

# Environmental niche patterns of native and non-native fishes within an invaded African river system

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## Abstract

To test ecological niche theory, this study investigated the spatial patterns and the environmental niches of native and non-native fishes within the invaded Great Fish River system, South Africa. For the native fishes, there were contrasting environmental niche breadths that varied from being small to being large and overlapped for most species, except minnows that were restricted to headwater tributaries. In addition, there was high niche overlap in habitat association among fishes with similar distribution. It was therefore inferred that habitat filtering-driven spatial organisation was important in explaining native species distribution patterns. In comparison, most non-native fishes were found to have broad environmental niches and these fishes showed high tolerance to environmental conditions, which generally supported the niche opportunity hypothesis. The proliferation of multiple non-native fishes in the mainstem section suggest that they form a functional assemblage that is probably facilitated by the anthropogenic modification of flow regimes through inter-basin water transfer. Based on the distribution patterns observed in the study, it was inferred that there was a likelihood of negative interactions between native and non-native fishes. Such effects are likely to be exacerbated by altered flow regime that was likely to have negative implications for native ichthyofauna.

## KEYWORDS

distribution patterns, environmental niche, invasions, native fishes, niche segregation, spatial organisation

## 1 | INTRODUCTION

Uncovering the mechanisms that describe species' spatial patterns and trophic resource use is fundamental in understanding what drives community organisation and maintains biological diversity (Chesson, 2000). Niche-based studies are often critical when evaluating the importance of spatial and trophic interrelationships, particularly when addressing questions related to both species' distributions and concerns over the effects of global environmental change (Broennimann *et al.*, 2012; Chase & Leibold, 2003; Soberon, 2007). Within natural communities, spatial organisation is considered to be a consequence of species responding differently to either environmental or trophic

resource niche axes (Chase & Myers, 2011; Colwell & Rangel, 2009; Soberon & Nakamura, 2009). Studies on environmental niches evaluate the importance of species–environment relationships, which considers that physical factors, such as microhabitat, natural disturbance regimes and dispersal limitations are likely to impose strong constraints on the membership of species in a particular community (Leibold, 1995; Myers & Harms, 2009). In comparison, studies on trophic niches assume that species resource requirements and their functional roles are determined largely by biotic interactions (Leibold, 1995; Newsome *et al.*, 2007). Biotic interactions, including competition and predation, are assumed to drive species to either occur in allopatry or to exhibit differential resource utilisation when

they occur in sympatry in order to minimise competitive exclusion (Gutierrez *et al.*, 2014).

Within invaded habitats, non-native species that have become invasive are assumed to have substantial breadth in both their ecological requirements and functional roles (Shea & Chesson, 2002). From a niche perspective, invasion success is driven by resource availability, natural enemy escape opportunities and novel physical environments, which all may create favourable conditions and niche opportunities (Shea & Chesson, 2002; Vazquez, 2005). Because of niche opportunities, successful invaders are assumed to utilise a wide range of environmental and resource axes since they are considered to be less constrained by resource availability and interspecific interactions compared with native species (Jeschke & Strayer, 2006). In many invaded ecosystems, the potential for niche opportunities, together with colonisation and propagule pressures have culminated in the successful establishment and co-occurrence of multiple invasive non-native species (Lockwood *et al.*, 2009; Simberloff, 2009). Within freshwater ecosystems, the establishment of multiple non-native fishes has been associated with both direct and indirect effects on native species and their environment (Strayer, 2010). Although several studies have provided unequivocal evidence on mechanisms that drive invasion success and their effects, many of these have focused on single invaders, with few addressing patterns and probable consequences associated with multiple invasions (Jackson & Britton, 2014; Preston *et al.*, 2012). Research on multiple invasions posits the likelihood of complex and synergistic interactions among these invaders (Ricciardi, 2005; Simberloff, 2011). Since most biological invasions are often associated with negative consequences, there is a need to understand the patterns associated with both native and non-native invaders from a community context (Ricciardi, 2005; Shea & Chesson, 2002).

The Great Fish River in the Eastern Cape, South Africa, provides an important case study for evaluating niche-based mechanisms for both native and non-native fishes. The Orange–Fish River interbasin water transfer (IBWT) scheme, which transfers water from the Orange River, has both acted as a conduit to multiple invasions into the Great Fish River and altered its flow from seasonal to perennial (Laurenson & Hocutt, 1985). Currently, the Great Fish River system is host to several non-native fishes because of the IBWT scheme and through deliberate angler introductions (Kadye & Booth, 2012a, 2013). While previous studies have focused on effects of single invaders (Kadye & Booth, 2012a, 2013), there is a need to understand the mechanisms associated with coexistence patterns of both native and non-native species, particularly within the context of human-mediated disturbances. In this regard, evaluating environmental niches is helpful in the understanding of community organisation, particularly where anthropogenic-induced habitat alteration and the prevalence of non-native species are likely to influence niche patterns (Sharma *et al.*, 2011). An important assumption on evaluating the role of environmental niches is that both large-scale (*e.g.*, catchment wide variables) and local-scale (*e.g.*, local habitat variables in the pool–riffle sequence) operate in a hierarchical sequence, which ultimately influences stream fishes and their community organisation

(Dembkowski & Miranda, 2014; Fitzpatrick *et al.*, 2001; Frissell *et al.*, 1986).

To better understand the patterns of coexistence associated with invasions, native and non-native ichthyofauna within the Great Fish River were compared in relation to environmental niche positioning. The study aims were: to evaluate the spatial patterns together with the associated environmental niches of both native and non-native fishes and to assess probable negative interactions between native species and non-native species. It was hypothesised that due to environmental niche filtering (Chase & Myers, 2011), native fish species were likely to exhibit spatial structuring that would be reflected by variable niche sizes as a response to different habitat and resource requirements. By comparison, it was hypothesised that due to niche opportunities (Shea & Chesson, 2002), non-native fishes would exploit a wide range of habitats and were unlikely to show any spatial organisation within their invaded range.

## 2 | MATERIALS AND METHODS

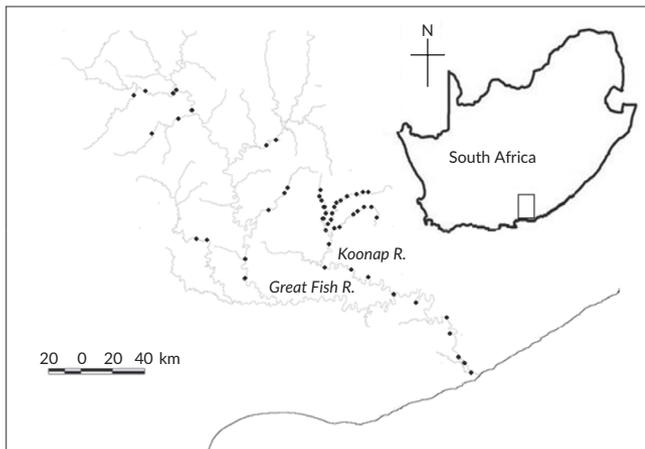
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### 2.1 | Study area

The Great Fish River originates in the Karoo region of south-central South Africa and flows through the Eastern Cape into the Indian Ocean. It has a longitudinal axis of *c.* 650 km, a catchment of 30,243 km<sup>2</sup> and flows through an arid region with mean annual precipitation ranging from 350 to 600 mm. Much of the water comes from the Orange River system through an 82 km underground tunnel connected to the Gariiep Dam. The IBWT scheme transfers approximately 350 × 10<sup>6</sup> m<sup>3</sup> into the Great Fish River annually (O'Keeffe & de Moor, 1988). In this way, the river's flow regime has been altered by the IBWT from one with seasonal fluctuations to a perennial state with little monthly variations. Most of its tributaries, however, are not influenced by the IBWT and maintain natural flow regimes that are characterised by high seasonal variability.

### 2.2 | Sample collection

Sampling was conducted at 52 sites in the mainstem of the Great Fish River and its tributaries, which included the Koonap River (Figure 1). Data were collected from several surveys that were conducted in two sampling periods; October 2009 to December 2010 and October 2012 to November 2013. Fish were captured using a variety of sampling gears, including gill nets, fyke nets, seine net and electrofishing. Gill nets were 30 m long with three 10 m panels of mesh sizes of 50, 75 and 100 mm. Double ended fyke nets were used, each with an 8 m guiding net and a first ring diameter of 55 cm and a 10 mm mesh



**FIGURE 1** Map of the study area showing the Great Fish River, its major tributary the Koonap River and the sampling sites. (●) Sampling site, (—) Rivers

size. Gill nets and fyke nets were set from the surface and were soaked overnight (16:00–07:00 hours). An 8 m seine net with 4 mm mesh size was also used to sample shallow and marginal habitats. Headwater sites were sampled by three-pass depletion electrofishing using a Samus 725GN backpack electric fisher ([www.gmdu.net](http://www.gmdu.net)) that was powered by a 12 V battery. Before electrofishing was conducted, a section of each site was blocked both upstream and downstream with 4 mm mesh nets that were secured to the streambed. Captured fish were identified to species and the total number of each species in each gear was recorded.

At each of the mainstem sites, a section of the river c. 100 m in length was sampled. Within each site, three main habitat types were identified; pools that were deep (> 1 m) with slow flow, riffles that were shallow (< 1 m) with fast flow and backwaters, which were sections along the main river that had little to no flow and had variable depth. Each habitat type was sampled separately using a combination of different methods. In addition, within each habitat type, average depth was measured and the presence or absence of submerged and emergent macrophytes was recorded as a proxy for physical structure. Average depth was recorded from 30 random points that were measured within each habitat type. Similarly, for headwater sites, river sections between 50–100 m in length were sampled. Pools and riffles were the main habitat types within headwater sites, which were characterised and sampled separately.

Captured fish were identified to species level following Skelton (2001) and the total number of each species from each sampling method was recorded. The fish were released alive, except for voucher samples that were kept for a separate study on stable-isotope analysis. For this separate study, the fishes were euthanised by a lethal dose of clove oil and transported to the laboratory for further processing. In addition to fish sampling, physical–chemical parameters at each site were recorded, including temperature ( $^{\circ}\text{C}$ ), pH, total dissolved solids (TDS,  $\text{mg ml}^{-1}$ ) and conductivity ( $\mu\text{S cm}^{-1}$ ) using a HANNA HI 98129 Combo meter and turbidity (NTU) using a HANNA HI 98703 turbidity meter ([www.hannainstruments.co.uk](http://www.hannainstruments.co.uk)). Furthermore, site characteristics

were measured at each collection point, including average stream width (m) and altitude. Average stream width was determined from three transects that were set perpendicular to the flow at the top, middle and bottom of each sampling site. Altitude was determined from a topographical map using the GPS coordinates that were recorded for each site. Physico-chemical variables and site characteristics were used as an adequate proxy for environmental variability within the study area (Kadye & Booth, 2013).

### 2.3 | Spatial patterns and environmental niches analysis

Environmental niche parameters along broad environmental gradients were tested for all species, as well as niche overlap for species with similar distribution. A total of 10 native and six non-native fish species, which were all sampled from at least three sites, were included in this analysis. In order to test environmental niche parameters for individual species, outlying mean index analysis was used ( $I_{\text{OM}}$ , Doledec *et al.*, 2000). Due to several sampling methods used to assess fish distribution, species niche parameters were analysed with data indicating either presence or absence. The  $I_{\text{OM}}$  characterises a species based on its niche position and niche breadth. Niche position measures the deviation of a species' mean habitat condition from a hypothetical species that is uniformly distributed and tolerates average habitat conditions. Habitat conditions were based on physico-chemical factors that were measured at each site. Species with high  $I_{\text{OM}}$  values have marginal niches, whereas those with low values have non-marginal niches. Niche breadth measures the dispersion of a species from the typically average environmental conditions that it uses, which is represented by its level of tolerance. Species with high tolerance values have wide niche breadths and occur across a wide range of environmental conditions (habitat generalists), whereas those with low values occur within a limited range of conditions (habitat specialists; Doledec *et al.*, 2000). In addition, residual tolerance, which represents variability that is not explained by the measured variables, was estimated for each species. A Monte Carlo permutation test (999 permutations) tested the null hypothesis that a species' niche position was not constrained by environmental variables. Canonical  $I_{\text{OM}}$  was used to compare broad scale niche overlap among species for both native and non-native fishes.

Habitat niche overlap was tested for species with similar distribution. For native fishes, species with similar distribution were categorised as being either widespread or less widespread. To test for niche overlap for different fishes, co-occurrences of pairwise species were analysed based on three microhabitat dimensions, including habitat type, depth and submerged vegetation. Niche overlap ( $O_N$ ) and null models were calculated using mixture models that incorporate different data types following Geange *et al.* (2011). Local realised niches were evaluated for each species along three dimensions that were measured at each site. For the habitat dimension (pool, riffle and backwater), the association of a species to a particular habitat type was treated as electivity data. The availability of the habitat types was weighted by the number of sampling sites. Manly's alpha indices were then used to calculate  $O_N$  for the electivity (Geange *et al.*, 2011). The

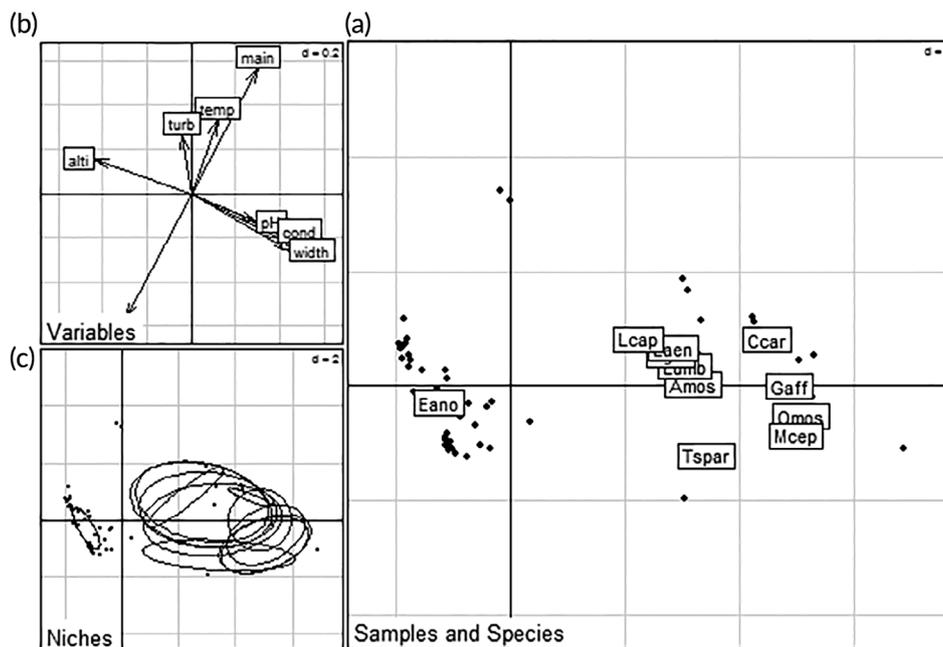
depth dimension (m) was treated as a continuous variable. Niche overlap along the depth gradient was therefore modelled based on non-parametric kernel density function (Mouillot *et al.*, 2005). The vegetation dimension (presence or absence) was treated as binary data and was modelled based on Bernoulli distribution. A unified measure of mean  $O_N$  was calculated by averaging the niche overlap between species  $i$  and  $j$  over each different axis  $t$ :  $O_{Nij} = \frac{\sum_{t=1}^T O_{Nij,t}}{T}$ , where  $O_{Nij,t} = \frac{\int \sum_{i=1}^T NO_{i,j,t}}{T}$ , where  $O_{Nij}$  is the niche overlap value that ranges from 0, when two distributions are completely separate, to 1, when they completely coincide and  $T$  is the number of axes (Geange *et al.*, 2011). Null models with randomisation permutations (999 permutations) were used to test  $H_0$  (no niche differentiation) for species with similar distribution that occupy the same niche. All analyses were conducted in R (www.r-project.org). Within R, we used the following packages; ade4 and adehabitatHS for environmental niche assessment. To meet the assumptions of multivariate normality all environmental variables were transformed into z-scores prior to  $I_{OM}$  ordinations.

### 3 | RESULTS

The first and second  $I_{OM}$  axes explained 96.7% and 2.7% of the variation of the data, respectively and we used the first axis to interpret the results. This axis was positively correlated with altitude and negatively correlated with stream width (Figure 2). High altitude represented tributary sites, whereas mainstream sites were characterised by high stream width. These mainstream sites exhibited a longitudinal gradient whereby stream width, TDS, conductivity and pH increased downstream (Figure 2). With the exception of mudfish *Labeo capensis* (Smith 1841), all fish species exhibited a significant deviation of their environmental niches from the average habitat conditions (Monte Carlo randomisation test,  $P < 0.01$ ), indicating that abiotic factors influenced species distribution (Table 1). Similarly, the global test on

marginality of all species was significant (Monte Carlo randomisation test,  $P < 0.001$ ), providing evidence of environmental niche segregation among the fishes along the  $I_{OM}$  axes. Most native fishes, including mottled eel *Anguilla marmorata* Quoy & Gaimard 1824, river goby *Glossogobius callidus* (Smith 1937), Cape moony *Monodactylus falciformis* Lacépède 1801, Mozambique tilapia *Oreochromis mossambicus* (Peters 1852), large-scale mullet *Planiliza macrolepis* (Smith 1846), freshwater mullet *Pseudomyxus capensis* (Valenciennes 1836) and flathead mullet *Mugil cephalus* L. 1758, occurred downstream within the mainstem (Figure 2) and all presented high  $I_{OM}$  (marginality) and low tolerance values, which showed that they were habitat specialists with narrow environmental niches (Table 1). These species were less widespread, occurring at  $< 10\%$  of all sampling sites. Within their distribution, most of these native species presented high mean niche overlap ( $O_N > 0.5$ ), with *A. marmorata* and *O. mossambicus* showing the most similar local realised niches (Table 2). However, two exceptions included the *G. callidus* and *M. falciformis*, whose niches differed significantly from that of the *P. macrolepis*.

One native species, the longfin eel *Anguilla mossambica* (Peters 1852), showed low marginality, indicating a ubiquitous presence, whereas another native species, the moggel *Labeo umbratus* (Smith 1841), presented high tolerance and evidence of occupying a wide environmental niche breadth. These two species were widespread, occurring at  $> 15\%$  of all sites in both the mainstem and in some of the tributaries, as well as showing high niche overlap (mean  $O_N = 0.76 \pm 0.20$ ). Another species with low marginality was chubbyhead barb *Enteromius anoplus* (Weber 1897), but it had low tolerance and high residual tolerance. *Enteromius anoplus* was widespread within the headwaters of tributaries and absent within the mainstem. At sites where it co-occurred with other species, *E. anoplus* had high niche overlap with *A. mossambica* and significantly low niche overlap with *L. umbratus* (Table 2). Overall, canonical  $I_{OM}$  revealed broad spatial organisation



**FIGURE 2** Outlying mean index analysis indicating the species and environmental variables vectors for the Great Fish River, South Africa: (a) projection of the sampling sites and the mean of the distribution of the utilisation weights of fishes; (b) the projection of the environmental variables scores; (c) the individual niches for different species. The species abbreviations are given in Table 2

**TABLE 1** Niche parameters for fish species collected in the Great Fish River system, Eastern Cape, South Africa

| Common name           | Species                                | Abbr. | $I_{OM}$ | Tol. | $R_{Tol}$ | $I_{OM}\%^a$ | Tol. $\%^a$ | $R_{Tol}\%^a$ | P       |
|-----------------------|--|-------|----------|------|-----------|--------------|-------------|---------------|---------|
| Mottled eel           | <i>Anguilla marmorata</i>              | Amar  | 25.68    | 2.23 | 3.93      | 80.70        | 7.00        | 12.30         | < 0.01  |
| Longfin eel           | <i>Anguilla mossambica</i>             | Amos  | 10.35    | 5.46 | 4.38      | 51.30        | 27.00       | 21.70         | < 0.001 |
| Chubbyhead barb       | <i>Enteromius anoplus</i>              | Eano  | 1.67     | 0.12 | 3.01      | 34.70        | 2.60        | 62.70         | < 0.001 |
| Moggel                | <i>Labeo umbratus</i>                  | Lumb  | 9.30     | 5.61 | 4.29      | 48.40        | 29.20       | 22.30         | < 0.001 |
| River goby            | <i>Glossogobius callidus</i>           | Gcal  | 26.00    | 1.85 | 3.69      | 82.40        | 5.90        | 11.70         | < 0.001 |
| Cape moony            | <i>Monodactylus falciformis</i>        | Mfal  | 26.48    | 2.33 | 4.42      | 79.70        | 7.00        | 13.30         | < 0.01  |
| Mozambique tilapia    | <i>Oreochromis mossambicus</i>         | Omos  | 26.00    | 1.85 | 3.69      | 82.40        | 5.90        | 11.70         | < 0.001 |
| Large-scale mullet    | <i>Planiliza macrolepis</i>            | Lmac  | 25.68    | 2.23 | 3.93      | 80.70        | 7.00        | 12.30         | < 0.001 |
| Freshwater mullet     | <i>Pseudomyxus capensis</i>            | Mcap  | 25.68    | 2.23 | 3.93      | 80.70        | 7.00        | 12.30         | < 0.001 |
| Flathead mullet       | <i>Mugil cephalus</i>                  | Mcep  | 25.68    | 2.23 | 3.93      | 80.70        | 7.00        | 12.30         | < 0.01  |
| Banded tilapia        | <i>Tilapia sparrmanii</i> <sup>b</sup> | Tspar | 13.64    | 5.03 | 6.32      | 54.60        | 20.10       | 25.30         | < 0.05  |
| Common carp           | <i>Cyprinus carpio</i> <sup>b</sup>    | Ccar  | 20.90    | 0.56 | 1.33      | 91.70        | 2.50        | 5.80          | < 0.01  |
| Sharptooth catfish    | <i>Clarias gariepinus</i> <sup>b</sup> | Cgar  | 8.13     | 5.59 | 5.00      | 43.40        | 29.90       | 26.70         | < 0.001 |
| Smallmouth yellowfish | <i>Labeobarbus aeneus</i> <sup>b</sup> | Laen  | 8.44     | 4.97 | 5.04      | 45.70        | 26.90       | 27.30         | < 0.001 |
| Mosquitofish          | <i>Gambusia affinis</i> <sup>b</sup>   | Gaff  | 23.75    | 1.31 | 3.14      | 84.20        | 4.70        | 11.10         | < 0.001 |
| Mudfish               | <i>Labeo capensis</i> <sup>b</sup>     | Lcap  | 6.40     | 1.99 | 3.13      | 55.50        | 17.30       | 27.10         | > 0.05  |

Species abbreviations used in the analysis;  $I_{OM}$ : outlying mean index (which indicates marginality); Tol.: tolerance (which indicates niche breadth);  $R_{Tol}$ : residual tolerance (which indicate unexplained variance).

<sup>a</sup>Percentages indicate the proportion of variability from total inertia for each species.

<sup>b</sup>Non-native species.

**TABLE 2** Mean ( $\pm$  SD) niche overlap between native fishes incorporating three axis; (1) habitat association (electivity data), (2) depth (measurement data) and (3) presence or absence of vegetation (categorical data)

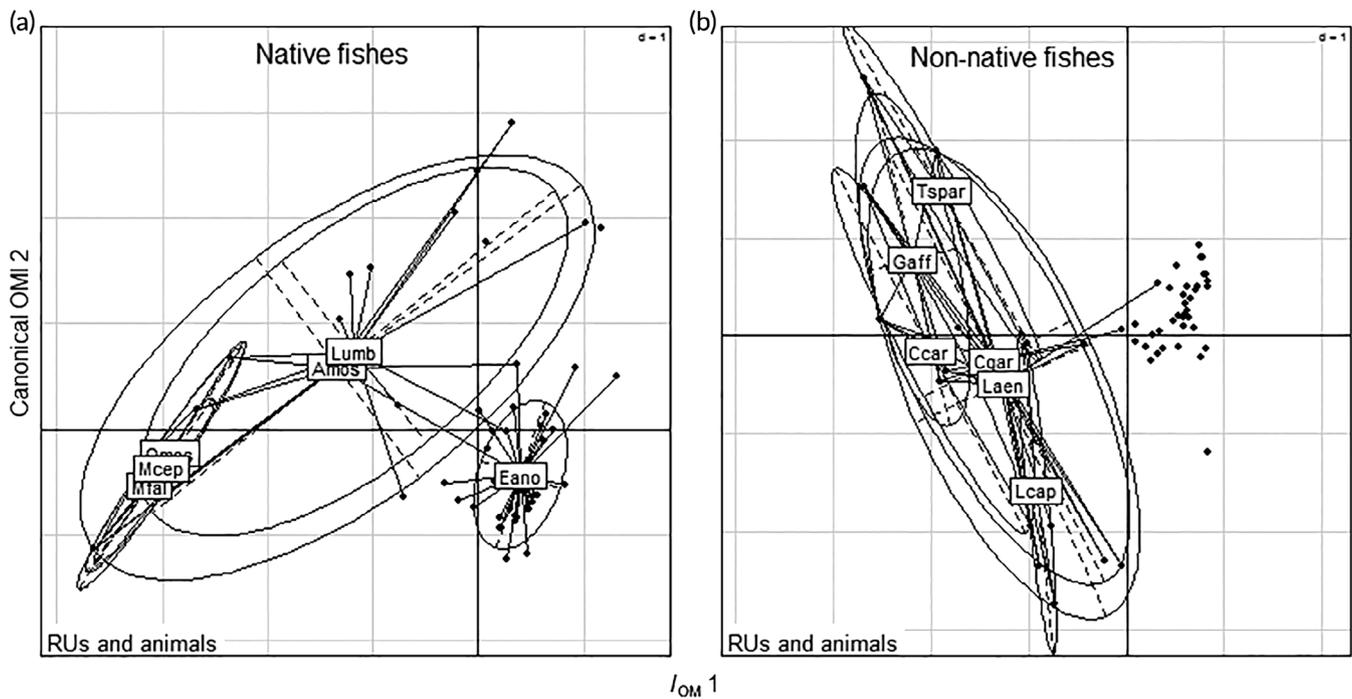
|                           | <i>Anguilla mossambica</i> | <i>Enteromius anoplus</i> | <i>Glossogobius callidus</i> | <i>Planiliza macrolepis</i>       | <i>Labeo umbratus</i>             | <i>Pseudomyxus capensis</i> | <i>Mugil cephalus</i> | <i>Monodactylus falciformis</i>   | <i>Oreochromis mossambicus</i> |
|---------------------------|----------------------------|---------------------------|------------------------------|-----------------------------------|-----------------------------------|-----------------------------|-----------------------|-----------------------------------|--------------------------------|
| <i>Anguilla marmorata</i> | 0.63 $\pm$ 0.27            | –                         | 0.77 $\pm$ 0.10              | 0.55 $\pm$ 0.32                   | 0.84 $\pm$ 0.11                   | 0.63 $\pm$ 0.21             | 0.59 $\pm$ 0.29       | 0.74 $\pm$ 0.22                   | 0.93 $\pm$ 0.06                |
| <i>A. mossambica</i>      |                            | 0.70 $\pm$ 0.19           | 0.73 $\pm$ 0.12              | 0.47 $\pm$ 0.47                   | 0.76 $\pm$ 0.20                   | 0.87 $\pm$ 0.11             | 0.48 $\pm$ 0.45       | 0.67 $\pm$ 0.25                   | 0.58 $\pm$ 0.20                |
| <i>E. anoplus</i>         |                            |                           |                              | –                                 | <b>0.52 <math>\pm</math> 0.03</b> | –                           | –                     | –                                 | –                              |
| <i>G. callidus</i>        |                            |                           |                              | <b>0.39 <math>\pm</math> 0.35</b> | 0.80 $\pm$ 0.08                   | 0.71 $\pm$ 0.09             | 0.42 $\pm$ 0.34       | 0.80 $\pm$ 0.08                   | 0.80 $\pm$ 0.18                |
| <i>P. macrolepis</i>      |                            |                           |                              |                                   | 0.57 $\pm$ 0.36                   | 0.47 $\pm$ 0.38             | 0.87 $\pm$ 0.23       | <b>0.33 <math>\pm</math> 0.52</b> | 0.53 $\pm$ 0.23                |
| <i>L. umbratus</i>        |                            |                           |                              |                                   |                                   | 0.75 $\pm$ 0.13             | 0.60 $\pm$ 0.34       | 0.73 $\pm$ 0.18                   | 0.79 $\pm$ 0.07                |
| <i>P. capensis</i>        |                            |                           |                              |                                   |                                   |                             | 0.51 $\pm$ 0.34       | 0.61 $\pm$ 0.19                   | 0.57 $\pm$ 0.14                |
| <i>M. cephalus</i>        |                            |                           |                              |                                   |                                   |                             |                       | 0.35 $\pm$ 0.50                   | 0.56 $\pm$ 0.22                |
| <i>M. falciformis</i>     |                            |                           |                              |                                   |                                   |                             |                       |                                   | 0.70 $\pm$ 0.16                |

Species occupying statistically different ( $P < 0.05$ ) local realised niches are indicated in bold.

among all native species, whereby the *A. mossambica* and *L. umbratus*, the most widespread species, had broad and overlapping environmental niches (Figure 3). By contrast, the *E. anoplus*, which was widespread within tributaries, had a narrow and non-overlapping environmental niche, whereas most of the native species that occurred downstream had narrow and overlapping environmental niches.

In general, most non-native fishes, including the banded tilapia *Tilapia sparrmanii* Smith 1840, sharptooth catfish *Clarias gariepinus* (Burchell 1822), smallmouth yellowfish *Labeobarbus aeneus* (Burchell 1822) and *L. capensis* showed relatively low marginality and high tolerance. In particular, the *C. gariepinus* and *L. aeneus* had the lowest marginality and highest tolerance, indicating that they were the most

ubiquitous. Marginality and tolerance values for these two species were comparable to those of the *A. mossambica* and *L. umbratus*, the most widespread native species. An exception to the general environmental niche patterns for the non-native fish species was observed for the common carp *Cyprinus carpio* L. 1758 and the mosquitofish *Gambusia affinis* (Baird & Girard 1853), which both presented high marginality and low tolerance, indicating that they were less ubiquitous (Table 1). Furthermore, *C. carpio* exhibited low niche overlap with *L. aeneus*, whereas *G. affinis* niche was significantly dissimilar to that of *C. gariepinus* and *Labeo capensis* (Table 3). Spatially, however, these non-native fishes generally showed broad and overlapping environmental niches (Figure 3).



**FIGURE 3** Spatial organisation and environmental niche breadth based on canonical outlying mean index ( $I_{OM}$ ) analysis for (a) native and (b) non-native fish species that were collected in the Great Fish River system, Eastern Cape, South Africa. The resource units (RU) and animals represent the environmental niche size (ellipse) and the fish species, respectively. The species abbreviations are given in Table 2

#### 4 | DISCUSSION

Niche partitioning predicts that co-occurring species and potential competitors would show differentiation in their niche breadth and extend of niche overlap as a response to either minimising competitive interference (Schoener, 1974) or due to having different environmental preferences (Myers & Harms, 2009). Consistent with the first hypothesis, this study showed probable environmental niche differentiation among native fishes. These results suggest that this pattern was closely matched to niche breadth and niche overlap. Specifically, this study indicated that among native fishes, there was spatial organisation that occurred at broad scale along the longitudinal profile of the study system. This was reflected by the presence of less ubiquitous species with narrow environmental niches, such as most species that occurred downstream within the mainstem, the presences of ubiquitous species and with broad environmental niches, such as *A. mossambica* and *L. umbratus* and the distribution pattern of *E. anoplus* that were widespread within the tributaries and whose environmental niche did not overlap with other species. This spatial pattern was consistent with the general observation on spatial organisation within lotic ecosystems, which has been illustrated by studies that show differential responses of species to environmental gradients (Darmon *et al.*, 2012; Vannote *et al.*, 1980). Spatial organisation reflects environment-mediated niche filtering that can occur when species have different tolerances to spatial heterogeneities, resulting in species either having segregated distribution and non-overlapping niches or having overlapping niches with different niche breadth (Chesson, 2000).

In general, the spatial pattern of the Great Fish River's native fishes appeared to be a consequence of a combination of the longitudinal hydro-morphological changes, which result in the upstream and downstream differences in assemblage composition, and the hydrological modification associated with the IBWT, which probably influenced assemblage structure of the upper mainstem section of the study system. Firstly, the Great Fish River's upstream section was marked by the dominance of the *E. anoplus* in the headwater streams and the occurrence of a few primary freshwater fishes (mainly *A. mossambica* and *L. umbratus*) in the mainstem. This was in contrast to the downstream section that was characterised by a distinct assemblage, which comprised both primary freshwater fishes and coastal and estuarine species, such as *A. marmorata*, *G. callidus*, *M. falciformis*, *P. macrolepis*, *P. capensis* and *M. cephalus*. In this study, the spatial pattern of native fishes was generally consistent with the fish diversity patterns associated with river continuum, primary due to increasing structural complexity from upstream to downstream (Carvalho & Tejerina-Garro, 2015; Montana & Winemiller, 2010). The longitudinal structural complexity of rivers is usually directly associated with additional habitats, which often facilitate the occurrence of different species (Angermeier & Karr, 1983; Casatti *et al.*, 2009; Schlosser, 1982) and indirectly associated with increasing food availability (Eros, 2005; Schlosser, 1998).

From a niche perspective, the broad spatial patterns that reflected the upstream–downstream differences in assemblage composition posits the likelihood of environmental filtering along the longitudinal gradient. Environmental filtering is assumed to drive functionally different species to occur in dissimilar habitat conditions (Kraft *et al.*,

**TABLE 3** Mean ( $\pm$  SD) niche overlap between non-native fishes incorporating three axis; (1) habitat association (electivity data), (2) depth (measurement data) and (3) presence or absence of vegetation (categorical data)

|                        | <i>Clarias gariepinus</i> | <i>Gambusia affinis</i>           | <i>Labeobarbus aeneus</i>         | <i>Labeo capensis</i>             | <i>Tilapia sparrmanii</i> |
|------------------------|---------------------------|-----------------------------------|-----------------------------------|-----------------------------------|---------------------------|
| <i>Cyprinus carpio</i> | 0.71 $\pm$ 0.12           | 0.72 $\pm$ 0.21                   | <b>0.56 <math>\pm</math> 0.13</b> | 0.57 $\pm$ 0.12                   | 0.73 $\pm$ 0.09           |
| <i>C. gariepinus</i>   |                           | <b>0.56 <math>\pm</math> 0.23</b> | 0.82 $\pm$ 0.07                   | 0.70 $\pm$ 0.06                   | 0.65 $\pm$ 0.15           |
| <i>G. affinis</i>      |                           |                                   | 0.40 $\pm$ 0.26                   | <b>0.34 <math>\pm</math> 0.24</b> | 0.68 $\pm$ 0.06           |
| <i>L. aeneus</i>       |                           |                                   |                                   | 0.79 $\pm$ 0.03                   | 0.60 $\pm$ 0.03           |
| <i>L. capensis</i>     |                           |                                   |                                   |                                   | 0.56 $\pm$ 0.25           |

Species occupying statistically different ( $P < 0.05$ ) local realised niches are indicated in bold.

2014; Mayfield & Levine, 2010), whereas different species with converging functional traits may co-occur with limited interspecific interactions (McGill *et al.*, 2006). Although there was evidence for spatial organisation, most native fishes showed high environmental niche overlap and appeared to have similar local realised niches. For the native fishes that co-occurred in the downstream section of the study systems, it is likely that their coexistence within similar habitat conditions may be mediated by trophic niche differentiation mechanisms. Studies elsewhere have shown that lower reaches of rivers are characterised by high richness that is mediated by trophic diversification that allows different fishes to occupy different trophic positions (Guo *et al.*, 2018; Ou *et al.*, 2017). Secondly, the general absence in the Great Fish River's upper mainstem section of the *E. anoplus*, which was historically widespread (Laurenson & Hocutt, 1985), suggest the likely impact of the IBWT in influencing both habitat availability for this species, together with the proliferation of multiple non-native fishes, which include generalist predators such as *C. gariepinus* (Kadye & Booth, 2012a, 2012b).

While niche differentiation is assumed to drive coexistence in natural communities, successful invaders appear to override this theory because they are assumed to utilise a wide array of habitats and resources within their invaded environments (Shea & Chesson, 2002). Results on environmental niches for non-native species appeared consistent with this hypothesis because most fishes had broad environmental niches and high tolerances to environmental factors. Two possible mechanisms were likely to explain the environmental niche patterns for these non-native fishes. Firstly, high environmental niche breadth observed for most non-native fishes was in agreement with studies that suggest that successful invaders comprise species that are either habitat generalists or those that have a high dispersal abilities beyond their natural range (Moyle & Marchetti, 2006; Vazquez, 2005). Large environmental niches for non-native species can be attributed to high dispersal ability within novel habitats that may be aided by resource opportunity and release from their native competitors and predators (Larson *et al.*, 2010). Results of this study suggest that most non-native fishes were less constrained by environmental requirements, particularly in the mainstem section and were therefore likely able to persist in a wide range of habitats. This was notably so for the *C. gariepinus* and *L. aeneus* that were generally the most ubiquitous. Secondly, the co-occurrence of multiple non-native fishes is consistent with the view that invaded systems can host functional assemblages of non-native species (Sax *et al.*, 2007). Emerging

evidence suggest that such recently formed assemblages of non-native species can coexist in the absence of a prolonged evolutionary co-adaptation (Sax *et al.*, 2007), often being facilitated by rapid adjustments and complex ecological interactions (Ackerly, 2003). In addition, both empirical evidence and theoretical views appear to suggest that multiple invasions may be facilitated by the trophic composition of the recipient communities (Bruno *et al.*, 2003; Gilbert & Parker, 2006). For example, communities that are characterised by either specialist predators and pathogens or generalist mutualists have been found to be susceptible to multiple invasions, often showing little invasion resistance (Callaway *et al.*, 2004). This is likely so for the Great Fish River system where the native predators, such as *Anguilla* spp. either have narrow ranges (Laurenson & Hocutt, 1985) or have a relatively narrow trophic range compared with non-native predators, such as *C. gariepinus*.

This study showed widespread occurrence of non-native species, particularly within the mainstem. The implications of these multiple invasions are far reaching as the non-native fishes are likely to contribute both individually and collectively to influence the integrity and functioning of the invaded system. Individual effects are likely to occur for species that share similar distribution and resource utilisation patterns. For example, results of this study suggest the likelihood of competition between two predators, non-native *C. gariepinus* and native *A. mossambica* that both had overlapping environmental niches. Similarly, there was a likelihood of competitive interference between non-native *T. sparrmanii* and native *O. massambicus* in habitats that they co-occur. Collective synergistic effects (Ricciardi, 2005; Simberloff, 2011) by non-native fishes could be inferred from their large environmental niche breadths, which suggest their ability to utilise a wide range of habitats and potentially compete with native species that share similar resources. Furthermore, results of this study indicated that these non-natives were widespread in the upstream section of the mainstem. It is postulated that the IBWT scheme has become a substantial human-mediated disturbance, especially on the upstream section. Disturbances, including altering flow regimes, are likely to create environmental conditions that promote the proliferation of non-native species (Byers, 2002) while weakening the invasion resistance of native species (Baltz & Moyle, 1993). This study therefore suggests that high non-native richness within the upstream may be a consequence of such flow-related disturbances. By acting as a conduit to translocation of non-native species, the

IBWT scheme is likely to enhance both colonisation and propagule pressures within this river.

To conclude, this study demonstrated the importance of examining environment niches when assessing patterns associated with co-occurring native and non-native species. This study further suggests that spatial organisation among species can reflect their differences in tolerance to environmental heterogeneities. Specifically, spatial organisation by native species suggest the role of environmental niche filtering along the longitudinal gradient, whereas the multiple non-native species appear to occur as a distinct functional assemblage within the mainstem section of the invaded river system. The findings from this study provided a critical assessment of the role of multiple invasions within aquatic ecosystems and potentially invokes questions on their functional role particularly through interspecific interactions. With the worldwide concerns on species distribution patterns, these findings advance our knowledge on patterns that explain species coexistence and the effects of environmental change.

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