



Research article

Environmental pressures on Mekong fish: Insights from temporal functional diversity dynamics



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ABSTRACT

The Mekong River faces increasing environmental threats. To understand fish community responses to these threats, we explored the links between functional diversity (FD) dynamics and environmental changes across four sites using trait-based methods and fish monitoring data for 347 species. We assessed functional richness (FRic) and divergence (FDiv) using standardized effect sizes to investigate the main assembly rules structuring fish communities and used generalized additive models to identify key environmental drivers. After dam construction, all four sites experienced significant changes in environmental conditions. Deterministic processes, particularly environmental filtering, dominated in structuring fish communities. The upstream Lao People's Democratic Republic site (LPB) influenced by deterministic and stochastic processes. The Cambodia sites in Stung Treng province (CST) and Tonle Sap (TLS) Lake primarily driven by deterministic process with a decline in FRic and FDiv. Conversely, the Viet Nam site (VCM) seemed primarily influenced by stochastic process with more subtle environmental effects, evidenced by an increase in FRic and FDiv over time. The upper sites (LPB, CST, and TLS) displayed a distinct seasonal pattern in FD indices, with values decreasing during the dry season and increasing during the wet season. Conversely, the lower site (VCM) exhibited the opposite. Water level emerged as the key driver across all sites, with temperature and total nitrogen as secondary drivers. Dam impacts and other anthropogenic factors not included in our analyses (e.g., unsustainable fishing and habitat degradation) probably contributed to the observed changes in FD at specific sites. These findings highlight potential strategies for conservation, offering national and regional practitioners an opportunity to develop and refine river management plans.

1. Introduction

Freshwater fish display remarkable biodiversity, holding a disproportionately high share (49%) of the world's fish species, despite occupying only 0.0093% of the planet's water (Facey et al., 2023). However, they face some of the most significant threats among vertebrates due to their vulnerability to human alterations, including species introductions, overexploitation, habitat fragmentation, watercourse degradation, and climate change (Barbarossa et al., 2021). For example, habitat fragmentation caused by dams is a major threat to freshwater fish, especially migratory species (Sor et al., 2023). Dams disrupt natural

water flow, transforming lotic (fast-flowing) environments into lentic (stagnant-water) ones. This shift favours generalist species over specialists, leading to changes in fish assemblages. Consequently, endemic species face a higher risk of extinction and, overall, biodiversity homogenization can occur (LeRoy et al., 2007; Rahel, 2000). Understanding how biological communities interact with their environment is key to successful conservation and restoration efforts (Mouillot et al., 2013).

To understand the link between biological communities and their environment, ecologists have traditionally employed taxonomic approaches, such as species richness and diversity indices (e.g., Huang

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et al., 2019; Ngor et al., 2018a,b; Sor et al., 2023). Yet, taxonomic approaches miss the finer details when it comes to small changes in habitat quality. Trait-based approaches, on the other hand, offer a powerful alternative. By analysing the functional characteristics of species within a community, they can uncover the impact of various disturbances, even when the overall species composition shows only minimal change (McLean et al., 2019; Mouillot et al., 2008, 2013). This reasoning has prompted the exploration of functional diversity (FD) indices to measure the diversity in traits that influence how species contribute to ecosystem processes (Mason et al., 2005; Petchey and Gaston, 2002; Villéger et al., 2008). The growing importance of FD has led to its incorporation in a wide range of ecological and environmental research, such as community assembly and the patterns and drivers of biodiversity (e.g., McLean et al., 2019; Ortega-Martínez et al., 2020).

Moreover, there has been a growing focus on using FD indices to understand the community assembly (e.g., deterministic and stochastic mechanisms) that govern biodiversity patterns (e.g., Ge et al., 2021; Mastrogianni et al., 2021; Ortega-Martínez et al., 2020). While a wide range of functional diversity (FD) indices, based on occurrence, abundance or biomass data, have been established, not all are equally effective in revealing community assembly (Mouchet et al., 2010). Deterministic mechanisms are defined by non-random processes, environmental filtering and limiting similarity. In ecology, some environments act like filters, favouring species with specific traits. These filters, driven by factors like water temperature or food availability, lead to communities with similar traits (trait underdispersion). In contrast, the principle of limiting similarity, building upon competitive exclusion, suggests that two species can coexist only when their niches, their ecological roles, do not overlap significantly. This concept can also be described as trait overdispersion, where successful species have traits that are distinct from each other (de Bello et al., 2021; Kraft et al., 2015; Weiher and Keddy, 1995). Stochastic mechanisms refer to the process by which ecological communities are assembled due to random or probabilistic factors. In stochastic community assembly, dispersal of individuals across space is the key driver, regardless of their specific traits. This means the structure and composition of communities are primarily determined by ecological drift and the dispersal capacity of the species (Hubbell, 2001; Zhou and Ning, 2017). To test community assembly processes (whether random or non-random), ecologists have widely employed null models (e.g., Cornell and Ackerly, 2009; Daniel et al., 2019; Ge et al., 2021; Ortega-Martínez et al., 2020). Null models used in phylogenetic and functional diversity analyses are typically categorized into two types of randomization: (i) community data matrix randomization and (ii) phylogenetic or functional trait data matrix randomization. The first type (community data matrix randomization) shuffles species abundance (or occurrence) data within samples while maintaining sample species richness (or preserving both species occurrence frequency and sample species richness). The second type (phylogenetic or functional trait data matrix randomization) keeps the entire community data matrix fixed while randomizing the phylogenetic or functional information (de Bello et al., 2021; Götzenberger et al., 2016; Swenson, 2014). Both approaches yield comparable outcomes, particularly when using a trait diversity index weighted by species abundances (Götzenberger et al., 2016).

The Mekong River, one of the world's largest rivers, is renowned for its biodiversity, particularly its diverse fish species and high fisheries productivity. Millions of people partially or wholly depend on the Mekong River for their subsistence (Mekong River Commission, 2018). Despite providing significant ecological and socioeconomic benefits, the river's ecosystem is under severe pressure, such as hydropower dam development, overfishing, and climate change (Allan et al., 2005; Nuon et al., 2020, 2024). Like elsewhere in the world, ecologists working in the Mekong River have traditionally relied on taxonomic approaches to understand community patterns as well as biodiversity-environment relationships (e.g., Chea et al., 2017; Ngor et al., 2023; Nuon et al., 2020; Sor et al., 2023). While trait-based approaches have been

implemented in some Mekong studies (Montaña et al., 2020; Ou et al., 2017; Zhang et al., 2021), they have primarily focused on the lower part of the Lower Mekong Basin (LMB), especially northeastern part of Cambodia. To date, no studies have employed trait-based approaches across a broad spatial extent of the LMB, from its upper to lower reaches, using long-term fish monitoring data to investigate temporal changes in fish functional diversity and their relationship with environmental factors.

To address this gap, here we employed a trait-based approach utilizing long-term fish monitoring data (spanning 13 years) from the upper part of the LMB to the Mekong delta. Functional richness and functional divergence were used since these indices show promise in revealing community assembly patterns due to their strong discriminatory power. Furthermore, they can provide an advanced warning of ecosystem disturbance before species loss and extinctions occur (Mouchet et al., 2010; Mouillot et al., 2013; Villéger et al., 2010). Our study aimed to first identify the processes governing fish community assembly along an environmental gradient in the Lower Mekong Basin. We then assessed how fish functional diversity changed over time. Finally, we identified the environmental factors that most significantly explained the variations in functional diversity.

2. Materials and methods

2.1. Study area

The study was conducted across four locations, encompassing eight fish sampling sites (or monitoring stations) within the LMB (Fig. 2). These locations were strategically selected to represent key fish habitats (nursery, spawning, and feeding grounds) within the Lower Mekong Basin, while also capturing a gradient of environmental conditions and human impacts. The first location (LPB) included one site, situated in the upper part of the LMB, within Luangprabang province, Lao People's Democratic Republic (Lao PDR). This site was upstream of the main-stream dam (Xayaburi hydropower dam) approximately 110 km away from the dam site. Characterized by a steep slope and fast, variable flows, LPB serves as a critical spawning ground for long- and short-distance white fishes and provides refuges for rhithron-resident species (Gupta and Liew, 2007; Poulsen et al., 2002). The second location (CST), near the Lao PDR border in Stung Treng province, Cambodia, also comprised a single site. Located approximately 10 km downstream of the Don Sahong hydropower dam, this site lies within the Stung Treng Ramsar site, one of the Mekong River's most ecologically significant protected wetlands. With its deep pools, flooded forests, and rapid water, CST provides essential spawning and refuge habitats for various fish species, including long- and short-distance white fishes. It also supports several flagship species, such as the Irrawaddy dolphin, Sarus crane, Mekong giant catfish, and Siamese crocodile (Nuon et al., 2020; Try and Chambers, 2006). The third location was within Tonle Sap Lake (TLS) in Cambodia, a UNESCO World Biosphere Reserve designated in 1997, which also encompasses two Ramsar sites: Boeng Chhmar and Prek Toal (Davidson, 2006). Home to approximately 296 fish species, TLS ranks third globally in fish diversity, following Lake Malawi and Lake Tanganyika (Baran et al., 2007, 2013). Its fisheries production is among the largest of any inland fishery worldwide, significantly contributing to local livelihoods (Baran, 2005; Baran et al., 2013). Due to its large area and ecological diversity, five sampling sites were selected within this location. Lastly, the fourth location (VCM) included a single site in the upper reaches of Viet Nam's Mekong Delta. This area is characterized by high habitat heterogeneity, encompassing floodplains, wetlands, mangrove forests, mudflats, and peatlands, supporting a diverse fish fauna of approximately 450 species (WWF, n.d.). The unique interplay of marine, brackish, and freshwater environments further enhances its species richness (Valbo-Jorgensen et al., 2009).

2.2. Environmental data

Environmental data were obtained from the Mekong River Commission (MRC; <https://www.mrcmekong.org/>), under two distinct monitoring programmes: the Water Quality Monitoring Program and the Hydrological Monitoring Program. We used ten environmental variables, which included water level (m), water temperature (°C), pH, dissolved oxygen (mg.L⁻¹), electrical conductivity (mS.m⁻¹), total nitrite and nitrate (mg.L⁻¹), total phosphorus (mg.L⁻¹), total nitrogen (mg.L⁻¹), ammonium (mg.L⁻¹), and total suspended solids (mg.L⁻¹), collected close to the fish sampling sites for the period from 2008 to 2021. These variables were selected for this study because (i) their time span encompasses the periods before, during, and after dam construction, and (ii) they are widely used to assess the environmental impacts of dams and other anthropogenic disturbances on freshwater ecosystems (e.g., Chen et al., 2022b; He et al., 2024; Liu and Wang, 2018; Mao et al., 2021; Mekong River Commission, 2022b). Moreover, the data from these programmes were collected through the teams from national water quality and hydrology-related agencies in Cambodia, Lao PDR and Viet Nam. The water quality data were collected monthly, while the hydrological data were collected daily. To ensure consistency with the monthly water quality data, daily hydrological data were averaged to monthly values. This approach has been previously employed in ecological studies to align high-frequency data with lower-frequency datasets (Ngor et al., 2023).

2.3. Fish data

2.3.1. Fish survey

Fish data were collected through a fisheries-dependent monitoring programme, which has been implemented by teams from national fisheries agencies in the MRC Member Countries: Cambodia, Lao PDR and Viet Nam. Each monitoring site had three fishers who were responsible for recording their daily fish catches (e.g. weight, number of fish and fishing effort) in a logbook. Multiple types of fishing gear were used, with stationary gillnets being the most common, accounting for 61% of usage. The fish sampling adhered to the MRC’s standard operation manual for fish abundance and diversity monitoring in the LMB as detailed in the Mekong River Commission (2021).

Fish data included 347 fish species from 51 families across 14 orders (Table S1). The Cyprinidae family was the most diverse, representing 38% of all families recorded. Similarly, three functional guilds—short-distance white fishes, floodplain spawners, and generalist fishes—dominated the catch, accounting for 68% of all guilds (Fig. 1). Daily

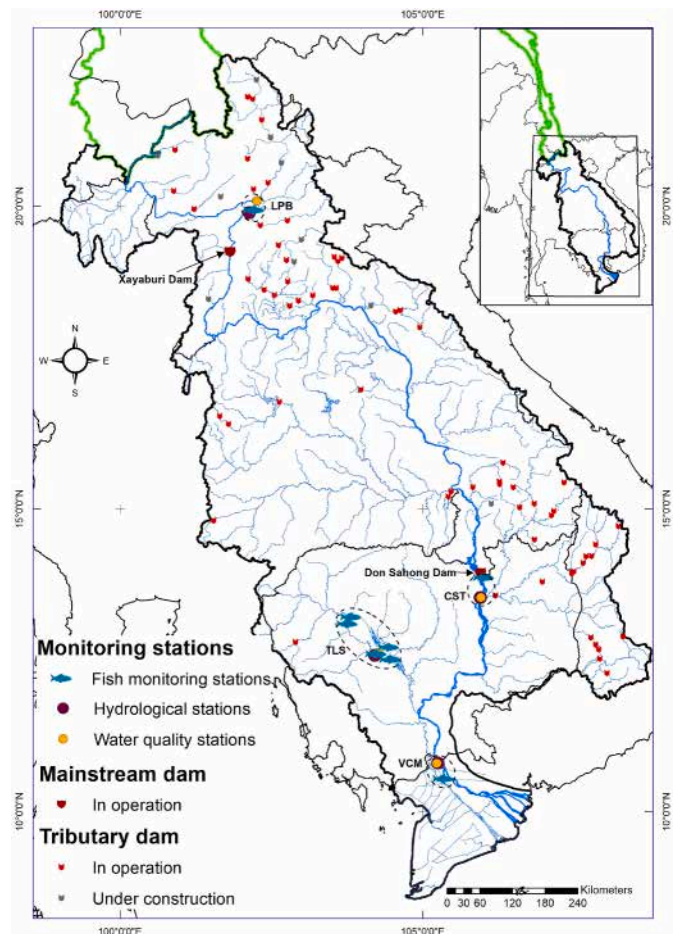


Fig. 2. Lower Mekong Basin and monitoring stations for fish, water quality and water level data. Location of dams (in operation or under construction) are indicated.

fish catch data were gathered from eight monitoring sites within the LMB (Fig. 2). Among these eight sites, only those within TLS were situated in the lake, while the remaining sites were located along the mainstream of the Mekong River. The collected data primarily covered the period from 2008 to 2021, except for the data from the five TLS sites in Cambodia, which were collected from 2012 to 2021. Daily fish abundance data from the three fishers per site were averaged and then aggregated into monthly data to align with the frequency of the water quality data. Given that there is only a single hydrological and water quality monitoring station in the TLS, we aggregated the fish abundance data from all five TLS sites.

2.3.2. Trait data

We used both morphological and ecological traits that were previously employed to compute functional diversity indices (Côte et al., 2023; Lin et al., 2021; Toussaint et al., 2016). Specifically, ten morphological traits were derived from the FISHMORPH database (Brosse et al., 2021), including maximum body length and nine morphological ratios related to food acquisition and locomotion (Table S2). In addition, ecological trait (i.e., 10 functional guilds) was sourced from the Mekong River Commission (2021), based on the work of Welcomme et al. (2006) according to fish species reproductive strategies and preferred habitat associations within the Mekong River basin (Table S2).

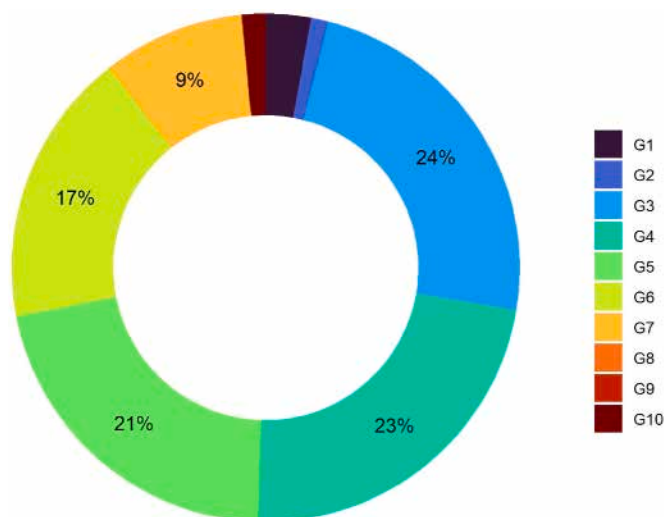


Fig. 1. Distribution of fish abundance across functional guilds.

2.4. Functional diversity indices

Functional diversity indices used were functional richness (FRic) and divergence (FDiv). FRic is defined as the volume of the functional space filled by the species in the community. FDiv, on the other hand, illustrates the distribution of abundances within the volume of functional trait space occupied by species. FDiv incorporate species abundance into its calculation, whereas FRic does not. In order to calculate the FRic and FDiv, we first utilized the Gower distance to generate a functional distance matrix based on the trait values of each species. Subsequently, a Principal Coordinates Analysis (PCoA) was conducted on this functional distance matrix to generate a multidimensional functional space (Mouillot et al., 2013). FRic was computed as the proportion of functional space filled by species of the studied assemblage (e.g., the volume inside the convex-hull shaping species), while FDiv quantified the proportion of the biomass/abundance supported by the species with the most extreme functional traits (e.g., the ones located at the edges of the convex-hull filled by the assemblage). FD indices were computed utilizing the function *alpha.fd.multidim* from the mFD package in R (Magneville et al., 2022).

Finally, null models were used to investigate the community assembly that structure the community types and define whether or not the observed FD indices were significantly different from the values expected by chance (de Bello et al., 2021). Importantly, null models can help control for the influence of species richness on FD indices. For each monthly sampling, we conducted 999 randomizations of fish assemblages, shuffling species abundance within each sample and keeping species richness constant (i.e., richness null model) and computed 999 null values for each FD index. These randomizations were performed independently for each site, to consider the potential for both varying species pools and distinct environmental impacts across different sites. We performed these randomizations using the *randomizeMatrix* function from the *picante* package in R (Kembel et al., 2010) and computed the standardized effect size (SES) values using the formula: $\frac{obs - \text{mean}(\text{rand})}{\text{sd}(\text{rand})}$ (Gotelli and McCabe, 2002), where *obs* represents the observed FD indices, and *rand* represents the 999 null values of the FD indices. Henceforth, SES values were used for all subsequent analyses.

2.5. Statistical analyses

Firstly, we investigated significant changes in environmental conditions throughout the study period, particularly in relation to dam construction. Kruskal-Wallis tests and pairwise comparisons were employed to assess differences between three distinct phases: pre-construction (2008–2012), during construction (2013–2019), and post-construction (2020–2021). These phases were defined based on the construction timeline of the Xayaburi Dam, the first mainstream hydropower dam on the Lower Mekong Basin. The groundbreaking ceremony for this dam occurred in November 2012 (International Rivers, n.d.). Thus, to ensure a clear demarcation between pre-construction and construction phases, we designated early 2013 as the start of construction.

Secondly, to investigate the assembly rules (i.e., stochastic vs deterministic) that structure fish community at each site, we used t-tests to examine whether or not the mean SES values at each site differed significantly from zero (de Bello et al., 2021). P-values less than 0.05 indicated a deterministic process, with positive and negative SES values suggested limiting similarity and environmental filtering, respectively. Conversely, non-significant ($p > 0.05$) values implied a stochastic process.

Thirdly, we assessed long-term and seasonal trends in FD indices at each site to understand the natural annual fluctuations and the gradual changes over the study period. Generalized additive models (GAMs) with Gaussian distributions were used to analyse these trends, allowing smooth, complex non-linear trends in FD indices to be estimated, while providing a statistically rigorous framework for inference and managing

the analysis of irregularly spaced time-series data (Simpson, 2018). Importantly, GAMs are capable to analyse seasonal trends, compared to the classical linear models. GAMs were employed to capture both long-term and seasonal trends in FD indices. GAMs achieved this by utilizing cubic regression splines to model non-linear changes in FD over time, while simultaneously incorporating cyclic cubic splines to account for recurring seasonal patterns within a year. GAMs were expressed as follows:

$$g(E(Y)) = \alpha + f_1(x_1) + f_2(x_2) + \dots + f_k(x_k)$$

where Y is the dependent variable and $E(Y)$ denotes the expected value of Y . Also, g is the link function that relates the expected value of Y to the predictor variables, α is the intercept term, and $f_i(x_i)$ is smooth functions of the predictor variables x_i .

Finally, GAMs were used to assess the influence of environmental variables on FD indices at each site. The models included smooth terms for all environmental variables, using cubic regression splines. All predictor variables were log-transformed and standardized, and no multicollinearity among predictors was detected (e.g., all variance inflation factors were lower than 2). To ensure optimal model selection and identify the key environmental factors influencing FD indices, an additional penalty was applied to each term during model fitting. This allowed the model to shrink non-contributing predictors to zero, effectively removing them from the final model. This process was achieved using the `select = TRUE` option in the `gam` function from the “*mgcv*” package in R (Wood, 2017). For all GAMs, we selected the optimal degree of smoothness using the REML (Restricted Maximum Likelihood) method as recommended by Simpson (2018) and Wood (2011).

3. Result

3.1. Environmental changes

All four study sites experienced significant changes in environmental conditions following dam construction (Fig. S1). At LPB site, water level (WL), temperature (TEMP), and total nitrogen (TOTN) increased significantly ($P < 0.05$) after dam construction. Conversely, total suspended solids (TSS) and ammonium levels exhibited a decreasing trend. Unlike the aforementioned variables, pH, dissolved oxygen (DO), and total nitrite and nitrate (NO32) showed no significant difference between the periods before and after dam construction. However, pH and DO declined, while NO32 increased during dam construction, making this period significantly different ($P < 0.05$) from the periods before and after dam construction. Additionally, conductivity and total phosphorus (TOTP) remained stable across the three periods. At CST, pH, conductivity, ammonium, and TOTP levels increased significantly ($P < 0.05$) after dam construction, while DO decreased. In contrast, WL, temperature, TSS, NO32, and TOTN showed no significant changes across all three periods. In TLS, temperature, DO, NO32, ammonium, and TOTN showed no significant differences across all three periods. Conversely, pH, TSS, conductivity and TOTP increased post-dam ($P < 0.05$) while WL decreased. At VCM, only WL remained stable over the three periods. Temperature, pH, conductivity, NO32, and TOTN significantly increased post-dam, while TSS, DO and TOTP significantly declined. Notably, ammonium showed a unique trend, with a significant mid-point increase during construction, but then returning to no significant difference between pre- and post-construction levels.

3.2. Assembly mechanisms and temporal changes of fish functional diversity

Overall, deterministic processes were the dominant drivers of fish community assembly across sites, with environmental filtering being the process most frequently observed (Table 1). At LPB, FRic exhibited signs of a stochastic process, while FDiv indicated environmental filtering

Table 1

Results from GAMs modelling the temporal changes (i.e., annual and seasonal trends) in functional richness (FRic) and divergence (FDiv), and assembly mechanisms including *t*-test P-value. **P*<0.05: Significant; ***P*<0.01: Highly significant; ****P*<0.001: Very highly significant.

Site	SES FD Indices	Annual P-value	Seasonal P-value	Deviance explained (%)	Assembly mechanisms	<i>t</i> -test P-value	Mean ± sd of FD Indices
LPB	FRic	***	***	54	Stochastic	0.9	0.01 ± 1.02
	FDiv	**	***	63	Environmental filtering	***	-0.35 ± 1.01
CST	FRic	**	0.06	25	Environmental filtering	***	-1.6 ± 0.4
	FDiv	***	**	45	Environmental filtering	***	-0.5 ± 0.8
TLS	FRic	***	**	35	Environmental filtering	***	-1.6 ± 0.55
	FDiv	**	***	46	Environmental filtering	***	-1.8 ± 1.08
VCM	FRic	***	***	46	Stochastic	0.5	-0.03 ± 0.65
	FDiv	***	***	53	Stochastic	0.6	0.03 ± 0.89

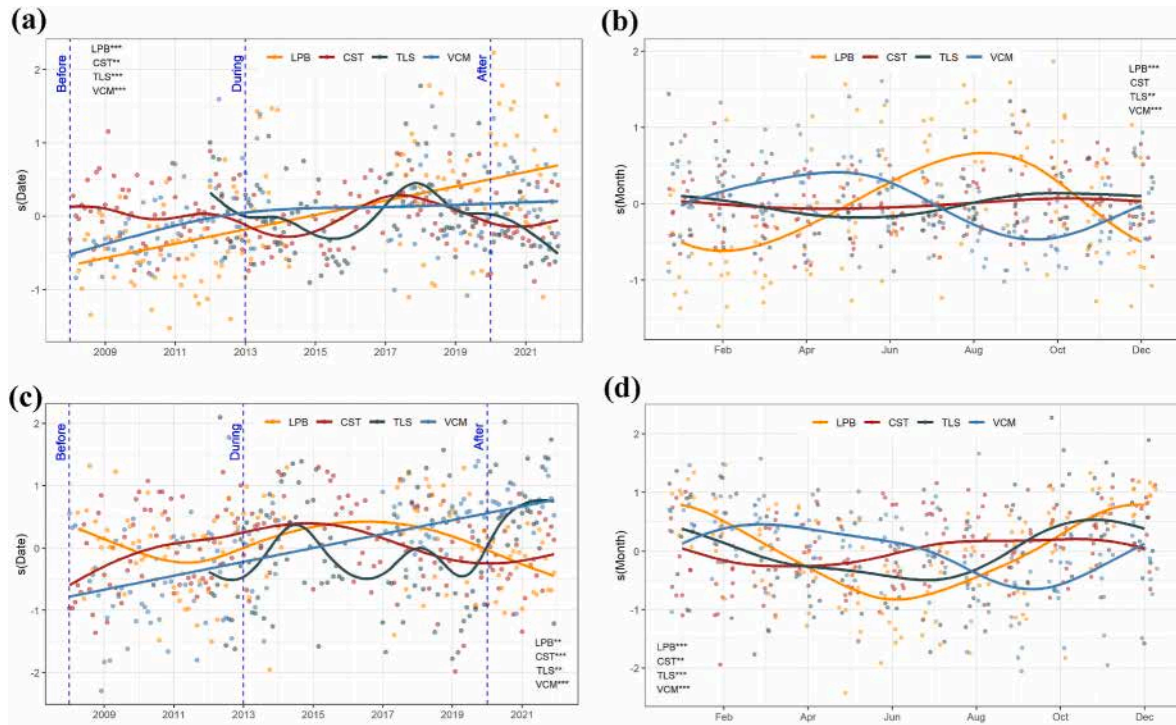


Fig. 3. GAM smoother estimation for long-term trend in functional richness (a) and functional divergence (c), and seasonal trend in functional richness (b) and functional divergence (d). Dots represent partial residuals and solid lines denote the fitted smooth function, showing the estimated relationship between the response variable (functional diversity indices) and the predictor variable (time). The y-axis represents the cubic regression splines function for long-term trend and cyclic cubic splines function for seasonal trend. **P*<0.05: Significant; ***P*<0.01: Highly significant; ****P*<0.001: Very highly significant.

through trait clustering. In contrast, FRic and FDiv at CST and TLS pointed towards a significant influence of environmental filtering, suggesting a clustering of traits within these communities. VCM, the most

downstream site, presented a distinct pattern since those of FRic and FDiv were not statistically different from zero, suggesting a stochastic process governing fish community assembly.

Table 2

Significant environmental variables influencing the functional richness and divergence identified by the GAMs. The relationships between response and predictor variables are labelled with + (positive), - (negative), U (initially positive and then negative), ∩ (initially positive and then negative). **P*<0.05: Significant; ***P*<0.01: Highly significant; ****P*<0.001: Very highly significant.

SES FD Indices	LPB		CST		TLS		VCM		Total		Important drivers
	FRic	FDiv	FRic	FDiv	FRic	FDiv	FRic	FDiv	FRic	FDiv	
Water level	(+)	***		(∩)**	(+)*	(U)*	(-)	***	3	3	First important driver
Temperature		(-)	***		(∩)*		(+)	**	2	2	Second important driver
pH						(+)*			-	2	-
Total suspended solids		(-)	**	(+)	***				1	1	-
Dissolved oxygen	(U)**	(U)**		(-)*					2	1	-
Electrical conductivity					(∩)*			(U)*	1	1	-
Total nitrite and nitrate				(∩)**		(-)	***		2	1	-
Ammonium									0	0	-
Total nitrogen	(∩)*			(∩)*	(+)*			(+)*	2	2	Second important driver
Total phosphorus				(+)*				(-)	1	1	-
Deviance explained (%)	46	35	24	21	30	24	40	60	-	-	-

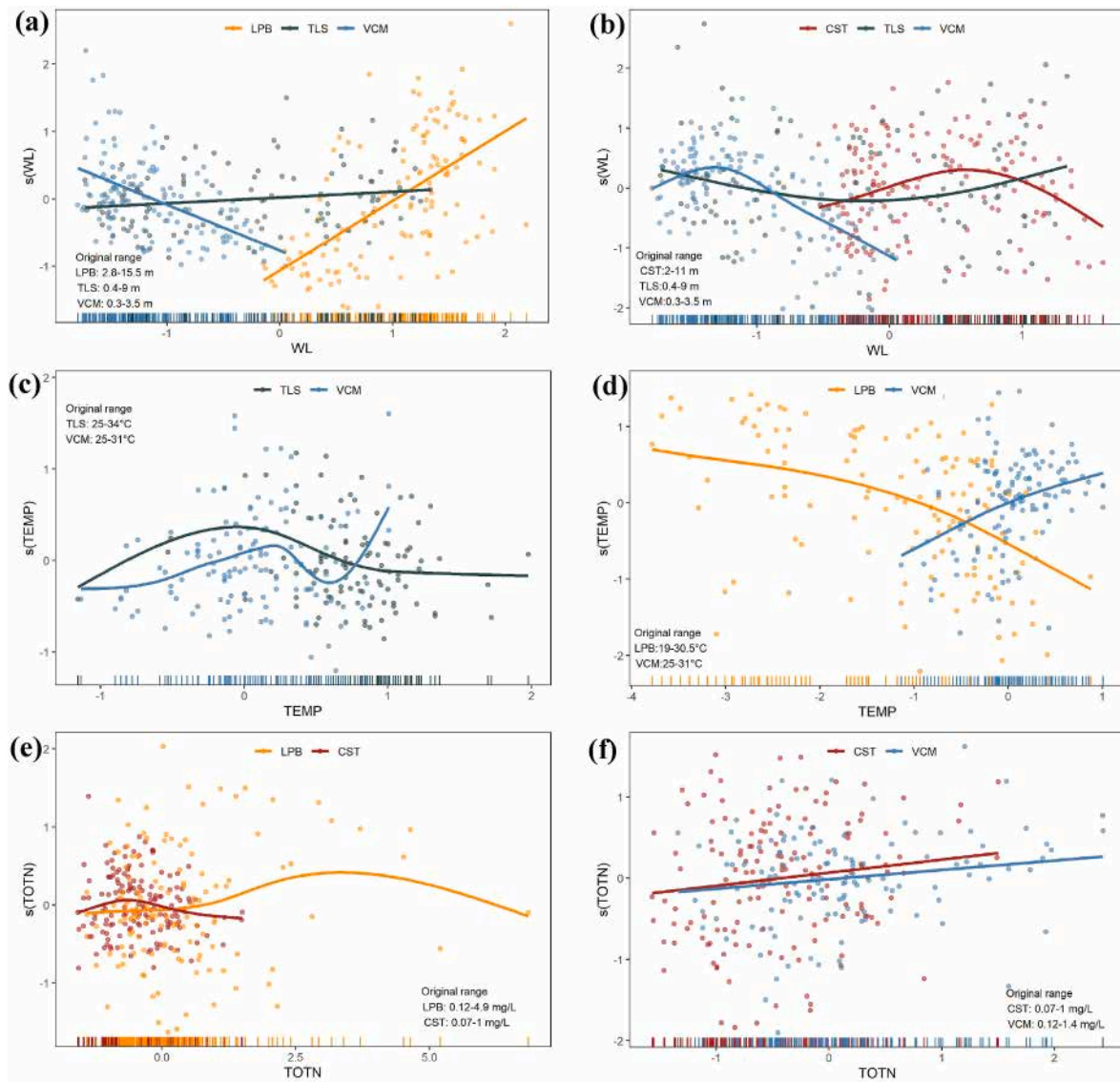


Fig. 4. GAM smoother estimation for the significant relationships between functional richness (a, c, e) or functional divergence (b, d, f) and environmental variables (water level: WL, temperature: TEMP and total nitrogen: TOTN). Dots represent partial residuals, and marks along the x-axis indicate the transformed values of the predictor variable. Solid line denotes the fitted smooth function, showing the estimated relationship between the response variable (functional diversity indices) and the predictor variables (WL, TEMP and TOTN). The y-axis represents the cubic regression splines function.

GAM models explained substantial deviance in both FRic (25%–54%) and FDiv (45%–63%) (Table 1). Significant ($P < 0.05$) long-term (annual) changes in FD indices were observed for all sites (Fig. 3a–c and S2). FRic at LPB and VCM showed increasing trajectories, while CST and TLS exhibited fluctuations. FRic at CST and TLS increased around 2017 and 2018, respectively, but then declined until 2021. FDiv trends varied across sites: LPB declined initially (around 2012), then increased (2013–2017), and declined again (2019–2021). CST had a rising trend (2008–2015) followed by a decrease (2016–2021). TLS showed fluctuating FDiv values with a period of lower values between 2016 and 2019, then an increase in 2021. VCM's FDiv linearly increased from 2008 to 2021.

Seasonal trends in FD indices showed different patterns between upstream and downstream sites (Fig. 3b–d and S2). Significant seasonal variations in FRic ($P < 0.05$) were observed at LPB, TLS, and VCM, except CST. At LPB, FRic declined during the late wet season (November), reached its lowest level in February, and increased during the late dry season (April–May), peaking in the wet season (around mid-August). TLS showed a similar pattern but with minimum values in May and a

peak in October. VCM exhibited an opposite pattern, peaking in May and reaching its lowest level in September. Seasonal FDiv followed similar trends with significant variations ($P < 0.05$) for all sites. At LPB, FDiv dropped in February, reached a minimum in June, and peaked in December. CST lacked distinct seasonal pattern but trended downwards in the dry season and upwards in the wet season. TLS's FDiv showed a minimum in July and a peak in mid-October. VCM's FDiv mirrored its FRic pattern, peaking in March and reaching a minimum in September.

3.3. Influence of environmental factors on functional diversity

Our results demonstrated complex relationships between environmental variables and FD indices as well as contrasted effects among sites. The explained deviance by GAMs varied from 24% to 46% for FRic and 21%–60% for FDiv (Table 2). Out of ten environmental variables, water level (WL) emerged as the most influential driver across multiple sites. It significantly impacted FRic in LPB, TLS and VCM, and FDiv in CST, TLS and VCM (Fig. 4a and b and S3). Temperature and total nitrogen (TOTN) were identified as secondary drivers (Fig. 4c–f and S3).

Temperature influenced FRic in TLS and VCM, and FDiv in LPB and VCM. Similarly, TOTN impacted FRic in LPB and CST, and FDiv in CST and VCM.

We observed a positive correlation between WL and FRic at LPB and TLS, but a negative correlation at VCM. For FDiv, a positive correlation with WL was found at TLS, while CST and VCM exhibited the opposite pattern. In relation to temperature, a positive correlation was found at VCM for FRic, but a negative correlation at TLS. Likewise, FDiv displayed a positive correlation at VCM but a negative one at LPB. TOTN exhibited contrasting effects compared to temperature on both FRic and FDiv. FRic showed a negative correlation with TOTN at LPB and CST, while FDiv displayed a positive correlation in CST and VCM.

4. Discussion

Trait-based approaches are increasingly valued for providing a deeper understanding of community assembly and ecological functioning compared to taxonomic approaches. Importantly, these approaches can detect different types of disturbances and their effects even with subtle changes in species composition (McLean et al., 2019; Mouillot et al., 2008, 2013). In this study, we employed a trait-based approach using long-term monitoring data to identify the processes governing fish community assembly at four sites along the Mekong River and examined how functional diversity changed over time. Furthermore, we explored the relationships between fish functional diversity and environmental factors throughout the four sites.

4.1. Assembly mechanisms and temporal changes of functional diversity

We found distinct assembly processes structuring fish communities which contributed to the variation in functional diversity between sites over the survey period. Fish community assembly in LPB exhibited a complex interaction between deterministic and stochastic mechanisms. This complex interaction resulted in contrasting temporal trends of FRic and FDiv. Although FRic does not decrease, a downward trend in FDiv indicates disturbance, such as dam and habitat alteration (Mekong River Commission, 2022b; Nuon et al., 2020). FRic is less sensitive with moderate disturbance intensity which is insufficient to drive local extinction of functionally distinct species (Mouillot et al., 2013). As disturbance increases to moderate levels, many species (including new species) with redundant traits accumulate in the community. This trend leads to a decrease in functional divergence (Gerisch et al., 2012; Jarquín-Martínez et al., 2024; Mouillot et al., 2013).

In contrast to LPB, CST and TLS appear to be more strongly influenced by deterministic mechanisms, particularly environmental filtering. FD indices at CST fluctuate and show a decreasing trend in the later years, demonstrating trait convergence. This can likely be attributed to high environmental disturbance in this river reach, such as dam, habitat alteration, and illegal fishing (Campbell et al., 2020; Herranz Muñoz et al., 2023; Nuon et al., 2020; Nuon and Gallardob, 2011). Supporting our observations, prior studies have linked decreasing FD indices to disturbance (Arantes et al., 2019; Feng et al., 2023; Martins et al., 2012; Villéger et al., 2010). The FD indices pattern at TLS differs slightly from CST. The decreasing FRic could result from an increasing level of disturbance, leading to the local extirpation of functionally distinct species (Mouillot et al., 2013). This decline can be attributed to various stressors, such as overfishing, rising temperatures, and habitat degradation (Allan et al., 2005; Chen et al., 2022a,b; Chheng and David, 2016; Daly et al., 2020; Nuon et al., 2020). Studies on both fish and plants support this link, demonstrating that sites experiencing significant impacts tend to have lower FRic (Bello et al., 2013; Feng et al., 2023; Lin et al., 2021). These stressors can further contribute to trait underdispersion in this site, reflected in the negative SES values of FDiv over the study period (Fig. S2). In essence, these stressors act like environmental filters, removing species unable to survive locally and leaving behind a community dominated by species with more similar

traits (Kraft et al., 2015).

Unlike the upper sites, stochastic mechanisms (i.e., ecological stochasticity) appeared to dominate fish community assembly at VCM, the most downstream location. Despite the absence of significant differences from zero, the increasing trends of SES values (Fig. S2) for both FRic and FDiv from negative to positive indicate a weakening of environmental filtering. These positive trends suggest the least impact from disturbances, especially from hydropower dams, likely due to the site's distance from them. A study in the undammed Ivinhema River, compared to the dammed Paraná and Baía Rivers in Brazil, reported similar patterns, with higher functional diversity in undammed fish communities due to more natural flow regimes (Oliveira et al., 2018). Located in the Mekong Delta, VCM serves as a transitional zone between freshwater and marine ecosystems, fostering a variety of microhabitats like wetlands, mangrove forests, mudflats, seagrasses, riparian vegetation, paddy fields, and peatlands (Valbo-Jorgensen et al., 2009; WWF, n.d.). The delta's environment is characterized by fluctuating water salinity, temperature, and other abiotic factors due to tidal influences and seasonal freshwater input from rivers during the wet season (Valbo-Jorgensen et al., 2009). This environmental heterogeneity promoted heterogeneous selection (Zhou and Ning, 2017), leading to a high degree of trait differences, evidenced by the presence of nine functional guilds (excluding Catadromous fishes) in this site. This suggests dispersal of various guilds from other local communities, indicating the emergence of randomly structured assemblages. This corresponds to previous studies on bird (Hidasi-Neto et al., 2012; Sobral and Cianciaruso, 2016) and beetles (Magura et al., 2018; Ortega-Martínez et al., 2020). The fluctuating delta environment, including changes in water salinity, tidal influences, and seasonal freshwater input, may promote ecological drift through stochastic immigration of various guilds into this community (Zhou and Ning, 2017). This randomness in the arrival of individuals each season can have significant consequences for the community assembly, as evidenced by a previous study on temporary wetlands (Daniel et al., 2019). Consistent with our findings, this study found that the annual re-establishment (periodic resetting) through individual or propagule dispersal (stochastic immigration) subjects these temporal systems to the stochasticity.

4.2. Environmental factors influencing functional diversity variation

GAM results enabled us to identify the key drivers influencing the variation in FD indices across the studied sites. We found that water level was a crucial environmental factor, as it was associated with most of the FD indices variation in all sites. The higher water level at LPB and TLS expanded the niche space in both areas, resulting in higher functional diversity (Fig. 4a and S3). These findings are consistent with those reported by Baumgartner et al. (2018) and Mao et al. (2021). The upper LMB (including LPB) is considered a vital spawning area during the wet season, particularly for migratory species (Poulsen et al., 2002), while the floodplain site serves as spawning and nursery habitats during wet season (Valbo-Jorgensen et al., 2009). Therefore, these habitats can support a more functionally diverse fish community during high water levels. However, the significant water level changes observed in these sites following dam construction (Fig. S1) may pose a major threat to fish functional diversity. While LPB experienced a significant increase in water level post-dam, we observed a concerning decline in the variation range between minimum and maximum water levels as well as the seasonal flow pattern. The river reach in LPB historically existed as a free-flowing system with a predictable seasonal pattern, yet its natural flow has been disrupted since late 2018 (Fig. S4). This disruption is due to the presence of the Xayaburi hydropower dam (backwater of Xayaburi impoundment) as reported by Mekong River Commission (2022b), which may cause alterations in the habitat. This impact can act as an environmental filter, driving trait convergence, as previously documented in the review article by Arantes et al. (2019). Prior to dam construction, guild 3 (short-distance white fishes) dominated the top ten

most abundant species, with eight out of ten belonging to this guild (Fig. S5). The most striking change occurred after dam construction. Guild 4 (floodplain spawners) became dominant, comprising nearly half of the top ten species. Additionally, a new guild (generalist fishes) emerged, along with seven new species (e.g., *Paralaubuca riveroi*, *Puntius spilopterus* and *P. stoliczkanus*). Supporting our findings, previous studies (Chen et al., 2023; Oliveira et al., 2018; Zhang et al., 2020) observed an increase in fish adapted to lentic environments and a decrease in lotic adapted fish after dam construction. This shift reflects a change in the functional diversity of the fish community (Arantes et al., 2019), with a decline in the relative abundance of species occupying extreme functional niches (Villéger et al., 2010). This aligns with our findings, as evidenced by the disappearance of half the dominant species from guild 3 after dam construction. In TLS, the seasonal flow appeared to be normal (Fig. S4), but the water level significantly decreased post-dam (Fig. S1). This decline contributes to the lower functional diversity. The positive correlation between water level and lake area (Mao et al., 2021) suggests that reduced water levels may limit habitat availability, thereby adversely impacting functional diversity.

In contrast to LPB and TLS, as well as findings by Baumgartner et al. (2018) and Mao et al. (2021), we observed a significant negative correlation between water level and FD indices in CST and VCM. In CST, FDiv initially increased as water level rises around 6 m; however, this trend reversed at higher water levels, with FDiv starting to decrease (Fig. 4b). This pattern aligns with the findings of Baran (2006) who observed a decline in both fish biomass and species richness in Khone Falls (located around 10 km from CST) with an increasing discharge. This suggests very high water levels in CST could act as an environmental filter, selectively removing fish species that cannot withstand strong currents. This selective removal ultimately leads to a reduction in functional diversity within the fish community. A similar pattern was observed in VCM, where low salinity during high water levels acts as a filter, excluding fish species (particularly marine visitors) unable to tolerate the relatively low salinity levels. During the wet season (high water level), particularly from August to October, salinity reportedly dropped to zero at both high and low tide (Nguyen et al., 2020). Similarly, a study conducted at the Mondego estuary in Portugal found a link between decreasing salinity and higher precipitation and river runoff (Baptista et al., 2015). During the wet season, high water levels and low salinity contributed to a decrease in FRic with high trait convergence, reflecting the seasonal differences observed in both FRic and FDiv in VCM (Fig. 3b–d and S2). However, it is important to note that not all estuaries exhibit the same response to salinity changes. For example, a study by Dolbeth et al. (2016) in two tropical estuaries of Brazil found that both FRic and FDiv did not show substantial differences along the salinity gradient between the dry and wet seasons. This suggests that the influence of salinity on fish communities can vary depending on the specific ecological characteristics of the site.

Following water level as the most important driver, temperature and TOTN emerged as the second most important factors influencing variations in FD indices at certain sites. We observed that FDiv and FRic decreases in LPB and TLS, respectively, at warmer temperatures (Fig. 4c, d and S3). The interaction between high temperatures and high nutrient levels (TOTN) may contribute to phytoplankton blooms (Dory et al., 2024) as documented at both upstream and impoundment of Xayaburi dam (Mekong River Commission, 2022b). These blooms can adversely impact fish communities (Plisnier et al., 2023), potentially leading to a decrease in FRic, as observed in LPB when TOTN increases. Since both temperature and TOTN significantly increased after dam construction (Fig. S1), phytoplankton blooms may pose a long-term threat to fish communities at this site. The fish community in TLS appears particularly sensitive to elevated temperatures, despite the absence of significant changes in water temperature post-dam. Documented fish kill events reported the mortality of approximately 65 tons of fish in 2016 and 20 tonnes in 2019 due to high temperatures (Cambodia News English, 2019; Chheng and David, 2016). This harsh environment likely acts as a

filter, selectively removing fish species less tolerant of these extreme temperatures. Consequently, species with traits enabling them to adapt to this novel environment may be favoured, leading to a reduction in functional diversity (McLean et al., 2019; Nagelkerken et al., 2023), as evidenced by the observed drop in FRic at TLS. The effect of temperature on functional diversity can be complex. VCM presents a contrasting case, where FD indices increase at higher temperatures. This might be explained by the interplay of water level, salinity, temperature, and nutrients. During the dry season, lower water levels likely lead to warmer water temperatures and higher salinity due to saltwater intrusion from the ocean. This influx of marine water may then trigger the migration of marine fish species into the delta (Valbo-Jorgensen et al., 2009). Consequently, this increase in marine species could lead to a rise in FD indices (FRic and FDiv), potentially explaining the observed increase in FD indices during the dry season (Fig. 3b–d and S2). Additionally, the increase in temporal FD indices might be further attributed to higher productivity. Significant higher temperatures and TOTN (Fig. S1)—within the acceptable range as reported by Mekong River Commission (2022a) for TOTN—may promote plankton growth, which serves as the base of the aquatic food web (Chatterjee, 2023; Cho, 2023; Kuang et al., 2021). This potential increase in food resources might contribute to the observed increase in FD indices alongside the arrival of marine fishes. Our findings are further supported by the work of Mao et al. (2021), who reported a similar increase in FD with rising Chlorophyll *a* concentrations (an indicator of plankton productivity) and higher temperatures. A slightly different pattern, compared to VCM, was observed in CST. Initially, FRic in CST increased with rising TOTN levels, but then declined at higher TOTN. This suggests that moderate nutrient levels may initially enhance some functional aspects of the fish community. However, excessive nitrogen can lead to negative impacts, potentially through algal blooms (Plisnier et al., 2023). Unlike FRic, FDiv increased with rising TOTN, indicating a greater variety of functional niches (high niches differentiation) being occupied by fish species tolerant of these conditions (Mason et al., 2005; Mayfield and Levine, 2010). These tolerant species might possess traits that allow for more efficient resource use in a high-nitrogen environment.

4.3. Other potential factors contributing to changes in functional diversity

We recognized that our models left a large portion of the variation unexplained, which may suggest other potential factors contributing to the changes in functional diversity observed, particularly in CST and TLS. While there may be numerous contributing factors, we focused on three well-documented threats to the fish communities in the Mekong Basin: hydropower dams, habitat degradation, and unsustainable fishing (Mekong River Commission, 2021; Nuon et al., 2020). CST, located around 10 km downstream of the Don Sahong hydropower dam. The river reach at the dam site is unique because the main river splits into numerous channels (e.g., Hoo Sahong, Hoo Som Yai, Hoo Sadam, Xang Peuak Noy). Among these, Hoo Sahong channel stands out for its critical role. This wide channel, with no natural barriers along its 7-km length, provides easy passage for the vast number of migratory fish species traveling up the Mekong River from Cambodia to the Khone Falls in Lao PDR (Baird, 1996). However, this channel has been blocked by the construction of Don Sahong dam. A previous study investigating the impact of dams on downstream fish communities found an increase in the abundance of migratory fish near the dam, likely because the dam prevents them from swimming upstream (Agostinho et al., 2016). However, migratory fish populations have been reported to decline in the downstream reaches over the long term (Ribeiro et al., 1995; Zhong and Power, 1996). Consistent with these findings, our observations following the construction of the Don Sahong dam revealed a predominance of migratory fish, particularly long- and short-distance white fishes (Fig. S5). Given the documented long-term declines observed elsewhere, it is likely that these migratory fish guild populations may also decrease in our study area over time. In addition to the impacts from

dam, illegal fishing practices further threaten the fish community at CST. These practices include using fine mesh sizes, dynamite, poison, and electrofishing gear, and fishing in conservation zones (Mekong River Commission, 2017, 2021; Nuon and Gallardob, 2011). This combination of stressors may have a devastating impact on fish functional diversity.

TLS is situated within the Tonle Sap floodplain, a natural reservoir that stores Mekong floodwaters during the wet season (Mekong River Commission, 2005). The Tonle Sap floodplain boasts approximately 650,000 ha of flooded forest (Pry, 2024), a crucial ecosystem for diverse species including fish, mammals, reptiles, birds, and even some marine life. However, these vital flooded forests are being destroyed at an alarming rate due to conversion for agricultural land and fires (Chen et al., 2022a,b; Lovgren, 2020). This critical habitat degradation is likely impacting the fish functional diversity, leading to a homogenization of traits within the community. This aligns with the results of Villéger et al. (2010) who observed a decline in functional divergence with deteriorating habitat quality. In addition to habitat degradation, this site has been critically threatened by overfishing, including illegal fishing. Intensive fishing pressure, characterized by increased fishing efforts and reliance on illegal methods, disrupts the fish community. This disruption manifested as a shift in species composition, with a decline in catches of medium- to large-bodied species (particularly long- and short-distance white fishes) occupying higher trophic levels and a corresponding stability or increase in catches of smaller-bodied fish (Ngor et al., 2018a,b; Nuon et al., 2020; Sovannara, 2020). Supporting this observed shift, fishers in the TLS reported a dominance of small-bodied species within their catch (Kc et al., 2017). The disproportionate loss of large-bodied fish, particularly commercial species, suggests a significant decline in functional diversity within the ecosystem (Martins et al., 2012), aligning with the findings of our study.

5. Conclusion

Our results demonstrated that functional diversity indices offer valuable insights into community assembly processes and temporal changes in response to disturbance levels. The results showed that deterministic processes were the dominant influence on fish communities, with environmental filtering being the process most frequently observed. In a highly dynamic environment like the Mekong River, characterized by a monsoon-driven hydrological cycle with distinct dry and wet seasons, fish communities exhibited pronounced seasonal fluctuations in FD. Additionally, FD shows complex and context-dependent long-term changes, with a general downward trend observed at most studied sites. The main factors explaining FD changes were water level, followed by temperature and total nitrogen.

The findings of this study provide valuable scientific information for conservation practitioners and policymakers in the region. Enhancement of river connectivity (longitudinal and lateral connectivity), flooded forest restoration, and robust law enforcement should be given strong consideration when developing or revising river basin management plans at both regional and national levels. While fish passages have been constructed at the Xayaburi and Don Sahong hydropower dams, their effectiveness may be limited—particularly the fish passage at Don Sahong where only four of 139 tagged fish (three *Pangasius larnaudii* and one *Hemibagrus filamentus*) were successfully detected migrating upstream (Robinson et al., 2023). Hence, key habitats and tributaries downstream of these dams should be prioritized for restoration and protection since they may serve as potential refuges and spawning areas. Additionally, fishing should be restricted immediately downstream of the dam, especially at Don Sahong, where the dam's outflow attracts large numbers of fish, consequently drawing a high concentration of fishers (Mekong River Commission, 2022b).

Future studies should investigate how fish trait composition has shifted over time to identify traits most responsive to environmental changes and which traits are linked to fish species vulnerability.

Moreover, while this study focused solely on functional diversity, future studies could employ taxonomic and phylogenetic diversities to provide complementary information for guiding conservation efforts. Factors such as dam construction (including river connectivity), conversion of flooded forests, and unsustainable fishing were not explicitly included in the model. Future studies should further investigate these variables further to fully understand their impacts on fish communities. Climate change can significantly affect fish communities by altering water temperature, flow regimes, and habitat suitability. We recommend that future research incorporate these factors to better disentangle the effects of dams, climate change, and their potential interactions. Gaining a clearer understanding of these impacts will support the development of robust, science-based management plans.

CRedit authorship contribution statement

Vanna Nuon: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Ratha Chea:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Bernard Huguency:** Writing – review & editing, Conceptualization. **Gaël Grenouillet:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.125138>.

Data availability

The authors do not have permission to share data.

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