Habitat alteration facilitates the dominance of invasive species through disrupting niche partitioning in floodplain wetlands

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Abstract

Aim: Exotic species invasion often leads to declines in local and regional biodiversity, particularly in freshwater ecosystems. This biodiversity loss is generally facilitated by human activities such as land cover change and hydrological alternation. Recent advances in stable isotope analysis (SIA) have been highlighted in many studies addressing fundamental issues in invasion ecology, especially in quantifying competition for resources between native and exotic species. However, how anthropogenic disturbance influences trophic relationships among invasive and native species remains poorly understood.

Location: Middle-lower Yangtze River Region, China.

Methods: To investigate the effects of human disturbance on interspecific trophic interactions, this study compared isotopic niche space and overlap of the introduced red swamp crayfish (*Procambarus clarkii*) and the native oriental river shrimp (*Macrobrachium nipponense*) and freshwater snail (*Bellamya aeruginosa*) in natural and modified wetlands.

Results: Based on carbon and nitrogen SIA, we found ubiquitous niche shifts in macroinvertebrates with increased competition, which might lead to significant niche contraction in modified habitats at both community and population scales. Moreover, the isotopic niche width of the exotic crayfish was twice as larger as that of natives at both habitats, suggesting that the exotic *P. clarkii* had great competitive superiority over the native species. However, the effects of habitat modification on niche overlap were inconsistent. While the niche overlap between crayfish and shrimp was significantly higher in modified habitats than in natural open waters, niche overlap between crayfish and the snail was significantly reduced.

Main conclusions: Collectively, our findings highlight that the competitive outcomes of interspecific trophic interactions can be dependent on the prey availability and diversity, which embraces both the classic optimal foraging theory and competition theory to understand how environmental change, such as habitat alternation, affects the biological invasion processes.
1 | INTRODUCTION

The introduction of exotic species, habitat change, climate change, overexploitation and pollution are the five leading drivers of biodiversity loss (Mazor et al., 2018). Freshwater ecosystems are often vulnerable to biological invasions of exotic species (Tricarico et al., 2016). Biological invasions can lead to changes in composition and structure of species assemblages and can have major complications for ecosystem processes and functioning (Hector & Bagchi, 2007; Olden et al., 2004; Pejchar & Mooney, 2009). Numerous invasions of non-native species into aquatic environments have been linked to human activities, especially by urbanization and agriculture (Ruaro et al., 2018).

The establishment of non-native species can (a) increase interspecific competition, which can result in negative consequences for native species; or (b) promote trophic niche divergence, which can facilitate integration of invaders into the community and their coexistence with native species (Tran et al., 2015). Therefore, the comparison of the trophic ecology of exotic and native species can provide insights into the mechanisms of invasive species expansion. As omnivory and high trophic plasticity are typical traits of successful invaders (Clavel et al., 2011), their trophic ecology may differ across their invasive range in a complex manner (Cucherousset et al., 2012; Tillberg et al., 2007). Environmental change can also influence the establishment of non-native species, as disturbance can act as a precursor to invasions (Allan & Flecker, 1993; Hobbs & Huenneke, 1992). Invasive species can severely disrupt the organization of native communities by excluding native species or reducing their abundance (Gurevitch & Padilla, 2004). Investigating the interactions among invaders and native species and how invaders are incorporated into local communities could not only improve our understanding of the impacts of biological invasion and habitat change on the structure and function of ecosystem, but also provide a sound scientific basis for effective ecosystem management and biodiversity conservation (Lodge et al., 2012).

Stable isotope analysis (SIA) has emerged as an important tool in trophic ecology for assessing resource use and trophic interaction among coexisting species, and for estimating trophic level and energy transfer in ecological communities (Bearhop et al., 2004; Fry, 2006). Moreover, SIA allows the estimation of the isotopic niche overlap among sympatric species to infer potential intra- and interspecies competition for resources (Balzani et al., 2016; Haubrock et al., 2020), niche partitioning (Mazumder et al., 2016) or foraging specialization (Parent et al., 2014). Among the stable isotopes common to all organisms, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes are the most frequently applied to address questions about trophic interactions (Kamenova et al., 2017). While $\delta^{13}C$ reveals the carbon origin of diets (e.g. foraging habitat; Bearhop et al., 2004), $\delta^{15}N$ informs the step-wise N enrichment within each trophic level (i.e. trophic position; Fry, 2006). Thus, isotopic niche based on $\delta^{13}C$ and $\delta^{15}N$ provides a quantitative estimate of trophic niche (Bearhop et al., 2004; Marshall et al., 2019) despite limitations (Hette-Tronquart, 2019), such as the temporal variance in the diet-tissue discrimination factor (Post et al., 2007).

Recently, SIA has been highlighted in a few studies addressing fundamental issues in invasion ecology (Kamenova et al., 2017), especially in answering questions relating to the ecological mechanisms underlying invasion processes, such as invasion pathway, and the impacts of invasive species (McCue et al., 2020). For example, Vander Zanden et al. (1999) demonstrated that the diet of the native lake trout (Salvelinus namaycush) was shifted from littoral to pelagic habitat with reduced trophic position following the invasion of exotic smallmouth bass Micropterus dolomieu and rock bass Ambloplites rupestris in North American boreal lakes. Fera et al. (2017) showed that the aquatic invasive species (Dreissenid mussels) had the potential to alter key ecosystem services through their impacts on energy pathways by tracing enrichment of $\delta^{13}C$ in benthivorous fish following Dreissenid mussel invasion. By comparing trophic niche size, SIA has also been a powerful tool to quantify resource competition between invasive and native species as documented for invaders such as crayfish (Olsson et al., 2009), fish (Costantini et al., 2018; Rush et al., 2012), turtles (Balzani et al., 2016) and the Argentine ant (Tillberg et al., 2007).

The red swamp crayfish (Procambarus clarkii) is native to North America, but it has invaded aquatic ecosystems of more than 40 countries across all continents except Australia and Antarctica (Officialdegui, 2019), and has become the most widely distributed crayfish in the world (Holdich, 2002). P. clarkii is an omnivore and can affect all levels of the freshwater food chain by reducing the abundance of macrophytes, preying on macroinvertebrates, and decreasing the abundances and growth of amphibians and fish (Gallardo et al., 2016; Twardochleb et al., 2013). In China, P. clarkii was first introduced from Japan to Nanjing in 1929 (Yue et al., 2010) and has rapidly spread to most provinces since. However, species distribution models predicted that the highly suitable habitats for P. clarkii concentrate at the eastern subtropical region, especially the middle and lower reaches of the Yangtze River (Zhao et al., 2016). This region is densely populated, and the majority of waterways and water bodies have been heavily modified. Since the 1970s, about 41.6% of the total lake area in this region has been reclaimed, and reclamation activities and other anthropogenic activities such as damming have had dramatic impacts on the regional hydrology and local water quality (Hou et al., 2020; Lu et al., 2018), which has led to declines in

**KEYWORDS**

floodplain wetland, interspecific trophic relationship, niche partitioning, niche shift, red swamp crayfish (Procambarus clarkii)
biodiversity (Fang et al., 2006; Li et al., 2020; Zeng et al., 2018). *P. clarkii* has become the main contribution to crustacean biomass in this region. For example, in Poyang Lake, the largest lake of this region, the average annual catch of *P. clarkii* from 2009 to 2013 reached 25,000 tons (Zhang et al., 2014), which exceeded the catch of natural fish in the same period (Wang et al., 2014). As part of the Chinese ecosystem protection policy, a 10-year total fishing ban has been initiated for the Yangtze River Basin since 2020, and both native fish and exotic crayfish cannot be legally harvested. Benchmark data on current *P. clarkii* population, its trophic niche and position, and the interactions with other native sympatric species would be invaluable for future ecological studies on topics such as how invasion alters the evolutionary responses to harvest pressure (Palkovacs et al., 2018).

Despite substantial growth in the use of SIA in invasion ecology over the past four decades (Kamenova et al., 2017; Mccue et al., 2020), especially in exploring the role of anthropogenic activities in the widespread introduction of exotic species through reconstructing invasion history (Strayer et al., 2006), very little attention has been directed at understanding the impacts of habitat modification on the post-invasion trophic interactions between invasive and native species. One of the direct consequences of biological invasion is greater competition for resources among coexisting species (Britton et al., 2018; Mccue et al., 2020). Increased interspecies competition exerts important effects on community structure and dynamics (Tilman, 1987). For example, the optimal foraging theory predicts niche expansion with increased competition, as individuals should add (the otherwise suboptimal) new food items to their diet, resulting in wider trophic niche (Stephens & Krebs, 1986). In contrast, the classic competition theory predicts that stable coexistence could be achieved through niche differentiation, leading to reduced dietary overlap (Svanbäck & Bolnick, 2007) and/or niche contraction (Sih & Christensen, 2001). There is empirical support for both hypotheses (Parent et al., 2014). We expect that both mechanisms could be in operation in our ecosystems depending on the competition strength and prey availability.

In this study, we investigated the isotopic niche size of and the niche overlap between three widespread coexisting species, including the exotic red swamp crayfish, a native oriental river shrimp (*Macrobrachium nipponense*) and a native freshwater snail (*Bellamya clarkii*), in relatively natural and heavily modified habitats in the middle Yangtze River basin. The main purpose of the study was to investigate the impacts of habitat modification on the trophic ecology of the three sympatric species. Specifically, we aimed to test the following predictions using δ¹³C and δ¹⁵N SIA: (a) the invasive *P. clarkii* has wider trophic niche than the native *M. nipponense* and *B. clarkii*; (b) human disturbances such as habitat alternation increase trophic niche overlap; and (c) intensive sympatric competition for resources leads to niche contraction. The findings will improve the knowledge of the mechanisms of post-invasion expansion of exotic species and the consequences on native species and local biodiversity.

### 2 METHODS

#### 2.1 Study site

Dongting Lake (112°40′-113°10′E, 28°38′-29°45′N, Figure 1), China’s second largest freshwater lake, is one of two large lakes that are freely connected with the Yangtze River. It is one of the biodiversity hubs of the Yangtze basin (Fang et al., 2006). There are three Ramsar wetlands of international importance located within the Dongting Lake, providing foraging grounds for hundreds and thousands of wintering migratory waterbirds (Guan et al., 2016). Due to sedimentation and intensive lake reclamation, the whole lake is divided into three sublakes, which are hydrologically connected through main river channels. Our study site, the West Dongting Lake (WDTL) (111°57′-112°17′E, 28°47′-29°07′N) is the most upstream section (Figure 1). Dongting Lake is a seasonally dynamic system; its hydrology is largely influenced by the prevailing subtropical monsoon climate, with large intra-annual variations in lake area and water level. However, the Three Gorges Dam has greatly changed the lake-river relationship and the natural hydrological regimes in the lake (Lu et al., 2018). During the low water winter season, five broad habitat types can be visually distinguished: open waters, mudflats, Carex sedges, Reed marshes and Black Poplar (*Populus nigra*) plantations, presenting a gradient of human disturbances from relatively natural to extensively alternated. Macroinvertebrate samples were taken from the ends of this gradient (i.e. open waters/mudflats and poplar plantations) to emphasize the contrast of the human modification.

From the late 1980s, plantation of *P. nigra*, an introduced fast-growing tree for wood pulp, started in WDTL. To ensure young trees would survive the summer flooding, high ridges were built through pushing up the lakebed sediments, leaving a network of artificial ditches with varying depth (1.0-2.5 m; Li et al., 2020). These ditches have substantially reduced hydrological connectivity in comparison with other habitats (Dong et al., 2021), leading to a less diverse aquatic community with higher density of *P. clarkii* (Li et al., 2020).

#### 2.2 Sample collection

From 8 to 18 August 2017, crayfish, oriental river shrimp and the freshwater snail were sampled using fyke nets (mesh size: 10 mm). Samples were collected at 32 locations across the WDTL, of which 21 were from the heavily modified ditches at *P. nigra* plantations (referred as modified thereafter) and 11 were from the relatively natural open waters near the wet meadows (referred as natural thereafter) with water depth less than 2.5 m according to crayfish habitat preferences (Figure 1). We set three repetitions of nets at each sample site. The nets were set at 9:00-10:00 a.m. for approximately 24 hr and retrieved the following morning. All samples were transferred to the laboratory for identification, and counting, weighing and crayfish relative abundance (catch per unit effort, CPUE) were calculated for each site.
2.3 | Environmental variable measurements

For each sample site, a range of environmental variables, including water depth (WD), water clarity (WC), pH, water temperature and redox potential (ORP), were measured in situ. Water samples were also taken for laboratory analyses. WD was measured with a hand-held sonar depth sounder SM-5A (Weatherhawk, USA). WC was measured using a Secchi disc. Water pH, temperature and ORP were recorded using a YSI multiprobe (YSI professional plus). In the laboratory, total nitrogen (TN), total phosphorus (TP), suspended solids (SS) and chlorophyll a (Chl-a) were analysed following the standard methods of APHA (1998).

2.4 | Stable isotope analysis

The tail muscle tissues of *P. clarkii* and *M. nipponense* and foot tissues of *B. aeruginosa* were cut using scalpel and scissors and used for stable isotopic analysis. After dried at 60°C to a constant weight, the samples were ground to fine homogeneous powder with mortar and pestle and wrapped in tin capsules.

Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) were measured using Finnegan MAT 253 (Thermo Scientific) coupled with a Flash Elemental Analyzer 1112 System (Chinese Academy of Sciences). Stable isotopic ratios were expressed as δ^{13}C (‰) and δ^{15}N (‰) relative to Pee Dee Belemnite limestone and atmospheric N_{2}, respectively, and calculated as:

\[ \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000. \]

Analytical precisions based on replicates of laboratory standards (urea) for δ^{13}C and δ^{15}N were ±0.1% and ±0.3%, respectively.

2.5 | Data analysis

We used Welch’s two-sample *t* test to compare the difference in macroinvertebrate abundance, environmental variables, δ^{13}C, δ^{15}N and isotopic niche size of the three macroinvertebrates, and isotopic niche overlap in modified and natural habitats. Prior to the *t* test, we checked the normality of the variables using a Shapiro–Wilk test. Variables that failed the Shapiro–Wilk test at 0.05 level were subjected either to logarithm (macroinvertebrate abundance) or square root (WD, TN, Chl-a and WC) transformations to achieve normality.

We used both convex hull and Bayesian standard ellipse area (SEA) to describe community and population niche width. Comparing with other methods such as convex hull (Layman et al., 2007) and frequentist standard ellipses, Bayesian SEA was superior to estimate niche width as it is unbiased and less affected by extreme values and sample size (Jackson et al., 2011); therefore, it is the preferred methods in most current studies (Eckrich et al., 2020). We also calculated and reported the 95% confidence intervals of SEA using 10,000 posterior Markov chain Monte Carlo draws. Interspecific niche overlap between sympatric species was based on 500 posterior draws of the Bayesian standard ellipses. The estimates of Bayesian SEA and niche overlap were carried out using the R package SIBER (Jackson et al., 2011) within the R environment (R 3.5.2. R Development Core Team, 2017).
### 3 | RESULTS

#### 3.1 | Environmental factors and crayfish abundance variation at natural and modified habitats

Crayfish CPUE and Chl-α were significantly higher in modified habitats than in natural ones. However, macroinvertebrate biomass and water depth were significantly lower in modified habitats (Table 1). The difference in other environmental variables, such as water temperature, transparency, SS, TN and TP, was not significant at 0.05 level (Table 1).

#### 3.2 | Community trophic interaction at natural and modified habitats

Macroinvertebrate assemblages at natural and modified habitats varied significantly (p < .001; Table 2) in isotopic niche space. At the natural open water sites, the macroinvertebrate assemblages had a smaller δ¹³C range and larger δ¹⁵N range than in the modified plantation sites. Also, the open water community had significantly larger niche-based TA (total area of convex hulls) and standard ellipses area (SEA) calculated from 10,000 posterior draws. In addition, the macroinvertebrates sampled from the natural open waters had higher δ¹⁵N values than those from plantation sites (Figure 2), suggesting these omnivores feed on higher trophic level prey species in natural habitats.

#### 3.3 | Interspecific niche differences at natural and modified habitats

The standard deviation was relatively small in comparison with the mean values (Table 4) for all species in both habitats, suggesting a normal distribution of the δ¹³C and δ¹⁵N. The exotic crayfish had significantly lower variations in δ¹³C and δ¹⁵N in modified habitats (p = .035 and <.001 for δ¹³C and δ¹⁵N, respectively; Table 3). For native species, the pattern was not consistent. For shrimp, although both δ¹³C and δ¹⁵N were higher in natural open waters, the difference in δ¹³C was not significant between the two habitats (p = .113; Table 3). For the snail, however, while δ¹³C was significantly lower at sites in the modified habitat (the average δ¹³C was −31.06‰ and −26.29‰ for modified and natural habitats, respectively, p < .001; Table 3), δ¹⁵N was slightly higher in the natural habitat (p = .107; Table 3).

Trophic niche size of all investigated species was significantly higher in natural habitats than in the modified plantations for both SEAc and TA (Table 4, Figure 3). The introduced crayfish had significantly larger trophic niche area than that of the native snail and shrimp, especially measured as SEAc in both natural and modified habitats (Table 4).

#### 3.4 | Interspecific niche overlaps at natural and modified habitats

It was clear that the niche size was smaller in modified habitats than in the more natural open waters, especially for the crayfish and the snail (see Table 4 for statistics). In addition, both the shape of the modelled ellipses and the range of overlap between species varied greatly for the modified and natural habitats. All species had wider δ¹⁵N ranges but narrower δ¹³C spectrums in natural habitats than in modified ones; thus, the variations in δ¹⁵N contributed more to the dietary overlaps among species (Figure 4).

The niche overlap estimated for the two native species (i.e. shrimp and snail) was small in both natural and modified habitats (mean overlap was 0.0247 and 0.0035 for modified and natural habitat, respectively; Table 5). However, the niche overlap between the introduced and native species was significantly higher based on the estimated 95% confidence intervals (Table 5). Finally, the niche

### TABLE 1 | Summary of macroinvertebrate abundance and environmental variables in modified and natural habitats

| Variable                    | Modified Mean (SD) | Natural Mean (SD) | p-value* |
|-----------------------------|--------------------|-------------------|----------|
| Water temperature (°C)      | 2.18               | 30.39 (1.89)      | .082     |
| Water depth (cm)            | 73.98 (58.76)      | 137.50 (50.83)    | .002     |
| Water clarity (cm)          | 35.95 (26.09)      | 34.00 (12.26)     | .768     |
| pH                          | 7.03 (1.03)        | 7.79 (2.19)       | .177     |
| Redox potential (mV)        | 173.96 (91.42)     | 205.89 (25.30)    | .978     |
| Suspended solids (mg/L)     | 0.13 (0.22)        | 0.08 (0.06)       | .337     |
| Total nitrogen (mg/L)       | 7.57 (1.73)        | 7.67 (1.97)       | .881     |
| Total phosphorus (µg/L)     | 0.33 (0.24)        | 0.50 (0.68)       | .823     |
| Chlorophyll a (µg/L)        | 2.87 (3.43)        | 1.02 (1.24)       | .032     |
| Macroinvertebrate biomass (g/m²) | 215.73 (305.94) | 604.80 (637.17)  | .028     |
| Crayfish CPUE (ind/net)     | 16.32 (16.34)      | 4.57 (8.68)       | .009     |

* p-value of the Welch two-sample t test (df = 30) of the difference between natural and modified habitats. Significant difference in bold.
overlaps between crayfish and shrimp and between shrimp and snail were significantly higher at the modified plantations than at the natural open waters. On the contrary, the niche overlap between crayfish and snail was significantly higher at natural habitats (Table 5).

### 4 | DISCUSSION

By comparing the isotopic niche size of three widespread coexisting species, including the invasive P. clarkii, captured at natural and modified habitats in a large floodplain lake of the Yangtze River in China, we demonstrated that habitat modification could lead to niche contraction at both community and population levels. This reduction in niche size could result from increased interspecific competition at the modified habitats, indicated by the significantly higher density of P. clarkii. Through estimating the niche overlap among the three sympatric species, we showed that habitat modification could have contrasting effects on trophic interaction. Specifically, human disturbance increased the degree of niche overlap between crayfish and shrimp, which are both omnivorous generalists (and cannibalistic) and have a high degree of similarity of their ecological niches. However, the niche overlap between crayfish and the algivorous snail was decreased in modified habitats, probably due to differences in food resources. Optimal foraging and competition theory could predict opposing trophic interactions results from intra- and interspecific competition (e.g. Sheppard et al., 2018). We found that these predictions can be strongly context-dependent (Costa-Pereira et al., 2018) and that the effect of competition on niche size and niche overlap is not necessarily consistent across populations and communities (Costa-Pereira et al., 2019; Parent et al., 2014). In fact, our results provided empirical support to both competition hypotheses (Svanbäck & Bolnick, 2007) and optimal foraging theory (Stephens & Krebs, 1986) by showing broad shifts in resource use of macroinvertebrates with increased competition.

#### 4.1 Environmental conditions in natural and modified habitats

Poplar plantations have significantly changed the environmental conditions in modified habitats in terms of water depth and Chl-a

### TABLE 2  Comparison of macroinvertebrate community niche indices at natural and modified habitats

| Metrics             | Modified Mean (SD) | Natural Mean (SD) | p-value<sup>a</sup> |
|---------------------|--------------------|-------------------|----------------------|
| δ<sup>15</sup>N range | 7.06 (0.57)          | 10.14 (0.54)       | <.001                |
| δ<sup>13</sup>C range | 14.02 (0.69)         | 12.95 (1.20)       | <.001                |
| TA (total area of convex hulls) | 68.97 (5.19)        | 92.48 (7.79)       | <.001                |
| SEA (standard ellipses area) | 22.09 (2.89)       | 30.31 (3.12)       | <.001                |
| SEAc (corrected SEA) | 22.55 (2.95)         | 30.94 (3.18)       | <.001                |

<sup>a</sup>p-value of the Welch two-sample t test of the mean overlap between natural and modified habitats. Significant difference in bold.

### FIGURE 2  Macroinvertebrate assemblage δ<sup>13</sup>C and δ<sup>15</sup>N niche space based on the convex hull (left) and standard ellipse (right). Blue points represent macroinvertebrate community from natural habitats. Black points represent macroinvertebrate community from modified habitats

### TABLE 3  Mean δ<sup>13</sup>C and δ<sup>15</sup>N (standard deviation in brackets) of the crayfish, shrimp and snail at natural and modified habitats

|                | N<sup>a</sup> | δ<sup>13</sup>C | δ<sup>15</sup>N | p-value<sup>b</sup> |
|----------------|--------------|----------------|----------------|---------------------|
| Crayfish       | 106, 23      | -25.81 (1.85)   | -24.88 (2.05)  | .035                |
| Shrimp         | 12, 35       | -27.09 (1.54)   | -26.29 (1.44)  | .113                |
| Snail          | 54, 16       | -31.06 (1.64)   | -26.67 (1.96)  | <.001               |

<sup>a</sup>Sample size for modified and natural habitats, respectively.

<sup>b</sup>Based on the Welch two-sample t test, Significant difference in bold.

#### TABLE 3  Mean δ<sup>13</sup>C and δ<sup>15</sup>N (standard deviation in brackets) of the crayfish, shrimp and snail at natural and modified habitats

|                | Modified Mean (SD) | Natural Mean (SD) | p-value<sup>b</sup> |
|----------------|--------------------|-------------------|---------------------|
| Crayfish       | -25.81 (1.85)      | -24.88 (2.05)     | .035                |
| Shrimp         | -27.09 (1.54)      | -26.29 (1.44)     | .113                |
| Snail          | -31.06 (1.64)      | -26.67 (1.96)     | <.001               |

<sup>b</sup>Based on the Welch two-sample t test, Significant difference in bold.
However, the difference in other measured variables was not significant, although water quality was generally worse at the modified sites (e.g. higher SS and TN and lower redox potential; Table 1). In a previous study of the same system, Dong et al. (2021) found that the hydrological connectivity was dramatically reduced from fully connected in the main river channels and open water habitats to 10% in the plantation, resulting in relatively stable hydrology in the highly modified sites (Li et al., 2021). The elevated nutrient level and stable hydrological condition could promote primary productivity, and this would be expected to favour some guilds of zooplankton (e.g. herbivores and detrivores) over others (Budria, 2017). These changes in composition of the lower trophic communities (i.e. prey items and abundance) could alter trophic niche and interaction at higher levels (Schmitz et al., 2004). As we did not sample and analyse food resources, further research is needed to confirm these trophic cascade effects and whether they are different in natural and modified habitats. Nevertheless, higher ecosystem productivity could lead to decreased niche size and niche overlap (Lesser et al., 2020), which is incongruent with our results; hence, other mechanisms, such as the mobility of studied species, may provide a more tenable explanation.

4.2 | Macroinvertebrate trophic niche width variations at natural and modified habitats

Successful invaders generally have wider niches with high abundance and higher resource use plasticity than their non-invasive counterparts (Correia et al., 2002), thus increasing their competitive capabilities (Tilman, 1999). The exotic crayfish collected at WDTL occupied a significantly larger trophic niche than the native shrimp and snail, and this was true for both natural and modified habitats. The larger trophic niche area suggested that this exotic species was opportunistic and could overcome possible changes in prey structure and have advantages in competition (Kondoh, 2003), which might explain its dominance, especially in the modified habitats (Córdova-Tapia et al., 2015).

Biological invasions may disrupt resource partitioning in aquatic ecosystems (Sagouis et al., 2015), potentially resulting in shifts in the resource use of native species (Rogosch & Olden, 2020) and even competitive exclusion (Britton et al., 2018). Our results demonstrated that human disturbance could exacerbate these negative impacts of biological invasions on native biodiversity (Sévêque et al., 2020). However, the increased competition in the modified habitat did not lead to niche

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**TABLE 4** Isotopic niche size calculated as corrected standard ellipse area (SEAc) and total area (TA) of the macroinvertebrates at natural and modified habitats

| Species | SEAc | Modified | p-value<sup>a</sup> | TA | Modified | p-value<sup>a</sup> |
|---------|------|----------|---------------------|----|----------|---------------------|
| Crayfish | 25.17 (0.86) | 23.78 (0.44) | .001 | 33.02 (2.06) | 32.02 (5.02) | .001 |
| Shrimp | 11.73 (0.38) | 7.93 (0.57) | <.001 | 47.49 (4.38) | 28.71 (1.27) | .008 |
| Snail | 14.20 (0.65) | 11.03 (0.28) | <.001 | Mean (SD) | Mean (SD) | <.001 |

<sup>a</sup>p-value of the Welch two-sample t test of the mean overlap between natural and modified habitats. Significant difference in bold.
expansion as speculated by classic optimal foraging theory, because under increased competition conditions, individuals should add new prey items to their diet, widening their trophic niche (Stephens & Krebs, 1986). This opposing result should not be regarded as a dispute to the optimal foraging theory as competition-driven niche expansion is dependent on resource breadth (Costa-Pereira et al., 2019).

4.3 | Macroinvertebrate trophic niche overlap at natural and modified habitats

Trophic niche overlap between species can be interpreted as a shared food source (Pilger et al., 2010; Vander Zanden et al., 1999) and therefore has been proposed as an indicator of potential competition in many studies (Kelly & Jellyman, 2007; Zambrano et al., 2010). According to competition theory (Pianka, 1981), increasing competition promotes resource partitioning between coexisting species, leading to reduction in dietary overlap between competitors (Svanbäck & Bolnick, 2007).

Our analysis showed the broad dietary shift in modified habitats. Specifically, while the algivorous snail increased the intakes of more $^{13}$C depleted food items such as phytoplankton (Hamilton & Lewis, 1992) in the modified habitats, the generalist crayfish and shrimp were much more $^{15}$N-enriched in natural habitats. The dietary shifts might have resulted from niche partitioning predicted by competition theory for coexisting species. However, the detected dietary shifts did not progenerate consistent reduction in niche overlap between the sympatric species (Svanbäck & Bolnick, 2007). The putative reduction in niche overlap was only found between crayfish and snail. On contrast, niche overlap between the crayfish and shrimp was significantly higher in the modified habitats, which could be linked to prey depletion and the loss of prey diversity (Parent et al., 2014; Sévêque et al., 2020). Similarly, although very small in comparison with the niche overlap between exotic and native species, the niche overlap between the two natives was significantly higher in the modified plantations.

Previous studies also found that the impact of anthropogenic disturbance on niche overlap between sympatric species was not unidirectional: both increase or decrease and no change in niche overlap have been reported to be associated with human disturbances (Sévêque et al., 2020), highlighting that niche overlap (or the way how it was measured) may not provide a direct estimate of the intensity of competition (Abrams, 1980). This contradictory effect of habitat modification on niche overlaps can be at least partially explained by the difference in ecological similarity of the compared pairs. A study of crayfish, shrimp and snails co-occurring in aquaculture ponds (Mao et al., 2016) found that epiphytes were the most important carbon sources for both shrimp and crayfish (a range of contributions: 52%–65%), while phytoplankton made up the highest contribution to molluscs (33%–47%). Our results suggested that the competitive outcomes of interspecific trophic interactions might depend on both the availability and diversity of prey and the dietary similarity among sympatric species (Lawlor, 1980).

5 | CONCLUSIONS

The exotic red swamp crayfish had a wider trophic niche with higher plasticity in resource use than native species, making it one of the most successful aquatic invaders worldwide (Oficialdegui, 2019). Our

![Graph showing niche overlap](image)

**FIGURE 4** Graphs show the niche overlap in natural (upper) and modified (lower) habitats based on 500 posterior Bayesian standard ellipses for each of the three macroinvertebrate species. Lines are fitted ellipses, and dots are measured $\delta^{13}$C and $\delta^{15}$N values.

**TABLE 5** Isotopic overlap among macroinvertebrate at natural and modified habitats based on predicted standard ellipses

|          | Modified                  | Natural                  | p-value$^b$ |
|----------|---------------------------|--------------------------|-------------|
|          | Upper CI$^a$ | Mean | Lower CI | Upper CI | Mean | Lower CI |             |
| Crayfish – Shrimp | 0.1667 | 0.1638 | 0.1610 | 0.1409 | 0.1381 | 0.1352 | 0.0000 |
| Crayfish – Snail | 0.1214 | 0.1201 | 0.1187 | 0.2469 | 0.2436 | 0.2404 | 0.0000 |
| Shrimp – Snail  | 0.0269 | 0.0247 | 0.0225 | 0.0042 | 0.0035 | 0.0029 | 0.0000 |

$^a$CI = 95% confidence interval based on 10,000 posterior draws;

$^b$p-value of the Welch two-sample t test of the mean overlap between natural and modified wetlands. Significant difference in bold.
findings demonstrated that human disturbances could facilitate the post-introduction expansion of the exotic species and exacerbate the negative impacts of biological invasions on native species, especially on species with similar ecological niches (Özdilek et al., 2019) such as the widespread oriental shrimp. First, niche size was significantly smaller in anthropogenically modified habitats than in natural open waters at both community and population levels, indicating that the overall reduction in food availability and diversity was caused by habitat modification (Li et al., 2020). Further, the significantly higher degree of niche overlap between species with similar trophic niches suggested that the reduced prey availability and diversity in modified habitats (Dong et al., 2021; Li et al., 2021) could prevent the coexisting species to achieve prey partitioning, leading to the declining population and the ultimate exclusion of the disadvantaged one, usually the natives (the Oriental Shrimp in our study system). In conclusion, our results highlight that the competitive outcomes of interspecific trophic interactions can depend on the prey availability and diversity (Costa-Pereira et al., 2019), which embraces the classic optimal foraging theory and competition theory to understand how environmental change, such as habitat modification and conversion, affects biological invasion processes and biodiversity loss.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All relevant data supporting the results are available from the Dryad: https://doi.org/10.5061/dryad.mkkwh710x.

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**BIOSKETCH**

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