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Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia

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Abstract

Although the Mekong River is one of the world's 35 biodiversity hot spots, the large-scale patterns of fish diversity and assemblage structure remain poorly addressed. This study aimed to investigate the fish distribution patterns in the Lower Mekong River (LMR) and to identify their environmental determinants. Daily fish catch data (i.e. from December 2000 to November 2001) at 38 sites distributed along the LMR were related to 15 physicochemical and 19 climatic variables. As a result, four different clusters were defined according to the similarity in assemblage composition and 80 indicator species were identified. While fish species richness was highest in the Mekong delta and lowest in the upper part of the LMR, the diversity index was highest in the middle part of the LMR and lowest in the delta. We found that fish assemblages changed along the environmental gradients and that the main drivers affecting the fish assemblage structure were the seasonal variation of temperature, precipitation, dissolved oxygen, pH and total phosphorus. Specifically, upstream assemblages were characterised by cyprinids and *Pangasius* catfish, well suited to low temperature, high dissolved oxygen and high pH. Fish assemblages in the delta were dominated by perch-like fish and clupeids, more tolerant to high temperatures, and high levels of nutrients (nitrates and total phosphorus) and salinity. Overall, the patterns were consistent between seasons. Our study contributes to establishing the first holistic fish community study in the LMR.

KEYWORDS
distribution patterns, environmental gradient, fish assemblage, fishery, Lower Mekong River

1 | INTRODUCTION

Large tropical rivers represent ecosystems of historically immense value for humanity, both in terms of the high biodiversity they support and of the number of people whose livelihoods depend directly upon that biodiversity (Coates, 2001). Mekong River, the largest tropical river in Asia, is known as one of the world's 35 biodiversity hot spots (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). It is a biologically diverse and highly productive ecosystem, ranked 3rd in terms of fish diversity (877 species, Ziv, Baran, So, Rodriguez-Iturbe, & Levin, 2012), just after the Amazon River Basin (3,000 species, Rainboth, 1996) and the Congo River Basin (991 species, Froese & Pauly, 2015); yet, on a per unit area basis and fish family diversity Mekong is indeed the richest. Annually, Mekong harvests 2.3 million tonnes of wild fish supporting the world's largest inland fishery and providing essential livelihoods, nutrition and food security for millions of people within the region (MRC 2015). The economic values of fisheries in Lower Mekong alone were estimated to be worth around 17 billion USD a year generating employments and constituting a safety net for more than 60 million people within the region, especially the poor households in rural communities (MRC 2015). More importantly, in combination with its socio-economic values, the Mekong River Basin accounts for high levels of endemism, for example among the known species, 219 are endemic to the basin (76% are cyprinids and 12% catfishes; Dudgeon, 2011). However, compared to other riverine ecosystems, that is temperate, neotropical and subtropical, still very little effort has

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been mobilised to study the ecological and biological compartments of this extremely productive system, for example fish, invertebrates and other primary producers (Coates, 2001; Dudgeon, 2003; Kottelat & Whitten, 1996). While previous studies have focused on the relationship between hydrology and fish production, the impact of dams as well as the migration patterns of certain common species, the spatial structure of the fish community as a whole has not been investigated (Baran, 2006; Dugan et al., 2010; Lucas, Baras, Thom, Duncan, & Slavik, 2001; Poulsen, Ouch, Sinthavong, Ubolratana, & Nguyen, 2002; Ziv et al., 2012) and the relative importance of environmental factors in structuring fish communities along the river remains to be studied. Accordingly, the large-scale distribution patterns of the fish community have neither been described nor documented, except some ecological and biological descriptions of single species (see Rainboth, 1996).

To date, the determination of factors structuring communities remains one of the major objectives in fish ecological studies and it is widely accepted that the structure of communities results from spatial variability of habitat, environmental variability and interactions among the organisms (Albert & Reis, 2011; Lujan et al., 2013; Olden et al., 2010; Zhao, Grenouillet, Pool, Tudesque, & Cucherousset, 2015). For instance, some authors revealed the prevailing roles of physicochemical factors in structuring fish communities (Pires, Pires, Collares-Pereira, & Magalhães, 2010; Tejerina-Garro, Fortin, & Rodríguez, 1998), while others reported the dominant effects of climatic factors (Buisson, Blanc, & Grenouillet, 2008; Guo et al., 2015). Considering large-scale patterns, the study of fish communities is always challenging, for example lack of environmental variables at the local scale, rarity of large data sets of fish composition, which are much more informative than simple presence–absence data, and limitation of modelling the nonlinear relationship between biotic and abiotic factors, especially for cross-border river basins (e.g. the Mekong; Amarasinghe & Welcomme, 2002; Oberdoff, Guegan, & Hugueny, 1995).

Furthermore, over the last 30 years, with the rapid growth of population, industrialisation, agriculture intensification and hydropower development in the basin, in both Upper and Lower Mekong Basins, it was reported that the basin is now facing increasing environmental degradation, that is water pollution, eutrophication, deforestation, which are adversely affecting the biodiversity within the whole region (Dudgeon, 2003, 2011; Vorosmarty et al., 2010). Therefore, biodiversity management and conservation efforts are needed to mitigate these impacts. Consequently, this requires an understanding of how environmental and anthropogenic factors shape the present biogeography of organisms (Olden et al., 2010; Pool, Olden, Whittier, & Paukert, 2010). In this context, the main objectives of the present work were: (i) to describe the fish diversity and assemblage structure in the Lower Mekong River (LMR) by examining the relative abundance of fish composition and the associated distribution patterns and (ii) to identify the physicochemical and climatic factors driving fish assemblage patterns. More specifically, our study contributes to establishing a baseline holistic fish community study in the LMR and to identifying the drivers controlling the fish assemblage patterns. These findings could have important implications for biodiversity management and conservation in the large river basins worldwide.

2 | MATERIALS AND METHODS

2.1 | Study area: The Lower Mekong River

The Mekong rises on the Tibetan plateau and runs for 4,350 km through six countries to the South China Sea, where it discharges annually on average 475,000 million m^3 (Lu & Siew, 2006). The Mekong River Basin covers an area of 795,000 km^2 and is functionally divided into two parts: the Upper Mekong Basin (UMB) and the Lower Mekong Basin (LMB; Lu & Siew, 2006). The upper part of the river, in China, is called the Lancang Jiang and is characterised by deep gorges and steep declines. At the Golden Triangle, where the borders of Laos, Myanmar and Thailand meet, the LMB starts, and the river (Lower Mekong River) runs for another 2,500 km to the sea (Fig. 1). The LMB consists of four riparian countries, that is Laos, Thailand, Cambodia and Vietnam and covers 77% of the total basin area with 60 million inhabitants. Geographically, the Lower Mekong River (LMR) forms a stretch of about 900 km, which marks the border between Laos and Thailand, and creates an inland delta at the Lao-Cambodian border known as Khone Falls (21 m high; Fig. 1; Roberts & Baird, 1995). Then, at Phnom Penh, the Mekong

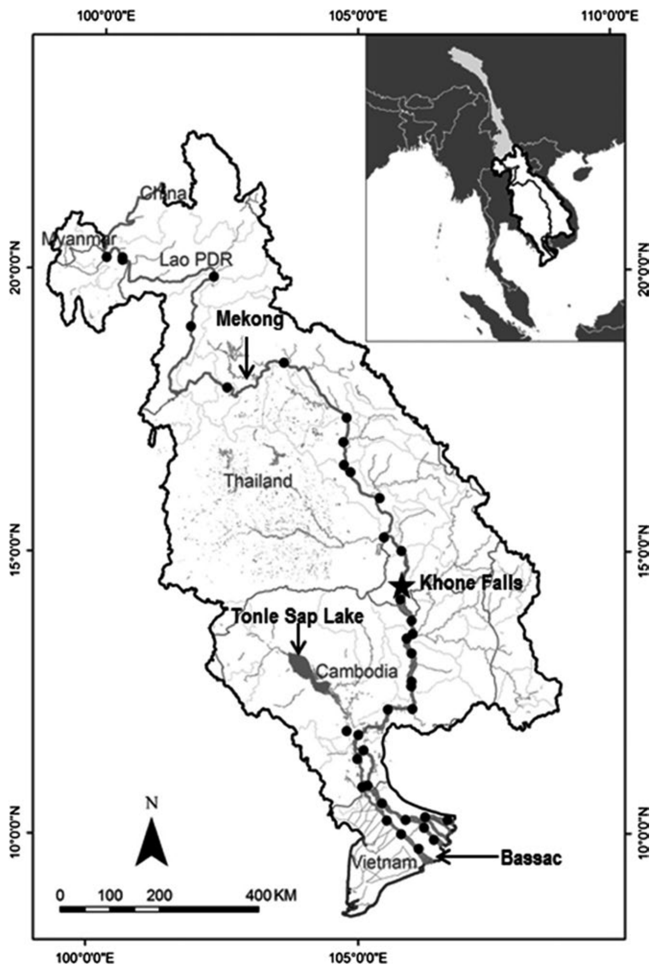

FIGURE 1 Lower Mekong Basin. Black dots represent the fish monitoring sites along the mainstream Lower Mekong River

TABLE 1 List of bioclimatic variables used in the study with the average and standard deviation

Variable	Unit	Variable type	Mean	*SD*
Bio1	(°C)	Annual Mean Temperature	26.76	0.90
Bio2	(°C)	Mean Diurnal Range (Mean of monthly (max temp − min temp))	9.15	1.71
Bio3	%	Isothermality (bio2/bio7); *100)	58.54	5.39
Bio4	(°C*100)	Temperature Seasonality (standard deviation *100)	1,569.82	736.45
Bio5	(°C)	Maximum Temperature of Warmest Month	34.23	0.98
Bio6	(°C)	Minimum Temperature of Coldest Month	18.39	3.57
Bio7	(°C)	Temperature Annual Range (bio5-bio6)	15.84	4.20
Bio8	(°C)	Mean Temperature of Wettest Quarter	27.20	0.31
Bio9	(°C)	Mean Temperature of Driest Quarter	24.83	2.19
Bio10	(°C)	Mean Temperature of Warmest Quarter	28.53	0.55
Bio11	(°C)	Mean Temperature of Coldest Quarter	24.50	2.03
Bio12	mm	Annual Precipitation	1,635.26	324.78
Bio13	mm	Precipitation of Wettest Month	329.85	90.95
Bio14	mm	Precipitation of Driest Month	4.18	3.27
Bio15	—	Precipitation Seasonality (Coefficient of Variation)	83.82	10.42
Bio16	mm	Precipitation of Wettest Quarter	869.21	251.89
Bio17	mm	Precipitation of Driest Quarter	25.31	12.84
Bio18	mm	Precipitation of Warmest Quarter	407.79	184.73
Bio19	mm	Precipitation of Coldest Quarter	63.51	46.40

Isothermality (bio3) is defined as the ratio of the diurnal range of temperature to the annual range.

connects with Tonle Sap Lake through Tonle Sap River. There, the river splits into two branches, that is Mekong proper and Bassac River, and forms a large estuarine delta before it empties in the sea. Under the influence of tropical Monsoon, the LMB's climate is basically divided into two seasons, that is dry (December–May) and wet (June–November) seasons, each lasting 6 months (Lu, Li, Kummu, Padawangi, & Wang, 2014). One of the important features of the Mekong's hydrological regime is the flow regulation by the Great Lake in Cambodia, that is the vast lake draining into the Mekong in the dry season and raising the water level in the delta for 5–6 months (Lu et al., 2014).

2.2 | Fish catch monitoring

The fish data used in this study were derived from the Mekong River Commission (MRC), under the Assessment of Mekong Fisheries Component of the MRC Fisheries Programme. The daily fish catches were monitored at 38 sites along the Lower Mekong mainstream from November 2000 to December 2001; the project was funded by the government of Denmark through DANIDA (Danish International Development Agency; Poulsen et al., 2002). Indeed, the fish survey was carried out along the main channel and consisted of eight sites located in Laos, seven in Thailand, 12 in Cambodia and 11 in Vietnam. Basically, at each location, fishermen recorded their daily catches in the logbooks, the maximum length of each species in every sample, the type of fishing gears used as well as the weather condition of the fishing day (e.g. high/low water level, rainy/sunny day). The catch monitoring methods were derived from the MRC's regional monitoring programme on Fish abundance and diversity in Lower Mekong Basin (FEVM 2007). Indeed, all fishermen were trained to use logbooks, sampling and subsampling techniques applied for the large catch during the peak seasons, identify the fish species, as well as measure length and weight of fish species. The taxonomic identification was performed to species level and to help with fish identification, the photograph flipcharts of more than 170 fish common species were provided to fishermen. Moreover, to ensure the quality of monitoring, all data were checked for errors and cleaned quarterly within the monitoring period by MRC's specialists. In total, about 14,368 observations have been recorded over the survey period and five main types of fishing gear were recorded, that is gillnets (47%), long lines and hooks (23%), traps (10%), bag nets (8%) and cast nets (7%; Sinthavong, 2006). The fishing efforts ranged from 1 to 24 hr depending on the seasons and type of the gear; nevertheless, the average efforts over the record period were between 6 to 7 hr/day. We used the whole data set for the statistical analyses.

2.3 | Climatic variables

Nineteen bioclimatic variables were derived from the WordClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), available at http://www.worldclim.org, describing the climate conditions for the period 1950–2000 with a spatial resolution of about 1 km^2 (Table 1).

2.4 | Physicochemical variables

Fifteen physicochemical variables were obtained from the MRC's water quality monitoring programme (Chea, Grenouillet, & Lek, 2016) and used to examine the link between physicochemical factors and fish assemblages (Table 2). The monitoring programme started in 1985 in Laos–Vietnam–Thailand and 1995 in Cambodia. At the basin scale, 117 sites were monitored monthly. The values of physicochemical variables of each fish site were attributed from the closest water quality monitoring sites (Table S1). In total, 22 of the whole number of monitoring sites were used for the analyses and the values of each parameter were expressed as annual median values (Table S1). The

TABLE 2 List of physicochemical variables used

Variables	Unit	Mean	*SD*
pH	—	7.38	0.33
Total suspended solids (TSS)	mg/L	124.47	84.70
Conductivity (EC)	μS/cm	202.19	105.07
Calcium (Ca^{+2})	mg/L	19.30	6.21
Magnesium (Mg^{+2})	mg/L	5.36	2.29
Sodium (Na^{+})	mg/L	12.56	17.22
Potassium (K^{+})	mg/L	1.85	1.01
Alkalinity (Alk)	mg/L	76.07	20.00
Chloride (Cl^{-})	mg/L	15.69	30.00
Sulphate (SO_4^{-2})	mg/L	14.22	5.99
Nitrate (NO_3^{-})	mg/L	0.23	0.07
Ammonium (NH_4^{+})	mg/L	0.05	0.02
Total phosphorus (TP)	mg/L	0.09	0.06
Dissolved oxygen (DO)	mg/L	7.09	0.69
Chemical oxygen demand (COD)	mg/L	2.59	1.13

average distance between fish and physicochemical sites was 27.36 (±27.08 *SD*) km.

2.5 | Statistical analysis

Here, we focused on patterns of community in terms of composition rather than abundance. Therefore, all fish catches were transformed into relative abundance to reduce the effect of varying fishing efforts between sites and averaged to annual mean relative abundance to summarise the data set. Next, we performed Ward hierarchical clustering based on the annual mean relative abundance to classify the fish sites into different groups according to their similarity in species composition (Murtagh & Legendre, 2014). Species richness and diversity index (i.e. inverse Simpson index) were computed to describe the clusters identified, and significant differences ($p < .05$) among clusters were tested using Tukey's HSD (Honest Significant Difference) tests.

Afterwards, the indicator species of each group of sites were determined using the "indicspecies" package to describe the differences in the clusters identified (De Cáceres, Legendre, & Moretti, 2010). For a given cluster, the indicator value of the species is the square root of the product of two quantities called A and B, that is predictive value and sensitivity. Quantity A is the probability of the target group of sites given that an individual species has been found and was defined as the mean abundance of the species in the target site group divided by the sum of the mean abundance value over all groups. Quantity B is the average relative abundance of individuals of the species at a site that belongs to the target site group and was determined as the relative frequency of occurrence of the species inside the target site group (De Cáceres et al., 2010). Hence, species with high indicator values were used as characteristic members of the cluster. The same procedure was performed simultaneously for dry and wet seasons of fish data sets.

To study the relationship between fish assemblages and environmental variables, ordination methods were performed on annual mean fish data. First, detrended correspondence analysis (DCA) was performed to select the appropriate ordination method for our study (i.e. redundancy analysis (RDA) versus canonical correspondence analysis (CCA; Legendre & Legendre, 2012). CCA was described as the most appropriate method as the calculated DCA ordination gradient was > 3 (i.e. 4.22 for our study), revealing that unimodal responses to environmental factors predominated (Ter Braak & Prentice, 1988). CCA is a constraint ordination method which reveals the relationships between community structure, sites and environmental variables (Legendre & Legendre, 2012). In the biplot of CCA, the importance of environmental variables is depicted by the length of the vectors, while the correlation between them is exhibited by the angle between the vectors. We used Monte Carlo permutation tests with 999 permutations to test whether the variables significantly ($p < .05$) explained the fish data (Legendre & Legendre, 2012).

Lastly, to examine the contribution of the two sets of environmental factors in explaining the variation in fish assemblages, variance partitioning was performed to see how the physicochemical and climatic variables contributed to explain fish assemblages (Borcard, Legendre, & Drapeau, 1992; Legendre & Legendre, 2012). Spatial vectors were also included in the variance partitioning to disentangle the influence of environmental and spatial factors on fish distribution. The geographic coordinates of the sites were modelled following the Asymmetric Eigenvectors Map (AEM) procedure proposed by Blanchet, Legendre, and Borcard (2008). Forward selection was performed on AEM vectors, and only significant environmental and AEM variables were kept for the analysis. The partitioning was performed through the "vegan" package and displayed in the form of a Venn diagram (Borcard et al., 1992). All statistical analyses were conducted in R 3.2.2 (R Core Team 2015).

3 | RESULTS

3.1 | Fish diversity and assemblage structure

A total of 182 species belonging to 110 genera, 42 families and 13 different orders were recorded by the fishermen at 38 monitoring sites. Three main orders accounted for 80% of the total number of species, that is Cypriniformes (54 species), Siluriformes (53 species) and Perciformes (39 species), while Anguilliformes, Batrachoidiformes, Beloniformes, Clupeiformes, Mugiliformes, Osteoglossiformes, Pleuronectiformes, Rajiformes, Synbranchiformes and Tetraodontiformes represented each of them < 5% of the total fish species richness.

The 38 monitoring sites were patterned into four different community assemblage clusters based on the similarity of their species composition (Fig. 2a). Two main community clusters were defined at the first split (clusters I and II), revealing the longitudinal characteristics of the Mekong system between the upper LMR and its delta. Subsequently, the main clusters were subdivided into four different groups considered as four different fish assemblages (Ia, Ib, IIa and

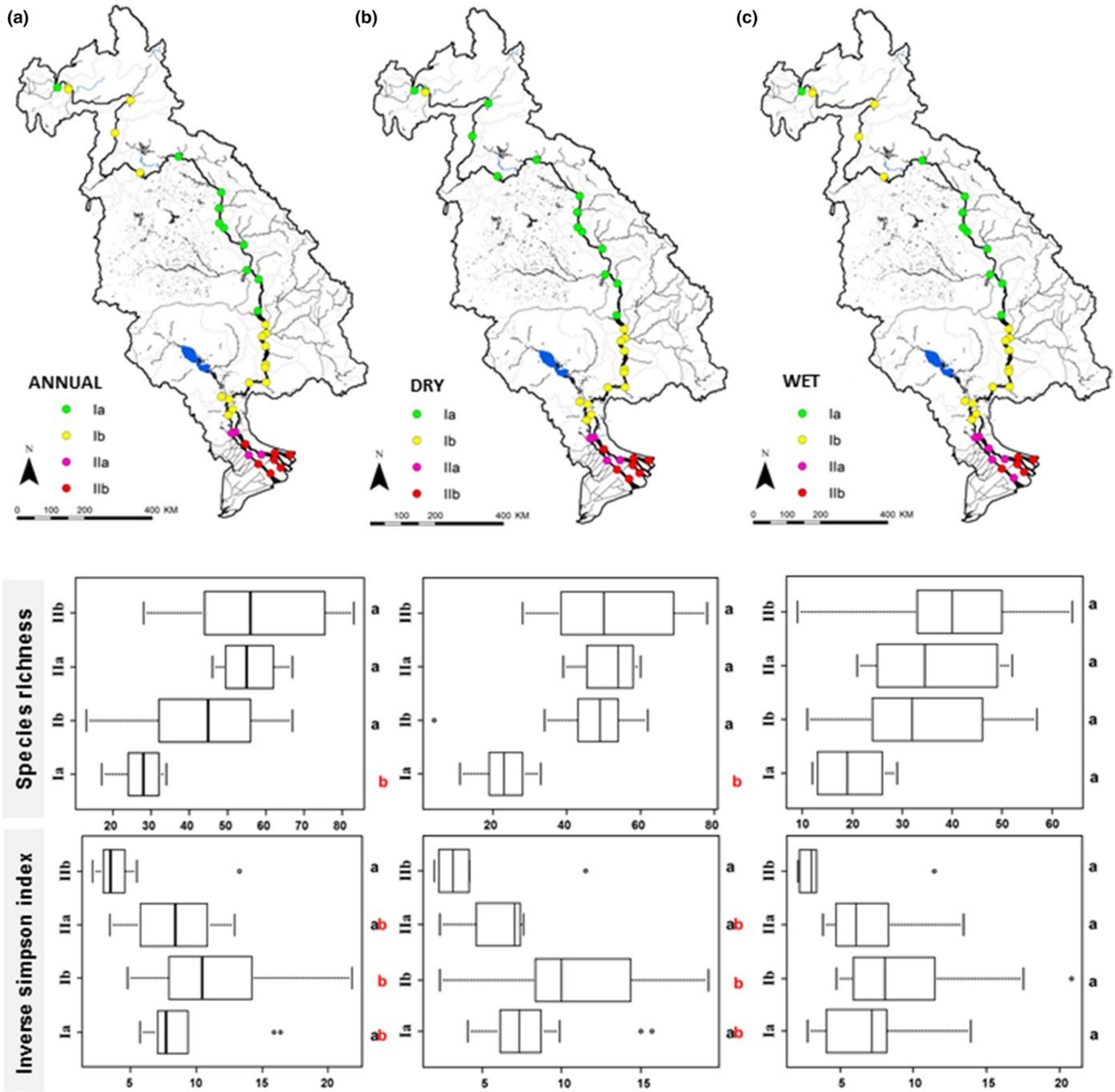

FIGURE 2 Fish distribution and assemblage patterns in Lower Mekong River. Annual (a), dry season (b) and wet season (c) clustering associated with species richness and Inverse Simpson index of each cluster (Ia, Ib, IIa, IIb). For each box plot, the dark line inside the box represents the median value, while the lines below and above indicate the 25 and 75 percentiles respectively. The whisker marks represent the minimum and maximum values. Mean values among clusters with a common letter are not significantly different at *p* = .05 (Tukey's HSD tests)

IIb) in the LMR (Fig. 2a). Indeed, cluster Ia was composed of 10 sites, stretching down in the upper part of the LMR, along the border between Laos and Thailand. Only one site of this cluster was found at the head of the LMB. Cluster Ib was composed of 17 sites, mainly located in Cambodia and four sites were found in upstream of the LMR, above Vientiane city. The smallest cluster IIa was made up of four sites, that is two sites located at the border of Cambodia and Mekong delta and other two sites in the middle part of the delta. Finally, the cluster IIb was characterised by seven sites in the lower part of the Mekong delta, known as the brackish zone; only one site of IIb was found in the middle part of the delta. Fish species richness of each assemblage ranged from 17 species at the head of the LMR to 82 at the mouth of the river (Fig. 2a). The highest species richness was found in IIb (median: 56 species), followed by IIa (55 species) and then Ib (45 species), and Ia contained the lowest species richness (28 species; Fig. 2a). Indeed, cluster Ia presented significantly lower species richness than the other three clusters, while no significant differences were observed between clusters Ib, IIa and IIb. Moreover, important variations in species richness were noticed between clusters Ib and IIb. In contrast, the diversity index was highest (median: 10.5) in Ib and lowest (median: 3.5) in IIb (Fig. 2a). Accordingly, the diversity in Ib was significantly different from IIb, while the others exhibited similar diversity indices (Fig. 2a).

The seasonal patterns were consistent between dry and wet season (Fig. 2b,c). During the dry season, fish assemblages were characterised by higher species richness than in wet season and the patterns of diversity were pronounced, especially between clusters Ib and IIb (Fig. 2b). By contrast, during the wet season, fish assemblage patterns were more similar to the annual patterns; and no significant differences in species richness and diversity were observed between the identified clusters (Fig. 2c).

Furthermore, the relative abundance of fish orders varied greatly along the longitudinal gradient of the LMR system, and this pattern was consistent between seasons for all except one fish order (i.e. Clupiformes, Fig. 3, Wilcoxon test, $p < .05$). Apart from the Mekong delta, that is particularly in Ia and Ib, Cypriniformes and Siluriformes dominated and occurred almost in every site, while their abundances decline dramatically in the delta. Additionally, Osteoglosiformes and Perciformes were found in some sites of Ib, that is the sites in Cambodia. In the delta (IIa and IIb), the fish composition was diverse and characterised by many species from different orders such as Clupeiformes, Perciformes, Pleuronectiformes, Synbranchiformes, Tetraodontiformes; among those, Perciformes and Clupeiformes were the most abundant (Fig. 3).

3.2 | Indicator species of clusters

A total of 80 indicator species were identified from the four annual clusters (Table S2). The highest number of indicator species was found in IIb (31 species), while the lowest was observed in Ia (11 species). The clusters in the delta (IIa and IIb) accounted for 66% of the total indicator species. The indicator species in Ia and Ib were mostly species from Cyprinidae, Pangasiidae, Siluridae and Bagridae families, that is *Cosmochilus harmandi*, *Bagnana behri*, *Helicophagus waandersii*, *Labeo chrysophekadion*, *Bagarius yarelli*, *Henicorhynchus* spp., *Micronema bleekeri and Hemibagrus nemurus*, which are known as potamodromous fish and indigenous to the LMB. Assemblage IIa contained 21 indicator species. Among them, many are known as freshwater and secondary freshwater fish such as *Glossogobius giuris*, *Macrognathus siamensis*, *Acanthopsis* sp., *Puntioplites proctozysron*, *Mastacembelus armatus and Mystus mysticetus*. Similarly, the main indicator species of IIb were mostly characterised by secondary freshwater fish and marine species, known as amphidromous and anadromous fish, that is *Clupeichthys aesarnensis*, *Rasbora trilineata*, *Scomberomorus sinensis*, *Eleotris* spp., *Liza* spp., *Arius stormi*, *Toxotes* spp., *Lates calcarifer*. Most of indicator species during the dry season were also identified as indicator species using annual assemblage compositions. Overall, dry season assemblages contained more indicator species (73 species) compared to wet season assemblages (51 species), while many indicators species from annual IIa and IIb were absent in the wet season (Table S2).

3.3 | Environmental determinants of the fish assemblages

The CCA model testing the association between annual fish assemblages and climatic variables was significant ($F = 1.55$, $p = .001$) and the first two axes explained 15.8% and 7.2% of the variation in fish composition respectively. Among the climatic variables tested, 18 had a significant ($p < .05$) effect on fish assemblage (Fig. 4a,b, Tables 1 and 3). Indeed, cluster Ia was mainly characterised by high values of bio15, bio16 and bio13 respectively the seasonal variation of precipitation,

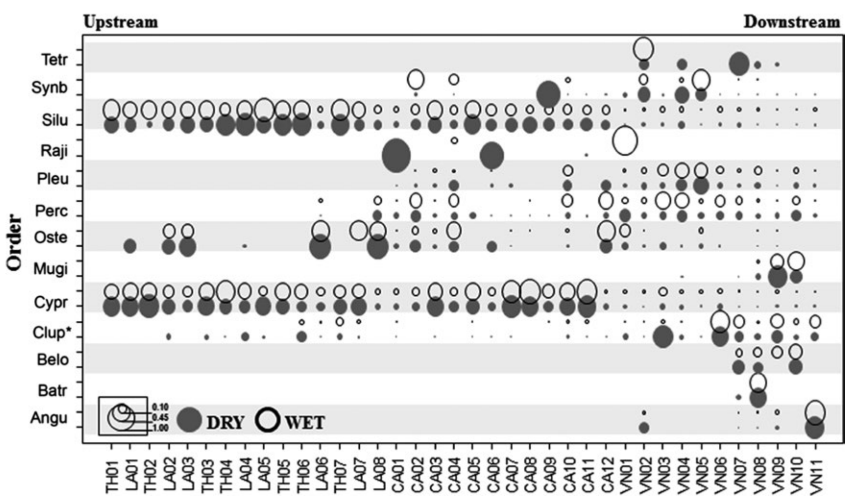

FIGURE 3 Relative abundances of fish order along the Lower Mekong River. Open and close circles denote the wet and dry season respectively. The acronyms in the vertical axis denote the species order: angu (Anguilliformes), batr (Batrachoidiformes), belo (Beloniformes), clup (Clupeiformes), cypr (Cypriniformes), mugi (Mugiliformes), oste (Osteoglossiformes), perc (Perciformes), pleu (Pleuronectiformes), raji (Rajiformes), silu (Siluriformes), synb (Synbranchiformes), tetr (Tetraodontiformes). The acronyms in the horizontal axis indicate the location of the sites: TH (Thailand), LA (Laos), CA (Cambodia) and VN (Vietnam). *denotes significant differences in fish relative abundance between seasons (Wilcoxon test, $V = 313$ and $p = .04$)

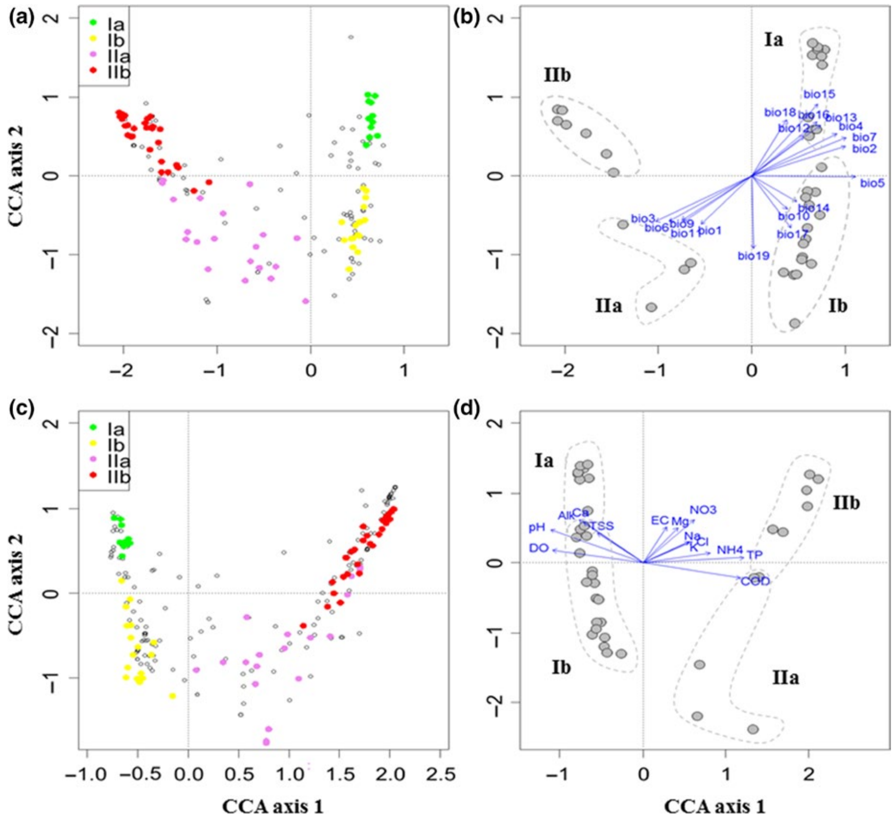

FIGURE 4 Canonical correspondence analysis (CCA) relating fish relative abundance to (a, b) climatic variables and (c, d) physicochemical variables. The different colour dots on the left plots represent the indicator species in each fish assemblage; while the grey dots on the right hand side indicate the fish monitoring sites. The blue arrows represent the vectors of environmental variables (i.e. climatic and physicochemical) and only significant variables ($p < .05$) are depicted. Details about the indicator species and environmental variables are given in Tables 1–3 and S2

the precipitation of the wettest month and wettest quarter. Similar climatic patterns were associated to Ib, except that high values of bio5 (maximal temperature of warmest month) and bio19 (precipitation of coldest quarter) were strongly associated with this cluster. In the Mekong delta, clusters IIa and IIb were characterised by high values of the isothermality (bio3), minimal temperature of the coldest month (bio6), the mean temperature of the driest quarter (bio9) and coldest quarter (bio11). Overall, in the upper part of the LMR, the clusters Ia and Ib were associated with high values of precipitation, while the delta clusters (IIa and IIb) were strongly characterised by high values of temperature.

In parallel, the CCA model testing the effect of physicochemical variables on annual fish assemblage composition was significant ($F = 1.77$, $p = .001$). The first two axes explained 22.5% of the variation in fish assemblage (15.5% and 7.0% respectively). Among the physicochemical variables tested, 14 had a significant effect on the fish assemblages ($p < .05$; Fig. 4c,d, Tables 2 and 3). Clusters Ia and Ib were strongly characterised by high values of DO, pH, Ca, alk and TSS; while the IIa and IIb were positively associated with high values of TP, COD and NH_4^+. In addition, cluster IIb was found to be associated with high levels of NO_3^- and Cl^- as well, especially for the sites close to the sea.

3.4 | Effects of environmental and spatial factors on the fish assemblages

Variance partitioning in fish assemblage composition indicated that both environmental (physicochemical and climatic) and spatial variables contributed significantly to explain patterns in fish assemblages (Fig. 5). The pure physicochemical factors explained 8.0% of variation in fish assemblages, while 10.9% and 4.0% were explained uniquely by climatic and spatial factors respectively. Physicochemical and climatic factors jointly explained 5.3% of the total variance, while the component shared by the three factors (physicochemical, climatic and spatial) explained 20.1% of the variation in fish assemblages. The adjusted R^2 from the model was 46.7%.

4 | DISCUSSION

4.1 | Fish diversity and assemblage structure

To our knowledge, this study is the first holistic fish community study to investigate the large-scale patterns of fish distribution and their environmental determinants in the lower Mekong river. In terms of fish diversity, the upstream part of the LMR exhibited the lowest species richness, while the highest richness was observed in the delta where fish species were composed of freshwater, brackish and marine species. Indeed, the longitudinal changes of species richness along the physical and chemical gradients, that is upstream–downstream, are well known in large-scale patterns of fish assemblages. Many discussions and explanations of the mechanisms responsible for such patterns have come up with the concept of “addition” leading to the increase in species richness from the headwaters to lower part of the river (see Matthews, 1998).

In contrast to species richness, cluster IIb exhibited the lowest diversity index, while the highest value was observed in Ib in Cambodia. Consequently, these patterns of diversity could reflect

TABLE 3 Canonical correlation coefficients of climatic and physicochemical variables with the first two canonical correspondence analysis axes (CCA1 and CCA2). The correlation of the explanatory variables to the final ordination (r^2) determines their importance in explaining fish assemblage composition, with their associated *p*-values computed from permutation tests. Variable codes are in Tables 1 and 2

Parameters	CCA1	CCA2	r^2	*p*
Climatic variables				
Bio1	−.664	−.748	.393	.001
Bio2	.937	.349	.676	.001
Bio3	−.870	−.493	.820	.001
Bio4	.861	.509	.658	.001
Bio5	1.000	−.010	.727	.001
Bio6	−.838	−.546	.656	.001
Bio7	.901	.434	.743	.001
Bio8	.272	−.962	.013	.756
Bio9	−.803	−.595	.518	.001
Bio10	.658	−.753	.191	.025
Bio11	−.783	−.622	.516	.001
Bio12	.736	.677	.336	.001
Bio13	.750	.662	.561	.001
Bio14	.830	−.557	.197	.020
Bio15	.613	.790	.788	.001
Bio16	.714	.700	.566	.001
Bio17	.538	−.843	.360	.002
Bio18	.463	.886	.382	.001
Bio19	.016	−1.000	.500	.001
Physicochemical variables				
pH	−.918	.397	.721	.001
TSS	−.789	.615	.236	.014
EC	.494	.869	.170	.043
Ca	−.780	.626	.476	.001
Mg	.637	.771	.213	.016
Na	.876	.482	.199	.023
K	.877	.480	.202	.021
Alk	−.768	.640	.415	.001
Cl	.890	.456	.217	.011
SO4	−.294	.956	.154	.066
NO3	.707	.708	.377	.001
NH4	.985	.174	.334	.005
TP	.998	.061	.736	.001
DO	−.987	.161	.600	.001
COD	.984	−.180	.703	.001

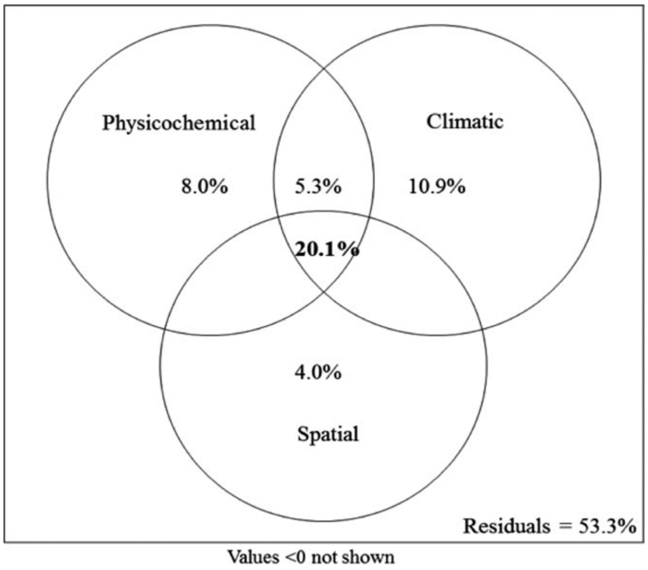

FIGURE 5 Venn diagram of variance partitioning results showing the relative effects of physicochemical, climatic and spatial factors alone and in combination with the variation of the fish assemblages. Numbers represent % variation explained by each factor. All pure factors were statistically significant (*p*-value < .05)

the river continuum concept (RCC) where the species richness is high at the lower part of the river and highest diversity is observed in the middle reach (Statzner & Higler, 1985; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980). However, RCC is more applicable to small- to medium-sized rivers, that is probably not the case for the lower Mekong. Another reason for the high diversity in Cambodia could be the geographical conditions of the region, where many species cannot migrate up the Khone Falls (Valbo-Jorgensen, Coates, & Hortle, 2009). In Cambodia, the river is characterised by low land and no barriers; thus, many species could move easily up and down this part (Baran, So, & Leng, 2008). Besides, the vital connectivity between the Tonle Sap Lake and Mekong provides favourable conditions for many species to complete their life cycle as the lake provides feeding and nursing grounds, while many deep pools below Khone Falls and at large tributaries (3S river system) are essential for spawning and dry season refuge.

Dry season fish assemblages were characterised by significant changes in species richness and diversity along the LMR, similar to observed annual patterns. It can be due to the fact that fish may be concentrated in deep pools, microhabitats or main river course during the dry season, while fish would probably disperse more as the river expands with increased inundated floodplains and habitat diversity during wet season (Ferreira & Stohlgren, 1999; Junk, Barley, & Sparks, 1989; Silvano, do Amaral, & Oyakawa, 2000). Consequently, this concentration would lead fishermen to catch easily the fish with variety of species compared to wet season. Moreover, different patterns in community composition between seasons could be explained by the migratory fish movement in the basin (Baran, 2006). Therefore, the seasonal turnover may be attributed to the different catchability, habitat diversity and migration of fish within the basin. Similar conclusions have been previously reported from fish community studies in tropical Amazonian rivers (Albert & Reis, 2011; Matthews, 1998; Winemiller, 1996).

At the upper part of LMR, the different patterns in Ia and Ib between dry and wet seasons revealed the association of community structure with migration patterns (Fig. 2a,c). For instance, many wet season indicator species from Ia and Ib, that is *C. harmandi*, *Henicorhynchus* spp., *Pangasianodon hypophthalmus*, *H. nemurus*, are long-distance migrants, and their spawning ground was identified at uppermost parts of LMR (Baran, 2006; Poulsen et al., 2004). Similarly, to many Amazonian fish, some of the Mekong species were reported to migrate upwards for reproduction, while others migrate downwards for feeding and nursing (Poulsen et al., 2004). Accordingly, in the middle part of LMR, most of the migrants feed in Tonle Sap Lake and spawn below Khone Falls; while at upper part, the river serves both, that is spawning and feeding, for all migrants (Poulsen et al., 2004; Rainboth, 1996). Nevertheless, as a result of fish movement, no significant difference in diversity was observed during the wet season, revealing that diversity patterns were more homogenous compared to dry season and annual patterns.

Clear patterns of the assemblage structure were observed between the upper LMR and its delta. Specifically, assemblages Ia and Ib were characterised by cyprinids and catfish, species known to be potamodromous, which frequently occur in a large-sized river, specifically in the Mekong mainstream, that is *C. harmandi*, *L. chrysophekadion*, *H. waandersii*, *B. yarelli and Bangana behri* (Lucas et al., 2001). Below Khone Falls, the cyprinids in Ib were dominated by opportunist species, that is *Henicorhynchus* spp., *Thynnichthys thynnoides* and *Paralaubucca typus*; these species are known as fast growing with short lifespan and are reported to do the long-distance migration as well, commonly between Tonle Sap Lake and upstream Cambodian Mekong (Baran et al., 2008).

In the Mekong delta, the fish assemblages changed significantly, with sharp declines in fish abundances observed for cyprinids and catfish, known as stenohaline species with low tolerance to salinity (Valbo-Jorgensen et al., 2009). Obviously, the perch-like fish (Perciformes) and clupeids (Clupeiformes) were common species in IIa and IIb; these groups of fish are tolerant to salinity and turbid water (Albert & Reis, 2011). Nevertheless, in IIa, many species were known as stenohaline species, that is *C. aesarnensis*, *Mastacembelus* spp., *Acanthopsis* sp., which are less tolerant to the brackish conditions of the delta. However, some of them need the marine environment to complete their life cycle, for example *Cynoglossus microlepis*, while others were believed to reside permanently in the estuary, for example *G. giuris* (Froese & Pauly, 2015; Valbo-Jorgensen et al., 2009). In IIb, we found mostly marine species, that is *Liza* spp., *Scomberomorus* sp., *Toxotes* spp., *Allenbatrachus grunniens*, *Boleophthalmus boddarti*, which are well suited to the marine environment with less light penetration (Moyle & Cech, 1988). Of course, these species are known as amphidromous fish and some of them are catadromous fish, for example *Anguilla* sp., *Ellochelon vaigiensis*, *Mugil cephalus*, which inhabit fresh-brackish water and live permanently in the estuary like the small anchovies (*Coilia* sp. and *Tenualosa toti*; Froese & Pauly, 2015; Motomura, Iwatsuki, Kimura, & Yoshino, 2002).

So far, the difference in fish assemblage patterns could result from the different migration routes of fish within the basin, where it was estimated that about 40% of lower Mekong species are "white fish" that conduct long-distance migrations (Baran, 2006; Poulsen et al., 2004).

4.2 | Relative importance of environmental and spatial factors structuring the fish assemblages

Overall, our study showed that the seasonal variation of precipitation (bio15), the precipitation of the wettest month (bio16), the maximal temperature of warmest month (bio5), the precipitation of coldest quarter (bio19), as well as the isothermality (bio3), the minimal temperature of the coldest month (bio6) and the mean temperature of the driest quarter (bio9) were the key climatic factors driving the changes in fish assemblage structure. Obviously, the seasonal variations of temperature and precipitation have proved to be important factors affecting the distribution of organisms in ecosystems (Buisson et al., 2008; Cheung et al., 2009). Alternatively, TP, DO, COD and pH significantly influenced the spatial structure of the fish assemblages as well. Indeed, many studies have revealed the link between physicochemical factors, particularly nutrients and DO, and the patterns of fish assemblages along river systems (Fialho, Oliveira, Tejerina-Garro, & de Mérona, 2007; Trujillo-Jiménez, López-López, Díaz-Pardo, & Camargo, 2009).

According to the results of our study, the differences between upstream (Ia and Ib) and delta assemblages (IIa and IIb) were mainly explained by temperature as well as nutrients and the natural effects of seawater intrusion. Consequently, the upstream species were specialised for upstream conditions with high altitude, lower temperature, high rainfall, DO and pH, particularly in cluster Ia. By contrast, the delta species were suited to high levels of nutrients and could tolerate high temperature and salinity. These conclusions were also consistent with previous studies which reported that the upper Mekong fish were dominated by Cyprinidae, Balitoridae, Cobitidae and Sisoridae that all prefer cold, oxygen-rich water bodies (Valbo-Jorgensen et al., 2009), while Gobiidae, Polynemidae, Toxotidae, Eleotridae, Clupeidae and Engraulidae dominated in the delta, with species known to tolerate estuarine conditions, that is low oxygen, high nutrient, eutrophication and salinity.

So far, many studies on the environmental determinants of fish assemblage structure have reported the main contribution of physicochemical factors (Braaten & Guy, 1999; Pires et al., 2010; Trujillo-Jiménez et al., 2009), while others revealed a predominant role of climatic factors in structuring the spatial distribution of fish (Buisson et al., 2008; Guo et al., 2015; Reash & Pigg, 1990; Zhao et al., 2015). However, in our study, the combination of environmental and spatial factors provided a better explanation of the variation in fish assemblages. Thus, the physicochemical or climatic factors alone would not optimally explain the distribution patterns of fish assemblages (Lujan et al., 2013).

4.3 | Fish diversity management and conservation

Our results provide the current baseline information on fish assemblage structure in the LMR system. According to our results, fish conservation zones should be prioritised in the middle part of the LMR, that is mainly cluster Ib, where the highest diversity was exhibited. Moreover, conservation planning should also consider the upstream part of the LMR (Cluster Ia), between Khone Falls and Vientiane city, where high levels of endemism to the LMR system are recorded (Coates, 2001). Accordingly, it was reported that the construction of natural reserves would be an effective approach to protect fish biodiversity (Park, Chang, Lek, & Brosse, 2003). Besides, the conservation strategies should be prioritised to specialist groups of fish as they are endangered and vulnerable to environmental changes (Kang et al., 2009). Alternatively, conservation practices should be carried out in a networked region rather than in single reserve and different conservation strategies should be proposed according to the different objectives and eco-regions, for example upstream LMR and Mekong delta.

Furthermore, the maintaining of the connectivity between upstream–downstream habitats (including deep pools as dry refuge) and major tributaries (3S river systems, Tonle Sap River, the Great Lake and its floodplains) is essential for many short- and long-distance migrants such as *Pangasianodon gigas* and *Pangasius kremfi* to complete their life cycle. Therefore, we strongly support the concerns of biodiversity losses due to the construction of dams across the main channel (Hortle, 2007; Valbo-Jorgensen et al., 2009; Ziv et al., 2012). Meanwhile, water quality monitoring and improvement need to be addressed rigorously within the region (Chea et al., 2016; Dudgeon, 2011). For instance, our study exhibited the lowest fish diversity in the delta, likely to reflect water pollution effects on the fish community. Thus, the cyprinids and *Pangasius* catfish, which are the main sources of proteins (Hortle, 2007), would be strongly affected as they are unable to withstand significant changes in water condition. Nevertheless, our study revealed that the combination of both environmental and spatial factors contributes significantly in structuring the fish community along the LMR. Taking these factors into account appears therefore crucial if we are to initiate management strategies to ensure the conservation and sustainable use of fisheries resources in the Lower Mekong River.

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