



Analysis of the elements of metacommunity structure in a Mediterranean basin: implications in the framework of global change

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Abstract

Metacommunity studies have been gaining in importance in recent decades due to their relevance when interpreting community dynamics. The elements of metacommunity structure (EMS), i.e. coherence, turnover and boundary clumping, are used to assess the assembly of metacommunities. In the present study we analysed the EMS of the Guadiana Hydrographic Demarcation, a prominent seasonal basin located in the southern Iberian Peninsula characterised by a Mediterranean climate, with dry reaches and disconnected pools frequent in streams during the summer. We studied the EMS of the four different taxocoenoses used to assess the ecological status of streams and rivers according to the European Water Framework Directive (diatoms, macrophytes, macroinvertebrates and fishes), both independently of each other and taken together. These analyses were carried out using three different approaches: (1) using a gradient from reciprocal averaging analysis; (2) following a geographical gradient; and (3) following an environmental gradient. We found that the four groups of organisms analysed had either a Clementsian metacommunity structure or a similar structure. When all groups were considered together, the structure of the metacommunity was Clementsian or quasi-Clementsian. Thus, in the framework of the current global change scenario, communities in this basin may be vulnerable to increasing isolation due to more frequent and larger dry periods; consequently, management measures should be considered.

Keywords Metacommunity structure · Diatoms · Macrophytes · Macroinvertebrates · Fishes · Spain

Introduction

The concept of a metacommunity, considered to be a set of local communities connected by the dispersal of several potentially interacting species (Leibold et al. 2004), has been gaining importance in recent years due to its significance in interpreting processes and dynamics that can be observed at regional and local scales (Leibold and Chase 2018). The metacommunity occupies a wide geographical space, i.e. the region, and each of the local communities are located in smaller sites within the region, i.e. the localities. Interspecific interactions, such as competition, occur at the local scale, while dispersal between local communities takes place at the regional level (Leibold et al. 2004). Local interspecific interactions modified by dispersal events and spatial heterogeneity result in species coexistence at different scales (HilleRisLambers et al. 2012; Leibold and Chase 2018; Chase et al. 2020). The study of metacommunities therefore involves investigating the structure of local communities,

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assuming that such structure is affected not only by local mechanisms but also by regional factors (Leibold et al. 2004; Heino et al. 2015b).

Three main factors are involved in the structuring process of a metacommunity: habitat heterogeneity, dispersal and ecological niche. The elements of metacommunity structure (EMS; Leibold and Mikkelsen 2002), namely coherence, turnover and boundary clumping (Presley et al. 2010), are used to assess metacommunity assembly. By determining these EMS, it is possible to identify different patterns of metacommunity structuring, with the main patterns being Clementsian gradients, Gleasonian gradients, checkerboard distribution, evenly spaced gradients, nested distribution, random subsets, as well as a number of other patterns within these major ones (quasi-structures; for more information see Presley et al. 2010).

Within this metacommunity context, streams and rivers are of great interest as the organisms that inhabit them use to be limited by terrestrial barriers, thus affecting their dispersal. Of particular interest are Mediterranean stream and river ecosystems, as these are characterised by their seasonality, with a marked decrease in flow in the summer which leaves many streams completely dry or with disconnected pools (Datry et al. 2017a), and, consequently, are among the ecosystems most vulnerable to the effect of climate change on a global scale (Markovic et al. 2017; Jorda-Capdevila et al. 2019). This seasonality has favoured the development of adaptations to these conditions in organisms living in Mediterranean streams to ensure their survival in these highly resilient and dynamic ecosystems (Bonada et al. 2007). A decrease in flow not only implies a reduction in habitat availability due to decreasing water depth and surface area, but also decreases habitat suitability, increases sedimentation, decreases water velocity, changes nutrient concentration, increases temperature, decreases oxygen concentration and even decreases the amount of available resources (Dewson et al. 2007). A clear example of the effects of seasonality on these environments is the appearance of disconnected pools that remain in some rivers, which serve as refuges for numerous organisms, resulting in high biotic densities in a very small space, where, in addition to all the conditions mentioned above, there is also a high level of competition (Mas-Martí et al. 2010). Moreover, these changing conditions throughout the hydrological year and the appearance—or not—of these disconnected pools will have a different effect on organisms with different biological traits and dispersal capacity. For example, diatoms do not possess significant active dispersal capabilities, but rather disperse by drift, anemochory and zoochory (Quevedo-Ortiz et al. 2024). Macrophytes do not have the ability to disperse actively, but they do disperse passively via water through their seeds and plant propagules (hydrochory) (Sarneel 2013), and although this is their predominant form of dispersal (Heidbüchel and

Hussner 2019), some species also disperse through anemochory and zoochory (Lesiv et al. 2020; Clausen et al. 2002). For their part, macroinvertebrates have an overall high dispersal capacity (Padiál et al. 2014) due to not only having the ability to disperse through river networks (Brown et al. 2018), but also some species are dispersed by zoochory and, in the case of many insects, they even have the ability to fly during their adult stage (Bohonak and Jenkins 2003; Stubbington et al. 2017). Lastly, fishes can only disperse, either actively or passively, along the course of the river while it has water (Kerezszy et al. 2017), as well as when floods connect water bodies (Thomaz et al. 2007). This is likely to affect their distribution, potentially giving rise to different metacommunity structures. Differences in dispersal ability among species have been pointed out (e.g. Bohonak and Jenkins 2003), conditioning the final composition of each community, resulting in some taxa being common to many different communities and others limited exclusively to particular sites under specific conditions. Such scenarios are also pertinent to the other groups, as suggested in previous studies (e.g. Heino et al. 2014 and references herein).

In the current global change scenario, where an increase in seasonality is expected to occur that would increase the frequency, intensity and severity of droughts, the aquatic systems of the Mediterranean region (mainly the small and medium-sized streams) and their biodiversity will be dramatically affected (Jorda-Capdevila et al. 2019). Synergistically to Climate Change, other anthropogenic effects (e.g. increase in urban areas, greater use of intensive irrigation, among others) contribute to the reduction of water and decreasing runoff (Best 2019). It is uncertain how species, their populations and communities will be able to respond to much more rapid changes than they have ever likely experienced throughout their evolutionary history, but knowing the structure of their metacommunities is a first step towards predicting what may occur under this scenario of change.

Several studies have attempted to analyse metacommunity structure in different aquatic ecosystems (e.g. Heino et al. 2015a; Tonkin et al. 2016; Brasil et al. 2017; Stoczynski et al. 2021), reporting different structures depending on the particular freshwater system and taxocoenosis. Despite these studies, to our knowledge, none has been conducted in a basin in which a seasonal regime of its streams prevails. This is the case of the Guadiana basin (southern Spain), which is mainly subject to a Mediterranean-continental climate, with marked temperature fluctuations, a well-defined dry season, high summer temperatures and low rainfall. Average rainfall also has a marked spatial variability, being very low in particular areas. Due to this marked seasonality in the basin, the Guadiana is exceptional in terms of the number of temporary streams it possesses, which are mostly small and medium-sized streams that either dry up completely during the summer period or leave only disconnected pools.

Due to these characteristics, the study of this basin is particularly interesting from a metacommunity point of view, and even more considering the current framework of global change, where Mediterranean ecosystems at a global scale are among the most vulnerable to the effect of climate change, with a notable increase in seasonality expected in the Mediterranean basin, affecting the aquatic ecosystems of this region and, consequently, its biodiversity (Tierno de Figueroa et al. 2013). Moreover, due to the aforementioned increase in the seasonality of other non-seasonal basins predicted by climatic models (Verdonschot et al. 2010), results from analyses of the metacommunity of this basin may be used as model of future conditions in other permanent drainages.

In addition, as some authors have recently suggested, reconsidering the methodology used to infer metacommunity structures from the traditional EMS approach (e.g. Dallas et al., 2016; Schmera et al. 2018), we performed the EMS analysis according to three different ordination gradients, i.e. traditional, geographic and environmental gradients, so that we could contrast the results for each of these.

Therefore, in this article we report the results of our analysis of the Guadiana basin, a basin subjected to a highly seasonal regime, in terms of the elements of metacommunity structure of four different biocoenoses, namely diatoms, macrophytes, macroinvertebrates and fishes, both independently and taken together, and discuss and describe the implications of each structure in the current Climate Change scenario from a conservation point of view. Our initial hypothesis is that the metacommunity is going to have a Clementsian structure in which the communities (considering the four studied groups together) are relatively discrete and quite well differentiated as conditioned by the marked seasonality, the presence of many anthropogenic barriers in the basin and the characteristics of each particular taxonomic group. Thus, the following hypotheses can be drawn for each taxocoenosis under the marked seasonality of the study area: (1) despite diatoms and macroinvertebrates having a high dispersal ability, their high taxonomic richness, including both generalist and specialist taxa, would promote a Clementsian structure; (2) macrophytes have also high dispersal capacity but, even if their taxonomic richness is much lower than that of the previous groups, the distribution of some of the species is restricted by ecological factors, so a Clementsian structure would be also expected; (3) finally, most fishes in the Guadiana Hydrographic Demarcation have wide tolerance ranges, and this, together with their fast aquatic displacement capacity through the river network, would promote relatively homogeneous communities, but due to the existence of many barriers in the basin together with the fact that fishes can only disperse through water, a Clementsian structure would be expected. Based on our analyses, we also discuss the possible effect of climate change on this type of

basin with a Mediterranean climate and its effect on their metacommunity and, therefore, on its biodiversity.

Material and methods

Study area

The Guadiana River Basin is located in the centre and southwest of the Iberian Peninsula, and its territorial scope extends over both Spain and Portugal. It has a surface area of just over 67,000 km², of which more than 55,500 km² are in Spanish territory, constituting what is known as the Guadiana Hydrographic Demarcation (Buonocore et al. 2021; MITECO 2023). This study focuses on the part of the basin forming the Guadiana Hydrographic Demarcation.

The Guadiana Hydrographic Demarcation has a high degree of heterogeneity, showing a clear asymmetry due to its geological characteristics, where the right bank is smaller and has a steeper morphology, while the left bank is larger and has a smoother relief (MITECO 2023). The climate is typically Mediterranean, watercourses within it are mainly seasonal and flow through terrains of different origin and nature until they flow into the Atlantic Ocean. The natural vegetation comprises Mediterranean forest, which changes with altitude, and cultivated vegetation is dominated by cereals, although in the upper basin, vines are the main cultivated crop, with areas of olive groves also being common (Canuto et al. 2019; Buonocore et al. 2021). The irrigation area covers over 400,000 ha, with 85% of derived water used for irrigation. A number of recent management projects are ongoing in the basin, which will result in the addition of 150,000 ha of irrigated land (Canuto et al. 2019). Livestock is also present in the study area at relatively high densities. In each of the water bodies of this basin, monitoring is carried out in accordance with the European Water Framework Directive (WFD), following the WFD protocols and monitoring programs; consequently, this study has been carried out in accordance with WFD regulations. There are 316 surface water bodies, of which 191 are classified as “natural stream” and 60 as “highly modified stream”. A number of barriers are present in these. A total of 67 reservoir dams have been defined, of which 37 are administered by the Guadiana Hydrographic Confederation and 30 are under the control of Autonomous Communities, individuals or municipalities (MITECO 2023). One or more control (i.e. sampling) sites are present in these different bodies of water. The network of sampling sites analysed in this study consist of 184 control sites, which were sampled in 2019, 2020 and 2021 (Fig. 1; Electronic Supplementary Material [ESM] Table S1). At each site, physical and chemical data were collected, as well as biological data on diatoms, macrophytes, macroinvertebrates and fishes.

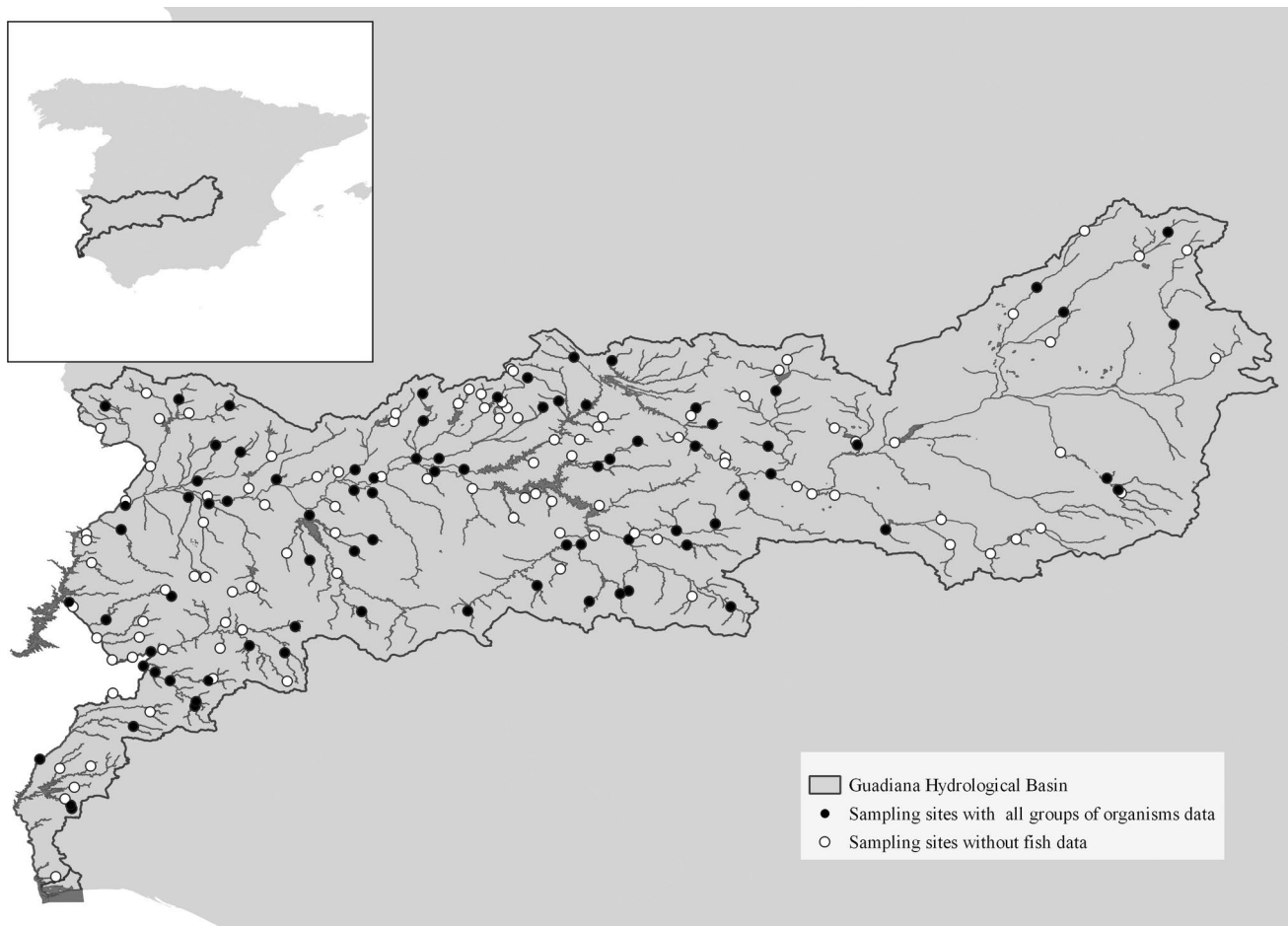


Fig. 1 Map of the Guadiana Hydrographic Demarcation (GHD) showing the 184 sampling sites considered in this study. Top left: Spain (with-out the Canary Islands, Ceuta and Melilla) showing the location of the GHD

Physical and chemical characterisation and biological sampling

Physical and chemical characterisation of the sampling sites were primarily determined using a multiparametric probe that measured pH, temperature, dissolved oxygen and conductivity in situ. Water samples were also taken in the field for subsequent analysis and determination of nitrates, ammonium, phosphates, total phosphorus and total nitrogen. The techniques and methods used to determine each of these parameters are shown in *ESM Table S2*. Data were collected monthly throughout 2020. An annual average was determined for each parameter, which was used for characterisation (*ESM Table S3*) and to relate the different communities to the physical and chemical parameters recorded in each site.

Biological sampling was carried out in accordance with Spanish regulations for the application of the WFD. Biological sampling of diatoms, macrophytes and macroinvertebrates was carried out in 184 sites between 17 February

and 25 May 2020, i.e. in the spring when macroinvertebrate communities reach their maximum diversity. This time period was in accordance with the dates established in the Spanish normative to apply the WFD (Royal Decree 817/2015; MAGRAMA, 2015c). Due to its greater complexity, sampling of fishes was carried out during 2019, 2020 and 2021. Samples were taken in different sites in each of those years, up to a total of 81 sites, so that the total number of samples for the 3 years would be representative of the basin, thus complying with the Spanish operational control programme (Royal Decree 817/2015; MAGRAMA, 2015c), which indicates that a complete sampling of fishes of a river basin is to be carried out every 3 years, always during the spring and autumn when the water temperature is suitable for electrofishing.

WFD sampling and laboratory protocols were followed for the collection and analysis of biological indicators (MAGRAMA 2015c). For the capture and determination of macroinvertebrates, we used the sampling and laboratory protocol for benthic invertebrate fauna in wadeable rivers

(MAGRAMA 2013b). A 100-m-long section representative of the water body was sampled at each sampling site and the different habitats present were identified for subsequent sampling. The section was sampled from downstream to upstream, and 20 sampling units were distributed. For each sampling unit, the substrate in the half metre in front of the mouth of the net (mesh size 500 μm) was removed. The net had a width of 0.25 m so each kick (agitation of substrate before the net mouth) corresponded to a rectangular area of approximately 0.125 m^2 ; therefore, a total of 2.5 m^2 was sampled. The samples were fixed with 96% ethanol and stored in cold storage. Once in the laboratory, macroinvertebrates were taken from the samples and identified using a Motic SMZ-168 stereo microscope (Motic, Speed Fair Co., Ltd, Hong Kong, China), mostly to the family level; the exceptions were *Corbicula fluminea* (O.F. Müller, 1774) and *Procambarus clarkii* (Girard, 1852), which were identified to species level as they are invasive species; oligochaetes and ostracods, which were identified to the class level; *Ferrisia*, which was identified to the genus level; and Acariformes, which was identified to the superorder level. Although *Ferrisia* is currently included in the family Planorbidae (Bouchet and Rocroi 2005), it is still identified and scored separately in the Iberian Biological Monitoring Working Party (IBMWP) quality index (Alba-Tecedor et al. 2004), which is why it has also been evaluated as a separate taxon in this study.

For the sampling and determination of diatoms, we used the sampling and laboratory protocol for aquatic flora (phytobenthic organisms) in rivers (MAGRAMA 2013c). A distance of 100 m was covered to identify a site with good current and luminosity. At this site, five or ten stones were collected (depending on size) and the top surface of each stone was brushed with a stiff toothbrush. An area of approximately 10 cm^2 per stone was scraped if ten stones were collected and 20 cm^2 per stone was scraped if five stones were taken. The total area sampled was therefore about 100 cm^2 . After scraping, the brush was placed in a jar with 25 ml of mineral water, where it was shaken, and the diatoms were resuspended. The samples were fixed by adding 25 ml of 96% ethanol and then stored in iceboxes. Once in the laboratory, two steps were followed for subsequent analysis. The first step was to eliminate all organic matter. To this end, the samples were sedimented and a large portion of the supernatant was removed. From the homogenised samples that remained, 3-ml samples were taken and placed in tubes under boiling conditions, with the subsequent addition of 7 ml of hydrogen peroxide to each tube; the samples were then placed in a water bath at 95 °C until completion of the reaction when they were removed from the heat source and a few drops of hydrochloric acid were added, thus removing possible inclusions of calcium carbonate. The samples, once cooled,

were centrifuged (3,000 rpm, 5 min), with the tubes filled with distilled water for flushing. To finish the preparation, a drop of each sample was taken with a Pasteur pipette and placed on a coverslip. This drop was left to dry and, once dry, naphrax was added, leaving the sample ready for the second step, namely the identification. Identification was carried out using a Leica DM-1000 optical microscope (Leica Microsystems, Wetzlar, Germany), with the aim to achieve the lowest possible level of taxonomic resolution, mostly at the species level; in a minority of samples, however, identification was only possible to the genus level.

For the study of macrophytes, we used the sampling and laboratory protocol for macrophytes in rivers (MAGRAMA 2015b), and the same section was sampled as that used for macroinvertebrates. Sampling consisted of taking the most relevant taxa and making a rough estimate of their abundance. Percent cover for each taxon present in the section was recorded. Sampling was carried out by zig-zagging upstream. Some taxa, due to their distinctiveness, were identified in situ, so collection was not necessary; for the other taxa, each taxon was labelled, fixed with Kew liquid and stored individually in vials. The samples were stored under cold conditions until identification. Identification required the use of both the Leica DM-1000 stereo microscope and the Motic SMZ-168 optical microscope, as described above. Vascular plants, bryophytes and some macroalgae were identified at the species level, but most of the latter were identified at the genus level. The term macrophyte designates a functional group of very heterogeneous plants, from both an evolutionary and systematic point of view, including vascular plants, bryophytes, charophytes and filamentous algae (MAGRAMA 2013a). Therefore, in this group we included diatoms that were found to have formed macroscopic colonies (in contrast to those considered in the study of diatoms explicitly as described above that do not form macroscopic colonies).

For the study of fishes, we used the sampling protocol for ichthyologic fauna in rivers (MAGRAMA 2015a). This sampling, unlike the sampling for the other groups of organisms, was done on a different day to the sampling of the previous groups of organisms to avoid fishes escaping. The most representative reach of the river was chosen, in terms of bank morphology and riverside vegetation, which provide refuges, habitat heterogeneity and shade. The reach also had to be delimited by natural obstacles or rapids that act as a natural partial barrier for fishes. The length of the sampling area was tenfold the average width of the river, with a minimum area of 100 m^2 and a minimum length of 100 m. The abundance of the taxa captured was expressed as catches per unit effort referring to the sampled area. The specimens collected by electrofishing were identified in situ at the species level and subsequently returned to the river.

Data analyses

To obtain a general view of the relationship between the analysed communities and the physical and chemical parameters recorded in each site, we performed a non-metric multidimensional scaling (NMDS) analysis using the metaMDS function in the vegan package (Oksanen et al. 2020) in R software (R Core Team 2021). A Wisconsin square root standardisation was applied to the community data (abundance), and dissimilarities among communities were calculated using the Bray–Curtis distance. The number of dimensions (“k” in function metaMDS) were adjusted to three in those cases in which the stress was > 0.2 . Function envfit in vegan package (Oksanen et al. 2020) was used to test the statistical significance of the physical and chemical parameters measured in each site, and those that were statistically significant were represented as vectors and isoclines in the NMDS bidimensional plots. These analyses were performed for the 184 studied sites for diatoms, macrophytes and macroinvertebrates, the 81 sites where data were available for fishes (see section [Physical and chemical characterisation and biological sampling](#)) and separately for each taxonomic group and for the whole community (the four taxocoenoses together). In the latter analysis, we performed one analysis for the 184 sites pooling together diatoms, macrophytes and macroinvertebrates, and another for the 81 sites where the four taxonomic groups coexisted.

Because the identification of fishes, macrophytes and diatoms was mostly done at the species level, while macroinvertebrates were identified at a higher level (family), a preliminary comparison of the EMS was carried out to check whether the metacommunity patterns obtained at different levels of taxonomic resolution differed or not. Although this has been previously tested and in the case of macroinvertebrates no different outcome between genus and family level was expected (e.g. Heino et al. 2015a; He et al. 2020), we wanted to verify this outcome with our own dataset. This allowed us to determine the taxonomic level at which we could work to obtain reliable conclusions. For this purpose, nine sampling sites were selected within a sub-catchment where there were no dispersal barriers (ESM Table S4). Once we verified that the results obtained at different taxonomic levels did not affect the outcome (ESM Table S5), the analyses of the EMS of the entire metacommunity of the organisms sampled as a whole (diatoms, macrophytes, macroinvertebrates and fishes together) and of each of the taxocoenoses independently were carried out applying three different approaches. The first approach followed Heino et al. (2015a), the second followed a geographical gradient and the third followed an environmental gradient. In this way, we could check whether or not there were differences in the results depending on the ordination gradient. The intention of performing the analysis with three different gradients

is to provide a comprehensive approach from three different points of view. The traditional gradient of Heino et al. (2015a) creates a matrix where sites with similar species and similar species distribution are located closer together. However, the possible effect of actual environmental conditions is lost. To include the possible effect of actual environmental conditions we performed the analysis including an environmental gradient, where abiotic factors take a considerable weight in the metacommunity structure. Finally, with the geographic gradient, the greatest structuring weight is given to dispersion, with the different local communities ordered by proximity. The metacommunity pattern of the taxocoenoses in isolation and the metacommunity as a whole was described according to the methodology of Leibold et al. (2004).

The analysis of metacommunity elements is based on three metrics: coherence, turnover and boundary clumping. It is important to emphasise that the metacommunity structure that best fits the empirical dataset in the EMS analysis is the combination of these three metacommunity elements. Prior to calculating these metrics, a presence-absence matrix of taxa was derived by ordering the different local sites along three different gradients. For the first approach, a presence-absence matrix of taxa was derived using reciprocal averaging (i.e. correspondence analysis) with the aim of ordering sites so that those with similar taxa composition are close to each other and ordering taxa so that those with similar occurrence among sites are also close. Ultimately, reciprocal averaging defines a latent environmental gradient (i.e. variation in unmeasured environmental characteristics sensu Presley et al. 2010) and an ordered metacommunity along this gradient, which incorporates multiple environmental factors that are presumably important for species distributions (Leibold and Mikkelsen 2002; Presley et al. 2010). For the second approach, a matrix with local sites ordered according to a geographic gradient was used. To order the local sites following the geographical gradient, the distance in kilometres between the points was taken using QGIS software (QGIS Development Team 2023), then sites were ordered based on proximity. Finally, for the third approach, a matrix ordered according to a physical and chemical gradient calculated with the parameters measured at each site was used. To obtain this matrix, we ordered by overall environmental gradients obtained from the first axis of a principal component analysis (PCA1) on the ten environmental variables using the vegan package (Oksanen et al. 2020) in R software (R Core Team 2021).

The EMS analyses were performed using the metacom package (Dallas 2013). The fixed proportional null model was used for the EMS analysis because it is not very sensitive to type I and II errors (Presley et al. 2009; Heino et al. 2015a). Random matrices were produced using the “r0” method for the fixed proportional null model as implemented

in the vegan package (Oksanen et al. 2020). A total of 100 simulations was used to provide random matrices. Statistical significance was then assessed by comparing the observed index value of the original matrix with the distribution of values derived from the randomisations (Manly 1995). EMS were assessed for each group of organisms and for the global metacommunity in all cases. Presley et al. (2010) was followed for the interpretation of the metrics.

We performed the EMS analyses at two different spatial scales, one which considered the 184 sampling sites with information on macroinvertebrates, macrophytes and diatoms (hereafter referred to as metacommunity A), and one considering only the 81 sites where fish data were also available (metacommunity B). In both cases we analysed the EMS considering each group independently, as well as considering all groups together. In this way, we were able to check whether or not there were differences in the results depending on the spatial scale.

Results

Abiotic environment and composition of the metacommunity

We found similar patterns in the physical and chemical parameter values, with few differences between the two metacommunities (Fig. 2). For example, total organic carbon

(TOC) was relatively low, with the exception of some particular sites with very high concentration, the pH rarely fell outside the range of 7 to 8.5, and the temperature ranged from 10°C to 22°C.

The NMDS ordinations for each taxonomic group (except for macrophytes, for which data were not enough for reliable interpretation due to the high number of zeros) and for the whole community considering 184 sites for diatoms, macrophytes and macroinvertebrates, and 81 sites for fishes plus the other three taxonomic groups, are shown in Figs. 3–7.

Diatoms were ordered along two main axes, one related to pH and the other related to temperature, conductivity, total nitrogen (TN) and nitrates (NO_3) (Fig. 3). The diatom community from one particular site (GN0000047) falls outside the main group of points in the figure, so for ease of representation, the axes have been restricted to all the remaining points.

Macroinvertebrate communities in the studied sites are ordered following three main gradients (Fig. 4): one physical, determined by temperature, conductivity (EC) and dissolved oxygen (DO), but not pH; one chemical, related to the main nutrients (forms of the nitrogen and phosphorous families, on the one hand, and total organic carbon [TOC], on the other, although this is not so clear); and one related exclusively to nitrates.

Pooling together the three taxocoenoses analysed in the 184 studied sites (macroinvertebrates, diatoms and macrophytes), the resulting communities were ranked along

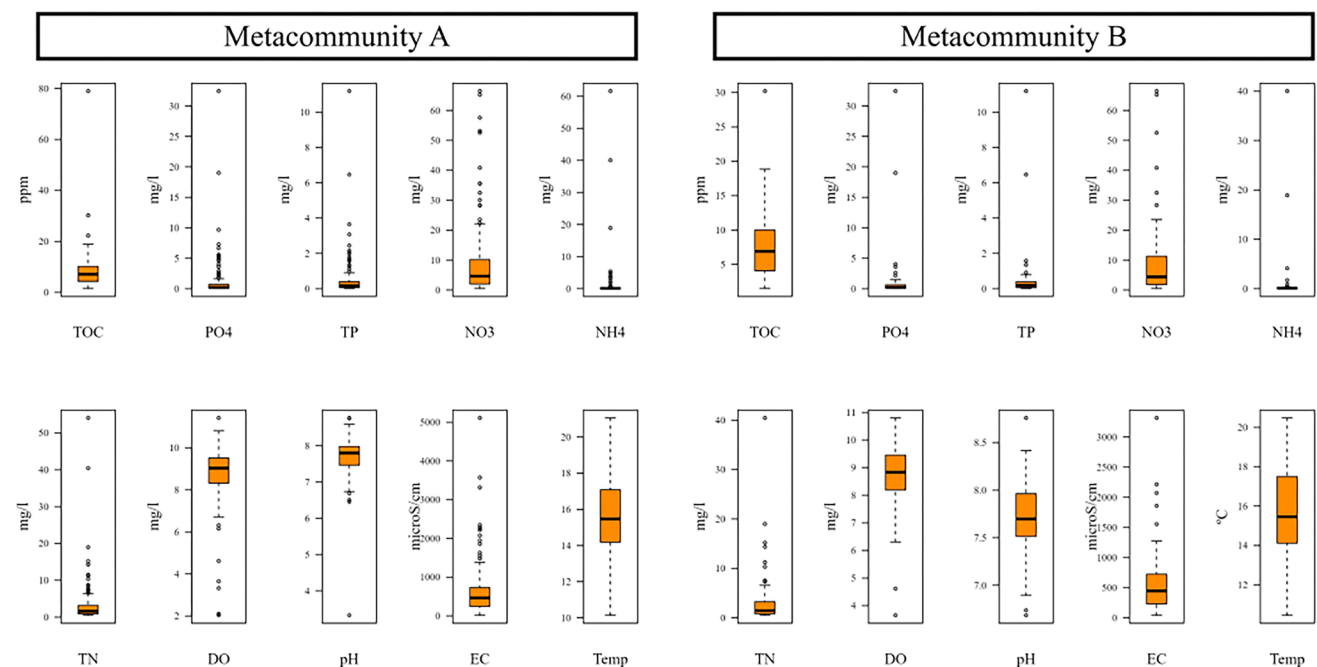


Fig. 2 Mean values of total organic carbon (TOC), phosphate (PO4), total phosphorus (TP), nitrate (NO3), ammonium (NH4), total nitrogen (TN), dissolved oxygen (DO), pH, conductivity (EC) and tem-

perature (Temp) for each of the sites forming metacommunity A (left) and metacommunity B (right)

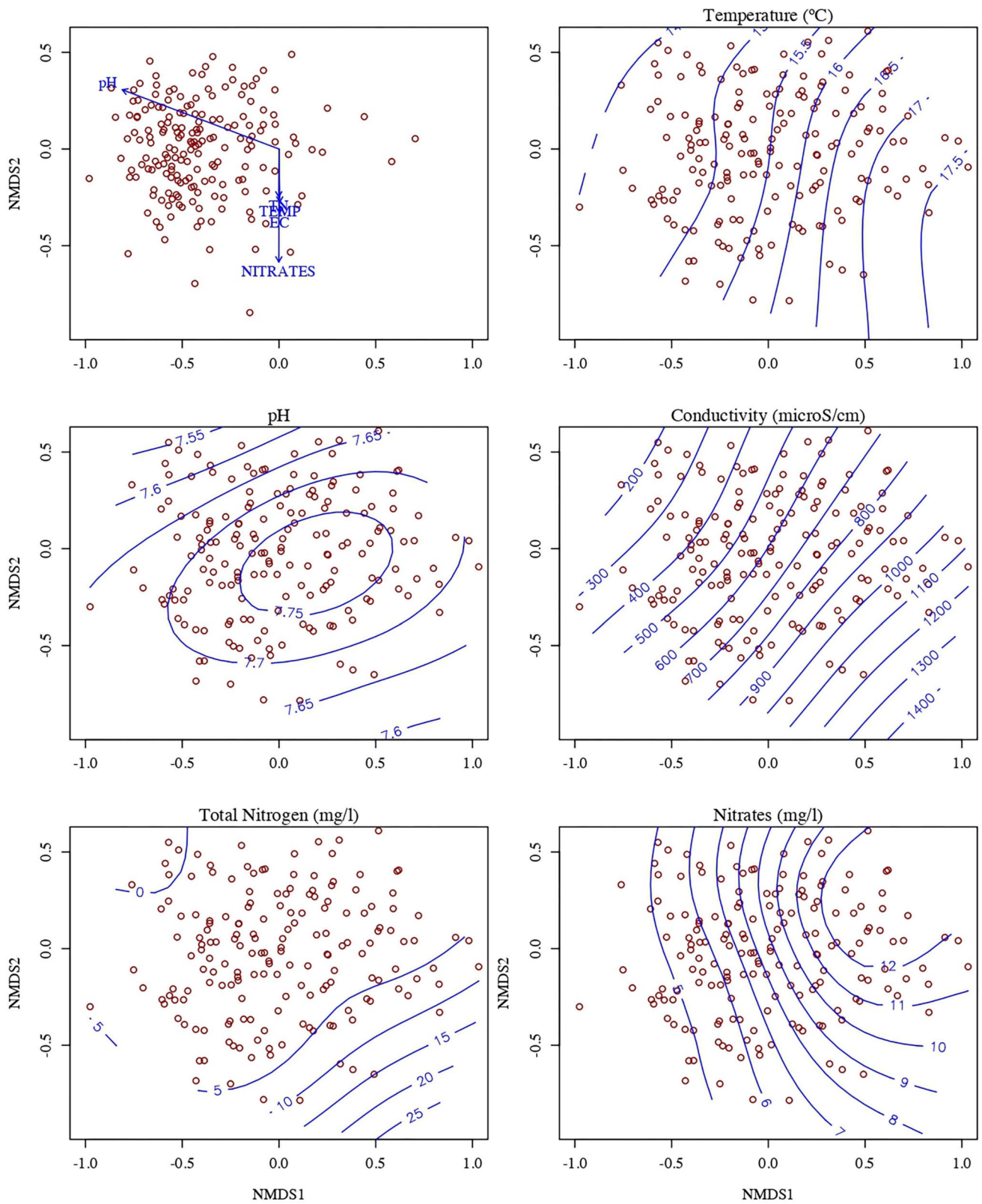
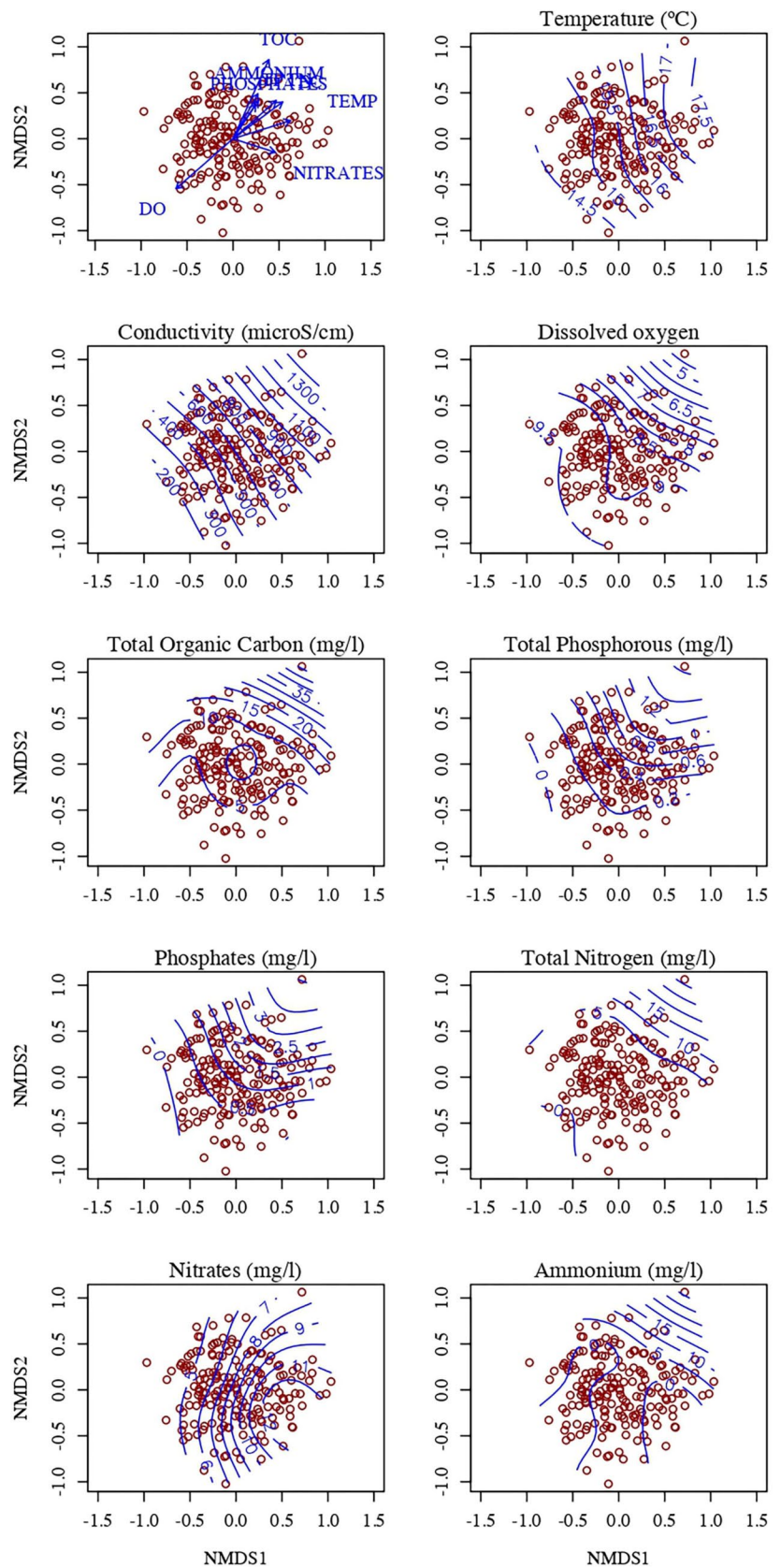


Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of the diatom communities present in the 184 sampled sites ($k=2$, stress=0.10). Top-left panel represents ordination of communities

and linear vectors for significant physical and chemical variables; the remaining panels represent smooth surfaces for each significant physical and chemical variable

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of the macroinvertebrate communities present in the 184 sampled sites ($k=3$, stress=0.20). Top-left panel represents ordination of communities and linear vectors for significant physical and chemical variables; the remaining panels represent smooth surfaces for each significant physical and chemical variable



gradients of several physical parameters, such as temperature, pH (in this case the gradient is not so clear), EC and DO, and several chemical parameters, such as TOC, total phosphorus (TP) and phosphates, and total nitrogen (TN) and nitrates (Fig. 5).

In the case of fishes, the ordination follows a gradient of temperature, on one side, and of TP, phosphates and ammonium (NH_4), on the other, with one community (GN00000594) clearly separated from the rest (Fig. 6).

We also considered the community formed by the four analysed taxocoenoses in the 81 sites where they coexist and found that all recorded physical and chemical parameters determined their distribution in the two-dimensional ecological space (Fig. 7). Of the physical parameters analysed, temperature shows the most linear gradient. In the case of the chemical parameters, NH_4 is the only compound for which no significant gradient is observed.

In total, more than 100,000 individuals were identified in the Guadiana Hydrographic Demarcation, including 172 macrophyte taxa, 527 diatom taxa, 108 macroinvertebrate taxa and 24 fish taxa (ESM Tables S6–S9).

The most abundant macroinvertebrate taxa with the highest frequency of occurrence in the sampled sites were Chironomidae, Oligochaeta, Ostracoda, Simuliidae and Baetidae. These taxa were found in more than 75% of the study sites, with Chironomidae occurring in 99% of study sites (ESM Table S6). Of the diatoms, the most abundant and frequent taxa among the sampling sites were *Achnanthydium minutissimum* (Kützing) Czarnecki, 1994, which was found in more than 60% of sites, *Navicula veneta* Kützing, 1844, identified in almost 66% of sites, *Planothydium frequentissimum* (Lange-Bertalot) Lange-Bertalot, 1999, present in 72% of sites and *Mayamaea permitis* (Hustedt) Bruder & Medlin, 2008, which was found in 74% of sites (ESM Table S7). With regard to macrophytes, *Spirogyra* and *Oedogonium* were the most frequent taxa; however, they appeared in only 47% of sites. The presence of the remaining taxa accounted for < 28% of the total number of sites (ESM Table S8). The fish taxa that stood out in terms of abundance were *Gambusia holbrooki* Girard, 1859, and two Iberian endemic species *Iberochondrostoma lemmingii* (Steindachner, 1866) and *Squalius alburnoides* (Steindachner, 1866). However, the most frequent taxa were *Lepomis gibbosus* (Linnaeus, 1758), *Gambusia holbrooki* Girard, 1859 and two endemic Iberian endemic species, *Squalius pyrenaicus* (Günther, 1868) and *Cobitis paludica* (de Buen, 1930), with a relatively low frequency of occurrence of around 40% (ESM Table S9).

In the preliminary analysis (family vs. genus) in macroinvertebrates, the same result was obtained when analysing the metacommunity of macroinvertebrates identified at the family level as when identification was carried out at the genus level, giving, in both cases, a Clementsian structure (ESM Table S5), which would support the use of both levels

of resolution indistinctly for this biocenosis in the Guadiana basin.

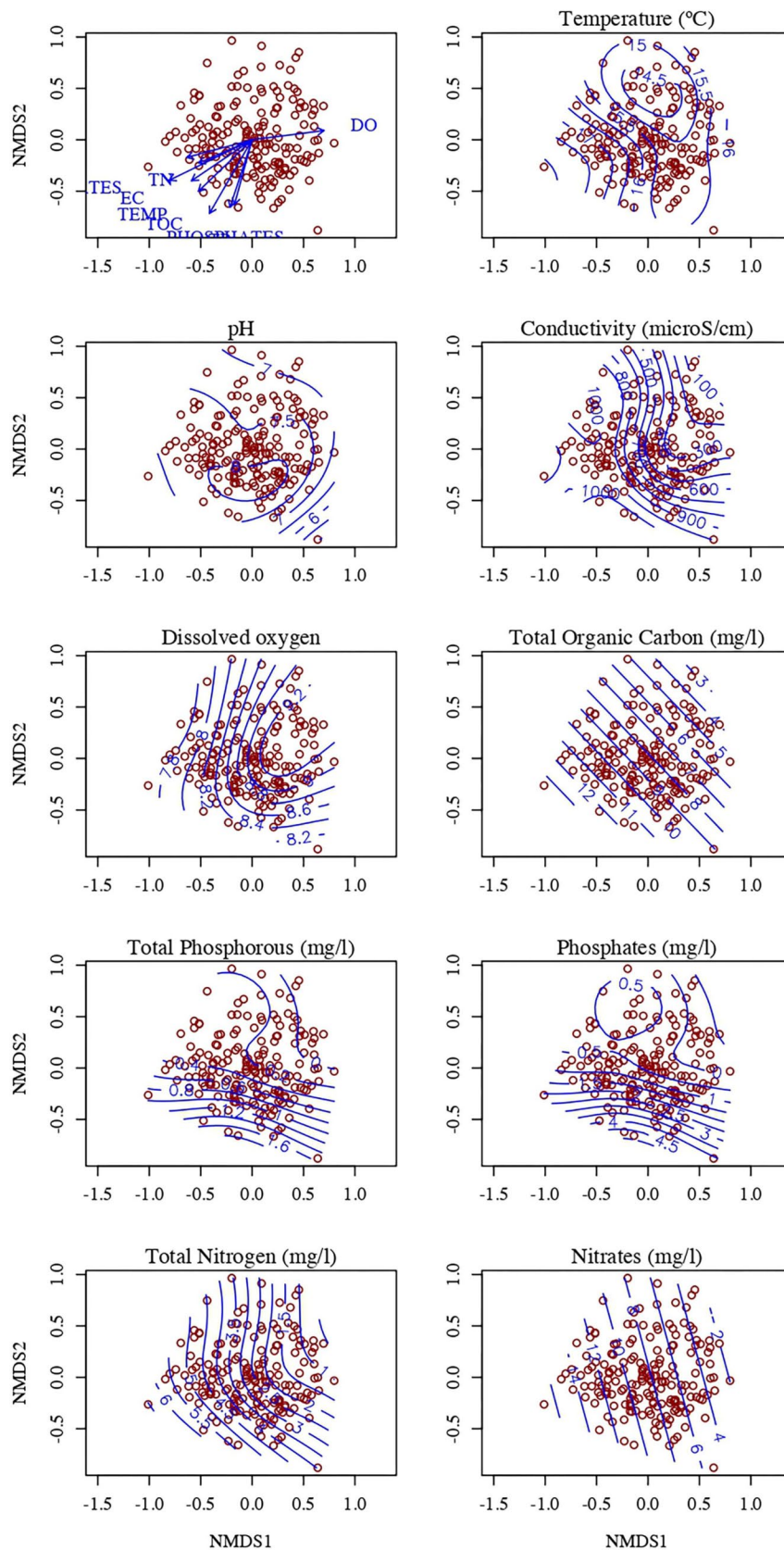
Analysis of elements of metacommunity structure by taxonomic groups

A comparison of the results of the EMS analyses obtained at the two different spatial scales (metacommunity A and metacommunity B) revealed almost no differences in outcomes for any of the taxa in which this comparison could be done, i.e. macroinvertebrates, diatoms and macrophytes using the three different gradients. When a latent gradient was used, the analysis of the EMS showed that both the macroinvertebrate and diatom metacommunities independently showed Clementsian gradients on both CA axes (ESM Table S10). The EMS of the macrophyte metacommunity, on the other hand, showed different interpretations on the primary and secondary axes in both metacommunity A and B, being quasi-nested (quasi-clumped species loss) and quasi-Clementsian, respectively, in the first CA axis, and following a Clementsian structure in the second CA axis in both (ESM Table S10). For fishes, the metacommunity showed a Gleasonian structure for the first axis and a quasi-Gleasonian structure for the second axis (ESM Table S10). When a geographical gradient was considered, macrophytes independently showed a quasi-Clementsian gradient in both metacommunities, the fish metacommunity showed a Clementsian structure and both macroinvertebrate and diatom metacommunities showed a Clementsian structure for metacommunity A and a quasi-Clementsian structure for metacommunity B (ESM Table S11). Finally, when an environmental gradient was used, both the macroinvertebrates and macrophytes showed a Clementsian structure for metacommunity A and a quasi-Clementsian structure for metacommunity B, and both fishes and diatoms showed a quasi-Clementsian structure for metacommunity A and a quasi-clumped species loss for the metacommunity B (ESM Table S12).

Analysis of elements of metacommunity structure as a whole

When metacommunity A was analysed, for which information on macroinvertebrates, diatoms and macrophytes was available, but no data on fishes were available, a Clementsian metacommunity structure was found for all the gradients. Similar results were obtained when studying the metacommunity formed by the 81 control sites with information from all four groups of organisms, i.e. including fishes (metacommunity B), the structure being Clementsian in all cases except when applying the environmental gradient, where a quasi-Clementsian structure was found (ESM Tables S13–S15).

Fig. 5 Non-metric multidimensional scaling (NMDS) ordination of the communities composed by macroinvertebrates, diatoms and macrophytes together present in the 184 sampled sites ($k=3$, stress=0.18). Top-left panel represents ordination of communities and linear vectors for significant physical and chemical variables; the remaining panels represent smooth surfaces for each significant physical and chemical variable



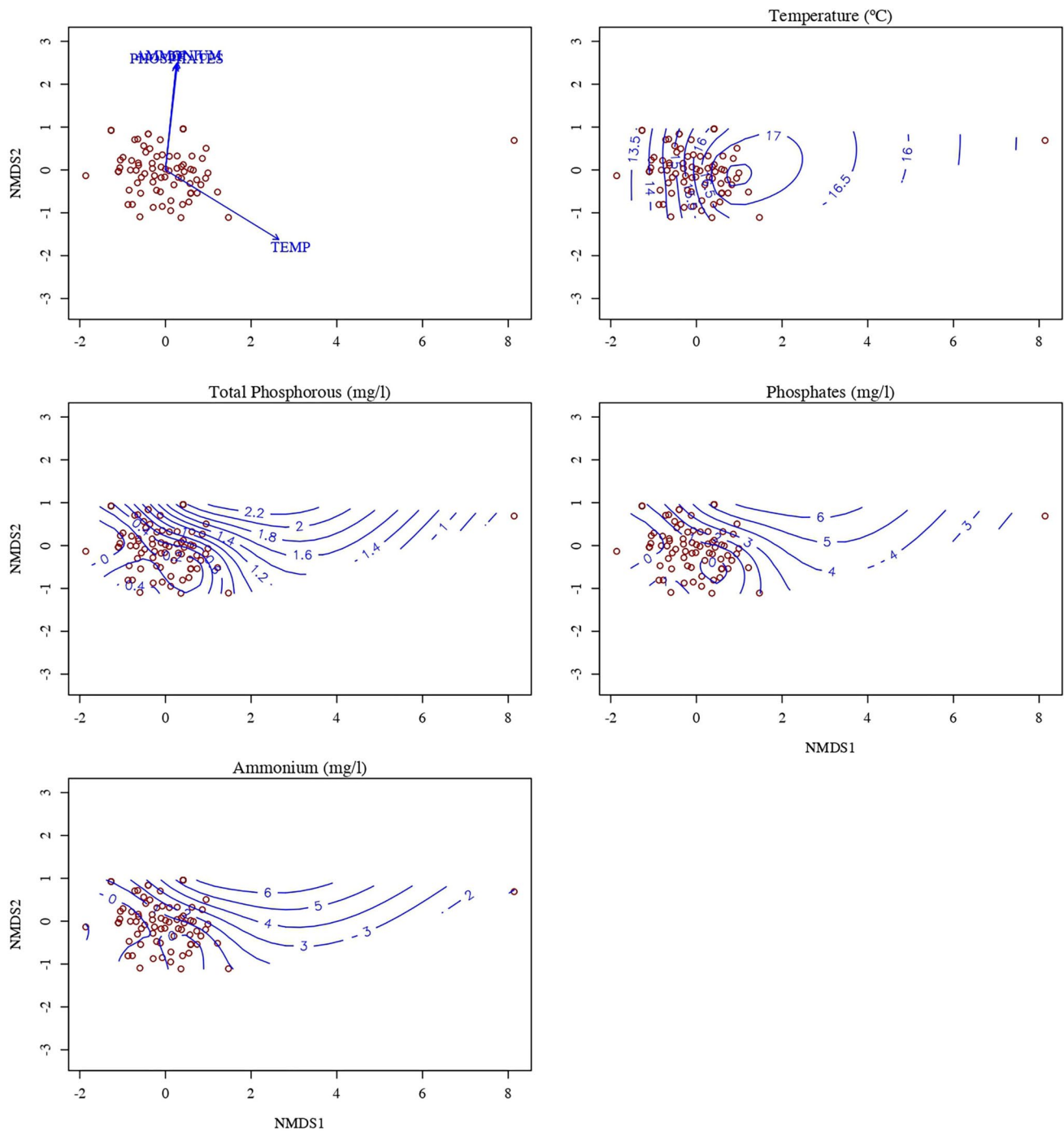


Fig. 6 Non-metric multidimensional scaling (*NMDS*) ordination of the fish communities present in 81 sampled sites ($k=2$, stress=0.14). Top-left panel represents ordination of communities and linear vec-

tors for significant physical and chemical variables; the remaining panels represent smooth surfaces for each significant physical and chemical variable

Discussion

Abiotic environment and composition of the metacommunity

The physical and chemical conditions in both

metacommunities were quite similar (Fig. 2; ESM Table S3). Overall, the high presence of livestock and agricultural practices in the basin (Canuto et al. 2019; Buonocore et al. 2021; MITECO 2023) results in high quantities of both TOC and nitrates. These components reach the rivers through both point-source and diffuse contamination, mainly due to agricultural

and livestock activities in the area. Both excrement and the excessive use of fertilisers end up in the rivers, modifying their natural abiotic conditions. Regarding temperature, the annual average value is relatively high, with most values between 14 °C and 17 °C, typical of the Mediterranean climate region in which the basin is located, where summers are characterised by high temperatures and winters are mild (Lionello et al. 2006). These particular conditions probably determined to a great extent the composition of the stream community in the Guadiana basin and may explain why the most frequent taxa within each taxonomic group in the studied sites were generalists. These taxa have low ecological requirements and wide tolerance ranges, so they used to be widely distributed (e.g. Cambra and Aboal 1992; Clavero et al. 2004; Heino 2005; Peeters and Ector 2018); consequently, their high frequency was expected. Among the fishes, *Gambusia holbrooki* stands out; this is an invasive exotic species whose presence and abundance in rivers is increasing, displacing other species and causing various problems to the native fauna (e.g. Cabrera-Guzmán et al. 2019).

The relationship between the measured environmental factors and each taxocoenosis, as well as the whole community (from the 184 sites for macroinvertebrates, diatoms and macrophytes, on one hand, and from the 81 sites including fishes, on the other) depicted in the NMDS analyses (Fig. 3–7) shows gradients for most of the recorded ecological parameters. Only macrophytes could not be represented within this analysis, as in many sites only a few species were present and these usually had a very low abundance due to their requirements and dependency on current, light and substrate conditions (in Mallin 2023); therefore, data are insufficient. In the case of diatoms and fishes, two particular sites (GN00000047 and GN00000594, respectively) lay outside the main trend. For diatoms, this is due to the high abundance of *Eunotia exigua* (Brébisson ex Kützing) Rabenhorst 1864, a species that inhabits waters with a very acidic pH (DeNicola 2000), as occurs at this site (ESM Tables S3, S6) with an average pH of 3.32, making life impossible for most diatoms and favoring this species. In the case of fishes, this is because in that site, only the exotic species *Cyprinus carpio* (Linnaeus, 1758) is present with relatively high abundances, as it is a highly disturbed site, located directly at the mouth of a dam, creating a pool which favours this exotic species over native species (Clavero et al. 2013). Thus, with only a few exceptions, the studied communities, independently of their taxonomic composition, are distributed along a gradient of conditions in the Guadiana basin.

Analysis of elements of metacommunity structure by taxonomic groups

Our analysis of the EMS of the Guadiana Hydrographic Demarcation for each taxonomic group individually,

independently of the gradient considered, revealed mainly Clementsian and quasi-Clementsian structures (ESM Tables S10–S12), following the interpretations of Presley et al. (2010) and supporting our initial hypotheses. Because fluvial systems have a high natural heterogeneity (Allan et al. 2021), Gleasonian and Clementsian structures are the most common in these environments (Heino et al. 2015a), being the most frequently obtained structures in studies of this type (e.g. López-González et al. 2012; Heino et al. 2015b; Tonkin et al. 2018). Due to this high heterogeneity, different organisms respond in complex ways to environmental gradients, so their structuring is often not simply due to species gain or loss along the ecological gradient (Heino et al. 2015a). In our studied region, the Clementsian structure we found in most cases is in line with the expected structure due to the conditions of the basin. The Guadiana basin is spatially and temporally heterogeneous under certain conditions, with many reaches drying out in summer and a relatively high presence of transversal barriers that promote the isolation of communities and thereby a high turnover of taxa. Nonetheless, Heino et al. (2015a) found that Clementsian structures appeared in basins with low environmental heterogeneity, contrary to their expectations; however, these authors only used the traditional EMS approach.

We did observe some differences in specific EMS of some of the studied groups (ESM Tables S10–S12), probably because different organisms are affected by environmental heterogeneity at different scales due to biological differences between them (Presley et al. 2012). In addition, differences such as the dispersal capacity contribute to the determination of metacommunity structure, with those groups having a lower dispersal capacity mostly structured by the spatial variables, and those with a higher dispersive capacity being more determined by environmental factors (Padial et al. 2014). In all EMS analyses conducted, a statistically significant positive coherence was observed, i.e. each taxon independently responded to a similar environmental gradient (Presley et al. 2010), which we verified with the NMDS analysis (Fig. 3–7). However, in the remaining EMS we found differences both between taxonomic groups and between metacommunities within the same group, and also between different analyses performed with different gradients.

In numerous studies, conductivity and TOC have been structural factors in river communities of macroinvertebrates (e.g. Kefford 1998; Yao et al. 2022), diatoms (e.g. Potapova and Charles 2003), macrophytes (e.g. Lévesque et al. 2017) and fishes (e.g. Barko et al. 2004). Also, Clementsian structure implies a > 1 and statistically significant boundary clumping, which implies clumped boundaries in the distribution of organisms that form each local community (Presley et al. 2010; Leibold and Chase 2018). Therefore, although environmental factors were very determinant, interspecific

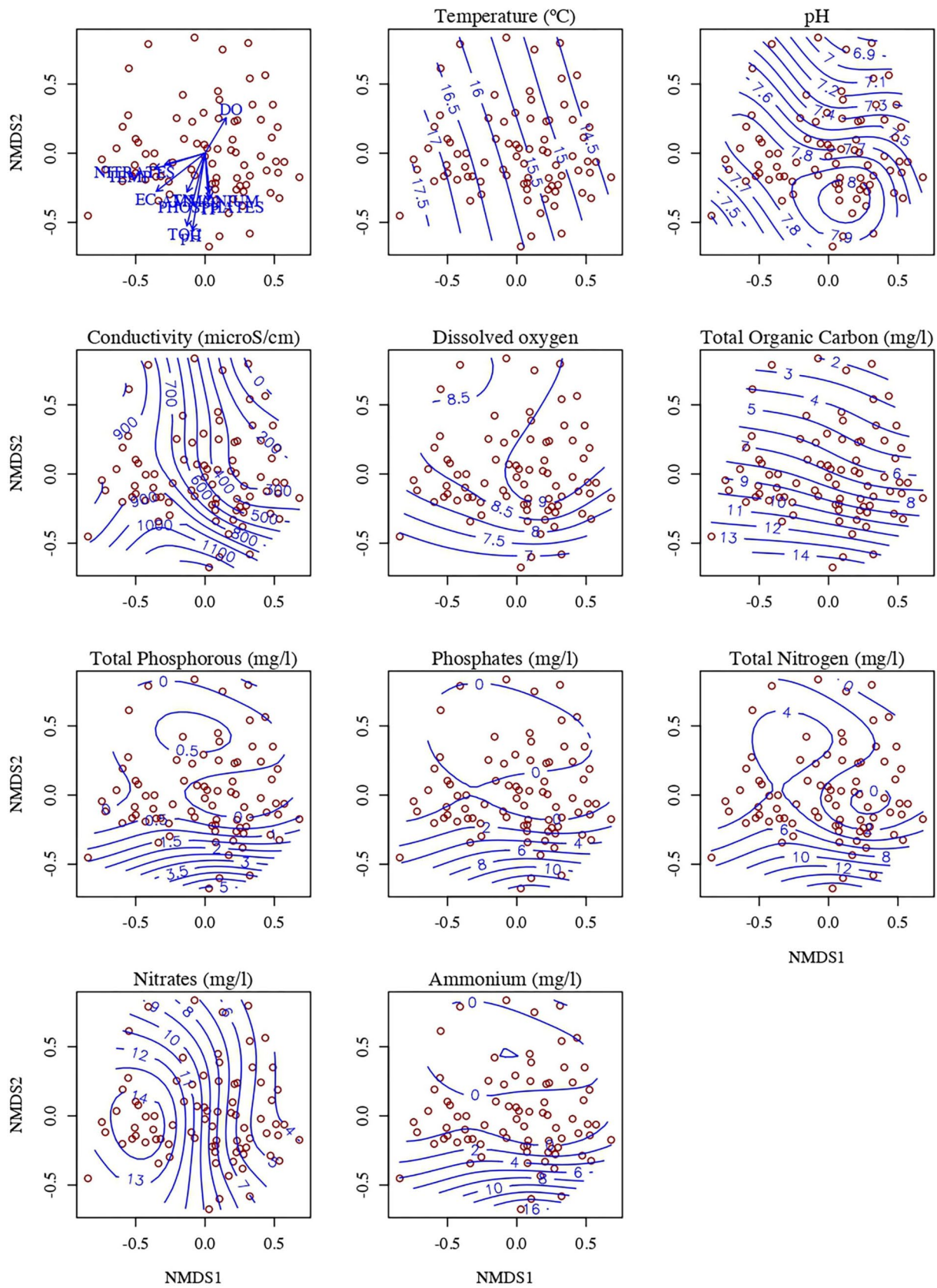


Fig. 7 Non-metric multidimensional scaling (NMDS) ordination of the communities composed by the four studied taxocoenoses together present in 81 sampled sites ($k=3$, stress=0.17). Top-left panel represents ordination of communities and linear vectors for significant physical and chemical variables; the remaining panels represent smooth surfaces for each significant physical and chemical variable

competition also probably played an important role in the structuring of these communities.

On the other hand, quasi-Clementsian structure differs only in that the replacement is not significant, i.e. the strength of the structuring mechanisms is less than that in the Clementsian structure. Given the temporality of our study basin, the Clementsian structure was the most expected structure. This would indicate well-defined, almost independent local communities with functionally similar species that, due to competition, could not coexist in the same local community (Presley et al. 2010). The structuring of these local communities and the coexistence of these biocoenoses relatively isolated from each other could reflect, in these kinds of environments, a storage effect (Chesson 2000). For a storage effect to occur, three components are needed (Mittelbach and McGill 2019): (1) the existence of taxon-specific responses to environmental variation; (2) the presence in the life cycle of strategies that allow organisms to increase recruitment under favourable years and buffer the negative effect of unfavourable years; and (3) covariance between environment and competition (i.e. strengthened intraspecific competitive effects when the environment favors a species' population growth). In all four groups studied, traits that may promote this storage effect are those related to the capacity of surviving the dry period. In general, such traits include the ability to survive in hyporheic zones or isolated pools (Mas-Martí et al. 2010; Kerezy et al. 2017; Sabater et al. 2017; Stubbington et al. 2017), having short life cycles and smaller body sizes (Elias et al. 2014) and the presence of resting or dormancy stages during their life cycle (e.g. López-Rodríguez et al. 2009a, 2009b; Sabater et al. 2017). In addition, many of these organisms are r-strategists (Williams 2006). These traits would favour a high recruitment of individuals of the species present in each local community during the favourable years and the capacity to buffer the effect on their populations of extended, or unpredicted, dry periods, and so would determine the structuring of each local community. As we found such community structures working at the family level in the case of macroinvertebrates, these forces are expected to have an even greater effect at the species level. The other metacommunity structure that appears in the present study is quasi-clumped species loss. This is a nested structure that arises due to negative turnover. The nesting itself indicates both low species replacement and the presence of some generalist species in all or almost all local communities. In addition, nestedness may indicate

that local sites are taxon-poor but located within a taxon-rich assemblage (Patterson and Atmar 1986); that is, along an environmental gradient, the ranges of taxa with more restricted distributions lie within the ranges of those with a wider distribution, leading to a pattern of taxon loss between sites (Heino et al. 2015a). This pattern of structuring is common in metacommunities from seasonal rivers (Datry et al. 2017a). This structure was found only in the analysis using an environmental gradient in diatom metacommunity B and in the one formed by fishes (ESM Table S12), as has been also found previously in fishes metacommunities by other authors (Bender et al. 2017). This pattern is common in cases of habitat fragmentation and areas with a high degree of isolation, as is the case of our study basin during the drought season. Also, in the latent gradient analysis, a quasi-clumped species loss in PCA1 in macrophytes metacommunity A (ESM Table S10). In this same analysis, the other CA axis shows a Clementsian structure (ESM Table S10), but the quasi-clumped species loss pattern can be associated with the Clementsian structure (Presley et al. 2010); therefore, both structures describing the macrophyte metacommunity are compatible.

The most notable change in metacommunity structure was seen in fishes, where, depending on the gradient used, we obtained different results. This difference may be because fishes are the only group whose dispersal is limited to the waterway, with dispersal prevented during the dry period and/or limited or even impossible due to the presence of dams in the riverbed. The largest difference was the structure from ordering according to the latent gradient, where we found a Gleasonian structure in the first CA axis and a quasi-Gleasonian in the second (ESM Table S10). Statistical non-significance of boundary clumping implies that the composition of different species varies with the environment in response to the gradient of abiotic factors, resulting in the coexistence of different taxa with similarities in tolerances or requirements (Heino et al. 2015b; Leibold and Chase 2018). This structure shows that the distribution of fish taxa is most determined by the environmental gradient, where each taxon shows different optima. This result is supported by other studies on fish communities (e.g. Barko et al. 2004) but especially those in perennial rivers (Vardakas et al. 2020).

The high ability of fishes to disperse through the river network indicates that the Gleasonian structure is feasible, making it easier for fishes to move from one particular site to another. Yet, due to the seasonality of the rivers in the Guadiana basin, there are months in which there are only disconnected pools, together with permanent rivers that carry water throughout the year, keeping some sites of the study connected. However, the structure obtained in the analysis with the geographic and environmental gradient were Clementsian and quasi-clumped species loss, respectively. It seems that the species that form this metacommunity do

not have such a high dispersive rate due to seasonality and anthropogenic barriers, and that they are limited by abiotic conditions and high interspecific competition (Leibold et al. 2004; Vieira et al. 2020).

However, the most important determinant of structuring is probably dispersion. In fact, Vardakas et al. (2020) argue that the metacommunity structure of fishes inhabiting Mediterranean-temporal environments is usually more determined by dispersal, and Padial et al. (2014) support that spatial predictors gain explanatory weight in those groups with lower dispersal capacity.

Analysis of elements of metacommunity structure as a whole

When we analysed the metacommunity as a whole, we obtained a clearly Clementsian structure in metacommunity A under all three gradients (latent gradient, geographical gradient and environmental gradient) (ESM Tables S13–S15). For metacommunity B, a Clementsian structure was found under the latent and the geographical gradients, but a quasi-Clementsian structure was found under the environmental gradient. The studied basin is notable for its above-mentioned seasonality, with long periods of dry rivers in which, in some cases, only isolated pools remain, isolating the different local sites from each other during those periods. Furthermore, although there is certain physical and chemical variability in the Guadiana basin (Fig. 1), one of the greatest limiting factors seems to be the marked seasonality, with months of drought, a condition to which most taxa are adapted evolutionarily and in a similar way to allow their survival (with resistance phases, short life cycles, parts of the life cycle with a terrestrial or aerial phase, burying themselves in the humid substrate, taking refuge in pools, among others; Williams 2006). Furthermore, one of the main factors determining water flow in Mediterranean rivers is precipitation, which in this climate, in particular, tends to be quite seasonal. Thus, in a basin such as the Guadiana, which is eminently seasonal in hydrological terms, this precipitation can generate greater or lesser connectivity between different river sections, which directly affects the structure of the metacommunity. Although the dispersive capacity of the different organisms will allow greater or lesser migration between the different communities, the intermittency of flows reduces aquatic migration and may reduce aerial dispersal of poor fliers giving spatially structured metacommunities (Cañedo-Argüelles et al. 2020). To all this, we must also add the existence of the large number of barriers present in the water masses (MITECO 2023), which make it difficult and, for some organisms, even prevent normal dispersal through the different sections of the river. All of which, in turn, defines, and favours the Clementsian structure, as it isolates some bodies of water from others.

Global change in the Guadiana basin

As shown by our results, communities within this basin are relatively isolated, and this isolation may be greater in the current global change framework. Climate change affects the dry period, increasing its intensity, frequency and severity (Jorda-Capdevila et al. 2019; Buonocore et al. 2021), which would lead to greater isolation between communities and an increasingly pronounced Clementsian structure (Jorda-Capdevila et al. 2019; Buonocore et al. 2021). This will be accentuated even more by the increase in urban areas (and so in water demand) and the effluents they will produce, as well as by the expansion of new hectares of irrigated land, among others (Canuto et al. 2019). Thus, the survival of the organisms composing these communities is determined by the composition of the community before the dry period, the presence or absence of residual pools and their size, the duration of the dry period, the speed of water withdrawal (Várbíró et al. 2020) and the presence of artificial barriers limiting repopulation between sites (Jones et al. 2020; Rodelles et al. 2020), despite these organisms being morphologically and physiologically adapted to the dry period through a strong selection of traits (Datry et al. 2017a; Várbíró et al. 2020). This increased isolation between communities may have negative effects as it affects both structural (increasing the distance between local sites) and functional connectivity (decreasing gene flow and dispersal between local sites) (Valenzuela-Aguayo et al. 2020). Due to this, potential migration would be reduced (Fahrig 2003; Datry et al. 2017b) and, with it, genetic diversity (due to increased inbreeding and genetic drift). This has an effect on genetic diversity at both the population (local) and regional (metacommunity) levels (Bonada et al. 2017), reducing fitness of the organisms (Brauer and Beheregaray 2020; Valenzuela-Aguayo et al. 2020) and, therefore, making them more vulnerable to extinction by stochastic demographic events (Brauer and Beheregaray 2020). Finally, as continued habitat fragmentation is expected in the Guadiana, hence decreasing the available habitat size, intra-community competition for resources is expected to increase significantly. All of these factors would contribute to make rivers from the Guadiana basin highly threatened from a conservation point of view. The vulnerability of these rivers is therefore extremely high and their conservation necessary, not only for their intrinsic value, but also for their geomorphological, biogeochemical, hydrological and ecological contributions to river networks and associated terrestrial systems (Chiu et al. 2017; Datry et al. 2017a; Kerezszy et al. 2017; Sabater et al. 2017; Stubbington et al. 2017).

Conclusion

In light of our results, we propose that the entire fluvial metacommunity of the Guadiana Hydrographic Demarcation formed by macroinvertebrates, diatoms, macrophytes and fishes follows a Clementsian gradient. Taking this gradient into consideration, one of the most determining factors in the study basin seems to be the isolation of communities due to the drought period, with the survival of the communities depending on the search by many organisms composing these communities for refuge during this period. In addition, migration, and so dispersal capacity of the organisms, is also a very important factor for their survival, taking into account the huge number of anthropogenic barriers present in the basin. This makes distances between sites and connectivity very important factors in the presence/absence of taxa from different communities, but the abiotic conditions also have an important role structuring these communities. Thus, despite these groups having such different characteristics, similar forces likely structure their communities.

Furthermore, the results of our three different analyses of ordination gradients did not reveal any notable differences, neither within each group nor in the global analyses. Only in the case of fishes were the results obtained under the latent gradient the most disparate compared to those obtained with the other, more realistic, two gradients.

For all of these reasons, we affirm that the different communities are relatively grouped and isolated. This isolation could be more accentuated in the current scenario of global change due to the increase of drought periods that could lead to a loss of biodiversity and even to the extinction of some endemic taxa due to the increasing fragmentation of the habitat. It is therefore necessary, in addition to other measures to mitigate other effects derived from global change, to cease the construction of barriers in water bodies, or even eliminate some of them, and control the extraction of groundwater and the discharge of both livestock and urban effluents, with the aim to reduce alterations in the discharge regime and water quality and, therefore, reduce the impacts that the Guadiana's water bodies and the organisms that inhabit them are suffering.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-024-01143-1>.

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Author contributions Conceptualisation, developing methods and conducting the research: ATC, JMTF, JMLO, MJLR. Data analysis, interpretation and preparation of figures and tables: ATC, MJLR. Writing the original draft: ATC. Reviewing, commenting and editing the draft of the manuscript: ATC, JMTF, JMLO, MJLR. Final approval of the version to be published and agreement for all aspects of the work: ATC, JMTF, JMLO, MJLR.

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Data availability Data are provided in the manuscript and the supplementary information file.

Declarations

Conflict of interest The authors declare no competing interests.

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