

Biological invasions undermine the functional diversity of fish community in a large subtropical river

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Abstract Biological invasions are considered to be one of the main threats to biodiversity. Invasions lead to a loss of native species, changes to species composition, and a shift in the functioning and stability of ecosystems. In this study, derived from nine consecutive years of monitoring data and based on morphological functional trait values measured at the individual-level, we quantified the functional differences between native and non-native fish species and further assessed how biological invasions impact on species richness and functional diversity in the large subtropical Pearl River in southern China. Specifically, we differentiated intraspecific functional variability by separating individuals of a species according to their different life stages. Our results

provided strong evidence that native and non-native fish were significantly different in their functional attributes. Invasion caused no obvious change in species richness; however, the yearly increase in non-native populations was accompanied by a significant decrease in functional niches of native species and change in several aspects of functional diversity in the fish community. Decreasing functional richness, and increasing functional divergence and specialization, indicated that most native species had been replaced by non-native species with different specific functional traits, which may affect ecosystem stability. Notably, this study provided empirical evidence that functional diversity was more sensitive to biological invasions than species richness. Our results show that control of non-native aquatic species is both necessary and urgent in the Pearl River. An understanding of the processes described in this study can form the basis of conservation in fish community, which is critical to sustainable and successful fisheries.

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Introduction

Biological invasions have become an important part of global change, and they are considered to be one of the

main threats to biodiversity (Chapin et al. 2000; Pysek et al. 2010; Simberloff et al. 2013). It is widely accepted that biological invasions can lead to dramatic changes in the taxonomic structure of recipient communities and may cause the extinction of some species (Clavero and García-Berthou 2005; Liao et al. 2008; Ehrenfeld 2010; Simberloff et al. 2013). However, the contribution of species to ecosystem processes are not equal, and it is the functional characteristics of a species (i.e., morphology, diet, swimming ability, and life history traits) rather than its taxonomic identity that drive species function in communities (Violle et al. 2007; Villéger et al. 2010; Díaz et al. 2013; Mouillot et al. 2013). Invasions represent a change in species composition and may represent the loss of species (with or without resulting changes in species richness), but also a shift in the functioning and stability of ecosystems. The effect of species loss on ecosystem processes and function depends largely on species traits and the niches that specific species fill (Petchey and Gaston 2002; Mori et al. 2013). It is critical to raise awareness about the consequences of biodiversity loss on ecosystem functioning and associated ecosystem services, which are fundamental to human well-being (Solan et al. 2004; Cardinale et al. 2012; Tomimatsu et al. 2013).

Biological invasion is a complex biological process, its success not only relating to abiotic characteristics, but also relating to the biological and ecological characteristics of the intruder itself and the vulnerability of the community (Tilman 2004; Catford et al. 2009). For instance, *Centaurea cyanus* has successfully invaded California's annual grassland, mainly because its roots are able to take advantage of water available at 60 cm depth (Muth and Pigliucci 2007), which native species cannot access. Invasive plants generally display a larger leaf area (Ordonez et al. 2010) and root biomass (Van Kleunen et al. 2010), and lower mean C:N ratio (Heard and Sax 2013) than native species, which confer a competitive advantage. Hejda and Bello (2013), through comparative analysis of different vegetation types, found that the success of an invasive species is often due to the functional difference with local species; i.e., an invasive species may invade successfully because it occupies a different niche. Invasive largemouth bass (*Micropterus salmoides*) occupies a different habitat from native fish species (Huskey and Turingan 2001), and invasive pumpkinseed (*Lepomis gibbosus*) exhibited a strong

trophic variability by exploiting a large array of prey (Wainwright et al. 1991). These findings reflect the existence of markedly different ecological characteristics and functions between invasive species and native species (MacDougall et al. 2009; Ordonez et al. 2010), which may be the key to successful invasion (Ricciardi et al. 2013).

There has been a gradual increase in functional approaches, particularly functional trait comparison, to evaluate the impact of biological invasions on communities and ecosystems. There are some studies that have explored the effect of non-native species on the functional diversity of freshwater fish, such as Blanchet et al. (2010), who found that non-native species disrupt global patterns in the size of freshwater fish. Introduced lake trout (*Salvelinus namaycush*) have been shown to replace native salmonids and induce major trophic cascades in some North American lakes (Eloranta et al. 2014). Based on multiple life-history traits, Olden et al. (2006) identified non-native fish species that have no, or minimal, overlap with the life history strategies of native fish species. Invasive species may promote variability of the trophic positions of species, thereby changing the functions of an ecosystem and may even disrupt ecosystem stability (Britton et al. 2010; Cucherousset et al. 2012; Matsuzaki et al. 2013). However, studies on the functional differences between native and non-native animal species, and empirical assessments of the impact of biological invasions on patterns in functional diversity are still lacking. The main difficulty encountered when assessing the impact of an invasion is that change tends to be cumulative and slow, and the impact may take many years to become obvious (Strayer et al. 2006). A functional approach can provide important and sensitive insights on how traits mediate community assembly and cause community disturbance (Sudin et al. 2005; Mouillot et al. 2013). Hence, a functional approach, which analyzes the relationships between invasive species and the patterns in functional diversity within the recipient community, may facilitate earlier detection of alterations in ecosystem function, which is not easily revealed by variations in species richness in a short period of time.

Although freshwater ecosystems account for less than 1% of the Earth's surface area, these ecosystems contain 9.5% of the total number of species (Balian et al. 2008) and provide humanity with rich

biodiversity and essential ecological services, such as drinking water and aquatic products (Lévêque et al. 2008). Freshwater ecosystems exhibit the highest species richness per unit area, and it has the highest extinction rates on the planet (Michelan et al. 2010). For many reasons, such as dam construction, pollution and overfishing, the functions of aquatic ecosystems have decreased sharply in recent years (Jenkins 2003), and they are considered to be one of the most endangered ecosystems on Earth (Carpenter et al. 1992; Dudgeon et al. 2006). The introduction of non-native freshwater fish, for instance recreational fishing, aquaculture and international trade, is a significant component of this global change (Leprieur et al. 2008; Marr et al. 2010). This phenomenon has been observed in freshwater fish assemblages in southern China (Shuai et al. 2017).

The Pearl River is a large subtropical river in southern China, stretching some 2400 km. It was once characterized by having rich aquatic biological resources due to its mild climate and abundant food supply, and it exhibited high endemism and a diverse gene pool, supporting 381 fish species, including 262 freshwater species and 119 estuarine species (Shuai et al. 2017). To restore and maintain fishery stocks, fishing moratoria, such as no fishing during the spawning season, has been introduced since 2010. Yet one of the most serious ecological problems in the Pearl River is the invasion of non-native species, such as *Oreochromis niloticus* and *Hypostomus plecostomus* (Shuai et al. 2015). However, to date, our knowledge about the effects of biological invasions on the functional diversity patterns in the Pearl River is still limited, despite its ecological importance and urgency. In this study, to provide insight on the processes of biological invasions of the Pearl River basin, we quantified the functional difference between native and established non-native fish species, and we assessed temporal changes in species richness and functional diversity patterns. It is crucial to understand the processes, such as those outlined in this study, to control non-native aquatics, conserve the diversity of fish community, sustain successful fisheries, and improve current conservation strategies in the Pearl River.

Materials and methods

Study site

Biological surveys were conducted at one single locality in the Fengkai to Deqing section (N 23°08'36", E 111°46'33") of the Pearl River in southern China, ~ 200 km upstream of the Pearl River estuary (Fig. 1). This section of the Pearl River is characterized by an average temperature of 23 °C with no obvious seasonal differences, and it is an important area for sustainable wild fishery resources. This section is a representation of other downstream river reaches or tributaries within the basin. To gain insight into ecosystem equilibrium and fish stock composition, as well as biological invasions, fish collections were performed in this river section from the year 2009 to 2017.

Sample collection

Samples were collected four times a year from 2009 to 2017 in one site. Fish community was sampled always using the same protocol, namely a combination of fishing gears distributed randomly in the sampling site to overcome selectivity effects, including 4 gillnets (length: 10 m, height: 2.5 m, mesh-size: 20 mm), 4 fishing hooks (length: 20 m, hooks: 50) and 4 lobster pots (total length: 15 m, radius: 18 cm). Sampling started in the early evening (approximately 18:00 h) and lasted 12 h through the night. Fish individuals captured with these three methods were immediately photographed, identified, labeled and measured for body length and weight. Specimens that could not be identified immediately were labelled, fixed in 5% formalin and brought back to the laboratory for further examination. The remnant fish were released if they are alive.

Many studies have demonstrated that different life-stages within a species can have different functional traits and effects on a community (Miller and Rudolf 2011) and ecosystem (Rudolf and Rasmussen 2013; Zhao et al. 2014). Intraspecific variability in functional traits cannot be negligible when using functional approaches in community ecology (Bolnick et al. 2011; Albert et al. 2012; Zhao et al. 2014). Therefore, each fish species in this study was divided into two to three functional entities, based on life stages (i.e., young-of-the-year, juveniles and adults).

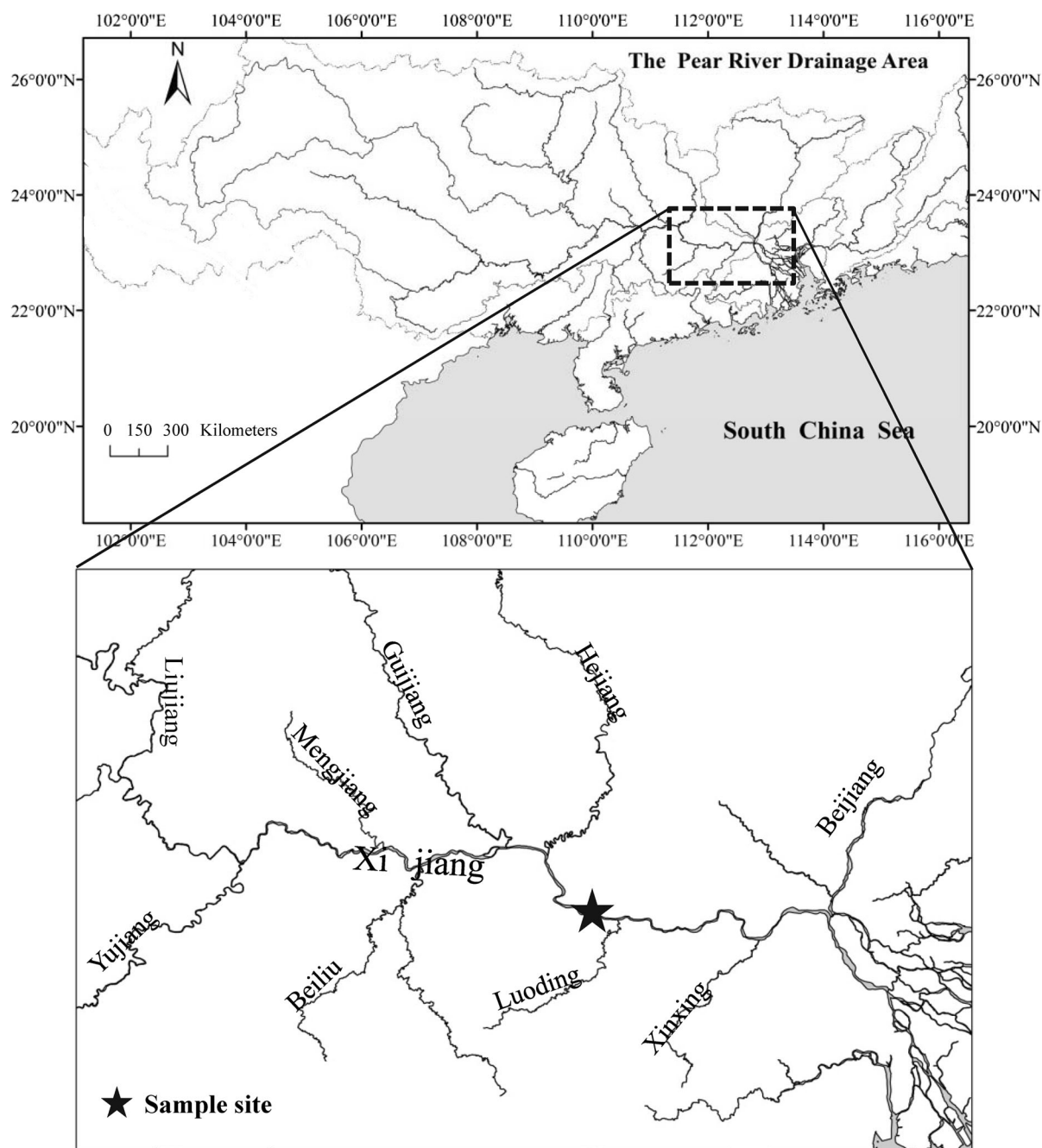


Fig. 1 Geographic location of the sampling site in the Pearl River

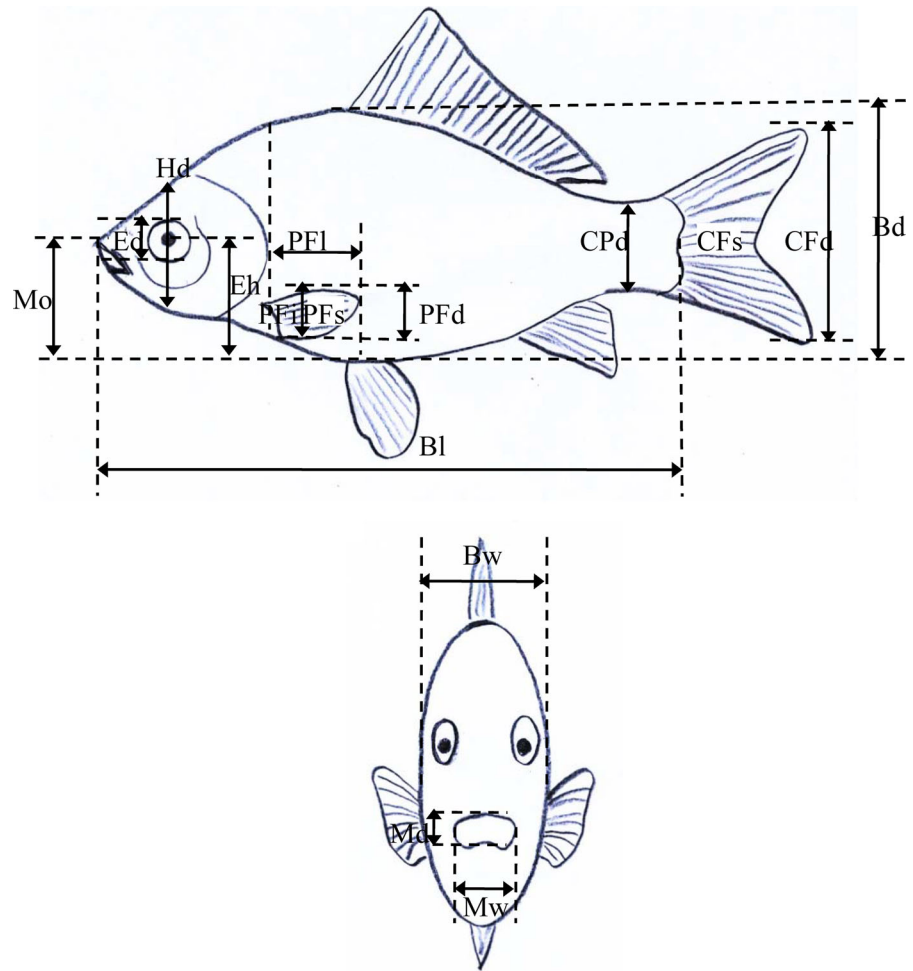
Morphological characteristics were measured directly using a scale and digital caliper or through picture analyses (software Image J; Fig. 2). Measurements were made to the nearest 0.01 mm. Specifically, these morphological traits were measured on at least 20 individuals (except some rare species whose total

sample number was < 20) for each species observed in the study site for the whole study. For all females, only non-pregnant individuals were measured.

Nineteen morphological trait measurements were obtained for each specimen (Dumay et al. 2004; Villéger et al. 2010; Fig. 2). These measurements

Fig. 2 The measurement of external morphology traits.

Bl body standard length, *Bd* body depth, *CPd* caudal peduncle minimal depth, *CFd* caudal fin depth, *CFs* caudal fin surface, *PFI* distance between the insertion of the pectoral fin to the bottom of the body, *PFb* body depth at the level of the pectoral fin insertion, *PFl* pectoral fin length, *PFs* pectoral fin surface, *Hd* head depth along the vertical axis of the eye, *Ed* eye diameter, *EH* distance between the center of the eye to the bottom of the head, *Mo* distance from the top of the mouth to the bottom of the head along the head depth axis, *Bw* body width, *Md* mouth depth, *Mw* mouth width, *Gl* total gut length, *GRL* gill raker length, *M* body weight



could be quantified easily for a large number of individuals. Food acquisition and locomotion are considered to be the most important survival functions performed by fish (Vill  ger et al. 2010) and usually involve coordinated use of multiple organs simultaneously (Mouillot et al. 2013). Therefore, measurements were converted into 16 complementary functional traits which were closely related to food acquisition and locomotion (details in Table 1).

Statistical analyses

To quantify the differences in functional traits between native and established non-native fish species, a multidimensional functional space was built using a principal component analysis (PCA), based on measured functional trait values (Vill  ger et al. 2008). The first five synthetic principal components (PC) of

the PCA (PC1 = 23.63%, PC2 = 20.60%, PC3 = 12.85%, PC4 = 11.32%, and PC5 = 8.05%, respectively) were subsequently selected to build the functional space of the species pool by selecting mean-squared deviation index > 0.002 (Maire et al. 2015). These five PC axes account for 76.45% of the initial inertia in trait values, demonstrating that the functional space accurately represented the initial distances between functional entities. We used permutational multivariate analysis (PERMANOVA, 9999 permutations, Anderson 2001) to test the differences in position in the functional space between native and non-native entities. We then tested if functional richness (the volume of the minimum convex hull) differed between the species pools of native and non-native species. Specifically, we calculated the observed functional richness of native and non-native entities separately (Vill  ger et al. 2008)

Table 1 List of the 16 functional traits associated with food acquisition and locomotion. Adapted from Villéger et al. (2010)

Functional traits	Code	Measurements	Ecological meaning
Mass (food and locomotion)	M	$\log (M + 1)$	Muscle mass
Oral gape surface (food)	OGSu	$\frac{Mw \times Md}{Bw \times Bd}$	Size of food items captured and ability to filter water
Oral gape shape (food)	OGSh	$\frac{Md}{Mw}$	Method to capture food item and food acquisition
Oral gape position (food)	OGP	$\frac{Mo}{Hd}$	Position of prey in the water
Gill raker length (food)	GRL	$\frac{GRL}{Hd}$	Filtration capacity or gill protection
Gut length (food)	GL	$\frac{Gl}{Bl}$	Digestibility of food
Eye size (food)	ES	$\frac{Ed}{Hd}$	Prey detection
Eye position (locomotion)	EP	$\frac{Eh}{Hd}$	Position in the water column
Body transversal shape (locomotion)	BTSh	$\frac{Bd}{Bw}$	Position in the water column and hydrodynamism
Body transversal surface (locomotion)	BTSu	$\frac{\ln\left(\left(\frac{2}{3} \times Bw \times Bd\right) + 1\right)}{\ln(M+1)}$	Mass distribution along the body and hydrodynamism
Pectoral fin position (locomotion)	PFP	$\frac{PFi}{PFb}$	Pectoral fin use for maneuverability
Pectoral fin shape (locomotion)	PFS	$\frac{PFi^2}{PFs}$	Propulsion and maneuverability
Caudal peduncle throttling (locomotion)	CPT	$\frac{CFd}{CFd}$	Caudal propulsion efficiency and endurance
Caudal fin shape (locomotion)	CFS	$\frac{CFd^2}{CPs}$	Propulsion, endurance, acceleration and direction
Fins surface ratio (locomotion)	FSR	$\frac{2 \times PFS}{CFs}$	Propulsion between caudal and pectoral fins
Fins area (locomotion)	FA	$\frac{(2 \times PFS) + CFs}{\frac{2}{3} \times Bw \times Bd}$	Acceleration and manoeuvrability

F means related to food acquisition and L related to locomotion

and used a bootstrap procedure (1000 randomizations) to calculate the expected functional richness values in a random pool. The level of functional overlap between the local species pools of native and established non-native entities was calculated following Villéger et al. (2013); i.e., the percentage of functional space shared by native and non-native species in the five-dimensional functional space. A high functional overlap indicates a high functional similarity between native and non-native species.

Functional richness represents the amount of functional space filled by the community. Functional evenness describes the evenness of abundance distribution in a functional trait space. Functional divergence represents how abundance is spread along a functional trait axis, within the range occupied by the community. Functional specialization represent the proportion of abundance on extreme strategies in the functional space. To determine how biological invasions (expressed as the relative abundance of non-native entities) affect the functional traits of the community, we also quantified for each year: functional richness of native species, functional richness of

non-native species, functional overlap between them. Moreover we also quantified for all species together, species richness, functional richness, functional evenness, functional divergence and functional specialization. Functional diversity indexes were calculated following Villéger et al. (2008). Functional diversity would responded nonlinearly to invasion intensity (Mouillot et al. 2013), so linear models with quadratic terms were used to quantify either monotonic (linear and nonlinear) or non-monotonic (hump-shape and U-shape) changes as a function of the biological invasion as a predictor variable, represented by the relative abundance of non-native entities

All statistical analyses were conducted in R 2.14.1 (R Development Core Team 2011). Variables were considered statistically significant at $P < 0.05$.

Results

Species composition

A total of 12,310 individuals belonging to 68 taxa, 18 families and eight orders were collected. Fifty-nine native species, including four species endemic to China, and nine non-native species, were recorded during the nine sampling years. The Cyprinidae represented 37 taxa and accounted for 54% of the total fish species richness captured. Among these, eight species were river-sea migratory and 16 species were river-lake migratory (Table 2). Overall, the most dominant species was *Cirrhinus molitorella*, which accounted for approximately 25.35% of all individuals, followed by *Megalobrama terminalis* (17.73%) and *Squaliobarbus curriculus* (16.17%). Nine non-native species were captured during the studied period. The non-native Nile tilapia (*Oreochromis niloticus*), was one of the top four dominant species, and its abundance accounted for 6.13% of all individuals in our study area. However, the proportional abundance of non-native species in the community increased significantly from around 1% at the beginning of the study in 2009 to 7% at the end of the study in 2017 (Spearman's Rho, two-tailed $P < 0.01$, Fig. 3).

Functional differences between native and non-native species

In the species pool, the position in the functional space significantly differed between native and non-native entities (PERMANOVA, $P < 0.001$; Fig. 4). Although they were composed of the same number of functional entities ($n = 16$), the observed functional richness of native entities (26.20% of the functional space available) was significantly larger than the richness of non-native entities (6.79%, mean = $0.3 \pm 0.08\%$; 95% confidence interval = 0.15%–0.47%). Functional overlap between native and non-native species was low, as only 3.55% of the total functional space was shared by native and non-native functional entities.

Relationship between biological invasion and functional niche

With the yearly increase in the intensity of invasion (i.e. relative abundance of non-native species),

functional niche of native species decreased significantly (quadratic term: $P = 0.038$), with maximal functional niche being observed at a slight level of invasion, whereas the functional niche of non-native species (quadratic term: $P = 0.04$) and the functional overlap between native and non-native species (quadratic term: $P = 0.036$) increased significantly (Fig. 5, Table 3).

Relationship between biological invasion and functional diversity

In the sampled fish community, annual species richness (SR) showed no obvious change against the invasion gradient ($P > 0.05$). Annual functional richness (FRic) (linear term: $P = 0.031$, quadratic term: $P = 0.017$) displayed a significant hump-shape relationship to the invasion gradient. Annual functional evenness (FEve) showed a linear curve but no significant response to the invasion gradient (linear term: $P = 0.385$). Annual functional divergence (FDiv) displayed a significant linear increase ($P = 0.047$) along the invasion gradient. In contrast, annual functional specialization (FSpe) displayed an U-shaped curve response to the invasion gradient (linear term: $P = 0.049$, quadratic term: $P = 0.029$) (Fig. 6, Table 4).

Discussion

Freshwater fish play a vital role in ecosystem stability and the loss of fish species can cause dramatic changes in freshwater ecosystems (Mims et al. 2010; Matsuzaki et al. 2013). Simultaneously, freshwater fish are one of the most endangered groups of vertebrates and they have a high priority for management and conservation (Dudgeon et al. 2006). In the present study, we found that the number of non-native species increased significantly over the study years in the subtropical Pearl River. Also, our results indicated that native and non-native fish species showed considerable differences in their ecological and biological attributes, and functional overlap between them was low. Non-native species had narrower functional niches than native species despite having the same number of functional entities. Simultaneously, the observed functional richness of native entities was 26.20%, only. This means there are 73.8% of

Table 2 List of fish species and their ecological characteristics in the Deqing section of the Pearl River (*H* herbivore, *I* invertivore, *P* piscivore, *Pl.* planktivore, *D* Detritivore,*O* omnivore, *E* endemic to China, *N* native species, *Non.* Non-native species, *RS* River-sea migratory, *RL* River–lake migratory, *SE* Sedentary; “+” indicates rare species)

Species	Code	Percentage	Trophic guild	Category	Life stage
Cypriniformes					
Cyprinidae					
<i>Cirrhinus molitorella</i>	CIRM	25.35	H	N;RL	YOY + Juvenile + Adult
<i>Megalobrama terminalis</i>	MEGA	17.73	O	N;RL	YOY + Juvenile + Adult
<i>Squaliobarbus curriculus</i>	SQUC	16.17	O	N;RL	YOY + Juvenile + Adult
<i>Hemiculter leucisculus</i>	HEMLE	4.22	O	N;SE	YOY + Juvenile + Adult
<i>Xenocypris davidi</i>	XEND	2.29	H	N;RL	Juvenile + Adult
<i>Parabramis pekinensis</i>	PARA	1.48	H	N;RL	Juvenile
<i>Cyprinus carpio</i>	CYPC	1.32	O	N;SE	YOY + Juvenile + Adult
<i>Pseudorasbora parva</i>	PSEP	1.32	O	N;SE	Juvenile
<i>Xenocypris argentea</i> Günther	XENA	1.32	H	N;RL	Juvenile + Adult
<i>Ctenopharyngodon idellus</i>	CTEI	1.21	H	N;RL	YOY + Juvenile + Adult
<i>Hypophthalmichthys molitrix</i>	HYPM	1.19	Pl.	N;RL	YOY + Juvenile + Adult
<i>Pseudolaubuca sinensis</i>	PSES	1.06	Pl.	N;SE	Juvenile
<i>Squalidus argentatus</i>	SQUA	0.97	I	N;RL	Juvenile
<i>Carassius auratus</i>	CARA	0.74	O	N;SE	Adult
<i>Pseudohemiculter dispar</i>	PSED	0.71	O	N;SE	Juvenile
<i>Erythroculter recurviceps</i>	ERYT	0.44	P	N;SE	YOY + Juvenile
<i>Aristichthys nobilis</i>	ARIN	0.28	Pl.	N;RL	YOY + Juvenile + Adult
<i>Ptychidio jordani</i>	PTYJ	0.19	I	E;SE	YOY + Juvenile
<i>Distoechodon tumirostris</i>	DIST	0.18	D	N;RL	YOY + Juvenile + Adult
<i>Culter alburnus</i>	CULA	0.16	P	N;SE	YOY + Juvenile + Adult
<i>Elopichthys bambusa</i>	ELOP	0.15	P	N;RL	Adult
<i>Osteochilus salsburyi</i>	OSTS	0.11	O	N;SE	Juvenile
<i>Megalobrama amblycephala</i>	MEGAL	0.11	H	Non;RL	Adult
<i>Saurogobio dabryi</i>	SAUD	0.10	I	N;SE	Juvenile
<i>Sinibrama wui</i>	SINW	+	O	E;RL	YOY
<i>Opsariichthys bidens</i> Günther	OPSB	+	P	N;SE	Juvenile + Adult
<i>Rhodeus ocellatus</i>	RHOO	+	O	N;SE	Juvenile
<i>Hemibarbus maculatus</i>	HEMB	+	O	N;SE	Juvenile
<i>Zacco platypus</i>	ZACP	+	O	N;SE	Adult
<i>Gobiobotia meridionalis</i>	GOBM	+	I	E;SE	YOY
<i>Mylopharyngodon piceus</i>	MYLP	+	I	N;RL	YOY + Juvenile
<i>Cirrhinus mrigala</i>	CIRMR	+	O	Non;SE	Juvenile + Adult
<i>Spinibarbus denticulatus</i>	SPID	+	O	N;RL	YOY
<i>Labeo rohita</i>	LARO	+	D	Non;SE	Juvenile
<i>Hemibarbus labeo</i>	HEMLA	+	O	N;SE	Juvenile
<i>Tinca tinca</i>	TINC	+	O	Non;SE	YOY
<i>Cyprinus carpio var. specularis</i> Lacepede	GERM	+	O	Non;SE	Adult
Cobitidae					
<i>Misgurnus anguillicaudatus</i>	MISA	0.95	D	N;SE	Adult
<i>Botia robusta</i>	BOTR	+	D	N;SE	Juvenile + Adult
<i>Botia pulchra</i>	PARA	+	I	E;SE	YOY + Juvenile

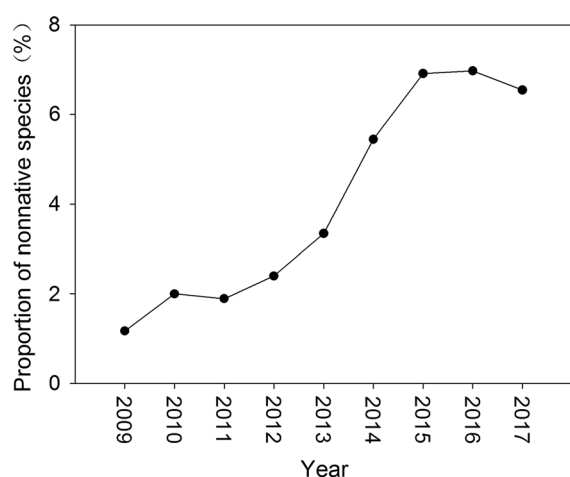
Table 2 continued

Species	Code	Percentage	Trophic guild	Category	Life stage
<i>Micronoemacheilus pulcher</i>	MICP	+	D	N;SE	YOY + Juvenile
Perciformes					
Cichlidae					
<i>Oreochromis niloticus</i>	OREN	6.13	O	Non;SE	YOY + Juvenile + Adult
Serranidae					
<i>Lateolabrax japonicus</i>	LATJ	0.22	P	N;RS	Adult
<i>Siniperca kneri</i>	SINK	0.11	P	N;SE	Juvenile + Adult
<i>Siniperca scherzeri</i>	SINS	+	P	N;SE	YOY
Channidae					
<i>Channa maculata</i>	CHAM	0.15	P	N;SE	Adult
<i>Channa argus</i>	CHAR	+	P	N;SE	Adult
Eleotridae					
<i>Eleotris oxycephala</i>	ELOX	0.58	P	N;SE	Juvenile
Gobiidae					
<i>Rhinogobius giurinus</i>	RHIG	1.73	P	N;SE	Juvenile
<i>Glossogobius giuris</i>	GLOG	0.44	P	N;SE	Juvenile
Mastacembelidae					
<i>Mastacembelus armatus</i>	MAAR	0.59	I	N;SE	Juvenile + Adult
Siluriformes					
Bagridae					
<i>Pelteobagrus fulvidraco</i>	PELF	3.80	P	N;SE	Juvenile + Adult
<i>Pelteobagrus vachelli</i>	PELV	1.49	P	N;SE	Juvenile + Adult
<i>Mystus guttatus</i>	MYSG	0.66	P	N;SE	YOY + Juvenile
<i>Leiocassis crassilabris</i>	LEIC	0.54	P	N;SE	Juvenile + Adult
Cranoglanididae					
<i>Cranoglanis boudierius</i>	CRAB	+	P	E;SE	Adult
<i>Ictalurus Punctatus</i>	LETP	+	O	Non;SE	Juvenile + Adult
Clariidae					
<i>Clarias fuscus</i>	CLFU	0.10	P	N;SE	Adult
<i>Clarias gariepinus</i>	CLAR	0.12	P	Non;SE	Adult
Siluridae					
<i>Silurus asotus</i>	SILA	0.18	P	N;SE	YOY + Juvenile + Adult
Clupeiformes					
Clupeidae					
<i>Clupanodon thrissa</i>	CLUT	2.20	O	N;RS	Adult
<i>Konosirus punctatus</i>	KONP	+	Pl.	N;RS	Adult
Engraulidae					
<i>Coilia grayii</i>	COIL	0.26	I	N;SE	Adult
Anguilliformes					
Anguillidae					
<i>Anguilla japonica</i>	ANGJ	0.15	P	N;RS	Juvenile
<i>Anguilla marmorata</i>	ANGM	+	P	N;RS	Juvenile
Synbranchiformes					
Synbranchidae					
<i>Monopterus albus</i>	MONA	+	I	N;RS	Adult

Table 2 continued

Species	Code	Percentage	Trophic guild	Category	Life stage
Characiformes					
Characidae					
<i>Colossoma brach ypomum</i>	COLO	+	O	Non;RS	YOY + Juvenile
Tetraodontiformes					
Tetraodontidae					
<i>Takifugu ocellatus</i>	TAKI	0.18	P	N;RS	YOY

The life history of each fish is divided into two to three stages, that is young-of-the-year (YOY), juveniles and adults

**Fig. 3** Annual proportion of non-native species in the community

functional niches empty. These findings indicate that our study site have low resistance to invasion and can explain why non-native species can quickly invade our study area (Burke and Grime 1996).

Previous studies have shown that colonization by non-native fish can lead to rapid establishment and population growth in the recipient community with large differences between the ecological and functional characteristics of invasive species and native species (Britton-Simmons 2006; MacDougall et al. 2009; Byun et al. 2012). Once established, invasive species can successfully invade recipient communities by reducing abundance, even extirpating native entities with similar functional traits (Hejda 2013). For example, the tilapia *Oreochromis niloticus*, which was one of the top four dominant species in our study area, have established viable feral populations in many

tropical and subtropical environments (Costa-Pierce 2003) and, currently, it is one of the most invasive fish worldwide (Shuai et al. 2015). Once established, the Nile tilapia (*Oreochromis niloticus*) can cause substantial ecological disturbance by altering the function of aquatic systems through competition (Starling et al. 2002) and local extinction of native fish populations (Lowe-McConnell 2000). Our results demonstrated that the control of non-native aquatics is very urgent and should be compulsory in the Pearl River.

Moreover, we found that after initial colonization by non-native fish species, functional richness of native species was decreased significantly, whereas functional richness of non-native species and the functional overlap between native and non-native species increased significantly with increasing intensity of invasion. This means that the increasing population of non-native species undermined the functional niche of native species and resulted in reduced abundance of some species, or even loss of some species. Specifically, the loss of species with unique functions may affect ecosystem stability given that ecosystem stability depend greatly on species traits and the niches that the species fill (Matsuzaki et al. 2016). For example, the introduced largemouth bass can eliminate native fish species with similar ecological attributes in lakes and rivers (Brown et al. 2009). The invasion of *Bythotrephes* reduced the proportion of herbivorous cladoceran biomass and increased the proportion of omnivorous and/or predatory copepod biomass, which may significantly increased the trophic position of zooplankton and lake herring, and leading to substantial increases in fish contaminant concentrations (Rennie et al. 2011).

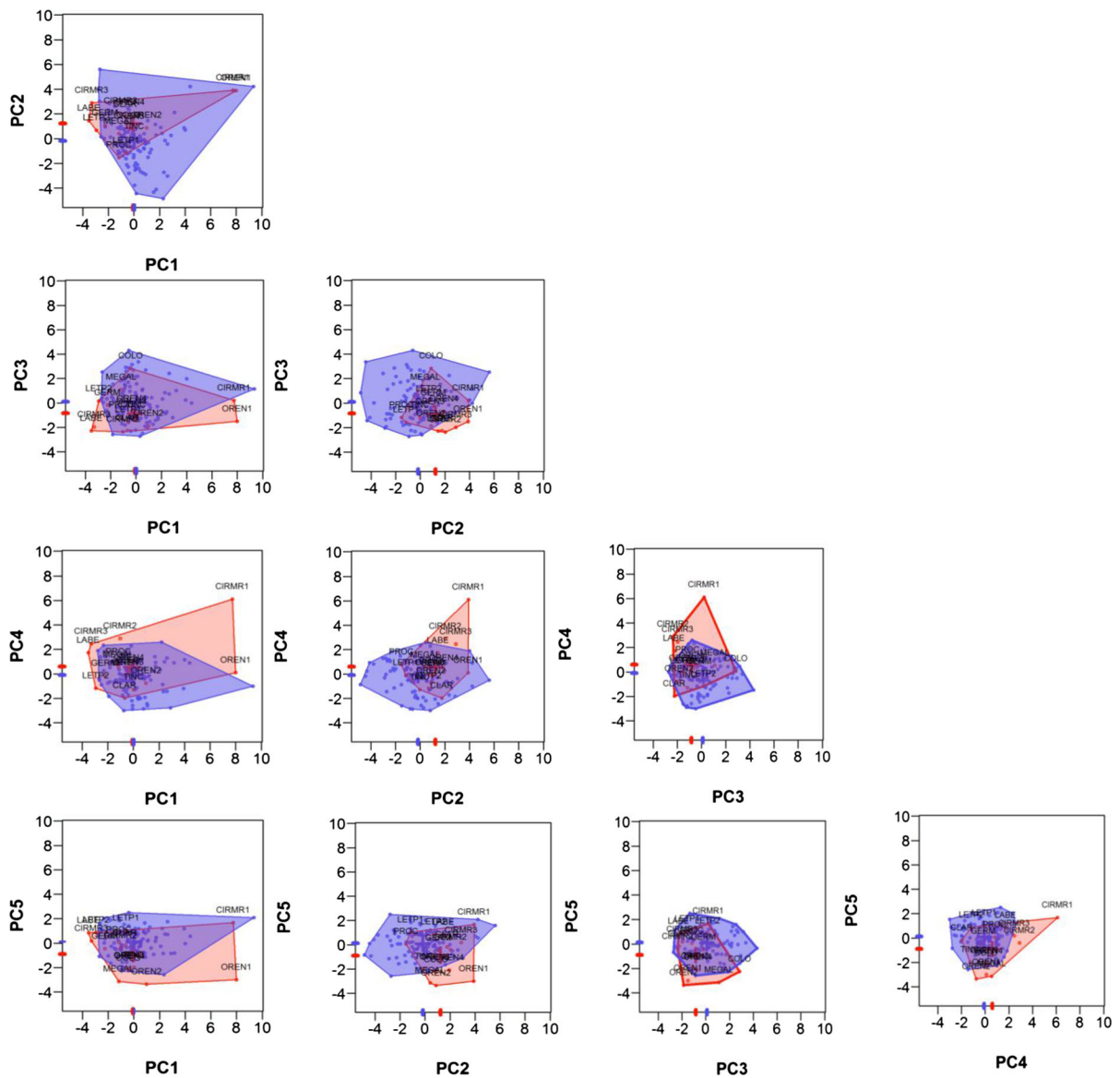


Fig. 4 Illustration of all the functional entities in the 5-dimensional functional space. Native entities are plotted in blue, non-native entities are plotted in red. All functional entities are plotted with circles. Projections of functional richness are illustrated by the colored areas. The cross represents the gravity

center of the functional space for native entities (blue) and non-native entities (red). Codes of functional entities are detailed in Table 1. “Code + no.” means different life stages; for instance, CIRM1 represents the juvenile of *Cirrhinus mrigala*

Those may ultimately affect the function of an ecosystem.

Much recent work on community assembly using trait based approaches has investigated the effects of biological invasions on the functional diversity of native communities at different spatial scales (Lambdon et al. 2008; Chabrierie et al. 2010; Monzon-Argueello et al. 2013; Matsuzaki et al. 2016). The

present study’s findings provided strong evidence that establishment of non-native fish species was accompanied by changes in the functional diversity patterns of the fish community, suggesting changes to the stability of the ecosystem of our studied area. Functional richness (FRic) displayed a hump-shape relationship to the invasion gradient and this can be explained by a gradual replacement of native entities

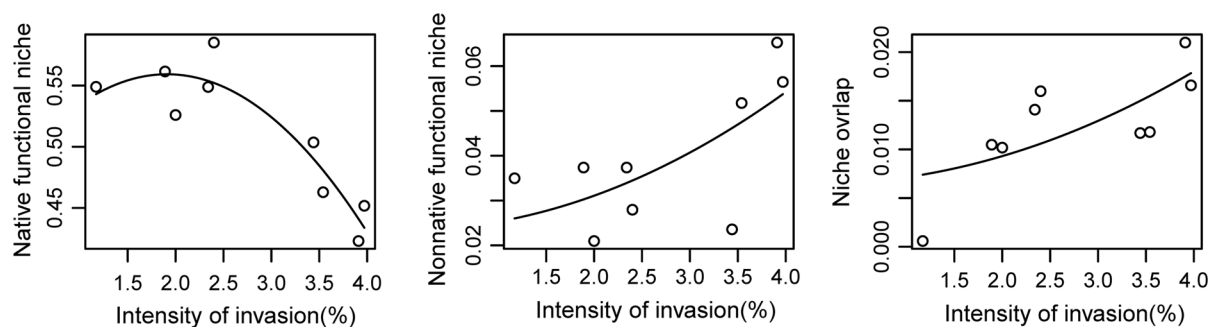


Fig. 5 Relationships between the intensity of biological invasion (%) and the functional niche size of native species, the functional niche size of non-native species, and the functional niche overlap between native and non-native species (details in Table 3)

Table 3 Results of linear models used to test the impact of biological invasion intensity on functional niche size

Response variable	Source of variation	Estimate (SE)	SE	P
Native niche	Intercept	0.451	0.07	< 0.001
	Intensity of invasion ²	−0.030	0.011	0.038
Non-native niche	Intercept	0.023	0.007	0.017
	Intensity of invasion ²	0.002	0.001	0.040
Niche overlap	Intercept	0.006	0.003	0.053
	Intensity of invasion ²	0.001	0.0002	0.036

Bold type represent significance at $p < 0.05$, based on a linear models with quadratic terms

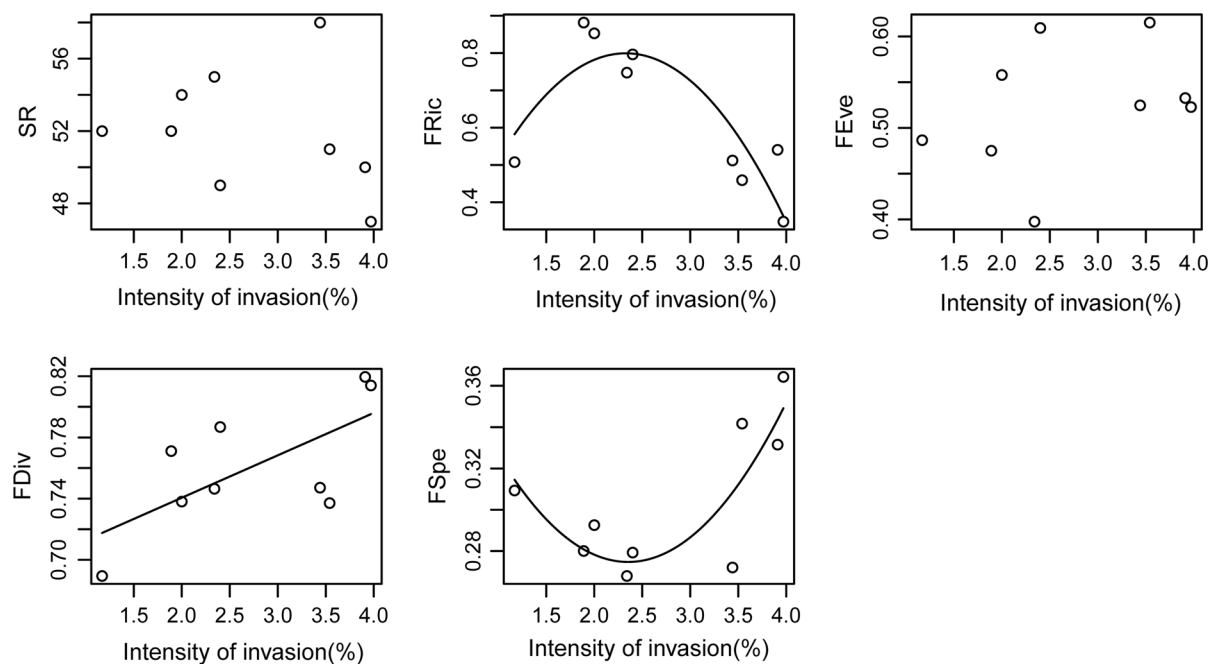


Fig. 6 Relationships between intensity of biological invasion (%), species richness and functional diversity indices (i.e. *SR* species richness, *FRic* functional richness, *FEve* functional

evenness, *FDiv* functional divergence, *FSpe* functional specialization); Solid and dashed lines represent significant and non-significant relationships, respectively (details in Table 4)

Table 4 Results of the linear models used to test the effects of the intensity of biological invasion on functional diversity indices

Response variables	Source of variation	Estimate (SE)	SE	<i>P</i>
SR	Intercept	43.98	10.85	0.007
	Intensity of invasion	7.88	8.76	0.403
	Intensity of invasion ²	− 1.62	1.61	0.354
FRic	Intercept	− 0.08	0.33	0.82
	Intensity of invasion	0.75	0.27	0.031
	Intensity of invasion ²	− 0.16	0.05	0.017
FEve	Intercept	0.46	0.07	< 0.001
	Intensity of invasion	0.02	0.02	0.385
FDiv	Intercept	0.69	0.033	< 0.001
	Intensity of invasion	0.03	0.012	0.047
FSpe	Intercept	0.43	0.07	< 0.001
	Intensity of invasion	− 0.13	0.05	0.049
	Intensity of invasion ²	0.03	0.01	0.029

Bold type represent a significant at $p < 0.05$, based on a linear models with quadratic terms

(which decrease in richness) by non-native species with unique functional traits (which increase in richness). These functional traits can be considered as the proxies for higher competitiveness and rapid adaptation in new environments following introduction, thus favoring the establishment of non-native species. For instance, we observed that tilapia is the most prominent non-native species, showing longer branch lengths in the functional dendrogram compared with native species. It displayed longer total gut length and larger fin area, which may facilitate higher digestive capacity (Karpouzi and Stergiou 2003), faster acceleration and greater maneuverability (Bellwood and Wainwright 2001) than native fish species. Besides, tilapia has tougher fins compared to native species, which means it has few natural predators. Functional divergence (FDiv) displayed a significant linear increase along the invasion gradient, suggesting that the proportional abundance of functional entities with extreme functional trait combinations should increase along the invasion gradient. Functional specialization (FSpe) displayed a U-shaped curve response to the invasion gradient, suggesting that the ecological function of the community tends to be specialized and homogenized with increasing invasion by non-native species, which may be detrimental to the stability of the ecosystem (Chabrerie et al. 2010).

Most important, in the sampled fish community species richness showed no obvious change with the invasion gradient, whereas several measures of functional diversity (i.e., functional richness, functional divergence and functional specialization) displayed a

significant change with the invasion temporal gradient. These findings suggest that the functional diversity index is sensitive when evaluating the effects of non-native species on a community compared with species richness (Mouillot et al. 2008). Species richness has some relationship with functional diversity, but it is not necessarily a positive relationship (Stuart-Smith et al. 2013). It is inappropriate to use any single diversity measure alone to assess the effects of biological invasions on a community. For instance, species richness indices implicitly assume that all species contribute equally to ecosystem functioning; however, these indices do not take into account biological identity and differences among species (Villéger et al. 2010; Matsuzaki et al. 2013). Following biological invasion, species richness at the local and regional scales will possibly increase when the number of non-native species greatly exceeds the number of native species that became extinct (Sax et al. 2002; Winter et al. 2009; Baiser and Lockwood 2011), while the function of the ecosystem will change due to changes in the functional traits of the species pool, which is difficult to reflect by species richness. Functional diversity, which is the value and range of functional traits of the organisms present in a given ecosystem, is considered to be an important determinant of ecosystem processes (Díaz and Cabido 2001; Petchey and Gaston 2002; Cadotte et al. 2011). Therefore, we can infer that using both functional and species richness indexes will be more accurate when assessing the influence of invasion on a community.

Overall, this study provided strong evidence that native and non-native fish were significantly different in their functional attributes in the Pearl River. The increased invasion of non-native species was accompanied by a change in functional diversity of the fish community which may have consequences for the stability of the ecosystem. Notably, this study provided empirical evidence that functional diversity was much more sensitive than species richness in response to biological invasions.

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