Invasive carp alter trophic niches of consumers and basal resources in African reservoirs

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HIGHLIGHTS

- Niche conservatism among reservoirs was generally higher in invertebrates.
- Niche conservatism was not based on reservoir condition (i.e. presence or absence of pollution and/or invasion).
- Invasion coupled with organic pollution may cause subtle yet differing effects on food web components.
- Results provide baseline measure in carp invasions and organic pollution detection and response strategies.

GRAPHICAL ABSTRACT
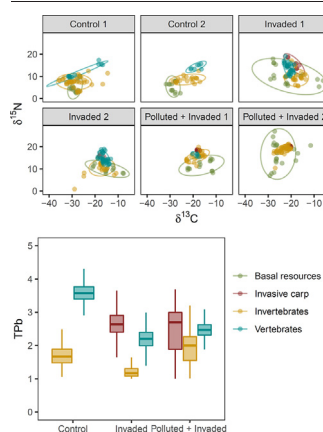
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ABSTRACT

Environmental pollution and biological invasions are key drivers of biodiversity change. However, the effects of invasion and pollution on food webs remain largely unexplored. Here, we used stable isotopes to examine the effects of common carp *Cyprinus carpio* and pollution on trophic dynamics in six small reservoirs. Our results revealed that the trophic niche widths of invertebrates, vertebrates, and invasive carp did not significantly differ among reservoirs with different pollution statuses. However, we found low niche conservatism among reservoirs, suggesting that while niche width may remain consistent, there is a shift in the position of the niches in isotopic space under both pollution and invasion scenarios. Niche conservatism among reservoirs was generally higher in invertebrates, but this was also regardless of reservoir condition (i.e. presence or absence of pollution and invasion). These results suggest that invasion by species coupled with organic pollution may cause subtle yet differing effects on components of a food web (basal end-members, invertebrates and vertebrates). Our findings provide a baseline measure of the potential in the development of detection and response strategies for carp invasions and organic pollution.

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1. Introduction

Globally, biodiversity loss and nutrient enrichment are two of the most pervasive drivers of changes in ecosystems (O'Connor et al., 2015; Alahuhta et al., 2019; Albert et al., 2021). Biological invasions are a major driver of biodiversity declines (Bellard et al., 2016), and while biodiversity loss and nutrient enrichment are recognised independently (Cook et al., 2018; Birk et al., 2020; Albert et al., 2021), little is known about how these disturbances interact to affect ecosystem functioning and their services. Invasive alien fishes have had pernicious impacts on ecosystems and economies, from displacement of native fishes, to alteration of trophic dynamics and damages to commercial or recreational fisheries (Cucherousset and Olden, 2011; Haubrock et al., 2021). Impacts of fish invasions are, however, potentially altered by context–dependencies (such as nutrient enrichment; Catford et al., 2021) which modulate the trophic niche (Almela et al., 2021), resulting in different impacts among invaded systems (Boets et al., 2019).

Invasive fishes are ubiquitous in South Africa, with most rivers containing several invaders (Ellender and Weyl, 2014; Weyl et al., 2020). The most widespread are species used for aquaculture (e.g., Nile tilapia *Oreochromis niloticus*) and the enhancement of fisheries e.g., black bass species (*Micropterus* spp.), trout (*Onchorhychus mykiss*, *Salmo trutta*) and common carp (*Cyprinus carpio*) (Ellender and Weyl, 2014). These species are a source of conflict because they can benefit society, but also cause environmental harm (Ellender and Weyl, 2014; Zengeya et al., 2017). As a result, their management is often complicated by the different value sets of stakeholders (Woodford et al., 2017; Haubrock et al., 2021). Proactive management approaches require an understanding of the drivers of invasions in the context of other stressors, and the extent of their impacts on South African environments. Unfortunately, these drivers are poorly researched for many of the conflict species, and particularly for carp where no studies have assessed impact in South African ecosystems.

Carp are globally invasive, often dominate ecosystems, and threaten native taxa such as fishes, aquatic plants and vertebrates via top–down and bottom–up processes (such as predation and modification of nutrient levels and turbidity; Weber and Brown, 2009; Winker et al., 2011). For instance, increased nutrient mobilisation from bottom-grubbing by carp can result in blue–green algal blooms, which affect the potability of water and subsequently the cost of water treatment (Eilers et al., 2011; Dalu et al., 2020). Its invasion success suggests that carp is equipped with a set of adaptable life history attributes that allow it to successfully colonise a wide range of habitats (Britton et al., 2007), including polluted water bodies (Dwivedi et al., 2018). However, the effect of nutrient pollution on carp invasions, and the combined effect of carp and pollution on native species is unknown. This knowledge gap is particularly important to fill in water–scarce regions such as South Africa, to aid in predictions of economic impacts relating to water provisioning.

An increasingly popular approach to examine the effects of organic pollution on fishes is via the use of biogeochemical tracers, such as stable isotopes (Baeta et al., 2017; Jackson et al., 2020; Prado et al., 2020; Almela et al., 2021). These studies are predicated on the principle that animals "are what and where they eat", with isotopic values of animal tissues reflecting the same biomarkers in their diet and surrounding food web (de Baeta et al., 2017; de Carvalho et al., 2020; Qin et al., 2021). For example, nitrogen isotopic values (δ^{15}N) are commonly used to infer consumer trophic level and diets (Post, 2002). Carbon isotopic values (δ^{13}C) show the use of basal carbon resources (Layman et al., 2012). The δ^{15}N and δ^{13}C values are thus complementary, and when quantified can characterize trophic structure and function, identify patterns of resource allocation and effects of pollution (e.g., Bode et al., 2021).

Using a number of small reservoirs with and without common carp and organic pollution, we characterize the independent and interacting effects of these two stressors using stable isotopes. Specifically, we predicted that common carp would benefit from pollution, which would result in wider trophic niches compared to carp in less polluted reservoirs (Hypothesis 1; H1). Furthermore, we predicted that a combination of carp invasion and pollution would result in simpler food webs dominated by lower trophic levels (H2). We expect that the findings from this research will provide data that will be instrumental in the development of detection and response strategies for carp invasions and organic pollution. In the long term, these data may be useful in the development of management interventions that include eradication of established populations in sensitive areas, as well as elucidation of context-dependencies underpinning invasion impacts.

2. Materials and methods

2.1. Study area

The study was conducted in Makhanda (formerly Grahamstown) and the Committees Drift region within the Eastern Cape Province, South Africa (Fig. 1). Six reservoirs were selected: 2 × polluted + invaded; 2 × unpolluted + invaded; and 2 × control [unpolluted + uninvaded]. Four sites were randomly selected within each reservoir to cover most of the surface area of the systems. The systems with carp were identified based on local fisherman knowledge and preliminary surveys, and the additional two polluted reservoirs were chosen primarily because porous sewage pipes were observed entering the system from surrounding settlements. The mean annual precipitation of the region is around 650 mm, with air temperatures of 1.5 °C (minimum) and 43 °C (maximum). The sampling was carried out on two temporal events (15th to 16th April and 14th to 15th August 2017) to capture both warm water and cold water periods.

2.2. Field sampling

Conductivity, temperature, total dissolved solids, salinity, and pH were measured at four locations within each reservoir for the two study months (i.e., April and August), using a YSI 6600 multi–parameter probe (Yellow Springs Instruments, Yellow Springs, OH). Water samples were used for ammonium (NH^+_4) and phosphate (PO^{3-}_4) determination with an HI 83203 multiparameter photometer (Hanna Instruments Inc., Rhode Island). Water samples (5 L; $n = 4$ per reservoir sampling event) were collected from each site for the determination of particulate organic matter (POM). Particulate organic matter water samples were then each sieved through 80 μm mesh to remove any zooplankton, before being filtered onto pre–combusted (500 °C, 5 h) Whatman GF/F filters (0.7 μm mesh size). Any visible zooplankton which passed through the pre–filtration were removed with forceps under a dissecting Olympus microscope operated at 60 × magnification.

Replicated basal food sources were sampled at each site and reservoir ($n = 3$–6 samples for each reservoir sampling event). Dominant submerged (e.g., *Potamogeton* sp.) and emergent (e.g., *Cyprus* sp., *Juncus* sp., *Schnoeplectus* sp., *Typha capensis*, *Persicaria* sp.) macrophyte stems and leaves ($n = 3$) were sampled and stored on ice in labelled pre–combusted (500 °C; 5 h) foil envelopes until further processing in the laboratory.

For the pelagic biota collections, a modified WP2 plankton net (40 cm mouth diameter, 63 μm mesh aperture size) was employed. The net, attached to a horizontal arm fixed to the bow of a 2.2 m inflatable boat, was submerged 30 cm below the water surface and towed along the selected sites at each reservoir for three minutes at a speed of between 1 and 2 knots. For the littoral zone macroinvertebrate collection, sampling was done using a nylon hand net (mesh aperture size 500 μm, dimension 30 × 30 cm) with an aluminium rim and a 1.5 m handle. For each sample, at a depth of between 1 and 1.2 m, the upward–facing net was hauled vertically, from the bottom to the water surface, through a clump of submerged macrophytes. Zooplankton and macroinvertebrate samples were collected in replicates ($n = 4$–10 per reservoir sampling event) for stable isotopic signatures.

Frogs and fishes were sampled using a seine net (30 m long, 5 mm mesh size) at each site per reservoir and representatives of all fish species captured were retained for isotope signatures. Retained fishes were placed in ice water for 1 h and then pithed prior to removal of muscle tissue from the flank of each individual. Fish tissue samples used for isotope samples were immediately stored in labelled, pre–combusted (500 °C; 5 h) foil
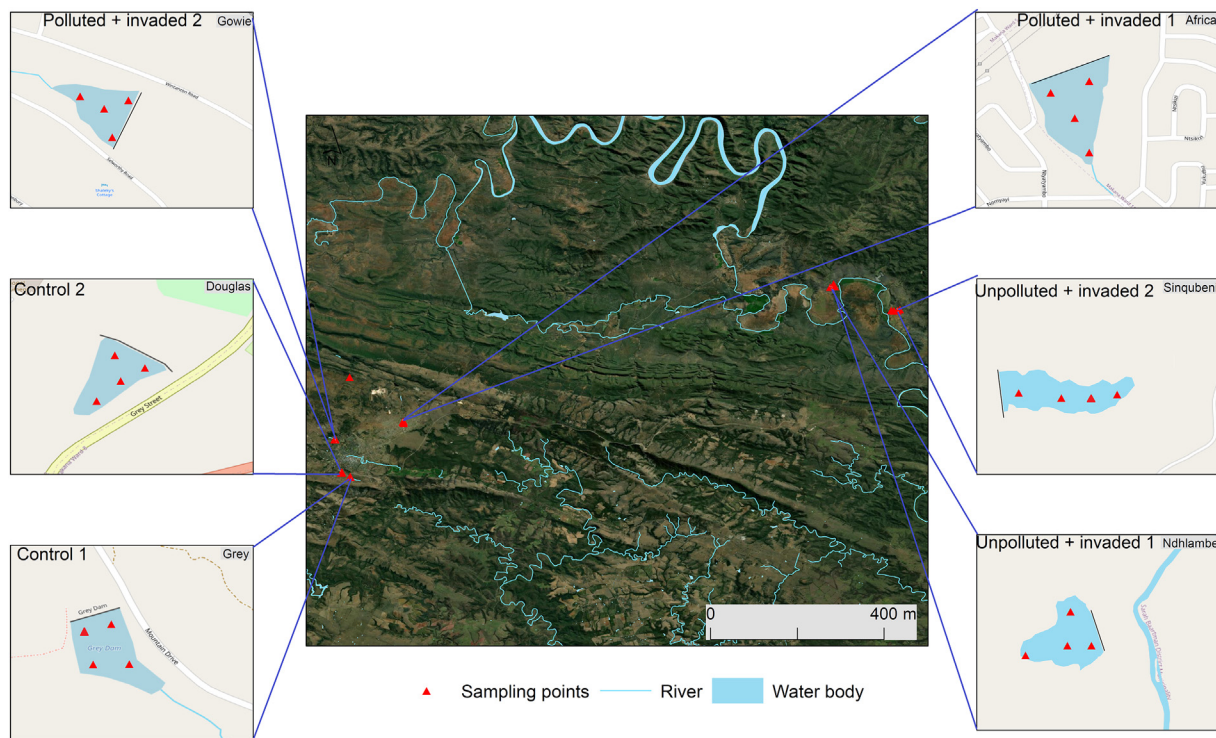
Fig. 1. Location of the study reservoirs in the Eastern Cape Province of South Africa.

envelopes placed on ice, until they were processed within two hours of collection.

2.3. Stable isotope analysis

Where possible, at least four replicates of each taxon from each site were processed for stable isotope values. All samples were dried in an oven on-site at 50 °C for 48 h. After drying, all material (e.g. aquatic macrophyte samples, selected invertebrates, frog and fish tissue) were ground to a fine, homogeneous powder using a mortar and pestle. Then, approximately 1 mg of each sample was placed in toluene-rinsed tin capsules. Prior to encapsulation, all sediment, POM samples on filters were vortexed for 2 min in 2 M hydrochloric acid (to remove any calcified components), centrifuged for 5 min at 3600 rpm, washed twice in deionised water followed again by centrifugation, dried at 50 °C and homogenised in a Retsch Mixer Mill (Jacob et al., 2005).

The $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios (‰) of all samples were determined using a Europa Scientific 20–20 Isotope Ratio Mass Spectrometer (IRMS), interfaced to an ANCA SL Elemental Analyser at the Stable Isotope Laboratory, University of Pretoria, South Africa. Values were normalised to internal standards calibrated to the International Atomic Energy reference materials (IAEA–CH6 for $\delta^{13}C$ and IAEA–N2 for $\delta^{15}N$). All $\delta^{13}C$ and $\delta^{15}N$ values are reported in per mil (‰) notation against Vienna PeeDee Belemnite (VPDB) and air, respectively. Carbon and nitrogen isotopic values are expressed in standard delta notation:

$$\delta^{13}C \text{ or } \delta^{15}N \text{ () } = \left[\left(R_{sample} / R_{standard} \right) - 1 \right] \times 1000$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The precision ranges for the determination of $\delta^{13}C$ and $\delta^{15}N$ were 0.01–0.15 and 0.04–0.16‰, respectively.

2.4. Data analyses

A two–way ANOVA was conducted to assess for reservoir (i.e., 1–6) and monthly (i.e., April, August) differences in physicochemical variables after the data were found to meet the assumptions of a parametric test. Some

parameters, specifically ammonium and turbidity, were not sampled for the two months, but only once due to logistical constraints, and hence analysis was done only to assess the reservoir differences alone in these cases.

Next, we grouped individual samples into broad taxonomic groups to make comparisons among the food webs in control, invaded, and invaded plus polluted reservoirs: autochthonous basal resources, invertebrates, vertebrates and invasive carp (in invaded reservoirs). Additionally, because Bayesian models display higher uncertainty with smaller sample size (Quezada-Romegialli et al., 2019) we pooled certain taxa data into broad trophic groups to avoid bias. We calculated Bayesian estimates of isotopic niche area and trophic position of each taxonomic group in each reservoir using the SIBER (Jackson et al., 2011a, 2011b) and tRophicPosition (Quezada-Romegialli et al., 2019) packages in R, respectively (R version 4.0.0, R Core Team, 2020, code included as Supporting Information). After centroid correction to make comparisons among sites with different baselines, isotopic niche area was calculated using standard Bayesian ellipses (SEA$_b$): this gives the bivariate variance of the isotope data of each taxonomic group (using 95% confidence intervals and 4000 Monte Carlo simulations, Jackson et al., 2011a, 2011b). For calculated SEA$_b$, Bayesian posterior probabilities (PP > 0.95) were used to test for significant differences among groups. Average trophic position of each group was calculated using a Bayesian model to estimate posterior modes (TP$_b$) with the full range of autochthonous basal resources as our baseline (Quezada-Romegialli et al., 2018). To test for trophic conservatism (i.e. shifts in isotopic space), we calculated the proportional overlap of SEA$_b$ using the 95% prediction ellipse area (Jackson et al., 2011a, 2011b) of each taxonomic group among control, invaded, and invaded plus polluted reservoirs.

3. Results

3.1. Physico–chemistry of sampled reservoirs

Generally, nutrients (i.e., ammonium, phosphates) were high in the polluted + invaded systems, with the invaded systems having high conductivity, TDS, pH and salinity levels (Table 1). A two–way ANOVA indicated significant differences ($p < 0.05$, Table S1) among the study reservoirs for

Table 1

Mean (± standard deviation) phyisco–chemical variables recorded from the six reservoirs (pooled across sites), in Makhanda Eastern Cape Province of South Africa. Abbreviations: TDS – total dissolved solids, NH_4^+ – ammonium, PO_4^{3-} – phosphate.

Variable	Unit	Polluted + invaded 1	Polluted + invaded 2	Invaded 1	Invaded 2	Control 1	Control 2
April							
Conductivity	$\mu S\ cm^{-1}$	919.8 ± 3.9	899.8 ± 2.4	1330.8 ± 1.4	1088.2 ± 2.4	232.3 ± 1.3	272.5 ± 0.7
Temperature	˚C	20.0 ± 0.2	22.1 ± 0.3	23.3 ± 0.3	25.1 ± 0.3	19.0 ± 0.1	19.2 ± 0.1
TDS	$mg\ L^{-1}$	652.3 ± 3.3	639.1 ± 1.8	935.3 ± 28.6	772.4 ± 1.1	165.4 ± 0.9	193.3 ± 0.8
Salinity	ppt	449.4 ± 1.1	440.8 ± 0.9	661.8 ± 1.7	538.2 ± 0.6	110.9 ± 0.3	130.3 ± 0.5
pH		8.9 ± 0.2	8.2 ± 0.1	9.6 ± 0.3	9.3 ± 0.1	8.0 ± 0.2	8.3 ± 0.1
Water depth	m	1.1 ± 0.3	2.9 ± 1.0	3.7 ± 1.3	4.8 ± 2.0	3.3 ± 0.9	2.3 ± 1.5
Transparency	m	0.4 ± 0.05	0.5 ± 0.05	0.5 ± 0.04	1.7 ± 0.2	1.1 ± 0.1	0.5 ± 0.03
NH_4^+	$mg\ L^{-1}$	1.0 ± 0.3	1.9 ± 0.1	0.3 ± 0.4	0.2 ± 0.1	0.5 ± 0.2	0.4 ± 0.3
PO_4^{3-}	$mg\ L^{-1}$	1.7 ± 0.4	1.0 ± 0.6	0.6 ± 0.6	0.4 ± 0.2	0.3 ± 0.1	0.2 ± 0.3
August							
Conductivity	$\mu S\ cm^{-1}$	1011.6 ± 2.9	977.8 ± 2.1	1408.1 ± 75.0	1150.4 ± 91.6	247.9 ± 18.2	295.5 ± 0.8
Temperature	˚C	12.6 ± 0.1	12.6 ± 0.1	18.8 ± 0.5	18.0 ± 0.6	12.0 ± 0.1	12.7 ± 0.1
TDS	$mg\ L^{-1}$	717.3 ± 0.9	693.4 ± 1.3	1010.8 ± 0.9	817.5 ± 64.2	182.5 ± 2.3	209.9 ± 0.6
Salinity	ppt	485.4 ± 2.1	470.1 ± 2.4	708.5 ± 3.6	562.5 ± 48.9	118.5 ± 0.5	137.9 ± 0.4
pH		9.6 ± 0.1	8.6 ± 0.03	9.8 ± 0.2	9.9 ± 0.03	8.7 ± 0.3	8.6 ± 0.1
Water depth	m	1.13 ± 0.3	2.9 ± 1.0	3.1 ± 1.7	5.3 ± 2.5	4.9 ± 2.4	3.3 ± 1.0
Transparency	m	0.5 ± 0.1	0.3 ± 0.04	0.3 ± 0.1	1.3 ± 0.3	0.7 ± 0.1	1.1 ± 0.2
PO_4^{3-}	$mg\ L^{-1}$	1.4 ± 0.2	1.0 ± 0.2	0.8 ± 0.7	0.5 ± 0.4	0.8 ± 0.4	0.5 ± 0.2
Turbidity	NTU	10.7 ± 0.6	13.0 ± 2.6	15.9 ± 7.7	2.3 ± 8.9	6.2 ± 1.1	4.3 ± 0.5

all variables, with also significant variations between months being observed for all variables ($p < 0.001$), with the exception of water transparency, depth and phosphate which were not significant ($p > 0.05$; Table S1). Significant interaction terms between reservoirs and months were found across all parameters ($p < 0.001$), except conductivity, pH, water depth and phosphate ($p > 0.05$, Table S1).

3.2. Trophic niche width and conservatism

Broadly, our estimates of the trophic niche widths of invertebrates, vertebrates, and invasive carp did not significantly differ among reservoirs with different conditions (Fig. 2a,b; Table S2; PP < 0.95). However, there was generally low niche conservatism among reservoirs (Table 2), suggesting that, although niche area (i.e. diet breadth) might remain relatively consistent, i.e., the location of the niche shifts in isotopic space (after baseline correction). Niche conservatism among reservoirs was generally higher in invertebrates, but this was also regardless of reservoir condition (i.e. presence or absence of pollution and invasion; Table 2). For example, with pollution, the niche shifts to higher trophic levels (Fig. 2a).

3.3. Trophic position

The average trophic position of invertebrates did not significantly differ with reservoir conditions, but vertebrates (other than invasive carp) had lower trophic positions at invaded sites (regardless of the presence or absence of pollution; Fig. 2a, c). The trophic position of invasive carp did not differ with pollution (Fig. 2a, c).

4. Discussion

In lentic systems, the feeding ecology of consumers is dependent on environmental conditions and can be affected by invasive species (Havel et al., 2015). The potential effects of invasive species on the trophic dynamics of consumers in reservoirs in Africa are understudied, despite their high invasion success across anthropogenically-altered systems (sensu McClain, 2013). This study presents insights into the trophic niche widths and positions, and possible influence of the invasive carp on trophic connections in six reservoirs under different pollution scenarios. We accept our first hypothesis that common carp would benefit from pollution, which would result in wider trophic niches compared to carp in less polluted reservoirs as highlighted by the Bayesian

estimates of average trophic position and that the niche area contracted in the presence of pollution (Fig. 2b). Furthermore, the predicted combination of carp invasion and pollution resulted in simpler food webs dominated by lower trophic levels i.e., basal food resources, as per our second hypothesis. This is likely because the presence of carp tends to lead to increased nutrient enrichment that favours basal food resource growth (Dalu et al., 2020), reducing the invertebrate and vertebrate diversity and SEA$_b$ values (Fig. 2). Similarly, Freedman et al. (2012) and Kaemingk et al. (2016) observed that carp depressed trophic levels by selective consumption of large predatory zooplankton, suggesting that carp presence in a system can exert substantial ecosystem structure and function effects and changes. This may be due to over-predation on large predatory zooplankton, and subsequent increases in small grazing zooplankton such as rotifers. Therefore, the increase in $\delta^{15}N$ in polluted and invaded reservoirs might have been due to increased anthropogenic inputs in these reservoirs, while the slight narrowing of $\delta^{13}C$ sources requires further investigation as to possible cause as well as effect of carp invasions.

We observed low niche conservatism among all reservoirs sampled and most analyses detected significant abiotic differences among reservoirs, although trophic niche width areas generally remained similar. Our analyses revealed little isotopic dietary trophic niche overlap across reservoirs, with limited overlap in isotopic δ-space and highly variable use of functional prey groups, similar to observations by Manlick et al. (2019). Our study is one of few to explicitly assess niche conservatism in aquatic invasions, and our results are consistent with recent studies illustrating the plasticity of carp dietary niches (Kaemingk et al., 2016) and low niche conservatism among fishes in particular (Comte et al., 2017; Keppeler and Winemiller, 2020). These results, however, indicate that the effects of pollutants were often unclear and site-specific, which may relate to a limited number of sampling sites and additional underlying variations in environmental conditions at the site-level. Furthermore, shifts in trophic niche sizes can emanate from emergent competitive interactions between carp and other fishes, with composition differing among reservoirs, which could also have resulted in changes to the isotopic signature in our results (Almela et al., 2021).

In conclusion, invasion ecology often assumes that the carp functional roles are conserved across ecosystems and clades, however, carp has been repeatedly observed to affect trophic relationships and functional roles within aquatic ecosystems. We demonstrated that introduced freshwater carp exhibited trophic position and resource use flexibility that was beyond natural variability levels observed in their native ranges (Weber and Brown,
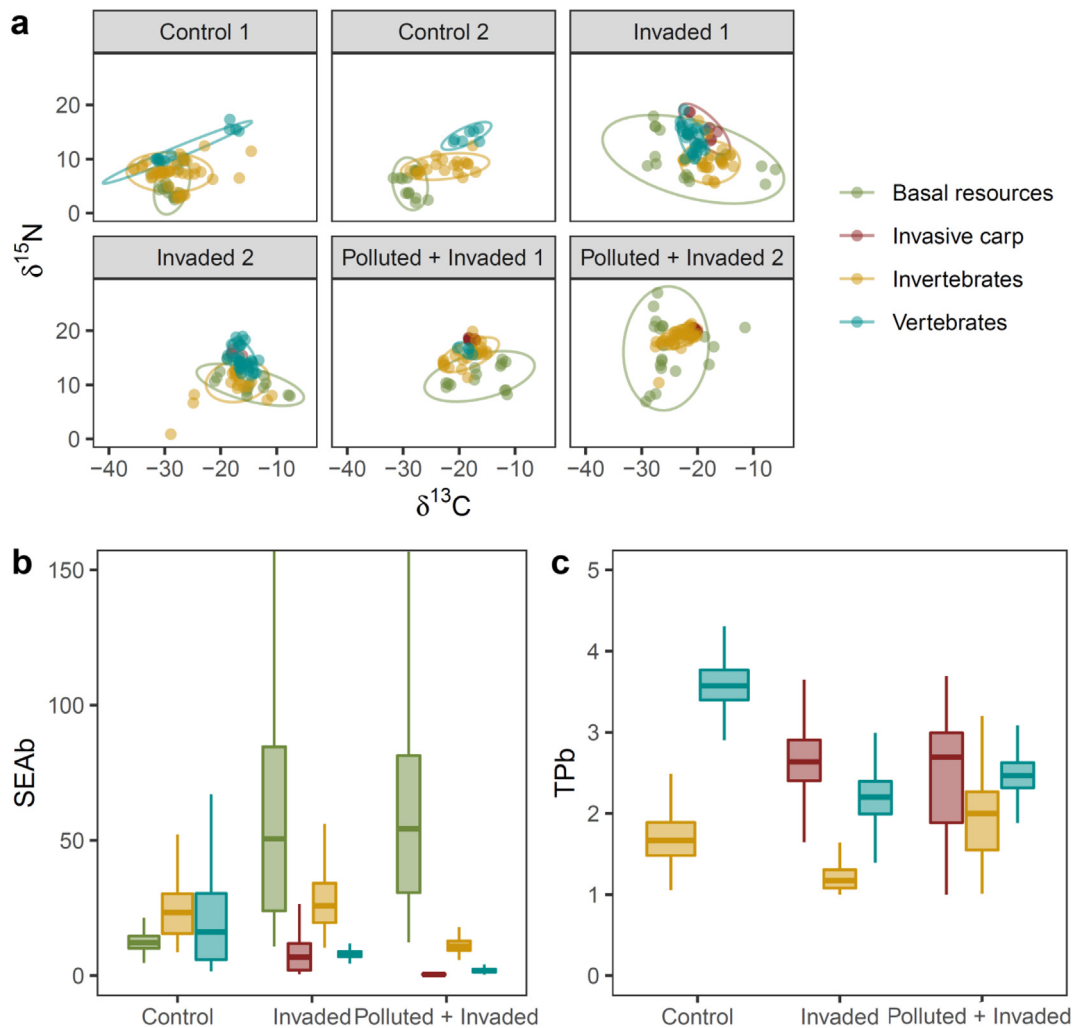
Fig. 2. (a) Stable isotope biplots of the six reservoirs, where points represent individuals and ellipses show the uncorrected isotopic niche of each taxonomic group. (b) Centroid–corrected Bayesian estimates of isotopic niche area (quantified using SEA_b) across each treatment for each taxonomic group. (c) Bayesian estimates of average trophic position of each taxonomic group in each treatment.

2009). This may relate to different characteristics of invading populations given the traits of founding populations or those at the invasion front, which in turn might promote invasion success or different behaviour (Shine et al., 2011; Perkins et al., 2013). However, such strategies are also contingent upon niche conservatism and trophic stationarity, and our results suggest that trophic niches and functional roles were not conserved among carp, and were highly variable and most conserved among invertebrate groups. Consequently, these findings suggest that feeding dynamics and the realized functional roles may not be transferable across systems, presenting additional complexity to carp invasion strategies and dynamics. The mechanisms that promote and/or inhibit species from shifting their trophic niche and conservatism remain unknown (Comte et al., 2017), however, trophic flexibility is likely to contribute to both the success and ecological impacts of invasive species under increased anthropogenic impacts, such as pollution and climate change.

Ethics approval

Permits for fish collection were obtained from the Eastern Cape Department of Economic Development and Environmental Affairs (DEDEA permit no. CRO 35/17CR and CRO 36/17CR). Ethical clearance was obtained from the South African Institute for Aquatic Biodiversity (SAIAB reference no. 25/4/1/5_2017/03).

Consent for publication

Not applicable, all data was collected by the authors.

Declaration of Competing Interest

All authors declare no conflict or financial interests exist for the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.152625.

Table 2

Niche conservatism among reservoirs (as percentage overlap of centroid corrected SEA$_b$). Higher conservatism is indicated by darker blue. Absence of a taxonomic group in one site is indicated by NA.

		Polluted + invaded 1	Polluted + invaded 2	Invaded 1	Invaded 2	Control 1	Control 2
Invertebrates	Polluted + invaded 1						
	Polluted + invaded 2	1.7					
	Invaded 1	39.8	3				
	Invaded 2	13.2	20.6	13.7			
	Control 1	47.3	3.9	57.1	16.5		
	Control 2	0	1.8	0	4.7	0.1	
Vertebrates	Polluted + invaded 1						
	Polluted + invaded 2	NA					
	Invaded 1	15.1	NA				
	Invaded 2	14.3	NA	2.7			
	Control 1	0.1	NA	0.4	0.7		
	Control 2	5.4	NA	2.9	12	5.9	
Invasive carp	Polluted + invaded 1						
	Polluted + invaded 2	10.8					
	Invaded 1	24.4	18.6				
	Invaded 2	9.6	29.2	22.1			
	Control 1	NA	NA	NA	NA		
	Control 2	NA	NA	NA	NA	NA	

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