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Coexistence mechanisms and individual trophic niche variation between functionally analogous non-native and native carp species

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Understanding the mechanisms that promote coexistence between functionally analogous non-native and native species that share similar prey is important for predicting the ecological consequences of their competitive interactions. Theory predicts that species coexistence is facilitated by stabilizing mechanisms that enhance inter-specific trophic niche partitioning, and/ or the equalizing mechanisms that reduce differences in the average fitness. Inter-specific niche partitioning, influenced by the ecological opportunity in prey resources, also affects intra-specific niche partitioning and individual niche expansion. These theories were tested using the non-native mrigal carp *Cirrhinus mrigala* and its congener native mud carp *C. molitorella* that coexist across the Pearl River basin, Southern China, with their trophic interactions analysed using DNA metabarcoding on fish gut contents sampled across the basin in both the dry and wet seasons of 2019 and 2021. The results revealed that the inter-specific trophic niche overlap was lower than their intra-specific trophic niche overlap, suggesting their coexistence was supported by stabilizing mechanisms. The ecological opportunity in prey resources was driving inter-specific niche partitioning and this partitioning then positively influenced intra-specific niche partitioning and individual niche expansion, especially in mrigal carp that had larger body sizes and occupied higher trophic positions at constricted individual niches. Fish body size also affected inter-specific niche partitioning and the relationship between inter- and intra-specific niche partitioning, with positive effects on both in mrigal carp but negative effects on both in mud carp. The results thus provide a mechanistic explanation on how closely related non-native and native species coexist and highlight the importance of dietary plasticity in facilitating the invasion of non-native species.

Keywords Stabilizing mechanisms, Inter-specific interactions, Ecological opportunity, DNA metabarcoding, Plasticity

Introductions of non-native species can lead to population establishment and their subsequent dispersal in introduced ranges[1,2]. These invasive populations must integrate into native food-webs[3], leading to competition between individuals and existing species for prey resources. The mechanisms driving these interactions are crucial in determining the ecological impact of the invader[4,5]. Where the strength of competition between the invasive and native species is high, native species may experience detrimental effects, including alterations in their trophic niche size and position, as well as the risk of competitive exclusion[6,7].

How functionally analogous non-native and native species co-exist is thus a question of fundamental ecological importance. Theory posits that this coexistence is determined by the extent of niche overlap between the species (see explanation in Table 1), and the difference in their competitive abilities (i.e. average fitness difference[8,9]). Stable coexistence can be achieved by stabilizing mechanisms that increase niche partitioning between the species, enabling intra-specific competition to be stronger than inter-specific competition, and/ or by

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Term	Explanation
Niche overlap	The degree to which two or more species use the same resources reflects the extent to which species share aspects of their ecological niches, such as food sources.
Inter-specific niche overlap	Niche overlap between or among individuals of different species
Intra-specific niche overlap	Niche overlap between or among individuals of the same species
Ecological opportunity	The availability of ecological resources that may be exploited with a specific space and time [1]
Individual niche width (INW)	An individual trophic trait relating to the richness and abundance of prey species consumed by a given individual [1]
Trophic position (TP)	TP refers to the level an organism occupies in a food web based on its feeding relationships and energy source, with primary producers at the base (TP = 1).

Table 1. Glossary.

Region	Mud carp			Mrigal carp		
	n	Mean SL (cm)	Mean weight (g)	n	Mean SL (cm)	Mean weight (g)
West River	117	19.3 ± 4.3	222.2 ± 186.8	58	24.6 ± 7.9	417.4 ± 430.2
North River	73	18.4 ± 4.9	185 ± 167.9	52	26.5 ± 7.6	493 ± 547.4
East River	53	21.5 ± 3.8	256.1 ± 143.6	28	26.8 ± 4.8	431.2 ± 270.8
Central Delta	124	19.7 ± 3	200.2 ± 76.3	108	27.7 ± 6.6	545.6 ± 456.6

Table 2. The number (n), standard length (SL, cm) and weight (g) of native mud carp and non-native mrigal carp sampled in the different regions of the Pearl River.

equalizing mechanisms that reduce average fitness differences between the species[10,11]. Stabilizing mechanisms can also promote stable coexistence at individual levels when niche partitioning is stronger between individuals of different species versus the same species, and niche overlap is higher within than between the species[10]. Equalizing mechanisms decrease fitness differences among individuals of competing species, thereby reducing the intensity of competition[10]. Body size is also a key trait influencing phenotypic plasticity of individuals and the competitive interactions among individuals[11,12]. Body size thus has implications for individual fitness, with larger individuals possessing anatomical and morphological features which contribute to their higher performance in accessing limited resources and/ or acquiring a mate versus smaller individuals[11,13,14].

Species coexistence is also influenced by prey abundance and diversity in the environment, i.e. the ecological opportunity (see explanation in Table 1), where there tends to be greater competitive exclusion in environments of low ecological opportunity, but reduced inter-specific trophic niche overlap and stable coexistence under high ecological opportunity[15]. This reduced overlap can also drive inter-individual niche partitioning and individual niche expansion, and result in population niche expansion, as individuals are released from the constraining inter-specific interactions of niche overlap (i.e. the niche variation hypothesis[16,17]).

Despite the theoretical framework, coexistence mechanisms involving the trophic niche variation between invasive and native species in fluctuating environments are yet to be fully understood. The coexistence of non-native and native species in subtropical rivers provides an opportunity for testing these theories, as these rivers have high variability in river discharge, temperature and ecological opportunity in prey resources between wet and dry seasons[18–20]. Accordingly, the focal non-native fish here is the mrigal carp *Cirrhinus mrigala*, which was introduced into southern China for aquaculture in 1982[21]. Its subsequent escape and dispersal have resulted in its coexistence with the its native congener and functional analogue mud carp *Cirrhinus molitorella* across much of southern China, including the Pearl River basin (the focal study area). With both species being ilyophagous, which involves feeding on soft sediments[22], this has raised concerns over the extent and intensity of their inter-specific trophic niche overlap and competition, particularly in comparison to intra-specific trophic niche overlap and competition. Mrigal carp (average size: 241 ± 13 g) are also generally larger in body size than mud carp (average size: 146 ± 5 g) in southern China[21]. We posit that the coexistence of these species across the basin is facilitated by the stabilizing mechanisms where inter-specific trophic niche overlap was smaller than intra-specific trophic niche overlap, and high ecological opportunity drives increases in inter-specific niche partitioning and, subsequently, in intra-specific niche partitioning and individual niche expansion. We also posit that larger body size range in mrigal versus mud carp results in higher phenotypic plasticity in inter- and intra-specific niche partitioning, individual trophic niche width (INW; Table 1) and individual trophic position (TP; Table 1), which facilitates their invasion of the basin. Our objectives were to test the hypothesis that inter-specific trophic niche overlap was smaller than intra-specific trophic niche overlap, to assess the role of ecological opportunity in both inter- and intra-specific niche partitioning and individual niche variation, and to evaluate the impact of body size on phenotypic plasticity in niche partitioning and individual niche variation.

Results
Inter-specific difference in body size
A total of 367 mud carp and 246 mrigal carp were captured across the sampling events (Table 2). Mrigal carp (SL: 26.6 ± 7.1 cm; weight: 491 ± 456 g) were larger than mud carp (SL: 19.6 ± 4.1 cm; weight: 212 ± 148 g) across each

	Intra-specific niche overlap	Inter-specific niche overlap
Mud carp	0.47 ± 0.20	0.44 ± 0.22
	$t = 1.37, P = 0.17$	
Mrigal carp	0.46 ± 0.20	0.40 ± 0.16
	$t = 1.99, P = 0.049*$	
Inter-specific difference	$t = 0.17, P = 0.87$	$t = 1.11, P = 0.27$

Table 3. Differences between the intra- and inter-specific niche overlap for each/ both species, and inter-specific differences in intra- and inter-specific niche overlaps. *, $P < 0.05$.

Dependent variable	Predictors	Estimate	SE	z value	$P (>|z|)$
inters_np	(Intercept)	-0.54	0.39	-1.39	0.16
	Ln (Ecological opportunity)	0.23	0.10	2.22	0.03*
intras_np	(Intercept)	-0.97	0.27	-3.54	<0.001***
	inters_np	1.89	0.40	4.67	<0.001***
	mrigal carp	-1.14	0.36	-3.21	0.001**
	inters_np: mrigal carp	1.81	0.57	3.16	0.001**
inters_np	(Intercept)	1.32	0.36	3.69	<0.001***
	SL	-0.04	0.01	-3.04	0.002**
	mrigal carp	-1.25	0.42	-2.97	0.003**
	SL: mrigal carp	0.06	0.02	3.20	0.001**
intras_np	(Intercept)	-2.77	0.68	-4.07	<0.001***
	inters_np	4.02	1.16	3.46	<0.001***
	Mrigal carp	4.53	1.33	3.41	<0.001***
	SL	0.08	0.03	2.94	0.003**
	inters_np: mrigal carp	-6.91	2.29	-3.01	0.003**
	inters_np: SL	-0.09	0.05	-1.90	0.06
	Mrigal carp: SL	-0.22	0.05	-4.42	<0.001***
	inters_np: mrigal carp: SL	0.34	0.09	3.80	<0.001***

Table 4. The relationships among ecological opportunity, inter-specific niche partitioning (inters_np), intra-specific niche partitioning (intras_np), individual standard length (SL), the two fish species and their interactions. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

sampling region (Table 2; $P < 0.001$ for both SL and weight), with an average body size ratio for standard length (SL) of 1.37 ± 0.21 and weight of 2.42 ± 1.27.

Trophic niche overlap

Intra-specific trophic niche overlap was larger than inter-specific trophic niche overlap, with this difference being significant for mrigal carp ($P = 0.049$), but not significant for mud carp ($P = 0.17$; Table 3), suggesting that intra-specific competition for prey resources tended to be stronger than inter-specific competition when prey resources are limited. The niche overlaps among con- / inter-specific individuals were both slightly higher for mud carp than for mrigal carp, but these differences were not significant ($P = 0.87$, $P = 0.27$; Table 3). This suggests that, compared to mrigal carp, limited prey resources may lead to slightly intensified competition in mud carp, both within their species and between species.

Effects of ecological opportunity on individual niche variation

Increased ecological opportunity in prey resources led to increased inter-specific niche partitioning (Table 4; Figs. 1 and 2a). This inter-specific niche partitioning then drove significant increases in intra-specific niche partitioning and increases in INW of lower significance (Fig. 2; intra-specific niche partitioning: regression coefficient = 0.65, $P < 0.001$; INW: regression coefficient = 0.65, $P = 0.06$), with intra-specific niche partitioning and INW being significantly correlated with each other (regression coefficient = 0.03, $P = 0.004$; Figs. 1 and 2). Additionally, the fish species had significant influences on the relationship between inter- and intra-specific niche partitioning and between intra-specific niche partitioning and INW, with higher regression slopes in mrigal carp than mud carp (Tables 4 and 5; Fig. 2b, c). The INW was negatively correlated with TP for both species, but with a significantly steeper slope and higher TPs at small INW for mrigal carp than mud carp (Table 5; Fig. 2d).

Effects of body size on individual niche variation

The effects of SL on inter-specific niche partitioning were significant ($P = 0.002$, Table 4), with a positive effect of SL in mrigal carp but a negative effect in mud carp (Fig. 2e). The SL was also significantly affecting the
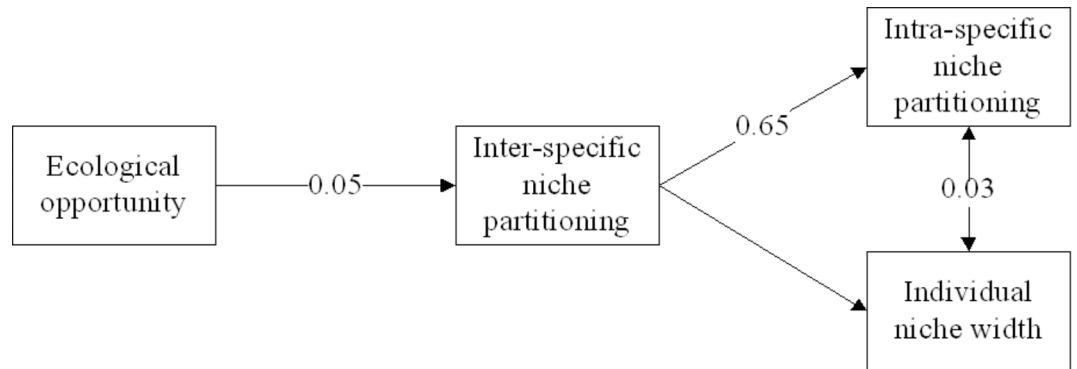
Fig. 1. Path from variation in ecological opportunity, to variation in inter-specific niche partitioning, intra-specific niche partitioning, and individual trophic niche width. Regression coefficients with $P < 0.05$ as shown.
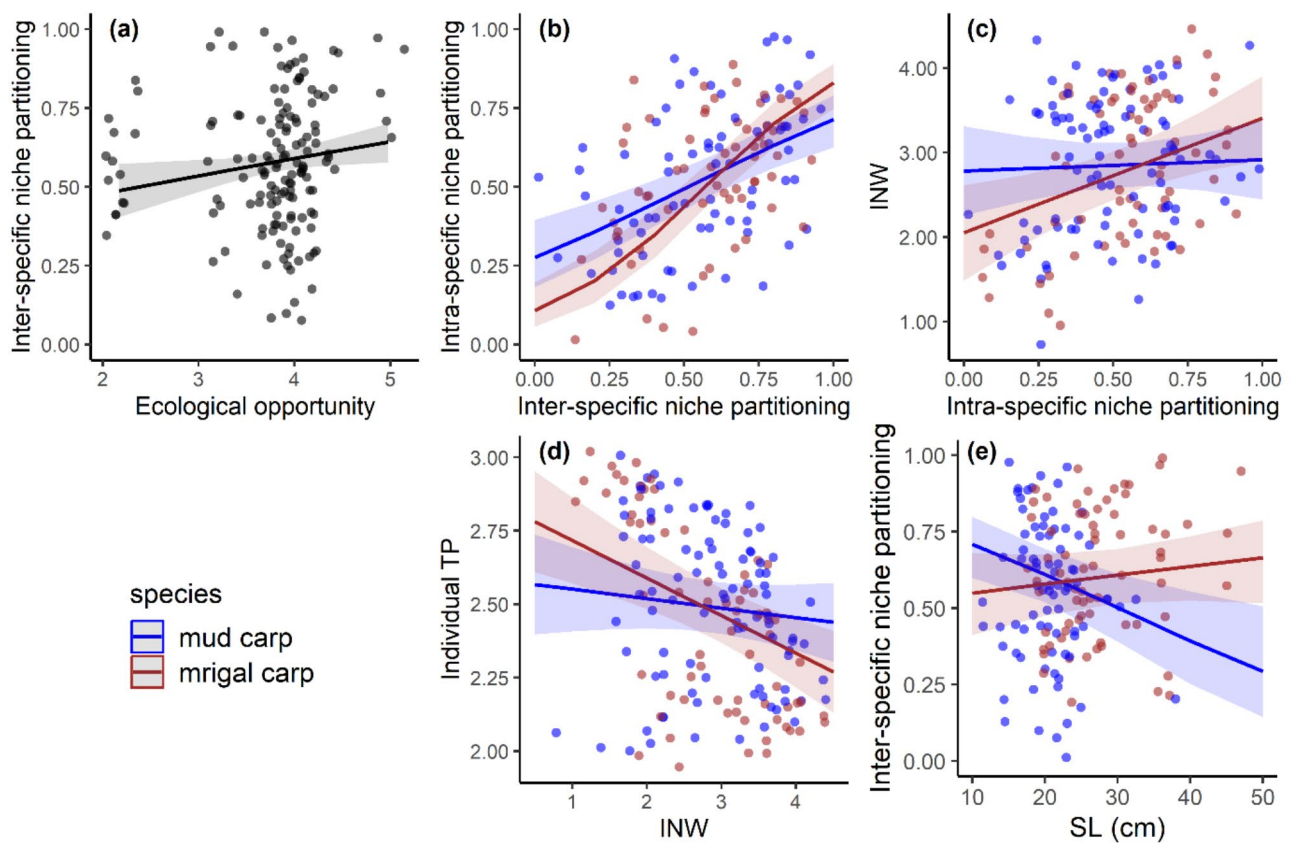

Fig. 2. The relationships between ecological opportunity, inter-specific niche partitioning, intra-specific niche partitioning, individual trophic niche width (INW), and individual trophic position (TP) and standard length (SL) of non-native mrigal carp and native mud carp.

association between intra- and inter-specific niche partitioning, with the regression slopes increasing with SL in mrigal carp and decreasing with SL in mud carp (Table 4; Fig. 3). However, no significant effects of SL were found on intra-specific niche partitioning ($P = 0.11$, Table S1), INW ($P > 0.1$, Table S1), or TP ($P > 0.1$, Table S1) for individuals of both species.

Discussion

Trophic interactions among individuals of differing body sizes of functionally analogous non-native mrigal carp and native mud carp were assessed across different regions of the Pearl River basin, China, based on individual diet composition revealed by DNA metabarcoding. A higher intra- than inter-specific trophic niche overlap was found in both species but with different levels of significance. The inter-specific niche partitioning, which

Dependent variable	Predictors	Estimate	SE	t value	P (>|t|)
INW	(Intercept)	2.77	0.27	10.39	< 0.001***
	intras_np	0.15	0.43	0.34	0.74
	mrigal carp	-0.72	0.33	-2.19	0.03*
	intras_np: mrigal carp	1.20	0.58	2.08	0.04*
Individual TP	(Intercept)	2.58	0.10	26.19	< 0.001***
	INW	-0.03	0.03	-0.94	0.35
	mrigal carp	0.26	0.11	2.35	0.02*
	INW: mrigal carp	-0.10	0.04	-2.54	0.01*

Table 5. The relationships between INW and intra-specific niche partitioning (inras_np), fish species, and their interaction, and between individual trophic position (TP), individual niche width (INW), fish species and their interactions. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.
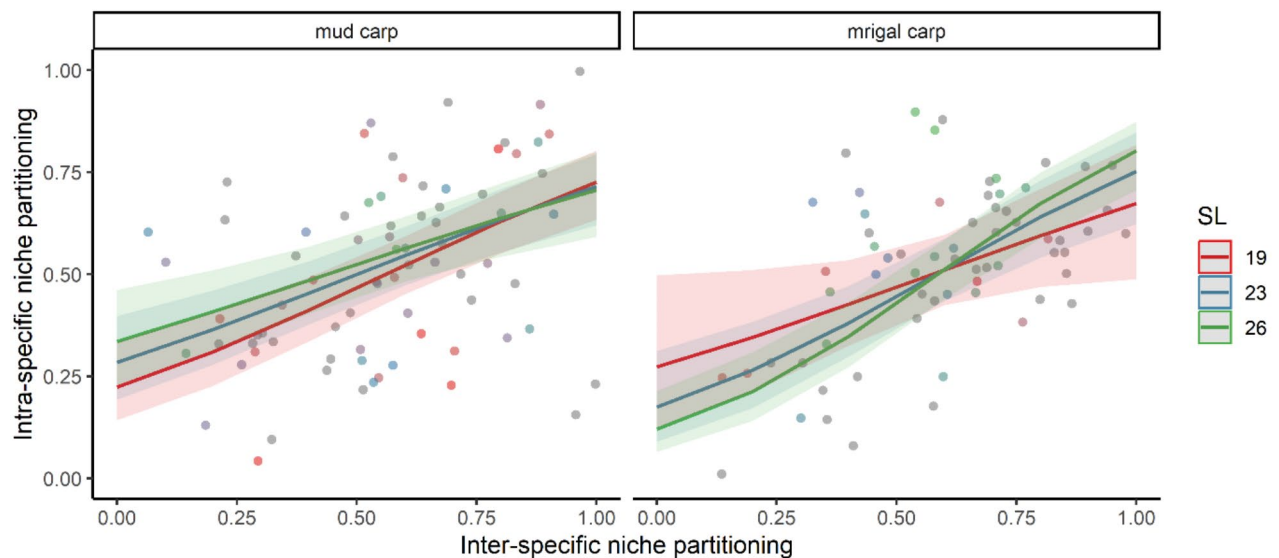
Fig. 3. Dependence of intra-specific niche partitioning on inter-specific niche partitioning across standard length (SL, cm) of mud carp and mrigal carp.

increased with ecological opportunity in prey resources, significantly affected intra-specific niche partitioning, where steeper regression slopes were demonstrated in mrigal carp than mud carp. The inter-specific niche partitioning and the subsequent variation in intra-specific niche partitioning were also affected by body size of the two species.

The higher intra- than inter-specific trophic niche overlap for both species indicate that their coexistence was facilitated by stabilizing mechanisms that resulted in higher niche partitioning between species, where intra-specific competition was then stronger than inter-specific competition, especially when the ecological opportunity in prey resources was limited[9,15,23]. However, when the ecological opportunity increases, it can enhance species coexistence by reducing inter-specific niche overlap or increasing niche partitioning[15]. Increased inter-specific niche partitioning, indicating a reduction in the constraining inter-specific interactions, will promote intra-specific niche partitioning and individual niche expansions[16,17]. These processes can collectively contribute to expansions of population niche width[17].

Both mud and mrigal carp demonstrated intra-specific niche partitioning and individual niche expansions, albeit with notable differences in strength. The significantly stronger variations of intra-specific niche partitioning in mrigal carp indicated that their individuals had higher dietary plasticity when released from inter-specific competitive interactions. The higher variation in its intra-specific niche partitioning also suggests the enhanced performance of mrigal carp individuals in reducing intra-specific competition compared to mud carp, as niche partitioning (low niche overlap) usually indicates diminished competition[23]. The dietary plasticity of mrigal carp was also demonstrated by its ability to occupy higher TP than mud carp to maintain energy requirements for individuals with constrained INW, with both species demonstrating negative relationships between INW and TP. These indicate that mrigal carp had higher adaptive capacity in foraging than mud carp. The high dietary plasticity and adaptive capacity of mrigal carp would have likely facilitated its population establishment and dispersal following introduction, which is consistent with patterns observed in other invasive species[24].

Mrigal carp had larger body sizes than mud carp across different regions of the Pearl River, indicating their potential to be a superior competitor than the coexisting mud carp, as larger individuals can physically restrict the access of smaller individuals to resources through interference competition[25]. As body size increased, mrigal carp tended to increase inter-specific niche partitioning with mud carp, which would promote their inter-specific coexistence[9]; they also exhibited a tendency to increase the strength of associations between intra- and inter-specific niche partitioning, which would facilitate population niche expansions when inter-specific niche partitioning occurred[16,17]. Conversely, the body size of mud carp demonstrated negative effects in variations in inter-specific niche partitioning and the associations between intra- and inter-specific niche partitioning. The different inter-specific effects of body size suggest that their coexistence can be facilitated by their high inter-specific niche partitioning between large mrigal carp and small mud carp, which might explain their stable size ratios in their coexisting ranges.

Larger fish body sizes enable larger jaw and gape sizes, allowing access to larger prey and a broad range of resources. This can result in niche expansion and increased TP[26]. However, this study found no significant effects of body size on individual niche width, TP, and intra-specific niche partitioning in both species. These effects may become significant in long-term dietary data, as DNA metabarcoding of fish gut content reflects only immediate feeding habits, providing a snapshot of their recent dietary choices[27]. Moreover, although ecological opportunities in prey resources are among the main factors influencing their trophic interactions, individual trophic traits (such as niche width, TP and inter-individual niche overlap) are also significantly shaped by the density of conspecifics and competitor species[28–31]. We quantified the ecological opportunity across different sampling events at each site and assessed its effect on inter-individual trophic interactions. This approach accounted for variability in sampling months across seasons between years, ensuring that no artifacts were introduced into the results. However, fish density in the wild environment could not be quantified in this study, nor were its effects addressed. Therefore, further research is needed to conduct experiments with both these species across a wider range of body sizes and varying densities of conspecifics and inter-specifics[11]. By combining gut content analysis and stable isotope analysis, we can enhance our understanding of individual resource use over extended periods, such as months[32–34]. This approach will help elucidate how density and body size influence the co-existence of these two species.

In summary, the testing of theory on how non-native and native species co-exist suggested stabilising mechanisms were important for the two focal fishes here, where these mechanisms were due, at least in part, to their significant inter-specific differences in body sizes, with both large mrigal carp and small mud carp having high inter-specific niche partitioning. This inter-specific niche partitioning can be further enhanced by increased ecological opportunities in prey resources. The results also demonstrated the higher adaptive dietary plasticity of non-native mrigal carp when their individuals were released from inter-specific interactions with native mud carp, with this adaptation facilitating their invasion in the Pearl River basin.

Methods

Fish gut contents and eDNA sampling

In the Pearl River, the dry season extends from October to March, while the wet season lasts from April to September[35]. Fish samples were collected during the dry and wet seasons of 2019 (November and July/September) and 2021 (January and July) in the West River, North River, East River, and the central delta of the Pearl River (Fig. 4). During the 2019 wet season, sampling occurred in July in the West River and in September for the other areas. For each sampling campaign, fish were collected from consistent locations across all sites, and a combination of fishing nets was consistently used, including gill nets, cast nets, and cage traps, following Zhang, et al.[36]. At each site, twelve gill nets (40 m long, 1.5 m high, with mesh sizes of 20 mm, 40 mm, and 60 mm) and twelve cage traps (9.5 m long, 38 cm wide, 25 cm high, with a mesh size of 18 mm) were separately deployed across the river, spaced 30 m apart, for 10 h from 8:00 PM to 6:00 AM. Three cast nets (6 m in diameter, 10 mm mesh size) were thrown into the river and retrieved twelve times at approximately 8:00 AM to collect fish. The combination of different fishing nets was aimed to capture individuals from various microhabitats, and target different size classes of fish, ensuring the samples accurately represent the populations. The fish were then transported on ice to the laboratory where they were measured (SL, to 0.1 cm) and weighed (nearest g), before they were dissected. During each fish sampling event, 1 L of river water was sampled at the depth ≤ 1 m to the riverbed and filtered using the precombusted Whatman® glass fiber filter (dia. 47 mm, pore size 0.7 μm) as environmental DNA (eDNA) samples. These samples were stored in liquid nitrogen before DNA extraction.

DNA extraction and sequencing

For individual fish with gut fullness of $> 50\%$, the gut contents were extracted by press gently on the fore-, mid- and hind-gut and used in DNA analyses. Accordingly, the genomic DNA of the gut contents and the eDNA water samples were extracted using the DP812 TGuide S96 Magnetic Soil/Stool DNA Kit (TIANGEN®, Beijing, China). The V4 region of the 18S rDNA was amplified from the genomic DNA using the primer with barcode TAReuk454FWD1 and TAReukREV3[37]. All the PCR-amplified DNA fragments were purified, quantified, and homogenized to obtain a sequence library. The qualified library, which meets the criterion of a concentration > 1ng/μl in the $380 \sim 630$ bp fragments, were sequenced on the Illumina® Novaseq 6000 system.

The raw paired sequences were demultiplexed and denoised using DADA2 methods in QIIME2[38]. The resulting feature table contains counts of different amplicon sequence variant (ASV). The ASV with counts < 10 or being present in a single sample were removed to avoid contamination. Then the taxonomy classification of the ASV with taxonomy confidence ≥ 0.85 was performed using a pre-trained Naive Bayes classifier of the Silva v138 database[39]. Before statistical analysis on the gut contents, we removed the ASVs assigned under the order of Teleostei to avoid contamination of mud carp/mrigal carp DNA, and the unassigned ASVs or ASVs assigned as bacteria or parasites as they were non-targeted taxa.
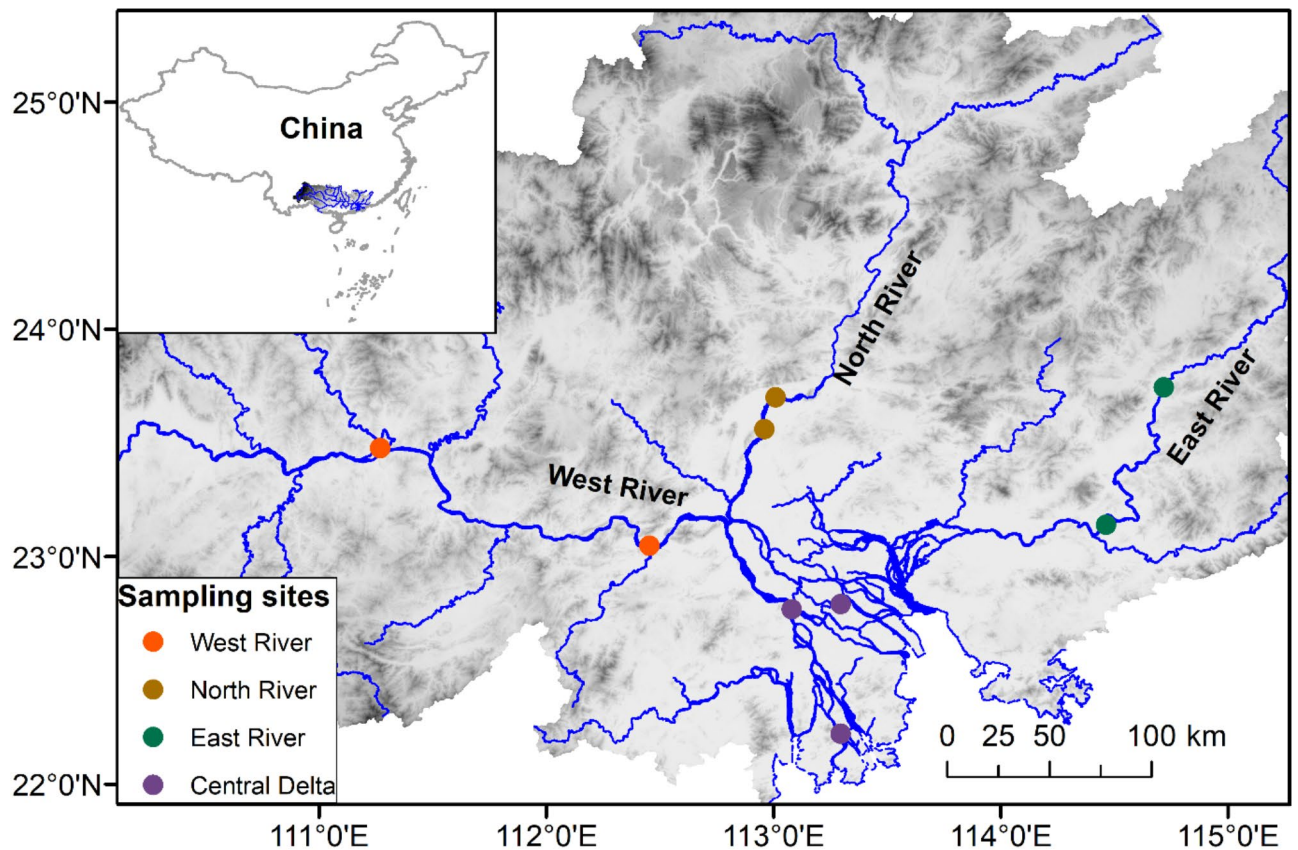
Fig. 4. Inset: the location of the Pearl River basin in China. Main: Locations of sampling sites in the West River, North River, East River, and the Central Delta of the Pearl River basin. The map was generated using ArcMap 10.8.2 (https://www.esri.com/en-us/arcgis/products/arcgis-desktop/resources).

Statistical analyses

Inter-specific difference in body size

Inter-specific differences in fish SL and weight were analysed separately for 24 of the total 28 sampling events (each representing a collection at a site on a specific date), where both mud and mrigal carp were captured. Inter-specific differences in SL and weight across sampling regions were tested separately using generalized linear mixed models with a gamma distribution, followed by multiple comparison tests. A gamma distribution was selected because of the right-skewed distribution of the residuals when modelled with a Gaussian distribution[40]. The analysis was conducted using the lme4 and emmeans packages, with fish species, sampling region and their interaction as fixed effects and sampling event treated as a random factor.

Inter-specific body size ratios were calculated separately for SL and weight. For each sampling event, the ratio of average SL of mrigal carp to average SL of mud carp was calculated, as well as the ratio of average weight of mrigal carp to average weight of mud carp. These ratios were then averaged across sampling events to obtain overall mean values.

Trophic niche metrics

The ecological opportunity in prey resources was estimated from data derived from the eDNA water samples and was expressed as the α diversity, being calculated as the Hill number (q = 1) in the hilldiv package[41]. For the fish gut data, the individual fish's INW (Table 1) was also evaluated by calculating the Hill number (q = 1). During each sampling event, inter-individual trophic niche overlap was calculated as the Sorensen overlap by running the *pair_dis* function in the hilldiv package. For each individual, trophic niche overlap was measured with all other individuals. Average overlap values were then calculated separately, resulting in inter-specific niche overlap for pairs between different species, and intra-specific niche overlap for pairs within the same species. Accordingly, inter-specific niche partitioning was calculated as 1 – inter-specific trophic niche overlap, and intra-specific niche partitioning as 1 – intra-specific trophic niche overlap. Difference between inter- and intra-specific trophic niche overlap were separately tested for mud and mrigal carp using Student's t-test in R. Similarly, the difference in inter- and intra-specific trophic niche overlap between the two species were also assessed using Student's t-test.

For each individual, their TP (Table 1) was calculated following Pauly, et al.[42] using the function $TP_i = 1 + \sum_{j=1}^{G} DC_{ij} \times TP_j$, where DC_{ij} is the proportion of prey item j in the diet of individual i, G is the number of

prey items in the diet, and TP_j is the trophic position of prey j in the diet of individual i. TP_j were assigned as 1 for the prey item of plants, algae, and fungi, as 2 for protozoa, rotifer, sponge, and other animals.

Effects of ecological opportunity on individual niche variation
The effects of ecological opportunity on inter- and intra-specific niche overlap, INW and individual TPs were tested using structural equation models (SEM), linear mixed models and generalized linear (mixed) models. Prior to testing, the ecological opportunity and INW were natural log transformed to minimise the magnitude of variances between variables and meet the requirements on normal distribution. SEM was performed in the lavaan package, where the model fit was assessed using a combination of Chi-square tests ($P > 0.05$ indicates a good match between the model and the data), the comparative fit index (CFI; CFI > 0.90 indicates good fit), the Tucker Lewis index (TLI; TLI > 0.90 indicates good fit), and the root mean square error of approximation (RMSEA; RMSEA < 0.50, close fit; 0.50 < RMSEA < 0.80, reasonable approximate fit)[43]. The SEM was a good fit to the data (Chi-square test: $P = 0.16$; CFI = 0.98; TLI = 0.94; RMSEA = 0.075). For dependent variables of inter- and intra-specific niche partitioning which are proportion data, we further built generalized linear (mixed) models with beta distributions. The association between ecological opportunity and inter-specific niche partitioning was analysed using a generalized linear model. The relationship between inter- and intra-specific niche partitioning was further analysed using generalized linear mixed models, where inter-specific niche partitioning, fish species and their interaction are predictors, sampling event were treated as a random factor. The associations between intra-specific niche partitioning and INW, and between INW and TPs were further analysed using linear mixed models, where sampling event was treated as a random factor.

Effects of body size on individual niche variation
Effects of individual body size (SL) on inter-/ intra-specific niche partitioning were tested by building generalized linear mixed models, and their effects on INW, and TP were tested by building linear mixed models, where SL and species were predictors and sampling event was treated as a random factor. Dependence of intra-specific niche partitioning on inter-specific niche partitioning, fish species, SL and their interactions were analysed using a generalized linear mixed model. All calculations and statistical analyses were completed in R 4.3.2[44].

Data availability
DNA sequences and relevant data are available in the NCBI repository (https://dataview.ncbi.nlm.nih.gov/object/PRJNA1092352).

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Author contributions

YZ conceived ideas and designed methodology; YZ, JL, DH, YH, YL, WC collected data; YZ analysed and interpreted data; YZ, RB wrote the manuscript. All co-authors contributed greatly to the revision of the manuscript and approved its final version.

Declarations

Competing interests

The authors declare no competing interests.

Ethical approval

The use of fish and all experiments were approved by the Laboratory Animal Ethics Committee, Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences. All experiments were performed in accordance with the protocols by the Institutional Animal Care and Use Committee in China. The study is reported in accordance with ARRIVE guidelines (Animal Research: Reporting In Vivo Experiments).

Additional information

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