appear in the final model.

SEM modelling results on the relationships of environment and biota abundances on each of the amphibian parameters.											
The explanatory variables in each SEM model include fish abundance and the abundance of macroinvertebrate groups (tadpole-predator macroinvertebrates, grazing macroinvertebrates, and others) and diatoms on total amphibian richness, adult and larval abundance, as well as adult and larval species richness. The table shows the coefficient (b) of the model parameter with its standard error (\pm SE) and associated p-values. The relationships between the explanatory variables (fish, macroinvertebrates, and diatoms) remain constant across models, so they are only represented in the total richness column. The grey spaces correspond to non-significant variables that do not appear in the final model.											
Explanitive variables		Total richness		Adults abundance		Adult richness		Larvae abundance		Larvae richness	
		b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value
Amphibians	IHF			0.15 \pm 0.03	<0.001	-0.09 \pm 0.03	0.007	-0.65 \pm 0.03	<0.001	-0.15 \pm 0.03	<0.001
	QBR	-0.38 \pm 0.05	<0.001	1.51 \pm 0.06	<0.001			-0.39 \pm 0.06	<0.001	-0.15 \pm 0.05	0.002
	Water availability	0.58 \pm 0.02	<0.001	0.31 \pm 0.02	<0.001	0.56 \pm 0.02	<0.001	0.26 \pm 0.02	<0.001	0.49 \pm 0.01	<0.001
	Fish abundance	0.74 \pm 0.05	<0.001	-1.33 \pm 0.06	<0.001	0.33 \pm 0.02	<0.001	0.72 \pm 0.06	<0.001	0.54 \pm 0.05	<0.001
	Tadpole-predators macroinvertebrate abundance	0.16 \pm 0.02	<0.001	-0.11 \pm 0.03	<0.001	0.16 \pm 0.02	<0.001	0.38 \pm 0.02	<0.001	0.11 \pm 0.02	<0.001
	Grazing macroinvertebrate abundance	-0.10 \pm 0.03	<0.001	0.18 \pm 0.04	<0.001	0.20 \pm 0.03	<0.001	-0.17 \pm 0.04	0.001	-0.10 \pm 0.03	0.001
	Other invertebrate abundance	0.22 \pm 0.02	<0.001	-0.13 \pm 0.03	<0.001			0.07 \pm 0.03	<0.001	0.37 \pm 0.02	<0.001
	Diatom abundance	0.04 \pm 0.02	0.03			0.11 \pm 0.02	<0.001	-0.11 \pm 0.02	<0.001	-0.16 \pm 0.02	<0.001
Fish	IHF	-0.04 \pm 0.01	<0.001								
	QBR	0.91 \pm 0.01	<0.001								
Tadpole-predator macroinvertebrates	IHF	0.53 \pm 0.02	<0.001								
	QBR	0.76 \pm 0.05	<0.001								
Grazing macroinvertebrates	Fish abundance	-0.87 \pm 0.05	<0.001								
	IHF	0.69 \pm 0.02	<0.001								
	QBR	-0.92 \pm 0.04	<0.001								
	Fish abundance	0.88 \pm 0.04	<0.001								
	Tadpole-predators macroinvertebrate abundance	0.26 \pm 0.02	<0.001								
	Diatom abundance	-0.06 \pm 0.02	<0.001								
Other macroinvertebrates	IHF	0.61 \pm 0.02	<0.001								
	QBR	-0.46 \pm 0.05	<0.001								
	Fish abundance	0.56 \pm 0.05	<0.001								
	Tadpole-predators macroinvertebrate abundance	0.05 \pm 0.03	0.04								
Diatoms	IHF	0.20 \pm 0.02	<0.001								
	QBR	-0.38 \pm 0.02	<0.001								

richness. Moreover, several indirect effects of faunistic and hydro-morphological variables on amphibian abundance and richness were identified within the multi-taxon path model (Table S5).

IHF has the largest direct positive effects for diatoms, tadpole-predators, grazing and other macroinvertebrates, while the QBR had positive effects on fish and tadpole-predator macroinvertebrates, but negative effects on diatoms, grazing and other macroinvertebrates (Table 1). Fish abundance showed a negative relationship with tadpole-predator macroinvertebrates and a positive relationship with grazing and other macroinvertebrates. Tadpole-predator macroinvertebrates positively affected grazing macroinvertebrates (Fig. 4). Finally, focusing on the diversity of organisms (Fig. 5), IHF had a direct positive effect on tadpole-predator macroinvertebrates and a negative effect on diatoms. QBR positively affected the diversity of fish, tadpole-predator and grazing macroinvertebrates. Fish diversity negatively affected the diversity of tadpole-predators and grazing macroinvertebrates, while tadpole-predators positively affected the other macroinvertebrates diversity (Table 2).

4. Discussion

The urgent challenge of predicting and preventing species loss (Díaz et al., 2018) can be complex due to the intricate interactions among species that sustain ecosystems (Harvey et al., 2017). In this sense, knowledge of amphibian biological interactions is crucial to identify relevant resources, dynamics or habitats which allow for effective conservation strategies in temporary rivers (Gallardo and Aldridge, 2013; Knights et al., 2015). Previous studies have already highlighted that factors such as altered discharge variability, drying events, floodplain alterations, and hydrological connectivity may be crucial in shaping faunal populations in temporary rivers in the future (Hill and Milner, 2018; Leigh and Datry, 2017). The presence of shelter during high and low-flow periods, the availability of suitable habitats like ponded sites,

and the influence of landscape composition have been also highlighted as key factors for amphibian abundance (Gibbons et al., 2006). Our study shows that a complex interaction of abiotic – water presence, habitat complexity – and biotic – presence and abundance of predators – shapes amphibian abundance and diversity in temporary rivers.

Amphibian larvae generally showed habitat occurrences consistent with previous studies, particularly regarding water permanence and presence of potential predators such as fish (Manenti and Pennati, 2016). However, in our case, both native *Barbus* species consume macroinvertebrates, but there have been no reports of them preying on amphibian larvae. In contrast, invasive *L. gibbosus*, detected in one stream, may prey on amphibian larvae, which can potentially affect amphibian populations. For instance, *P. perezi* and *B. spinosus* larvae were predominantly found in areas with permanent flow and fish presence, coinciding with previous studies and observations (García-Salmerón et al., 2022; Richter-Boix et al., 2007). Toxicity in *B. spinosus* tadpoles (Bókonyi et al., 2016) allows the breeding in presence of fish, while *P. perezi*'s phenotypic plasticity (Gomez-Mestre and Díaz-Panigagua, 2011) aids tadpoles to survive high predation pressure in permanent water bodies. On the other hand, *A. almogavarii* tadpoles were mostly found in fish-free areas but with abundant, favourable water conditions, which is also consistent with their usual preference for small and permanent water bodies in the area (García-Salmerón et al., 2022). This species seems to find its ecological niche clearly differentiated from the other two species in the riparian habitats surveyed. In our study, *S. salamandra* larvae tended to be found in areas with more scarce water permanence, typically in predator-free watercourses (Bylak, 2018). Lastly, although not implied by the results, it is important to note that *E. calamita* larvae exhibited a unique ecological niche. They utilized dynamic riparian microhabitats such as small ponds prone to desiccation, avoiding predators and competitors, consistent with their pond preferences (Richter-Boix et al., 2006; Richter-Boix et al., 2007; Richter-Boix et al., 2011; Pujol-Buxó et al., 2019). Thus, this last species did not

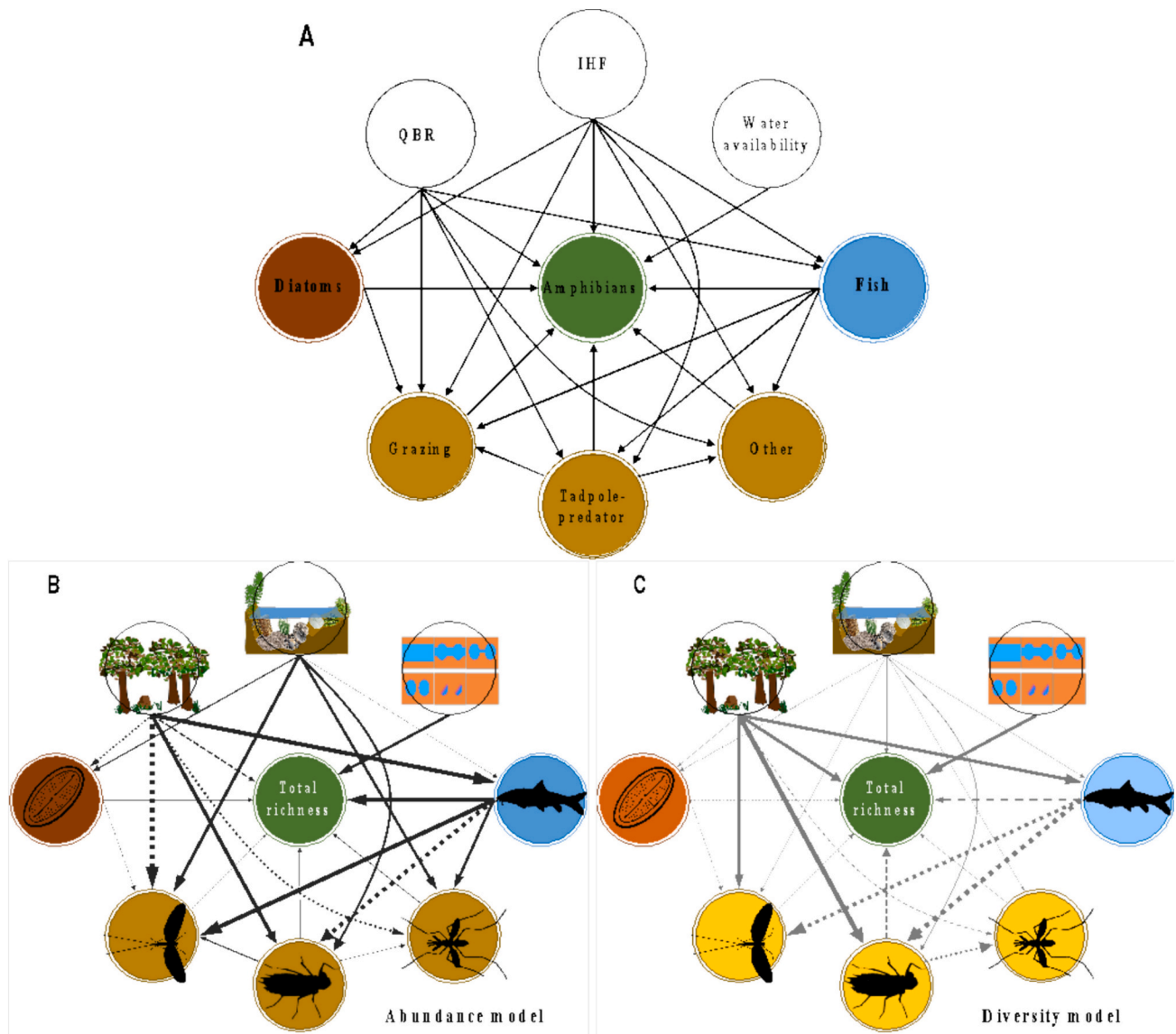


Fig. 3. Structural equation model (SEM) for total amphibian richness. Initial structural equation model (SEM) (A) with all the trajectories considered for the five amphibian models to study (adults, larvae, adult richness, larval richness, total richness). Final model relationships are also shown for total amphibian richness (B) using the fish abundance, and the abundance of macroinvertebrates groups (tadpole-predator, grazing and other) and diatoms; and (C) using the Shannon index for fish, macroinvertebrates groups and diatoms. Here, the arrow width corresponds to the coefficients, continuous lines represent positive relationships, while discontinuous lines indicate negative relationships. Non-significant relationships are not shown. For more information on the model relationships, see Table S4.

show a clear pattern of larvae occurrence in this study, occupying each stream depending on the presence of these microhabitats. The absence of the other species in larval stages are most probably due to an incomplete detection, as surveys omitted dip-netting or trapping in order to allow for extensive surveys in large areas while preventing disease spread and minimising sampling effort. Therefore, the possibility of low larval densities of other or the same species in habitats other than those in which each larval species has been mainly reported should not be discarded. These species-level results should be taken as the situation in which the larvae of each species is most commonly found, but not as a complete separation or avoidance of the other ecological situations. In fact, even if some species seem to prefer areas without fish, globally the relationship between fish and amphibian larvae contradicts our initial hypotheses. Higher fish abundance was associated, in fact, with greater abundance and diversity of amphibian larvae. These results however, could be partially influenced by the high relative abundance of *B. spinosus* and their lower predation risk due to its toxicity, and also by the fact that permanent water bodies most probably become more

important for amphibian dynamics during droughts (Moss et al., 2021) a possibility which is further discussed later. Despite fish being primary aquatic predators capable of decimating entire amphibian populations in pools (Woodward, 1983), some species like *B. spinosus* and *P. perezi* (Manenti and Pennati, 2016) are adapted to fish presence. On the other hand, the natural dynamics of rivers and the availability of microhabitats that make predation difficult for fish may allow fish-avoiding amphibian species to persist. In this sense, conserving habitat complexity becomes paramount.

Conversely to the larval results, interpreting adult species results was difficult in some cases. As a first clear result, *H. meridionalis* adults decidedly preferred vegetated areas, consistent with their climbing adaptations (García-Salmerón et al., 2022). Although the similar habitat preference of *P. perezi* was not necessarily expected, it might be either linked to an indirect link of abundant vegetation to water permanence, or to the direct preference for juveniles and adults of the species for vegetated areas. On the other hand, *A. almogavarii* adults seem to choose areas reflecting the tadpole ecological niche, showing consistent

Table 2
SEM modelling results on the relationships of environment and biota diversity on each of the amphibian parameters. The explanatory variables in each SEM model include the Shannon index for fish, macroinvertebrate groups (tadpole-predator, grazing and others) and diatoms on total amphibian richness, adult and larval abundance, as well as adult and larval species richness. The table shows the coefficient (b) of the model parameter with its standard error (\pm SE) and associated p-values. The relationships between the explanatory variables (fish, macroinvertebrates, and diatoms) remain constant across models, so they are only represented in the total richness column. The grey spaces correspond to non-significant variables that do not appear in the final model.

SEM modelling results on the relationships of environment and biota diversity on each of the amphibian parameters.											
The explanatory variables in each SEM model include the Shannon index for fish, macroinvertebrate groups (tadpole-predator, grazing and others) and diatoms on total amphibian richness, adult and larval abundance, as well as adult and larval species richness. The table shows the coefficient (b) of the model parameter with its standard error (\pm SE) and associated p-values. The relationships between the explanatory variables (fish, macroinvertebrates, and diatoms) remain constant across models, so they are only represented in the total richness column. The grey spaces correspond to non-significant variables that do not appear in the final model.											
Explanatory variables		Total richness		Adults		Adult richness		Larvae		Larvae richness	
		b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value	b \pm SE	p-value
Amphibians	IHF	0.16 \pm 0.02	<0.001	0.23 \pm 0.02	<0.001	0.19 \pm 0.02	<0.001	-0.14 \pm 0.02	<0.001		
	QBR	0.68 \pm 0.04	<0.001	0.75 \pm 0.04	<0.001	0.97 \pm 0.04	<0.001	0.25 \pm 0.04	<0.001	0.41 \pm 0.02	<0.001
	Water availability	0.64 \pm 0.02	<0.001	0.29 \pm 0.02	<0.001	0.56 \pm 0.02	<0.001	0.42 \pm 0.02	<0.001	0.59 \pm 0.02	<0.001
	Fish diversity	-0.37 \pm 0.04	<0.001	-0.63 \pm 0.04	<0.001	-0.79 \pm 0.04	<0.001	0.26 \pm 0.04	<0.001		
	Tadpole-predator macroinvertebrate diversity	-0.36 \pm 0.03	<0.001	-0.13 \pm 0.03	<0.001	-0.46 \pm 0.03	<0.001	-0.31 \pm 0.03	<0.001		
	Grazing macroinvertebrate diversity	-0.11 \pm 0.02	<0.001	-0.09 \pm 0.02	<0.001	-0.29 \pm 0.02	<0.001	0.24 \pm 0.02	<0.001	0.07 \pm 0.02	<0.001
	Other invertebrate diversity	0.07 \pm 0.02	<0.001	0.27 \pm 0.02	<0.001	0.29 \pm 0.02	<0.001	-0.42 \pm 0.02	<0.001	-0.18 \pm 0.02	<0.001
	Diatom diversity	-0.05 \pm 0.02	0.007	0.07 \pm 0.02	<0.001	-0.23 \pm 0.02	<0.001	0.26 \pm 0.02	<0.001	-0.06 \pm 0.02	<0.001
Fish	IHF	0.05 \pm 0.02	0.005								
	QBR	0.69 \pm 0.02	<0.001								
Tadpole-predator macroinvertebrates	IHF	0.15 \pm 0.02	<0.001								
	QBR	1.10 \pm 0.02	<0.001								
Grazing macroinvertebrates	Fish diversity	-0.98 \pm 0.02	<0.001								
	IHF	0.11 \pm 0.02	<0.001								
	QBR	0.61 \pm 0.03	<0.001								
	Fish diversity	-0.81 \pm 0.03	<0.001								
Other macroinvertebrates	Diatom diversity	-0.13 \pm 0.02	<0.001								
	IHF	0.09 \pm 0.02	<0.001								
	QBR	-0.14 \pm 0.03	<0.001								
	Tadpole-predator macroinvertebrate diversity	0.54 \pm 0.02	<0.001								
Diatoms	IHF	-0.22 \pm 0.03	<0.001								
	QBR	0.07 \pm 0.03	0.004								

preference for water-abundant and fish-free areas across life stages. Unexpectedly, adults of *E. calamita* and *B. spinosus*, in breeding season, showed habitat preferences opposing their larval stages, suggesting that the habitats in which they breed are subsequently rapidly abandoned. Bufonidae species are highly terrestrial and can be very mobile (Van Bocxlaer et al., 2010), being this the possible explanation to these differences between life stages. In general, amphibian adults were more abundant and diverse in areas associated with low fish abundance and richness.

Globally, riparian vegetation appears more relevant for adult amphibians than for larvae, although this relationship seems species-specific. Riparian vegetation can offers shelter for juvenile amphibian and supports their development (Battaglin et al., 2016). Additionally, it may indirectly affect amphibians by influencing water quality and stream sedimentation, which in turn impacts the entire biotic community (Sweeney and Newbold, 2014; Ferreira and Beja, 2013). Besides riparian quality, instream habitat heterogeneity, which determines macroinvertebrate community structure and diversity (Mellado-Díaz et al., 2019), may also influence amphibian abundance and diversity in temporary rivers. At the species level, we observe that adults of *P. perezi*, *H. meridionalis*, *E. calamita*, and *B. spinosus* are more common in areas with high QBR index values, while fewer species are present where this index is lower. Larvae of *P. perezi* and *B. spinosus* also seem to be more prevalent in areas with a high QBR index, whereas in areas with a low QBR index, larvae are fewer and predominantly correspond to *S. salamandra*. Higher IHF values occur in rivers with diverse rapids, which increasing habitat diversity, and increased flow rates enhance river connectivity. Furthermore, this facilitate frequent movement of macroinvertebrates and increase the available shelters and microhabitats (Bonada et al., 2006). Globally, the IHF index seems to increase the adult presence while decreasing the larvae abundance and diversity. This reinforce the idea that the abundance of adults and larvae of amphibian species can be uncorrelated at small geographic scales. The relationship between habitat heterogeneity and amphibian abundance appears complex and demands further study, as not all species

amphibians and developmental stages benefit equally from increased habitat heterogeneity. For example, *P. perezi*, *H. meridionalis*, *E. calamita*, and *B. spinosus* adults seem to be more common where the IHF index is high, while fewer species are present where this index is low. Interestingly however, it is the low IHF values, which correlate with the presence of *P. perezi* and *B. spinosus* larvae, while in turn *A. almogavarii* larvae occupy habitats with higher heterogeneity. The relationship between macroinvertebrates and amphibians in freshwater ecosystems could be intricate and multifaceted. Macroinvertebrates can act as both food sources for adult amphibians and predators of amphibian tadpoles. However, these interactions do not always directly correlate with adult amphibian abundance or richness, as our results showed. Nevertheless, tadpole-predator diversity exhibited a negative correlation with amphibian adult richness, suggesting that the diversity of predators targeting tadpoles can affect the overall richness of adult amphibians (Skelly and Werner, 1990). Certain macroinvertebrate groups, including Odonata, Coleoptera, Heteroptera, and crayfish may prey on anuran tadpoles and urodele larvae in fishless temporary habitats, inducing great predation tolls, and force morphological and life-history responses in anurans (Pujol-Buxó et al., 2017; Pujol-Buxó et al., 2013; Van Buskirk, 2001). Consequently, adult amphibians may prefer to breed in water bodies with few predators to minimise egg and larval loss during breeding. The composition and structure of macroinvertebrate communities can be affected by various environmental factors (Bonada and Resh, 2013) and can have cascading effects on the amphibian community (Valdez, 2019), underscoring the interconnectedness of these ecosystems.

Considering that water availability is one of the two main factors that determines amphibian abundance and diversity in our study, it is plausible to infer its crucial role in shaping future amphibian community trends (Datry et al., 2014; Leigh et al., 2016). The dynamic nature of temporary rivers presents challenges during dry periods, serving as a model for resilience to climate change. Reduced water residence time may disrupt certain species' life cycles (Segura and Palomar, 2023). Species with adult adaptations, like aestivation or habitat migration,

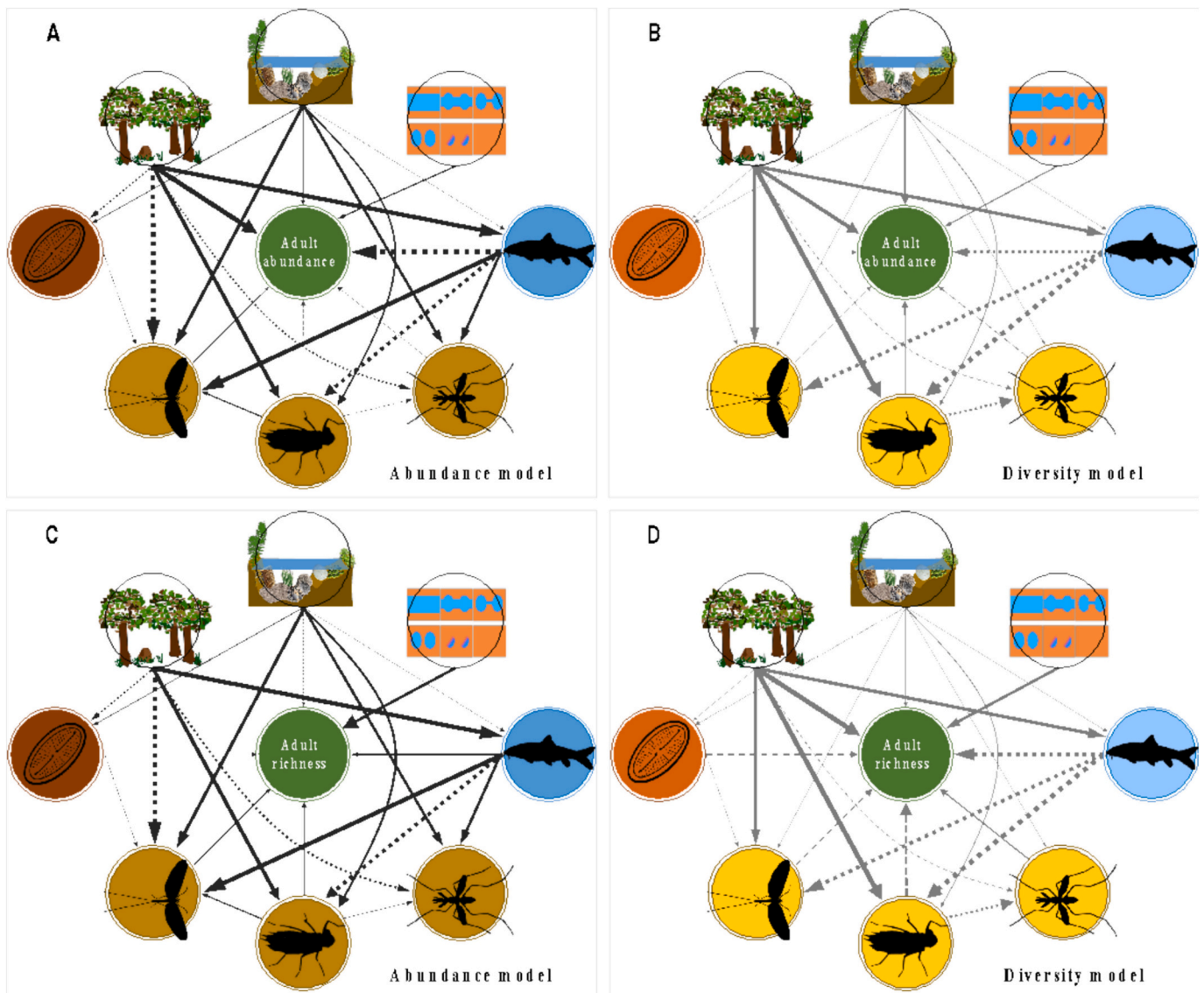


Fig. 4. Structural equation model (SEM) for adult amphibians. Final model relationships for adult amphibian abundance and richness are shown. The arrow width corresponds to the coefficients, continuous lines represent positive relationships, while discontinuous lines indicate negative relationships. (A) represents the relationships between fish abundance, and the abundance of macroinvertebrate groups (tadpole-predator, grazing and others) and diatoms on the abundance of adult amphibians; while in (B) the relationships are represented using the Shannon index for fish, macroinvertebrate and diatoms. Graphs (C) and (D) show the same relationships as (A) and (B), respectively, but using the species richness of adult amphibians. Non-significant relationships are not shown. For more information on the model relationships, see Table S4.

may be more resistant. For example, dry periods have been linked to declines in macroinvertebrate richness in temporary rivers (García-Roger et al., 2011), accompanied by increased predation risk (Petranka and Kennedy, 1999). Studies highlight assessing species-habitat relationships to enhance connectivity and conservation efforts for fragmented amphibian populations in the Mediterranean region (Gutiérrez-Rodríguez et al., 2023). In arid and semiarid zones, the lack of temporary ponds may pose challenges for amphibians, impacting their breeding habitats. Man-made temporary ponds have shown potential benefits for amphibian species in this region (Ruhí et al., 2012). Therefore, our findings suggest that future scenarios of reduced water availability may decrease amphibian abundance and diversity, particularly impacting species reliant on permanent water bodies and unable to reproduce under ephemeral conditions, as observed by other researchers (Segura and Palomar, 2023).

From mid-2020 to early 2024, our study area experienced a 4-years prolonged drought. While the biota in these Mediterranean temporary

rivers are adapted to summer drying, the impact of such extended climatic events amphibian demographic parameters is not well documented. Therefore, the effects of a 4-year drought period on various species remain unclear. Under a similar climate in California, an extreme 7-year drought led to a general but species-specific reduction in pond occupancy, with a temporary increase in the importance of the permanent ponds for amphibian community resilience, followed by a strong recovery immediately post-drought (Moss et al., 2021). Our 2023 data, collected during a 3-year drought, showed relatively stable amphibian diversity but greater variability in abundance (unpublished data). Consistent with Moss et al. (2021), it is possible that water availability was overemphasized in our results, as it may have been more crucial than ever during this period. Despite these conditions, we were able to detect species-specific idiosyncrasies, which can be explained by their habitat use. Therefore, although the drought likely influenced our findings, this climatic event in fact may only prevent extensive generalisation of our results. Future research should continue to elucidate the

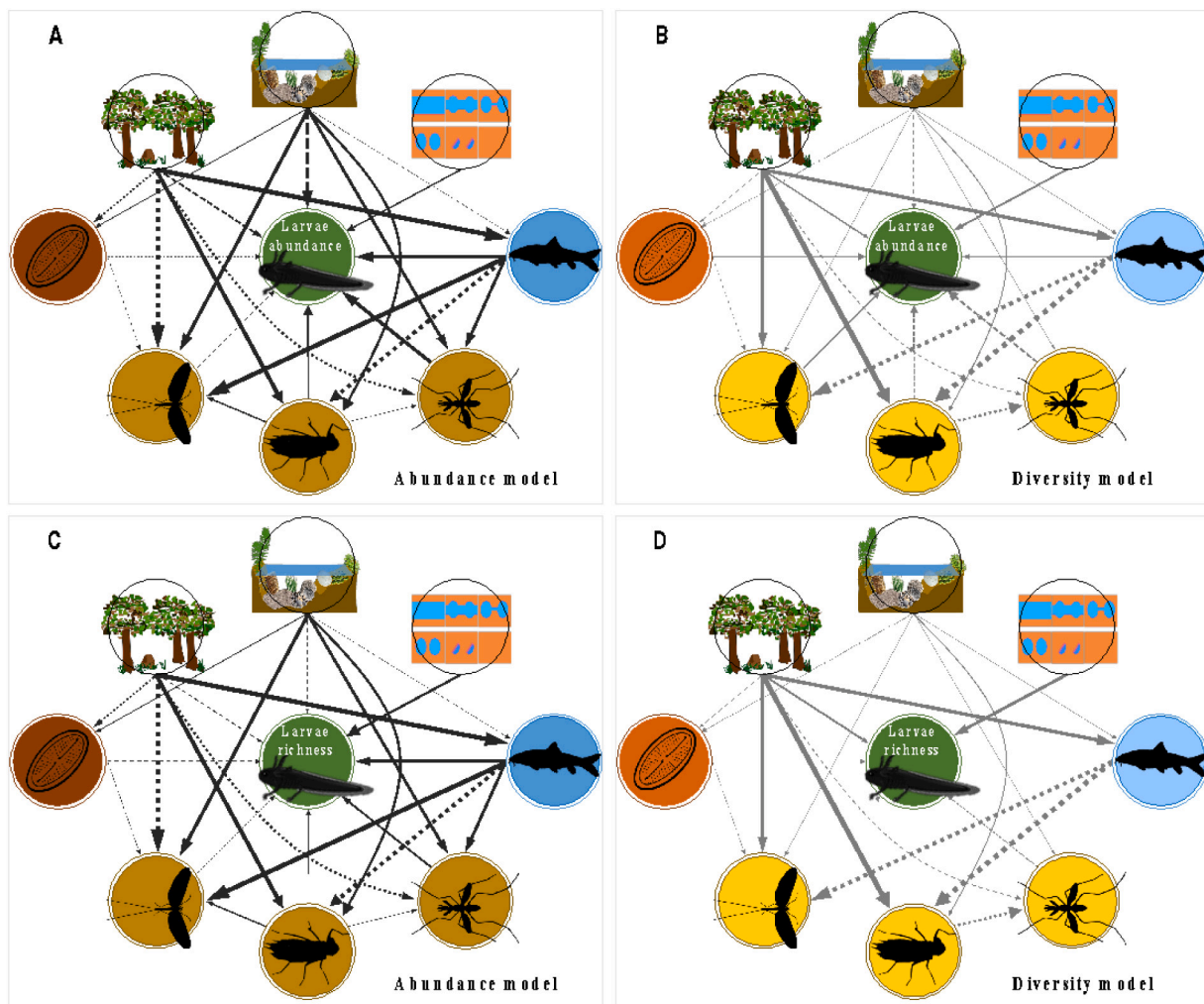


Fig. 5. Structural equation model (SEM) for larvae amphibians. Final model relationships for larvae amphibian abundance and richness are shown. The arrow width corresponds to the coefficients, continuous lines represent positive relationships, while discontinuous lines indicate negative relationships. (A) represents the relationships between fish abundance, and the abundance of macroinvertebrate groups (tadpole-predator, grazing and others) and diatoms on the abundance of larvae amphibians; while in (B) the relationships are represented using the Shannon index for fish, macroinvertebrate and diatoms. Graphs (C) and (D) show the same relationships as (A) and (B), respectively, but using the species richness of larvae amphibians. Non-significant relationships are not shown. For more information on the model relationships, see Table S4.

amphibian dynamics in temporary rivers in wet periods.

The positive interaction between fish abundance and grazing macroinvertebrates and other macroinvertebrate abundance also challenges our expectations, as macroinvertebrates may serve as a food source for fish during specific life stages. Hence, we presumed that macroinvertebrate availability would influence fish abundance (Osenberg et al., 1992). One plausible explanation is the co-tolerance, the ability of different species to coexist in a shared ecosystem by utilising resources in a complementary manner (Vinebrooke et al., 2004). On the other hand, the negative relationships observed between fish and tadpole-predators (abundance and richness), along with grazing macroinvertebrate richness, reinforce the idea that high predation pressure on certain species can decrease diversity. This unexpected finding may indicate that other factors, such as habitat complexity, competition dynamics, or trophic cascades, could be influencing the relationship between fish and macroinvertebrates. The native species of fish captured in the study area and the minnow were *Cyprinidae*, being mostly insectivorous or omnivorous, like the *B. meridionalis* often prefers the larvae of Chironomidae and Ephemeroptera (Aparicio et al., 2016; Rodríguez-Lozano et al., 2016). The *L. gibbosus* is a hungry fish that feeds on invertebrates, but also on fish and amphibian larvae and juvenile, being able to reduce the presence of other fish species. Consequently,

increased fish abundance and diversity may reduce both the number and diversity of specific macroinvertebrate species, favouring non-predated species.

Diatoms respond quickly to environmental changes and are consumed upon by, among others, amphibian tadpoles (Connelly et al., 2008). Diatom beta diversity, for example, was positively related to environmental heterogeneity, while their community variation was linked to physical habitat structure and grazer abundance (Jyrkänkallio-Mikkola et al., 2016). Surprisingly, our association between diatoms and amphibians is generally weak, even with larvae and grazing macroinvertebrates exhibiting negative interactions with diatoms. Furthermore, abiotic variables like QBR and IHF minimally affect diatoms, and the models explain little variance in their abundance. Nevertheless, higher habitat heterogeneity seems to result in higher diatom abundance but lower diversity. Thus, our results suggest that amphibians prefer heterogeneous habitats with diverse shelters and macroinvertebrates over the presence of high diatom abundance, possibly because tadpoles can feed on other resources like detritus (Barrett et al., 2017). Accumulated detritus and algae in temporary streams (not analysed here) likely provide sufficient nutrients for tadpoles, reducing their dependence on the growth and abundance diatoms, as observed in non-permanent ponds (Arribas et al., 2015), potentially mitigating

competition with macroinvertebrates for resources.

Globally, our results suggest that, concerning abiotic factors, water availability in temporary rivers increases amphibian abundance and diversity even if it comes with the addition of predators. This, however, does not seem to be linked to food availability but to the possibility to breed. Indeed, concerning biotic interactions, amphibians in temporary rivers seem more affected by top-down than bottom-up interactions. While results linked to the presence of predators and habitat complexity (interpreted as refugia and the presence of microhabitats) were often present in our study, interactions linked to food resources were unclear or weak. In this sense, a relevant variable missing for a comprehensive understanding of amphibian interactions in sampling sections is the macrophyte population. The abundance of submerged macrophyte species significantly influences fish-macroinvertebrate interactions, as diverse macrophyte habitats may provide resources for macroinvertebrates, reducing their vulnerability to fish predation (Diehl and Eklöv, 1995). This, in turn, affects fish habitat selection, survival, and growth, impacting fish population dynamics and predatory pressure on several stream trophic components (Diehl and Eklöv, 1995). Thus, the macrophyte population may also significantly influence amphibians, especially those with a distinct aquatic character, or with long larval periods which are prone to suffer from intense predation risk, a possibility that could not be addressed in this study.

Our study provides insights into the complex interplay between faunal and hydro-morphological variables and their implications for amphibian communities in temporary rivers that could inform effective conservation strategies in the Mediterranean region (Fernández-Calero et al., 2024). The scarcity of research in this area highlights the novelty and importance of studies focused on amphibians in temporary rivers, particularly given the projected impacts of climate change on both rivers and amphibians. These findings also have significant implications for conservation efforts, highlighting the importance of maintaining the water hydroperiod, natural dynamics, and habitat complexity to safeguard the integrity of temporary river amphibian biodiversity. Additionally, water extraction (wells, canals, dams, ...) exacerbates the flow during drought periods, and some direct discharges of wastewater create highly negative synergies that must be addressed.

CRediT authorship contribution statement

Roger Puig-Gironès: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gemma Bel:** Writing – original draft, Methodology, Investigation, Data curation. **Miguel Cañedo-Argüelles:** Writing – review & editing, Writing – original draft, Visualization, Methodology. **José María Fernández-Calero:** Writing – review & editing, Methodology. **Guillermo Quevedo-Ortiz:** Writing – review & editing, Methodology. **Pau Fortuño:** Writing – review & editing, Methodology. **Dolors Vinyoles:** Writing – review & editing, Methodology. **Joan Real:** Writing – review & editing, Project administration, Funding acquisition. **Eudald Pujol-Buxó:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Núria Bonada:** Writing – review & editing, Writing – original draft, Visualization, Methodology.

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.2024.175917>.

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