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Integrating spatiotemporal hydrological connectivity into conservation planning to protect temporary rivers

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Abstract

1. Temporary rivers (TRs) have been largely overlooked in conservation assessments. Because TRs are such dynamic ecosystems, spatial and temporal aspects of their hydrology and ecology need to be taken into account when designing conservation plans.
2. The aim of this paper is to propose a set of recommendations that could be useful for managers to do this, using seasonal diatom and macroinvertebrate data from north-eastern Spain as a case study. Beta diversity was partitioned into local and species contributions to beta diversity (LCBD and SCBD). Additionally, priority conservation sites covering the spatial distribution of all species were identified using Marxan and the selection frequency (MSF) of the sites served as a measure of the relative irreplaceability of each site.
3. Using both approaches (beta diversity and Marxan), the effects of changing spatiotemporal connectivity and habitat heterogeneity on the selection and prioritization of sites to be conserved were assessed.
4. It was found that LCBD and MSF ranged widely both in space and time. However, LCBD and MSF were weakly related. Marxan adequately represented all taxa by selecting a few sites, while LCBD selected communities with higher differentiation but not necessarily those with rare species. In addition, SCBDs assigned low values to rare taxa, thus care must be taken when using this index for conservation planning.
5. Spatiotemporal connectivity and local habitat heterogeneity played a critical role at the regional and local scales, driving site prioritization.
6. Overall, we recommend: 1) monitoring multiple hydrological phases to encompass the different community types and capturing total diversity; 2) using Marxan and LCBD in combination, to benefit from their complementary insights; and 3) integrating spatiotemporal isolation and habitat heterogeneity into conservation

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plans, since they are the main drivers of community variation over space and time in TRs.

KEYWORDS

aquatic macroinvertebrates, conservation planning, diatoms, habitat connectivity, habitat heterogeneity, local contribution to beta diversity, Marxan, species contribution to beta diversity, temporary rivers

1 | INTRODUCTION

Preserving freshwater biodiversity is one of the most pressing global challenges of our time (IPBES, 2019). Pressures on freshwater biodiversity and freshwater habitats have exponentially increased during the last decades, mainly due to habitat destruction, fragmentation, pollution, invasive species, and overexploitation (Albert et al., 2021; Harrison et al., 2018). Consequently, freshwater species are disappearing at alarming rates (over 83% have become extinct since 1970), faster than their marine and terrestrial counterparts (Harrison et al., 2018). This is expected to worsen in the future, as a result of climate change and increasing human water demands (Dudgeon, 2019). Within this context, there is an urgent need to improve current conservation efforts to address the particular management needs of freshwater ecosystems, mostly overlooked under current conservation priorities (Hermoso et al., 2016).

Temporary rivers (hereafter TRs) are generally described as watercourses that stop flowing in both space and time (Acuña et al., 2014; Datry, Bonada & Boulton, 2017), and are also known as non-perennial, intermittent, ephemeral, or episodic. TRs are one of the most common freshwater habitats in the planet (Messenger et al., 2021), and they are expected to become even more widespread in the future because of water scarcity (Kumar et al., 2014; Mekonnen & Hoekstra, 2016; van Vliet et al., 2021). TRs are characterised by shifting wet and dry phases (Gallart et al., 2012), which change spatiotemporal hydrological connectivity (Cunillera-Montcusí et al., 2023), constraint species dispersal, and affect metacommunity dynamics (Cañedo-Argüelles et al., 2020). This dynamism can have challenging implications for the conservation and biomonitoring of TRs (Datry et al., 2023) because available habitats and species to be potentially protected and/or used as bioindicators change dramatically in space and through time. Additionally, TRs are among the most damaged and vulnerable freshwater habitats in the world (Datry et al., 2014; Fovet et al., 2021; Skoulikidis et al., 2017). Despite some efforts have been done in some parts of the world (e.g., partial recognition in the EU Water Framework Directive and Habitats Directive; Fritz et al., 2017), they still remain neglected by policy-makers (Datry et al., 2023; Leigh et al., 2015), and conservation plans have largely ignored them (Bruno et al., 2022). The few existing studies on the conservation of TRs argue that priority sites for conservation can vary over time in these ecosystems (Rodríguez-Lozano et al., 2023; Ruhí et al., 2017). For example, when present, disconnected pools might play a vital role as biodiversity refugia

during the dry season (e.g., fish or amphibians) (Bonada et al., 2020; Hermoso et al., 2013), or can be used as stepping-stones habitats, favouring connections across the disconnected river network (Datry, Boulton, et al., 2017; Sánchez-Montoya et al., 2022). However, the integration of spatiotemporal changes of TRs into conservation plans remains neglected.

There are different conservation approaches that could be used to select and prioritise sites to be preserved. One of them is to partition beta diversity to obtain the relative contribution of sites or species as in Legendre & De Cáceres (2013). This framework allows assessing the relative contribution of each sampling unit to beta diversity, that is, local contribution to beta diversity (LCBD), and the relative contribution of each species to beta diversity (SCBD). Considering a set of sites (i.e., regional scale), LCBD is an indicator of the biological uniqueness of each site, that is, a very different community composition compared with the regional mean. Thus, large values of LCBD could be considered as indicators of priority sites for conservation (high LCBD and high alpha diversity) or species-poor sites with restoration needs (high LCBD and low alpha diversity) (Legendre, 2014; Legendre & De Cáceres, 2013). The LCBD value identifies relatively unique communities in terms of their community differentiation, although not necessarily the communities with the rarest species. Therefore, setting conservation priorities based only on LCBD could lead to underrepresenting these rare species, which are often the most threatened ones. Importantly, LCBD values can change over time, reflecting metacommunity dynamics processes (i.e., habitats that may operate as sources, or sinks, to whole river networks) (Ruhí et al., 2017). In turn, SCBD indicates species with high variation in abundance between different sites in a region. Usually, species with high SCBD values have a large, or moderate, occupancy across sites and high abundance, resulting in the most important species contributing to the uniqueness (LCBD) of the different sites (Heino & Grönroos, 2017). These beta partitioning approaches have increasingly been used for identifying conservation sites based on different organisms, such as diatoms and macroinvertebrates (Heino & Grönroos, 2017; Rodríguez-Lozano et al., 2023; Vilmi et al., 2017), fish (Xia et al., 2022), terrestrial arthropods (Sánchez-Montoya et al., 2020), and terrestrial plants (Kirk et al., 2021).

An alternative approach for selecting and prioritising sites to be conserved are systematic planning (Margules & Pressey, 2000), which have been used in rivers (Linke et al., 2011) and, only recently, in TRs (Bruno et al., 2022). Among these tools, one of the most widely used

is Marxan (Ball et al., 2009), which relies on the principle of complementarity to find the best combination of sites to be protected to meet a set of conservation targets at the minimum cost. Unlike LCBD-based approaches, Marxan may be used to identify priority sites based on a specific predefined target, rather than just considering sites very far from the median community composition in a regional pool. Thus, Marxan-based conservation planning may be particularly beneficial when community composition (and thus centroids) vary strongly over space and time and the main conservation target is total regional gamma diversity.

In this study, we aim to propose a set of recommendations that can be useful for managers when designing conservation plans in TRs. To do so, the above-mentioned conservation prioritisation approaches were used to identify priority conservation sites in TRs, and to assess the effects of changing spatiotemporal connectivity on the selection and prioritisation of sites. Since connectivity plays an important role in structuring aquatic communities in TRs (Cid et al., 2022), the focus was on two groups of organisms with contrasting dispersal abilities: diatoms and macroinvertebrates. Diatoms are widely dispersed (Bogan et al., 2017; Kristiansen, 1996) by water flow, wind, or animal vectors such as mammals and birds (Leone et al., 2014; Liu et al., 2013; Manning et al., 2021; Romero et al., 2003). Macroinvertebrates have two main dispersal modes (Bilton et al., 2001): i) active dispersers (e.g., adult dragonflies) can reach very long distances and they usually fly oriented upstream (Bogan & Boersma, 2012; French & McCauley, 2019); whereas ii) passive dispersers (e.g., larvae of non-biting midges) might drift downstream (Brown et al., 2011; Sarremejane et al., 2020) or restrict their movements to the benthic zone (Kappes & Haase, 2012).

Firstly, we hypothesised that priority conservation sites and species should change across seasons in response to changes in hydrological conditions, because drying determines biodiversity and habitat availability (Leigh & Datry, 2017; Ruhí et al., 2017). This would suggest that conservation actions should be adaptive and priority sites to be conserved should vary in space and time. Secondly, we hypothesised that both conservation approaches mentioned above are complementary. Whereas LCBD can identify sites with unique species composition, systematic planning tools are based on the complementarity principle and, therefore, these sites might not necessarily be selected. In addition, SCBD is not designed to select rare species but those that occur in a moderate number of sites in high abundances or have narrow niche breadth (Pozzobom et al., 2020; Xia et al., 2022), whereas rare species could be used as a selection criteria in systematic planning tools. Thirdly, we hypothesised that environmental drivers behind selected sites could inform us whether the conservation of local habitat or spatiotemporal connectivity should be preserved (or enhanced) to ensure current conservation status. For example, when local habitat variables are relevant, measures to enhance habitat diversity or to improve water quality should be implemented, whereas if drying is important, measures should consider solutions that reduce its effects and increase connectivity (Datry et al., 2015).

2 | METHODS

2.1 | Study area

The study was carried out in the Sant Llorenç del Munt i l'Obac Natural Park, a 140 km² protected area in northeast Spain with a typical Mediterranean climate (i.e., dry summers and heavy rains during autumn). The geology of the area is mainly karstic with permeable substrates (Anglés et al., 2017), but with abundant exposed bedrock in some areas. The flora of the natural park is typically Mediterranean, dominated by evergreen oaks (*Quercus ilex*) and several species of pines (*Pinus halepensis*, *P. nigra*, and *P. sylvestris*). Some of the main species of shrubs are the common box (*Buxus sempervirens*) or heath species (*Erica* spp.). Two species of native barbels (*Barbus haasi* or *B. meridionalis*, depending on river basin) inhabit the study area, as well as the native *Squalius laietanus*, and the invasive exotic cyprinid (*Phoxinus septimaniae* x *P. dragarum*) (Corral-Lou et al., 2019). Thirty sites were sampled distributed among seven TRs: Vall d'Horta (H), Sanana (SA), Santa Creu (SC), Rellinars (R), Talamanca (T), Castelló (CA) and Mura (MU). These TRs covered a wide hydrological gradient, with Flow Permanence values (i.e., percentage of days with wet reaches in each site, FP) ranging from 33.14% to 99.80% for the 513 monitored days (from July 2018 to December 2019) (see Supporting information S2 for all FP values) (Pineda-Morante et al., 2022). The samples were collected once per season during 2019: winter (January), spring (May), summer (July), and autumn (November).

2.2 | Diatom and macroinvertebrate data

Diatoms were sampled by brushing the surface of three submerged stones with a toothbrush. The samples were preserved in the freezer using 70% ethanol. Then, organic matter was removed with hydrogen peroxide at 100 °C, rinsed with distilled water and prepared permanent slides with Naphrax®. Afterwards, diatoms were identified to species level with a DIC Polyvar Zeiss microscope with a built-in camera, counting a minimum of 500 diatom valves per sample. Macroinvertebrates were collected along 100 m reaches using a 250 µm mesh size hand net by kicking all the available habitats. Before sampling, each studied reach was carefully inspected to identify all the available habitats based on expert judgement (including different items, such as substrate type, flow conditions, and aquatic vegetation). The samples were preserved in 96% ethanol and stored them in the freezer until their sorting and identification. Likewise, all macroinvertebrates were identified and counted using a binocular stereoscope to the lowest possible taxonomic resolution (usually genus). Once all diatoms and macroinvertebrates were identified and counted, a logarithmic transformation was applied ($\log x + 1$) to abundances values of each taxon.

2.3 | Environmental and hydrological data

The abiotic variables were measured once per reach in each season. Dissolved oxygen (DO mg/L), oxygen saturation (DO %), water temperature (T °C), pH, conductivity (EC $\mu\text{S}/\text{cm}$), specific conductivity (SPC $\mu\text{S}/\text{cm}$) and total dissolved solids (TDS mg/L) were measured using a multiparameter probe (YSI Professional plus Multiparameter Probe). A characterisation of the habitat heterogeneity was also conducted by calculating the “Fluvial Habitat Index” (IHF) (Pardo et al., 2002), which accounts for the embeddedness in riffles and sedimentation in pools (B1), the frequency of riffles (B2), the substrate composition (B3), the flow velocity and depth regimes (B4), the percentage of shade in the channel (B5), the presence of habitat heterogeneity elements (e.g., leaf litter, branches and woods, or roots) (B6) and the aquatic vegetation coverage (B7). Presence/absence of water was registered from July 2018 to December 2019 using temperature data loggers deployed at each sampling site (Pineda-Morante et al., 2022). This information was used to calculate different hydrological metrics: the total number of dry days or duration of drying events (hereafter TotDur), the frequency of drying events or number of drying events (hereafter TotNum) and the average length of each drying event (hereafter TotLeng) (Arias-Real et al., 2021; Crabot et al., 2020; Pineda-Morante et al., 2022). In addition, the flow permanence was calculated as the percentage of the days that reaches were wet along two different time windows: 50 days before each sampling campaign (FP50), and 100 days before each sampling campaign (FP100). Two different time windows were considered, since organisms with different life cycles will be affected differently depending on when and how long sites were dried.

A presence/absence of water dataset was utilized to calculate spatiotemporal hydrological connectivity variables (hereafter STcon) for each sampling site, and considering the two scenarios proposed in Cunillera-Montcusí et al. (2023): a binary scenario (i.e., connection between sites as 1 and no connection as 0) and a weighted scenario (i.e., connection between sites weighted by the Euclidean distance between them). In addition, two types of network structures were considered for each of these two scenarios: directed (i.e., with an upstream to downstream directionality) and undirected (i.e., where all sites are connected between each other). Four STcon values were finally obtained: directed and binary, undirected binary, directed weighted and undirected weighted (DirBin, UndBin, DirWei, and UndWei, respectively). For binary scenarios, higher STcon values imply that a site has been highly connected with all its potential neighbours during the monitored time (i.e., high connectivity), whereas weighted scenarios with higher values imply that a site has been highly disconnected during the monitored time and it is located in an isolated position from its neighbours (i.e., high dispersal resistance). As distances between sampling sites for each stream were small, and streams were relatively straight, Euclidean distances could be used to weight both Binary and Undirected scenarios. See more details about STcon in Cunillera-Montcusí et al. (2023).

2.4 | Beta diversity partitioning: LCBD and SCBD

Community uniqueness results from partitioning beta diversity indices between sites (LCBD) and species (SCBD). LCBD calculates the uniqueness of the community across several sites and indicates how far each individual site is with respect to the mean centroid sample. The sum of the LCBDs across all sites equals 1, being the highest values of LCBD corresponding to communities with different species composition (Legendre, 2014). Then, sites with significantly different LCBD values were identified (p -value < 0.05 after Holm correction for multiple comparisons; Borcard et al., 2011; Holm, 1979). In order to identify sites with significant LCBD values, a Holm-corrected test was used (Holm, 1979). To explore the temporal variation of selected sites with high LCBD, LCBD values for each season were plotted. Moreover, SCBD calculates the species contribution to beta diversity, which represents the relative contribution of each taxa to beta diversity. For this, a “rose plot” was plotted to visually explore the different contributions of each taxa to beta diversity and the relationship with occupancy and abundance. The “beta.div” function (Legendre & De Cáceres, 2013) in the R package “Adespatial” (Dray et al., 2022) was used to calculate LCBD and SCBD, and the “ggplot” function in the ggplot2 v. 3.4.1 (Wickham, 2016) to plot the results of the analyses.

2.5 | Systematic planning tools: MSF

To identify a minimum set of sites that collectively achieve a coverage target, the systematic planning tool Marxan was used (Ball et al., 2009). Marxan relies on a simulated annealing optimization algorithm to identify a minimum set of sites that meet user-defined targets at a minimum cost. A representation target of 20% of the sites where each species was found was set (i.e., occupancy of each specie*0.2), keeping a minimum target of 1 for those taxa that were present in less than five sites. Given the high rate of taxa turnover in our dataset, with most taxa restricted to a few sites, high representation targets could only be achieved for all taxa at the same time by selecting almost all sites simultaneously. To address this problem, a bootstrap analysis was conducted (Bruno et al., 2022), by attempting to achieve the targets for a given proportion of all taxa each time. For this, 1,000 random samples were selected containing 50% of the taxa from the total pool and identified the minimum set of locations to cover the representation targets explained above. This decision was based on the work of Bruno et al. (2022), who tested three different thresholds (50%, 75%, 90%) and found that the results were consistent across the different bootstrap thresholds used. Given the lack of estimates of conservation costs across the study area, a constant cost across all locations were used (e.g., Hermoso et al., 2021) and no connectivity penalty measure was included, similar to Bruno et al. (2022). With this configuration, Marxan was ran 100 times, using a million iterations each, and kept the solution with the lowest objective function score across those runs as our best solution, for each of the bootstrap selection of taxa. All best solutions

were summarised by calculating the selection frequency of each location across the 1,000 solutions, calling this variable Marxan Selection Frequency (MSF). In this way, the irreplaceability of each site at representing the taxa was measured, regardless of the particular combination of taxa selected in each of the 1,000 bootstraps. As previously described above for LCBD, MSF values for each season were plotted to explore changes in space and time.

Finally, in order to compare results obtained by LCBD and MSF approaches, taxa richness per site was calculated using the “vegan” package (Oksanen et al., 2022), and compared values among seasons using a Kruskal-Wallis test. In case of differences between seasons, a Mann-Whitney-Wilcoxon test was conducted.

2.6 | Environmental and hydrological models

Finally, all predictor variables were normalised (i.e., water chemistry, hydrology, habitat, spatiotemporal connectivity) using the “scale” function from R Base Package and tested their correlation between them using the function “findCorrelation” from “caret” R package (Kuhn, 2008). The Spearman correlation cut-off was set at 0.7 and then calculated the mean absolute correlation of each variable with the rest of the variables in the dataset, eliminating those with the highest mean absolute correlation. For the diatom data, a total of 16 variables were considered to test with LCBD and MSF. Previously, seven variables were deleted (TotDur, TotNum, FP100, B6, EC, SPC and DO %) that had a high Spearman correlation. For the macroinvertebrate dataset, six of the 23 variables were eliminated because of their high Spearman correlation (TotDur, TotNum, FP100, EC, SPC and DO %), resulting in a total of 17 variables to test with LCBD and MSF.

In order to analyse the complementarity of LCBD and MSF, we compared data obtained by the two approaches and with richness using beta regression models for LCBD, and linear mixed-effect models (LMM) for MSF. All models included streams and sites as random effects, and season as fixed effect. For LMM, the “lme” function in the package “nlme” was used (Pinheiro et al., 2022), whereas for beta regression models, the “glmmTMB” function in the glmmTMB v. 1.1.5 (Brooks et al., 2017) was employed. Finally, in order to determine the environmental drivers behind selected sites by LCBD and MSF, similar models were run between each approach and the predictor variables. Two different coefficients of determination were reported, denoted R^2 . Marginal R^2 (R^2_m) describes the proportion of variance of fixed factors and conditional R^2 (R^2_c), that takes into account fixed and random effects (i.e., the total model) (Nakagawa & Schielzeth, 2013).

Rstudio 4.3.0 was used for all the analyses and Muff et al. (2022) was followed to report the results in the language of evidence.

3 | RESULTS

A total of 55,654 diatoms belonging to 222 species and 144,846 macroinvertebrates belonging to 178 different taxa were collected

(diatom species and macroinvertebrate taxa can be found in Supporting Information S3). Diatoms richness ranged between 14 and 65, with an average of 34. The Kruskal-Wallis test showed no significant difference in richness among seasons ($p = 0.141$). Macroinvertebrates richness ranged between 6 and 62, with an average of 34. The Kruskal-Wallis test showed strong differences in richness among seasons ($p < 0.001$). The strongest differences were found between autumn and the rest of the seasons (see Mann-Whitney-Wilcoxon test for further information in Supporting Information S1).

According to the Holm-corrected LCBD values, four sites strongly contributing to beta diversity which belonged to the same stream and two different seasons for diatoms were found (H1W, $p = 0.009$; H2W, $p = 0.009$; H3A, $p = 0.037$; H5A, $p = 0.037$). Four sites were also found for macroinvertebrates, belonging to three different streams and three different seasons (H5W, $p = 0.039$; MU2A, $p = 0.01$; SC2SP, $p = 0.01$; SC3A, $p = 0.03$). A high spatiotemporal variability in LCBD for both diatoms and macroinvertebrates was found (Figure 1). For example, some ephemeral sites (e.g., R1 and R2) were completely dry for most of the year and LCBD ranged from 0 to 0.011, whereas some perennial reaches (e.g., H1) maintained very similar LCBD values throughout the seasons for macroinvertebrates (Figure 1c,d). MSF also showed a very strong seasonal variation for both diatoms and macroinvertebrates. For example, for diatoms, only two sites were selected by MSF during summer (T3 and CA1) (Figure 1b).

No strong relationship was found between LCBD and MSF (diatoms: $p = 0.641$; $R^2_m = 0.002$; $R^2_c = 0.125$; macroinvertebrates: $p = 0.264$; $R^2_m = 0.012$; $R^2_c = 0.211$). LCBD showed a negative relationship with species richness, which was weak for diatoms ($p = 0.026$; $R^2_m = 0.077$; $R^2_c = 0.445$) and very strong for macroinvertebrates ($p < 0.0001$; $R^2_m = 0.355$; $R^2_c = 0.411$). Contrarily to LCBD, MSF showed a strong positive relationship with richness for both, diatoms ($p < 0.0001$; $R^2_m = 0.298$; $R^2_c = 0.304$) and macroinvertebrates; ($p < 0.0001$; $R^2_m = 0.443$; $R^2_c = 0.46$) (Figure 2).

SCBD values ranged from 0 to 0.024 for diatoms, and from 0.0001 to 0.035 for macroinvertebrates. SCBD showed an unimodal relationship with species occupancy when presence/absence data was used (Figure 3b-d), whereas it increased exponentially with occupancy when using abundances (Figure 3a-c).

A great seasonal variability was found in the contribution of each taxa to beta diversity (Figure 4). For diatoms, several species showed high SCBD values in three seasons (e.g., *Brachysira neoexilis*, *B. neglectissima*, *Encyonopsis subminuta*, *Gomphonema lateripunctatum*, *Gomphonema tergestinum*, *Amphora pediculus* and *Achnanthisium pyrenaicum*) whereas other species showed high SCBD values for only one season (e.g., few *Fragilaria* spp. in winter, *Cocconeis placentula* in spring or *Navicula antonii* in autumn). In the case of macroinvertebrates there were seasonal variations in SCBD. For example, *Bidessus* exclusively contributed to beta diversity in spring, whereas *Habroleptoides* greatly contributed in winter. However, some taxa (e.g., *Dasyhelea* or *Cloeon*) greatly contributed

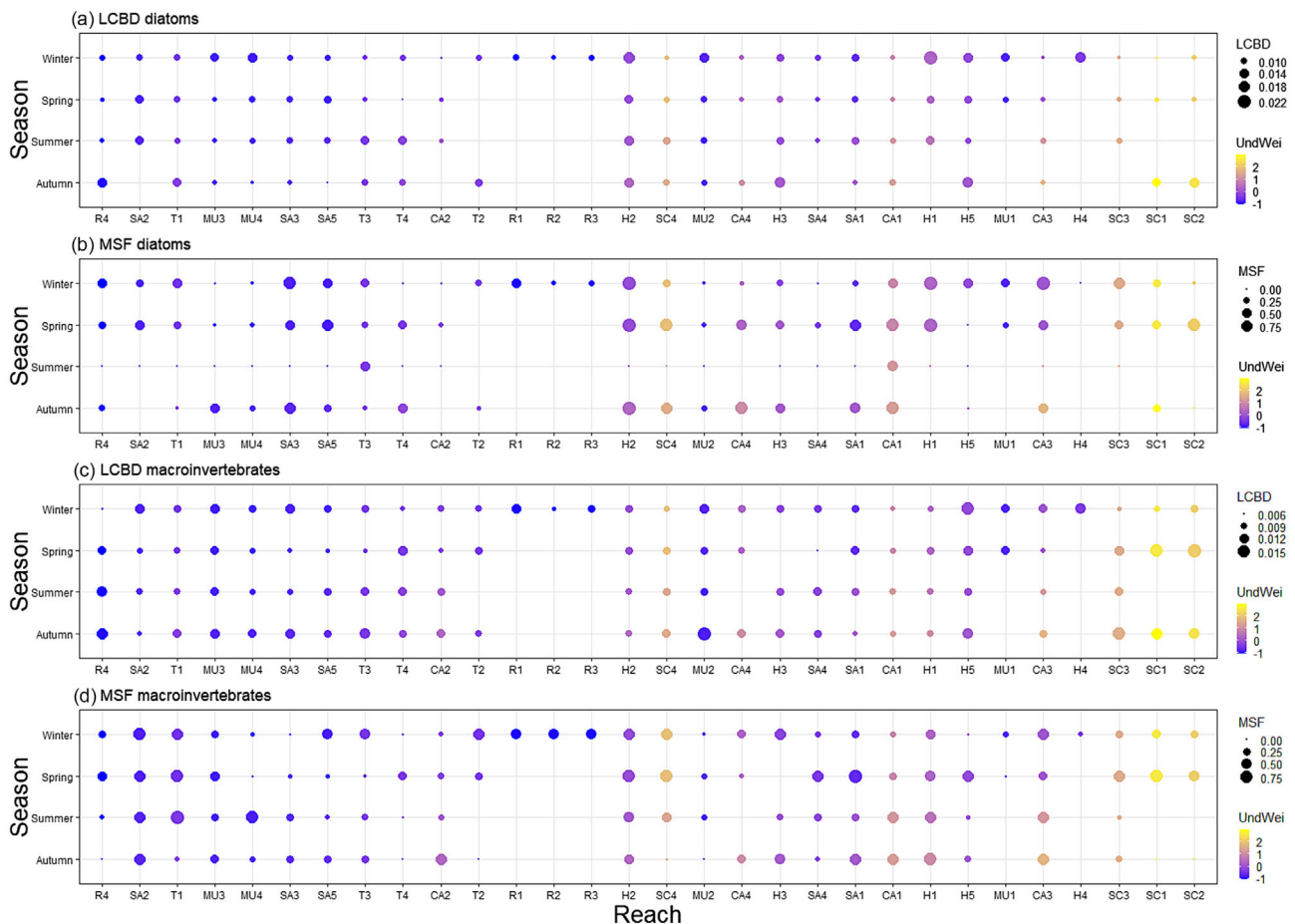


FIGURE 1 Bubble plots showing Local Contribution to Beta Diversity (LCBD) values and Marxan's Selection Frequency (MSF) for the four seasons and across sites. (a,b) Diatoms and (c,d) macroinvertebrates values. Bubble plot size represents LCBD and MSF values. The order of the reaches is in increasing order of dispersal resistance (UndWei) values.

to beta diversity across seasons (Figure 4). SCBD did not seem to be related to the rarity of the taxa, since some taxa that were exclusively found in ephemeral streams (e.g., *Tyrrhenoleuctra* and *Mesophylax*), showed very low SCBD values (0.003 and 0.001, respectively).

According to beta regression models using diatoms, LCBD did not show any relationship with the predictor variables, whereas MSF showed a strong positive relationship with two variables: dissolved oxygen (DO mg/L) ($F = 7.61$; $p = 0.007$) and temperature ($F = 7.81$; $p = 0.007$); and a weak relationship with two spatiotemporal connectivity metrics: connectivity (UndBin) ($F = 3.021$; $p = 0.087$) and dispersal resistance (UndWei) ($F = 3.559$; $p = 0.064$) (Figure 5) (for more information about the rest of the variables see Supporting Information S1). For macroinvertebrates, there was a strong relationship between LCBD and three habitat heterogeneity variables: embeddedness in riffles and sedimentation in pools (B1) ($Z = 2.98$; $p = 0.003$), frequency of riffles (B2) ($Z = -2.62$; $p = 0.008$) and the substrate composition (B3) ($Z = 3.08$; $p = 0.002$). Other two variables related to spatiotemporal connectivity showed a moderate relationship with LCBD: directed weighted scenario (DirWei: $Z = 2.27$; $p = 0.023$) and undirected binary scenario (UndBin:

$Z = -2.52$; $p = 0.012$). Finally, two habitat heterogeneity variables showed a weak relationship with LCBD: flow velocity and depth regimes (B4) ($Z = -1.86$; $p = 0.062$) and aquatic vegetation cover (B7) ($Z = -1.65$; $p = 0.098$). For MSF using macroinvertebrates models only showed a strong relationship with aquatic vegetation cover (B7) ($F = 10.37$; $p = 0.02$) (for more information about the rest of the variables see Supporting Information S1).

The relationship of LCBD with the variables selected by the beta regression models experienced seasonal variations (Figure 6). For example, DirWei (i.e., the dispersal resistance, or spatiotemporal isolation, between reaches following a downstream direction) was positively related with LCBD in all seasons, whereas UndBin (i.e., the connectivity between each pair of reaches without any given direction) was negatively correlated with LCBD in all seasons except for winter (Figure 6e).

4 | DISCUSSION

In spite of covering a small study area with similar climatic, geological, and habitat characteristics, selected sites for conservation using LCBD

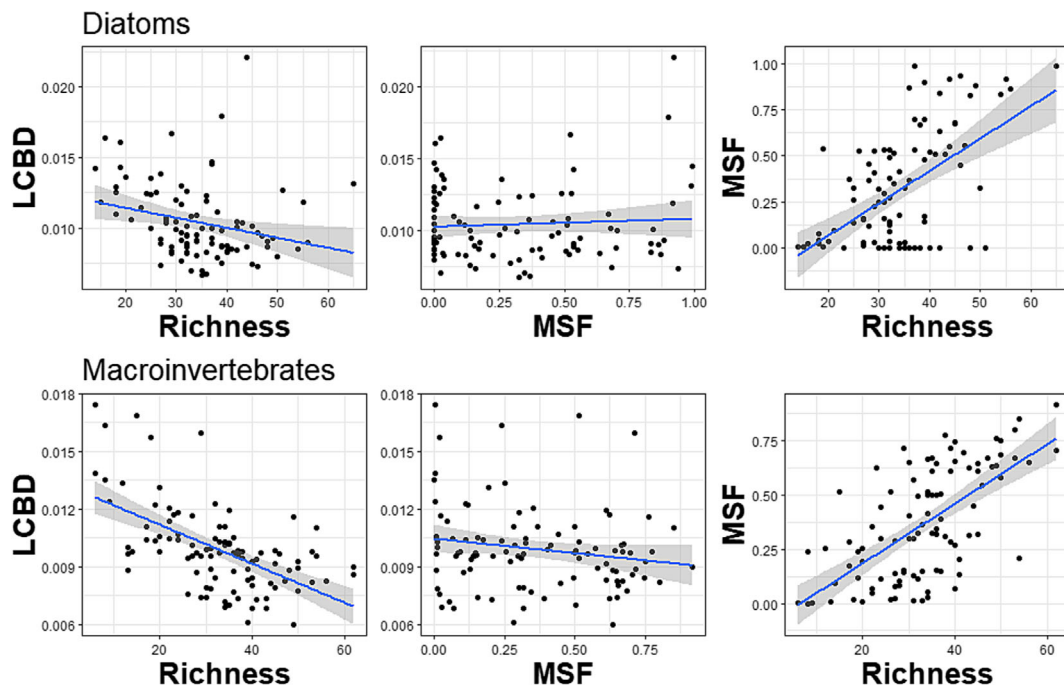


FIGURE 2 Relationship between Local Contribution to Beta Diversity (LCBD), Marxan's Selection Frequency (MSF) and taxa richness for diatoms and macroinvertebrates.

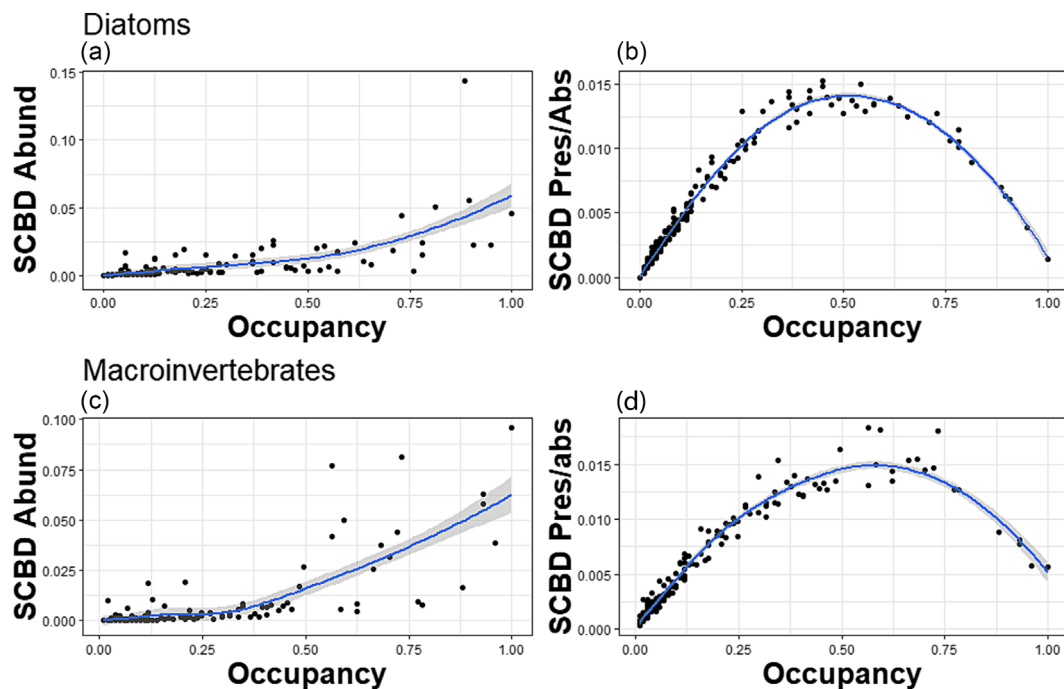


FIGURE 3 Relationship between occupancy and abundance or presence/absence data for diatoms (a,b) and macroinvertebrates (c,d).

and MSF varied widely in space and time, which agrees with our first hypothesis. Given our results, we advise conservation plans to properly capture the spatiotemporal hydrological variability of TRs and be able to accommodate the changing conditions. As we have hypothesised, TRs are highly dynamic systems that create a patchy landscape in which flowing reaches can co-occur with disconnected

pools and dry riverbeds within a single network. This favours the co-existence of different communities (e.g., aquatic and terrestrial) because of multiple factors, such as habitat heterogeneity or the existence of spatially isolated sites that serve as a refugia for weak competitors (Bonada et al., 2020; Larned et al., 2010). Moreover, this landscape drastically changes over time. For example, in late summer,

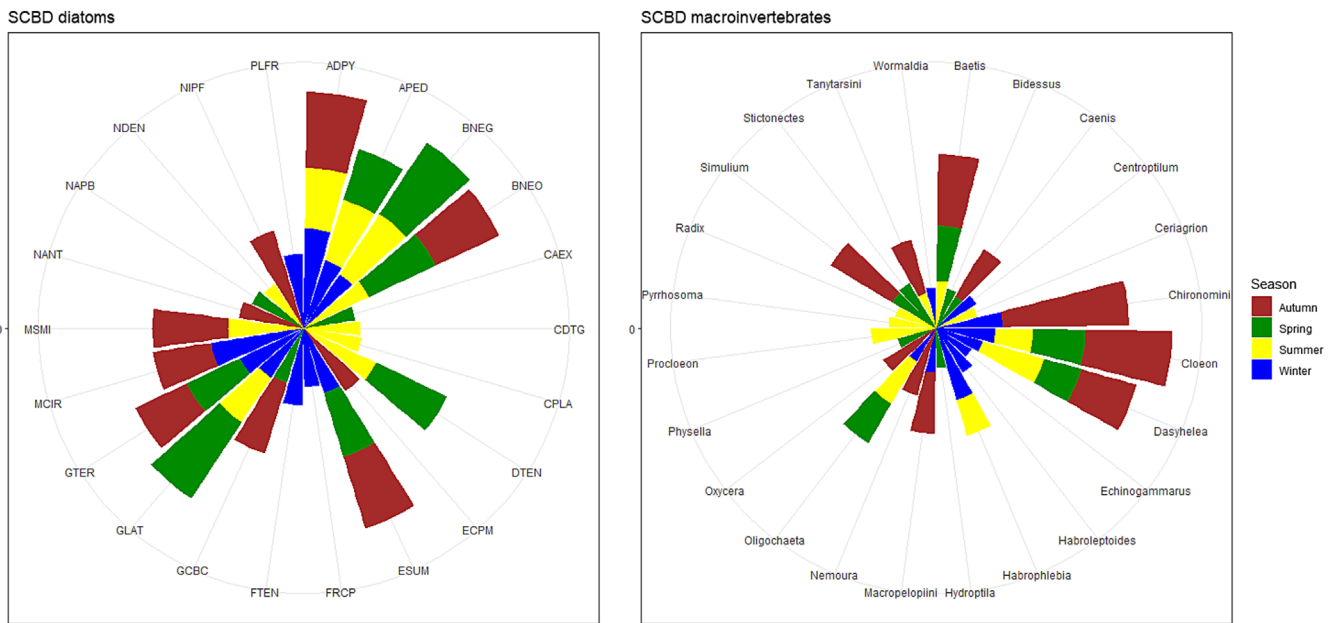


FIGURE 4 Rose plot of the most contributing taxa to beta diversity (SCBD) across seasons for diatoms and macroinvertebrates. Diatom species codes can be found in Supporting Information S3.

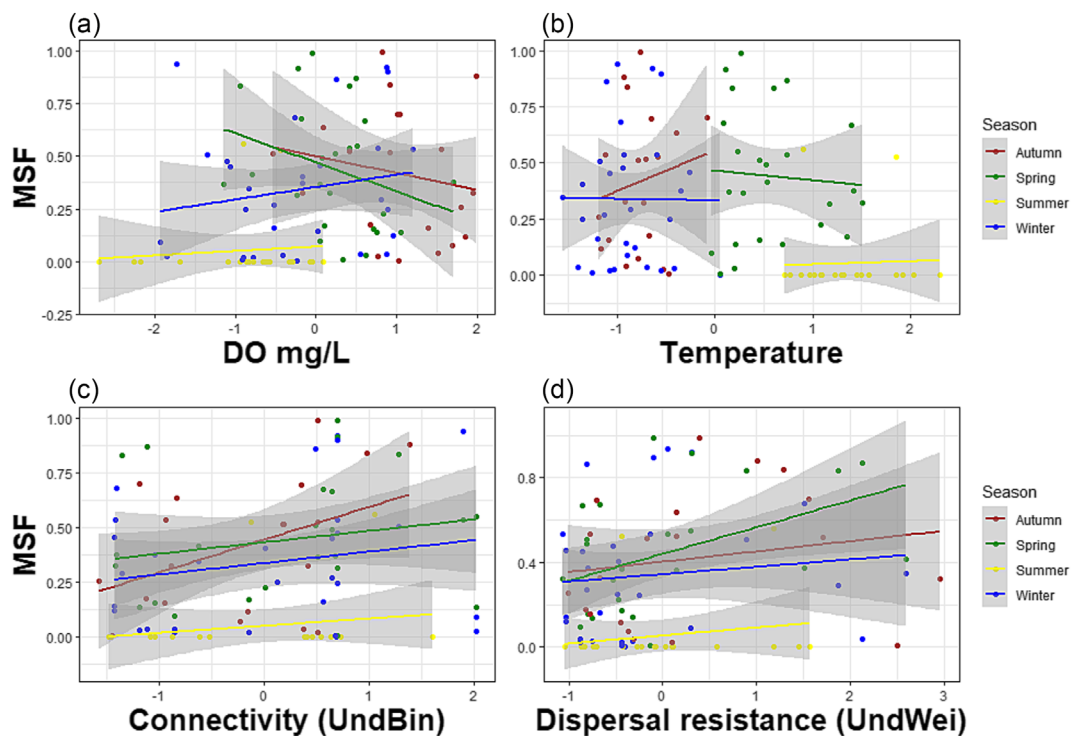


FIGURE 5 Relationships between predictor variables and Marxa's selection frequency (MSF) for diatoms with p -values < 0.1 in each season. DO mg/L refers to dissolved oxygen, temperature to the temperature on water, UndBin to the connectivity between each pair of reaches without any given direction, and UndWei to the dispersal resistance (or spatiotemporal isolation) between reaches not following a downstream direction.

a dry fragmented stream network can be rapidly transformed into a fully connected network after heavy precipitation events (Pineda-Morante et al., 2022). Taking this into account, planning conservation on the basis of snap-shot aquatic biodiversity surveys

would lead to strongly biased and misguided decisions that could hamper conservation efforts.

MSF and LCBD showed a strong spatiotemporal variability, but they were weakly related. In agreement with our second

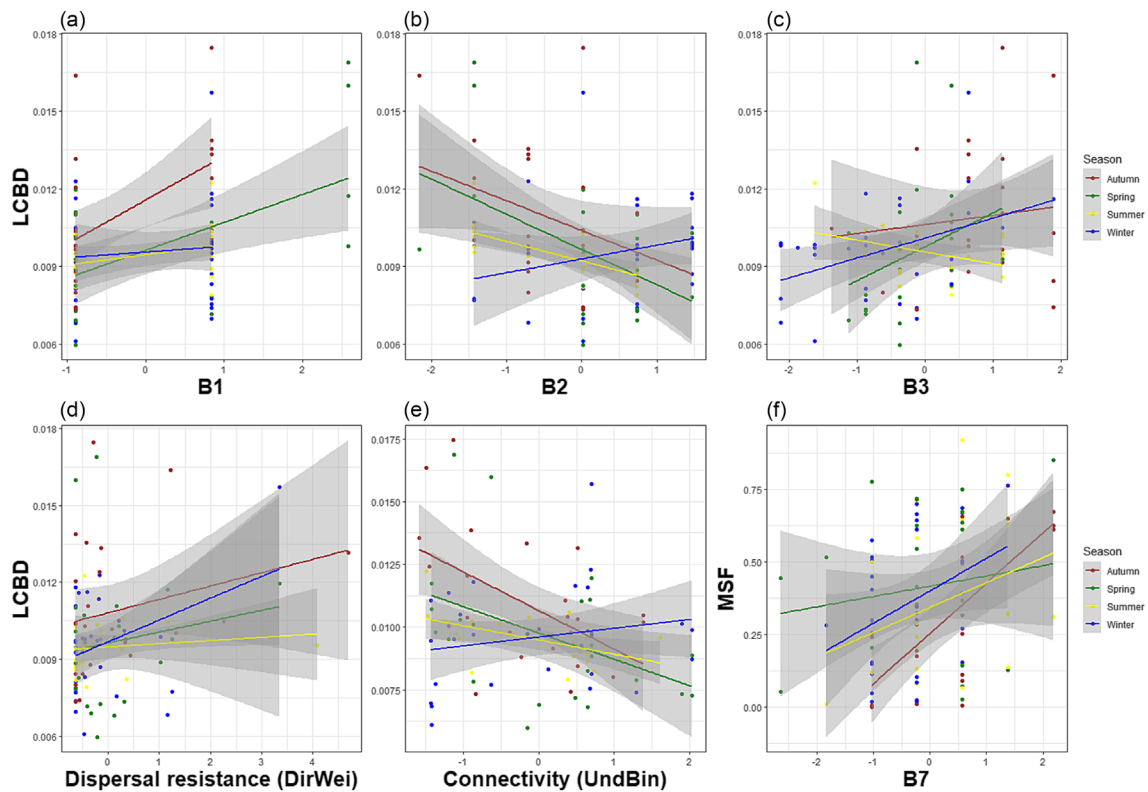


FIGURE 6 Relationships between predictor variables and Local Contribution to Beta Diversity (LCBD) or Marxan's Selection Frequency (MSF) values for macroinvertebrates with p -values < 0.05 in each season. “B1” refers to embeddedness in riffles and sedimentation in pools, “B2” to the frequency of riffles, “B3” to the substrate composition, “DirWei” to the dispersal resistance (or spatiotemporal isolation) between reaches following a downstream direction, “UndBin” to the connectivity between each pair of reaches without any given direction, and “B7” to the aquatic vegetation cover.

hypothesis, MSF usually selects a combination of sites with high local richness and very rare taxa (Epele et al., 2021). In our study, under some circumstances, MSF was able to adequately represent all taxa by selecting a few sites (e.g., only two sites for diatoms in summer). On the contrary, LCBD selected the communities with a higher relative weight at the level of community differentiation but not necessarily the communities with rare or endemic species. Thus, this approach does not seem adequate to design conservation strategies in rivers when these rare or endemic species occur and have a high conservation value, such as in TRs (Bogan, 2017; Fernández-Calero et al., 2022; Stubbington et al., 2017). In these cases, MSF with its principle of complementarity and its flexibility in the application of specific targets, would be a more reliable tool. However, LCBD selected communities with higher differentiation and low richness that were not necessarily selected by MSF (e.g., site R4 in autumn or H5 in winter (Figure 1)). This highlights the conservation value of TRs and specially of those with low richness as a result of low flow permanence (Datry et al., 2014).

According to previous studies (Heino & Grönroos, 2017; Siqueira et al., 2009) taxa with high abundances and occupancy across sites, which are often the least threatened taxa, present a greater contribution to beta diversity. Concordantly, we found a very strong

relationship between species occupancy and abundance with SCBD for diatoms and macroinvertebrates. This suggests that SCBD alone is not a suitable metric to assess the conservation value of a given taxa, since it is strongly driven by locally abundant and regionally common species, rather than rare or endemic species with high conservation value (Rodríguez-Lozano et al., 2023). For example, the genus *Tyrrenoleuctra*, a specialist taxon of ephemeral rivers, whose nymphal presence only occurs in winter and early spring, did not strongly contribute to SCBD in our study. However, this is a rare and vulnerable taxa with restricted geographical distribution (Fernández-Calero et al., 2022; Fochetti et al., 2009) that should be considered in conservation plans and probably requires specific conservation actions.

Despite the use of SCBD is not recommended for conservation, we found different diatom and macroinvertebrate taxa strongly contributing to beta diversity depending on the season. In the case of diatoms, species characteristic of oligotrophic calcareous rivers contributed the most to beta diversity (e.g., *Brachysira neoexilis*, *Gomphonema lateripunctatum*, *G. tergestinum* and *Encyonema subminuta*), as well as generalist species (e.g., *Achnanthyidium pyrenaicum* and *A. pediculus*). This aligns with previous studies showing that commonly occurring diatom taxa greatly contribute to beta diversity (Szabó et al., 2019; Vilmi et al., 2017). For

macroinvertebrates, the differential seasonal contribution of taxa might be explained by changes in habitat variability and flow permanence (Bonada et al., 2007), which influences habitat preference and phenology (Porst et al., 2012; Woods et al., 2022). For example, in agreement with previous studies (Bogan et al., 2017; Bonada et al., 2007), Ephemeroptera, Plecoptera, and Trichoptera (EPT) were more abundant in winter and autumn, during flowing conditions and mild temperatures, whereas Odonata, Coleoptera, and Hemiptera (OCH) dominated in spring and summer, when many stream reaches might have disconnected pools and temperatures are high. Thus, riffle-adapted taxa, such as *Simulium* and *Habroleptoides* (Horne et al., 1992), showed high SCBD values in winter and autumn, whereas in spring and summer lentic-adapted taxa, such as *Bidessus*, *Stictonectes*, *Gerris*, or *Sympetrum* (Buffagni, 2021; Letsch et al., 2016), showed the highest SCBD values. However, there were many generalist taxa that contributed significantly to beta diversity throughout most of the year (e.g., *Cloeon* and *Dasyhelea*).

Concerning our third hypothesis, local conditions largely determined the conservation importance of our study sites. Physicochemical and habitat variables were the most important drivers of LCBD and MSF for diatoms and macroinvertebrates, respectively. We found that dissolved oxygen and temperature drove diatom MSF, in line with previous works showing that local physicochemical conditions shaped diatom communities (Soininen & Teittinen, 2019). Diatoms also responded to environmental heterogeneity, but this might be directly related to the species-area relationship (SARs) (i.e., larger samples, more richness) (Soininen & Teittinen, 2019). For macroinvertebrates, embeddedness in riffles and sedimentation in pools (B1), along with substrate composition (B3), and aquatic vegetation cover (B7), determined LCBD across seasons, suggesting that, in general, increasing habitat heterogeneity might promote community turnover through a niche partitioning. For example, rock characteristics can determine caddisfly oviposition patterns and influence population dynamics (Reich et al., 2011). Overall, our findings illustrate the importance of preserving local habitat heterogeneity to support diverse macroinvertebrate communities.

Our results agree with that more spatiotemporally isolated sites in TRs showed a stronger contribution to LCBD (Crabot et al., 2020; Ruhí et al., 2017). However, there were important temporal variations in the relationship between LCBD and hydrological connectivity. When the network was fully connected in winter (after the rewetting), LCBD values linearly increased with spatiotemporal connectivity, most likely because there are fewer dispersal restrictions and each species occupies its preferential niche (Fletcher et al., 2016; Leibold & Chase, 2017; Thompson et al., 2017; Warfe et al., 2012). In the remaining seasons, the communities with highest LCBD values were located in the most spatiotemporally isolated sites, suggesting that isolation promotes beta diversity (e.g., by allowing rare species with low competitive advantage to persist), which has already been shown for high mountain streams (Finn et al., 2011). Hydrological connectivity also played a role in the selection of sites by MSF, with spatially isolated sites being often

selected to represent rare taxa. Overall, our results suggest that conservation plans should adequately capture the natural hydrological variability of drying river networks, because the networks can also have temporary reaches with high conservation value (Hamdhani et al., 2020; Hermoso et al., 2013; Naia et al., 2021; Vander Vorste et al., 2020).

TRs are one of the most widespread and vulnerable river systems on the planet (Chiu et al., 2017; Datry et al., 2023; Messenger et al., 2021), but host unique freshwater biodiversity adapted to these ecosystems (e.g., *Mesophylax*, *Tyrrhenoleuctra*) (Bonada et al., 2020; Magoulick & Kobza, 2003; Vander Vorste et al., 2020; Yu et al., 2022). In addition, TRs also support semi aquatic and terrestrial taxa (i.e., invertebrates and vertebrates) that use dry channels and riparian habitats as new habitats and migration corridors (Sánchez-Montoya et al., 2017). These singular river ecosystems should have specific conservation strategies to ensure their biodiversity and functionality. However, specific protection plans including TRs are still lacking (Datry et al., 2023). For example, in Europe, even though the Annex I of the Habitats Directive (Council Directive 92/43/EEC, 1992) describes habitat types that refer to TRs (i.e., Intermittently flowing Mediterranean rivers of the Paspalo-Agrostidion, and Riparian formations on intermittent Mediterranean watercourses with *Rhododendron ponticum*, *Salix*, and other species), this has resulted in limited conservation and policy actions related to the protection of these ecosystems (Datry et al., 2023; Fritz et al., 2017; Magand et al., 2020). In the United States, many temporary waterbodies are protected under a range of policy instruments at the local, State, and Federal levels. However, protections for TRs at the Federal level have been increasingly threatened over the past decades, owing to Supreme Court rulings (Sulliván & Gardner, 2023). A recent Supreme Court decision (Sackett v. US Environmental Protection Agency) has ruled that for a “wetland” (including streams and rivers) to receive protection under the Clean Water Act of 1972, it must have a continuous surface connection with a larger body of water (i.e., an ocean, a lake, or a larger perennial river). This decision threatens protection to TRs, which strongly dominate the subarid and arid regions of the U.S. Southwest (Levick et al., 2008). Moreover, as many rivers across the U.S. Southwest continues to lose flow because of climate change and overallocation of freshwater resources (Ruhí et al., 2016), often shifting from perennial to intermittent flow regimes, using physical but not biological connectivity as a condition for stream protection may enable further degradation in the near future.

In addition, many rivers around the world are expected to become temporary and unpredictable during the next decades because of climate change (Döll & Schmied, 2012). Thus, conservation plans that incorporate the spatiotemporal variability of TRs, will become increasingly needed to effectively protect freshwater biodiversity. Therefore, based on our results, we suggest a set of recommendations to guide future conservation plans for TRs that help to ensure their biodiversity and functionality. Firstly, we strongly recommend regular assessments across seasons or, at least, during the dry season (including disconnected pools), the

rewetting period, and the fully connected period to have a full characterization of biodiversity. Secondly, we recommend the use of beta diversity components such as LCBD and conservation planning methods (MSF) as complementary approaches to determine and prioritize sites to be conserved. LCBD is able to detect unique species composition even in sites with low richness as a result of low flow permanence (Datry et al., 2014), whereas MSF could be used as a tool to design specific criteria, for example, to include rare or singular species. Thirdly, focusing on a local perspective, we encourage the preservation of local habitat heterogeneity such as the substrate composition or instream aquatic vegetation. Fourthly, in a regional perspective, we encourage the conservation of spatiotemporal isolated communities with low species richness because these sites usually host unique communities with high LCBD values. Fifthly, we argue that natural spatiotemporal connectivity should be enforced and be case specific (Cid et al., 2022). For example, in historically isolated populations and communities such as the ones in our study, anthropogenic water discharges that could increase hydrological connectivity but decrease biodiversity of the TRs should be avoided.

Although our study provides valuable insights about the spatiotemporal dynamics of biodiversity patterns in TRs and how it can influence conservation decisions, it also has limitations that should be considered if our approach is applied to other areas. Firstly, our study area covers a small spatial scale with very homogeneous environmental conditions, which could potentially result in homogeneous community dynamics. However, we showed that even under similar environmental conditions community dynamics differ because of differences in spatiotemporal hydrological dynamics. Secondly, the temporal duration of the study was only one year, and the patterns observed may not reflect long-term trends. Although the year of the study was a normal hydrological year in the area, in a drier year, communities can behave completely different (Cid et al., 2017). This highlights the need to incorporate data coming from multiple years in conservation planning studies, especially in areas with high interannual variability, such as the Mediterranean region (Bonada et al., 2020; Cid et al., 2017). Thirdly, our study only considers diatoms and macroinvertebrates, which may not represent the full complexity of the ecosystem. Data on other aquatic or even terrestrial organisms (e.g., fish, amphibians) would be recommended if the approach needs to be applied to other areas. Future research should address these limitations when applying our approach to other TRs (and even perennial) in order to increase the performance of conservation strategies.

Finally, conservation plans need to be flexible and adapted to each hydrological scenario. For example, in the wet season the connectivity of the river network and microhabitat heterogeneity (riffles and pools) should be maintained at the reach scale. However, during the dry season, maintaining disconnected pools is key to sustaining refuges for aquatic biodiversity. All these recommendations stand as broad guidelines that should be specifically adapted to the particular characteristics of each TR but keeping in mind the relevance of these ecosystems at the global

scale (Messenger et al., 2021), especially considering future global change scenarios.

AUTHOR CONTRIBUTIONS

José María Fernández-Calero led the paper in the contextualization, analysis, writing, interpretation and edition. He also collected the data, sorted and identified macroinvertebrates. Núria Bonada conceptualised the paper, interpreted the results, wrote and edited the manuscript and obtained funding. Miguel Cañedo-Argüelles collected the data, conceptualised the paper, interpreted the results, wrote and edited the manuscript and obtained funding. David Cunillera-Montcusí calculated spatiotemporal connectivity metrics, interpreted the results, wrote and edited the manuscript. Núria Cid collected the data, interpreted the results, edited the manuscript and obtained funding. Albert Ruhí conceptualised the paper, interpreted the results and edited the manuscript. Dolors Vinyoles collected the data and edited the manuscript. Guillermo Quevedo-Ortiz identified diatom and edited the manuscript. Joan Gomà interpreted diatom results and edited the manuscript. Virgilio Hermoso interpreted the results, wrote and edited the manuscript. Pau Fortuño and Raúl Acosta collected the data, identified macroinvertebrates and edited the manuscript.

CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Check list of taxa available as Supporting Information S3.

Models results available as Supporting information S1 and S2.

Code used is available on Github: <https://github.com/Josefernandezcalero/Conservation-paper-from-the-MECODISPER-project>.

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