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RESEARCH ARTICLE

Analysing the contribution of intermittent rivers to beta diversity can improve freshwater conservation in Mediterranean rivers

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Abstract

In Mediterranean climate regions, intermittent rivers (IRs) harbor highly dynamic communities with species and trait composition changing over time and space. Simultaneously considering multiple biodiversity facets and a spatiotemporal perspective is, therefore, key to developing effective conservation strategies for these ecosystems. We studied the spatiotemporal dynamics of aquatic macroinvertebrates in rivers of the western Mediterranean Basin by analysing (1) the taxonomic and functional richness and the local contribution to beta diversity (LCBD; measured considering taxonomic and functional facets) of perennial rivers and IRs over five sampling times, and (2) their relation with flow intermittence, local environmental uniqueness, and the number of anthropogenic impacts. Both analyses were also conducted for the subset of data including only IRs to compare values between their flowing and disconnected pool phases. According to our results, taxonomic and functional richness tended to be higher in perennial rivers than in IRs, while taxonomic and functional LCBD tended to be higher in IRs than in perennial rivers. When comparing IR sites over time, higher values of taxonomic and functional LCBD corresponded mostly to their disconnected pool phase. Flow intermittence, the number of anthropogenic impacts and the environmental uniqueness were significant predictors of taxonomic and functional richness, but only flow intermittence was an important predictor of taxonomic LCBD. For the IR-only data subset, disconnected pool permanence was the main predictor explaining spatiotemporal patterns. Our results highlight the importance of IRs to biodiversity conservation of Mediterranean climate rivers, especially during the disconnected pool phase, suggesting that these ecosystems cannot be ignored in conservation planning strategies.

Keywords LCBD · Functional traits · Non-perennial rivers · Macroinvertebrates · Temporal beta-diversity · Temporary rivers

Introduction

Incorporating spatiotemporal alpha (α), beta (β) and gamma (γ) diversity information into community composition analysis is crucial to developing effective biodiversity and ecosystem conservation strategies (Pereira et al. 2013; Hill et al. 2016). Commonly, conservation efforts have focused on protecting the number of species within a site (taxonomic α-diversity) or region (taxonomic γ-diversity or regional diversity), while efforts to characterize and incorporate the variation in species composition (taxonomic β-diversity) are relatively more recent (Koleff et al. 2003; Anderson et al. 2011; Socolar et al. 2016; Bush et al. 2016). Taxonomic β-diversity can be measured as the compositional dissimilarity in species assemblages, either across space (Baselga 2010; Anderson et al. 2011) or time (Legendre and Gauthier 2014; Legendre 2019; Shimadzu et al. 2015). Spatial taxonomic β-diversity aims to understand the processes governing spatial variation in community composition, while temporal taxonomic β-diversity provides information on how species composition changes over time (Anderson et al. 2011; Legendre and Gauthier 2014; Legendre and Condit 2019). The combination of spatial and temporal β-diversity has therefore the potential to better represent how and why community composition changes over time, particularly in response to environmental changes (Legendre and Condit 2019; Vander Vorste et al. 2021; Faustino de Queiroz et al. 2022). As a result, this integrated approach can help to better

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identify areas that may be more resilient to change and those that may be more vulnerable, allowing for targeted conservation efforts (McGill et al. 2015).

Functional diversity can provide complementary insights into the impacts of disturbance on ecosystem functioning (Flynn et al. 2011; Gross et al. 2017). For instance, the use of functional diversity allows us to clarify the role of each species in ecosystem processes and their resistance and/or resilience capacity to environmental changes, either natural or anthropogenic (Tobias and Monika 2011; Villéger et al. 2013, 2017; Soria et al. 2020). Functional β-diversity can be defined as the dissimilarity in trait composition across space (Villéger et al. 2013; Aspin et al. 2019) or time (Baselga et al. 2015; Magurran et al. 2019). As the increase in multiple anthropogenic impacts is threatening the stability of ecosystems, understanding how both taxonomic and functional diversity influence ecosystem functioning can contribute to better predicting the ecological consequences of biodiversity loss (Hooper et al. 2005; Flynn et al. 2011; Gutiérrez-Cánovas et al. 2015).

Intermittent rivers (IRs) are non-perennial watercourses that typically shift among flowing, disconnected pool and dry phases, and are therefore highly dynamic ecosystems (Gallart et al. 2012, 2017). Flow intermittence exerts a primary control on IR ecosystem structure and function over time and, consequently, biodiversity patterns typically follow these changes (Datry et al. 2014; Arroita et al. 2018; Arias-Real et al. 2020). In the case of aquatic macroinvertebrates, surface flow cessation and the subsequent formation of disconnected pools imply the disappearance of riffle-dwelling species and the appearance of pool-dwelling species (Bonada et al. 2006; Bogan et al. 2017; Tonkin et al. 2017). With the complete drying of the riverbed, some taxa may emerge, move to other wet habitats or to the hyporheic zone, or enter a desiccation-resistant life stage (Lytle and Poff 2004; Bogan et al. 2017; Stubbington et al. 2019). Shifts from dry to flowing phases following rewetting favour recolonization, contributing to the recovery of local communities in IRs (Leigh et al. 2016; Bogan et al. 2017). IR communities are highly variable in time, with species and trait composition changing from one period to another (Datry et al. 2014; Bogan et al. 2017). Nevertheless, climate change and increasing human water demand are altering biodiversity patterns and functional processes of IRs (Datry et al. 2014; Leigh et al. 2019), and thus a better understanding of their contribution to biodiversity is timely.

In comparison to IRs from other climatic regions, those in Mediterranean climate areas are characterized by being highly predictable in terms of seasonality, resulting in well-known community shifts between flowing and non-flowing phases (Hershkovitz and Gasith 2013; Tonkin et al. 2017). In addition, Mediterranean-climate IRs are global biodiversity hotspots, possessing high levels of endemism, but also being particularly vulnerable to anthropogenic impacts (Bonada and Resh 2013; Cid et al. 2017; Newbold et al. 2020). Considering their high spatiotemporal variability, identifying key sites and periods of time that contribute the most to regional diversity could be informative for conservation management (Ruhí et al. 2017; Sánchez-Montoya et al. 2020; Rodríguez-Lozano et al. 2023).

Here, we studied the spatial and temporal dynamics of aquatic macroinvertebrates in 20 rivers of the western Mediterranean Basin over different aquatic phases by analysing the taxonomic and functional richness (hereafter TRic and FRic) and the local contribution to overall taxonomic and functional β-diversity (hereafter T-LCBD and

F-LCBD, respectively; Legendre and De Cáceres 2013) of each site over five sampling times. Specifically, we analysed (1) the values of TRic, FRic, T-LCBD and F-LCBD of perennial rivers and IRs over five sampling times, and (2) their relationship with three main predictors: flow intermittence, number of anthropogenic impacts and local environmental uniqueness. Both analyses were also conducted for the subset of data including only IRs to compare values between their flowing and disconnected pool phases. Perennial rivers and IRs were sampled along gradients of natural flow intermittence and anthropogenic impacts to investigate their influence on LCBD. We used the LCBD because it allows identifying which sites and times contribute the most to total β-diversity. We hypothesized that TRic and FRic would be higher in perennial rivers than in IRs, whereas T-LCBD and F-LCBD would be higher in IRs than in perennial rivers. Macroinvertebrate communities in IRs from Mediterranean climatic regions are exposed to and adapted to higher spatiotemporal variability, and consequently host unique species adapted to non-flowing conditions (Bonada et al. 2006, 2020; Bonada and Resh 2013; Leigh et al. 2019). However, evolutionarily acquired macroinvertebrate resistance traits in response to drying (e.g. aerial respiration, diapause or dormancy resistance forms) are less frequent than resilience traits (e.g. life cycle duration, aerial dispersion) in these ecosystems (Datry et al. 2014; Leigh et al. 2016; Bogan et al. 2017), which may result in higher dispersal of individuals during the dry period (i.e. increase in β-diversity or LCBD) than individuals that remain (i.e. TRic and FRic). Moreover, we hypothesized that T-LCBD and F-LCBD values would be even higher during IRs' periods of disconnected pools than during their flowing phase because species adapted to non-flowing conditions with some kind of resilience trait will move from dry river reaches in search of any site with water (i.e. disconnected pool). Finally, in addition to TRic, FRic, T-LCBD and F-LCBD being related to flow intermittence, we also expected them to be positively correlated with environmental uniqueness (Castro et al. 2019; Heino et al. 2022), as sites and sampling times with differentiated

environmental conditions may have unique species or trait composition (Ruhí et al. 2017; Bonada et al. 2020).

Methods

Study sites and sampling design

This study was conducted in 20 rivers located in the Mediterranean climate region of the Iberian Peninsula (Fig. 1). Sites were located in three predominantly calcareous catchments, comprising the Ebro, Júcar and Catalan basins. A 100-m site was defined in each river. Ten sites were intermittent and ten were perennial. The study area is characterized by a Mediterranean climate, with high seasonal and inter-annual variability in precipitation and flow regime (Bonada and Resh 2013; Cid et al. 2017). Sites ranged in altitude from 6 to 1100 m.a.s.l., and experienced different hydrological phases over the five sampling times (Table S1), with discharges ranging from 0 to 0.417 m^3/s. See Table S2 and the following section on the Mediterranean Reference Criteria (MRC index)for further details on the study sites, such as riparian vegetation (e.g. cover and composition, lateral connectivity), introduced species, pollution (e.g. urban or industrial effluents), diffuse pollution sources and land use (e.g. agriculture, intensive grazing, urban use, burned vegetation), river morphology and habitat conditions (e.g. substrate diversity, canalization, gravel extraction), and hydrological alteration and regulation.

Biological dataset

Macroinvertebrates were collected during flowing and disconnected pool phases by sampling each site five times during a 6-week interval between April and December 2015: April–May (henceforth t1; spring in the Northern Hemisphere), June (t2; spring), July–August (t3; summer), September (t4; summer) and December (t5; autumn). Therefore, sampling included flowing (t1), drying (t2–t4) and rewetting (t5) periods with their corresponding flowing, disconnected pools and dry riverbed aquatic phases (see Table S1 for further details). Because five sites were dry on one to three occasions, a total of 91 samples were obtained. Our sampling procedure followed the official standardized protocol used by water agencies in Spain (MAGRAMA 2013). Samples were collected using a 250-µm-mesh D-net across all available microhabitats (i.e. hard substrates, plant detritus, vegetated banks, submerged macrophytes, sand and other fine sediments) and preserved in 4% formaldehyde (see Appendix S1 for more details). Macroinvertebrates were identified to the lowest taxonomic resolution possible, usually genus, but with some Chironomidae and Ceratopogonidae identified to subfamily or tribe. Overall, 194 macroinvertebrate taxa were identified (Soria et al. 2020).

As suggested in Soria et al. (2020), categories from seven specific resistance and resilience traits from Tachet et al. (2010) related to flow intermittence and anthropogenic impacts were used to study the functional facet of biodiversity: asexual reproduction, resistance forms (i.e. diapause or dormancy, cocoons), aerial respiration (i.e. spiracle, hydrostatic vesicle), flier and burrower (i.e. epibenthic) or interstitial (i.e. endobenthic) locomotion and substrate relation, less than a year life cycle duration, more than one reproduction cycles per year, aerial active and aquatic passive (i.e. drift) dissemination (Table S3).

Predictors of spatiotemporal β-diversity

Hydrology, anthropogenic impacts and general water quality parameters of the studied rivers were included as predictors of LCBD. The TREHS (Temporary Rivers Ecological and Hydrological Status) software (http://www.lifet rivers.eu/products/trehs-software/; Gallart et al. 2017) was used to classify rivers' hydrological regime (i.e. perennial and IRs) and to differentiate river sites affected by natural flow intermittence from those with human-driven flow intermittence. To infer the IRs' phases (i.e. flow, disconnected pools, dry riverbed), two temperature data loggers (UA-002 HOBO) were installed at each river site, which recorded data during the 30-week study period (see details in Soria et al. 2020). Thermal amplitude was then used to calculate the total zero-flow days (i.e. disconnected pools or dry riverbed) during the 30-week study period (hereafter ZF_T) and the number of days in the disconnected pool phase since the last sample was taken (hereafter DP_i) (Soria et al. 2020). The ZF_T hydrological predictor was 0 for perennial rivers and ranged from 17 to 209 days of total zero-flow days for IRs. The DP_i predictor ranged from 5 to 90 days in the disconnected pool phase since the last sample was taken (Table S1) and was only available for IRs. Thus, the ZF_T provides information on the total cumulative drying period of each site, and thus informed on the degree of intermittency of an IR. The DP_i provides information on the permanence of the disconnected pool phase between sampling times. For example, one IR may have been disconnected, connected and then disconnected again between t1 and t2, while another IR may have been disconnected for the entire time between t1 and t2. Since there was a moderate positive correlation between ZF_T and DP_i, the ZF_T was used to test the spatiotemporal patterns of taxonomic and functional richness and LCBD between perennial rivers and IRs, while the DP_i was used when analysing IRs' spatiotemporal dataset.

Anthropogenic impacts were measured at each river site by using the number of impacts according to the Mediterranean Reference Criteria (MRC index) (Sánchez-Montoya

et al. 2009). The MRC index includes information on invasive species, diffuse pollution sources, land-use intensity, riparian vegetation, river geomorphology, instream habitat conditions and hydrological alterations (Table S2), and ranges from 0 (highly impacted) to 20 (non-impacted). The information for each site was obtained from the list of pressures and impacts of the three different river basin water authorities included in our study combined with field observations (e.g. detection of invasive species) and, in the case of hydrological alterations, from the TREHS software. To facilitate interpretation, the inverse of the MRC index values was used (i.e. from 0 = non-impacted to 20 = highly impacted, hereafter number of impacts; see Soria et al. 2020). As a result, the number of impacts ranged from 0 (non-impacted) to 13.

For each sampling site and time, the following water quality parameters were measured in situ and analysed in the laboratory when required: conductivity (µS/cm), pH, temperature (ºC), dissolved oxygen (mg/l), chlorophyll-a (mg/m^3), HCO_3, Ca, TOC, Mg and SO_4 (µg/l). Chlorophyll-a concentration, however, was not used because there was a moderate negative correlation with the number of impacts (Soria et al. 2020). Following Castro et al. (2019), the method described by Legendre and De Cáceres (2013) was used to calculate the local contribution to environmental heterogeneity (hereafter environmental uniqueness), a measure describing the environmental uniqueness of each site, which in this study was in terms of physicochemical characteristics. To do so, all physicochemical variables (except pH) were log-transformed and then a standardized Euclidean distance matrix was used to calculate the environmental uniqueness of each site. Samples with high values (closer to one) of the resultant vector are more unique in terms of environmental conditions (Castro et al. 2019). The predictor of environmental uniqueness ranged from 0.006 to 0.025, with a mean value of 0.011.

Statistical analysis

The TRic and FRic of each site and sampling time were calculated (Table S1). Data were rarefied prior to diversity calculations. FRic was obtained from Soria et al. (2020) and estimated as suggested by Villéger et al. (2008). T-LCBD and F-LCBD were estimated for each sample, i.e. for each site and sampling time (spatiotemporal approach; Legendre and De Cáceres 2013; Legendre and Gauthier 2014). T-LCBD and F-LCBD

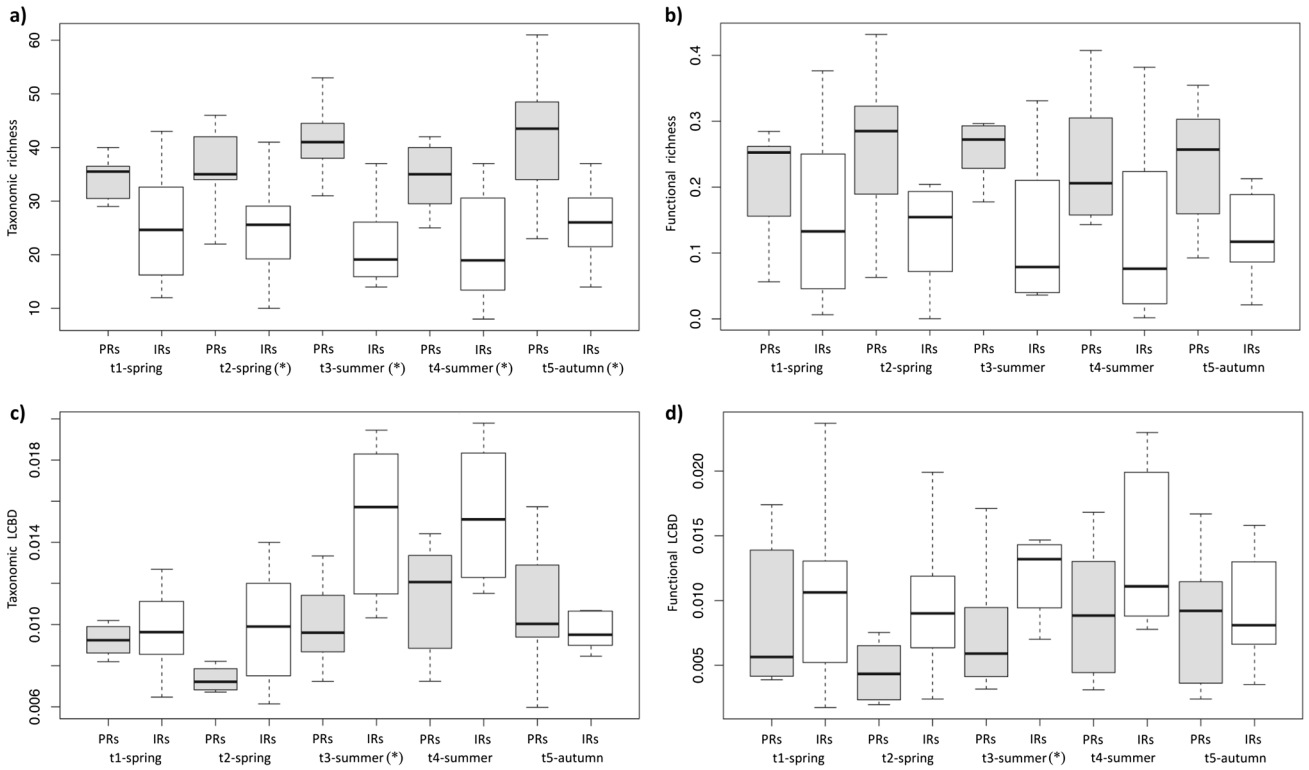

Fig. 1 Boxplots showing taxonomic and functional local richness (**a**, **b**, respectively) and LCBD (c and d, respectively) over the five sampled times: flowing (t1: spring), drying (t2: spring and t3–t4: summer) and rewetting (t5: autumn) periods with their corresponding flowing, disconnected pools and dry riverbed aquatic phases. The thick horizontal bar indicates the median. The box indicates the interquartile range. Vertical bars indicate minimum and maximum values. Full boxes represent perennial rivers (PRs) and empty ones IRs. Significant differences ($P < 0.05$) between perennial rivers and IRs are indicated with (*)

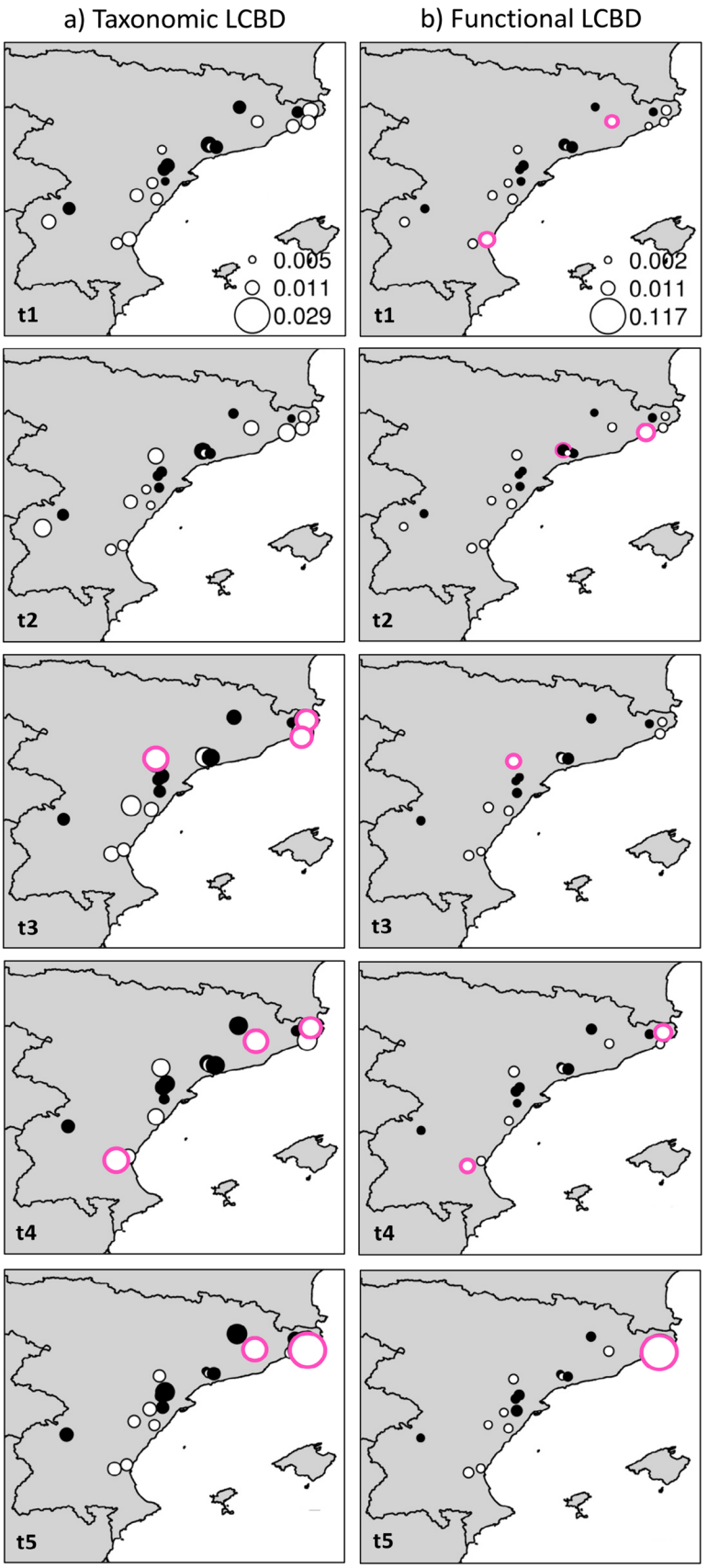

Fig. 2 Taxonomic (**a**) and functional (**b**) LCBD plots of each site through the five sampled times: flowing (t1: spring), drying (t2: spring and t3–t4: summer) and rewetting (t5: autumn) periods with their corresponding flowing, disconnected pools and dry riverbed aquatic phases. Circle size is proportional to the contribution to overall β-diversity for each period. Filled circles: observed perennial rivers; empty circles: observed intermittent rivers. Sites with significant values of LCBD ($P < 0.05$) are indicated in pink. See Table S2 for further details

values indicate the degree of ecological uniqueness of each site at each sampling time in terms of taxa abundance or trait composition, respectively (Legendre and De Cáceres 2013). The T-LCBD was calculated using the taxa abundance matrix (Legendre and De Cáceres 2013). The F-LCBD was calculated using a matrix with the relative abundance of each trait category (columns) across the samples (rows) (Rodrigues-Capítulo et al. 2009). Following the procedures described by Legendre and De Cáceres (2013), T-LCBD and F-LCBD were estimated using the Euclidean distance on Hellinger-transformed data (Legendre and Gallagher 2001) and the significance of each LCBD value (i.e. each site in each sampling time) was tested with 999 permutations. For IRs, TRic ranged from 8 to 56 (mean: 24.63), FRic ranged from 0.002 to 0.418 (mean: 0.145), T-LCBD ranged from 0.006 to 0.029 (mean: 0.012) and F-LCBD ranged from 0.002 to 0.117 (mean: 0.013). For perennial rivers, TRic ranged from 18 to 61 (mean: 37.88), FRic ranged from 0.056 to 0.432 (mean: 0.2427), T-LCBD ranged from 0.005 to 0.016 (mean: 0.009) and F-LCBD ranged from 0.002 to 0.021 (mean: 0.008). A non-parametric Mann–Whitney *U* test with a Bonferroni correction was used to test significant differences between perennial rivers and IRs over the sampling times.

Linear mixed-effect models (LME) were used to test the relationship between TRic, FRic, T-LCBD and F-LCBD, and our set of environmental predictors. Specifically, the ZF_T predictor was used when considering the whole dataset to compare the response variables along an intermittency gradient (i.e. including perennial rivers with $ZF_T = 0$), while DP_i was used when considering data from IRs only to compare the response variables between IRs' periods of disconnected pools and their flowing phase. The number of impacts and environmental uniqueness predictors were used in both datasets to test whether TRic, FRic, T-LCBD and F-LCBD are negatively correlated with the number of impacts and positively correlated with environmental uniqueness. All models included sampling time (t1–t5) as a random factor to assess whether the relationship between TRic, FRic, T-LCBD and F-LCBD and predictors changed among sampling campaigns (i.e. spatial effects were assessed directly while time effects were assessed indirectly).

All analyses were conducted in R software version 3.6.2 (R Core Team 2015), using the packages "ade4" (Dray et al. 2007), "adespatial" (Dray et al. 2018), "car" (Fox and Weisberg 2011), "maptools" (Bivand and Lewin-Koh 2020), "nlme" (Pinheiro et al. 2016), "raster" (Hijmans 2020), "rgdal" (Bivand et al. 2020), "rgeos" (Bivand and Rundel 2020) and "vegan" (Oksanen et al. 2013). The code and functions used to run these analyses are available in the data availability statement.

Results

Our results suggest that both TRic and FRic tended to be higher in perennial rivers than in IRs over time (Fig. 1a, b and Table S1), while T-LCBD and F-LCBD showed the opposite pattern (Fig. 1c, d and Table S4), especially in summer. Significant differences ($P < 0.05$) between perennial rivers and IRs were found in t2–t5 sampling times

Table 1 Partial regression coefficients of the explanatory predictors used in linear mixed-effects models

Response	Predictors variables	Value	SE	df	t-value	*P*
TRic	Intercept	46.3253	2.5133	83	18.4324	0.00
	ZF_T	**−0.0676**	**0.0145**	**83**	**−4.6705**	**0.0001**
	Environmental uniqueness	**−712.0431**	**222.9353**	**83**	**−3.1939**	**0.002**
	Number of impacts	**−0.9814**	**0.1923**	**83**	**−5.0935**	**0.0001**
FRic	Intercept	0.3385	0.0263	83	12.8647	0.00001
	ZF_T	**−0.0004**	**0.0002**	**83**	**−2.8748**	**0.0051**
	Environmental uniqueness	**−6.8186**	**2.3778**	**83**	**−2.8676**	**0.0052**
	Number of impacts	**−0.0109**	**0.0021**	**83**	**−5.3094**	**0.00001**
T-LCBD	Intercept	0.0086	0.0013	83	6.8149	0.00001
	ZF_T	**0.00002**	**0.00001**	**83**	**2.9259**	**0.0044**
	Environmental uniqueness	0.1850	0.0942	83	1.9654	0.0527
	Number of impacts	−0.0001	0.0001	83	−0.7269	0.4693
F-LCBD	Intercept	0.0061	0.0038	83	1.5978	0.1149
	ZF_T	0.00003	0.00002	83	1.5599	0.1226
	Environmental uniqueness	0.1175	0.3434	83	0.3421	0.7331
	Number of impacts	0.0004	0.0003	83	1.3407	0.1837

The response variables were the local taxonomic and functional richness (TRic and FRic, respectively) and the taxonomic and functional local contribution to β-diversity (T-LCBD and F-LCBD, respectively). TRic and FRic were tested T-LCBD and F-LCBD, ZF_T: total zero-flow days

Significant coefficients ($P < 0.05$) are indicated in bold

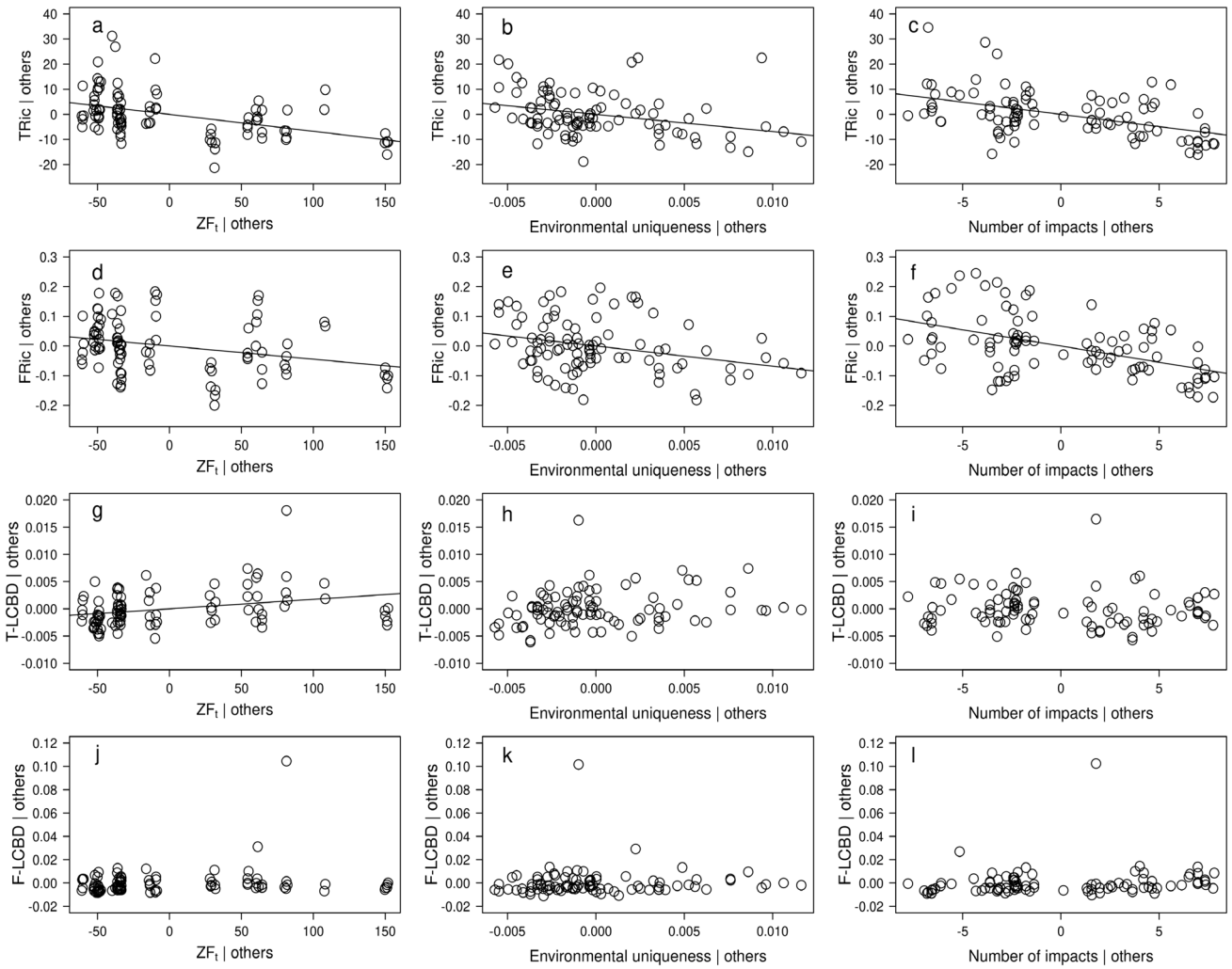

Fig. 3 Partial relationship between taxonomic and functional richness (TRic and FRic, respectively), taxonomic and functional LCBD (T-LCBD and F-LCBD, respectively), and the total zero-flow days (ZF_T) during the 30-week study period, environmental uniqueness, and the number of impacts for all dataset including perennial and intermittent rivers. Regression lines are only shown in those plots with statistically significant relationships in the models

for TRic (Fig. 1a) and t3 sampling time for T-LCBD and F-LCBD (Fig. 1c, d).

When comparing the contributions of perennial rivers and IRs with overall taxonomic and functional β-diversity through the five sampling times, IR sites were the largest contributors. Specifically, significant site contributions to T-LCBD were found in five IRs corresponding to their disconnected pool phase (t3–t5; Fig. 2a and Tables S1 and S4). These five IRs had unique taxa that were found only at these sites, such as *Hydrellia*, *Lispe*, *Diamesa*, *Anisops*, *Batracobdella* and *Hippeutis*, or taxa that were found in these IRs and one (i.e. *Eristalis*, *Sepedon*, *Naucoris*, *Stictotarsus*, *Cyphon*, *Aeschna*, *Parasigara*) or two other rivers (i.e. *Telmatoscopus*, *Hydroglyphus*, *Chaoborus*, *Helobdella*, *Sialis*, *Peltodytes*). For F-LCBD, significant site contributions were observed at one specific sampling time (t2) of a perennial river, three IRs during its flowing phase (t1 and t3) and four IRs during its disconnected pool phase (t2, t4–t5; Fig. 2b and Tables S1 and S4).

When considering perennial rivers and IRs, TRic and FRic showed a significant negative correlation with all three predictors: ZF_T, the number of impacts and environmental uniqueness (Table 1 and Fig. 3a–f). Our results also showed a significant and positive relationship between T-LCBD and ZF_t, but no significant results were observed for the number of impacts and environmental uniqueness (Table 1 and Fig. 3g–i). None of the explanatory variables were correlated with F-LCBD (Table 1 and Fig. 3j–l).

For the subset of data including only IRs, TRic showed a significant negative correlation with all three predictors, but FRic was only significantly and negatively correlated with the number of impacts (Table 2 and Fig. 4a–f). T-LCBD

Table 2 Partial regression coefficients of the explanatory predictors used in linear mixed-effects models for intermittent rivers only

Response	Predictors variables	Value	SE	*df*	*t*-value	*P*
TRic	Intercept	39.2470	3.3143	43	11.8419	0.00001
	DP_i	**−0.1030**	**0.0474**	**43**	**−2.1744**	**0.0352**
	Environmental uniqueness	**−531.5054**	**252.4283**	**43**	**−2.1058**	**0.0411**
	Number of impacts	**−1.0494**	**0.2123**	**43**	**−4.9423**	**0.00001**
FRic	Intercept	0.2921	0.0425	43	6.8757	0.00001
	DP_i	−0.0003	0.0006	43	−0.5590	0.5791
	Environmental uniqueness	−4.5424	3.2356	43	−1.4039	0.1675
	Number of impacts	**−0.0133**	**0.0027**	**43**	**−4.8987**	**0.00001**
T-LCBD	Intercept	0.0099	0.0019	43	5.2038	0.00001
	DP_i	**0.0001**	**0.00002**	**43**	**3.2005**	**0.0026**
	Environmental uniqueness	0.1091	0.1367	43	0.7984	0.4291
	Number of impacts	−0.00003	0.0001	43	−0.2444	0.8080
F-LCBD	Intercept	0.0048	0.0064	43	0.7532	0.4555
	DP_i	**0.0004**	**0.0001**	**43**	**4.1734**	**0.0001**
	Environmental uniqueness	0.1494	0.4890	43	0.3054	0.7615
	Number of impacts	0.0003	0.0004	43	0.8482	0.4010

The response variables were the taxonomic and functional local contribution to β-diversity (T-LCBD and F-LCBD, respectively), and the local taxonomic and functional richness (TRic and FRic, respectively). DP_i: the number of days in the disconnected pool phase since the last sample was taken

Significant coefficients ($P < 0.05$) are indicated in bold

and F-LCBD were significantly correlated with DP_i, but no significant patterns were observed for the other predictors (Table 2 and Fig. 4g–l).

Discussion

Overall, our results showed that IRs had significantly higher taxonomic LCBD than perennial rivers, despite their lower local taxonomic and functional diversity. In early summer and in response to the loss of surface flow, the observed decline in taxonomic and functional richness in IRs can be explained by the disappearance of lotic species inhabiting riffle habitats (Bogan et al. 2017; Tonkin et al. 2017). Yet, during the disconnected pool phase in summer, the increase in taxonomic and functional LCBD in IRs can be related to the colonization of species with specific traits adapted to cope with such conditions (Bonada et al. 2006, 2020). A similar pattern, where sites with higher LCBD are those with lower richness, has been found in other studies of macroinvertebrates (e.g. Heino et al. 2017; da Silva et al. 2018; Valente-Neto et al. 2020) and other biological groups (e.g. Legendre and De Cáceres 2013; Vilmi et al. 2017; Landeiro et al. 2018). This negative relationship indicates that sites with low taxonomic and functional richness tend to hold unique species and trait compositions, highlighting the complementarity of alpha and beta diversity indices in describing biodiversity (Heino et al. 2017; da Silva et al. 2018). Incorporating temporal patterns of LCBD is therefore key to capturing the full variation in community composition that exists in these highly dynamic ecosystems (Ruhí et al. 2017; Sánchez-Montoya et al. 2020; Rodríguez-Lozano et al. 2023).

Our study also showed that higher values of taxonomic and functional LCBD occur mostly during the disconnected pool phase of IRs. During this phase, taxa inhabiting flowing conditions tend to be lost, while lentic taxa progressively colonize the remaining disconnected pools from nearby sites that are drying up, such as Odonata, Coleoptera and Hemiptera (Bogan et al. 2017; Bonada et al. 2020). Indeed, there are studies showing that lentic-dwelling species have higher dispersal abilities than lotic species (e.g. Ribera and Vogler 2000; Hjalmarsson et al. 2015). Disconnected pools can act as refuges for some aquatic taxa such as fish or amphibians during IRs' dry season, which are fundamental for recolonizing the river network upon flow resumption (Hermoso et al. 2013; Gallart et al. 2017). In addition, for some species of macroinvertebrates (and for amphibians and fish), disconnected pools are also used as stepping-stones for their dispersal or as key sites for laying eggs and, thus, completing their life cycle (Bonada et al. 2006, 2020; Stubbington et al. 2017; Moidu et al. 2023). Considering that up to 60% of the world's rivers by length are IRs and that they are expected to increase worldwide (Döll and Schmied 2012; Messager et al. 2021), it is expected that disconnected pools will become more abundant and, consequently, management actions will be needed to conserve them (Gallart et al. 2017; Bonada et al. 2020).

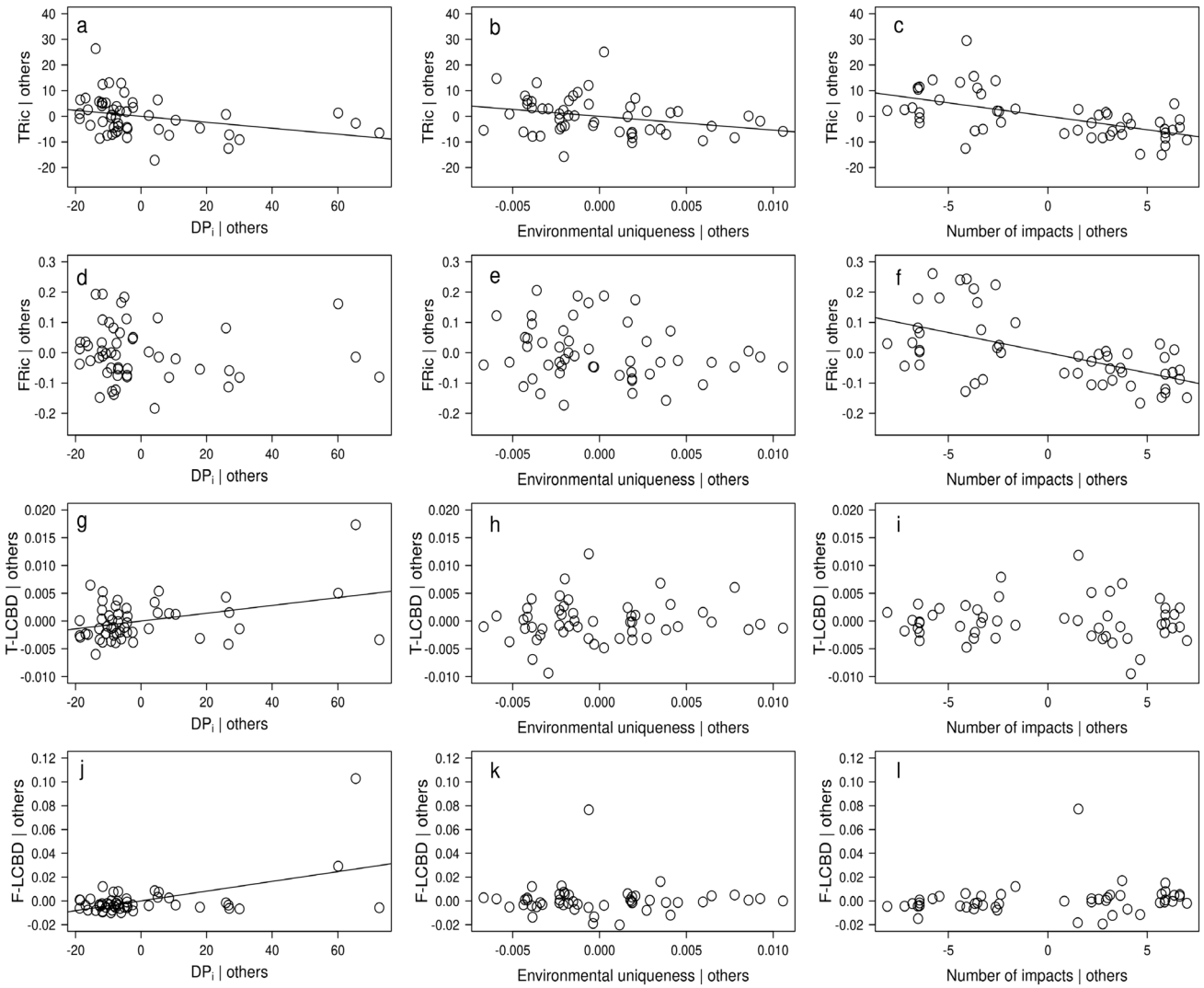

Fig. 4 Partial relationship between taxonomic and functional richness (TRic and FRic, respectively), taxonomic and functional LCBD (T-LCBD and F-LCBD, respectively), and the number of days in the disconnected pool phase (DP_i) since the last sample was taken, environmental uniqueness and the number of impacts for only intermittent rivers. Regression lines are only shown in those plots with statistically significant relationships in the models

On the other hand, our results suggest that flow intermittence (i.e. indicated by ZF_T), the number of impacts and the environmental uniqueness were significant predictors of taxonomic and functional richness, but only flow intermittence was an important predictor of taxonomic LCBD. Indeed, the permanence of disconnected pools (i.e. indicated by DP_i) was the main predictor explaining the spatiotemporal patterns of IRs. However, there was no significant correlation with the number of impacts, despite some impacted IRs also showing higher LCBD values. This could be explained by the fact that resistance and resilience traits that can cope with flow intermittence in IRs (e.g. multi-voltinism, aerial respiration or mechanisms to tolerate low dissolved oxygen concentrations) may also be useful in coping with anthropogenic impacts (Bonada and Resh 2013; Stubbington et al. 2017; Soria et al. 2020), a phenomenon known as co-tolerance (Boulton et al. 2000). In fact, Mediterranean IRs hold unique species composition adapted to natural flow intermittence, such as a dominance of pool-dwelling species during the disconnected pool phase (Bonada et al. 2006, 2020; Cid et al. 2017), which could give them the ability to resist and to recover from drying periods and, at the same time, from anthropogenic impacts. However, persistent and intensifying anthropogenic impacts over time could reduce the ability of these species to cope with flow intermittence (Datry et al. 2017).

Considering that IRs have been commonly ignored in conservation planning (Bogan and Lytle 2007; Leigh et al. 2019), it is timely to provide complementary measures

to adequately assess their biodiversity. In this sense, the LCBD approach shows a high potential to be used for conservation purposes, as the ecological uniqueness of a site can be compared with other sites sampled in a region (Legendre and De Cáceres 2013; da Silva et al. 2018; Valente-Neto et al. 2020). In highly dynamic systems such as IRs, not only spatial but temporal patterns should also be considered to better identify key sites (Ruhí et al. 2017; Rogosch and Olden 2019; Stubbington et al. 2019; Sánchez-Montoya et al. 2020). However, analysing only spatiotemporal species richness and community composition might not be sufficient to design conservation plans aimed at protecting the processes that maintain their ecosystem functioning (Leigh et al. 2016, 2019; Villéger et al. 2017; Crabot et al. 2020). Therefore, given the hydrological variability of IRs and the increasing anthropogenic impacts they receive, freshwater conservation planning should consider monitoring the temporal variability of both taxonomic and functional biodiversity in these ecosystems. This might be even more relevant in Mediterranean climate regions worldwide where IRs constitute one of their predominant freshwater ecosystems (Bonada and Resh 2013; Cid et al. 2017). Special attention should also be given to the disconnected pool phase, as this is key to maintaining local and regional aquatic biodiversity (Gallart et al. 2017; Bonada et al. 2020). In this regard, several management-related tools have recently been developed to better predict the flow patterns of IRs, such as wet-dry mapping, remote sensing (e.g. satellite images, fixed cameras), field sensors (e.g. conductivity, temperature, water level and/or presence/absence of water), hydrological metrics (e.g. zero-flow days) or models (e.g. IHACRES [Identification of unit Hydrographs And Component flows from Rainfall, Evaporation and Streamflow data] or SWAT [Soil & Water Assessment Tool]) (Datry et al. 2017). Indeed, as the distribution of disconnected pools in IR networks can vary spatially and temporally from one year to another, tools have been developed even to account for their temporal and spatial occurrence (e.g. TRESH software; Gallart et al. 2017), as well as to assess their priority as biodiversity refuges and incorporate them into conservation planning (Hermoso et al. 2013; Yu et al. 2022). Citizen science can also result in a powerful tool to fully understand the hydrological characteristics of these ecosystems (e.g. RiuNet app, DRYRivERS app). The integration of these tools in the conservation management of IRs, together with the use of community metrics able to capture their spatiotemporal biodiversity patterns, are key to improving freshwater conservation in the Mediterranean climate region.

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Author contributions MS, JO, NC, LMB and NB conceived the ideas and designed the methodology; NC, PR-L, PF and DV collected the data; RA identified the macroinvertebrate data; MS, JO and LMB analysed the data; MS, JO, LMB, NB and NC led the writing of the manuscript; and CG-C, RA, PR-L, PF, DV, FG and NP contributed to the drafts. All authors gave final approval for submission.

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Data availability Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n2z34tms5 (Soria et al. 2019).

Declarations

Competing interests The authors declare no competing interests.

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