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ORIGINAL ARTICLE

The introduced *Arapaima gigas* in the Bolivian Amazon: Trophic position and isotopic niche overlap with native species

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Abstract

Non-native fish species may generate major ecological impacts on native assemblages. This study aims to assess the potential impact of the introduced *Arapaima gigas* on native fish assemblages in two oxbow lakes of the Bolivian Amazon. Stable isotope data were used to determine trophic position (TP) and isotopic niche overlap, to evaluate potential predation and competition interactions, respectively. Results suggest that *A. gigas* is more an omnivore than a top predator, as often claimed. *Arapaima gigas* occupied an intermediate TP between detritivore/herbivore and piscivore fish species and showed broader isotopic niche compared to most native species analysed. The isotopic niche of *A. gigas* significantly overlapped with most native fish species in one lake (i.e. Lake Mentiroso), while there was low niche overlap in the second (i.e. Lake Miraflores). Given its omnivorous tendencies, the predation impact of *A. gigas* on other fish species is likely less than currently claimed and likely varies with the food web structure of the ecosystem. More precise data on resource availability and use are necessary to infer whether niche overlap will have negative impacts on native fish species through potential competitive interactions. Increasing our understanding on the processes generating impact of these introductions on resident communities through food web ecology will pave the way for better resource management and conservation efforts.

KEYWORDS

competition, fish, floodplain lakes, non-native species, predation, upper Madeira basin

1 | INTRODUCTION

Introduction of non-native fish species in freshwater ecosystems is continuously increasing and has become a matter of concern among ecologists, who are frequently asked to evaluate the potential risks of intentional or unintentional introductions (Gozlan, 2008). The impact of these introductions on native communities is often difficult to evaluate; some may have rather subtle effects, while others may exert strong ecological impacts (Cucherousset & Olden, 2011).

Major ecological impacts range from behavioural shifts and severe population declines in native species, to local extinctions of some species and even to the extirpation of entire faunas (Cucherousset & Olden, 2011; Ricciardi & Kipp, 2008). Predation and competition are usually considered the main mechanisms driving the impact of non-native introduced fish species (Levine, 2008). Predation by introduced species is expected to cause major detrimental effects on resident communities (Salo et al., 2007; Sih et al., 2010) through strong top-down control (Carpenter et al., 2001). Competition may

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also strongly impact native species when the novel environment is colonised by a species with superior competitive ability (competition hypothesis). On the contrary, when colonisation occurs through occupation of niches not yet used by native species (opportunistic hypothesis), low competition and impact are expected (Pagani-Núñez et al., 2018).

To determine ecological impacts of introduced fishes is particularly challenging for Amazonian fish assemblages, which typically present high species diversity and trophic complexity (Jepsen & Winemiller, 2002). The recent introduction of one of the largest freshwater fish in the world into Bolivian waters is considered a serious threat. *Arapaima gigas*, known as Pirarucú in Brazil and as Paiche in Peru and Bolivia, reaches 3 m in length and up to 200 kg in weight (Saint-Paul, 2017). *Arapaima gigas* natural distribution is broad and includes different sub-basins of the Amazon, Tocantins-Araguaia and Essequibo Rivers that flow across Brazil, Ecuador, Colombia, Guyana and Peru (Castello & Stewart, 2010; Dubos et al., 2022). However, *A. gigas* natural distribution does not include any area of the Bolivian Amazon (i.e. the upper Madeira basin), probably due to the historical presence of a series of rapids along the main course of Madeira River between Puerto Paez (Bolivia) and Porto Velho (Brazil), which have acted as a natural barrier to migration and therefore as a natural boundary for the distribution of this species (Hrbek et al., 2005). According to Miranda-Chumacero et al. (2012), *A. gigas* first colonised Bolivian waters via the Peruvian part of the upper Madre de Dios River following its introduction on different occasions in several lagoons between the mid-1960s and early 1980s. During flood events, some of these fishes started a colonisation process towards the Bolivian territory (Carvajal-Vallejos et al., 2011; Farias et al., 2019; Miranda-Chumacero et al., 2012). Multiple secondary introductions, mainly coming from aquaculture practices, may have advanced this colonisation process (Catâneo et al., 2022). At present, *A. gigas* has been reported virtually in all the Bolivian tributaries of the Madre de Dios and Orthon Rivers and in the lower reaches of the Beni, Mamoré and Iténez Rivers (Carvajal-Vallejos et al., 2011; Catâneo et al., 2022; Miranda-Chumacero et al., 2012).

Arapaima gigas is often considered a top predator due to its large size and piscivorous feeding habits (Martinelli & Petrere, 1999; Sarmiento et al., 2014). Given that large populations of this species are now established in Bolivian waters, it may potentially cause strong ecological impacts on the colonised ecosystems. Local fishermen and indigenous people already blame *A. gigas* for decline in catches of traditional commercial species and changes in the composition of native fish assemblages (Doria et al., 2020; Miranda-Chumacero et al., 2012; Van Damme et al., 2015). However, there is yet no real scientific evidence supporting these statements, all the more as some recent studies have suggested that the species may feed lower in the food web than previously thought (Carvalho et al., 2018; Jacobi et al., 2020; Queiroz, 2000; Villafan et al., 2020; Watson et al., 2013).

The trophic position (TP) of an introduced species and the proportion of trophic niche overlap between species in an assemblage provide a good approach for assessing the potential occurrence of

predation and competition between introduced and native species (Cornell & Lawton, 1992). Fish stomach content data offer detailed information on their diets but are challenging to collect, and may only represent recently ingested food, and include unidentifiable and non-digestible biomass (Gu et al., 1997; Manetta et al., 2003). This complexity and methodological problems in measuring the trophic niche using stomach content analysis hindered the development of this approach (Bearhop et al., 2004; Inger et al., 2006; Robb et al., 2012). Development of stable isotope-based approaches and associated statistical methods helped to largely overcome these difficulties. Layman et al. (2007) proposed the use of stable isotope data as a proxy for trophic niche, as stable isotopes ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are indicative of a species' feeding niche. The concept of the isotopic niche was formalised later (Newsome et al., 2007), and further developments in statistical methods allowed the inference of characteristics of the isotopic niche width, comparisons between populations/communities and estimation of niche overlap (Jackson et al., 2011). Currently, the isotopic niche concept is frequently used to assess trophic niche overlap (Larocque et al., 2021) to evaluate the potential impact of introduced species on native communities (Pennock et al., 2021; Yalçın Özdilek et al., 2019).

Our study aims to test whether *A. gigas* is a top predator in food webs of colonised Bolivian habitats by describing the trophic structure of the fish assemblages using ^{15}N and ^{13}C stable isotope estimations and the TP as an indicator of potential predation processes and to analyse the extent to which the isotopic niches of native species with various feeding habits (i.e. detritivorous, herbivorous, invertivorous and piscivorous habits) overlap with *A. gigas* as an indicator of potential competitive interactions.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

We collected samples from two *várzea* lakes (Mentiroso and Miraflores) located between 11.05–11.16°S and 66.30–66.70°W in the floodplain of the white-water Bolivian Madre de Dios River (Figure 1). White-water rivers are characterised by turbid, ochre-coloured and rich in nutrients waters due to high loading rates of suspended sediments (Sioli, 1984). The study area is located at 140–170 m above sea level, with mean annual temperatures above 25°C and annual average precipitations around 1350 mm. *Várzea* lakes are abundant in the floodplain of the Madre de Dios River and are connected to the river channel during high-water periods. The main primary carbon sources are phytoplankton, aquatic macrophytes (the C4 West Indian marsh grass *Hymenachne* and water grass *Paspalum*; and the C3 water hyacinth *Eichhornia* and water lettuce *Pistia*) and allochthonous organic matter supplied by the riparian rainforest.

We sampled fishes and basal carbon sources during the low water season in Lake Mentiroso (October 2015) and in Lake Miraflores (July 2017). During this period of the year, the lakes are totally isolated from the river, preventing sampling recently arrived

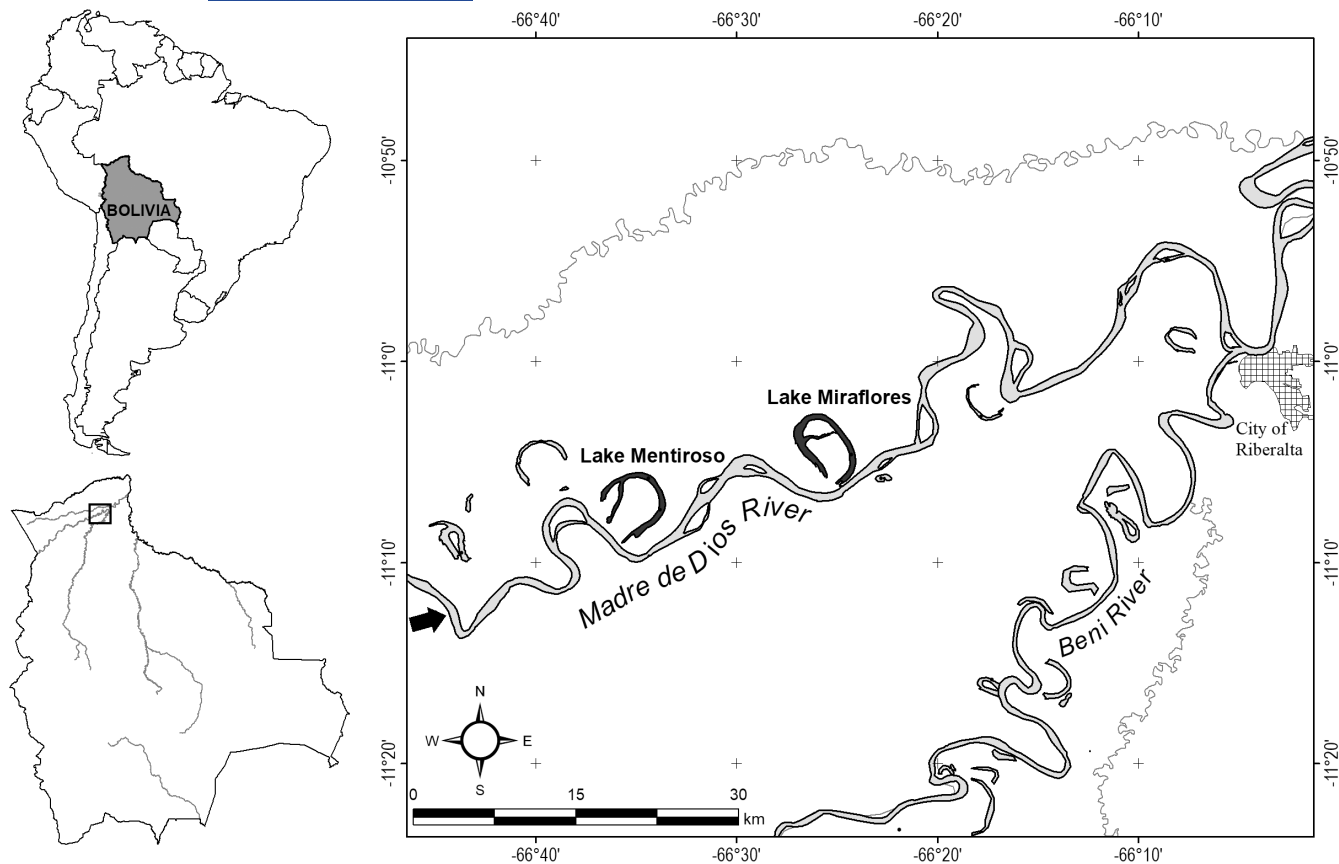


FIGURE 1 Location of the study area, showing Bolivia in South America, the study area in Bolivia, and the floodplain of River Madre de Dios. Waterbodies in black represent sampled lakes. The black arrow shows the direction of colonisation of *Arapaima gigas*.

migrants. Due to logistical difficulties, sampling effort was lower in Lake Miraflores compared to Lake Mentiroso. Consequently, data presented in this study are not representative of species richness and abundance. We captured fishes with the cooperation of local fishermen, fishing with hook and lines and a set of gillnets with knot-to-knot distances of 30–100 mm. Fish were identified and their standard length (SL) measured. We collected samples of adult individuals only, to avoid potential consequences of ontogenetic dietary shifts on analyses (Carvalho et al., 2018; Sánchez-Hernández et al., 2019). We chose the fish species most frequently captured and traded by local fishermen and representing all trophic guilds; that is, the introduced non-native *Arapaima gigas* (Schinz, 1822), the detritivores *Potamorhina altamazonica* (Cope, 1878) and *Potamorhina latior* (Spix & Agassiz, 1829), the herbivores *Colossoma macropomum* (Cuvier, 1816), *Mylossoma duriventre* (Cuvier, 1818), *Piaractus brachypomus* (Cuvier, 1818) and *Prochilodus nigricans* (Spix & Agassiz, 1829), the invertivores *Hypophthalmus* sp. (Spix & Agassiz, 1829) and *Triporthus albus* (Cope, 1872), and the piscivores *Hoplias malabaricus* (Bloch, 1794), *Plagioscion squamosissimus* (Heckel, 1840), *Pseudoplatystoma fasciatum* (Linnaeus, 1766), *Pygocentrus nattereri* (Kner, 1858), and *Serrasalmus spilopleura* (Kner, 1858). Each species was assigned to its specific trophic guild based on available literature data on gut content analyses (see Rejas, 2018 for review).

For stable isotope analyses, a sample of ~10 g of muscle tissue was taken from the dorsal part of each fish. In addition, we sampled basal carbon sources: C3 and C4 aquatic macrophytes and particulate organic matter (POM) as a surrogate for phytoplankton. Terrestrial plants from the surrounding rainforest were also sampled. POM samples were collected using water from the upper 1.5 m of the water column, screened through 20- μ m mesh to exclude zooplankton and filtered onto precombusted glassfibre Whatman GF/F filters. All samples were rinsed with deionised water and stored frozen in cryovials. Samples were thawed, freeze-dried and ground to a fine powder using a mortar and a pestle. Approximately 1 mg of dry sample material was packed into tin capsules. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements were performed at the UC Davis Stable Isotope Facility laboratory (University of California, Davis, USA).

We analysed samples from 158 fishes (39 from *A. gigas* and 119 from other species) and 31 basal carbon sources. Stable isotope ratios are reported in parts per thousand (‰) relative to international standards: Pee Dee belemnite (PDB) and atmospheric N for carbon and nitrogen, respectively. Isotope ratios are defined as: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$ (Fry, 2006). Samples with positive δ values indicate relatively more of the heavy isotope than present in the standard. Samples with negative δ values indicate relatively less of the heavy isotope than present in the standard (Jepsen & Winemiller, 2002).

2.2 | Data analyses

We used two-way ANOVA to assess interaction effects of lake and origin (i.e. C3 and C4 aquatic macrophytes, POM and terrestrial vegetation) on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of basal carbon sources. We then tested for differences in isotopic ratios between carbon sources within each of the lakes using one-way ANOVAs followed by Tukey's HSD test. To assess differences in isotopic ratios between fish trophic guilds (assigned from literature), we applied one-way ANOVAs followed by Tukey's HSD test, using individual fish as replicates. *Arapaima gigas* was treated separately since we aimed at determining its TP within the fish assemblages. Since SL range was broad for *A. gigas* (SL = 600–2290 mm), we used linear regressions for each lake to determine if SL and ^{15}N isotope ratios were correlated. We used $\delta^{15}\text{N}$ to estimate consumer's TP (Minagawa & Wada, 1984). Relative individual TP was calculated using the formula: $\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{base}}) / \Delta$, where λ is the TP of the organism used to estimate $\delta^{15}\text{N}_{\text{base}}$ and Δ is the N isotopic fractionation (in ‰) that occurs between each trophic level (Post, 2002). The isotopic fractionation value Δ was set at 2.8 ‰ (McCutchan et al., 2003). $\delta^{15}\text{N}_{\text{base}}$ was estimated for each lake using mean nitrogen signals of the fish species showing the lowest $\delta^{15}\text{N}$ value and with at least three replicates: *Potamorhina latior* and *Prochilodus nigricans* for Lake Mentirosos and Lake Miraflores, respectively. The TPs for these baseline species were then arbitrarily set to a value of 2.

We calculated isotopic niche widths using the 'Stable Isotope Bayesian Ellipses in R' package (SIBER; Jackson et al., 2011). The program calculates metrics describing the data in a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space for each population: that is, the total amount of isotopic niche area occupied (total area; TA), the standard ellipse area (SEA) and the sample size-corrected standard ellipse area (SEA_c). We retained all species with at least four sampled individuals for calculation. Bayesian inference was used to generate a distribution of covariance matrices that describe the observed data and to calculate the posterior ellipse and derived parameters, specifically the posterior Bayesian estimates of the SEA (SEAb). We further calculated the proportion of the isotopic niche of each native species that overlapped with the isotopic niche of *A. gigas* based on the posterior distributions of the fitted ellipses. All Data analyses were performed using R 4.1.2 (R Core Team, 2022).

3 | RESULTS

Significant interaction effects between carbon source origin and lakes were identified for both $\delta^{13}\text{C}$ (ANOVA, $p < .01$) and $\delta^{15}\text{N}$ values ($p < .05$), meaning that the effect of origin on isotopic ratios varied between lakes (Tables S1 and S2). Subsequent analyses were performed independently for each lake. C4 aquatic macrophytes showed significantly higher $\delta^{13}\text{C}$ values than all other carbon sources in both lakes ($p < .001$). $\delta^{13}\text{C}$ values for the remaining carbon sources varied in a relatively narrow range. In Lake Mentirosos, no significant differences in $\delta^{15}\text{N}$ values of carbon sources were observed ($p = .06$). In

lake Miraflores, C4 aquatic macrophytes showed significantly higher $\delta^{15}\text{N}$ values than terrestrial vegetation ($p < .05$). No significant differences in $\delta^{15}\text{N}$ values for the remaining pairwise comparisons were observed (Figure 2, Table S3).

Arapaima gigas was the largest fish species with mean SL varying between 1306 ± 491 and 975 ± 313 mm in lakes Mentirosos and Miraflores, respectively (Table 1). SL and $\delta^{15}\text{N}$ values for *A. gigas* were not significantly related, neither in Lake Mentirosos ($r^2 = .05$; $p = .24$) nor in Lake Miraflores ($r^2 = .41$, $p = .11$), indicating that variations in $\delta^{15}\text{N}$ values for this species were not due to potential ontogenetic dietary shifts. $\delta^{13}\text{C}$ values in fishes varied within a relatively narrow range, from -35.0 ± 1.5 ‰ (*P. nigricans*) to -26.8 ‰ (*M. duriventre*). Mean $\delta^{15}\text{N}$ values varied from 6.0 ± 0.9 ‰ (*P. latior*) to 11.8 ± 0.3 ‰ (*P. nattereri*).

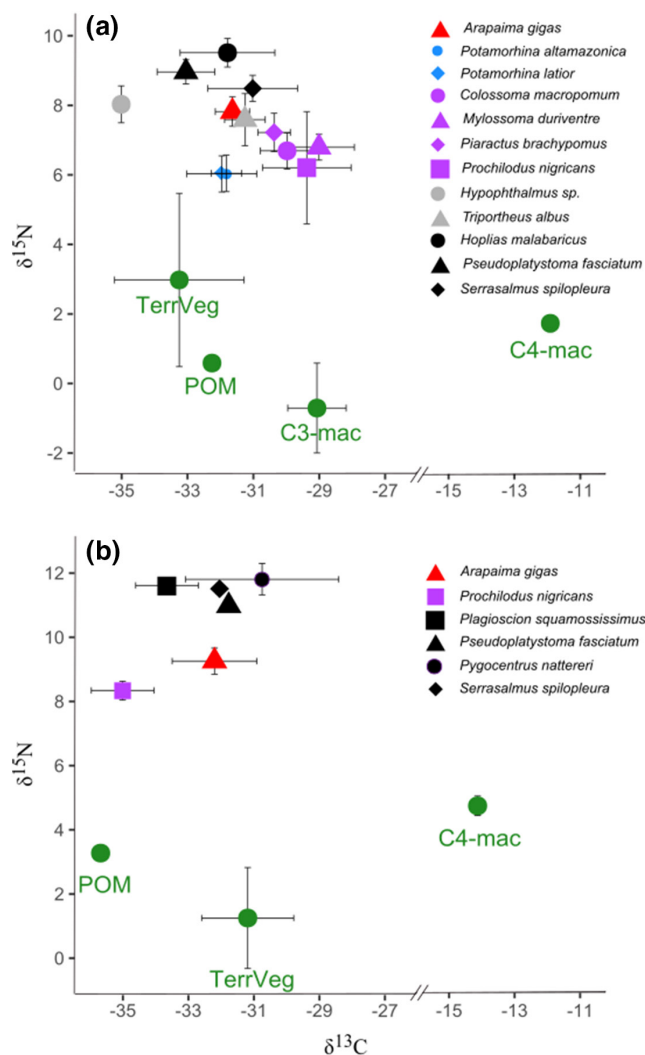


FIGURE 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values ($\pm 2\text{SE}$) of potential carbon sources and fish in lakes (a) Mentirosos and (b) Miraflores, located in the floodplain of River Madre de Dios, Bolivia. With carbon sources in dark green (C3-mac = C3 aquatic macrophytes, C4-mac = C4 aquatic macrophytes, POM = particulate organic matter, TerrVeg = terrestrial vegetation), *Arapaima gigas* in red, detritivores in light blue, herbivores in purple, invertivores in grey and piscivores in black.

TABLE 1 Sample size (*n*), standard length (SL; mean \pm standard deviation [SD] and range), mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SD) and trophic position (TP) for the introduced non-native fish *Arapaima gigas* and native fish species from lakes Mentiroso and Miraflores, located in the floodplain of river Madre de Dios.

Fish species	<i>n</i>	SL (mm)		Stable isotope ratios (‰)		TP
		Mean \pm SD	Range	Mean $\delta^{13}\text{C} \pm$ SD	Mean $\delta^{15}\text{N} \pm$ SD	
Lake Mentiroso						
<i>Arapaima gigas</i>	32	1306 \pm 491	645–2290	-31.6 \pm 1.5	7.8 \pm 1.2	2.6
Detritivores						
<i>Potamorhina altamazonica</i>	10	210 \pm 12	195–230	-31.8 \pm 0.7	6.0 \pm 0.8	2.0
<i>Potamorhina latior</i>	12	199 \pm 10	185–215	-32.0 \pm 1.8	6.0 \pm 0.9	2.0
Herbivores						
<i>Colossoma macropomum</i>	12	389 \pm 122	225–630	-30.0 \pm 1.4	6.7 \pm 0.9	2.2
<i>Mylossoma duriventre</i>	13	131 \pm 25	105–185	-29.0 \pm 1.9	6.8 \pm 0.7	2.3
<i>Piaractus brachypomus</i>	4	352 \pm 75	254–436	-30.4 \pm 0.5	7.2 \pm 0.6	2.4
<i>Prochilodus nigricans</i>	3	235 \pm 28	205–260	-29.4 \pm 1.2	6.2 \pm 1.4	2.1
Invertivores						
<i>Hypophthalmus sp</i>	7	315 \pm 56	190–350	-35.0 \pm 0.3	8.0 \pm 0.7	2.7
<i>Triportheus albus</i>	9	234 \pm 7	225–240	-31.3 \pm 0.9	7.6 \pm 1.1	2.6
Piscivores						
<i>Hoplias malabaricus</i>	5	334 \pm 141	230–582	-31.8 \pm 1.6	9.5 \pm 0.5	3.2
<i>Pseudoplatystoma fasciatum</i>	9	628 \pm 182	500–1055	-33.0 \pm 1.3	9.0 \pm 0.5	3.0
<i>Serrasalmus spilopleura</i>	6	129 \pm 14	110–150	-31.0 \pm 1.7	8.5 \pm 0.5	2.9
Lake Miraflores						
<i>Arapaima gigas</i>	7	975 \pm 313	600–1630	-32.2 \pm 1.7	9.3 \pm 0.5	2.3
Herbivores						
<i>Prochilodus nigricans</i>	8	339 \pm 44	290–410	-35.0 \pm 1.5	8.3 \pm 0.4	2.0
Piscivores						
<i>Pseudoplatystoma fasciatum</i>	1	530		-31.8	11.0	3.0
<i>Serrasalmus spilopleura</i>	1	250		-32.0	11.5	3.1
<i>Plagioscion squamosissimus</i>	17	425 \pm 78	275–540	-33.7 \pm 2.0	11.6 \pm 0.4	3.2
<i>Pygocentrus nattereri</i>	2	184 \pm 12	175–192	-30.8 \pm 1.7	11.8 \pm 0.3	3.3

Note: Species were assigned to trophic guilds based on available literature (see Rejas, 2018 for review).

$\delta^{15}\text{N}$ values matched well with our a priori trophic guild classification for native fish. In Lake Mentiroso, all pairwise comparisons between fish trophic guilds and *A. gigas* showed significantly different $\delta^{15}\text{N}$ values ($p < .05$), except the invertivores trophic guild ($p = .99$) (Table S4). Detritivores showed the lowest $\delta^{15}\text{N}$ values, whereas piscivores presented significantly higher mean $\delta^{15}\text{N}$ values compared to all other trophic guilds and *A. gigas* (p -values $< .01$). In consequence, TP estimations based on $\delta^{15}\text{N}$ values placed detritivore species at the bottom level (TP 2) and increased gradually from herbivores (TP values from 2.1 to 2.4) to invertivores (TP values from 2.6 to 2.7) and piscivores (TP values from 2.9 to 3.2). TP values for herbivorous fishes in Lake Mentiroso were higher than the TP value (2) expected for primary consumers. TP value for *A. gigas* was 2.6, positioning the species within the range of invertivores.

In Lake Miraflores, all pairwise comparisons between fish trophic guilds and *A. gigas* were significantly different (p -values $< .001$)

(Table S4). The herbivorous fish *P. nigricans* showed the lowest $\delta^{15}\text{N}$ values being at the bottom level (TP = 2), TP value for *A. gigas* was intermediate (2.3), and piscivores were on top with TP values varying between 3.0 and 3.3. Due to the limited number of species and individuals sampled in Lake Miraflores, no specific pattern emerged except that piscivores had higher TP values compared to *A. gigas* (Table 1).

A. gigas showed larger isotopic niche areas (SEAc 4.30 ‰² and 2.66 ‰² in lakes Mentiroso and Miraflores, respectively) compared to most native species. The proportion of isotopic niche area of native species overlapping with *A. gigas*, estimated from the range of SEAb and expressed as the mode, varied from 0% (*P. squamosissimus* from Lake Miraflores) to 100% (*P. brachypomus* from Lake Mentiroso) but exceeded 50% for most species, independently of their respective trophic guilds. In Lake Mentiroso, the isotopic niche overlap between *A. gigas* and curimatid detritivores

of the genus *Potamorhina* ranged from 44% to 55%. Both detritivores overlapped almost completely with *A. gigas* on the $\delta^{13}\text{C}$ axis, and there was also a considerable overlap on the $\delta^{15}\text{N}$ axis, even if *A. gigas* had on average higher $\delta^{15}\text{N}$ -values. Relatively high $\delta^{15}\text{N}$ -values for herbivore fishes and the wide range of $\delta^{15}\text{N}$ -values for *A. gigas* in Lake Mentirosos resulted in a high overlap on the $\delta^{15}\text{N}$ axis. $\delta^{13}\text{C}$ ranges for *C. macropomum* and *P. brachypomus* also mostly overlapped with that of *A. gigas*, resulting in high isotopic niche overlaps between these species and *A. gigas* (77% and 100%, respectively). In contrast, the herbivorous *P. nigricans* from Lake Miraflores showed the lowest isotopic niche overlap (26%) with that of *A. gigas*, mainly because showing lower $\delta^{13}\text{C}$ -values. Invertivorous fishes from Lake Mentirosos overlapped considerably with *A. gigas* on the $\delta^{15}\text{N}$ axis, resulting in similar TP-values. $\delta^{13}\text{C}$ -values for *T. albus* were found within the range of *A. gigas*, resulting in high isotopic niche overlap (70%) between the two species. On the contrary, *Hypophthalmus* sp. presented lower $\delta^{13}\text{C}$ -values than *A. gigas*, resulting in low isotopic niche overlap (10%; Table 2, Figure 3).

4 | DISCUSSION

Here we investigated potential effects of the non-native species *A. gigas* on native fish in the Bolivian Madre de Dios river-floodplain system, by determining its trophic position within the colonised fish assemblages and evaluating the extent of its isotopic niche overlap with that of the native fish species constituting these assemblages.

4.1 | *Arapaima gigas*: A generalist species with piscivorous tendencies

Overall, *A. gigas* occupied an intermediate TP, higher than detritivore and herbivore fish species, lower than piscivores and similar to invertivore species (data for detritivores and invertivores available only for Lake Mentirosos). Related to piscivores, differences in TP were relatively small in Lake Mentirosos but reached up to one full TP in Lake Miraflores. It should be noted that the piscivore fishes sampled here are usually reported for feeding almost exclusively on fishes

TABLE 2 Isotopic niche area (%²) estimates and proportion of isotopic niche overlap with the introduced non-native fish *Arapaima gigas* for native fish species in lakes Mentirosos and Miraflores, located in the floodplain of river Madre de Dios.

Species	TA	SEA	SEAc	SEAb	95% CI	Proportion overlap	
						Mode	95% CI
Lake Mentirosos							
<i>Arapaima gigas</i>	14.45	4.16	4.30	4.12	2.91–5.98		
Detritivores							
<i>Potamorhina altamazonica</i>	2.45	1.50	1.68	1.46	0.77–2.91	0.55	0.29–0.85
<i>Potamorhina latior</i>	9.09	4.66	5.13	4.57	2.35–8.36	0.44	0.25–0.58
Herbivores							
<i>Colossoma macropomum</i>	2.79	1.52	1.67	2.01	1.02–3.71	0.77	0.55–1.00
<i>Mylossoma duriventre</i>	7.68	4.06	4.43	3.88	2.06–6.91	0.51	0.29–0.71
<i>Piaractus brachypomus</i>	0.33	0.42	0.63	0.51	0.17–1.92	1.00	0.77–1.00
Invertivores							
<i>Hypophthalmus</i> sp.	0.96	0.71	0.86	0.64	0.29–1.53	0.10	0.00–0.75
<i>Triplocheilichthys albus</i>	5.73	3.25	3.71	3.10	1.28–6.25	0.70	0.44–0.98
Piscivores							
<i>Hoplias malabaricus</i>	1.98	1.78	2.37	1.70	0.61–5.04	0.59	0.16–0.95
<i>Pseudoplatystoma fasciatum</i>	2.08	1.31	1.49	1.38	0.70–2.98	0.88	0.60–1.00
<i>Serrasalmus spilopleura</i>	2.74	2.23	2.78	2.02	0.82–5.32	0.66	0.37–0.95
Lake Miraflores							
<i>Arapaima gigas</i>	3.77	2.22	2.66	2.20	0.95–5.11		
Herbivores							
<i>Prochilodus nigricans</i>	2.64	1.70	1.98	1.57	0.81–3.53	0.26	0.00–0.72
Piscivores							
<i>Plagioscion squamosissimus</i>	6.82	2.56	2.73	2.43	1.47–4.21	0.00	0.00–0.24

Note: Estimates of isotopic niche area are given as total area (TA), standard ellipse area (SEA), sample size-corrected standard ellipse area (SEAc) and the mode of the Bayesian (posterior) standard ellipse area (SEAb) estimates. Upper and lower 95% credible intervals (CI) indicate the uncertainty in the SEAb estimates. Isotopic niche overlap and credible intervals were calculated based on the posterior distributions of the fitted ellipses.

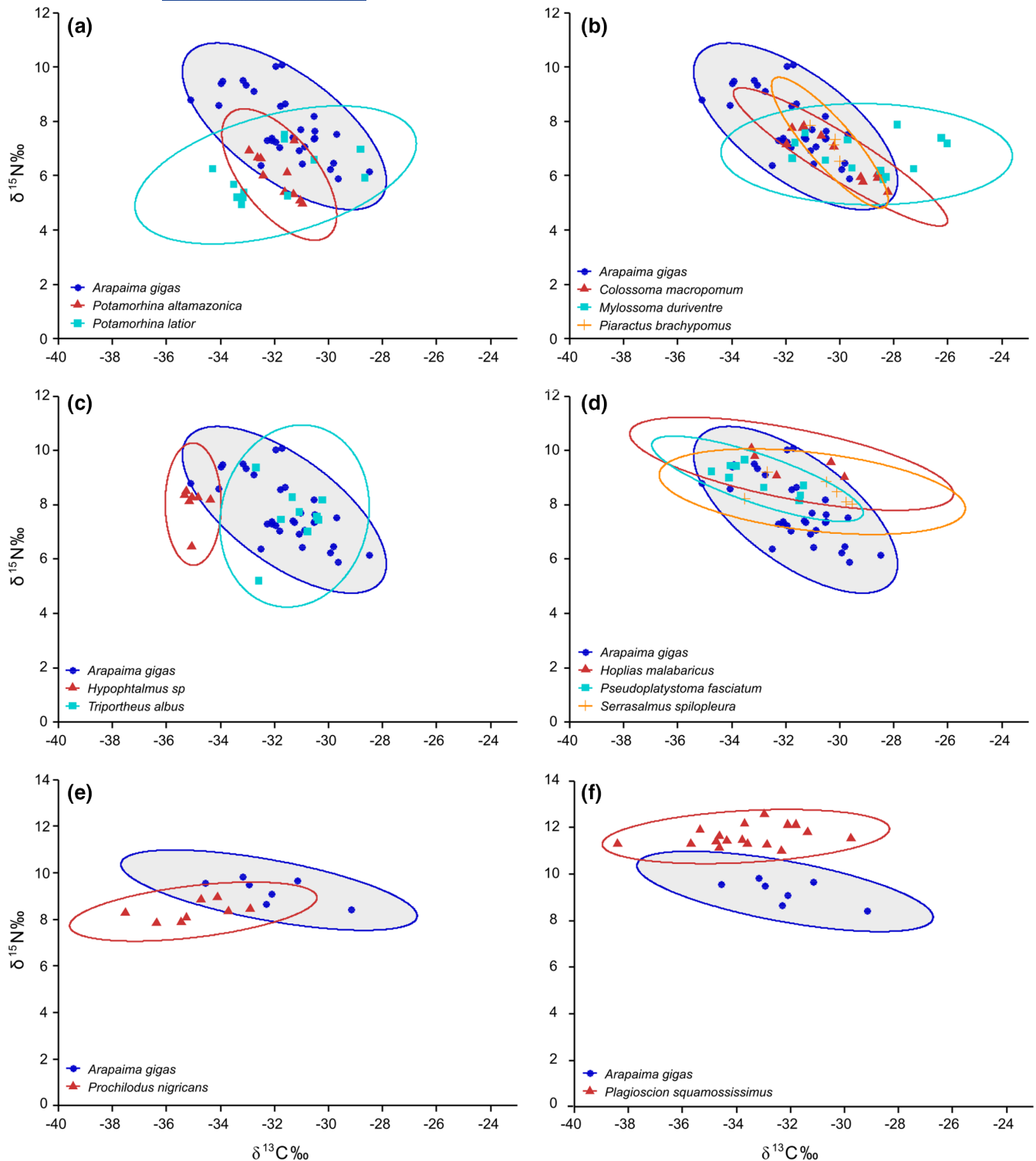


FIGURE 3 Isotopic niches estimated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) of *Arapaima gigas* in comparison to (a) detritivores, (b) herbivores, (c) invertivores and (d) piscivores in Lake Mentiroso; and (e) herbivores and (f) piscivores in Lake Miraflores. Ellipses represent 95% confidence interval.

(Mérona & Rankin-de-Mérona, 2004; Pouilly et al., 2004; Sarmiento et al., 2014), and our data confirm that they do behave as specialist piscivores deriving a high proportion of their energy from primary consumer fishes. Our results on the TP of *A. gigas* are in line with a previous study analysing isotopic signatures of *A. gigas* and

its fish preys (exclusively) in the Essequibo River basin and where *A. gigas* showed higher $\delta^{15}\text{N}$ values than algivorous/detritivorous and omnivorous fishes but lower values compared to piscivorous ones, indicating that the latter were not important energy sources for *A. gigas* (Watson et al., 2013). The intermediate position of *A. gigas*

between primary consumers and piscivores strongly suggests that other sources than fish, such as plants and invertebrates, form an important component of its diet. This finding is corroborated by some earlier studies analysing stomach contents for this species (e.g. Carvalho et al., 2018; Queiroz, 2000; Villafan et al., 2020). For example, Queiroz (2000) showed that individuals of *A. gigas* from the Central Amazon (Solimões River) fed on fishes, but that piscivorous species were a minor fraction of their diet and that invertebrates were also important items, especially during the high-water period. Furthermore, plant material was found virtually in all *A. gigas* stomachs, although the author concluded that plants were ingested accidentally, while suctioning preys into their mouths (Queiroz, 2000). A later study in Central Amazon (Carvalho et al., 2018) confirmed that fishes in stomachs of *A. gigas* were mostly omnivores/invertivores and detritivores, while the occurrence of piscivore fishes was low. This later study also found several stomachs containing plant material. Finally, a stomach content analysis of *A. gigas* individuals performed concurrently with our study in Lake Mentiroso showed that diet was composed mainly by small (<20cm) detritivorous and invertivorous fishes of the Curimatidae and Characidae families, invertebrates and a large portion of plant material (Villafan et al., 2020). In this later study and the one of Watson et al. (2013), the *A. gigas* alimentary tract length to body length ratio (Intestine index, I_i), a morphological feature frequently used to estimate general feeding habits of fishes, ranged between 1.45 (Watson et al., 2013) and 1.48 (Villafan et al., 2020). This range is typically assigned to omnivorous fishes ($1 < I_i < 2$; Nikolsky, 1963).

Piscivorous fish feeding mainly on low-trophic-level preys may show low TPs (East et al., 2017), especially in neotropical fish assemblages where primary consumers are dominant (Winemiller, 1990; Wootton & Oemke, 1992). However, the significantly lower $\delta^{15}\text{N}$ values found for *A. gigas* compared to all other piscivorous species and additional results from stomach content and morphological studies (e.g. Carvalho et al., 2018; Queiroz, 2000; Villafan et al., 2020) indicate that *A. gigas* feeds low in the food web and that its diet consists of plant material, invertebrates and low-trophic-level fishes. Here, we define omnivores as species that consume and can digest considerable amounts of both plant and animal foods (Karr et al., 1986; Schlosser, 1982). Therefore, according to our results and the ones of earlier studies analysing stomach contents (e.g. Villafan et al., 2020), *A. gigas* should be classified as an omnivorous species with piscivorous tendencies rather than as a top predator. This is in line with results from various studies in aquatic environments, indicating that invasive species most often have a flexible and generalist diet (McCue et al., 2020; Su et al., 2023).

4.2 | Potential competition between *A. gigas* and native species

Species arrival in a new environment inevitably cause some shifts in the food web structure by creating new feeding interactions (Jackson et al., 2017). Overlap of species in isotopic niche space

can be an indication of potential competition for food resources (Zambrano et al., 2010). Here, the broad isotopic niche width of *A. gigas* results in an overall significant overlap with the ones of native fish species, regardless of their respective trophic guilds. This significant niche overlap of *A. gigas* with the native species is especially true for Lake Mentiroso, whereas the overlap in Lake Miraflores was much less pronounced. The fish species studied in the two lakes mainly derive their carbon from phytoplankton, terrestrial vegetation and C3-macrophytes, with $\delta^{13}\text{C}$ -values varying in a relatively narrow range. This result agrees with several studies, indicating that C4-macrophytes, also very abundant, contribute little carbon to fish biomass in river-floodplain systems (Jackson et al., 2013; Mortillaro et al., 2015; Pouilly et al., 2013; Rejas, 2018; Winemiller et al., 2023). In consequence, we observed high overlap in $\delta^{13}\text{C}$ ranges among most fish species analysed (but see results obtained for the herbivorous species *M. duriventre*). With little exceptions, isotopic niches differentiation was mainly attributable to differences in $\delta^{15}\text{N}$ -values.

In Lake Mentiroso, the isotopic niches of the detritivorous species *Potamorhina* spp. substantially overlapped with the one of *A. gigas*. Given that tropical fishes are often opportunistic in their feeding habits (Lowe-McConnell, 1987) and that *Potamorhina* are reported to feed occasionally on benthic invertebrates (Sarmiento et al., 2014), our findings suggest that these detritivore species are also consuming some invertebrates and that our detritivore baseline could be slightly above that of strictly primary consumers. The isotopic niches of two out of our three native herbivores (i.e. *C. macropomum* and *P. brachypomus*) also substantially overlapped with the one of *A. gigas*. These two species are known to feed mainly on fruits and seeds, but also occasionally on invertebrates and fishes (Mérona & Rankin-de-Mérona, 2004; Sarmiento et al., 2014) potentially sharing resources with *A. gigas*. The third herbivore species *M. duriventre* showed the highest $\delta^{13}\text{C}$ -values of all fishes studied here, suggesting the assimilation of carbon from C4-macrophytes as previously reported in the Paraná River (Manetta et al., 2003) and other Amazon watersheds (Mortillaro et al., 2015; Rejas, 2018), resulting in a much lower isotopic niche overlap with *A. gigas*. Competition between *A. gigas* and these herbivorous species seems unlikely as floodplain lakes are not likely limited on this resource. Results were somewhat contrasted for invertivorous species. While, on the one hand, the isotopic niche of the invertivore *T. albus* highly overlapped with the one of *A. gigas* suggesting potential competition for this resource, on the other hand, the isotopic niche of the invertivore *Hypophthalmus* sp. overlapped little with *A. gigas* due to lower $\delta^{13}\text{C}$ -values, suggesting that the former feeds on invertebrates that obtain their carbon from phytoplankton and/or terrestrial vegetation. Finally, piscivores showed significant isotopic niche overlap with *A. gigas*, indicating also potential competitive interactions. However, our data on TP and isotopic niche indicate that the piscivorous species studied herein are more trophic specialists compared to *A. gigas*. Competition potentially occurs when resources are limiting and, in this case, *A. gigas* may be a stronger competitor due to its generalist feeding strategy.

In Lake Miraflores, the herbivore *P. nigrificans* showed low isotopic niche overlap with *A. gigas* as a result of low $\delta^{13}\text{C}$ -values. Low $\delta^{13}\text{C}$ -values are frequently found for detritivores in neotropical floodplain lakes and indicate carbon assimilation from phytoplankton or an even more ^{13}C depleted source, such as methanotrophic bacteria from the sediment (Azevedo-Silva et al., 2016; Rejas et al., 2020; Sanseverino et al., 2012). This is in line with the feeding mode of *P. nigrificans* that mainly scrapes algae from trunks and frequently ingests sediment from the benthic zone (Pouilly et al., 2004; Sarmiento et al., 2014). The specialist piscivore *P. squamosissimus* (Pouilly et al., 2004) presented low overlap with *A. gigas* as well, in this case as a result of higher $\delta^{15}\text{N}$ -values. No other piscivorous species were captured in high enough numbers to calculate their isotopic niches. However, TPs of the few individuals collected were consistently nearly one TP higher than *A. gigas*, positioning the former higher in the food web than the latter. This last result indicates that food web structure may differ among sites and that potential competitive interactions between native fish and *A. gigas* in Lake Mentiroso may not be the general rule.

A limitation of this study was the uneven sampling effort between the two lakes, which led to a large disparity in sample sizes. To control, as far as possible, for sample size bias between lakes, we calculated SEAc (a measure of SEA corrected for small sample size) and used the Bayesian estimate SEAb (having the same properties as SEAc) to determine niche overlaps (Jackson et al., 2011). Nevertheless, we cannot fully discard the possibility that differences in the niche space occupied by *A. gigas* and the degree of niche overlap between *A. gigas* and the other species may be due to differences in sample size between the two lakes. It is thus important to acknowledge that the limited sample size in Lake Miraflores prevents drawing strong conclusions for this lake.

In addition, it should be noted that our sampling methodology limited fish species sampled to individuals larger than 100mm. By doing this, we may have missed smaller specialised species and potentially a link in our fish trophic chain. However, we are confident that this limitation is unlikely to have fundamentally affected our main findings.

5 | CONCLUSION

It is generally assumed that top predators have stronger detrimental effects than omnivores by altering the distribution of total biomass across all trophic levels (Carpenter et al., 2001; Salo et al., 2007) and that omnivores dampen top-down control, releasing low trophic levels from predation (Fei & Kong, 2021). Under this view, our finding that *A. gigas* is an omnivore rather than a specialist piscivore suggests that the impact of its introduction may be weaker than expected for a large strictly piscivore species. Moreover, since piscivores are diverse and abundant in the native assemblages, massive effects of a new predator are not likely, since prey have effective antipredator responses (Levine, 2008; Sih et al., 2010). However, these assertions should be carefully analysed as there is also evidence that omnivorous fishes in lakes may occasionally enable stronger and persistent

top-down control (Vadeboncoeur et al., 2005). Local food web structure will, to a great degree, determine the impact of *A. gigas* on the native fish assemblages of the Madre de Dios river-floodplain system. In lakes with relatively short food webs, isotopic niches of *A. gigas* and native fish will overlap more than in lakes with longer food chains. Potential competition will be higher in the former, not only with piscivore fishes but with all trophic guilds. In lakes with longer food chains, niche overlap will be lower, releasing native species from competition. However, whatever the size of food chains, it remains unclear whether isotopic niches overlapping will have negative impacts on native populations through competition without precise data on the availability of food resources. The impact of the introduced non-native *A. gigas* on colonised waterbodies can be expected to vary depending on composition of the native fish assemblage and food web structure.

AUTHOR CONTRIBUTIONS

Conceptualisation: D.R. Developing methods: D.R., T.O., S.D. and M.W. Conducting the research: D.R. and T.O. Data analysis: D.R. and M.W. Data interpretation: D.R., T.O., S.D. and M.W. Preparation of figures and tables: D.R. and M.W. Writing: D.R., T.O., S.D. and M.W.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the first author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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