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Effects of Lateral Hydrological Connectivity on the Taxonomic and Functional Structure of Fish Communities in Saône River Floodplains (France): Implications for Non-Native Species Distribution

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ABSTRACT

1. Large alluvial plain rivers provide a complex mosaic of freshwater habitats characterised by a lateral hydrological connectivity (LHC) gradient between the main channel and floodplains. This connectivity plays a key role in structuring aquatic communities, influencing species distribution, diversity, and ecosystem processes. The aims of our study were to assess the effects of the LHC gradient on both fish taxonomic and functional diversity, and to characterise the effects of this connectivity on the distribution of non-native species.
2. Community data were gathered through electrofishing at five sites in the main channel of the Saône River (France), and in four permanently (parapotamic) and four occasionally (plesiopotamic) connected oxbows. Functional diversity was investigated using a trait-based approach as surrogates of ecosystem processes.
3. A total of 28 fish species were identified, including 14 non-native species. Our results show that main channel and plesiopotamic oxbows exhibited distinct compositional and structural patterns of fish communities, while parapotamic oxbows displayed an intermediate composition and community structure. Taxonomic and functional diversity decreased along the lateral continuum from the main channel to plesiopotamic waterbodies. In contrast, while non-native species richness was similar between the main channel and floodplains, their densities were higher in floodplain oxbows.
4. These findings highlight the prominent role of hydrological connectivity in sustaining both taxonomic and functional diversity in riverine ecosystems. Fish community variations between habitats may be explained by physical changes resulting from reduced connectivity, primarily characterised by a loss of depth and surface area, which in turn affect a broad spectrum of abiotic and biotic factors. High densities of non-native species in lentic environments like oxbows can be attributed to specific abiotic conditions (e.g., hypoxia, rapid temperature fluctuations and eutrophication) and the greater tolerance and plasticity

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of non-native species compared to native species. Additionally, the absence of predators reduces top-down control and intensifies competition with native species for resources.

5. Conservation and management strategies should prioritise preserving and restoring connectivity to support native fish communities, limit the dominance of non-native species, and maintain the ecological integrity of freshwater ecosystems.

1 | Introduction

Large alluvial plain rivers host numerous meanders and side arms that are partially or fully hydrologically disconnected from the main channel. These perifluvial habitats, known as side channels, oxbow lakes or "*lônes*" (local term used exclusively for the Saône, Rhône and Isère rivers) are structured along a lateral hydrological connectivity (LHC) gradient (Amoros and Bornette 2002). Their morphological diversity results from complex interactions between hydrological and sedimentary processes (Doyle et al. 2005), which are significantly and synergistically influenced by water discharge and river management practices. By exhibiting a broad range of environmental conditions (e.g., temperature regime, dissolved oxygen, flow regime, water depth, sediment and nutrient loading, and various degrees of connectivity to the main river channel), and thus habitat heterogeneity, perifluvial freshwater habitats hold major ecological importance and support rich diversity (Ward et al. 1999). The ecological functioning of these habitats largely depends on their hydrological connectivity with the main river channel, which plays a key role in structuring aquatic communities (Heino et al. 2015; Virgilio et al. 2022). Several studies have reported a substantial influence of hydrological dynamics and connectivity levels with the main channel of the river as drivers of the composition and structure of fish species assemblages (Fernandes et al. 2014; Manfrin et al. 2020; Virgilio et al. 2022). Depending on the degree of connectivity, oxbow habitats may serve as spawning grounds, shelters and nurseries for fry, as well as feeding and wintering grounds for a wide range of aquatic organisms (e.g., ichthyofauna) (Hohausová et al. 2003; Osorio et al. 2011). They also provide refuge from predators (Sedell et al. 1990), as well as from environmental (e.g., river floods, droughts, and ebbing periods) and anthropogenic (e.g., pollution) disturbances (Obolewski et al. 2009). However, intensified management of waterways has often profoundly altered flood regimes, thereby disrupting the functioning of floodplain habitats and accelerating sedimentation processes. These alterations can disrupt environmental filters, leading to changes in species composition, and potentially facilitating the spread of non-native species (Bunn and Arthington 2002).

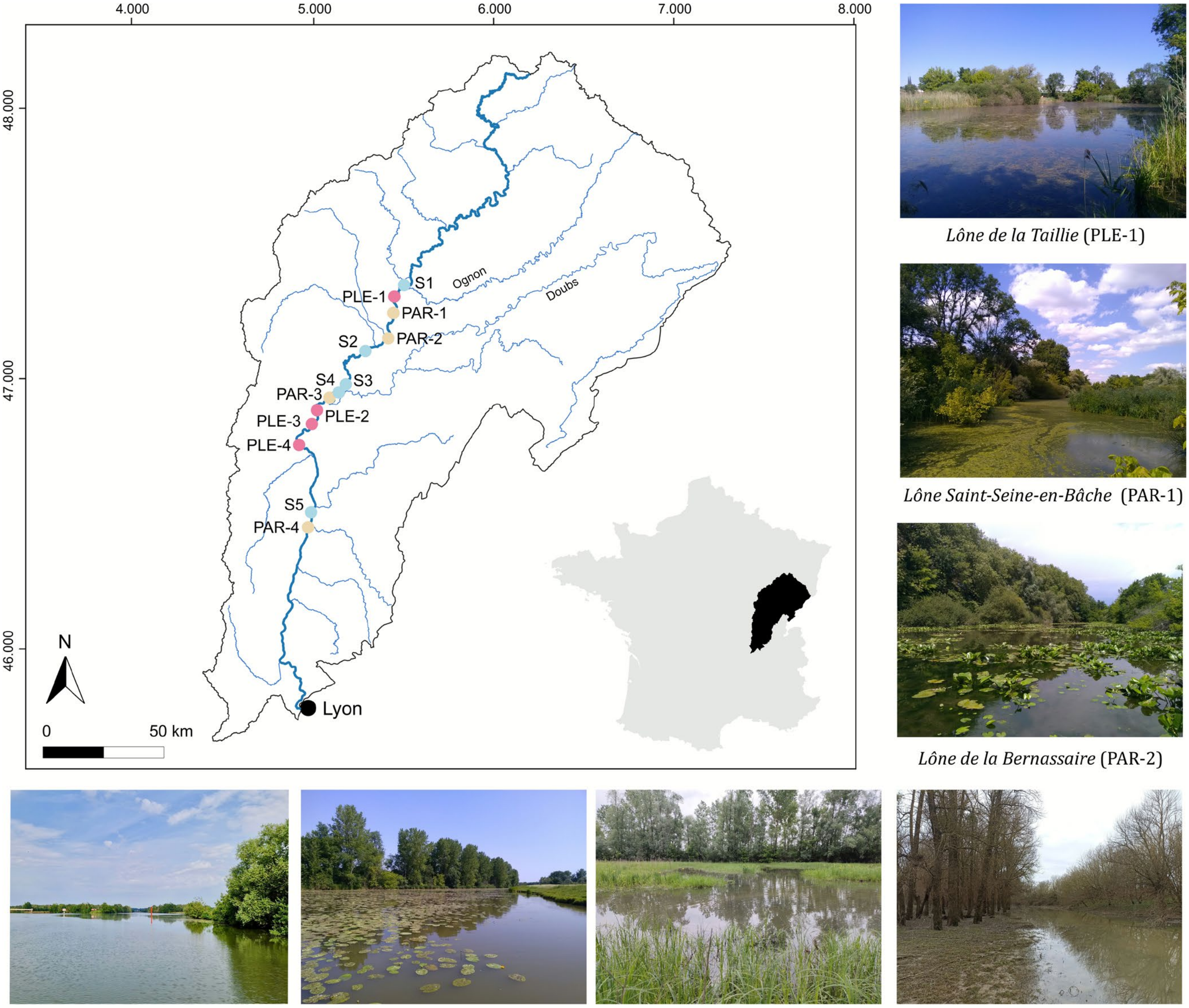
Freshwater environments are highly sensitive to species introductions (Dudgeon et al. 2006; Olden et al. 2010; Strayer 2010). Non-native species are defined as species living outside their native distributional range, introduced by humans, either intentionally or accidentally. These species may have various effects on the local ecosystem, potentially spreading uncontrollably and becoming invasive, which affects native biodiversity as well as ecosystem functions and services. Colonisation of freshwater ecosystems by non-native species may drastically modify the natural habitat, leading to a compositional and structural reshuffling of native species assemblages (Cucherousset and Olden 2011). Several mechanisms may drive these changes: (1) habitat alteration causing the disappearance of microhabitats and associated diversity (including species potentially subject to conservation measures) (Hermoso et al. 2011); (2) alteration of the food web structure (Vander Zanden et al. 1999; Sagouis et al. 2015; David et al. 2017); (3) modification of biotic interactions (Gallardo et al. 2016); and/or (4) the creation of new habitats for a new range of species (Rodriguez 2006). The preservation and management of freshwater ecosystems against biological invasions must be a top priority in order to maintain biodiversity as well as the ecological processes and services they provide. Therefore, in response to the increasing degradation of aquatic environments, and more specifically of riparian and perifluvial areas, numerous restoration strategies have been proposed and implemented to reconnect or enhance connectivity between these habitats with the river's main channel (Obolewski and Glińska-Lewczuk 2011; Seidel et al. 2017). Understanding the role of perifluvial habitats in the spread of non-native species is urgently needed to better predict the future of aquatic communities, prevent their possible degradation, and set guidelines for optimal conservation and management of these habitats.

Despite their high ecological value, the influence of perifluvial habitats on fish communities, and consequently on non-native species, remains poorly studied in French rivers. Located in eastern France, the Saône River is a prime example of a large river system where both natural and anthropogenic factors influence aquatic habitats and species distributions. The numerous oxbows present along the river offer an opportunity to investigate the relationship between lateral hydrological connectivity and ichthyofauna communities. In this context, the present study aims (1) to describe and compare the composition and structure of fish communities associated with the Saône River and oxbow sites; to assess (2) the influence of lateral hydrological connectivity on fish taxonomic (i.e., species composition, community structure) and functional diversity (i.e., through a trait-based approach); and (3) to characterise the effects of this connectivity on the distribution of non-native species.

2 | Materials and Methods

2.1 | Study Site

Located in eastern France, the Saône River draws its source from the Vosges Mountains (Vioménil) at an altitude of 405 m and flows to its confluence with the Rhône River at Lyon at an altitude of 160 m (Figure 1). With a Strahler order 6, the Saône River receives 20 major tributaries, of which the Doubs and the Ognon are the largest, and it is the largest tributary of



Lône de la Taillie (PLE-1)

Lône Saint-Seine-en-Bâche (PAR-1)

Lône de la Bernassaire (PAR-2)

S4 - *Écuelles*

Lône d'Uchizy (PAR-4)

Lône du Breuil (PLE-3)

Lône du Pâquier des Bordes (PAR-3)

FIGURE 1 | The Saône River basin and location of the electrofishing sampling sites, with S1: Heuilley-sur-Saône, S2: Chaugey, S3: Seurre, S4: Écuelles, S5: Uchizy, PAR-1: *Lône de Saint-Seine-en-Bâche*, PAR-2: *Lône de la Bernassaire*, PAR-3: *Lône du Pâquier des Bordes*, PAR-4: *Lône d'Uchizy*, PLE-1: *Lône de la Taillie*, PLE-2: *Lône du Triot*, PLE-3: *Lône du Breuil*, and PLE-4: *Lône de Teppe Turenne*. Blue corresponds to Saône River main channel sites, brown to parapotamic oxbows, and pink to plesiopotamic oxbow sites.

the Rhône River. The Saône extends for approximately 473 km with an average slope of 4 cm per kilometre, an average discharge of 160 m^3/s before the confluence with the Doubs and 450 m^3/s at the confluence with the Rhône River in Lyon, as well as a catchment area of around 30,000 km^2. This slight slope promotes the existence of a wide range of freshwater habitats (e.g., oxbows). Among the 47 oxbows currently identified along the Saône River, eight were selected, including: (1) four parapotamic oxbows (permanently connected with the main channel of the Saône River; PAR-1: *Lône de Saint-Seine-en-Bâche*, PAR-2: *Lône de la Bernassaire*, PAR-3: *Lône du Pâquier des Bordes*, and PAR-4: *Lône d'Uchizy*); and (2) four plesiopotamic oxbows (connected with the main channel only during inundation periods; PLE-1: *Lône de la Taillie*, PLE-2: *Lône du Triot*, PLE-3: *Lône du Breuil*, and PLE-4: *Lône de Teppe Turenne*) (Figure 1). These oxbows were selected to represent a wide range of physical characteristics (e.g., surface area, depth, connectivity) (Table S1). In addition, five stations (S1: Heuilley-sur-Saône, S2: Chaugey, S3: Seurre, S4: Écuelles, and S5: Uchizy) were sampled in the Saône main channel (Figure 1, Table S1).

2.2 | Fish Sampling Design in Saône and Oxbow Habitats

According to their presence within each site, four different types of microhabitats were identified and sampled: (1) open water microhabitat (no macrophyte, rock, or branches), (2) macrophyte-dominated microhabitat, (3) rock microhabitat, and (4) branch-dominated microhabitat. Fish communities were sampled by electrofishing from May to July 2024.

Depending on the depth (Table S1), sites were fished by wading or using a boat, with a straight DC electrofishing device (EFKO FEG 8000, EFKO-Elektrofischfanggeräte GmbH, Leutkirch, Germany). Each sampling point corresponded to the immersion of the anode three times (~6.5 m^2 sampled per immersion) in the same type of habitat, resulting in a total surface area of approximately 20 m^2 per sampling point. Overall, between 10 and 18 sampling points were carried out at each site, depending on the surface of each available microhabitat. Captured fish were then sorted into tanks with continuous water flow to ensure they remained oxygenated and to minimise stress associated with handling. Fish were identified to species level and counted. Species listed as non-native and invasive species were euthanised using an eugenol solution, as releasing them into the natural environment is strictly prohibited in France (Articles L.411-5 to L.411-10 of the Environmental Code and Articles R.411-37 to R.411-47 of the Environmental Code and Decrees related to the prevention of the introduction and spread of invasive alien species).

2.3 | Sampling Effort, Taxonomic Diversity Metrics, and Fish Communities' Variation Across Sites

Hill's number of order q were calculated on fish community densities for each sampling site, with species richness ($q=0$), Shannon diversity ($q=1$), and Simpson's inverse ($q=2$) (Jost 2006). To assess sampling effort and compare diversity variation across sites, rarefied diversity was computed from individual-based rarefaction curves for fish communities (rarefied to the lowest number of individuals among sites: 181 individuals). Non-parametric Kruskal–Wallis tests followed by Dunn's post hoc pairwise tests were conducted to test for significant differences in species richness and diversity among Saône River sites and the type (parapotamic or plesiopotamic) of oxbow sites, as well as to compare the proportion and density of non-native fish species between these environments. Principal Coordinates ordination Analyses (PCoA) were performed on Hellinger-transformed fish densities to investigate variation in fish community composition and structure between sites and microhabitat types (i.e., open water microhabitat, macrophyte-dominated microhabitat, rock microhabitat, as well as branch-dominated microhabitat). The Hellinger transformation was applied in order to minimise the greater weight given to rare species (Legendre and Gallagher 2001). All statistical analyses were performed using R software (version 4.2.0, R Core Team 2022). Rarefaction curves and diversity metrics were conducted using the *iNEXT* package (Hsieh et al. 2016). PCoA were conducted using the *vegan* package (Oksanen et al. 2020).

2.4 | Trait Collection and Functional Diversity Analyses

Sixteen functional traits, divided into 50 modalities, were selected to reflect the diversity of fish strategies (Table 1). These traits are commonly used in studies on fish functional diversity and are suitable proxies for freshwater ecosystem functioning (Mason et al. 2008; Pool et al. 2014; Villéger et al. 2014). Trait information was compiled from peer-reviewed literature, *FishBase* (Froese and Pauly 2025) and freshwaterecology.info (Schmidt-Kloiber and Hering 2015) databases, as well as expert knowledge. Fish species were scored for each trait modality based on their affinity using a fuzzy coding procedure (Chevenet et al. 1994), with a score ranging from 0 (no affinity) to 4 (exclusive affinity) (Table S2). This approach allows for the integration of intra-specific variability in certain traits (e.g., feeding diet), providing a more realistic representation of species functional roles within the ecosystem. A species-trait density matrix, containing the total densities of each modality within sites, was generated by multiplying the fish species density matrix (species densities within fishing sites) with the species-trait matrix, which contains the relative expression of trait modalities by species after standardisation of scores to 1 per trait and per species. This procedure ensures that all traits contribute equally to the functional analysis by assigning a weight to each modality, regardless of the number of modalities associated with each trait.

The functional structure (functional α diversity) of fish communities within each site was characterised using five complementary indices computed using a subset of Principal Coordinates ordination Analysis axes (first 8 PCoA axes that accounted for 76.4% of the total variance of the multidimensional functional space), based on Euclidean distance of the standardised species-trait density matrix (Villéger et al. 2008; Laliberté and Legendre 2010): the (1) functional richness (FRic); within a community, each species has a unique position in the multidimensional functional space based on the combination of its individual traits. FRic represents the proportion of functional space (convex hull volume [Cornwell et al. 2006]) filled by the species community. Sites with high functional richness are characterised by species with a broad range of functional traits, playing many different roles within the ecosystem; the (2) functional evenness (FEve) that describes the regularity of spacing of species within the multidimensional functional space and the evenness of distribution of abundance across species. FEve may be used as an indicator of under- or over-use of environmental niches and resources (Mason et al. 2005). A low FEve indicates a less regular species placement in functional space and may be interpreted as a high proportion of functionally similar species; the (3) functional divergence (FDiv), that indicates the placement of species weighted by abundance in the multidimensional functional space relative to the centroid. FDiv indicates whether abundant species are located close to the centroid (functional convergence, low FDiv values) or towards the edges of the functional space defined by the whole community (functional divergence, high FDiv values) (Mason et al. 2005); (4) the functional dispersion (FDis), defined as the mean-weighted distance of individual species in the functional space to the centroid (Laliberté and Legendre 2010), that measures the spread and diversity of traits in the functional space. High FDis values indicate that species within the community are functionally diverse and spread out in trait space, representing different functional roles or strategies; and the (5) functional redundancy (FR), defined as the portion of functional traits shared by species within a community or ecosystem, was also calculated. FR can serve as an indicator of ecosystem resilience (Schmera et al. 2017). A high FR value reflects a community with many functionally similar species, suggesting greater ecological stability and buffering capacity, making it less sensitive to environmental upheavals or species

TABLE 1 | Overview of the functional traits and their modalities used to characterise functional diversity of fish communities in Saône main channel and oxbow sites.

Traits	Trait modalities	Definition	Labels	Ecological meaning
Common adult length (cm)	Very small (< 10)	Very small size	VS	Habitat use, trophic interactions, growth rate, fish mobility
	Small (10–20)	Small size	S	
	Medium (21–40)	Medium size	M	
	Large (≥ 40)	Large size	LS	
Habitat	Bentho-pelagic	Living in both the bottom and open water	Ben-Pel	Environmental niche, habitat use
	Pelagic	Living in the open water	Pel	
	Demersal	Living near the bottom	Dem	
Habitat rheophily	Eurytopic	Adapted for a wide range of flow types	Eury	Local hydrodynamic, fish ecological niche, trophic interactions, habitat use
	Limnophilic	Living in slow flows	Limno	
	Rheophilic	Living in fast flows	Rheo	
Reproduction habitat	Phytophilic	Lay their eggs on vegetation	Phyto	Environmental niche, habitat use
	Phyto-lithophilic	Lay their eggs on both vegetation and stones	Phy-Li	
	Lithophilic	Lay their eggs on rocky substrates	Lith	
	Other	Other	RH-O	
Migration	No migration	Sedentary species	NoMi	Dispersal ability, habitat use
	Potamodromous species	Migrate exclusively within freshwater	Pota	
	Diadromous species	Migrate between freshwater and saltwater	Diad	
Feeding diet	Invertivore	Feed primarily on invertebrates	Inver	Thophic interactions, nutrient cycling, habitat use
	Piscivore	Feed primarily on fish	Pisci	
	Herbivore	Feed primarily on vegetation	Herb	
	Carnivore	Feed primarily on other animals	Carn	
	Omnivore	Feed on both vegetation and animals	Omni	
Feeding habitat	Benthivorous	Feed on benthic organisms	Benth	Thophic interactions, habitat use
	Water column	Feed on pelagic organisms	WC	
Female reproductive maturity (year)	Very short (≤ 2)	Very short reproductive maturity	VS-RM	Life-history strategies, dispersal ability, recovery and resilience
	Short (2.1–3)	Short reproductive maturity	S-RM	
	Medium (3.1–4)	Medium reproductive maturity	M-RM	
	Long (4.1–5)	Long reproductive maturity	L-RM	
	Very long (> 5)	Very long reproductive maturity	VL-RM	
Spawning time	Winter	Breeding during the winter period	Win	Life-history strategies, dispersal ability, recovery and resilience
	Summer	Breeding during the summer period	Sum	

(Continues)

TABLE 1 | (Continued)

Traits	Trait modalities	Definition	Labels	Ecological meaning
Fecundity (number of oocytes)	Low (< 10,000)	Low fecundity	LF	Life-history strategies, dispersal ability, recovery and resilience
	Medium (10,000–100,000)	Medium fecundity	MF	
	High (> 100,000)	High fecundity	HF	
Egg diameter (mm)	Small (< 1.35)	Small egg diameter	S-ED	Life-history strategies, dispersal ability
	Medium (1.35–2)	Medium egg diameter	M-ED	
	Large (> 2)	Large egg diameter	L-ED	
Larval length (mm)	Small (≤ 4.2)	Small larval length	S-LL	Life-history strategies, dispersal ability
	Medium (4.3–6.3)	Medium larval length	M-LL	
	Long (> 6.3)	Long larval length	L-LL	
Parental care	No protection	No protection	NoPro	Life-history strategies
	No protection, but nesters	No protection, but nesters or eggs hiders	Nest	
	Protection with nesters	Protection with nesters or eggs hiding	Pro	
Origin	Native	Originate from a specific area	NAT	Life history
	Exotic	Introduced outside their natural range	EXO	
Activity	Diurnal	Active during the day	Diurn	Habitat use, trophic interactions
	Nocturnal	Active during the night	Noct	
Lifespan (year)	Low (≤ 8)	Low lifespan	L-LS	Life history, growth rate, recovery and resilience
	Medium (8–15)	Medium lifespan	M-LS	
	High (> 15)	High lifespan	H-LS	

loss. Functional indices were computed using the *FD* package (Laliberté et al. 2014).

3 | Results

3.1 | Electrofishing Sampling Effort

A total of 7420 individual fish were sampled and identified across the five sites in the main channel of the Saône River (2541 individuals) and the eight oxbow sites (4879 individuals); encompassing 28 fish species spanning nine families (Table S3). Nineteen species were shared between oxbows and Saône River main channel sites, while eight species were found exclusively in the Saône River channel. Combining data from all 13 studied sites, the overall individual-based rarefaction curve (Figure 2; black curve at the bottom right) showed that a plateau was reached at about 28 fish species, giving a fair representation of fish communities in the Saône River. At the site level, individual-based rarefaction curves showed that the sampling effort tended to reach an asymptote, indicating a sufficient effort to capture the fish diversity in oxbows and Saône main channel sites (Figure 2).

3.2 | Saône River and Oxbows Fish Communities' Description

Among the 28 identified fish species, 14 were classified as non-native (the freshwater blenny *Salariopsis fluviatilis*, the pumpkinseed *Lepomis gibbosus*, the black bass *Micropterus salmoides*, the gibel carp *Carassius gibelio*, the volga nase *Chondrostoma variabile*, the common carp *Cyprinus carpio*, the asp *Leuciscus aspius*, the stone moroko *Pseudorasbora parva*, the European bitterling *Rhodeus amarus*, the round goby *Neogobius melanostomus*, the black bullhead *Ameiurus melas*, the ruffe *Gymnocephalus cernua*, the zander *Sander lucioperca*, and the wels catfish *Silurus glanis*) (Table S3). The most diversified families were Cyprinidae with 17 species, followed by Percidae and Centrarchidae with three and two fish species, respectively. For sites sampled on the Saône River main channel, the site of Heuilley-sur-Saône (S1) was dominated by the bleak *A. alburnus* (32.9%), the rudd *S. erythrophthalmus* (16.3%), and both the roach *R. rutilus* and the European bitterling *R. amarus* (9.5%). Like S1, Chaugey (S2) was characterised by a high density of the bleak *A. alburnus* (46.5%), followed by the roach *R. rutilus* (16%) and the pumpkinseed *L. gibbosus* (8.2%). The site Seurre (S3) was

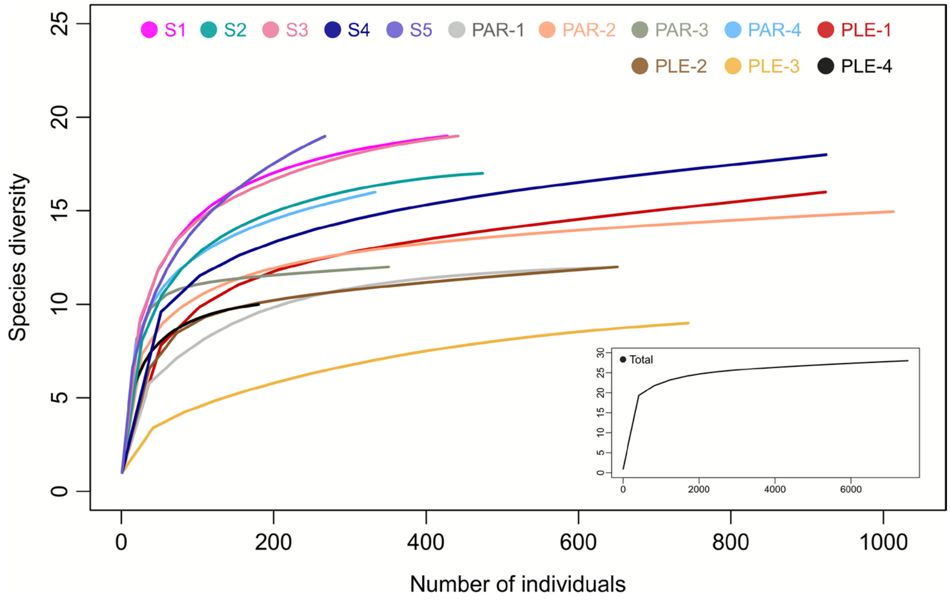


FIGURE 2 | Rarefaction curves for fish communities within the 13 sites sampled in the Saône River, including Saône main channel (S1 to S5), parapotamic oxbows (PAR-1 to PAR-4), and plesiopotamic oxbows (PLE-1 to PLE-4) sites. The black line at the bottom right represents the rarefaction curve for all sites combined.

also dominated by the bleak *A. alburnus* (21.9%), followed by the roach *R. rutilus* (16.6%) and the rudd *S. erythrophthalmus* (16.4%). Écuelles (S4) was highly dominated by the bleak *A. alburnus* (59.2%), followed by the roach *R. rutilus* (7.7%) and the pumpkinseed *L. gibbosus* (6.3%). Finally, as the previous five sites of the Saône main channel, Uchizy (S5) was dominated by the bleak *A. alburnus* (26.7%), closely followed by the chub *Squalius cephalus* (26%) and the rudd *S. erythrophthalmus* (13.3%). For parapotamic oxbows, the *Lône de Saint-Seine-en-Bâche* (PAR-1) was dominated by the white bream *Blicca bjoerkna* (29.9%), closely followed by the bleak *Alburnus alburnus* (27.8%) and the *P. parva* (25.6%). The *Lône de la Bernassaire* (PAR-2) was dominated by the bleak *A. alburnus* (43.3%), the stone moroko *P. parva* (17.5%), and the roach *Rutilus rutilus* (9.8%). The *Lône du Pâquier des Bordes* (PAR-3) was dominated by the bleak *A. alburnus* (29.5%), followed by the white bream *B. bjoerkna* (11.9%) and the pumpkinseed *Lepomis gibbosus* (11.4%). Finally, the *Lône d'Uchizy* (PAR-4) was characterised by a high density of the bleak *A. alburnus* (25.4%), followed by the non-native invasive stone moroko *P. parva* (19.2%) and the non-native gibel carp *C. gibelio* (11.7%). For plesiopotamic oxbows, the *Lône de la Taillie* (PLE-1) was dominated by three non-native species, the stone moroko *P. parva* (61.8%), the pumpkinseed *L. gibbosus* (12%), and the gibel carp *C. gibelio* (8.9%). The *Lône du Triot* (PLE-2) was dominated by a high density of the bleak *A. alburnus* (74.8%), and to a lesser extent by the European bitterling *R. amarus* (4.7%) as well as the white bream *B. bjoerkna* (4.1%). As for PAR-3, the *Lône du Breuil* (PLE-3) was dominated by a high density of the bleak *A. alburnus* (80.3%), followed by the stone moroko *P. parva* (15.2%) and the rudd *Scardinius erythrophthalmus* (2.8%). Finally, the *Lône de Teppe Turenne* (PLE-4) was dominated by the non-native stone moroko *P. parva* (52.5%), followed by the non-native gibel carp *C. gibelio* (14.3%) and the roach *R. rutilus* (9.4%) (Table S3).

3.3 | Fish Community Variations Among Sites and Microhabitat Types

At the site scale, the PCoA highlighted distinct communities between the Saône River main channel and oxbow sites (Figure 3). While the Saône main channel sites displayed similar fish communities, the oxbow sites showed greater heterogeneity with distinct compositional and structural patterns between parapotamic and plesiopotamic oxbows. No clear differences were found between the four parapotamic oxbows (PAR-1 to PAR-4). However, plesiopotamic oxbows PLE-1 and PLE-4 exhibited compositional and structural differences from the plesiopotamic oxbows PLE-2 and PLE-3 (Figure 3).

At the microhabitat scale, the PCoA emphasised compositional and structural variations of fish communities among habitats from the Saône River, parapotamic oxbows, and plesiopotamic oxbows (Figure 4). Habitats in parapotamic oxbows exhibited an intermediate composition and structure of fish communities between those of the Saône River and plesiopotamic oxbow sites. Open-water microhabitats were mainly characterised by high densities of the bleak *A. alburnus*, highlighting a clear distinction from the other microhabitat types (i.e., macrophyte-dominated microhabitat, rock microhabitat, and branch-dominated microhabitat). With the exception of Saône main channel sites, no compositional and structural differences in fish communities were observed between microhabitats dominated by macrophytes and those characterised by the presence of branches. In the Saône River main channel, branch microhabitats were characterised by the presence of the spirlin *Alburnoides bipunctatus* and the ruffe *G. cernua*, and macrophyte microhabitats were predominantly dominated by the chub *S. cephalus*, the European perch *Perca fluviatilis*, the pike *Esox lucius*, and the pumpkinseed *L. gibbosus*. In oxbows, microhabitats dominated by macrophytes

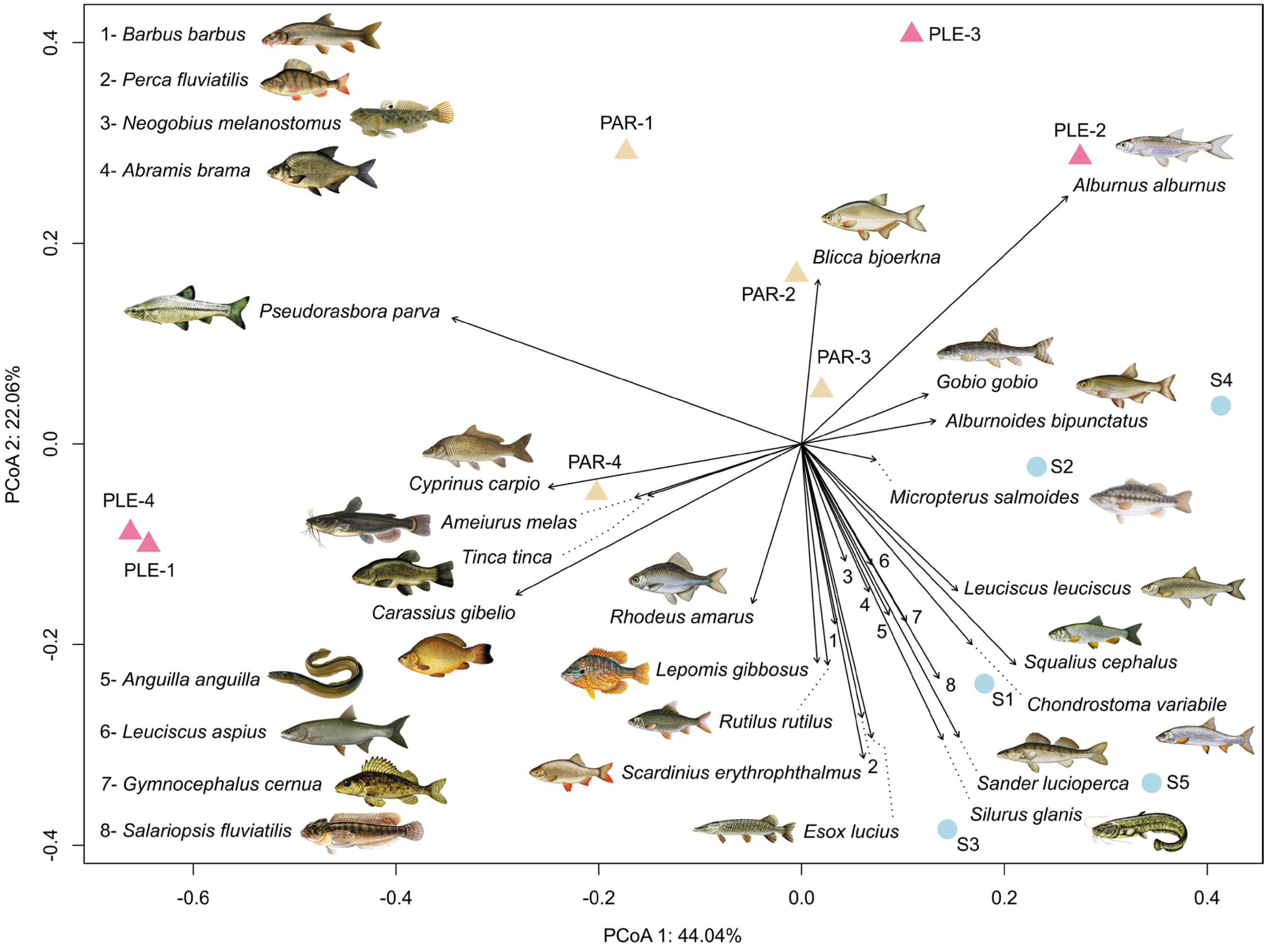


FIGURE 3 | Principal Coordinates ordination Analysis (PCoA) based on Hellinger-transformed fish densities. Blue circles correspond to Saône main channel sites, and triangles to parapotamic (brown) and plesiopotamic (pink) oxbow sites. The first two canonical axes captured 66.10% of the total variance of Hellinger-transformed species composition.

and branches were primarily characterised by the presence of the rudd *S. erythrophthalmus*, the European bitterling *R. amarus*, the common carp *C. carpio*, the tench *Tinca tinca*, and the white bream *B. bjoerkna*, as well as non-native species such as the stone moroko *P. parva*, the gibel carp *C. gibelio*, and the black bullhead *A. melas*. Finally, the fish composition of rock microhabitats in Saône River main channel sites was similar to that of macrophyte microhabitats, although the community structure differed.

3.4 | Taxonomic Diversity Across Saône Main Channel and Oxbow Sites

Overall, the highest levels of species richness and diversity indices were found in Saône River sites (average $R_{rar} = 15.555 \pm 1.676$; average $N_{rar} = 7.406 \pm 1.870$; average $1/\lambda_{rar} = 5.026 \pm 1.768$) compared to oxbow sites (average $R_{rar} = 10.526 \pm 2.482$; average $N_{rar} = 5.145 \pm 2.396$; average $1/\lambda_{rar} = 3.781 \pm 2.020$) (Table 2). For Saône main channel sites, the highest species richness were found at Uchizy (S5; $R_{rar} = 17.024$), Heuilley-sur-Saône (S1; $R_{rar} = 16.717$), and Seurre (S3; $R_{rar} = 16.350$), while the lowest species richness was found at Écuelles (S4; $R_{rar} = 13.049$) (Table 2). However, diversity values were highest at S3 ($N_{rar} = 9.349$; $1/\lambda_{rar} = 7.109$), followed by S1 ($N_{rar} = 8.734$; $1/\lambda_{rar} = 5.915$) and S5 ($N_{rar} = 7.914$; $1/\lambda_{rar} = 5.630$). Finally, S4 showed the lowest diversity values ($N_{rar} = 4.793$; $1/\lambda_{rar} = 2.678$) (Table 2). Among oxbow sites, the highest species richness and diversity values were observed for the *Lône d'Uchizy* (PAR-4) ($R_{rar} = 14.258$; $N_{rar} = 8.590$; $1/\lambda_{rar} = 6.756$), while the lowest species richness and diversity values were found at the *Lône du Breuil* (PLE-3) ($R_{rar} = 5.577$; $N_{rar} = 1.906$; $1/\lambda_{rar} = 1.494$) (Table 2). Whereas a closely similar level of species richness was observed among the *Lône de la Bernassaire* (PAR-2; $R_{rar} = 11.727$), *Lône de la Taillie* (PLE-1; $R_{rar} = 11.496$), and *Lône du Pâquier des Bordes* (PAR-3; $R_{rar} = 11.488$), diversity values were highest at PAR-3 ($N_{rar} = 8.396$; $1/\lambda_{rar} = 6.608$), followed by PAR-2 ($N_{rar} = 5.887$; $1/\lambda_{rar} = 4.037$) and PLE-1 ($N_{rar} = 3.927$; $1/\lambda_{rar} = 2.423$).

3.5 | Impacts of Hydrological Connectivity on Taxonomic Diversity and Non-Native Species

No significant differences were observed in total fish density between the habitats, that is, Saône River main

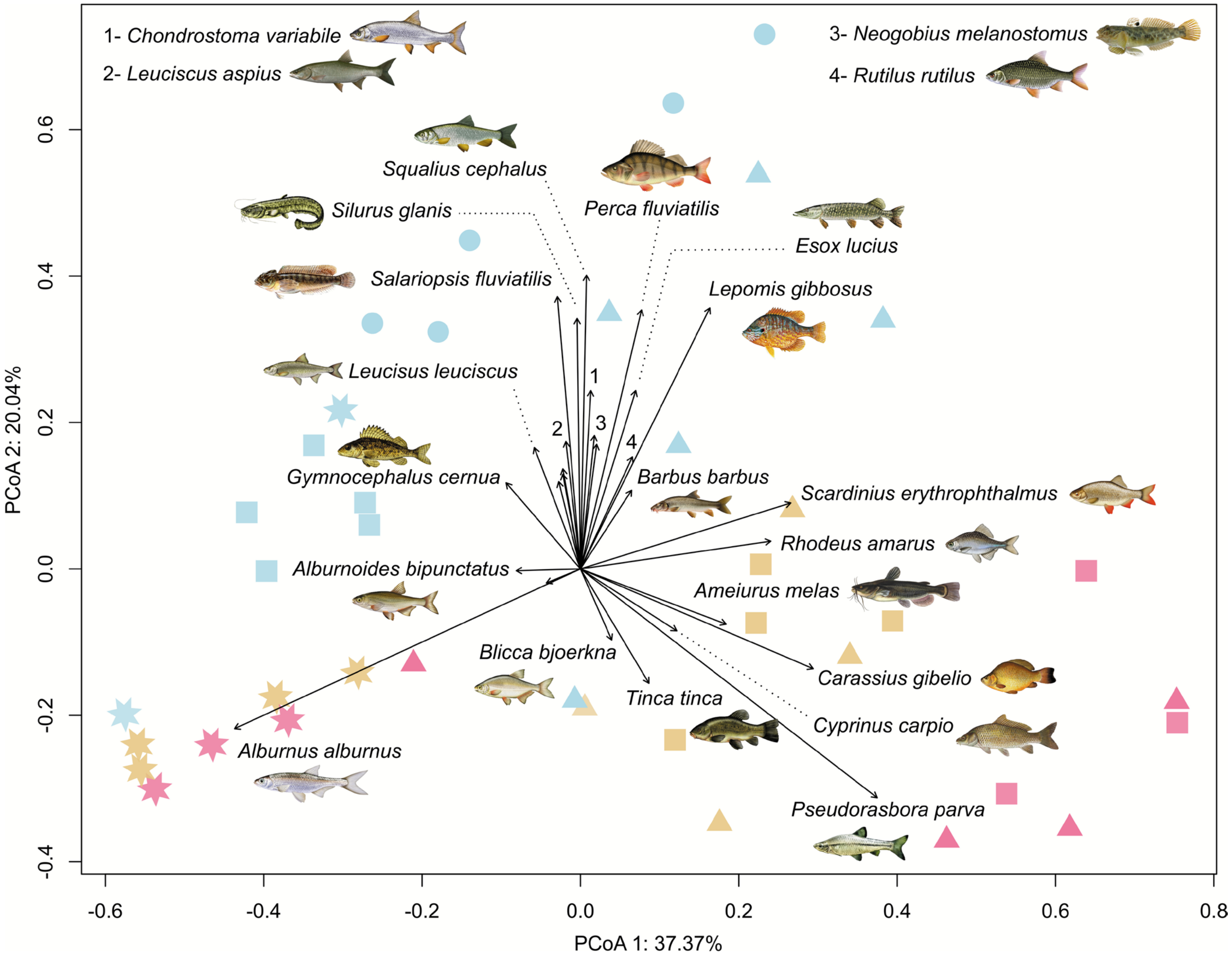


FIGURE 4 | Principal Coordinates ordination Analysis (PCoA) based on Hellinger-transformed fish densities of the different microhabitat types, with open water microhabitat (stars), macrophyte-dominated microhabitat (triangles), rock microhabitat (circles), and branch-dominated microhabitat (squares). Blue corresponds to habitats sampled in the Saône River main channel sites, brown in habitats sampled in parapotamic oxbows, and pink in plesiopotamic oxbow sites. The first two canonical axes captured 57.41% of the total variance.

channel, parapotamic (PAR) and plesiopotamic (PLE) oxbows (Figure 5a). While species richness and Shannon diversity indices showed no variations between Saône River main channel sites and parapotamic oxbows, these indices were significantly higher in Saône River main channel sites compared to plesiopotamic oxbows (species richness: $p = 0.006$; Shannon diversity: $p = 0.014$) (Figure 5b,c). However, no significant differences in species richness variation were observed between parapotamic and plesiopotamic oxbows. A similar trend was observed for Simpson diversity, with no significant differences between the Saône River and parapotamic oxbows. However, Simpson diversity was significantly lower in plesiopotamic oxbows (Figure 5d). Regarding non-native species, their proportion was similar between the Saône River main channel sites and oxbows (Figure 5e). However, their densities were significantly higher in oxbows (parapotamic oxbows: $p = 0.028$; plesiopotamic oxbows: $p = 0.006$) compared to the river main channel (Figure 5f).

3.6 | Functional Diversity Among Saône Main Channel and Oxbow Sites

Overall, Saône River main channel sites displayed significantly ($p = 0.008$) greater functional richness (FRic) values ($\text{FRic}_{\text{mean}} = 0.169 \pm 0.071$) compared to oxbows ($\text{FRic}_{\text{mean}} = 0.027 \pm 0.033$) (Table 2; FRic). Seurre (S3) showed the highest functional richness, followed by Uchizy (S5) and Heuilley-sur-Saône (S1). However, no significant variations were found for functional evenness between Saône River main channel ($\text{FEve}_{\text{mean}} = 0.508 \pm 0.086$) and oxbow ($\text{FEve}_{\text{mean}} = 0.588 \pm 0.129$) sites (Table 2; FEve). The highest FEve values were found for the *Lône d'Uchizy* (PAR-4), *Lône de Teppe Turenne* (PLE-4), and *Lône de la Taillie* (PLE-1). Significant differences ($p = 0.013$) were reported for functional divergence between Saône River main channel ($\text{FDiv}_{\text{mean}} = 0.827 \pm 0.051$) and oxbow ($\text{FDiv}_{\text{mean}} = 0.906 \pm 0.047$) sites (Table 2; FDiv). Similarly, no

TABLE 2 | Taxonomic and functional diversity indices of fish communities for each Saône main channel and oxbow sampling site. Taxonomic indices include species richness (R), rarefied species richness (R_{rar}), Shannon diversity (N), rarefied Shannon diversity (N_{rar}), Simpson diversity ($1/\lambda$), and rarefied Simpson diversity ($1/\lambda_{rar}$). Functional indices include functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and functional redundancy (FR).

	Taxonomic diversity						**Functional diversity**				
Site	**R**	**R_{rar}**	**N**	**N_{rar}**	**$1/\lambda$**	**$1/\lambda_{rar}$**	**FRic**	**FEve**	**FDiv**	**FDis**	**FR**
Saône main channel											
S1—Heuilley-sur-Saône	19	16.717	9.069	8.734	6.021	5.915	$1.758*10^{-1}$	0.553	0.865	2.565	0.344
S2—Chaugey	17	14.633	6.427	6.241	3.835	3.800	$6.245*10^{-2}$	0.524	0.882	2.258	0.352
S3—Seurre	19	16.350	9.715	9.349	7.280	7.109	$2.608*10^{-1}$	0.587	0.826	2.666	0.342
S4—Écuelles	18	13.049	4.973	4.793	2.696	2.678	$1.611*10^{-1}$	0.364	0.811	1.877	0.265
S5—Uchizy	19	17.024	8.045	7.914	5.666	5.630	$1.844*10^{-1}$	0.513	0.752	2.488	0.300
Parapotamic oxbows											
PAR-1—*Lône de Saint-Seine-en-Bâche*	12	9.576	4.841	4.724	4.081	4.033	$8.518*10^{-3}$	0.410	0.878	2.379	0.335
PAR-2—*Lône de la Bernassaire*	15	11.727	6.083	5.887	4.094	4.037	$5.168*10^{-2}$	0.552	0.887	2.312	0.340
PAR-3—*Lône du Pâquier des Bordes*	12	11.488	8.542	8.396	6.717	6.608	$3.662*10^{-3}$	0.546	0.892	2.531	0.310
PAR-4—*Lône d'Uchizy*	16	14.258	8.783	8.590	6.857	6.756	$6.743*10^{-2}$	0.778	0.846	2.642	0.354
Plesiopotamic oxbows											
PLE-1—*Lône de la Taillie*	16	11.496	4.055	3.927	2.435	2.423	$7.655*10^{-2}$	0.644	0.955	2.089	0.317
PLE-2—*Lône du Triot*	12	10.083	2.995	2.921	1.759	1.753	$3.662*10^{-3}$	0.494	0.891	1.297	0.161
PLE-3—*Lône du Breuil*	9	5.577	1.940	1.906	1.497	1.494	$7.270*10^{-6}$	0.519	0.993	1.075	0.122
PLE-4—*Lône de Teppe Turenne*	10	10	4.808	4.808	3.141	3.143	$1.181*10^{-3}$	0.758	0.906	2.451	0.229

significant variations were reported for functional dispersion between Saône River main channel ($FDis_{mean} = 2.371 \pm 0.314$) and oxbow ($FDis_{mean} = 2.097 \pm 0.588$) sites (Table 2; FDis). Finally, no significant differences were found for functional redundancy (FR) between Saône River main channel ($FR_{mean} = 0.321 \pm 0.037$) and oxbow ($FR_{mean} = 0.271 \pm 0.089$) sites (Table 2; FR).

3.7 | Impacts of Hydrological Connectivity on the Functional Diversity

Sites from the Saône River main channel showed a significant ($p = 0.010$) higher functional richness (FRic) compared to plesiopotamic oxbows (Figure 6a). However, no significant variations were found between the main channel and the parapotamic oxbows, as well as between parapotamic and plesiopotamic oxbows. The same pattern was observed for functional divergence (FDiv; $p = 0.003$) (Figure 6c). While the functional redundancy (FR) was similar between the Saône River main channel and parapotamic oxbows, FR was significantly lower in plesiopotamic oxbows (Figure 6e). For all other functional indices, no significant differences were found between the Saône River main channel, parapotamic oxbows, and plesiopotamic oxbows (Figure 6b,d). However, with the exception of functional evenness, which is relatively consistent across habitats (Figure 6b), strong trends were observed between Saône River main channel, parapotamic oxbows, and

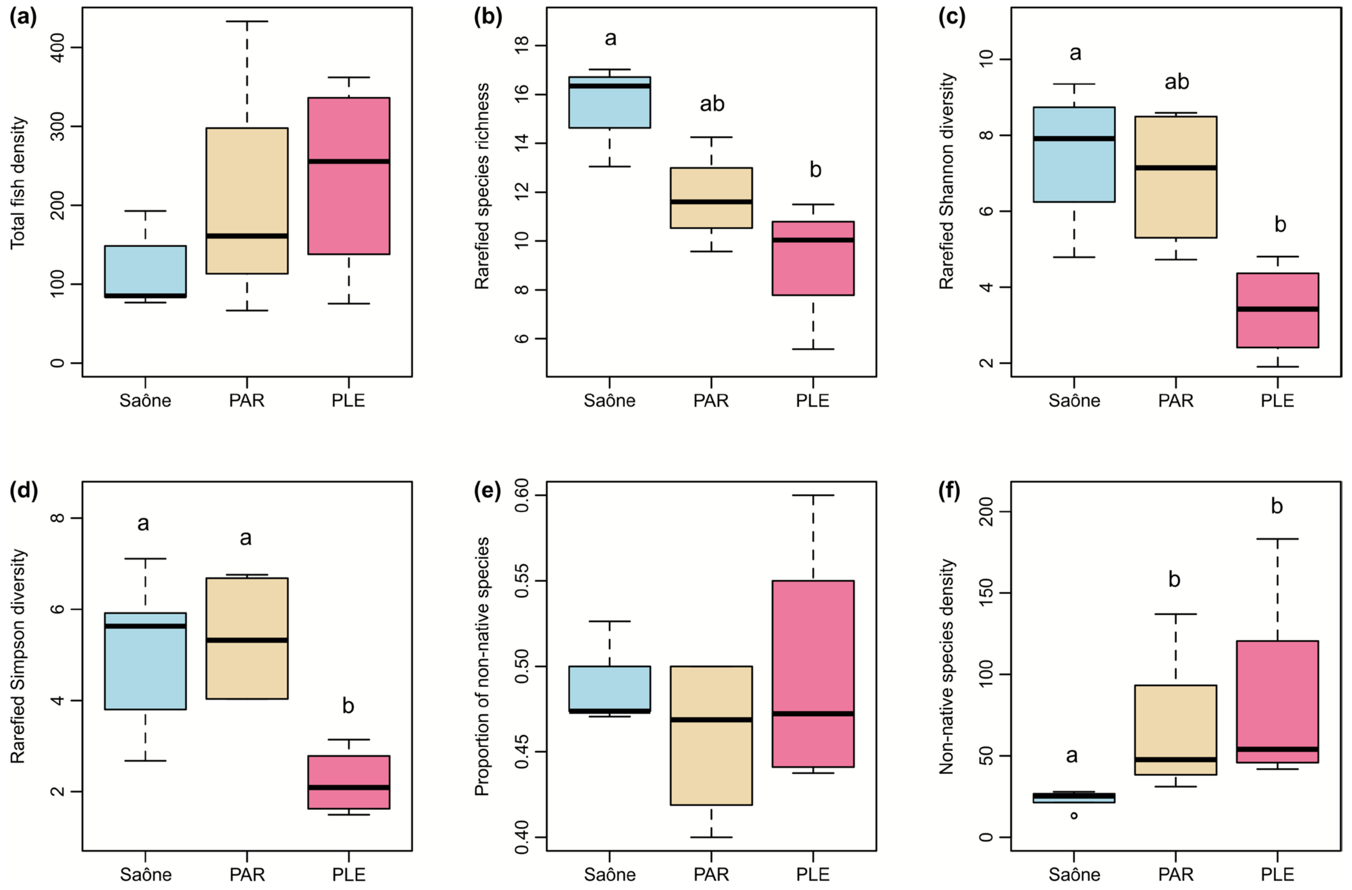


FIGURE 5 | Comparison of (a) total fish density and rarefied diversity metrics, including (b) rarefied species richness, (c) rarefied Shannon diversity, and (d) rarefied Simpson diversity; as well as the (e) proportion and (f) density of non-native species among Saône main channel (S1 to S5), parapotamic oxbow (PAR; PAR-1 to PAR-4), and plesiopotamic oxbow (PLE; PLE-1 to PLE-4) sites. Letters above boxplots indicate significantly different statistical groups resulting from Dunn tests.

plesiopotamic oxbows. Functional dispersion (FDis) was lower in the plesiopotamic oxbows compared to both the Saône main channel and the parapotamic oxbows, which exhibited similar values (Figure 6d).

4 | Discussion

4.1 | Fish Communities of the Saône River and Floodplain Environments

This study identified a total of 28 fish species in the Saône River system, primarily represented by cyprinid species, and comprising 14 native as well as 14 non-native species. At the end of the 19th century, the fish fauna of the Saône River reached 30 native species, including three migratory species that have now disappeared, the European sturgeon *Acipenser sturio*, the American shad *Alosa fallax*, and the sea lamprey *Petromyzon marinus* (Olivier et al. 2022). This significant decline in native species is attributed to the complex interplay of cumulative stressors, including the loss and degradation of freshwater habitats (e.g., river fragmentation due to dams and channelisation), water pollution related to intensified agriculture, as well as the increasing impacts of climate change and biological invasions (Dudgeon et al. 2006; Reid et al. 2019). The upper 13 km of the Saône River, near the source, is characterised by three species, the planer lamprey *Lampetra planeri*, the bullhead *Cottus gobio*, and the brown trout *Salmo trutta* (Huet 1959). This area was not included in the sampling of this study, which explains the absence of these fishes in the collected samples. Finally, the typical native species of the two sections of the river were identified, with the barbel zone covering 93 km and the bream zone extending over the last 366 km (Huet 1959). The fish composition of the Saône River main channel was characterised by a few rheophilic species and numerous eurytopic species. In contrast to most oxbows, the main channel was characterised by the presence of top predators, including the zander *Sander lucioperca*, the asp *Leuciscus aspius*, the wels catfish *Silurus glanis*, the European perch *Perca fluviatilis*, and the pike *Esox lucius*. The low abundance of top predators in the *Lône de la Taillie* is likely related to the greater depth of this oxbow compared to the others. Oxbow habitats were particularly occupied by high densities of limnophilic and eurytopic species such as the native bleak *Alburnus alburnus*, the white bream *Blicca bjoerkna*, the roach *Rutilus rutilus*, the tench *Tinca tinca*, as well as non-native species such as the black bullhead *Ameiurus melas*, the common carp *Cyprinus carpio*, the pumpkinseed *Lepomis gibbosus*, the stone moroko *Pseudorasbora parva*, and the European bitterling *Rhodeus amarus*.

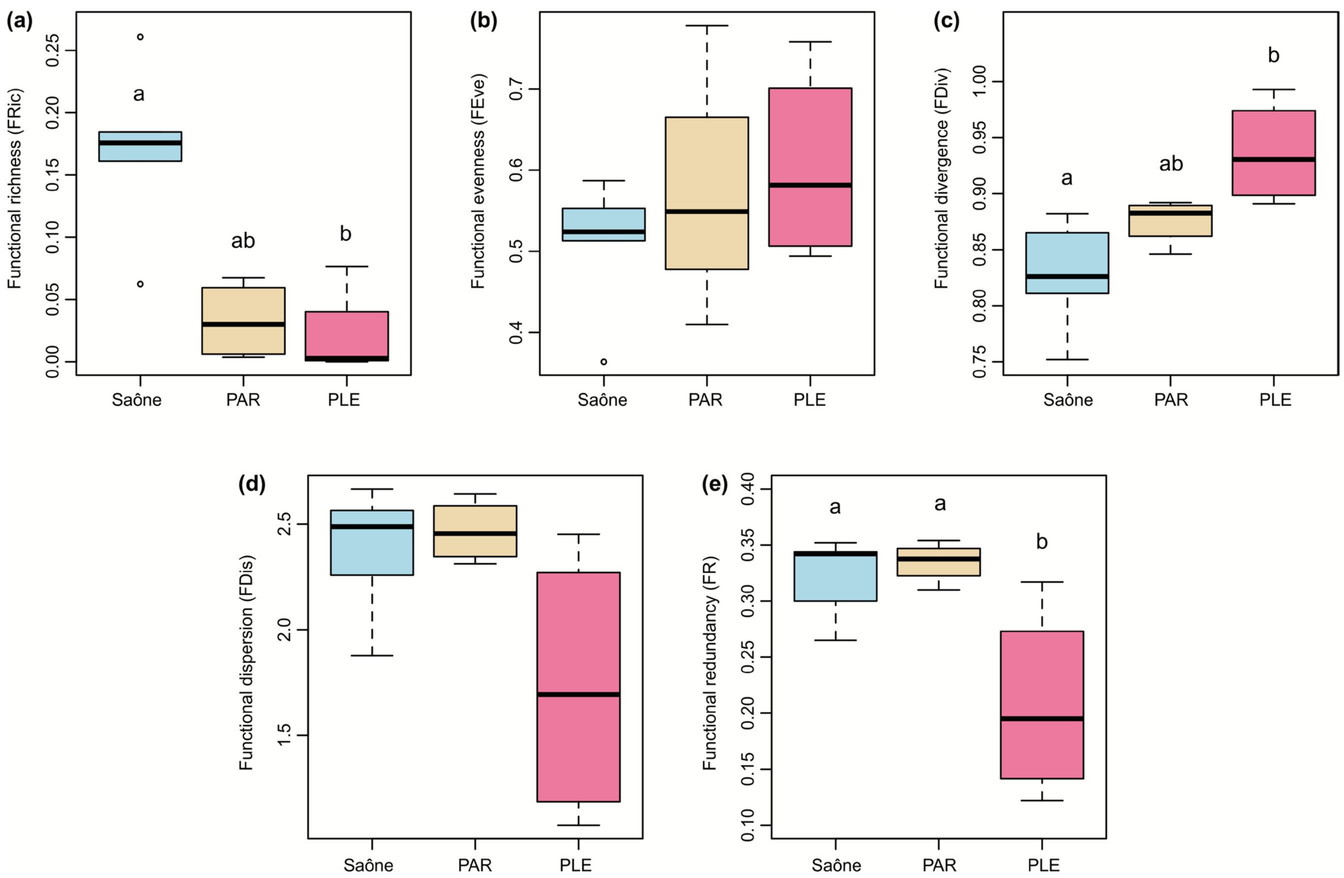


FIGURE 6 | Comparison of functional diversity indices, including the (a) functional richness (FRic), (b) functional evenness (FEve), (c) functional divergence (FDiv), (d) functional dispersion (FDis), and (e) functional redundancy (FR) among Saône main channel (S1 to S5), parapotamic oxbow (PAR; PAR-1 to PAR-4), and plesiopotamic oxbow (PLE; PLE-1 to PLE-4) sites. Letters above boxplots indicate significantly different statistical groups resulting from Dunn tests.

4.2 | Influence of the Lateral Hydrological Connectivity on Diversity Patterns

The composition and structure of fish communities gradually changed as oxbows progressively disconnected from the Saône River. Main channel sites and plesiopotamic oxbows exhibit distinct compositional and structural patterns of fish communities, with parapotamic oxbows displaying an intermediate fish composition and community structure. This pattern has been reported in previous studies across Europe, such as in the French Rhône and Rhine Rivers (Ward et al. 1999), Austrian Danube River (Ward et al. 1999), and German Lippe River (Manfrin et al. 2020), as well as in America in the Mississippi River (Miranda 2005). Consistent with previous studies (Tockner et al. 1998; Ward et al. 1999; Bolland et al. 2012; Manfrin et al. 2020), fish taxonomic diversity—species richness and diversity indices—declined in floodplain waterbodies with increasing isolation from the main river (from the main channel to plesiopotamic oxbows). Significantly higher species richness and diversity were found in the Saône River main channel compared to plesiopotamic oxbows, whereas parapotamic oxbows exhibited intermediate levels of species richness and diversity. These compositional and structural variations between habitats may be explained by physical changes resulting from reduced connectivity, primarily characterised by a loss of depth and surface area, which in turn affect a broad spectrum of abiotic and biotic factors that indirectly influence fish community structure (Amoros and Bornette 2002; Miranda 2005, 2011; Lubinski et al. 2008; Goetz et al. 2015). Due to reduced connectivity with the main channel and depth reduction, oxbow habitats are characterised by stagnant waters, hypoxia, elevated turbidity, warmer temperatures, and eutrophication (Winemiller et al. 2000; Miranda 2011; Goetz et al. 2015). Greater lateral hydrological connectivity may result in higher nutrient exchange, water quality, and habitat availability, enhancing fish species richness and diversity. In addition, shallow oxbows promote riparian vegetation and the growth of a wide range of macrophyte, reducing light penetration through the water column and depleting oxygen levels (Scheffer 1998; Beaufort et al. 2020). These abiotic factors may influence the availability of environmental niches as well as biotic interaction (i.e., predation) and trophic dynamics, thereby resulting in significant compositional and structural changes within fish communities.

The functional richness (FRic) followed a similar trend to taxonomic richness, with greater functional richness observed in environments with stronger lateral hydrological connectivity to the river. The loss of functional richness with the loss of lateral hydrological connectivity is in agreement with previous studies (Schleuter et al. 2012; Liu and Wang 2018). Plesiopotamic oxbows displayed significantly lower FRic than Saône main channel sites. In addition, the strong correlation ($R^2 = 0.81$) between taxonomic and functional richness, along with the presence of fish species with distinct traits, suggests that sites with greater species diversity have more extensive functional space, leading to higher ecological functionality (Petchey and Gaston 2006; Morelli et al. 2018). The higher species richness in the Saône main channel compared to oxbows may explain the higher FRic in the main channel. However, the *Lône d'Uchizy* exhibited comparable or even greater FRic than Saône main channel sites. Its permanent connection to the Saône River, along with its unique morphology—being deeper and wider—could facilitate greater species exchange, leading to increased functional diversity. In contrast to FRic, hydrological connectivity did not appear to influence functional evenness (FEve). Some specific sites, such as *Lône de Saint-Seine-en-Bâche* and Écuelles, displayed lower FEve, which may suggest an imbalance in the distribution of ecological roles. This imbalance could reflect a higher proportion of functionally similar fish species, suggesting that some parts of the niche space, whilst occupied, are under-used (Mason et al. 2005). On the other hand, moderate FEve values observed in the other Saône River and oxbow sites indicate that fish species occupy diverse functional niches and that ecological roles are relatively well distributed. This is supported by high levels of functional divergence (FDiv) within all sites, indicating a high degree of niche differentiation and low resource competition (Mason et al. 2005). Nevertheless, FDiv decreases with increasing hydrological connectivity, with FDiv significantly higher in plesiopotamic oxbows compared to the Saône River. The higher species diversity in connected environments—Saône River and parapotamic oxbows—may lead to increased competition for resources. In addition, the potential abundance of these resources may reduce niche specialisation. In contrast, functional dispersion (FDis) was similar between the Saône River and oxbows but tended to decrease in plesiopotamic oxbows. The lack of a significant difference in FDis, despite strong trends, could be attributed to an insufficient sample size to detect the effect of connectivity on FDis. This result warrants further investigation in future studies. While higher FDiv values indicated a wide range of functional roles among fish species in plesiopotamic oxbows, lower FDis values indicate fish species with similar traits, making plesiopotamic oxbows more vulnerable to disturbances than connected habitats. Lower FDis values are characteristic of environments undergoing significant disturbances (Mouillot et al. 2013). Alongside the lower-moderate FEve values, all sites exhibited low functional redundancy (FR). Although FR levels were closely similar between the main river and the parapotamic oxbows, plesiopotamic oxbows showed significantly lower FR. These lower FEve and FR values emphasise the vulnerability and sensitivity of these ecosystems to potential disturbances (Fonseca and Ganade 2001), such as global warming, pollution, changes in hydrological regimes, and the introduction of non-native species. Fish species occupy specific niches without sufficient functional overlap, which makes certain ecological functions and species traits particularly vulnerable to disturbances. The loss of species can exacerbate this vulnerability, potentially leading to vacant or poorly occupied functional niches, increasing opportunities for potential invaders. This highlights the importance of lateral hydrological connectivity in enhancing functional redundancy and, consequently, ecosystem resilience.

These findings highlight the critical role of hydrological connectivity in enhancing both taxonomic and functional diversity within freshwater ecosystems in the Saône River. Increased connectivity fosters greater species richness and functional richness, contributing to a more resilient ecosystem capable of withstanding disturbances. The significant correlation between taxonomic and functional diversity indicates that diverse species assemblages lead to more extensive functional space, enhancing ecological functionality. Conversely, reduced connectivity, as observed in plesiopotamic oxbows, may lead to decreased diversity and functional redundancy, leaving ecosystems more vulnerable to environmental changes and biological invasions. Consequently, maintaining and restoring lateral hydrological connectivity is crucial for promoting biodiversity and enhancing ecosystem health and resilience.

4.3 | Distribution of Non-Native Species in Saône Freshwater Habitats

Our results show that Saône River freshwater ecosystems are heavily impacted by invasive species, with non-native species accounting for 50% of the fish communities. This high proportion of non-native fish species may be explained by the role that inland waterways play in the dispersal of non-native fish that have been voluntarily or involuntarily introduced mostly since the 19th century onwards in Europe (Keith and Poulet 2020). The Saône River is connected to four major river basins: the Rhône to the south, of which the Saône is the main tributary; the Rhine to the northeast, linked via the *Canal du Rhône* and the *Canal de l'Est*, which connect the Meuse and Moselle rivers to the Saône; the Seine to the northwest, connected by the *Canal de Bourgogne* and the *Canal de la Marne*; as well as the Loire River, linked by the *Canal du Centre* (Bollache et al. 2004). This geographical position, coupled with a well-developed and connected hydrographic network, makes the Saône River both a corridor and a recipient area for fish species, including non-native ones.

Although the presence of non-native species poses a threat to ecosystems, their impact on native species and ecosystem functions is density-dependent (DeRoy et al. 2020). The Saône main channel and oxbows highlighted a similar proportion of the non-native species richness. However, densities of non-native species were significantly higher in oxbows. This pattern may be explained by the specific abiotic conditions of these environments, as well as the greater tolerance and plasticity of non-native species compared to native species in response to environmental stressors (Perdikaris et al. 2012; Christensen et al. 2021; Dickey et al. 2021). With their low water volume and weak or non-existent flow, lentic ecosystems such as oxbows are more susceptible to rapid temperature fluctuations than the main river channel. Many non-native species, with broader thermal tolerances, are better adapted than native species to exploit these conditions, finding the warmer waters more favourable for their growth and reproduction (Leuven et al. 2011). This reduced water flow may also lead to lower dissolved oxygen levels and nutrient accumulation, creating hypoxic and eutrophic conditions that further advantage non-native species (Byers et al. 2023). In addition to abiotic conditions, oxbows were characterised by the absence or very low density of top-predators (e.g., pikeperch *Sander lucioperca*, pike *Esox lucius*, wels catfish *Silurus glanis*). This absence of predators may reduce the

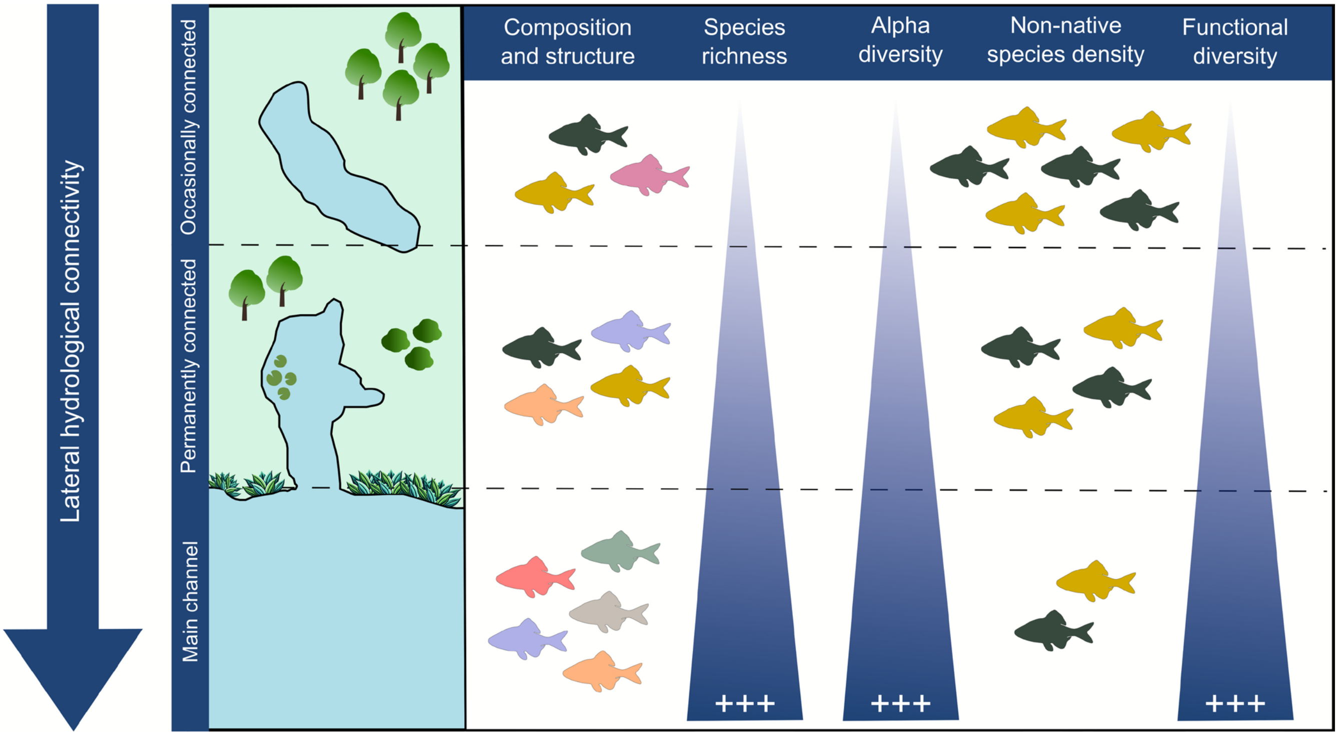


FIGURE 7 | Schematic representation of the effects of lateral hydrological connectivity on the taxonomic and functional structure of fish communities, as well as on non-native species.

top-down control they typically exert on lower trophic levels and therefore non-native species, enhancing the greater competitive advantage of non-native species and intensifying their competition with native species for resources such as food and space (Rettig and Smith 2021; Beshai et al. 2023).

The prevalence and high densities of non-native species in Saône River freshwater ecosystems, especially in oxbows, could have significantly detrimental impacts on local fish populations, potentially altering ecosystem functions and biodiversity. The interactions between climate change, habitat alterations, and the expansion of waterway networks are expected to accelerate the introduction and spread of invasive species, making native species and freshwater ecosystems more vulnerable (Dudgeon et al. 2006; Reid et al. 2019). Warming temperatures will likely increase habitat suitability in oxbows for a number of non-native species, expanding their current distribution areas and leading to significant ecological and economic damage (van der Veer and Nentwig 2015).

4.4 | Ecological and Conservation Implications of Hydrological Connectivity

European floodplains have been significantly impacted by human activities, often leading to their disconnection from the main river channels (Belletti et al. 2020). Restoring lateral connectivity between wetlands, oxbows, and riparian areas with the adjacent river systems is crucial for maintaining the natural functioning of floodplain ecosystems (Gumiero et al. 2013). Floodplain restoration not only supports the natural hydrological processes but also plays an important role in enhancing biodiversity. One of the most significant benefits is the improvement of spawning habitats for species such as the northern pike *Esox lucius*, which rely heavily on seasonally flooded wetlands for reproduction (Neveldine et al. 2019). These areas provide ideal conditions—shallow waters rich in vegetation—for pike eggs to hatch and fry to develop safely (Neveldine et al. 2019). This study highlights the beneficial effects of the lateral hydrological connectivity on both taxonomic and functional diversity of fish communities in Saône River floodplain. These findings suggest that decision-makers and conservation policies should assess not only the taxonomic diversity but also, and more importantly, the functional diversity to set appropriate conservation strategies for a sustainable and effective management of riverine ecosystems. This integrative approach ensures that conservation efforts not only focus on preserving species but also the preservation of the diversity of functional traits in order to sustain the functional integrity of freshwater habitats and ecosystem processes taking place there.

Enhancement of hydrological connectivity in restoration and conservation programmes of freshwater ecosystems often aims to increase fish dispersal, richness and diversity. However, restoring connectivity between rivers and floodplains also carries certain risks, particularly the spread of invasive species. Indeed, enhanced connectivity can facilitate the movement of non-native species, such as invasive fish, which may thrive in these newly accessible habitats. Once established, these species can outcompete native fauna, disrupt food webs, and alter the natural dynamics of floodplain ecosystems. Limited connectivity can thus be seen as a tool to reduce the spread of non-native species (Melles et al. 2015). Nevertheless, in habitats already occupied by non-native species, restoring connectivity can also have the positive effect of enhancing biotic resistance (Glen et al. 2013). In this study, the densities of non-native species were found to be lower in areas with greater hydrological connectivity. By reconnecting floodplains to their rivers, a more diverse and dynamic habitat is created, supporting a wider range of native species. This increase in biodiversity can strengthen ecosystem resilience, as native species compete more efficiently for resources such as space, light, and nutrients, making it harder for invasive species to establish themselves. In addition to the risks posed by alien species, hydrological connectivity may also produce antagonistic effects on other biological components (e.g., amphibians, macrozoobenthos, macrophytes) (Tockner et al. 1998; Amoros and Bornette 2002). For example, several studies reported that amphibian species richness and abundance declined with increased hydrological connectivity (Tockner et al. 1998; Hamer et al. 2023). Hydrological connectivity facilitates the establishment of fish species, especially in waterbodies that were previously fish-free before restoration (Tockner et al. 1998), leading to increased predation rates on larval amphibians and competition for resources. These studies highlight the need to provide and preserve hydrologically disconnected waterbodies. Restoring freshwater ecosystems through lateral hydrological connectivity requires thus a more nuanced approach, where trade-offs are inevitable. A careful consideration of both connected and disconnected waterbodies and their biodiversity is key to sustainable freshwater ecosystem restoration.

5 | Conclusion

By combining both taxonomic and trait-based approaches, this study is the first to provide a detailed description of the structure and functional diversity of fish communities across freshwater ecosystems of the Saône River, each with varying levels of lateral hydrological connectivity. Our results highlight compositional and structural changes in fish communities as the oxbows progressively disconnect from the main channel (Figure 7). These community changes are accompanied by a decrease in both taxonomic and functional diversity along the hydrological gradient (Figure 7). Future studies should investigate how seasonal variations of the hydrological connectivity, and consequently, changes in abiotic factors (e.g., water temperature, water levels and flow rates) affect fish communities within these interconnected habitats. However, the low functional redundancy of these habitats, especially in plesiopotamic oxbows, makes freshwater ecosystems vulnerable and sensitive to potential disturbances. The loss of fish species resulting from both natural and human-induced activities could significantly alter ecosystem functioning. In addition to its positive influence on taxonomic and functional diversity, hydrological connectivity also reduces the density of non-native species (Figure 7). Enhancing lateral connectivity therefore not only supports greater fish diversity but also reinforces biotic resistance, resilience, and the ecological integrity of riverine systems. This study provides valuable insights to encourage conservation and restoration efforts, ensuring the long-term health of freshwater ecosystems along the Saône River.

Author Contributions

Conceptualisation: Y.L., L.B. Developing methods: Y.L. Conducting the research: Y.L., E.G., G.M., J.-P.C., J.Ma. Data analysis, preparation of figures and tables: Y.L. Data interpretation, writing: Y.L., E.G., G.G., G.M., J.Mo., J.-P.C., J.Ma., S.M., R.W., M.T., F.-X.D.-M., L.B.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Location and environmental information on fish sampling sites, including the coordinates, the type of site, the oxbow surfaces (S_{total}), the sampling effort with the sampled surface (S_s), as well as oxbow depths. **Table S2:** Trait categorisation using the fuzzy coding procedure for each fish species. In our coding procedure, a species expresses each modality of a given trait on a scale from 0 to 4, with 4 being an exclusive affinity for a modality (all other modalities of the trait being 0 for that species), 3 a strong affinity for a modality, 2 a mean or uncertain affinity for a modality, 1 an occasional behaviour or observed value for the species, and 0 for the absence of the modality. Traits were compiled from peer-reviewed literature, online databases, and expert knowledge. **Table S3:** List and density (individuals/100m^2) of the 28 fish species sampled in the Saône main channel (S1 to S5), parapotamic oxbows (PAR-1 to PAR-4), and plesiopotamic oxbows (PLE-1 to PLE-4) sites; as well as their geographic origin (N: Native; NN: Non-native).