

Trophic consequences of invasive mrigal carp for native mud carp by comparing the results of intra- and inter-specific competition

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Abstract

Predicting the ecological impacts of invasive species on analogous native species has great significance for native population conservation. We tested how the strength of interspecific competition from a coexisting invasive species varies with abundance and how this compares with intraspecific competition. The model species was the native mud carp, and the coexisting invasive species was mrigal carp. The replicated mesocosm used each species in an allopatric control ($n = 10$), in intraspecific competition treatments ($n = 20, 30$), in a sympatric control ($n = 5$ for both species) and in interspecific competition treatments ($n = 10, 15, 20$ for both species). The treatment effects were the specific growth rate (SGR), position and size of trophic (isotopic) niches. Compared to mrigal carp, mud carp had a significantly lower survival rate (median: 0.8) and SGR. The mud carp SGR significantly decreased when the con- and inter-specific densities increased, showing a density dependence, but there was no significant difference between intra- and inter-specific competition. Compared to intraspecific competition in which mud carp expanded their niche, the presence of mrigal carp drove the mud carp trophic niche toward broader sizes at lower trophic positions, but intensified interspecific competition drove the mud carp trophic niche toward constriction. Both mud carp and mrigal carp expanded their niches in invaded communities, and their niches overlapped with each other. Their niche expansions implied plasticity in resource utilization. These results also suggested a complexity in how ilyophagous invasive species integrate into food webs and alter their structure.

Introduction

Being introduced intentionally and unintentionally, invasive alien species has spread globally in geographic distribution (Turbelin et al. 2017), causing substantial ecological and economic impacts (Haubrock et al. 2021). Negative ecological impacts of alien species include the displacement and extinction of native species, alteration of trophic interactions, transmitting new pathogens and parasites, threatening native species' genetic diversity through hybridization and disruption of ecosystem functioning (Cucherousset, Olden 2011; Goodenough 2010; Haubrock et al. 2021). Thus, predicting the ecological impacts of invasive species is important for ecosystem management and biodiversity maintenance. The impacts of invasive species on analogous native species in the same trophic guilds have received great attention. Understanding such impacts has great implications for determining the mechanisms by which invasive species integrate into native food webs and coexist with native species (Dominguez Almela et al. 2021). Through competition for shared foods, invasive species can lead to displacement or even extinction of native species (Huxel 1999). As MacArthur, Levins (1967) suggested, competition sets a limit on the similarity of coexisting species. Invasive species are often deemed super competitive, and their coexistence with closely related native species will probably drive the niche divergence or competitive exclusion of native species (Britton et al. 2018).

The Volterra-Gause principle states that species are not able to co-occur when they occupy identical niches, and if the two species are forced to compete in an undiversified environment, one inevitably becomes extinct (Hutchinson 1957). According to ecological niche theory, when closely related

invasive species and native species coexist, (1) niche opportunities for invaders exist when the resources are not fully exploited, and invaders occupy an empty trophic niche, avoiding competition with native species and facilitating species coexistence and food web integration (Shea, Chesson 2002). (2) Niche divergence occurs between invaders and native species when resources are fully exploited (Tran et al. 2015). Under intensified interspecific competition, their trophic niche sizes will be reduced compared with their allopatric contexts (De Santis et al. 2020; Tran et al. 2015). More seriously, when the invader and native species compete for the same key resources, they cannot coexist, and the more competitive species will exclude and take the place of the weaker species (Competitive exclusion principle or Gause principle, Gause, 1934).

Given the apparent importance of interspecific competition in driving the alteration of the trophic ecology of populations, population density is one of the most important factors in modifying the strength of interspecific competition (De Santis et al. 2020). The impacts of invasive species increase both linearly and nonlinearly with population density (Jackson et al. 2015). On the other hand, increased intraspecific competition caused by increased numbers of conspecific individuals can have greater ecological consequences due to conspecifics having virtually identical traits that can result in a greater extent of resource sharing (Buoro et al. 2016).

Therefore, this study tested how the trophic ecology of a model species is altered by the increased abundance of an invasive species with analogous traits, and we compared these impacts with those from increased intraspecific competition. The model animals were freshwater fish, which are adaptable and tractable in competitive experiments (De Santis et al. 2020). The model species was mud carp *Cirrhinus molitorella* (Fig. S1), a native species widely distributed in southern China and Vietnam (Froese, Pauly 2021). The coexisting species was the invasive mrigal carp *C. mrigala* (Fig. S1). Mrigal carp, a native species to the Indian subcontinent (Froese, Pauly 2021), was introduced to Guangdong Province in China in 1982 and has become one of the most abundant invasive species in a wide geographical range of the southern China rivers, including the Yangtze River, Pearl River, Han River, Yang River and Jian River (Yu et al. 2019). Mud carp and mrigal carp are both filter-feeding species that feed on soft sediments (Bowen et al. 2006). Compared to mud carp, mrigal carp have a larger body size and are more capable of tolerating cold water temperature and eutrophic water conditions and are more competitive in snatching food in sympatry with mud carp (Yu et al. 2019).

Using a pond mesocosm experiment with mud carp as the model fish and mrigal carp as the coexisting invasive species, this study tested the relative strength of increased intra- and inter-specific competition on mud carp somatic growth rates and their niche position and niche breadth. Due to the large body size of mrigal carp and its competitiveness in snatching food from mud carp (Yu et al. 2019), Hypothesis 1 was that the mud carp growth rate would decrease with densities more greatly when in sympatry with mrigal carp than that in allopatric treatments. Second, interspecific competition could reduce the trophic niches of coexisting species (De Santis et al. 2020; Tran et al. 2015). Hypothesis 2 was that the trophic niche of sympatric mud carp and mrigal carp would be highly divergent, with the trophic niche of sympatric mud carp being smaller than that in allopatric treatments. Moreover, to complement the

mesocosm experiment, we also tested the consistency of the interspecific niche divergence pattern between the experiment and the invaded community.

Materials And Methods

Experimental design

Following the experimental designs by Britton (2019) and Britton et al. (2018), we used 10 additive and substitutive treatments across a combination of allopatric and sympatric contexts and replicated each treatment three times (Table 1). Two control treatments used each species in allopatry (“Allopatry”; $N=10$; Table 1). One substitutive treatment combined these two species in sympatry (“Sympatry”; $n=5+5$, $N=10$; Table 1). Three additive treatments then used these two species in sympatry across three different abundances (“Interspecific competition”, $n=10+10, 15+15, 20+20$; $N=20, 30, 40$; Table 1). Four intraspecific competitions used mud carp and mrigal carp in allopatry in higher abundances (“Intraspecific competition”; $N=20, 30$; Table 1). All the fish we used were juveniles and had been hatchery reared in May 2019 simultaneously for these two species. Their starting lengths were 3–3.5 cm and 1.5–2 cm, and they weighed 0.5–0.7 g (on average 0.63 g) and 0.1–0.2 g (on average 0.11 g) for mud carp and mrigal carp, respectively. The predicted stable isotope half-life for their dorsal muscle was 36 and 38 days for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Thomas, Crowther 2015).

We completed the experiment using the treatments within enclosures in a large pond (50 m long \times 50 m wide, 1–2 m deep) at the Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou, China. The enclosures were net cages (length: 2 m; width: 1 m; height: 2 m; mesh: 4 mm², 10 mesh) fixed at the pond bottom using bamboo poles tied to the four top/bottom corners (Fig. S2). Our net cages prevent bird predation and fish ingress and egress but allow movements of small invertebrates and suspended materials. The 30 enclosures were numbered and placed neatly in the pond with a 2 m distance between them and 5 m distance from the pond edge. For each treatment, the enclosures were drawn randomly based on the enclosure number. During the experiment, we kept the pond without artificial disturbance; thus, sediments and organisms in the pond are the primary sources of food for mud carp and mrigal carp.

The experiment ran for one and half years (547 days) from 21 June 2019 to 19 December 2020. This period enabled fish dorsal muscle to undergo more than 10 half-lives and would represent their diet in a pond (Thomas, Crowther 2015). During the experiment, the temperature in the larger pond ranged from 14.5 to 33.5 °C, as revealed by temperature loggers (Wdsen Electronic Technology Co., Ltd). All fish were weighed prior to release into the enclosures. In December 2020, all fish were recovered from the enclosures, euthanized and returned to the laboratory. For each individual, the standard length and total length were measured to 1 mm, and the weight was measured to 0.1 g. Then, a dorsal muscle sample was taken for stable analysis. In addition, the benthic surface grazing snail *Cipangopaludina chinensis* was sampled for stable isotope analysis.

The survival rate (SR) of each species in each cage net ranged from 0 to 1 but was not normally distributed. Thus, the difference in SR between species and treatments was examined using the Mann–Whitney test. The mean specific growth rate (SGR) in mass per replicate and species was calculated as $(\ln W_{s+t}) - (\ln W_s) / t$ (De Santis et al. 2020), where W_s = mean starting weight of the species in the replicate, W_{s+t} = mean end weight of the species in the replicate, and t = the duration of the experiment in days. By running the `rlmer()` function in the *robustlmm* package in R (Koller 2016), we performed robust linear mixed models to analyze SGR variation with species, treatments, and their interactions, in which the cage net number was set as a random factor, i.e., $SGR \sim \text{species} * \text{treatments} + (1 | \text{cage net number})$. The P value in robust linear mixed models was calculated for a two-tailed test following Cutler et al. (2021). Furthermore, multiple comparisons of the SGR between the allopatry treatment and each other treatment for each species were finished using the *emmeans* package (Lenth 2021). The P value in multiple comparison results was adjusted using the Bonferroni method.

Invaded wild fish communities

In four wild fish communities where they coexist, mud carp and mrigal carp were sampled. The sampling sites are located downstream of the Pearl River basin in China, i.e., the North River downstream (S1) and the central area of the Pearl River delta (S2-S4) (Fig. S3). At each site, we sampled fish using a combination of gillnets, fish traps, and cast nets (see details in Zhang et al. (2021)). Following their capture, they were euthanized and returned to the laboratory. In the laboratory, each of the individuals was identified to species and measured for the standard length (mm) and the total weight (g). For stable isotope detection, a small part (approximately 2 g) of dorsal muscle of each individual was cut and frozen at -20 °C.

Stable isotope analysis

Muscle samples of mud carp, mrigal carp and snails were freeze dried at -45 °C for 48 hours to constant weight in an FD-1-50 plus freeze-dryer (Beijing Biocool Experimental Instruments Co., Ltd.). The dried muscles were then ground to powder using a GT200 grinder (Beijing Grinder Instrument Co., Ltd.). Then, 0.5 mg of the ground muscle of each individual was encapsulated in a tin (Sn) capsule to ensure that they remained intact and did not leak or contaminate. The stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and elemental concentrations of the tissues were detected using a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Waltham, MA, USA) coupled with an elemental analyzer (Flash EA 1112, Thermo Fisher Scientific, Milan, Italy).

The CN ratios of mud carp and mrigal carp ranged from 3.14 to 3.30, which was consistently below 3.5, indicating very low lipid content (Post et al. 2007); thus, the data were analyzed without lipid correction. Because both species in the mesocosm treatments were cultured in the same pond ecosystem, they had the same trophic baseline. $\delta^{15}\text{N}$ was used to estimate fish trophic positions. Trophic position was calculated as follows: $\text{trophic position} = (\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n + \lambda$, where $\delta^{15}\text{N}_{\text{base}}$ is the mean $\delta^{15}\text{N}$ of the baseline organism of the benthic surface grazing snails *C. chinensis*, Δ_n is the enrichment in $\delta^{15}\text{N}$

per trophic level and equals 3.4 ‰, and λ is the trophic position of the baseline organisms and equals 2 (Post 2002). Robust linear mixed models were constructed to analyze the effects of species, experimental treatment and their interactions on individual trophic position and $\delta^{13}\text{C}$ through the *robustlmm* package (Koller 2016). Multiple comparisons of the dependent variables among each level of the treatments for each species were performed in the *emmeans* package (Lenth 2021).

To describe trophic niches, we selected the most commonly used stable isotope ratios, which are defined as quantitative indicators of trophic niches (Marshall et al. 2019). To determine the trophic niche of the studied fish across different experimental designs or different wild communities, we calculated the Layman et al. (2007) niche metrics of $\delta^{13}\text{C}$ range (CR) and $\delta^{15}\text{N}$ range (NR). The niche size was estimated using the corrected standard ellipse area (SEA_C) and Bayesian standard ellipse area (SEA_B) by running the *SIBER* package (Jackson et al. 2011). All data analyses were completed in R 4.1.1 (R Core Team 2020).

Results

SR varied significantly between species but not among experimental treatments. The SR of mud carp ranged from 0 to 1, with a median of 0.8, which was significantly lower than that of mrigal carp, which ranged from 0.2 to 1, with a median of 1. The main losses of mud carp were the replication of *intraspecific_20* and *sympatry*, located at the corners of the cage net arrays, which are assumed to be due to netting failure during summer storms.

Specific growth rate

The mud carp SGR was significantly lower than that of the mrigal carp ($b = 0.005$, $Z = 21.68$, $P < 0.001$), as suggested by the robust linear mixed models (Table 2). The SGR of the native mud carp (0.0086 ± 0.0006) (mean \pm SD) was significantly lower than that of the invasive mrigal carp (0.0142 ± 0.0003). The mud carp SGR decreased significantly with increasing density in the intra- and inter-specific competition treatments compared to the allopatry control (Fig. 1, Table 2). Mrigal carp SGR also decreased with increasing density under intra- or inter-specific treatments, but it showed no significant differences until the severe interspecific condition (*interspecific_40*) compared to the allopatry control (Fig. 1). The SGR of both species showed density dependence, but there was no significant difference between the intra- and inter-specific competition treatments at the same density level.

Intra- and inter-specific competition affects the trophic niches of native mud carp and invasive mrigal carp

The isotopic niches of mud carp and mrigal carp diverged distinctly across all experimental treatments. Mud carp had a significantly higher trophic position ($b = -0.200$, $Z = -6.43$, $P < 0.001$) (Table S1) and a significantly higher $\delta^{13}\text{C}$ than did mrigal carp ($b = -0.910$, $Z = -6.58$, $P < 0.001$) (Table S2).

The experimental treatments also had significant effects on both the trophic position and $\delta^{13}\text{C}$ of mud carp, as indicated by the multiple comparison results (Fig. 2–3, Table S1–S2). Interspecific competition at high densities drove significant declines in both the trophic position and $\delta^{13}\text{C}$ of the mud carp, but intraspecific competition showed no significant effects. However, under severe interspecific competition (interspecific_40), mud carp trophic position and $\delta^{13}\text{C}$ returned to those in the allopatry control.

As suggested by SEA_c and SEA_B in Table 3 and Fig. 3, the trophic niche size of mud carp increased with conspecific densities in allopatric treatments, indicating a shift to a more generalized diet as intraspecific competition increased. However, the trophic niche size of mud carp was largest in the sympatry control but decreased with increasing interspecific competition with mrigal carp (Table 3, Fig. 3). This indicated that mud carp shifted to a generalized diet in the presence of mrigal carp but shifted to more specialized diets under increased interspecific competition. This finding can be summarized as “niche expansion in sympatry, niche constriction in severe interspecific competition”.

For mrigal carp, its trophic position and $\delta^{13}\text{C}$ also declined with increasing density under intra- and interspecific competition but rebounded to the same level in the allopatry control under severe interspecific conditions. Such density dependence patterns were consistent with those of mud carp, although the multiple comparisons suggested no significant differences between experimental treatments (Fig. 2). In the interspecific_20 treatment, the trophic position of mrigal carp was highest among all treatments, indicating a tendency of increasing trophic position when in sympatry with native mud carp. The trophic niches of mrigal carp also showed a high dependence on density. The size of its trophic niche decreased with increasing intra- or inter-specific competition.

Trophic niches in invaded communities vs. the experiment

In invaded communities, both mud carp and mrigal carp expanded their trophic niches, as indicated by higher NR, CR, SEA_c and SEA_B than those in the sympatry control (Table 4). The mud carp niche had relatively high trophic positions (indicated by $\delta^{15}\text{N}$) and relatively stable breadths among communities, but the mrigal carp niche varied significantly in size and CR across communities (Table 4). Moreover, isotopic niches overlapped greatly between species across invaded communities, although niches diverged with no overlap between species in the sympatry control, as indicated by the SEA_c in Fig. 4.

Discussion

The presence of coexisting mrigal carp in the sympatric treatments had marked impacts on the growth and trophic niches of the native mud carp when compared to allopatric treatments. Generally, the native mud carp had a lower SGR and broader and higher-level trophic niche than the invasive mrigal carp. The mud carp SGR decreased when the con- and inter-specific densities increased, showing a density dependence. At the same density level, there were no significant differences in mud carp SGR between

sympatric and allopatric treatments, which rejected Hypothesis 1. Compared to the allopatry treatment, mrigal carp presence drove the mud carp trophic niche toward broader sizes at lower trophic levels, which rejected Hypothesis 2, but intensified interspecific competition drove the mud carp trophic niche to be constricted, which corroborated Hypothesis 2. However, mrigal carp had a higher SGR than mud carp, and its trophic niche in sympatric treatments became smaller at higher trophic levels compared to the allopatry treatment. The niche divergence pattern in the invaded community was consistent with that in the pond experiment in terms of relative trophic position but different in terms of niche breadth and niche overlap.

Specific growth rate

The substantial differences in SGR among the allopatry and other treatments for both species were considered to primarily be an effect of the intensified competition for prey resulting from higher fish densities (De Santis et al. 2020), but such effects were the same between intra- and inter-specific competition. The density dependence in mud carp growth rejected Hypothesis 1. Invasive mrigal carp affected mud carp growth by increasing density (i.e., mud carp growth decreases as density increases). The density dependence in growth was consistent with De Santis et al. (2020) and Britton et al. (2018), where similar effects were observed in the growth rates of native chub *Squalius cephalus* and native tench *Tinca tinca*, respectively, between allopatry and sympatry with invasive species.

The significantly low SGR of mud carp and its SGR significantly declined as density increased compared with those of mrigal carp, providing evidence of the strong divergence in growth rate between native species and invasive species. The invasive mrigal carp appear to be better suited than native mud carp in capturing and utilizing prey resources, which is also evidenced by the fact that mrigal carp snatches food from mud carp when in sympatry (Yu et al. 2019).

Intra- and inter-specific competition affects the trophic niches of native mud carp and invasive mrigal carp

In addition to changes in fish growth rate, there were also marked differences in position and size of the trophic niche among treatments. Compared with the allopatric treatments, the trophic niche of mud carp shifted to a lower trophic level and was broader in size when in sympatry with mrigal carp, i.e., niche expansion in sympatry, contrary to Hypothesis 2. These increased niche sizes and reduced trophic positions implied that mud carp in sympatric treatments shifted to a generalized but more herbivorous diet. When interspecific competition intensified due to increasing density, the trophic niche of mud carp shrank compared to the sympatry control, as per Hypothesis 2. The changes suggested that mud carp shifted to a specialized diet when interspecific competition intensified, a result consistent with the niche variation hypothesis predicting that populations become less generalized in their diet under conditions of increased interspecific competition (De Santis et al. 2020; van Valen 1965). In allopatric treatments, the trophic niche size of mud carp increased under intraspecific competition compared to the allopatry control. The increase in niche size in intraspecific competition is consistent with trophic niche theory, which suggests that when resource competition increases, species will expand

their niche and explore a wider dietary base to maintain their energetic requirements (De Santis et al. 2020; Svanbäck, Bolnick 2007). Thus, mud carp will generally expand their trophic niche under intraspecific competition, sympatry control and interspecific competition compared to the allopatry control, but there are fundamental differences in the impact between increased intraspecific competition (niche expansion) and interspecific competition (niche constriction). This is consistent to some extent with “niche expansion in allopatry and niche constriction in sympatry” from De Santis et al. (2020).

Another pattern in mud carp trophic position variation is that its trophic position and $\delta^{13}\text{C}$ decreased with increased intra- and inter-specific competition, but under severe interspecific competition (interspecific_40), they rebounded to the same level in the allopatry control. This is probably because the shortage in low trophic level prey resources, e.g., phytoplankton, caused by intensified competition drove mud carp to expand its trophic niches toward high trophic levels again.

The niche breadth of mrigal carp became constricted in intraspecific competition, sympatry control and interspecific competition compared to the allopatry control. These changes suggested that mrigal carp shifted to a specialized diet in sympatry, intra- and inter-specific competition treatments. This pattern is consistent with the niche variation hypothesis, which predicts that populations become less generalized in their diet under increased competition (De Santis et al. 2020; van Valen 1965). The reduced niche size along the increased density also suggested a limitation of representative samples in large populations.

Therefore, when in sympatry, mud carp and mrigal carp used different strategies to maintain their energy input, as supported by the divergent patterns of growth rate and niche partitioning between populations. Mud carp tend to forage a wide variety of resources, as suggested by their relatively large niche size. However, mrigal carp that are superior in body size tend to prey primarily on a small variety of resources. The higher specialization in the trophic niche of mrigal carp is probably due to its high competitiveness and efficiency in foraging (snatching food from mud carp when in sympatry (Yu et al. 2019)) and digestion (Bowen et al. 2006). In contrast, mud carp, having inefficient digestion (Bowen et al. 2006), had to rely on a wide variety of food sources by expanding the trophic niche to avoid interspecific competition.

Trophic niches in invaded communities

Although the relative niche positions between species in the invaded communities were consistent with the experimental results, inconsistent patterns occurred due to the complex environments. The niche expansion in both species in the invaded communities suggested an increase in niche variation and plasticity in resource utilization. The niche expansions and niche variation could be driven by the increase in resource breadth in the environment (Pastore et al. 2021). However, when resources are not fully exploited, niche opportunities exist for invasive species (Shea, Chesson 2002). The rich and diverse detrital resources in the subtropical Pearl River delta likely created niche opportunities for mrigal carp invasion. However, the niche overlap between mrigal carp and mud carp in the invaded communities indicated the possibility of interspecific dietary competition. Intensified competition in biologically diverse

communities could also drive individuals to become increasingly opportunistic and thus have greater niche variation (Britton et al. 2019; Rossi et al. 2015; Svanbäck, Bolnick 2007). The higher niche variation in position and size in mrigal carp than in mud carp showed a higher plasticity in resource utilization of the invasive species than that of the native species.

Conclusion

When they coexisted, the invasive mrigal carp drove the native mud carp toward a lower SGR (density dependence), and the mud carp trophic niche shifted toward a lower trophic position and broader niche size but the niche constricted when interspecific competition intensified. However, mrigal carp maintained relatively stable SGR and trophic position but constricted trophic niche size in sympatric experiments compared to the allopatry control. The high SGR of mrigal carp was probably due to its high efficiency in foraging and digestion. In wild communities, the niche expansions of both species suggested their plasticity in resource utilization. These results also suggested a complexity in how ilyophagous invasive species integrate into food webs and alter their structure.

Declarations

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Competing interests

The authors declare no conflicts of interest.

Author contributions

Yingqiu Zhang conceived the study. Yingqiu Zhang and Jie Li obtained the research funding. Yingqiu Zhang, Fangcan Chen, Yuefei Li, Xinhui Li, Shouhui Dai, and Jie Li performed the experiments and sampling. Yingqiu Zhang, Fangcan Chen, Yuefei Li, Xinhui Li, Shouhui Dai, and Jie Li analyzed and interpreted the data. Yingqiu Zhang led the writing of the manuscript with input from all other coauthors. All authors gave final approval for publication.

Availability of data and code

The datasets and R code generated during the current study are available from the corresponding author upon reasonable request.

Ethics approval

The use of fish was authorized by the Laboratory Animal Ethics Committee, Pearl River Fisheries Research Institute, CAFS.

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Tables

Table 1 Treatments used in the experiment, showing the number of fish per species per treatment (n) and the total number of fish per treatment (N).

Treatment	code	Mud carp (n)	Mrigal carp (n)	N
Allopatry (mud carp)	allopatry	10	0	10
Allopatry (mrigal carp)	allopatry	0	10	10
Intraspecific competition (20 mud carps)	intraspecific_20	20	0	20
Intraspecific competition (20 mrigal carps)	intraspecific_20	0	20	20
Intraspecific competition (30 mud carps)	intraspecific_30	30	0	30
Intraspecific competition (30 mrigal carps)	intraspecific_30	0	30	30
Sympatry	sympatry	5	5	10
Interspecific competition (10)	interspecific_20	10	10	20
Interspecific competition (15)	interspecific_30	15	15	30
Interspecific competition (20)	interspecific_40	20	20	40

Table 2 The robust linear mixed model (specific growth rate ~ species * treat + (1 | cage net number)) suggested that the specific growth rate varied significantly between species, among treatments, and among their interaction term.

	beta	2.5 %	97.5 %	SE	Z	P
Intercept	0.009	0.009	0.010	0.000	53.48	<0.001
Species (mrigal carp vs mud carp)	0.005	0.005	0.005	0.000	21.68	<0.001
Treat (intraspecific_20 vs allopatry)	-0.001	-0.001	-0.000	0.000	-3.32	<0.001
Treat (intraspecific_30 vs allopatry)	-0.001	-0.002	-0.001	0.000	-5.77	<0.001
Treat (sympatry vs allopatry)	-0.000	-0.001	0.000	0.000	-1.15	0.25
Treat (interpecific_20 vs allopatry)	-0.001	-0.001	-0.000	0.000	-2.92	0.003
Treat (interpecific_30 vs allopatry)	-0.001	-0.002	-0.001	0.000	-5.18	<0.001
Treat (interpecific_40 vs allopatry)	-0.002	-0.002	-0.001	0.000	-6.43	<0.001
Species * Treat (intraspecific_20 vs allopatry)	0.001	-0.000	0.001	0.000	1.62	0.10
Species * Treat (intraspecific_30 vs allopatry)	0.001	0.000	0.001	0.000	2.83	0.005
Species * Treat (sympatry vs allopatry)	0.000	-0.000	0.001	0.000	1.25	0.21
Species * Treat (interpecific_20 vs allopatry)	0.001	0.000	0.001	0.000	2.05	0.040
Species * Treat (interpecific_30 vs allopatry)	0.001	0.000	0.001	0.000	2.56	0.010
Species * Treat (interpecific_40 vs allopatry)	0.001	0.000	0.001	0.000	3.34	<0.001

Table 3 $\delta^{15}\text{N}$ range (NR), $\delta^{13}\text{C}$ range (CR), corrected standard ellipse area (SEA_c) for small samples and the Bayesian standard ellipse (SEA_B) of the native mud carp and the invasive mrigal carp in the experimental treatments

Species	treatment	NR	CR	SEA _c	SEA _B
mud carp	allopatry	0.6	1.283	0.227	0.205
	intraspecific_20	0.766	1.908	0.398	0.358
	intraspecific_30	0.793	2.323	0.376	0.322
	sympatry	0.725	1.526	0.420	0.358
	interspecific_20	0.694	1.848	0.316	0.280
	interspecific_30	0.875	1.364	0.318	0.286
	interspecific_40	0.939	1.077	0.259	0.231
	mrigal carp	allopatry	0.694	0.891	0.125
intraspecific_20		0.713	0.564	0.078	0.073
intraspecific_30		0.465	0.648	0.086	0.075
sympatry		0.361	0.671	0.065	0.055
interspecific_20		0.312	0.574	0.048	0.043
interspecific_30		0.435	0.599	0.048	0.043
interspecific_40		0.623	0.509	0.068	0.060

Table 4 Sample size (N), standard length (SL, cm), $\delta^{15}\text{N}$ range (NR) and $\delta^{13}\text{C}$ range (CR), the corrected standard ellipse area (SEA_c) for small samples and the Bayesian standard ellipse (SEA_B) of the native mud carp and the invasive mrigal carp in invaded communities and the sympatry control

species	community	N	SL	NR	CR	SEA _c	SEA _B
mud carp	S1	11	12.8–24	14.362	4.579	17.133	14.302
	S2	12	13–20	9.048	6.378	14.759	11.809
	S3	9	15.5–22	16.73	3.938	22.752	17.784
	S4	11	16–21.1	10.758	5.59	16.529	14.593
	sympatry			0.725	1.526	0.420	0.358
mrigal carp	S1	11	16–23	7.386	3.888	6.882	6.214
	S2	13	14.9–27.4	8.027	3.117	4.450	3.868
	S3	10	21.5–27.9	11.931	6.464	28.318	22.994
	S4	14	17.2–40	11.805	10.642	34.842	30.568
	sympatry			0.361	0.671	0.065	0.055

Figures

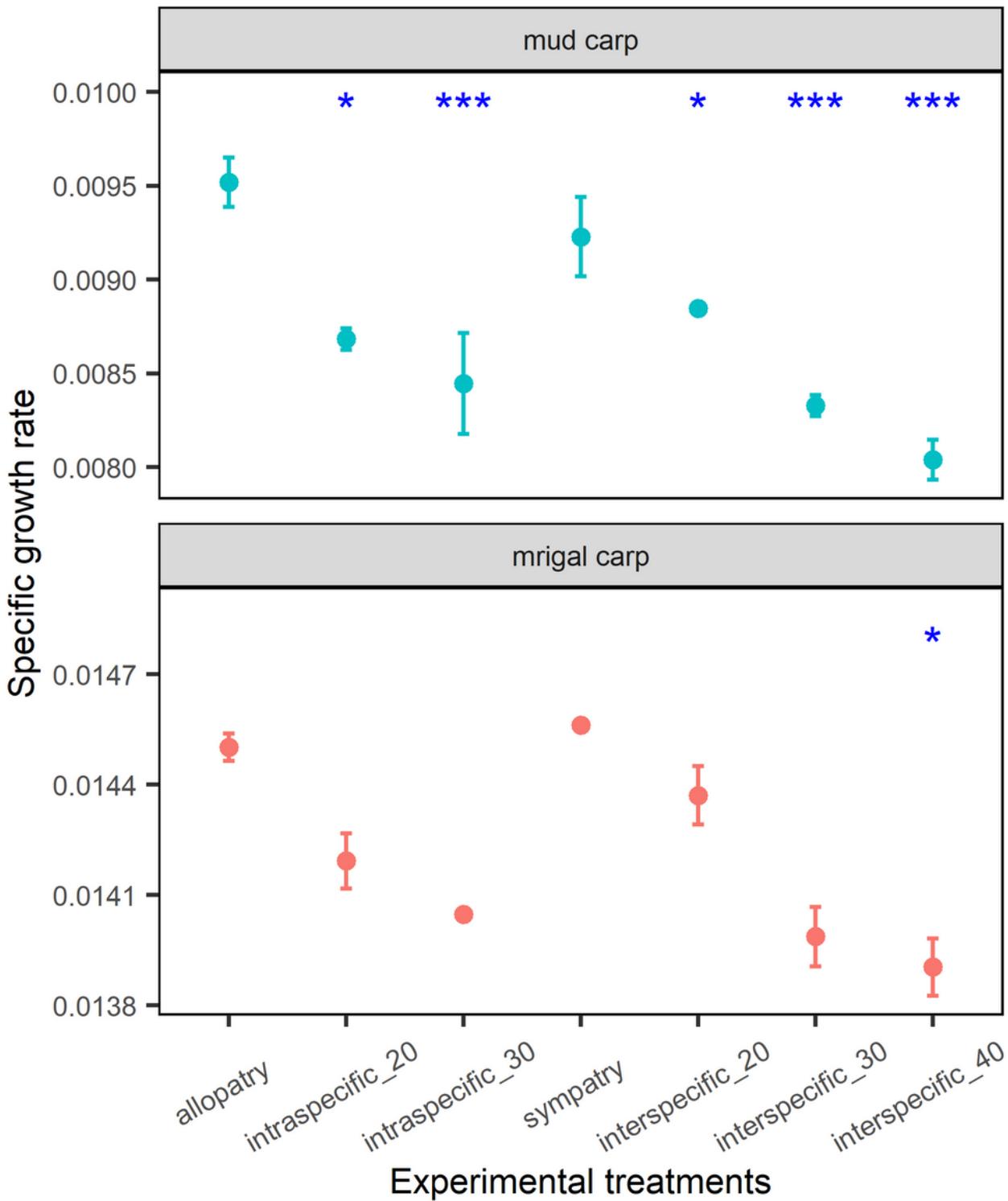


Figure 1

Specific growth rate (mean ± SE) of the invasive mrigal carp and the native mud carp among different experimental treatments. Asterisks indicate significant differences between treatments as suggested by the multiple comparison test: * for $P < 0.05$; ** for $P < 0.01$; *** for $P < 0.001$.

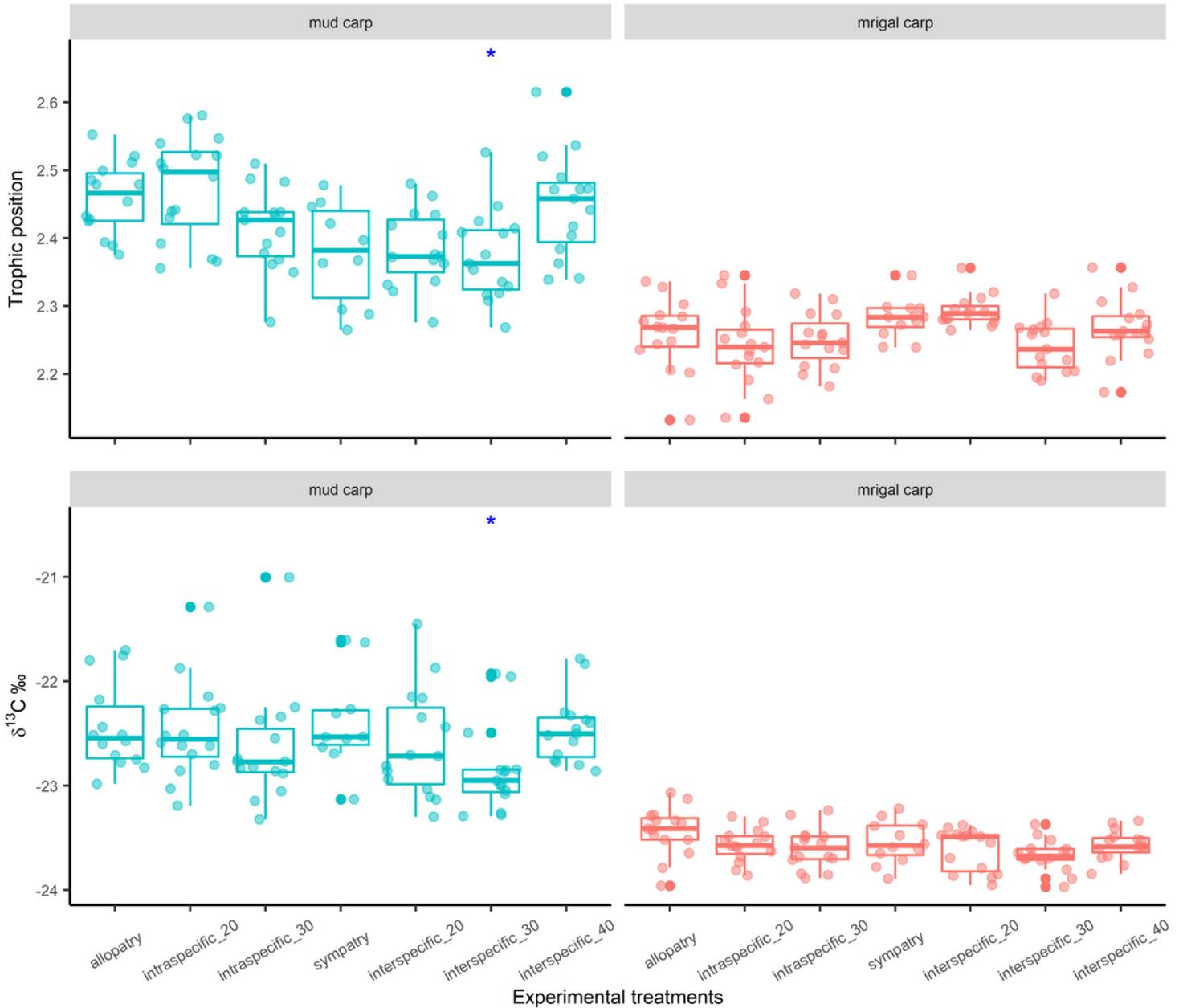


Figure 2

Variations in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of mud carp and mrigal carp among the experimental treatments. The absence of the same letters on top of the boxplot indicates a significant difference between treatments suggested by the multiple comparison test. Asterisks indicate significant differences between treatments as suggested by the multiple comparison test: * for $P < 0.05$; ** for $P < 0.01$; *** for $P < 0.001$.

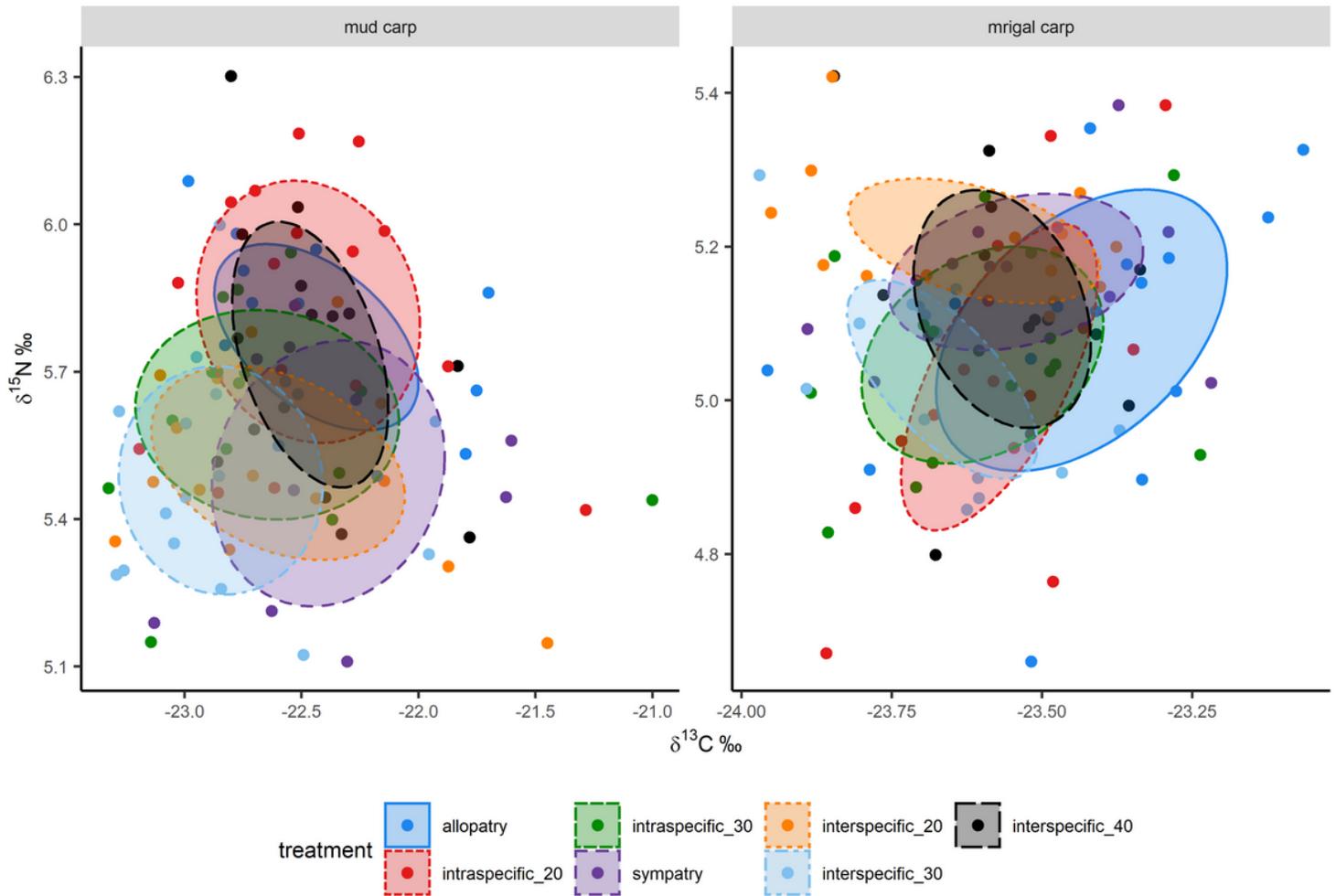


Figure 3

The trophic niche of mud carp and mrigal carp, indicated as the corrected standard ellipse area (SEA_c) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, varied among experimental treatments. Points represent individual $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and ellipses represent SEA_c

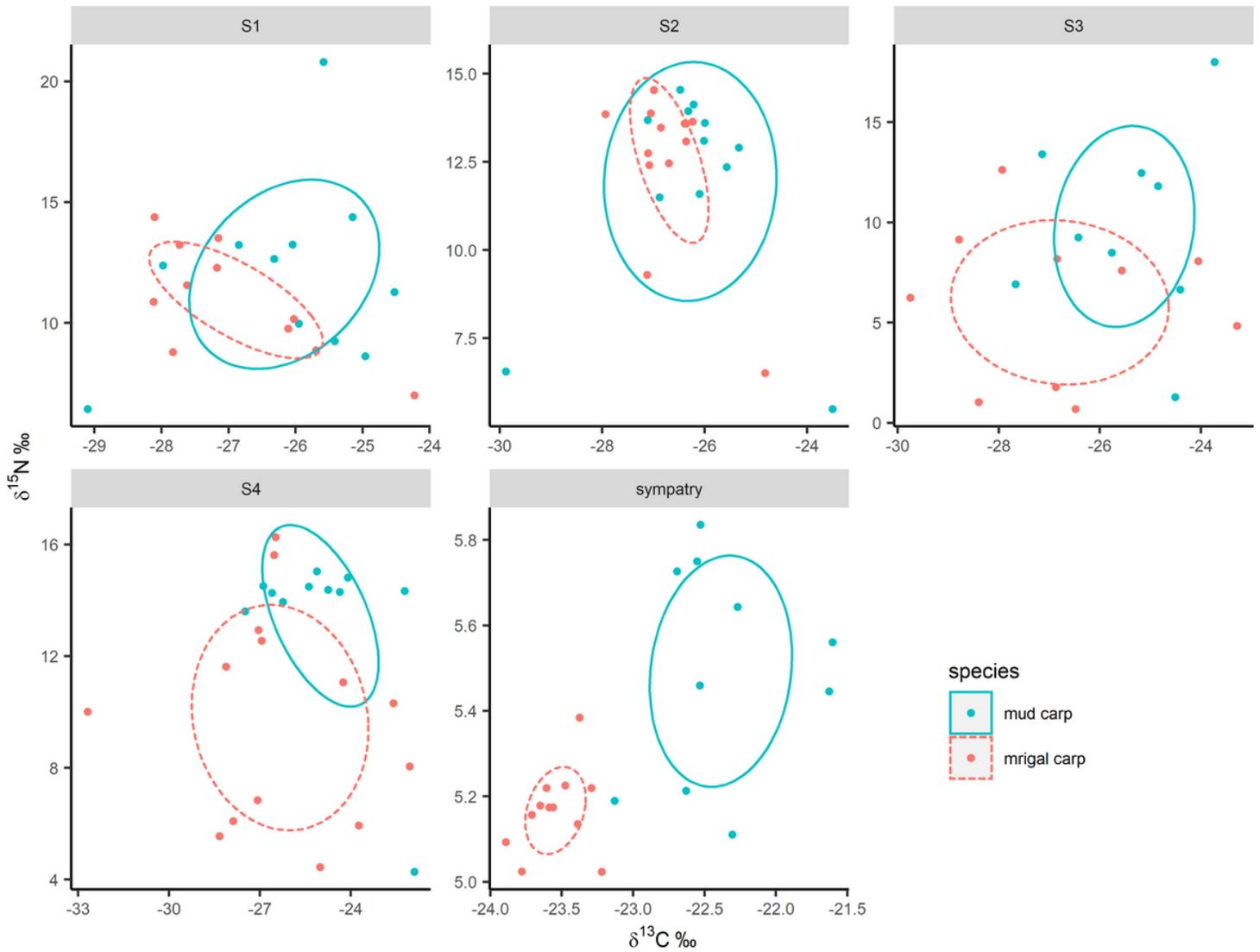


Figure 4

Stable isotope biplots comparing the corrected standard ellipse areas (SEAc) of sympatric mud carp and mrigal carp between the invaded communities (S1–S5) and the sympatry control in the experiment

Supplementary Files

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