

ARTICLE

Does invasion by armored catfish shift trophic ecology of native fishes? Evidence from stable isotope analysis

Yasmín Quintana¹  | Friedrich Wolfgang Keppeler^{2,3}  | Kirk O. Winemiller¹ 

¹Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas 77843, USA

²Center for Limnology, University of Wisconsin–Madison, Madison, Wisconsin, USA

³Núcleo de Ecologia Aquática e Pesca da Amazônia, Federal University of Pará, Belém, Brazil

Correspondence

Yasmín Quintana
Email: yquintana@tamu.edu

Funding information

American Association of University Women, Grant/Award Number: 2020-21; Rufford Foundation, Grant/Award Number: 26506-1; Russell E. Train Education for Nature Program-WWF, Grant/Award Number: # RH31; Faculty for the Future Fellowship-Schlumberger Foundation; Tom B. Slick Fellowship-Texas A&M University

Handling Editor: Andrea Kirkwood

Abstract

Popular as aquarium fish, armored catfishes from South America (*Pterygoplichthys* spp.) have been introduced and become invasive in tropical and subtropical regions worldwide. These ecosystem engineers can deplete basal resources (e.g., periphyton and detritus), with potential negative effects for native fauna. We studied the trophic ecology of fishes in the Usumacinta River Basin, Guatemala, where *Pterygoplichthys* is now widespread and locally abundant. We analyzed stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in fish tissues and basal resources to assess the potential impact of *Pterygoplichthys* on the trophic ecology of six co-occurring native fishes that feed at a similar trophic level (*Astyanax aeneus*, *Dorosoma petenense*, *Thorichthys pasionis*, *Oscara heterospila*, *Poecilia mexicana*, and *Gambusia sexradiata*). The study was conducted during the dry season in the La Pasion (LPR; high invasion) and San Pedro (SPR; low invasion) rivers. We compared isotopic spaces occupied by native fish and *Pterygoplichthys*, estimated isotopic overlap, and evaluated the trophic displacement of native species. We also evaluated the relationships of environmental factors, including the relative biomass of the invasive catfish, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. Except for *P. mexicana*, native species had lower isotopic overlap with the catfish in LPR. Native fish isotopic spaces were compressed and shifted toward higher trophic positions in LPR relative to SPR. Benthic food resources were important for *Pterygoplichthys* in both rivers, and water-column resources had greater relative importance (RI) for native species in LPR. Native fish $\delta^{13}\text{C}$ was significantly associated with *Pterygoplichthys* biomass, conductivity, and water flow velocity; and water depth and sedimentation had a significant association with native fish $\delta^{15}\text{N}$. Findings provide evidence that invasive *Pterygoplichthys*, along with environmental factors, impact the trophic ecology of native fish in the Usumacinta Basin. Additional field research conducted over longer time periods and mesocosm experiments that account for fish assemblage and environmental variation could elucidate *Pterygoplichthys* impacts via food resource depletion or habitat alteration.

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KEYWORDS

benthic ecology, biological invasion, food web, resource competition, river, species displacement, Usumacinta Basin

INTRODUCTION

Fishes are commonly moved among freshwater ecosystems, with the aquarium hobby being a major source for introductions (Padilla & Williams, 2004). In recent years armored catfish in the genus *Pterygoplichthys* (family Loricariidae) have invaded freshwater systems worldwide (Orfinger & Goodding, 2018). Native to South America, these fish are popular in the aquarium trade because they feed on periphyton and other organic films that accumulate on substrates (Elfidasari et al., 2020; German & Miles, 2010). *Pterygoplichthys* tolerate a wide range of water quality conditions, have bony plates, stout pectoral and dorsal spines, brood guarding behavior, and accessory aerial respiration, all of which facilitate invasion under a wide range of environmental conditions (Armbruster, 1998; Capps et al., 2011; Gibbs et al., 2017; Hoover et al., 2004).

Given that biofilms are ubiquitous in aquatic ecosystems and detritus is rarely limiting (Moyle & Light, 1996), *Pterygoplichthys* often attain high densities where introduced (e.g., Escalera-Vázquez et al., 2019). Grazing intensity has the potential to reduce the quality and quantity of benthic primary and secondary production (Capps & Flecker, 2015; Flecker, 1996; Juárez-Sánchez et al., 2019; Power, 1990; Winemiller et al., 2014). The impacts of *Pterygoplichthys* on native fish remain poorly documented and probably are context dependent. The *invader density-impact model* proposes that invasion impact may increase or decrease either linearly or nonlinearly as a function of invasive species abundance (Kornis et al., 2014; Yokomizo et al., 2009). A comparative study of invasion scenarios suggests that invasion generally produces a nonlinear decline in populations of native species at a similar trophic level (Bradley et al., 2019).

Pterygoplichthys pardalis and *Pterygoplichthys disjunctivus* were introduced in the Usumacinta River Basin in Mexico several decades ago. These catfish are now broadly distributed and locally abundant in the basin. The Usumacinta Basin has long been recognized as a distinct ichthyological province in Nuclear Middle America (Miller, 1966), with ~59% of the endemic fish species in Mesoamerica occurring within the basin. Cichlidae and Poeciliidae are the most species-rich and ecologically diverse families in the region (Matamoros et al., 2015). Several species exploit benthic food resources and could

compete with *Pterygoplichthys*. Even if direct competition between *Pterygoplichthys* and native fish was minimal or absent, grazing by the invasive catfish could have indirect effects within the food web (e.g., Flecker, 1996). *Pterygoplichthys* were shown to have trophic niche overlap with native fish in southern Mexico (Sepúlveda-Lozada et al., 2015). However, trophic overlap does not necessarily indicate competition, which depends on the ratio of resource demand/supply, ecosystem productivity, and population densities (García et al., 2020). Low niche overlap is generally interpreted as evidence of resource partitioning between invasive and native species (e.g., Ludovisi et al., 2022).

Stable isotope analysis (SIA) is widely used to investigate the potential for trophic overlap between invasive and native species (Haubrock et al., 2020; Jackson et al., 2012; Lamb et al., 2021; Layman et al., 2007; Pagani-Núñez et al., 2018; Vander Zanden et al., 1999). Analysis of $\delta^{13}\text{C}$ ($^{13}\text{C}/^{12}\text{C}$ ratio) and $\delta^{15}\text{N}$ ($^{15}\text{N}/^{14}\text{N}$ ratio) has been used to infer trophic niche partitioning and displacement of native species by invaders (Gargano et al., 2022). Mixing models can be used to estimate the relative contributions of material from different sources to consumer biomass as well as a trophic position relative to a known or inferred baseline (Quezada-Romegialli et al., 2018).

Here, we use SIA to examine the potential impact of *Pterygoplichthys* on native fish species that feed at a similar trophic level. We conducted this study in two major tributaries of the Usumacinta River in Guatemala: La Pasion River (LPR) where *Pterygoplichthys* are abundant, and San Pedro River (SPR) where the catfish is still uncommon. The two rivers have similar fish species richness and functional groups (e.g., trophic guilds, taxonomic family composition) (Quintana, unpublished manuscript). We compared these rivers with high versus low invasion intensity with regards to (1) sizes and positions of the isotopic spaces (areas within plots of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) occupied by *Pterygoplichthys* and native fish; (2) isotopic space overlap between *Pterygoplichthys* and native fish; (3) proportional contributions to fish biomass from benthic and water-column basal resources; (4) estimated species trophic positions; and (5) variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fish in relation to invader abundance versus other local environmental factors. Based on models for invasion intensity-impact (Kornis et al., 2014; Yokomizo et al., 2009) and interspecific competition-niche compression (Pianka,

1974), we predicted that a high level of *Pterygoplichthys* invasion would be associated with trophic niche displacement of native species and reduction in isospace area and overlap.

METHODS

Study area

The Usumacinta River Basin is the largest in Mesoamerica (~74,000 km²). The river emerges in northern Guatemala (where 58% of the basin is located) and Belize, and flows through southern Mexico before entering the Gulf of Mexico. This basin contains diverse aquatic habitats, including streams, tributary rivers, lakes, lagoons, and marshes (Gandin, 2012). At least 172 freshwater and estuarine fish species (Soria-Barreto et al., 2018) are reported from the basin, with ~60% of freshwater species being endemic (Eliás et al., 2020). Much of the basin has been impacted by deforestation, agriculture, and natural resource extraction (Dürr, 2017; Gandin, 2012; Tapia-Silva et al., 2015), and African palm oil plantations have propagated mainly in LPR and SPR in Guatemala (Camacho-Valdez et al., 2022), although some of these plantations in SPR are not yet documented. In recent decades, *P. pardalis*, *P. disjunctivus*, and their hybrids have been reported in various locations

(Gaitán et al., 2020; Wakida-Kusunoki et al., 2007; Wakida-Kusunoki & Amador del Ángel, 2008). By 2010, these invasive catfish expanded throughout the Usumacinta, reaching Río Salinas-Chixoy, Río La Pasion, and Río San Pedro in Guatemala, the latter two sub-basins with high abundances (Eliás et al., 2022). Our study was conducted in two major tributaries within the Usumacinta: SPR (17.134803° N, 89.902668° W) and LPR (16.480881° N, 90.543095° W) (Figure 1).

Field surveys

We surveyed 18 locations in SPR and 18 locations with similar environmental characteristics (channel width, substrate, hydrology, and riparian cover) in LPR from April to July 2019. In each river, we distributed survey locations among upper, middle, and lower sections in an attempt to capture spatial variability. Each survey location had a river reach of ~500 m, and stations were separated by at least 2 km. At each survey location, we measured conductivity, pH, dissolved oxygen, and temperature using a multiparameter water meter (YSI Pro 2030). We collected water samples (250 mL) for measurement of total P and total N. We recorded littoral depth, sediment depth, transparency (Secchi depth), channel

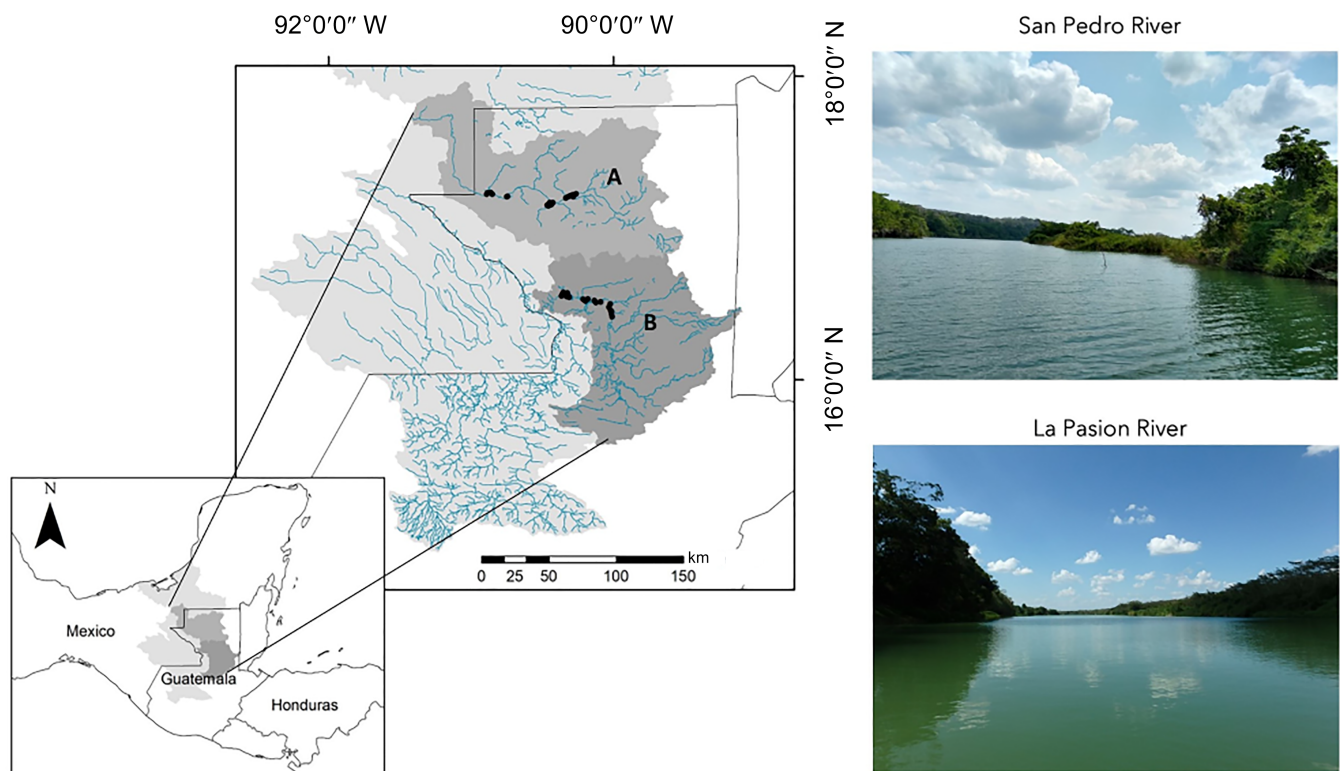


FIGURE 1 Map of sites surveyed (black points) within the Usumacinta River Basin: 18 sites in San Pedro River (A) and 18 sites at La Pasion River (B). Photograph credit: Yasmin Quintana.

width, water flow velocity in the littoral zone (Flomate 2000 flow meter), and percent forest cover in the riparian zone (visual estimate) (Appendix S1: Table S1).

We collected fish and basal production sources (dominant C3 riparian and aquatic plants, C4 plants, plankton, and macroinvertebrates) at each location. We surveyed fish using complementary fishing gears (seine, cast net, and gill nets) and consistent effort (Appendix S1: Table S2). We anesthetized fish using tricaine methane sulfonate (MS222) and then euthanized them via an overdose. In this study, we grouped all the specimens from the genus *Pterygoplichthys* due to difficulties in taxonomic identification and the high incidence of hybridization observed between *P. pardalis* and *P. disjunctivus*. To contrast isotopic space overlap between *Pterygoplichthys* and native fish, we selected native species according to the following criteria: (1) species common in both rivers and representing diverse families, and (2) low trophic position with potential dietary overlap with *Pterygoplichthys* (i.e., detritivores, algivores, and omnivores). To select these species, we assessed relative abundance based on our survey data (Quintana, unpublished manuscript), and trophic position values from FishBase (Froese & Pauly, 2022) and our own preliminary samples. Native species selected for analyses were *D. petenense* (Clupeidae), *A. aeneus* (Characidae), *G. sexradiata* (Poeciliidae), *P. mexicana* (Poeciliidae), *O. heterospila*, and *T. passionis* (Cichlidae). We included *G. sexradiata* and *T. passionis* even though these species feed mostly on invertebrates because they ingest minor fractions of filamentous algae and fine particulate organic matter (Pease et al., 2018; Rakocinski & Greenfield, 1985). Moreover, aquatic invertebrate abundance could decline due to *Pterygoplichthys* grazing (Capps & Flecker, 2015).

We collected samples of C3 and C4 plants, and plankton samples were collected using a 40-cm diameter and 80- μ m mesh net. Plankton samples contained mostly zooplankton and a few large phytoplankton (Pal & Choudhury, 2014; Takarina et al., 2019), and could contain a fraction of suspended coarse particulate organic matter. We attempted to collect 20–30 specimens of each fish species from each river, and a minimum of 10 samples of each basal source from each river (Jackson et al., 2011). Expected turnover for fish muscle tissue is 1–3 months (Buchheister & Latour, 2010), we therefore assumed that our samples reflected diet assimilation during the dry season.

Stable isotope analysis

We obtained muscle tissue samples from the dorso-lateral region of euthanized fish. For small fish specimens, we removed bones and viscera, and the remainder of the body

was used for SIA. We stored samples of fish tissue and basal sources in individual bags with non-iodized table salt (NaCl) for preservation. We followed methods by Arrington and Winemiller (2002) for the laboratory processing of tissue samples. We ground dried samples to a fine powder using mortar and pestle, then weighed (fish and source samples to the nearest 1.5–3 mg) and stored them in UltraPure tin capsules (Costech) for determination of percent carbon, percent nitrogen, and isotopic ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) using mass spectrometry.

To estimate trophic niche breadth (Vander Zanden et al., 2015) we used isotopic ratios, expressed in standard delta (δ) notation in parts per thousand (‰), standardized in relation to reference material, and reported as: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where $R = \delta^{13}\text{C}$ or $\delta^{15}\text{N}$. We did not correct isotope samples for lipid content, because the vast majority of samples fell below or were close to C:N = 3.5 (Post et al., 2007) and because exploratory analysis indicated that the standardized and raw values were virtually the same, not affecting the results.

Data analysis

Catch-per-unit effort (CPUE)

We used CPUE as a measure of fish abundance. CPUE (mean $\pm$ SD) indicates the total number of fish captured per day at each locality. We estimated the species relative frequency for each river as ($N_{\text{sites present}}/\text{Total } N_{\text{sites}}$) and relative biomass as ($P_{\text{terygoplichthys biomass (g)}/\text{Total fish biomass (g)}}$) per sampling location.

Trophic position and source assimilation estimation

We used a two baseline full model from the package tRophicPosition (Quezada-Romegialli et al., 2018; R Core Team, 2022) to estimate the species trophic position and the proportional contribution of benthic (macroinvertebrates) and water-column (plankton) sources for each fish species at each river. Macroinvertebrates and plankton have distinct $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and provide a good representation of benthic detrital and water-column carbon, respectively. The two baseline full model accounts for individual variability, propagating sampling error of basal sources and consumers, and from trophic fractionation, using a Bayesian approach. The model follows two basic equations:

$$\delta^{15}\text{N}_c = \Delta N(\text{TP} + \lambda) + \alpha(\delta^{15}\text{N}_{b1} + \delta^{15}\text{N}_{b2}) - \delta^{15}\text{N}_{b2} \quad (1)$$

and

$$\delta^{13}\text{C}_c = \delta^{13}\text{C}_{b1} \alpha + \delta^{13}\text{C}_{b2}(1 - \alpha) \quad (2)$$

where ΔN is the trophic fractionation value for nitrogen, λ is the trophic position of the baseline (Vander Zanden et al., 1997), $\delta^{15}\text{N}_{b1}$, $\delta^{13}\text{C}_{b1}$, and $\delta^{15}\text{N}_{b2}$, $\delta^{13}\text{C}_{b2}$, are the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the two baselines, and α is the proportion of N derived from baseline 1 (Post, 2002). We used the trophic fractionation of $3.4 (\pm 0.98 \text{ SD})$ for $\delta^{15}\text{N}$ and $0.39 (\pm 1.3 \text{ SD})$ for $\delta^{13}\text{C}$ (Post, 2002), parallel chains = 5, adaptive iterations = 40,000, burn in = 20,000, $\lambda = 2$, and thin = 50. We estimated the probability of similar trophic positions for conspecifics from the two rivers, and between native species and *Pterygoplichthys* from the same river using the function “pairwiseComparisons” from the package *tRophicPosition*, which provides the proportion of posterior samples that are equal or less among compared samples.

We investigated the association of environmental factors and *Pterygoplichthys* relative biomass with native species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures using linear mixed-effects models (LMM). The relative biomass of *Pterygoplichthys* reflects the potential for impact on local ecosystems and communities. We explored a series of models: (1) including environmental variables and *Pterygoplichthys* relative biomass, (2) excluding *Pterygoplichthys* relative biomass, (3) containing only *Pterygoplichthys* relative biomass, and (4) containing only significant environmental variables. This was necessary to explore the effect of *Pterygoplichthys* in the presence/absence of confounding factors. We included native species as random factors in all models. We standardized the fixed variables to zero mean and unit variance because they were measured at different scales. We used the variance inflation factor (VIF) to test multicollinearity. To compute the models, we used the R package *lme4* (Bates et al., 2015). We selected the best model using the Akaike Information Criterion (AIC) and assessed the goodness-of-fit of each model through the marginal R^2 (R_m^2 = variance explained by fixed factors) and conditional R^2 (R_c^2 = variance explained by fixed and random factors) (Nakagawa et al., 2017) using the performance package (Lüdtke et al., 2021). We estimated the average R^2 based on all models. To obtain the RI of the fixed variables included in the global model, we used the functions “dredge” and “sw” from the *MuMIn* R package (Version 1.47.1. R) (Barton, 2022).

Estimation of isotopic space and overlap

For each river, we estimated the size of the isospace occupied by each species and the pairwise overlap of isotopic spaces of *Pterygoplichthys* and native species. We

estimated isospaces as the area occupied by species within $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ plots using the R package *nicheROVER* (Lysy et al., 2021; Swanson et al., 2015). This package provides a probabilistic method to estimate isospace size and overlap in a Bayesian framework, accounting for uncertainty due to sample size and producing elliptical projections of core isotopic regions (Swanson et al., 2015). To estimate the isotopic spaces, we computed 25 random pairs of posterior distributions of the mean (μ) and variance (Σ) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using the default prior: $\pi(\mu, \Sigma) \propto |\Sigma|^{-n-1}$ (Swanson et al., 2015), with alpha (i.e., scalar vector of niche region sizes) set to 0.95. The statistical significance of differences in the size of species isospaces in the two rivers was the probability that LPR was more than SPR ($\Pr[\text{pred}[\text{LP}] > \text{pred}[\text{SP}]]$; Ovaskainen & Abrego, 2020). We considered differences to be significant if the probability was more than 0.95.

We estimated the probability that the isospace of *Pterygoplichthys* overlaps with the isospace of native fish using the equation $O(\frac{A}{B}) = \Pr(X_A \in N_R(B))$, where A and B are the species to be compared, and $O(\frac{A}{B})$ is the probability that individuals from species A (X_A), belong to the isospace of species B ($N_R(B)$) (Swanson et al., 2015). We estimated isotopic overlap from the posterior distribution of species μ and Σ , with 10,000 Monte Carlo draws and 95% CI. To account for the spatial variability of $\delta^{15}\text{N}$ isotopic baselines in each river, we normalized the consumers $\delta^{15}\text{N}$ signature prior analysis as follows: baseline-calibrated $\Delta^{15}\text{N} = \delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}}$ (Potapov et al., 2019; Vander Zanden et al., 1997). For data normalization, we selected a set of C3 basal sources collected in both rivers, excluding C4 grasses that appeared to contribute little to consumer biomass.

In addition, we used the similar methodology described above to estimate the trophic niche size and overlap for each species in each river using trophic position and α variables. This was necessary to confirm results derived from $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variables that do not completely account for spatial variation in baseline values.

RESULTS

Fish abundance

In total, 3098 fish was captured, 54% in LPR and 45% in SPR. In LPR, *Pterygoplichthys* was captured at every survey site and had greater CPUE than native fish, except for *G. sexradiata* (Table 1). In SPR, *Pterygoplichthys* was rare, with a relative frequency of 0.4 and negligible CPUE compared with those of native species.

Isotopic space and overlap

Analyses were based on 372 fish tissue samples, 71 samples of primary consumers, and 140 samples of basal production sources (Appendix S1: Table S3). Trophic space and overlap occupied by *Pterygoplichthys* and native species according to TP and α were consistent with elliptical projections of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Thus, here we provided estimates of trophic space and overlap derived only from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (see Appendix S1: Figure S3 for estimates derived from TP and α values).

The isospace of *Pterygoplichthys* was significantly larger in LPR, where it was abundant, with a median value almost double that for SPR. The opposite was observed for native fish that had significantly larger isospaces in SPR, with the only exception being *P. mexicana* (Figure 2; Appendix S1: Table S4).

In SPR, isospace elliptical projections of native species tended to have wider ranges with higher $\delta^{15}\text{N}$ compared with *Pterygoplichthys*. $\delta^{13}\text{C}$ signatures of *A. aeneus*, *T. pasionis*, *O. heterospila*, and *G. sexradiata* in SPR had wider ranges compared with conspecifics in LPR, with most SPR native species having distributions shifted toward more negative values (Figure 3). *Pterygoplichthys* had a wider range of $\delta^{13}\text{C}$ signatures in LPR compared with SPR. Isotopic ellipses (encompassing 95% probability) indicated substantial overlap between *Pterygoplichthys* and native fish in both rivers (Figure 2), with higher overlap occurring in SPR. In this river, the highest overlap was observed in *D. petenense* (96.9%), *T. pasionis* (83.5%), and *P. mexicana* (74.0%) (Appendix S1: Table S4). In LPR, native species occupied smaller isospaces and their overlap with *Pterygoplichthys* was smaller compared with the overlap in SPR, particularly *A. aeneus* (21.6%), *O. heterospila* (22.2%),

TABLE 1 Comparison of catch-per-unit effort (CPUE) and relative frequency (Rf) of native species and *Pterygoplichthys* collected in La Pasion River and San Pedro River in the dry season.

Family	Species	La Pasion River			San Pedro River		
		<i>n</i>	CPUE mean $\pm$ SD	Rf	<i>n</i>	CPUE mean $\pm$ SD	Rf
Characidae	<i>Astyanax aeneus</i>	233	12.9 $\pm$ 12.7	1	354	19.7 $\pm$ 12.1	1
Clupeidae	<i>Dorosoma petenense</i>	236	13.9 $\pm$ 21.5	0.7	427	25.1 $\pm$ 37.2	0.9
Cichlidae	<i>Thorichthys pasionis</i>	46	2.6 $\pm$ 3.7	0.6	166	9.2 $\pm$ 6.1	1
	<i>Oscara heterospila</i>	28	1.6 $\pm$ 1.8	0.5	197	10.9 $\pm$ 9.8	1
Poeciliidae	<i>Poecilia mexicana</i>	101	6.7 $\pm$ 7.3	0.8	68	4.5 $\pm$ 7.9	0.5
	<i>Gambusia sexradiata</i>	704	39.0 $\pm$ 27	1	169	9.0 $\pm$ 14.0	0.55
Loricariidae	<i>Pterygoplichthys</i> spp.	352	19.6 $\pm$ 10.6	1	17	0.94 $\pm$ 1.35	0.4

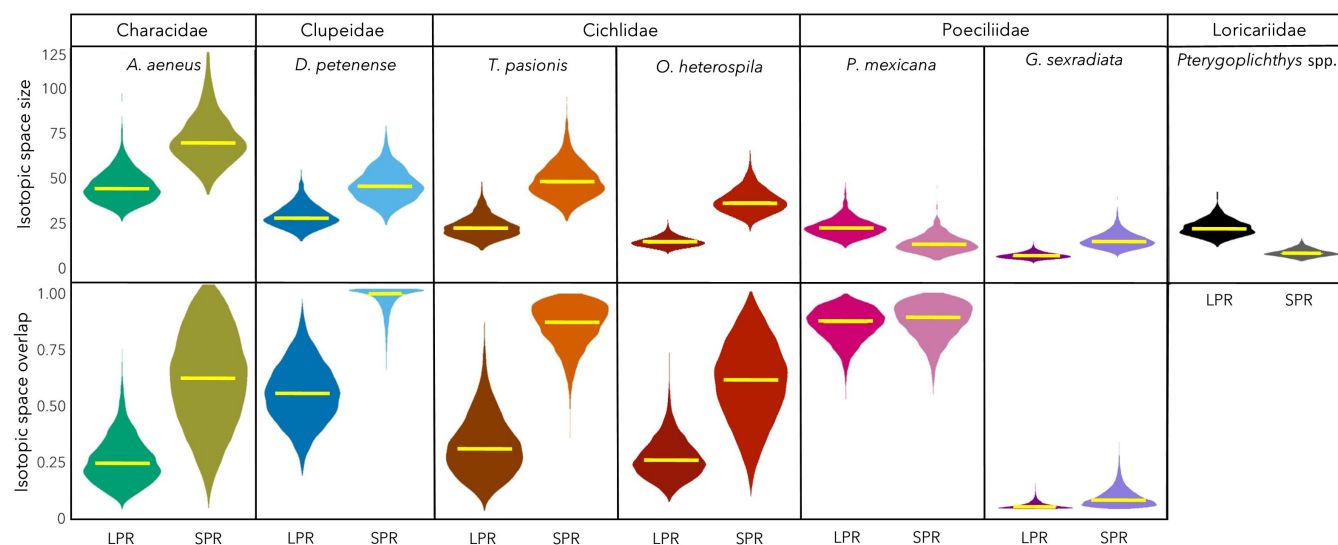


FIGURE 2 Comparison of isotopic space size of native species and *Pterygoplichthys* (top row), and isotopic overlap probability between *Pterygoplichthys* and native species (bottom row), in La Pasion (LPR) and San Pedro (SPR) rivers (horizontal yellow bar = median value based on posterior probability distribution).

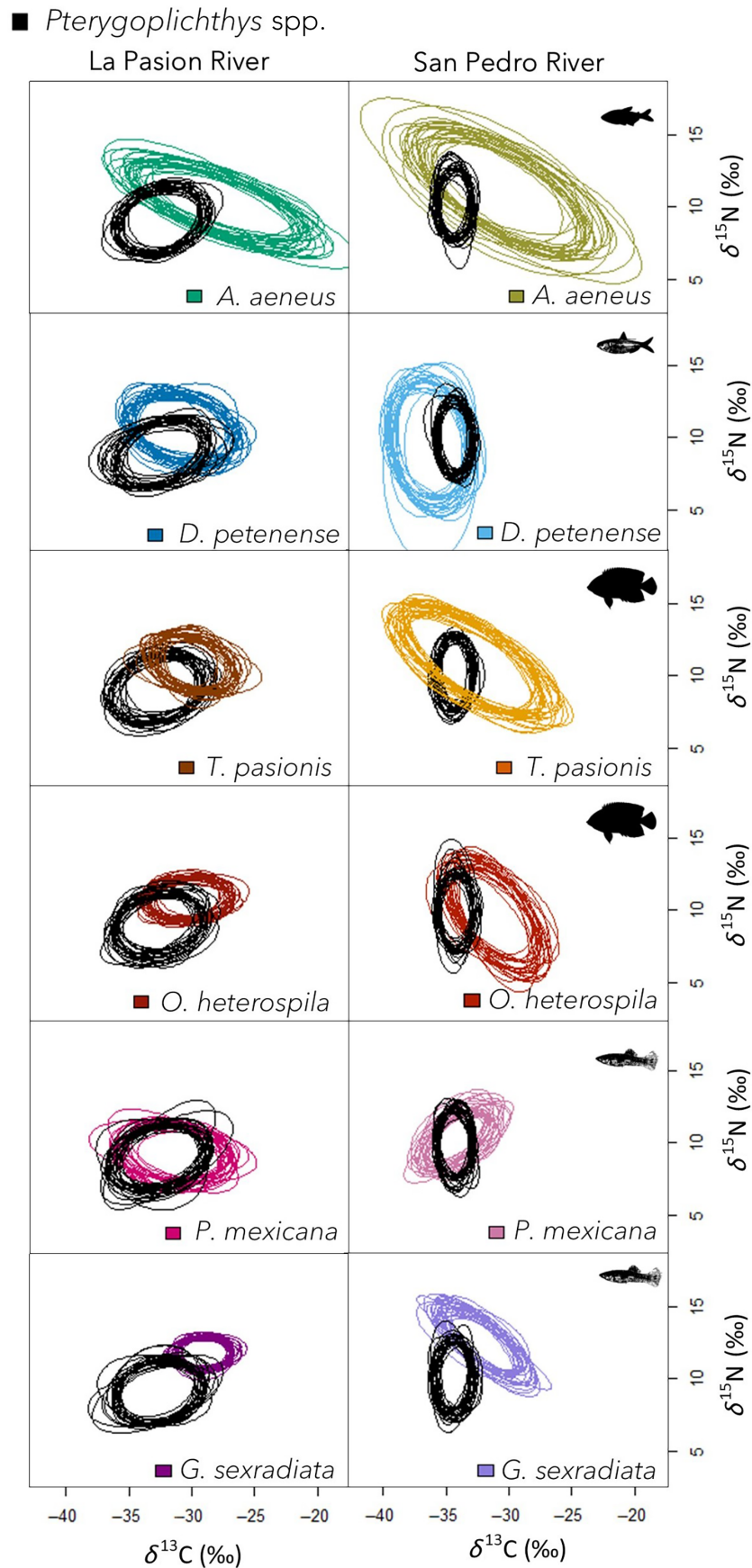


FIGURE 3 Random elliptical projections of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic spaces for native fish (colored ellipses) and *Pterygoplichthys* (black ellipses) from La Pasion River and San Pedro River. Projections were generated with “nicheROVER” using 95% CI (Swanson et al., 2015).

D. petenense (31.3%), and the *T. passionis* (32.5%). Among poeciliids, *P. mexicana* occupied similar isospaces and had similar overlap with *Pterygoplichthys* in the two rivers (Figure 2), and *G. sexradiata* had minimal overlap with the invasive catfish.

Trophic position and source assimilation

All native species had a significantly higher trophic position in LPR (Figure 4; Appendix S1: Table S5), and this was especially the case for *D. petenense*, *O. heterospila*, and *T. passionis* (Figure 4). The lowest trophic position recorded among fish for LPR was for *Pterygoplichthys*. *Dorosoma petenense* had the lowest trophic position among fish from SPR. The pairwise comparison indicated that *Pterygoplichthys* had a significantly lower trophic position than most native species in each river (pairwise comparison probability ≥ 0.8), the only exception being *D. petenense* in SPR (Figure 4; Appendix S1: Table S5).

Basal sources from the water-column were the most important contributor to the biomass of native species in LPR ($\alpha \geq 0.5$; Figure 4; Appendix S1: Figure S1), but this source was estimated to be less important in supporting native fish in SPR where the invader is rare ($\alpha \leq 0.3$; Figure 4; Appendix S1: Figure S2). Most native species in both rivers appeared to be supported by a mixture of benthic and water-column production sources. The exceptions were *A. aeneus* in LPR almost exclusively assimilated water-column sources ($\alpha = 0.91$) and *D. petenense* ($\alpha = 0.05$)

and *P. mexicana* ($\alpha = 0.1$) in SPR, similar to *Pterygoplichthys*, assimilated mostly benthic sources ($\alpha = 0.1$).

Statistical models (Appendix S1: Table S6) consistently found significant correlations for $\delta^{13}\text{C}$ with *Pterygoplichthys* biomass (RI = 0.99), conductivity (RI = 0.78), and water flow velocity (RI = 0.51) ($R_c^2 = 0.56\text{--}0.58$, $R_m^2 = 0.22\text{--}0.23$), the former being considered the most important variable. Conductivity had high multicollinearity with *Pterygoplichthys* relative biomass (VIF = 10.54 and 9.03, respectively). The significance effect of *Pterygoplichthys* biomass on native species $\delta^{13}\text{C}$ was not impacted by the inclusion of environmental variables in the models ($\beta = 0.79$, $t = 3.47$, $p < 0.05$; Figure 5). The model with the highest AIC showed a significant correlation for $\delta^{13}\text{C}$ with total phosphorous. We also found a significant effect from water depth (RI = 0.89) and sediment depth (RI = 0.48) on $\delta^{15}\text{N}$, but R_c^2 and R_m^2 were low ($R_c^2 = 0.25\text{--}0.3$, $R_m^2 = 0.001\text{--}0.005$) indicating weak associations.

DISCUSSION

Where invasive *Pterygoplichthys* are abundant, native fish at similar trophic positions were found to occupy smaller isotopic spaces and had less overlap from the invader when compared with conspecifics in a river where the invader is uncommon. The degree of isotopic overlap varied depending on the identity of native species. Among the significant factors affecting fish isotopic signatures we found invasion intensity to play an important role, along with a

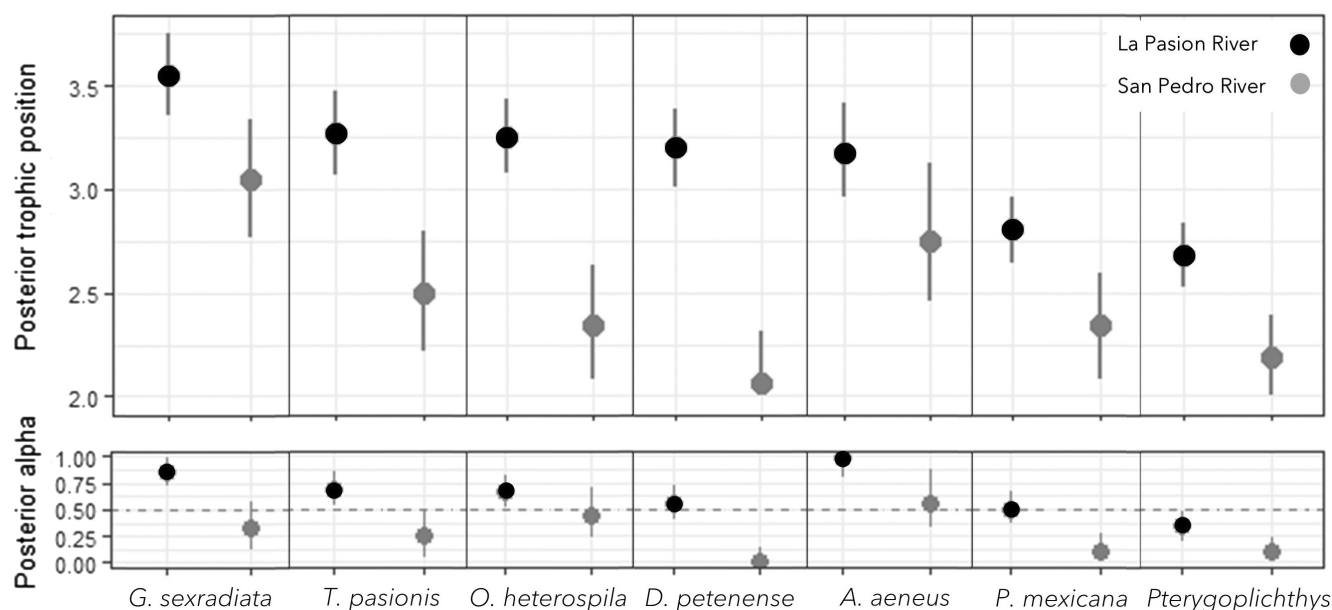


FIGURE 4 Estimated posterior trophic position of native fish and *Pterygoplichthys* in La Pasion River and San Pedro River, and posterior α indicating the relative contribution of water-column-derived $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The model accounts for trophic discrimination values ΔN (3.4 ± 0.98 SD) and ΔC (0.39 ± 1.3 SD) (Post, 2002). The circles indicate the mean value and bars show the 95% CI.

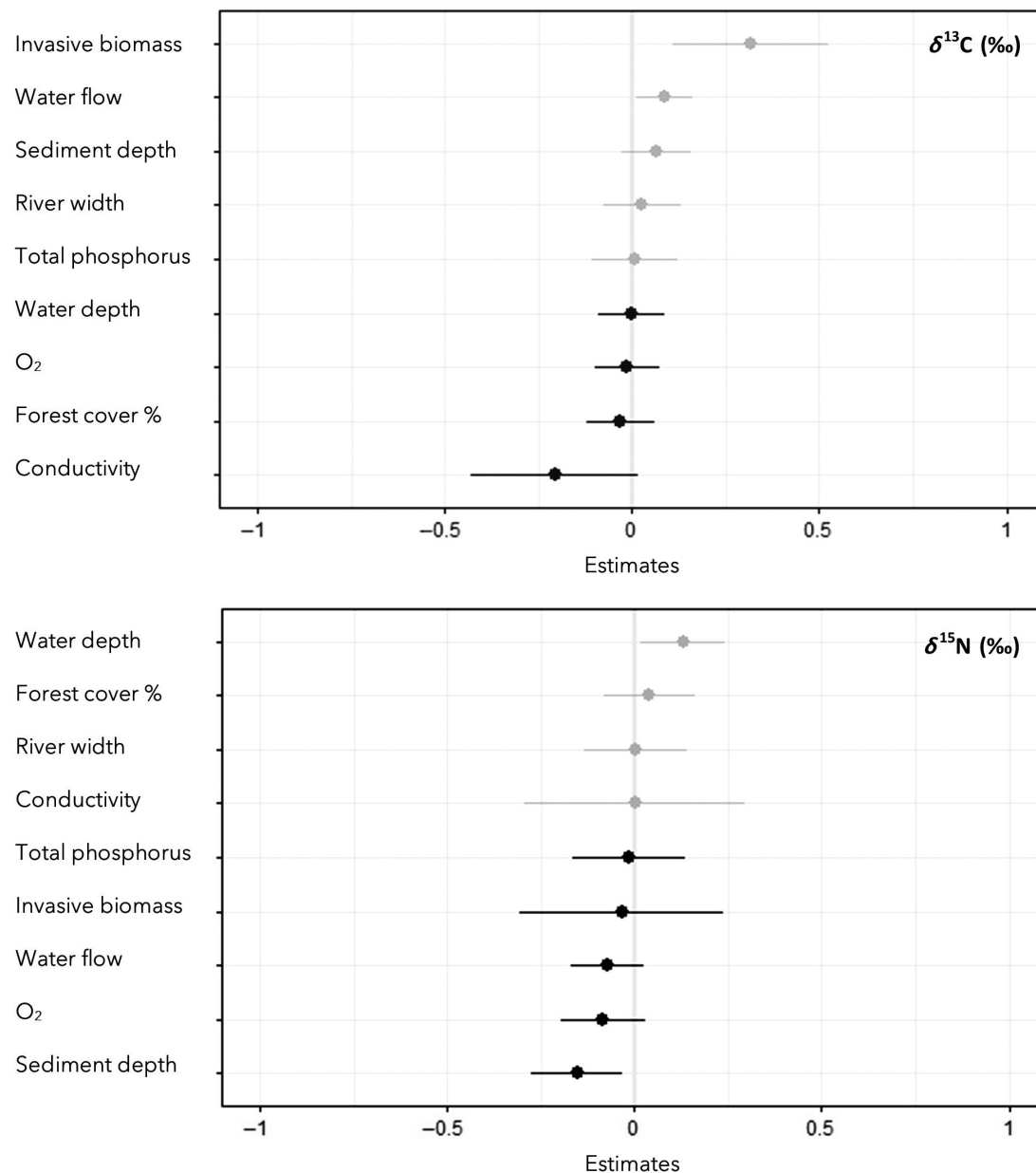


FIGURE 5 Results of the linear mixed effects models with statistical effects of environmental variables on $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) with 95% CI.

few local environmental factors. This evidence suggests trophic niche displacement, in response to competition for limited food resources during the dry season. *Pterygoplichthys* has invaded ecosystems throughout the world, with documented impacts on native fish (e.g., Chaichana et al., 2011; Escalera-Vázquez et al., 2019). Local people first reported *Pterygoplichthys* in LPR and SPR more than 10 years ago. The first ecological effect documented in LPR and SPR after 7 years of *Pterygoplichthys* invasion was the major shift in the diet of river otters (*Lontra longicaudis*) toward *Pterygoplichthys* (~49% occurrence in scats), accompanied by the reduction in diet breadth and trophic level (Juárez-Sánchez et al., 2019). The current study found

Pterygoplichthys to be very abundant in LPR but uncommon in SPR during the dry season. The two rivers have similar environmental conditions, but LPR is located higher in the drainage basin. It is unclear why *Pterygoplichthys* has not yet attained densities (CPUE, biomass) in SPR as those observed in LPR and other rivers in Mexico and Guatemala.

Predicting the impact of invasive species on food webs is challenging because they can affect ecosystems via multiple mechanisms (David et al., 2017). For example, when invasive and native species compete for limited resources, native species may expand their trophic niches (Harris et al., 2022), show no change in niche breadth (García et al., 2020), or compress and partition niches

(David et al., 2017; Tran et al., 2015). Our findings suggest the latter response to the high abundance of *Pterygoplichthys*. *Pterygoplichthys* had low isotopic overlap with five of the six native species (i.e., *A. aeneus*, *D. petenense*, *T. pasionis*, *O. heterospila*, *P. mexicana*) in LPR compared with the interspecific overlap in SPR where the invader is rare. A similar pattern was previously observed for fish in the Illinois and Mississippi rivers in the USA, where the invasive bigheaded carps (i.e., *Hypophthalmichthys molitrix* and *H. nobilis*) had high overlap with native planktivorous fish at low densities, but the overlap was lower where the density of invasive carp was high (Harris et al., 2022). Low isotopic overlap observed in LPR was accompanied by compression of native species isospaces with varying degrees of positional shifts (*P. mexicana* was the only exception). Native fish tended to have higher $\delta^{15}\text{N}$ (a proxy for trophic position) in LPR compared with conspecifics from SPR.

Smaller isospace area and lower interspecific overlap with *Pterygoplichthys* in LPR relative to SPR was especially the case for *D. petenense*, *O. heterospila* and *T. pasionis*. *Pterygoplichthys* had a larger isospace in LPR than SPR. A study of fish invasion in mesocosms found that the isotopic space of the invader expanded when it was the most abundant species in the system (Tran et al., 2015). From the perspective of optimal foraging theory (MacArthur & Pianka, 1966; Svanbäck & Bolnick, 2007), expansion of the invader's trophic niche could occur if the strength of intraspecific competition is more than interspecific competition (Bolnick et al., 2003). Like native species, *Pterygoplichthys* had a higher trophic position in LPR, which might indicate lower availability or depletion of preferred basal production resources, such as periphyton and other biofilms.

Pterygoplichthys biomass was estimated to derive mostly from benthic production sources in both rivers, with contribution from water-column sources slightly greater in LPR. Grazing by *Pterygoplichthys* can alter the quality and quantity of benthic resources (Capps & Flecker, 2015), and the high abundance of this invader in LPR could have reduced the availability of benthic production sources. *Pterygoplichthys* grazing reduced algal biomass and primary production in an experiment conducted in the Chacamax River, Mexico (Capps et al., 2015). Periphyton C:P and C:N were lower when a similar loriciid, *Hypostomus plecostomus*, was present in a mesocosm experiment conducted in the spring-fed San Marcos River, Texas (Scott et al., 2012). In the SPR, the biomass of native species was estimated to have been derived mostly from benthic production sources, but in the LPR, where *Pterygoplichthys* was dominant, native fish were estimated to have derived >50% of their

biomass from water-column sources. For *D. petenense*, the estimated contribution from water-column sources was <10% in SPR and >50% in LPR. This between-site difference in estimates of material assimilated from basal sources could have been influenced by competition from the invasive catfish, differences in availability of various basal sources, local environmental conditions (e.g., higher vs. lower turbidity), species composition, or some combination of these factors. Other studies have shown that seasonal changes can modify the availability and assimilation of basal production sources in rivers. For example, in rivers of the Lower Mekong River Basin, isotopic signatures of fish tended to be more strongly associated with aquatic production sources during the dry season and riparian macrophytes sources during the rainy season (Ou & Winemiller, 2016). Although aquatic sources were less important during the wet season when rivers flooded and water was turbid with suspended sediments, seston (water-column basal source) had a higher estimated contribution than benthic algae for nearly all benthivorous cyprinids feeding at low trophic positions (i.e., detritivores, algivores, and omnivores).

In our study, native fish $\delta^{13}\text{C}$ was positively correlated with both *Pterygoplichthys* biomass and water flow velocity and negatively correlated with conductivity. Higher $\delta^{13}\text{C}$ tended to reflect the assimilation of water-column sources. LPR has a larger watershed than SPR, which could increase the nutrient load and aquatic productivity. Eutrophication of fluvial systems can increase water-column productivity and turbidity which then reduce light penetration to the benthos. We did not find significant associations between $\delta^{13}\text{C}$ signatures and most other environmental variables measured in this study, only one model showed total phosphorus to be significant, but this was not consistent in all the models explored. Land use and land cover changes, especially propagation of oil palm plantations, have affected LPR whereas much of the SPR watershed remains lies within the Maya Biosphere Reserve. However, SPR has not escaped impacts entirely and agricultural development and wildfires have occurred in its watershed over the past 20 years, with likely consequences for nutrient loading (Camacho-Valdez et al., 2022; Juárez-Sánchez et al., 2019). Water depth was positively correlated with native fish $\delta^{15}\text{N}$ signatures, and sediment depth showed the opposite trend. Sedimentation has been shown to change the composition of benthic feeding guilds and result in lower $\delta^{15}\text{N}$ signatures of primary consumers (Burdon et al., 2020). Some sectors of the LPR and SPR catchments have been deforested and converted to agriculture and receive high sediment inputs. When environmental factors were included along with *Pterygoplichthys* biomass in statistical analyses, *Pterygoplichthys* biomass

consistently had the strongest association with $\delta^{13}\text{C}$ signatures of native fish, followed by conductivity and water flow velocity.

Smaller isospace size of native fish with lower overlap with the abundant invader in LPR is interpreted here as strong evidence of response to competition for benthic food resources. If this is indeed the case, then these native fish may be capable of adjusting their trophic ecology in order to coexist with *Pterygoplichthys*. The most common species in LPR, *G. sexradiata*, was probably minimally affected by the invasion because it feeds mainly on small invertebrates, including those found at the surface and in the water column (Greenfield et al., 1983; Horstkotte & Strecker, 2005; Rakocinski & Greenfield, 1985). Isospace overlap between *G. sexradiata* and *Pterygoplichthys* was very low in both rivers. Capps and Flecker (2015) found evidence of macroinvertebrate biomass decline in areas foraged by *Pterygoplichthys* in the Chacamax River. Grazers not only can compete with macroinvertebrates for resources, but also can disrupt their habitat (Flecker, 1996).

The clupeid *D. petenense* was abundant in LPR. This filter-feeder had almost complete isospace overlap with *Pterygoplichthys* in SPR but a low overlap in LPR. *D. petenense* was estimated to have assimilated mostly benthic source material in SPR and approximately half water-column sources in LPR. Ingram and Ziebell (1983) suggested that while *D. petenense* prefers water-column to benthic food resources, it shifts its feeding according to resource availability. The characid *A. aeneus* is a trophic generalist and assimilated more material derived from water-column sources and also had lower isotopic overlap with *Pterygoplichthys* in LPR compared with SPR. The two cichlids, *T. pasionis* and *O. heterospila*, also are trophic generalists that had smaller isotopic spaces and lower overlap with *Pterygoplichthys* in LPR, with the former revealing a smaller overlap.

A robust assessment of the competition in nature can be achieved with well-designed and long-term field experiments or ecological modeling with strong empirical support. Our comparative study provides insight into the trophic ecology of freshwater fish in two similar rivers under different levels of invasion using stable isotopes, which allowed us to integrate the assimilation of consumed items over time (Layman et al., 2012). However, trophic dynamics and armor catfish invasion in our study system are also likely to be influenced by differences between rivers, including variation in fish assemblage composition, local or regional environmental conditions (e.g., rivers productivity) (Burdon et al., 2020; Didham et al., 2005) or interactions between the invasion and environmental conditions. For example, *Pterygoplichthys* often thrives in modified habitats, especially those that have

undergone eutrophication (Wei et al., 2018), although, we did not find *Pterygoplichthys* abundance to have a strong correlation with total phosphorous and further research is needed to understand the role of productivity on *Pterygoplichthys* invasion. Also, *Pterygoplichthys* nest excavation can increase sedimentation (Nico et al., 2009) that can reduce primary productivity and abundance of primary consumers (Burdon et al., 2020). Indeed, our analysis indicated that conductivity and other physical-chemical parameters were associated with changes in stable isotope signature, but these associations were overall weaker when compared with the influence of armor catfish abundance. This suggests that armor catfish abundance is the primary driver of the trophic niche changes observed. However, the collinearity between *Pterygoplichthys* abundance and conductivity deserves to be further studied. Although the gradient in conductivity is primarily related to the karstic soils within the Yucatan Peninsula and SPR sub-basin (Mejia-Ortiz et al., 2021) and is likely not to be a byproduct of the invasion, the distinction between the influence of conductivity and the invasive abundance should clarify the mechanisms underlying the changes in the trophic niche of native species.

Local people claimed that *Pterygoplichthys* populations are more common in SPR during the rainy season and, if accurate, would be consistent with seasonal patterns described for in La Palizada River in the lower Usumacinta, Mexico, where *Pterygoplichthys* density can increase four-fold during the rainy season (Escalera-Vázquez et al., 2019). In this sense, analysis of seasonal variation in fish assemblage composition, functional diversity, food sources, and habitat characteristics and habitat use/availability, as well as isotopic signatures, could further reveal the trophic dynamics of native and invading fish populations and clarify the extension of the invasion impact. Integration of available information (occurrence/abundance) from all the sub-basins in the upper and lower Usumacinta, and the Yucatan region is also needed to identify the environmental conditions (e.g., karst conditions, allochthony vs. autochthony, eutrophication, and proximity to urban centers and fish farms) of the most affected ecosystems and to plan contingency and management plans.

CONCLUSIONS

Invasive *Pterygoplichthys* was shown to overlap broadly in isotopic space with algivorous, detritivorous, and omnivorous native fish under low invasion conditions where estimates of basal source assimilation stressed benthic production sources. In the river with a high abundance of *Pterygoplichthys*, this invader probably reduced the availability of benthic basal resources and competed

with native fish at similar trophic positions, as evidenced by their smaller isotopic spaces and lower overlap with *Pterygoplichthys*. Moreover, native fish coexisting with abundant invaders may have shifted from the assimilation of mostly benthic sources to mostly water-column sources. However, we cannot rule out the potential influence of variation in local fish assemblage composition and environmental factors on isotopic signatures. It is also important to note that biological invasions and habitat degradation often interact to influence community trophic dynamics, and invasive species can be “drivers or passengers of ecological change” (Didham et al., 2005). In addition to niche partitioning, other mechanisms could explain the coexistence of native and invasive species (Chesson, 2000). For example, *Pterygoplichthys* had almost complete isotopic overlap (inferred as trophic overlap) with *P. mexicana* in both rivers. Coexistence under conditions of high invasion in LPR could have been achieved by partitioning microhabitats or some other mechanism. Except for poeciliids, native species were less common in LPR relative to SPR, and therefore could be more susceptible to high levels of invasion or habitat degradation (Table 1). Understanding not only environmental tolerance, but also trophic plasticity will be important for predicting *Pterygoplichthys*’ potential for establishment in freshwater ecosystems, particularly those previously identified as preferred by the species (Escalera-Vázquez et al., 2019). Consumption of a broad spectrum of food resources probably facilitates invasion as well as the potential for impacts on native species. To prevent the loss of native biological diversity and alteration of ecosystem function, further introductions of *Pterygoplichthys* and other invasive loricariids must be prevented, and areas already invaded would benefit from research for management options to control invader populations and mitigate impacts.

AUTHOR CONTRIBUTIONS

The study was conceived and carried out by Yasmín Quintana, and Yasmín Quintana analyzed the data and wrote the manuscript with input from Kirk O. Winemiller and Friedrich Wolfgang Keppeler. All authors approved the final manuscript prior to submission.

ACKNOWLEDGMENTS

The authors thank the Russell E. Train Education for Nature-Word Wildlife Fund, the Faculty for the Future Fellowship-Schlumberger Foundation, the American Association of University Women International Fellowship, The Rufford Foundation, and the Tom B. Slick Fellowship-Texas A&M University for the financial support. We thank the Estación Biológica Las Guacamayas, AMPI, CONAP-Sayaxché, and Universidad de San Carlos

de Guatemala for the logistical support. Also, we thank J. Perkin, and W. Rogers for their comments to improve the manuscript. Thanks to Marlon Córdoba, Diego Juárez, Diego Elías, Emily Parker, Hunter Parker, Lucía López, César Fuentes, and Francis Santos, for assistance during fieldwork and laboratory work. IACUC 2018-0454. CONAP No. 00375-B and No. 3927. The procedures followed the Guidelines for the Use of Fishes in Research (Use of Fishes in Research Committee, joint committee of the American Fisheries Society, the American Institute of Fishery Research Biologists 2014).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Quintana, 2023) are available in the Texas Data Repository at <https://doi.org/10.18738/T8/513KIQ>.

ORCID

Yasmín Quintana  <https://orcid.org/0000-0002-1051-0202>

Friedrich Wolfgang Keppeler  <https://orcid.org/0000-0002-5165-1298>

Kirk O. Winemiller  <https://orcid.org/0000-0003-0236-5129>

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SUPPORTING INFORMATION

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

How to cite this article: Quintana, Yasmín, Friedrich Wolfgang Keppeler, and Kirk O. Winemiller. 2023. “Does Invasion by Armored Catfish Shift Trophic Ecology of Native Fishes? Evidence from Stable Isotope Analysis.” *Ecology* e4024. <https://doi.org/10.1002/ecy.4024>