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Influences of local habitat and stream spatial position on fish assemblages in a dammed watershed, the Qingyi Stream, China

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Abstract – Identifying the underlying mechanisms that explain the spatial variation in stream fish assemblages is crucial for the protection of species diversity. The influences of local habitat and stream spatial position on fish assemblages were examined from first-order through third-order streams within a dammed watershed, the Qingyi Stream, China. Based on linear regression models, the most important environmental variables influencing fish species richness were water temperature and wetted width, but stream spatial position variables were less important. Using canonical correspondence analysis, five environmental variables were identified to significantly influence fish assemblages, including three habitats (elevation, substrate and water depth) and two spatial variables (C-link and Link). Our results suggest that, in a heavily dammed watershed, by blocking the migration routes of fishes, dams weaken the influence of stream spatial position on fish species richness. However, fish species compositions are significantly influenced by both local habitat environment and stream spatial position, which is perhaps owing to the distribution of fish species according to ecological requirements not related to spatial processes.

Key words: stream fish assemblage; species richness; dam; local habitat; stream spatial position

Introduction

Traditionally, streams are regarded as a linear hierarchy that presents a notably upstream–downstream gradient (Vannote et al. 1980). Along this gradient, fish assemblages vary spatially and temporally, associated with the variations in local habitat diversity, complexity and stability (Grossman et al. 1990; Matthews 1998). Although fish species richness often increases downstream with increasing stream size (Matthews 1986), the river continuum concept assumes that the maximum species diversity is observed at the mid-sized, not large, streams (Vannote et al. 1980). However, the riverscape, a newly developing perspective, claims that streams should be viewed as an entire interconnected network architecture with a complex but definable 'network geometry', instead of just a relatively simple linear hierarchy (Fausch et al. 2002; Wiens 2002). Grant et al. (2007) further emphasised the importance of the architecture of dendritic ecosystem network (DEN) in structuring biotic assemblages and highlighted the importance of movement among branches and the heterogeneity of habitats associated with a branch-node structure. When looking at an entire watershed, adventitious streams, defined as streams at least three stream orders smaller than streams into which they flow, often hold more diverse fish assemblages than similar-sized headwater streams (Osborne & Wiley 1992). This could be explained by the proximity of adventitious streams from the colonising source, the mainstream, in contrast with headwater tributaries (Gorman 1986). Therefore, at a watershed scale, stream fish

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assemblages are influenced both by the position along upstream–downstream gradient, which reflects stream size and habitat condition, and by the spatial position within the drainage network, which determines the rate of fish immigration and extinction (Grenouillet et al. 2004; Smith & Kraft 2005).

The spatial pattern of fish assemblages along upstream–downstream gradient is well established, especially in American temperate and European Mediterranean areas (Matthews 1998). However, the pattern of how stream spatial position influences fish assemblages still remains debated and unclear (Smith & Kraft 2005). This question was raised by Fausch et al. (1984), who observed higher species richness in collections near mouth of tributaries entering large rivers. Gorman (1986) found fish assemblages in adventitious streams were more diverse than headwater streams. Osborne & Wiley (1992) examined the effects of four measures of stream size (i.e., drainage area, stream order, link magnitude and downstream link) on fish assemblages. They revealed that downstream link explained the greatest portion of the variance in species richness, indicating that downstream processes significantly influence fish assemblages. Grenouillet et al. (2004) described the relative influence of local habitat and stream spatial position on species richness of fish assemblages. They discovered significant influence of both habitat (stream width and gradient) and spatial variables. But the spatial autocorrelation was only significant downstream (from fourth- to seventh-order streams), suggesting the relative importance of local habitat and biotic processes may depend on the position along the longitudinal gradient. Smith & Kraft (2005) evaluated the relative influence of habitat and stream spatial position on both species richness and abundance of fish assemblages, especially compared the effects of five spatial variables, i.e., stream order, link magnitude, branch link, confluence link and downstream link. They revealed that confluence link, but not downstream link as described by other researchers, was the significant factor among spatial variables influencing fish assemblages.

In this study, the relative influence of local habitat and spatial position on fish assemblages was surveyed in a dammed stream, the Qingyi Stream, in China. Associated with extensive agricultural and industrial productions, urbanisation development and hydraulic engineering constructions, most stream ecosystems in China are experiencing massive ecological perturbation, which threatens freshwater fishes in these systems (Chen 2005). In the Qingyi Stream, numerous and diverse dams were constructed for electricity generation, farmland irrigation and domestic water consumption in the mid–late 20th century. Dams can significantly alter the distribution and abundance of stream fishes by blocking migratory pathways (March et al. 2003), altering natural flow regime (Bonner & Wilde 2000), decreasing (Clarkson & Childs 2000) or increasing (Lessard & Hayes 2003) downstream water temperature, decreasing current velocity upstream (Bennett et al. 2002), increasing flow velocity downstream (Kondolf 1997), altering food webs (Power et al. 1996), disrupting riparian plant communities (Nilsson et al. 1997) and shifting water chemistry (Humborg et al. 1997). Grant et al. (2007) stated that mediating the movement pattern of specific species within a dendritic network is one of the most important mechanisms that explain how the network architecture of DENs influences community dynamic. Therefore, we hypothesise that fish assemblages in dammed streams are determined mainly by local habitat conditions, while the influence of spatial position could be weakened by dams, if the immigration or emigration of fish is the underlying mechanism that explains the importance of stream spatial position. This study was aimed to (i) determine the pure and combined influences of local habitat and spatial position on fish species richness; (ii) determine the influence of habitat and spatial position on fish assemblages and (iii) test our hypothesis that local habitat conditions are more important than spatial position in influencing fish assemblages in a dammed stream.

Materials and methods

Study area

The Qingyi Stream watershed originates in the northern portion of the Huangshan Mountain, Anhui Province, China, and flows northeast toward its confluence with the lower reach of the Yangtze River. This watershed is 309 km long at mainstem and 7195 km^2 of area. Because of the subtropical monsoon climate, the Qingyi Stream is characterised by asymmetry in seasonal temperature and precipitation. Mean annual air temperature, ranging from −22.1 °C (January) to 27.5 °C (July), is 17.8 °C. Annual rainfall is quite abundant (approximately 2000 $mm \cdot year^{-1}$), but about 79% of rainfall occurs during spring and summer (from April to September) and less than 5% during the cold and dry winter. In the mid–late 20th century, numerous and diverse dams were built in this area. Among them, there are at least 200 hydropower stations (including the Chencun Hydropower Station, being the largest station at the lower reach of the Yangtze River) and almost 1000 low-head dams (<4 m in height) built for irrigation and drinking water supply.

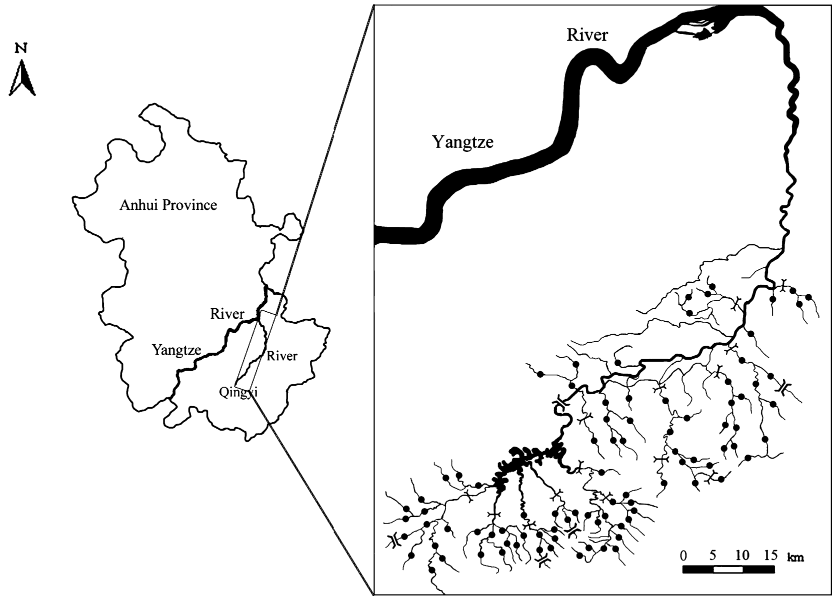


Fig. 1. Map of the Qingyi Stream watershed in Anhui Province, China. Solid circles marked the 89 sampling sites. Part hydropower stations (⊏⊐) and low-head dams (⋊⋉) were shown.

Fish sampling

Derived from Anhui Province topographic maps (1:300,000 scale), the Qingyi Stream is fifth order (Strahler 1957) at its mainstream. Within this watershed, 75 first-order, 34 second-order, 12 third-order, 4 fourth-order and 1 fifth-order streams have been numbered. A total of 60 first-order, 22 second-order and 7 third-order segments were surveyed once during October 2009 in this study (Fig. 1). Sample sites, each 50 m long and not more than 1 m depth, were selected in the field based on habitat representativeness and accessibility. Each site was far from dams upstream (>1.0 km) and encompassed at least two mesohabitat units such as pools and riffles. Fish were collected using backpack electro-fishing gear (CWB-2000 P, China; 12 V import, 250 V export) by wading in two passes with comparable effort (30–40 min). Fish were identified to species (except for *Ctenogobius* fish because of the deficiency in identifying tools), counted and returned to the sampling sites if alive. Voucher specimens were soaked in 8% formaldehyde solution for further identification.

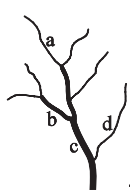
Habitat survey

Each sampling site was characterised using 10 variables to describe local environmental conditions: elevation (m), wetted width (m), water depth (m), water temperature (°C), pH, conductivity ($mS \cdot cm^{-1}$), dissolved oxygen (ppm), current velocity ($m \cdot s^{-1}$), discharge ($m^3 \cdot s^{-1}$) and substrate size (%). Elevation was determined by global positioning system (GPS). Wetted width was measured along five transects, regularly spaced across the stream channel. Water depth, temperature, dissolved oxygen, pH and conductivity were surveyed at four equal interval points along each transect. Current velocity was taken at 60% of water depth at each point of each transect. Discharge of each channel was determined at the transect that yielded the most accurate measurement (smooth bottom and laminar flow). Along each transect, the proportion of substrate categories (particle size 1 = 0–1 mm; 2 = 1–5 mm; 3 = 5–25 mm; 4 = 25–50 mm; 5 = 50–100 mm; 6 = 100–500 mm; 7 = 500–1000 mm; 8 ≥ 1000 mm) was visually estimated, and an index of substrate coarseness ranging from 1 to 8 was derived for each site following Bain et al. (1985).

Spatial position description

In addition to stream order (Strahler 1957), three other watershed-level metrics were described to evaluate the influence of stream spatial position on fish assemblages: stream link magnitude, confluence link and

Fig. 2. Hypothetical example of a stream network for delineating spatial position variables: stream order, link magnitude (Link), confluence ink (C-link) and downstream link (D-link) – for a simplified watershed.



Site	Stream order	Link	C-link	D-link
a	1	1	4	2
b	2	2	2	5
c	3	5	1	6
d	1	1	1	6

downstream link (Fig. 2). Stream link magnitude (Link) is defined as the number of unbranched source stream upstream from a given segment in the drainage network (Shreve 1966). Confluence link (C-link) is the number of confluences downstream from each stream segment (Fairchild et al. 1998). Downstream link (D-link) is the link magnitude of the next downstream confluence (Osborne & Wiley 1992). Descriptions of these spatial variables were assigned to each segment derived from Anhui Province topographic maps (1:300,000 scales).

Data analysis

Importance value index (IVI), a synthetically quantitative index indicating the functional status and role of a specific species within a community, was assessed for each species as following: IVI = F_i (%) × P_i (%), where F_i and P_i are the frequency of occurrence and relative abundance of species i, respectively (Krebs (1989). Linear regression was used to estimate the influence of local habitat and stream spatial position on local species richness (Legendre & Legendre 1998). The procedures included separate stepwise analysis for each group of factors, to select the reduced subset of variables that maximally accounted for variation in each response variable. This method isolates three components of explained variation: pure habitat variation, pure stream spatial position and combined habitat/spatial variation. Prior to analysis, log-transformations were used to reduce the influence of extreme value in elevation, width, depth and spatial factors. The SPSS 11.5 statistics package (SPSS Inc., Chicago, IL, USA) was used to perform statistical analysis, and statistical significance was accepted at $P < 0.05$.

Discrete spatial pattern in fish assemblages was identified using PRIMER 5.0. (PRIMER-E Ltd., Plymouth, UK). Species richness and abundance data were $\log(X + 1)$ transformed to meet assumptions of multivariate normality and to moderate the influence of extreme data. Following a Bray–Curtis similarity matrix calculation, a two-way crossed ANOSIM was used to test the influences of stream order and headwater/adventitious attribute on fish assemblages. The contribution of each species to differences among assemblage groups was identified using the SIMPER (Clarke & Warwick 2001). Using CANOCO 4.5 (Microcomputer Power, Ithaca, NY, USA) software package, a canonical correspondence analysis (CCA) was performed to evaluate the variability in fish assemblages in relation to local habitat and stream spatial position variables. Subsequently, all the variables entered the analysis after a forward selection procedure, showing their importance in explaining the total variability in the species composition. The significance ($P < 0.05$) of the CCA gradients was assessed by Monte Carlo permutation tests and their importance measured by the eigenvalues of the first two axes (ter Braak & Verdonschot 1995). Remaining variables were ordered by their importance in accounting for additional variance in the species data, and this procedure was repeated for each variable included in this model. The remaining species were analysed separately, and excluded from the analysis if occurring in less than two sites, to avoid negligible weighting (Gauch 1982).

Results

Overview of species diversity

A total of 9875 fish were captured throughout this study watershed, representing 36 species, 11 families and four orders. Species of family Cyprinidae comprised, on average, 69.3% of total species richness. Species richness per sample amounted to 7.3 ± 2.7 (mean ± SD) species and abundance per site 110.6 ± 80.8 specimens. *Siniperca chuatsi*, *Cirrhinus molitorella*, *Hemibarbus labeo*, *Erythroculter ilishaeformis* and *Channa argus* were only collected in one site. *Zacco platypus* was the most common (92.1% of samples) and dominant (3832.8% of IVI) species. *Ctenogobius*, *Acrossocheilus fasciatus*, *Rhodeus ocellatus*, *Misgurnus anguillicaudatus* and *Vanmanenia stenosoma* were also common (>40% of occurring frequency) and dominant (>100% of IVI). Whereas, 12 species were restricted (<40% of frequency) but relatively important (>10%), and other 24 species were rare (<10% of IVI). These species collected varied in their habitat preferences (i.e., small, mid-sized and large streams) and trophic ecology (i.e., omnivorous, invertivore, herbivore and piscivore) (Table 1).

Environmental characteristics

Local habitat environmental conditions and stream spatial position were described at 89 sampling sites. Mean wetted width of channel was 11.6 ± 9.7 m (mean ± SD), ranging from 1.7 to 48.6 m, and depth was 0.4 ± 0.2 m, from 0.1 to 0.9 m. Current velocity ranged from 0.1 to 1.4 $m \cdot s^{-1}$ with the average of 0.3 $m \cdot s^{-1}$. Discharge ranged from 0.04 to 11.7 $m^3 \cdot s^{-1}$. Temperature and dissolved oxygen ranged from 17.1 to 22.1 °C and 6 to 9 ppm, respectively. The water conductivity ranged from 0.01 to 0.99 $ms \cdot cm^{-1}$. For spatial position variables, Link ranged from 1 to 10, C-Link ranged from 1 to 26, and D-Link ranged from 2 to 13.

Correlation between local habitat and stream position descriptors showed that width and discharge

Table 1. Occurring frequency (*F*), relative abundance (*P*), index of relative importance (IVI), habitat preference (HP) and trophic ecology (TE) of fish collected from 89 sites in the Qingyi Stream.

Order/family/species	Common name	Code	*F* (%)	*P* (%)	IVI (%)	HP	TE
Cypriniformes							
Cyprinidae							
Zacco platypus	Pale chub	PAC	92.1	41.6	3832.8	SS	O
Opsarrichthys bidens	Hooksnout carp	HSC	19.1	0.9	18.2	SMS	O
Acrossocheilus fasciatus	Slippylip barbel	SLB	57.3	7.4	423.0	SS	H
Cyprinus carpio	Carp	CAR	2.2	0.1	0.1	LS	O
Carassius auratus	Crucian carp	CRC	28.1	2.1	58.6	MLS	O
Pseudorasbora parva	Topmouth gudgeon	TMG	31.5	1.5	48.1	MLS	O
Abbottina rivularis	False gudgeon	FAG	21.3	2.4	50.6	MLS	I
A. tafangensis	Jiangde false gudgeon	JFG	2.2	0.2	0.46	MS	I
Squalidus argentatus	Silver gudgeon	SIG	8.9	0.3	2.5	MS	I
Pseudogobio vaillanti	Horsehead gudgeon	HHG	21.3	2.1	45.6	SS	O
Sarcocheilichthys parvus	Small gudgeon	SMG	4.5	0.4	1.8	MS	O
Sarcocheilichthys nigripinnis	Rainbow gudgeon	RBG	4.5	0.1	0.4	MS	O
Gnathopogon imberbis	Jawbeard gudgeon	JBG	2.2	0.03	0.1	MS	H
Saurogobio dabryi	Longnose gudgeon	LNG	2.2	0.04	0.1	MLS	I
Hemiculter leucisculus	White semiknife carp	WSC	3.4	0.7	2.2	LS	O
*Erythroculter ilishaeformis**			1.1	0.04	0.05		
Phoxinus oxycephalus	Spikyhead minnow	SHM	5.6	2.3	13.2	SS	O
*Hemibarbus labeo**			1.1	0.1	0.1		
*Cirrhinus molitorella**			1.1	0.02	0.02		
Rhodeus ocellatus	Rosy bitterling	ROB	48.3	5.5	268.1	MLS	O
Acheilognathus barbatulus	Shortbeard betterling	SBB	15.7	1.5	24.1	MS	H
Cobitidae							
Misgurnus anguillicaudatus	Mud loach	MUL	53.9	2.1	113.1	MS	O
Cobitis sinensis	Chinese spotted loach	CSL	24.7	1.8	43.8	MS	O
C. rarus	Rare spotted loach	RSL	22.7	3.1	103.7	SMS	O
Parabotia fasciata	Spotsand loach	SSL	9.0	0.5	4.1	MS	O
Homalopteridae							
Vanmanenia stenosoma	Flatfin loach	FFL	43.8	5.1	222.3	SS	I
Siluriformes							
Siluridae							
Silurus asotus	Catfish	CAF	2.2	0.02	0.1	MLS	P
Pseudobagrus truncatus	Sphenoidtail bullhead	STB	14.6	0.3	5.0	SS	P
Amblycipitidae							
Liobagrus styani	Si's bullhead	SIB	15.7	0.5	8.0	SS	P
Perciformes							
Gobiidae							
Ctenogobius sp.	Goby	GOB	75.3	14.3	1080.2	SMS	P
Eleotridae							
Odontobutis obscurus	Dark sleeper	DAS	32.6	2.6	84.5	MLS	P
Hypseleotris swinhonis	Yellow sleeper	YES	3.4	0.2	0.5	MLS	P
Mastacembelidae							
Mastacembelus aculeatus	Spiny eel	SPE	4.5	0.1	0.3	MLS	I
Serranidae							
*Siniperca chuatsi**			1.1	0.01	0.01		
Channidae							
*Channa argus**			1.1	0.01	0.01		
Synbranchiformes							
Synbranchidae							
Monopterus alba	Ricefield eel	RFE	11.2	0.1	1.6	MLS	I

SS, MS, LS, SMS and MLS in 'HP' column represent small, mid-sized, large, small and mid-sized, and mid-sized and large streams, respectively. O, I, H and P in 'TE' column represent omnivorous, invertivore, herbivore and piscivore, respectively. The ecological traits of species were determined by Chen (1998), Chu et al. (1999), Yue (2000), and Wu & Zhong (2008).

*The rare species only collected in one site, not included in the statistic analysis.

Table 2. Matrix of correlation between environmental variables and spatial position descriptors.

Variables	Wetted width*	Water depth*	Velocity	Discharge	Substrates	pH	Elevation*	Temperature	Dissolved oxygen	Conductivity*	Stream order	LINK*	D-LINK*	C-LINK*
Local habitat														
Wetted width*		<0.01	ns	<0.01	0.024	<0.01	ns	ns	ns	0.037	<0.01	<0.01	0.017	ns
Depth*	0.328		ns	<0.01	ns	ns	ns	ns	0.024	ns	<0.01	<0.01	ns	ns
Velocity	0.115	0.207		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Discharge	0.669	0.418	0.134		ns	<0.01	ns	ns	<0.01	ns	<0.01	<0.01	<0.01	ns
Substrates	−0.239	−0.012	−0.049	−0.185		ns	<0.01	ns	ns	ns	ns	ns	0.03	0.02
pH	0.431	0.156	0.135	0.396	−0.178		0.026	0.037	<0.01	0.011	<0.01	<0.01	ns	ns
Elevation*	−0.101	−0.138	−0.117	0.049	0.327	−0.236		<0.01	ns	0.01	ns	ns	ns	<0.01
Temperature	0.017	0.137	0.052	0.035	−0.261	0.221	−0.581		0.04	ns	ns	ns	ns	<0.01
Dissolved oxygen	−0.186	−0.24	−0.169	−0.283	0.097	−0.37	0.155	−0.218		0.045	<0.01	<0.01	ns	ns
Conductivity*	0.221	0.147	0.019	0.026	−0.008	0.268	−0.273	0.02	−0.213		ns	ns	ns	<0.01
Spatial position														
Stream order	0.607	0.384	0.125	0.589	−0.220	0.409	−0.021	0.108	−0.379	0.046		<0.01	<0.01	ns
LINK*	0.565	0.342	0.153	0.507	−0.256	0.428	−0.098	0.202	−0.291	0.073	0.836		<0.01	ns
D-LINK*	0.252	0.147	0.19	0.364	−0.136	0.156	0.162	−0.017	−0.03	−0.128	0.375	0.423		ns
C-LINK*	−0.073	−0.097	−0.144	0.037	0.324	−0.196	0.823	−0.414	0.178	−0.319	0.031	−0.046	0.192	

Above the diagonal, P (Bonferroni probabilities) values (ns, not significant).
*Variables expressed in logarithmic values.

were significantly correlated with the three spatial position descriptors except for the C-Link, but the highest correlation occurred between elevation and C-Link ($P < 0.01$). Link had significant correlation with wetted width, depth, discharge, pH and dissolved oxygen ($P < 0.01$), and C-Link had significant correlation with elevation, substrates, temperature and conductivity ($P < 0.01$). Velocity was not significantly correlated with the spatial position ($P > 0.05$) (Table 2).

Local species richness

Results from the linear regression model of species richness and local habitat variables showed that wetted width and temperature were the main indicators influencing local fish richness. When analysing the correlation between species richness and spatial position factors only, it indicated that stream order was the significant descriptor. However, combining habitat and spatial variables with species richness indicated the significant influence of habitat conditions (i.e., wetted width and temperature) on fish richness, but spatial variables showed no significant effect. Therefore, local species richness in the Qingyi Stream was positively correlated with stream width and water temperature (Table 3).

Fish assemblage

Two-way crossed ANOSIM testing for both stream order and headwater/adventitious attribute influencing fish assemblages suggested that stream order did not have a significant influence ($R = 0.039$, $P > 0.05$), but fish assemblages were significantly different between headwater and adventitious streams ($R = 0.382$, $P < 0.01$). Following the SIMPER procedure, shifts in abundance of *Z. platypus* (10.3% of contribution), *R. ocellatus* (9.6%), *Ctenogobius* sp. (9.4%), *Odontobutis obscurus* (8.2%), *Abbottina rivularis* (7.6%) and *Acrossocheilus fasciatus* (7.2%) contributed most to the difference between headwater and adventitious streams. *Zacco platypus*, *C.* sp., and *Ac. fasciatus* were common in headwaters, but *R. ocellatus*,

Table 3. Stepwise linear regression model of local species richness versus habitat and spatial position.

Variables	Independent variables	Coefficients	t value	P	R^2
Local habitat	Wetted width	3.092 (0.324)	3.197	<0.01	0.105
	Temperature	0.763 (0.256)	2.610	<0.01	0.171
Spatial position	Stream order	1.413 (0.313)	3.073	<0.01	0.098
Habitat and position	Wetted width	3.092 (0.324)	3.197	<0.01	0.105
	Temperature	0.763 (0.256)	2.610	<0.01	0.171

Table 4. Canonical correspondence analysis summary statistics for the Qingyi Stream. Total inertia was 2.000.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.217	0.055	0.051	0.048
Species–environment correlation	0.778	0.603	0.673	0.651
Cumulative percentage variance of				
Species data only	10.8	13.6	16.2	18.6
Species + environmental relation	42.6	53.5	63.6	73.0
Interset correlations of environmental variables with axes				
Spatial position				
Stream order	0.095	0.356	0.051	0.212
Link	0.037	0.382	0.108	0.306
C-Link	−0.555	0.120	−0.290	−0.144
D-Link	−0.005	0.375	0.039	−0.115
Local habitat				
Wetted width	0.136	0.204	0.110	0.129
Depth	0.305	0.074	−0.007	−0.157
Discharge	0.142	−0.219	−0.095	−0.052
Elevation	−0.643	−0.013	0.041	−0.248
Temperature	0.307	0.010	−0.354	0.253
Conductivity	0.098	0.232	0.414	0.191
Dissolved oxygen	−0.176	−0.114	−0.150	−0.179
pH	0.263	0.286	0.145	0.074
Velocity	−0.040	0.091	−0.103	0.194
Substrates	−0.443	−0.097	0.054	−0.038

O. obscures and *A. rivularis* were common in adventitious streams.

Correlations of habitat variables and spatial position factors with the four canonical correspondence axes were shown in Table 4. The first two axes of the CCA ordination reflected the dominant patterns of variation in the species data as explained by local habitat and spatial position variables and accounted for 18.6% of the total variance in fish species abundance and richness among sites. Eigenvalues, which ranged between 0 and 1, measured the importance of each axis. The first ordination axis accounted for 42.6% of the variance of the species data and environmental relation, whereas the second axis accounted for 10.9% of this variance (Table 4).

According to the CCA statistics, C-Link (−0.555), elevation (−0.643), substrates (−0.443) and temperature (0.307) were highly correlated with the axis 1, and Link (0.476), D-Link (0.375), stream order (0.356) and pH (0.286) had the highest correlation with axis 2 (Fig. 3a). Species near the centre of the diagram had maximal relative abundances at sites somewhat intermediate with respect to many of the environmental variables. After the Monte Carlo tests, elevation, substrates, depth, C-Link and Link were selected as the variables significantly influencing fish assemblages (Fig. 3b). From the CCA, two main gradients were observed. The first gradient separated assemblages based on C-link, elevation and substrate on the left, but depth on the right. The species associated with this gradient were *Phoxinus oxycephalus*, *Ac. fasciatus*, *Pseudogobio vaillanti*, *V. stenosoma*, *Cobitis rarus*, *Z. platypus*, *C.* sp., *Liobagrus styani*, *Silurus asotus*, *Cobitis sinensis*, *Odontobutis obscurus*, *Hemiculter leucisculus*, *R. ocellatus*, *Carassius auratus*, *A. rivularis*, *Mastacembelus aculeatus* from the left to right. The second gradient was caused by Link, along which *Sarcocheilichthys parvus*, *Abbottina tafangensis*, *Acheilognathus barbatulus*, *Parabotia fasciata*, *Squalidus argentatus*, *Monopterus alba*, *Gnathopogon imberbis*, *M. anguillicaudatus*, *Pseudorasbora parva*, *Hypseleotris swinhonis* were distributed from the top to bottom.

Discussion

Numerous researchers have found that the factors influencing stream fish assemblages involve physiochemical environment, which is spatially heterogeneous and temporally variable, and biotic interactions such as

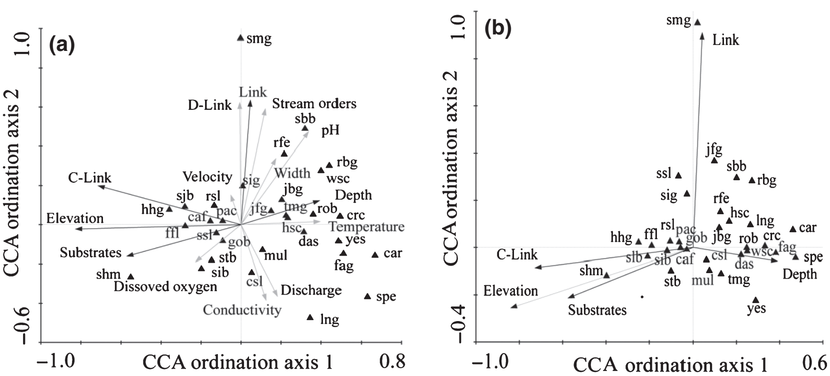


Fig. 3. Canonical correspondence analysis diagrams for environmental variables (habitat and spatial position) and fish assemblages in the Qingyi Stream. (a) Ten habitat environmental variables and four spatial location variables were examined with fish assemblage; (b) using the forward selection by using the Monte Carlo permutation test, as a result, removing those subordinate factors, then depth, substrates, elevation and Link & C-Link were selected as the main indicators about fish assemblage. The black arrows indicated the most important factors, and the grey arrows showed the other factors. Species codes as in Table 1.

competition and predation (Gorman 1988; Harvey & Stewart 1991; Grossman et al. 1998; Dauwalter et al. 2008). The variability in habitat complexity and diversity along upstream–downstream gradient is one of the underlying mechanisms that explain why stream fish assemblages vary spatially (Matthews 1986). Shelter availability (Abes & Agostinho 2001), substrate (Aadland 1993), water depth (Harvey & Stewart 1991), current velocity (Magoulick 2004), water temperature (Wang et al. 2003), woody debris (Gregory et al. 1991) and relative bed stability (Kaufmann & Hughes 2006) have all been shown to influence stream fish assemblages. In this study, 10 variables were measured to determine the influence of local habitat on fish assemblages. Based on linear regression models, wetted width and water temperature were the factors significantly influencing species richness in the Qingyi Stream. In addition, elevation, substrate and water depth were identified to determine fish assemblages according to the CCA. Our findings are consistent with the well-established notion that stream size is the most important factor influencing fish assemblages (including species richness), because the variation in stream size is often associated with the changes of water depth and width, elevation and substrate (Matthews & Robison 1988). The differing thermal tolerances of different species also affect fish distributions (Petts 2000) and thus fish assemblage composition.

Because of the differential rates of immigration and extinction of fishes among different streams within a watershed, fish assemblages are also influenced by the stream spatial position determining ‘immigration–extinction’ rates (Osborne & Wiley 1992). The importance of immigration and extinction dynamics in structuring stream fish assemblages has been underlined in a number of studies (e.g., Angermeier & Schlosser 1989; Gotelli & Taylor 1999; Taylor & Warren 2001). However, the pattern of how stream spatial position structures fish assemblages is not well established and remains debated. Osborne & Wiley (1992) found a significant relationship between D-link and fish species richness in a central Illinois watershed, but Grenouillet et al. (2004) found the similar result using downstream local species richness (D-LSR). Smith & Kraft (2005) revealed that fish species richness was affected by stream order, D-link and C-link within a Beaverkill–Willowemoc watershed in New York. In addition, B-link (branch link), the number of branches along a path to the right (+) or left (−) of the central axis of mainstream, was also shown to affect species richness (Nieman 1996). As B-link is considered to be limited by only providing information about how the watershed differs on one side or the other of a mainstream branch (Smith & Kraft 2005), stream order, Link, D-link and C-link are selected to identify how stream spatial position influences fish assemblages in this study. Our results show that only stream order significantly structures fish species richness when examining the relationship between species richness and pure spatial variables. However, only habitat variables are screened out to significantly affect species richness when considering the combined influences of local habitat and spatial position, but spatial variables are all less important.

In addition, our result also presents that, by using the forward selection procedure of the CCA, Link and C-link, rather than stream order and D-link, significantly influence fish assemblages in the study stream. In our result, *P. oxycephalus*, *Pseudogobio vaillanti*, *Ac. fasciatus* and *V. stenosoma* are most abundant in streams with high C-link, but *Mastacembelus aculeatus*, *A. rivularis*, *C. carpio* and *C. auratus* display the opposite pattern. This can be well explained by their specific ecological traits, because the former four species always inhabit small streams characterised by high elevation, fast flow and coarse substrate, but the latter are common in the lentic systems (i.e., lakes) and tranquil flows (i.e., large rivers) (Chen 1998; Yue 2000). For example, most *Phoxinus* fishes are endemic in montane headwaters, and their distributions are often intensively constrained by cold water temperature (Chen 1998). Adult *Ac. fasciatus* usually inhabit beneath cobbles or boulders in deep lotic waters with spawning occurring in shallow lotic riffles (Yan et al. 2009), while *C. carpio* is widely naturally distributed in most lakes, reservoirs and large rivers in China (Yue 2000). However, *Sarcocheilichthys parvus*, *A. tafangensis*, *Parabotia fasciata*, *Squalidus argentatus* and *Acheilognathus barbatulus* often prefer middle-sized streams or pools in small streams to dwell (Chen 1998; Yue 2000), which could perhaps explain why the distributions of these species are closely correlated with Link but not C-link in our study. Fairchild et al. (1998) found a similar result in a CCA ordination of fish assemblages with a south-eastern Pennsylvania watershed: C-link and Link accounted for 13.5% of the variation in species composition among sites. Smith & Kraft (2005) found the significant effect of C-link and stream order on species composition by the CCA and stated that C-link was greatly informative in determining the influence of tributary spatial position on fish assemblage because of its ability to distinguish between headwater and adventitious streams. The utility of C-link is also supported by the relevance of stream confluences to geomorphological processes within DENs that are likely to influence ecological processes (Grant et al. 2007).

Dams can extensively impact stream fish assemblages in diverse ways, such as the blocking of migration routes and the loss of navigational cues (Drinkwater & Frank 1994), the fragmentation of habitat with associated isolation of larvae and juveniles at water intakes (Travnichek et al. 1993), the alteration of natural of hydrologic and geomorphic regimes (Ligon et al. 1995), the decline in biodiversity and the alteration of natural food webs (Power et al. 1996) and the shift in water chemistry (Humborg et al. 1997). Based on the Serial Discontinuity Concept (Stanford & Ward 2001), dams and other anthropic activities (e.g., pollution and erosion.) should disrupt the underlying stream continuum, causing longitudinal shifts in the abiotic and biotic parameters and processes. Our result suggests that local habitat conditions are more important in influencing fish species richness than spatial position in the dammed Qingyi Stream watershed. This could be explained by the fact that dams block the immigration routes of fishes from mainstream to tributaries, which weakens the effect of stream spatial position on species richness. However, our result also presents that fish assemblages are significantly different between headwater and adventitious streams in spite of the similar species richness, which is associated with the variation in relative abundance of *Z. platypus*, *C.* sp., *Ac. fasciatus* (common in headwaters), *R. ocellatus*, *O. obscures* and *A. rivularis* (common in adventitious streams). Thornbrugh & Gido (2010) found that fish assemblage structure in adventitious streams was different from headwater streams, but species richness was also significantly higher in adventitious streams in the Kansas River basin. In addition, two spatial position variables, C-link and Link, are discovered to significantly influence species compositions among tributaries in our study. Therefore, our results suggest that, in a heavily dammed watershed, the importance of the relative influences of local habitat and stream spatial position on fish assemblages depends on the community descriptor used. Fish species richness is mainly determined by local habitat environment, but not stream spatial position, which could be a result of the negative effect of dams on fish movements between tributary and confluence. But both local habitat and stream spatial position are important in structuring fish species composition, which suggests that the distribution of specific species in a DEN is determined by its inherent ecological traits (e.g., habitat preference) despite the fact that dams possibly constrain the potential movement of fishes.

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