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RESEARCH

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Nile tilapia (*Oreochromis niloticus*) invasion impacts trophic position and resource use of commercially harvested piscivorous fishes in a large subtropical river

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Abstract

Background Although freshwater ecosystems cover less than 1% of the earth's surface, they support extremely high levels of biodiversity and provide vital ecosystem services. However, due to the introduction of non-native fishes, aquatic ecosystem functioning has been altered, and in some cases, declined sharply. Quantifying the impacts of invasive species has proven problematic. In this study, we examined the relative trophic position of native piscivorous fishes to estimate the effects of invasive Nile tilapia on food webs in the downstream sections of an invaded large subtropical river, the Pearl River, China. Furthermore, we quantified how native piscivorous fish diets changed as the Nile tilapia invasion progressed.

Results The trophic position of the widely distributed and locally important economically harvested piscivorous culter fish (*Culter recurviceps*), mandarinfish (*Siniperca kneri*), and catfish (*Pelteobagrus fulvidraco*) lowered significantly in the invaded Dongjiang River compared to an uninvaded reference Beijiang River. The lower trophic position of these piscivorous fishes was reflected by a major reduction in the proportion of prey fish biomass in their diets following the Nile tilapia invasion. Small fishes in the diet of culter fish from the reference river (33% small fishes, 17% zooplankton) shifted to lower trophic level zooplankton prey in the invaded river (36% zooplankton, 25% small fish), possibly due to the presence of Nile tilapia. Additionally, small fishes in the diet of mandarinfish in the reference river (46% small fishes, 11% aquatic insects) declined in the invaded river (20% aquatic insects, 30% small fishes). Similarly, the diet of catfish from the reference river shifted from fish eggs (25% fish eggs, 25% aquatic insects) to aquatic insects in the invaded river (44% aquatic insects, 5% fish eggs).

Conclusions The results of this study contributed to a growing body of evidence, suggesting that Nile tilapia can modify trophic interactions in invaded ecosystems. It is crucial to understand the processes outlined in this study in order to better assess non-native aquatic species, conserve the stability of freshwater ecosystems, and improve current conservation strategies in reaches of the Pearl River and other similar rivers that have experienced invasions of non-native species.

Keywords Nile tilapia, Invasion, Stable isotope ratio, Trophic position, Stable isotope mixing model

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Background

Although freshwater ecosystems cover less than 1% of the earth's surface, they support extremely high levels of biodiversity and provide vital ecosystem services, including providing rich fish products to humans (Lévéque et al.

2008). Freshwater ecosystems exhibit the greatest species richness per unit area of all ecosystems (Balian et al. 2008). However, due to global changes (e.g., global warming) and anthropogenic influences (e.g., urbanization, agriculture), aquatic ecosystem functionality has been drastically altered, and in some cases, declined sharply (Jenkins 2003). In fact, freshwater ecosystems are commonly considered to be one of the most endangered ecosystems on Earth (Dudgeon et al. 2006), owing primarily to the fact that they contain the highest extinction rates compared to other ecosystems (Michelan et al. 2010).

The introduction of non-native fishes for aquacultural and/or ornamental uses is widely regarded as a serious threat to freshwater ecosystem functions (Ehrenfeld 2010; Lockwood et al. 2011; Marr et al. 2010). Both directly and indirectly, invasive fishes affect a wide range of native organisms from zooplankton to mammals across multiple levels of biological organizations ranging from the genome to the ecosystem (Cucherousset and Olden 2011). A number of studies have reported that fish invasions can destabilize natural communities by altering food web structure and stability (Attayde et al. 2011; Eby et al. 2006; Goto et al. 2020). Although knowledge concerning how invasive species establishment drives changes in the trophic structure of native food webs remains poorly understood, it may potentially be an important aspect of global change caused by biological invasions (Wainright et al. 2021).

Quantitative predictions of trophic responses to non-native species invasions remain challenging because food web structures are variable and complex. In addition, invasive species often have varied diets, so they have greater potential to interact with a wide variety of co-occurring species (Polis and Winemiller 2013; Theoharides and Dukes 2007). Ongoing improvements in stable isotope technology have revolutionized this field and made it more feasible to assess invasive fish species effects on food web structure, and thus, improve understanding of the subsequent impacts on ecosystem functioning (Cardinale et al. 2012; González-Bergonzoni et al. 2020; Thompson et al. 2012; Whitinger et al. 2022). For instance, using stable isotopes, Vander-Zanden et al. (1999) first documented significant changes in the trophic positions of native lake trout (*Salvelinus namaycush*) following the invasion of two invasive fishes (*Micropterus dolomieu* and *Ambloplites rupestris*), caused a diet of shift from consuming littoral fishes to pelagic zooplankton. Baxter et al. (2004) suggested the invasion of rainbow trout (*Oncorhynchus mykiss*) predatorily consumed terrestrial prey that fell into the stream, causing native Dolly Varden charr (*Salvelinus malma*) to shift their diet towards aquatic insects, which resulted in the restructuring of stream and forest food webs. Non-native species invasion has also been shown to increase food chain length in aquatic ecosystems and threatening human health by elevating contaminant levels (e.g., heavy metals) in top predators (Vörösmarty et al. 2010).

Nile tilapia, which is native to Africa, grows rapidly and shows a range of biological responses to environmental conditions, including increased disease resistance and environmental tolerance (Attayde et al. 2011). Nile tilapia has been introduced to at least 100 countries and has become one of the most important aquaculture species in the world (Grammer et al. 2012; Martin et al. 2010). However, this species has established viable wild populations in most tropical and subtropical environments (Zengeya et al. 2013). Wild populations were first reported from Australia in the 1970s (Ovenden et al. 2015), and now exist in at least 114 countries (Deines et al. 2016). Tilapia species are currently one of the most widely distributed invasive fishes, second only to Asian carps (Rutten et al. 2004). In China, Nile tilapia was initially introduced into Hubei Province for aquaculture purposes in 1978. In 1979, Nile tilapia began to be farmed in Guangdong Province, with aquacultural practices developing rapidly throughout southern China (Fisheries and Fishery Administration Bureau of Ministry of Agriculture 2021; Yao and Ye 2014). Nile tilapia invasion can reduce local biodiversity and result in the extinction of native fish species due to competitive replacement (Figueredo & Giani 2005; Starling et al. 2002). Therefore, the establishment of Nile tilapia has detrimental effects on aquatic food web structure in native habitats (Attayde et al. 2011; Martin et al. 2010; Russell et al. 2012). In China, little attention has been paid to the negative effects of Nile tilapia introduction before 2000. The earliest survey record of Nile tilapia in the Pearl River was in 2006. Nile tilapia was found in all the sections from Sanshui of Xijiang River to Shilong of Liujiang River in the Pearl River basin. The lowest proportion of Nile tilapia was 0.15% in the Wuzhou section, while the highest proportion of Nile tilapia was 26.6% in the Dongjiang River. The ratio of Nile tilapia in Beijiang River was 0.95% (Tan et al. 2012). In 2014, Nile tilapia was officially listed as one of the world's top 100 invasive species in the list of non-native invasive species in China (https://www.mee.gov.cn).

The subtropical Pearl River is over 2400 km in length and is the largest river in southern China. It is characterized by an average annual temperature of 23 ℃, with a very expansive and diverse aquatic biological resource. The Pearl River supports high levels of biodiversity and is a popular area for global biodiversity research. The Pearl River supports 381 fish species, exhibits a high degree of endemism and a diverse gene pool (Lu 1990; Shuai et al. 2017). To restore and maintain fisheries stocks, fishing moratoria, including fishing bans during spawning seasons, were introduced in 2010. Since 2018, commercial fishing has been prohibited in the Pearl River basin from March through June annually. One of the most serious ecological issues in the Pearl River basin has been the invasion of Nile tilapia in some of its downstream tributaries (Gu et al. 2015; Shuai et al. 2019).

Although the top–down impacts of Nile tilapia invasions on ecosystems has gained much attention in recent years (Attayde et al. 2011; Córdova-Tapia et al. 2015; Russell et al. 2012), the ecological importance of this issue is still not fully understood how this species competes with native species for food resources or how this competition might impact the trophic structure of aquatic ecosystems. Trophic position, which represents the food resource utilization characteristics of organisms at the local scale, is a key property linking ecosystem functioning with species invasions (Thompson et al. 2012). In addition, trophic position is the most intuitive and accurately measured ecological index of food web change provided the baseline is accurately estimated (Post 2002).

In this study, our objectives were to (1) examine the relative trophic position of native piscivorous fishes to assess the effects of invasive Nile tilapia on food webs in the downstream sections of the Pearl River, China. Furthermore, we used stable isotope mixing models (SIMMs) to quantify how diets of native piscivorous fish changed as the Nile tilapia invasion progressed. We selected the widely distributed and locally important commercially harvested culter fish (Hainan culter [*Culter recurviceps*], pelagic habit), mandarinfish (bigeye mandarinfish [*Siniperca kneri*], mesopelagic habit), and catfish (yellow catfish [*Pelteobagrus fulvidraco*], demersal habit) as our representative native piscivorous fishes. (2) Utilizing a combination of long-term abundance monitoring data and stable isotope analyses, we addressed how invasion-induced trophic dynamics changed in downstream food webs. It is crucial to understand the processes outlined in this study, in order to better assess impacts of non-native aquatic species, conserve the stability of freshwater ecosystems, and improve current conservation strategies in the Pearl River.

Methods

Study area

The Dongjiang River, a tributary of the lower Pearl River, was selected as the treatment river (i.e., impacted by Nile tilapia), with a parallel tributary, the Beijiang River, selected as reference river. The two parallel tributaries, the Dongjiang River, and Beijiang River are similar geographically and exhibit similar environmental conditions (see Additional file 1: Table S1 for details). However, there is a significant Nile tilapia invasion in the Dongjiang River as a result of the prevalent aquaculture industry existing within the basin. In fact, the Nile tilapia alone accounts for about 13% of the total fish catch (Gu et al. 2015; Shuai et al. 2015). By comparison, the Nile tilapia population in the Beijiang River is relatively small and inconsequential, accounting for only about 4% of the total catch due to an underdeveloped aquaculture industry. A total of eight sampling sites (four in the invaded Dongjiang River and four in the reference Beijiang River) were established for this study (Fig. 1, Table 1). The distance between each sampling site is approximately 100 km.

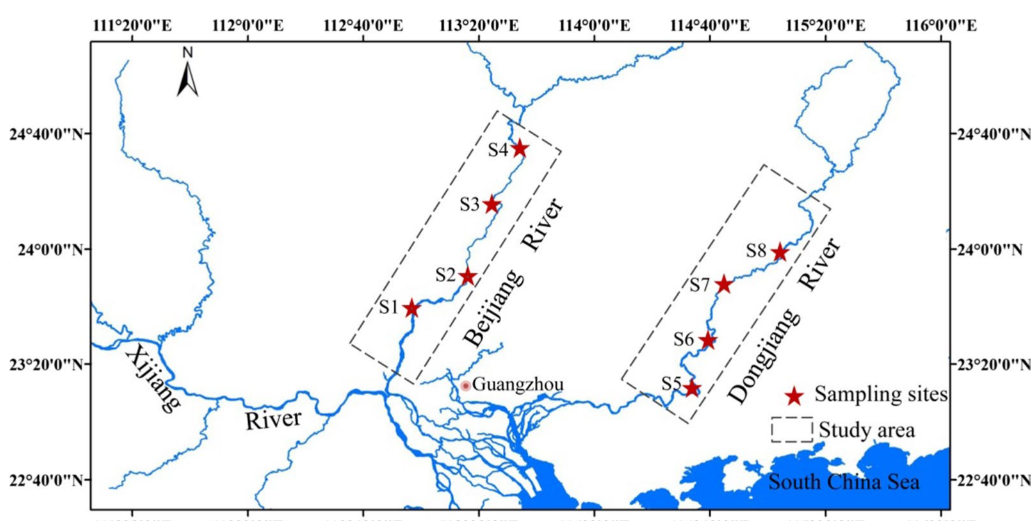

Fig. 1 Sampling sites within the Dongjiang and Beijiang rivers within the Pearl River basin, China

Table 1 The coordinates of sampling sites along the Pearl River basin

Sites	Name	Coordinates	Width (m)	Subordinate river
S1	Lubao	112°53′23″E, 23°20′53″N	791	Beijiang
S2	Shijiao	112°57′59″E, 23°33′41″N	882	Beijiang
S3	Qingyuan	113°3′49″E, 23°41′50″N	935	Beijiang
S4	Lianjiang	113°18′16″E, 24°1′29″N	635	Beijiang
S5	Hengli	114°36′55″E, 23°10′26″N	770	Dongjiang
S6	Guzhu	114°41′26″E, 23°30′25″N	462	Dongjiang
S7	Heyuan	114°42′45″E, 23°44′18″N	714	Dongjiang
S8	Huangtian	114°59′36″E, 23°53′17″N	341	Dongjiang

Sampling collection and preparation

Fishing is prohibited in the entire Pearl River basin from March to June annually and climate in the downstream stretches of the Pearl River basin is non-seasonal. Thus, fish community samples were collected twice during spring (January–February), summer (July–October) and autumn (November–December) at each sampling site annually from 2013 through 2021. Community sampling was conducted using a set of gillnets (length: 10 m, height: 2.5 m; mesh size: 20 mm), fishing hooks (a 20 m line with 50 attached hooks), and lobster pots (15 m in length and with a square mouth 18 cm) to reduce some selectivity effects. All sampled fishes were identified to species level and measured for total length (mm) and wet weight (g). Gillnet sets were distributed randomly at each sampling site. Sampling started in the afternoon (approx. 1800 and last 12 h for a whole night. Fish individuals captured with these three methods were immediately photographed, identified, logged and measured for body length and weight. Specimens that could not be immediately identified were labeled, fixed in 5% formalin and brought back to the laboratory for further examination. We used Sorensen similarity coefficient to analyze the similarity of the two communities (Pietsch et al. 2003).

Isotope sample collection was only done during summer 2020, to reduce seasonal effects. Stable isotopes were measured on at least six individuals per species per site in the treatment river except for rare species which total abundance < 5 individuals. For fish isotope sample collection, the white muscles were dissected from the upper side of the body adjacent to the dorsal fins and placed into 5-mL centrifuge tubes. Isotope samples for fish was limited to only adult individuals to reduce possible confounding effects of life stage on isotopic values (Rennie et al. 2009). Phytoplankton and zooplankton samples were collected using a 250-mm plankton net with zooplankton then filtered out using a 130-mm plankton net. Aquatic insects (e.g., mayflies and caddisflies) were collected with a small handmade net customized for scraping the bottom of the river. Benthic snails collected by hand and shrimp collected by lobster pots. Benthic snails and shrimp were placed in clean water for 24–48 h, the shell was then removed, and the muscle tissue was placed into a 5-mL centrifuge tube. Any attached benthic algae and leaves of aquatic plants were collected and washed along with the attached sediment in deionized water. Fish eggs and larvae were collected on spawning substrates, largely aquatic plants. All samples were stored in a mobile refrigerator at − 20 ℃ and brought to the laboratory for processing. In the laboratory, samples were dried to constant weight at 60 ℃, powdered, and stored in a dryer. Each sample contained at least six replicates and weighted between 0.5 and 1.0 mg.

Stable isotope analyses

Samples were wrapped in tin capsules (volume: 48-μL, Thermo Fisher Scientific, U.S.) and weighed using a microbalance (Sartorius Service, Göttingen, Germany) with an accuracy of 0.001 g. The C and N isotope analysis was conducted using a Finnigan Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS, Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.) and a Flash 2000 HT Elemental Analyzer (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.) using a Conflo IV interface (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, U.S.) (Shuai and Li 2022).

In this study, the trophic position of fishes was estimated relative to a primary "baseline" consumer given that basal trophic levels vary among seasons and rivers (Cabana and Rasmussen 1996). Consumer trophic position was estimated using the formula: Trophic $\text{position}_{\text{consumer}} = ((\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/3.4) + 2$, where 3.4 is the assumed increase in $\delta^{15}N$ per trophic level (Vander-Zanden and Rasmussen 1999). We chose snail (*Bellamya purificata*) as our baseline consumer as they were abundant in all rivers sampled and collected in sufficient numbers. In addition, *Bellamya purificata* is a long-lived species that integrates isotopic signatures over time, and therefore, would be superior to many other species as a baseline consumer (Post 2002). Our entire isotope analysis was based on the measurement of $\delta^{15}N$ and $\delta^{13}C$ signatures from 684 samples collected across the eight study sites in the Diongjiang and Beijiang rivers.

Diet analyses

Stomach contents were used to make preliminarily inferences on the diet of the representative fishes. Representative fish individuals ($n=30$ per site, 120 per river) were captured alive and measured to the nearest 1 mm (total length, TL). Diet analysis was conducted based on the contents in the upper portion of the gut to the first bend in the digestive tract. The stomach contents were removed from each individual and stored in 70% ethanol before being analyzed to identify the food source in the digestive tract. Stomach content analyses were mainly used to determine the composition of diet and correct the next isotope analysis. The prey fishes of each species are listed in Table 2.

Changes in the $\delta^{13}C$ or $\delta^{15}N$ signature of an organism indicate a change in food sources (Rennie et al. 2009; Vander-Zanden and Rasmussen 1999). To compare the feeding ecology of the three piscivorous fishes (i.e., culter fish, mandarinfish, and catfish) between the two rivers, we estimated the change of the potential contribution of food sources using a Bayesian Stable Isotope Mixing Model (SIMM) for R 3.5.3 (R Core Team 2019). SIMM was used to infer dietary proportions of organisms consuming various food sources from the stable isotope values taken from the organisms' tissue samples. SIMM is considered an upgrade of the Stable Isotope Bayesian Ellipses in R (SIBER or SIAR) model, which fits bivariate ellipses to stable isotope data using Bayesian inference with the goal of describing and comparing their isotopic niches. SIBER contains a slightly more sophisticated mixing model and uses a Just Another Gibbs Sampler (JAGS) algorithm to run the model (Parnell et al. 2013). The replicates for this model are the means of $\delta^{13}C$ and $\delta^{15}N$ isotope values among sites within a river. $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of the three piscivorous fishes were used in the model as consumers. Means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ information of small prey fishes, fish eggs, crustaceans, aquatic insects, zooplankton, snails, and aquatic plants were incorporated into the model as source means and source variance data. Default values (NULL) were used for other parameters in the model (e.g., concentration and correction coefficients). Gelman–Rubin convergence diagnostics were conducted to test whether the model ran properly, with Gelman diagnostic values near 1.0 indicating that the model ran sufficiently. The posterior distribution for each source was reported as 95% confidence intervals. The combination netting provided catch-per-unit-effort (CPUE, fish per net per day), estimates of relative densities of the piscivorous fishes (i.e., culter fish, mandarinfish, and catfish), and their prey. Spearman's correlation coefficients were used to assess the changes in fish abundance over time. All analyses were conducted using R Statistical Software, version 3.3.1 (R Core Team 2019). Variables were considered statistically significant at $P < 0.05$.

Results

Fish community structure and variation

A total of 10,623 individual fishes belonging to 74 taxa, 20 families, and seven orders were sampled during the present study in the invaded Dongjiang River. Of these, 66 were native species and eight were non-native species. Cyprinids were the most dominant species, and accounted for 59% of total number of species collected. Of the eight non-native species, Nile tilapia was the most abundant, accounting for 13% of all individuals collected in the Dongjiang River (Table 2). Abundances of all other non-native species was relatively low. In the reference Beijiang River, a total of 10,288 fishes belonging to 77 taxa, 17 families, and seven orders were collected. Of these species, 71 were native and six were non-native. Cyprinids also were the most dominant species, and accounted for 62% of the total number of species collected. The abundance of all the non-native species was relatively low in this river, with Nile tilapia only accounting for about 4.5% of all individuals collected (Table 2). The Sorensen similarity index of the two communities is 0.71, indicating that the species composition of the two communities is very similar.

The main piscivorous fish in the Dongjiang and Beijiang River are culters, mandarinfish, and catfishes. These fishes are the most common and widely distributed fishes in the lower tributaries of the Pearl River basin. Moreover, the relative abundance of these three piscivorous fishes has remained relatively stable over time in the reference Beijiang River, while culter fish (Rs, two-tailed $P<0.01$, Fig. 2a) and catfish (Rs, two-tailed $P<0.005$, Fig. 2c) abundance decreased significantly in the invaded Dongjiang River. This is especially noteworthy given that the number of prey fish species had not varied through time in either the invaded or reference rivers (Fig. 2d–f). Finally, the relative densities of prey fishes of the three piscivorous fishes also did not vary through time in the reference Beijiang River, while all prey species for the three piscivorous fishes decreased significantly through time in the invaded Dongjiang River (Rs, two-tailed $P<0.05$, Fig. 2g–i).

For the three piscivorous fishes, there was no significant difference in the number of prey fish species in the invaded Dongjiang River and the reference Beijiang River (Fig. 3a). However, catch data revealed that there were significantly lower catch rates (as fish per net per day) of prey fishes for culter fish ($t=6.705$, $d.f.=62$, $P<0.05$), mandarinfish ($t=5.009$, $d.f.=62$, $P<0.001$), and catfish ($t=6.452$, $d.f.=62$, $P<0.05$) in the invaded Dongjiang

Table 2 Fish community structure in the Dongjiang and Beijiang rivers within the Pearl River basin, China

Species	English name	Percentage (%)		Feeding habit	Category	Prey fish
		Beijiang	Dongjian			
Cypriniformes						
Cyprinidae						
Squalidus argentatus	Chub	19.28	8.04	I	N;RL	Ca
Hemiculter leucisculus	Common sawbelly	15.05	17.63	O	N;SE	Cu
Cirrhinus molitorella	Mud carp	4.06	12.31	H	N;RL	Ma
Culter recurviceps	Hainan culter	3.70	0.85	P	N;SE	
Pseudohemiculter dispar		3.59	0.37	O	N;SE	Cu
Zacco platypus	Pale chub	3.45	0.09	O	N;SE	Ca
Squalidus wolterstorffi	Dot chub	3.22	0.08	I	N;RL	Ca
Squaliobarbus curriculus	Barbel chub	2.91	1.52	O	N;RL	Cu
Abbottina rivularis	Amur false gudgeon	2.62	0.02	O	N;SE	Cu
Cyprinus carpio	Carp	1.92	1.51	O	N;SE	Ma
Carassius auratus	Goldfish	1.82	2.55	O	N;SE	Ma
Megalobrama terminalis	Black amur bream	1.69	5.47	O	N;RL	Cu, Ma
Saurogobio dabryi	Longnose gudgeon	1.94	4.79	I	N;RL	Ca
Cirrhinus mrigala	Mrigal carp	1.29	1.07	O	Non;SE	Ma
Hemibarbus labeo		1.29	0.71	O	N;SE	Ca
Hemibarbus maculatus		1.20	1.14	O	N;SE	Ca
Hypophthalmichthys molitrix	Silver carp	1.14	1.50	PL	N;RL	Cu
Opsariichthys bidens	Chinese hooksnout carp	1.07	0.93	I	N;SE	Ca
Culter dabryi	Dashi culter	1.05		P	N;SE	
Sarcocheilichthys parvus		0.91		O	N;SE	
Ctenopharyngodon idellus	Grass carp	0.80	0.81	H	N;RL	Ma
Aristichthys nobilis	Bighead carp	0.75	0.38	PL	N;RL	Cu
Platysmacheilus exiguus		0.71		I	N;RL	
Rhodeus sinensis	Light's bitterling	0.58		O	N;SE	
Sinibrama wui	Bigeye bream	0.40	0.09	O	E;RL	Cu
Xenocypris davidi	Yellow tailed xenocypris	0.35	2.28	H	N;RL	Ma
Onychostoma gerlachi	Largescale shoveljaw fish	0.29		H	N;SE	
Hemiculterella wui		0.28		O	E;SE	
Puntius semifasciolatus	Chinese barb	0.26		O	N;SE	
Acrossocheilus beijiangensis		0.13		H	N;SE	
Osteochilus salsburyi		0.11	1.01	O	N;SE	Ma
Parabramis pekinensis	White bream	0.10	0.06	H	N;RL	Cu
Xenocypris argentea	Silver xenocypris	0.10	0.04			Ma
Culter alburnus	Topmouth culter	0.08	0.57	P	N;SE	
Culter hypselonotus	Bigeye culterfish	0.07	+	p	N;SE	
Megalobrama amblycephala	Wuchang fish	0.05	0.02	O	N;RL	
Distoechodon tumirostris	Round mouth	0.05	0.02	H	N;RL	Ma
Acheilognathus tonkinensis	Vietnamese bitterling	0.03	0.66	O	N;SE	Cu
Sinibrama melroseib	Hainan bream	0.02	0.06	O	N;SE	Cu
Mylopharyngodon piceus	Black carp	0.02	0.01	I	N;RL	
Acrossocheilus parallens		0.02		H	N;SE	
Acrossocheilus labiatus		0.02		H	N;SE	
Acrossocheilus stenotaeniatus		0.02		H	N;SE	
Elopichthys bambusa	Yellow cheek carp	0.02		P	N;RL	
Acheilognathus macropterus	Largefin bitterling	0.02		O	N;SE	
Rectoris posehensis		0.01		H	N;SE	

Table 2 (continued)

Species	English name	Percentage (%)		Feeding habit	Category	Prey fish
		Beijiang	Dongjian			
Cyprinus carpio var.*specularis*	German mirror carp	0.01		O	N;SE	
Labeo rohita	Roho labeo	0.10		D	Non;SE	
Huigobio chenhsienensis	Huigobio gudgeon		+	I	N;RL	
Pseudogobio vaillanti			0.08	I	N;RL	
Acheilognathus chankaensis	Khanka spiny bitterling		0.26	O	N;SE	
Sarcocheilichthys nigripinnis			0.15	O	N;SE	
Garra orientalis	Oriental sucking barb		0.04	H	N;SE	
Pseudolaubuca sinensis			0.03	PL	N;SE	
Pseudorasbora parva	Stone moroko		0.02	O	N;SE	
Tinca tinca	Tench		0.02	O	Non;SE	
Spinibarbus denticulatus			0.02	O	N;RL	
Gobiobotia meridionalis			0.02	I	E;SE	
Rhodeus spinalis Oshima			0.01	O	N;SE	
Parasinilabeo assimilis			0.01	H	N;SE	
Cobitidae						
Misgurnus anguillicaudatus	Oriental weatherfish	4.06	3.53	D	N;SE	Ca
Micronoemacheilus pulcher		0.21	0.08	D	N;SE	Ca
Cobitis sinensis	Siberian spiny loach	0.01	0.38	I	N;SE	Ca
Homalopteridae						
Vanmanenia hainanensis			0.01	I	E;SE	
Perciformes						
Cichlidae						
Oreochromis niloticus	Nile tilapia	4.52	13.07	O	Non;SE	
Tilapia zillii	Zillii tilapia	0.32	0.17	O	Non;SE	
Serranidae						
Lateolabrax japonicus	Spotted sea bass	1.20		I	N;RS	
Siniperca kneri	Bigeye mandarinfish	0.34	0.05	P	N;SE	
Siniperca scherzeri	Spotted mandarinfish	0.16		P	N;SE	
Channidae						
Channa asiatica	Chinese snakehead	0.02	0.27	P	N;SE	
Channa maculata	Taiwan snakehead	0.01	0.18	P	N;SE	
Channa argus	Snakehead	0.01		P	N;SE	
Eleotridae						
Eleotris oxycephala	Sharphead sleeper	0.49	0.20	I	N;SE	Ca
Hypseleotris hainanensis			0.01	I	N;SE	
Gobiidae						
Rhinogobius giurinus	Amur goby	0.17	1.74	I	N;SE	Ca
Glossogobius giuris	Tongue goby		2.67	I	N;SE	Ca
Anabantidae						
Anabas testudineus	Climbing perch		0.01	O	Non;SE	
Mastacembelidae						
Mastacembelus armatus	Tire track eel	0.41	0.55	I	N;SE	
Siluriformes						
Bagridae						
Pelteobagrus fulvidraco	Yellow catfish	1.43	0.70	I	N;SE	
Pelteobagrus vachelli	Darkbarbel catfish	1.27	1.48	I	N;SE	
Leiocassis crassilabris	Ussuri catfish	1.07	0.02	I	N;SE	
Mystus guttatus	Spotted longbarbel catfish	0.54	0.38	I	N;SE	

Table 2 (continued)

Species	English name	Percentage (%)		Feeding habit	Category	Prey fish
		Beijiang	Dongjian			
Leiocassis argentivittatus		0.25	0.34	I	N;SE	
Mystus macropterus	Largefin longbarbel catfish	0.01		I	N;SE	
Leiocassis virgatus	Striped catfish		0.37	I	N;SE	
Sisoridae						
Glyptothorax fukiensis			0.09	I	N;SE	
Ictaluridae						
Ictalurus punctatus	Channel catfish		0.08	I	Non;SE	
Clariidae						
Clarias fuscus	Oriental catfish	0.08	0.65	O	N;SE	
Clarias gariepinus	Fuscous catfish	0.01	0.18	O	Non;SE	
Siluridae						
Silurus asotus	Catfish	0.36	0.18	P	N;SE	
Loricariidae						
Hypostomus plecostomus	Suckermouth catfish	0.05	0.05	O	Non;SE	
Clupeiformes						
Clupeidae						
Clupanodon thrissa	Chinese gizzard shad	0.19		PL	N;RS	
Konosirus punctatus	Dotted gizzard shad	0.05		PL	N;RS	
Engraulidae						
Coilia grayii	Gray's grenadier anchovy	2.60	3.20	I	N;SE	Cu
Anguilliformes						
Anguillidae						
Anguilla japonica	Japanese eel		0.03	P	N;RS	
Synbranchiformes						
Synbranchidae						
Monopterus albus	Finless eel	0.08	0.06	I	N;RS	
Characiformes						
Anostomidae						
Prochilodus scyofa		0.17	0.01	O	Non;SE	
Tetraodontiformes						
Tetraodontidae						
Takifugu ocellatus	Ocellated puffer	+		I	N;RS	

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, *Cu* prey fish of culter fish, *Ma* prey fish of mandarinfish, *Ca* prey fish of catfish

River compared to the reference Beijiang River (Fig. 3b, Table 3).

Changes in trophic position of piscivorous fishes post-Nile tilapia invasion

The trophic position of the three piscivorous fishes was also lower in the invaded river compared to the reference river (Fig. 4a). The trophic position of culter fish averaged 3.91 in the invaded Dongjiang River, which was significantly lower than 4.62 in the Beijiang River ($t=-2.46$, $d.f.=46$, $P=0.03$). Similarly, the trophic position of mandarinfish averaged 4.13 in the invaded Dongjiang River compared to 5.11 in the Beijiang River ($t=-3.31$, $d.f.=46$, $P=0.008$). Finally, the trophic position of catfish averaged 3.40 in the invaded Dongjiang River, which was significantly lower than 4.33 in the reference Beijiang River ($t=-2.567$, $d.f.=46$, $P=0.03$).

The $\delta^{13}C$ signatures provide additional evidence for food web structural differences between the invaded and reference rivers. The $\delta^{13}C$ values for culter fish from the reference river averaged − 26.95%, indicative of reliance on small prey fishes. By comparison, $\delta^{13}C$ values in culter fish from invaded rivers was − 29.01%, which indicated greater use of zooplankton prey at lower trophic levels ($t=3.355$, $d.f.=46$, $P<0.01$, Table 4). As with culter fish, $\delta^{13}C$ values

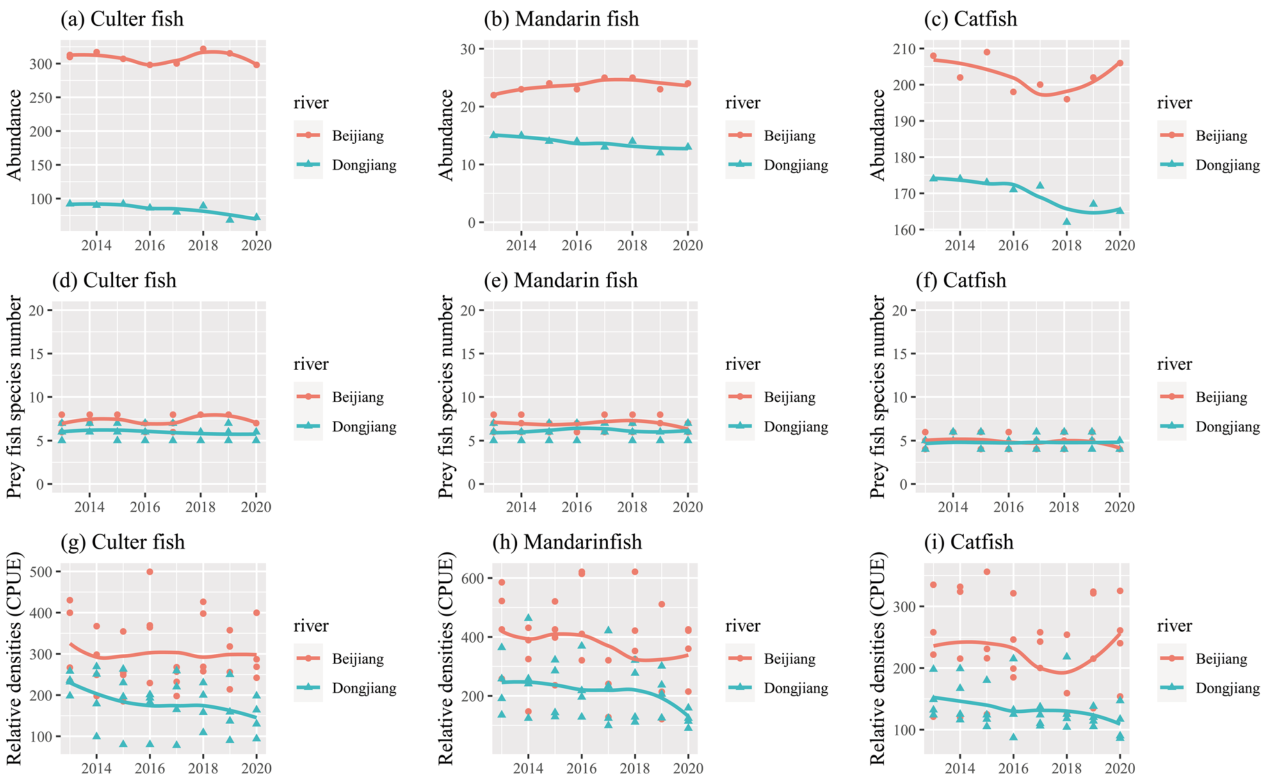

Fig. 2 Temporal dynamics of three piscivorous fishes (culter fish [*Culter recurviceps*], mandarinfish [*Siniperca kneri*], catfish [*Pelteobagrus fulvidraco*] and their prey fishes. **a** Abundance of culter fish, **b** abundance of mandarinfish, **c** abundance of catfish, **d** species number of culter fish prey fishes, **e** species number of mandarinfish prey fishes, **f** species number of catfish prey fishes, **g** relative abundance (CPUE, g per net per day) of culter fish prey fishes fish, **h** relative abundance (CPUE) of mandarinfish prey fishes, **i** relative abundance (CPUE) of catfish prey fishes in the Dongjiang and Beijiang rivers from 2013 to 2020

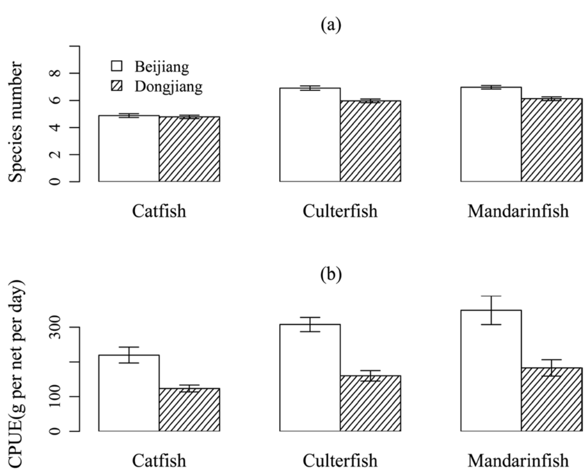

Fig. 3 Prey fish data of the three piscivorous fishes from the invaded and reference rivers (mean ± SD). **a** Comparison the number of prey fish species, **b** comparison of the relative densities (i.e., CPUE, g) of prey fishes caught in each net each day

for mandarinfish from the reference river averaged − 25.21%, which also indicated small fishes as their main food source. Conversely, $\delta^{13}C$ values from the invaded rivers were − 28.13%, indicating greater use of zooplankton and aquatic insects ($t = 3.840$, $d.f. = 46$, $P < 0.05$, Table 4). Finally, $\delta^{13}C$ values in catfish from the reference river averaged − 25.32% compared to − 27.43% in the invaded river, which also indicated significant differences in food resource use between rivers ($t = 6.003$, $P < 0.01$, Table 4).

SIMMs using food source data indicated that the diets of culter fish from the reference river averaged 33% small fishes and 17% zooplankton, compared to only 25% small fish and 36% zooplankton in the invaded river (Fig. 5a, b). The diet of mandarinfish from the reference river averaged 46% small fishes and 10% aquatic insects, which compared to 30% small fishes and 20% aquatic

Table 3 Prey fish data of three piscivorous fish in invaded Dongjiang River and the reference Beijiang River

Species	River	Site	Mean no. of prey species (SD)	Mean prey catch rate as grams per net per day (SD)
Culter fish				
	Dongjiang			
		Hengli	5.25 (0.46)	184.00 (63.79)
		Guzhu	6.13 (0.64)	196.75 (65.60)
		Heyuan	6.63 (0.52)	204.88 (48.94)
		Huangtian	5.88 (0.64)	138.00 (50.55)
		Mean	5.97 (0.57)	180.91 (60.82)
	Beijiang			
		Lubao	7.00 (0.93)	317.13 (105.29)
		Shijiao	7.00 (1.19)	302.75 (75.84)
		Qingyuan	6.87 (0.83)	303.50 (65.26)
		Lianjiang	6.75 (0.89)	276.12 (78.25)
		Mean	6.91 (0.12)	299.88 (79.84)*
Mandarinfish				
	Dongjiang			
		Hengli	6.63 (0.52)	243.13 (128.77)
		Guzhu	6.50 (0.76)	175.50 (80.46)
		Heyuan	6.13 (0.35)	229.88 (99.40)
		Huangtian	5.25 (0.46)	213.38 (95.67)
		Mean	6.42 (0.26)	215.47 (100.84)
	Beijiang			
		Lubao	7.00 (0.76)	483.88 (116.46)
		Shijiao	7.25 (0.71)	334.25 (170.95)
		Qingyuan	7.13 (0.83)	315.88 (79.78)
		Lianjiang	6.50 (0.53)	306.88 (125.04)
		Mean	6.97 (0.33)	369.56 (141.87)**
Catfish				
	Dongjiang			
		Hengli	4.5 (0.76)	129.38 (26.65)
		Guzhu	5.25 (0.70)	150.00 (37.99)
		Heyuan	4.88 (0.64)	134.38 (45.34)
		Huangtian	4.5 (0.53)	118.00 (25.42)
		Mean	4.78 (0.36)	132.94 (35.11)
	Beijiang			
		Lubao	5.00 (0.76)	231.38 (95.89)
		Shijiao	5.38 (0.92)	246.12 (55.81)
		Qingyuan	4.88 (0.64)	211.00 (75.08)
		Lianjiang	4.25 (0.46)	221.38 (79.03)
		Mean	4.88 (0.47)	227.47 (75.07)*

*$0.01 < P \leq 0.05$

insects in the invaded river (Fig. 5c, d). SIMMs indicated that catfish diets from the reference river averaged 25% fish eggs and 25% aquatic insects, which compared to only 5% fish eggs and 44% aquatic insects in the invaded river (Fig. 5e, f).

Discussion

This is the first study to estimate how the invasion of Nile tilapia affects the feeding habits and trophic position of native species. We provided strong evidence of a diet shift and a decline in trophic position of three fish

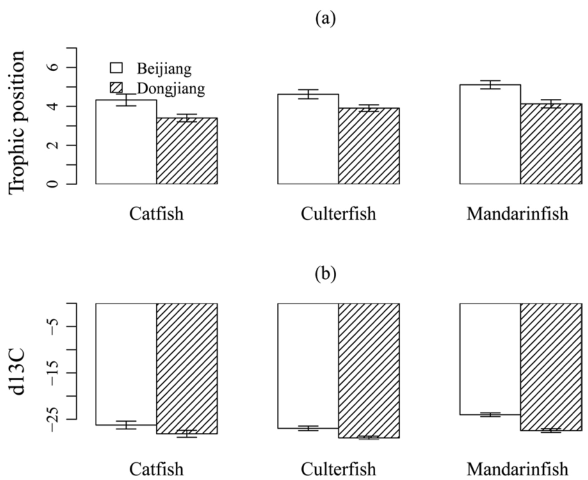

Fig. 4 Trophic position and $\delta^{13}C$ values (mean + SD). **a** Comparison of mean trophic position of piscivorous culter fish, mandarinfish, and catfish from invaded and reference rivers. **b** Comparison of mean $\delta^{13}C$ values of piscivorous culter fish, mandarinfish, and catfish from invaded and reference rivers

piscivores in the invaded Dongjiang River. These observations also coincided with apparent changes in prey availability. The trophic position of culter fish, mandarinfish, and catfish in the invaded Dongjiang River, was significantly lower than in the reference Beijiang River. Compared with the reference river, the invasive Nile tilapia forced other fish to reduce the consumption of small fish and fish eggs, and increasingly rely on zooplankton and aquatic insect resources in the tropical river.

This dietary shift was accompanied by a prolonged reduction in the abundance of native fish species. The sampling data showed that the relative densities of native prey fishes decreased significantly through time in the invaded Dongjiang River. Previous studies have documented that increases of Nile tilapia in rivers affect the native species CPUE and the overall fish community structure (Gu et al. 2015). These effects often involve the most abundant native species, including mud carp (*Cirrhinus molitorella*), black amur bream (*Megalobrama terminalis*), barbel chub (*Squaliobarbus curriculus*) and common sawbelly (*Hemiculter leucisculus*) (Shuai et al. 2019). The larvae of these fishes are important food sources for top piscivores. A significant reduction in the CPUE of other commercially important species also was observed post-introduction of Nile tilapia in a northeastern Brazil reservoir (Attayde et al. 2011). In fact, there is often substantial diet overlap between Nile tilapia and native fishes in most tropical and subtropical systems (Henson et al. 2016). In the current 9-year study in the Pearl River basin, native fish densities decreased with increasing Nile tilapia density. In addition, progressive decreases in body size of native fishes (e.g., fish plumpness, body length, and body weight) coincided with the increasing prevalence of Nile tilapia in the basin (Shuai et al. 2019). We interpret this observation as increased competition between Nile tilapia and local native species for food resources.

Trophic position stability is considered to be an important variable in the structural stability of food webs (Rennie et al. 2011; Thomsen et al. 2014). Analyzing trophic position variation can be helpful in detecting the effects of invasive fish species on the structure of food webs and understanding subsequent impacts on ecosystem functioning (Cardinale et al. 2012; Thompson et al. 2012). Stable trophic position of predators and prey typify stable food webs (Johnson et al. 2014), while trophic dispersion implies variability in trophic position (i.e., trophic instability). In this study, the Nile tilapia invasion appeared to induce significant trophic dispersion, thereby disrupting trophic positions and destabilizing food webs of the impacted aquatic community in the Dongjiang River. We documented that native top fish piscivores increasingly shifted from small fishes to zooplankton and aquatic insects as the invasion of Nile tilapia proceeded. This invasion appeared to have destabilized food webs and facilitated the transition to a Nile tilapia-dominated fish community. Given that food web instability is a precursor to ecological state change (Rooney and McCann 2012), biological invasions are likely to produce alternative ecological states (Scheffer and Carpenter 2003). In the case of this Nile tilapia invasion, it is probable that these food web changes ultimately produced a new ecological regime in the Dongjiang River (Wainright et al. 2021).

These results demonstrated how invasive Nile tilapia initiated disruption of native food webs through trophic displacement that ultimately impacts ecosystem stability. Results of this study further provide a basis for understanding and predicting the directional effects of invasive species on recipient food webs. Trophic changes due to fish invasions also can exhibit biotic homogenization through trophic downgrading (Singh 2021). For example, the invasion of lake trout (*Salvelinus namaycush*) into the northern Rocky Mountains, USA increased fish diet variability, disrupted food webs by reorganizing macro-invertebrate communities, and displaced native fishes from their baseline dietary state (Wainright et al. 2021). Similarly, the invasion of dreissenid mussels, including the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostiformus bugensis*) into the Great Lakes, USA-Canada caused commercially harvested native whitefish (*Coregonus clupeaformis*) to become more

Table 4 Trophic position, $\delta^{13}C$ and mixing-model results (numbers in parentheses are SDs)

Species	River	Trophic position (± SD)	Prey fish trophic position (± SD)	$\delta^{13}C$ (‰) (± SD)	Prey fish $\delta^{13}C$ (‰) (± SD)	Diet (%) (± SD)				
Culter fish						Small fish	Crustacean	Aquatic insects	Zooplankton	Phytoplankton
	Beijiang									
	Lubao	4.40 (0.43)	4.47 (0.19)	− 26.08(0.63)	− 24.23 (1.83)					
	Shijiao	4.35 (0.29)	2.59 (0.71)	− 26.72(0.45)	− 25.96 (0.62)					
	Qingyuan	4.62 (0.15)	4.62 (0.38)	− 27.19(2.12)	− 26.72 (0.97)					
	Lianjiang	4.89 (0.10)	4.17 (0.40)	− 25.69(0.96)	− 24.86 (0.24)					
	Mean	4.57 (0.24)	3.96 (0.42)	− 26.95(1.28)	− 25.16 (1.28)	32.7(0.21)	20.9(0.15)	13.0(0.10)	17(0.13)	16.5(0.13)
	Dongjiang									
	Hengli	4.12 (0.17)	4.89 (0.17)	− 28.17(0.52)	− 25.16 (1.49)					
	Guzhu	3.94 (0.33)	2.62 (0.85)	− 28.54(0.93)	− 25.51 (3.76)					
	Heyuan	3.89 (0.35)	3.67 (0.41)	− 29.72(0.71)	− 28.03 (1.17)					
	Huangtian	3.90 (0.17)	3.98 (0.42)	27.88(0.63)	− 23.25 (4.10)					
	Mean	3.96 (0.26)	3.79 (0.46)	− 29.01(0.10)	− 25.46 (2.87)	25.5(0.23)	12.7(0.12)	11.9(0.10)	36.3(0.24)	13.6(0.12)

Species	River	Trophic position (± SD)	Prey fish trophic position (± SD)	$\delta^{13}C$ (‰) (± SD)	Prey fish $\delta^{13}C$ (‰) (± SD)	Diet (%) (± SD)					
Mandarinfish						Small fish	Crustacean	Aquatic insects	Zooplankton	Snail	Aquatic plants
	Beijiang										
	Lubao	4.94 (0.06)	3.77 (1.19)	− 24.14(1.09)	− 23.90 (1.07)						
	Shijiao	5.22 (0.41)	2.69 (0.42)	− 27.20(0.31)	− 24.62 (0.33)						
	Qingyuan	5.13 (0.60)	4.69 (0.30)	− 25.08(1.41)	− 23.78 (0.86)						
	Lianjiang	4.72 (0.10)	4.42 (0.55)	− 26.28(3.11)	− 24.18 (0.01)						
	Mean	5.00 (0.29)	3.89 (0.62)	− 25.21(2.07)	− 24.03 (0.78)	46.7(0.15)	13.6(0.11)	10.4(0.08)	4.5(0.05)	12.1(0.10)	12.8(0.10)
	Dongjiang										
	Hengli	4.31 (0.26)	3.89 (0.24)	− 26.38(1.72)	− 22.82 (3.67)						
	Guzhu	4.09 (0.45)	3.67 (0.50)	− 27.33(3.07)	− 26.11 (3.98)						
	Heyuan	3.91 (0.12)	2.79 (1.49)	− 28.35(1.63)	− 26.02 (0.19)						
	Huangtian	4.15 (0.11)	3.11 (0.43)	− 29.65(0.71)	− 26.27 (0.53)						
	Mean	4.11 (0.24)	3.37 (0.59)	− 28.13(1.84)	− 25.21 (3.29)	29.9(0.22)	8.21(0.07)	20.3(0.17)	17.9(0.18)	8.9(0.08)	14.7(0.13)

Table 4 (continued)

Species	River	Trophic position (± SD)	Prey fish trophic position (± SD)	$\delta^{13}C$ (‰) (± SD)	Prey fish $\delta^{13}C$ (‰) (± SD)	Diet (%) (± SD)					
Catfish						Small fish	Crustacean	Aquatic insects	Fish eggs	Snail	Aquatic plants
	Beijiang										
	Lubao	4.37 (0.13)	3.67 (1.14)	− 25.10(1.08)	− 23.13 (0.58)						
	Shijiao	4.76 (0.52)	4.25 (0.26)	− 26.62(1.25)	− 24.96 (0.02)						
	Qingyuan	4.28 (1.29)	3.40 (0.57)	− 24.37(0.15)	− 23.34 (0.13)						
	Lianjiang	4.22 (1.23)	3.89 (0.12)	− 25.95(1.32)	− 24.62 (0.33)						
	Mean	4.41 (0.79)	3.80 (0.52)	− 25.32(0.98)	− 24.95 (1.09)	12.9(0.12)	8.9(0.06)	24.8(0.18)	25.1(0.14)	11.4(0.10)	17.1(0.14)
	Dongjiang										
	Hengli	3.49 (0.10)	3.24 (0.41)	− 27.52(2.00)	− 24.64 (2.79)						
	Guzhu	3.55 (0.21)	4.31 (0.29)	− 27.08(0.66)	− 25.68 (1.50)						
	Heyuan	3.04 (0.12)	3.52 (0.11)	− 26.98(0.12)	− 24.32 (2.28)						
	Huangtian	3.79 (0.09)	3.79 (0.09)	− 27.67(0.18)	− 26.01 (2.01)						
	Mean	3.47 (0.13)	3.72 (0.23)	− 27.43(0.99)	− 24.10 (1.83)	9.8(0.07)	12.7(0.11)	43.5(0.17)	4.8(0.03)	13.2(0.11)	15.9(0.14)

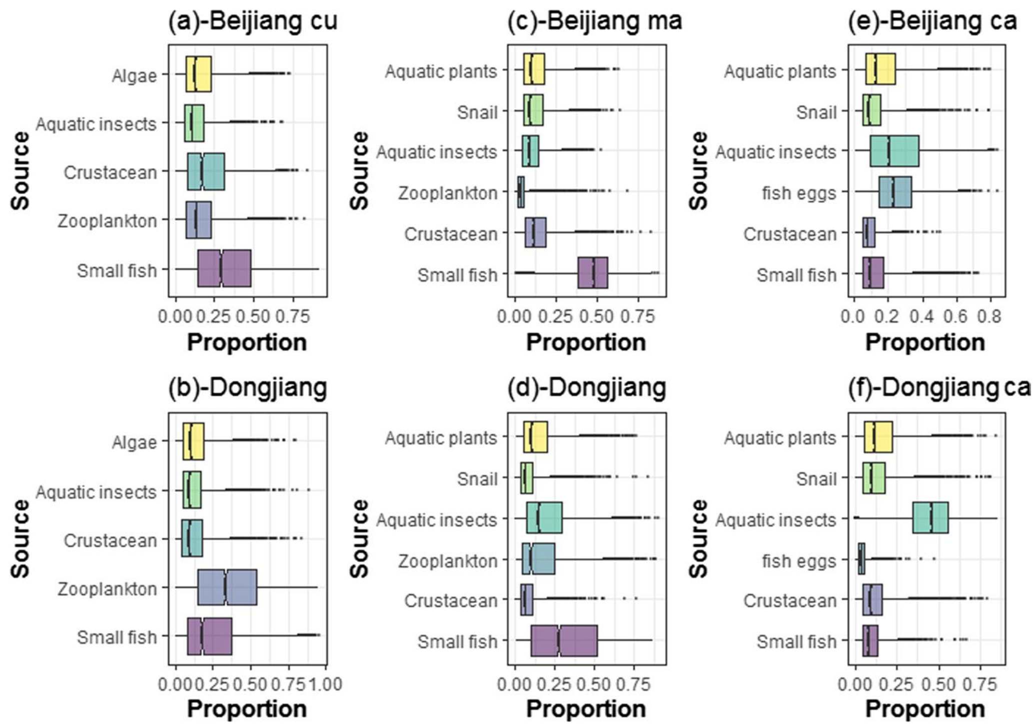

Fig. 5 Food resource structure of uninvaded and invaded rivers

dependent on near shore benthic production, which altered the fundamental energy pathways in the systems (Fear et al. 2017).

Further invasions of Nile tilapia in southern China is likely to alter the trophic positions of many species in native fish communities. We advise that these likely negative impacts on native fisheries and ecosystems should not be underestimated. Protecting native fish populations often involves stopping the intentional introduction of non-native fishes. The potential damage associated with invasive species has prompted recent efforts to predict the vulnerability of ecosystems to species invasions and prioritize them for management (McDonald-Madden et al. 2016; Strassburg et al. 2020). Ultimately, protecting entire landscapes from biological invasions may be required to sustain native biodiversity and ecosystems. This strategy may require strict prohibition on the introduction of invasive species, including non-native fish stocking programs, and using innovative bio-surveillance monitoring techniques like environmental DNA (*e*DNA; Evans et al. 2017) aimed at early detection of potential invaders.

Understanding the consequences of invasive species on ecosystem functioning through changes in trophic interactions among species has received considerable interest over the past decade (Thébault and Loreau 2003). Most of these studies have used stable isotopes to quantify changes in the trophic structure of communities (Cucherousset et al. 2012), as carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can provide an accurate quantitative method for the study of the changes of nutritional structure in aquatic ecosystems (Bearhop et al. 2004). Recent methodological developments have facilitated the quantification of multiple facets of the trophic structure of communities, such as isotopic diversity metrics that have been widely used to assess the effects of biological invasions on a multitude of food webs and ecosystem functioning at both local and global scales (Cucherousset and Villéger 2015; Jackson et al. 2011; Sagouis et al. 2015; Spurgeon et al. 2014; Walsworth et al. 2013; Zambrano et al. 2010). While theoretical and methodological approaches have been recently developed, empirical studies are still needed to assess the effects of biological invasions on the trophic structure of recipient communities. The changes in food webs described in the current study have serious implications for native fish populations and food resources. An increased understanding of the interactions between Nile tilapia and native fish is necessary for fishery management in many regions. Our findings emphasize the need to implement proactive control efforts to restore invaded ecosystems, particularly during colonization and early stages of establishment, to avoid food web disruptions that may be difficult to reverse.

Conclusions

This study provided strong evidence of a diet shift and a decline in trophic position of three fish piscivores in the invaded Dongjiang River. The Nile tilapia invasion appeared to induce significant trophic dispersion, thereby disrupting trophic positions and destabilizing food webs of the impacted aquatic community in the Dongjiang River. Native top fish piscivores increasingly shifted from small fishes to zooplankton and aquatic insects as the invasion of Nile tilapia proceeded. These food web changes ultimately produced a new ecological regime in the Dongjiang River. Results of this study provide a basis for understanding and predicting the directional effects of invasive species on recipient food webs. Our findings highlight the need to implement proactive control efforts to restore invaded ecosystems and improved regulatory practices that limit the spread of this species.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00430-3.

Additional file 1: Table S1. Background data for the study rivers.

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Author contributions
FS and JL performed the field sampling; FS, SL performed the data analysis; FS wrote the manuscript. SL and JL edited the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare they have no competing interests.

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References

Attayde JL, Brasil J, Menescal RA (2011) Impacts of introducing Nile tilapia on the fisheries of a tropical reservoir in north-eastern brazil. Fisheries Manag Ecol 18(6):437–443. https://doi.org/10.1111/j.1365-2400.2011.00796.x

Balian EV, Segers H, Lévèque C, Martens K (2008) The freshwater animal diversity assessment: an overview of the results. Hydrobiologia 595:627–637. https://doi.org/10.1007/s10750-008-9302-7

Baxter CV, Fausch KD, Murakami M, Chapman PL (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85(10):2656–2663. https://doi.org/10.1890/04-138

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis: stable isotopes as measures of niche width. J Anim Ecol 73:1007–1012. https://doi.org/10.1111/j.0021-8790.2004.00861.x

Cabana G, Rasmussen JB (1996) Comparison of aquatic food chains using nitrogen isotopes. PNAS 93:10844–10847. https://doi.org/10.1073/PNAS.93.20.10844

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. https://doi.org/10.1038/nature11148

Cucherousset J, Olden JD (2011) Ecological impacts of nonnative freshwater fishes. Fishes 36(5):215–230. https://doi.org/10.1080/03632415.2011.574578

Cucherousset J, Villéger S (2015) Quantifying the multiple facets of isotopic diversity: new metrics for stable isotope ecology. Ecol Indic 56:152–160. https://doi.org/10.1016/j.ecolind.2015.03.032

Cucherousset J, Blanchet S, Olden JD (2012) Non-native species promote trophic dispersion of food webs. Front Ecol Environ 10(8):406–408. https://doi.org/10.1890/12.WB.018

Córdova-Tapia F, Contreras M, Zambrano L (2015) Trophic niche overlap between native and non-native fishes. Hydrobiologia 746(1):291–301. https://doi.org/10.1007/s10750-014-1944-z

Deines AM, Wittmann ME, Deines JM, Lodge DM (2016) Trade-offs among ecosystem services associated with global tilapia introductions. Rev Fish Sci Aquac 2(24):178–191. https://doi.org/10.1080/23308249.2015.1115466

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z, Knowler D, Lévèque C, Naiman RJ, Prieur-Richard A, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81:163–182. https://doi.org/10.1017/S1464793105006950

Eby LA, Roach WJ, Crowder LB, Stanford JA (2006) Effects of stocking-up freshwater food webs. Trends Ecol Evol 21(10):576–584. https://doi.org/10.1016/j.tree.2006.06.016

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Evans NT, Shirey PD, Wieringa JG, Mahon AR, Lamberti GA (2017) Comparative cost and effort of fish distribution detection via environmental DNA analysis and electrofishing. Fisheries 42:90–99. https://doi.org/10.1080/03632415.2017.1276329

Fear SA, Rennie MD, Dunlop ES (2017) Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. Ecology 98(6):1681–1692. https://doi.org/10.1002/ecy.1836

Figueredo CC, Giani A (2005) Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). Freshw Biol 50:1391–1403. https://doi.org/10.1111/j.1365-2427.2005.01407.x

Fisheries and Fishery Administration Bureau of Ministry of Agriculture (2021) China Fisheries Statistical Yearbook. China Agricultural Publishing House, Beijing

González-Bergonzoni I, Silva I, Mello FT, D'Anatro A, Boccardi L, Stebniki S, Brugnoli E, Tesitore G, Vidal N, Naya DE (2020) Evaluating the role of predatory fish controlling the invasion of the Asian golden mussel *limnoperna fortunei* in a subtropical river. J Appl Ecol 57(4):717–728. https://doi.org/10.1111/1365-2664.13573

Goto D, Dunlop ES, Young JD, Jackson DA (2020) Shifting trophic control of fishery-ecosystem dynamics following biological invasions. Ecol Appl 30(8):e02190. https://doi.org/10.1002/eap.2190

Grammer GL, Slack WT, Peterson MS, Dugo MA (2012) Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) establishment in temperate Mississippi, USA: multi-year survival confirmed by otolith ages. Aquat Invasions 7:367–376. https://doi.org/10.3391/ai.2012.7.3.008
Gu D, Ma G, Zhu Y, Xu M, Luo D, Li Y, Wei H, Mu X, Luo J, Hu Y (2015) The impacts of invasive Nile tilapia (*Oreochromis niloticus*) on the fisheries in the main rivers of Guangdong Province, China. Biochem Syst Ecol 59:1–7. https://doi.org/10.1016/j.bse.2015.01.004
Henson MN, Aday DD, Rice JA, Layman CA (2016) Assessing the influence of tilapia on sport species in North Carolina reservoirs. T Am Fish Soc 147(2):1248–1254. https://doi.org/10.1002/tafs.10031
Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. J Anim Ecol 80:595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x
Jenkins M (2003) Prospects for biodiversity. Science 302:1175–1177. https://doi.org/10.1126/science.108866
Johnson S, Domínguez-García V, Donetti L, Muñoz MA (2014) Trophic coherence determines food–web stability. PNAS 111:17923–17928. https://doi.org/10.1073/pnas.1409077111
Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA (2008) Global diversity of fish (Pisces) in fresh water. Hydrobiologia 595:545–567. https://doi.org/10.1007/978-1-4020-8259-7_53
Lockwood JL, Hoopes MF, Marchetti MP (2011) Non-natives: plusses of invasion ecology. Nature 475(7354):36–36. https://doi.org/10.1038/475036c
Lu KX (1990) Pearl river fishery resources. Guangdong Science and Technology Press, Guanghzou, pp 91–121
Marr SM, Marchetti MP, Olden JD, García-Berthou E, Morgan DL, Arismendi I, Day JA, Griffiths CL, Skelton PH (2010) Freshwater fish introductions in Mediterranean–climate regions: are there commonalities in the conservation problem? Divers Distrib 16:606–619. https://doi.org/10.1111/j.1472-4642.2010.00669.x
Martin CW, Valentine MM, Valentine JF (2010) Competitive interactions between invasive Nile tilapia and native fish: the potential for altered trophic exchange and modification of food webs. PLoS ONE 5(12):e14395. https://doi.org/10.1371/journal.pone.0014395
McDonald-Madden E, Sabbadin R, Game ET, Baxter P, Chadès I, Possingham HP (2016) Using food-web theory to conserve ecosystems. Nat Commun 7:10245. https://doi.org/10.1038/ncomms10245
Michelan TS, Thomaz SM, Mormul RP, Carvalho P (2010) Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. Freshw Biol 55(6):1315–1326. https://doi.org/10.1111/j.1365-2427.2009.02355.x
Ovenden JR, Macbeth GM, Pope L, Thuesen P, Street R, Broderick D (2015) Translocation between freshwater catchments has facilitated the spread of tilapia in eastern Australia. Biol Invasions 17(2):637–650. https://doi.org/10.1007/s10530-014-0754-6
Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Inger R (2013) Bayesian stable isotope mixing models. Environmetrics 24(6):387–399. https://doi.org/10.1002/env.2221
Pietsch TW, Bogatov VV, Amaoka K, Zhuravlev YN, Barkalov VY, Gage S (2003) Biodiversity and biogeography of the islands of the kuril archipelago. J Biogeogr 30(9):1297–1310. https://doi.org/10.1046/j.1365-2699.2003.00956.x
Polis GA, Winemiller KO (2013) Food webs: integration of patterns & dynamics. Springer Science & Business Media, Berlin
Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3):703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2
R Core Team (2019) R: a language and environment for statistical computing. R Foundation for statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Rennie MD, Sprules WG, Johnson TB (2009) Resource switching in fish following a major food web disruption. Oecologia 159:789–802. https://doi.org/10.1007/s00442-008-1271-z
Rennie MD, Strecker AL, Palmer ME (2011) Bythotrephes invasion elevates trophic position of zooplankton and fish: implications for contaminant biomagnification. Biol Invasions 13:2621–2634. https://doi.org/10.1007/s10530-011-0081-0
Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. Trends Ecol Evol 27:40–46. https://doi.org/10.1016/j.tree.2011.09.001
Russell DJ, Thuesen PA, Thomson FE (2012) A review of the biology, ecology, distribution and control of Mozambique tilapia, *Oreochromis mossambicus* (Peters 1852) (Pisces: Cichlidae) with particular emphasis on invasive Australian populations. Rev Fish Biol Fisher 22:533–554. https://doi.org/10.1007/s11160-011-9249-z
Rutten MJM, Komen H, Deerenberg RM, Siwek M, Bovenhuis H (2004) Genetic characterization of four strains of Nile tilapia (*Oreochromis niloticus* L.) using microsatellite markers. Anim Genet 35:93–97. https://doi.org/10.1111/j.1365-2052.2004.01090.x
Sagouis A, Cucherousset J, Villéger S, Santoul F, Boulêtreau S (2015) Non-native species modify the isotopic structure of freshwater fish communities across the globe. Ecography 38:979–985. https://doi.org/10.1111/ecog.01348
Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656. https://doi.org/10.1016/j.tree.2003.09.002
Shuai FM, Li J (2022) Nile tilapia (*Oreochromis niloticus* Linnaeus, 1758) invasion caused trophic structure disruptions of fish communities in the South China River—Pearl River. Biology 11(11):1665. https://doi.org/10.3390/biology11111665
Shuai FM, Li XH, Li YF, Li J, Yang JP, Lek S (2015) Forecasting the invasive potential of Nile tilapia (*Oreochromis niloticus*) in a large subtropical river using a univariate approach. Fundam Appl Lim 187:165–176. https://doi.org/10.1127/fal/2015/0828
Shuai FM, Li XH, Chen FC, Li YF, Lek S (2017) Spatial patterns of fish assemblages in the Pearl River, China: environmental correlates. Fundam Appl Lim 189(4):329–340. https://doi.org/10.1127/fal/2016/0922
Shuai FM, Li XH, Liu QF, Zhu SL, Wu Z, Zhang YQ (2019) Nile tilapia (*Oreochromis niloticus*) invasions disrupt the functional patterns of fish community in a large subtropical river in China. Fisheries Manag Ecol 26(6):578–589. https://doi.org/10.1111/fme.12368
Singh AK (2021) State of aquatic invasive species in tropical India: an overview. Aquat Ecosyst Health 24(2):13–23
Spurgeon JJ, Paukert CP, Healy BD, Kelley CA, Whiting DP (2014) Can translocated native fishes retain their trophic niche when confronted with a resident invasive? Ecol Freshw Fish 24:456–466. https://doi.org/10.1111/eff.12160
Starling F, Lazzaro X, Cavalcanti C, Moreira R (2002) Contribution of omnivorous tilapia to eutrophication of a shallow tropical reservoir: evidence from a fish kill. Freshw Biol l47:2443–2452. https://doi.org/10.1046/j.1365-2427.2002.01013.x
Strassburg BBN, Iribarrem A, Beyer HL, Cordeiro CL, Crouzeilles R, Jakovac CC, Junqueira AB, Lacerda E, Latawiec AE, Balmford A (2020) Global priority areas for ecosystem restoration. Nature 586:724–729. https://doi.org/10.1038/s41586-020-2784-9
Tan XC, Li XH, Li YF, Jie Li (2012) Early development and spatial distribution of the Nile tilapia (*Oreochromis niloticus*) in the Pearl River. J Biosaf 21(4):295–299 **(In Chinese)**
Thébault E, Loreau M (2003) Food-web constraints on biodiversity-ecosystem functioning relationships. PNAS 100(25):14949–14954. https://doi.org/10.1073/pnas.2434847100
Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273. https://doi.org/10.1111/j.1469-8137.2007.02207.x
Thompson RM, Brose U, Dunne JA, Hall RO, Hladyz S, Kitching RL, Martinez ND, Rantala H, Romanuk TN, Stouffer DB, Tylianakis JM (2012) Food webs: reconciling the structure and function of biodiversity. Trends Ecol Evol 27:689–697. https://doi.org/10.1016/j.tree.2012.08.005
Thomsen MS, Byers JE, Schiel DR, Bruno JE, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and function similarity. Mar Ecol Prog Ser 495:39–47. https://doi.org/10.3354/meps10566
Vander-Zanden MJ, Rasmussen JB (1999) Primary consumer δ^{15}N and δ^{13}C and the trophic position of aquatic consumers. Ecology 80:1395–1404

Vander-Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467. https://doi.org/10.1038/46762
Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Reidy-Liermann C, Davies PM (2010) Global threats to human water security and river biodiversity. Nature 467:555–561. https://doi.org/10.1038/nature09440
Wainright CA, Muhlfeld CC, Elser JJ, Bourretd SL, Devlina SP (2021) Species invasion progressively disrupts the trophic structure of native food webs. PNAS 118(45):e2102179118. https://doi.org/10.1073/pnas.210217911
Walsworth TE, Budy P, Thiede GP (2013) Longer food chains and crowded niche space: effects of multiple invaders on desert stream food web structure. Ecol Freshw Fish 22:439–452. https://doi.org/10.1111/eff.12038
WhitingerJA ZTG, Gerig BS (2022) Stable isotopes and movement of walleye change following ecological shifts driven by Dreissenid Mussels. N Am J Fish Manage 42(3):572–584. https://doi.org/10.1002/nafm.10733
Yao GC, Ye W (2014) New technology of ecological and efficient culture of tilapia. China Ocean Press, Beijing
Zambrano L, Valiente E, Vander-Zanden MJ (2010) Food web overlap among native axolotl (*Ambystoma mexicanum*) and two exotic fishes: carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*) in Xochimilco, Mexico City. Biol Invasions 12:3061–3069. https://doi.org/10.1007/s10530-010-9697-8
Zengeya TA, Robertson MP, Booth AJ, Chimimba CT (2013) Ecological niche modeling of the invasive potential of Nile tilapia *Oreochromis niloticus* in African river systems: concerns and implications for the conservation of indigenous congenerics. Biol Invasions 15:1507–1521. https://doi.org/10.1007/s10530-012-0386-7

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