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The importance of riverine islands: scaling and linking hydro-morphological and fish diversity in a very large river

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Riverine islands are keystone geomorphic features that enhance hydro-morphological heterogeneity in large rivers; how island-associated main and side channels contribute to the taxonomic and functional diversity of fish assemblages in regulated rivers, however, remains poorly understood. Therefore, we applied a hierarchical spatial framework to examine how hydro-morphological variation between main and side channels would structure fish assemblages along three islands in the Middle Danube (Hungary). Principal component analyses of physical habitat variables revealed that main channel habitats were characterized by higher velocities and coarser substrates, whereas side channels exhibited slower flow, finer sediments, and greater macrophyte and herbaceous cover. Overall, habitat-type effects in physical structure were stronger and more consistent than regional differences among islands. Shoreline electrofishing revealed pronounced differences in fish assemblages associated with hydro-morphological variation. Specifically, rarefaction analyses justified higher species richness in side channels and complementarity between habitat types, indicating that each harbored some unique species that contributed to gamma diversity. Multivariate analyses demonstrated clear separation in the taxonomic structure of fish assemblages between main and side channels. Functional analyses mirrored taxonomic patterns, showing distinct trait compositions along hydro-morphological gradients. Velocity and substrate composition emerged as the key environmental drivers that structure both taxonomic and functional structure, thus highlighting the importance of hydro-morphological heterogeneity. Our findings identify riverine islands and their side channels as biodiversity amplifiers that sustain lateral habitat complexity and increase hydro-morphological, taxonomic, and functional diversity in regulated large rivers. Protecting and restoring island–side-channel complexes should therefore be prioritized in process-based river restoration strategies, such as the EU Nature Restoration Regulation, to counteract habitat homogenization and enhance lateral connectivity and functional resilience.

KEYWORDS

Danube, fish assemblages, functional structure, lateral connectivity, nature restoration regulation, side-arms

Introduction

Riverine ecosystems are among the most dynamic and heterogeneous environments on Earth, where hydrology, geomorphology, and biotic interactions jointly shape biodiversity patterns (Boys and Thoms, 2006; Erős and Lowe, 2019). The physical template of a river, often referred to as “hydro-morphological diversity” or more generally “geodiversity”, plays a fundamental role in structuring aquatic communities by determining habitat availability, diversity, connectivity, and stability across spatial and temporal scales (Ward, 1989; Brierley and Fryirs, 2005; Kärnä et al., 2018). Hydro-morphological features such as riffles, pools, gravel bars, and islands create mosaics of hydraulic conditions and substrate types that provide critical habitats for fish and other aquatic organisms (Ward et al., 2002; Allan and Castillo, 2007).

Riverine islands and their associated side arms represent especially unique yet vulnerable features of large river systems. Islands act as keystone geomorphic structures that maintain the multi-thread character of river channels and sustain lateral habitat complexity (Thorp, 1992; Gurnell and Petts, 2002). Their geomorphological diversity fosters a wide range of hydrodynamic and substrate conditions that benefit both aquatic and riparian biota. However, the persistence of these geomorphic and ecological functions is increasingly threatened (Bunn and Arthington, 2002; Tockner and Stanford, 2002). River regulation and channelization, including the construction of groins, embankments, and navigation-enhancing structures, have altered sediment dynamics and flow regimes, accelerating island succession and promoting the siltation or disconnection of side arms (Hohensinner et al., 2004; 2021; Ricaurte et al., 2012; Raška et al., 2017). As a result, many islands become incorporated into the riverbank, leading to reduced channel width, loss of hydro-morphological complexity, and ultimately the homogenization of aquatic, side-channel habitats (Raška et al., 2017; Hohensinner et al., 2004; 2021; Ádám and Malatinszky, 2022). These processes pose major challenges for biodiversity conservation and sustainable river management, especially in the mainstem of intensively used large rivers such as the Danube (Habersack et al., 2016; Hein et al., 2019; Erős and Bányai, 2020).

For fish, side channels often serve as refuges, feeding grounds, and reproductive habitats, contributing significantly to the overall diversity of riverine assemblages (Aarts et al., 2004; Stoffers et al., 2022). Lateral habitats, in general, are particularly important for the early life stages of rheophilic species, providing low-velocity nursery areas with suitable substrate and food resources (Zeug and Winemiller, 2008; Stoffers et al., 2022; Ramsey et al., 2024). However, despite the ecological significance of lateral connectivity, the quantitative contribution of islands and their associated side arm habitats to the fish diversity of the main channel remains largely unexplored (Hintz et al., 2015). For example, it has been shown how the structure of fish assemblages changes along long ecological gradients of lateral connectivity from permanently isolated oxbows to the main channel (Aarts et al., 2004; Manfrin et al., 2020; Feng et al., 2024). It has been also examined how fish assemblages develop in individual side arms or flood plains after reconnection to the main channel (Pander et al., 2015; Marin et al., 2026). However, standardized comparisons of fish assemblages among island associated main- and side-channel habitats remain limited. In particular, it is still unclear how species richness and the

taxonomic and functional structure of fish assemblages vary among these habitat types and to what extent finer-scale hydro-morphological characteristics shape these patterns. A notable exception in this regard is Johnson and Jennings (1998), who examined associations between fish assemblages and habitat features surrounding alluvial islands in the upper Mississippi River; they found that mesohabitat characteristics, particularly vegetation abundance, were more important than island-scale macrohabitat features in determining fish density. Understanding how hydro-morphological diversity at different spatial scales underpins fish assemblage structure is critical for developing effective restoration and conservation strategies (Langhans et al., 2016; Wohl et al., 2024). Such insights are essential for the spatial prioritization of biodiversity and restoration measures in large river systems, where balancing navigation, flood protection, and ecological integrity is a key management challenge (Weigelhofer et al., 2020; Díaz-Redondo et al., 2018; Erős and Bányai, 2020).

Here, we apply a hierarchical spatial framework to quantify hydro-morphological and fish diversity in the littoral zone of the Danube River, Hungary, and to assess their associations. Such an approach is particularly suitable for riverine island systems, where reaches, islands, and side-channel habitats are clearly organized across multiple nested spatial scales (Ward et al., 2002; Pegg and Taylor, 2007). Specifically, we examine how hydro-morphological patterns vary within and between the main and side channels adjacent to Danubian islands, and how these physical attributes influence fish diversity and taxonomic and trait-based assemblage structure. Since species turnover may mask underlying functional patterns that cannot be directly resolved through taxonomic analyses alone, we were particularly interested in examining how traits reflect ecological strategies at both the species and assemblage levels, as well as how they respond to hydro-morphological conditions (see also Pease et al., 2012; Feng et al., 2024). By linking habitat heterogeneity to assemblage organization across spatial scales, we aim to advance our understanding of how physical complexity sustains biodiversity in the mainstem of large, regulated rivers and to provide a scientific basis for conservation-oriented river management.

Based on the keystone role of islands in shaping fluvial habitat diversity, we predict that hydro-morphological patterns will differ significantly between main and side channels, with the latter exhibiting greater habitat heterogeneity driven by more variable flow conditions and dynamic sedimentation processes (Amoros, 2001; Gurnell and Petts, 2002). We further hypothesize that this spatial variation in physical attributes will be reflected in fish assemblage structure and can be detected through our analyses of environmental variables, species composition, and functional traits (for floodplain systems, see Copp, 1989; Persat et al., 1994; Williams et al., 2024). Specifically, we expect systematic differences in flow velocity, substrate composition, and vegetation cover among habitat types, with side channels characterized by lower flow velocities, finer sediments, and higher macrophyte or riparian vegetation cover than main-channel habitats, which are expected to exhibit higher velocities, coarser substrates, and reduced vegetation. These environmental gradients are expected to drive corresponding shifts in species richness, assemblage composition, and the occurrence of indicator species, with slow-water specialists and habitat-generalist taxa being more prevalent in the side channels,

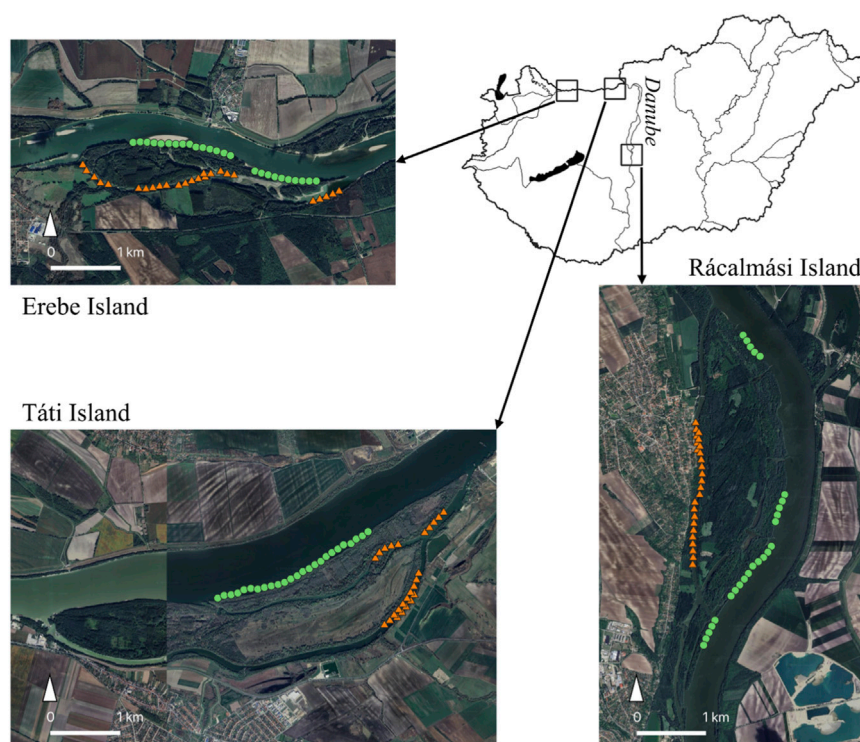


FIGURE 1
Map of the study area in the main channel of the Danube River, Hungary. The 100 m long sampling units in the main arm and side arms are indicated with filled green circles and filled orange triangles, respectively.

whereas rheophilic species associated with higher flow velocities and coarse substrates are expected to dominate main-channel habitats. In terms of trophic structure, we anticipate a higher dominance of omnivore species in side arms, reflecting more vegetated conditions, while insectivore species are expected to be more abundant in main-channel habitats. Regarding life-history strategies, we expect opportunistic species to be more prevalent in the main channel, whereas equilibrium strategists are predicted to be relatively more common in the more benign and slower flowing side arms. We also predicted a relatively even distribution of large-bodied periodic species, which are widespread in the Danube, while expecting differences in species-specific abundances between the main channel and the side arms. Overall, we expect trait-based structure (e.g., flow preference, trophic guild, and life-history strategy) to vary predictably along these physical habitat gradients, thereby identifying key environmental drivers of assemblage differentiation. Collectively, these patterns are expected to result in higher overall fish diversity and greater functional heterogeneity within and among island-associated reaches of the Danube.

Materials and methods

Study area

With a length of 2,847 km and a drainage area of 796,250 km², the Danube is the second largest river in

Europe. River regulation, including the construction of hydroelectric schemes in the Upper Danube (Germany and Austria) and extensive channelization, has profoundly altered its physical structure along much of its course. The Hungarian section, referred to as the “Middle Danube,” extends for 417 km and has a mean annual discharge of approximately 2,000 m³ s⁻¹. The main channel is 300–600 m wide, with a substrate dominated by gravel and sand, a mean water depth of approximately 4 m, and an average current velocity of 0.6 m s⁻¹. Although large portions of the riverbanks remain relatively natural, particularly outside the Budapest metropolitan area, the system has been substantially modified over the past century and a half through river regulation, including channelization, bank stabilization, and the construction of embankments and rip-rap shorelines that occur intermittently along reaches of approximately 100–1,000 m. In addition, historical navigation improvements and flood protection works have contributed to the simplification of channel morphology and the progressive siltation and disconnection of former side arms and floodplain habitats (Erős and Bányai, 2020; Ádám and Malatinszky, 2022; Erős et al., 2023). Despite this degree of regulation, the Middle Danube still retains a mosaic of semi-natural and altered habitats, making it a highly relevant study system for river conservation research aimed at understanding how hydro-morphological modification influences habitat heterogeneity and aquatic biodiversity responses.

Environmental data

Data on habitat characteristics and fish assemblages were collected along three islands between 5 and 26 September 2023 (Figure 1). The islands were chosen to represent the largest remaining relatively natural island systems along this river segment. Along the shore, five 500-m-long sections were selected in the inner (side arm) and outer (main channel) side of each island. Site selection depended on water level related habitat availability (i.e., only boatable sections were chosen with sufficient depth for fish surveys). Each section was subdivided into five 100-m-long sections delineated using a GPS unit to characterize habitat and fish assemblages, but they were subsequently pooled depending on the type of analyses in order to provide robust, easily interpretable and visualized data in multivariate analyses (for details, see below).

Habitat measurements were conducted during the daytime to quantify mean distance from the bank, water velocity, water depth, and large woody debris (LWD) as numeric variables, while substrate composition, macrophyte cover, and riparian vegetation were visually estimated as proportional (%) values for each 100 m stretch (Erős et al., 2008). Boat distance from the bank (m) was calculated as the mean of visual estimates made by three team members at 30 m intervals (i.e., at the upper, middle, and lower portions of each 100 m unit), with high consistency among observers (± 1 m). Mean water velocity (cm s^{-1}) was measured at 30 m intervals using an FP201 Global Flow Probe (Global Water Instrumentation, Inc.) at a depth corresponding to 60% of the water column within the electro-fished zone. Mean water depth (cm) was recorded with a meter stick at the same intervals. Substratum composition was visually estimated at each 30 m point and classified into the following categories: silt or clay (<0.25 mm), sand (0.25–2 mm), gravel (2–64 mm), and cobble or stone (>64 mm). Proportional composition of emergent and submerged macrophytes and the quantity of LWD (logs and branches, predominantly of willow sprouts of *Salix* spp.) was visually estimated for the entire 100 m unit along the ~ 1 m wide littoral strip where fish sampling occurred. Finally, the proportional composition of herbaceous and woody bank vegetation was visually estimated for the entire 100 m unit along a ~ 5 m wide strip of the bank.

Fish collections

Fish assemblages were sampled by boat electrofishing using a Hans-Grassl GmbH EL64 II GI, DC, 7.5 kW device and one handheld anode (2.5 m long pole with a 40 cm diameter ring anode and 6 mm net mesh) while slowly moving downstream (Wolter and Bischoff, 2001; Wolter and Freyhof, 2004). At the end of each 100 m section, captured fish were identified, counted, measured for standard length (SL, cm), and stored until the whole 500 m long section was sampled. Fish were then released in the upper end of each section to minimize the risk of recapture (Erős et al., 2008). All age groups were included in the samples; however, this shoreline electrofishing method is most efficient for juvenile to intermediate size classes and less effective for very small individuals (<2 cm) and very large adults. Consequently, 0+ fish inhabiting extremely shallow areas (<30 cm), as well as larger, offshore-dwelling individuals, may be underrepresented. Although such

bias is typical for boat electrofishing (Simon, 1999; Goffaux et al., 2005), our results are explicitly based on samples collected with conventional boat-based electrofishing in riverine littoral zones (Erős et al., 2008).

Trait-based characterization

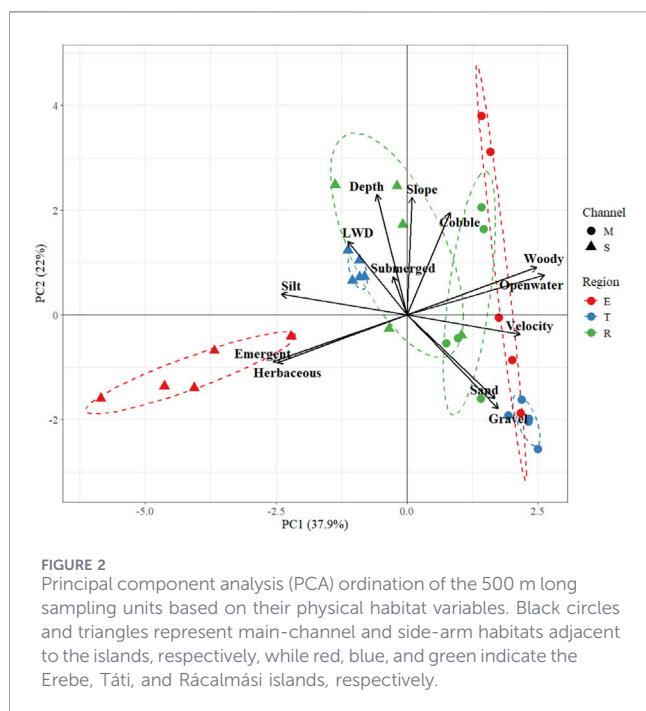
To characterize trait-based fish assemblage structure, each species was assigned to five ecological guilds based on published biological and ecological classifications for Central European freshwater fish and standardized trait databases (Froese and Pauly, 2023; Erős, 2005; Noble et al., 2007). In cases of inconsistencies, we assigned trait categories based on our expert knowledge of the Middle Danube region. The guilds included vertical position in the water column (VG: benthic, benthopelagic, or pelagic), flow preference (FG: rheophil, eurytop, or stagnophil), migration behavior (MG: non-migratory or potamodromous), trophic guild (TG: herbivore, omnivore, invertivore, piscivore, or planktivore), and life-history strategy (LG: equilibrium, opportunistic, or periodic). Detailed descriptions, abbreviations, ecological meanings, and references for all functional guilds are provided in Supplementary Table S1, while species-specific trait assignments are presented in Supplementary Table S2. The latter reflect species-level variation in habitat use, feeding strategies, reproductive traits, and ecological specialization to ensure consistent characterization across sites and comparability between ecological or biogeographic regions (Hoeinghaus et al., 2007; Feng et al., 2024).

Statistical analysis

We used both sample-unit and individual-based rarefaction analyses to compare the diversity of fish assemblages (Gotelli and Colwell, 2001; Chao et al., 2014). The analyses were carried out at the 100-m sampling-unit scale, which were subsequently pooled to inform scale dependent changes in alpha, beta, and gamma diversity (see Erős and Schmera, 2010). The rarefaction curves were computed separately for each side-arm and main-channel site of each island, as well as for the pooled datasets. However, for brevity, only the pooled dataset is presented here.

We used the 500 m long sections as sampling units to characterize patterns in the environmental variables, taxonomic and guild-based fish assemblage structure, and taxonomic and guild-based fish environmental relationships. Environmental variation was assessed using standardized principal component analysis (PCA) (based on the correlation matrix; Legendre and Legendre, 2012). Continuous variables were log-transformed and proportional variables arcsine-square root transformed prior to analysis (Zar, 2010).

Fish assemblage structure was analyzed using species abundances, including only species occurring in at least three 500 m long sample units. Abundances were Hellinger-transformed to reduce the influence of dominant species (Legendre and Gallagher, 2001), and principal coordinates analysis (PCoA) based on Bray–Curtis dissimilarities was used to visualize gradients in assemblage structure (Anderson et al., 2011). Weighted-average species coordinates were calculated, and abundance-based indicator value (IndVal) analysis identified



significant indicator species ($p < 0.05$), thus distinguishing main versus side-arm channels (Dufrêne and Legendre, 1997).

Guild based functional composition was assessed using community-weighted means (CWM) of fish traits, expressed as percentages (Lavorel et al., 2008). Categorical traits were converted to one-hot matrices, and CWM values were square-root arcsine transformed prior to standardized PCA to visualize functional gradients among sites (Villéger et al., 2008).

For all three data types, multivariate differences among sites were formally tested using PERMANOVA on Euclidean distance matrices, considering hierarchical contrasts including channel (main vs. side-arm) across all sites, within each region, among regions across channels, and among regions within each channel (Anderson, 2001; McArdle and Anderson, 2001). Pairwise regional comparisons were corrected for multiple testing using the false discovery rate. The homogeneity of multivariate dispersion (β -dispersion) was assessed prior to PERMANOVA to ensure that observed differences were not confounded by unequal within-group variability (Anderson, 2006).

Finally, redundancy analysis (RDA) was used to quantify relationships between fish assemblage structure, guild-based functional composition, and environmental variables (Legendre and Legendre, 2012). RDAs were performed separately for the Hellinger-transformed fish abundance matrix and the CWM trait matrix described above. Environmental predictors were standardized prior to analysis, and variance inflation factors (VIF) were examined to control for multicollinearity (Dormann et al., 2013). The significance of the overall models, individual axes, and single environmental variables was assessed using permutation tests.

All analyses were performed in the R environment (version 4.4.3; R Core Team, 2025). Rarefaction and extrapolation curves were generated using the *iNEXT* function in the *iNEXT* package (Hsieh et al., 2025). PCA was conducted using the *PCA* function in the

FactoMineR package (Lê et al., 2008), while PCoA was performed using the *cmdscale* function from the *stats* package. Indicator species analysis was conducted using the *multipatt* function in the *indicspecies* package (De Cáceres and Legendre, 2009). CWM were computed using the *dbFD* function in the *FD* package (Laliberté et al., 2014). Dissimilarity matrices were calculated using the *vegdist* function in the *vegan* package, which was also used for PERMANOVA (*adonis2*), tests of homogeneity of multivariate dispersion (β -dispersion; *betadisper* and *permutest*), RDA (*rda*), and the calculation of VIF (*vif.cca*) (Oksanen et al., 2022). All graphical visualizations were produced using the *ggplot2* package (Wickham, 2016).

Results

Habitat characteristics

The first two components of the habitat PCA explained 59.9% of the total variance and indicated good interpretable correlation among many environmental variables (Figure 2). Component 1 characterized a gradient which was determined by a mixture of within-channel and riparian variables. Samples with strong positive loadings characterized main channel sites with woody riparian vegetation and open-water, higher velocity habitats with gravel and sand substrate. Conversely, sites with strong negative loadings characterized the side arms of the islands, with a higher proportion of herbaceous vegetation on the bank, higher macrophyte coverage in the channel, slower velocity, and a silty substrate. Component 2 further delineated sites with deeper habitats, higher bank steepness, and coarser substrate at one end of the gradient (positive loadings), while sites had opposite characteristics on the other side (negative loadings). PERMANOVA analyses indicated that environmental characteristics differed significantly between side-arm and main-channel sites, both within individual regions and among regions (Table 1). However, regional differences became non-significant when main- and side-channel samples were pooled. This pattern suggests that habitat-type differences were stronger than regional variation and dominated the overall environmental structure.

These results suggests that habitat-type differences (side arm vs. main channel) were stronger than regional variation and dominated the overall environmental structure.

Diversity of fish assemblages

We collected a total of 37 species and 9,203 specimens during the study (Table 2). Both sample-based (Figure 3a) and individual-based (Figure 3b) rarefaction curves indicated higher species richness in the side arms than in the main channel. Rarefaction curves derived from pooled data (i.e., combining side arms and the main channel) showed significantly higher species richness at a standardized sample size for both sample- and individual-based analyses, indicating that each habitat type harbors several unique species not shared with the other (see also Table 2).

The first two axes of the PCoA explained 54.2% of the total variance in fish relative abundance data (Figure 4). Side-channel habitats were clearly separated from main-channel sites along the first axis, whereas the second axis reflected variation among

TABLE 1 Summary results of the PERMANOVA analyses for habitat characteristics.

Comparison	df_model	df_residual	PERMANOVA R ²	PERMANOVA F	PERMANOVA p	β- dispersion F	β- dispersion p
Channel M vs. S (all region)	1	28	0.451	22.986	0.001	0.002	0.957
Channel M vs. S (region E)	1	8	0.621	13.108	0.007	2.779	0.141
Channel M vs. S (region R)	1	8	0.311	3.618	0.022	0.596	0.503
Channel M vs. S (region T)	1	8	0.967	235.470	0.007	0.258	0.613
Region E vs. R vs. T (all channel)	2	27	0.092	1.369	0.221	2.106	0.151
Region E vs. R vs. T (channel M)	2	12	0.547	7.258	0.001	16.816	0.001
Region E vs. R vs. T (channel S)	2	12	0.360	3.380	0.016	2.481	0.130

Abbreviations: M and S, respectively, denote main-channel and side-arm habitats adjacent to the islands, while E, T, and R represent the Erebe, Táti, and Rácalmási islands, respectively. Beta-dispersion tests indicated no significant differences in within-group dispersions in any case (except for Region E vs. R vs. T in channel M, as noted in the results table), confirming that significant PERMANOVA results reflect true differences in group centroids. Bold values indicate variables that are statistically significant at $p < 0.05$.

individual sites within both habitat types. Side-channel habitats exhibited greater regional separation than main-channel habitats in the ordination space. Indicator species analysis identified several species that were significantly associated with either main- or side-channel habitats (Figure 4). PERMANOVA results (Table 3) were fully consistent with the environmental analyses, revealing a significant separation of fish assemblage structure between side- and main-channel habitats both within and among regions (i.e., for the pooled samples). In contrast, regional differences in fish assemblage structure were significant when main- and side-channel habitats were analyzed separately, but only marginally significant when samples from both habitat types were pooled (Table 3). This suggests that variation associated with habitat type exceeded regional variation and partly obscured regional differences in the pooled analysis.

The first two axes of the PCA explained 77.1% of the total variance in the functional structure of fish assemblages based on community-weighted means (Figure 5). Both PC1 and PC2 axes contributed to the clear separation of side- and main-channel habitats. However, individual sites within both habitat types exhibited substantial variability in each region along these two axes. PERMANOVA analyses indicated a significant separation between main- and side-channel habitats both within regions and for the pooled samples (Table 4). In contrast, regional differences were not significant for main-channel habitats, side-channel habitats, or the pooled samples.

Fish–habitat associations

The first two axes of the redundancy analysis explained 50.2% of the constrained variation in fish–environment relationships based

on relative fish abundances (Figure 6). The first axis represented a gradient separating side- and main-channel sites, primarily driven by differences in substrate composition (primarily silt) and flow velocity. Further separation of sites was jointly influenced by the first and second axes, with additional substrate (e.g., gravel, sand, and cobble), riparian, and other environmental variables (e.g., depth, slope, emergent vegetation) shaping fish assemblage structure.

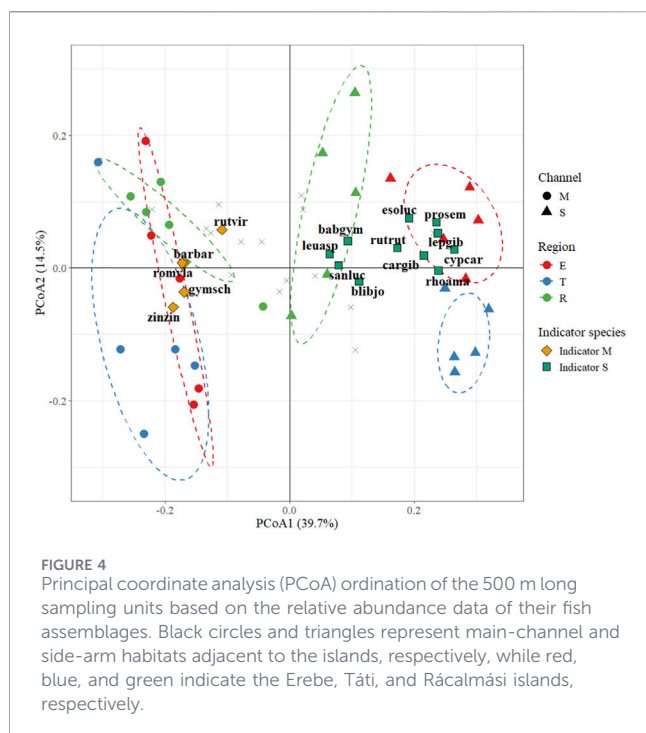
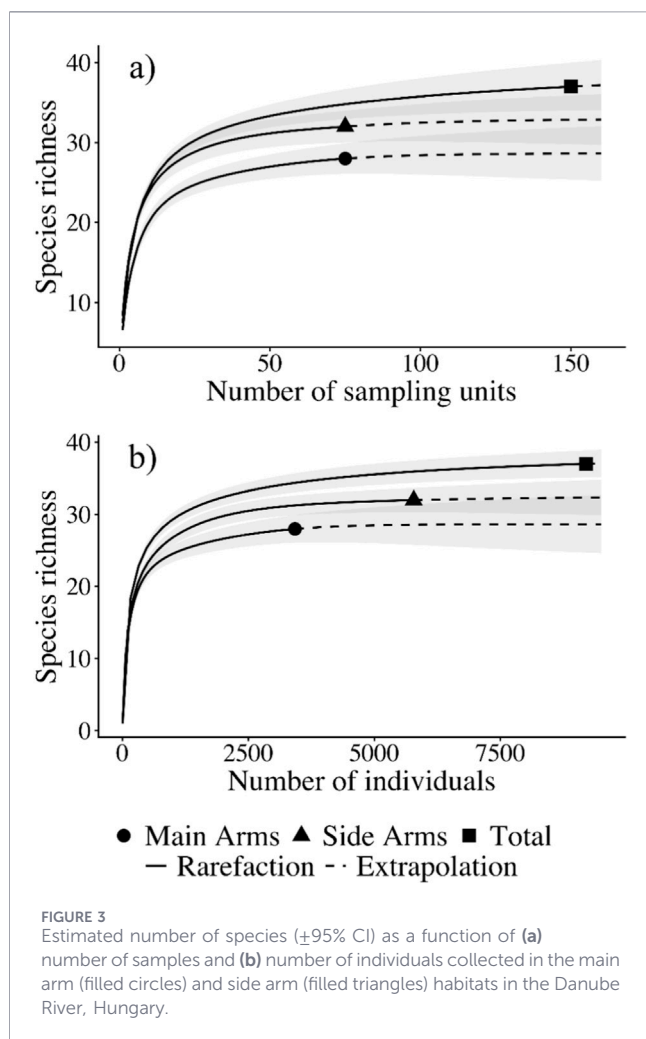
The first two axes of the redundancy analysis explained 57.1% of the constrained variation in fish–environment relationships based on functional structure (Figure 7). As with taxonomic structure, a well-defined environmental gradient was associated with fish assemblage structure along the side–main channel gradient, with velocity and gravel and sand substrates representing one end, whereas silt, emergent in-channel vegetation, LWD, and herbaceous riparian vegetation characterized the other end of the gradient.

Discussion

Our results demonstrate that riverine islands and their associated side channels play a central role in sustaining hydro-morphological heterogeneity and fish assemblage diversity in the mainstem of the Danube River. Across all analyses, side-channel habitats consistently differed from main-channel habitats in their physical structure, taxonomic composition, and functional organization, supporting our initial hypotheses regarding the keystone role of islands in shaping habitat mosaics and biodiversity patterns. Importantly, habitat-type effects were stronger and more consistent than regional differences among islands, suggesting that local hydro-morphological conditions

TABLE 2 List of species, their species name codes, and relative abundance values in side- and main-arm habitats.

Species name	Common name	Code	Side arms	Main arm
<i>Abramis brama</i>	Freshwater bream	Abrbra	1.07	2.46
<i>Alburnus alburnus</i>	Bleak	Albalb	48.17	55.63
<i>Babka gymnotrachelus</i>	Racer goby	Babgym	2.66	0.73
<i>Ballerus sapa</i>	White-eye bream	Balsap	0.07	0.35
<i>Barbus barbus</i>	Barbel	Barbar	0.05	0.76
<i>Blicca bjoerkna</i>	White bream	Blibjo	7.63	1.37
<i>Carassius gibelio</i>	Prussian carp	Cargib	2.11	0.06
<i>Chondrostoma nasus</i>	Common nase	Chonas	1.57	7.02
<i>Cobitis elongatoides</i>	Spined loach	Cobelo	0.02	
<i>Cyprinus carpio</i>	Common carp	Cypcar	0.78	
<i>Esox lucius</i>	Northern pike	Esoluc	0.54	
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Gasacu	0.09	
<i>Gymnocephalus baloni</i>	Danube ruffe	Gymbal		0.06
<i>G. cernua</i>	Ruffe	Gymcer	0.1	0.06
<i>G. schraetser</i>	Schraetzer	Gymsch		0.94
<i>Lepomis gibbosus</i>	Pumpkinseed	Lepgib	0.16	
<i>Leuciscus aspius</i>	Asp	Leuasp	0.76	0.35
<i>L. idus</i>	Ide	Leuidu	0.73	0.23
<i>Neogobius fluviatilis</i>	Monkey goby	Neoflu	0.52	0.38
<i>Neogobius melanostomus</i>	Round goby	Neomel	0.64	1.46
<i>Perca fluviatilis</i>	European perch	Perflu	0.29	0.26
<i>Ponticola kessleri</i>	Bighead goby	Ponkes	0.24	0.79
<i>Proterorhinus semilunaris</i>	Western tubenose goby	Prosem	0.14	
<i>Pseudorasbora parva</i>	Stone moroko	Psepar	0.07	
<i>Rhodeus amarus</i>	European bitterling	Rhoama	2.14	0.03
<i>Romanogobio vladkovi</i>	White-finned gudgeon	Romvla	0.42	18.33
<i>Rutilus rutilus</i>	Roach	Rutrut	25.3	0.5
<i>R. virgo</i>	Cactus roach	Rutvir	1.09	3.98
<i>Sander lucioperca</i>	Pike-perch	Sanluc	1.9	0.76
<i>S. volgensis</i>	Volga pikeperch	Sanvol	0.14	0.18
<i>Scardinius erythrophthalmus</i>	Rudd	Scaery	0.09	
<i>Silurus glanis</i>	Wels catfish	Silgla		0.12
<i>Squalius cephalus</i>	Chub	Squcep	0.38	2.25
<i>Tinca tinca</i>	Tench	Tintin	0.03	
<i>Vimba vimba</i>	Vimba bream	Vimvim	0.1	0.41
<i>Zingel streber</i>	Danube streber	Zinstr		0.03
<i>Z. zingel</i>	Zingel	Zinzin		0.53
Number of individuals			5,782	3,421
Number of species			32	28



linked to channel position outweigh broader longitudinal or regional variation in structuring fish assemblages along this section of the Danube.

Hydro-morphological differentiation between main and side channels

Environmental ordinations revealed clearly interpretable gradients separating main- and side-channel habitats in the Danube islands studied, primarily driven by flow velocity, substrate composition, and riparian and in-channel vegetation. Main-channel sites were characterized by higher flow velocities and coarser substrates, whereas side channels exhibited slower flow, finer sediments, and greater macrophyte and herbaceous riparian cover. Although some variability occurred among islands, the consistent separation of habitat types indicates that island-associated side channels constitute a distinct and functionally important component of the habitat mosaic in this Danube reach. Furthermore, the limited regional differentiation observed when samples were pooled suggests that similar hydro-geomorphological processes operate across islands despite differences in local geomorphic setting and regulation history.

Beyond the Danube, these findings support general conceptual models of island-braided and ana-branching rivers, in which islands generate hydraulic shelter, promote sediment retention, and create low-energy habitats adjacent to the main flow (Tockner and Stanford, 2002; Gurnell et al., 2001; Gurnell and Petts, 2002). The recurrence of these habitat patterns across multiple islands suggests that island-driven habitat heterogeneity represents a scalable feature of large river systems rather than a site-specific phenomenon. Consequently, our results reinforce the broader view that islands function as repeating geomorphic units that maintain physical habitat complexity and contribute to ecological resilience in regulated large rivers worldwide (Belletti et al., 2015; Wu et al., 2024).

Taxonomic diversity patterns and the role of habitat heterogeneity

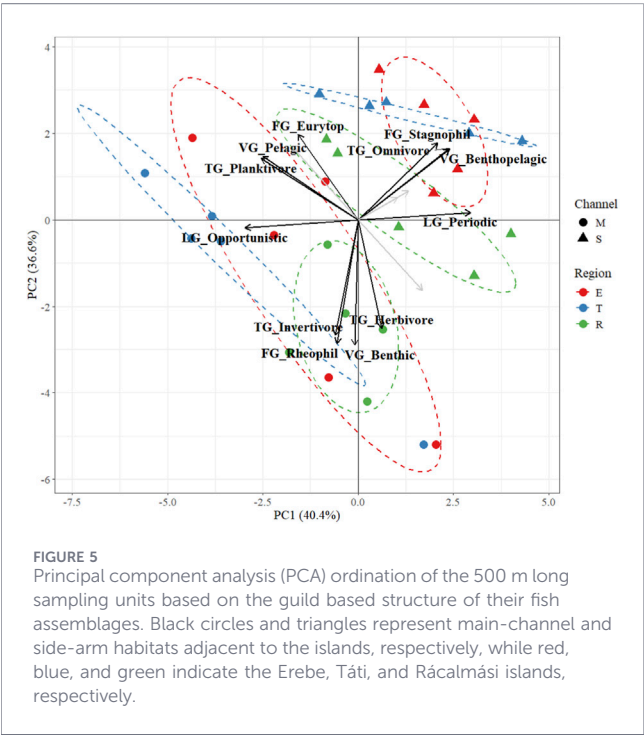
Fish assemblage diversity patterns closely mirrored the observed environmental gradients. In the Danube islands studied, both sample- and individual-based rarefaction analyses indicated higher species richness in side channels than in the main channel and revealed additional species unique to each habitat type. Species occurring exclusively in side channels were primarily stagnophilic or eurytopic, including the spined loach (*Cobitis elongatoides*), northern pike (*Esox lucius*), three-spined stickleback (*Gasterosteus aculeatus*), and rudd (*Scardinius erythrophthalmus*). In contrast, species recorded exclusively along the main-channel side of islands were predominantly rheophilic specialists, such as Danube streber (*Zingel streber*), zingel (*Z. zingel*), Danube ruffe (*Gymnocephalus baloni*), and schraetzer (*G. schraetzer*). This complementarity demonstrates that side channels substantially increase gamma diversity by supporting species that are absent from the adjacent main channel.

Multivariate analyses further showed that fish assemblage composition differed consistently between side- and main-channel habitats, whereas regional differences among islands were comparatively weak. Although regional effects became

TABLE 3 Summary results of PERMANOVA analyses for taxonomic structure of fish assemblages based on relative abundance data.

Comparison	df_model	df_residual	PERMANOVA <i>R</i> ²	PERMANOVA <i>F</i>	PERMANOVA <i>p</i>	β- dispersion <i>F</i>	β- dispersion <i>p</i>
Channel M vs. S (all region)	1	28	0.383	17.370	0.001	0.009	0.932
Channel M vs. S (region E)	1	8	0.525	8.847	0.008	1.944	0.198
Channel M vs. S (region R)	1	8	0.377	4.831	0.016	0.197	0.621
Channel M vs. S (region T)	1	8	0.662	15.667	0.010	1.228	0.271
Region E vs. R vs. T (all channel)	2	27	0.122	1.881	0.059	0.719	0.473
Region E vs. R vs. T (channel M)	2	12	0.269	2.207	0.014	0.802	0.504
Region E vs. R vs. T (channel S)	2	12	0.502	6.047	0.001	0.390	0.658

Abbreviations: M and S, respectively, denote main-channel and side-arm habitats adjacent to the islands, while E, T, and R represent the Erebe, Táti, and Rácalmási islands, respectively. Beta-dispersion tests indicated no significant differences in within-group dispersions in any case, confirming that significant PERMANOVA results reflect true differences in group centroids. Bold values indicate variables that are statistically significant at *p* < 0.05.



significant when habitat types were analyzed separately, habitat type explained a substantially larger proportion of the variation. This suggests that island-specific environmental conditions influence fish assemblages, but their effects are secondary to the stronger and more consistent environmental filtering associated with channel type. The high dispersion of both side- and main-channel assemblages in the ordination space

also indicates considerable beta diversity within each habitat, reflecting fine-scale habitat heterogeneity generated by variation in substrate composition, sediment deposition, aquatic vegetation, and flow refugia around islands.

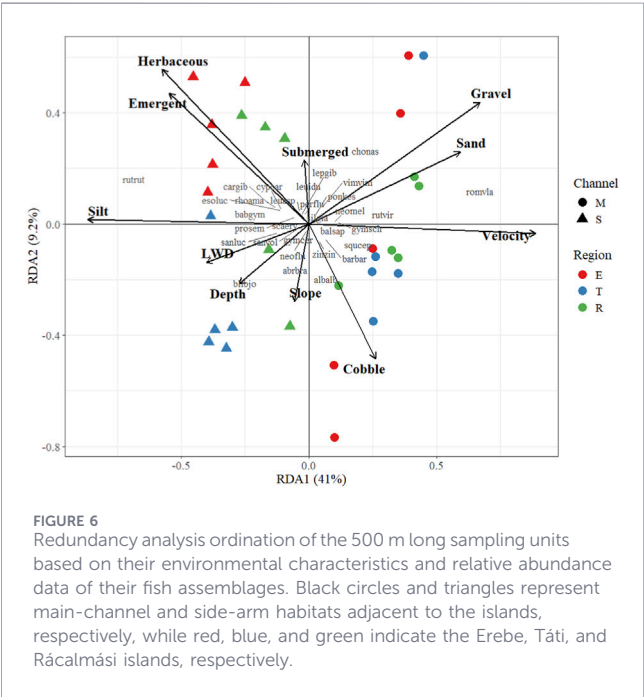
Indicator species analysis further emphasized this ecological differentiation. Characteristic side-channel species included the eurytopic roach (*Rutilus rutilus*), white bream (*Blicca bjoerkna*), pikeperch (*Sander lucioperca*), and the more stagnophilic northern pike (*E. lucius*) and bitterling (*Rhodeus amarus*). In contrast, indicator species of the main-channel habitats were exclusively rheophilic benthic insectivores, including barbel (*Barbus barbus*), zingel (*Z. zingel*), schraetzer (*G. schraetser*), cactus roach (*Rutilus virgo*), and white-finned gudgeon (*Romanogobio vladykovi*).

Beyond the segment under study, these findings reinforce the general importance of channel diversity within island complexes for sustaining fish biodiversity in large rivers. The role of habitat complementarity has been reported from other segments of the Danube or from other large river systems, where off-channel and low-energy habitats support additional lentic and semi-lentic species that are absent from the main channel (Johnson and Jennings, 1998; Loisl et al., 2014; Meulenbroek et al., 2018). More broadly, our results support the concept that mesoscale habitat heterogeneity, rather than geographic location alone, is a primary driver of fish assemblage organization in large rivers (Boys and Thoms, 2006; Pegg and Taylor, 2007; Wolter et al., 2016; Erős et al., 2017). The repeated occurrence of these patterns across multiple Danube islands suggests that island-associated side channels function as recurring biodiversity hotspots and that conserving or restoring these habitats is likely to enhance fish diversity and ecological resilience in regulated large rivers worldwide.

TABLE 4 Summary results of PERMANOVA analyses for functional structure of fish assemblages based on CWM data of ecological guilds.

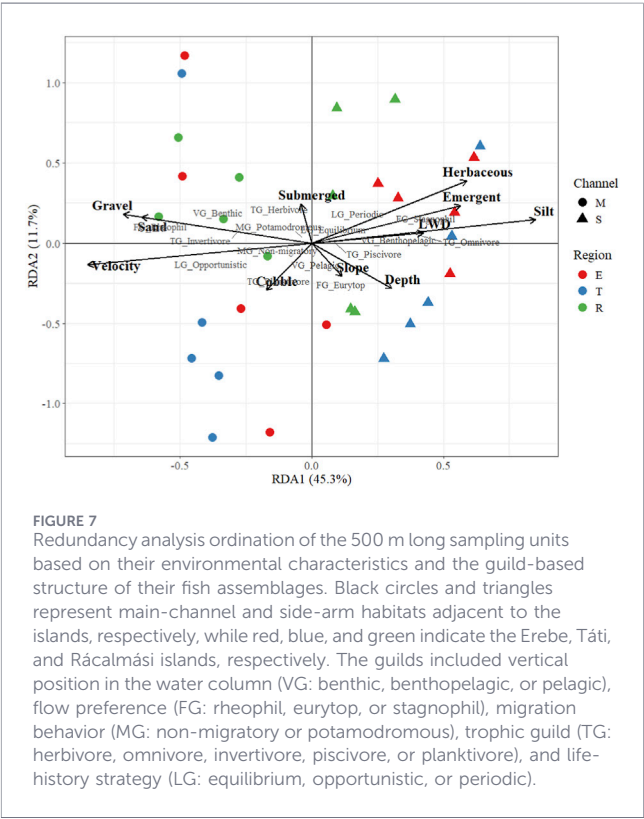
Comparison	df_model	df_residual	PERMANOVA R ²	PERMANOVA F	PERMANOVA p	β- dispersion F	β- dispersion p
Channel M vs. S (all region)	1	28	0.365	16.093	0.001	1.596	0.205
Channel M vs. S (region E)	1	8	0.452	6.603	0.008	2.719	0.160
Channel M vs. S (region R)	1	8	0.491	7.719	0.014	0.085	0.789
Channel M vs. S (region T)	1	8	0.386	5.039	0.009	0.918	0.374
Region E vs. R vs. T (all channel)	2	27	0.072	1.051	0.382	1.399	0.283
Region E vs. R vs. T (channel M)	2	12	0.164	1.180	0.324	0.740	0.517
Region E vs. R vs. T (channel S)	2	12	0.243	1.931	0.116	0.187	0.845

Abbreviations: M and S, respectively, denote main-channel and side-arm habitats adjacent to the islands, while E, T, and R represent the Erebe, Tāti, and Rácalmási islands, respectively. Beta-dispersion tests indicated no significant differences in within-group dispersions in any case, confirming that significant PERMANOVA results reflect true differences in group centroids. Bold values indicate variables that are statistically significant at $p < 0.05$.



Functional structure and trait-based responses to environmental gradients

Trait-based analyses revealed that differences between main and side channels extend beyond species identities to encompass fundamental aspects of functional organization. Functional PCA based on community-weighted means showed a strong



separation of assemblages along the side-main channel gradient, indicating that habitat filtering operates on ecological traits related primarily to flow preference, habitat use, and substrate association. Side channels were associated

with functional traits linked to slower flow, finer sediments, and increased structural complexity (vegetation, LWD), whereas main-channel assemblages were dominated by traits adapted to higher velocities and coarser substrates.

As predicted, trophic guild structure also changed between habitat types, with omnivore and predator species being relatively more dominant in side-channel habitats, whereas invertivore species were more strongly associated with the main channel. This pattern likely reflects fundamental differences in habitat complexity, flow and substrate conditions, and food-resource availability between the two habitat types. Side channels are typically characterized by lower current velocities, finer sediments, and higher macrophyte and shoreline vegetation cover, which increase habitat heterogeneity and promote the accumulation of organic matter and diverse food resources. Such conditions favor species feeding on plant materials, such as omnivore species with broader feeding plasticity (Loisl et al., 2014; Silva et al., 2021; Thomaz et al., 2025), as well as more sedentary predatory fishes such as pike and pike-perch, that benefit from structurally complex habitats providing both feeding opportunities and shelter (Pauwels et al., 2017; Ramler and Keckeis, 2019; Pelz et al., 2026). In contrast, the main channel was dominated by benthic invertivore species, likely because higher flow velocities and coarser substrates support benthic macroinvertebrate production (Rempel et al., 2000; Duan et al., 2008) and favor rheophilic species specialized for feeding under lotic conditions. The analysis also revealed that an interesting exception of these differences was the herbivore nase (*Chondrostoma nasus*), which preferred main channel habitats. This rheophilic species prefers flowing water, feeding on benthic algae from the stony-gravelly bottom (Ovidio and Nzau Matondo, 2024). Overall, our results are consistent with those of previous studies, although those investigations did not specifically focus on island-associated main and side channels. Research at the mesohabitat (Hirzinger et al., 2004; Loisl et al., 2014), reach (Pelz et al., 2026), and river-segment scales (Erős et al., 2017) reported similar distribution patterns for the Danubian fish species examined in this study around Danubian islands. For example, omnivore species such as roach and predatory species such as pike-perch were also found to prefer slow-flowing habitats, while the benthic invertivore nase, barbel, and zingel species were more abundant in the fast flowing zones of the main channel in these studies (Hirzinger et al., 2004; Loisl et al., 2014; Pelz et al., 2026).

Differences were also observed in life-history strategies, albeit not so contrasting as in the case of vertical position and flow preference guilds—that is for traits indicating habitat use patterns. For example, opportunistic species, such as the genera *Zingel*, *Gymnocephalus*, and *Romanogobio*, were relatively more abundant in the main channel, while periodic strategists were more characteristic of side-channel habitats. The higher relative abundance of opportunistic species in the main channel can be linked to the more dynamic and hydrologically variable conditions of these habitats, where rapid colonization ability, early maturation, and flexible reproductive strategies provide advantages under frequent disturbance. Conversely, the RDA analysis revealed that the relatively higher abundance of large-bodied periodic species was associated with side-channel habitats in samples characterized by steeper banks and greater water depths. However, the literature also suggests that both trophic guild structure and life-history strategies

often exhibit only moderate responses to lateral connectivity, with these responses varying according to hydrological conditions and the degree of connectivity (Silva et al., 2021; Feng et al., 2024).

Overall, redundancy analyses directly linked environmental variables to both taxonomic and functional assemblage structure. The strong explanatory power of velocity and substrate composition across both RDAs underscores their role as master variables structuring fish communities in rivers (Poff and Allan, 1995). Notably, the comparable proportion of variance explained by taxonomic and functional RDAs suggests that trait-based approaches may provide integrative and mechanistic understanding of fish–habitat relationships, particularly in systems where species composition may vary regionally but functional roles remain conserved (Lamouroux et al., 2002). This finding aligns with growing evidence that functional traits capture key ecological responses to environmental gradients and disturbance in riverine ecosystems (Logez et al., 2013; Lima et al., 2017).

Islands as biodiversity amplifiers in regulated large rivers

Taken together, our results highlight riverine islands as biodiversity amplifiers that enhance both hydro-morphological, taxonomic, and functional diversity by maintaining side-channel habitats within the mainstem (Johnson and Jennings, 1998; Thorp, 1992; Hintz et al., 2015). In regulated rivers such as the Danube, where channel simplification and flow stabilization have reduced habitat diversity, islands represent critical nodes of physical and ecological complexity (Hohensinner et al., 2004; Ádám and Malatinszky, 2022). Their capacity to generate both high- and slow-flowing habitats, promote sediment sorting, and sustain riparian–aquatic linkages makes them particularly valuable for fish assemblages that depend on habitat heterogeneity across life stages (Zeug and Winemiller, 2008; Stoffers et al., 2022).

The concept of islands as biodiversity amplifiers extends beyond simple species richness to encompass multiple dimensions of diversity. Islands enhance alpha diversity within local habitats by increasing niche availability, beta diversity by creating distinct habitat types, and gamma diversity at the landscape scale by maintaining habitat mosaics (Thorp, 1992; Gurnell and Petts, 2002). This multi-scale enhancement of diversity is particularly critical in regulated rivers, where homogenization of physical habitats has led to corresponding losses in biological diversity (Aarts et al., 2004; Schmutz et al., 1999; Tockner and Stanford, 2002).

The finding that habitat-type differences outweighed regional differences has important implications for conservation planning. It suggests that protecting or restoring side-channel habitats around islands may yield biodiversity benefits regardless of their exact longitudinal position, provided that key hydro-morphological processes are maintained (Riquier et al., 2015; Díaz-Redondo et al., 2018). Conversely, the loss or disconnection of side channels through island attachment, siltation, or bank fixation is likely to lead to the functional homogenization of fish assemblages and loss of key habitats, with potential consequences for ecosystem resilience and food-web dynamics.

Study limitations

Although our study encompassed multiple riverine islands spanning a broad section of the Danube in Hungary, several limitations should be acknowledged. Firstly, the analyses were based on a single sampling period and therefore do not capture seasonal or interannual variability in hydrological conditions and fish assemblage dynamics. Because habitat use and lateral connectivity can vary substantially with discharge regime, future studies incorporating repeated sampling across different flow conditions would improve our understanding of the temporal stability of the observed patterns (see [Feng et al., 2025](#); [Pelz et al., 2026](#)). Secondly, our analyses focused on littoral fish assemblages associated with island habitats and did not include deeper offshore environments (see [Szalóky et al., 2021](#)) or larval stages that may respond differently to hydro-morphological gradients (see [Stoffers et al., 2025](#)). Finally, while the consistent relationships between habitat characteristics and both taxonomic and functional assemblage structures suggest strong ecological mechanisms, the observational nature of the study precludes direct inference of causal processes. Nevertheless, the concordance of hydro-morphological, taxonomic, and functional patterns across multiple islands provides robust evidence that island-associated habitat heterogeneity is a major driver of fish biodiversity in the Danube.

Implications for river management and restoration

From a management and policy perspective, our study directly supports the objectives of the European Union's Nature Restoration Regulation (NRR), which explicitly calls for the restoration of river connectivity, hydro-morphological processes, and habitat diversity in degraded river systems. While much of the current policy discourse has focused on longitudinal connectivity (e.g., dam removal and fish passage), our results emphasize that lateral functional connectivity, maintained by islands and their associated side channels, is equally critical for sustaining fish diversity in large rivers. Measures that preserve or restore side-channel dynamics, such as maintaining hydraulic exchange, preventing excessive siltation, and safeguarding sediment transport processes around islands, are therefore highly relevant tools for achieving the NRR's targets for river ecosystem recovery ([Wohl et al., 2024](#); [Clarke, 2025](#)). In navigation-dominated rivers such as the Danube, this may include the selective removal or modification of bank reinforcements, reconnection or partial reopening of side arms, and sediment management practices that counteract channel incision and island stabilization, thereby reinstating habitat mosaics essential for diverse fish assemblages.

More broadly, our findings align with the NRR's shift away from static, reach-scale restoration toward process-based and spatially explicit strategies that recognize rivers as hierarchically structured, patchy systems ([Wohl et al., 2024](#); [Beechie et al., 2010](#)). By demonstrating strong and consistent links between hydro-morphological heterogeneity, lateral habitat differentiation, and both taxonomic and functional fish assemblage structure, this study provides empirical evidence

that riverine islands function as key landscape elements that underpin biodiversity in large rivers. Consequently, restoring and maintaining the dynamic character of island-side-channel complexes should be considered a priority action in the mainstem of very large rivers within EU river restoration frameworks. Such an approach not only enhances species richness but also supports functional resilience and ecological integrity, thereby contributing to the NRR's long-term goals under ongoing climatic and anthropogenic pressures.

Conclusion

Our study demonstrates that riverine islands are key drivers of hydro-morphological heterogeneity and fish biodiversity in the mainstem of the Danube River. By creating distinct main- and side-channel habitats, islands generate environmental gradients that shape both the taxonomic and functional structure of fish assemblages. Habitat-type differences consistently outweighed regional variation, highlighting that local hydro-morphological conditions associated with island-side-channel complexes are the primary determinants of fish community structure in this segment of the river. Maintaining this habitat mosaic is therefore essential for preserving ecological processes and supporting diverse fish communities in large rivers that have been simplified by regulation and channel modification.

Data availability statement

The datasets presented in this article are not publicly available due to their ongoing use by the authors in continuing research projects. Requests to access the datasets should be directed to the corresponding author.

Ethics statement

The animal study was approved by A HUN-REN BLKI Munkahelyi Állatkísérleti Bizottságának (MÁB) szabályzata (<https://www.blki.hun-ren.hu/node/15592> <https://www.blki.hun-ren.hu/node/15593>). The study was conducted in accordance with local legislation and institutional requirements.

Author contributions

TE: Writing – original draft, Supervision, Formal Analysis, Visualization, Data curation, Project administration, Resources, Methodology, Validation, Funding acquisition, Investigation, Conceptualization. KF: Methodology, Conceptualization, Writing – review and editing, Visualization, Software, Formal Analysis. BT: Writing – review and editing, Methodology, Conceptualization, Investigation. AS: Methodology, Investigation, Writing – review and editing. ZS: Conceptualization, Investigation, Writing – review and editing, Visualization, Methodology, Formal Analysis.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript. The authors used ChatGPT (OpenAI) to assist in condensing human-written text. All artificial intelligence (AI)-assisted edits were limited to

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2026.1864609/full#supplementary-material>

References

- Aarts, B. G. W., Van Den Brink, F. W. B., and Nienhuis, P. H. (2004). Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Res. Appl.* 20, 3–23. doi: 10.1002/RRA.720
- Ádám, Sz., and Malatinszky, Á. (2022). How many real islands have existed along a mid-danube section during the past 250 years? *Sustainability* 14 (3), 1829. doi: 10.3390/su14031829
- Allan, J. D., and Castillo, M. M. (2007). *Stream Ecology: Structure and Function of Running Waters*. Dordrecht. XIV: Springer, 436. doi: 10.1007/978-1-4020-5583-6
- Amoros, C. (2001). The concept of habitat diversity between and within ecosystems applied to river side-arm restoration. *Environ. Manag.* 28, 805–817. doi: 10.1007/s002670010263
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253. doi: 10.1111/j.1541-0420.2005.00440.x
- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., et al. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. doi: 10.1111/j.1461-0248.2010.01552.x
- Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., et al. (2010). Process-based principles for restoring river ecosystems. *BioScience* 60, 209–222. doi: 10.1525/bio.2010.60.3.7
- Belletti, B., Dufour, S., and Piégay, H. (2015). What is the relative effect of space and time to explain the braided river width and island patterns at a regional scale? *River Res. Appl.* 31, 1–15. doi: 10.1002/rra.2714
- Bellwood, D. R., Hoey, A. S., and Choat, J. H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.* 6, 281–285. doi: 10.1046/j.1461-0248.2003.00432.x
- Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B* 57, 289–300. doi: 10.1111/j.2517-6161.1995.tb02031.x
- Boys, C. A., and Thoms, M. C. (2006). A large-scale, hierarchical approach for assessing habitat associations of fish assemblages in large dryland rivers. *Hydrobiologia* 572, 11–31. doi: 10.1007/s10750-005-0004-0
- Brierley, G. J., and Fryirs, K. A. (2005). *Geomorphology and River Management: Applications of the River Styles Framework*. Oxford: Blackwell Publishing.
- Bunn, S., and Arthington, A. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ. Manag.* 30, 492–507. doi: 10.1007/s00267-002-2737-0
- Cáceres, M. D., and Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology* 90 (12), 3566–3574. doi: 10.1890/08-1823.1
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67. doi: 10.1890/13-0133.1
- Clarke, S. J. (2025). Full floodplain connectivity: realising opportunities for 'Stage 0' river restoration. *River Res. Appl.* 41 (1), 152–158. doi: 10.1002/rra.4283
- Copp, G. H. (1989). The habitat diversity and fish reproductive function of floodplain ecosystems. *Environ. Biol. Fishes* 26, 1–27. doi: 10.1007/bf00002472
- Díaz-Redondo, M., Egger, G., Marchamalo, M., Damm, C., de Oliveira, R. P., and Schmitt, L. (2018). Targeting lateral connectivity and morphodynamics in a large river-floodplain system: the upper rhine river. *River Res. Applic.* 34, 734–744. doi: 10.1002/rra.3287
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x
- Dray, S., and Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20. doi: 10.18637/jss.v022.i04
- Duan, X., Wang, Z., and Tian, S. (2008). Effect of streambed substrate on macroinvertebrate biodiversity. *Front. Environ. Sci. and Eng. China* 2 (1), 122–128. doi: 10.1007/s11783-008-0023-y
- Dufrène, M., and Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. doi: 10.1890/0012-9615(1997)067[0345:SAIST]2.0.CO;2
- Erős, T. (2005). Life history diversification in the Middle Danubian fish fauna – a conservation perspective. *Arch. Hydrobiol. Suppl. 158 Large Rivers* 16, 289–304. doi: 10.1127/lr/16/2005/289
- Erős, T., and Bányai, Zs. (2020). Sparing and sharing land for maintaining the multifunctionality of large floodplain rivers. *Sci. Total Environ.* 728, 138441. doi: 10.1016/j.scitotenv.2020.138441

- Erős, T., and Lowe, W. H. (2019). The landscape ecology of Rivers: from patch-based to spatial network analyses. *Curr. Landsc. Ecol. Rep.* 4 (4), 103–112. doi: 10.1007/s40823-019-00044-6
- Erős, T., and Schmera, D. (2010). Spatio-temporal scaling of biodiversity and the species-time relationship in a stream fish assemblage. *Freshw. Biol.* 55, 2391–2400. doi: 10.1111/j.1365-2427.2010.02450.x
- Erős, T., Tóth, B., Sevcsik, A., and Schmera, D. (2008). Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (River Danube, Hungary). *Int. Rev. Hydrobiology* 93, 88–105. doi: 10.1002/iroh.200710976
- Erős, T., Bammer, V., György, Á. I., Pehlivanov, L., Schabuss, M., Zornig, H., et al. (2017). Typology of a great river using fish assemblages: implications for the bioassessment of the Danube river. *River Res. Appl.* 33, 37–49. doi: 10.1002/rra.3060
- Erős, T., Petrovski, J., and Mórocz, A. (2023). Planning for sustainability: historical data and remote sensing-based analyses aid landscape design in one of the largest remnant European floodplains. *Landsc. Urban Plan.* 238, 104837. doi: 10.1016/j.landurbplan.2023.104837
- EU (2024). *Regulation (EU) 2024/1991 of the European Parliament and of the Council on Nature Restoration*. Official Journal of the European Union L, 2024/1991.
- Fausch, K. D., Torgersen, C. E., Baxter, C. V., and Li, H. W. (2002). Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52, 483–498. doi: 10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2
- Feng, K., Czeglédi, I., Funk, A., Hein, T., Pont, D., Meulenbroek, P., et al. (2024). Composition, divergence and variability: a comprehensive analysis of fish trait responses to connectivity. *Ecol. Indic.* 167, 112670. doi: 10.1016/j.ecolind.2024.112670
- Feng, K., Czeglédi, I., Funk, A., Hein, T., Pont, D., Meulenbroek, P., et al. (2025). Drivers of metacommunity dynamics in river-floodplain fish: a path modeling approach. *Ecol. Monogr.* 95 (3), e70036. doi: 10.1002/ecm.70036
- Froese, R., and Pauly, D. (2023). *Fishbase*. World Wide Web Electronic Publication.
- Goffaux, D., Grenouillet, G., and Kestemont, P. (2005). Electrofishing versus gillnet sampling for the assessment of fish assemblages in large rivers. *Arch. für Hydrobiol.* 162, 73–90. doi: 10.1127/0003-9136/2005/0162-0073
- Gotelli, N. J., and Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. doi: 10.1046/j.1461-0248.2001.00230.x
- Gurnell, A. M., and Petts, G. E. (2002). Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshw. Biol.* 47, 581–600. doi: 10.1046/j.1365-2427.2002.00923.x
- Gurnell, A. M., Petts, G. E., Hannah, D. M., Smith, B. P. G., Edwards, P. J., Kollmann, J., et al. (2001). Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surf. Process. Landforms* 26, 31–62. doi: 10.1002/1096-9837(200101)26:1<31::AID-ESP155>3.0.CO;2-Y
- Habersack, H., Hein, T., Stanica, A., Liska, I., Mair, R., Jäger, E., et al. (2016). Challenges of river basin management: current status of, and prospects for, the river Danube from a river engineering perspective. *Sci. Total Environ.* 543, 828–845. doi: 10.1016/j.scitotenv.2015.10.123
- Hein, T., Funk, A., Pletterbauer, F., Graf, W., Zsuffa, I., Haidvogel, G., et al. (2019). Management challenges related to long-term ecological impacts, complex stressor interactions, and different assessment approaches in the Danube river basin. *River Res. Appl.* 35 (5), 500–509. doi: 10.1002/rra.3243
- Hermoso, V. (2025). Restoring free-flowing rivers: planning for longitudinal and lateral connectivity recovery. *J. Appl. Ecol.* 62, 2048–2060. doi: 10.1111/1365-2664.70095
- Hintz, W. D., Porreca, A. P., Garvey, J. E., Phelps, Q. E., Tripp, S. J., Hrabik, R. A., et al. (2015). Abiotic attributes surrounding alluvial islands generate critical fish habitat. *River Res. Appl.* 31, 1218–1226. doi: 10.1002/RRA.2829
- Hirzinger, V., Keckeis, H., Nemeschkal, H. L., and Schiemer, F. (2004). The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. *River Res. applic.* 20, 137–149. doi: 10.1002/rra.739
- Hoeinghaus, D. J., Winemiller, K. O., and Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *J. Biogeogr.* 34 (2), 324–338. doi: 10.1111/j.1365-2699.2006.01587.x
- Hohensinner, S., Habersack, H., Jungwirth, M., and Zauner, G. (2004). Reconstruction of the characteristics of a natural alluvial river-floodplain system and hydromorphological changes following human modifications: the Danube river (1812–1991). *River Res. Appl.* 20, 25–41. doi: 10.1002/RRA.719
- Hohensinner, S., Lager, B., Sonnlechner, C., Haidvogel, G., Gierlinger, S., Schmid, M., et al. (2021). Changes in water and land: the reconstructed Viennese riverscape from 1500 to the present. *Water Hist.* 5, 145–172. doi: 10.1007/s12685-013-0074-2
- Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456. doi: 10.1111/2041-210X.12613
- Hsieh, T. C., Ma, K. H., and Chao, A. (2025). iNEXT: interpolation and extrapolation for species diversity (R package version 3.0.2). Available online at: http://chao.stat.nthu.edu.tw/wordpress/software_download/ (Accessed June 30, 2026).
- Johnson, B. L., and Jennings, C. A. (1998). Habitat associations of small fishes around islands in the upper Mississippi river. *North Am. J. Fish. Manag.* 18 (2), 327–336. doi: 10.1577/1548-8675(1998)018<0327:HAOSFA>2.0.CO;2
- Kärnä, O. M., Heino, J., Grönroos, M., and Hjort, J. (2018). The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity. *Ecol. Indic.* 94, 420–429. doi: 10.1016/j.ecolind.2018.06.034
- Laliberté, E., Legendre, P., and Shipley, B. (2014). *FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology*.
- Lamoureux, N., Poff, N. L., and Angermeier, P. L. (2002). Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83, 1792–1807. doi: 10.1890/0012-9658(2002)083[1792:ICOSFC]2.0.CO;2
- Langhans, S. D., Gessner, J., Hermoso, V., and Wolter, C. (2016). Coupling systematic planning and expert judgement enhances the efficiency of river restoration. *Sci. Total Environ.* 560–561, 266–273. doi: 10.1016/j.scitotenv.2016.03.232
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Gardén, D., Dorrough, J., et al. (2008). Assessing functional diversity in the field – methodology matters. *Funct. Ecol.* 22, 134–147. doi: 10.1111/j.1365-2435.2007.01339.x
- Lê, S., Josse, J., and Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25 (1), 1–18. doi: 10.18637/jss.v025.i01
- Legendre, P., and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. doi: 10.1007/s004420100716
- Legendre, P., and Legendre, L. (2012). *Numerical Ecology*. 3rd English ed. Amsterdam: Elsevier.
- Lima, A. C., Wrona, F. J., and Soares, A. M. V. M. (2017). Fish traits as an alternative tool for the assessment of impacted rivers. *Rev. Fish. Biol. Fish.* 27, 31–42. doi: 10.1007/s11160-016-9446-x
- Logez, M., Bady, P., Melcher, A., and Pont, D. (2013). A continental-scale analysis of fish assemblage functional structure in European rivers. *Ecography* 36, 80–91. doi: 10.1111/j.1600-0587.2012.07447.x
- Loisl, F., Singer, G., and Keckeis, H. (2014). Method-integrated fish assemblage structure at two spatial scales along a free-flowing stretch of the Austrian Danube. *Hydrobiologia* 729, 77–94. doi: 10.1007/s10750-013-1588-4
- Manfrin, A., Bunzel-Drüke, M., Lorenz, A., Maire, A., Scharf, M., Zimball, O., et al. (2020). The effect of lateral connectedness on the taxonomic and functional structure of fish communities in a lowland river floodplain. *Sci. Total Environ.* 719, 137169. doi: 10.1016/j.scitotenv.2020.137169
- Marin, V., Archambault, V., Barillier, A., Gouraud, V., Staentzel, C., and Tales, E. (2026). How does floodplain restoration of a highly anthropized river enhance aquatic biodiversity? Lessons from a decade of macroinvertebrate and fish recolonization. *Ecol. Eng.* 226, 107934. doi: 10.1016/j.ecoleng.2026.107934
- McArdle, B. H., and Anderson, M. J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297. doi: 10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2
- Meulenbroek, P., Drexler, S., Huemer, D., Gruber, S., Krumböck, S., Rauch, P., et al. (2018). Species-specific fish larvae drift in anthropogenically constructed riparian zones on the Vienna impoundment of the River Danube, Austria: species occurrence, frequencies, and seasonal patterns based on DNA barcoding. *River Res. Applic.* 34, 854–862. doi: 10.1002/rra.3303
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., and Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. and Evol.* 28, 167–177. doi: 10.1016/j.tree.2012.10.004
- Noble, R. A. A., Cowx, I. G., Goffaux, D., and Kestemont, P. (2007). Assessing the health of European rivers using functional ecological guilds of fish communities: standardising species classification and approaches to metric selection. *Fish. Manag. Ecol.* 14, 381–392. doi: 10.1111/j.1365-2400.2007.00575.x
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., et al. (2022). *Vegan: Community Ecology Package*. R package version 2.6-2. Available online at: <https://cran.r-project.org/package=vegan> (Accessed June 30, 2026).
- Ovidio, M., and Nzau Matondo, B. (2024). Ecology and sustainable conservation of the nase, *chondrostoma nasus*: a literature review. *Sustainability* 16 (14), 6007. doi: 10.3390/su16146007
- Pander, J., Mueller, M., and Geist, J. (2015). Succession of fish diversity after reconnecting a large floodplain to the upper Danube river. *Ecol. Eng.* 75, 41–50. doi: 10.1016/j.ecoleng.2014.11.011
- Pauwels, I., Goethals, P., Coeck, J., and Mouton, A. (2017). Habitat use and preference of adult pike (*Esox lucius* L.) in an anthropogenically impacted lowland river. *Limnologia* 62, 151–160. doi: 10.1016/j.limno.2016.10.001
- Pease, A. A., González-Díaz, A. A., Rodiles-Hernández, R., and Winemiller, K. O. (2012). Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment. *Freshw. Biol.* 57, 1060–1075. doi: 10.1111/j.1365-2427.2012.02768.x
- Pegg, M. A., and Taylor, R. M. (2007). Fish species diversity among spatial scales of altered temperate rivers. *J. Biogeogr.* 34, 549–558. doi: 10.1111/j.1365-2699.2006.01624.x

- Pelz, D., Grohmann, M., Neuburg, J., Auer, S., Schmutz, S., Hein, T., et al. (2026). Disrupted currents and shifting riverbanks: unveiling the structure of fish assemblages in the fragmented Austrian Danube. *Hydrobiologia* 853, 4313–4336. doi: 10.1007/s10750-026-06208-w
- Persat, H., Olivier, J. M., and Pont, D. (1994). Theoretical habitat templates, species traits, and species richness: fish in the upper Rhone river and its floodplain. *Freshw. Biol.* 31, 439–454. doi: 10.1111/j.1365-2427.1994.tb01750.x
- Poff, N. L., and Allan, J. D. (1995). Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76, 606–627. doi: 10.2307/1941217
- R Core Team (2025). R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available online at: <https://www.r-project.org/> (Accessed June 30, 2026).
- Ramler, D., and Keckeis, H. (2019). Occurrence of non-native fishes in the Danube east of Vienna (Austria) and potential interactions of invasive gobiids with native fishes. *J. Appl. Ichthyol.* 35, 850–862. doi: 10.1111/jai.13916
- Ramler, D., Wanzenböck, J., Guttman, S., Keckeis, H., Schludermann, E., Schabuss, M., et al. (2019). Effects of large-river restoration measures on ecological fish guilds and focal species of conservation in a large European river (Danube, Austria). *Sci. Total Environ.* 689, 1076–1093. doi: 10.1016/j.scitotenv.2019.05.373
- Ramsey, P. Q., Dattilo, J., DeVries, D. R., and Brewer, S. K. (2024). Evaluating the context dependency of large river nursery habitats for fishes in the lower red river catchment. *River Res. Appl.* 40, 761–779. doi: 10.1002/rra.4259
- Raška, P., Dolejš, M., and Hofmanová, M. (2017). Effects of damming on long-term development of fluvial islands, Elbe river (N Czechia). *River Res. Appl.* 33, 471–482. doi: 10.1002/RRA.3104
- Rempel, L. L., Richardson, J. S., and Healey, M. C. (2000). Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshw. Biol.* 45, 57–73. doi: 10.1046/j.1365-2427.2000.00617.x
- Ricaurte, L. F., Boesch, S., Jokela, J., and Tockner, K. (2012). The distribution and environmental state of vegetated islands within human-impacted European rivers. *Freshw. Biol.* 57, 2539–2549. doi: 10.1111/fwb.12026
- Riquier, J., Piégay, H., and Šulc Michalková, M. (2015). Hydromorphological conditions in eighteen restored floodplain channels of a large river: linking patterns to processes. *Freshw. Biol.* 60, 1085–1103. doi: 10.1111/FWB.12411
- Schmutz, S., Kaufmann, M., Vogel, B., Jungwirth, M., and Muhar, S. (1999). Fish as indicators of large river connectivity: the Danube and its tributaries. *Arch. für Hydrobiol. Suppl.* 115, 329–348. doi: 10.1127/LR/11/1999/329
- Silva, P. B., Arantes, C. C., Freitas, C. E. C., Petrere, M., Jr., and Ribeiro, F. R. V. (2021). Seasonal hydrology and fish assemblage structure in the floodplain of the lower Amazon river. *Ecol. Freshw. Fish* 30 (2), 162–173. doi: 10.1111/eff.12572
- Simon, T. P. (1999). *Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Assemblages* (Boca Raton, Florida: CRC Press).
- Stoffers, T., Buijse, A. D., Verreth, J. A. J., and Nagelkerke, L. A. J. (2022). Environmental requirements and heterogeneity of rheophilic fish nursery habitats in European lowland rivers: current insights and future challenges. *Fish Fish.* 23, 162–182. doi: 10.1111/faf.12606
- Stoffers, T., Buijse, A. D., Poos, J. J., Verreth, J. A. J., and Nagelkerke, L. A. J. (2025). Ontogenetic shifts by juvenile fishes highlight the need for habitat heterogeneity and connectivity in river restoration. *Limnol. Oceanogr.* 70, 732–748. doi: 10.1002/lno.12797
- Szalóky, Z., Füstös, V., Tóth, B., and Erős, T. (2021). Environmental drivers of benthic fish assemblages and fish habitat associations in offshore areas of a very large river. *River Res. Appl.* 37, 712–721. doi: 10.1002/rra.3793
- Thomaz, S. M., Cardozo, A. L. P., Quirino, B. A., Yofukuji, K., Aleixo, M. H. F., and Fugi, R. (2025). A review of the ecological role of aquatic macrophytes on freshwater fish. *Hydrobiologia* 852 (13), 3257–3290. doi: 10.1007/s10750-025-05819-z
- Thorp, J. H. (1992). Linkage between islands and benthos in the Ohio river, with implications for riverine management. *Can. J. Fish. Aquatic Sci.* 49 (9), 1873–1882. doi: 10.1139/f92-207
- Thorp, J. H., Thoms, M. C., and Delong, M. D. (2006). The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Res. Appl.* 22, 123–147. doi: 10.1002/rra.901
- Tockner, K., and Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environ. Conserv.* 29, 308–330. doi: 10.1017/S037689290200022X
- Villéger, S., Mason, N. W. H., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301. doi: 10.1890/07-1206.1
- Ward, J. V. (1989). The four-dimensional nature of lotic ecosystems. *J. North Am. Benthol. Soc.* 8, 2–8. doi: 10.2307/1467397
- Ward, J. V., Tockner, K., and Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul. Rivers Res. and Manag.* 15, 125–139. doi: 10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E
- Ward, J. V., Tockner, K., Arscott, D. B., and Claret, C. (2002). Riverine landscape diversity. *Freshw. Biol.* 47, 517–539. doi: 10.1046/j.1365-2427.2002.00893.x
- Weigelhofer, G., Feldbacher, E., Trauner, D., Pölz, E., Hein, T., and Funk, A. (2020). Integrating conflicting goals of the EC water framework directive and the EC habitats directives into floodplain restoration schemes. *Front. Environ. Sci.* 8, 538139. doi: 10.3389/fenvs.2020.538139
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Williams, J. E., Gregory, S., and Wildman, R. (2024). Fish assemblage structure and habitat relationships of a large floodplain river in Western North America. *River Res. Appl.* 40 (5), 809–820. doi: 10.1002/rra.4273
- Wohl, E., Rathburn, S., Dunn, S., Iskin, E., Katz, A., Marshall, A., et al. (2024). Geomorphic context in process-based river restoration. *River Res. Appl.* 40 (3), 322–340. doi: 10.1002/rra.4236
- Wolter, C., and Bischoff, A. (2001). Seasonal changes of fish diversity in the main channel of the large lowland river Oder. *Regul. Rivers Res. and Manag.* 17, 595–608. doi: 10.1002/rrr.645
- Wolter, C., and Freyhof, J. (2004). Diel distribution patterns of fishes in a temperate large lowland river. *J. Fish Biol.* 64, 632–642. doi: 10.1111/j.1095-8649.2004.00327.x
- Wolter, C., Buijse, A. D., and Parasiewicz, P. (2016). Temporal and spatial patterns of fish response to hydromorphological processes. *River Res. applic.* 32, 190–201. doi: 10.1002/rra.2980
- Wu, J., Fan, M., Zhang, H., Shaikat, M., Best, J. L., Li, N., et al. (2024). Decadal evolution of fluvial islands and its controlling factors along the lower Yangtze river. *Front. Environ. Sci.* 12, 1388854. doi: 10.3389/fenvs.2024.1388854
- Zar, J. H. (2010). *Biostatistical Analysis*. 5th ed. Upper Saddle River, NJ: Prentice Hall.
- Zeug, S. C., and Winemiller, K. O. (2008). Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Res. Appl.* 25, 90–102. doi: 10.1002/RRA.1061