

Predicting the competitive interactions and trophic niche consequences of a globally invasive fish with threatened native species

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Abstract

1. Novel trophic interactions between invasive and native species potentially increase levels of interspecific competition in the receiving environment. However, theory on the trophic impacts of invasive fauna on native competitors is ambiguous, as while increased interspecific competition can result in the species having constricted and diverged trophic niches, the species might instead increase their niche sizes, especially in omnivorous species.
2. The competitive interactions between an omnivorous invasive fish, common carp *Cyprinus carpio*, and a tropically analogous native and threatened fish, crucian carp *Carassius carassius*, were tested using comparative functional responses (CFRs). A natural pond experiment then presented the species in allopatry and sympatry, determining the changes in their trophic (isotopic) niche sizes and positions over 4 years. These predictive approaches were complemented by assessing their trophic relationships in wild populations.
3. Comparative functional responses revealed that compared to crucian carp, carp had a significantly higher maximum consumption rate. Coupled with a previous cohabitation growth study, these results predicted that competition between the species is asymmetric, with carp the superior competitor.
4. The pond experiment used stable isotope metrics to quantify shifts in the trophic (isotopic) niche sizes of the fishes. In allopatry, the isotopic niches of the two species were similar sized and diverged. Conversely, in sympatry, carp isotopic niches were always considerably larger than those of crucian carp and were strongly partitioned. Sympatric crucian carp had larger isotopic niches than allopatric conspecifics, a likely response to asymmetric competition from carp. However, carp isotopic niches were also larger in sympatry than allopatry. In the wild populations, the carp isotopic niches were always larger than crucian carp niches, and were highly divergent.
5. The superior competitive abilities of carp predicted in aquaria experiments were considered to be a process involved in sympatric crucian carp having larger isotopic

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niches than in allopatry. However, as sympatric carp also had larger niches than in allopatry, this suggests other ecological processes were also likely to be involved, such as those relating to fish prey resources. These results highlight the inherent complexity in determining how omnivorous invasive species integrate into food webs and alter their structure.

KEYWORDS

Carassius carassius, comparative functional response, *Cyprinus carpio*, invasive species, isotopic niche, stable isotope analysis

1 | INTRODUCTION

Ongoing globalisation is driving increases in biological invasions (McNeely, 2001). Besides driving biological homogenisation, invasive species can have substantial consequences upon the receiving communities, including the transmission of novel pathogens, habitat degradation and hybridisation with native species (García-Vásquez et al., 2017; Hitt et al., 2003; Matsuzaki et al., 2009). As ecological impacts can also occur via direct predation or indirectly through competition for resources (Foley et al., 2017), then determining the mechanisms involved in determining the severity of these impacts is integral for invasion risk management to avoid negative and cascading effects on food webs (Britton et al., 2010).

Although predicting the ecological impacts of alien species is an important aspect of invasion risk assessment, it remains highly challenging (Dick, Laverty, et al., 2017). Considerable progress has been made in predicting the trophic impacts of aquatic invasive species in recent years using comparative functional responses (CFRs), where relatively simple aquarium experiments using alien species and their native analogues have successfully predicted high impacting invaders (e.g. Laverty et al., 2017; Paterson et al., 2015). However, a potential issue of CFRs is their experimental designs, where exposing consumer species to single prey species within tank aquaria can represent an over-simplification of more complex natural systems in which a wider range of prey resources are available (Britton, 2018; Dick et al., 2014). Scaling-up experimental approaches for predicting the trophic impacts of alien freshwater fishes to mesocosms and pond enclosures have provided considerable insights into their trophic interactions with native species (Britton, 2018), with suggestions that rather than share and potentially compete for similar prey resources, functionally analogous native and alien fishes often demonstrate strong patterns of trophic niche partitioning (Britton et al., 2018; Raby et al., 2020).

Determining mechanisms by which novel species integrate into native food webs and coexist with native species can provide the basis for understanding the success of highly invasive alien species (Catford et al., 2009). For example, the use of unexploited resources by the alien species minimises their competitive interactions with native species (the empty niche hypothesis [ENH]; Mason et al., 2008; Juncos et al., 2015). Conversely, in scenarios where

the prey resources are all being exploited then the increased competitive interactions can result in population niche constrictions as each species increasingly develops dietary specialisms (Jackson et al., 2016; Mason et al., 2008), which can also result in strong niche partitioning. Although it is commonly referred to as the niche variation hypothesis (Britton et al., 2019), here we refer to it as the trophic specialisation hypothesis (TSH) to emphasise the mechanism. Alternatively, as interspecific competition increases, the niche sizes of each species might increase as individuals diversify their diet as the prey resources deplete (Svanbäck & Bolnick, 2007). While this has been referred to as the trophic niche hypothesis, here we refer it as the trophic generalisation hypotheses (TGH). In more extreme cases, asymmetric interspecific competition can result in the weaker species being competitively excluded from their original trophic niche, resulting in their reduced energetic intake that can lead to slower growth rates and lower population abundances (Chase et al., 2002).

The trophic niches of omnivorous species have the potential to be highly plastic in response to different biotic and abiotic contexts. Accurately predicting their trophic interactions with native species is then challenging, as intraspecific and interspecific variability can result in the same species generating different impacts in disparate systems (Klose & Cooper, 2013). A strong example of a globally invasive omnivorous species is the common carp *Cyprinus carpio* ('carp' hereafter), a freshwater fish that whose domination of many aquatic ecosystems causes a severe threat to native fish, aquatic plants and invertebrates (Weber & Brown, 2009). Consequently, the aim of this study was to initially use carp as the model alien species to predict, using two experimental approaches, their trophic interactions with a threatened native fish, the crucian carp *Carassius carassius*, a species with similar functional traits and feeding behaviours (Busst & Britton, 2017). As both species are aggregative and compete exploitatively (Bajer et al., 2011; Baumgartner et al., 2008; Penne & Pierce, 2008), they were used in both a CFR experiment based on using paired fish and in a relatively long-term (4 years) pond experiment in southern England, where stable isotope analysis (SIA) was used to assess the extent of their trophic interactions. Then, the results of both experiments were compared to their actual trophic relationships in wild, invaded ponds in southern England, also using SIA.

Hypotheses on the trophic interactions of carp and crucian carp can be designed from recently completed feeding studies involving the two species. First, a co-habitation aquaria experiment, which used the two species in allopatry and sympatry and exposed them to fixed feeding rations, suggested their asymmetry in their competitive interactions, as crucian carp length increments were significantly smaller in sympatry than allopatry (Busst & Britton, 2015). Therefore, Hypothesis 1 was that the CFR experiment would show that carp have a higher magnitude functional response and associated parameters than crucian carp, indicating higher resource consumption efficiency. Second, a co-habitation pond enclosure experiment indicated that when the two species are in sympatry, their trophic niches do not overlap, and for crucian carp, their niche shifts to a higher trophic position than when in allopatry (Busst & Britton, 2017). Consequently, in the natural pond experiment and wild ponds, Hypothesis 2 is that the trophic niches of sympatric carp and crucian carp will be highly divergent, with the trophic niche of sympatric crucian carp being smaller and at a higher trophic position than in allopatry as a result of diet specialisation (i.e. TSH).

2 | MATERIALS AND METHODS

2.1 | Study species

The crucian carp is considered native in ponds and lakes in Britain, Europe and central Asia (Wheeler, 1997, 2000), although more recent evidence suggests it might have actually been introduced into Britain around 600 years ago (Jeffries et al., 2017). It is considered as threatened in England due to the loss of its preferred pond habitats and the presence of alien species, especially carp and brown goldfish *Carassius auratus* (Copp et al., 2010; Sayer et al., 2011). The carp, listed on the list of the World's Worst Global Invaders (Lowe et al., 2000), is highly invasive in many countries (Escobar et al., 2018) and has been present in England since at least the 15th century, but perhaps since Roman times (Hoole et al., 2001).

2.2 | Comparative functional responses

The crucian carp used in the CFRs were captured using baited traps from natural populations in two adjacent ponds in Southern England. Both populations had been seeded from the source and so did not differ genetically, with two ponds used to ensure the appropriate number of fish were collected. The carp were sourced from a local hatchery where they had been pond-reared on a mix of natural and supplemental food, before being held in small outdoor ponds (1,000 L) for 2 months without supplemental feeding to promote natural foraging behaviours. Both species were then moved into an aquarium facility and held in species-specific holding tanks (90 L; 10 fish per tank) at 17°C for 21 days, with daily feeding (ad libitum) with frozen chironomid larvae. The CFR experiment was completed

at 17°C to represent typical summer water temperatures in England (Britton, 2007). Given the two species are aggregative in nature (Bajer et al., 2011; Baumgartner et al., 2008; Penne & Pierce, 2008), then rather than complete the experiment on individuals, the fish were used in conspecific pairings. Prior to the CFR trials, the fish were measured with callipers (standard length [SL] to 0.1 mm), with mean lengths (\pm SD) of crucian carp being 66.3 ± 6.7 mm and common carp being 66.6 ± 7.7 mm, and were thus considered as size-matched.

The CFR trials were all completed in rectangular tanks (20 L volume) without substrate or refugia, and to eliminate external stimuli, were covered with a lid and the sides were also covered. Hunger levels were standardised by the experimental fish not being fed for 24 hr prior to experiments. The paired conspecifics were selected randomly from their holding tanks, released into the experimental tanks and then acclimated for 2 hr. The food resource was pelletised fishmeal ('pellets') of 2 mm diameter, as these provide a resource of standard dimensions that have been consumed readily by similar fish species in functional response experiments (e.g. Murray et al., 2013). The pellets were released into the tanks at one of seven specific amounts (2, 4, 8, 16, 32, 48 and 96 pellets), with each amount replicated at least three times. Each individual trial lasted 4 hr and, at their conclusion, the fish were removed from the tank and the number of unconsumed pellets counted. The derived number of consumed pellets thus represents the number consumed per conspecific pair, rather than per individual fish.

Following the conclusion of all trials, the CFRs were modelled in the R package 'frair' (Pritchard, 2014) using maximum likelihood estimation (MLE; Bolker, 2010) and Rogers' (1972) Random Predator Equation (Equation 1), as the prey were not being replaced as they were consumed. Where the proportion of prey consumed decreased as prey density increased then the logistic regression produces a significantly negative result representing a 'Type II response'; in contrast, if it produces a significantly positive result then it represents a 'Type III' response (Juliano, 2001). Given both species indicated a significant Type II response, then Rogers' random predator equation was determined from:

$$N_e = N_0(1 - \exp(a(N_e h - T))),$$

where N_e is the number of pellets eaten, N_0 is the initial density of pellets, a is the attack parameter, h is the handling parameter and T is the total time available (fixed at 1). The FR data were non-parametrically bootstrapped (bias corrected and accelerated; $n = 2,000$) to generate 95% confidence intervals around the mean FR curve of each species, with comparison of the 95% confidence intervals enabling these data to be considered in a phenomenological manner with regard to population-level inferences (Pritchard et al., 2017) and with overlapping confidence intervals considered as indicating non-significant differences in the FR curves of the two species. In addition, parameter estimates [a , h] between the two species were compared using the z-method (Juliano, 2001) via *frair:fair_compare*.

2.3 | Natural pond experiment

Predicting the trophic interactions of crucian carp and carp was completed in a natural pond experiment completed in southern England between 2016 and 2019. In January 2016, juveniles of both species were sourced from local hatcheries where they had been reared in ponds, and were released into three adjacent (but unconnected), fishless (following their draining, drying and re-filling), former aquaculture ponds of approximately 400 m², maximum depths of 1.2 m, and with relatively clear water (secchi disk depths > 0.75 m) and highly abundant macrophyte growth (mainly *Elodea* spp.), with the water clarity remaining largely unchanged throughout the experimental period. The ponds were used as three distinct treatments, but with these not replicated due to logistical reasons preventing use of a greater number of ponds. Two of the ponds were used as allopatric controls, with 100 juvenile carp released into one pond and 100 crucian carp into the other (all < 100 mm). The third pond was used as a sympatric treatment, where the same number of fish was used (100) but split 50:50 between both species. As both species lack external features to enable differentiation of the sexes, then the sex ratios were unknown. While all three ponds had an increasing number of invasive signal crayfish *Pacifastacus leniusculus* present during the study ('crayfish' hereafter), only in the sympatric treatment in 2018 and 2019 were sample sizes sufficiently high to enable samples to be analysed ($n \geq 6$).

The ponds were then left until September 2017 to enable their tissues to become isotopically equilibrated to their new prey resources. The fish were then sampled in September 2017, 2018 and 2019 using baited fish traps set overnight. After lifting, the captured fish were removed, measured (fork length, FL, nearest mm), anaesthetised and a fin biopsy taken, and were then released back into their pond. Concomitantly, samples of macro-invertebrates (as fish putative prey resources) were taken using a sweep net and sorted for stable isotope analysis (SIA). The samples of fish fin, crayfish and macroinvertebrates were then taken to the laboratory, dried to constant mass at 60°C and then analysed at the Cornell University Stable Isotope Laboratory (New York) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific) interfaced to a NC2500 elemental analyser (CE Elantach Inc.). Analytical precision of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sample runs was estimated against an internal standard sample of animal (deer) material every 10 samples, with the overall standard deviation estimated at 0.08 and 0.04‰, respectively. Ratios of C:N were generally between 3.5 and 4.0, and so were not mathematically corrected for lipid (Winter et al., 2021).

Prior to further analyses, the SI data of the fish putative prey were compared within each pond by year and between the ponds. As these revealed some considerable differences (Table S1), then the fish SI data could not be compared directly between the ponds and years without correction (De Santis et al., 2021). Consequently, the $\delta^{15}\text{N}$ muscle data were converted to trophic position (TP) according to (Olsson et al., 2009):

$$\text{TP} = 2 + \delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{prey}}/3.4,$$

where TP and $\delta^{15}\text{N}_{\text{fish}}$ are the trophic positions and the nitrogen ratios of each individual fish, $\delta^{15}\text{N}_{\text{prey}}$ is the mean nitrogen ratio of the putative macroinvertebrate prey resources (Table S1), 2 is the trophic position of these prey resources (as primary consumers) and 3.4 is the generally accepted fractionation factor between adjacent trophic levels (Post, 2002). The fish $\delta^{13}\text{C}$ data were converted to corrected carbon ($\delta^{13}\text{C}_{\text{corr}}$) according to the following equation (Olsson et al., 2009):

$$\delta^{13}\text{C}_{\text{corr}} = (\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{meanMI}}) / \text{CR}_{\text{MI}},$$

wherein $\delta^{13}\text{C}_{\text{fish}}$ is the $\delta^{13}\text{C}$ value of each fish, $\delta^{13}\text{C}_{\text{meanMI}}$ is the mean $\delta^{13}\text{C}$ of the macroinvertebrate prey (Table S1) and CR_{MI} is the carbon range ($\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{min}}$) of the same macroinvertebrates (Olsson et al., 2009).

Following the correction of the SI data to $\delta^{13}\text{C}_{\text{corr}}$ and TP, the initial data analysis tested differences in these data between the two fish species in the sympatric treatment using ANCOVA, where the covariate was fish length and data for all years were combined. Then, to account for the presence of crayfish in the sympatric treatment, the significance of differences between their corrected SI data with the fish corrected SI data was tested in one-way ANOVA (with Tukey multiple comparisons of means with 95% family-wise confidence levels). The corrected SI data were then used to calculate the trophic niche size of each fish species per pond and sampling year, using the isotopic niche as a proxy of the trophic niche (Jackson et al., 2011). While closely related to the trophic niche, the isotopic niche is also influenced by factors including growth rate and metabolism (Jackson et al., 2011). The isotopic niches were calculated as standard ellipse areas (SEA) in SIBER (Jackson et al., 2011, 2012). SEAs are a bivariate measure of the distribution of individuals in isotopic space and as the ellipses enclose the core 40% of data, they represent the typical resource use of the analysed population (De Santis et al., 2021; Jackson et al., 2011). A Bayesian estimate of SEA (SEA_{B}) tested differences in niche sizes between the treatments per species, calculated using a Markov chain Monte Carlo simulation (10^4 iterations per group; Jackson et al., 2011, 2012). Differences in the size of isotopic niches (as SEA_{B}) were evaluated by calculating the probability that the relative posterior distributions of the niche size of the allopatric treatment were significantly smaller or larger than those of each of their sympatric niches ($\alpha = 0.05$) in SIBER. The SI data were then used to calculate isotopic niche overlap (%) between the species using SEA_{c} also calculated in SIBER, where subscript 'c' indicates a small sample size correction was used (Jackson et al., 2012). The use of SEA_{c} was mainly to get a representation of the extent of niche overlap between species, as it is more strongly affected by small sample sizes (<30) than SEA_{B} (Jackson et al., 2012). Overlaps between the isotopic niches were calculated based on SEA_{c} with 95% confidence tested for the species between their allopatric and sympatric treatments each year.

2.4 | Wild ponds with sympatric carp and crucian carp

There were four wild ponds sampled for their populations of sympatric carp and crucian carp between July and September 2019. The ponds were all located in southern England, were between 0.5 and 1.5 ha in area and had depths to 2 m. Their exact locations are unable to be provided to protect business confidentiality, as each was run as a private fishery for catch-and-release angling. All of the fish had been present in the ponds for at least 3 years (i.e. there had been no recent stocking of fish). The fish were sampled by a combination of baited fish traps and rod and line angling during stock assessment exercises, where the species were identified, measured (FL, nearest mm) and scale samples taken (3 to 5 scales per fish), originally for age and growth analyses for fishery management purposes. It was these scales that were used for stable isotope analysis, with scales tending to have a longer isotopic half-life than fin tissue (Busst & Britton, 2018). The scales were not decalcified prior to isotopic analysis, as the removal of inorganic carbonates has no significant effect on scale $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Ventura & Jeppesen, 2010; Woodcock & Walther, 2014). They were prepared by their cleaning with distilled water before the outer portion of the scale was removed for SIA, as this ensures that the analysed tissue is from the most recent growth of each fish (e.g. the last full year of growth; Hutchinson & Trueman, 2006). Only one scale was analysed per individual fish as this provided sufficient material for SIA. The samples were then prepared and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as per the natural pond experiment. As these SI data were only compared between the two species within each pond and not between ponds, no corrections were made to these data. As per the natural pond experiment, differences in the SI data between the species were initially tested in ANCOVA before their isotopic niches were calculated (as SEA_B and SEA_C) in SIBER.

The ethical approval process and all regulated procedures were completed under UK Home Office licence PPL 30/3277. All data analyses were completed in R version 4.0.5 (R Development Core Team, 2021).

3 | RESULTS

3.1 | Comparative functional responses

In the CFR experiments, the first-order linear coefficient from logistic regressions revealed the functional responses of both species were Type II and significant (first-order linear coefficients from logistic regressions: carp: -0.03 , $p < 0.001$; crucian carp: -0.02 , $p < 0.001$). Parameter estimates [a , h] were significant for both species. There was no difference between attack parameter estimates of carp (mean \pm SE: 8.62 ± 2.72) and crucian carp (4.53 ± 1.65 ; $z = 1.16$, $p = 0.25$). However, carp (0.025 ± 0.001) had a significantly shorter handling parameter estimate compared to crucian carp (0.12 ± 0.01 ; $z = 7.82$, $p < 0.001$). The maximum feeding estimate of carp (40.0)

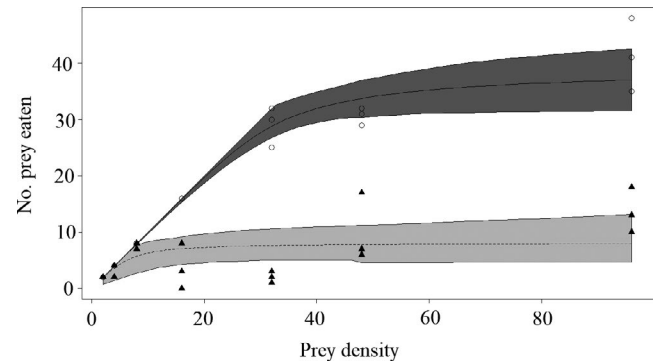


FIGURE 1 Comparative functional response plot of common carp *Cyprinus carpio* (clear circles, solid line) versus crucian carp *Carassius carassius* (black triangles, dashed line) fitted with Type II functional response curves calculated using Rogers' random predator equation. Shaded regions indicate 95% confidence intervals around the fitted functional response from bootstrapping 999 iterations

was considerably higher than crucian carp (8.1), with no overlap in their 95% confidence intervals (Figure 1).

3.2 | Natural pond experiments

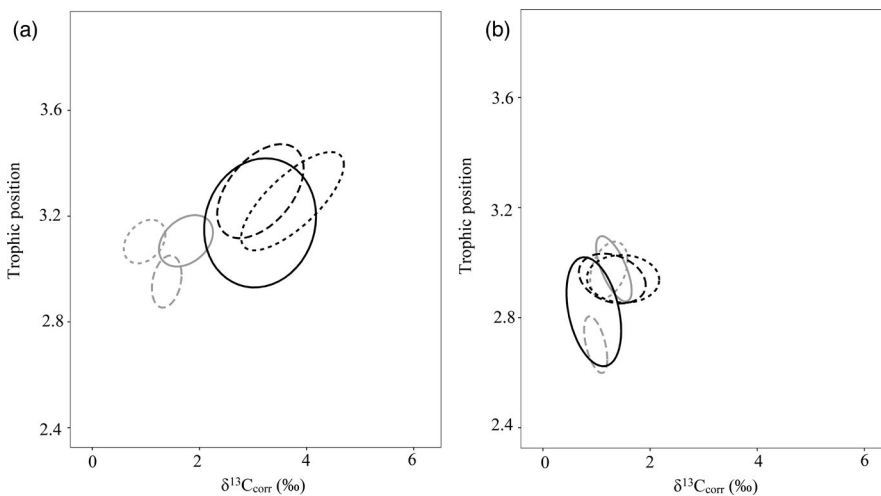
Across the three sampling years, there were considerable differences in the fish lengths of the two species due to reproduction and recruitment in the crucian carp, but with this not occurring in common carp; the differences in lengths within each species were relatively minor (Table 1; Table S1). In the sympatric treatment across all sampling years, there were significant differences in the corrected SI data between the two species ($\delta^{13}\text{C}_{\text{corr}}$: $F_{1,88} = 16.33$, $p < 0.01$; TP: $F_{1,88} = 5.18$, $p = 0.02$), where the effects of fish length as a covariate were not significant ($\delta^{13}\text{C}_{\text{corr}}$: $F_{1,88} = 0.09$, $p = 0.77$; TP: $F_{1,88} = 2.21$, $p = 0.14$; Figures 2 and 3). In the sympatric treatment, the carapace lengths of the analysed crayfish were 35 to 45 mm, with their corrected SI data differing significantly from the two fish species (ANOVA: $\delta^{13}\text{C}_{\text{corr}}$: $F_{2,91} = 43.81$, $p < 0.01$; TP: $F_{2,91} = 122.52$, $p < 0.01$; Figure S1). The Tukey multiple comparisons of means indicated that the differences in $\delta^{13}\text{C}_{\text{corr}}$ between crucian carp and crayfish were significant ($p < 0.01$), but were not between carp and crayfish ($p = 0.21$). For TP, the Tukey multiple comparisons indicated the differences between the species were all significant ($p < 0.01$; Figure S1).

The range of SI values of corrected $\delta^{13}\text{C}$ and TP was higher for both species in sympatry than in allopatry (Table S1). This was then reflected in their isotopic niches always being larger in sympatry than allopatry in each sampling year (Figure 2). Comparisons of the relative posterior distributions of the ellipse areas (as SEA_B) indicated that for carp, their isotopic niches were always significantly larger in sympatry than allopatry, whereas for crucian carp, this was only the case in 2019 (Table 1).

Comparison of the SI metrics for the two species in their allopatric treatments indicated similar isotopic niche sizes that slightly overlapped in their isotopic space in 2017 and 2018 (2% and 1%,

TABLE 1 Mean fork length ($\pm 95\%$ CL) and isotopic niche sizes (as standard ellipse areas, SEA_c and SEA_b , with 95% CI) per species, year and treatment, in the natural pond experiment

| Treatment | Species | Year | Mean length (mm) | SEA_c (CI) | SEA_b (CI) |
|------------|----------|------|------------------|-------------------|-------------------|
| Allopatric | Carp | 2017 | 171 \pm 9 | 0.18 (0.10, 0.28) | 0.17 (0.10, 0.28) |
| Sympatric | Carp | 2017 | 166 \pm 6 | 1.18 (0.63, 1.72) | 1.01 (0.55, 1.89) |
| Allopatric | Carp | 2018 | 206 \pm 9 | 0.13 (0.09, 0.17) | 0.11 (0.07, 0.20) |
| Sympatric | Carp | 2018 | 215 \pm 7 | 0.46 (0.24, 0.70) | 0.43 (0.26, 0.75) |
| Allopatric | Carp | 2019 | 244 \pm 9 | 0.10 (0.07, 0.12) | 0.08 (0.05, 0.16) |
| Sympatric | Carp | 2019 | 252 \pm 8 | 0.57 (0.20, 0.99) | 0.52 (0.33, 0.88) |
| Allopatric | Crucian | 2017 | 86 \pm 13 | 0.14 (0.07, 0.20) | 0.12 (0.07, 0.23) |
| Sympatric | Crucian | 2017 | 86 \pm 12 | 0.42 (0.16, 0.71) | 0.37 (0.22, 0.64) |
| Allopatric | Crucian | 2018 | 103 \pm 12 | 0.15 (0.10, 0.19) | 0.13 (0.07, 0.25) |
| Sympatric | Crucian | 2018 | 87 \pm 9 | 0.28 (0.13, 0.42) | 0.24 (0.14, 0.43) |
| Allopatric | Crucian | 2019 | 118 \pm 6 | 0.08 (0.04, 0.11) | 0.07 (0.06, 0.08) |
| Sympatric | Crucian | 2019 | 82 \pm 9 | 0.24 (0.11, 0.37) | 0.21 (0.13, 0.36) |
| Sympatric | Crayfish | 2018 | n/a | 0.15 (0.06, 0.23) | 0.14 (0.08, 0.24) |
| Sympatric | Crayfish | 2019 | n/a | 0.20 (0.10, 0.29) | 0.17 (0.11, 0.31) |

**FIGURE 2** The isotopic niches (represented as standard ellipse areas, SEA_c) of (a) allopatric carp (grey ellipses) versus sympatric carp (black ellipses) and (b) allopatric crucian carp (grey ellipses) versus sympatric crucian carp (black ellipses) in 2017 (continuous line), 2018 (dotted line) and 2019 (dashed line), in the natural pond experiment

respectively), but not in 2019 (Table 1; Figure 3a). In the sympatric treatment, the isotopic niches of carp were always larger than crucian carp in each sampling year (Figure 3b), although their relative posterior distributions of the ellipse areas (as SEA_b) indicated these differences were not significant (Table 1). Their isotopic niches (as SEA_c) also did not overlap in any sampling year (Figure 3b). This was also the case for the crayfish in the sympatric treatment, whose isotopic niche did not overlap with the fish species in 2018 or 2019 (Figure S1).

3.3 | Wild ponds with sympatric carp and crucian carp

The mean lengths of the two species analysed in each pond were relatively similar, with some overlaps in their length ranges (Pond

1: carp 181 \pm 58, crucian carp 134 \pm 8 mm; Pond 2: carp 118 \pm 46, crucian carp 69 \pm 8 mm; Pond 3: carp 154 \pm 15, crucian carp 179 \pm 23 mm; Pond 4: carp 141 \pm 10, crucian carp 147 \pm 10 mm; Table S2). There were significant differences in both stable isotopes between the species in each pond ($p < 0.05$ in all cases; Table S3), where the effect of fish length as a covariate was not significant ($p > 0.05$; Table S3), other than for $\delta^{13}C$ in Pond 2 ($p = 0.04$; Table S3). The range of the SI data of carp was higher than crucian carp in all ponds except Pond 2 (Table S2), with this reflected in carp having larger isotopic niches than crucian carp in these ponds (Figure 4). However, the relative posterior distributions of the ellipse areas (as SEA_b) indicated these isotopic niches were only significantly larger in carp in Pond 3 (Table 2). In Ponds 2–4, there were no overlaps in the species' isotopic niches (as SEA_c), but with minor overlap apparent in Pond 1 (Figure 4).

FIGURE 3 The isotopic niches (represented as standard ellipse areas, SEA_c) for (a) allopatric and (b) sympatric treatments for carp (filled circles) and crucian carp (filled triangles) in 2017 (black continuous line), 2018 (grey dotted line) and 2019 (blue dashed line), in the natural pond experiment

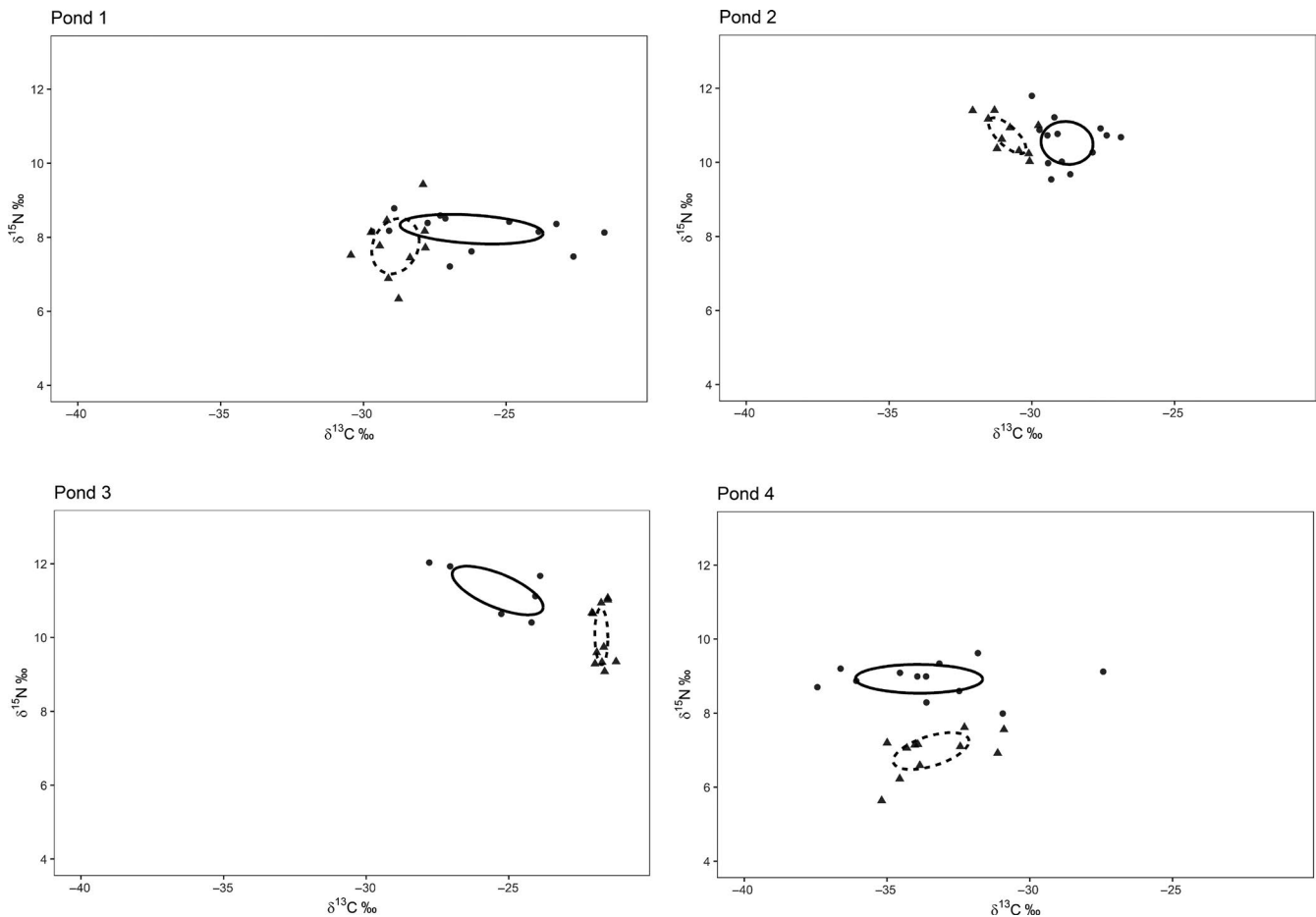
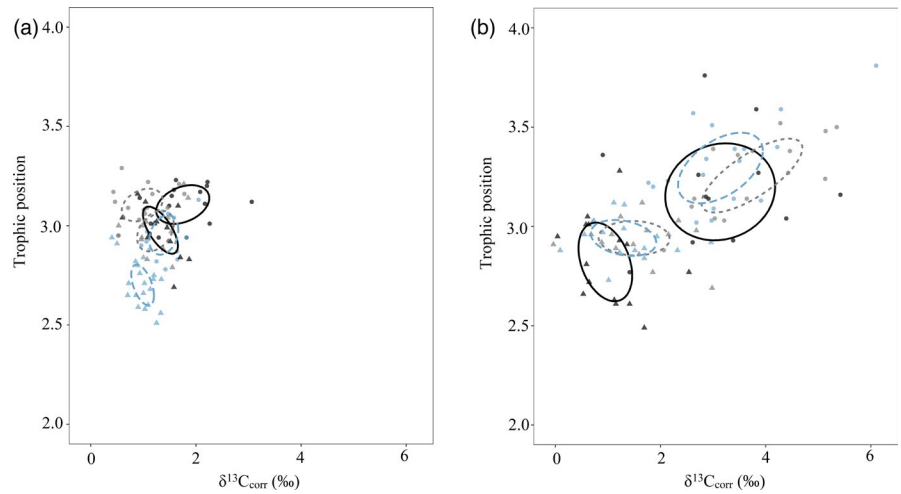


FIGURE 4 The isotopic niches (represented as standard ellipse areas, SEA_c) of carp (filled dots; continuous ellipses) and crucian carp (filled triangles; dotted ellipses) in each wild pond

4 | DISCUSSION

Predicting outcomes of trophic interactions between native and invasive species is a prerequisite for invasive species risk assessment and subsequent management. The CFR experiment completed here corroborated Hypothesis 1, with carp having a higher maximum feeding rate than crucian carp. When this result is considered in conjunction with the co-habitation aquarium experiment of Busst and

Britton (2015), these results suggest that their competitive interactions are asymmetric, with carp accessing more prey than crucian carp. Previous pond enclosure experiments also indicated when the species are in sympatry in more natural contexts, there are considerable shifts in the position of the crucian carp trophic niche compared to allopatry, suggesting that the presence of invasive carp results in some dietary shifts in crucian carp (Busst & Britton, 2017). Here, the natural pond experiment, which seeded three similar, fishless ponds

| | Pond 1 | Pond 2 | Pond 3 | Pond 4 |
|--------------|----------------|----------------|----------------|----------------|
| Carp | 3.4 (1.9, 6.3) | 1.9 (1.0, 3.3) | 2.5 (1.2, 7.0) | 3.6 (2.0, 6.7) |
| Crucian carp | 2.1 (1.1, 4.3) | 0.9 (0.5, 1.8) | 0.6 (0.3, 1.1) | 2.2 (1.1, 4.2) |

TABLE 2 Isotopic niches sizes of carp and crucian carp in each wild pond (as SEA_b) and their 95% confidence intervals (CI)

with equal numbers of carp and crucian carp in allopatry and sympatry, revealed that over 4 years, there were consistent patterns of larger isotopic niches in carp than crucian carp, with these niches being strongly partitioned, as per Hypothesis 2. However, the isotopic niches for both species were considerably larger in sympatry than allopatry and there was also no consistent pattern in the change in trophic position of their niches between allopatry and sympatry. Both of these results are contrary to Hypothesis 2. In the four natural pond populations, carp also had larger isotopic niches than crucian carp, with these niches also being partitioned.

High impact invasive species are consistently predicted by CFRs (Dick et al., 2014; Dickey et al., 2020). This has been confirmed across a broad range of invasive taxa (Dick et al., 2013; Laverty et al., 2017; Madzivanzira et al., 2021), including piscivorous fish (Alexander et al., 2014). The CFR results from the present study clearly show capacity for more efficient resource consumption by invasive carp as driven by shorter handling estimates. Type II functional responses and high maximum feeding estimates are ostensibly destabilising for prey populations (Dick et al., 2014). Nevertheless, CFRs have rarely been used to imply that the invasive species are superior competitors, given that any displacement of native species by an invader might also be driven by other mechanisms (Dick, Alexander, et al., 2017; Luger et al., 2020). When in sympatry, invasive fish can outcompete native species through more efficient resource consumption when compared to each species in allopatry, even where there is no net loss on prey populations (Mofu et al., 2019). Here, we show that carp impact is driven by lower handling parameters rather than attack (i.e. search and encounter rates), indicating that in a given period of time carp are able to consume more food than crucian carp. These results are supported by the results of the growth co-habitation experiment of Busst and Britton (2015), which indicated the growth increments of carp were considerably higher than crucian carp when in sympatry as they accessed a greater proportion of the fixed food resources. In combination, these results suggest that asymmetric competition should enable carp to monopolise higher proportions of shared prey resources when in sympatry with functionally analogous species (such as crucian carp), at least in contexts where these resources are limited.

Hypothesis 2 had predicted that these isotopic niches would be constricted when the two species were in sympatry versus allopatry, indicating a more specialist diet (i.e. TSH). In these scenarios, populations become more specialised in their diet under conditions of increased interspecific competition and thus reduce their niche size (Olsson et al., 2009; Thomson, 2004; Van Valen, 1965). To increase the experimental complexity beyond aquaria experiments and the co-habitation pond enclosure experiments of Busst and Britton (2017), the longer-term pond experiment was used to assess the trophic interactions of invasive carp and native crucian carp, using two

allopatric and one sympatric treatment (but was unable to be replicated). The allopatric treatments indicated that the isotopic niches of the two species would be similar sized and largely distinct from each other, with only minor overlap. In sympatry, the actual isotopic niches of carp were considerably larger than those of crucian carp, and these niches were strongly partitioned, with no overlap between them. Moreover, their sympatric isotopic niches were considerably larger than in allopatry, with a much wider range isotopic range evident in both species when in sympatry versus allopatry, indicating their use of a greater range of prey resources where they coexist. The isotopic niche expansion evident in our natural pond experiment thus rejects Hypothesis 2 and suggests that as resource competition (both intraspecific and interspecific) increases, each species will exploit a broader diet to maintain their energetic requirements (De Santis et al., 2021; Svanbäck & Bolnick, 2007). Indeed, this has been documented in carp populations in China as a mechanism for persistence when in sympatry with invasive transgenic carp (Wang et al., 2021). The potential role of intraspecific competition on this increased trophic generalisation in the natural pond experiment was also suggested, given that the crucian carp had reproduced in the sympatric treatment and so their numerical abundance was relatively high by the end of the experiment when compared to carp.

The results from both the pond experiment and the wild pond populations indicated strong partitioning between the isotopic niches of carp and crucian carp. Partitioning was evident in the allopatric treatments of the pond experiment, thus indicating that this occurs regardless of interspecific competitive interactions, albeit the partitioning was considerably stronger in the sympatric treatment. Carp are superior competitors towards crucian carp (as per the aquaria experiments). Thus, while we posit that crucian carp increase their resource breadth in response to strong competition from carp, there is some uncertainty in how this asymmetric competition influenced the isotopic niche sizes. Despite carp being superior competitors, their niche sizes also increased in sympatry and actually had minimal overlap with the carp from the allopatric treatments, which suggests that they were displaced. During the experiment, the ponds were purposely left unmanipulated between sampling events to enable the relationships between the species to develop over time without disturbance, and thus the abundances of the prey resources were not measured. It is plausible that the increased niche size of both species in the sympatric treatment could have also been due to prey resources becoming more depleted than in the allopatric ponds, thus forcing fish to exploit a broader range of resources. Although this cannot be explicitly tested, inferences from the CFR experiments suggest that both species consume comparable amounts of prey even at low resource densities in a resource population destabilising manner. Furthermore, carp are ecosystem engineers which can alter prey communities in both abundance and richness (e.g. Kloskowski, 2011;

Stuart et al., 2021; Zambrano & Honojosa, 1999). The larger niches in sympatry might have also been related to density dependence, given that the crucian carp reproduced in the sympatric pond (producing an established population where there were abundant individuals of 60–100 mm), whereas the carp did not as they did not reach sufficient size to be sexually mature (generally > 300 mm; Brown et al., 2005; Winker et al., 2011). There were thus higher total fish abundances in the sympatric pond versus the carp allopatric pond. However, the crucian carp also recruited strongly in their allopatric pond, where the isotopic niches were smaller versus sympatry, with little indication of displacement. This is potentially important, given dietary shifts are often apparent in fishes as their lengths increase (Davis et al., 2012; Gutmann Roberts & Britton, 2018). Indeed, there was a mismatch in the lengths of the carp versus crucian carp that increased over the experimental period (differences in mean lengths in the sympatric pond in 2017 was 80 mm vs. 170 mm in 2019). This was at least partially overcome in some analyses using fish length as a covariate, where its effect on the stable isotope data was primarily non-significant, and with length differences being relatively minor between the species in the wild ponds.

In entirety, these results and inferences suggest greater complexity in the relationships between the species than was possible to be elucidated from the experimental approaches used here. Indeed, predicting trophic interactions of generalist and omnivorous native and alien species is challenging, given their dietary plasticity (Klose & Cooper, 2013). Short-term simplistic—yet data intensive—controlled aquaria experiments enable precise mechanisms to be deduced, while in more complex and natural experiments, the ecological signals may take longer to become apparent or become diluted by other processes. Complementary approaches should be developed to improve predictive capacity to overcome these issues regarding ecological scale (Korsu et al., 2009; Spivak et al., 2011). This was at least partially overcome here by the complementary use of the pond experiments (enclosures in Busst and Britton (2017); entire ponds here). In this case, the results of the pond experiments were from contexts that were closer to natural scenarios but that still had some initial control over the experimental conditions, for example, ponds being fishless prior to start (Spivak et al., 2011; Tran et al., 2015). Other options for future work include the use of wild-sourced fish for all experiments. While the use of hatchery-reared carp here provided the experimental approaches with access to appropriate numbers of fish that could be size-matched to the crucian carp, hatchery-reared fish often have, compared to wild fish, lower genetic variability and poorer anti-predator responses, and can differ in aspects of their foraging behaviours (Milla et al., 2021; Tang et al., 2017; Xu et al., 2012). As such, the use of wild-sourced fish in future experiments would eliminate this potential confound, although it could also introduce new issues, such as increasing the difficulty of obtaining appropriate sample sizes of fish of the required lengths for size-matching within the trials. In addition, the presence of invasive signal crayfish in the natural pond experiment increased over time, especially in the sympatric treatment, with this unable to be avoided as the species started recolonising the ponds (as they

had been extirpated when the ponds were drained and dried prior to the experiment). However, their presence was not considered as a major driver of the fish trophic ecology in the ponds due to their relatively low trophic position and isotopic niches that were strongly partitioned from the fish species, with this also consistent with previous studies on these species in pond environments (e.g. Jackson & Britton, 2014).

The common carp has been described as one of the world's worst vertebrate pests (Stuart et al., 2021), implicated in the decline of threatened crucian carp in Norfolk (Sayer et al., 2020), but is highly valued for recreational angling and aquaculture (Vilizzi, 2012). While aspects of the ecological impacts of invasive carp are well chronicled (e.g. Vilizzi, 2012; Vilizzi et al., 2015; Weber & Brown, 2009), knowledge regarding trophic impacts and outcomes for native species is limited. The approaches here demonstrate that invasive carp can act as a strong competitor with functionally analogous native species, even when they have potentially been present in sympatry for sustained periods, given carp were first introduced into Britain at least 600 years ago (Britton et al., 2010). Where invasive carp are able to increase the size of their trophic niche to facilitate persistence in sympatry then this will ultimately alter the food web structure in resource-limited pond environments. This presents a plausible mechanism for the widespread decline of crucian carp via indirect impacts of carp invasions (Sayer et al., 2020) and one that has relevance for other native fishes threatened by the invasion of alien omnivorous fishes.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors contributed to the study design; J.S. and J.R.B. carried out the experiments and collected the data; V.D.A. led analyses and writing, assisted by J.S. and J.R.B. All authors contributed to revising the manuscript and approved its submission.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.w3r2280r8> (Dominguez Almela et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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