



The effects of longitudinal fragmentation on riverine beta diversity are modulated by fragmentation intensity

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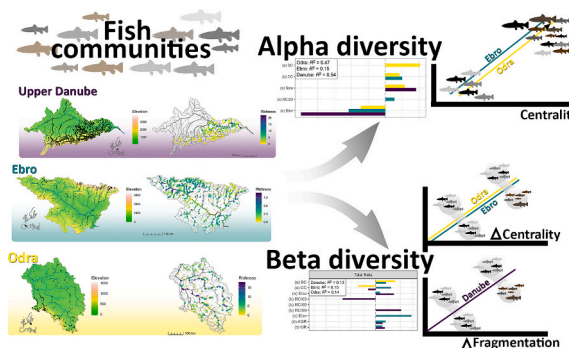
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HIGHLIGHTS

- Fragmentation due to barriers affects metacommunity dynamics.
- Reach-scale indices for fragmentation used with network centrality and environmental covariates
- Fish alpha and beta diversity predicted by network centrality and fragmentation
- Fragmentation importance higher in highly fragmented catchment
- Fragmentation indices useful for modeling fish metacommunity

GRAPHICAL ABSTRACT



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ABSTRACT

The loss of longitudinal connectivity affects river systems globally, being one of the leading causes of the freshwater biodiversity crisis. Barriers alter the dispersal of aquatic organisms and limit the exchange of species between local communities, disrupting metacommunity dynamics. However, the interplay between connectivity losses due to dams and other drivers of metacommunity structure, such as the configuration of the river network, needs to be explored. In this paper, we analyzed the response of fish communities to the network position and the fragmentation induced by dams while controlling for human pressures and environmental gradients. We studied

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beta diversity
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three large European catchments covering a fragmentation gradient: Upper Danube (Austrian section), Ebro (Spain), and Odra/Oder (Poland). We quantified fragmentation through reach-scaled connectivity indices that account for the position of barriers along the dendritic network and the dispersal capacity of the organisms. We used generalized linear models to explain species richness and Local Contributions to Beta Diversity (LCBD) and multilinear regressions on the distance matrix to describe Beta Diversity and its Replacement and Richness Difference components. Results show that species richness was not affected by fragmentation. Network centrality metrics were relevant drivers of beta diversity for catchments with lower fragmentation (Ebro, Odra), and fragmentation indices were strong beta diversity predictors for the catchment with higher fragmentation (Danube). We conclude that in highly fragmented catchments, the effects of network centrality/isolation on biodiversity could be masked by the effects of dam fragmentation. In such catchments, metapopulation and metacommunity dynamics can be strongly altered by barriers, and the restoration of longitudinal connectivity (i. e. the natural centrality/isolation gradient) is urgent to prevent local extinctions.

1. Introduction

River systems and the biodiversity they host are threatened by a multiple array of pressures (Albert et al., 2021; Harrison et al., 2018; Reid et al., 2019), with the proliferation of dams worldwide being one of the most important (Almond et al., 2020; Couto and Olden, 2018; Grill et al., 2019). Reductions in longitudinal connectivity are especially relevant as even local disconnections can lead to large-scale impacts due to the dendritic arrangement of river systems (Altermatt, 2013; Fagan, 2002; Larsen et al., 2021). Fragmented rivers display strongly isolated sections where the movement of water, sediments, energy, and organisms is impeded, resulting in declines of migratory species, increased local extinction risks, and genetic drifting of isolated populations (Jumani et al., 2020; Lange et al., 2018). Thus, understanding the impacts of longitudinal fragmentation on biodiversity patterns at the catchment scale is critical for designing effective monitoring and conservation strategies (Cid et al., 2022).

The connectivity among habitats determines the exchange of species between local habitat patches, driving metacommunity dynamics (Gianuca et al., 2017; Leibold and Chase, 2017; Tonkin et al., 2018a). Different movement types, including dispersal and migration, are relevant for metacommunity dynamics (Gounand et al., 2018) and are often linked (Tamarío et al., 2019). Communities in more isolated habitats will tend to receive less dispersal propagules, and will be mainly modulated by local environmental characteristics (i.e. species sorting). On the contrary, communities located in more central reaches are not limited by dispersal and present a weaker association with the local environment (i.e. mass effects; Borthagaray et al., 2015; Thompson et al., 2020). Accordingly, communities located in central habitats should have higher species richness (alpha diversity) and be more similar between each other (lower beta diversity) than communities located in more isolated habitats (network position hypothesis, Economo and Keitt, 2010; Gianuca et al., 2017; Henriques-Silva et al., 2019).

Longitudinal barriers such as dams can greatly affect river connectivity in river catchments (Edge et al., 2017), where the dendritic structure of the network defines the centrality-isolation gradient (Altermatt, 2013). However, it is still unclear how barriers might disrupt the exchange of individuals at the metacommunity level and the balance between assembly drivers (i.e., species sorting and mass effects). On one side, barriers increase site fragmentation, reducing organisms exchange rates and altering the relative position of habitats along the centrality/isolation gradient (Barbarossa et al., 2020). Ultimately, sites that are hardly reachable due to multiple sequential barriers will become spatially isolated and undergo local stochastic extinctions (Brauer and Beheregaray, 2020; Carvajal-Quintero et al., 2017). On the other side, barriers also alter the hydrological dynamics (Chalise et al., 2021; Palmer and Ruhí, 2019) and the habitat structure (Poff and Schmidt, 2016; Tonkin et al., 2018b), potentially promoting species sorting (Loures and Pompeu, 2019; Valente-Neto et al., 2020). All these changes are also determined by the spatial distribution of barriers along the catchment as well as by their number and characteristics (e.g. size, passability), which might modulate the intensity of their impact on

metacommunity dynamics (Perkin and Gido, 2012; Poff and Hart, 2002). Most studies on the effects of connectivity loss caused by dams on aquatic organisms (Perkin and Gido, 2012; Mahlum et al., 2014; Wang et al., 2021; Díaz et al., 2021) focus on small, highly fragmented catchments without considering the additional effect of the centrality/isolation gradient. Furthermore, in large catchments, dispersal could be a limiting factor, but it is not represented in commonly used indices such as the Dendritic Connectivity Index (Mahlum et al., 2014). Indices that describe the effects of fragmentation and dispersal limitation simultaneously have been recently developed (Rodeles et al., 2021), compared with other fragmentation indices (Jumani et al., 2020), and included in software packages (Baldan et al., 2022b), but never used to explain biodiversity patterns at the catchment scale. The simultaneous assessment of the effects of habitat centrality/isolation and connectivity loss (weighted by both the spatial arrangement of the barriers and the dispersal ability) could therefore advance our current understanding of how physical barriers are impacting metacommunity dynamics (Patrick et al., 2021).

The objective of this paper was to test the usefulness of landscape connectivity indices to explain fish communities and meta-community structure. We analyzed three large European catchments (Ebro, Odra, and Upper Danube) and tested predictors accounting for a) network position, b) connectivity loss due to dams, c) bioclimatic constraints, and d) human alterations. The catchments cover a fragmentation gradient, with the Upper Danube being much more fragmented than Odra and Ebro. We tested the following hypotheses. (i) We expected sites with high centrality (predictors a) and low fragmentation (predictors b) to have higher species richness due to mass effect (Economo and Keitt, 2010). (ii) We expected both centrality and fragmentation to be drivers of beta diversity (Gianuca et al., 2017). Accordingly, we also expected isolation and fragmentation dissimilarities to drive species replacement and richness difference. (iii) We expected the relative importance of the predictors (a - b) to differ depending on the extent of fragmentation. We expected fragmentation indices to have a higher importance in catchments with greater number of dams than in less impacted catchments, where network position should have a greater influence on fish biodiversity. (iv) We expected the same pattern for Local Contributions to Beta Diversity (LCBDs). Since LCBDs represent sites with higher uniqueness in species assemblages, in catchments with a lower extent of fragmentation, isolated sites should have higher LCBDs than well connected sites because they host more unique communities due to species sorting and higher likelihood of stochastic extinctions.

2. Methods

2.1. Ebro, Odra, and Upper Danube catchments

We performed our study in three large European catchments: Ebro (85,600 km², NE Iberian Peninsula), Odra (119,000 km², Western Poland), and the Upper Danube upstream of Vienna (101,800 km², Central Europe). The average annual temperature is 11 °C, 8.1 °C, and 6.6 °C for Ebro, Odra, and Upper Danube, respectively; the average

annual precipitation is 659 mm, 582 mm, and 969 mm, respectively; the average elevation is 778 m, 165 m, and 791 m, respectively; and the average discharge at the outlet is $430 \text{ m}^3 \text{ s}^{-1}$, $590 \text{ m}^3 \text{ s}^{-1}$, and $1960 \text{ m}^3 \text{ s}^{-1}$ (Linke et al., 2019). The catchments belong to three different freshwater ecoregions: Eastern Iberia, Central and Western Europe and Upper Danube, respectively (Abell et al., 2008).

2.2. River network and barriers data

We conceptualized the riverscape as a network (graph) where river reaches are nodes, and confluences or barriers are links (Erős et al., 2012). We used the hydrographic data from the 'European Catchments and Rivers Network Systems' dataset (ECRINS; EEA, 2012). To keep the size of the network low, we removed segments classified as first order reaches. For the barriers, we used the European-scale dataset generated in the project 'Adaptive Management of Barriers in European Rivers' (AMBER; Belletti et al., 2020). Objects classified as 'dams' were retained and assigned to the closest reach segment. Dams whose distance from the river network was higher than 1 km (i.e. where incongruences between ECRINS and AMBER exist) were not included in the analysis. We thus retained 6796 dams ($0.28 \text{ dams km}^{-1}$) for the Danube, 320 dams ($0.017 \text{ dams km}^{-1}$) for the Ebro, and 268 dams ($0.014 \text{ dams km}^{-1}$) for the Odra.

Following the tutorial described in Baldan et al. (2022b), we used the hydrographic and barriers data to generate a graph representing the river network including barriers with the 'igraph' package (Csardi and Nepusz, 2006) in R v4.1.2 computing environment. The resulting networks have 4393 nodes for the Ebro, 9283 nodes for the Danube, and 2658 nodes for the Odra. As detailed information on each dam's passability (the likelihood a fish can pass across the dam) was not available, we used a uniform value of 0.5 for each dam (see Section 2.3). To assess the sensitivity of this choice, we recalculated connectivity indices with different passability values (ranging from 0.2 to 0.7) and checked that the connectivity rankings of the different reaches did not change dramatically (Fig. S1).

2.3. Connectivity indices

We adopted the definition of connectivity as the probability of a successful movement between two reaches located in different positions along the river network (Pascual-Hortal and Saura, 2006). For a given reach i (network node), we calculated the Reach Connectivity Index (RCI_{*i*}) as the sum of the probabilities of connectivity (I_{ij}) between a given reach and any other reach j in the network:

$$RCI_i = \sum_{j=1}^n I_{ij} = \sum_{j=1}^n c_{ij} B_{ij} \quad (1)$$

where n is the total number of reaches in the network. The probability of connectivity is decomposed into a term that accounts only for the spatial arrangement of barriers in the catchment (c_{ij}), and a term that accounts for the ability of fish to move across the distance between the reaches (B_{ij}).

We express the term that accounts for barriers as the product of barriers passability along the path that connects reaches i and j across the network:

$$c_{ij} = \prod_{m=1}^k p_m \quad (2)$$

where m denotes a barrier that is located on the path between reach i and j (total: k barriers are located along the path), p_m is the passability of barrier m . We express the term that accounts for dispersal with an exponential function:

$$B_{ij} = PD^{d_{ij}} \quad (3)$$

where PD is a parameter that ranges between 0 and 1 and describes the movement/dispersal capacity of a class of organisms (Rodeles et al., 2021) and d_{ij} is the network-distance between reaches i and j (see Section 2.4).

The RCI values range from zero to one, and should be interpreted as a dispersal probability. Lower RCI values represent reaches that are less connected to the catchment, and higher RCI values for sites more connected to the catchment (Baldan et al., 2022b).

2.4. Fish data and predictors

We collected fish data from national surveys (Fig. 1). Multiannual data for the Odra were obtained from the Chief Inspectorate of Environmental Protection (GIOŚ, see Baldan et al., 2022a for details). To avoid bias resulting from temporal replicated measurements, we retained sampling events occurred in 2019, the year with the largest spatial coverage (174 points). Data for the Ebro were collected by several EU-level projects and were obtained from the Geoportal of the Ebro Hydrographic Confederation (CHEBRO, see Filipe et al., 2013 for an example of application). The sampling was conducted in 2007 and has a spatial coverage of 596 points. Multiannual data for the Austrian part of the Upper Danube were acquired from Austrian Federal Ministry of Agriculture. We merged data from 2011 and 2012 (total: 294 points), which have no spatial overlap. The sampled sites cover all the centrality, elevation, and fragmentation gradients existing in the three catchments, even in the Danube, where data cover only part of the analyzed geographic extent (Fig. S2). We removed non-native species from all three databases to consider only the impact of fragmentation on native species. To check for differences in dispersal traits between the three catchments, we retrieved movement traits for each species from the freshwaterecology.info database for Danube and Odra (Schmidt-Kloiber and Hering, 2015) and from Cano-Barbacid et al. (2020) for Ebro.

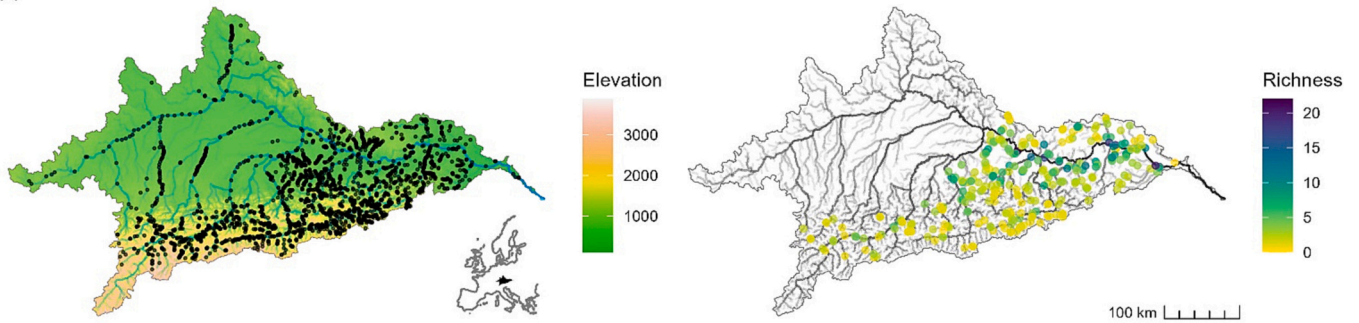
We built four classes of predictors, accounting for: a) centrality in the river network, b) fragmentation due to dams, c) bioclimatic constraints, and d) human alterations. (Table 1).

To derive network centrality predictors (a), we first built river networks like those described in Section 2.2 but without barriers. Then, we calculated the Betweenness Centrality (BC) and the Out Closeness Centrality (CC) for each reach in the network. We used those indices to describe the natural centrality/isolation patterns stemming from the dendritic structure of the network (Borthagaray et al., 2020). BC has higher values in the middle sections of the main channel, and CC has higher values at the outlet. We also included a stream size parameter measured in the field during the biotic sampling: the flow depth in the Odra, the discharge for the Ebro, and the wetted width for the Upper Danube. Such parameters are interrelated and scale proportionally with the network position (Leopold and Maddock, 1953).

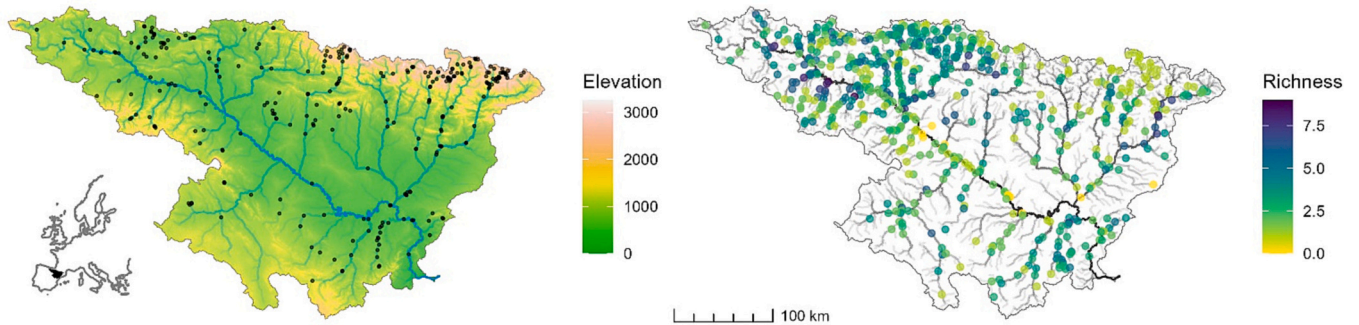
We used the 'riverconn' package (Baldan et al., 2022b) to calculate connectivity indices (b). For each reach, we calculated the RCI with different PD values corresponding to different classes of fish. Following the analysis carried out in the Iberian Peninsula by Rodeles et al. (2021), we used three different probabilities of dispersal to generate three indices (RCI03, RCI06, and RCI09). We used PD = 0.3 for fish with low swimming and leaping capacity (e.g. small benthic species like bullhead *Cottus gobio* L. and stone loach *Barbatula barbatula* L.; Tudorache et al., 2008). We used PD = 0.6 for fish with medium swimming and leaping capacity (e.g. medium distance migratory species like *Barbus barbus* or *Chondrostoma nasus*, Panchan et al., 2022). We used PD = 0.9 for fish with high swimming and leaping capacity, representing species that migrate medium to long distances during the reproductive season (e.g. salmonids). We also calculated the RCI for PD = 1, which mirrors the widely used Dendritic Connectivity Index (Jumani et al., 2020). Both DCI and RCI range from zero to one, with zero corresponding to sites with higher fragmentation, and one to sites with lower fragmentation.

We used the site elevation as a predictor accounting for bioclimatic

Upper Danube



Ebro



Odra

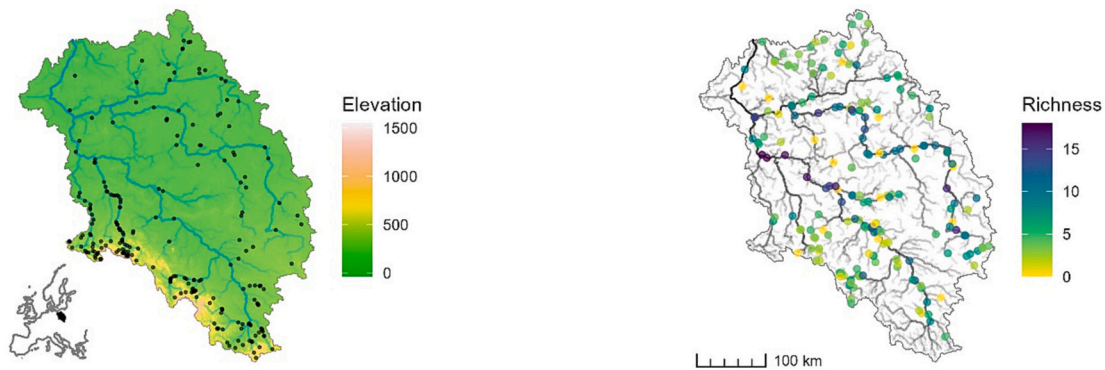


Fig. 1. Maps of the studied catchments. The left column shows the spatial distribution of the dams considered in this study. The right column shows the position of the fish sampling points used. Only streams with stream order greater than two are displayed.

Table 1

Modal (minimum - maximum) values of the predictors in the three catchments. Note that the flow depth (Odra) was measured during low flow. Letters refer to predictors' classes: a) centrality in the river network, b) fragmentation due to dams, c) bioclimatic constraints, and d) human alterations.

Name	Class	Description	Danube	Ebro	Odra
BC	a	Site Betweenness Centrality (log-transformed)	3.9 (0–12.1)	7.2 (0–11.6)	5.6 (0–10.5)
CC	a	Site Closeness Centrality (values are in 10^{-3} units)	10.4 (6.2–14.9)	13.3 (8.1–18.4)	15.41 (9.3–22.9)
Size	a	Discharge (Ebro, m^3s^{-1}), river width (Upper Danube, m), flow depth (Odra, m)	9.4 (0.5–300)	0.69 (0–235.55)	0.6 (0.4–2.95)
RCI03	b	RCI index for PD = 0.3 (values are in 10^{-3} units)	1.3 (0.2–6.2)	1.4 (0.2–6.5)	1.3 (0.4–5.2)
RCI06	b	RCI index for PD = 0.6 (values are in 10^{-3} units)	4.9 (0.45–21.1)	4.87 (0.64–20.29)	4.19 (0.67–13.04)
RCI09	b	RCI index for PD = 0.9 (values are in 10^{-3} units)	74.8 (14.5–126.4)	60.3 (18.4–101.2)	47.8 (11.7–111.8)
Elevation	c	Site elevation (m)	518 (150–1271)	542 (11–1881)	110 (–0.8–488.1)
UR	d	Fraction of urban land use in a 1 km circular buffer	0.08 (0–0.7)	0 (0–0.9)	0.08 (0–0.9)
FR	d	Fraction of forest land use in a 1 km circular buffer	0.4 (0–1)	0.53 (0–1)	0.16 (0–1)
AGR	d	Fraction of agricultural land use in a 1 km circular buffer	0.44 (0–1)	0.4 (0–1)	0.64 (0–1)

conditions (c), as it correlates with temperature and resources availability (Kirk et al., 2022; Vannote et al., 1980). As indicators for human alteration (d), we calculated the percentage of agricultural, urban, and forested land use (CORINE land cover data) in a 1 km circular buffer from the sampling point (Mwajengo et al., 2020). Due to differences in sampling methodologies, it was not possible to include indicators for

hydromorphological modifications. Some reaches in the Ebro catchment might experience flow intermittency. However, the fish monitoring was focused on permanent streams, and only few sampling points (< 20 over a total of 596) are located in streams with high likelihood of drying periodically according to the global flow intermittency model built by Messenger et al. (2021). No intermittent streams were sampled in the

Odra and in the upper Danube.

We did not include predictors accounting for the presence of non-native species because their distribution might depend on human activities such as intentional release for recreational fishing. A preliminary analysis showed that the log-abundance of non-native species was positively (but weakly) correlated with the species richness (negative binomial generalized linear model, $R^2 = 0.16$ in the Ebro, $R^2 = 0.16$ in the Danube).

2.5. Data analysis

We used presence-absence data to calculate the biodiversity metrics. We calculated alpha diversity as the number of species recorded for each sampling point. We used Sørensen-based indices of the Podani family to calculate the distance matrix representing beta diversity (Legendre and De Cáceres, 2013) and its decomposition into the replacement and richness difference components (Legendre, 2014). The replacement matrix describes differences between sites due to the replacement of species by others because of environmental changes. The richness difference matrix describes differences between sites due to a change in the number of species. We then calculated the Local Contribution to Beta Diversity (LCBD) for the three beta diversity matrices (package 'adespatial'), obtaining for each site an LCBD score for its contribution to beta diversity, an LCBD score for its contribution to richness difference, and an LCBD score for its contribution to species replacement.

We used uncorrelated predictors (spearman correlation <0.7 , Fig. S3, S4, S5 in the supplementary material) to fit the model. We verified the used predictors do not have collinearity issues by checking the Variance Inflation Factors with the `vifstep` function from the package 'usdm'. We log-transformed the predictors to remove excessive skewness in their distribution, except for the land use fractions, which were logit-transformed. All predictors were scaled (zero mean and unit variance) to allow for a comparison of the relative effects. We used a generalized linear model with a negative Poisson link function (nbGLM, 'MASS' package) to explain alpha diversity, distributed as count data when the species richness is low. We used a generalized linear model with a logit link function (betaGLM, 'betareg' package) to explain LCBDs, whose values are constrained between 0 and 1. For both model types, we used a forward stepwise selection procedure based on AIC to select parsimonious predictor sets.

We used Multilinear Regression on the Distance Matrix (MRM, 'ecodist' package) to explain beta diversity patterns (Lichstein, 2007). Compared to univariate Mantel test, MRM uses multiple distance matrices as explanatory variables (Goslee and Urban, 2007), thus allowing for comparing their relative importance. To select a parsimonious subset of predictors, we first calculated pairwise Mantel tests for each couple of predictors and excluded the correlated predictors; then we fitted iteratively the MRM model and removed manually non-significant predictors (Noguerales et al., 2016). Significance was assessed via permutations of the beta distance matrix (1000 permutations). Finally, we checked if the slopes predicted in the retained MRM model were concordant with those from univariate Mantel tests, and we interpreted the lack of change as a sign that the retained MRM predictors were relatively uncorrelated. For the interpretation of the results, we examined the retained predictors with a positive slope, i.e. predictors whose dissimilarity is correlated with increased beta diversity (a negative slope would relate predictor's dissimilarities to more homogeneous communities).

To avoid biases arising from differences in the sampling methods, all analyses were repeated separately for each catchment and predictors' importance was compared only within the same catchment. Since the Ebro data are available only as presence/absence, we did not rarefy the data used to fit the models to keep the analyses consistent between the three catchments. However, we repeated the analysis with rarefied data (R package 'BAT') in Danube and Odra (where count data are available) and verified that the models' results do not differ compared to the same

models fitted to the original count data (Fig. S6, S7, S8).

3. Results

The total native species richness was 43 in the Danube, 13 in the Ebro, and 39 in the Odra (Table S1). The mean species richness per site was 4 in the Danube, 3 in the Ebro, and 7 in the Odra. The maximum species richness per site was 22 in the Danube, 9 in the Ebro, and 18 in the Odra. The Danube fish community was composed of 8 non migratory, 21 potamodromous, and 1 diadromous fish. The Ebro fish community was composed of 4 potamodromous, 7 non-migratory, and 1 diadromous fish. The Odra fish community was composed of 23 potamodromous, 6 non migratory, and 3 diadromous fish.

The fragmentation indices have a catchment-dependent degree of correlation, with higher correlation (spearman's correlation between all RCI indices >0.95) in the Danube, and lower correlation in the Ebro and in the Odra (correlation <0.25 between RCI03 and RCI09; Fig. S3, S4, S5). In all catchments, the correlation with centrality indices is low.

The results from the nbGLM models (Fig. 2) confirmed our hypothesis on alpha diversity (i): centrality predictors had a positive effect on species richness in the three catchments, and connectivity indices had a positive effect only in the Ebro. Additionally, elevation was a relevant driver of alpha diversity (negative slope) in all the three catchments.

The results of the MRM models (Fig. 3) supports our hypothesis of an effect of centrality and connectivity on beta diversity and its components (ii). Regarding the total beta diversity, all centrality predictors were significant in the Ebro, while Betweenness Centrality was significant in the Odra, and size in the Danube. Among connectivity indices, RCI09 was significant only in the Danube. Additionally, elevation was relevant in the Ebro. Regarding the replacement component, all centrality predictors were significant in the Ebro, no centrality index was significant in the Odra, and size was significant in the Danube. Among fragmentation indices, RCI09 was significant only in the Danube. Additionally, elevation was relevant in the Ebro and in the Odra. Regarding the richness difference component, no centrality predictor was significant in the Ebro, Size was significant in the Danube and in the Odra, and Betweenness centrality in the Odra. Among connectivity indices, RCI06 was significant only in the Danube. Additionally, elevation was relevant in all the three catchments.

Our hypothesis on the dependence of the relative importance of centrality and connectivity predictors from the extent of fragmentation (iii) was supported: in the Danube (higher fragmentation extent), fragmentation indices had higher slopes than centrality indices, while we found the opposite in Ebro and Odra (lower fragmentation).

The results of the betaGLM models (Fig. 4) partially supported our hypothesis of an effect of centrality and fragmentation on LCBDs mediated by the fragmentation intensity (iv). Regarding LCBDs calculated on the beta diversity matrix, a significant effect of centrality was observed in all the three catchments, and a small effect of fragmentation indices was observed only in the Ebro. Regarding the LCBDs calculated on the replacement matrix, an effect of centrality is detected in the Ebro and in the Danube, and an effect of fragmentation was detected in the Odra. Regarding the LCBDs calculated on the richness difference matrix, an effect of centrality (size) was detected in the Danube, and an effect of fragmentation in the Odra. The direction of the effect of fragmentation on species replacement LCBDs aligns with our hypothesis, with a negative effect in the Odra (RCI09) and Ebro (RCI06), and a positive effect (RCI09) in the Danube. Neither total beta diversity nor richness difference LCBDs align with our hypothesis.

Land use predictors were never among the top ranked predictors for alpha diversity, beta diversity, and LCBDs.

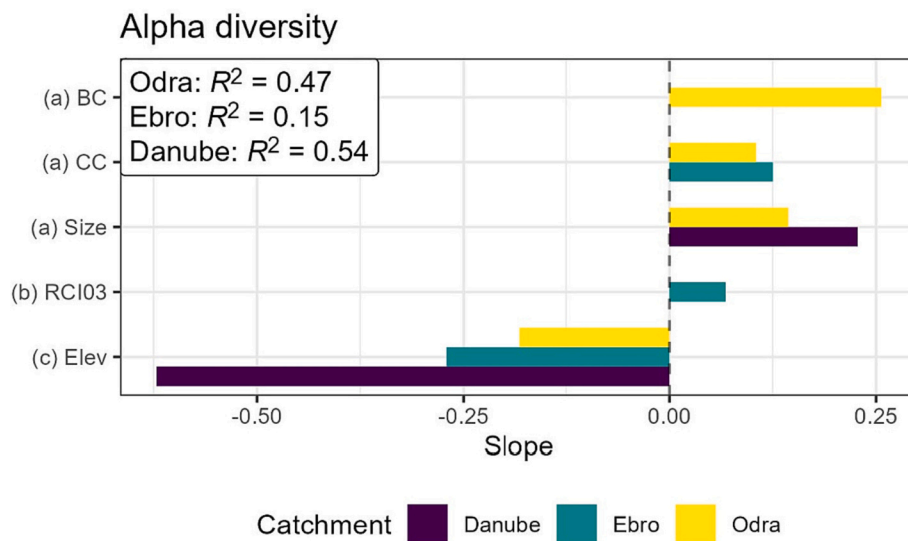


Fig. 2. Relative importance of predictors to explain alpha diversity, as measured by each predictor's slope in the Negative Poisson generalized linear models. See Table 1 for abbreviations. Predictors with higher slope have higher relevance. Only significant ($p < 0.05$) predictors are reported. Refer to table S2 for confidence intervals and significance levels. The insert on the top-left reports the explanatory power of the models (3 models in total) as measured by R^2 .

4. Discussion

4.1. Effects of connectivity losses in the analyzed catchments

Our results confirm that dam-induced fragmentation has catchment-specific effects on alpha, beta diversity, and LCBD. The diverse spatial arrangement (i.e. position in the river network) and density of dams could explain the different responses to fragmentation patterns (the different distributions of RCI in the three catchments are compared in Fig. S9). The Ebro catchment has a high density of dams in the north-eastern mountainous sections, but some tributaries with a low number of dams still exist (Rodeles et al., 2021). Since part of the original centrality/isolation gradient is preserved, predictors describing the position along the network (betweenness centrality and out closeness centrality) are among the most important for both alpha and beta diversity. Sites that are more central in the network have higher alpha diversity, and centrality dissimilarities drive community dissimilarities, with species being replaced along the centrality/isolation gradient. The Odra has a high density of dams in the southern high-elevation sections, and a small number of dams in the lowland sections. In this catchment, centrality indices also play a key role in structuring biodiversity, with more central sites having higher species richness, and centrality dissimilarities driving communities' dissimilarities. These results are in agreement with the network position hypothesis, where central reaches are more likely to align to mass effects archetypes due to a higher propagule/dispersal pressure (Henriques-Silva et al., 2019).

The Upper Danube is impacted by a large number of barriers that are distributed uniformly along the network, with few free-flowing reaches left in the lowland mid-section (Hein et al., 2019). Beta diversity in the Upper Danube is driven by the fragmentation gradient generated by the presence of barriers rather than by centrality/isolation position in the river network. This result is in agreement with studies comparing catchments with different fragmentation extents showing that inter-catchment beta diversity is driven by the length of the longest fragment (Díaz et al., 2021), or by the extent of fragmentation (Perkin and Gido, 2012).

The Local Contribution to Beta Diversity is related to the site uniqueness in terms of beta diversity (Valente-Neto et al., 2020). Our hypothesis regarding the replacement component of LCBDs is partially supported by our results. In Ebro and Odra, sites with higher fragmentation also have higher replacement LCBD scores. This is probably due to

stochastic processes that cause communities in fragmented sites to drift from those located in the remaining section of the network (Erós, 2017). One of the mechanisms causing this drift could be the disappearance of long-range dispersers and their replacement by less mobile fish species (Zhang et al., 2019). In the Odra catchment, richness difference also plays a role: here, fragmented sites have different communities probably because of barriers that filter out some species. The lack of response of the richness difference to fragmentation in the Ebro catchment could be related to the low regional native species pool ($n = 13$), the high presence of invasive species ($n = 15$) and the wide range of distribution of some fish (Cañedo-Argüelles et al., 2019), which limits the potential difference in the number of species between local communities. On the contrary, in the Upper Danube, we observed a positive correlation of replacement LCBDs with betweenness centrality, which is associated with mainstream reaches in dendritic networks. This relation could indicate a stronger community differentiation between mainstream and midstream reaches caused by intensive fragmentation that isolates mainstream reaches leading to more unique communities (Díaz et al., 2021; Pool and Olden, 2012).

The poor explanatory power of land use predictors could be related to regional land use information failing to capture fine scale drivers of fish assemblages such as riparian habitat quality, sediment deposition or nutrient enrichment (Guse et al., 2015; Meador and Goldstein, 2003; Nerbonne and Vondracek, 2001). However, previous studies have shown that land use can have a strong effect on fish communities (Diana et al., 2006; Mantyka-Pringle et al., 2014; Utz et al., 2010). Thereby our results should be interpreted within the context of being compared with other explicative variable that might play a global main role against alpha, beta and LCBD patterns. In this sense, their small relevance should be properly framed in the context of the current study and taken with caution.

Overall, our results demonstrate that the effect of fragmentation on metacommunity dynamics strongly depends on the degree of fragmentation and the spatial arrangement of the barriers. This aligns with recent studies on drying river networks, which showed how the position of the dry river reaches (acting as a barrier to dispersal) had a strong influence on beta diversity patterns (Jacquet et al., 2022; Pineda-Morante et al., 2022). Further research is needed to explore the combined effects of other drivers of fragmentation, such as weirs, culverts, and road crossings, that might have high relevance, especially in smaller streams (Sun et al., 2023). To this end, accurate assessments of barriers

Beta diversity

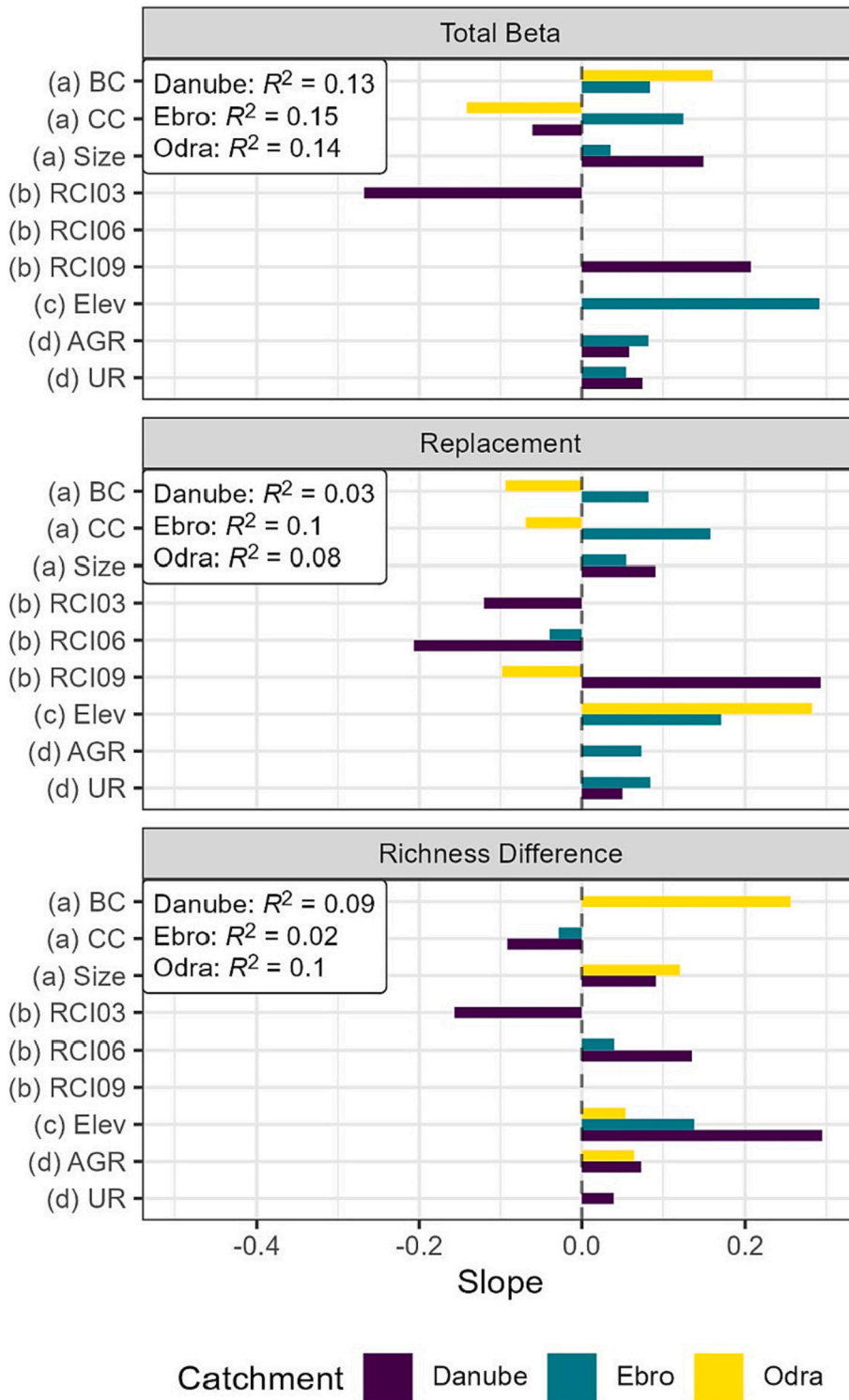


Fig. 3. Relative importance of predictors to explain beta diversity and its replacement and richness difference components, as measured by each predictor's slope in the multilinear regression on the distance matrix models. See Table 1 for abbreviations. Predictors with higher slope have higher relevance. Only significant ($p < 0.05$) predictors are reported. Refer to table S3 for significance levels. The inserts on the top-left reports the explanatory power of the models (9 models in total) as measured by R^2 .

passabilities are needed to parametrize better the connectivity indices used in this paper since this can determine more precisely fish distribution (Januchowski-Hartley et al., 2014; Kemp and O'hanley, 2010). Finally, recently developed global datasets such as HydroATLAS (Linke et al., 2019) and Hydrography90m (Amatulli et al., 2022) have the potential for providing additional high resolution environmental predictors.

4.2. Metacommunity aspects

Traditionally, metacommunity ecology has focused on disentangling the effects of environmental and spatial drivers, respectively linked with species sorting and mass effect archetypes (Heino et al., 2015; Viana et al., 2022). Within this framework, the attribution of the explained variance to environmental and spatial processes can be biased by the

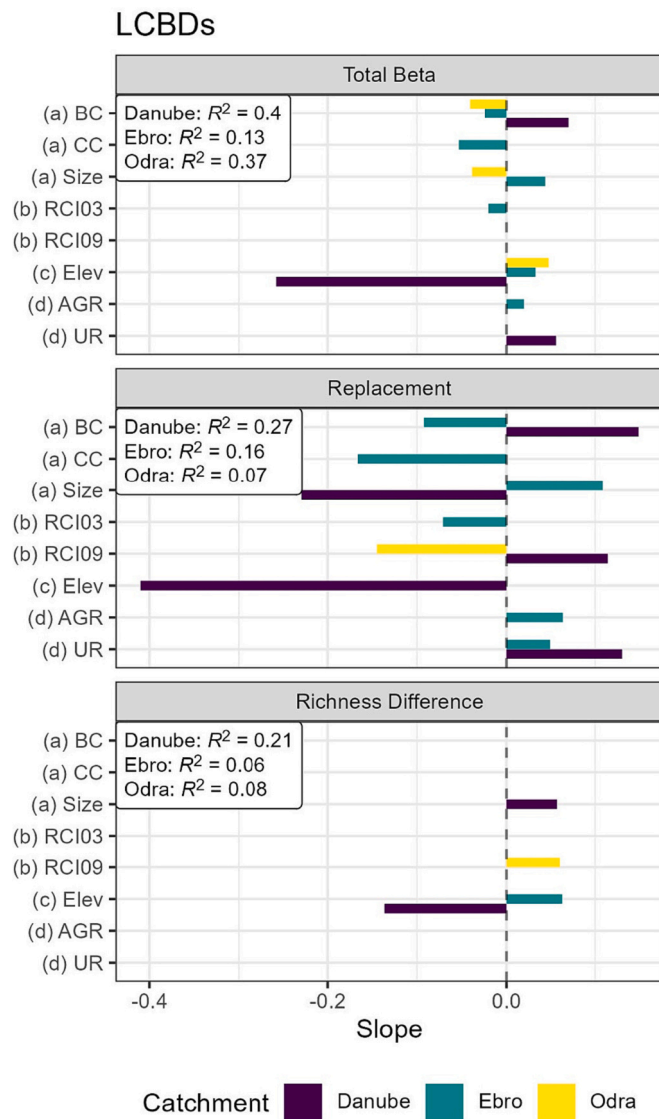


Fig. 4. Relative importance of predictors to explain the local contribution to beta diversity, as measured by each predictor's slope in the negative binomial generalized linear models. Predictors with higher slope have higher relevance. See Table 1 for abbreviations. Only significant ($p < 0.05$) predictors are reported. Refer to table S4 for confidence intervals and significance levels. The inserts on the top-left reports the explanatory power of the models (9 models in total) as measured by R^2 .

choice of spatial predictors. Classical spatial statistical methods in community ecology such as Moran's Eigenvalues Maps (MEMS) or the Principal Components of the Neighboring Matrix (PCNM) have limited capacity to accommodate network properties (Erős and Lowe, 2019). On the other hand, spatial predictors based on the network position can capture the structure of dendritic systems (Altermatt, 2013). Still, they are expected to be of little use in systems experiencing high connectivity losses (Tonkin et al., 2018a). These methods do not account for the position of barriers, which are highly relevant in dendritic networks (Altermatt, 2013). As discussed in the introduction, barriers impact the mechanisms that regulate metacommunities, e.g. by altering the balance between species sorting and mass effects because of reduced movement/dispersal of propagules between local communities. We show that the connectivity indices correlate well with biodiversity metrics in the studied catchments. These findings might be common across other fluvial networks and, therefore, connectivity indices have great potential as spatial predictors in metacommunity ecology.

Our results suggest that the spatial distribution of barriers (dams, weirs, culverts) can become more important than natural drivers to explain fish distribution patterns in highly fragmented systems. We show that in such systems, the centrality/isolation gradient can be replaced by a fragmentation gradient. Further research could focus on the factors governing the transition between those two spatial gradients. In this regard, modeling approaches showed that the spatial arrangement of barriers and its interaction with environmental factors are critical drivers of metacommunities (Lee et al., 2022). Biogeographic legacy effects, which can determine the regional species pool, are also supposed to play a role (Carvajal-Quintero et al., 2019). This fragmentation threshold will depend, among other things, on the interaction of connectivity losses with the distribution of dispersal traits in the metacommunity (e.g. relative share of migratory, rheophilic, eurytopic organisms). The replication of the approach used in this paper to catchments with different extents of fragmentation, other biogeographic constraints and different human pressures can support the detection of this critical tipping point.

As barriers construction proliferates worldwide (Zarfl et al., 2015) and free-flowing rivers disappear (Grill et al., 2019), it is becoming increasingly important not only to understand and minimize the effects of fragmentation on the biodiversity associated with river networks. In this regard, the passability of barriers can be improved with technical solutions such as the construction of a fishpass for upstream migration and less impactful turbines for downstream movement (Radinger et al., 2022). Removing obsolete barriers is also an increasingly considered option (Verhelst et al., 2021). These actions need to be carefully planned to maximize the connectivity gain under economic constraints (King et al., 2017; O'Hanley, 2011; Poff and Hart, 2002). The prioritization of barriers for removal or improvement is performed generally using connectivity indices such as those used in this paper (Baldan et al., 2022b). Consequently, barriers are prioritized based on the relative length of the reconnected river segments (Cote et al., 2009) or the potential reconnected habitat area (Rodeles et al., 2021). However, this prioritization does not account for the interactions with the natural centrality/isolation gradient. Based on our results, we suggest that conservation and restoration planning should directly account for the natural isolation/centrality gradient that arises from the dendritic network structure. For example, barrier removal prioritization is generally carried out based on the maximization of the connected length or the connected catchment area (Jumani et al., 2022; Jumani et al., 2020). We suggest weighting the connected length by the potential to act as a link between central and isolated sites could be an additional criterion. Our results are valid for communities composed of native species, and managers should bear in mind that connectivity improvements could also lead to the undesired expansion of non-native species. This is an additional criterion that needs to be accounted for when prioritizing barriers for removal (Cooper et al., 2021).

Finally, it is important to consider a fragmentation tipping point that should not be trespassed to preserve natural metacommunity dynamics. These considerations should be incorporated into conservation and restoration plans, e.g. by integrating fragmentation indices, such as the ones developed here, into systematic planning tools (Hermoso et al., 2018).

5. Conclusions

In this paper, we analyzed the effects of habitat fragmentation induced by barriers in three catchments. We found context dependent responses: in two catchments, beta diversity was best explained by elevation and by network position predictors, while in one catchment, the best predictors were related to fragmentation due to dams. Since the fragmentation-related drivers are almost as relevant as the environmental drivers, we suggest that the restoration of the natural centrality/isolation gradient driven by network position should be considered among the objectives in future plans for mitigating the impacts of

barriers.

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CRediT authorship contribution statement

DB, DCM, and AF conceived the study. DB analyzed the data with contributions from DCM and AF. DB led the writing of the manuscript with inputs from all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166703>.

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