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Morphologic and trophic diversity of fish assemblages in rapids of the Xingu River, a major Amazon tributary and region of endemism

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Abstract Increasing hydropower expansion in hyper-diverse tropical river basins is currently threatening aquatic biodiversity on an unprecedented scale. Among the largest and most controversial of these projects is the Belo Monte Hydroelectric Complex being constructed on the Xingu River, a major Amazon tributary in Brazil. Despite the potentially large impacts, almost no baseline ecological data are available for the river's diverse ichthyofauna. This study uses ecomorphology and stable isotope analysis to explore the functional and trophic relationships among four of the dominant families within the Xingu River rapids (Loricariidae, Cichlidae, Anostomidae, and Serrasalmidae). Morphological analysis revealed clear separation of these families based on functional traits associated with microhabitat use and foraging strategies, with the Loricariidae and Cichlidae displaying greatest functional diversity. The four families analyzed were not clearly differentiated in isotopic space defined by $\delta^{13}C$ and $\delta^{15}N$ values. Considerable overlap was observed among isotopic niches and all four families primarily assimilated material originating from phytomicrobenthos (assumed to be mainly benthic algae). Differences between morphological and trophic diversity within families provide insight into how this diverse assemblage may be partitioning niche space, which in turn has implications for population responses to hydrologic alteration.

Keywords Rheophilic · Neotropics · Anostomidae · Cichlidae · Loricariidae · Serrasalmidae · Stable isotope · Functional traits

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Introduction

Traits-based approaches provide increased mechanistic understanding of species responses to biotic and abiotic conditions, and an effective means to address issues of biodiversity conservation and fisheries management (McGill et al. 2006; Frimpong and Angermeier 2010; Mouillot et al. 2013; Verberk et al. 2013). The functional composition of fish assemblages in fluvial systems is strongly associated with patterns of variation within hydrologic regimes (Lamouroux et al. 2002; Mims and Olden 2012; Pease et al. 2012; Poff and Allan 1995). River impoundments impact a variety of abiotic conditions, including water discharge, flow velocities, sediment dynamics, substrate composition, and water quality, which may in turn result in predictable shifts in the functional composition of fish assemblages (Gido et al. 2009; Franssen et al. 2013; Rolls and Sternberg 2015). In addition to predicting community response to habitat modification, an understanding of trait-environment relationships and the distribution of functional traits within intact assemblages may also help define functional targets

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for restoration or management efforts designed to maintain ecosystem functioning (Laughlin 2014).

Analysis of food web structure offers a complimentary approach to describe community dynamics, and provides a convenient framework for monitoring highly diverse tropical rivers for which obtaining functional traits data for an entire assemblage is not feasible. Food web dynamics are strongly influenced by the hydrologic regime (Junk et al. 1989; Roach 2013; Roach et al. 2014), and river impoundments have been shown to significantly impact the food web structure of fish communities (Wootton et al. 1996; Albrecht and Caramaschi 2003; Hoeinghaus et al. 2008). Understanding the dynamics of energy flow through intact river systems is critical to maintaining fishery yields after flow regulation (Winemiller 2005). Stable isotope analysis is commonly used to estimate trophic structure because it provides information that is integrated over both space and time (Layman et al. 2012). In addition, stable isotopes provide quantitative measures of trophic relationships that can be used to compare trophic diversity or trophic niches through multivariate metrics similar to those used in traits-based approaches (Jackson et al. 2011; Layman et al. 2007; Abrantes et al. 2014).

Increasing hydropower expansion in hyper-diverse tropical river basins is currently threatening aquatic biodiversity on an unprecedented scale (Winemiller et al. 2016). Among the largest and most controversial of these projects is the Belo Monte Hydroelectric Complex being constructed on the Xingu River in Brazil. The Xingu River is the largest clear water tributary to the Amazon, famously known for a 130 km expanse of rapids and braided channels known as the Volta Grande, or Big Bend. This section of the Xingu contains over 450 fish species, with at least 26 micro-endemics found only in the rapids (Camargo et al. 2004). The Xingu River supports a large ornamental fishery targeting the high diversity of rheophilic species, many of which possess numerous adaptations to life in high velocity habitats (Lujan and Conway 2015) that also make them particularly vulnerable to hydrologic alteration (Winemiller et al. 2016). Our understanding of this diverse ichthyofauna is limited to taxonomic assessments (Camargo et al. 2004), with almost no data available on habitat use, feeding ecology, and niche relationships (Zuanon 1999; Jegu and Zuanon 2005). The Belo Monte Hydroelectric Complex will divert a significant portion of the river's flow to a series of man-made canals and reservoirs (Fearnside 2006). This design will result in the flooding of the upper portion of the Volta Grande and the dewatering of the lower portion, significantly altering flow dynamics. With construction nearing completion, baseline data on the functional ecology and trophic structure of these fishes are critically needed. This study analyzes morphologic and trophic diversity among the four most abundant families of the Xingu rapids in order to understand the functional and trophic relationships among fishes within the rapids and provide baseline data for ongoing monitoring efforts.

Material and methods

Study site

This study was conducted in the Xingu River, one of the major tributaries of the Amazon River. The Xingu River originates in the Serra do Roncador region of Brazil's Mato Grosso state, flowing 2050 km in a northerly direction to its confluence with the Amazon River in Brazil's Pará state. The Xingu drains a 500,000 km^2 area of the Brazilian Shield, an ancient geologic formation that gives the river its characteristic oligotrophic waters, low conductivity (mean = 0.03 μS/cm), high transparency (Secchi depth = 1 to 5 m), and nearly neutral pH (mean = pH 6.7). The hydrologic regime is strongly seasonal, with daily discharge ranging from 32,000 m$^3 \cdot$s^{-1} during the high-water period (January to May) to 500 m$^3 \cdot$s^{-1} during the low-water period (August to November).

Surveys were conducted along a 10-km reach of the main channel within the Volta Grande, or Big Bend region, approximately 45 km downstream from the city of Altamira (Fig. 1). Samples of primary producers and fishes were collected in November 2012, during the low-water period, from rapids near the town of Paquiçamba (3° 35′ S; 51° 50′ W). Fishes were collected using gillnets of ten different mesh sizes (between 20 and 180 mm stretched), cast nets (20 to 60 mm mesh), and a hand net, the latter while free diving. After capture, fishes were identified to the lowest feasible taxonomic level based on available literature (Gery 1977; Planquette et al. 1996; Santos et al. 2004). To minimize the effects of temporal and spatial variation in isotopic signatures, sampling was performed during one week within an area of ~24 km^2 dominated by rapids. This area lies within the zone that will be partially dewatered by the Belo Monte Hydroelectric Complex, which is

currently nearing completion. The strong elevation gradient in this region (Rodrigues 1993) combined with numerous outcrops of metamorphic and igneous rocks creates a complex maze of rapids. In areas with swift current, many rocks are covered with rheophilic macrophytes, particularly species of the family Podostemaceae. In areas with slower currents, plants of the families Myrtaceae, Asteraceae and Mimosaceae dominate. Riparian forests are seasonally flooded and provide feeding, spawning, and nursery habitat for many fishes.

Morphological analysis

Twenty-two morphological characters related to feeding, locomotion, and habitat use were measured for 166 specimens of 20 fish species (2 to 28 specimens per species). Trait definitions are provided in Table 1. All measurements, except mouth position, were taken as the straight-line distance between points and recorded to the nearest 0.01 mm using digital calipers. These morphological traits were selected following Montana and Winemiller (2013) for their ease of measurement and clear functional relationships to various aspects of species ecology.

Stable isotope analysis

Tissue samples were collected from potential basal production sources, including aquatic and riparian vascular plants, filamentous algae, microphytobenthos, and seston, with the latter two samples presumed to be dominated by microalgae. Multiple leaves, fruits, and seeds of the dominant riparian plants and aquatic vascular plants were clipped from live plants. Samples of filamentous algae were collected with forceps from the substratum and microphytobenthos samples were scraped from rock surfaces. To sample seston, approximately 200 l of river water were passed through a 45-μm screen to remove large particles and zooplankton, then filtered onto pre-combusted Whatman GF/F glass fiber filters (GE Healthcare Bio-Sciences, Pittsburg, Pennsylvania, USA).

Twenty of the most common fish species, representing four families and three orders, were retained for isotopic analyses. To minimize intraspecific variation associated with ontogeny, tissue samples were obtained from fish specimens of a similar size class, and with few exceptions these were adult size classes. Standard length was measured to the nearest 0.1 cm

using calipers and total weight was measured to the nearest 0.01 g using an electronic balance. Following euthanasia via lethal cold shock, white muscle tissue (1 to 2 g) was extracted from the flank below the anterior margin of the dorsal fin. Dermal bone was removed from muscle tissue samples of armored catfishes (Loricariidae). Tissue samples of fish and primary producers were stored on ice in the field and later placed in a freezer in the laboratory where they were kept until processing. Voucher specimens were fixed in 10 % formalin solution and deposited at the Universidade Federal do Para.

Fifty-eight fish samples comprising 18 genera and 20 species were analyzed for C and N stable isotope ratios. In addition, 103 primary production sources consisting of 33 aquatic macrophytes from the family Podostemaceae, six microphytobenthos scrapes, three filamentous algae samples, three seston samples, and 58 terrestrial plants representing 12 species and eight families were also analyzed. Tissue samples were rinsed with distilled water to remove debris, dried to constant weight in an air-circulating oven at 60 °C, and pulverized to a fine homogeneous powder using a mortar and pestle. Subsamples of 1.5 to 3.0 mg were weighed and placed in Ultra-Pure tin capsules (Costech Analytical, Valencia, California, USA). Carbon and nitrogen isotope ratios were determined using a Delta-V isotope ratio mass spectrometer coupled to an NA1500 CHN Carlo Erba combustion analyzer via a Thermo Conflo III Interface. Stable isotope ratios were expressed in standard delta (δ) notation and defined as parts per thousand (‰) relative to a standard as follows:

$$\delta X = \left[\left(R_{Sample}/R_{Standard} \right) - 1 \right] \times 10^3$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively. $R_{standard}$ for ^{13}C was the Vienna Pee Dee Belemnite (VPDB) limestone formation and $R_{standard}$ for ^{15}N was atmospheric N_2. Because all fish samples displayed C/N ratios <3.5, lipid corrections of $\delta^{13}C$ values were not considered appropriate (Post et al. 2007).

Statistical analyses

Principal components analysis (PCA) was used to describe the morphological space occupied by each family and examine patterns of functional traits between

families. PCA was performed on the correlation matrix of all 166 specimens and all 22 traits. With the exception of mouth position, all morphological characters were converted to proportions of standard length to remove the effect of body size and to retain components describing body shape (Relyea 2004). Ratios of body size can introduce allometric bias into shape analysis, but these influences should be negligible for interspecific comparisons in which a restricted size interval (e.g., adult size class) is chosen to characterize a given species (Winemiller 1991). Prior to the analysis, morphometric variables were log-transformed to improve normality. A permutational analysis of variance (PERMANOVA) was used to test for morphological differences between families. PERMANOVA uses Bray-Curtis similarity matrices of log-transformed morphological data with 9999 permutations. Similarity between species was represented graphically by clustering based on distances between family centroids. PCA, PERMANOVA and cluster analysis were performed with PERMANOVA+ and PRIMER version 6.4 (PRIMER-E Ltd., Plymouth, U.K.).

Trait-based and stable-isotope-based community-wide metrics were used to infer morphologic and trophic structure of families using the SIAR package (Layman et al. 2007; Parnell et al. 2010; Parnell and Jackson 2013). This method uses Bayesian inference to compare patterns in data sets with different sample sizes (Jackson et al. 2012). Three metrics were used to describe the relative positions of the four families within morphologic and isotopic space (Layman et al. 2007; Jackson et al. 2012; Abrantes et al. 2014): i) mean Euclidian distance of each species to its group centroid (CD), ii) mean nearest-neighbor distance (MNND), and iii) standard deviation of nearest-neighbor distance (SDNND). CD provides an estimate of average morphologic/isotopic diversity, MNND estimates the relative density of species within the group's space (i.e., smaller MNND values indicate greater morphologic/trophic similarity), and SDNND estimates evenness (i.e., lower values indicate more even distributions of species within morphologic/trophic space). Morphologic and isotopic niches of the various families were calculated as Bayesian standard ellipse areas (SEA), expressed in ‰^{2} using the package Stable Isotope Bayesian Ellipses in R (Jackson et al. 2011). The correction for small sample size (SEA$_C$) was used to increase accuracy (Jackson et al. 2011). This method is robust for comparisons between different and/or small sample sizes, and assesses statistical significance of differences in SEA$_C$ between groups based on the proportional outcome of 10^6 repeated measures.

To estimate contributions of basal production sources to fish biomass, we ran isotopic mixing models using Stable Isotope Analysis in R (SIAR) version 4 (Parnell and Jackson 2013) and R version 2.13.1 for Windows (R Core Team 2015). The SIAR model uses variation in isotopic discrimination factors and Bayesian inference to produce the most likely set of proportional contributions of sources for a given consumer. Because specific trophic fractionation values have been estimated for few Amazonian fishes, we used average values obtained from previous meta-analyses, with trophic fractionation of $\delta^{13}C = 0.5 \pm 0.13$ SD (McCutchan et al. 2003) and trophic fractionation of $\delta^{15}N = 2.5 \pm 0.11$ SD (Vanderklift and Ponsard 2003). Default SIAR modeling specifications with 200,000 iterations were used, and estimated proportional contributions of each source item to biomass of consumers were graphically summarized using 95 %, 75 % and 25 % Bayesian credibility intervals.

Nitrogen isotopic signatures were used to estimate trophic positions (TP) of consumers according to the following equation:

$$TP = \left[\left(\delta^{15}N_{consumer} - \delta^{15}N_{reference} \right) / 2.54 \right] + 1$$

Where $\delta^{15}N_{reference}$ was the mean $\delta^{15}N$ of the five most common primary producers in the system, and 2.54 ‰ was the mean trophic fractionation value found in a previous meta-analysis (Vanderklift and Ponsard 2003).

Results

Relationships within morphological space

A total of 503 fish specimens belonging to five orders and 11 families was collected in the rapids of the Xingu River. Twenty species from the four most abundant families were selected for analysis. Results from PCA and PERMANOVA (Pseudo-F = 156.0; $p < 0.0001$) both show that these four families occupy distinct regions of morphological space. The first two principal components modeled 75.2 % of total morphological
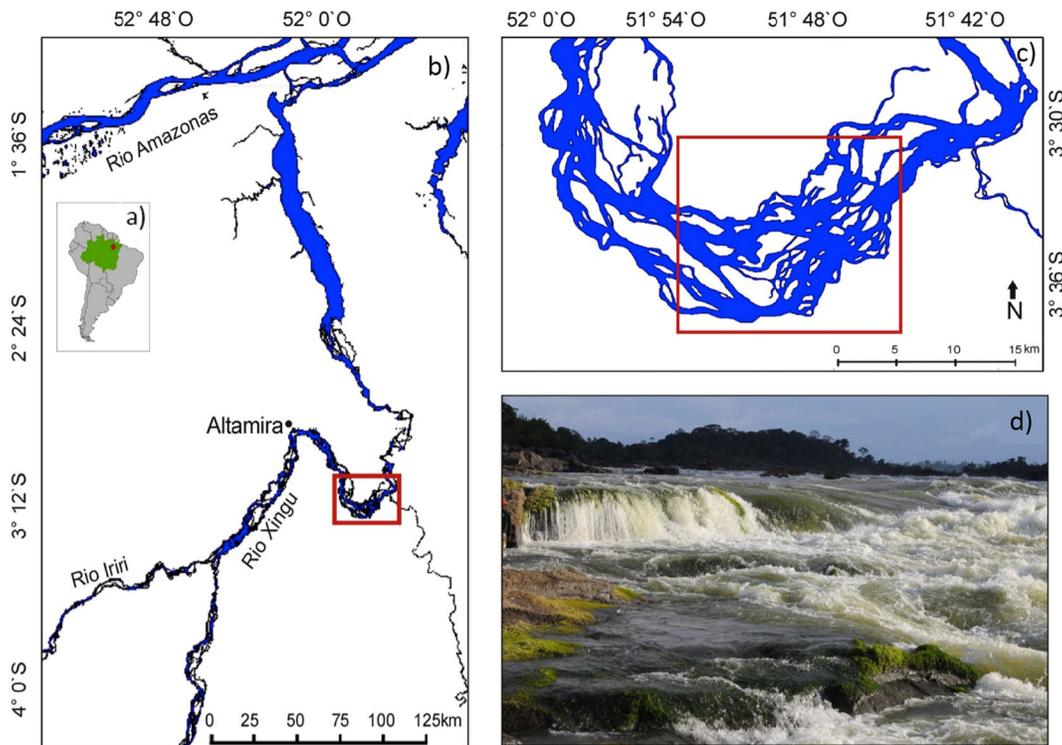
Fig. 1 Study location, showing the Amazon River Basin (green) in South America **a**, the Lower Xingu River from the Iriri River to the confluence with the Amazon River **b**, study site within the Volta Grande **c**, and a characteristic section of rapids **d**. River flow proceeds generally in a northerly direction

variation in the dataset. The first axis (43.2 % of variation) described a gradient between species with a long anal fin, deeper body, shorter caudal peduncle, superior mouth, and shorter snout at one end, and species with a wide, dorso-ventrally flattened body, short anal fin, and inferior mouth at the other extreme (Fig. 2). Species of the family Loricariidae, all of which have relatively elongate, dorso-ventrally compressed bodies, long caudal peduncles, short heads, and ventrally oriented mouths, occupied high values on PC1, while species of the family Serrasalmidae occupied low values of PC1. The second axis (32.0 % of variation) described a gradient contrasting species with a deeper head, eyes positioned higher on the head, wider mouth and longer dorsal fin with species displaying the opposite traits. Species of the families Anostomidae and Cichlidae were differentiated primarily according to position on PC2, with anostomids characterized by relatively small heads and mouths and wide fusiform bodies compared to the deep, laterally compressed bodies of cichlids (Fig. 2).

Functional diversity, estimated as CD, was higher for cichlids and loricariids based on 25 % credibility intervals,

although 95 % credibility intervals overlapped for all four families (Fig. 3a). No significant differences were found for estimates of morphologic similarity (MNND) or evenness (SDNND) between families (Fig. 3c, e). Species dispersion within morphological space differed significantly between families (Fig. 4), with loricariids displaying the greatest inter-specific morphological variation ($SEA_C = 0.47$) and anostomids the least ($SEA_C = 0.11$). Serrasalmids ($SEA_C = 0.28$) and cichlids ($SEA_C = 0.21$) showed intermediate morphological dispersion.

Relationships within isotopic space

The four families were not as clearly differentiated in isotopic space based on $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 5). Overlap between families ranged from no overlap between Anostomidae and Loricariidae to 69.1 % overlap between Anostomidae and Cichlidae. Trophic diversity, estimated as CD based on $\delta^{13}C$ and $\delta^{15}N$ values, was greatest for Loricariidae and Serrasalmidae (Fig. 3b). Cichlids displayed the lowest trophic diversity, with 75 % credibility intervals well below those of other

Table 1 Morphological traits used in analyses with definition of measurements

Trait	Definition
Standard length	Distance from tip of snout to posterior end of last vertebra
Snout length closed	Horizontal distance between an imaginary vertical line passing through the anterior edge of the orbit and an imaginary vertical line passing through the anterior tip of the upper jaw
Eye position	Vertical distance from the center of the pupil to ventrum
Eye diameter	Horizontal distance from eye margin to eye margin
Body depth	Maximum vertical distance from dorsum to ventrum
Dorsal fin length	Distance from anterior proximal margin to posterior proximal margin of the dorsal fin
Peduncle length	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra
Peduncle depth	Minimum vertical distance from dorsum to ventrum of the caudal peduncle
Dorsal fin height	Maximum distance from proximal to distal margin of the dorsal fin (excluding filaments)
Pectoral fin length	Maximum distance from proximal to distal margin of the pectoral fin
Pelvic fin length	The distance from the base of the pelvic fin to the tip of the longest ray (excluding filaments)
Anal fin length	Distance from anterior proximal margin to posterior proximal margin of the anal fin base
Anal fin height	Maximum distance from the proximal to distal margin of the anal fin (excluding filaments)
Caudal fin length	Maximum distance from proximal to distal margin of the caudal fin (excluding filaments)
Interorbital distance	Maximum horizontal distance between dorsal margins of both orbits
Body width	Maximum horizontal distance from side to side
Caudal peduncle width	Width of the caudal peduncle in horizontal plane at midlength
Head length	Distance from tip of upper jaw to the most caudal extension of the operculum
Gape width	Horizontal distance inside fully open mouth at widest point
Head height	Vertical distance from dorsum to ventrum passing through the center of the pupil
Caudal fin depth	Maximum vertical distance across the fully spread caudal fin
Mouth position	Estimated as the angle between an imaginary line connecting the tips of the open jaws and one connecting the corner of the mouth to the posterior most vertebra

families. Analysis of isotopic niche breadth based on standard ellipse area further confirmed that serrasalmids displayed the largest isotopic dispersion ($SEA_c = 20.2$ ‰^{2}) and cichlids had the lowest dispersion (Fig. 4; $SEA_c = 5.1$ ‰^{2}). Loricariids and cichlids revealed low values of MNND (Fig. 3d), and were more tightly packed within family trophic space than anostomids or serrasalmids based on 75 % credibility intervals. A similar pattern was displayed for SDNND, indicating that loricariids and cichlids were more evenly spaced within isotopic space than serrasalmids or anostomids, although credibility intervals overlapped between families (Fig. 3f).

Five potential production sources were evaluated for their contributions to consumer biomass. C and N isotopic signatures were significantly different between basal sources (PERMANOVA, pseudo-F = 127.58 $p < 0.0001$). According to mixing model estimates, phytomicrobenthos, which is assumed to be composed mainly of benthic algae, was the most important basal production source supporting biomass of fishes from all four families. This was particularly true for the family Loricariidae, for which the proportional contribution of phytomicromenthos ranged from 70 to 90 % (Fig. 6). Fishes of the family Cichlidae were primarily supported by phytomicrobenthos and C3 vascular plants. The families Anostomidae and Serrasalmidae revealed relatively even estimates of proportional contributions of the five sources, though phytomicrobenthos appeared to be the most important source for these groups as well. Filamentous algae contributed very little to fish biomass in all four families.

Trophic position of Loricariidae averaged 3.2 and ranged from 2.8 for *Spectracanthicus zuanoni* to 3.2 for *Scobinancistrus pariolispos*. Serrasalmidae displayed the largest range in TP from 2.6 for *Myloplus schomburgkii* to 4.2 for *Serrasalmus*
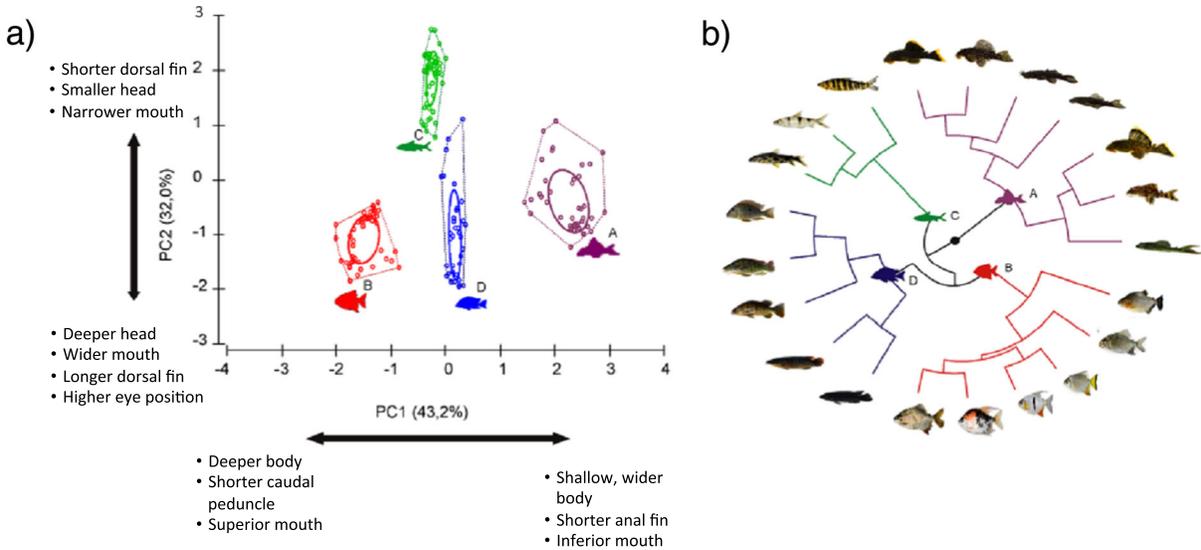
Fig. 2 Results of principal components analysis of 22 morphological traits related to habitat use and feeding strategies **a**. Symbols represent individual fish, dotted lines represent convex hulls, and solid lines represent Bayesian standard ellipses. Text below PC axes show morphological traits with highest PC loadings. Twenty species from the four dominant families in the Xingu rapids were analyzed **b**. Family symbols represent Loricariidae (A; purple), Serrasalmidae (B; red), Anostomidae (C; green), and Cichlidae (D; blue)

rhombeus, with an average TP of 3.25. Trophic position varied relatively little within the Anostomidae and Cichlidae, with means of 3.5 and 3.7, respectively.

Discussion

This study analyzed relationships among morphology and trophic structures of the four dominant families of fishes in rapids of the Xingu River prior to completion of the Belo Monte Hydroelectric Complex, which will cause large-scale ecosystem changes. The four families were separated based on morphological traits associated with microhabitat use and feeding. At one end of the gradient were dorso-ventrally compressed species of the family Loricariidae, which are well adapted for benthic habitats, often in swift water. Many Xingu loricariids inhabit interstices of rocky substrates within high-velocity, shallow waters, although species in this diverse family occupy a wide range of microhabitats (Zuanon 1999). The highly modified oral disk not only allows for efficient foraging of benthic resources, but also provides a strong suction apparatus that allows species to maintain position in swift waters (Lujan and Armbruster 2012). In addition, the shallow body depth of many species allows them to seek refuge from swift-flowing water within narrow crevices. The other end of the morphological gradient was occupied by serrasalmids, species with laterally compressed, discoid bodies that facilitate precise lateral movements within the water column. With the possible exception of *Serrasalmus rhombeus*, these reophilic species inhabit rapids flowing over cobble, rocks, and boulders, spending the major portion of their time within hydraulic refuges (Jégu 2003).

The families Cichlidae and Anostomide occupied intermediate positions along the dominant morphological gradient, with most cichlids differentiated from anostomids by having larger heads, wider mouths, and deeper bodies. These differneces probably reflect a greater range of habitats occupied and prey sizes consumed by cichlids (Montana and Winemiller 2013). Most anostomid species in the Xingu River would be characterized as rheophilic (Zuanon 1999). Some Cichlid species (e.g. *Crenicihla spp.* and *Retroculus xinguense*) co-occur with anostomids in rapids, whereas others (e.g., *Geophagus altifrons* and *Cichla melaniae*) are generally found near channel margins where current is slower.

The four families analyzed were less differentiated in isotopic space than morphological space (Fig. 5). The Serrasalmidae and Loricariidae generally displayed the

Fig. 3 Morphologic and Isotopic diversity metrics calculated based on Bayesian standard ellipses using the package SIBER in R. Left three panels display diversity metrics for morphologic analysis and right three panels display diversity metrics for isotopic analysis. Box plots represent 50, 75, and 95 % Bayesian credibility intervals. Mean distance to centroid (CD) estimates total morphologic **a** and trophic **b** diversity. Mean Nearest Neighbor Distance (MNND) estimates species packing within morphologic **c** and isotopic **d** space. Standard Deviation of Nearest Neighbor Distance (SDNND) estimates evenness of spacing within morphologic **e** and isotopic **f** space. Family symbols represent Loricariidae (A; purple), Serrasalmidae (B; red), Anostomidae (C; green), and Cichlidae (D; blue)
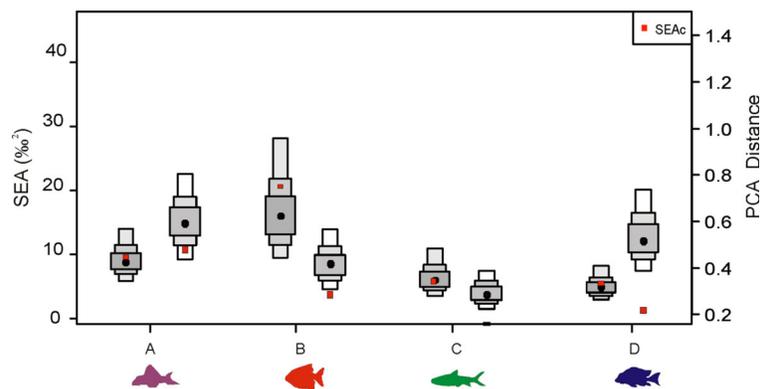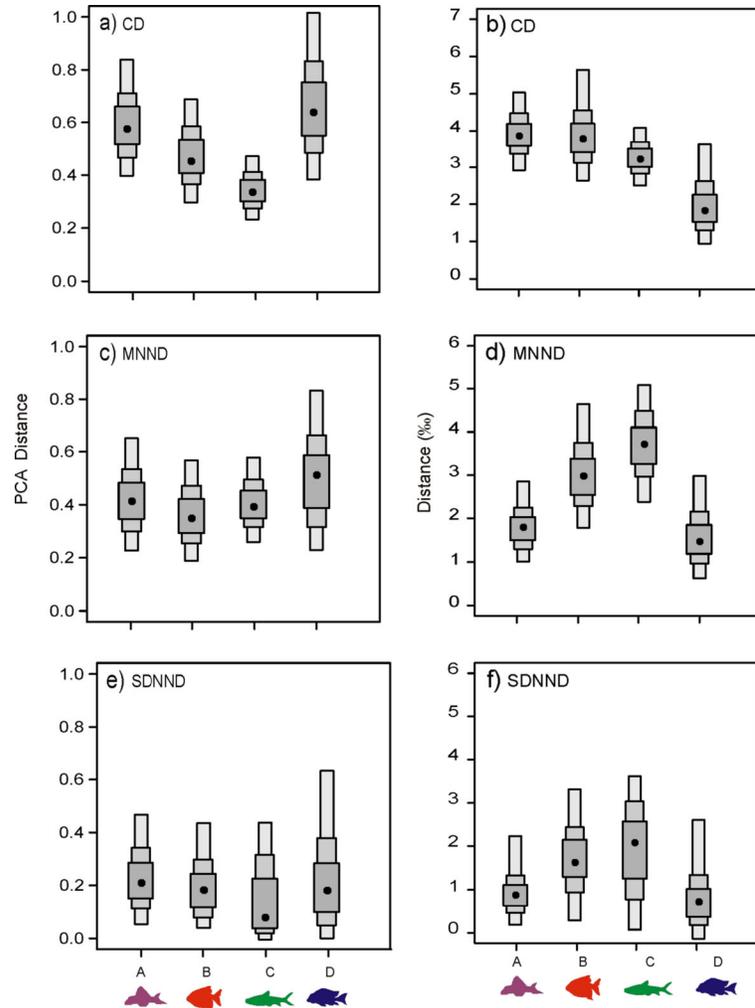
Fig. 4 Morphologic (right) and trophic (left) niche breadth for each family based on Bayesisan standard ellipse areas calculated using the package SIBER in R. Box plots represent 50, 75, and 95 % Bayesian credibility intervals. Family symbols represent Loricariidae (A; purple), Serrasalmidae (B; red), Anostomidae (C; green), and Cichlidae (D; blue). Red squares represent standard ellipse areas calculated using the correction for small sample sizes

Fig. 5 Distribution of families in isotopic space based on δC and δN values. Open symbols represent individual fish and solid black squares represent the major primary production sources. Dotted lines represent convex hulls, and solid lines represent Bayesian standard ellipses for each family. Family symbols represent Loricariidae (A; purple), Serrasalmidae (B; red), Anostomidae (C; green), and Cichlidae (D; blue). Primary production sources include phytomicrobenthos (PMB), aquatic macrophytes of family Podostemacea, C3 riparian plants, filamentous algae, and phytoplankton
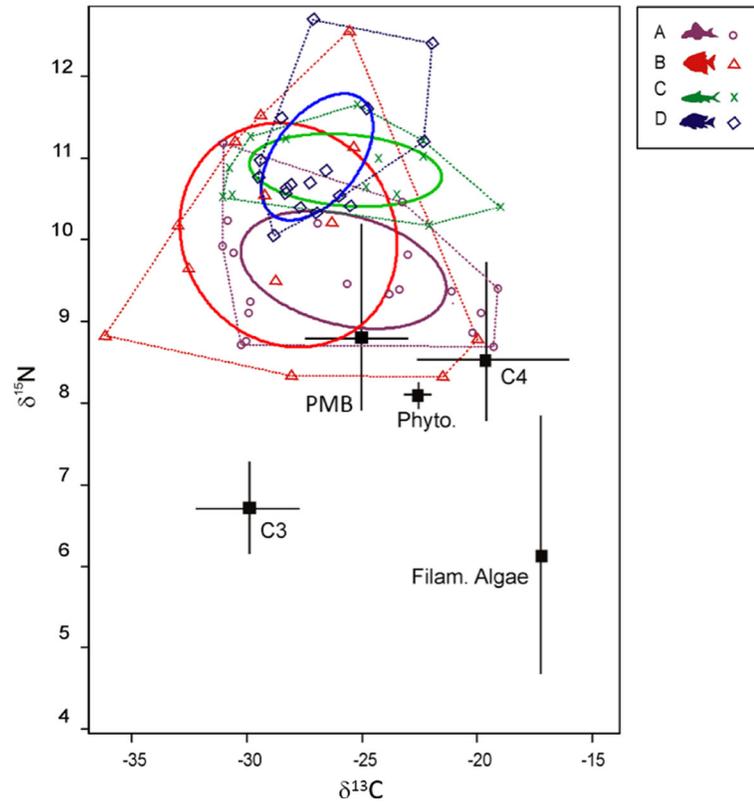
lowest $\delta^{15}N$ values, however both families revealed large isotopic variation. Anostomids and cichlids revealed lower isotopic diversity with generally higher $\delta^{15}N$ values, which presumably reflects higher trophic

Fig. 6 Percent contribution of the various primary production sources to consumer biomass for each family. Box plots represent 50, 75, and 95 % Bayesian credibility intervals. Box plots represent 25, 75, and 95 % Bayesian credibility intervals. Primary production sources include phytomicrobenthos (PMB), aquatic macrophytes of family Podostemacea, C3 riparian plants, filamentous algae, and phytoplankton. Family symbols represent Loricariidae (A; purple), Serrasalmidae (B; red), Anostomidae (C; green), and Cichlidae (D; blue)
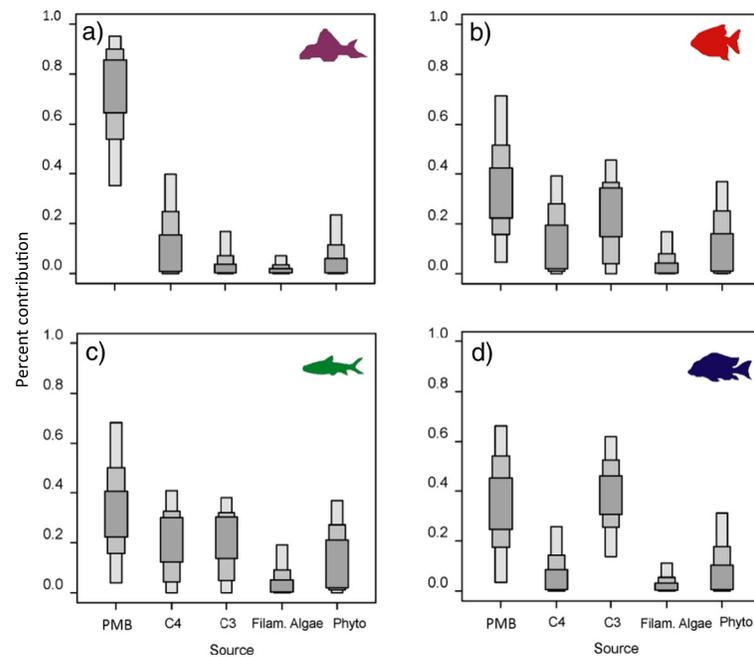
positions associated with consumption of aquatic insects and fishes. While the high trophic diversity of serrasalmids and loricariids could be influenced by differences in sample sizes across families, this finding is also consistent with interspecific dietary variation within these families. Most of the serrasalmid species analyzed are considered to be omnivores that consume aquatic insects, grasses, seeds, and some aquatic macrophytes (Jégu 2003). This is reflected in their wide range of δ^{13}C values (Fig. 5). *Serrasalmus rhombeus*, on the other hand, is a carnivore whose consistently higher δ^{15}N values contributed to the high trophic diversity within this family. Endemic *Ossubtus xinguense*, a serrasalmid with dentition thought to indicate herbivory, displayed higher δ^{15}N values than omnivorous serrasalmids (e.g., *Myloplus schomburgkii*). Herbivores have been found to have significantly higher ^{15}N/^{14}N trophic fractionation values compared to fishes of other trophic guilds (Mill et al. 2007). Consequently, use of a single trophic fractionation value for all consumers could have artificially elevated estimates of trophic position for some herbivores. Loricariids also displayed significant interspecific variation in trophic position. While most species displayed low δ^{15}N values consistent with the primarily algivorous-detritivorous diet typical for this family, others (e.g., *Scobinancistrus pariolispos*) revealed isotopic signatures more consistent with an insectivorous diet. This is further supported by *S. pariolispos* having relatively few robust teeth compared to the numerous comb-like teeth characteristic of known herbivore-detritivores, such as *Baryancistrus xanthellus* (Lujan et al. 2012; Lujan et al. 2015).

Differences between morphologic and trophic diversity within families provide insight into how this diverse assemblage may be partitioning niche space. For example, cichlids had highest functional diversity, but the lowest isotopic diversity (Fig. 3). This pattern suggests that functional differentiation may reflect adaptations to exploit similar resources in a variety of microhabitats. For example, *Crenicichla* spp. tend to swim just above the substrate or in the mid water column when swimming rapidly between hydraulic refuges, whereas *R. xinguense* has a reduced swimbladder and generally rests upon gravel substrates between short bursts to change locations. This benthic species also forages in a specialized manner, using its long orobranchial chamber to winnow ingested particles to sort aquatic invertebrates from sand and gravel substrate; Zuanon 1999). Other invertivorous cichlids (e.g., *G. altifrons*) inhabit

slower-moving waters between rapids with sandy substrates. *Cichla melanie* and large *Crenicichla* species are piscivores, however, body shapes of these taxa are quite different, which suggests differences in swimming performance and habitat use.

Patterns of niche partitioning within the species-rich family Loricariidae are less clear, as both trophic and morphologic diversity were among the highest observed (Fig. 3). Loricariid catfishes possess adaptations that promote efficient foraging on benthic detritus, algae, and plant matter, such as ventrally positioned jaws and large fleshy lips (Lujan et al. 2012). Nonetheless, several species have evolved to exploit additional resources and microhabitats. High δ^{15}N values and the presence of fewer and larger teeth suggest that some species, such as *S. pariolispos*, consume aquatic invertebrates. Species with extremely shallow body depths, such as *Ancistrus ranunculus* and *Parancistrus* spp., are able to exploit microhabitats inaccessible to other species, which may aid in acquiring their specialized diet of loosely aggregated, flocculant detritus (Zuanon 1999; Lujan et al. 2015). However, the clear contribution of phytomicrobenthos to Loricariid biomass and low δ^{15}N values suggests that the majority of species maintain a generalized diet of detritus and benthic algae (Figs. 5, 6). How such a high diversity of apparent trophic equivalents coexist within rapids remains an open question, and may involve niche partitioning based on chemical cues (Hall 2004; Lujan et al. 2012) or fine-scale aspects of microhabitat complexity.

While this study analyzed a small portion of the species richness within rapids of the Xingu River, the relationships between trophic and morphologic diversity among the dominant families have clear implications for impending hydrologic alteration. The river's high habitat heterogeneity clearly plays a role in sustaining the diversity and endemism present. High siltation behind impoundments and decreased aquatic habitat in the dewatered portion of the river will decrease the amount of interstitial space available, removing a key aspect of niche segregation within this fish assemblage. The regulation of flow will also significantly decrease habitat heterogeneity, further limiting available environmental gradients for niche segregation. In addition, all four families assimilated significant amounts of material originating from phytomicrobenthos, a resource that depends on the clear, shallow waters typical of the river during the dry season. Changes in water depth and clarity within newly flooded reservoirs will alter the

availability of this key resource, and species persistence may largely depend on ability to shift feeding strategies accordingly (Albrecht and Caramaschi 2003). Regulation of flow through the Volta Grande will undoubtedly alter the environmental conditions that have promoted and sustained some of the most impressive freshwater diversity on Earth, and future research should track food web dynamics in response to changing hydrology.

References

Abrantes KG, Barnett A, Bouillon S (2014) Stable isotope-based community metrics as a tool to identify patterns in food web structure in east African estuaries. Funct Ecol 28(1):270–282. doi:10.1111/1365-2435.12155

Albrecht MP, Caramaschi ÉP (2003) Feeding ecology of *Leporinus friderici* (Teleostei; Anostomidae) in the upper Tocantins River, Central Brazil, before and after installation of a hydroelectric plant. Stud Neotropical Fauna Environ 38(1):33–40

Camargo M, Giarrizzo T, Isaac V (2004) Review of the geographic distribution of fish fauna of the Xingu River Basin, Brazil. Ecotropica 10:123–147

Core Team R (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Fearnside PM (2006) Dams in the Amazon: Belo Monte and Brazil's hydroelectric development of the Xingu River basin. Environ Manag 38(1):16–27. doi:10.1007/s00267-005-0113-6

Franssen NR, Harris J, Clark SR, Schaefer JF, Stewart LK (2013) Shared and unique morphological responses of stream fishes to anthropogenic habitat alteration. P Roy Soc B-Biol Sci 280(1752). doi:10.1098/rspb.2012.2715

Frimpong EA, Angermeier PL (2010) Trait-based approaches in the analysis of stream fish communities. Am Fish Soc Symp 73:109–136

Gery J (1977) Characoids of the world. Publications, Neptune City, NJ, T.F.H

Gido KB, Schaefer JF, Falke JA (2009) Convergence of fish communities from the littoral zone of reservoirs. Freshw Biol 54(6):1163–1177. doi:10.1111/j.1365-2427.2008.02162.x

Hall SR (2004) Stoichiometrically explicit competition between grazers: Species replacement, coexistence, and priority effects along resource supply gradients. Am Nat 164(2):157–172. doi:10.1086/422201

Hoeinghaus DJ, Winemiller KO, Agostinho AA (2008) Hydrogeomorphology and river impoundment affect food-chain length of diverse Neotropical food webs. Oikos 117:984–995

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80(3):595–602. doi:10.1111/j.1365-2656.2011.01806.x

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS One 7(2):e31757. doi:10.1371/journal.pone.0031757

Jégu M (2003) Serrasalminae (Pacus and piranhas). In: Reis RE, Kullander SO, Feraris CJ (eds) Checklist of the Freshwater Fishes of South and Central America. Edipucrs, Porto Alegre, Brasil, pp. 182–196

Jegu M, Zuanon J (2005) Threatened fishes of the world: *Ossubtus xinguense* (Jegu 1992) (Characidae: Serrasalminae). Environ Biol Fish 73(4):414–414. doi:10.1007/s10641-004-4230-5

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dogde DP (ed) Proceedings of the international large rivers symposium, Ottawa, p 110–127

Lamouroux N, Poff NL, Angermeier PL (2002) Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83(7):1792–1807. doi:10.2307/3071765

Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecol Lett 17(7):771–784. doi:10.1111/ele.12288

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure? Ecology 88(1):42–48

Layman CA et al. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol Rev 87(3):545–562. doi:10.1111/J.1469-185x.2011.00208.X

Lujan NK, Armbruster JW (2012) Morphological and functional diversity of the mandible in suckermouth armored catfishes (Siluriformes: Loricariidae). J Morphol 273(1):24–39. doi:10.1002/Jmor.11003

Lujan NK, Conway KW (2015) Life in the fast lane: a review of rheophily in freshwater fishes. In: Tobler M, Plath M (eds) Riesch R. Springer International Publishing, Extremophile Fishes, pp. 107–136

Lujan NK, Winemiller KO, Armbruster JW (2012) Trophic diversity in the evolution and community assembly of loricariid catfishes. BMC Evol Biol 12:124 doi:10.1186/1471-2148-12-124

Lujan NK, Armbruster JW, Lovejoy NR, Lopez-Fernandez H (2015) Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. Mol Phylogenet Evol 82:269–288. doi:10.1016/j.ympev.2014.08.020

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102(2):378–390. doi:10.1034/j.1600-0706.2003.12098.x

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21(4):178–185. doi:10.1016/j.tree.2006.02.002

Mill AC, Pinnegar JK, Polunin NVC (2007) Explaining isotope trophic-step fractionation: why herbivorous fish are different. Funct Ecol 21(6):1137–1145. doi:10.1111/j.1365-2435.2007.01330.x

Mims MC, Olden JD (2012) Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 93(1):35–45

Montana CG, Winemiller KO (2013) Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. Biol J Linn Soc 109(1):146–164. doi:10.1111/Bij.12021

Mouillot D, Graham NAJ, Villeger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28(3):167–177. doi:10.1016/J.Tree.2012.10.004

Parnell A, Jackson A (2013) siar: stable isotope analysis in r. R package version 4.2: http://CRAN.R-project.org/package=siar

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS One 5(3):e9672. doi:10.1371/journal.pone.0009672

Pease AA, Gonzalez-Diaz AA, Rodiles-Hernandez R, Winemiller KO (2012) Functional diversity and trait-environment relationships of stream fish assemblages in a large tropical catchment. Freshw Biol 57(5):1060–1075. doi:10.1111/j.1365-2427.2012.02768.x

Planquette P, Keith P, Le Bail P-Y (1996) Atlas des poissons d'eau douce de Guyane Tome 1 edn. Museum National d'Histoire Naturelle, Service du Patrimoine Naturel, Paris.

Poff NL, Allan JD (1995) Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76(2):606–627

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152(1):179–189. doi:10.1007/s00442-006-0630-x

Relyea RA (2004) Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. Ecology 85(1):172–179

Roach KA (2013) Environmental factors affecting incorporation of terrestrial material into large river food webs. Freshw Sci 32(1):283–298 doi:10.1899/12-063.1

Roach KA, Winemiller KO, Davis SE (2014) Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity and nutrients. Freshw Biol 59(6):1278–1293. doi:10.1111/fwb.12347

Rodrigues SK (1993) Neotectônica e sedimentação quaternária da região a "Volta Grande" do rio Xingu, Altamira. PA. Universidade de São Paulo, São Paulo, Brazil

Rolls RJ, Sternberg D (2015) Can species traits predict the susceptibility of riverine fish to water resource development? An Australian case study. Environ Manag 55(6):1315–1326. doi:10.1007/s00267-015-0462-8

Santos GM, Mérona B, Juras AA, Jégu M (2004) Peixes do Baixo Rio Tocantins: vinte anos depois da Usina Hidrelétrica de Tucuruí. Electronote, Brasília, p. 215

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet delta(15)N enrichment: a meta-analysis. Oecologia 136(2):169–182. doi:10.1007/s00442-003-1270-z

Verberk WCEP, van Noordwijk CGE, Hildrew AG (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. Freshw Sci 32(2):531–547. doi:10.1899/12-092.1

Winemiller KO (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecol Monogr 61(4):343–365

Winemiller KO (2005) Floodplain river food webs: generalizations and implications for fisheries management. In: Welcomme R, Petr T (eds) International Symposium on the Management of Large Rivers for Fisheries. Bangkok, Thailand, pp. 285–309

Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T, Nam S, Baird IG, Darwall W, Lujan NK, Harrison I, et al. (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351(6269):128–129

Wootton JT, Parker MS, Power ME (1996) Effects of disturbance on river food webs. Science 273(5281):1558–1561

Zuanon J (1999) História natural da ictiofauna de corredeiras do rio Xingu, na região de Altamira. Universidade Estadual de Campinas, Campinas, Brazil, Pará