

Influence of Floodplain Area on Fish Species Richness in Waterbodies of the Chao Phraya River Basin, Thailand

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Abstract

River-floodplain ecosystems are in delicate balance and are impacted by even minor changes in water availability. In this study, we surveyed fish assemblages and investigated environmental and landscape parameters in a total of 135 floodplain waterbodies (rivers, diversion canals, ponds, irrigation ditches, paddy fields, and wetlands) in the Chao Phraya River Basin in rainy (September 2014) and dry (March 2015) seasons. Factors affecting fish species richness in each type of waterbody were analyzed using generalized linear mixed models. Floodplain area around each surveyed waterbody was a major factor determining fish species richness in rivers, diversion canals, and ponds in the region. The contribution of floodplain area was equivalent to that of hydrology (current velocity, water depth) and water quality (dissolved oxygen, turbidity) in the waterbodies. The population of juvenile fishes was increased in temporarily connected floodplain waterbodies to main rivers compared with isolated waterbodies, and fluvial and lacustrine fishes were observed in the temporary inundated floodplain waterbodies during the rainy season. The high dependence of fish species richness on floodplain area in the region appeared to be a result of the use of inundated floodplains by fish species to forage and breed. Our results highlight the impact of flood control measures that reduces floodplain area. These measures must be reviewed to ensure the conservation of fish biodiversity in the Chao Phraya River Basin, one of the world's most threatened floodplain systems.

Keywords

Floodplain, Fish Species Richness, Lateral Fish Migration, Chao Phraya River Basin, Flood Pulse Concept

1. Introduction

Floodplains are riparian ecotones in which there is a transition between terrestrial and aquatic communities [1]. These areas feature high biodiversity and are a highly productive part of the aquatic ecosystem [2] [3]. Previous studies on river-floodplain ecosystems have demonstrated the importance of flooding, which allows aquatic organisms to migrate into inundated floodplains and to use resources from the submerged terrestrial landscape for feeding and breeding. Therefore, the area of floodplains affects the recruitment of aquatic organisms [2] [4] [5]. Changes in or disturbance of the natural flooding cycle creates habitat heterogeneity and gradients in the hydrochemical environment in floodplain waterbodies, which in turn affect the distribution and species richness of aquatic organisms [6]-[8].

Many studies have shown that the species richness of various biota is affected by floods in large river systems around the world, for example, fishes and phytoplankton in the Danube River in Europe [7] [9], hydrochorous plants in the Twentekanaal Canal in the Netherlands [10], zooplankton and phytoplankton in the La Plata River in South America [11] [12], and fishes and zooplankton in the Amazon River in South America [13] [14]. Although Southeast Asia is home to some of the world's most threatened floodplains, particularly as a result of human activities, there have been few studies conducted on the impact of flooding on species diversity in this region [15].

The Chao Phraya River is one of the major rivers of Southeast Asia, and its basin has a vast floodplain system. The floodplains are maintained by regular and sustained flood events, and the life cycles of many fish species in the basin depend on these floods [16]. However, flood control measures have been implemented in the Chao Phraya River Basin following the devastation caused by the 2011 Thailand flood. Understanding of the impact of floodplain area and flood events on fishes in the basin is essential to ensure that the flood control measures are adapted to minimize negative effects on the river-floodplain ecosystem. Previous studies about fishes in the basin have focused on taxonomy and biodiversity (e.g., [17]-[19]), whereas ecological aspects have received little attention [16] [20]. In particular, the importance of floodplain area and flood events for fish species richness remains largely unknown. In the present study, fish assemblages and the hydrochemical environments of the main tributaries and floodplain water bodies in the mid-Chao Phraya River Basin were investigated. General linear mixed model (GLMM) analysis was used to determine the importance of flood events and the area of floodplains for the fishes in the region.

2. Materials and Methods

2.1. Study Area

The study was conducted in the floodplains of the mid-Chao Phraya River Basin (**Figure 1(a)**) where the three main tributary rivers of the Chao Phraya River meet. The tributaries are the Ping River with an average discharge of $158 \text{ m}^3 \cdot \text{s}^{-1}$ and a maximum discharge of $403 \text{ m}^3 \cdot \text{s}^{-1}$ (P.7A water level station 2014), the Yom River with an average discharge of $101 \text{ m}^3 \cdot \text{s}^{-1}$ and a maximum discharge of $443 \text{ m}^3 \cdot \text{s}^{-1}$ (Y.16 water level station 2014), and the Nan River with an average discharge of $201 \text{ m}^3 \cdot \text{s}^{-1}$ and a maximum discharge of $862 \text{ m}^3 \cdot \text{s}^{-1}$ (N.7A water level station 2014) [21]. There are no barriers to the dispersal of fishes, such as large dams, on the rivers in the study area. This region has three seasons: a rainy season, typically from mid-May to mid-October, and cool and hot dry seasons, typically from mid-October to mid-May [22]. In the rainy season, floods generally occur from September to October. Flood characteristics among the three sub-basins differ in terms of floodplain area. The floodplain area in the Ping River sub-basin is smaller than that in the Yom and Nan River sub-basins (**Figure 1(b)**).

2.2. Fish Sampling and Environmental Parameter Assessment

Fish sampling was conducted using cast nets with a 20 mm mesh size and scoop nets with a 2 mm mesh size. The fishing effort at all sampling sites was 20 man-minutes for cast nets and 10 man-minutes for scoop nets. In total, 135 waterbodies were sampled in the Ping River sub-basin, the Yom River sub-basin, and the Nan River sub-basin (**Figure 1(a)**) in September 2014 (the rainy season: 15 rivers, 19 diversion canals, 12 ponds, 5 irrigation ditches, 18 paddies, and six wetlands) and March 2015 (the dry season: 15 rivers, 18 diversion canals, 12 ponds, 5 irrigation ditches, 11 paddies, and one wetland). The different waterbody types are shown in **Figure 2**. For safety reasons, sampling from rivers and ponds with a water depth $> 2 \text{ m}$ was carried out from the edge of

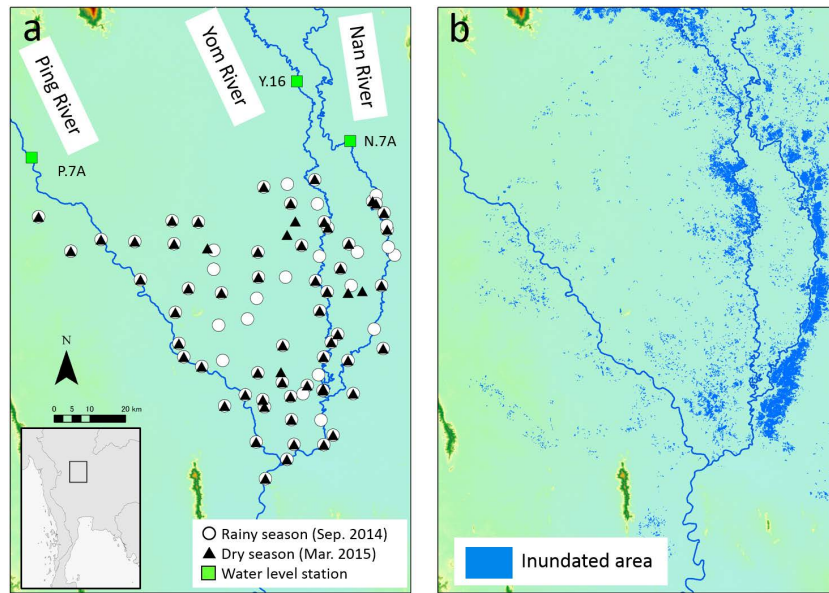


Figure 1. Maps of the study area. (a) Open circles indicate the sites surveyed in the rainy season (September 2014). Black triangles indicate the sites surveyed in the dry season (March 2015), (b) Inundated areas in 2014.

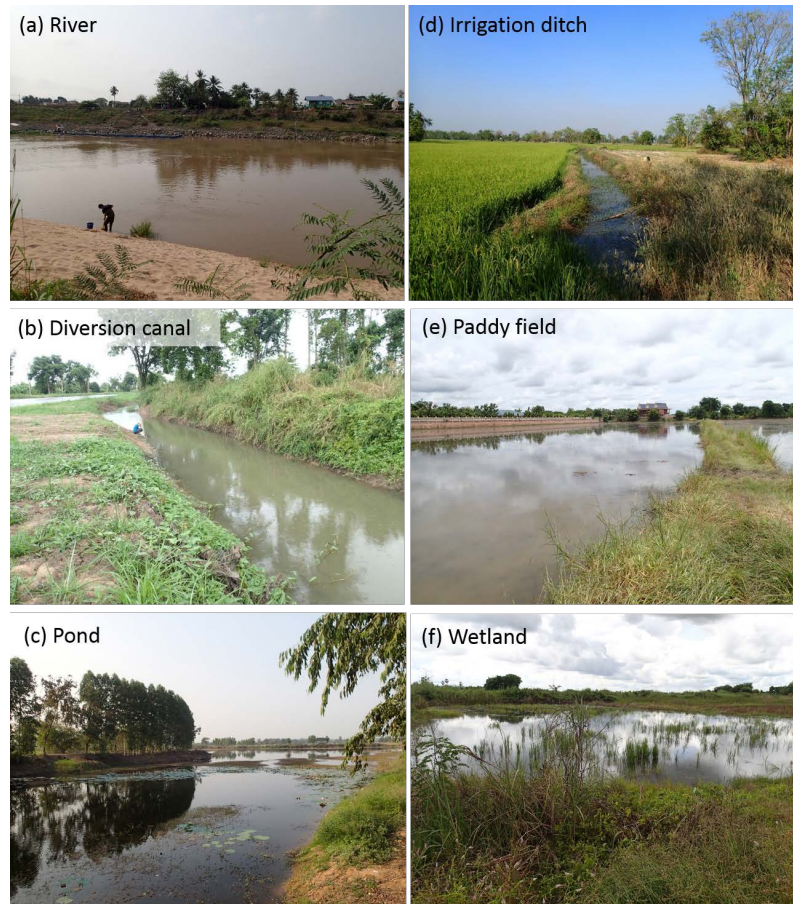


Figure 2. Photographs of the types of waterbodies surveyed. (a) River, (b) Diversion canal, (c) Pond, (d) Irrigation ditch, (e) Paddy field, and (f) Wetland.

the waterbody. Captured fishes were identified at species level and their total length was measured. Most individuals were released at the same site where they were caught, but some were preserved in 4% formalin when further identification was required. The fishes were identified according to [16], Apinun (unpublished data), and the online database of Fishes of Mainland Southeast Asia (<http://ffish.asia/>; [23]), their scientific names following [19].

At each study site, the following environmental parameters were measured in the field: electric conductivity (EC, μS ; PCS Tester 35, Oakton Instruments, IL, USA), turbidity (Turb, NTU; HI 93703; Hanna Instruments Japan, Tokyo, Japan), dissolved oxygen (DO, $\text{mg}\cdot\text{L}^{-1}$; DO-5509; Mother Tool Co., Ltd., Ueda, Japan), water depth (Dep, m), and current velocity (Vel, $\text{m}\cdot\text{s}^{-1}$; CR-11; Cosmo-riken Co., Ltd., Kashiwara, Japan). These environmental parameters were measured once at the surface in the center of each study site. In addition to the above environmental parameters, waterbodies were classified as temporarily connected to main rivers by an annual flood or as isolated at the time of survey (Con; 1 for temporary connection, 0 for no connection).

2.3. Landscape Parameter Assessment

At each sampling location, the following landscape parameters were measured by geographic information system (GIS) manipulation: route distance of each waterbody via the channel network from the nearest river (Dist, km), and the floodplain area around each survey site (FA, km^2). The floodplain area was calculated within a buffered circle around each survey site according to [24] and [25]. Because the spatial scale at which the floodplain area should be extracted was not clear, buffers of a given radius (500 m, 1000 m, 2000 m, 3000 m, and 4000 m) were generated around the center of each study site. The floodplain GIS data were obtained from the Thailand Flood Monitoring System [26]. Data for the 2014 inundation range were used and areas that experienced flooding in that year were classified as floodplains. The landscape parameters were calculated using ArcGIS ver. 10.2 (ESRI Japan, Tokyo, Japan).

2.4. Data Analysis

To determine the size composition of fishes in the waterbodies connected to main rivers by an annual flood and in isolated waterbodies, total length histograms were constructed for the species with more than 50 individuals captured from both connected and isolated waterbodies during the rainy season survey (*Esomus metallicus*, *Trichopsis vittata*, *Trichopodus trichopterus*, and *Trichopodus microlepis*).

A GLMM [27] was used to identify the environmental and landscape parameters that influence fish species richness (Table 1). The analysis was performed for overall fish species richness and for each waterbody type surveyed at twenty or more locations (rivers, diversion canals, ponds, and paddy fields). A correlation matrix between environmental and landscape parameters was calculated to avoid multicollinearity. The Pearson's correlation coefficients (R) were <0.7 , indicating that multicollinearity did not distort the GLMMs using these variables as predictors (Table 2) [28].

In the GLMMs, the dependent values were the species richness of native fish species, migratory native fish species, and non-migratory native fish species in each waterbody type. The floodplain migratory behavior for each fish species was defined according to FishBase (<http://www.fishbase.org/>). The independent variables were EC, Turb, DO, Dep, Vel, Con, Dist, and FA as fixed factors, and season (rainy season, dry season) and waterbody

Table 1. Variables used during GLMM and model selection.

Variables	Description	Variable type	Unit
EC	Electric conductivity of survey site	Continuous	μS
Dep	Water depth of survey site	Continuous	m
Do	Dissolved oxygen of survey site	Continuous	$\text{mg}\cdot\text{L}^{-1}$
Turb	Turbidity of survey site	Continuous	NTU
Vel	Current velocity of survey site	Continuous	$\text{m}\cdot\text{s}^{-1}$
Con	Connected by an annual flood or not	Dummy	0, 1
Dist	Route distance from the nearest river	Continuous	km
FA	Floodplain area around each survey site	Continuous	km^2

Table 2. Correlation matrix of variables used during GLMM and model selection.

Total		1	2	3	4	5	6	7	8
1	EC	1							
2	Dep	-0.26	1						
3	Do	-0.02	-0.03	1					
4	Turb	0.03	-0.09	0.06	1				
5	Vel	-0.25	0.31	0.27	0.13	1			
6	Con	-0.15	0.00	-0.03	-0.11	-0.09	1		
7	Dist	0.14	-0.16	-0.05	0.20	-0.29	-0.14	1	
8	FA [†]	0.09	0.06	-0.16	-0.27	-0.06	0.33	-0.46	1
River		1	2	3	4	5	6	7	8
1	EC	1							
2	Dep	-0.32	1						
3	Do	0.21	-0.27	1					
4	Turb	0.06	0.69	0.15	1				
5	Vel	-0.11	0.46	0.46	0.53	1			
6	Con	-	-	-	-	-	-		
7	Dist	-	-	-	-	-	-	-	
8	FA [†]	-0.36	0.2	-0.38	-0.21	-0.01	-	-	1
Canal		1	2	3	4	5	6	7	8
1	EC	1							
2	Dep	-0.37	1						
3	Do	0.00	-0.15	1					
4	Turb	0.10	-0.22	0.07	1				
5	Vel	-0.12	0.48	-0.10	-0.07	1			
6	Con	-	-	-	-	-	-		
7	Dist	0.17	0.06	-0.15	0.16	0.26	-	1	
8	FA [†]	0.19	-0.08	0.1	-0.26	-0.1	-	-0.40	1
Paddy		1	2	3	4	5	6	7	8
1	EC	1							
2	Dep	-0.34	1						
3	Do	-0.07	-0.02	1					
4	Turb	0.04	-0.31	0.06	1				
5	Vel	-0.10	0.29	-0.26	-0.08	1			
6	Con	-0.32	0.59	-0.09	-0.31	0.32	1		
7	Dist	0.10	-0.42	0.16	0.33	-0.17	-0.36	1	
8	FA [†]	0.02	0.48	-0.27	-0.41	0.27	0.54	-0.59	1
Pond		1	2	3	4	5	6	7	8
1	EC	1							
2	Dep	-0.18	1						
3	Do	0.12	0.12	1					
4	Turb	0.07	-0.28	0.27	1				
5	Vel	-0.04	-0.16	-0.15	0.25	1			
6	Con	-0.32	-0.06	0.23	-0.07	-0.06	1		
7	Dist	-0.02	-0.16	0.52	0.23	-0.13	-0.16	1	
8	FA [†]	-0.03	0.13	-0.43	-0.13	0.12	0.21	-0.65	1

[†]Radius of buffer is 2000 m; -: Unused; Variable name abbreviation is indicated in **Table 1** and text.

type (river, diversion canal, pond, irrigation ditch, paddy field, and wetland) as random effect intercepts. A Poisson distribution with log link function was applied to the GLMMs, which were performed for all possible sets of independent variables. Model selection was made using Akaike's information criterion (AIC; [29]). The model with the lowest AIC was defined as the best model.

It is possible that fish species richness showed spatial autocorrelation among the study sites (e.g., the fish species richness was less in the Ping River sub-basin study sites compared with the Yom and Nan River sub-basins). Species-environment models that have spatial autocorrelation in the residuals may be not appropriate because they can overestimate or underestimate the importance of environmental variables [30]–[32]. To test for spatial autocorrelation, Moran's I [33] was computed using the residuals from the best models. Moran's I is widely used to assess the existence and effect of spatial autocorrelation in species–environment regression models (e.g., [34]). Moran's I ranges from -1 to $+1$; a positive and high value indicates a spatial dispersion distribution pattern (positive autocorrelation), a zero value indicates a random distribution pattern, and a negative and low value indicates a spatial correlation distribution pattern (negative autocorrelation). The significance of Moran's I was tested by computing the Z score. According to the two-tailed Z test with a significance threshold (P value) of 0.05, P values <0.05 were considered significantly spatially autocorrelated. All statistical analyses were conducted using R statistical software (ver. 3.1.1; R Development Core Team) and its optional packages “lme4” for GLMM, “MuMIn” for model selection, and “spdep” for Moran's I test.

3. Results

3.1. Fish Species Richness and Environmental Characteristics

In total, 103 species (6555 individuals) belonging to 27 families were recorded (Table 3). Of the 135 study sites, 11 were inundated by the annual flood when the survey was conducted during the rainy season. The general characteristics of environmental and landscape parameters for each waterbody type during the rainy and dry seasons are shown in Table 4. No major differences were observed between the seasons except for Turb. Turb tended to be higher during the rainy season in all waterbody types except for diversion canal. Turb in diversion canal tended to be higher during the dry season. Figure 3 shows the total-length histograms for fishes captured in the study sites connected to main rivers by an annual flood and in isolated study sites during the rainy season survey. For all species, the proportion of small fish tended to be higher in connected study sites compared with isolated waterbodies.

Table 3. Summary of fish sampling data.

Order	Family	Scientific name	Lateral migration †	Alien	Sites	N	Prevalence at each waterbody type					
							River	Diversion canal	Pond	Irrigation ditch	Paddy field	Wetland
Beloniformes												
	Adrianichthyidae	<i>Oryzias sp.</i>			22	108	○	○	○	○	○	○
	Belonidae	<i>Xenentodon cancila</i> (Hamilton 1822)	○		6	10	○		○		○	
		<i>Xenentodon sp.</i>			2	2	○					
	Hemiramphidae	<i>Dermogenys siamensis</i> (Fowler 1934)			27	103	○	○	○	○	○	○
Clupeiformes												
	Clupeidae	<i>Corica laciniata</i> (Fowler 1935)			1	1	○					
		<i>Clupeoides borneensis</i> (Bleeker 1851)			1	4	○					
		<i>Clupeichthys aesarnensis</i> (Wongratana 1983)			6	15	○					
		<i>Clupeichthys sp.</i>			2	4	○					
Cypriniformes												
	Cobitidae	<i>Acantopsis spp.</i>			16	42	○	○				

Continued

	<i>Lepidocephalichthys hasselti</i> (Cuvier & Valenciennes 1846)	○	4	7	○	○	○	○	○
	<i>Lepidocephalichthys (c.f. hasselti)</i> (Cuvier & Valenciennes 1846)		2	10	○				
	<i>Lepidocephalichthys (c.f. bermorei)</i> (Blyth, 1860)		1	1	○				
	<i>Pangio anguillaris</i> (Vaillant 1902)	○	3	3	○	○			
	<i>Yasuhikotakia eos</i> (Taki 1972)		1	11	○				
Cyprinidae	<i>Amblypharyngodon chulabhornae</i> (Vidthayanon & Kottelat 1990)	○	22	75		○	○	○	○
	<i>Barbichthys laevis</i> (Cuvier & Valenciennes 1842)	○	1	1	○				
	<i>Barbonymus altus</i> (Günther, 1868)	○	15	98	○	○	○	○	
	<i>Barbonymus gonionotus</i> (Bleeker, 1849)	○	22	109	○	○	○	○	○
	<i>Barbonymus schwanefeldii</i> (Bleeker 1854)	○	10	78	○	○			
	<i>Barbonymus sp.</i>	○	2	6	○				
	<i>Crossocheilus reticulatus</i> (Fowler 1934)	○	2	3	○				
	<i>Cyclocheilichthys armatus</i> (Cuvier & Valenciennes 1842)	○	13	82	○	○	○		
	<i>Cyclocheilichthys apogon</i> (Cuvier & Valenciennes 1842)	○	13	211	○	○	○	○	
	<i>Cyclocheilichthys lagleri</i> (Sontirat 1985)	○	7	15	○	○	○		
	<i>Cyclocheilichthys repasson</i> (Bleeker 1853)	○	1	2	○	○	○	○	○
	<i>Cyclocheilichthys sp.</i>		4	10		○			
	<i>Cyclocheilos enoplos</i> (Bleeker 1849)	○	9	11		○		○	
	<i>Esomus metallicus</i> (Ahl 1924)	○	72	1572	○	○	○	○	○
	<i>Gymnostomus siamensis</i> (Sauvage 1881)	○	19	54	○	○	○	○	○
	<i>Henicorhynchus sp.</i>	○	1	37	○				
	<i>Hypsibarbus malcolmi</i> (Smith 1945)		6	73	○				
	<i>Hypsibarbus vernayi</i> (Norman 1925)		5	14	○				
	<i>Hypsibarbus wetmorei</i> (Smith 1931)		2	64	○				
	<i>Labeo chrysopehadion</i> (Bleeker 1849)	○	1	1		○			

Continued

<i>Labeo rohita</i> (Hamilton 1822)	○	2	5		○	○			
<i>Labeo sp.</i>	○	1	3		○				
<i>Labiobarbus siamensis</i> (Sauvage 1881)		22	73	○	○	○		○	
<i>Labiobarbus leptocheilus</i> (Cuvier & Valenciennes 1842)		8	24	○	○	○			○
<i>Labiobarbus sp.</i>		4	13	○	○			○	
<i>Mystacoleucus obtusirostris</i> (Cuvier & Valenciennes 1842)		26	298	○	○				
<i>Osteochilus vittatus</i> (Cuvier & Valenciennes 1842)	○	13	19	○	○				
<i>Osteochilus waandersii</i> (Bleeker 1853)	○	1	1	○					
<i>Osteochilus sp.</i>		6	11	○	○				○
<i>Paralaubuca typus</i> (Bleeker 1864)	○	13	83	○	○		○	○	
<i>Paralaubuca sp.</i>		3	5		○			○	
<i>Parachela oxygastroides</i> (Bleeker 1852)	○	6	43	○	○				
<i>Parachela siamensis</i> (Günther 1868)	○	1	1	○					
<i>Parachela williaminae</i> (Fowler 1934)		1	1				○		
<i>Parachela sp.</i>	○	4	4	○	○			○	
<i>Puntioplites proctozysron</i> (Bleeker 1864)	○	18	45	○	○			○	
<i>Puntius brevis</i> (Bleeker 1849)	○	17	125	○	○	○	○	○	○
<i>Puntius</i> (cf. <i>masyai</i>) (Smith 1945)		3	4			○		○	
<i>Puntius sp.</i>		1	2					○	
<i>Raiamas guttatus</i> (Day 1870)	○	4	20	○					
<i>Systemus rubripinnis</i> (Cuvier & Valenciennes 1842)	○	1	3	○					
<i>Thynnichthys thynnoides</i> (Bleeker 1852)	○	1	10	○					
<i>Rasbora aurotaenia</i> (Tirant 1885)		5	15	○	○	○		○	
<i>Rasbora borapetensis</i> (Smith 1934)	○	10	20	○		○	○	○	○
<i>Rasbora dusonensis</i> (Bleeker 1850)		10	52	○		○			

Continued

	<i>Rasbora paviana</i> (Tirant 1885)		11	51	○	○	○	○	○
	<i>Rasbora sp.</i>		4	14		○			○
	<i>Systemus rubripinnis</i> (Cuvier & Valenciennes 1842)	○	2	6		○	○		
Gasterosteiformes									
Syngnathidae	<i>Doryichthys martensii</i> (Peters 1868)		1	1	○				
Osteoglossiformes									
Notopteridae	<i>Chitala ornate</i> (Gray 1831)		1	1	○				
	<i>Notopterus notopterus</i> (Pallas 1769)	○	6	8	○	○		○	○
Perciformes									
Ambassidae	<i>Parambassis siamensis</i> (Fowler 1937)	○	40	418	○	○	○	○	○
	<i>Parambassis wolffii</i> (Bleeker 1850)	○	4	14	○	○			○
Anabantidae	<i>Anabas testudineus</i> (Bloch 1792)	○	24	78	○	○	○	○	○
Channidae	<i>Channa striata</i> (Bloch 1793)	○	13	110	○	○	○		○
Cichlidae	<i>Oreochromis niloticus</i> (Linnaeus 1758)	○	13	66	○	○	○	○	○
Eleotrididae	<i>Oxyeleotris marmorata</i> (Bleeker 1852)	○	5	8	○	○	○		○
Gobiidae	<i>Gobiopterus chuno</i> (Hamilton 1822)		9	23	○	○	○		○
	<i>Mugilogobius rambaiae</i> (Smith 1945)		3	11	○	○			
	<i>Mugilogobius sp.</i>		1	1		○			
	<i>Rhinogobius sp.</i>		2	4		○			○
	<i>Brachygobius sp.</i>		3	4		○	○		○
Nandidae	<i>Pristolepis fasciata</i> (Bleeker 1851)		14	38	○	○	○		○
Osphronemidae	<i>Osphronemus goramy</i> La Cepède 1801)		2	2	○				
	<i>Trichopsis pumila</i> (Arnold 1936)		24	99	○	○	○	○	○
	<i>Trichopsis vittata</i> (Cuvier & Valenciennes 1831)	○	70	576	○	○	○	○	○
	<i>Trichopodus microlepis</i> (Günther 1861)		39	409	○	○	○	○	○

Continued

	<i>Trichopodus pectoralis</i> (Regan 1910)	○	8	23		○	○		○
	<i>Trichopodus trichopterus</i> (Pallas 1770)	○	67	682	○	○	○	○	○
Pleuronectiformes									
Soleidae	<i>Brachirus harmandi</i> (Sauvage 1878)		8	14	○				
Cynoglossidae	<i>Cynoglossus feldmanni</i> (Bleeker 1854)		1	1	○				
Siluriformes									
Bagridae	<i>Hemibagrus filamentus</i> (Chaux & Fang 1949)	○	4	6	○				
	<i>Hemibagrus spilopterus</i> (Ng & Rainboth 1999)	○	2	8			○		○
	<i>Mystus albolineatus</i> (Roberts 1994)		11	22	○	○		○	○
	<i>Mystus multiradiatus</i> (Roberts 1992)	○	11	40	○	○	○	○	○
	<i>Mystus mysticetus</i> (Roberts 1992)	○	9	43	○	○	○		○
	<i>Pseudomystus siamensis</i> (Regan 1913)		3	11	○	○			
Clariidae	<i>Clarias macrocephalus</i> (Günther 1864)		1	1		○			
	<i>Clarias batrachus</i> (Linnaeus, 1758)		1	1			○		
Loricariidae	<i>Pterygoplichthys</i> sp.	○	3	5		○		○	
Pangasiidae	<i>Pangasius sanitwongsei</i> (Smith 1931)		2	5	○				
	<i>Pangasius macronema</i> (Bleeker 1850)	○	3	4	○				
	<i>Pangasius</i> sp.		1	2	○				
Silurida	<i>Kryptopterus cryptopterus</i> (Bleeker 1851)		1	14	○				
	<i>Phalacronotus bleekeri</i> (Günther 1864)	○	2	3	○				
Sisoridae	<i>Bagarius yarrelli</i> (Sykes 1839)		1	1	○				
Synbranchiformes									
Mastacembelidae	<i>Mastacembelus armatus</i> (La Cepède 1800)	○	6	8	○				
Synbranchidae	<i>Monopterus javanensis</i> (La Cepède, 1800)		1	1			○		
Tetraodontiformes									
Tetraodontidae	<i>Pao cambodgiensis</i> (Chabanaud 1923)		1	1	○				

†: According to Fish Base (<http://www.fishbase.org>).

Table 4. General characteristics of environmental and landscape parameters at each waterbody type.

Unit	River		Diversion canal		Irrigation ditch		Pond		Paddy field		Wetland		
	Mean (SD)		Mean (SD)		Mean (SD)		Mean (SD)		Mean (SD)		Mean (SD)		
	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	
EC	μS	214 (39.4)	207 (61.2)	239 (45.7)	357 (156)	345 (143)	665 (257)	318 (104)	533 (328)	344 (163)	586 (549)	263 (91.0)	199 (0)
Dep	m	1.05 (0.367)	0.691 (0.311)	1.10 (0.505)	0.581 (0.356)	0.680 (0.232)	0.452 (0.142)	0.997 (0.328)	1.10 (0.498)	0.426 (0.317)	0.218 (0.126)	0.365 (0.0946)	0.47 (0)
Do	mg·L ⁻¹	5.61 (1.41)	4.76 (1.48)	3.40 (1.28)	3.66 (1.56)	3.35 (1.51)	3.68 (1.24)	3.68 (3.05)	3.66 (2.02)	3.96 (2.31)	4.11 (2.08)	4.19 (2.29)	0.300 (0)
Turb	NTU	130 (85.3)	12.6 (8.04)	70.9 (79.6)	141 (228)	108 (70.8)	51.2 (58.4)	47.8 (36.4)	19.6 (22.5)	156 (167)	36.9 (34.1)	21.9 (7.44)	0.640 (0)
Vel	ms ⁻¹	0.824 (0.419)	0.38 (0.303)	0.183 (0.184)	0.0189 (0.0621)	0.0267 (0.0533)	0(0)	0.0139 (0.0461)	0(0)	0.0456 (0.167)	0(0)	0(0)	0(0)
Con	0, 1	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0.167 (0.373)	0(0)	0.4444 (0.4969)	0(0)	0.167 (0.373)	0(0)
Dist	km	0.152 (0.132)	0.152 (0.132)	0.144 (0.165)	0.166 (0.185)	0.206 (0.127)	0.239 (0.0987)	0.428 (0.206)	0.387 (0.204)	0.397 (0.250)	0.333 (0.249)	0.325 (0.173)	0.0662 (0)
FA	km ²	3.90 (2.58) [†]	3.902 (2.58) [†]	2.80 (3.02) [†]	3.05 (3.18) [†]	3.41 (2.09) [†]	3.88 (1.79) [†]	6.05 (2.92) [†]	5.44 (2.82) [†]	5.17 (3.25) [†]	4.99 (3.47) [†]	5.23 (2.71) [†]	1.11 (0) [†]

[†] Radius of buffer is 2000 m; Variable name abbreviation is indicated in Table 1 and text.

3.2. GLMM Analysis and Model Selection

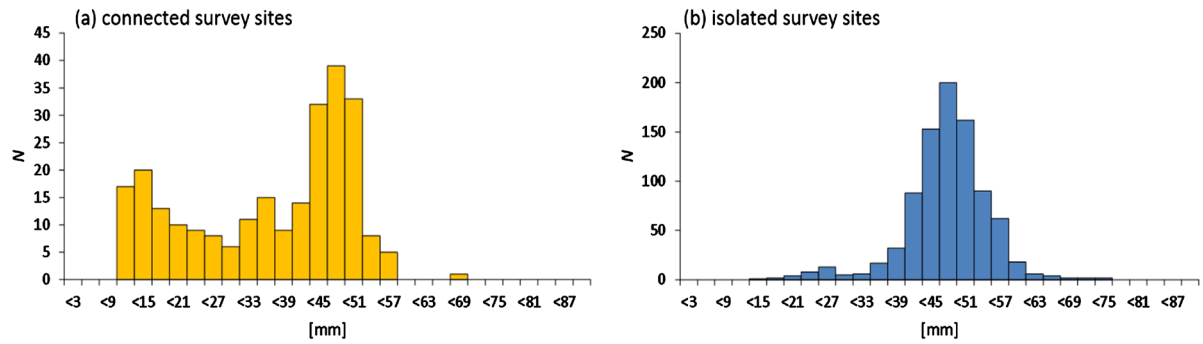
Table 5 shows the results of GLMM analysis with AIC model selection for fish species richness. The differences between the AIC value for the best models and null models (ΔAIC) were >4 except for the model for non-migratory fish species richness in canals, indicating substantial support for the best models [35]. No spatial autocorrelation was detected in the residuals of the best models. Figure 4 shows the relationship between floodplain area (2000 m buffer size; the best buffer size for GLMM analysis of the richness of all native fish in a waterbody) and richness of all native species in each waterbody type. The broken lines represent linear regression lines for significant correlations ($P < 0.05$). Significant positive correlations between native fish richness and floodplain area were found for rivers and ponds, but not for other waterbody types.

4. Discussion

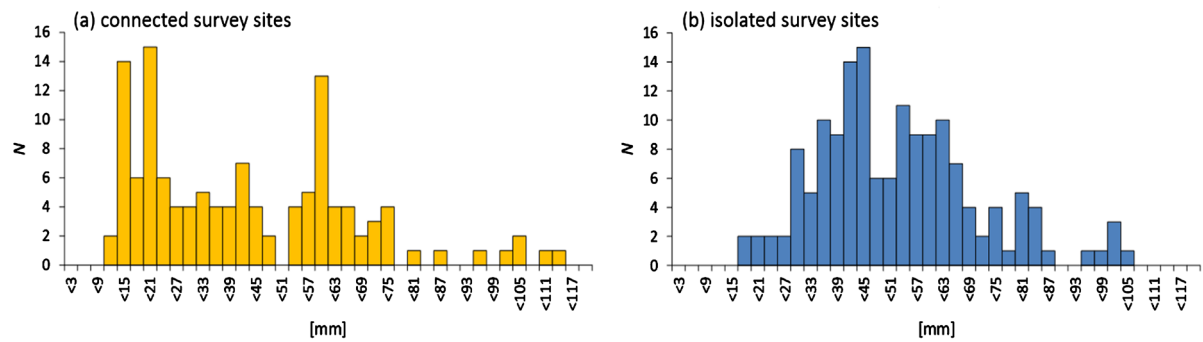
The most important finding of the present study is that the area of floodplains around each study site is a primary factor that determines fish species richness in rivers, diversion canals, and ponds in the study area. The contribution of floodplain area to fish species richness was equivalent to hydrology (Con, Vel, and Dep) and water quality (DO, Turb) parameters. This was supported by the fact that the best models for richness of all native fish species, floodplain migratory native fish species, and floodplain non-migratory native fish species showed a positive effect of floodplain area, and most were significant (Table 5; Figure 4), and by the fact that floodplain area was one of the top three parameters in all model selections (Table 5).

In paddy fields, the parameters EC and Con were the major determinants of fish species richness (Table 5). This may reflect the usage of fertilizers and pesticides, which increase electric conductivity, and the difficult access into isolated paddy field waterbodies because of migration barriers between paddy fields and ditches. The biological importance of submerged floodplains in fish ecology is well known. Shallow standing water and water with low dissolved oxygen provide refuge habitats from predators and flood disturbance [13]; high nutrient inputs from rivers and high concentrations of feed organisms, such as phytoplankton [36], zooplankton [11], and fish [37] [38], provide foraging and nursery habitats [37] [38], and new connections between waterbodies and water level fluctuations caused by floods, trigger lateral spawning migration and egg deposition in some species [39]-[41].

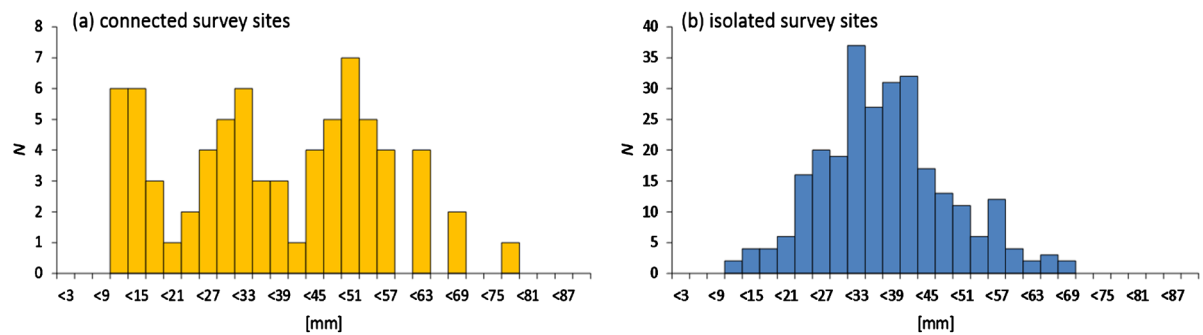
E. metallicus



T. microlepis



T. trichopterus



T. vittata

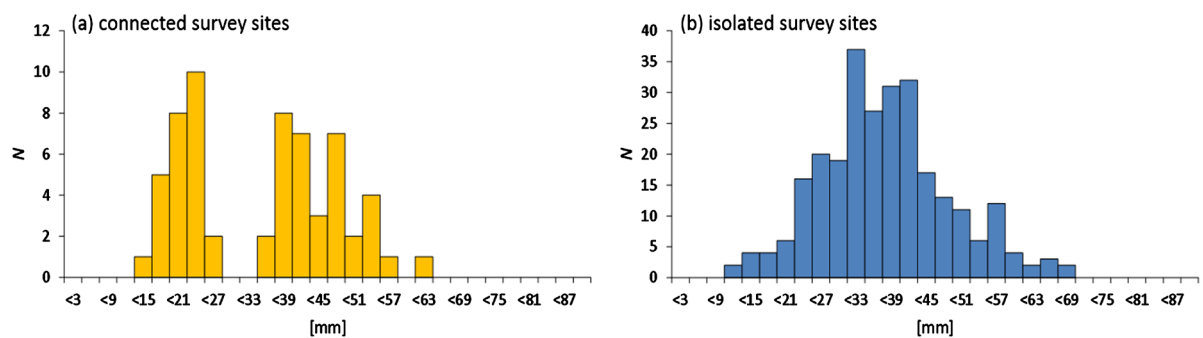


Figure 3. Total-length histograms for four common fish species (more than 50 individuals captured from both temporarily connected and isolated waterbodies) recorded during the rainy season survey. (a) Temporarily connected study sites and (b) Isolated study sites.

Table 5. Results of the general linear mixed model analysis of richness of all native species, floodplain migratory native species, and floodplain non-migratory native species in each waterbody type.

Waterbody type	Species richness	Random intercept												
		AIC	ΔAIC (from Null)	Wi	Morn's I	Intercept	Season		Waterbody Type					
							Rainy	Dry	River	Diversion Canal	Pond	Irrigation Ditch	Paddy	Wetland
Total	All native fish	765.8	96.6	0.296	0.0346 ^{NS}	1.35 ^{***}	-0.0486	0.0486	0.600	0.178	-0.0743	0.0969	-0.651	-0.125
	Floodplain migratory	650.4	48.4	0.145	0.0596 ^{NS}	0.698 ^{**}	-0.00203	0.00203	0.579	0.143	-0.135	0.171	-0.648	-0.0756
	Floodplain non-migratory	509	46.6	0.128	0.0390 ^{NS}	-0.0291	0	0	1.13	0.240	-0.350	-0.270	-0.609	-0.0659
River	All native fish	143.8	54.1	0.159	-0.0844 ^{NS}	3.14 ^{***}	1.25e-17	-1.25e-17	-	-	-	-	-	-
	Floodplain migratory	133.5	40.3	0.177	-0.0136 ^{NS}	2.01 ^{***}	0	0	-	-	-	-	-	-
	Floodplain non-migratory	119.4	14.7	0.117	0.0107 ^{NS}	2.72 ^{***}	1.13e-18	-1.13e-18	-	-	-	-	-	-
Canal	All native fish	214.5	14.7	0.178	0.0707 ^{NS}	1.37 ^{***}	0	0	-	-	-	-	-	-
	Floodplain migratory	182.3	12.2	0.161	0.0646 ^{NS}	0.904 ^{***}	0	0	-	-	-	-	-	-
	Floodplain non-migratory	140.0	1.39	0.0479	-0.0106 ^{NS}	0.380 ⁻	0	0	-	-	-	-	-	-
Paddy	All native fish	147.6	49.0	0.0730	0.105 ^{NS}	1.17 ^{**}	0	0	-	-	-	-	-	-
	Floodplain migratory	120.0	19.6	0.0757	-0.107 ^{NS}	0.978 [*]	0	0	-	-	-	-	-	-
	Floodplain non-migratory	85.4	33.8	0.0816	0.0137 ^{NS}	1.65 ⁺	0	0	-	-	-	-	-	-
Pond	All native fish	107.8	8.89	0.0765	-0.216 ^{NS}	1.02 ^{***}	0	0	-	-	-	-	-	-
	Floodplain migratory	97.2	4.55	0.0651	-0.205 ^{NS}	0.835 ^{**}	0	0	-	-	-	-	-	-
	Floodplain non-migratory	85.4	4.92	0.0519	-0.0878 ^{NS}	-0.475 ^{NS}	0	0	-	-	-	-	-	-

Waterbody type	Species richness	Coefficient of independent variables								FA [Buffer Size]
		EC	Dep	Do	Turb	Vel	Con	Dist	FA [Buffer Size]	
		(appearance) [†]	(appearance) [†]	(appearance) [†]	(appearance) [†]	(appearance) [†]	(appearance) [†]	(appearance) [†]	(appearance) [†]	
Total	All native fish	-0.000399 ⁻			0.000955 ^{***}	-0.347 ⁺	0.867 ^{***}	0.00709 ⁺	0.106 ^{***}	[2000]
	Floodplain migratory	(50%)	(100%)	(33.3%)	(100%)	(100%)	(100%)	(66.7%)	(100%)	
	Floodplain non-migratory	-0.000454 ⁻	0.698 ^{NS}		0.00119 ^{***}	-0.288 ^{NS}	0.764 ^{***}	0.00877 ⁺	0.118 ^{***}	[2000]
River	All native fish	(50%)	(100%)	(37.5%)	(43.8%)	(93.8%)	(100%)	(37.5%)	(93.8%)	
	Floodplain migratory	(42.9%)	(50%)	(100%)	(50%)	(42.9%)	ND	-	0.166 ^{***}	[2000]
	Floodplain non-migratory	(28.6%)	(38.1%)	(95.2%)	(38.1%)	(38.1%)	ND	-	0.202 ^{***}	[2000]
Canal	All native fish	(36.4%)	(36.4%)	(36.4%)	(100%)	(36.4%)	ND	0.0102 ^{***}	0.0957 ^{**}	[500]
	Floodplain migratory	(35.7%)	(28.6%)	(28.6%)	(100%)	(28.6%)	ND	0.0121 ^{**}	0.0872 ⁺	[500]
	Floodplain non-migratory	(28.8%)	(40.4%)	(21.2%)	(50%)	(51.9%)	ND	(25%)	(65.4%)	[1000]
Paddy	All native fish	-0.00198 ^{**}			0.0684 ^{NS}	0.00133 ⁺	1.27 ^{***}			
	Floodplain migratory	(100%)	(38.9%)	(63.9%)	(58.3%)	(36.1%)	(100%)	(27.8%)	(47.2%)	
	Floodplain non-migratory	-0.00160 ⁺			0.00162 ⁺		1.12 ^{***}			
Pond	All native fish	(100%)	(44.8%)	(37.9%)	(65.5%)	(31%)	(100%)	(24.1%)	(27.6%)	
	Floodplain migratory	-0.00432 ^{**}			1.83 ^{***}				-0.171 ⁻	[1000]
	Floodplain non-migratory	(100%)	(28.6%)	(42.9%)	(28.6%)	(32.1%)	(100%)	(25%)	(57.1%)	
Pond	All native fish	(23.3%)	(26.7%)	(86.7%)	(56.7%)	(36.7%)	(23.3%)	(23.3%)	(100%)	[2000]
	Floodplain migratory	(23.3%)	(23.3%)	(23.3%)	(23.3%)	(23.3%)	(23.3%)	(26.7%)	(96.7%)	[2000]
	Floodplain non-migratory	(24.4%)	(31.1%)	(100%)	(51.1%)	(26.7%)	(26.7%)	(42.2%)	(68.9%)	[1000]

[†] Appearance rate of containing model in the models with ΔAIC < 4 from the best model [%]; Level of significance: ^{***}P < 0.001, ^{**}P < 0.01, ^{*}P < 0.05, ⁻P < 0.1, ^{NS}P > 0.1; ND: No data, -: Unused; Variable name abbreviation is indicated in Table 1 and text.

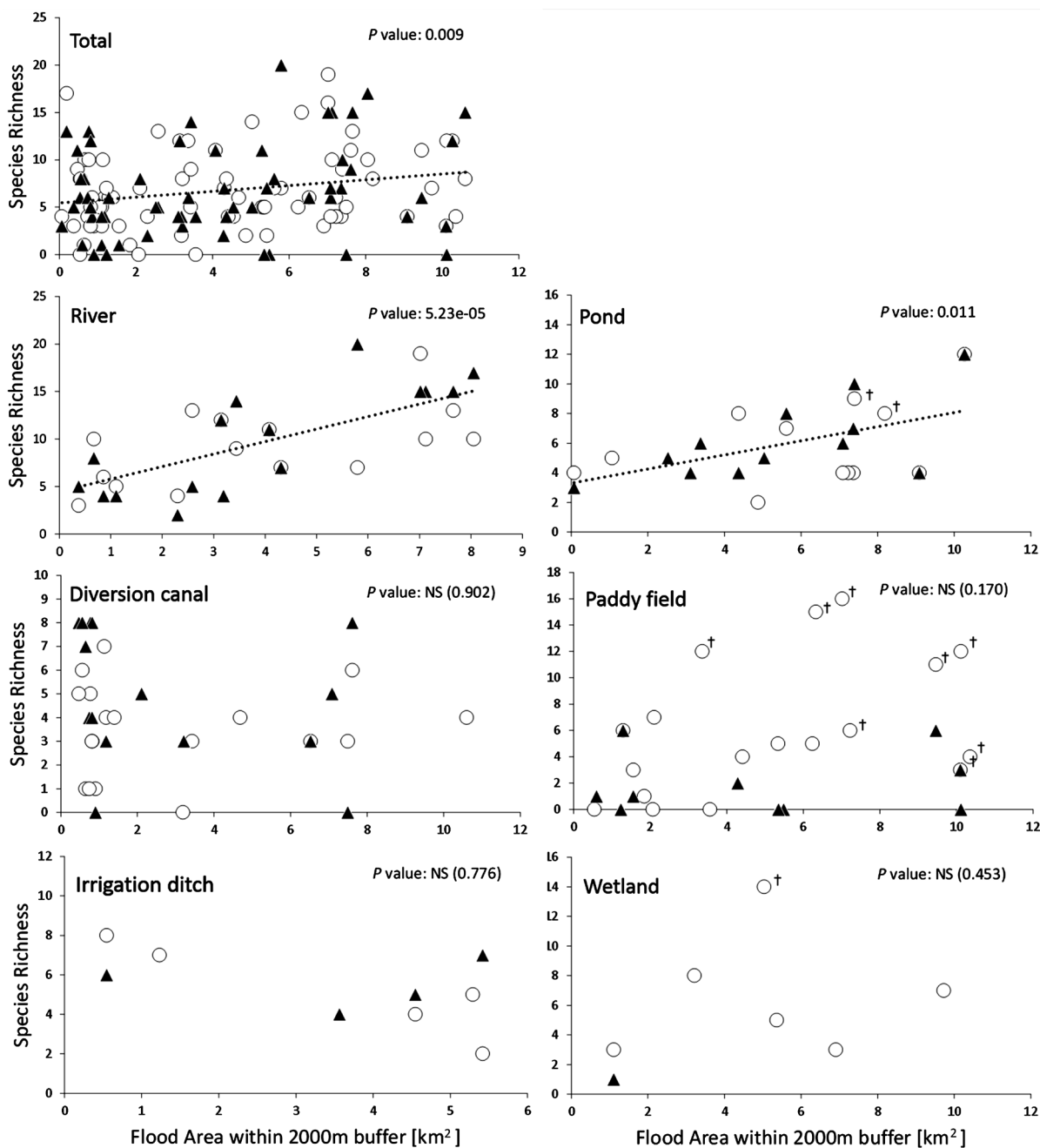


Figure 4. The relationship between floodplain area (2000 m buffer size) and richness of all native fish species for each waterbody type. The broken lines represent significant linear regressions ($P < 0.01$). P values are shown in the top right of each plot. Open circles indicate sites surveyed in the rainy season. Black triangles indicate sites surveyed in the dry season. Crosses to the upper right open circles represent the study sites temporarily connected to main rivers by floodwaters in the rainy season survey.

In the present study, increasing fish richness with increasing floodplain area probably reflected a direct association with floodplain utilization by migratory fish species. The parameter FA was retained with relatively higher frequency in model selections for floodplain migratory species compared with those for non-migratory species in every waterbody type except paddy fields (Table 5). In addition, the proportion of small size fishes (<20 mm total length) of four common species (*Esomus metallicus*, *Trichopsis vittata*, *Trichopodus trichopterus*, and *Trichopodus microlepis*), classified as 0+ juveniles, was increased in temporarily connected survey sites

compared with isolated survey sites (Figure 3). Furthermore, although numbers were less than for the four common species mentioned above, some fluvial and lacustrine fish species, such as *Xenentodon cancila*, *Barbonymus gonionotus*, *Cyclocheilichthys apogon*, *Cyclocheilichthys lagleri*, *Puntius brevis*, and *Amblypharyngodon chulabhornae* (Table 3), were captured in temporarily inundated study sites. This finding indicates that individuals of these species moved into floodplains from permanent waterbodies in the early part of the rainy season, even before maximum flood levels occurred.

This study revealed the importance of floodplain area for fishes in the mid-region of the Chao Phraya River basin. The conservation of floodplains and fishes in the region is important for many reasons. The Chao Phraya River Basin is known for its high fish biodiversity. More than 690 freshwater fish species have been recorded and many utilize the floodplains during their life cycle [16] [18]. Moreover, inland fisheries have long been a part of Thai culture and are an important source of protein, especially for rural populations. Based on catch, the Thailand inland fishery ranked 13th in the world in 2012 [42]. Floodplains are maintained by dynamic interactions between flooding and landscape, and floodplains are disappearing at an accelerating rate in Southeast Asia, primarily as a result of changing hydrology caused by large-scale irrigation schemes and dams [15]. [43] investigated the impact of the operation of large-scale dams since the 2011 Thailand flood and found that the inundated area in the Chao Phraya River Basin was reduced by 40%. In the present study, the main stream of the Ping River, which has a smaller floodplain area compared with the other two rivers, showed a relatively low fish species richness (Figure 5). The reduction in floodplain area secondary to flood control measures (e.g., the Bhumibol Dam) may affect species richness, especially of migratory species in the Ping River Basin. On the other hand, flooding has the potential to cause serious damage to the economy of Thailand (e.g., the 2011 Thailand flood). Further studies are needed to assess the respective advantages and disadvantages of flood control measures in the Chao Phraya River Basin and to identify the best approach to protect both the economy and biodiversity. Future research should consider the detailed relationship between aquatic organisms and the characteristics of flood events, such as velocity, duration, timing, and the degree of fluctuation.

5. Conclusion

Fish assemblages and environmental, landscape parameters in floodplain waterbodies (rivers, diversion canals, ponds, irrigation ditches, paddy fields, and wetlands) in the mid-Chao Phraya River Basin were investigated in rainy (September 2014) and dry (March 2015) seasons. Factors affecting fish species richness in each type of waterbody were analyzed using generalized linear mixed models. The analysis showed that floodplain area around each surveyed waterbody was a major factor determining fish species richness in rivers, diversion canals, and ponds in the region. The observation of the study also showed that the population of juvenile fishes was increased in temporarily connected floodplain waterbodies to main rivers compared with isolated waterbodies. The high dependence of fish species richness on floodplain area in the region appeared to be a result of the use of inundated floodplains by fish species to forage and breed.

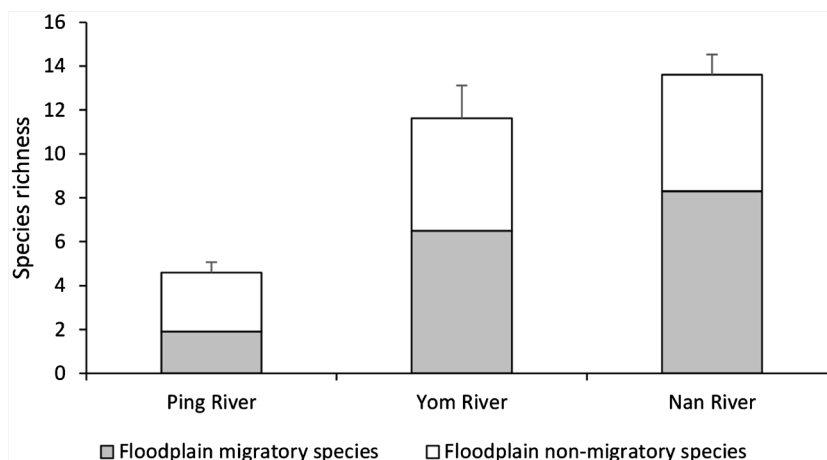


Figure 5. Native fish species richness and composition for each of the three rivers surveyed. Bars indicate the standard error.

Acknowledgements

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